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A reevaluation of early amniote phylogeny

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A new phylogenetic analysis of early amniotes based on 124 characters and 13 taxa (including three outgroups) indicates that synapsids are the sister-group of all other known amniotes. The sister-group of Synapsida is Sauropsida, including Mesosauridae and Reptilia as its two main subdivisions. Reptilia is divided into Parareptilia and Eureptilia. Parareptilia includes Testudines and its fossil relatives (Procolophonidae, Pareiasauria and Millerettidae), while Eureptilia includes Diapsida and its fossil relatives (*Paleothyris* and Captorhinidae). Parts of the phylogeny are robust, such as the sister-group relationship between procolophonids and testudines, and between pareiasaurs and the testudinomorphs (the clade including procolophonids and testudines). Other parts of the new tree are not so firmly established, such as the position of mesosaurs as the sister-group of reptiles. The new phylogeny indicates that three major clades of amniotes extend from the present to the Palaeozoic. These three clades are the Synapsida (including Mammalia), Parareptilia (including Testudines), and Eureptilia (including Sauria). In addition, the Procolophonidae, a group of Triassic parareptiles, are the sister-group of Testudines.

ADDITIONAL KEY WORDS:—Amniota – Sauropsida – Mesosauridae – Reptilia – Parareptilia – Eureptilia – Testudines – phylogenetics – evolution – Palaeozoic.

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* The order in which the names appear is alphabetical; no priority of authorship is implied.

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INTRODUCTION

Amniotes are by far the most successful and diverse vertebrates. Their present diversity encompasses thousands of species of mammals, testudines and diapsids that have occupied most major environments. Amniotes are also well represented in the fossil record, and the origins of modern groups can be traced at least to the Triassic and, in most cases, to the Pennsylvanian (Reisz, 1981, 1986; Reisz & Laurin, 1991). Because of this great diversity and rich fossil record, amniote phylogeny has been extensively studied and the interrelationships within the major groups of early amniotes are well understood. The origin of diapsids from within eureptiles is fairly well supported (Gauthier, Estes & de Queiroz, 1988a; Reisz, 1981), and their early evolution has been studied extensively (Benton, 1985; Carroll & Currie, 1991; Evans, 1988; Gauthier, 1984; Gauthier *et al.*, 1988a; Laurin, 1991; Rieppel, 1993a). The similarities between the published phylogenies indicate that a consensus exists on the broadest outlines of diapsid history. Similarly, the evolution of early synapsids is well understood (Laurin, 1993; Reisz, 1986). Testudine phylogeny has also been studied extensively (Gaffney, 1975a; Gaffney & Meylan, 1988; Gaffney, Meylan & Wyss, 1991), although turtle origins have been poorly understood.

In spite of early incorrect assignment of certain microsaurs to the Reptilia (Carroll & Gaskill, 1978) and previous debates about the taxonomic position of seymouriamorphs (White, 1939), there is now a broad consensus about the composition of the Amniota. This taxon is generally defined as a crown-group bounded by synapsids, testudines and diapsids (Gauthier, Kluge & Rowe, 1988b). In addition to these extant groups, the Amniota is believed to include mesosaurs, millerettids, pareiasaurs, procolophonids, captorhinids and ‘protorothyridids’, and a few other early and poorly understood tetrapods. Their closest relatives are believed to be diadectomorphs (Gauthier *et al.*, 1988b). However, Berman, Sumida & Lombard (1992) suggested as an alternative hypothesis that diadectomorphs were the sister-group of synapsids and that they should perhaps be included in the Amniota. However, Berman *et al.* (1992) based their conclusions on an analysis of only nine osteological characters scored onto seven taxa, including the outgroup. The characters used by Berman *et al.* (1992) have been included in our matrix to test their hypothesis.

Despite extensive phylogenetic studies (Baur, 1887; Gregory, 1946; Osborn, 1903), the relationships between many groups of early amniotes are still poorly understood (Gauthier *et al.*, 1988b). In the last three decades, several papers have discussed amniote phylogeny (Carroll, 1969, 1982; Clark & Carroll, 1973; Gaffney, 1980; Heaton & Reisz, 1986), but an extensive analysis was not published until Gauthier *et al.* (1988b) performed the first large-scale, computer-assisted cladistic analysis of early amniotes.

Carroll has been an influential, although somewhat conservative, student of amniote phylogeny. Carroll (1969) argued that *Paleothyris* and its presumed relatives (then known as 'romeriids') were ancestral to most other amniotes. He believed that captorhinids, mesosaurs, *Bolosaurus* and synapsids were derived from early, still unknown 'romeriids', and he held this view in all his subsequent discussions of amniote phylogeny (Carroll, 1982, 1988, 1991; Clark & Carroll, 1973). He also expanded his theory (Carroll, 1982) by including poorly known taxa such as pareiasaurs, millerettids, and procolophonids as having been independently derived from within the 'Protorothyrididae' (Carroll refers to this group as the Protorothyridae for aesthetic reasons). This last taxon replaced the Romeriidae when it was discovered that *Romeria* was a captorhinid, and currently includes *Paleothyris, Hylonomus, Cephalerpeton, Brouffia, Coelostegus* and *Protorothyris* (Reisz, 1980a). However, Carroll's (1982, 1991) phylogeny of amniotes was based on non-cladistic arguments and is no longer accepted by the majority of the palaeontological community (Gauthier *et al.*, 1988b).

In their detailed analysis of amniote relationships, Gauthier *et al.* (1988b) suggested that synapsids were the sister-group of all other amniotes (Fig. 1). Testudines, diapsids and their presumed fossil relatives (captorhinids and *Paleothyris*) were classified in the Reptilia (Fig. 1) and defined as a crown-group. Gauthier *et al.* (1988b) suggested that mesosaurs, procolophonids, millerettids, and pareiasaurs formed a clade of extinct amniotes that they collectively called parareptiles, thus resurrecting Olson's (1947) terminology. However, a major pitfall of their analysis was that the authors did not have the opportunity to

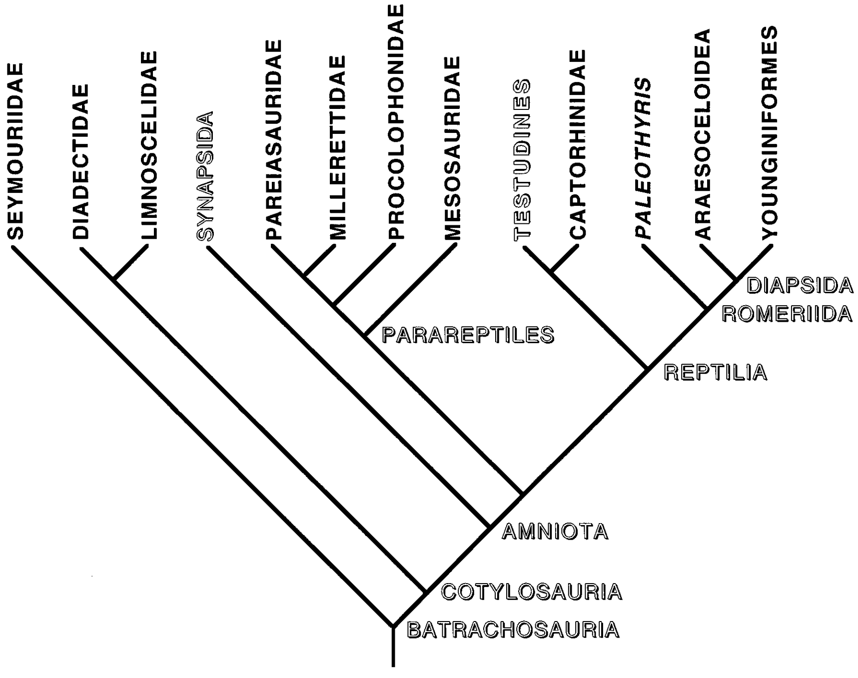

Figure 1. Amniote phylogeny according to Gauthier *et al.* (1988b). In this tree, parareptiles are an extinct taxon.

restudy many of the relevant taxa and were forced to rely heavily on outdated and inadequate descriptions. To their credit, Gauthier *et al.* (1988b) admitted that they had little faith in their parareptile clade. Their work represents a major breakthrough in studies of amniote phylogeny because it was the first large-scale cladistic analysis of early amniotes, and partly because it was the only phylogeny of early amniotes supported by a large data matrix that was analysed by computer. Publication of the data matrix allowed others to evaluate objectively the conclusions reached by Gauthier *et al.* and to focus on potential weaknesses of this phylogeny.

The origin of turtles has been probably the most controversial and most poorly documented problem in amniote phylogeny. Its solution has eluded palaeontologists for decades, and few detailed arguments have been put forward to link testudines with any group of early amniotes (Gregory, 1946; Lee, 1993; Reisz & Laurin, 1991). Around the turn of the century, palaeontologists suggested that turtles were related to diadectids, sauropterygians (which then included placodonts) and cotylosaurs (then considered to have included *Seymouria*, diadectomorphs, pareiasaurs, procolophonids, and captorhinids, or various combinations of these taxa). Gregory (1946) reviewed these studies and went further in comparing testudines with diadectids, placodonts, captorhinomorphs, and pareiasaurs. He believed that diadectids were not closely related to testudines because they had highly specialized jaws and dentitions while lacking a bony carapace and plastron. Similarly, he rejected the possibility of close affinities between placodonts or captorhinomorphs and testudines. He believed that placodonts could not be ancestral to turtles because they were more specialized than early testudines. Furthermore, he showed that early suggestions of affinities between placodonts and testudines were based on misleading comparisons between modern testudines and late placodonts. According to Gregory, early testudines were much more primitive and less similar to placodonts than modern turtles were. In addition, early placodonts were less similar to testudines and displayed more similarities with nothosaurs than with turtles. Gregory (1946) finally argued that pareiasaurs were closely related to testudines because of similarities in the skull, vertebrae, ribs, girdles, and appendicular skeleton. Gregory's characters included a mixture of primitive and derived traits, but several of them were quite convincing. For instance, he noticed that testudines and pareiasaurs both have dermal armour, a high and narrow scapula bearing an acromion, a reduced phalangeal formula in manus and pes, and strong, blunt claws. Gregory's (1946) review of turtle origins was extremely perceptive and convincing. Unfortunately, most later students of amniote phylogeny did not accept its conclusions.

Clark & Carroll (1973) argued that testudines were derived from captorhinids because captorhinids retain an anapsid skull, because turtles and captorhinids have large post-temporal fossae separated by a narrow supraoccipital, and because the paroccipital process was thought to be braced against the squamosal in both groups. These arguments have been largely rejected since then. The anapsid skull is a primitive character. The large post-temporal fossa is found in all reptiles (as defined below). The supraoccipital is narrow in all reptiles, and is even narrower in pareiasaurs, procolophonids and testudines than in captorhinids. Finally, the connection between the paroccipital process and the cheek is a problematic character for several reasons. In testudines, the paroccipital is sutured solidly against the quadrate and the squamosal whereas in captorhinids it ends freely, medial to the squamosal, and would have been braced against it through a cartilaginous extension. This configuration is not especially reminiscent of testudines and is found in captorhinids, *Paleothyris* and diapsids. Despite these problems, the conclusion that captorhinids were the closest known relatives of testudines was accepted by most subsequent workers (Gaffney & Meylan, 1988; Gaffney *et al.*, 1991; Gauthier *et al.*, 1988b). However, Gaffney & Meylan (1988) and Gauthier *et al.* (1988b) used none of the characters proposed by Clark & Carroll (1973). They believed that captorhinids were related to testudines because both groups lack a tabular and an ectopterygoid, and both taxa have an alary process of the jugal and an orbitonasal foramen.

Our understanding of the origin of turtles drastically changed with the suggestion by Reisz & Laurin (1991) that testudines were closely related to procolophonids. This study, based on a preliminary analysis of the data found below, showed that turtles were more closely related to procolophonids than to captorhinids. Because of this, some characters found in pareiasaurs and even millerettids, in addition to characters unique to testudines and procolophonids, were discussed.

More recently, Lee (1993) proposed that pareiasaurs were the closest known relatives of testudines. According to Lee, *Sclerosaurus*, Procolophonoidae and Nyctiphruretida are successively more remote relatives of the Pareiasauridae and Chelonia. Lee (1993) discussed briefly the thesis that procolophonids are the sister-group of turtles, but he dismissed most of the characters used by Reisz & Laurin (1991). Lee used 16 characters to support his claim that pareiasaurids are the closest known relatives of testudines and nine others to link *Sclerosaurus* to pareiasaurs and turtles. Several of his characters were initially suggested by Gregory (1946) in linking pareiasaurs to testudines. Lee's characters were incorporated into the present analysis.

The origin of turtles had eluded generations of palaeontologists largely because parareptile anatomy and phylogeny were poorly understood. The location of the best specimens of parareptiles in Eastern Europe and South Africa has hampered comparisons with the rich North American and Western European fauna of Palaeozoic tetrapods. Few scientists have had the opportunity to study North American, Eastern European, and South African specimens of early amniotes. We have tried to improve on this by travelling to various institutions housing many of the materials and preparing several parareptile specimens (R. Reisz went to Russia and South Africa to study early parareptiles). R. Reisz also borrowed two juvenile specimens of the pareiasaur *Deltavjatia vjatkensis.* Most sutures were clear in these two specimens, whereas they are often obscured by extensive fusion in adult pareiasaurs. The study of *Seymouria*, the dissertation topic for M. Laurin, has helped with the polarization of many previously problematic characters. Furthermore, our analysis was greatly strengthened by a wealth of data on the postcranial anatomy of procolophonids and mesosaurids generously provided by Michael deBraga and Sean P. Modesto, respectively.

METHODS

The phylogeny discussed below is based on an analysis of a matrix comprising 13 taxa (including outgroups) and 124 characters. Some of the characters used in this phylogenetic analysis (see Appendix 1) come from Gauthier *et al.* (1988b) and a few come from Lee (1993) and Berman *et al.* (1992). All the characters were recoded by studying specimens and the literature. In addition, new characters were added, and those found to be invariant in the taxa subject to this analysis were deleted.

Most of the taxa included in the analysis of Gauthier *et al.* (1988b) are also included in this analysis. We reconstructed a primitive morphotype for Synapsida on the basis of previous work on this group (see Appendix 2), instead of coding all variations occurring in the clade, as Gauthier *et al.* (1988b) did. Thus, the condition present in eothyridids, caseids, varanopseids, and ophiacodontids was used to establish the primitive condition for synapsids. The phylogeny suggested by Reisz (1986) was used to optimize the states present in the four most basal families on a tree of the Synapsida. The condition at the ingroup node was then considered to be primitive for synapsids. However, this difference is of no consequence because when more than one state was present in a particular taxon, Gauthier *et al.* (1988b) considered the state 0 as ancestral for that taxon. This approach was necessary because only one state could be coded per character and per taxon in PAUP 2.3.

Instead of including an ill-defined and possibly paraphyletic Procolophonoidea as a terminal taxon, we have included the Procolophonidae. The latter is restricted to *Procolophon, Hypsognathus* and other closely related procolophonids. Thus defined, the Procolophonidae excludes early ‘procolophonoids’ such as *Nyctiphruretus, Nycteroleter, Macroleter, Barasaurus* and *Owenetta. Owenetta* was excluded from this analysis because, while coding an early version of this matrix, it became apparent that it was quite different from the more mature, better known specimens of *Procolophon* and *Hypsognathus*. Further, Michael deBraga is working on a detailed phylogeny of parareptiles that will clarify the relationships of procolophonoids, including *Owenetta*. The Sauria is replaced by the Younginiformes in this analysis; Laurin (1991) demonstrated that younginiforms are the sister-group of saurians, whereas they were formerly thought to be closely related to lepidosaurs, and as such, to be saurians (Benton, 1985; Evans, 1988; Gauthier *et al*., 1988a). The composition of other terminal taxa included in our analysis (see Appendix 2) follows the current taxonomy. For taxa other than Synapsida, no internal relationships were postulated and all the variations occurring within the terminal taxa were noted and coded as polymorphism when two or more states were present. This procedure was necessary because the phylogeny of most of these taxa (such as Captorhinidae, Procolophonidae and Pareiasauria) is poorly understood.

All the characters were equally weighted, and reversals were considered to be as probable as convergence. Character optimization was performed using the delayed transformation (DELTRAN) algorithm of PAUP 3.1 (Swofford, 1993). Character polarity was determined by comparison with the outgroup (*Seymouria*). The resultant data matrix was subjected to the branch and bound algorithm of PAUP 3.1, which guarantees to find all the most parsimonious trees.

A few characters were ordered in this study (Appendix 1). The controversy over whether multi-state characters should be ordered or left unordered is not settled. Some have argued against the use of ordered characters (Hauser & Presch, 1991; Mabee, 1989), while others have argued that characters should be ordered when possible (Mickevich & Lipscomb, 1991; Slowinski, 1993). We have used a mixed approach. All multi-state characters exhibiting what seemed to be a morphocline were mapped on the shortest tree (found with unordered characters only) using MacClade 3.0 (Maddison & Maddison, 1992). When the optimization of the character supported the existence of a morphocline, the character was ordered. Support for the morphocline required that all state transformations for the relevant character be compatible with the morphocline. If a single transformation was ambiguous, the character was not ordered. This procedure allowed us to order six characters (Appendix 1). Because of our procedure, none of our conclusions would be altered if all the characters were unordered. This procedure may be useful to reveal the existence of morphoclines and test evolutionary trends.

RESULTS

Only one tree was found (Fig. 2); it requires 323 steps and has an overall consistency index of 0.669 and a consistency index excluding uninformative characters (i.e. unique autapomorphies) of 0.569.

The tree topology differs substantially from the cladogram obtained by Gauthier *et al.* (1988b). A revised taxonomy including new definitions and lists of synapomorphies and autapomorphies, based only on the characters used in this analysis, is given below. Whenever possible, the taxonomy of amniotes and their relatives was left unaltered. Therefore, the new definition of the Batrachosauria and Cotylosauria approximates that used by Gauthier *et al.* (1988b). In this study, the Batrachosauria is the clade including the last common

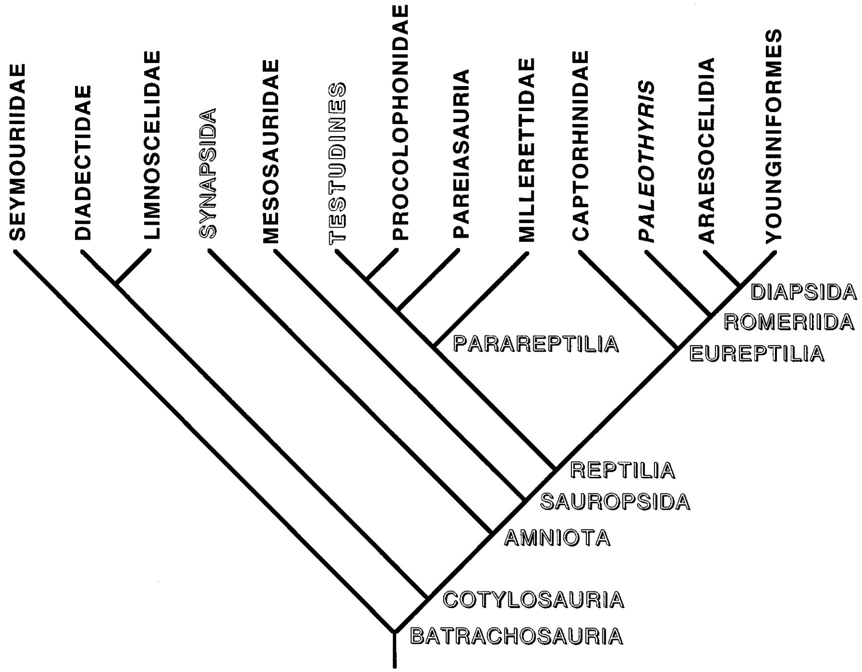

Figure 2. Amniote phylogeny used in this study. In this phylogeny, Parareptilia include Testudines. Taxa with extant members are in bold, outline font.

ancestor of *Seymouria* and amniotes, and all its descendants. The Cotylosauria is the taxon including the last common ancestor of *Limnoscelis, Tseajaia, Diadectes* and amniotes, and all its descendants. This analysis supports the monophyly of Diadectomorpha and its position as sister-group of Amniota (see Discussion).

AMNIOTE TAXONOMY

The new hypothesis of amniote phylogeny proposed here (Fig. 2) can be summarized by the following indented classification:

- Cotylosauria Cope 1880
  - Diadectomorpha Watson 1917
  - Amniota Haeckel 1866
    - Synapsida Osborn 1903
    - Sauropsida Huxley 1864
      - Mesosauridae Baur 1889
      - Reptilia Linnaeus 1758
        - Parareptilia Olson 1947
          - Millerettidae Watson 1957
          - Procolophonia Seeley 1888
            - Pareiasauria Seeley 1888
            - Testudinomorpha, new taxon
              - Procolophonidae Lydekker 1890
              - Testudines Linnaeus 1758
        - Eureptilia Olson 1947
          - Captorhinidae Case 1911
          - Romeriida Gauthier, Kluge & Rowe 1988
            - *Paleothyris* Carroll 1969
            - Diapsida Osborn 1903
              - Araeoscelidia Williston 1913
              - Younginiformes Romer 1945

To avoid taxonomic clutter, new names were avoided whenever possible. Widely used taxa are bounded by extant members, to ensure maximum stability of their content and diagnosis; therefore, the Amniota and the Reptilia are defined as crown-groups (see below). The character numbers given below correspond to the numbers in the appendices 1 to 3. Characters marked by an asterisk are ambiguous and could apply at other levels. Negative signs indicate reversals. When the derived condition is not 1 but rather 2, 3 or a higher number, the number is indicated in parentheses. Reversals to conditions other than 0 are also identified by a number in parentheses. A reversal is here defined as any transition to a state of lower numerical value than the state present at the next most inclusive node. In the character discussions, the primitive state and its distribution are described immediately after the character name is given. The derived state that defines the clade and its distribution follow the primitive condition. The state numbers are also given in parentheses in the character descriptions. Each character is only discussed once, where it first appears in the discussion (usually in the most basal or inclusive node). Subsequent change in the same character is briefly noted and the reader is referred to the complete character description.

Cotylosauria Cope 1880

Definition. The most recent common ancestor of diadectomorphs and synapsids, and all its descendants. Therefore, Cotylosauria is now a large, monophyletic group. Its synapomorphies need not be discussed here.

Cope (1880) erected the Cotylosauria for diadectids, but subsequent authors have used this nomen in a more inclusive manner. In addition to diadectids, Case (1911) included *Bolosaurus,* pareiasaurs, captorhinids, *Seymouria,* procolophonids and *Pantylus* into the Cotylosauria. At the time, *Seymouria* was thought to be the most primitive amniote and *Pantylus* was believed to be an early reptile. Therefore, Cotylosauria included the earliest, basal, anapsid amniotes and their closest relatives. This concept of Cotylosauria was widely accepted and remained in use into the sixties (Romer, 1966). Our definition of Cotylosauria as a monophyletic group includes all amniotes, but remains similar to established usage. The main difference consists in the exclusion of seymouriamorphs.

Diadectomorpha Watson 1917

Definition. The last common ancestor of diadectids, limnoscelids, *Tseajaia,* and all its descendants.

Watson (1917) erected the Diadectomorpha for diadectids, pareiasaurs and procolophonids. Subsequently, limnoscelids were shown to be closely related to diadectids, while pareiasaurs and procolophonids were included into the Amniota.

Diadectomorphs are united by the following synapomorphies:

4 Postparietal median (Figs 3–5). *Seymouria* and all amniotes, except testudinomorphs and some pareiasaurs, have a paired postparietal (0). Diadectomorphs have a single, median postparietal (1). Testudinomorphs lack a postparietal (2).

23* Quadratojugal not reaching level of orbit (Fig. 6). The quadratojugal of pareiasaurs, procolophonids, mesosaurs, some synapsids and *Seymouria* extends anteriorly at least to the level of the posterior edge of the orbit (0). This condition may be primitive for cotylosaurs. The quadratojugal of diadectomorphs is shorter and fails to extend to the level of the orbit (1). The polarity of this character is difficult to assess because the quadratojugal of testudines, millerettids, most eureptiles and some synapsids is also short (1). Therefore, this character could also be primitive for batrachosaurs.

