

Classification and phylogeny of the diapsid reptiles

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Reptiles with two temporal openings in the skull are generally divided into two groups—the Lepidosauria (lizards, snakes, *Sphenodon*, ‘eosuchians’) and the Archosauria (crocodiles, thecodontians, dinosaurs, pterosaurs). Recent suggestions that these two are not sister-groups are shown to be unproven, whereas there is strong evidence that they form a monophyletic group, the Diapsida, on the basis of several synapomorphies of living and fossil forms. A cladistic analysis of skull and skeletal characters of all described Permo-Triassic diapsid reptiles suggests some significant rearrangements to commonly held views. The genus *Petrolacosaurus* is the sister-group of all later diapsids which fall into two large groups—the Archosauromorpha (Pterosauria, Rhynchosauria, Prolacertiformes, Archosauria) and the Lepidosauromorpha (Younginiformes, Sphenodontia, Squamata). The pterosaurs are not archosaurs, but they are the sister-group of all other archosauromorphs. There is no close relationship between rhynchosaurs and sphenodontids, nor between *Prolacerta* or *Tanystropheus* and lizards. The terms ‘Eosuchia’, ‘Rhynchocephalia’ and ‘Protosauria’ have become too wide in application and they are not used. A cladistic classification of the Diapsida is given, as well as a phylogenetic tree which uses cladistic and stratigraphic data.

KEY WORDS:—Reptilia – Diapsida – taxonomy – classification – cladistics – evolution – Permian – Triassic.

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INTRODUCTION

Reptiles are normally classified into subclasses on the basis of their temporal openings, although those with two, the diapsids, have been further subdivided into the Subclasses Lepidosauria (lizards, snakes, *Sphenodon*, various extinct groups) and Archosauria (crocodiles, dinosaurs, pterosaurs, other extinct groups) (Romer, 1956, 1966, 1967). In recent years, palaeontological and neontological evidence has suggested to many workers (e.g. Cruickshank, 1972a; Carroll, 1975a, 1976c, 1977, 1981; Evans, 1980; Gaffney, 1980; Wild, 1980; Reisz, 1981; Benton, 1982, 1983b) that the diapsids form a monophyletic group. An opposing viewpoint has been presented by Løvtrup (1977) who argued that crocodiles share more derived characters with turtles than with lepidosaurs. Further, Gardiner (1982) has presented synapomorphy lists in favour of his view that Testudines are the sister-group of (Crocodylia + Aves + Mammalia), and that Lepidosauria are the sister-group of all four groups. It will be argued here that the most parsimonious arrangement of living reptiles is to accept the monophyly of the diapsids—that the archosaurs (including birds) are the sister-group of the lepidosaurs. The outline of the cladogram to be presented here is based solely on living forms.

There was a great diversity of diapsid reptiles in the Permo-Triassic, and their relationships have become extremely confused (cf. Romer, 1966; Kuhn, 1969; Evans, 1980; Wild, 1980; Benton, 1982; Sues, 1982). The main part of this paper consists of a cladistic analysis of the characters of the early diapsids. The well-known genera are classified on the basis of an assessment of shared derived characters, so far as can be determined from the fossil material. Certain genera

were hard to assign either because the material was too poorly preserved to allow a consideration of key characters or because convincing synapomorphies could not be found. Thus the cladogram erected on the basis of living forms was substantially extended by a study of the fossil forms.

Standard cladistic techniques were used in the character analysis (see Platnick, 1979; Eldredge & Cracraft, 1980; Wiley, 1981), and fossils were treated as terminal taxa. The polarity of characters was determined by means of out-group comparison, where the out-group was 'all other tetrapods' for the assessment of diapsid monophyly, and 'all early reptiles' for the consideration of major divisions within the Diapsida. The remainder of the analysis is presented in a step-wise fashion in which major groups are established, and then individual genera within them analysed. Polarity decisions at these levels are determined by a comparison with other members of the larger monophyletic group that has already been established. A classification is presented on the basis of the cladogram, and a phylogenetic tree is given which consists of the cladogram with the addition of stratigraphic data. A preliminary account has been given in Benton (1983b, 1984).

The main fossil taxa to be considered in the second part of the study (listed stratigraphically here for ease of reference) are:

Upper Carboniferous: *Petrolacosaurus*.

Upper Permian: *Weigeltisaurus*, *Coelurosauravus*, *Claudiosaurus*, *Protorosaurus*, *Youngina*, *Tangasaurus*, *Hovasaurus*, *Kenyasaurus*, *Thadeosaurus*, *Paliguana*, *Saurosternon*, *Galesphyrus*, *Heleosaurus*.

Lower Triassic: *Prolacerta*, *Mesosuchus*, *Howesia*, *Chasmatosaurus*, *Erythrosuchus*, *Euparkeria*, *Palaeagama*, *Noteosuchus*.

Middle Triassic: *Macrocnemus*, *Tanystropheus*, *Stenaulorhynchus*, *Rhynchosaurus*, *Clarazia*, *Hescheleria*, *Askeptosaurus*.

Upper Triassic: *Tanytrachelos*, *Trilophosaurus*, *Hyperodapedon*, *Scaphonyx*, *Malerisaurus*, *Clevosaurus*, *Brachyrhinodon*, *Kuehneosaurus*, *Icarosaurus*, *Gephyrosaurus*, *Thalattosaurus*.

In the interests of brevity, the post-Triassic diapsids are not considered here, nor is there any discussion of the relationships among different genera of middle and late Triassic thecodontians, dinosaurs, crocodiles or pterosaurs.

HISTORICAL SURVEY

Osborn (1903) established the reptilian subclass Diapsida to include all forms that we currently regard as diapsid, as well as the Pelycosauria, the Procolophonia, the Proganosauria (*Mesosaurus*) and the Ichthyosauria. These groups were defined as "primarily with double or divided temporal arches" and they were distinguished from all other reptiles which had "single or undivided temporal arches" (Osborn's Synapsida). The characters he used to define his Diapsida (Osborn, 1903: 459) are as follows.

- "(1) Roof of cranium open with two distinct temporal arches, which may secondarily, one or both, disappear.
- (2) Squamosal relatively small, frequently separate from prosquamosal [= anterior part of squamosal], not entering into articulation with the lower jaw.
- (3) Quadrate relatively large, uncovered and sometimes secondarily movable.

- (4) Coracoid and procoracoid early coalesced into a single bone, or procoracoid degenerate.
 (5) Phalangeal formula primitively 2,3,4,5,3-4."

Osborn assigned the pelycosaurs to the Diapsida since his reconstruction showed two temporal fenestrae. He called *Procolophon* a diapsid because he considered that it had an upper temporal fenestra and because of features of its hand and foot. *Mesosaurus* was considered to be a diapsid on the basis of supposed similarities with *Sphenodon* and rhynchosaurs, and the inclusion of the ichthyosaurs was not explained at all.

The classification of living and fossil reptiles on the basis of their temporal fenestrae was carried further by Watson (1917) and others. Williston (1925) presented a revised classification of reptiles in which many of Osborn's dubious diapsids were placed elsewhere. Williston's Subclass Diapsida included the following:

?Order Proterosuchia

?Order "Eosuchia"

Superorder Diaptosauria

Order Rhynchocephalia

Superorder Archosauria

Order Parasuchia

Order Crocodilia

Order Saurischia

Order Ornithischia

Order Pterosauria

He placed the lizards and snakes (Order Squamata) in the Subclass Parapsida with *Mesosaurus* and the ichthyosaurs on the assumption that all of these forms had always had only an upper temporal opening. Broom (1925) argued strongly that lizards were true diapsids that had lost the lower temporal bar, and that view is generally held now. Williston (1925: 212-213) gave the following characters of the Diapsida:

"Two temporal openings, separated by postorbito-squamosal arch; no supratemporals or tabulars (?*Youngina*). A single coracoid; no cleithrum. Phalangeal formula primitive. Often reduced postaxially."

This kind of classification of reptiles, in which the two-arched forms were regarded as a single group distinct from those with no temporal fenestrae (Anapsida: primitive groups, turtles) and those with only a lower (Synapsida: mammal-like reptiles) or only an upper ('Parapsida': plesiosaurs, ichthyosaurs) was followed by several subsequent authors (e.g. Kuhn, 1938, 1966; Camp, 1945; Olson, 1947; Huene, 1948, 1956; Parrington, 1958). However, Romer (1933, 1956, 1966, 1967, 1968, 1971) argued repeatedly that there were two distinct lineages within the diapsids, namely the Subclass Lepidosauria (Eosuchia, Squamata, Rhynchocephalia) and the Subclass Archosauria (Thecodontia, Crocodylia, Pterosauria, Saurischia, Ornithischia), each of which had a distinct origin within the captorhinomorphs. The separation of Lepidosauria from Archosauria is still accepted in many quarters because of Romer's influence, and because of the great anatomical differences between crocodiles on the one hand and lizards, snakes and *Sphenodon* on the other.

Five further hypotheses of diapsid relationships should be noted here: that millerosaurs are the sister-group of all diapsids (Watson, 1957), or of lepidosaurs

alone (Gow, 1972), that varanopsid pelycosaurs are the sister-group of diapsids (Reig, 1967, 1970), that turtles are the sister-group of crocodiles (Løvtrup, 1977), or of crocodiles + birds + mammals (Gardiner, 1982).

Watson (1957) suggested that the diapsid reptiles evolved from seymouriamorph anthracosaurs via the Millerosauria. The late Permian millerosaurs (*Milleretta*, *Millerosaurus*, etc.) from S Africa shared such characters with the diapsids as a lower temporal fenestra surrounded by jugal, postorbital, squamosal and quadratojugal, an otic notch, and lizard-like stapes. Watson's ideas were an extension of Goodrich's (1916) division of reptiles into theropsids (mammal-like reptiles, leading to mammals) and sauropsids (turtles, diapsid forms, leading to birds), but Watson expressly ruled out the Captorhinomorpha as diapsid ancestors and placed them among the Theropsida. Gow (1972) modified Watson's (1957) theory, and suggested that millerosaurs were directly ancestral to lizards since the quadrate was apparently freely movable and the lower temporal bar was reduced in some genera. However, as Carroll (1977: 388–391) noted, the supposed 'lizard-like' features are not homologous: the quadrate of *Millerosaurus* is like that of a captorhinomorph and the tympanum is supported by both the squamosal and quadratojugal, and not the quadrate.

Reig (1967, 1970) proposed that archosaurs arose from varanopsid pelycosaurs on the basis of a long list of shared characters. Romer (1971) and Cruickshank (1972a) pointed out that nearly all of these shared characters are primitive features present in captorhinomorphs and this theory is apparently no longer held by Reig himself (Charig, 1976b: 10).

At present, the classification of early diapsid reptiles is in a state of some confusion. There is no reliable framework into which new finds may be fitted, and many major taxa are effectively undefined (e.g. *Lepidosauria sensu lato*, *Eosuchia*, *Rhynchocephalia*, *Protorosauria*). This confusion has arisen from the reliance on the authority of certain eminent workers, the mixing of primitive and derived characters, and attempts to classify material that is unclassifiable. In the present work a classification of all early diapsid reptiles is given, with all taxa defined by synapomorphies and areas of uncertainty made clear.

Two cladistic analyses have been made recently that suggest that the lepidosaurs and the archosaurs are not sister-groups. Løvtrup (1977) argued that Testudines are the sister-group of Crocodylia + Aves, that *Rhynchocephalia* are the sister-group of these three, and *Squamata* of all four. Thus, he denied the monophyly of the Diapsida and of the *Lepidosauria*. Gardiner (1982) developed the hypothesis that the turtles are the sister-group of crocodiles + birds + mammals, and that the lepidosaurs are the sister-group of these four. Thus, he has also proposed that the crocodiles share synapomorphies with the turtles rather than with the lepidosaurs.

MONOPHYLY OF THE DIAPSIDA

In this section, the arguments that have been presented against the monophyly of the Diapsida are considered. The three main critics have been Romer (1966, 1968, 1971) who presented his arguments in a non-cladistic way, and the cladists Løvtrup (1977) and Gardiner (1982). Romer's arguments and the supposed synapomorphies between turtles and crocodiles will be discussed,

and a case will be made that, among living forms, the lepidosaurs are in fact the sister-group of the crocodiles.

Romer (1968)

Romer suggested at times that primitive eosuchians could have given rise to the archosaurs (e.g. Romer, 1956: 473; 1966: 127), but he tended to regard this as unlikely: "there is little proof of a monophyletic origin of two-arched reptiles" (Romer, 1967: 832; see also Romer, 1968: 126; 1971: 108). He argued that even the earliest lepidosaurs, and in particular *Youngina* from the late Permian of S Africa, had advanced characters that excluded them from the ancestry of the more 'primitive' early archosaurs such as *Chasmatosaurus* from the early Triassic of S Africa. These characters of *Youngina* were (Romer, 1968: 126–127):

- (1) short jaw, not extending behind the plane of the occiput;
- (2) incipient otic notch.

Romer implied that these two characters are shared derived characters of lepidosaurs that prove an independent origin of the archosaurs, which supposedly retain the primitive state. However, it is not acceptable to argue in this way that the Archosauria are the sister-group of some unspecified captorhinomorphs on the basis of shared primitive characters. Furthermore, these two characters are not valid. *Youngina* is now known to have a retroarticular process that extends behind the plane of the occiput (Gow, 1975; Carroll, 1981) and this is a synapomorphy of all diapsids except for *Petrolacosaurus* from the late Carboniferous (Reisz, 1981). Further, the polarity of this character is the opposite to that assumed by Romer (i.e. the short jaw is primitive by comparison with an outgroup of early reptiles in general—captorhinomorphs, pareiasaurs, pelycosaurs, etc.). The "incipient otic notch" is also a synapomorphy of all diapsids except *Petrolacosaurus* (Reisz, 1981). *Chasmatosaurus* has an otic notch (Cruickshank, 1972a: 98; Charig & Sues, 1976: 13). The "otic notch" seen in millerosaurs is almost certainly convergent (Carroll, 1977). Thus, I consider that Romer's evidence against the monophyly of the Diapsida is unconvincing.

The three-taxon statements

In the remainder of this discussion, we shall consider whether crocodiles are the sister-group of turtles or of lepidosaurs. Three arrangements of these three groups are possible (Fig. 1), although only the first two have been considered in the literature to my knowledge. Fig. 1A (Lepidosauria the sister-group of Crocodylia + Testudines) is favoured by Løvtrup (1977: 179–185) and Gardiner (1982), while Fig. 1B is a more standard arrangement accepted by Carroll (1977, 1982b), Reisz (1977, 1981), Gaffney (1980), and numerous others in recent years. It is necessary, first of all, to establish the monophyly of the three major groups: Testudines, Lepidosauria and Crocodylia.

Gaffney (1975) has argued for turtle monophyly on the basis of the absence or reduction of the teeth, the horny sheath of the jaws, the fused basiptyergoid articulation, the hypertrophy of the middle ear, the absence of the pineal foramen, the absence of lacrimal, postfrontal, supratemporal, postparietal and septomaxilla, the single vomer, the paroccipital process of the opisthotic sutured to the quadrate, and the shell. This view has not been opposed (Gaffney, 1980).

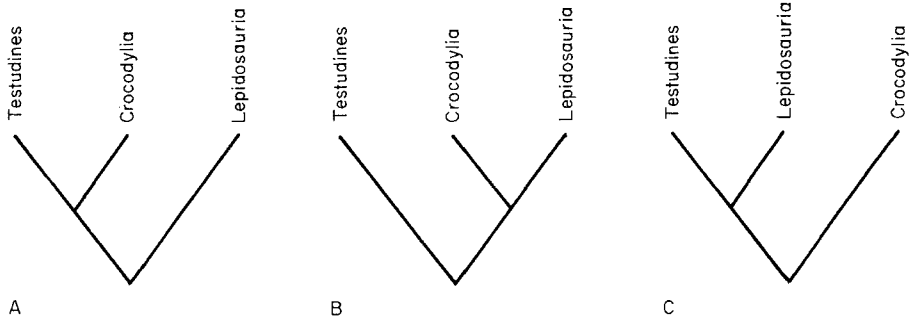


Figure 1. Three 3-taxon statements representing possible relationships of the three groups of living reptiles.

The living lepidosaurs (lizards, snakes, amphisbaenians, *Sphenodon*) share numerous derived characters such as determinant growth, bony epiphyses on the long bones, specialized ulna-ulnare joint, fused astragalus and calcaneum, supraparachordal course of the notochord, formation of a median hypocentral occipital condyle, kidney provided with a sexual segment, and so on (Carroll, 1977; Gardiner, 1982; Rage, 1982; see also below, p. 143). Løvtrup (1977: 183–184) disputed the monophyly of the Lepidosauria and noted that *Sphenodon* shares several characters with turtles + crocodiles + birds: uncinat processes on the ribs, solid ovary, lime-impregnated shell, albumen, and horny caruncle. However, uncinat processes are not present in turtles, and the polarity of the other characters may be wrongly determined. On the other hand, the monophyly of the Lepidosauria is supported by the numerous synapomorphies just noted.

The living crocodiles are also regarded as a monophyletic group here on the basis of the following synapomorphies: elongation of the snout, secondary palate, sculpture on the external surface of the skull, upper temporal opening small or closed, rectangular skull table behind the orbits, pterygoid and quadrate tightly applied to the lateral wall of the braincase, closure of the otic notch by union of squamosal and quadrate posteriorly, procoelous dorsal vertebrae, elongated waisted coracoid, rod-like pubis excluded from acetabulum, reduced carpus with elongate waisted radiale and ulnare (Romer, 1956; Steel, 1973).

Løvtrup (1977) and Gardiner (1982)

The supposed synapomorphies shared by Testudines and Crocodylia, but not by Lepidosauria, are listed from Gardiner (1982) (characters 1–10) and Løvtrup (1977) (characters 3, 4, 9, 11–15).

- (1) Epipterygoid joins parietal
- (2) Stapes unites with Mëckel's cartilage
- (3) Penis single and with erectile tissue
- (4) Solid ovaries
- (5) Ciliary process
- (6) Upper eyelid cartilage
- (7) Tendon of nictitans to pyramidalis muscle
- (8) Thyroid and cricoid cartilages

- (9) Cartilaginous cones at ends of long bones
- (10) Subclavian arteries displaced cephalad
- (11) Type of scutes
- (12) Lime-impregnated shell
- (13) Albumen
- (14) Horny caruncle
- (15) Blood proteins

The choice of an out-group for these comparisons is not easy. Amongst living tetrapods, we must consider the Lissamphibia, and for hard-part characters we can also consider the large set of extinct early tetrapods, on the assumption that the tetrapods form a monophyletic group.

Gardiner (1982: 216–217) notes that the epipterygoid meets the parietal in turtles, crocodiles, birds and mammals, and that this does not occur in lepidosaurs. This is incorrect. First, this proposal assumes the homology of the pleurospenoid of birds and crocodiles with the epipterygoid (or alisphenoid) of other reptiles and mammals. The epipterygoid of *Sphenodon*, lizards and primitive reptiles is homologous with that of cryptodire turtles in that it is an ossification of the ascending process of the pterygoquadrate lateral to the cavum epiptericum (de Beer, 1937; Bellairs & Kamal, 1981). The mammalian alisphenoid may be a neomorph that arose from an upgrowth of the epipterygoid root of reptiles (Presley & Steel, 1976). The laterosphenoid of snakes develops in the prootic notch: it may be entirely a membrane bone, or it may incorporate a portion that originated from a cartilage on the edge of the basal plate. Snakes have no obvious cavum epiptericum, but the laterosphenoid has similar relationships to the trigeminal nerve as the epipterygoid. The snake laterosphenoid may be a neomorph whose cartilaginous portion is related to a vestigial pterygoquadrate derivative and in that respect it could be seen as a possible homologue of the mammalian alisphenoid (Bellairs & Kamal, 1981). On the other hand, the pleurospenoid of crocodiles and birds is formed from the ossified pila antotica, and is not homologous with the lizard or turtle epipterygoid, mammal alisphenoid or snake laterosphenoid (Rieppel, 1976; Bellairs & Kamal, 1981). Even if these homologies were accepted, the character 'epipterygoid joins parietal' occurs in lepidosaurs. In certain lizards the epipterygoid may articulate with the parietal and in some cases, such as scincomorph lizards, a process from the parietal descends towards it (Jollie, 1960; Rieppel, 1981). Further, in snakes, the laterosphenoid meets a descending process of the parietal.

There is a temporary connection between the stapes and Meckel's cartilage via an interhyal during the early development of some turtles and crocodiles (character (2); de Beer, 1937). This has not been reported in lepidosaurs, but, according to Goodrich (1930: 455) and Bellairs & Kamal (1981: 246), this may be a trivial non-homologous feature.

There is a problem in assessing the polarity of the penis character (character (3)) since it occurs in several different states in the living groups. Among living amphibians, male caecilians and the frog *Ascaphus* have copulatory organs that are muscular extensions of the cloaca. Other amphibians, as well as *Sphenodon*, have no penis. Snakes and lizards have paired hemipenes, and turtles and crocodiles have a single erectile organ. This latter could be the primitive condition just as readily as the derived.

Crocodiles and turtles have solid ovaries, whereas those of lizards, snakes and amphisbaenians are saccular and hollow (character (4)). However, *Sphenodon* also has a solid ovary, which suggests that this is either non-homologous or a primitive amniote character.

Ciliary processes are seen in the eyes of crocodiles, chelonians, birds and mammals, but they are absent in lepidosaurs (character (5); Underwood, 1970). However, anurans and urodeles have ciliary processes, so that these are probably primitive for tetrapods and they have been secondarily lost in lepidosaurs (Walls, 1942).

Gardiner (1982: 217) states that crocodiles and turtles have cricoid and thyroid cartilages around the larynx, and that these are absent in lepidosaurs (character (8)). This is incorrect. All living amphibians and reptiles have paired arytenoid cartilages and, except for salamanders, they all have a single cricoid cartilage. Turtles have an additional single procricoid cartilage in front of the cricoid. Out-group comparison suggests that the turtle procricoid is an autapomorphy. The turtle cricoid has occasionally been named the 'thyreocricoid', but this is not homologous with the mammalian thyroid (Goodrich, 1930; Schumacher, 1973). Crocodiles have no thyroid cartilage either, and simply show the primitive tetrapod pattern.

Gardiner (1982) notes that crocodiles and chelonians have temporary massive cartilaginous cones at the ends of long bones during development (character (9)). Lizards and *Sphenodon* have bony epiphyses, but this is apparently the derived condition. Living amphibians and birds have cartilaginous epiphyses, as did various early tetrapods (Haines, 1969; Ricqlès, 1972). Further, although it is difficult to comment on snake epiphyses in the absence of limbs, they have cartilaginous epiphyses on the tips of their vertebrae, and thus may be said to have endochondral ossification of the turtle-crocodile type (Haines, 1969).

Løvtrup (1977: 182) states that in crocodiles and turtles "the type of scutes is the same (Boas, 1931)" (character (11)). Boas (1931) makes no such assertion and no out-group is indicated. This supposed synapomorphy cannot be considered unless it is adequately defined.

A lime-impregnated egg shell (character (12)) is present in living turtles, crocodiles, *Sphenodon*, and in some gekkos. Numerous calcified eggshells of dinosaurs and other fossil reptiles are also known, so that this is probably a primitive amniote feature.

The presence of albumen in the egg of crocodiles and turtles (character (13)) is linked with the calcified shell and the need to ensure a supply of water to the embryo. *Sphenodon* also has albumen in the egg.

The young of crocodiles and turtles have a horny caruncle (character (14)) instead of an egg tooth as in lizards and snakes. However, *Sphenodon* also has a horny caruncle (de Beer, 1937) so that this may be the primitive amniote condition.

Finally, Løvtrup (1977: 182) quotes Dessauer (1970: 51–52) that "serology demonstrates the fairly close relationship of some lizards and snakes, indicates a very remote affinity between turtles and crocodiles, and shows the wide divergence of the Squamata from the Testudines and Crocodylia" (character (15)). I am uncertain which side of the argument Løvtrup is supporting with this quotation! Further, in the absence of out-group comparison, and greater precision, this character must be regarded as trivial.

Thus, of the 15 supposed synapomorphies of turtles and crocodiles presented by Løvtrup (1977) and Gardiner (1982), two are incorrect (1, 8), three have no out-group defined (3, 11, 15), and six are probably primitive for amniotes or tetrapods (4, 5, 9, 12, 13, 14). The remaining characters are:

- (2) stapes unites with Meckel's cartilage;
- (6) upper eyelid cartilage;
- (7) tendon of nictitans to pyramidalis muscle;
- (10) subclavian arteries displaced cephalad.

An opposing synapomorphy list will be presented below in support of the view that crocodiles are the sister-group of lepidosaurs rather than chelonians. Recent molecular data that bears on this question will be considered briefly first.