27*(3) Occipital flange of squamosal absent. In *Seymouria*, an otic flange of the squamosal defines the otic notch and lines the tympanic cavity (0), while a ventromedial flange overlaps the ventrolateral surface of the quadrate ramus of the pterygoid (personal observation; some of these structures are visible in White, 1939: figs 1, 2, and 5). In synapsids, mesosaurs and most eureptiles, the squamosal wraps around the posterior surface of the quadrate (1) and forms a gently convex flange that defines the posterolateral edge of the skull (Fig. 5). Either of these states may be primitive for cotylosaurs, and the latter is certainly primitive for amniotes. In diadectomorphs, the squamosal is bordered posteriorly either by the quadratojugal and the tabular (in limnoscelids) or by the quadrate (in diadectids); the squamosal has no occipital flange (3) in these taxa (Fig. 5). This condition (3) may be an autapomorphy of diadectomorphs, but it may also be primitive for cotylosaurs. Younginiforms convergently lost the occipital

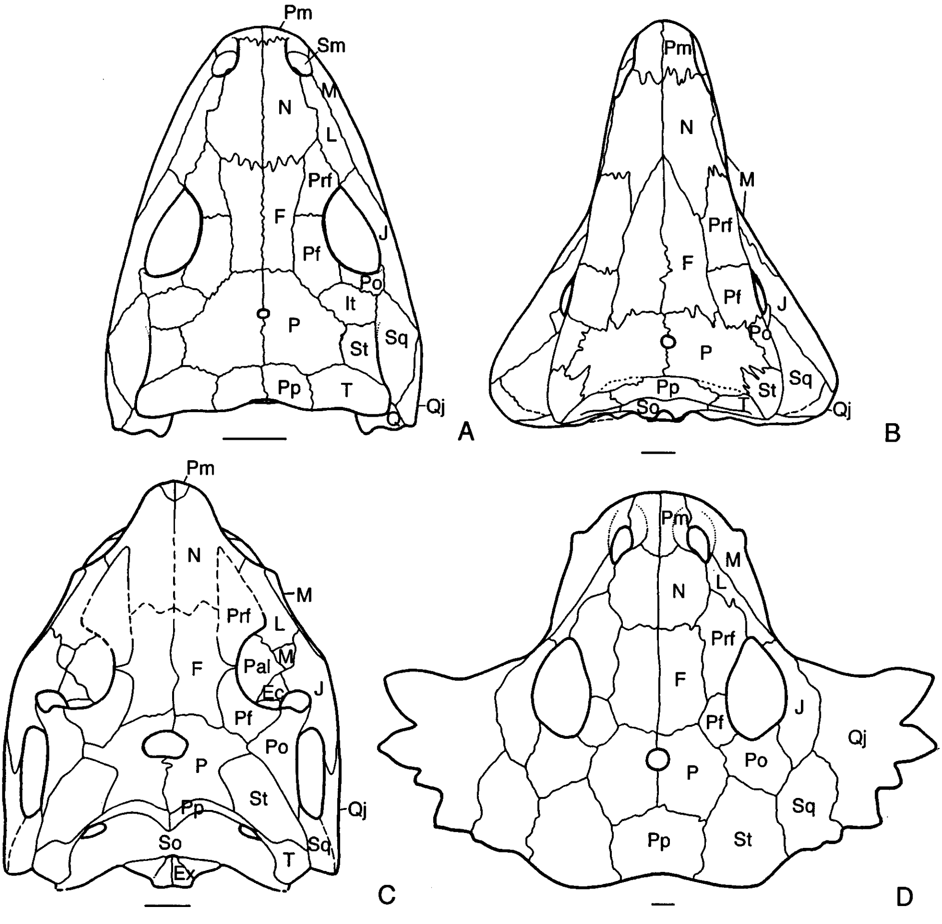

Figure 3. Skulls of batrachosaurs in dorsal view. A, *Seymouria*. B, *Limnoscelis*. C, *Cotylorhynchus*. D, *Scutosaurus*. B was redrawn from Fracasso (1983) and Berman *et al.* (1992). D was redrawn from Ivachnenko (1987). Scale bars = 1 cm.

flange (3). The evolution of the squamosal is complex in parareptiles. The occipital flange is convex above the quadrate emargination and concave medial to the tympanic ridge in millerettids (Watson, 1957: figs 13, 14) (2). The occipital flange of pareiasaurs is anteromedial to a posterolateral ridge and faces posteromedially (4). The occipital flange of the squamosal of testudinomorphs is located in the temporal emargination and is concave (5). In procolophonids, the flange is large, faces posterolaterally and lines most of the temporal emargination (Carroll & Lindsay, 1985: figs 1, 3 and 5). In testudines, the occipital flange is smaller (although it is fairly large in *Proganochelys*) and restricted to the dorsal portion of the emargination. Conditions 2, 4, or 5 could be primitive for parareptiles.

58 Otic trough in ventral flange of opisthotic. In *Seymouria*, reptiles (Heaton, 1979: fig. 27) and some synapsids, the opisthotic is flat or convex posterior to the fenestra ovalis and lacks a distinct ventral projection (0). In diadectomorphs, the opisthotic has a distinct, concave ventral flange posterior

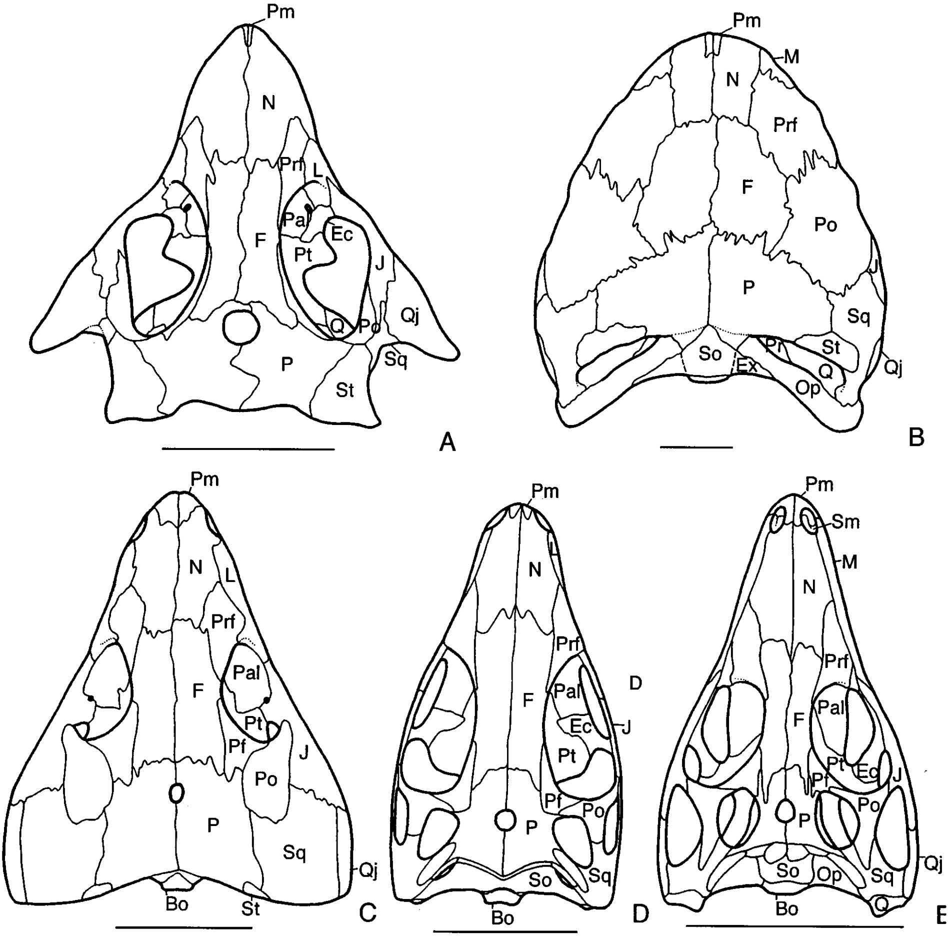

Figure 4. Skulls of reptiles in dorsal view. A, *Procolophon*. B, *Proganochelys*. C, *Captorhinus*. D, *Petrolacosaurus*. E, *Youngina*. A was redrawn from Carrol & Lindsay (1985), B from Gaffney (1990), C from Heaton (1979), D from Reisz (1981), and E from Carroll (1981). Scale bars = 1 cm.

to the fenestra ovalis (1). Some synapsids seem to have convergently acquired an otic trough (Reisz, Berman & Scott, 1992: fig. 13).

84 Axial intercentrum with strong anterior process. In *Seymouria* (Berman, Reisz & Eberth, 1987: fig. 9F) and amniotes, the axial intercentrum has a gently rounded anterior margin (0). In diadectomorphs (Sumida & Lombard, 1991: figs 2–16) the axial intercentrum has a strong anteroventral process (1).

104 Humerus short and robust, without a shaft. The humerus of *Seymouria*, synapsids (Reisz, 1986: fig. 24), most parareptiles, captorhinids and younginiforms has robust heads between which extends a short but distinct shaft (and the distal head width/humeral length ratio is between 35% and 65%) (0). The humerus of diadectomorphs (Berman & Sumida, 1990: fig. 12) has two robust heads that merge into each other without a discrete shaft between them (and the distal head width/humeral length ratio is over 65%) (1). Pareiasaurs convergently acquired a similar condition (1). The humerus of mesosaurs, *Paleothyris* (Carroll, 1969: fig. 2) and araeoscelidians is slender (the width of its

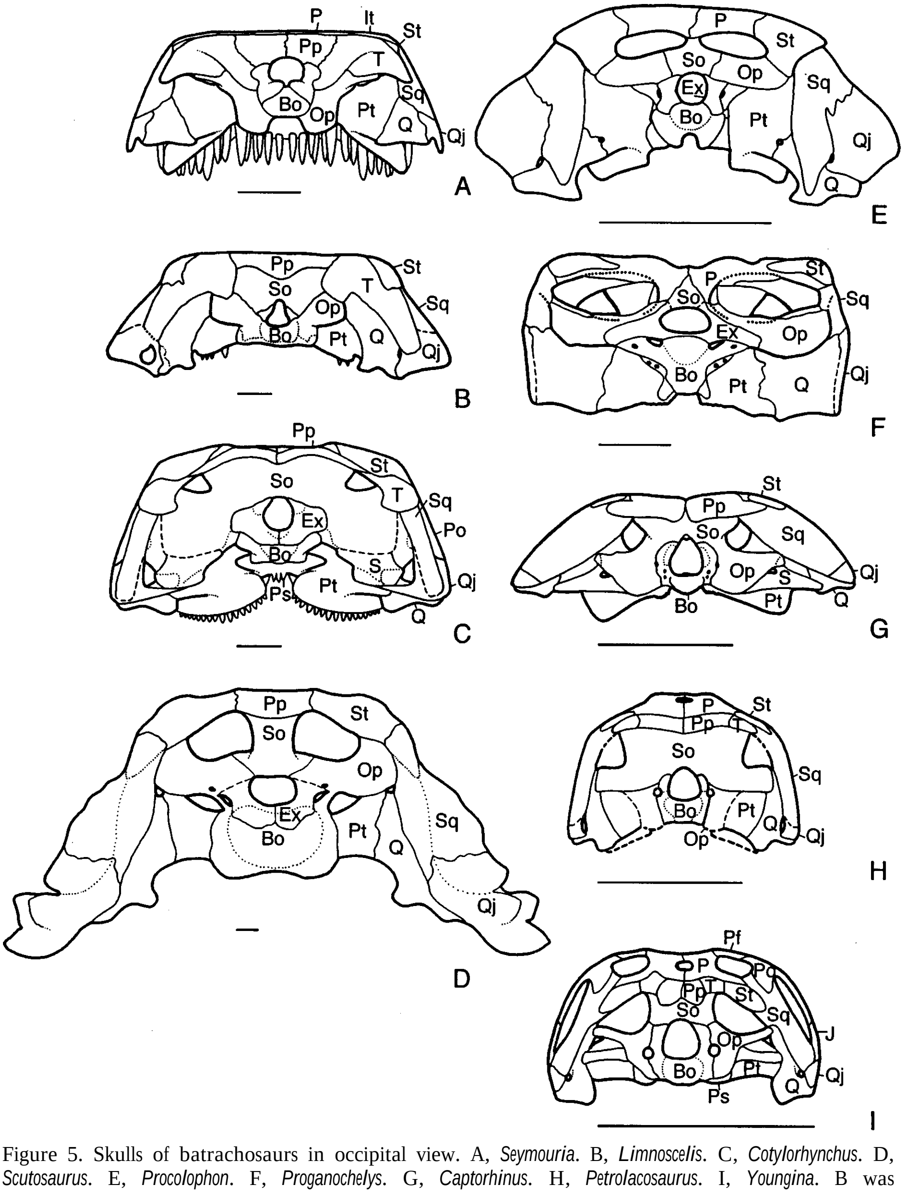

Figure 5. Skulls of batrachosaurs in occipital view. A, *Seymouria*. B, *Limnoscelis*. C, *Cotylorhynchus*. D, *Scutosaurus*. E, *Procolophon*. F, *Proganochelys*. G, *Captorhinus*. H, *Petrolacosaurus*. I, *Youngina*. B was redrawn from Fracasso (1983) and Berman *et al.* (1992), D from Ivachnenko (1987), E from Carroll & Lindsay (1985), F from Gaffney (1990), G from Heaton (1979), H from Reisz (1981), and I from Carroll (1981). Scale bars = 1 cm.

distal head is less than 35% of the length of the bone) (2). This condition may have appeared independently in all these taxa, or romeriids may have had a slender humerus primitively and younginiforms reverted to the primitive condition.

107 Dorsolateral shelf on iliac blade. The iliac blade of *Seymouria* and amniotes is a simple, relatively flat structure (0). There is a dorsolateral shelf on the iliac blade of diadectomorphs (Heaton, 1980: fig. 10) (1).

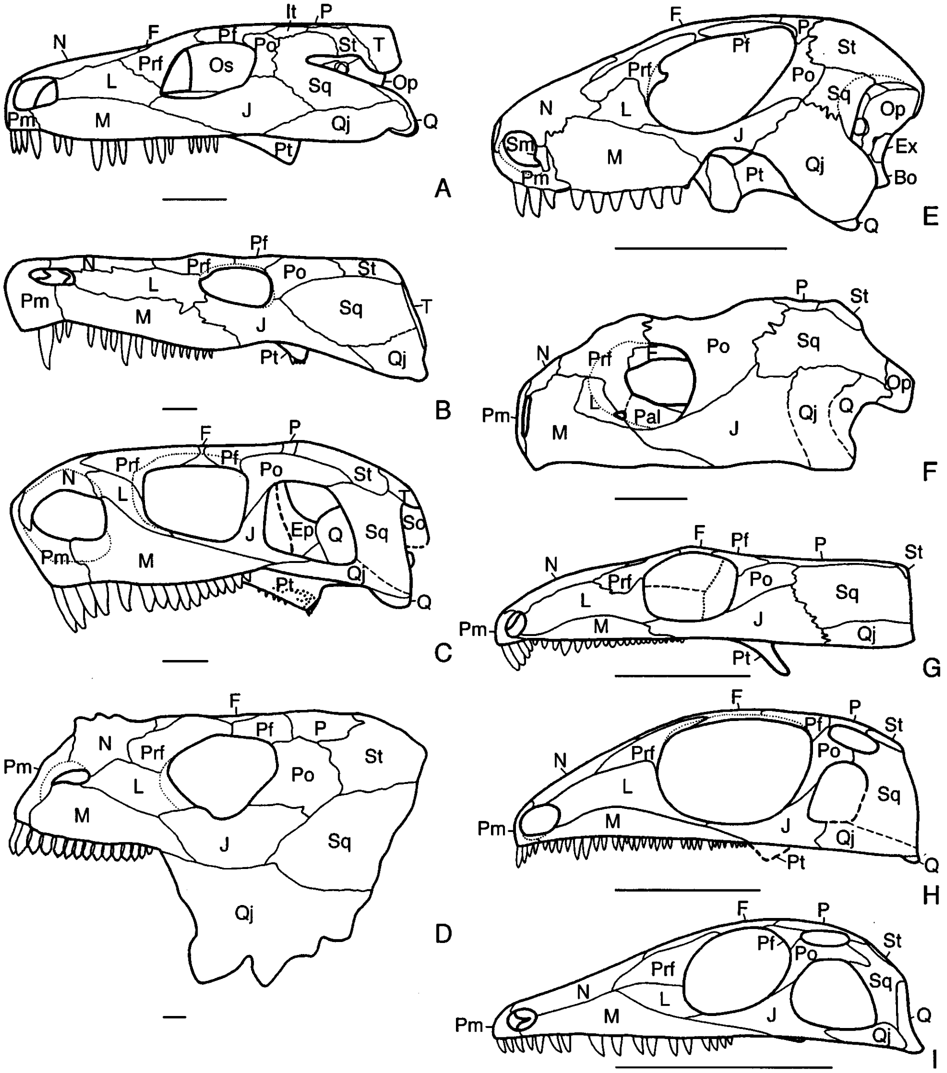

Figure 6. Skulls of batrachosaurs in lateral view. A, *Seymouria*. B, *Limnoscelis*. C, *Cotylorhynchus*. D, *Scutosaurus*. E, *Procolophon*. F, *Proganochelys*. G, *Captorhinus*. H, *Petrolacosaurus*. I, *Youngina*. B was redrawn from Fracasso (1983), D from Ivachnenko (1987), E from Carroll & Lindsay (1985), F from Gaffney (1990), G from Heaton (1979), H from Reisz (1981), and I from Carroll (1981). Scale bars = 1 cm.

Amniota Haeckel 1866

Definition. The most recent common ancestor of synapsids, testudines and diapsids, and all its descendants. Thus defined, Amniota is a crown-group. This definition of Amniota has been used recently (Gaffney, 1980; Gauthier *et al.*, 1988b).

The definition and composition has not varied significantly since this taxon was erected by Haeckel (1866). However, several authors (Broom, 1924a; Carroll, 1988; Olson, 1947; Romer, 1966; Williston, 1917) have not used this taxon and have divided the Amniota into Mammalia, Aves and a paraphyletic

Reptilia including all modern amniotes, except mammals and birds, and most fossil amniotes.

This taxon is supported by nine autapomorphies:

2 Frontal contacting orbit. In *Seymouria* and diadectomorphs, the frontal is separated from the orbit (0) by a contact between the prefrontal and the postfrontal (Fig. 3). In all amniote groups except pareiasaurs (Figs 3, 4), the frontal contributes to the dorsal rim of the orbit (1) and separates the prefrontal from the postfrontal (Figs 3, 4).

27* Occipital flange of squamosal gently convex (1). See Diadectomorpha.

46* Transverse flange bearing a row of large teeth on its posterior edge. The transverse flange of the pterygoid of diadectids and *Seymouria* is covered in a shagreen of small denticles of uniform size (0). This may be the primitive condition for cotylosaurs. Most amniotes have a row of large teeth on the posterior edge of their transverse flange (1), and this may be a synapomorphy of the group (Figs 7, 8). The optimization of this character is ambiguous because limnoscelids also have a row of large teeth on their transverse flange. Therefore, this character could also diagnose the Cotylosauria. In testudinomorphs, there are no fangs on the posterior edge of the transverse flange, but there is a narrow ventral ridge instead (2). Captorhinids have lost the row of teeth and reverted to the primitive condition for batrachosaurs (0).

62 Occipital condyle rounded. In *Seymouria* and diadectomorphs (Fig. 5), the occipital condyle is much broader than high (0). The occipital condyle of amniotes is more rounded and is almost as high as it is broad (1).

68* Labyrinthodont infolding of enamel absent (Gauthier *et al.*, 1988b). The teeth of *Limnoscelis* and *Seymouria* are infolded (0). This is probably a primitive condition inherited from their distant ancestors. No amniote surveyed had labyrinthine infolding of the enamel (1). Therefore, the loss of labyrinthine infolding may be an amniote synapomorphy. However, the teeth of *Diadectes* lack labyrinthine infolding. Therefore, the loss of infolding may also be a synapomorphy of cotylosaurs (amniotes and diadectomorphs). Under this second hypothesis, the infolding of *Limnoscelis* represents a reversal to the primitive condition.

82 Axial centrum tilted anterodorsally (Gauthier *et al.*, 1988b). The axial centrum is oriented along the main axis of the vertebral column in diadectomorphs (Sumida & Lombard, 1991: figs 1 and 2) and *Seymouria* (0). The axial centrum of all amniotes surveyed is oriented anterodorsally relative to the centra posterior to it (Romer & Price, 1940: fig. 44) (1).

94 Cleithrum restricted to anterior edge of scapulocoracoid (Gauthier *et al.*, 1988b). The cleithrum of diadectomorphs (Case, 1911: plate 5) and *Seymouria* widens dorsally and covers the anterodorsal corner of the scapula (0). In most amniotes (Romer & Price, 1940: fig. 55), the cleithrum does not expand nearly as much dorsally and does not cover the anterodorsal corner of the scapula (1). Testudinomorphs and some captorhinids have lost the cleithrum (2).

95 Presence of three scapulocoracoid ossifications. The scapulocoracoid of diadectomorphs and *Seymouria* consists of two ossifications, a scapula and a coracoid (0). Amniotes have three centres of ossification, an anterior and a posterior coracoid, and a scapula (1). Testudines and younginiforms independently reverted to the primitive condition.

115* Presence of astragalus. The tarsus of diadectomorphs and *Seymouria* is poorly known, but as far as we know, *Seymouria* retains a discrete tibiale, intermedium, and perhaps a proximal centrale (0). Diadectids have an astragalus that includes incompletely fused tibiale and intermedium, and probably the fourth centrale (1). The third (proximal) centrale may have remained discrete. The astragalus of diadectids has been argued not to be homologous to the amniote astragalus (Rieppel, 1993b) and is coded as a separate condition. The astragalus of amniotes shows no traces of its possible compound origin (2). The optimization of this character is ambiguous because its polarity is uncertain.

Synapsida Osborn 1903

Definition. The last common ancestor of *Eothyris, Varanops* and mammals, and all its descendants.

Synapsida was originally erected (Osborn, 1903) as a subclass of Reptilia for taxa with a single or undivided (unbroken) temporal arch. Osborn included Cotylosauria, Anomodontia, Testudinata and Sauropterygia in Synapsida because all these taxa were believed to have a single temporal fenestra or a solid skull roof. All other known reptiles were classified into Diapsida, a taxon characterized by the presence of two temporal fenestrae.

Even though Williston (1917) did not give a formal classification of amniotes, his phylogenetic tree and discussions influenced our perception of Synapsida. Williston restricted Synapsida to reptiles with a single lower lateral temporal fenestra and included Theromorpha (pelycosaurs), Therapsida (excluding mammals) and Sauropterygia (which were at the time believed to possess a single temporal fenestra). Williston (1917) believed that Diapsida and Mammalia were derived from Synapsida, but he did not consider these taxa to be synapsids.

Later authors restricted Synapsida to reptiles that were believed to be more closely related to mammals than to extant reptiles. Thus, Synapsida included Pelycosauria and Therapsida (Carroll, 1988; Kemp, 1985; Reisz, 1986; Romer, 1966). Romer & Price (1940) contributed to amniote taxonomy by arguing that the nomen Synapsida should be used instead of Theromorpha and Anomodontia.

The latest change in the definition of Synapsida is the inclusion of Mammalia (Hopson, 1991; Laurin, 1993; Rowe, 1986, 1988). Thus defined, Synapsida is for the first time a monophyletic group.

This taxon is supported by five autapomorphies:

22* Maxilla contacting quadratojugal. In eureptiles, testudinomorphs, millerettids, mesosaurs, and the outgroups, the maxilla is separated in lateral view from the quadratojugal by the ventral margin of the jugal (0). There may still be a medial contact between these elements, but it is not visible in lateral view. In most early synapsids, the jugal reaches the ventral edge of the skull (1). Pareiasaurs have convergently acquired a contact between maxilla and quadratojugal.

25 Caniniform maxillary tooth present. Parareptiles, mesosaurs, diadectomorphs and *Seymouria* have a relatively homodont dentition and lack a distinctly enlarged caniniform tooth (0). Basal synapsids (Langston, 1965: fig. 5) have a caniniform tooth (1). A caniniform was convergently acquired in eureptiles (1) and lost in younginiforms (0).

30 Lower temporal fenestra present. Among the tetrapods studied here,

only araeoscelidians, younginiforms, synapsids and some millerettids (Fig. 6) have a lower temporal fenestra (1). This structure seems to have appeared at least three times in amniotes: in synapsids, in diapsids and in some millerettids.