Molecular data and diapsid relationships

In the last few years, new data on the protein sequences of various reptiles have become available (e.g. Dene *et al.*, 1980; Leclercq *et al.*, 1981; Maeda & Fitch, 1981a, b; Perutz *et al.*, 1981; Leclercq *et al.*, 1982; Litman *et al.*, 1983; Watts *et al.*, 1983), and these have led to some reinterpretations of the relationships of the groups. On the basis of myoglobin sequences, alligators are the sister-group of turtles, and squamates are the sister-group of those two (Dene *et al.*, 1980; Maeda & Fitch, 1981b). On the basis of cytochrome-*c* sequences, snakes are the sister-group of mammals, and birds are the sister-group of those two (Maeda & Fitch, 1981b). According to one analysis of α -haemoglobin sequences (Maeda & Fitch, 1981b), birds are the sister-group of mammals, and squamates are the sister-group of (fish + salamanders + birds + mammals). However, according to another analysis of α -haemoglobin sequences (Leclercq *et al.*, 1981; Perutz *et al.*, 1981), birds and crocodiles are sister-groups, mammals are the sister-group of those two, and squamates the sister-group of (mammals + birds + crocodiles). A third tree produced on the basis of α -haemoglobin sequences (Goodman *et al.*, 1982) shows crocodiles and birds as sister-groups, squamates as the sister-group of those two, and mammals the sister-group of (squamates + crocodiles + birds).

Some of these protein sequence data, then, have suggested phylogenies in which crocodiles are separated from the squamates and made the sister-group of (birds + mammals). Some of the authors who reached these conclusions (Dene *et al.*, 1980; Leclercq *et al.*, 1982) have proceeded to rewrite tetrapod phylogeny, and to propose that birds (and dinosaurs) evolved from a common ancestor with the mammals in the Permian, and that the crocodiles came from a different ancestor within the captorhinomorphs.

Other authors (e.g. Romero-Herrera *et al.*, 1978; Perutz *et al.*, 1981; Goodman *et al.*, 1982), however, treat the molecular data more cautiously. They recognize that the most parsimonious tree may only be slightly more parsimonious than a range of quite different trees by a narrow margin. For example, in the cases noted above, the differences, in terms of numbers of nucleotide substitutions, between the most parsimonious tree and a 'biological' tree that reflects the consensus of anatomical and palaeontological opinion, are small: 801 and 813 or 630 and 638 for myoglobin (Maeda & Fitch, 1981b; Dene *et al.*, 1980), 143 and 145 for cytochrome-*c* (Maeda & Fitch, 1981b), and 940 and 950 for α -haemoglobin (Maeda & Fitch, 1981b).

The most parsimonious trees from different proteins and different data sets are not self-consistent, and this suggests that the proteins may have evolved in different ways. There are probably different rates of molecular evolution in different lineages, and a constant rate of nucleotide substitution in all lineages cannot be assured. Further, parallel and convergent evolution of substitutions may occur (Romero-Herrera *et al.*, 1978; Goodman *et al.*, 1982).

Biochemical and immunological studies of other tetrapod proteins have only offered the conclusion that the main groups of living reptiles diverged from each other a long time ago (Dessauer, 1970, 1974; Densmore, 1983). Strong evidence has not been found in favour of a close pairing of Squamata and Crocodylia, or of any other grouping.

In conclusion, some molecular data support the sister-group relationship of Squamata and (Crocodylia + Aves), while other data suggest different arrangements. More data and more consideration of the nature of protein evolution are required before firm phylogenies of the amniotes can be drawn up on the sole basis of molecular data.

Monophyly of the Diapsida

Gaffney (1980) and Reisz (1981) have presented synapomorphy lists for the Diapsida, and several more characters are added here to strengthen the conclusion that, amongst living forms, crocodiles are the sister-group of lepidosaurs rather than of chelonians (Fig. 4A). The out-group for this section is living amphibians (non-amniote tetrapods), on the assumption that the Tetrapoda are monophyletic. Note that we are not concerned here with the relationships of birds and mammals. Where relevant, birds are assumed to be diapsids, and mammals are not considered to be part of the out-group for testing the Testudines-Crocodylia-Lepidosauria cladograms since they may be the sister-group of Diapsida as a whole (Gaffney, 1979, 1980), or of Aves alone (Gardiner, 1982).

Character list A: Diapsida

- (1) Presence of a superior temporal fenestra.
- (2) Presence of an upper temporal arch formed by a triradiate postorbital and a triradiate squamosal which have a small contact with each other; the parietal has small contacts with the postorbital and quadrate and it has a lateral process.
- (3) Presence of a well developed suborbital fenestra.
- (4) Maxilla, palatine, ectopterygoid and jugal bones and their interrelationships modified as a result of the presence of the suborbital fenestra. The maxilla/palatine suture is reduced in length; the ectopterygoid is reduced and the contact between the ectopterygoid and the cheek is reduced; there is no ectopterygoid/maxilla contact.
- (5) Presence of a Jacobson's organ that develops as a ventromedial outpocketing of the early embryonic nasal cavity (Parsons, 1967, 1970; Gaffney, 1980). A true Jacobson's organ is present in adults of Squamata and *Sphenodon*, and in some mammals. In birds and crocodiles, the organ develops in the embryo, but disappears in the adult. In squamates, Jacobson's organ is a separate structure lying ventral to the posterior part of the vestibulum or the anterior part of the cavum, and vomeronasal epithelium is restricted to its roof

and sides. In *Sphenodon*, Jacobson's organ is a tubular structure lying along the nasal septum that opens into the antero-ventral part of the nasal sac. Again, the vomeronasal epithelium is restricted to the roof of the organ. Turtles and amphibians have sensory tissues that have been termed Jacobson's organs, but these are best called simply vomeronasal organs (Parsons, 1967). In both structures, Bowman's glands are absent (these are present in the normal olfactory epithelium of most tetrapods), the innervation is to the accessory olfactory bulb (instead of the main olfactory bulb), and the region is ventrally located in the nasal cavity. However, the vomeronasal organs of amphibians and turtles lack the ventromedial outpocketing seen in the true Jacobson's organ.

(6) Olfactory bulbs anterior to the eyes and linked to the forebrain by the stalk-like olfactory tract. In turtles and living amphibians, the bulb sits directly on the telencephalon with no olfactory tract: the bulbs are said to be sessile (Starck, 1979).

(7) Presence of one or more nasal conchae in the *cavum nasi proprium* (Parsons, 1967, 1970; Bellairs & Kamal, 1981). *Sphenodon* has two conchae, nearly all lizards have one, crocodiles have three, while turtles and amphibians have none. (Note that birds have three nasal conchae, and mammals have several.)

(8) Presence of a 'Huxley's foramen' at the distal end of the extracolumella, surrounded medially by the processus dorsalis and intercalary, and laterally by a laterohyal which links the intercalary to the distal extracolumellar plate (de Beer, 1937; Wever, 1978; Bellairs & Kamal, 1981). The laterohyal is cartilaginous in *Sphenodon*, and ligamentous in geckos and crocodiles. This feature is present in birds also, but absent in turtles and amphibians.

(9) Low levels of urea in the blood. Lizards, snakes and crocodiles have low levels of urea in the blood (<5 mg%), or none at all, while living amphibians and turtles have high levels (5–55 mg%) (Dessauer, 1974).

On the basis of these characters (1–9), it is argued that the Diapsida are monophyletic, with crocodiles as the sister-group of lepidosaurs rather than of turtles.

In his discussion of the relationships of *Petrolacosaurus*, Reisz (1981) suggested four more synapomorphies of early diapsids: presence of well developed post-temporal fenestrae, relatively small skull, relatively long limbs, locked tibio-astragalar joint. However, these cannot be used as apomorphies of the Diapsida: turtles also have large post-temporal fenestrae, small heads, and limited movement between tibia and astragalus. Crocodiles have relatively large heads and short limbs. The tibio-astragalar joint is not 'locked' in living lepidosaurs, although this feature is present in early diapsids, crocodiles and dinosaurs.

CLASSIFICATION OF THE PERMIAN AND TRIASSIC DIAPSID REPTILES

Introduction

Having established the monophyly of the Diapsida and the sister-group relationship of lepidosaurs to crocodiles (+ birds), the fossil forms may now be added to the cladogram. The oldest known diapsid reptile is *Petrolacosaurus* from the late Carboniferous of Kansas. There are no true diapsid reptiles known from

the early Permian (except for a ?diapsid parietal from Oklahoma: Carroll, 1968), but a range of families appeared in the late Permian, and these radiated worldwide in the Triassic. Some of these groups have been well studied, and families and suborders have been defined. However, others are poorly known, and they are classified in a great range of positions in taxonomic summaries (cf. Huene, 1956; Romer, 1966; Kuhn, 1969). Hitherto, no cladistic analysis of the relationships of these reptiles has been attempted.

At the start of this work, it seemed that there were no clear larger monophyletic groups within the Diapsida, and therefore that the diapsids had radiated along numerous separate lines during the Permo-Triassic (cf. Evans, 1980; Benton, 1982). However, in the search for synapomorphies, strong evidence was found for several major clades. *Petrolacosaurus* is the sister-group of all later diapsids, which are termed here the Neodiapsida. The Neodiapsida split into two large monophyletic groups: the Archosauromorpha (Huene, 1946), which includes Rhynchosauria, Prolacertiformes and Archosauria, and the Lepidosauromorpha (Benton, 1983b, 1984), which contains the Younginiformes and Lepidosauria (*sensu stricto*). The crocodiles (and birds) are the living representatives of the Archosauromorpha, and the lizards, snakes, amphisbaenians and *Sphenodon* are the living representatives of the Lepidosauromorpha. The cladistic relationships of the members of each of these groups were then tested, and a cladogram was constructed (Figs 4, 9, 10, 15) which represents the most parsimonious arrangement of synapomorphies. In the supporting text, the taxa are introduced, their relationships are established on the basis of a character analysis, and apparently conflicting synapomorphies are discussed. The synapomorphy lists for each clade are matched by letter designations (A–Z) in the text and cladograms. Poorly defined taxa are noted briefly, and currently unassignable taxa are discussed in more detail at the end. Most of these are not shown on the cladogram, but they are listed as *incertae sedis* in the classification.

The order of treatment of taxa is as follows:

Neodiapsida

Archosauromorpha

Prolacertiformes

(Protorosauridae, Prolacertidae, Tanystropheidae)

Archosauria

(?Proterosuchidae, Erythrosuchidae, Euparkeriidae, Pseudosuchia, later archosaurs)

Heleosaurus

Rhynchosauria

(Mesosuchidae, Rhynchosauroidae, Howesiidae, Rhynchosauridae)

Trilophosauridae

Pterosauria

Lepidosauromorpha

Younginiformes

Younginoidea (Younginidae, Tangasauridae)

Lepidosauria

Squamata, the “paliguanids”, Kuehneosauridae, Gephyrosauridae

Sphenodontia

Others

(Galesphyridae, Weigeltisauridae, Claudiosauridae, Claraziidae, Thalattosauridae)

Petrolacosaurus and diapsid relationships

The earliest diapsid reptile is *Petrolacosaurus kansensis* from the Conemaugh Series (Stephanian, Upper Pennsylvanian, uppermost Carboniferous) of Garnett, Kansas. It shows all diapsid synapomorphies (Fig. 4, character list A). This animal was 60–70 cm long (snout-tail tip) and it had a long neck (elongate cervical vertebrae) and long fore- and hind-limbs of equal length (Fig. 2). The skull was typically diapsid, high, and with conical subthecodont teeth (Reisz, 1981). *Petrolacosaurus* was probably an agile terrestrial reptile that may have fed on large insects and other arthropods.

Petrolacosaurus shows numerous plesiomorphies of other contemporary reptiles, but shares a suite of derived characters with the protorothyridids. The Family Protorothyrididae includes six Pennsylvanian genera (*Hylonomus*, *Palaeothyris*, *Cephalerpeton*, *Anthracodromeus*, *Brouffia*, *Coelostegus*) and two early Permian genera (*Protorothyris* and an undescribed form) from various localities in Canada, the U.S.A. and Czechoslovakia (Carroll, 1964, 1969, 1982b; Carroll & Baird, 1972; Clark & Carroll, 1973; Reisz, 1980). The protorothyridids were small reptiles, about 100 mm in snout to vent length, with relatively small skulls and light limbs. Their size, jaws and dentition suggest that they had an insectivorous diet, rather like many living lizards.

The best-known protorothyridid, *Palaeothyris* (Fig. 3) shows the typical derived features of other early reptiles when compared with amphibians—the

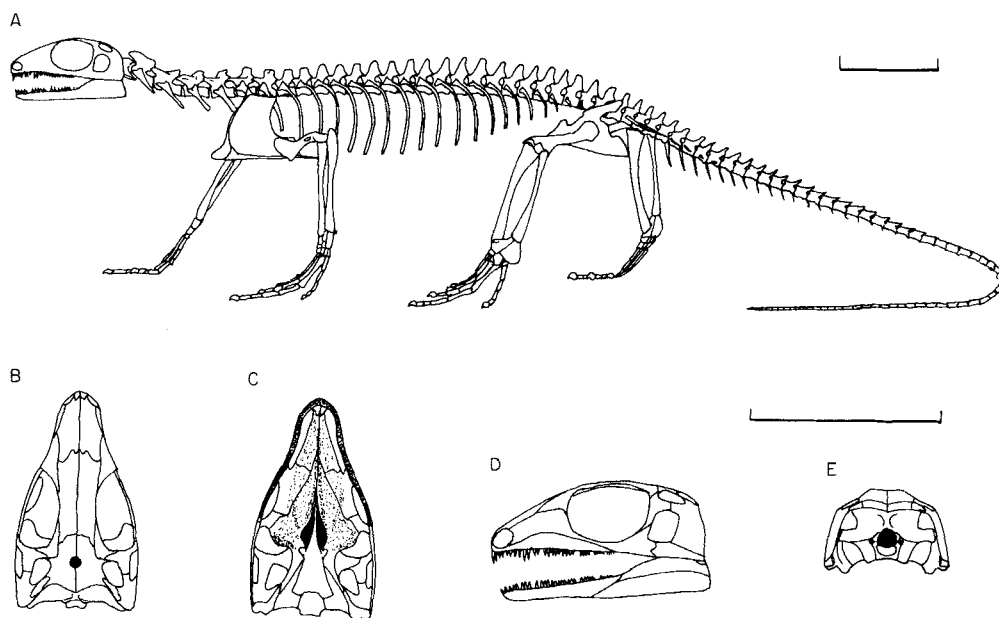


Figure 2. *Petrolacosaurus* (late Carboniferous of Kansas), the oldest known diapsid. A, skeleton; B–E, skull in B, dorsal; C, palatal; D, lateral; and E, occipital views. (After Reisz, 1981.)

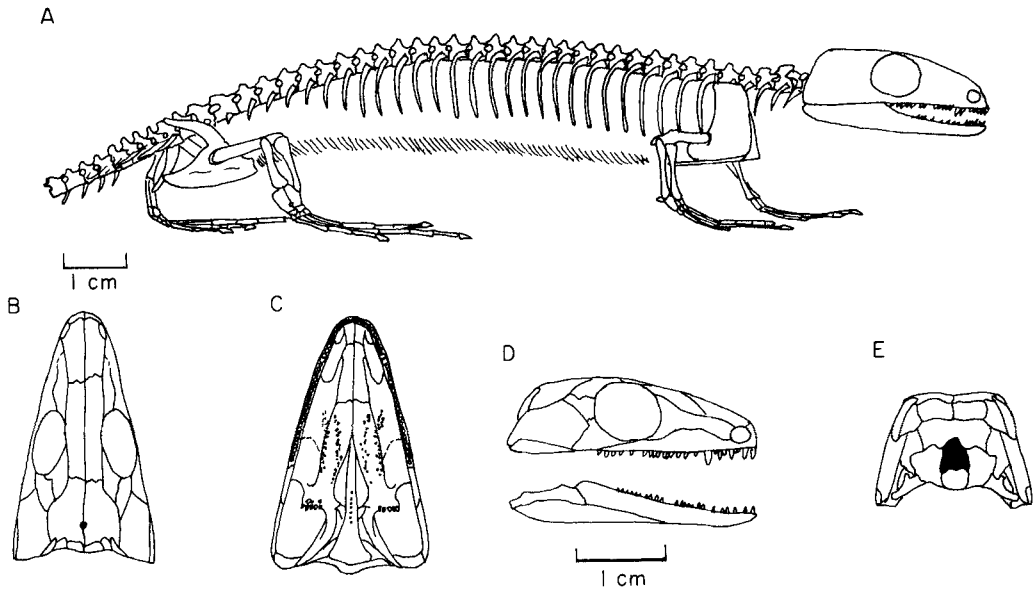


Figure 3. *Paleothyris* (late Carboniferous of Nova Scotia), a protorothyridid captorhinomorph. A, skeleton; B-E, skull in B, dorsal; C, palatal; D, lateral; and E, occipital views. (A, after Carroll & Baird, 1972; B-E, after Carroll, 1982a.)

posterior margin of the cheek is vertical; the chamber for the jaw muscles extends to the skull roof posteriorly; the palatal ramus of the pterygoid is deflected ventrally, which provides the origin for a large anterior pterygoideus muscle; the occiput is deep; the supraoccipital is present as a separate centre of ossification; the otic capsule does not contribute to the attachment of the braincase to the dermal bones of the skull; the occipital condyle is roughly circular and well developed; there is a characteristically specialized atlas-axis complex; the limbs are light; and in the ankle, the tibiale, intermedium and proximal centrale have fused into a single unit, the astragalus. However, these features are shared with many other reptiles, and it has proved difficult to identify synapomorphies that are unique to the Protorothyrididae (Reisz, 1981; 59; Carroll, 1982b).

Nevertheless, Reisz (1981: 61-62) argues that the sister-group of Diapsida is *Paleothyris*, as a typical protorothyridid, on the basis of the following synapomorphies (out-group: all other early reptiles—pareiasaurs, procolophonians, millerosaurs, mesosaurs, pelycosaurs, other captorhinomorphs):

- (1) loss of contact between the postorbital and supratemporal;
- (2) reduction in the size of the supratemporal bone;
- (3) reduction in size or loss of the tabular bone;
- (4) proximal and distal limb elements elongate and lightly built;
- (5) manus and pes narrow and long with overlapping metatarsals and metacarpals;
- (6) presence of a single centrale in the pes.

Aræoscelis from the Arroyo Formation (early Permian) of Texas has a single upper temporal opening and robust teeth. However, it is otherwise very like

Petrolacosaurus and it may be a true diapsid (apomorphy: closure of its lower temporal opening), or it may be a sister-group of the Diapsida (synapomorphy: presence of only the upper temporal fenestra) (Carroll, 1981: 373, 376; Reisz, 1981: 64–65).

Neodiapsida nov.

The term Neodiapsida is introduced here to include all diapsid reptiles except for *Petrolacosaurus* and a few other groups that will be noted later. All neodiapsids share numerous synapomorphies that are absent in *Petrolacosaurus* by comparison with an out-group consisting of Protorothyrididae and other early non-diapsid reptiles (see Fig. 4B).

Character list B: Neodiapsida

(1) Reduced lacrimal. The lacrimal does not reach the naris (excluded by premaxilla and/or maxilla), and in some cases it does not enter the orbital border (excluded by prefrontal and/or jugal), or it may be completely absent.

(2) Presence of ventro-medial flanges on the parietal. These flanges beneath the parietal allow the attachment of jaw adductor muscles.

(3) Absence of ‘caniniform’ maxillary teeth. All diapsids other than *Petrolacosaurus* lack the pair of long maxillary teeth seen in many other Permian reptiles.

(4) Reduced quadratojugal with a short contact with the squamosal. In most diapsids, the quadratojugal is reduced in size because the lower temporal fenestra becomes large; indeed, the quadratojugal is actually absent in several groups. *Petrolacosaurus* and other early reptiles have a long quadratojugal/squamosal contact.

(5) Quadrate not completely covered in lateral view by a large plate-like squamosal. In *Petrolacosaurus*, and early reptiles, the quadrate is not seen in lateral view. In neodiapsids, the squamosal is positioned higher up, which exposes the quadrate and quadratojugal.

(6) Quadrate emarginated or notched posteriorly. The lateral exposure of the quadrate shows that the bone is slightly notched. This may be connected with the presence of a tympanum and a light stapes which permits the reception of high-frequency air-borne sound by the middle ear.

(7) Stapes more slender. *Petrolacosaurus* and other early reptiles have heavy stapes and probably lacked the impedance-matching transducer system of neodiapsids.

(8) Reduction in numbers of teeth on the pterygoid. *Petrolacosaurus* and most early reptiles had large numbers of teeth on the pterygoid. Most neodiapsids have a reduced number of rows (1–4), or none at all.

(9) Absence of teeth on the parasphenoid.

(10) Retroarticular process developed. Neodiapsids have a retroarticular process which extends behind the glenoid, and is turned up in some cases.

(11) Ulna lacks a well developed olecranon and sigmoid notch. However, lizards may have a specialized epiphyseal “olecranon” (Haines, 1969), which is regarded as non-homologous to *Petrolacosaurus* and primitive reptiles.

(12) Acetabulum rounded. The acetabulum in *Petrolacosaurus* and protorothyridids is elongate and restricted largely to the posterior and ventral

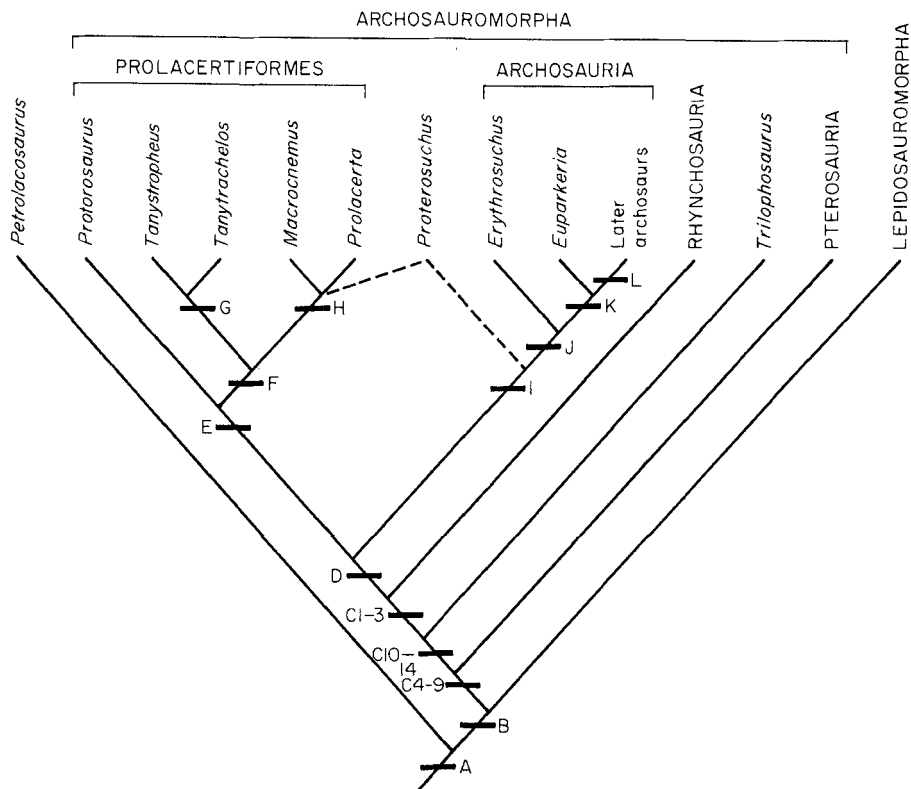


Figure 4. Cladogram representing the relationships of the early diapsid reptiles, particularly the Archosauromorpha (Rhynchosauria, see Fig. 9; Lepidosauromorpha, see Fig. 10). Genera and main monophyletic groups are indicated. Synapomorphies are: A, superior temporal fenestra, upper temporal arch, suborbital fenestra, modified palatal bones, Jacobson's organ in a ventromedial outpocketing of the nasal cavity, olfactory bulbs anterior to eyes and on stalk, one or more nasal conchae, Huxley's foramen at end of extracolumella, low levels of urea in blood; B, reduced lacrimal, ventro-medial flanges on parietal, absence of caniniform maxillary teeth, reduced quadratojugal, quadrate exposed in lateral view, quadrate notched posteriorly, stapes slender, reduced number of teeth on pterygoid, no teeth on parasphenoid, retroarticular process, ulna lacks good olecranon and sigmoid notch, acetabulum rounded, femur sigmoidal and slender, distal articular surfaces on femur level, femur more than 10% longer than humerus; C, premaxilla extends up behind naris, nares elongate and close to midline, quadratojugal behind lower temporal fenestra, loss of tabulars, stapes without foramen, vertebrae not notochordal, transverse processes on dorsal vertebrae elongate, cleithrum absent, no entepicondylar foramen in humerus, loss of foramen in carpus, lateral tuber on calcaneum, complex articulation between astragalus and calcaneum, 5th distal tarsal lost, 5th metatarsal hooked without lepidosaur specializations; D, long snout and narrow skull, nasals longer than frontals, post-temporal fenestrae small or absent, recurved teeth, parasphenoid/basiphenoid in side wall of braincase, long thin tapering cervical ribs with two or three heads; E, lower temporal bar incomplete, 7-12 elongate cervical vertebrae, cervical vertebrae have long low neural spines, short ischium; F, quadratojugal much reduced or absent, quadrate partially streptostylic; G, very long neck, postcloacal bones, 5th metatarsal short; H, squamosal tetradiate, choanae very long, midline gap in palate between pterygoids and posterior part of vomers; I, antorbital fenestra, orbit shaped like an inverted triangle, teeth laterally compressed, 4th trochanter on femur; J, high skull, antorbital fenestra close to naris, loss of supratemporal, lateral mandibular fenestra, coronoid reduced or absent, ossified portion of scapula tall and narrow, coracoid small and glenoid faces backwards, deltopectoral crest extends well down humerus shaft, distal end of humerus narrow, hand is short, pubis has strongly downturned anterior tuber, iliac blade has small anterior process, ischium has large postero-ventral process, tarsus contains only four elements; K, antorbital fenestra large and lies in a depression, parietal foramen absent, otic notch well developed, thecodont dentition, ribs all one or two-headed, pelvis markedly 3-rayed, hind limbs under the body, significant rotation between astragalus and calcaneum, dermal armour; L, postparietals absent, pterygoids meet medially, palatal teeth absent, ?presence of pleurosphenoid, presacral intercentra absent. The relationships of *Proterosuchus* are uncertain. Full details are given in the text.

portion of the ilium. The acetabulum is more circular and centrally placed on the side of the pelvis in neodiapsids.

(13) Femur sigmoidal and slender. In neodiapsids, the femur is slim and slightly curved, with the proximal head often inflected medially.

(14) Distal articular surfaces on femur for fibula and tibia level with each other. In *Petrolacosaurus* and other early reptiles the distal articular surfaces on the femur consist of two distinct condyles with the posterior one extending much further distally than the anterior one.

(15) Femur more than 10% longer than humerus. In *Petrolacosaurus* the femur is about the same length as the humerus. In protorothyridids and other early reptiles, the femur is about the same length or only a little longer than the humerus.

CLASSIFICATION OF THE ARCHOSAUMORPHA

Archosauromorpha

The Neodiapsida are divided into two major groups here on the basis of numerous synapomorphies for each: the Archosauromorpha (Archosauria + Rhynchosauria + Prolacertiformes) and the Lepidosauromorpha (Lepidosauria *sensu stricto* + Younginiformes). A diapsid assemblage consisting of (Prolacertiformes + Thecodontia + Rhynchosauria) has been suggested in one form or another by several authors (e.g. Hughes, 1968; Cruickshank, 1972a; Carroll, 1975a; Gow, 1975; Brinkman, 1981). The last author gave the best evidence in the shared nature of the ankle structure in all three groups, and he also included the trilophosaurids, specialized late Triassic forms with a herbivorous dentition (see p. 134). The name Archosauromorpha was established by Huene (1946) to include various early diapsids, rhynchosaur, thecodontians, dinosaurs, crocodiles, pterosaurs and birds.

Another subdivision of the Neodiapsida has been suggested in which *Youngina* is the sister-group of all later diapsids (Gaffney, 1980). Indeed *Youngina* and its close relatives (the Younginiformes), are primitive with respect to four characters shared by Archosauromorpha and all other Lepidosauromorpha. The Younginiformes have tabulars, a cleithrum, a foramen in the carpus and a fifth distal tarsal. However the Younginiformes share six synapomorphies with Lepidosauria (R1–6; see below, p. 136) and it is more parsimonious at present to assume that these four characters are parallelisms of Archosauromorpha (C4, 8, 10, 13) and Lepidosauria (X5, 12).

The following characters are derived from the *Petrolacosaurus* condition, and they are shared by the Archosauria, Prolacertiformes, and Rhynchosauria, but not by the Younginiformes, Squamata or Sphenodontia (see Fig. 4C and Figs 5–8).

Character list C: Archosauromorpha

(1) Premaxilla extends up behind naris. This character is absent in certain thecodontians (aetosaurs, phytosaurs) and crocodiles, in which the external nares have become very long, or have moved back.

(2) Nares elongate and close to midline. In prolacertiforms and archosaurs, the nares are close together and elongate, and in rhynchosaur, they fuse into a

single median naris. In contrast, the nares of *Petrolacosaurus*, *Youngina*, *Sphenodon* and most lizards are rounded and well separated in the midline by processes of the premaxillae and nasals.

(3) Quadratojugal (if present) located mainly behind the lower temporal fenestra. If a lower temporal bar is present, it is formed largely by the jugal, and the squamosal has a short ventral process. In *Petrolacosaurus*, *Youngina*, *Sphenodon* and other lepidosaurs that have one, the quadratojugal is mainly ventral to the lower temporal fenestra. Later lizards and snakes have lost the quadratojugal.

(4) Loss of the tabulars. *Petrolacosaurus*, *Youngina* and tangasaurids (aquatic Younginiforms) and the early 'lizard' *Paliguana* retain tabulars (Carroll, 1975b, 1977; Gow, 1975; Currie, 1981c), although such elements are absent in *Sphenodon* and Squamata.

(5) Stapes without a foramen. As far as is known, this applies to all Archosauromorpha (*Prolacerta*, Gow, 1975: 106; *Tanystropheus*, Wild, 1973: 17; Pseudosuchia, Krebs, 1976: 47; general, Romer, 1956: 419–420). *Youngina* retains a heavier stapes with a foramen (Gow, 1975: 94), as does the tangasaurid *Hovasaurus* (Currie, 1981c: 129), many groups of living lizards and *Sphenodon* (Baird, 1970).

(6) Vertebrae not notochordal. This appears to apply to all Archosauromorpha. On the other hand, *Youngina* (Gow, 1975: 95), *Hovasaurus* (Currie, 1981c: 129), *Sphenodon* and geckos retain notochordal vertebrae (Romer, 1956: 223).

(7) Transverse processes on dorsal vertebrae project as distinctive narrow elongate processes. In prolacertiforms, rhynchosaur, thecodontians and later archosaurs there is a clear process that extends well beyond the centrum and which is very long in some archosaurs. On the other hand, the transverse processes in *Petrolacosaurus*, *Youngina*, *Hovasaurus*, lizards and snakes project very little.

(8) Cleithrum absent. *Petrolacosaurus* and some Younginiformes at least (*Hovasaurus*) primitively retain the cleithrum.

(9) No entepicondylar foramen in the humerus. The entepicondylar foramen is retained by *Youngina* (Gow, 1975: 95), *Hovasaurus* (Currie, 1981c: 150), the early 'lizard' *Saurosternon* (Carroll, 1977: 373), and *Sphenodon*, although lizards have lost this structure (Romer, 1956: 356).

(10) Loss of foramen in carpus between ulnare and intermedium. This foramen is present in *Petrolacosaurus* (Reisz, 1981: 46), the tangasaurids *Thadeosaurus* (Carroll, 1981: 328) and *Hovasaurus* (Currie, 1981c: 152), the ?younginid *Acerosodontosaurus* (Currie, 1980: 503), although absent in *Saurosternon* (Carroll, 1977: 374) and later Squamata.

(11) Presence of a lateral tuber on the calcaneum. This is seen in early rhynchosaur, prolacertiforms (Gow, 1975), proterosuchids and later thecodontians (Brinkman, 1981), although some dinosaurs and crocodiles have lost it. Such a tuber is not seen in younginids and tangasaurids (Carroll, 1976b; Harris & Carroll, 1977; Brinkman, 1981; Currie, 1981c), *Saurosternon* (Carroll, 1975b), lizards or *Sphenodon* (Romer, 1956: 396–397) (cf. Figs 7, 14).

(12) Complex concave-convex articulation between the astragalus and calcaneum. Proterosuchids, rhynchosaur, prolacertiforms and trilophosaurids have two interlocking ball and socket joints between the astragalus and calcaneum. Most later thecodontians have a peg on the astragalus or on the

calcaneum only (Cruickshank, 1979; Thulborn, 1980; Brinkman, 1981; Chatterjee, 1982) and the ankle joint runs partly between these two proximal elements. This kind of ankle joint is not seen in lepidosauromorphs.

(13) Fifth distal tarsal lost. Younginids and tangasaurids (Broom, 1921; Carroll, 1976b: 66; 1981: 333; Currie, 1981c: 159) retain the 5th distal tarsal, although it may have fused with the 4th in some tangasaurids (Harris & Carroll, 1977: 146; Currie, 1982: 259). *Saurosternon* also has the 5th distal tarsal (Carroll, 1977: 376–377). The 5th distal tarsal is lost in lizards and *Sphenodon*.

(14) Fifth metatarsal hooked without lepidosaur specializations. This character is absent in younginids, tangasaurids and *Saurosternon* (see references for character 13). A hooked 5th metatarsal is present in later Squamata and *Sphenodon*, but is probably not homologous. In squamates and *Sphenodon* the 5th metatarsal is 'hooked' in two planes, it bears specialized plantar tubercles, and it passes into the tarsus over the proximal end of the 4th metatarsal (Robinson, 1975). None of these specialized features occurs in archosauromorphs.

Prolacertiformes + Archosauria

Within the Archosauromorpha, the Prolacertiformes (*Protorosaurus*, *Prolacerta*, *Macrocnemus*, *Tanystropheus*) share numerous synapomorphies with the Archosauria (thecodontians, crocodiles, dinosaurs) that are not present in Rhynchosauria. For the present, the Pterosauria are considered separately from the Archosauria (see below, p. 134). The particularly close similarity of *Proterosuchus* (*Chasmatosaurus*) as a thecodontian, and *Prolacerta* as a prolacertiform has already been noted (Gow, 1975; Brinkman, 1981). It is argued here that the Prolacertiformes and Archosauria are sister-groups, and together form the sister-group of the Rhynchosauria (out-group: Lepidosauromorpha). They share the following derived characters (Fig. 4D).

Character list D: Prolacertiformes + Archosauria

(1) Long snout and narrow skull. The ratio of snout length (anterior margin of orbit—anterior tip of snout) to total skull length is generally greater than, or equal to, a half. This is not true of rhynchosaur, *Youngina*, lizards or *Sphenodon*, although mosasaurs convergently show this character (cf. Figs 5, 8, 12).

(2) Nasals longer than frontals.

(3) Post-temporal fenestrae small or absent. Such fenestrae are large in rhynchosaur and Lepidosauromorpha.

(4) Recurved teeth. Prolacertiforms and thecodontians have recurved teeth, while rhynchosaur and lepidosauromorphs have peg-like teeth. The simple tooth shape is modified in later herbivorous thecodontians and dinosaurs into a variety of different forms.

(5) Extensive participation of the parasphenoid/basisphenoid in the side wall of the braincase. This character was emphasized by Gow (1975: 118–121) as a means of distinguishing archosaurs from lizards. He noted this condition in *Prolacerta* and the thecodontians *Proterosuchus*, *Euparkeria* and *Stagonolepis*. It was absent in *Youngina* and lizards. Likewise, the basisphenoid does not enter the side wall of the rhynchosaur braincase (Chatterjee, 1974; Benton, 1983b).

(6) Long, thin, tapering cervical ribs with two or three heads and an anterior

dorsal process. The Prolacertiformes had very long, splint-like cervical ribs (Gow, 1975: 108; Wild, 1973: 59–60), as did *Proterosuchus* (Cruickshank, 1972a: 105) and pseudosuchians (Krebs, 1976: 51–52). The anterior dorsal process is emphasized in the ‘plough-shaped’ cervical ribs of many crocodiles and dinosaurs (Romer, 1956: 286, 290). Rhynchosaurs had relatively short broad cervical ribs with two heads. Younginids and tangasaurids had simple short cervical ribs with broad proximal ends, and a reduced capitular head (Currie, 1980: 506–507; 1981c: 135–136), and in Squamata and *Sphenodon*, the cervical ribs are short single-headed pegs.

Prolacertiformes

Camp (1945) erected the order Prolacertiformes to include *Protorosaurus*, *Prolacerta*, *Tangasaurus* and *Youngina*. Romer (1945) included *Prolacerta* in the Younginiformes and *Protorosaurus*, *Macrocnemus* and *Tanystropheus* in the Araucoscelidia, a suborder of the Euryapsida (which also included nothosaurs, plesiosaurs and placodonts). Romer (1966) reinstated the Prolacertiformes with *Prolacerta*, *Macrocnemus* and two other less well-known forms, but retained *Protorosaurus* and *Tanystropheus* as euryapsids. Kuhn-Schnyder (1967) returned *Protorosaurus* and *Tanystropheus* to the Prolacertidae, and Gow (1975) named a new Order Parathecodontia to include *Prolacerta*, *Macrocnemus* and *Tanystropheus*. However, in more recent studies of this assemblage of early diapsids, the older name Prolacertiformes has been retained. Wild (1980) includes *Protorosaurus*, *Prolacerta*, *Macrocnemus* and *Tanystropheus* in this group, while Chatterjee (1980b) includes these, *Petrolacosaurus* and two recently described genera, *Malerisaurus* and *Tanytrachelos*. These assignments are supported here except for *Petrolacosaurus*.

Chatterjee (1980b: 192, 197) placed *Petrolacosaurus* in the Prolacertiformes because of its long neck and gracile body. However, the long neck of *Petrolacosaurus* with six cervical vertebrae is not necessarily a synapomorphy with that of *Prolacerta* which has eight cervicals. Further, it has been shown that *Petrolacosaurus* is the sister-group of later diapsids and lacks all synapomorphies of the Neodiapsida.

The genus *Protorosaurus* (Fig. 5A) from the Kupferschiefer (late Permian) of E Germany appears to be related to *Prolacerta*. *Protorosaurus* has been described, or discussed, by several authors (e.g. Meyer, 1856; Seeley, 1888; Huene, 1926; Peyer, 1937: 105–111; Camp, 1945: 85–87, 93–94; Romer, 1947; Vaughn, 1955: 432–434; Kuhn-Schnyder, 1962: 127; Chatterjee, 1980b: 189–190; Wild, 1980: 18; Carroll, 1981: 374–375), but there are many important aspects of its anatomy that are still controversial. The following list of synapomorphies tests the monophyly of the Prolacertiformes by comparison with other archosauromorphs (Fig. 4E). Note that two of these characters (E1, 2) are uncertain in *Protorosaurus*, so that these synapomorphies might actually apply to (*Prolacerta* + *Macrocnemus* + *Tanystropheus*) alone.

Character list E: Prolacertiformes

(1) Lower temporal bar incomplete. This character is shared by *Prolacerta*, *Macrocnemus*, *Tanystropheus*, and possibly also *Protorosaurus* (Carroll, 1981: 374–375). Several authors have assumed that *Protorosaurus* had a complete lower

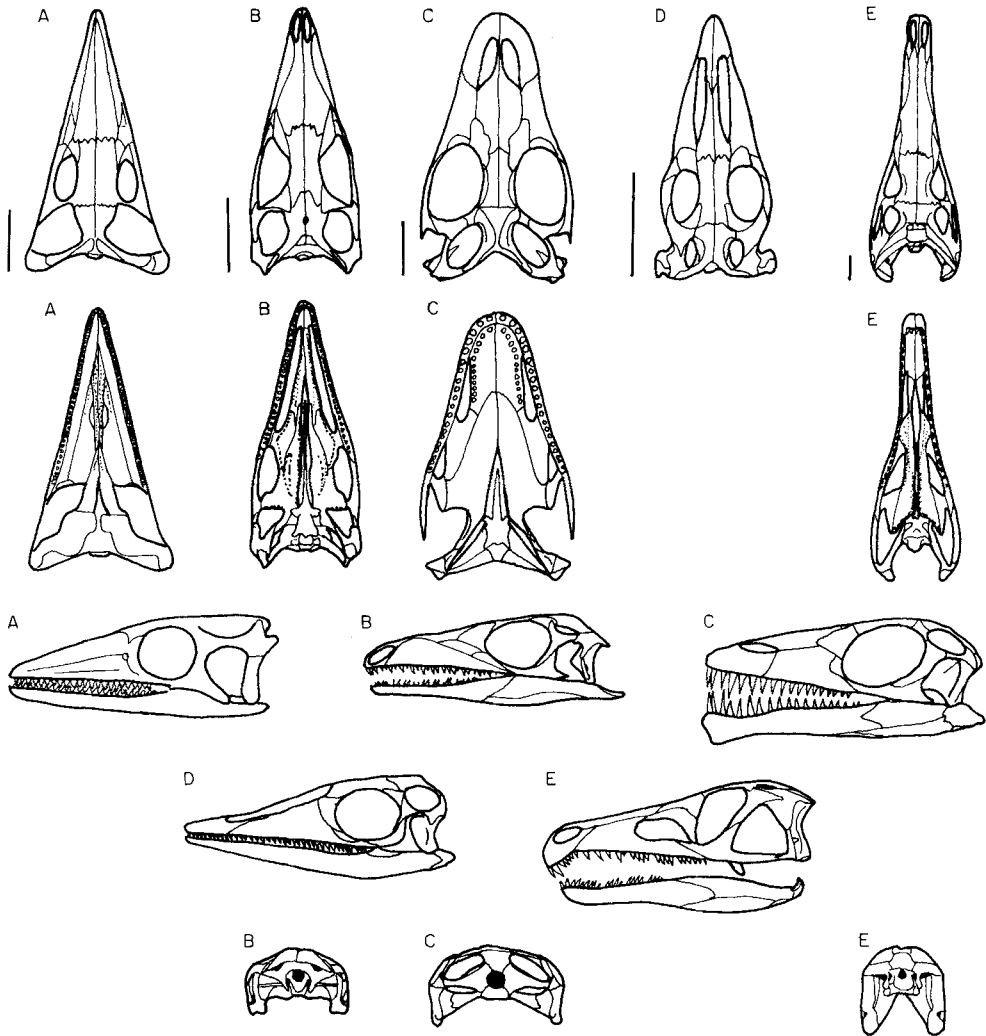


Figure 5. The skulls of A, *Protorosaurus*; B, *Prolacerta*; C, *Tanystropheus*; D, *Macrocnemus*; and E, *Proterosuchus* in dorsal (top row), palatal (second row), lateral (third, fourth rows), and occipital (bottom row) views. The skulls have been drawn to a standard length. Scale bars = 2 cm. The reconstructions of *Protorosaurus* are tentative. The palate of *Macrocnemus* and the occiputs of *Protorosaurus* and *Macrocnemus* have not been reconstructed. (A, after Seeley, 1888; B, after Gow, 1975; C, after Wild, 1973; D, after Kuhn-Schnyder, 1962 and Wild, 1973; E, after Cruickshank, 1972a.)

temporal bar, but Seeley (1888: pl. 16) restored the lower cheek as open, although he noted (p. 206) that "there is no evidence whether the malar arch connected with the quadrate bone" (Fig. 5). In the original specimen (Royal College of Surgeons No. 308), the relevant area is obscured.

(2) 7–12 elongate cervical vertebrae. Prolacertiforms are characterized by very long necks in which cervical vertebrae may be twice as long as dorsals. This is taken to an extreme in *Tanystropheus* where some are five or six times as long as dorsals. *Protorosaurus* has either 7 or 8 elongate cervical vertebrae (Peyer, 1937:

108; Wild, 1980: 18), while *Prolacerta* and *Macrocnemus* have 8 and *Tanystropheus* has 12. *Proterosuchus* has 9 cervical vertebrae that are longer than the dorsal, but rhynchosaurs and other thecodontians have 7–9 short cervicals.

(3) Cervical vertebrae have long low neural spines. The neural spines in all prolacertiforms approach, or exceed, the length of the centrum, and yet they are always very low compared with the neural spines of dorsal vertebrae. Rhynchosaurs, *Proterosuchus* and thecodontians have higher neural spines on the cervical vertebrae (Charig & Sues, 1976; Krebs, 1976).

(4) Short ischium. The ischium does not extend back further than the posterior limit of the iliac blade (Fig. 7). The ischium is only slightly longer in proterosuchids (see below), but runs well back in rhynchosaurs, *Erythrosuchus*, *Euparkeria* and later thecodontians (Krebs, 1976).

Cosesaurus from the Muschelkalk of Spain, claimed to be a bird ancestor (Ellenberger & Villalta, 1974) may be a prolacertiform (Olsen, 1979), although in the original description “la fosse anté-orbitale” is said to be long.

Malerisaurus, a diapsid reptile recently described from the late Triassic Maleri Formation of India, has been placed in the Protorosauridae with *Protorosaurus* (Chatterjee, 1980b) on the basis of its closed lower temporal bar and fixed quadrate, improved middle ear and great limb disparity. The first two characters are primitive diapsid features, and the second two are seen in all Archosauromorpha. The other characters of *Malerisaurus* confirm that it is an archosauromorph, although it is restored with large post-temporal fenestrae (D3) and has only very slightly recurved teeth (D4). In all respects, it is also a prolacertiform, except in one character which Chatterjee (1980b) emphasizes—the closed lower temporal bar. This is not certain, however: Chatterjee (1980b: 169) states “the lower temporal arcade is probably complete”. *Malerisaurus* lacks prolacertid and tanystropheid characters and may be the sister-group of those two, or of the Prolacertiformes as a whole.

Prolacertidae + Tanystropheidae

Prolacerta (Figs 5B, 6A, 7A) from the *Lystrosaurus* Zone of S Africa (Parrington, 1935; Camp, 1945; Gow, 1975) and the Fremouw Formation of Antarctica (Colbert, 1978) (both early Triassic) has been regarded as an ancestral lizard, as an ‘eosuchian’ and as a relative of the thecodontians by different authors (Parrington, 1935; Robinson, 1967a; Gow, 1975).

Tanystropheus, a large long-necked form from the early, middle and late Triassic of central Europe was classified as a euryapsid by Romer (1956, 1966), but is now normally placed in the Prolacertiformes close to *Prolacerta* (e.g. Wild, 1973, 1980; Gow, 1975; Carroll, 1977; Chatterjee, 1980b). There are several species of *Tanystropheus*, but the best known is *T. longobardicus* (Figs 5C, 6B, 7B) from the Grenzbitumenzone (middle Triassic) of Monte San Giorgio, Switzerland (Wild, 1973). The enormously long neck, consisting of 12 elongate cervical vertebrae, seems to set *Tanystropheus* apart from all other early diapsids, but it displays all the prolacertiform characters listed above (list E). In addition, the relationship of *Tanystropheus* to *Prolacerta* may be tested by the following synapomorphies in comparison with *Protorosaurus* and other archosauromorphs (Fig. 4F).

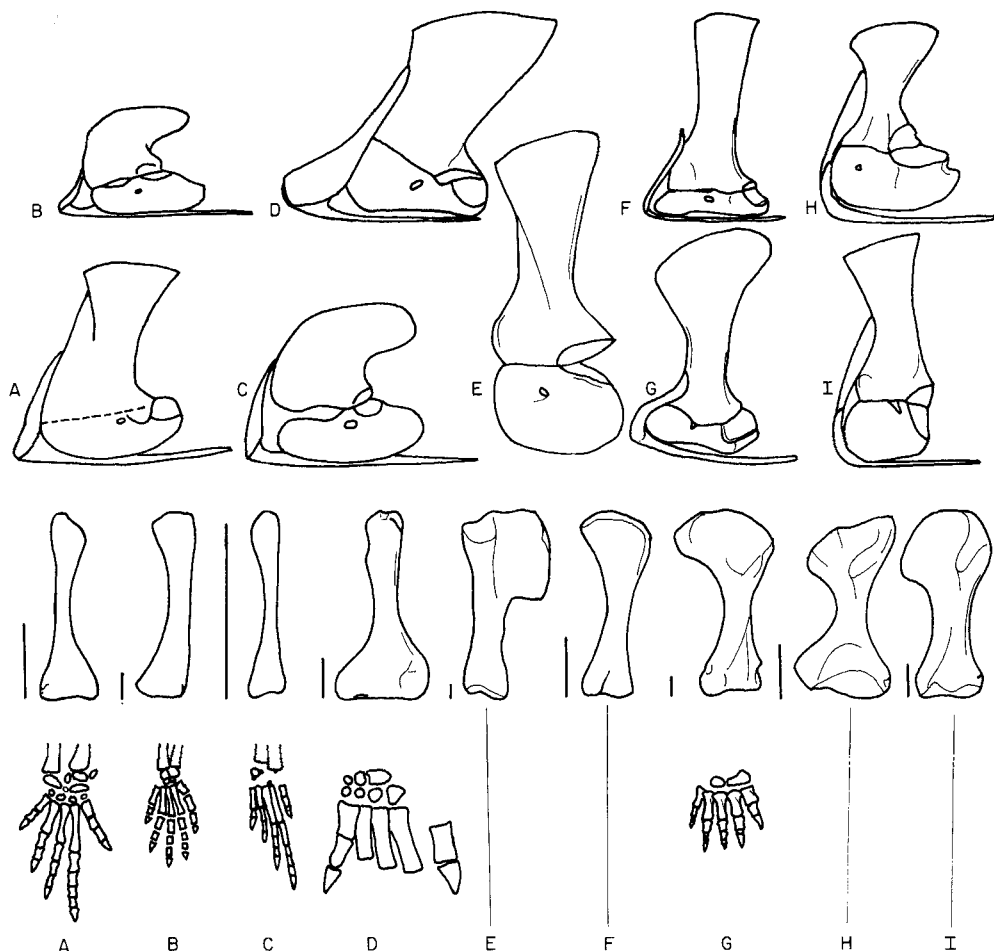


Figure 6. The pectoral girdle (left lateral view), humerus (left, ventral or medial view) and hand (dorsal view) of A, *Prolacerta*; B, *Tanystropheus*; C, *Macrocnemus*; D, *Proterosuchus*; E, *Erythrosuchus*; F, *Euparkeria*; G, *Stagonolepis*; H, *Stenaulorhynchus*; and I, *Hyperodapedon*. The shoulder girdle of *Erythrosuchus* (E) is not shown here—that figured by Broom, Huene and Charig & Sues (1976) may belong to the dicynodont *Kannemeyeria* (A. R. I. Cruickshank, pers. comm., 1983). The scapulo-coracoid of *Vjushkovia* (Huene, 1960) is shown instead. The humeri have been drawn to a standard length, and the shoulder girdles and hands to scale. Scale bars for each genus = 2 cm. The hands of *Erythrosuchus*, *Euparkeria*, *Stenaulorhynchus*, and *Hyperodapedon* are too poorly known for reconstruction. (A, after Gow, 1975; B, after Wild, 1973; C, after Peyer, 1937; D, after Cruickshank, 1972a; E, after Charig & Sues, 1976; F, after Ewer, 1965; G, after Walker, 1961; H, after Huene, 1938 and Romer, 1956; I, after Benton, 1983b).