57*(2) Paroccipital process contacting tabular and squamosal distally. The relationships of the paroccipital to the dermatocranium are complex and highly variable in batrachosaurs. Because of this, the primitive condition for amniotes can only be guessed. The paroccipital process contacts the tabular in *Seymouria* (White, 1939: figs 5, 7) and limnoscelids (0). This is the primitive condition for batrachosaurs. In millerettids and pareiasaurs it is sutured to the squamosal and the supratemporal (3). This is a synapomorphy of parareptiles. In eureptiles, it ends freely (6), although its cartilaginous extension probably contacts the squamosal (Heaton, 1979). Any of these configurations, or even the synapsid configuration, could be primitive for amniotes. Therefore, it is unclear if the contact between the paroccipital process and the tabular and squamosal (2) is an autopomorphy of synapsids. This character varies in other cotylosaurs. The paroccipital process of diadectids contacts the supratemporal and the tabular (1). In procolophonids, the paroccipital process only contacts the supratemporal distally (4) whereas it contacts the squamosal and the quadrate distally in testudines (5). It is unclear which condition is primitive for testudinomorphs.

86* Trunk neural arches narrow. The trunk neural arches of mesosaurs, captorhinids, araeoscelidians, diadectomorphs and *Seymouria* are swollen (0) and have wide zygapophyseal buttresses (White, 1939: fig. 12). Broad neural arches are certainly primitive for cotylosaurs and may represent the primitive condition for amniotes. Basal synapsids (Romer & Price, 1940: fig. 44) have narrow neural arches (1). This may be an autapomorphy of synapsids as well as millerettids, testudines, *Paleothyris* and younginiforms. Alternatively, the presence of narrow neural arches in all these taxa may suggest that it is primitive for amniotes. Pareiasaurs (Seeley, 1888: plate 12) and procolophonids also have swollen neural arches, but their zygapophyseal buttresses are narrow (2). It is unclear whether this represents a procolophonian synapomorphy that was lost in testudines or if it represents convergence.

Sauropsida Huxley 1864

Definition. The last common ancestor of mesosaurs, testudines and diapsids, and all its descendants.

Huxley (1864) erected Sauropsida to include reptiles and birds. This taxon has not been widely used, but its meaning has been fairly constant (Baur, 1887; Watson, 1957). The redefinition of Reptilia as a monophyletic group including birds (Gauthier *et al.*, 1988b) would make Sauropsida redundant if the latter were restricted to the last common ancestor of testudines and diapsids and all its descendants. Therefore, the nomen Sauropsida is available for the clade including mesosaurs and reptiles. This new definition of Sauropsida is consistent with previous usage because most early amniotes (including mesosaurs) have been considered to be reptiles.

This taxon is supported by seven synapomorphies:

22* Maxilla separated from quadratojugal by jugal (1). See Diadectomorpha.

33* Ventral margin of postorbital region of skull rectilinear. In some synapsids, diadectomorphs and *Seymouria*, the posterior part of the ventral skull margin is expanded ventrally (0). This is the primitive condition for cotylosaurs. The ventral margin of the postorbital region of the skull of most sauropsids is rectilinear (1), and this may be a synapomorphy of this clade. However, the presence of a rectilinear skull margin may also diagnose the Amniota because some synapsids share this condition. Pareiasaurs have reverted to the primitive condition (0) and their quadratojugal is greatly expanded ventrally, while procolophonids have an emarginated ventral skull margin (2). Testudines possess states 1 and 2. Therefore, the optimization of this character in procolophonians is ambiguous.

74 Presence of a single coronoid. Early synapsids, limnoscelids and *Seymouria* have at least an anterior and a posterior (0) coronoid (*Seymouria* has three coronoids). Mesosaurs (Modesto, personal communication), parareptiles and eureptiles retain a single coronoid (1), probably the posterior one, judging by its shape and location. This condition developed in parallel in diadectids.

101 Supinator process parallel to humeral shaft and separated from it by a groove. In synapsids (Romer & Price, 1940: fig. 31) and the outgroups, the supinator process is strongly angled relative to the shaft (0). In mesosaurs, millerettids, testudines, and romeriids (Carroll, 1969: fig. 2), the supinator process is almost parallel to the shaft of the humerus (1). This is a synapomorphy of sauropsids. In pareiasaurs, procolophonids and captorhinids (Holmes, 1977: fig. 8), the supinator process is confluent with the distal head of the humerus and is almost parallel to the shaft (2). This condition may have appeared independently in these three taxa, but it may also be a synapomorphy of procolophonians that was lost in testudines.

113* Femoral shaft long and slender. The femur of diadectomorphs, *Seymouria* (White, 1939: fig. 28) and some synapsids has a short and broad shaft (0). This condition is primitive for cotylosaurs and may be primitive for amniotes. Mesosaurs and most reptiles (Carroll, 1969: fig. 11) have a long and slender femoral shaft (1). This may be a synapomorphy of the Sauropsida, but it may also be an amniote synapomorphy, because some synapsids also have a slender shaft. The femoral shaft of pareiasaurs is short, broad and flat (0). The femur of pareiasaurs is also autapomorphic in having broad and flat heads and a very strong adductor crest located along its posterior edge. The femoral shaft of captorhinids convergently became short and broad (0).

118 Presence of a single pedal centrale. The tarsus of synapsids (Romer & Price, 1940: fig. 41) and diadectomorphs has a medial and a lateral centrale (0). Mesosaurs (Huene, 1941) and reptiles (Heaton & Reisz, 1986: fig. 6) retain only the lateral centrale in their tarsus (1).

Mesosauridae Baur 1889

Definition. The last common ancestor of *Mesosaurus, Brazilosaurus* and *Stereosternum,* and all its descendants (Baur, 1889; Carroll, 1988; Lydekker, 1889).

This taxon is supported by eleven synapomorphies:

24* Caniniform region absent. The anterior maxillary teeth of eureptiles, some millerettids, synapsids, *Limnoscelis* and *Seymouria* are enlarged into a caniniform region (0). This is the primitive condition for amniotes and perhaps for sauropsids. The anterior maxillary teeth of mesosaurs (Romer, 1966: fig.

171) are only about as long as the numerous premaxillary teeth (1). A similar condition is found in some millerettids, pareiasaurs and procolophonids. Therefore, parareptiles or procolophonians may share the loss of a caniniform region (1). The history of this character is ambiguous, because it is possible that the loss of the caniniform region occurred at the base of the Sauropsida, and that eureptiles and some millerettids re-evolved a caniniform region.

32 Short postorbital region of skull. The postorbital region constitutes at least 15% of the skull length (0) in all batrachosaurs included in this analysis, except for mesosaurs, in which the postorbital region (1) accounts for only 12% of the skull length (Modesto, personal communication).

42* Arcuate flange absent. The pterygoid of parareptiles, synapsids and diadectomorphs bears an arcuate (tympanic) flange (0). This condition may be primitive for sauropsids. The ventral edge of the quadrate ramus of the pterygoid of mesosaurs is not bent (1) into an arcuate flange (Huene, 1941). This may be an autapomorphy of mesosaurs, but the polarity of this character is uncertain because eureptiles and *Seymouria* also lack an arcuate flange (1). Therefore, this character could be primitive for batrachosaurs and the flange may have appeared independently in diadectomorphs, synapsids, and parareptiles.

47*(2) Ectopterygoid absent. *Paleothyris,* synapsids and the outgroups (Figs 7 and 8) have a large ectopterygoid (0). This may be the primitive condition for sauropsids. Mesosaurs have lost (2) this element (Modesto, personal communication). This may be an autapomorphy of mesosaurs, but the evolution of this character is ambiguous because the ectopterygoid is also absent in captorhinids and testudines, and it is small (1) in diapsids and early parareptiles. Therefore, this element may have been lost in sauropsids and then reappeared in parareptiles and romeriids.

76 Retroarticular process transversely broad, dorsally concave. The retroarticular process of millerettids, eureptiles, synapsids and the outgroups is small and narrow, when it is present (0). The retroarticular process of mesosaurs is distinctly larger (1) and it is dorsally concave (Modesto, personal communication). A similar condition appeared in parallel among procolophonians.

91* Caudal hemal arches attached to anterior centrum only. In eureptiles, procolophonids, synapsids and *Seymouria* (White, 1939: fig. 12), the hemal arches are wedged between adjacent centra (0). This condition is primitive for amniotes and may be primitive for sauropsids. The hemal arches of mesosaurs are attached to the posterior edge of the centrum anterior to it (Modesto, personal communication). This may be an autapomorphy of mesosaurs (1), but the polarity of this character is uncertain because pareiasaurs and testudines have a similar condition (Lee, 1993: fig. 4). Therefore, this character could also be a sauropsid synapomorphy that was lost in procolophonids and eureptiles.

97* Supraglenoid foramen absent. Most eureptiles, synapsids, diadectomorphs and *Seymouria* (White, 1939: fig. 17) have a supraglenoid foramen (0). The presence of this foramen is primitive for amniotes, and it may also be primitive for sauropsids. The lack of a supraglenoid foramen (1) may be an autapomorphy of mesosaurs (Modesto, personal communication). However, the optimization of this character is ambiguous because parareptiles also lack a supraglenoid foramen (Boonstra, 1932b: fig. 4). Therefore, this character may be a sauropsid synapomorphy that was reversed in eureptiles. Younginiforms also lost the supraglenoid foramen (1).

104 Humerus long and slender (2). See Diadectomorpha.

105 Olecranon process small. The olecranon process of pareiasaurs, most eureptiles, synapsids (Romer & Price, 1940: fig. 46) and diadectomorphs is large and its articular surface faces medially (0). The olecranon process of mesosaurs is small (1) and its articular surface faces proximally (Modesto, personal communication). Testudinomorphs and younginiforms have convergently reduced the olecranon process (Gaffney, 1990: fig. 156).

110 Oblique ventral ridge of femur absent. The ventral surface of the femur of captorhinids, *Paleothyris*, pareiasaurs, procolophonids, synapsids (Romer & Price, 1940: plate 46), diadectomorphs and *Seymouria* bears an adductor crest (0). Mesosaurs have lost the adductor crest (1). Testudines and diapsids have also lost the adductor crest (Gaffney, 1990: fig. 163).

111 Femoral proximal articulation round. In pareiasaurs, millerettids, eureptiles, synapsids (Romer & Price, 1940: plate 46) and the outgroups, the proximal articular surface of the femur is antero-posteriorly long and narrow (0). The proximal articular surface of the femur of mesosaurs is more compact (1) and is almost round (Modesto, personal communication). Testudinomorphs have convergently acquired a round proximal femoral articulation (Gaffney, 1990: fig. 163).

Reptilia Linnaeus 1758

Definition. The most recent common ancestor of testudines and diapsids, and all its descendants.

Linnaeus (1758) erected Reptilia to include testudines, crocodiles, and lepidosaurs. The composition of Reptilia was subsequently altered by the inclusion of most early amniotes, including the early relatives of mammals and birds (Carroll, 1988; Case, 1911; Lydekker, 1888, 1889, 1890; Romer, 1966). Finally, Reptilia was redefined as a monophyletic group including testudines and diapsids, and all their fossil relatives (Gauthier *et al.*, 1988b). Thus defined, Reptilia is the crown-group of sauropsids and includes birds.

Reptilia is supported by seven synapomorphies:

17 Tabular small or absent. Mesosaurs, synapsids, diadectomorphs, and *Seymouria* retain a large tabular (0). The tabular of reptiles is small (1), when it is present. The tabular was lost (2) convergently in procolophonians and captorhinids.

49* Suborbital foramen present. In early synapsids, diadectomorphs and *Seymouria* the palate is unbroken (Fig. 7) where the palatine, pterygoid and ectopterygoid meet (0). Reptiles have a foramen (or a fenestra) in this region (1). The optimization of this character is ambiguous because this area is poorly known in mesosaurs. Therefore, the suborbital foramen could also diagnose Sauropsida. The suborbital fenestra (2) of diapsids seems to be an enlargement of the suborbital foramen of other reptiles (Fig. 8). The suborbital fenestra may diagnose diapsids or romeriids because this region of the palate is poorly known in *Paleothyris.*

50* Parasphenoid recess for cervical musculature absent. The posterior part of the ventral surface of the parasphenoid of mesosaurs, some early synapsids (Romer & Price, 1940: plate 3) and limnoscelids has a recess where the hypaxial cervical musculature is thought to have inserted (0). The posterior

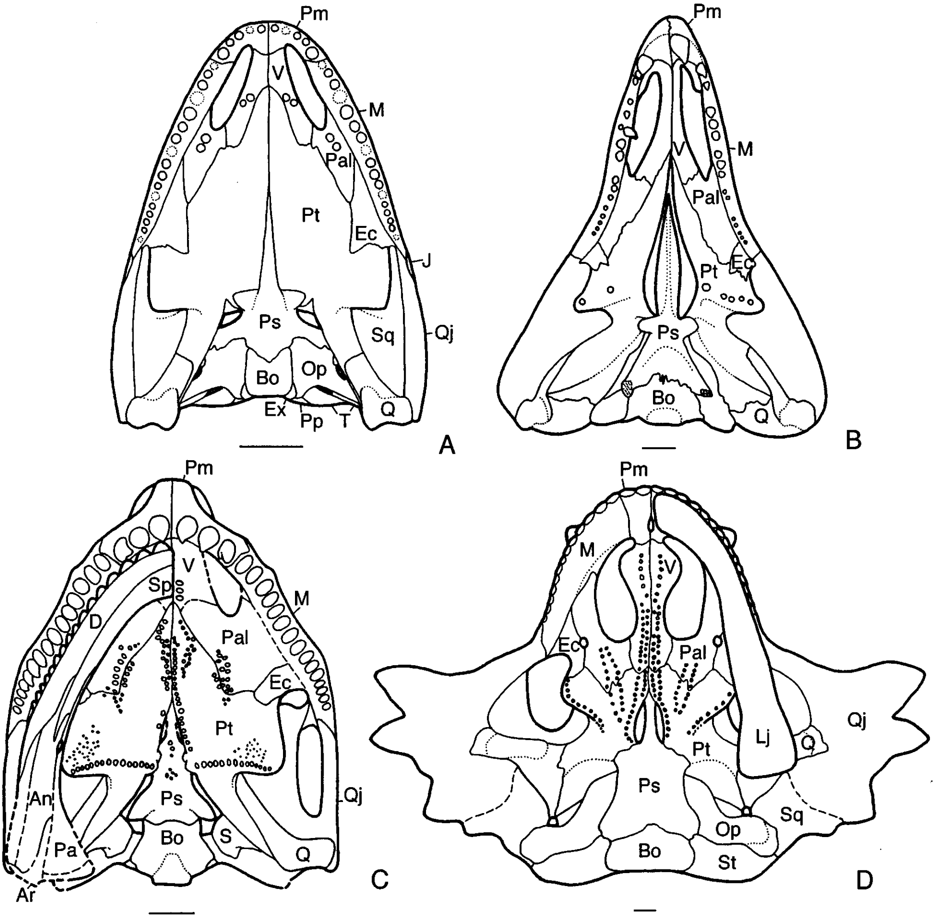

Figure 7. Skulls of batrachosaurs in palatal view. A, *Seymouria*. B, *Limnoscelis*. C, *Cotylorhynchus*. D, *Scutosaurus*. B was redrawn from Fracasso (1983) and D from Ivachnenko (1987). Scale bars = 1 cm.

part of the ventral surface of the parasphenoid of reptiles is relatively flat and lacks a recess (Heaton, 1979: fig. 27) (1). A similar condition convergently appeared in *Seymouria*.

51 Parasphenoid wings absent. In mesosaurs, early synapsids (Romer & Price, 1940: plate 19), diadectomorphs and *Seymouria*, the parasphenoid has a broad, paired posterolateral wing (0). The parasphenoid of reptiles (Heaton, 1979: fig. 27) is more narrow posteriorly and only has a narrow crista ventrolateralis (1).

54 Supraoccipital anterior crista present. The supraoccipital of mesosaurs, synapsids (Romer & Price, 1940: fig. 9) and diadectomorphs lacks anterior parasagittal flanges (0). The supraoccipital of reptiles (Heaton, 1979: fig. 27) has a paired anterior parasagittal flange called the anterior crista (1).

55(2) Supraoccipital plate narrow. The occipital plate of mesosaurs, early synapsids and diadectomorphs (Berman *et al.*, 1992: fig. 7) is broad and extends

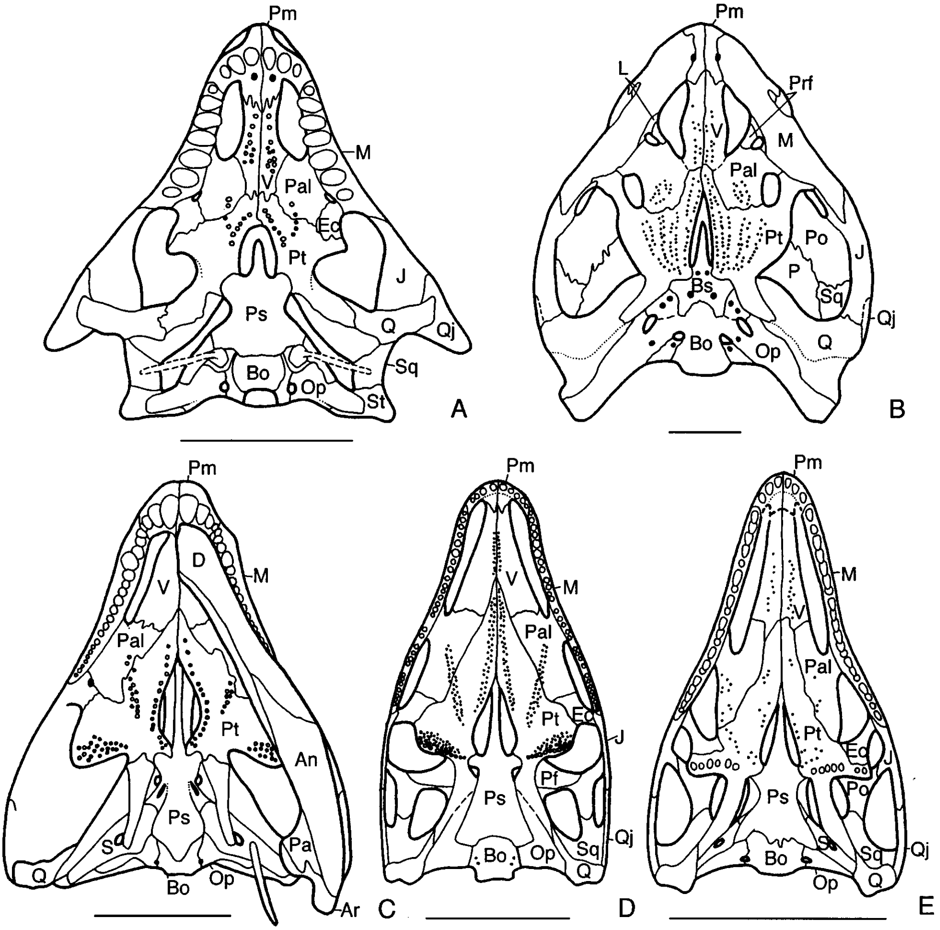

Figure 8. Skulls of reptiles in palatal view. A, *Procolophon*. B, *Proganochelys*. C, *Captorhinus*. D, *Petrolacosaurus*. E, *Youngina*. A was redrawn from Carroll & Lindsay (1985), B from Gaffney (1990), C from Heaton (1979), D from Reisz (1981), and E from Carroll (1981). Scale bars = 1 cm.

laterally farther than the postparietal (1). The occipital plate of all reptiles is reduced (Heaton, 1979: fig. 1) (2). The supraoccipital plate is reduced to a sagittal pillar in procolophonians (3).

60* Post-temporal fenestra large. The post-temporal fenestra of early synapsids and diadectids (Berman *et al.*, 1992: fig. 7) is a small opening wedged between the opisthotic, supraoccipital and tabular (0). The post-temporal fenestra of *Seymouria* is also small, but it is located between the tabular and the opisthotic. This is the primitive condition for amniotes. The post-temporal fenestra of reptiles is large (1), partly because the supraoccipital and the tabular are small (Heaton, 1979: fig. 1). The optimization of this character is ambiguous because mesosaurs could not be coded for this character. Therefore, the presence of a large post-temporal fenestra could be a sauropsid synapomorphy.

Parareptilia Olson 1947

Definition. Testudines and all amniotes more closely related to them than to diapsids.

Olson (1947) erected Parareptilia as a subclass of Reptilia. He divided Parareptilia into the order Diadecta, including Seymouriamorpha, Diadectomorpha, Procolophonia and Pareiasauria, and the order Chelonia. Olson believed that the reptilian condition had been achieved at least twice, once in Eureptilia and at least once within the Parareptilia, since he believed Seymouriamorpha not to be fully reptilian. Olson's ideas were accepted by Ivachnenko (1987), who added Lanthanosuchida and Nycteroleterida to Parareptilia.

Gauthier *et al.* (1988b) recognized a parareptile assemblage including only mesosaurs, procolophonids, pareiasaurs and millerettids. However, Gauthier *et al.* were not confident in the monophyly of this group and did not name it Parareptilia, even though they referred to its members as parareptiles.

This taxon is supported by 14 synapomorphies:

6* Prefrontal-palatine contact present. In romeriids, mesosaurs, early synapsids and limnoscelids, the prefrontal does not reach the palate (0). This condition may be primitive for reptiles. In millerittids and pareiasaurs, the prefrontal has a weak contact with the palatine (1). This may be a synapomorphy of parareptiles. The optimization of this character is ambiguous because captorhinids, diadectids and *Seymouria* also have a weak contact between the prefrontal and the palate (1). Therefore, this character could be a synapomorphy of reptiles and be reversed in romeriids, or it could be primitive for batrachosaurs. Testudinomorphs have a strong contact between the prefrontal and the palatine that encloses the orbitonasal foramen (Carroll & Lindsay, 1985: fig. 6) (2).

10(2) Foramen orbito-nasale enclosed between prefrontal, lacrimal and palatine. Diapsids, synapsids, limnoscelids and *Seymouria* have no foramen between the lacrimal, palatine and prefrontal (0). The nerves and blood vessels that pass through the foramen orbito-nasale, in the taxa that possess such a structure, pass medial to the prefrontal in diapsids, synapsids, limnoscelids and *Seymouria*. Most parareptiles have an orbitonasal foramen located between the lacrimal, palatine and prefrontal bone (2). In captorhinids, the foramen orbitonasale is represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine.

20 Anterior lateral maxillary foramen distinctly larger than other foramina. In eureptiles, mesosaurs, synapsids and the outgroups, several small foramina may be present on the lateral surface of the maxilla, but none of these foramina is much larger than the others (0). In millerettids, pareiasaurs and procolophonids (Carroll & Lindsay, 1985: fig. 3), the anterior lateral maxillary foramen is much larger than other foramina (1). This is a synapomorphy of parareptiles that was lost in testudines, which have no large foramina on the lateral surface of the maxilla (2). The foramina may have disappeared because of the horny beak found in all testudines. However, foramina are found on the medioventral surface of this element in testudines.

28 Quadratojugal expanded dorsally. In eureptiles, mesosaurs, synapsids and the outgroups, the quadratojugal is a long and relatively narrow triangular element (0). In parareptiles, the posterior end of the quadratojugal is expanded dorsally (1).

31 Temporal emargination bordered by quadratojugal and squamosal. In eureptiles, mesosaurs and synapsids, there is no temporal emargination (0). Millerettids, procolophonids and testudines have a temporal emargination bordered anteriorly by the quadratojugal and the squamosal (2). This is a synapomorphy of parareptiles. The quadrate of these taxa is also emarginated, but it does not define the edge of the emargination. In pareiasaurs, the massive quadratojugal and squamosal hide the tympanic emargination in lateral view (3). However, the emargination is still visible in posterior view. Furthermore, a slight incision in the squamosal posteriorly may represent the edge of an external auditory meatus.

36 Jaw articulation to occiput. The jaw articulation of eureptiles, mesosaurs, synapsids and diadectomorphs is even with the occiput (1). In parareptiles, the jaw joint is located slightly anterior to the occiput (2).

47* Ectopterygoid small (1). See Mesosauridae.

48 Edentulous ectopterygoid. The ectopterygoid is a dentigerous element carrying a shagreen of denticles (0) in *Paleothyris*, araeoscelidians, early synapsids and the outgroups. This condition is primitive for reptiles. The ectopterygoid of parareptiles is always edentulous (1).