Character list F: *Prolacertidae* + *Tanystropheidae*

(1) Quadratojugal much reduced or absent. *Prolacerta* has a tiny splint-like quadratojugal (Gow, 1975: 102), but the quadratojugal is apparently absent in *Tanystropheus* (Wild, 1973) (Fig. 5).

(2) Quadrate partially streptostylic (Kuhn-Schnyder, 1962; Wild, 1973; Gow, 1975). This is difficult to assess in fossil material, and some doubts have been expressed as to the degree of quadrate movement possible in these genera (Robinson, 1967a; Evans, 1980: 250–255; Rieppel & Gronowski, 1981: 205–207).

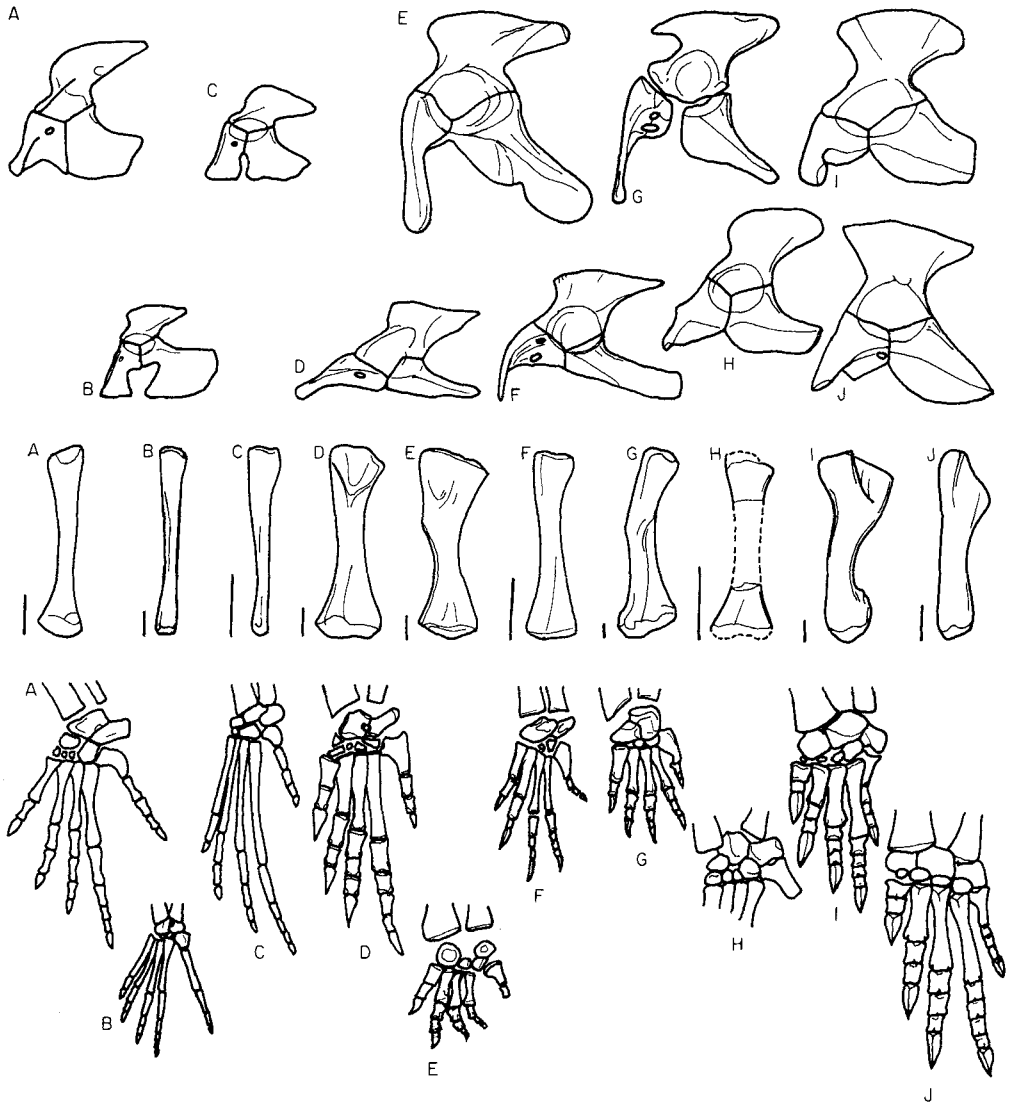


Figure 7. The pelvis (left lateral view), femur (postero-lateral view) and foot (dorsal view) of A, *Prolacerta*; B, *Tanystropheus*; C, *Macrocnemus*; D, *Proterosuchus*; E, *Erythrosuchus*; F, *Euparkeria*; G, *Stagonolepis*; H, *Howesia*; I, *Stenaulorhynchus*; and J, *Hyperodapedon*. The femora have been drawn to a standard length, and the pelvis and feet to scale. Scale bars for each genus = 2 cm. (A, after Gow, 1975; B, after Wild, 1973; C, after Peyer, 1937 and Wild, 1973; D, after Cruickshank, 1972a; E, after Charig & Sues, 1976 and Cruickshank, 1978; F, after Ewer, 1965; G, after Walker, 1961; H, after Broom, 1906 and Carroll, 1976a; I, after Huene, 1938; J, after Benton, 1983b.)

Tanystropheidae

A recently described small diapsid, *Tanytrachelos* from the Cow Branch Formation of the Newark Supergroup (late Triassic) of northern Carolina (Olsen, 1979), has been associated with *Tanystropheus* in the Family Tanystropheidae on the basis of several common features (Olsen, 1979: Chatterjee, 1980b: 191, 198; Wild, 1980: 31). Although *Tanytrachelos* is much

smaller than *Tanystropheus* (20 cm long, compared with a range of 50–600 cm in the latter), and it has procoelous vertebrae, the following characters shared between the two genera are derived in comparison with *Prolacerta* and other prolacertiforms (Fig. 4G).

Character list G: Tanystropheidae

(1) Very long neck (nearly as long as, or longer than, the trunk) with 9–12 elongate cervical vertebrae.

(2) Presence of postcloacal bones (cartilaginous elements which are interpreted as (?) penis elements: Wild, 1973, 122–123).

(3) Fifth metatarsal short and proximal phalanx of digit V elongate and metapodial-like (Olsen, 1979: 6).

There may be further synapomorphies of the skull, but *Tanytrachelos* has not been fully described yet.

Prolacertidae

Macrocnemus from the Grenzbitumenzone (middle Triassic) of Monte San Giorgio, Switzerland (Figs 5D, 6C, 7C), has usually been associated closely with *Prolacerta* (e.g. Peyer, 1937; Kuhn-Schnyder, 1962, 1963, 1974; Wild, 1973, 1980; Gow, 1975; Carroll, 1977; Chatterjee, 1980b). *Macrocnemus* appears to be more closely related to *Prolacerta* than to *Tanystropheus*, and the following synapomorphies of *Macrocnemus* and *Prolacerta* test this hypothesis, by comparison with *Tanystropheus* and other prolacertiforms (Fig. 4H).

Character list H: Prolacertidae

(1) Squamosal has a tetra-radiate shape. In *Prolacerta* and *Macrocnemus*, four wings of the squamosal run forward to meet the postorbital, down to the quadrate, medially to the parietal, and backwards over the top of the quadrate. Other early diapsids have a tri-radiate squamosal and *Tanystropheus* has a sickle-shaped squamosal (Fig. 5).

(2) Choanae very long and bones of palate long and narrow. The bones of the palate in *Tanystropheus* are broad, as in most other early diapsids.

(3) Presence of a midline gap in the palate between the pterygoids and the posterior part of the vomers, and a long cultriform process of the parasphenoid runs forward in the gap. This character is not seen in *Tanystropheus*.

Several authors have noted similarities between *Macrocnemus* and *Tanystropheus* (e.g. Peyer, 1937: 97–105; Kuhn-Schnyder, 1962: 124–126; Wild, 1973). Wild (1980) noted detailed resemblances between *Macrocnemus* and an early form of *Tanystropheus*, *T. antiquus* from the Upper Buntsandstein and Muschelkalk (early and early middle Triassic) of central Europe—the same number of cervical vertebrae, and a similar dentition. However, there were differences in the length of the cervical vertebrae and in the foot skeleton. There are two apparent synapomorphies between *Macrocnemus* and the more typical *Tanystropheus longobardicus*, in comparison with *Prolacerta*, and these support an opposing hypothesis that *Macrocnemus* is the sister-group of the Tanystropheidae: low, largely ventral shoulder girdle; large thyroid fenestra between pubis and ischium (Figs 6, 7; Wild, 1973: 104–105, 112–114). The most parsimonious arrangement is to group *Prolacerta* and *Macrocnemus* together as sister-group of

the Tanystropheidae and to assume that these limb-girdle characters are parallelisms. This is the decision taken also by Kuhn-Schnyder (1974), Gow (1975: 118), Chatterjee (1980b: 197–198) and Wild (1980).

Boreopricea from the Lower Triassic (Vetluzhian Series) of Kolguyev Island, Russia (Tatarinov, 1978) is probably a prolacertid. Many key characters are uncertain, and it appears to lack some: the nasals are short (D2), and the squamosal is not tetraradiate (H1). *Kadimakara* from the Lower Triassic (Rewan Formation) of central Queensland, Australia, has also been interpreted as a prolacertid rather like *Prolacerta* on the basis of incomplete skull pieces (Bartholomai, 1979).

As a result of the above analysis, the Prolacertiformes (ranging from the late Permian to the late Triassic) are divided into three families: Protorosauridae (*Protorosaurus*), Prolacertidae (*Prolacerta*, *Macrocnemus*), and Tanystropheidae (*Tanystropheus*, *Tanytrachelos*). The Protorosauridae are the sister-group of the (Prolacertidae + Tanystropheidae). The tentative nature of parts of this scheme must be stressed because of our inadequate knowledge of most of these genera, and of *Protorosaurus* in particular. The Prolacertiformes are considered to be the sister-group of the Archosauria.

The Prolacertiformes and lizards

A very different interpretation of *Prolacerta* has been that it is an ancestral lizard, and that the Prolacertiformes are closely related to early lizards. Parrington (1935), Watson (1957), and Robinson (1967a) placed *Prolacerta* directly between *Youngina* (or some other early 'cosuchian') and the lizards on the basis of several characters that were regarded as intermediate, and in particular the broken lower temporal arcade and the reduced quadratojugal. Camp (1945: 95) regarded *Prolacerta* as "probably ancestral to the lizards in a general way" but retained it in the Prolacertiformes, while Kuhn-Schnyder (1962) concluded that the Prolacertidae should be classed as early lepidosaurs. Wild (1973: 155) noted that *Tanystropheus* shares numerous characters with recent lizards which "have obviously been developed by convergence", but concluded that "*Tanystropheus* is a true, highly specialized lacertilian which takes a special place among the 'ancient lizards' of the Triassic". Wild (1980: 21–24) clarified his viewpoint, and proposed that the Prolacertiformes are the sister-group of the modern lizards on the basis of the following characters:

- (1) loss of lower temporal bar and streptostyly;
- (2) three-pointed teeth in juvenile *Tanystropheus* and in several families of lizards;
- (3) elongate cervical vertebrae also in *Varanus* and *Lanthanotus*;
- (4) two-headed ribs;
- (5) caudal autotomy in *Tanystropheus*;
- (6) postcloacal bones in *Tanystropheus* and in living gekkonids, pygopodids and xantusiids.

These characters were presented as general similarities that reinforce each other rather than as individual testable synapomorphies. Thus, no out-group and no polarity are defined, and the characters all fail for that reason. In addition, character (4) is primitive for diapsids, characters (2), (3) and (5) occur in several other groups: three-pointed teeth in a late Triassic pterosaur

(Wild, 1978), elongate cervical vertebrae in *Petrolacosaurus*, and caudal autotomy in a range of lizards, sphenodontids, 'eosuchians', captorhinomorphs, *Mesosaurus*, and possibly also *Araeoscelis* (Evans, 1981b). Further, it is much more likely that characters (2), (3) and (6) are homoplasies of both lizards and prolacertiforms than that they are synapomorphies since they are known only in a very small proportion of living lepidosaurs, and characters (2), (5) and (6) are known only in *Tanystropheus* amongst the prolacertiforms.

The broken lower temporal arch and streptostyly (1) may be seen as the best synapomorphy of Prolacertiformes and Squamata. These two features must be considered separately since several early diapsids with incomplete lower temporal bars (such as the sphenodontids *Clevosaurus* and *Planocephalosaurus*, the ?squamate *Gephyrosaurus*, and the late Permian *Claudiosaurus*) had fixed quadrates (Robinson, 1973; Evans, 1980; Carroll, 1981). There is also evidence that *Prolacerta*, *Macrocnemus* and *Tanystropheus* may have had restricted streptostyly, or none at all (Robinson, 1967a; Rieppel & Gronowski, 1981). In any case, the nature of the quadrate articulation is quite different in these prolacertiforms from that of true lizards (Evans, 1980: 250–255). Further, streptostyly is not unique to lizards, but occurs also in birds and in some early crocodiles. Several other authors have also pointed out objections to any particularly close relationship between the Prolacertiformes and the Squamata: Carroll (1975a, 1977), Gow (1975) and Chatterjee (1980b).

Both Chatterjee (1980b: 190–191) and Wild (1980: 18) have argued against the association of the Prolacertiformes with the Archosauria. Chatterjee noted the absence of an antorbital fenestra in *Prolacerta* and the supposed lack of derived characters shared between *Prolacerta* and *Proterosuchus*. Wild noted similar criticisms, and he also stated that neither group could be ancestral to the other since these two genera are of about the same geological age. However, synapomorphies of Prolacertiformes and Archosauria have been listed above, and Chatterjee's and Wild's other arguments are not convincing.

Archosauria

The Archosauria have been difficult to define. Charig (1976a) stressed two archosaur characters: the trend to acquisition of an erect gait and the presence of an antorbital fenestra. The first character is hard to define and not unique to archosaurs. Marked limb disparity is seen in many other groups of diapsids (younginids, certain lizards, prolacertids, tanystropheids, rhynchosaurs) and several were probably facultatively bipedal (Carroll, 1976c; Chatterjee, 1980b; Carroll & Thompson, 1982). Early archosaurs did not have an erect gait, and several non-archosaurian groups acquired similar kinds of 'semi-erect' stances (e.g. cynodonts (Kemp, 1980) and rhynchosaurs (Benton, 1983b)). Arguments have also been presented against the validity of that archosaur trademark, the antorbital fenestra, as a synapomorphy. It has been reported in the pelycosaur *Varanodon* (Reig, 1970), and it is absent in modern crocodiles. There is further evidence that it evolved twice, since it occurs in the Pterosauria, which are not regarded as members of the Archosauria (see below, p. 134 and Wild, 1978: 246–253). Nevertheless, it is tentatively retained in the following list of synapomorphies of Archosauria in comparison with other archosauromorphs (Fig. 4I).

Character list I: Archosauria (1)

- (1) Possession of an antorbital fenestra.
- (2) Orbit shaped more like an inverted triangle than a circle.
- (3) Teeth laterally compressed.
- (4) Possession of a fourth trochanter on the femur.

Proterosuchidae

Proterosuchus (*Chasmatosaurus*), a varanid-shaped carnivore from the *Lystrosaurus* Zone (early Triassic) of the Karoo, S Africa (Figs 5E, 6D, 7D), has generally been placed at the base of the archosaur radiation (Hughes, 1963; Romer, 1966; Charig & Sues, 1976). This genus, and its close relatives, are known from China, Bengal, northern Russia, Australia, and Antarctica, as well as S Africa. The oldest archosaur, *Archosaurus* from the late Permian of Russia, is probably related, but it is less well known.

There is a problem in deciding whether *Proterosuchus* is an archosaur or a prolacertiform. The Proterosuchidae display the four archosaur characters (I1–4), but they lack a whole suite of synapomorphies that *Erythrosuchus* and *Euparkeria* from the early Triassic, and all later archosaurs possess (list J below). Further, *Proterosuchus* is very like *Prolacerta* in several respects. It shows one prolacertiform character:

E3, more than 7 elongate cervical vertebrae;
as well as the three prolacertid characters:

H1, tetraradiate squamosal;

H2, long choanae, and long bones in the palate;

H3, gap between pterygoids and vomers with long parasphenoid cultriform process.

The resemblance to *Prolacerta* is even greater—the two genera share two further synapomorphies:

(1) Premaxilla downturned and projects forward beyond the lower jaw (Fig. 5B, E).

(2) Haemapophyses laterally compressed and broad at the distal end. They are very long, being 2–2½ times the length of the preceding caudal vertebra.

On the other hand, *Proterosuchus* lacks these prolacertiform characters: the broken lower temporal bar, the low cervical neural spines, and the short ischium, as well as the prolacertid/tanystropheid characters (reduced quadratojugal, partially streptostylic quadrate; F1, 2). Thus, if *Proterosuchus* were to be called a prolacertiform and placed as sister-group of *Prolacerta*, we would have to assume five reversals and four cases of convergence with archosaurs. If *Proterosuchus* is made the sister-group of all other archosaurs, we must assume six cases of convergence with *Prolacerta*. I will not make a decision between these alternatives for two reasons: the definition of the Prolacertiformes may be significantly altered by a re-study of *Protorosaurus*, and the definition of the Archosauria could depend on *Proterosuchus* (if it is the sister-group of all later archosaurs), so that an independent parsimony test is difficult.

Erythrosuchidae

Erythrosuchus, a massive 5 m long quadruped with a 1 m skull from the *Cynognathus* Zone (late early Triassic) of the Karoo Basin, S Africa (Figs 6E, 7E,

8A), and its relatives from Russia and China (the Erythrosuchidae), have generally been classified with the Proterosuchidae as the Suborder Proterosuchia (Romer, 1956; Charig & Sues, 1976). However, I have been unable to find synapomorphies in support of this relationship. One erythrosuchid, *Garjainia* from the early Triassic of Russia, shares a slightly downturned premaxilla with *Proterosuchus*, but in other respects the incomplete material appears to represent an erythrosuchid (Charig & Sues, 1976).

On the other hand, *Erythrosuchus* shares numerous synapomorphies with *Euparkeria*, also from the *Cynognathus* Zone, and the later archosaurs, that are not present in the Proterosuchidae or Prolacertiformes (Fig. 4J).

Character list J: Archosauria (2)

(1) Skull is high. The ratio of the greatest height of the skull to its length is greater than one-third in *Erythrosuchus*, *Euparkeria*, other thecodontians and dinosaurs. The value is less than one-third for *Proterosuchus* and prolacertiforms (Figs 5, 8).

(2) Antorbital fenestra close to naris. In *Proterosuchus*, the antorbital fenestra is separated by a long stretch of premaxilla and maxilla from the naris, while in *Erythrosuchus*, *Euparkeria* and other archosaurs this distance is much less.

(3) Loss of the supratemporal. This element is present in *Proterosuchus* (Cruickshank, 1972a: 97), as well as in prolacertiforms.

(4) Possession of a lateral mandibular fenestra. This is a character of *Erythrosuchus*, *Euparkeria* and other archosaurs that is absent in *Proterosuchus* (Charig & Sues, 1976; Krebs, 1976) and archosauromorphs.

(5) Coronoid reduced or absent. *Proterosuchus* (Broili & Schroeder, 1934), prolacertiforms, and rhynchosaurs had a coronoid, but this element is apparently reduced or absent in *Erythrosuchus*, *Euparkeria* and later archosaurs (Charig & Sues, 1976; Krebs, 1976: 47–48).

(6) Ossified portion of the scapula very tall and narrow. The ratio of minimum width to height is less than one-quarter. The figure is about one-half in *Prolacerta* and *Proterosuchus* (Fig. 6D–G).

(7) Coracoid small and glenoid faces largely backwards (Charig & Sues, 1976: Fig. 10I; Krebs, 1976: 52–53). In *Proterosuchus* the coracoid is long and the glenoid faces postero-laterally (Cruickshank, 1972a: fig. 5a). This is the case also in prolacertiforms.

(8) Deltopectoral crest on humerus extends far down the shaft. In *Proterosuchus*, the deltopectoral crest is strongly developed, but it does not extend down the shaft (Charig & Sues, 1976: 15), and this is the case also in rhynchosaurs and prolacertiforms.

(9) Distal end of humerus reduced in width. In *Erythrosuchus*, *Euparkeria* and later archosaurs, the ectepicondylar and entepicondylar areas of the humerus are reduced, and the ratio of the width of the distal end to that of the proximal is about two-thirds. If anything, the distal end is wider than the proximal in *Proterosuchus* (Cruickshank, 1972a: fig. 6a–c). This is also the case in prolacertiforms and early rhynchosaurs.

(10) Hand is short. The carpus and manus is less than half the length of the tarsus and pes. The hand is long in *Proterosuchus* and prolacertiforms.

(11) Pubis has a strongly downturned anterior tuber. There is a slight tuber in *Proterosuchus* (and in *Prolacerta*, but not in *Macrocnemus* or *Tanystropheus*), but it

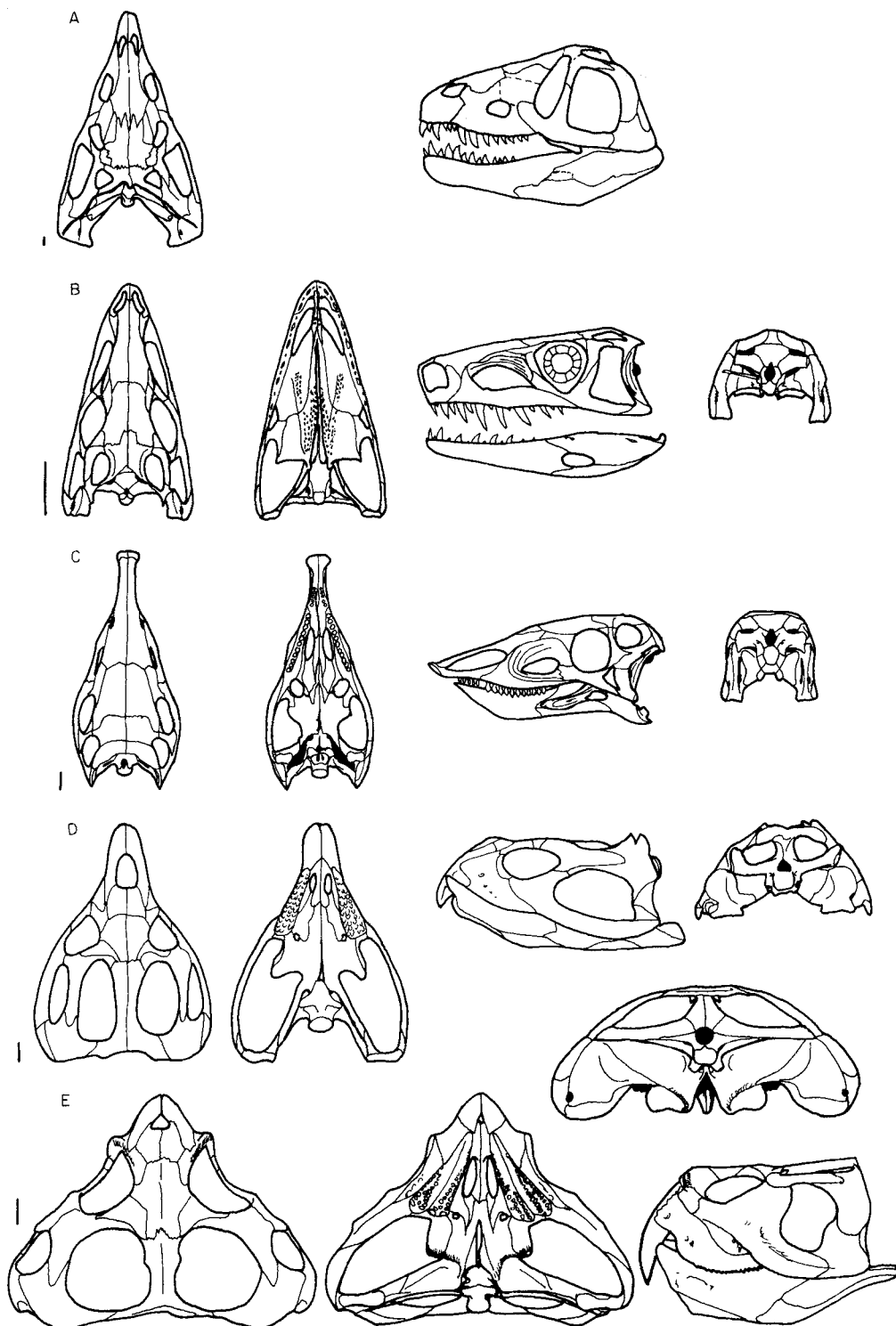


Figure 8. The skulls of A, *Erythrosuchus*; B, *Euparkeria*; C, *Stagonolepis*; D, *Stenaulorhynchus*; and E, *Hyperodapedon* in dorsal, palatal, lateral and occipital views. The skulls have been drawn to a standard length. Scale bars = 2 cm. The skull of *Erythrosuchus* is incompletely known. (A, after Charig & Sues, 1976; B, after Ewer, 1965; C, after Walker, 1961; D, after Huene, 1938, 1956; E, after Benton, 1983b.)

is not at all as clearly developed as in *Erythrosuchus*, *Euparkeria* or later archosaurs (Charig & Sues, 1976; Krebs, 1976).

(12) Iliac blade has a small anterior process. This is very poorly developed in *Proterosuchus* (Charig & Sues, 1976: 15) and other early archosauromorphs.

(13) Ischium has a large postero-ventral process. This extends a long way back in *Erythrosuchus*, *Euparkeria* and later archosaurs, but not in *Proterosuchus*, prolacertiforms or rhynchosaurs.

(14) Tarsus contains only four elements. The centrale and distals 1 and 2, which *Proterosuchus* and *Prolacerta* have, are lost in *Erythrosuchus* (Charig & Sues, 1976: 30; Cruickshank, 1978), *Euparkeria* and later archosaurs (Romer, 1956; Krebs, 1976: 59).

Euparkeriidae

Euparkeria, a small 65 cm long quadruped and possibly facultative biped from the *Cynognathus* Zone (late early Triassic) of the Karoo basin, S Africa (Figs 6F, 7F, 8B), displays many features of the typical later thecodontians. It has been placed in a separate family as the most primitive member of the Pseudosuchia by most authors (e.g. Romer, 1956, 1966; Charig & Reig, 1970: 135–136; Bonaparte, 1975; Krebs, 1976), although others have argued for its being allied more closely with *Erythrosuchus* and *Proterosuchus*.

Hughes (1963) concluded that *Euparkeria* was an erythrosuchid on the basis of shared primitive characters. Cruickshank (1972b) described the braincase of *Euparkeria*, and proposed that it was a proterosuchian—again on the basis of shared primitive characters. Cruickshank (1978: 174–176; 1979: 175) further argued that *Euparkeria* was more primitive than *Erythrosuchus* on the basis of the following characters:

- (1) the foot of *Erythrosuchus* has relatively shorter digits than that of *Euparkeria*;
- (2) the ankle of *Erythrosuchus* is mesotarsal with a much modified astragalus, a simplified calcaneum, and it may lack phalanges 2 and 3 on the 5th digit. This pattern may be derived from that seen in *Euparkeria*;
- (3) *Erythrosuchus* may possess a pleurosphenoid ('laterosphenoid');
- (4) the vertebrae of *Erythrosuchus* may be 'sculptured' as in later thecodontians and dinosaurs.

The ankle characters are the most significant, but three subsequent authors (Thulborn, 1980: 249–251; Brinkman, 1981: 18–19; Chatterjee, 1982: 318–319) have argued that the ankle of *Euparkeria* was in fact advanced over the primitive mesotarsal condition. Movement was possible between the proximal elements by means of a ball (calcaneum) and socket (astragalus) joint (the 'crocodile-reversed' condition). Thulborn (1980: 251) discounted Cruickshank's other advanced characters of *Erythrosuchus* on the basis of the great size difference between this genus and *Euparkeria*. Brinkman (1981: 18–20) considered that the *Erythrosuchus* tarsus was simply a poorly ossified proterosuchid tarsus (Fig. 7E, F).

In most features of the skeleton, *Euparkeria* is advanced over *Erythrosuchus*. The following synapomorphies test the hypothesis that *Euparkeria* is the sister-group of later archosaurs by comparison with *Erythrosuchus*, *Proterosuchus* and prolacertiforms (Fig. 4K).

Character list K: Archosauria (3)

(1) Antorbital fenestra large and lies in a depression. The antorbital fenestra in proterosuchids and erythrosuchids is of variable size—some erythrosuchids may have two small ones—and it is not clearly set off in a depression (Fig. 8; Charig & Sues, 1976; Krebs, 1976: 67).

(2) Parietal foramen absent. A small foramen is present in *Proterosuchus* and *Erythrosuchus*.

(3) Otic notch well developed. *Proterosuchus* and *Erythrosuchus* show only a moderate otic notch on the quadrate (Charig & Sues, 1976: 13), whereas this feature is better developed in *Euparkeria* and later archosaurs (Krebs, 1976: 67).

(4) Thecodont dentition. The Proterosuchidae and Erythrosuchidae have subthecodont teeth (Charig & Sues, 1976: 13), as in *Prolacerta*.

(5) Ribs all one or two-headed. In *Proterosuchus* and *Erythrosuchus*, the cervical and anterior dorsal ribs are three-headed.

(6) Pelvis markedly 3-rayed with long narrow ventral processes on the pubis and the ischium. The pelvis of *Euparkeria* and *Pseudosuchia* shows a long thin posterior iliac blade, a long antero-ventral pubic tuber and a long postero-ventral ischium process. These features are not at all present in *Proterosuchus* which has a heavy ventral pelvic plate (Cruickshank, 1972a: fig. 8a), but erythrosuchids show an intermediate position (Charig & Sues, 1976: figs 8L, 9A, C), but still with relatively broad pubes and ischia (Fig. 7D–G).

(7) Hind limbs brought in under the body and they move parallel to the sagittal plane (Krebs, 1976: 68).

(8) Significant rotation between astragalus and calcaneum apparently possible—whether ‘crocodile normal’ (*Pseudosuchia*) or ‘crocodile reversed’ (*Euparkeria*, Ornithosuchidae) (Chatterjee, 1982). Loss of the foramen between astragalus and calcaneum.

(9) Dermal armour developed. *Euparkeria* had a row of overlapping scutes along the length of the body on either side of the backbone (Ewer, 1965: 414–415). Similar armour was also present in most *Pseudosuchia* (Krebs, 1976: 62–63). *Proterosuchus* and *Erythrosuchus* show no dermal armour at all (Charig & Sues, 1976: 15).

Later archosaurs

As stated at the beginning, no attempt is made here to classify the later archosaurs. However, we may test the monophyly of that assemblage. All *Pseudosuchia* (middle-late Triassic), such as *Stagonolepis* (Figs 6G, 7G, 8C) and later archosaurs (including birds), share several synapomorphies that are absent in *Euparkeria*, *Erythrosuchus* and *Proterosuchus* (Fig. 4L).

Character list L: higher Archosauria

(1) Postparietals absent. *Euparkeria* retains a tiny postparietal (‘interparietal’: Ewer, 1965: 387) (Fig. 6F, G).

(2) Pterygoids meet medially. There is a broad interpterygoid vacuity in *Euparkeria* (Ewer, 1965: fig. 1b).

(3) Palatal teeth absent. *Euparkeria* has several rows of teeth on the pterygoid and on the palatine. Such teeth are absent in later archosaurs, but also absent in *Erythrosuchus* (Charig & Sues, 1976: 30).

(4) ?Presence of a pleurospenoid. This element is apparently absent in *Euparkeria*, although possibly present in *Erythrosuchus* (Cruickshank, 1972b). It has also been identified in *Stagonolepis* (Walker, 1961), as well as in crocodiles and birds, and it may be typical of all later archosaurs (Romer, 1956: 76), although it is a very difficult structure to identify in fossil material.

(5) Presacral intercentra absent. No intercentra are known behind the axis in later pseudosuchians (Krebs, 1976: 51) or other archosaurs. *Euparkeria* had intercentra along the length of the presacral column (Ewer, 1965: 406). *Proterosuchus* had intercentra from the neck to the tail (Cruickshank, 1972a: 104), and their presence in erythrosuchids is probable (Charig & Sues, 1976: 30).

Numerous papers have been written recently on the systematics of later thecodontians (e.g. Romer, 1972; Bonaparte, 1975, 1982; Krebs, 1976; Cruickshank, 1979; Thulborn, 1980; Brinkman, 1981; Chatterjee, 1982). Some authors (Romer, 1972; Bonaparte, 1975, 1982) regard the late Triassic Proterochampsidae as proterosuchians, and the middle Triassic Rausisuchidae as direct relations of the Erythrosuchidae. Several authors (e.g. Bonaparte, 1975; Cruickshank, 1979; Brinkman, 1981; Chatterjee, 1982) also postulated a separate group of thecodontians containing *Euparkeria* and the Ornithosuchidae, late Triassic bipedal thecodontians. These questions, as well as the relationships of the aetosaurs, phytosaurs, crocodiles, and dinosaurs, are not considered further here.

Heleosaurus and the archosaurs

Carroll (1975a, 1976c) redescribed *Heleosaurus*, a small diapsid from the *Cistecephalus* Zone of the Karoo Basin, S Africa (early part of the late Permian), on the basis of one poorly preserved skeleton. He suggested that it was a younginid 'eosuchian' ancestral to the archosaurs. The archosaur-like characters he noted were:

- (1) thecodont dentition;
- (2) teeth laterally compressed and recurved;
- (3) dermal armour consisting of small plates scattered along the vertebral column;
- (4) crocodile-like femur, with possibility of bipedality.

Wild (1978: 251) has noted that the teeth of *Heleosaurus* are subthecodont, and Reisz (1981: 59–60) has stated that its femur was misinterpreted by Carroll and is, in fact, quite primitive. Nevertheless, characters (2) and (3) are archosaur-like.

In assessing the relationships of *Heleosaurus*, Carroll (1976c) considered that it was a younginid. However, most of the typical younginid characters are not preserved, and *Heleosaurus* lacks the accessory intervertebral articulations considered by Currie (1981a, c: 164) as typical of the younginids and tangasaurids. Of the characters that may be assessed, *Heleosaurus* exhibits those of the Neodiapsida (list B). However, it lacks typical archosauromorph characters such as the posterior position of the quadratojugal, non-notochordal vertebrae, and transverse processes well developed (C3, 6, 7). In all respects, *Heleosaurus* is primitive, and it must be left as Neodiapsida, *incertae sedis* until more diagnostic skull and limb material is available. The archosaur-like features are regarded as convergences.

Rhynchosauria

The rhynchosaur—small to medium-sized herbivorous reptiles of the Triassic—have classically been associated with sphenodontids in the Order Rhynchocephalia (e.g. Williston, 1925; Romer, 1956, 1966; Kuhn, 1969). This viewpoint has been questioned recently (Hughes, 1968; Cruickshank, 1972a; Carroll, 1975a, 1976a, 1977; Brinkman, 1981; Benton, 1983b) and strong similarities have been noted between rhynchosaur and archosaur, and between rhynchosaur and prolacertiforms. Rhynchosaur clearly share a suite of synapomorphies with these groups, as has been shown above (character list C).

The earliest so-called rhynchosaur, *Noteosuchus* from the *Lystrosaurus* Zone (earliest Triassic) of S Africa, is represented by the incomplete posterior part of a skeleton (Carroll, 1976a). It was identified by Carroll as a rhynchosaur on the basis of general postcranial resemblances to the early rhynchosaur *Mesosuchus* and *Howesia*, and on the basis of features of the ankle in particular. However, *Noteosuchus* shares all of these characters with other early archosauromorphs. In the absence of a skull, *Noteosuchus* is treated as Archosauromorpha *incertae sedis* here.

Two early rhynchosaur have been described from the *Cynognathus* Zone (late early Triassic) of S Africa: *Howesia* (Broom, 1906; Malan, 1963; Carroll, 1976a) and *Mesosuchus* (Broom, 1913, 1925; Haughton, 1921, 1924; Malan, 1963; Carroll, 1976a). *Mesosuchus* is the least typical rhynchosaur, and it has often been separated from the Family Rhynchosauridae (*Howesia* and later rhynchosaur) as the Family Mesosuchidae. The hypothesis of a monophyletic Rhynchosauria is tested by the following synapomorphies between the Mesosuchidae and the Rhynchosauroidae which are derived in comparison with other early archosauromorphs (Fig. 9M).

Character list M: Rhynchosauria

(1) Premaxilla bearing a small number of acrodont teeth, or none at all (Fig. 8D, E).

(2) Single median naris. The anterior part of the snout has not been described in *Howesia* (Broom, 1906), but Robert Reisz (pers. comm., 1983) notes that it has a single median naris as in *Mesosuchus* and other rhynchosaur.

(3) Fused parietals. The parietals are fused and form a narrow strip between the large upper temporal fenestrae in all genera. In all cases, the parietal seems to be peaked in the midline and triangular in cross-section.

(4) Presence of three proximal tarsals, with the centrale closely associated with the astragalus (Fig. 7H–J). In archosauromorphs that have a centrale, this element is in the middle of the ankle, whereas in all rhynchosaur, including *Mesosuchus* and *Howesia* (Carroll, 1976a), the centrale has moved proximally and is firmly applied to the side of the astragalus. The tarsus of *Noteosuchus* does not show this character.

Rhynchosauroidae

Howesia and later rhynchosaur show many important differences from *Mesosuchus*. The members of the Rhynchosauroidae share the following characters which are derived in comparison with *Mesosuchus* and other archosauromorphs (Fig. 9N).

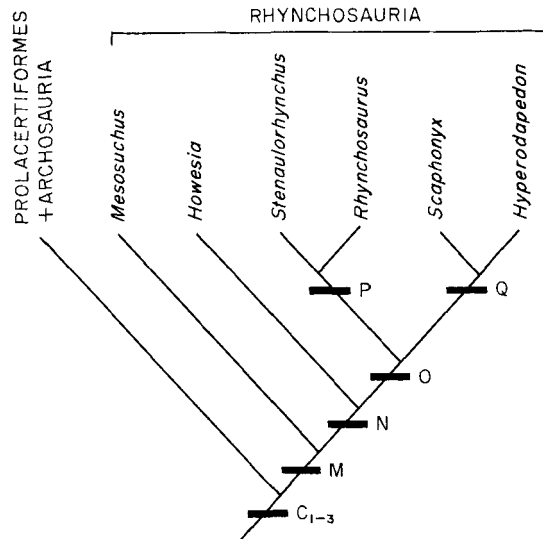


Figure 9. Cladogram representing the relationships of the rhynchosaur (other Archosauromorpha, see Fig. 4; Lepidosauromorpha, see Fig. 10). Genera and main monophyletic groups are indicated. Synapomorphies are: C_{1-3} , premaxilla extends up behind naris, nares elongate and close to midline, quadratojugal mainly behind lower temporal fenestra; M, premaxilla bears a small number of acrodont teeth or none at all, single median naris, fused parietals, three proximal tarsals; N, premaxilla beak-like and lacks teeth, parietal foramen absent, teeth have ankylothecondont implantation, batteries of functional teeth on maxilla and dentary; O, loss of supratemporal, interlocking groove and blade jaw apparatus, centrale large and united with astragalus; P, two grooves on maxilla, occipital condyle well in front of quadrates, single row of teeth on pterygoid; Q, breadth of skull greater than length, jugal occupies large area of cheek, single groove on maxilla, no teeth on lingual side of maxilla, no teeth on pterygoid, lower jaw very deep, dentary has only one or two rows of teeth, coracoid has no posterior process, femur approximately as long as humerus. Full details are given in the text.

Character list N: *Rhynchosauroidae*

(1) Premaxilla beak-like and lacks teeth. *Mesosuchus* has two acrodont teeth on its premaxilla (Haughton, 1924; Malan, 1963: 218). The status of this character is not known in *Howesia*.

(2) Parietal foramen absent. *Mesosuchus* and other early archosauromorphs retain this foramen.

(3) Teeth have ankylothecondont implantation. Rhynchosauroid teeth are implanted in deep sockets and fused to the jaw by bone of attachment. They show a mixture of the characters of acrodont and thecodont teeth (Chatterjee, 1974; Benton, 1983b). *Howesia* also apparently had this mode of implantation ('hyperacrodont': Malan, 1963: 217–218). The teeth of *Mesosuchus* were acrodont according to Broom (1913: 628) and Haughton (1924: 18).

(4) Batteries of functional teeth on the maxilla and dentary. The dentary tooth rows are reduced in late Triassic rhynchosaur, but multiple tooth rows on the maxilla are shared by all. *Mesosuchus* has a curious slightly zig-zag single-row dentition (Malan, 1963).

Mesosuchus also shows several autapomorphies when compared with other rhynchosaur—the dentition, (?) a broken lower temporal bar and streptostylic quadrate (Haughton, 1924; although Broom, 1925 strongly disagreed), a

reduced quadratojugal, and a possible mandibular fenestra (Broom, 1913, 1925).

Rhynchosauridae

Howesia may be distinguished from later rhynchosaurids (the Rhynchosauridae) since it lacks a number of characters that they share. The synapomorphies of Rhynchosauridae are (Fig. 9O):

Character list O: Rhynchosauridae

(1) Loss of supratemporal. This element has been identified in *Mesosuchus* (Haughton, 1924: 19; Broom, 1925: 6–7, as ‘tabular’) and *Howesia* (Haughton, 1924: 24).

(2) Interlocking groove and blade jaw apparatus. The tooth-bearing elements of *Howesia* have rounded occlusal surfaces (Broom, 1906; Malan, 1963), while grooves are present in the maxilla of later rhynchosaurids.

(3) Centrale large and firmly united with the astragalus.

The remaining well represented rhynchosaurids come from the middle Triassic (*Stenaulorhynchus* from Tanzania (Figs 6H, 7I, 8D), *Rhynchosaurus* from England) and the late Triassic (*Scaphonyx* from Brazil and Argentina, *Hyperodapedon* from Scotland and India) and they fall neatly into two subfamilies that match these stratigraphic divisions. *Stenaulorhynchus* and *Rhynchosaurus* (the Rhynchosaurine) share the following synapomorphies (Fig. 9P).

Character list P: Rhynchosaurinae

- (1) Two grooves on the maxilla and two matching ridges on the dentary.
- (2) Occipital condyle set well forward of the quadrates.
- (3) Single row of teeth on the pterygoid.

The late Triassic genera *Hyperodapedon* (Figs 6I, 7J, 8E) and *Scaphonyx* (the Hyperodapedontinae) share the following synapomorphies (Fig. 9Q).

Character list Q: Hyperodapedontinae

- (1) Breadth of the skull across the temporal region greater than its length.
- (2) Jugal occupies a large area of the cheek and has a heavy lateral ridge.
- (3) Single longitudinal groove on maxillary tooth plate.
- (4) No teeth on lingual side of maxilla.
- (5) No teeth on the pterygoid.
- (6) Lower jaw very deep.
- (7) Dentary has only one or two rows of teeth.
- (8) Coracoid has no posterior process.
- (9) Femur approximately as long as humerus.

There has been some disagreement in recent years over the classification within the Rhynchosauria. Most authors have classed *Howesia* with *Mesosuchus* in the Mesosuchidae or Mesosuchinae (e.g. Chatterjee, 1969, 1974, 1980a; Sill, 1971), but *Howesia* is clearly the sister group of the later rhynchosaurids, and it should be included in the Rhynchosauridae. The later genera have normally been placed into two subfamilies, as suggested here, namely the Rhynchosaurinae for the middle Triassic forms, and the Hyperodapedontinae

for the late Triassic forms (Chatterjee, 1969, 1974; Sill, 1971). However, Chatterjee (1980a) has recently proposed a geographic split into an American/Indian group and a European/African group on the basis of the relative widths of the maxillary tooth plate on either side of the groove. This character is not consistent with the proposed groups and the classification is without foundation (Benton, 1983b).

Trilophosauridae

Trilophosaurus from the Dockum Group (late Triassic) of Texas was a 2.4 m long herbivore with broad cheek teeth (Gregory, 1945). It has normally been classified as a protosaur (Euryapsida) (e.g. Romer, 1956, 1966) and compared with *Araeoscelis* from the early Permian. Recently, it has been suggested that *Trilophosaurus* has diapsid affinities (e.g. Chatterjee, 1980b: 191–192), and in particular with the archosauromorph group (Brinkman, 1981).

Trilophosaurus shows numerous specialized features in the skull and skeleton, but it shows all the hard-part characters of a diapsid (A1–4), including a small suborbital fenestra, although there is no lower temporal fenestra. As far as can be determined, *Trilophosaurus* also appears to belong to the Neodiapsida—it shares all characters B1–15, although the sutures of the lacrimal and other skull bones are partially fused and hard to determine. *Trilophosaurus* may be tentatively placed in the Archosauromorpha since it shares characters C4–14 (C3 doubtful, C1–2 absent). Brinkman (1981) has already noted the archosauromorph tarsal synapomorphies—tuber on the calcaneum, complex astragalus/calcaneum joint—and other important ones include stapes with no foramen, non-notochordal vertebrae, tall waisted scapula, no entepicondylar foramen in humerus, loss of 5th distal tarsal, hooked 5th metatarsal. The Family Trilophosauridae is here classified as the sister-group of (Rhynchosauria + Prolacertiformes + Archosauria).

Pterosauria

Pterosaurs have typically been regarded as archosaurs that had their ancestry among the thecodontians (e.g. Romer, 1966; Wellnhofer, 1978). However, Wild (1978) has described two late Triassic genera on the basis of good material (*Eudimorphodon*, *Peteinosaurus*), and he has made the proposal that the pterosaurs arose directly from 'eosuchians' and are not true archosaurs. Pterosaurs possess an antorbital fenestra, but Wild (1978: 247) considered that this may be a convergence. Further, Wild (1978: 246–253) reviewed numerous similarities between the early pterosaurs and various 'eosuchians' and differences from early thecodontians. The characters shared with *Youngina*, *Prolacerta* and others are all primitive to diapsids as a whole, except for the reduced quadratojugal, the ossified sternum, the 'hooked' 5th metatarsal, and the 3-pointed teeth seen in *Eudimorphodon*.