57* Paroccipital process sutured to squamosal and supratemporal (3). See Synapsida.

67 Stapedial dorsal process unossified. The stapes of most early eureptiles (Heaton, 1979: fig. 29), mesosaurs, synapsids and diadectids contacts the paroccipital process by an ossified dorsal process (0). The stapes of parareptiles is cylindrical and lacks an ossified dorsal process (Gaffney, 1990: figs 52 and 53) (1). The dorsal process was convergently lost in younginiforms.

89 Sacral ribs with narrow distal contact. The sacral ribs of eureptiles, mesosaurs, synapsids (Romer & Price, 1940: plate 25) and the outgroups are broad and are expanded distally (0). Contact over a significant portion of their length leaves only a small gap between the ribs. The sacral ribs of parareptiles (Watson, 1914: fig. 5) are more slender and contact each other only distally (1).

97* Supraglenoid foramen absent. See Mesosauridae.

102 Ectepicondylar groove and foramen present. In most romeriids (as defined by Gauthier *et al.*, 1988b), some mesosaurs, synapsids and the outgroups, a groove for the radial nerve is present on the anterodorsal surface of the distal head of the humerus (Carroll, 1969: fig. 2) (0). Millerettids and testudines (Gaffney, 1990: fig. 148) have an ectepicondylar foramen and groove (1). This is an autapomorphy of Parareptilia. Pareiasaurs (Boonstra, 1932: fig. 7) have only the ectepicondylar foramen (the foramen leads into a canal that enters the bone at a steep angle instead of the usual shallow angle), (2) while procolophonids lack both foramen and groove (3). Both of these conditions represent autapomorphies of pareiasaurs and procolophonids, respectively. Captorhinids independently lost the ectepicondylar foramen and groove (Holmes, 1977: fig. 8) (3).

108 Iliac blade dorsally expanded. The iliac blade of most eureptiles, mesosaurs, synapsids (Romer & Price, 1940: fig. 49), limnoscelids and *Seymouria* is primitive in having a long, low posterodorsal process and lacking an anterior expansion (0). The iliac blade of parareptiles (Watson, 1914: fig. 4) has a dorsal expansion directly above the acetabulum, a short anterior process, and is short posteriorly (1). This configuration appeared convergently in younginiforms.

Millerettidae Watson 1957

Definition. The most recent common ancestor of *Milleretta, Milleropsis* and *Millerosaurus,* and all its descendants (Gow, 1972).

This taxon is supported by ten autapomorphies:

23* Quadratojugal not reaching level of orbit. See Diadectomorpha.

27* Occipital flange of squamosal convex above quadrate emargination and concave medial to tympanic ridge (2). See Diadectomorpha.

34 Quadrate exposed laterally. The lateral surface of the quadrate is covered by the squamosal in procolophonids (Carroll & Lindsay, 1985: fig. 1), pareiasaurs, most eureptiles, mesosaurs, synapsids and most of the outgroups (0). The quadrate of millerettids is exposed laterally posterior to the posteromedian flanges of the squamosal and quadratojugal (Watson, 1957: fig. 13) (1). A lateral exposure of the quadrate (1) developed convergently in testudines and younginiforms.

38 Dermal sculpturing composed of tuberosities. The dermal cranial elements are relatively smooth (0) in romeriids, in procolophonids, some testudines, mesosaurs, synapsids and limnoscelids. The presence of gently domed tuberosities (1) on the dermal bones of millerettids is an autapomorphy (Gow, 1972: plate 1). Similar tuberosities also appeared convergently in diadectids and some testudines (*Proganochelys*) (1). Pareiasaurs have sculpturing in the form of large tuberosities and deep pits (2). The dermal cranial elements of captorhinids (Heaton, 1979: fig. 2) and *Seymouria* are ornamented by a pattern of ridges defining pits arranged in a honeycomb pattern (3).

39*(2) Interpterygoid vacuity long. In pareiasaurs, procolophonids (Carroll & Lindsay, 1985: fig. 1), mesosaurs, some synapsids and diadectids, the interpterygoid vacuity is short (it extends over less than 15% of the skull length). This may be the primitive condition for parareptiles (0). Millerettids have a long interpterygoid vacuity that extends over 15% of the skull length (2). *Proganochelys,* eureptiles, some synapsids and limnoscelids also have a long interpterygoid vacuity (Heaton, 1979: fig. 2). All of these taxa may have acquired this condition in parallel, or this could be a synapomorphy of reptiles, amniotes, or even cotylosaurs.

53 Parasphenoid teeth present. The parasphenoid is edentulous (0) in procolophonians (members of the Procolophonia as redefined in this paper: pareiasaurs, procolophonids and testudines), some captorhinids, some araeoscelidians, younginiforms, mesosaurs, some early synapsids, diadectids and *Seymouria*. The parasphenoid of millerettids bears denticles on its cultriform process and on part of its ventral plate (1). Denticles convergently appeared on the parasphenoid of limnoscelids, some captorhinids, *Paleothyris* and some araeoscelidians.

61 Presence of a ventral cranial fissure between the basioccipital and the basisphenoid (Lee, 1993). In pareiasaurs, testudines (Gaffney, 1990: fig. 48). captorhinids, synapsids and the outgroups, the basioccipital is sutured to the basisphenoid (0). The presence of a gap between the basisphenoid and the basioccipital (visible in dorsal view of the braincase) is an autapomorphy of millerettids (1). Procolophonids convergently developed a ventral cranial fissure (Carroll & Lindsay, 1985: fig. 1) (1). However, this character may simply reflect the fact that most of the described braincases of procolophonids come from

juvenile specimens. The braincase of the largest specimens of *Procolophon* have not been described.

86* Trunk neural arches narrow (1). See Synapsida.

114 Carpus and tarsus long and slender (Heaton & Reisz, 1986: fig. 6). The carpus and tarsus are short and broad (0) in procolophonians, captorhinids, mesosaurs, some synapsids and diadectomorphs. The carpus and tarsus of millerettids are long and slender (1). A similar condition appeared in romeriids.

123 First metatarsal less than half as long as fourth metatarsal. The first metatarsal of procolophonians, captorhinids, *Paleothyris*, mesosaurs, synapsids and the outgroups is more than half as long as the fourth metatarsal (Heaton & Reisz, 1986: fig. 6) (0). In these taxa, the ratio between the length of these two metatarsals is around 2/3. The first metatarsal of millerettids is shorter (1). A similar condition appeared convergently in diapsids (Reisz, 1981: fig. 24) (1).

Procolophonia Seeley 1888

Definition. The most recent common ancestor of pareiasaurs, procolophonids and testudines, and all its descendants.

Seeley (1888) erected Procolophonia as a subgroup of Anomodontia. At that time, Anomodontia also included Pareiasauria, Dicynodontia, Gennetotheria (which included genera now classified as Gorgonopsia) and Pelycosauria. It is unclear which genera were included in Seeley's Procolophonia in addition to *Procolophon.* His Procolophonia excluded pareiasaurs and testudines.

Case (1911) considered Procolophonia to be a suborder of the Cotylosauria and included Procolophonidae and Telerpetidae (both taxa are now included in the Procolophonidae). To this list, Olson (1947) and Carroll (1988) added a few poorly known groups of parareptiles, such as Nyctiphruretidae and Sclerosauridae.

Romer (1966) further expanded Procolophonia by adding the superfamilies Pareiasauroidea and Millerosauroidea to the taxa already included in this taxon. Therefore, Romer's Procolophonia is equivalent to our Parareptilia except that it does not include Testudines. However, Romer believed that the origins of turtles were to be found in his Procolophonia. Therefore, Romer's views on parareptile phylogeny were fairly similar to ours, even though this is not obvious from his taxonomy.

Procolophonia is supported by 29 synapomorphies:

3 Pineal foramen close to fronto-parietal suture. The pineal foramen of millerettids, most eureptiles, mesosaurs, synapsids and the outgroups is located close to the mid-length of the interparietal suture, or slightly anterior to this (0). The pineal foramen of procolophonians (when it is present) is located very close to the fronto-parietal suture (1). Testudines usually have no pineal foramen, but in the mutants that have a foramen, it is located close to the frontal (Lee, 1993).

-13* Postorbital far from occiput. In millerettids, younginiforms, some araeoscelidians, mesosaurs, synapsids and diadectomorphs, the postorbital extends far posteriorly toward the occiput (1). In procolophonians, the postorbital ends far from the occiput (0), partly because it is bordered posteriorly by a large supratemporal. This may be a procolophonian synapomorphy. The presence of the same condition in captorhinids, *Paleothyris* and some araeoscelidians may be an autapomorphy of all these taxa (0), or it could be a synapomorphy of reptiles.

17 Tabular absent (2). See Reptilia.

21* Anterior maxillary narial foramen present. Procolophonids and pareiasaurs have a foramen at the base of the posterior wall of the nasal cavity (1), close to the floor of the nasal chamber (R. Reisz, personal observation). This foramen may be homologous to the anterior opening of the canalis alveolare superius or foramen alveolare superius of testudines (Gaffney, 1979a: figs 53, 54 and 57). In the latter, the foramen is sometimes located farther medially and closer to the premaxilla than in procolophonids and pareiasaurs, but it is probably homologous in all these taxa and probably carries the alveolar artery in all procolophonians. Most other batrachosaurs lack this foramen (0). The optimization of this character is ambiguous because the presence of this foramen could not be verified in millerettids. Therefore, the presence of the anterior maxillary narial foramen could also be a parareptile synapomorphy.

24* Caniniform region absent (1). See Mesosauridae.

43 Cranio-quadrate space large. In millerettids, eureptiles (Heaton, 1979: fig. 2), synapsids and the outgroups, the cranio-quadrate space (the space between the braincase and the quadrate ramus of the pterygoid) is narrow and the paroccipital process and the quadrate ramus of the pterygoid converge posterolaterally (0). Both structures extend posterolaterally, although the paroccipital process is angled slightly more laterally than the quadrate ramus of the pterygoid. In all procolophonians, the cranio-quadrate space is wide and the paroccipital process is parallel to the quadrate ramus of the pterygoid (Carroll & Lindsay, 1985: fig. 1) (1). Both structures extend more or less laterally.

44 Pterygoid palatal ramus not reaching level of choana. In millerettids, eureptiles, mesosaurs, early synapsids and the outgroups, the palatal ramus extends between the choana (0). In pareiasaurs, procolophonids and testudines, the palatal ramus of the pterygoid is shorter and does not reach the level of the choana (1).

45 Transverse flange of pterygoid directed anterolaterally. In millerettids, most eureptiles, mesosaurs, early synapsids, limnoscelids and *Seymouria*, the transverse flange of the pterygoid extends posterolaterally from the area of the basicranial articulation (0). In procolophonians, the transverse flange of the pterygoid extends anterolaterally from the basicranial area (1). A similar condition appeared convergently in diadectids and araeoscelidians.

52 Cultriform process short. In millerettids, eureptiles, mesosaurs, early synapsids and the outgroups, the cultriform process is longer than the body of the parasphenoid (0). In procolophonians, the cultriform process is shorter than the body of the parasphenoid (1).

55 Supraoccipital plate reduced to a sagittal pillar (3). See Reptilia.

56 Paroccipital process antero-posteriorly expanded. In millerettids, most eureptiles, mesosaurs, early synapsids (Romer & Price, 1940: fig. 9) and diadectomorphs, the paroccipital process is a broad, thin, vertical flange (0). In procolophonians (Boonstra, 1934b: fig. 4), the paroccipital process seems to have been rotated toward the horizontal plane (1). Other batrachosaurs have different configurations. *Seymouria* has a thick, tubular paroccipital process

composed of the opisthotic (3). Captorhinids (Heaton, 1979: fig. 27) and younginiforms convergently acquired a narrow, cylindrical paroccipital process (2).

65 Quadrate condyle articular surfaces nearly flat and antero-posteriorly short. In millerettids, eureptiles (Heaton, 1979: fig. 26), mesosaurs, synapsids and the outgroups, the articular surfaces of the quadrate condyles are strongly convex and antero-posteriorly long (0). In procolophonians (Gaffney, 1990: fig. 27), the articular surfaces of the condyles are much shorter and almost flat (1).

69* Foramen intermandibularis posterior located below coronoid process or farther posteriorly. This foramen, when present, is located between the prearticular, angular and splenial. In captorhinids (Heaton, 1979: fig. 30), diadectomorphs and some synapsids, the posterior intermandibular foramen is located below the tooth row, in front of the coronoid process (1). The posterior intermandibular foramen of procolophonians (Carroll & Lindsay, 1985: fig. 13) is located at the level of the coronoid process, or farther posteriorly (2). The optimization of this character is ambiguous because the foramen could not be located in millerettids. Therefore, this character could also be a parareptile synapomorphy.

70 Meckelian fossa facing dorsally. In millerettids, eureptiles (Heaton, 1979: fig. 30), early synapsids, diadectids and *Seymouria*, the prearticular is narrow and the adductor fossa faces mediodorsally (0). The prearticular of pareiasaurs, procolophonids (Carroll & Lindsay, 1985: fig. 13) and testudines is tall and the meckelian fossa faces dorsally (1). A similar condition evolved in parallel in limnoscelids (1).

71 Fossa meckelii short. The meckelian fossa of millerettids, eureptiles (Heaton, 1979: fig. 30), mesosaurs, early synapsids and the outgroups is long and occupies at least 20% of the length of the lower jaw (0). In procolophonians (Carroll & Lindsay, 1985: fig. 13), the meckelian fossa is reduced in length (1).

72 Surangular not reaching coronoid eminence. In millerettids, most eureptiles (Heaton, 1979: fig. 2), mesosaurs, some early synapsids, limnoscelids and *Seymouria*, the surangular extends anteriorly beyond the coronoid eminence (0). In pareiasaurs, procolophonids (Carroll & Lindsay, 1985: fig. 1) and testudines, the surangular is shorter and does not extend beyond the coronoid eminence (1).

75 Prearticular extending no farther than coronoid eminence. In millerettids, most eureptiles (Heaton, 1979: fig. 30), synapsids and the outgroups, the prearticular extends from the posterior end of the jaw to below the tooth row, anterior to the coronoid eminence (0). In procolophonians (Carroll & Lindsay, 1985: fig. 13), the prearticular extends no farther anteriorly than the level of the coronoid eminence (1).

76 Retroarticular process transversely broad and dorsally concave (1). See Mesosauridae.

86* Trunk neural arches swollen, with narrow zygapophyseal buttresses (2). See Synapsida.

90* Transverse processes or caudal ribs present on at least 13 caudals. In most eureptiles, mesosaurs, synapsids, limnoscelids and *Seymouria*, transverse processes or caudal ribs are present on a few (0) proximal caudals (usually no more than eight). In procolophonians, transverse processes or ribs are present farther distally in the tail (1) and can be seen on at least 13 caudal vertebrae (Gaffney, 1990: fig. 129). The optimization of this character is ambiguous because millerettids could not be coded for this character. Therefore, the presence of transverse processes on at least 13 caudal vertebrae could be a parareptile synapomorphy. Younginiforms are convergent in the possession of transverse processes or ribs on at least 13 caudals (1).

92 T-shaped interclavicle. In millerettids, most eureptiles (Holmes, 1977: fig. 1), mesosaurs, early synapsids and the outgroups, the head of the interclavicle is diamond-shaped because the lateral processes of the head are broad (0). The head of the interclavicle of pareiasaurs and procolophonids (Watson, 1914: fig. 4) has slender, lateral processes giving it the appearance of a T (1). The interclavicle of most turtles has been modified by its incorporation into the plastron, but in *Proganochelys* it also has slender lateral processes, even though the latter extend posterolaterally rather than laterally. Younginiforms convergently acquired a T-shaped interclavicle.

93 Anteriorly directed groove on interclavicle for clavicle attachment. In millerettids, eureptiles (Holmes, 1977: fig. 1), mesosaurs, synapsids and the outgroups, the clavicle overlaps the interclavicle ventrally on a large sutural surface (0). In pareiasaurs (Boonstra, 1932b: fig. 24) and procolophonids, the interclavicle bears an anteriorly directed groove into which the head of the clavicle fits (1). This is a synapomorphy of procolophonians that became modified in turtles (2) by the appearance of the plastron (the turtle morphology cannot be easily compared with either of the other configurations).

96 Scapula narrow and flat. In millerettids, eureptiles, mesosaurs, synapsids and the outgroups, the scapula is a fairly broad, low blade (Holmes, 1977: fig. 5). The height of the scapula of these taxa is no more than two and a half times greater than its width (0). In pareiasaurs and procolophonids (deBraga, personal communication; Boonstra, 1932b: fig. 2), the scapula is a high, narrow blade (1). In turtles (Gaffney, 1990: fig. 135), the scapula is further modified in being cylindrical and narrower (2).

98 Glenoid short, bipartite. In millerettids, eureptiles (Holmes, 1977: fig. 5), mesosaurs, synapsids and the outgroups, the glenoid is long and helical (0). In procolophonians, the glenoid is short and composed of two facets (1), one on the coracoid and one on the scapula (deBraga, personal communication; Gaffney, 1990: fig. 135).

109* Acetabular buttress large, overhanging strongly above the acetabulum. In eureptiles (Sumida, 1989a: fig. 6), mesosaurs, synapsids and the outgroups, the acetabular buttress is small and overhangs only slightly above and lateral to the acetabulum (0). In procolophonians, the acetabular buttress is large (1), thick and overhangs strongly (deBraga, personal communication; Boonstra, 1932a: fig. 4). The optimization of this character is ambiguous because the acetabular buttress of millerettids is poorly known. Therefore, this character could be a parareptile synapomorphy. Younginiforms convergently acquired a large acetabular buttress (1).

112 Femoral greater trochanter present on posterior edge of femur (Lee, 1993). In millerettids, eureptiles, mesosaurs, synapsids (Romer & Price, 1940: fig. 36) and the outgroups, there is no greater trochanter (0). In procolophonians, there is a greater trochanter on the posterior edge of the proximal head of the femur (1). This structure may not be entirely homologous in all parareptiles. In pareiasaurs, it is represented by a particularly robust crest that extends along the posterior edge of the femur from the proximal to the distal head. It is

located slightly distal to the proximal head of the bone (Boonstra, 1932a: fig. 1). In procolophonids (deBraga, personal communication) and testudines, the greater trochanter is a small process on the posterior surface of the femur, close to the proximal end of the bone (Gaffney, 1990: fig. 163). If there is a ridge distal to the trochanter of testudinomorphs, it tapers quickly and disappears where the proximal head merges into the shaft. The greater trochanter of procolophonians is not homologous to the mammalian structure of the same name.

117 Astragalus and calcaneum sutured or fused to each other (Lee, 1993). In millerettids, eureptiles, mesosaurs and synapsids (Romer & Price, 1940: fig. 52), the astragalus and calcaneum, when present, are discrete elements (0). They are usually disarticulated because they are only loosely linked to each other. In procolophonians (Gaffney, 1990: fig. 171), the astragalus and calcaneum are either sutured or fused to each other (1). This character had not previously been observed in procolophonids, but newly prepared specimens show that the astragalus and calcaneum were at least tightly sutured to each other in mature specimens of *Procolophon* (deBraga, personal communication). Some mature specimens of diadectids have a fused astragalus and calcaneum, but this is a convergent feature.

119 Loss of the fifth distal tarsal. In millerettids, most eureptiles, mesosaurs, early synapsids and the outgroups, there are five distal tarsals (0). Pareiasaurs, procolophonids and testudines never have more than four (1) distal tarsals (deBraga, personal communication).

124 Dorsal dermal ossifications present. No dorsal dermal ossifications have been reported in millerettids, eureptiles, mesosaurs, synapsids or the outgroups (0). Pareiasaurs, testudines and at least some procolophonids (Sues, personal communication) have dorsal dermal ossifications (1). If the dermal ossifications of these three groups are homologous, their presence is a synapomorphy of the Procolophonia. However, at least two patterns of ossification are found in these three taxa. In pareiasaurs, they are represented by numerous osteoderms (Boonstra, 1934a: plate 24). According to Boonstra (1934a), there are three longitudinal rows of scutes above the vertebrae in *Bradysaurus.* In small specimens of the same genus, the external surface of the scutes is smooth, but in large individuals, it bears a central knob surrounded by radial ridges. A canal pierces the side of the knob and extends through the scute to open on its medial surface. There is no evidence that these osteoderms were covered by horny scutes. The scutes of pareiasaurs are not fused to the postcranial axial skeleton. In testudines, the dorsal ossifications are represented by large dermal plates (vertebrals, cervicals, marginals, pleurals etc.), fused to the vertebrae and ribs, that form part of the carapace. These dermal scutes are overlapped by epidermal, horny scutes. The dorsal dermal ossifications of procolophonids have not been described yet. Therefore, this character is somewhat problematic and definite conclusions must await more descriptive work on pareiasaurs and procolophonids.

Pareiasauria Seeley 1888

Definition. The most recent common ancestor of *Anthodon, Bradysaurus, Deltavjatia, Elginia, Embrithosaurus, Nanoparia, Parasaurus, Pareiasaurus, Scutosaurus* and *Shihtienfenia,* and all its descendants.

The history of Pareiasauria is relatively simple, and the composition of this taxon has only been expanded since its erection by Seeley (1888) by the addition of new genera and species (Boonstra, 1935; Gauthier *et al.*, 1988b; Gao, 1989; Ivachnenko, 1987).

This taxon is supported by 25 autapomorphies:

-2 Frontal excluded from orbit (0). See Amniota.

-5* Postparietal dorsally exposed. In millerettids, eureptiles, mesosaurs, synapsids (Romer & Price, 1940: plate 19) and diadectomorphs, the postparietal is an occipital element (1). This may be the primitive condition for procolophonians. In pareiasaurs (Boonstra, 1934b: plate 2), the postparietal is part of the skull table, as in *Seymouria* (0). This is a reversal to the primitive batrachosaur condition. The optimization of this character is ambiguous because testudinomorphs lack postparietals.

11* Jugal anterior process extending to anterior orbital rim. In testudines, millerettids, *Paleothyris*, some araeoscelidians, mesosaurs, synapsids, diadectids and some species of *Seymouria*, the anterior process of the jugal does not reach the anterior rim of the orbit (0). This condition is primitive for sauropsids and may be primitive for procolophonians. In pareiasaurs, the anterior process of the jugal is longer and extends at least to the anterior rim of the orbit, and usually beyond it (1). This could be an autapomorphy of pareiasaurs. The presence of this character in procolophonids, younginiforms, captorhinids and some araeoscelidians may be an autapomorphy of all these taxa or it may be a reptilian synapomorphy that was lost in millerettids, testudines, *Paleothyris* and some araeoscelidians. Limnoscelids convergently acquired a long jugal (1).

19* Low anterodorsal process of the maxilla not reaching nasal. In millerettids, most eureptiles, mesosaurs, synapsids and the outgroups, the maxilla is a low element that does not expand much dorsally in front of the orbit (0). It is bordered dorsally by the lacrimal from the level of the external naris to the orbit. This is the primitive condition for parareptiles. In pareiasaurs, the maxilla expands dorsally in front of the orbit (1). The optimization of this character is ambiguous because procolophonids and testudines have a high anterodorsal process of the maxilla that reaches the nasal (2). Therefore, the low anterodorsal process could be a synapomorphy of procolophonians that was further modified in testudinomorphs. Younginiforms convergently acquired a high anterodorsal maxillary process (2).

22 Maxilla and quadratojugal in contact (1). See Diadectomorpha.

27* Occipital flange of squamosal medial to tympanic ridge and facing posteromedially (4). See Diadectomorpha.

31 Temporal emargination visible in posterior view only (3). See Parareptilia.

-33* Convex ventral margin of postorbital region of dermatocranium (0). See Sauropsida.

38 Dermal sculpturing present in the form of large tuberosities and deep pits (2). See Millerettidae.

40* Choana located far medially and bordered posterolaterally by palatine. In procolophonids, millerettids, eureptiles, mesosaurs, synapsids, limnoscelids and *Seymouria*, the choana is more or less parallel to the maxilla and the palatine forms only its posterior and a small part of its lateral edge (0). This may be the primitive condition for procolophonians. In pareiasaurs, the choana is almost parasagittal, but it usually curves slightly medially in its posterior half (1).