Pterosaurs display all of the characters of the Neodiapsida as far as can be determined, except B2 (ventral processes on parietals) and B6 (emarginated quadrate). They show some archosauromorph synapomorphies (C4–10), but lack others: C1–3, 11–14. Pterosaurs share two characters with the Lepidosauromorpha: the single ossified sternum, and specialized sternal

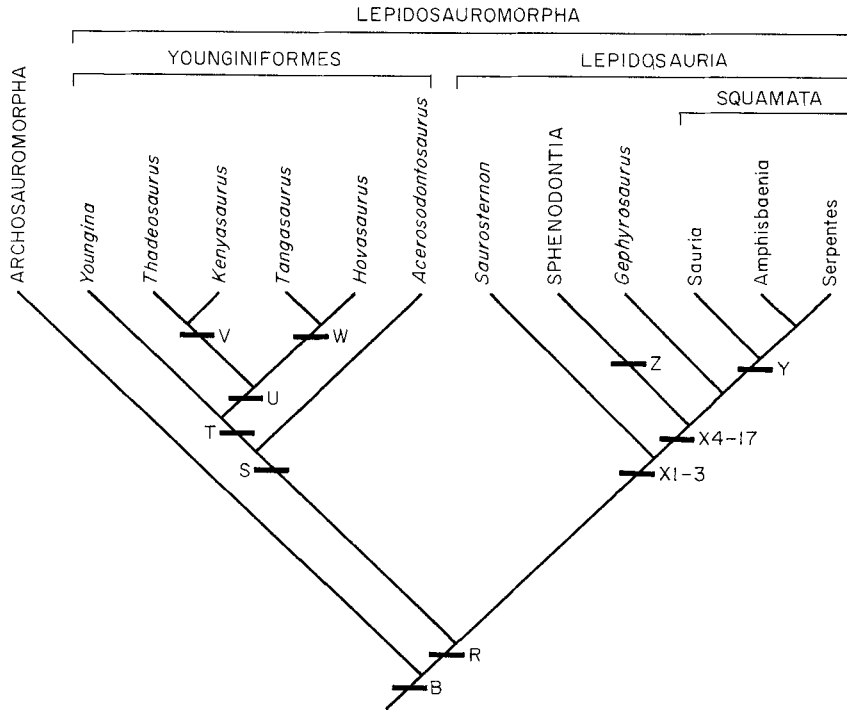


Figure 10. Cladogram representing the relationships of the Lepidosauromorpha (Archosauromorpha, see Figs. 4, 9). Genera and main monophyletic groups are indicated. Synapomorphies are: B (see Fig. 4); R, postfrontal enters border of upper temporal fenestra, accessory intervertebral articulations on neural arch, cervical centra shorter than dorsals, dorsal ribs single-headed, co-ossification of paired sternal plates in adult, specialized sternal rib connections; S, distinctive sutures on the parietal for the frontal and postfrontal, reduced rod-like quadratojugal running to a point, neural spines of dorsals high and rectangular, entepicondyle of humerus well developed, lateral centrale loses contact with distal carpal; T, short neck of 4–5 vertebrae, radius longer than shaft of ulna; U, humerus as long as or longer than femur, scapula low and ventral, coracoid as large as scapula, 5th distal tarsal not a discrete element; V, 19–28 pairs of caudal ribs; W, neural spines high, 9–12 pairs of caudal ribs, anterior caudal ribs expand distally, haemal spines large and plate-like, presacral intercentra ossify only in adult; X, determinant growth, specialized articulating surfaces on long bones, specialized joint between ulna and ulnare, lacrimal reduced or absent, postparietal and tabular absent, supraparachordal course of notochord, fusion of proatlas with tip of odontoid process, 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 and with plantar tubercles, loss of ciliary process in eye, kidney with a sexual segment; Y, skull roof bones often fused, postfrontal and postorbital often fused, pterygoids do not reach vomers, pterygoids do not meet in midline, supratemporal deep between squamosal and parietal, specialized articulation surface for dorsal wing of quadrate, squamosal reduced or absent, no lower temporal bar, no quadratojugal, quadrate ramus of pterygoid reduced, quadrate notched posteriorly forming a conch, mesokinesis, fenestra rotunda, vidian canal, ossification of anterior braincase, prearticular fused with articular, vertebrae usually procoelous, all ribs holocephalous, dorsal intercentra seldom developed, hypapophyses on cervicals, no true sacral ribs, loss of entepicondylar foramen, fenestrated anterior margin of scapulocoracoid, vomeronasal apparatus covered by septomaxilla, Jacobson's organ independent of nasal cavity, Jacobson's organ has a fungiform body, salivary glands anatomically separate; Z, lacrimal absent, parietals narrow, supratemporal absent, quadrate not emarginated, teeth acrodont, large fused teeth on premaxillae, tiny juvenile teeth, tooth replacement by addition at the back, single row of large teeth on palatine, maxillo-palatine groove, no other teeth on palate, splenial absent, broad mandibular symphysis, dentary forms most of lower jaw, large mandibular foramen. Full details are given in the text.

attachments for the ribs. The most parsimonious position for the pterosaurs at present is within the Archosauromorpha, as sister-group to all other archosauromorphs. Further work is needed on this question as well as on the suggestion that Pterosauria are the sister-group of Aves (Gardiner, 1982).

CLASSIFICATION OF THE LEPIDOSAUROMORPHA

Lepidosauromorpha

A second large assemblage of diapsids may be recognized in the late Permian and Triassic. The younginids and tangasaurids have been combined as the Younginiformes (Currie, 1982) and Currie (1981c: 163–164) noted resemblances between these and the late Permian and early Triassic ‘paliguanids’ (*Paliguana*, *Palaeagama*, *Saurosternon*). The ‘paliguanids’ have been interpreted as ancestral lizards, together with the kuehneosaurids (e.g. Robinson, 1962, 1967b; Carroll, 1975a, b, 1977), and these lizards and lizard-like animals have also been associated with the sphenodontids (e.g. Carroll, 1977; Rage, 1982). It is not easy to establish the monophyly of the Lepidosauromorpha. Nevertheless, the Younginiformes and Lepidosauria share a number of synapomorphies in comparison with *Petrolacosaurus* and the Archosauromorphs (Fig. 10R).

Character list R: Lepidosauromorpha

- (1) Postfrontal enters border of upper temporal fossa.
- (2) Accessory intervertebral articulations present on the midline of the neural arch between the zygapophyses (Fig. 11). This character was identified in the younginiforms *Youngina*, *Kenyasaurus*, *Hovasaurus*, *Tangasaurus* and *Thadeosaurus* (Currie, 1981a) and regarded as characteristic of this group (Currie, 1982: 260). In both *Youngina* and *Hovasaurus*, these articulations are variable throughout the vertebral column and may be seen as small facets between the zygapophyses or as processes higher up the neural spine. Currie (1981c: 163) notes their presence “on the midline of the neural arch in *Saurosternon* (Carroll, 1975b), but because the neural spine is so low in paliguanids, these processes do not resemble those of *Youngina* and the tangasaurids”. Carroll (1975b: 79) described these processes in *Saurosternon* as follows: the neural spine “bifurcates, as in some lizards, to form laterally facing accessory articulating processes. These are also developed in *Sphenodon*”. In certain groups of living lizards (Iguanidae, Cordylidae, Lacertidae, Teiidae), a zygosphen-zygantrum articulation is developed (“a condition in which an anteriorly facing tenon, situated between the prezygapophyses and provided with articular facets, is engaged by a posteriorly facing mortise between the postzygapophyses of the preceding vertebra” (Hoffstetter & Gasc, 1969: 250)). This pattern is also present in *Sphenodon*, while in all snakes the zygantrum and zygosphen are elevated on the neural spine and quite separate from the zygapophyseal facets (Hoffstetter & Gasc, 1969: 236, 249–252, 284–285). This joint is characteristic of most living squamates (although absent in amphisbaenians) and it could well be homologous with the younginiform condition, a point not discussed by Currie (1981a, c, 1982).
- (3) Cervical centra shorter than average mid-dorsal centra. This is the case in

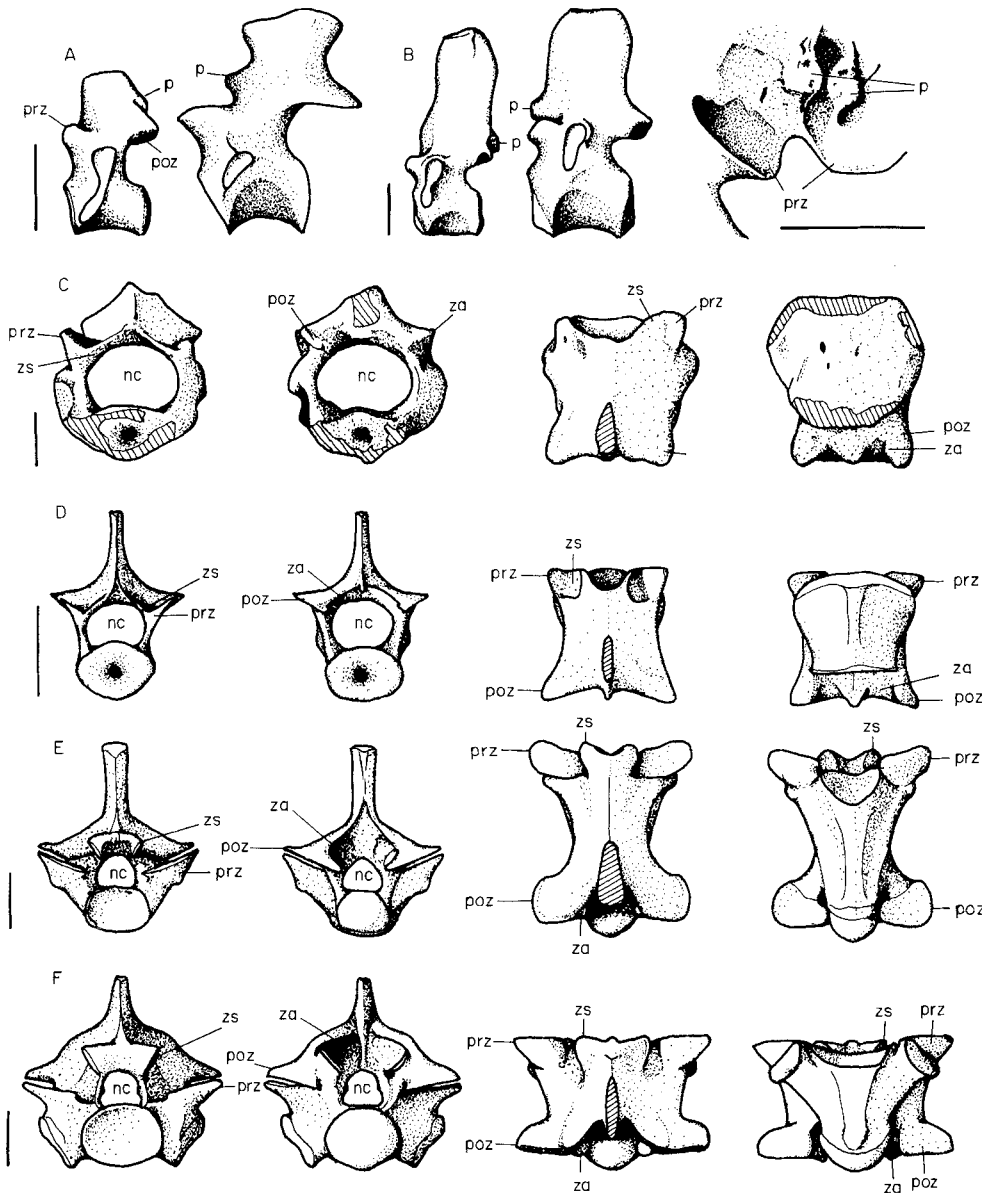


Figure 11. Accessory intervertebral articulation in lepidosauromorphs. A, cervical and dorsal vertebra of *Youngina*; B, anterior and posterior dorsal vertebra of *Hovasaurus*; and magnified view of anterior face of base of neural spine; C-F, dorsal vertebrae of C, *Gephyrosaurus*; D, *Sphenodon*; E, *Iguana*; and F, *Python* in anterior, posterior, dorsal and ventral views. Scale bars = 0.5 cm. Abbreviations: nc, neural canal; p, accessory intervertebral process; poz, postzygapophysis; prz, prezygapophysis; za, zygantrum; zs, zygosphene. (A, after Currie, 1981a; B, after Currie, 1981c; C, after Evans, 1981a; D-F, original.)

the younginiforms *Youngina* (Gow, 1975), *Thadeosaurus* (Carroll, 1981), *Hovasaurus* (Currie, 1981c) and *Acerosodontosaurus* (Currie, 1980). It is also true of *Sphenodon* and many lizards (Hoffstetter & Gasc, 1969) as well as kuehneosaurids (Colbert, 1970). The situation in *Saurosternon* and *Palaeagama* is uncertain

(Carroll, 1977). In *Petrolacosaurus* and the Prolacertiformes, the cervical centra are longer than the dorsals.

(4) Dorsal ribs single-headed. *Petrolacosaurus* and the archosauromorphs have primitive two-headed ribs in all or part of the dorsal region.

(5) Co-ossification of paired sternal plates in the adult. *Saurosternon* has an ossified sternum (Carroll, 1975b, 1977), and this character is typical of younginiforms (Currie, 1982: 260). *Sphenodon* and modern lizards have a sternum, or a series of sternal cartilages or bones of cartilaginous origin. A cartilaginous sternum is also present in crocodiles, and paired oval ossified plates are known in some dinosaurs (Romer, 1956: 295–297). However, the younginiform and *Saurosternon* sternum, a broad plate fitting closely behind the coracoids and which is overlapped by the posterior portion of the interclavicle, is most like that of modern lizards (Lécure, 1968), and quite unlike that of crocodiles and dinosaurs. The large sternum of pterosaurs (Wellnhofer, 1978: 13–14) is similar in shape and position, but it has a heavy anterior process.

(6) Specialized sternal rib connections. The sternum of *Hovasaurus* has lateral facets for the attachment of 4–5 ribs (Currie, 1981c: 145), *Thadeosaurus* probably had a similar number (Carroll, 1981: 326), and *Kenyasaurus* had at least three (Harris & Carroll 1977: 145). The rib attachments are not present in *Saurosternon* (Carroll 1977: 372–373). Lizards have 3–5 costal attachments in just the same arrangement as in younginoids (Lécure, 1968).

Younginiformes

The genus *Acerosodontosaurus* from the late Permian of Malagasy was described by Currie (1980) as a younginid on the basis of cranial similarities. However, he noted later (Currie, 1981a: 817; 1981c: 162; 1982) that *Acerosodontosaurus* lacks the accessory intervertebral articulations of the younginoids. *Acerosodontosaurus* has a number of synapomorphies with younginoids and it is tentatively treated as a younginiform, the sister-group to the Younginoidea. If the accessory intervertebral articulations are characteristic of Lepidosauromorpha, it must be assumed that *Acerosodontosaurus* has lost them. The synapomorphies of *Acerosodontosaurus* and the Younginoidea, by comparison with other early diapsids, are (Fig. 10S):

Character list S: Younginiformes

(1) Distinctive sutures on the parietal for the frontal and postfrontal (Currie, 1982: 260). The parietals send long processes forwards in the midline between the two frontals, and antero-laterally between frontal and postfrontal (Fig. 12A).

(2) Reduced triangular rod-like quadratojugal lying below the lower temporal fenestra and running to a point anteriorly. This feature is seen in *Youngina* (Gow, 1975; Carroll, 1981), *Hovasaurus* (Currie, 1981c), and in *Acerosodontosaurus* (Currie, 1980), but not in *Petrolacosaurus*, *Prolacerta* or *Paliguana*.

(3) Neural spines of dorsal vertebrae high and rectangular. This is the case in *Youngina* (Gow, 1975), *Kenyasaurus* (Harris & Carroll, 1977), *Thadeosaurus* (Carroll, 1981), *Hovasaurus* (Currie, 1981c), and in *Acerosodontosaurus* (Currie, 1980: 505). *Petrolacosaurus* (Reisz, 1981) has shorter, more triangular neural spines on anterior dorsals, while *Prolacerta* has medium to long, but tapering,

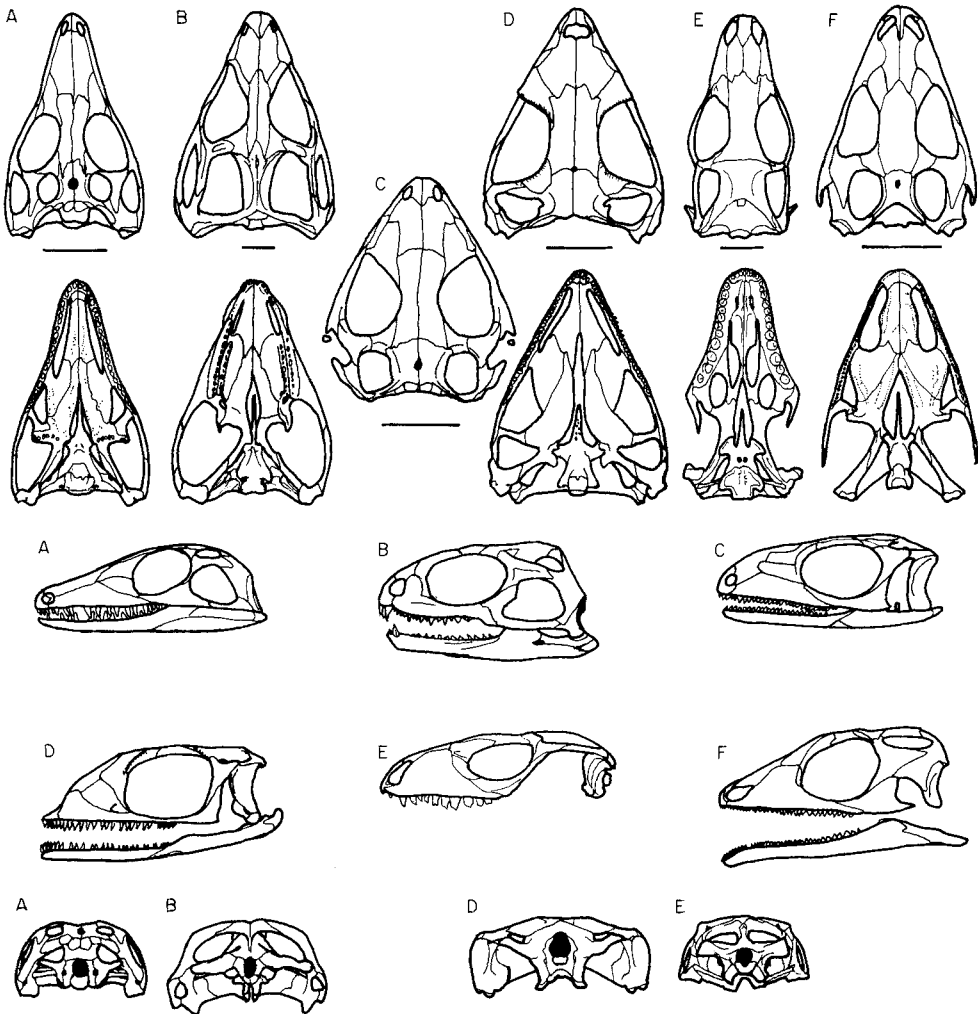


Figure 12. The skulls of A, *Youngina*; B, *Sphenodon*; C, *Paliguana*; D, *Kuehneosaurus*; E, *Tupinambis*; and F, *Gephyrosaurus* in dorsal (top row), palatal (second row), lateral (third, fourth rows) and occipital (bottom row) views. The skulls have been drawn to a standard length. Scale bars = 1 cm. The skull of *Paliguana* is incompletely known. (A, after Carroll, 1981; B, after Romer, 1956; C, after Carroll, 1975b; D, after Robinson, 1962; E, after Rieppel, 1980; F, after Evans, 1980).

spines (Gow, 1975), and *Saurosternon* has triangular spines (Carroll, 1975b, 1977).

(4) Entepicondyle of the humerus strongly developed at maturity. This is a character of younginoids (Currie, 1982) and of *Acerosodontosaurus* (Currie, 1980: 507–508), although the distal end of the humerus is not as strongly developed as in tangasaurids (Fig. 13A–C).

(5) Lateral centrale loses contact with 3rd distal carpal in the wrist. This is a feature of tangasaurids, *Acerosodontosaurus*, and possibly also *Youngina* (Currie, 1981b, 1981c: 162), and it is caused by the new contact between the small medial centrale and the 4th distal carpal.

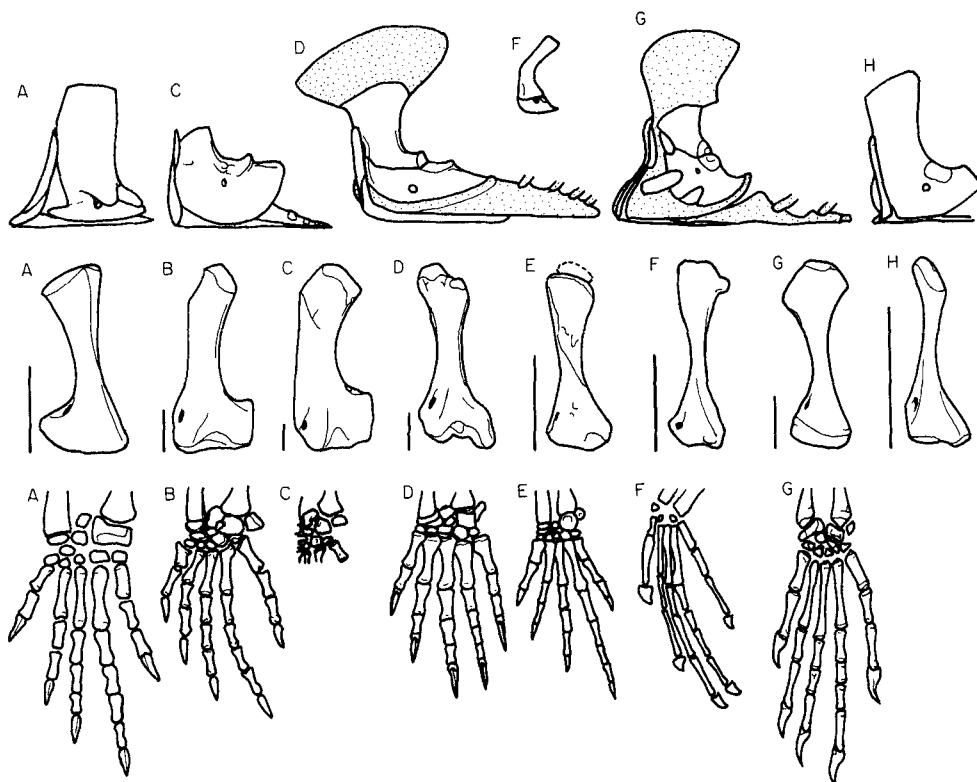


Figure 13. The pectoral girdle (left lateral views), humerus (left, dorsal view) and hand (left, dorsal view) of A, *Youngina*; B, *Thadeosaurus*; C, *Hovasaurus*; D, *Sphenodon*; E, *Saurosternon*; F, *Icarosaurus*; G, *Varanus*; and H, *Gephyrosaurus*. The humeri have been drawn to a standard length, and the shoulder girdles and hands to scale. Scale bars for each genus = 1 cm. Cartilage is shown by stippling. The pectoral girdles of *Thadeosaurus* and *Saurosternon*, and the hand of *Gephyrosaurus* are incompletely known. (A, after Gow, 1975; B, after Carroll, 1981; C, after Currie, 1981c; D, after Romer, 1956; E, after Carroll, 1975b, 1977; F, after Colbert, 1970; G, after Romer, 1956 and specimens; H, after Evans, 1981a.)

Younginoidea

Youngina, a 40 cm long diapsid reptile from the *Daptocephalus* Zone (late Permian) of the Karoo Basin, S Africa (Figs 12A, 13A, 14A), is rather better known than some other forms discussed so far (Broom, 1914, 1924; Olson, 1936; Watson, 1957: 367–372; Gow, 1975; Carroll, 1981; Currie, 1981a). It has hitherto been regarded as central to the ‘eosuchian’ concept and a suitable ancestor for later diapsids (e.g. Romer, 1956, 1966), but it is clearly specialized in several ways.

Currie (1982) has defined the Superfamily Younginoidea in terms of a series of synapomorphies of *Youngina* (Family Younginidae) and the Family Tangasauridae. Several of his characters (1–5) have already been used to diagnose the Neodiapsida (5), the Lepidosauromorpha (2, 3), and the Younginiformes (1, 4). If it is shown that the accessory intervertebral articulations of younginoids are not homologous with the zygosphenes-zygantrum articulations of lepidosaurs, then this character would be reinstated for younginoids. *Youngina* shares the

following synapomorphies with the tangasaurids in comparison with *Acerosodontosaurus* and other early lepidosauromorphs (Fig. 10T).

Character list T: Younginoidea

(1) Short neck consisting of four or five vertebrae. *Hovasaurus* has five cervicals (Currie, 1981c: 129), as was probably also the case in *Tangasaurus* (Currie, 1982: 253). Gow (1975: fig. 10) shows *Youngina* with 4–5 cervicals. The situation in *Thadeosaurus*, *Kenyasaurus*, *Acerosodontosaurus* and 'paliguanids' is uncertain. *Petrolacosaurus* had six cervicals, and prolacertiforms had 7–12. *Sphenodon* has 8 cervicals, most lizards have 7–9 (Hoffstetter & Gasc, 1969).

(2) Radius longer than the shaft of the ulna. This is not the case in *Acerosodontosaurus* (Currie, 1980), nor in other early diapsids.

Tangasauridae

Four recently described, or redescribed, younginoids are included in the Tangasauridae. These are *Thadeosaurus* (Figs 13B, 14B) from the Lower

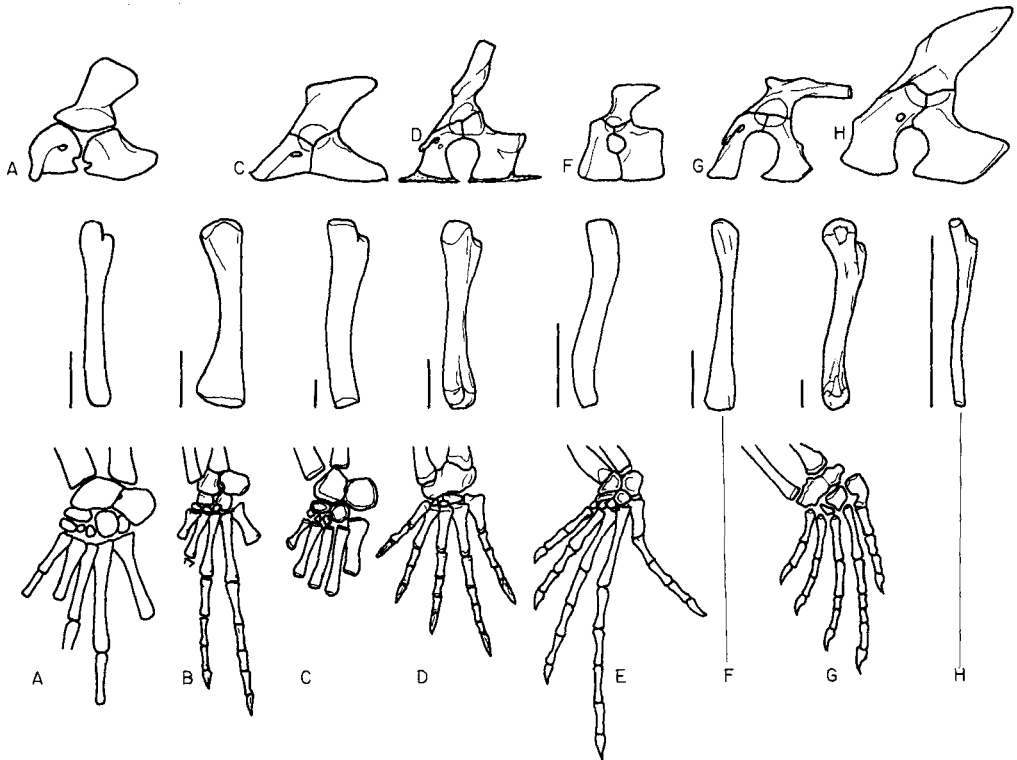


Figure 14. The pelvis (left lateral view), femur (postero-lateral view (A, C–E, G, H) or ventral view (B, F)) and foot (dorsal view) of A, *Youngina*; B, *Thadeosaurus*; C, *Hovasaurus*; D, *Sphenodon*; E, *Saurosternon*; F, *Icarosaurus*; G, *Varanus*; and H, *Gephyrosaurus*. The femora have been drawn to a standard length, and the pelves and feet to scale. Scale bars for each genus = 1 cm. Cartilage is shown by stippling. The pelvis of *Thadeosaurus* and *Saurosternon*, and the feet of *Icarosaurus* and *Gephyrosaurus* are incompletely known. (A, after Gow, 1975; B, after Carroll, 1981; C, after Currie, 1981c; D, original; E, after Carroll, 1975b, 1977; F, after Colbert, 1970; G, original; H, after Evans, 1981a.)

Sakamena Formation (late Permian) of SW Malagasy (Carroll, 1981), *Kenyasaurus* from the Middle Duruma Sandstone Series (late Permian/early Triassic?) of Kenya (Harris & Carroll, 1977), *Tangasaurus* from the late Permian of Tanzania (Currie, 1982), and *Hovasaurus* (Figs 13C, 14C) from the Lower Sakamena Formation of SW Malagasy (Currie, 1981c). These four genera share a number of synapomorphies in comparison with *Youngina* and *Acerosodontosaurus* (Currie, 1982: 262) (Fig. 10U).

Character list U: Tangosauridae

- (1) Humerus as long as, or longer than, femur in mature animal.
- (2) Scapula low in lateral aspect and mainly a ventral element.
- (3) Coracoid as large as the scapula.
- (4) Fifth distal tarsal not a discrete element.

The carpal character, in which the lateral centrale does not contact the 3rd distal carpal, is present in tangasaurids and *Acerosodontosaurus* (Currie, 1981b, c), and it has been used as a character of the Younginiiformes above. If this feature is shown to be absent in *Youngina*, then the character would be reinstated as a tangasaurid character. *Acerosodontosaurus* would then be difficult to place taxonomically.

The tangasaurids fall neatly into two groups, the terrestrial Kenyasaurinae and the aquatic Tangasaurinae. *Kenyasaurus* and *Thadeosaurus* have one synapomorphy (Currie, 1982: 262) (Fig. 10V).

Character list V: Kenyasaurinae

- (1) 19–28 pairs of caudal ribs and transverse processes present, all of which taper distally.

Tangasaurus and *Hovasaurus*, the Tangasaurinae, have the following synapomorphies (Currie, 1982: 262) (Fig. 10W).

Character list W: Tangasaurinae

- (1) Neural spines high in dorsal region and higher in proximal and mid-caudal regions.
- (2) 9–12 pairs of caudal ribs.
- (3) Anterior caudal ribs expanded distally.
- (4) Haemal spines large and plate-like.
- (5) Presacral intercentra, with the exception of the first three, do not ossify until animal is mature.

Lepidosauria

The term Lepidosauria was established by Duméril & Bibron (1839: 511, as 'Lépidosaures') as an alternative name for their scincoid group of lizards, which included a selection of Gekkota, Scincomorpha and Anguimorpha. Haeckel (1866: vol. 2, CXXXVIII) established the Subclass Lepidosauria, without reference to Duméril & Bibron, for lizards and snakes, and presumably also *Sphenodon*, which was regarded as an agamid lizard until Günther's (1867) restudy and establishment of the Order Rhynchocephalia. The term Lepidosauria was then either not used, or it was equated with Squamata by

later authors (e.g. Zittel, 1890). Lizards and snakes were then classed as Diapsida (Osborn, 1903) or Parapsida (Williston, 1925), until Romer (1933) revived the term Lepidosauria for Squamata + 'Rhynchocephalia' + some 'eosuchians'. Further 'eosuchians', millerosaurs, rhynchosauroids, and other unrelated groups were subsequently added (e.g. Romer, 1956; Kuhn, 1969). It is probably appropriate to return closer to Haeckel's original usage of 'Lepidosauria' to include Squamata and Sphenodontidae only.

The main groups to be considered as Lepidosauria are: the Squamata (lizards, amphisbaenians and snakes), the Sphenodontidae (*Sphenodon* and fossil relatives), and *Gephyrosaurus* (an early Jurassic form). The Paliguaniae (five late Permian and early Triassic genera—*Blomosaurus*, *Kudnu*, *Palaeagama*, *Paliguana*, *Saurosternon*—that probably do not form a natural assemblage) and the Kuehneosauridae (late Triassic gliding forms), both of which have been regarded as early lizards, will then be discussed.

The Lepidosauria display several synapomorphies when compared with Younginiformes and other early diapsids. They also show further synapomorphies when compared with other living reptiles (de Beer, 1937; Carroll, 1977: 392; Rage, 1982), and these are all listed (Fig. 10X).

Character list X: Lepidosauria

(1) Determinant growth. There is a particular adult size at which growth stops, and this is connected with the mode of bone growth. This is true of *Sphenodon*, lizards, and *Gephyrosaurus* (Evans, 1981a). It should be noted that some lizards may grow very slowly after maturity if the epiphyses do not fuse completely to the diaphysis (Bellairs, 1969). Further, snakes do not have bony epiphyses (Haines, 1969) and they do not appear to show determinant growth.

(2) Specialized articulating surfaces of the long bones. The long bones in *Sphenodon*, lizards and *Gephyrosaurus* are capped by secondary bony or calcified cartilage epiphyses (Haines, 1969; Carroll, 1977; Evans, 1981a).

(3) Specialized joint between the ulna and ulnare. A specialized distal portion of the ulna ossifies to form a ball-like surface for articulation with the ulnare in lizards and sphenodontids (Carroll, 1977).

(4) Lacrimal reduced or absent.

(5) Postparietal and tabular absent.

(6) Supraparachordal course of the notochord.

(7) Fusion of the pleurocentrum of the proatlas vertebra with the tip of the odontoid process.

(8) Formation of a median hypocentral occipital condyle (de Beer, 1937).

(9) Thyroid fenestra in the pelvis.

(10) Fusion of astragalus and calcaneum.

(11) Loss of the centrale by incorporation into the fused astragalo-calcaneum.

(12) Loss of distal tarsals 1 and 5.

(13) Hooking of the 5th metatarsal in two planes and with specialized plantar tubercles (Robinson, 1975). This is different from the simple hooking seen in archosauromorphs (character C14).

(14) Loss of the ciliary process in the eye.

(15) Kidney provided with a sexual segment (Rage, 1982).

(16) Shared pattern of the pituitary gland (Gardiner, 1982).

(17) Shared adrenal characters (Gardiner, 1982).

Squamata

Living Squamata (lizards, amphisbaenians, snakes) show numerous synapomorphies that are absent in *Sphenodon* and other lepidosauromorphs. These are listed briefly here (data from Romer, 1956; Evans, 1980: 256; Rage, 1982; Estes, 1983) (Fig. 10Y; Figs 12–14).

Character list Y: Squamata

- (1) Premaxillae, frontals, and parietals often fused (also nasals occasionally).
- (2) Postfrontal and postorbital often fused or one element lost.
- (3) Pterygoids do not reach vomers.
- (4) Pterygoids do not meet in the midline.
- (5) Supratemporal situated deep between the squamosal and parietal, above the quadrate.
- (6) Specialized articulation surface for the dorsal wing of the quadrate, formed by squamosal, supratemporal and opisthotic.
- (7) Squamosal reduced to a slender bar, or absent.
- (8) No lower temporal bar.
- (9) No quadratojugal.
- (10) Quadrate ramus of pterygoid reduced and no suture between quadrate and pterygoid.
- (11) Quadrate notched posteriorly with an anterior ridge, forming a conch for the tympanum.
- (12) Mesokinesis (fronto-parietal hinge).
- (13) Fenestra rotunda in the braincase.
- (14) Vidian canal in the braincase.
- (15) Ossification of the braincase anterior to the otic capsule.
- (16) Prearticular fused with the articular.
- (17) Vertebrae usually procoelous.
- (18) All ribs holocephalous.
- (19) Dorsal intercentra seldom developed.
- (20) Hypapophyses generally present on cervical vertebrae.
- (21) No true sacral ribs.
- (22) Loss of entepicondylar foramen in the humerus.
- (23) Fenestration of anterior margin of scapulocoracoid, with a procoracoid process.
- (24) Vomeronasal apparatus covered by a septomaxilla.
- (25) Jacobson's organ independent of the nasal cavity in the adult.
- (26) Jacobson's organ has a fungiform body (Rage, 1982).
- (27) Salivary glands are anatomically separate (Rage, 1982).

The 'paliguanids'

The Family Paliguanidae Broom 1926 has been interpreted (Carroll, 1975a, 1977) to include three genera from the late Permian and early Triassic of the Karoo, S Africa: *Palaeagama*, a partial skeleton and skull; *Paliguana*, a partial skull (Fig. 12C); and *Saurosternon*, a skeleton lacking the skull (Figs 13E, 14E). Tatarinov (1978) has described *Blomosaurus*, a partial skull from the early

Triassic of Russia, as a saurosternid, and Bartholomai (1979) has described *Kudnu*, a partial snout from the early Triassic of Australia, as a paliguanid. The exact relationships of these forms to each other, and to other early 'lizard-like' forms are unclear (Carroll, 1975a, b, 1977; Currie, 1981c: 163–164; Estes, 1983: 12–15). Indeed, the group cannot be defined by any apomorphy, and the genera must be considered separately. As far as can be determined, all of these genera are lepidosauromorphs.

Palaeagama is too poorly preserved to show many diagnostic features. Of those that can be recorded, it lacks the lepidosaur synapomorphies X4, 9, 10 and 13, and the squamate synapomorphies Y1, 2, 12, 17–19, 21 and 22. It shares no lepidosaur characters (list X), and it may share the squamate temporal characters Y7–9 and 11, but these are not at all clear in the specimen. *Palaeagama* also shows a primitive feature in that the lacrimal appears to border the naris (Carroll, 1975b: 74). It is regarded as a non-lepidosaur, and it is termed Lepidosauromorpha, *incertae sedis* for the present.

Paliguana, known only from a crushed skull, lacks the lepidosaur synapomorphies X4 and 5, and the squamate synapomorphies Y1, 2, 9 and 12. It shows no lepidosaur characters, but possibly the squamate characters Y7, 8 and 11. These latter are regarded as convergences, and *Paliguana* is also classified as Lepidosauromorpha, *incertae sedis* here.

Saurosternon is slightly better preserved than *Palaeagama* or *Paliguana*, but lacks the lepidosaur characters X9–13 and all of the squamate characters X17–19, 21 and 22 that may be determined. It appears to share the lepidosaur characters X1–3 (Carroll, 1975b, 1977). *Saurosternon* may be the primitive sister-group of the Lepidosauria.

Blomosaurus shows the lepidosaur character X4, and the squamate characters Y1, 2 and 16. *Kudnu* lacks the lepidosaur character X4 and the squamate character Y1, but none of the others may be determined. *Blomosaurus* and *Kudnu* are classified here as Lepidosauromorpha, *incertae sedis*.

Two recently described lizard-like forms may be mentioned here. *Lacertulus*, a very poorly preserved skeleton without data has been named as a possible early lizard on the basis of its size and proportions (Carroll & Thompson, 1982). As these authors note, there is no evidence as to its affinities, and it can only be recorded as Neodiapsida, *incertae sedis*. The second animal, *Colubrifer*, an elongate form with short legs from the *Lystrosaurus* Zone of S Africa (Carroll, 1982a), is described as a lizard. However, it lacks the lepidosaur characters X1–3, 5 and 9, but may show X10. Further, it shares the squamate characters Y11, 22 and 23(?), but not Y1, 9, 12, 17, 19 or 20, and the others are indeterminate. *Colubrifer* is tentatively referred to Lepidosauromorpha, *incertae sedis*.

Kuehneosauridae

The Kuehneosauridae, *Kuehneosaurus* (Fig. 12D) and *Kuehneosuchus* from the (?)late Triassic fissure deposits of the Bristol area, England (Robinson, 1962, 1967b) and *Icarosaurus* from the late Triassic of New Jersey, U.S.A. (Colbert, 1966, 1970), are clearly related to each other. They share a number of remarkable adaptations for gliding: elongate transverse processes on dorsal vertebrae; mid-dorsal ribs elongate and extended horizontally, and can be folded back; bones of skeleton light, many hollow; as well as two other derived

characters: very large orbit; lacrimal excluded from border of orbit by the prefrontal.

The taxonomic assignment of the Kuehneosauridae is not easy, not least because of the incomplete descriptions of *Kuehneosaurus*. They have hitherto been assigned to the Eolacertilia, as the sister-group of Lacertilia by Romer (1966), Robinson (1967b), Colbert (1970), Estes (1983: 15–19) and others, but this position is most unlikely. Kuehneosaurids show most of the synapomorphies of the Neodiapsida, although there are teeth on the parasphenoid (B9). Of the lepidosauromorph characters, *Kuehneosaurus* and/or *Icarosaurus* apparently lack R1, 2, 5 and 6, but they show short cervical centra (R3) and single-headed dorsal ribs (R4). The kuehneosaurids show lepidosaur synapomorphies Y5 and 9, but not Y4 or 10 and the other characters cannot be determined at present. Of the squamate synapomorphies, kuehneosaurids share Y4, 7–11, 19, 21 and 22, but not Y1–3, 5, 6, 12–15, 17, 18 or 23, with Y16 and 20 undetermined.

The kuehneosaurids share some archosauromorph characters. The nares are medially placed and confluent (C1) and the premaxillae run up behind the nares for a short distance (C2). Other archosauromorph characters are less certain, but the tabulars may be lost (C4), the vertebrae are non-notochordal (C6), the transverse processes of the dorsal vertebrae project laterally (C7), a cleithrum is not reported (C8), and there was no entepicondylar foramen (C9). The other archosauromorph synapomorphies cannot be determined.

The Family Kuehneosauridae could be made the sister-group of Neodiapsida since they lack one neodiapsid character. However, such an assignment would demand a large amount of convergence with archosauromorphs or lepidosauromorphs. Kuehneosaurids share only two lepidosauromorph characters, and lack the other four, but they show small numbers of lepidosaur and squamate synapomorphies. There is more evidence for an assignment to the Archosauromorpha. The kuehneosaurids show at least seven of the 14 archosauromorph synapomorphies. More information is required on the skull and ankle of kuehneosaurids before a taxonomic decision can be taken. The Family Kuehneosauridae is termed Neodiapsida, *incertae sedis* here.

Gephyrosauridae

Gephyrosaurus (Figs 12F, 13H, 14H) from the early Jurassic fissure infills of Bridgend, S Wales (Evans, 1980, 1981a), appears to be a lepidosaur. This small animal (25–30 cm long) has numerous primitive 'eosuchian' characters as well as some lizard-like ones, which has made its taxonomic assignment difficult. Estes (1983: 10) considers that *Gephyrosaurus* is probably a squamate, but he notes striking resemblances to Sphenodontia.

It shows four lepidosauromorph synapomorphies: the postfrontal enters the border of the upper temporal fenestra (R1); all presacral vertebrae, and some caudals, display a primitive zygosphenes-zygantrum arrangement (R2), the cervical centra are shorter than the dorsals (R3), and the dorsal ribs are single-headed (R4). However, no trace of sternal ossifications has been found (characters R5, 6). Further, *Gephyrosaurus* shows numerous lepidosaur synapomorphies: determinant growth (X1), discrete bony epiphyses (X2), reduced lacrimal (X4), no postparietal or tabular (X5), thyroid fenestra in pelvis (X9), fused astragalo-calcaneum (X10), ?loss of centrale (X11), ?loss of

distal tarsals 1 and 5 (X12), and hooked 5th metatarsal (X13). The other characters are unknown. Finally, *Gephyrosaurus* may be regarded as the sister-group of Squamata on the basis of the possession of a number of synapomorphies: fused parietal and frontal (Y1), reduced lower temporal bar (Y8), quadrate notched with a well rounded lateral conch (Y11), articular fused to the prearticular (Y16), all ribs holocephalous (Y18), and sacral ribs fused indistinguishably to the sacral vertebrae (Y21). In all other respects, *Gephyrosaurus* is primitive with respect to later squamates.

Sphenodontia

The name Sphenodontia is selected for *Sphenodon* and its close extinct relatives in preference to the name Rhynchocephalia since the latter has become too wide in application. The Order Rhynchocephalia was named by Günther (1867) for *Sphenodon* because of its great differences from lizards. He made no reference to fossil forms, although Owen (1863: 467) had already noted the supposed affinities of *Sphenodon* and *Rhynchosaurus*. However, subsequent authors (e.g. Huxley, 1869; 1871: 195; 1887; Newman, 1878; Lydekker, 1885, 1888; Zittel, 1890; Boulenger, 1890; Woodward, 1898) stated that rhynchosaurs were rhynchocephalians. Burckhardt (1900) and Osborn (1903: 477–479) questioned the closeness of this relationship, but most later authors have included all kinds of reptiles in the Rhynchocephalia (e.g. Williston, 1925; Hoffstetter, 1955; Huehne, 1956; Romer, 1956, 1966; Kuhn, 1969), such as champsosaurs, thalattosaurs, younginids, paliguanids, tangasaurids, pleurosaurs, and claraziids. The group has clearly got completely out of hand, and the use of the name Rhynchocephalia for *Sphenodon* and its relatives alone would be confusing. Other names that have been proposed are: Sphenodontoidea Lydekker 1888 and Rhynchocephalia *vera* Boulenger 1891 (both for sphenodontids and rhynchosaurs), and Sphenodontia Williston 1925 and Sphenodontoidea Nopcsa 1928 (both for sphenodontids). Williston's name Sphenodontia has priority, and is used here for *Sphenodon* and fossil relatives such as *Clevosaurus*, *Brachyrhinodon*, *Homoeosaurus*, and possibly *Sapheosaurus*. Estes (1983: 8) has erected the new Order Sphenodontida for *Sphenodon* and its close relatives, but Williston's name is considered appropriate here.

Sphenodon possesses numerous apomorphies when compared with early lepidosauromorphs and with the Squamata, and it is worth listing some of these as a guide to assessing which of the numerous fossil 'rhynchocephalians' are true sphenodontians (Figs 12B, 13D, 14D; Fig. 10Z).

Character list Z: Sphenodon

- (1) Lacrimal absent.
- (2) Parietals narrow and reduced to two nearly vertical back-to-back plates with ventro-lateral flanges that contact the supraoccipital.
- (3) Supratemporal absent.
- (4) Quadrate not emarginated.
- (5) Teeth acrodont.
- (6) One to three fused teeth on the premaxilla which are longer than the maxillary teeth and give a 'beaked' appearance to the skull.
- (7) Tiny juvenile teeth at the front of the maxilla and dentary.

(8) Tooth replacement occurs by addition at the back of the maxilla (as well as on the palatine and dentary).

(9) A single row of large teeth on the palatine which are separated from the maxillary teeth by a deep groove.

(10) The dentary teeth fit tightly into the maxilla-palatine groove and the propalinal jaw action polishes the teeth and bone in a uniform way.

(11) No teeth on the palate except for the palatine row. Occasional teeth on the vomer of *Sphenodon* have been noted (Howes, 1890).

(12) Splenial absent.

(13) Broad mandibular symphysis formed entirely by the dentary.

(14) Dentary runs well back, forming most of the lateral side of the lower jaw. It occupies nine-tenths of the length of the lower jaw measured to its most posterior point.

(15) Large mandibular foramen bounded by the dentary and the surangular.

In assessing the multitudes of fossil 'rhynchocephalians' listed by, for example, Romer (1966) and Kuhn (1969), it is soon evident that most of them are represented by insufficient material for a decision as to their status. A member of the Order Sphenodontia ought to possess a selection of the characters listed above. The possession of acrodont teeth alone is not enough to define a sphenodontian since this character is present in several lizards (e.g. *Uromastix*, *Agama*, *Chamaeleo*), amphisbaenians (*Trogonophis*), and some extinct captorhinids and procolophonids (Edmund, 1969).

Palacrodon from the early Triassic of S Africa is represented by a jaw fragment with six acrodont teeth. It could be a procolophonid, a lizard, or a sphenodontian (Malan, 1963: 214–215).

Brachyrhinodon from the late Triassic of Elgin, Scotland, was very small (c. 15 cm long), and it had a short-snouted skull with an apparent premaxillary beak. None of the sphenodontian characters listed above can be assessed—even the teeth are not visible (Huene, 1910, 1912). *Polysphenodon* from the late Triassic of Hannover, W Germany, also had a short snout, and multiple rows of teeth on the palate. It shows sphenodontian characters such as a groove between the maxilla and palatine for the dentary, and (?) absence of a lacrimal (Jaekel, 1911: 146; Huene, 1929: 44–47). *Elachistosuchus* from the latest Triassic of Halberstadt, E Germany, originally described as a thecodontian (Janensch, 1949), and reinterpreted as sphenodontian (Walker, 1966), apparently has acrodont teeth, no lacrimal, and other features of early sphenodontians. *Pachystropheus* from the latest Triassic of the Bristol area, England, and Germany, was identified as a 'rhynchocephalian' (E. von Huene, 1935) on the basis of the similarity of its vertebrae and ribs to *Champsosaurus*. The argument is not convincing. Two final late Triassic genera from the Bristol region, *Clevosaurus* (Swinton, 1939; Robinson, 1973, 1976) and *Planocephalosaurus* (Fraser, 1982), do share several diagnostic sphenodontid characters. However, they differ from *Sphenodon* in having teeth on the palate, a broad parietal, an emarginated quadrate, a retroarticular process, a broken lower temporal bar, and precision-shear bite. The late Triassic sphenodontians may fall into groups; such as short-snouted forms (*Brachyrhinodon*, *Polysphenodon*), and forms with a broken lower temporal bar (*Clevosaurus*, *Planocephalosaurus*); but a proper analysis cannot be made until these and later forms are better known.

Seven genera of late Jurassic sphenodontians may be mentioned here briefly.

Homoeosaurus and *Kallimodon* were small forms (less than 20 cm long) with small temporal fenestrae, broad parietals, partially fused astragalus and calcaneum, and antero-posteriorly elongated teeth that overlap (Cocude-Michel, 1963). *Opisthias*, known only from lower jaws, had *Sphenodon*-like teeth and a propalinal jaw action (Gilmore, 1909; Throckmorton *et al.*, 1981). Two deep-jawed forms with very wide grinding teeth (?herbivory)—*Eilenodon* and *Toxolophosaurus* (early Cretaceous; Rasmussen & Callison, 1981; Throckmorton *et al.*, 1981)—may form a further subgroup of sphenodontians, but they are known only from mandibles. *Monjurosuchus* (Endo, 1940; Huene, 1942: geological age uncertain) is hard to determine—even the descriptions are conflicting. It is almost certainly not a sphenodontian, and is left as Neodiapsida, *incertae sedis*. *Sapheosaurus* has several sphenodontian characters (Z1, 2, 3?, 12, 16), but it has no teeth, and so is hard to assign (Cocude-Michel, 1963).

CLASSIFICATION OF SOME UNCERTAIN FORMS

Several genera of Permo-Triassic diapsid reptiles that have not yet been discussed are hard to place taxonomically. These are: *Galesphyrus*, *Weigeltisaurus*, *Coelurosauravus*, *Claudiosaurus*, *Clarazia*, *Hescheleria*, *Askeptosaurus* and *Thalattosaurus*. As far as can be determined, the first four genera fall in the cladogram between *Petrolacosaurus* and the Neodiapsida, *Clarazia* and *Hescheleria* are hard to assign, and the last two genera are neodiapsids.

Galesphyridae

Galesphyrus, a small poorly preserved headless specimen from the *Cistecephalus* Zone of S Africa, has been classed as a younginid on the basis of its general resemblance to *Youngina* (Carroll, 1976b). However, it lacks the accessory intervertebral articulations and the high rectangular neural spines of younginiforms (Currie, 1981a: 509). Further, the characters of its tarsus and limbs (Brinkman, 1979; Currie, 1981c: 162) indicate that it is primitive. Of the characters that may be assessed, the type specimen of *Galesphyrus* shows the neodiapsid characters B14 (distal articular surface of femur level) and B15 (femur more than 10% longer than humerus). It is primitive with respect to all archosauromorph and lepidosauromorph apomorphies that may be observed. *Galesphyrus* is made a plesion of Neodiapsida until more material becomes available (Fig. 15).