Consequently, the posterior end of the choana is located far medial to the maxilla and the palatine defines the posterior and almost half of the lateral edge of the choana. The optimization of this character is ambiguous because a similar configuration is found in testudines. Therefore, this character could be a synapomorphy of procolophonians that was reversed in procolophonids. Diadectids also convergently acquired this condition (1).

41* Suborbital foramen located far medially and without a jugal or maxillary contact. In millerettids and eureptiles, the suborbital foramen (foramen palatinum posterius of Gaffney, 1990) is located close to the lateral edge of the skull and its lateral edge is defined by the jugal and/or the maxilla (0). In pareiasaurs, the suborbital foramen is located farther medially and its lateral edge is defined by the palatine anteriorly and the ectopterygoid posteriorly (1). The optimization of this character is ambiguous because the suborbital foramen of testudines is also located far medially. Therefore, this character may also be a procolophonian synapomorphy that was reversed in procolophonids. However, this scenario is less likely because in turtles the posterior edge of the suborbital foramen is defined by the pterygoid, whereas in pareiasaurs it is defined by the ectopterygoid.

64* Lateral flange of exoccipital extending beneath paroccipital process. In procolophonids, millerettids, eureptiles, synapsids and the outgroups, the exoccipital is restricted to the occipital condyle, the lateral edges of the foramen magnum and the immediate vicinity (0). In pareiasaurs, the exoccipital sends a lateral flange behind the paroccipital process of the opisthotic (1). This may be a pareiasaur autapomorphy, but the optimization of this character is ambiguous because testudines have a similar condition. Therefore, the lateral flange of the exoccipital may also be a procolophonian synapomorphy that was lost in procolophonids. Furthermore, this flange may have been present in procolophonids, but the immaturity and poor ossification of most specimens prevents confirmation of this character.

78 Lateral shelf on articular. In procolophonids, millerettids, eureptiles, mesosaurs, synapsids and the outgroups, the articular is not expanded laterally and its lateral surface (usually covered by the surangular) extends dorsally (0). In pareiasaurs, the articular is expanded laterally and its lateral surface extends dorsolaterally (1). Testudines also have a laterally expanded lower jaw, but in this case the surangular is expanded instead of the articular (2). Further, the surangular of testudines contributes to the articular surface of the mandible. Therefore, we do not consider these two conditions (1 and 2) homologous.

81* Presacral vertebral count of 20 or less. Procolophonids, millerettids, eureptiles, mesosaurs and the outgroups (0) have more than 20 presacral vertebrae (usually about 27). Pareiasaurs never have more than 20 presacral vertebrae (1). This may be an autapomorphy of pareiasaurs, but the optimization of this character is ambiguous because testudines have at the most 18 presacral vertebrae. Therefore, a reduction in the number of presacral vertebrae could be a synapomorphy of procolophonians that was reversed in procolophonids.

-85 Atlantal pleurocentrum not fused to axial intercentrum. In testudinomorphs, millerettids, eureptiles, mesosaurs, some early synapsids and diadectomorphs, the atlantal pleurocentrum is tightly attached or fused to the dorsal surface of the axial intercentrum (1). In pareiasaurs, the two elements remain separate and can move relative to each other (0).

88*(2) Presence of three or four sacral vertebrae. Testudines, millerettids, eureptiles, mesosaurs, early synapsids and diadectomorphs have two sacral vertebrae (1). This condition may be primitive for procolophonians. Pareiasaurs have four sacral vertebrae (2). This may be an autapomorphy of the Pareiasauria, but the optimization of this character is ambiguous because procolophonids have three sacral vertebrae. Therefore, an increase in the number of sacral vertebrae may be a procolophonian synapomorphy that was lost in testudines.

91* Caudal hemal arches attached to anterior centrum (1). See Mesosauridae.

99* Acromion present. In procolophonids, millerettids, eureptiles (Holmes, 1977: fig. 5), mesosaurs, synapsids and the outgroups, the anterior edge of the scapula is gently convex and continuous with the coracoid; there is no acromion (0). The scapula of pareiasaurs bears a strong acromion (Lee, 1993: fig. 4) (1). This may be an autapomorphy of pareiasaurs, but the optimization of this character is ambiguous because testudines also have an acromion. Therefore, the presence of an acromion could be a procolophonian synapomorphy that was lost in procolophonids. However, the acromion of testudines may not be homologous to the acromion of pareiasaurs. In testudines, the acromion is anteroventromedially directed, whereas the acromion of pareiasaurs is anterolaterally directed. Furthermore, the acromion of pareiasaurs is a distinct process that arises from the scapular blade well above the level of the scapulo-coracoid suture, whereas the acromion of testudines merges into the ventral portion of the scapula (Gaffney, 1990: fig. 135). Therefore, anatomical differences suggest that these structures may not be homologous.

101* Supinator process parallel to shaft and not separated by a groove (2). See Sauropsida.

102 Ectepicondylar foramen present without a radial groove (2). See Parareptilia.

104 Humerus short and robust, without a shaft (1). See Diadectomorpha.

106* Manual phalangeal formula reduced to 2 3 3 3 3 or less. In some procolophonids, millerettids, eureptiles (Holmes, 1977: fig. 11), mesosaurs, synapsids and the outgroups, the manual phalangeal formula is 2 3 4 5 3 (0). The manual phalangeal formula of pareiasaurs (Gregory, 1946: fig. 25) never exceeds 2 3 3 3 2 (2). The optimization of this character is ambiguous because the manual phalangeal formula of testudines is also reduced. Therefore, this character could be procolophonian synapomorphy that was reversed in procolophonids. However, this scenario is unlikely since the primitive phalangeal formula for testudines is believed to be 2 3 3 3 3 (Gaffney, 1990).

-113 Femoral shaft short and broad (0). See Sauropsida.

120* Fifth pedal digit more slender and no longer than first digit (Lee, 1993). In procolophonids, millerettids, eureptiles (Sumida, 1989a: fig. 10), mesosaurs, synapsids and the outgroups, the fifth pedal digit is more robust and longer than the first digit (0). In pareiasaurs (Lee, 1993: fig. 4), the fifth pedal digit is more slender and never longer than the first digit (1). This may be an autapomorphy of pareiasaurs, but the optimization of this character is ambiguous because testudines also have a short and slender fifth pedal digit. Therefore, this character could be a procolophonian synapomorphy that was reversed in procolophonids.

122* Pedal phalangeal formula reduced to 2 3 3 4 3 or less (Lee, 1993). In some procolophonids, millerettids, eureptiles (Sumida, 1989a: fig. 10), mesosaurs, synapsids, and the outgroups, the pedal phalangeal formula is 2 3 4 5 4 or 2 3 4 5 3 (0). The pedal phalangeal formula of pareiasaurs (Lee, 1993: fig. 4) never exceeds 2 3 3 4 2 (2). The optimization of this character is ambiguous because the pedal phalangeal formula of testudines is also reduced. Therefore, this character could be a procolophonian synapomorphy that was reversed in procolophonids. However, this scenario is unlikely since the primitive phalangeal formula for testudines is believed to be 2 3 3 3 3 (Gaffney, 1990).

Testudinomorpha, new taxon

Definition. The last common ancestor of the Procolophonidae and testudines, and all its descendants.

This taxon was erected because we are not aware of any name already in the literature that would link procolophonids to testudines.

Seventeen synapomorphies (14 of which are unambiguous) support Testudinomorpha:

4 Postparietal absent (2). See Diadectomorpha.

6 Strong prefrontal-palatal contact (2). See Parareptilia.

7 Wide prefrontal medial flange. In pareiasaurs, millerettids, eureptiles, mesosaurs, synapsids and the outgroups (0), the medial flange of the prefrontal is narrow (less than 45% of the interorbital width). In procolophonids and testudines, the anterior orbital rim is much broader than the posterior rim because the ventral flange of the prefrontal is very thick (1).

9 Lacrimal not reaching external naris. In pareiasaurs, millerettids, most eureptiles, mesosaurs, most early synapsids and the outgroups, the lacrimal reaches the external naris (0). In procolophonids and testudines, the lacrimal is short and no longer reaches the external naris (1). Younginiforms convergently acquired a short lacrimal.

19* Maxilla with a high anterodorsal process (2). See Pareiasauria.

27* Occipital flange of squamosal medial to tympanic ridge and concave (5). See Diadectomorpha.

46 Transverse flange of pterygoid edentulous, with a ventral ridge (2). See Amniota.

63 Basioccipital tubera paired. In pareiasaurs, millerettids, eureptiles (Heaton, 1979: fig. 27), mesosaurs, synapsids and the outgroups, the basioccipital lacks ventrolateral tubera (0). Procolophonids (Carroll & Lindsay, 1985: fig. 1) and most testudines have paired, ventrolateral tubera (1).

66* Stapes slender, imperforate. In millerettids, eureptiles (Heaton, 1979: fig. 29), mesosaurs, synapsids and the outgroups, the stapes is massive and is perforated by the stapedial foramen (0). This may be the primitive condition for procolophonians. Procolophonids and testudines (Gaffney, 1990: fig. 53) have a slender, imperforate stapes that may have functioned as part of a tympanic middle ear (1). This may be a synapomorphy of testudinomorphs, but the optimization of this character is ambiguous because the stapes of pareiasaurs is not known. Therefore, this character may be a synapomorphy of the Procolophonia. A potential stapes was recently found in *Scutosaurus* (M. S. Lee, personal communication). It is large, but its poor preservation precludes identification of a dorsal process or a foramen. This new datum suggests that the slender stapes is a testudinomorph character.

73 Accessory lateral shelf on dorsal surface of surangular. The dorsal surface of the surangular is gently convex in pareiasaurs, millerettids, eureptiles, mesosaurs, some synapsids, and the outgroups (0). In procolophonids and testudines, the dorsal surface of the surangular bears a narrow lateral shelf that is especially prominent between the articular and the meckelian fossa (1). The shelf tapers gradually anteriorly to the level of the anterior end of the adductor fossa.

77 Retroarticular process composed of at least three bones. In pareiasaurs, millerettids, eureptiles (Heaton, 1979: fig. 32), mesosaurs, synapsids, and the outgroups, the retroarticular process, when present, is made up entirely of the articular (0). In procolophonids and testudines (Gaffney, 1990: Fig. 57), the retroarticular process is composed of the articular, prearticular, surangular and, sometimes, the angular (1). The prearticular, surangular and angular extend posteriorly well beyond the jaw articulation and support the articular from beneath.

79 Coronoid process high and made up of coronoid only. In pareiasaurs, millerettids, eureptiles, mesosaurs, synapsids and the outgroups, there is only a low coronoid eminence composed of the dentary, surangular and coronoid (0). Procolophonids and testudines have a high coronoid process composed exclusively of the coronoid (1). Although most pareiasaurs lack this condition, a few pareiasaurs (such as juvenile specimens of *Deltavjatia*) have a small, short coronoid spike.

80 Splenial excluded from symphysis. In pareiasaurs, millerettids, eureptiles (Heaton, 1979: fig. 30), mesosaurs, synapsids and the outgroups, the splenial contributes to the mandibular symphysis (0). In procolophonids and testudines (Gaffney, 1990: fig. 61), the splenial is short and does not reach the symphysis (1).

94 Cleithrum absent (2). See Amniota.

105 Olecranon process small, articular facet of ulna faces proximally (1). See Mesosauridae.

111 Femoral proximal articulation short and wide (1). See Mesosauridae.

121 Metapodials overlapping. In pareiasaurs, captorhinids, mesosaurs, synapsids and diadectids, the proximal heads of the metapodials barely contact each other (0). In procolophonids and testudines, the proximal heads of the metapodials are proximally expanded and overlap dorsally the proximal end of the metapodial lateral to them (1). This character is especially obvious in the metatarsus, but it is also developed to a lesser extent in the metacarpus. Romeriids convergently acquired overlapping metapodials (Heaton & Reisz, 1986: fig. 6).

Procolophonidae Lydekker 1890

Definition. The last common ancestor of *Anomoiodon, Burtensia, Candelaria, Contritosaurus, Eumetabolodon, Hypsognathus, Kapes, Koiloskiosaurus, Leptopleuron, Macrophon, Microphon, Microthelodon, Myocephalus, Myognathus, Neoprocolophon, Orenburgia, Paoteodon, Procolophon* and *Thelegnathus*, and all its descendants (Carroll, 1988; Ivachnenko, 1979; Li, 1989).

This taxon is supported by 11 autapomorphies:

1 Narial shelf present. In all the taxa studied here except procolophonids and some synapsids, the nasal is thin and smooth above the external naris; this portion of the nasal is not differentiated from the rest of the bone (0). In procolophonids, the portion of the nasal above the external naris is thickened into a shelf visible in lateral view (1).

8 Prefrontal medial process present. In all amniotes except procolophonids, the orbital flange of the prefrontal has a relatively smooth medial edge (0). In procolophonids, there is a distinct, medial process on the orbital flange of the prefrontal (Fig. 6) (1).

11* Jugal anterior process extending anterior to level of anterior orbital rim. See Pareiasauria.

33* Ventral margin of postorbital region of skull emarginated (2). See Sauropsida.

37 Orbit enlarged posteriorly. In all amniotes except procolophonids, the orbit is circular or ellipsoidal (0). In procolophonids, the orbit is expanded posteriorly and it is no longer circular (1).

57* Paroccipital process sutured to supratemporal (4). See Synapsida.

61 Unossified region present between basioccipital and basisphenoid (1). See Millerettidae.

87*(2) Anterior pleurocentra bearing a double ridge. In pareiasaurs, millerettids, captorhinids, mesosaurs, some early synapsids and the outgroups, the ventral surface of the anterior pleurocentra is rounded ventrally (0). This is the primitive condition for procolophonians and may also be primitive for testudinomorphs. In procolophonids, the ventral surface of the anterior pleurocentra bears a double ridge (deBraga, personal communication). This may be an autapomorphy of procolophonids (2). However, the optimization of this character is ambiguous because the ventral surface of the anterior pleurocentra of testudines bears a single, median ridge (1). Because this character is unordered, three equally parsimonious scenarios are possible; the double ridge of procolophonids and the single ridge of testudines could have appeared independently of each other, or either derived condition could have given rise to the other. Romeriids convergently acquired a single, median ridge on their centra (1).

88* Presence of three sacral vertebrae (2). See Pareiasauria.

101* Supinator process parallel to shaft and without a groove (2). See Sauropsida.

102 Ectepicondyle without a foramen or a groove (3). See Parareptilia.

Testudines Linnaeus 1758

Definition. The last common ancestor or *Proganochelys* and modern turtles, and all its descendants.

The definition of Testudines has been expanded since its erection (Linnaeus, 1758) by the addition of several fossil and extant genera (Carroll, 1988). Unfortunately, fourteen synonymous nomina were proposed for this taxon, and three have prevailed (Chelonia, Testudinata and Testudines). The nomen Testudines is by far the oldest and should be used instead of other nomina (see Hunt, 1958, for an excellent review).

This taxon is supported by 25 autapomorphies:

-12 Postorbital not contacting the supratemporal. In procolophonids, pareiasaurs, millerettids, mesosaurs, synapsids and diadectomorphs, the postorbital contacts the supratemporal (1). In testudines that have a supratemporal (*Proganochelys*), a contact between the parietal and the squamosal separates the postorbital from the supratemporal (0). Eureptiles convergently lost the contact between postorbital and supratemporal (0).

20 No foramina on lateral surface of maxilla (2). See Parareptilia.

23* Quadratojugal not reaching level of orbit (1). See Diadectomorpha.

26 Squamosal bordering post-temporal fenestra. In procolophonids, pareiasaurs, millerettids, synapsids and the outgroups, the paroccipital process of the opisthotic articulates with the tabular or supratemporal (among other elements), thereby excluding the squamosal from the post-temporal fenestra (0). In testudines, the paroccipital process is directed more ventrally and usually articulates with the squamosal. Therefore, the squamosal defines the lateral edge of the post-temporal fenestra dorsal to the paroccipital process (1). A similar condition was independently acquired in eureptiles (1).

34 Quadrate exposed laterally (1). See Millerettidae.

39* Interpterygoid vacuity short or absent. In testudines, the interpterygoid vacuity is either (2) long (more than 15% of the skull length), as in *Proganochelys*, or absent (1), as in all other known testudines. See Millerettidae.

40* Choana inflected medially posteriorly and bordered by palatine posterolaterally (1). This character is discussed under the Pareiasauria.

41* Suborbital foramen located far medially and without a jugal or maxillary contact (1). See Pareiasauria.

47 Ectopterygoid absent (2). See Mesosauridae.

57* Paroccipital process sutured to squamosal and quadrate (5). See Synapsida.

59* Medial wall of inner ear ossified with acoustic nerve foramina (Gaffney, 1990: fig. 40). In early synapsids and *Seymouria*, the medial wall of the inner ear seems to have remained cartilaginous (0). This may be the primitive condition for testudinomorphs. The optimization of this character is ambiguous because some pareiasaurs (mostly large, fully mature individuals) and diadectids also have an ossified medial wall (1). This character cannot be evaluated in other cotylosaurs. The medial wall of the inner ear could be a cotylosaur character or a procolophonian character, among other possibilities.

64* Lateral flange of exoccipital beneath paroccipital process (1). See Pareiasauria.

78 Lateral shelf of articular region of mandible composed of surangular (2). See Pareiasauria.

81* 18 presacral vertebrae (Romer, 1956) (1). See Pareiasauria.

-86* Trunk neural arches narrow (1). See Synapsida.

87* Anterior pleurocentra keeled ventrally (1). See Procolophonidae.

91* Caudal hemal arches attached to anterior centrum (1). See Mesosauridae.

93 Interclavicle tightly sutured to plastron (2). See Procolophonia.

96 Scapula narrow and cylindrical (2). See Procolophonia.

99* Acromion present on scapula (1). See Pareiasauria.

103 Entepicondylar foramen absent. In procolophonids, pareiasaurs,

millerettids, eureptiles, mesosaurs, synapsids and the outgroups, the entepicondyle of the humerus is perforated by a foramen (0). Testudines lack the entepicondylar foramen (1).

106* Manual phalangeal formula reduced to 2 3 3 3 3 or less (2). See Pareiasauria.

110 Oblique ventral ridge of femur absent (1). See Mesosauridae.

120* Fifth pedal digit slender, not longer than first toe (1). See Pareiasauria.

122* Pedal phalangeal formula reduced to 2 3 3 4 3 or less (Lee, 1993) (2). See Pareiasauria.

Eureptilia Olson 1947

Definition. Diapsids and all amniotes more closely related to them than to testudines.

Olson (1947) erected Eureptilia to include Captorhina, Synapsida, Parapsida, Euryapsida and Diapsida. Thus defined, Eureptilia included extant diapsids (except birds), and all extinct amniotes except Procolophonia and Pareiasauria. Even though various authors have classified taxa into Eureptilia (Fox & Bowman, 1966; Laurin & Reisz, 1989; Reisz & Baird, 1983), few major reviews of amniote phylogeny and taxonomy have used it (Gaffney, 1980).

Based on a phylogenetic analysis of extant amniotes, Gaffney (1980) argued that Synapsida and Diapsida formed a clade excluding Testudines, and named this taxon Eureptilia. However, subsequent work has shown that, defined as such, the Eureptilia was probably not a clade (Gaffney & Meylan, 1988).

A major departure from previous studies is our exclusion of Synapsida and inclusion of Aves in Eureptilia. However, as in previous studies, our Eureptilia includes Captorhinidae, *Paleothyris* (and probably most, if not all protorothyridids) and Diapsida.

Eureptilia is supported by ten synapomorphies:

-12 Postorbital not reaching supratemporal (0). See Testudines.

15 Posterolateral corner of skull formed by parietal and small supratemporal. The posterolateral corner of the skull of most parareptiles, mesosaurs, synapsids and diadectomorphs is formed in large part by the supratemporal (1). Eureptiles have a smaller supratemporal and the posterolateral corner of the skull is formed mostly by the parietal and to a small extent by the reduced supratemporal (2).

18 Supratemporal small. The supratemporal is a large, broad bone (0) in all the taxa studied here except for eureptiles. Eureptiles have a small, narrow supratemporal (1).

23* Quadratojugal not reaching level of orbit (1). See Diadectomorpha.

25 Caniniform maxillary tooth present (1). See Synapsida.

26 Squamosal bordering post-temporal fenestra (1). See Testudines.

35 Quadrate anterior process short. The anterior process of the quadrate is long (0) in parareptiles, mesosaurs, synapsids and the outgroups. In these taxa, the anterior process of the quadrate extends anteriorly along more than 55% of the quadrate ramus of the pterygoid. In eureptiles, the anterior process of the quadrate only extends along less than 55% of the length of the quadrate ramus of the pterygoid (1). Diadectids convergently reduced the length of their quadrate (1).

39* Interpterygoid vacuity long (2). See Millerettidae.
42* Arcuate flange of pterygoid absent (1). See Mesosauridae.
-57* Paroccipital process ending freely (6). See Synapsida.

Captorhinidae Case 1911

Definition. The last common ancestor of *Captorhinus, Captorhinikos, Captorhinoides, Hecatogomphius, Kahneria, Labidosaurikos, Labidosaurus, Moradisaurus, Protocaptorhinus, Rhiodenticulatus, Romeria* and *Rothianiscus*, and all its descendants (Carroll, 1988; Case, 1911; Ricqlès, 1984; Romer, 1966).

This taxon is supported by 12 synapomorphies:

6* Prefrontal-palatine contact present (1). See Parareptilia.

10 Foramen orbito-nasale represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine (1). See Parareptilia.

11* Jugal suborbital process extending to anterior orbital rim (1). See Pareiasauria.

-13* Postorbital far from occiput (0). See Procolophonia.

17 Tabular absent (2). See Reptilia.

38 Dermal sculpturing composed of ridges and pits arranged in honeycomb pattern (3). See Millerettidae.

-46 Transverse flange of pterygoid bearing a shagreen of denticles (0). See Amniota.

47* Ectopterygoid absent (2). See Mesosauridae.

56 Paroccipital process narrow (2). See Procolophonia.

101 Supinator process parallel to shaft and ectepicondylar groove absent (2). See Sauropsida.

102 Ectepicondylar foramen and groove absent (3). See Parareptilia.

-113 Femoral shaft short and broad (0). See Sauropsida.

Romeriida Gauthier, Kluge & Rowe 1988

Definition. The last common ancestor of *Paleothyris* and diapsids, and all its descendants.

Romeriids (family Romeriidae) traditionally included several genera of uncertain taxonomic affinities (collectively called protorothyridids) and *Romeria*, a captorhinid. The altered taxonomic unit Romeriida (Gauthier *et al.*, 1988b) now includes diapsids in addition to *Paleothyris* and perhaps other protorothyridids, but *Romeria* must be excluded from this taxon.

This taxon is supported by four synapomorphies:

16* Tabular separated from opisthotic. In millerettids, mesosaurs, synapsids and the outgroups, the paroccipital process of the opisthotic contacts the tabular distally (0). In *Paleothyris* and early diapsids, the paroccipital process is incompletely ossified but extends toward the squamosal rather than toward the tabular (1). The optimization of this character is ambiguous because captorhinids lack a tabular. Therefore, this character could also be a eureptilian synapomorphy.

87 Anterior pleurocentra keeled ventrally (1). See Procolophonidae.

114 Carpus and tarsus long and slender (1). See Millerettidae.

121 Metapodials overlapping (1). See Testudinomorpha.

Paleothyris Carroll 1969

We have used *Paleothyris* instead of Protorothyrididae because the latter is ill-defined and possibly paraphyletic. This taxon has only been used to refer to MCZ 3481 and closely related specimens (Carroll, 1969).

This taxon is supported by four autapomorphies:

-13* Postorbital far from occiput (0). See the discussion of this character under Procolophonia.

53 Parasphenoid teeth present (1). See Millerettidae.

86* Trunk neural arches narrow (1). See Synapsida.

104* Humerus long and slender (2). See Diadectomorpha.

Diapsida Osborn 1903

Definition. The last common ancestor of araeoscelidians and younginiforms, and all its descendants.

Osborn (1903) erected Diapsida to encompass reptiles with double or divided temporal arches and forms having secondarily lost one or both arches. His Diapsida included taxa currently included in this taxon, in addition to Pelycosauria (Permo-Carboniferous synapsids), Procolophonia and Proganosauria (Mesosauridae).

Williston (1925) removed several taxa from the Diapsida. Most of these are not classified today as diapsids. These include Pelycosauria, Procolophonia and Proganosauria. However, he also removed taxa that are now believed to be diapsids, such as Squamata, Ichthyosauria and Protorosauria (which included araeoscelidians, prolacertiforms, pleurosaurs and some, but not all, sphenodontids).

Olson's (1947) Diapsida included Lepidosauria and Archosauria (without Aves), and this view has been accepted by most subsequent scientists (Carroll, 1988). Most subsequent modifications to Diapsida consisted in the inclusion of more fossil amniotes (Laurin, 1991; Reisz, 1981; Reisz, Berman & Scott, 1984). The definition of Diapsida has been further modified by the inclusion of Aves (Benton, 1985; Gauthier *et al.*, 1988a). This modification was required to make Diapsida monophyletic. Early students of diapsid phylogeny knew that birds were derived from some diapsids (Romer, 1966; Williston, 1917), but had no objections to erecting paraphyletic taxa.

Diapsida is supported by eight synapomorphies:

29 Upper temporal fenestra present. Of all the taxa studied here, only diapsids possess an upper temporal fenestra defined by the postorbital, parietal, squamosal and, sometimes, by the postfrontal (1).

30 Lower temporal fenestra present (1). See Synapsida.

47* Ectopterygoid small (1). See Mesosauridae.

49* Suborbital fenestra present (2). See Reptilia.

100 Mineralized sternum. The sternum of all batrachosaurs except diapsids remains cartilaginous and unmineralized throughout ontogeny (0). In araeoscelidians and younginiforms, the sternum (when known) is composed of calcified cartilage or bone (1).

110 Oblique ventral ridge of femur absent (1). See Mesosauridae.

116 Complex tibio-astragalar joint. The joint between the tibia and astragalus is a simple, flat joint (0) in all the taxa studied here (Sumida, 1989a: fig. 10) except for diapsids. In the latter, the distal head of the tibia has a ridge that fits into a groove in the proximal surface of the astragalus (Reisz, 1981: fig. 24) (1).

123 First metatarsal less than half as long as fourth metatarsal (1). See Millerettidae.

Araeoscelidia Williston 1913

Definition. The last common ancestor of *Araeoscelis* and *Petrolacosaurus* and all its descendants.

The history of Araeoscelidia is relatively simple. Williston (1913) erected this taxon for *Araeoscelis.* Subsequently, various closely related genera were added to Araeoscelidia, such as *Zarcasaurus* (Brinkman, Berman & Eberth, 1984) and *Petrolacosaurus* (Reisz, 1981).

This taxon is supported by two autapomorphies:

45 Transverse flange of pterygoid directed anterolaterally (1). See Procolophonia.

104* Humerus long and slender (2). See Diadectomorpha.

Younginiformes Romer 1945

Definition. The most recent common ancestor of *Youngina, Acerosodontosaurus* and *Hovasaurus*, and all its descendants.

When Younginiformes was erected (Romer, 1945), it included Younginidae, Prolacertidae (a group of early archosauromorphs) and Tangasauridae (close relatives of *Youngina*). At that time, Younginidae included genera now considered to be early lepidosauromorphs (*Paliguana, Palaeagama* and *Saurosternon*), eosuchians of uncertain affinities (*Galesphyrus* and *Heleosuchus*), an early archosaur (*Heleosaurus*) and a possible millerettid (*Heleophilus*), as well as taxa still included today in Younginiformes. Therefore, Younginiformes was a large and fairly diverse taxon. Romer (1966) later removed Prolacertidae from Younginiformes.

More recently, Younginiformes has been restricted to the last common ancestor of *Acerosodontosaurus, Hovasaurus* and *Youngina*, and all its descendants (Benton, 1985; Evans, 1988; Gauthier *et al.*, 1988a; Laurin, 1991). Thus defined Younginiformes only retains *Youngina* and Tangasauridae from Romer (1945).

Several of the characters listed as autapomorphies of younginiforms (17 altogether) in Appendix 3 are actually synapomorphies with saurians (extant diapsids) and will not be discussed. Most of these characters were discussed recently (Laurin, 1991). Saurians were excluded from the present analysis because they are extremely variable. They would be difficult to code as a terminal taxon and they would introduce much polymorphism in the data matrix. Their presence was not necessary in this analysis since this study deals with early amniote phylogeny, and diapsid monophyly is currently well supported, as several recent studies have demonstrated (Carroll & Currie, 1991; Evans, 1988; Gauthier *et al.*, 1988a; Laurin, 1991).

DISCUSSION

Comparisons with previous phylogenies

Our results support amniote monophyly and suggest that synapsids are the sister-group of sauropsids (including all other known amniotes). Our results also suggest that mesosaurs are the sister-group of reptiles. The Reptilia can be divided into the Parareptilia, including millerettids, pareiasaurs, procolophonids and testudines, and the Eureptilia, including captorhinids, *Paleothyris* and diapsids.

Using only monophyletic taxa has considerably altered the definition and concepts of various taxa. For instance, our Reptilia includes Aves, since the latter are a group of diapsids. Therefore, reptiles can no longer be viewed as 'primitive' amniotes lacking the features associated with endothermy found in mammals and birds (hair, feathers, a large brain, etc.). Furthermore, no reptile was the ancestor of mammals, and early synapsids should not be called mammal-like reptiles. The Cotylosauria, a taxon that has been poorly defined in the past and often considered to be paraphyletic, now includes all amniotes and diadectomorphs rather than only a few early amniotes.

A comparison of our tree with the cladogram of Gauthier *et al.* (1988b) reveals some similarities and extensive differences. In both trees, synapsids are the sister-group of all other amniotes, and *Paleothyris* is the sister-group of diapsids. However, in our tree, mesosaurs are the sister-group of all non-synapsid amniotes, and procolophonids, pareiasaurs and millerettids are consecutively more remote relatives of testudines (Fig. 2). Gauthier *et al.* (1988b) believed that mesosaurs, procolophonids, pareiasaurs and millerettids formed a group that they called parareptiles, and testudines were allied to captorhinids (Fig. 1). However, Gauthier *et al.* (1988b) were very perceptive in doubting their hypothesis of parareptile relationships. They stated: ''Mesosauridae, Millerettidae, Pareiasauria, and Procolophonia are informally referred to here as parareptiles. We doubt that the proposed monophyly will withstand further study . . .''. We are reasonably confident that the monophyly of the taxa defined above will withstand future studies, with the possible exception of the Reptilia and Romeriida. The new position of testudines in our tree may be one of the most surprising results, as they were linked to captorhinids by three unambiguous synapomorphies by Gauthier *et al.* (1988b). However, in the present analysis, testudines are united to procolophonids by 14 unambiguous and three ambiguous synapomorphies. Indeed, the taxon uniting testudines with procolophonids is one of the most strongly supported clades in our analysis.

Suggestions by Berman *et al.* (1992) that the Diadectomorpha (including the Limnoscelidae, Tseajaiidae and Diadectidae) may be the sister-group of the Synapsida and that the diadectomorph-synapsid clade is the sister-group of their Reptilia (represented in their analysis by captorhinomorphs and *Petrolacosaurus*) cannot be supported. Diadectomorphs are not amniotes according to this analysis, because they lack the amniote synapomorphies listed above and seem to be the sister-group of Amniota. Furthermore, the Amniota requires four extra steps to be collapsed (Table 1). Berman *et al.* (1991) used three shared derived characters to link diadectomorphs to synapsids: posterolateral corner of the skull table formed nearly entirely by the supratemporal; long posterior expansion of postorbital contacts supratemporal to exclude parietal lappet from contacting squamosal; and possession of an otic trough. Our evidence indicates

TABLE 1

Taxa	Extra steps	Statistical significance	Number of unambiguous characters	Total number of characters
Diadectomorpha	2	75	5	7
Amniota	4	87	6	9
Sauropsida	2	80	3	6
Reptilia	1	67	4	7
Parareptilia	5	96	10	14
Procolophonia	22	100	21	28
Testudinomorpha	5	82	14	17
Eureptilia	4	69	6	10
Romeriida	2	59	3	4
Diapsida	5	76	6	8

Relative strength of the nodes. The second column refers to the number of extra steps required to break the nodes of our new phylogeny. These numbers were obtained by doing a branch-and-bound search of all the trees requiring up to 331 steps with PAUP.MAC 3.1. Strict consensus trees of all the trees requiring one step more than the shortest tree were obtained. The same procedure was done for all the trees requiring up to two extra steps, then three, four, etc. Each consensus tree was examined to see which nodes collapsed. The procedure was repeated until all the nodes had collapsed. Column three evaluates the statistical significance of the clades established with the bootstrap algorithm of PAUP.MAC 3.1. 200 replications were performed with the heuristic algorithm. All trees found in each iteration were saved. The numbers following the taxa represent the percentage of times that the relevant clade was supported by the search. Some believe that a taxon is not significant unless it is found in at least 95% of the iterations, but such a stringent requirement is clearly too severe. Nevertheless, the numbers below indicate the relative robustness of the taxa. Columns four and five indicate the number of unambiguous characters and the total number of characters supporting the nodes (obtained by the DELTRAN optimization of PAUP 3.1).

that their first character is primitive for diadectomorphs and amniotes because the posterolateral corner of the skull table is formed mostly by the supratemporal in diadectomorphs, synapsids, mesosaurs, millerettids, at least some pareiasaurs, procolophonids and some testudines. The second character is also primitive for cotylosaurs because the postorbital contacts the supratemporal in diadectomorphs, synapsids, mesosaurs and most parareptiles (but not testudines). The third character may have evolved convergently in diadectomorphs and some synapsids, because several early synapsids have no otic trough. We saw no trough in *Eothyris, Varanops* or *Aerosaurus.* A ventral flange of the opisthotic is present in the last two genera, but it is convex and appears anatomically different from the otic trough. Therefore, even if the trough is present in *Casea* as Berman *et al.* (1992) have indicated, synapsids are polymorphic for this character. No other amniotes seem to have the trough. Consequently, we are forced to reject their list of synapomorphies for diadectomorphs and synapsids. However, the analysis of Berman *et al.* (1992) agrees with the present analysis in all other aspects.

Lee (1993) used 16 synapomorphies to argue that pareiasaurids were the closest relatives of testudines, and nine others to argue that *Sclerosaurus* was the sister-group of pareiasaurids and testudines. We were unable to locate the holotype and only known specimen of *Sclerosaurus*, and we prefer not to include it in our analysis because the only source of information would be the literature. Of the 25 characters used by Lee, it appears that only nine may be valid synapomorphies of pareiasaurs and testudines. These are the medially located choana (A1 in his study), the medially located suborbital foramen (A2), the long lateral flange of the exoccipital (A4), the chevrons attached to the anterior centrum only (A11), the acromion process (A12), the reduced fifth pedal digit (A15), the reduced presacral vertebral count (B1), the manual phalangeal formula reduced to 2 3 3 3 3 or less (B5), and the pedal phalangeal formula reduced to 2 3 3 4 3 or less (B7). However, even these characters are not without problems.

The attachment of the chevrons to the anterior centrum (A11 in Lee, 1993, but 91 in this analysis) is problematic because anatomical differences raise doubts about the homology of this character. The haemal arches of testudines attach to a prominent knob located on the posteroventral surface of the centrum, whereas the arch of pareiasaurs articulates in an indentation between successive centra. The latter configuration is more reminiscent of mesosaurs than of testudines.

The acromion process (A12 in Lee, 1993, and 99 in the present analysis) is anatomically different and may not be homologous (see the discussion of this character under Pareiasauria in the results section). In pareiasaurs, the acromion originates high on the scapular blade, but in turtles it extends from the ventral portion of the scapula.

The reduced manual phalangeal formula (B5) and the reduced pedal phalangeal formula (B7) can be considered together and may be a single character because they are usually correlated. These two characters have been kept separate in our analysis to ensure a fair test of Lee's hypothesis. A reduction in the formula (to 2 3 4 4 3) may be present in some procolophonids such as *Tichvinskia* (Ivachnenko, 1979). Lee (1993) argued that pareiasaurs and testudines share a manual phalangeal formula of 2 3 3 3 2, but several testudines have three phalanges in the fifth digit. Therefore, pareiasaurs lost more phalanges than early testudines and the potential synapomorphy between these two taxa should be a manual formula of 2 3 3 3 3. Lee (1993) believed that pareiasaurs and testudines shared a pedal phalangeal formula of 2 3 3 4 3, but no testudine has more than three phalanges in the fourth digit. Therefore, the phalangeal count of pareiasaurs is not identical to the count of testudines. A significant difference between these two taxa is that in pareiasaurs, the phalanges are discoid, suggesting graviportal modifications, whereas the phalanges of testudines are moderately long, possibly for digging or swimming rather than supporting a heavy body.

The other characters (A3, A5, and A6) cited by Lee (1993) cannot be potential synapomorphies of pareiasaurs and testudines because Lee did not establish their correct distribution in amniotes and their close relatives. A longer, unpublished version of his phylogenetic analysis may deal with this problem, but it was not available for study. The massive horizontal paroccipital process sutured to the squamosal and supratemporal (A3) is problematic because this configuration is not really similar to the condition found in testudines. In testudines, the paroccipital process is sutured to the squamosal and the quadrate. In pareiasaurs, the paroccipital process is sutured to the squamosal and the supratemporal. This condition is also found in millerettids and seems to be primitive for parareptiles (see the discussion of character 57 above).

The basisphenoid–basioccipital suture (A5) is problematic and seems to be primitive for cotylosaurs because it is found in captorhinids, synapsids, diadectomorphs and *Seymouria*, as well as in pareiasaurs and testudines (see discussion of character 61 above). This character cannot be evaluated in mesosaurs and romeriids. Furthermore, this character depends partly on size and growth; juvenile individuals often retain the ventral cranial fissure even when adults have a solid contact between basisphenoid and basioccipital. Among amniotes, only procolophonids and millerettids seem to lack the contact, and both taxa are known from juvenile specimens. Therefore, the lack of contact between these two elements in procolophonids and millerettids seems to be an autapomorphy of these taxa, if this condition is retained in adults.

The fully ossified medial wall of the prootic (A6) has an ambiguous and poorly documented history. The ossified wall is present in testudines, some pareiasaurs (the wall is present in large, adult individuals) and diadectids. It is absent in synapsids and *Seymouria*. Its presence cannot be established or refuted in any of the other taxa included in this analysis. Therefore, the presence of the wall could be primitive for cotylosaurs. Furthermore, the significance of this character is dubious because diadectids, pareiasaurs and testudines typically have a large, massively ossified skull and braincase, and the cranial anatomy of these taxa (except diadectomorphs) is well represented by dozens of specimens. The skulls of most other taxa are often smaller and are poorly known, and their braincase is often not as well ossified.

Several of the characters used by Lee (1993) to unite pareiasaurs and *Sclerosaurus* to testudines are procolophonian synapomorphies. These include the reduced and anteriorly directed transverse flange of the pterygoid (A7), the supraoccipital represented by a long, high, narrow, solid median ridge sutured to the skull roof along its entire length (A8), the greater trochanter (A14), the prominent supra-acetabular buttress (A16), the tall, narrow scapular blade (B2), the bipartite glenoid (B3), the fusion of the astragalus and calcaneum (B6), and the thick dermal armour (B8; see the discussion of character 122 above).

We consider that the dorsal location of the palate (A9) is difficult to assess because the palate does not appear to be higher in pareiasaurs than in other amniotes. In most Palaeozoic amniotes the palatal surface is domed, but its exact relationship to the rest of the skull is difficult to define and is often poorly reconstructed.

The prominent transverse processes on at least 14 caudals (A10) was changed into ‘‘prominent transverse processes or ribs on at least 13 caudals’’ for this analysis, because procolophonids have ribs on 13 caudal vertebrae. No procolophonid specimen that we have been able to examine has more than 13 caudal vertebrae preserved (deBraga, personal communication). A distinct increase in the number of transverse processes or ribs is a synapomorphy of the Procolophonia (see discussion of character 90 above).

The presence of an ectepicondylar foramen (A13) seems to be primitive for parareptiles because the foramen is present in millerettids and some mesosaurs, in addition to pareiasaurs and testudines (see discussion of character 102 above).

The anterodorsal orientation of the long axis of the glenoid (B4) is a dubious character because the presence of this condition in pareiasaurs is difficult to verify. The tilting is modest, at best, in *Proganochelys* and is present in procolophonids. Therefore, this character, if valid, may unite procolophonians.

The loss of gastralia (B9) is present in pareiasaurs, but this character is difficult to evaluate in testudines. The plastron is made of dermal bone, and the presence of ventral dermal ossifications in testudines is believed to reflect a primitive developmental potential homologous to that of other vertebrates (Burke, 1989). Therefore, the plastron may represent modified gastralia or a drastic reorganization of the tissues giving rise to gastralia. Whether or not this is homologous to the loss of gastralia in pareiasaurs seems to be dubious at best. The loss of gastralia may be an autapomorphy of pareiasaurs.

Amniote phylogeny and the fossil record

The oldest known amniotes were found in the Middle Pennsylvanian locality of Joggins, Nova Scotia (Carroll, 1964). The specimens found at Joggins usually consist of disarticulated skeletons preserved at the bottom of fossil tree stumps. At least two amniotes are present at Joggins: *Hylonomus*, believed to be a close relative of *Paleothyris*, and *Protoclepsydrops.* The affinities of the latter are difficult to assess because of the fragmentary nature of the known specimens, but it has usually been considered to be a synapsid (Reisz, 1986). Even if *Protoclepsydrops* does not belong to Synapsida, the latter is represented by ophiacodontids from only slightly younger localities (Reisz, 1972).

The presence at Joggins of an early synapsid and an early eureptile and the new phylogeny indicate that two important dichotomies in amniote evolution occurred before the appearance of the oldest known amniotes in the fossil record. These are the synapsid–sauropsid and the parareptile–eureptile dichotomies. This line of evidence suggests that the initial stages of evolutionary radiations of these taxa are indeed poorly represented in the fossil record (Fig. 9). Our phylogeny also indicates that extant amniotes are part of three separate clades that extend well into the Palaeozoic (Synapsida, Parareptilia and Eureptilia). These three clades are represented in the Palaeozoic by large evolutionary radiations that form the bulk of terrestrial fossil remains of that era.

Previous reports of Lower Pennsylvanian or Mississippian amniotes are inaccurate. *Romeriscus* was erected as a new limnoscelid at a time when limnoscelids were believed to be early amniotes (Baird & Carroll, 1967). However, limnoscelids are now unanimously believed to be diadectomorphs (Berman *et al.*, 1992), and *Romeriscus* has been reinterpreted as a nomen dubium (Laurin & Reisz, 1992).

Westlothiana, believed initially to be a Lower Carboniferous amniote, has been described from the East Kirkton Limestone (Smithson, 1989). However, a recent analysis of early tetrapods suggests that it does not belong to Amniota but is closely related to diadectomorphs (Carroll, in press).

The new phylogeny indicates that the fossil record of early turtles may not be as incomplete as previously believed (Fig. 9). The phylogeny advocated by Gauthier *et al.* (1988b) implied that turtles arose at the beginning of the Lower Permian, if not earlier, because their proposed sister-group (captorhinids) is known from almost the base of the Permian (Clark & Carroll, 1973). This implied a gap of about 80 million years in the fossil record of early turtles (Fig. 9). By comparison, the phylogeny presented here implies that the lineages that led to turtles and procolophonids differentiated no later than toward the end of the Upper Permian, because the earliest procolophonids are known

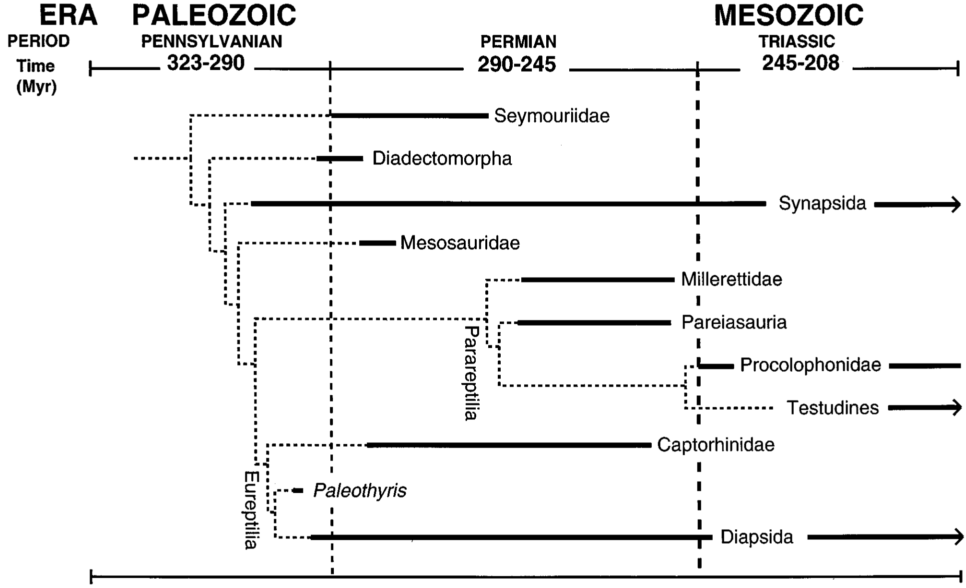

Figure 9. Amniote phylogeny and the fossil record. Notice that of all the suggested fossil relatives of testudines (procolophonids, pareiasaurs and captorhinids), procolophonids are the youngest. Therefore, this phylogeny minimizes the implied gap in the fossil record of testudines and its relatives.

from the Lower Triassic. This gap spans approximately 40 million years. The stratigraphic fit of our phylogeny was compared with that of Gauthier *et al.* (1988b) using the stratigraphic parsimony option of MacClade 3.0 (Maddison & Maddison, 1992). Our phylogeny had a slightly better fit, with nine steps instead of ten (see Appendix 4), even though it was not the stratigraphically shortest tree (which required only six steps). If pareiasaurs were the sister-group of turtles as Lee (1993) suggested, the lineage that led to testudines would have originated in the Lower Permian.

Strengths of the new phylogeny

The proposed phylogeny for parareptiles is fairly well supported. If we use the number of extra steps required to collapse nodes as an index of their strength (Table 1), the strongest node is the Procolophonia, and the next strongest are the Parareptilia and the Testudinomorpha. The overwhelming support for the Procolophonia is partly the result of incorporating the characters used by Lee (1993) to link pareiasaurs to testudines. Several of his characters are found in procolophonids and strongly support the monophyly of the Procolophonia.

A bootstrap analysis was also undertaken to assess the relative strength of the clades (Table 1). Bootstrapping in this case consists of sampling with replacement the original list of characters to produce a matrix of the same size as the original matrix. The shortest tree(s) are found, and the procedure is repeated for a second iteration. At least 20 such iterations should be undertaken, but a higher number is preferable (Swofford, 1993). For this study, 200 iterations were done. There is a loose correlation between the number of extra steps required to break a node and its statistical significance as estimated by a bootstrap analysis (Table 1). The only taxa that are statistically significant at a 95% threshold are the Procolophonia and the Parareptilia.

Weaknesses of the new phylogeny

Some parts of our amniote phylogeny are somewhat problematic (see Table 1 and Appendix 3). Because the focus of our study was parareptiles, we did not search intensively for new characters that would resolve relationships in eureptiles. Therefore, the low number of extra steps required to break the Romeriida (two steps) should not be interpreted strictly as representing a weakness within the eureptile clade. Nevertheless, eureptile phylogeny needs to be corroborated by more characters and detailed anatomical studies. Furthermore, the potential relatives of *Plaeothyris*, such as *Protorothyris, Hylonomus* and *Anthracodromeus*, need to be restudied. As currently defined, the Protorothyrididae may be paraphyletic. If the monophyly of the Protorothyrididae were supported, more meaningful studies of eureptile phylogeny could be attempted.

The low number of steps required to break the Reptilia and the Sauropsida is problematic. Despite detailed preliminary studies and comparisons of original materials (performed by Sean P. Modesto), we were unable to establish with great confidence the position of mesosaurs. Making mesosaurs the sister-group of Parareptilia requires a single extra step.

The Romeriida is the weakest taxon in our phylogeny according to the bootstrap analysis (Table 1). Paradoxically, although the Sauropsida requires fewer extra steps than the Romeriida to collapse, it is much stronger according to the bootstrap analysis. The difference is difficult to interpret.

The bootstrap algorithm of PAUP found a few trees (about 13%) in which pareiasaurs were the sister-group of testudines, as suggested by Lee (1993), but this clade was less frequently found than a group including mesosaurs and parareptiles (25%), parareptiles and younginiforms (22%), and limnoscelids and amniotes (21%). Therefore, Lee's (1993) phylogeny cannot be supported using our data.