Weigeltisauridae (= *Coelurosauravidae*)

Several specimens of gliding reptiles are known from the late Permian (*Weigeltisaurus* from the Kupferschiefer of Germany and the Marl Slate of England, and *Coelurosauravus* (= *Daedalosaurus*) from the Lower Sakamena Formation of SW Malagasy). These animals were small (30 cm long) and they had expanded dorsal ribs that presumably supported wing membranes. Their general adaptations were very similar to those of the late Triassic kuehneosaurids and the living lizard *Draco*, but they are clearly not lizards (Carroll, 1978; Evans, 1982).

The characters of the Weigeltisauridae are a mixture of apomorphies (e.g.

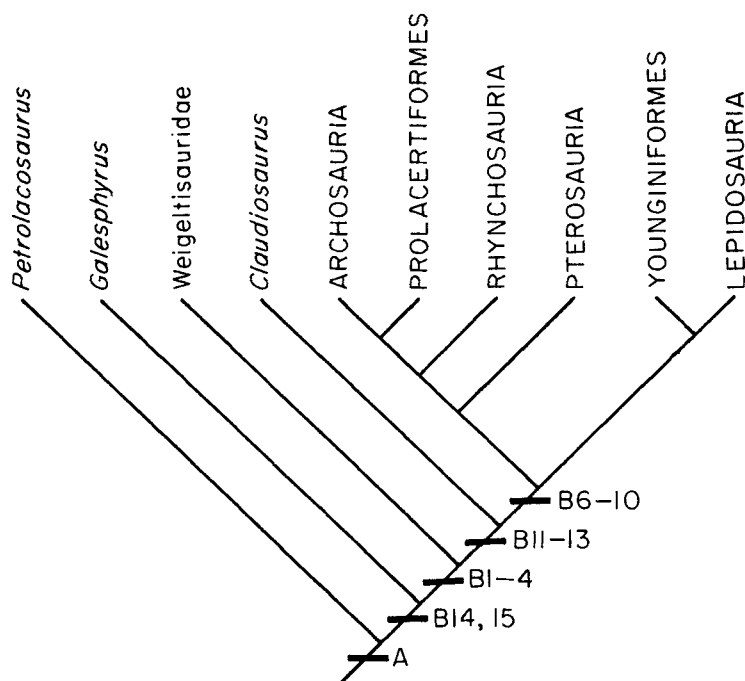


Figure 15. Cladogram representing the relationships of the main groups of the diapsids (summary of Figs 4, 9, 10), and some problematic forms. Synapomorphies are: A (see Fig. 4); B1, reduced lacrimal; 2, ventro-medial flanges on parietal; 3, absence of caniniform maxillary teeth; 4, reduced quadratojugal with short contact with squamosal; 5, quadrate not completely covered in side view; 6, quadrate notched posteriorly; 7, stapes slender; 8, reduction in numbers of teeth on pterygoid; 9, no teeth on parasphenoid; 10, retroarticular process developed; 11, ulna lacks well developed olecranon and sigmoid notch; 12, acetabulum rounded; 13, femur sigmoidal and slender; 14, distal articular surfaces on femur level; 15, femur more than 10% longer than humerus. Full details are given in the text.

pleurodont teeth, ornamented squamosal, incomplete lower temporal arcade, reduced quadratojugal, lacrimal small or absent, elongate jointed ribs, no dorsal intercentra) and diapsid plesiomorphies (e.g. large parietal foramen, ?presence of a cleithrum, solid puboischiadic plate, unfused astragalus and calcaneum, 4–5 distal tarsals, straight 5th metatarsal). The Weigeltisauridae, as far as can be seen, show some neodiapsid synapomorphies (B1–4, 14, 15), but are primitive with respect to others (B5, 6, 10(?), 11, 13). They are thus made a plesion of Neodiapsida just above *Galesphyrus* in the cladogram (Fig. 15).

The Claudiosauridae and the plesiosaurs

Claudiosaurus from the Lower Sakamena Formation of SW Malagasy has been described as a true sauropterygian with affinities to the younginids (Carroll, 1981). This 60 cm long animal had a small skull, a long neck, and paddle-like hands and feet, which suggest that it was a good swimmer.

Carroll's reasons for calling *Claudiosaurus* a plesiosaur ancestor seem to consist of general features of the skull (including the loss of the lower temporal bar) and the paddle-like hands and feet. He states (p. 380), "*Claudiosaurus* shows some

features that might be expected in any group beginning adaptation toward an aquatic way of life, but little that approaches the specifically nothosaurian pattern". Romer (1956: 660–662) gives a definition of the Nothosauria that consists of a mixture of primitive and derived characters. Of the derived characters, *Claudiosaurus* displays the following: premaxillae extend back between external nares, bones of palate broad, post-temporal fenestrae reduced, numerous gastralia, carpus and manus poorly ossified, broad hand. However, *Claudiosaurus* lacks many nothosaur synapomorphies, such as flattening of the skull with shift of the openings to the dorsal surface, reduction or loss of nasal bones, reduction in extent of parietals, closure of the palate so that the braincase is barely visible from below, increase in the number of cervical vertebrae (13–22 in nothosaurs; eight in *Claudiosaurus*), stout clavicles and reduced interclavicle with shoulder girdle elements forming a strong ventral 'circle', broad flattened short limb bones. Further study of the relationships of the nothosaurs and plesiosaurs is required before a definite conclusion can be reached, but *Claudiosaurus* cannot be convincingly assigned to the Sauropterygia. The question of the diapsid relationships of nothosaurs and plesiosaurs is, however, worth exploring.

Claudiosaurus displays all of the synapomorphies of the Diapsida (A1–4), and many of the neodiapsid synapomorphies (B1–4, 11–15). Of the characters not shared (B5–6, 8–10), the status of one is unknown (stapes), and the others display the primitive state. Thus, the quadrate in *Claudiosaurus* is largely covered by squamosal and quadratojugal in lateral view; the quadrate is not emarginated or notched; the pterygoid is covered with a shagreen of fine teeth; there are teeth on the parasphenoid; and there is no clear retroarticular process. *Claudiosaurus* lacks all archosauromorph synapomorphies (C1–14) and all lepidosauromorph synapomorphies (R1–6), as far as can be determined. The primitive features of *Claudiosaurus* suggest that the Claudiosauridae, like the Galesphyridae and the Weigeltisauridae, are to be located as a plesion on the diapsid line between *Petrolacosaurus* and the Neodiapsida (Fig. 15).

Claraziidae

The genera *Clarazia* and *Hescheleria* from the middle Triassic Grenzbitumen Zone of Monte San Giorgio, Switzerland, are normally tentatively placed in the 'Rhynchocephalia' (e.g. Hoffstetter, 1955; Romer, 1956, 1966; Kuhn, 1969) or even the Squamata (Huene, 1956) on the basis of their acrodont dentition and generalized 'lepidosaur' skeleton. The jaws are heavy, the teeth durapagous, the premaxilla overhangs, there are 30–32 presacral vertebrae, a long tail, reduced limb bones and large paddle-like hands and feet. The adaptations suggest an aquatic mollusc-eating existence. However, from the descriptions (Peyer, 1936a, b), it is not clearly established whether the skulls are diapsid or not. The postorbital and jugal of *Hescheleria* (Peyer, 1936b: 10) do appear to circumscribe an upper and lower temporal opening, but the identification and exact shape of these bones is not certain. *Clarazia* appears to have had a suborbital fenestra between the palatine and the lower border of the orbit (Peyer, 1936a: 7–8).

The limb girdles are not diagnostic and the limbs themselves could belong to any of several aquatic groups (short propodials with broad short epipodials,

poorly ossified carpus and tarsus, and broad hand and foot with fingers of similar lengths). If anything, the pelvis of both forms (Peyer, 1936a: 30–32; 1936b: 30–33) is sauropterygian, with the broad ventral elements, low acetabulum, and narrow rod-like ilium sloping backwards. At present, neither *Clarazia* nor *Hescheleria* can be identified more confidently than ?*Diapsida incertae sedis*.

Thalattosauridae

Askeptosaurus from the Grenzbitumen Zone (middle Triassic) of Monte San Giorgio, Switzerland (Kuhn, 1952; Kuhn-Schnyder, 1971) and *Thalattosaurus* from the Hosselkus Limestone (late Triassic) of California (Merriam, 1905) were large aquatic diapsids up to 2.5 m long. They are generally classed as 'Eosuchia' (Romer, 1956, 1966) or 'Rhynchocephalia' (Kuhn, 1969). These two genera share numerous synapomorphies such as an elongate snout; external nares placed far back and dorsally; the premaxillae elongate and meeting the frontals in the midline, separating the nasals; upper temporal fenestra slit-like or closed; lower temporal fenestra open below, or bounded by a weak lower temporal bar; occiput set well forward of the quadrates; recurved thecodont teeth; 13–14 cervical vertebrae; scapula and coracoid short and broad; clavicles expanded; thyroid fenestra in the pelvis; no posterior process on the ischium; limbs relatively small; no foramina in the humerus; phalangeal formula slightly reduced. Kuhn-Schnyder (1971) considered that *Askeptosaurus* was rather less closely related to *Thalattosaurus* than had been assumed—*Askeptosaurus* has no teeth on the vomer or pterygoid, the teeth are 'pleurothecodont', the neck is longer than that of *Thalattosaurus*, and the limbs are less paddle-like.

The thalattosaurs are clearly diapsids. They also belong within the Neodiapsida since they share all of the synapomorphies (B1–15). However, they cannot be placed with confidence in either the Archosauromorpha or Lepidosauromorpha. Several characters do indicate affinities with the archosauromorphs: the vertebrae are not notochordal, there is no entepicondylar foramen, the 5th distal tarsal is lost, the teeth are thecodont. Currie (1981c: 163) also suggested tentatively that thalattosaurs show closer relationships to the prolacertiforms than to the tangasaurids. Their status is left as Neodiapsida, *incertae sedis* for the present.

TAXONOMIC CONCLUSIONS

The present study of the relationships of the diapsids has produced a cladogram (Figs 4, 9, 10, 15) that is markedly different from the standard view of Romer (1966) and most subsequent authors. The main changes have consisted in a reassignment of several 'lepidosaur' groups, such as the Rhynchosauria and the Prolacertiformes, to the Archosauromorpha, and the removal of the Pterosauria from the Archosauria to an independent position within the Archosauromorpha. The cladogram must be translated into a classification. Some cladists (e.g. Hennig, 1966; Rosen, 1973; McKenna, 1975) have argued that a taxonomic hierarchy must be no more and no less than a direct equivalent of the relevant cladogram. However, I follow Cracraft (1974), Nelson (1974), Wiley (1976, 1981), Patterson & Rosen (1977) and others in

adopting an approach in which the classification is closely based on the cladogram, but is simplified by several conventions.

Within monophyletic groups, the taxa are listed in order of their sequence of branching, so that each is the sister-group of those below it (sequencing is described by Nelson, 1974 and Wiley, 1976, 1981). This technique avoids the necessity of naming and ranking every dichotomy. Further, redundant high rank names are not introduced for forms like *Petrolacosaurus*—the indented list system of Farris (1976) is used. In addition, the term plesion (Patterson & Rosen, 1977) is used to denote fossil forms in the stem-group of a monophyletic clade with living representatives, and their rank is indicated by their indented position. The designation *incertae sedis* is used several times, in different places and with qualifications, to indicate uncertainty about the assignment of certain genera and larger groups.

The major groups of the Diapsida are classified below with most emphasis on the Permo-Triassic forms. The only new names introduced are Neodiapsida and Lepidosauromorpha (Gauthier, 1983; Benton, 1983b). The names 'Eosuchia', 'Protorosauria', and 'Rhynchocephalia' have been dropped since they have become so wide in application. The Order Eosuchia was established by Broom (1914) to include *Youngina*, but so many odd forms have been added and removed over the years (cf. Huene, 1956; Romer, 1956, 1966; Kuhn, 1969; Evans, 1980) that the name cannot be restricted to a monophyletic group. The Order Protorosauria was used by Huxley (1871) to refer to *Protorosaurus* alone but, as with the 'Eosuchia', numerous early diapsids and other unrelated forms have been added so that its exact meaning is uncertain. Similarly, the Order Rhynchocephalia was named by Günther (1867) for *Sphenodon*, but rhynchosauroids were soon added, and then a whole range of other diapsids until the meaning of the name has become much altered. The classification of the Archosauria given below is provisional, and it includes some information based on additional work by Benton & Norman (in prep.).

Superseries Tetrapoda

Series Amphibia Latreille 1825 (Linnaeus 1758)

Series Amniota

Subseries Testudines Batsch 1788

Subseries Euplethia Olson 1947

Infraseries Synapsida Osborn 1903

Infraseries Diapsida Osborn 1903

Diapsida, *incertae sedis*

?†Family Claraziidae Peyer 1936

(†Family Champsosauridae Cope 1876)

(†Family Pleurosauridae Lydekker 1888)

plesion †Petrolacosauridae Peabody 1952 *Petrolacosaurus*

plesion †Galesphyridae Currie 1981 *Galesphyrus*

plesion †Weigeltisauridae Romer 1933

Weigeltisaurus, *Coelurosauravus*

plesion †Claudiosauridae Carroll 1981 *Claudiosaurus*

Superdivision **Neodiapsida nov.**

Neodiapsida, *incertae sedis*

†Family Heleosauridae Houghton 1924 *Heleosaurus*

†*Lacertulus*

†Family Kuehneosauridae Romer 1966

Kuehneosaurus, Kuehneosuchus, Icarosaurus

†Family Monjurosuchidae Endo 1940 *Monjurosuchus*

†Family Thalattosauridae Merriam 1904

Askeptosaurus, Thalattosaurus

Division Archosauromorpha Huene 1946

Archosauromorpha, *incertae sedis* †*Noteosuchus*

plesion †Pterosauria Owen 1840 (Kaup 1834)

plesion †Trilophosauridae Gregory 1945 *Trilophosaurus*

plesion †Rhynchosauria Osborn 1903 (Gervais 1859)

Suborder Mesosuchia Haughton 1924

Family Mesosuchidae Haughton 1924 *Mesosuchus*

Suborder Rhynchosauroidea Nopcsa 1928 (Gervais 1859)

Family Howesiidae Watson 1917 *Howesia*

Family Rhynchosauridae Huxley 1887 (Cope 1870)

Subfamily Rhynchosaurinae Nopcsa 1923

Stenaulorhynchus, Rhynchosaurus

Subfamily Hyperodapedontinae Chatterjee 1969

Hyperodapedon, Scaphonyx

plesion †Prolacertiformes Camp 1945

Prolacertiformes, *incertae sedis*

?*Cosesaurus, Malerisaurus*

Family Protorosauridae Baur 1889 (Cope 1871)

Protorosaurus

Family Prolacertidae Parrington 1935

Prolacerta, Macrocnemus, ?Boreopricea, ?Kadimakara

Family Tanystropheidae Romer 1945 (Gervais 1859)

Tanystropheus, Tanytrachelos

Incertae sedis (Prolacertiformes or Archosauria)

†Family Proterosuchidae Huene 1908

Chasmatosaurus, Proterosuchus, Chasmatosuchus, etc.

Subdivision Archosauria Cope 1869

plesion †Erythrosuchidae Watson 1917

Erythrosuchus, Vjushkovia, Garjainia, Shansisuchus, etc.

plesion †Proterochampsidae Romer 1966

plesion †Euparkeriidae Huene 1920 *Euparkeria*

Infradivision Neoarchosauria nov.

Cohort Suchia Krebs 1974

(includes most pseudosuchians, crocodiles)

Cohort Dinosauromorpha nov.

(includes ornithosuchids, dinosaurs, birds)

Division Lepidosauromorpha Benton 1983

Lepidosauromorpha, *incertae sedis*

†*Palaeagama, Paliguana, Blomosaurus, Kudnu,*

†*Colubrifer*

plesion †Younginiiformes Romer 1933

plesion †*Acerosodontosaurus*

Superfamily Younginoidea Currie 1982

	NORTH AMERICA	WESTERN EUROPE	EASTERN EUROPE	SE ASIA	SOUTH AMERICA	SOUTH AFRICA	EAST AFRICA	MALAGASY	INDIA	AUSTRALIA	ANTARCTICA
TRIASSIC	LOWER JURASSIC	South Wales/ Bristol fissures				Clarens F					
	RHAETIAN	Newark G			Las Coleradas	Elliot F					
	UPPER	Chinle F	Knollenmergel		Ischigualasto				Maleri F		
		Dockum G	Lössiemerel		Santa Maria F						
	CARNIAN	Hoselkus Lst									
	LADINIAN		Bromsgrove Sst F, etc	Sol'iletsk Ser Z VII							
	ANISIAN		Grenzbitumen Z				Manda F		Yerrapalli F		
	LOWER			Ehrmayin Ser							
				Baskunchak Ser Z VI		Cynognathus Z					
	SCYTHIAN			Vetluga Ser Z V		Lystrosaurus M Z			Panchet F	Rewan F	Fremouw F
PERMIAN	TATARIAN			Tatarian Ser Z IV							
	KAZANIAN										
	UPPER		Kupferschiefer /Mari Slate						L. Sakamena F		
						Daplocephalus Z					
UPPER CARBONIFEROUS	LOWER										
	UPPER	Conemaugh Ser									

Figure 16. The major reptile-bearing formations of the Permo-Triassic that have yielded diapsids. Stratigraphic assignments are based on Anderson & Cruickshank (1978), Tucker & Benton (1982), Benton (1983a) and Cruickshank (pers. comm.). The Rhaetian is tentatively retained as a stage between the Norian and the Hettangian (Lower Jurassic). Abbreviations: F, Formation; G, Group; L, Lower; Lst, Limestone; M, Middle; Ser, Series; Sst, Sandstone; U, Upper; Z, Zone.

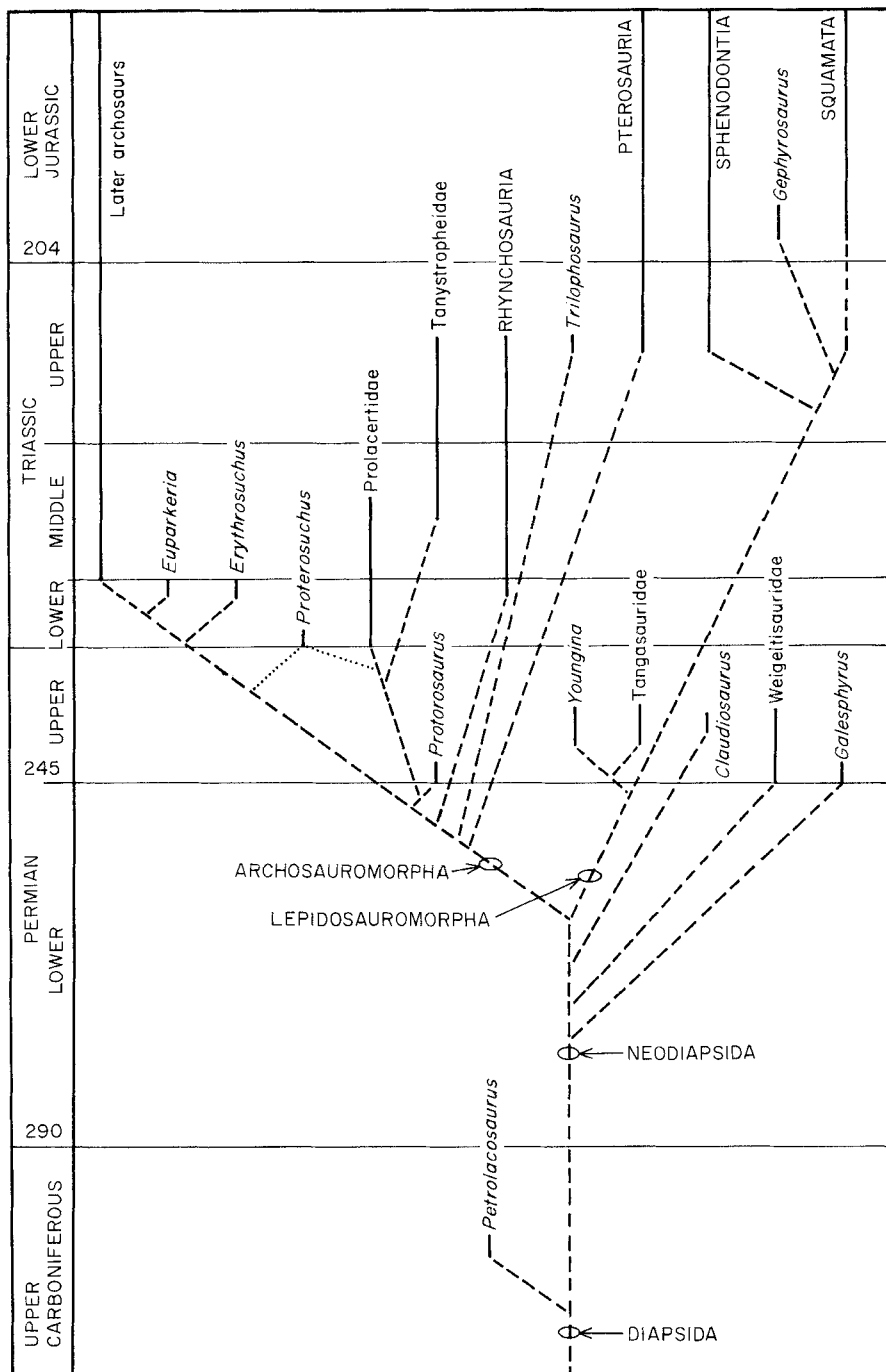


Figure 17. Phylogenetic tree of the Permo-Triassic diapsid reptiles. Data on relationships are taken from the cladograms (Figs 4, 9, 10, 15). Stratigraphic information is from Anderson & Cruickshank (1978), Tucker & Benton (1982) and Benton (1983a) and age dates from Odin (1982). The known stratigraphic ranges of families and genera are shown with solid lines; conjectured ancestor-descendant relationships are shown by dashed lines. *Protorosuchus* could fit in two places.

- Family Younginidae Broom 1914 *Youngina*
- Family Tangasauridae Camp 1945 (Piveteau 1926)
 - Subfamily Kenyasaurinae Currie 1982
 - Kenyasaurus*, *Thadeosaurus*
 - Subfamily Tangasaurinae Piveteau 1926
 - Tangasaurus*, *Hovasaurus*
- Subdivision †Saurosternidae Haughton 1924 *Saurosternon*
- Subdivision Lepidosauria Haeckel 1866 (Duméril & Bibron 1839)
 - Order Sphenodontia Williston 1925
 - Family Sphenodontidae Cope 1870
 - Sphenodon*, *Brachyrhinodon*, *Clevosaurus*, *Homoeosaurus*, *Toxolophosaurus*, etc.
 - ?Family Sapheosauridae Bau 1895 *Sapheosaurus*
 - Subdivision †Gephyrosauridae Evans 1980
 - Gephyrosaurus*
- Order Squamata Oppel 1811
 - (Suborder Sauria Macartney 1802)
 - (Suborder Amphisbaenia Gray 1844)
 - (Suborder Serpentes Linnaeus 1758)

PHYLOGENY OF THE EARLY DIAPSID

The evolution of the early diapsids may be represented in the form of a tree. This involves the input of stratigraphic and taxonomic information. The stratigraphy of the Permo-Triassic reptile beds that have yielded diapsids is summarized in Fig. 16 (data from Anderson & Cruickshank, 1978; Tucker & Benton, 1982; Benton, 1983a). A phylogenetic tree is presented (Fig. 17) with the major genera and families of early diapsids indicated in correct time relation and with their taxonomic assignments as proposed in this paper.

Evolutionary scenarios that are based on this phylogeny are given in Tucker & Benton (1982) and Benton (1983a, 1984). The first two papers concentrate on the rise of the thecodontians and dinosaurs, with statistics for all well-known late Permian and Triassic faunas. The third paper describes the succession of adaptive radiations of Permo-Triassic diapsids: the mid to late Permian lepidosauromorphs and archosauromorphs, the early Triassic thecodontians and 'paliguanids', the middle Triassic thecodontians, prolacertiforms and rhynchosaurs, and the late Triassic thecodontians, dinosaurs, crocodiles, squamates, sphenodontians and pterosaurs.

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NOTE ADDED IN PROOF

Four recent papers add significant data to the present paper. Reisz *et al.* (1984) confirm that *Araucoscelis* is a diapsid, and they classify it as the sister-group of *Petrolacosaurus*. Benton (1984) summarizes the results of a number of recent preliminary analyses of the relationships of archosaurs. Padian (1983) regards the pterosaurs as archosaurs, and classifies them as a sister-group of the Dinosauria. Finally, Evans (1984) reviews the classification of the lepidosauromorphs, and offers details of the relationships of 'paliguonids', kuehneosaurids, *Gephyrosaurus* and Squamata.

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