The relative strength of clades has often been assessed by the number of characters supporting them (Gauthier *et al.*, 1988a and b; Lee, 1993). We consider that this procedure (Table 1) is somewhat misleading in that it greatly overestimates the support for clades when convergence is a major component in a matrix. For instance, the Reptilia requires only one extra step to collapse (Table 1) and was found in only 67% of the trees in the bootstrap analysis (Table 1), but it is supported by four unambiguous and three ambiguous characters. The difference between the number of extra steps required to collapse the Reptilia and the number of unambiguous characters supporting it reflects convergent characters that could support alternative clades. In this case, three unambiguous characters could support the inclusion of mesosaurs in the Reptilia as the sister-group of the Parareptilia. The number of unambiguous characters supporting various clades also gives a poor estimate of the relative strength of the taxa because the Sauropsida is supported by only three unambiguous characters, but it requires two extra steps to collapse (more than the Reptilia). Therefore, authors should assess the relative strength of the clades found in their analyses by the number of extra steps required to collapse the nodes or by bootstrapping.

We hope that this phylogeny is a significant improvement on previous phylogenetic analyses, but at the very least it has exposed the weaknesses within the amniote clade. The Reptilia, Eureptilia, Romeriida, and Diapsida were only weakly supported by our data. A thorough reexamination of protorothyridids and their relationships to captorhinids and diapsids may lead to a strengthening of the Eureptilia and Romeriida, or a different taxonomic arrangement. Furthermore, the Parareptilia needs to be studied in greater detail. Russian parareptiles such as *Lanthanosuchus, Nycteroleter, Nyctiphruretus* and *Macroleter* do not seen to fit into the Procolophonidae, the Pareiasauria or the Millerettidae. A consideration of these taxa is beyond the scope of this study and would be premature because they are under study. However, their inclusion in a phylogeny of amniotes will certainly be informative and may change our perception of parareptile evolution. Mature specimens of millerettids are also under study (by C. E. Gow) but we chose to include millerettids in this study because of the large body of literature and the specimen that we were able to examine. Nevertheless, the publication of a description of a well-ossified, mature millerettid will certainly improve our knowledge of these early parareptiles, because published descriptions were based on juvenile individuals.

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REFERENCES

Baird D, Carroll RL. 1967. *Romeriscus*, the oldest known reptile. *Science* **157:** 56–59.

Baur G. 1887. On the phylogenetic arrangement of the Sauropsida. *Journal of Morphology* **1:** 93-104.

Baur G. 1889. *Palaeohatteria* Credner, and the Proganosauria. *American Journal of Science and Arts* **37:** 310–313.

Benton MJ. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* **84:** 97–164.

Berman DS. 1971. A small skull of the Lower Permian reptile *Diadectes* from the Washington formation, Dunkard group, West Virginia. *Annals of the Carnegie Museum of Natural History* **43:** 33–46.

Berman DS, Martens T. 1993. First occurrence of *Seymouria* (Amphibia: Batrachosauria) in the Lower Permian Rotliegend of central Germany. *Annals of the Carnegie Museum of Natural History* **62:** 63–79.

Berman DS, Reisz RR. 1982. Restudy of *Mycterosaurus longiceps* (Reptilia, Pelycosauria) from the Lower Permian of Texas. *Annals of the Carnegie Museum of Natural History* **51:** 423–453.

Berman DS, Reisz RR. 1986. Captorhinid reptiles from the Early Permian of New Mexico, with description of a new genus and species. *Annals of the Carnegie Museum of Natural History* **55:** 1–28.

Berman DS, Reisz RR, Eberth DA. 1987. *Seymouria sanjuanensis* (Amphibia, Batrachosauria) from the Lower Permian Cutler Formation of north-central New Mexico and the occurrence of sexual dimorphism in that genus questioned. *Canadian Journal of Earth Sciences* **24:** 1769–1784.

Berman DS, Sumida SS. 1990. A new species of *Limnoscelis* (Amphibia, Diadectomorpha) from the Late Pennsylvanian Sangre de Cristo formation of central Colorado. *Annals of the Carnegie Museum of Natural History* **59:** 303–341.

Berman DS, Sumida SS, Lombard RE. 1992. Reinterpretation of the temporal and occipital region in *Diadectes* and the relationships of diadectomorphs. *Journal of Paleontology* **66:** 481–499.

Boonstra LD. 1930. A contribution of the cranial osteology of *Pareiasaurus serridens* (Owen). *Annale van die Universiteit van Stellenbosch* **8:** 1–18.

Boonstra LD. 1932a. Pareiasaurian studies. Part VII. On the hind limb of the two little-known pareiasaurian genera: *Anthedon* and *Pareiasaurus. Annals of the South African Museum* **28:** 429–435.

Boonstra LD. 1932b. Pareiasaurian studies. Part VIII. The osteology and myology of the locomotor apparatus. B—Fore limb. *Annals of the South African Museum* **28:** 437–503.

Boonstra LD. 1934a. Pareiasaurian studies. Part X. The Dermal Armour. *Annals of the South African Museum* **31:** 39–48.

Boonstra LD. 1934b. Pareiasaurian studies. Part IX. The Cranial Osteology. *Annals of the South African Museum* **31:** 1–38.

Boonstra LD. 1935. On a pareiasaurian reptile from South Africa, *Bradyasurus whaitsi. American Museum Novitates* **770:** 1–4.

Brinkman D. 1988. Size-independent criteria for estimating relative age in *Ophiacodon* and *Dimetrodon* (Reptilia, Pelycosauria) from the Admiral and Lower Belle Plains formations of West-central Texas. *Journal of Vertebrate Paleontology* **8:** 172–180.

Brinkman DB, Berman DS, Eberth DA. 1984. A new araeoscelid reptile, *Zarcasaurus tanyderus*, from the Cutler Formation (Lower Permian) of north central New Mexico. *New Mexico Geology, 1984:* 34–39.

Broom R. 1924a. On the classification of the reptiles. *Bulletin of the American Museum of Natural History* **51:** 39–65.

Broom R. 1924b. Further evidence on the structure of the Eosuchia. *Bulletin of the American Museum of Natural History* **51:** 67–76.

Broom R. 1938. On a new type of primitive fossil reptile from the Upper Permian of South Africa. *Proceedings of the Zoological Society of London* **108:** 535–542.

Burke AC. 1989. Development of the turtle carapace: implications for the evolution of a novel bauplan. *Journal of Morphology* **199:** 363–378.

Carroll RL. 1964. The earliest reptiles. *Zoological Journal of the Linnean Society* **45:** 61–83.

Carroll RL. 1969. A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology* **43:** 151–170.

Carroll RL. 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society* **B293:** 315–383.

Carroll RL. 1982. Early evolution of reptiles. *Annual Review of Ecology and Systematics* **13:** 87–109.

Carroll RL. 1988. *Vertebrate Paleontology and Evolution.* New York: W. H. Freeman.

Carroll RL. 1991. The origin of reptiles. In: Schultze H-P, Trueb L, eds. *Origins Of The Higher Groups Of Tetrapods—Controversy And Consensus.* Ithaca: Comstock Publishing Associates, 331–353.

Carroll RL. in press. Phylogenetic analysis of Paleozoic choanates. In: Janvier P, Arsenault M, eds. *Proceedings Of The 7th International Symposium On Early Vertebrates.* Lawrence: University of Kansas.

Carroll RL, Currie PJ. 1991. The early radiation of diapsid reptiles. In: Schultze H-P, Trueb L, eds. *Origins Of The Higher Groups Of Tetrapods—Controversy And Consensus.* Ithaca: Comstock Publishing Associates, 354–424.

Carroll RL, Gaskill P. 1978. *The Order Microsauria.* Memoirs of the American Philosophical Society. Philadelphia: American Philosophical Society.

Carroll RL, Lindsay W. 1985. Cranial anatomy of the primitive reptile *Procolophon. Canadian Journal of Earth Sciences* **22:** 1571–1587.

Case EC. 1907. Restoration of *Diadectes. Journal of Geology* **15:** 556–559.

Case EC. 1911. A revision of the Cotylosauria of North America. *Carnegie Institution of Washington Publication* **145:** 1–122.

Case EC, Williston SW. 1912. A Description of the Skulls of *Diadectes lentus* and *Animasaurus carinatus. American Journal of Science* **33:** 339–348.

Clark J, Carroll RL. 1973. Romeriid Reptiles from the Lower Permian. *Bulletin of the Museum of Comparative Zoology* **144:** 353–407.

Colbert EH, Kitching JW. 1975. The Triassic Reptile *Procolophon* in Antarctica. *American Museum Novitates* **2566:** 1–23.

Cope ED. 1880. The skull of *Empedocles. The American Naturalist* **14:** 304.

Currie PJ. 1980. A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. *Canadian Journal of Earth Sciences* **17:** 500–511.

Currie PJ. 1981a. The vertebrae of *Youngina* (Reptilia: Eosuchia). *Canadian Journal of Earth Sciences* **18:** 815–818.

Currie PJ. 1981b. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. *Palaeontologia Africana* **24:** 99–168.

Currie PJ. 1982. The osteology and relationships of *Tangasaurus mennelli* Haughton (Reptilia, Eosuchia). *Annals of the South African Museum* **86:** 247–265.

Currie PJ, Carroll RL. 1984. Ontogenetic changes in the eosuchian reptile *Thadeosaurus. Journal of Vertebrate Paleontology* **4:** 68–84.

Dilkes DW, Reisz RR. 1986. The axial skeleton of the Early Permian reptile *Eocaptorhinus laticeps* (Williston). *Canadian Journal of Earth Sciences* **23:** 1288–1296.

Evans SE. 1987. The branicase of *Youngina capensis* (Reptilia: Diapsida; Permian). *Neuen Jahrbuch für Geologie und Paläeontologie. Monatsshefte, 1987:* 193–203.

Evans SE. 1988. The early history and relationships of the Diapsida. In: Benton MJ, ed. *The phylogeny and classification of the tetrapods.* Oxford: Clarendon Press, 221–260.

Fox RC, Bowman MC. 1966. Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). *Paleontological Contributions. University of Kansas* **11:** 1–79.

Fracasso MA. 1983. Cranial Osteology, Functional Morphology, Systematics and Paleoenvironment of *Limnoscelis paludis* Williston. Ph.D thesis, Yale, 1–624.

Gaffney ES. 1975a. A phylogeny and classification of the higher categories of turtles. *Bulletin of the American Museum of Natural History* **155:** 387–436.

Gaffney ES. 1975b. *Solnhofia parsoni*, a new cryptodiran turtle from the Late Jurassic of Europe. *American Museum Novitates* **2576:** 1–25.

Gaffney ES. 1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys. Bulletin of the American Museum of Natural History* **157:** 487–544.

Gaffney ES. 1979a. Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History* **164:** 65–376.

Gaffney ES. 1979b. The Jurassic turtles of North America. *Bulletin of the American Museum of Natural History* **162:** 91–136.

Gaffney ES. 1980. Phylogenetic relationships of the major groups of amniotes. In: Panchen AL, ed. *The Terrestrial Environment and the Origin of Land Vertebrates.* London: Academic Press, 593–610.

Gaffney ES. 1990. The comparative osteology of the Triassic turtle *Proganochelys. Bulletin of the American Museum of Natural History* **194:** 1–263.

Gaffney ES, Hutchinson JH, Jenkins FA, Jr, Meeker LJ. 1987. Modern turtle origins: The oldest known cryptodire. *Science* **237:** 289–291.

Gaffney ES, McKenna MC. 1979. A Late Permian captorhinid from Rhodesia. *American Museum Novitates* **2688:** 1–15.

Gaffney ES, Meylan PA. 1988. A phylogeny of turtles. In: Benton MJ, ed. *The Phylogeny and Classification of the Tetrapods.* Oxford: Clarendon Press, 157–219.

Gaffney ES, Meylan PA, Wyss AR. 1991. A computer assisted analysis of the relationships of the higher categories of turtles. *Cladistics* **7:** 313–335.

Gao K. 1989. Pareiasaurs from the Upper Permian of north China. *Canadian Journal of Earth Sciences* **26:** 1234–1240.

Gauthier J. 1984. A Cladistic Analysis of the Higher Systematic Categories Of The Diapsida. Ph.D thesis, University of California at Berkeley.

Gauthier J, Estes R, de Queiroz K. 1988a. A phylogenetic analysis of Lepidosauromorpha. In: Estes R, Pregill G, eds. *Phylogenetic Relationships Of The Lizard Families.* Stanford: Stanford University Press, 15–98.

Gauthier J, Kluge AG, Rowe T. 1988b. The early evolution of the Amniota. In: Benton MJ, ed. *The Phylogeny And Classification Of The Tetrapods*. Oxford: Clarendon Press, 103–155.

Gow CE. 1972. The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). *Journal of Zoology (London)* **167:** 219–264.

Gow CE. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana* **18:** 89–131.

Gregory WK. 1946. Pareiasaurs versus placodonts as near ancestors to the turtles. *Bulletin of the American Museum of Natural History* **86:** 275–326.

Haeckel E. 1866. *Generelle Morphologie Der Organismen.* Berlin: Reimer.

Harris JM, Carroll RL. 1977. *Kenyasaurus*, a new eosuchian reptile from the Early Triassic of Kenya. *Journal of Plaeontology* **51:** 139–149.

Hauser DL, Presch W. 1991. The effect of ordered characters on phylogenetic reconstruction. *Cladistics* **7:** 243–265.

Heaton MJ. 1979. Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas. *Bulletin of the Oklahoma Geological Survey* **127:** 1–84.

Heaton MJ. 1980. The Cotylosauria: A Reconsideration of a Group of Archaic Tetrapods. In: Panchen AL, ed. *The Terrestrial Environment and the Origin of Land Vertebrates.* London: Academic Press, 497–551.

Heaton MJ, Reisz RR. 1980. A skeletal reconstruction of the Early Permian captorhinid reptile *Eocaptorhinus laticeps* (Williston). *Journal of Paleontology* **54:** 136–143.

Heaton MJ, Reisz RR. 1986. Phylogenetic relationships of captorhinomorph reptiles. *Canadian Journal of Earth Sciences* **23:** 402–418.

Holmes R. 1977. The osteology and musculature of the pectoral limb of small captorhinids. *Journal of Morphology* **152:** 101–140.

Hopson JA. 1991. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids. In: Schultze HP, Trueb L, eds. *Origins Of The Higher Groups Of Tetrapods—Controversy And Consensus.* Ithaca: Comstock Publishing Associates, 635–693.

Huene F. von. 1941. Osteologie und systematische Stellung von *Mesosaurus. Palaeontographica. Abteilung A. Palaeozoologie-Stratigraphie* **92:** 45–58.

Hunt TJ. 1958. The ordinal name for tortoises, terrapins and turtles. *Herpetologica* **14:** 148–150.

Huxley TH. 1864. *Lectures On The Elements Of Comparative Anatomy.* London, J. Churchill.

Ivachnenko MF. 1979. Permian and Triassic procolophonoids of the Russian platform. *Akademiya Nauk SSSR* **164:** 1–80 (in Russian).

Ivachnenko MF. 1987. Permian parareptiles of U.S.S.R. *Akademiya Nauk SSSR* **223:** 1–159 (in Russian).

Kemp TS. 1974. The braincase and associated structures of the cotylosaur reptile *Procolophon trigoniceps* Owen. *Annals of the South African Museum* **64:** 11–26.

Kemp TS. 1985. Synapsid reptiles and the origin of higher taxa. *Special Papers in Palaeontology* **33:** 175–184.

Langston W. 1965. *Oedaleops campi* (Reptilia: Pelycosauria) new genus and species from the Lower Permian of New Mexico, and the family Eothyrididae. *Bulletin of the Texas Memorial Museum* **9:** 1–47.

Langston W, Reisz RR. 1981. *Aerosaurus wellesi*, new species, a varanopseid mammal-like reptile (Synapsida: Pelycosauria) from the Lower Permian of New Mexico. *Journal of Vertebrate Paleontology* **1:** 73–96.

Laurin M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society* **101:** 59–95.

Laurin M. 1993. Anatomy and relationships of *Haptodus garnettensis*, a Pennsylvanian synapsid from Kansas. *Journal of Vertebrate Paleontology* **13:** 200–229.

Laurin M, Reisz RR. 1989. Taxonomic position and phylogenetic relationships of *Colobomycter pholeter*, a small reptile from the Lower Permian of Oklahoma. *Canadian Journal of Earth Sciences* **26:** 544–550.

Laurin M, Reisz RR. 1992. A reassessment of the Pennsylvanian tetrapod *Romeriscus. Journal of Vertebrate Paleontology* **12:** 524–527.

Lee MSY. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science* **261:** 1716–1720.

Li JL. 1989. A new genus of Procolophonidae from Lower Triassic of Shaanxi, China. *Vertebrata Palasiatica* **27:** 248–267.

Linnaeus C. 1758. *Systema Naturae.* 10 ed., Stockholm.

Lydekker R. 1888. *Catalogue Of The Fossil Reptilia And Amphibia In The British Museum (Natural History), Part I. Containing The Orders Orinthosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, And Proterosauria.* London: British Museum (Natural History).

Lydekker R. 1889. *Catalogue Of The Fossil Reptilia And Amphibia In The British Museum (Natural History), Part II. Containing The Orders Ichthyopterygia And Sauropterygia.* London: British Museum (Natural History).

Lydekker R. 1890. *Catalogue Of The Fossil Reptilia And Amphibia In The British Museum (Natural History), Part IV. Containing The Orders Anomodontia, Ecaudata, Caudata, And Labyrinthodontia; And Supplement.* London: British Museum (Natural History).

Mabee PM. 1989. Assumptions underlying the use of ontogenetic sequences for determining character state order. *Transactions of the American Fisheries Society* **118:** 151–158.

MacGregor JH. 1908. On *Mesosaurus brasiliensis* nov. sp. from the Permian of Brasil. In: White IC, ed. *Commissao de Estudos Minas de Carvao de Pedras do Brasil.* Rio de Janeiro: National Press, 301–336.

Maddison WP, Maddison DR. 1992. *Macclade: Analysis Of Phylogeny And Character Evolution. Version 3.0.* Sunderland, Massachusetts: Sinauer Associates.

Mickevich MF, Lipscomb D. 1991. Parsimony and the choice between different transformations for the same character set. *Cladistics* **7:** 111–139.

Olson EC. 1936. Notes on the skull of *Youngina capensis* Broom. *Journal of Geology* **44:** 523–533.

Olson EC. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana Geology* **11:** 1–53.

Olson EC. 1950. The temporal region of the Permian reptile *Diadectes. Fieldiana Geology* **10:** 63–77.

Olson EC. 1965. Relationships of *Seymouria, Diadectes,* and *Chelonia. The American Zoologist* **5:** 295–307.

Olson EC. 1966. Relationships of *Diadectes. Fieldiana Geology* **14:** 199–227.

Olson EC. 1968. The family Caseidae. *Fieldiana Geology* **17:** 225–349.

Osborn HF. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs from the American Museum of Natural History* **1:** 265–270.

Parsons TS, Williams EE. 1961. Two Jurassic turtle skulls: a morphological study. *Bulletin of the Museum of Comparative Zoology* **125:** 43–107.

Piveteau J. 1926. Paléontologie de Madagascar. XIII. Amphibiens et reptiles Permiens. *Annals de paléontologie* **15:** 53–180.

Reisz RR. 1972. Pelycosaurian reptiles from the Middle Pennsylvanian of North America. *Bulletin of the Museum of Comparative Zoology* **144:** 27–62.

Reisz RR. 1975. Pennsylvanian pelycosaurs from Linton, Ohio and Nyrany, Czechoslovakia. *Journal of Paleontology* **49:** 522–527.

Reisz RR. 1980a. A protorothyridid captorhinomorph reptile from the Lower Permian of Oklahoma. *Life Sciences Contributions, Royal Ontario Museum* **121:** 1–16.

Reisz RR. 1980b. The Pelycosauria: A review of phylogenetic relationships. In: Panchen AL, ed. *The Terrestrial Environment And The Origin Of Land Vertebrates.* London: Academic Press, 553–592.

Reisz RR. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *University of Kansas Publications of the Museum of Natural History* **7:** 1–74.

Reisz RR. 1986. Pelycosauria. *Encyclopedia of Paleoherpetology* **17A:** 1–102.

Reisz RR, Baird D. 1983. Captorhinomorph 'stem' reptiles from the Pennsylvanian coal-swamp deposit of Linton, Ohio. *Annals of the Carnegie Museum of Natural History* **52:** 393–411.

Reisz RR, Berman DS, Scott D. 1984. The anatomy and relationships of the Lower Permian reptile *Araeoscelis. Journal of Vertebrate Paleontology* **4:** 57–67.

Reisz RR, Berman DS, Scott D. 1992. The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Pelycosauria: Sphenacodontidae) from the early Permian of Texas. *Zoological Journal of the Linnean Society* **104:** 127–184.

Reisz RR, Laurin M. 1991. *Owenetta* and the origin of turtles. *Nature* **349:** 324–326.

Ricqlès A. de 1984. Remarques systématiques et méthodologiques pour servir à l'étude de la famille des Captorhinidés. *Annales de paléontologie* **70:** 1–39.

Rieppel O. 1980. The skull of the Upper Jurassic cryptodire turtle *Thalassemys*, with a reconsideration of the chelonian braincase. *Paleontographica. Abteilung A. Palaeozoologie-Stratigraphie* **171:** 105–140.

Rieppel O. 1993a. Euryapsid relationships: A preliminary analysis. *Neuen Jahrbuch für Geologie und Paläontologie. Abhandlungen* **188:** 241–264.

Rieppel O. 1993b. Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *Journal of Vertebrate Paleontology* **13:** 31–47.

Romer AS. 1937. New genera and species of pelycosaurian reptiles. *Proceedings of the New England Zoological Club* **16:** 89–96.

Romer AS. 1945. *Vertebrate Paleontology.* 2nd ed., Chicago: University of Chicago Press.

Romer AS. 1946. The primitive reptile *Limnoscelis* restudied. *American Journal of Science* **244:** 149–188.

Romer AS. 1956. *Osteology of the reptiles.* Chicago: The University of Chicago Press.

Romer AS. 1966. *Vertebrate Paleontology* 3rd ed., Chicago: The University of Chicago Press.

Romer AS, Price LI. 1940. *Review of the Pelycosauria.* Vol. 28. Geological Society of America, Special Papers, New York: Arno Press.

Rowe T. 1986. Osteological diagnosis of Mammalia, L. 1758, and its Relationship to Extinct Synapsida. Ph.D thesis, University of California at Berkeley.

Rowe T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* **8:** 241–264.

Seeley HG. 1888. Researches on the structure, organisation, and classification of the fossil Reptilia. VI. On the anomodont Reptilia and their allies. *Proceedings of the Royal Society of London* **44:** 381–383.

Sigogneau-Russell D, Russell DE. 1974. Étude du premier caséidé (Reptilia, Pelycosauria) d'Europe occidentale. *Bulletin du Muséum national d'Histoire naturelle de Paris 3ème série* **38:** 145–215.

Slowinski JB. 1993. 'Unordered' versus 'Ordered' characters. *Systematic Biology* **42:** 155–165.

Smithson TR. 1989. The earliest known reptile. *Nature* **342:** 676–678.

Stovall JW, Price LI, Romer AS. 1966. The postcranial skeleton of the giant Permian pelycosaur *Cotylorhynchus romeri. Bulletin of the Museum of Comparative Zoology* **135:** 1–30.

Sumida SS. 1987. Two different vertebral forms in the axial column of *Labidosaurus* (Captorhinomorpha: Captorhinidae). *Journal of Paleontology* **61:** 155–167.

Sumida SS. 1989a. The appendicular skeleton of the Early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. *Journal of Vertebrate Paleontology* **9:** 295–313.

Sumida SS. 1989b. Reinterpretation of vertebral structure in the Early Permian pelycosaur *Varanosaurus acutirostris* (Amniota, Synapsida). *Journal of Vertebrate Paleontology* **9:** 451–458.

Sumida SS, Lombard RE. 1991. The atlas-axis complex in the Late Paleozoic genus *Diadectes* and the characteristics of the atlas-axis complex across the amphibian to amniote transition. *Journal of Paleontology* **65:** 973–983.

Swofford DL. 1993. *PAUP: Phylogenetic Analysis Using Parsimony.* Version 3.1. Champaign: Illinois Natural History Survey.

Thommasen H, Carroll RL. 1981. *Broomia*, the oldest known millerettid reptile. *Palaeontology* **24:** 379–390.

Vaughn PP. 1955. The Permian reptile *Araeoscelis* restudied. *Bulletin of the Museum of Comparative Zoology* **113:** 305–467.

Vaughn PP. 1966. *Seymouria* from the Lower Permian of Southeastern Utah, and possible sexual dimorphism in that genus. *Journal of Paleontology* **40:** 603–612.

Watson DMS. 1914. *Procolophon trigoniceps*, a cotylosaurian reptile from South Africa. *Proceedings of the Zoological Society of London, 1914:* 735–747.

Watson DMS. 1917. A sketch classification of the pre-Jurassic tetrapod vetebrates. *Proceedings of the Zoological Society of London, 1917:* 167–186.

Watson DMS. 1918. On *Seymouria*, the most primitive known reptile. *Journal of Zoology (London)* **2:** 267–301.

Watson DMS. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. *Philosophical Transactions of the Royal Society* **B240:** 325–400.

Welles SP. 1941. The mandible of a diadectid cotylosaur. *Bulletin of the Department of Geological Sciences of the University of California* **25:** 423–432.

White TE. 1939. Osteology of *Seymouria baylorensis* Broili. *Bulletin of the Museum of Comparative Zoology* **85:** 325–409.

Wild R. 1985. Ein Schädelrest von *Parasaurus geinitzi* H. v. Mayer (Reptilia, Cotylosauria) aus dem Kupferschiefer (Perm) von Richelsdorf (Hessen). *Geologische Blätter für Nordost-Bayern und angrenzende Gebiete* **34/35:** 897–920.

Williston SW. 1911. A new family of reptiles from the Permian of New Mexico. *American Journal of Science* **31:** 378–398.

Williston SW. 1912. Restoration of *Limnoscelis*, a cotylosaur reptile from New Mexico. *American Journal of Science* **34:** 457–468.

Williston SW. 1913. An ancestral lizard from the Permian of Texas. *Science* **38:** 825–826.

Williston SW. 1917. The phylogeny and classification of reptiles. *Contributions from the Walker Museum* **2:** 61–71.

Williston SW. 1925. *The Osteology Of The Reptiles.* Cambridge: Harvard University Press.

APPENDIX 1

List of characters used in this study. Only characters 6, 17, 36, 49, 55, and 94 were ordered.

1. Narial shelf: absent (0); present (1).
2. Frontal orbital contact: absent (0); present (1).
3. Pineal foramen position: in center of parietal or farther posteriorly (0); close to frontoparietal suture (1).
4. Postparietal: paired (0); median (1); absent (2).
5. Postparietal position: dorsally exposed (0); occipital (1).
6. Prefrontal-palatal contact: absent (0); weak (1); strong (2).
7. Prefrontal medial flange: narrow (0); wide (1).
8. Bulbous medial process of prefrontal: absent (0); present (1).
9. Lacrimal narial contact: present (0); absent (1).
10. Foramen orbitonasale: absent (0); represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine (1); enclosed between prefrontal, lacrimal and palatine (2).
11. Jugal anterior process: does not extend to anterior orbital rim (0); extends at least to level of anterior orbital rim (1).
12. Postorbital-supratemporal contact: absent (0); present (1).
13. Postorbital: far from occiput (0); close to occiput (1).
14. Intertemporal: present (0); absent (1).

15. Posterolateral corner of skull roof: formed by tabular (0); formed mostly by supratemporal (1); formed by parietal and small supratemporal (2).

16. Tabular and opisthotic: in contact (0); separated (1).

17. Tabular size: large (0); small (1); absent (2).

18. Supratemporal size: large (0); small (1); absent (2).

19. Anterodorsal process of the maxilla: absent (0); low, does not reach nasal or mid-height of external naris (1); high, reaches nasal and mid-height of external naris (2).

20. Anterior lateral maxillary foramen: equal in size to other maxillary foramina (0); larger than other foramina (1); the lateral surface of the maxilla lacks large foramina (2).

21. Maxillary anterior narial foramen: absent (0); present in maxilla only or between maxilla and premaxilla (1).

22. Maxilla and quadratojugal: in contact (0); separated (1).

23. Quadratojugal: reaches orbit (0); does not reach orbit (1).

24. Caniniform region: present (0); absent (1).

25. Caniniform maxillary tooth: absent (0); present (1).

26. Squamosal and post-temporal fenestra: separated (0); in contact (1).

27. Occipital flange of squamosal: in otic notch and overlaps pterygoid (0); gently convex all along the posterior edge of the skull (1); convex above quadrate emargination and concave medial to tympanic ridge (2); absent (3); medial to tympanic ridge, facing posteromedially (4); medial to tympanic ridge, concave, facing posterolaterally or ventrolaterally (5).

28. Quadratojugal shape: narrow (0); dorsally expanded (1).

29. Upper temporal fenestra: absent (0); present (1).

30. Lower temporal fenestra: absent (0); present (1).

31. Temporal emargination: absent (0); with squamosal and supratemporal (1); with quadratojugal and squamosal (2); facing posteriorly and exposed on occiput, bordered by squamosal, quadratojugal, and quadrate (3).

32. Postorbital region of skull: long (more than 15% of skull length) (0); short (15% of skull length or less) (1).

33. Ventral margin of postorbital region of skull: expanded ventrally (0); rectilinear (1); emarginated (2).

34. Quadrate lateral exposure: absent (0); present (1).

35. Quadrate anterior process: long (0); short (1).

36. Jaw articulation position: posterior to occiput (0); even with occiput (1); anterior to occiput (2).

37. Posterior extension of orbit: absent (0); present (1).

38. Dermal sculpturing: absent (0); tuberosities (1); tuberosities and pits (2); honeycomb pattern of ridges and pits (3).

39. Interpterygoid vacuity: short, less than 15% of skull length (0); absent (1); long, at least 15% of skull length (2).

40. Choana: parallel to maxilla; palatine forms its posterior edge only (0); curved posteromedially; palatine forms its posterior and part of its lateral edge (1).

41. Suborbital foramen: bordered by maxilla or jugal laterally (0); bordered by palatine, pterygoid and in some cases by ectopterygoid laterally (1).

42. Arcuate flange of pterygoid: present (0); absent (1).

43. Cranio-quadrate space: small, quadrate ramus of pterygoid and paroccipital process of opisthotic converge posterolaterally (0); large, quadrate ramus of pterygoid and paroccipital process of opisthotic are parallel to each other (1).

44. Pterygoid anterior extent: reaches level of posterior end of choana (0); posterior to choana (1).

45. Transverse flange of pterygoid orientation: directed posterolaterally or transversely (0); directed anterolaterally (1).

46. Transverse flange of pterygoid dentition: shagreen of denticles, no ventral ridge (0); row of large teeth, no ventral ridge (1); edentulous with ventral ridge (2).

47. Ectopterygoid: large (0); small (1); absent (2).

48. Ectopterygoid dentition: present (0); absent (1).

49. Suborbital foramen: absent (0); present (1); fenestra present (2).

50. Parasphenoid pocket for cervical musculature: present (0); absent (1).

51. Parasphenoid wings: present, parasphenoid broad posteriorly (0); absent, parasphenoid narrow posteriorly (1).

52. Cultriform process: long (0); short (1).

53. Parasphenoid teeth: absent (0); present (1).

54. Supraoccipital anterior crista: absent (0); present (1).

55. Supraoccipital plate: absent (0); broad, plate-like (1); narrow (2); very narrow, reduced to sagittal pillar (3).

56. Paroccipital process: vertically broad (0); antero-posteriorly expanded (1); narrow (2); tabular, composed of opisthotic (3).

57. Contact between paroccipital process and dermatocranium: to tabular (0); to supratemporal and tabular (1); to tabular and squamosal (2); to squamosal and supratemporal (3); to supratemporal (4); to squamosal and quadrate (5); ends freely (6).

58. Otic trough in ventral flange of opisthotic: absent (0); present (1).

59. Medial wall of inner ear (made of prootic): unossified (0); ossified with acoustic nerve foramina (1).

60. Post-temporal fenestra: small (0); large (1).

61. Osseous contact between basioccipital and basisphenoid: present (0); absent (1).

62. Occipital condyle shape: transversely broad (0); reniform to circular (1).

63. Basioccipital tubera: absent (0); paired (1); median (2).

64. Lateral flange of exoccipital: absent (0); present (1).

65. Quadrate condyle articular surfaces: strongly convex, antero-posteriorly long (0); nearly flat, antero-posteriorly short (1).

66. Stapes: massive, perforated (0); slender, imperforate (1).

67. Stapedial dorsal process: ossified (0); unossified (1).

68. Labyrinthodont infolding: present (0); absent (1).

69. Foramen intermandibularis: anterior symphysial foramen (0); two foramina, a symphysial and a posterior foramen located anterior to coronoid process (1); two foramina, a symphysial and a posterior foramen located posterior to or at level of coronoid process (2).

70. Meckelian fossa orientation: faces mediodorsally, prearticular narrow (0); faces dorsally, prearticular broad (1).

71. Fossa meckelii: long, occupies at least 20% of lower jaw length (0); short, occupies less than 20% of lower jaw length (1).

72. Surangular length: extends beyond coronoid eminence (0); does not extend beyond coronoid eminence (1).

73. Accessory lateral shelf on surangular anterior to articular region: absent (0); present (1).

74. Coronoid number: two or three (0); one (1).

75. Prearticular extends: beyond the coronoid eminence (0); no farther than the coronoid eminence (1).

76. Retroarticular process: absent or small and narrow (0); transversely broad, dorsally concave (1).

77. Retroarticular process composition: articular only (0); three or more elements (articular, prearticular, angular and surangular) (1).

78. Lateral shelf on articular region: absent (0); on articular (1); on surangular (2).

79. Coronoid process: small eminence composed of several elements (0); high process composed of coronoid only (1).

80. Splenial: contributes to symphysis (0); excluded from symphysis (1).

81. Presacral vertebral count: more than twenty (0); twenty or less (1).

82. Axial centrum orientation: in plane of axial skeleton (0); sloping anterodorsally (1).

83. Atlantal neural spine size: nearly as tall as axial spine (0); reduced to small spinous process (1).

84. Axial intercentrum: with rounded anteroventral edge (0); with strong anterior process (1).

85. Atlantal pleurocentrum and axial intercentrum: separate elements (0); attached or fused (1).

86. Trunk neural arches: swollen with wide zygapophyseal buttresses (0); narrow (1); swollen with narrow zygapophyseal buttresses (2).

87. Ventral surface of anterior pleurocentra: rounded (0); keeled (1); with double ridge (2).

88. Number of sacral vertebrae: one (0); two (1); three or four (2).

89. Sacral rib distal overlap: broad with narrow gap between ribs (0); small or absent with wide gap between ribs (1).

90. Transverse process or ribs: present on only a few anterior caudals (0); present on at least thirteen caudals (1).

91. Caudal hemal arches: wedged between centra (0); attached to anterior centrum (1).

92. Interclavicle: diamond-shaped (0); T-shaped, with long, slender lateral processes (1).

93. Interclavicle attachment for clavicle: ventral sutural area (0); anteriorly directed groove (1); tightly sutured into plastron (2).

94. Cleithrum: caps scapula anterodorsally (0); does not cap scapula at all (1); absent (2).

95. Scapulocoracoid ossifications: two (0); three (1).

96. Scapula: broad (0); narrow, thin (1); narrow, cylindrical (2).

97. Supraglenoid foramen: present (0); absent (1).

98. Glenoid: anteroposteriorly long, helical (0); short, bipartite (1).

99. Acromion: absent (0); present (1).

100. Sternum: not mineralized (0); mineralized (1).

101. Supinator process: strongly angled relative to shaft, separated from it by a groove (0); parallel to shaft, separated from it by a groove (1); parallel to shaft, not separated from shaft (2).

102. Ectepicondylar foramen and groove: only groove present (0); groove and foramen present (1); only foramen present (2); both absent (3).

103. Entepicondylar foramen: present (0); absent (1).

104. Humerus: with robust heads and a short shaft (0); short and robust, without a distinct shaft (1); slender with long shaft (2).

105. Olecranon process: large, proximal articular facet of ulna faces medially (0); small, proximal articular facet of ulna faces proximally (1).

106. Manual phalangeal formula: 2 3 4 5 3 (0); 2 3 4 4 3 (1); 2 3 3 3 3 or less (2).

107. Dorsolateral shelf on iliac blade: absent (0); present (1).

108. Iliac blade: low, with long posterior process (0); dorsally expanded, distally flaring (1).

109. Acetabular buttress: small, overhangs acetabulum only moderately (0); large, overhangs acetabulum strongly (1).

110. Oblique ventral ridge of femur (adductor crest): present (0); absent (1).

111. Femoral proximal articulation: antero-posteriorly long (0); round (1).

112. Greater trochanter of femur: absent (0); present on posterior edge of femur (1).

113. Femoral shaft: short and broad (0); long and slender (1).

114. Carpus and tarsus: short and broad (0); long and slender (1).

115. Astragalus: absent (0); incorporates incompletely fused tibiale, intermedium, and perhaps centrale 4 (1); without traces of a compound origin.

116. Tibio-astragalar joint: flat (0); tibial ridge fits into astragalar groove (1).

117. Astragalus and calcaneum: separate (0); sutured or fused (1).

118. Medial pedal centrale: present (0); absent (1).

119. Number of distal tarsals: five (0); four or less (1).

120. Fifth pedal digit: longer than first digit (0); more slender and no longer than first digit (1).

121. Metapodials: not overlapping (0); overlapping (1).

122. Pedal phalangeal formula: 2 3 4 5 4 or 3 (0); 2 3 4 4 3 (1); 2 3 3 4 3 or less (2).

123. Ratio between length of metatarsal one to length of metatarsal four: at least 0.5 (0); less than 0.5 (1).

124. Dorsal dermal ossifications: absent (0); present (1).

APPENDIX 2

Data matrix used in this study. Polymorphism is indicated by the states present in the second line below the relevant taxa.

```
                           11111111112222222222333333333344444444445555555555
Taxon             12345678901234567890123456789012345678901234567890123456789
-----------------------------------------------------------------------------
Seymouria         000001000000000000000000000000100000031 0?100000001000?03000
                            1
Limnoscelidae     0001100000111110000000100030000000010020?00001000000101001?
Diadectidae       000111000?011110000000110030001001110101?00010000?000010111
Synapsida         0100100000011110000001001010010000010000?000010000000010200
                  1                     1         1     2          1  1    1
Mesosauridae      010010000?011110000000010?10000110010000?1?0012??0000010???
Millerettidae     01001100020111101001?0100021002011020120000001111110112030?
                                         1     1
Pareiasauria      001001000211011?201111010041003000020201101111111111 0131300
                     1                                                      1
Procolophonidae   1112?2111211011?202110010051002020021000001112111111013140?
Testudines        0012?2101200011?2022101??1510020110200111011122?11110131501
                   1          1 2  2              2    12         2
Captorhinidae     010011000110012?2100001011100000101103200100002?1110012260?
                    1                                                 1
Paleothyris       010010000?000121110000101110000010110020?1000100?11011206??
Araeoscelidia     01001000000001211100000010101100101100200100101021100120?0?
                            1 1         1  1                   1      1
Younginiformes    0100100010101121112000100130110011110020010001112110012260?

                                                          1111111111111111111
                  66666666667777777777888888888899999999990000000000111111111
Taxon             01234567890123456789012345678901234567890123456789012345678
-----------------------------------------------------------------------------
Seymouria         00000011000000000000000000000000000000000000010000000 0?0???
Limnoscelidae     100000??01100000000000011100100?000000000000100100000000???0
Diadectidae       000000001100?01000000001110010??000000000000100110000001?00
                                                                           1
Synapsida         00100000100000000000000110010100000110000000000000000002000
                           1  11           1 1                         11
                           2
Mesosauridae      ??10?0001??0001?1000?01101001001001101000100210000110102001
                                                            1
Millerettidae     111000011?00001000000011011011??0011010001100?001??00112001
Pareiasauria      101011??121110111010011100202111111111110220102011001002011
Procolophonidae   11110111121111111101101101222110112111100230010011011102011
                                                                1
Testudines        10111111?21111111121111101111111122021110111012011111102011
                     2
Captorhinidae     10100000110000100000000110100100000110000230000000000002001
                                                    2
Paleothyris       1?10?0001??0?01?00?0001101111000001100000100200000000112001
Araeoscelidia     1?1000001?0000100000001101011000001100001100200000100112101
                                      1                    21
Younginiformes    1?1000011??0?01?00000??10?111010101001001100010011100112101
                                                            1
```

	1	1	1	1	1	1
	1	2	2	2	2	2
Taxon	9	0	1	2	3	4
Seymouria	?	0	?	0	0	0
Limnoscelidae	?	0	?	0	0	0
Diadectidae	?	0	0	0	0	0
Synapsida	0	0	0	0	0	0
Mesosauridae	0	0	0	0	0	0
Millerettidae	0	0	?	0	1	0
Pareiasauria	1	1	0	2	0	1
Procolophonidae	1	0	1	0	0	0
				1		1
Testudines	1	1	1	2	0	1
					1	
Captorhinidae	0	0	0	0	0	0
Paleothyris	0	0	1	0	0	0
Araeoscelidia	0	0	1	0	1	0
Younginiformes	0	0	1	0	1	0
	1					

APPENDIX 3

List of autapomorphies of taxa. When the level of generality of a character is unknown because of missing data, the character has been placed in the smallest group in which it is found (this is the DELTRAN option in PAUP); therefore, several of these characters could apply to larger taxa than suggested here. The ambiguous status of these characters is identified by an asterisk. Reversals are indicated by a negative sign. When a derived state other than '1' is present, it is indicated in brackets. Reversals to states other than '0' are also indicated in brackets. The presence of polymorphism in a terminal taxon is indicated by at least two numbers in brackets. Several of the characters listed under Younginiformes are actually synapomorphies with saurians. Most characters were unordered. Only characters 6, 17, 36, 49, 55, and 94 were ordered.

Diadectomorpha: 4, 23*, 27*(3), 58, 84, 104, 107.
Diadectidae: 6*, 24, 31*, 34, 35, 38, 40, 45, 57, 59*, 68*, 74, 108, 115*.
Limnoscelidae: 11, 39*(2), 46*, 53, 60, 70.
Amniota: 2, 27*, 46*, 62, 68*, 82, 94, 95, 115*(2).
Synapsida: 22, 25, 30, 57*(2), 86*.
Sauropsida: 33*, 74, 101, 113*, 118.
Mesosauridae: 24*, 32, 42*, 47*(2), 76, 91*, 97*, 104(2), 105, 110, 111.
Reptilia: 17, 49*, 50*, 51, 54, 55(2), 60*.
Parareptilia: 6*, 10(2), 20, 28, 31(2), 36(2), 47*, 48, 57*(3), 67, 89, 97*, 102, 108.
Millerettidae: 23*, 27*(2), 34, 38, 39*(2), 53, 61, 86*, 114, 123.
Procolophonia: 3, -13*, 17(2), 21*, 24*, 43, 44, 45, 52, 55(3), 56, 65, 69*(2), 70, 71, 72, 75, 76, 86*(2), 90*, 92, 93, 96, 98, 109*, 112, 117, 119, 124.
Pareiasauria: -2, -5*, 11*, 19*, 22, 27*(4), 31(3), -33*, 38(2), 40*, 41*, 64*, 78, 81*, -85, 88*(2), 91*, 99*, 101*(2), 102(2), 104, 106*, -113, 120*, 122*.
Testudinomorpha: 4(2), 6(2), 7, 9, 19*(2), 27*(5), 46(2), 63, 66*, 73, 77, 79, 80, 94(2), 105, 111, 121.
Procolophonidae: 1, 8, 11*, 33*(2), 37, 57*(4), 61, 87*(2), 88*(2), 101*(2), 102(3).
Testudines: -12, 20(2), 23*, 26, 34, 39*(1,2), 40*, 41*, 47(2), 57*(5), 59*, 64*, 78(2), 81*, -86*(1), 87*, 91*, 93(2), -95, 96(2), 99*, 103, 106*(2), 110, 120*, 122*(2).
Eureptilia: -12, 15(2), 18, 23*, 25, 26, 35, 39*(2), 42*, -57*(6).
Captorhinidae: 6*, 10, 11*, -13*, 17(2), 38(3), -46, 47*(2), 56(2), 101(2), 102(3), -113.
Romeriida: 16*, 87, 114, 121.
Paleothyris: -13*, 53, 86*, 104*(2).
Diapsida: 29, 30, 47*, 49*(2), 100, 110, 116, 123.
Araeoscelidia: 45, 104*(2).
Younginiformes: 9, 11*, 19(2), -25, 27(3), 34, 48, 56(2), 67, 86*, 90, 92, -95, 97, 105, 108, 109.

APPENDIX 4

Stratigraphic matrix used to evaluate the stratigraphic fit of phylogenies. The age range of the taxa is represented by the states. Therefore, polymorphism here represents temporal duration. The stratigraphic algorithm determines the stratigraphic length of the tree. A shorter tree fits the sequence of appearance of taxa better than a long tree. The geological time was broken into Pennsylvanian (0), Lower Permian (1), Upper Permian (2), Lower and Middle Triassic (3), and Upper Triassic and post-Triassic (4).

Taxa	Age range
Seymouria	Lower Permian
Limnoscelidae	Pennsylvanian and Lower Permian
Diadectidae	Pennsylvanian and Lower Permian
Synapsida	Pennsylvanian to Post-Triassic
Mesosauridae	Lower Permian
Millerettidae	Upper Permian
Pareiasauridae	Upper Permian
Procolophonidae	Lower Triassic to post-Triassic
Testudines	Upper Triassic and post-Triassic
Captorhinidae	Lower Permian and Upper Permian
Paleothyris	Pennsylvanian
Araeoscelidia	Pennsylvanian and Lower Permian
Younginiformes	Upper Permian and Lower and Middle Triassic

APPENDIX 5

Sources of anatomical data for the taxa included in this analysis. These sources were complemented by study of specimens of all the taxa except limnoscelids and younginiforms.

Seymouria: Berman & Martens, 1993; Berman *et al.*, 1987; Vaughn, 1966; Watson, 1918; White, 1939.

Limnoscelidae: Berman & Sumida, 1990; Fracasso, 1983; Romer, 1946; Williston, 1911, 1912.

Diadectidae: Berman, 1971; Berman *et al.*, 1992; Case, 1907; Case & Williston, 1912; Olson, 1947, 1950, 1965, 1966; Rieppel, 1993b; Sumida & Lombard, 1991; Welles, 1941.

Synapsida: Berman & Reisz, 1982; Brinkman, 1988; Langston, 1965; Langston & Reisz, 1981; Olson, 1968; Reisz, 1972, 1975, 1980b, 1986; Romer, 1937; Romer & Price, 1940; Sigogneau-Russell & Russell, 1974; Stovall, Price & Romer, 1966; Sumida, 1989a.

Mesosauridae: Huene, 1941; MacGregor, 1908.

Millerettidae: Broom, 1938; Gow, 1972; Thommasen & Carroll, 1981; Watson, 1957.

Pareiasauria: Boonstra, 1930, 1932a and b, 1934a and b; Gao, 1989; Gregory, 1946; Ivakhnenko, 1987; Lee, 1993; Wild, 1985.

Procolophonidae: Carroll & Lindsay, 1985; Colbert & Kitching, 1975; Ivakhnenko, 1979; Kemp, 1974; Li, 1989; Watson, 1914.

Testudines: Gaffney, 1975b, 1976, 1979a and b, 1990; Gaffney *et al.*, 1987; Parsons & Williams, 1961; Rieppel, 1980.

Captorhinidae: Berman & Reisz, 1986; Dilkes & Reisz, 1986; Fox & Bowman, 1966; Gaffney & McKenna, 1979; Heaton, 1979; Heaton & Reisz, 1980; Holmes, 1977; Sumida, 1987, 1989b.

Paleothyris: Carroll, 1969; Heaton & Reisz, 1986.

Araeoscelidia: Reisz, 1981; Reisz *et al.*, 1984; Vaughn, 1955.

Younginiformes: Broom, 1924b; Carroll, 1981; Currie, 1980, 1981a and b, 1982; Currie & Carroll, 1984; Evans, 1987; Gow, 1975; Harris & Carroll, 1977; Olson, 1936; Piveteau, 1926.