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Reptile phylogeny and the interrelationships of turtles

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A comprehensive analysis of amniote interrelationships is presented in an attempt to test turtle interrelationships. The results refute earlier hypotheses that turtles are related to parareptiles, i.e. to procolophonids or pareiasaurs. Instead, turtles are shown to be the sister-group of Sauropterygia, the two clades being nested within Sauria as sister-group of Lepidosauriformes. This scenario is also supported by several developmental and soft tissue characters which are shown to be congruent with the current phylogeny. The analysis strongly supports a monophyletic Parareptilia, sister-group of a monophyletic Eureptilia. The Diapsida, however, is paraphyletic unless it includes turtles and sauropterygians. Additionally, the position of turtles within Diapsida has major implications for the evolutionary history and/or significance of many characters, i.e. temporal fenestration.

ADDITIONAL KEY WORDS:—Sauropterygia – Eureptilia – Parareptilia – Diapsida – Sauria – turtle – phylogeny – evolution.

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INTRODUCTION

With his discovery that *Sphenodon* differs from agamid lizards by the presence of a lower temporal arch, Günther (1867) set the stage for the classification of reptiles on the basis of the configuration of the temporal region of the skull. In the succeeding years, Baur (1889, 1895) and Cope (1892) developed a theory of fenestration of the reptilian skull. Baur (1895) compared patterns of reduction in the turtle skull to that seen in other (diapsid) reptiles and concluded than even if advanced stages of reduction of the dermatocranium in turtles may result in a *pattern* that resembles the presence of an upper temporal arch, the *process* of reduction is still fundamentally different from temporal fenestration observed in other (diapsid) reptiles. Cope (1892) followed Baur (1895) in the conclusion that the temporal region of the skull in turtles is reduced by emargination from below (from the margin of the subtemporal fossa) and from behind (from the margin of the posttemporal fossa), rather than by fenestration as in other reptiles. Cope (1892) furthermore compared the Chelonia to the Sauropterygia, as he thought that both groups share temporal emargination from below (from the margin of the subtemporal fossa).

On the basis of this earlier work on the fenestration of the temporal region of the skull, Osborn (1903) subdivided the class Reptilia into two subclasses, viz. the Synapsida (none or a single lower temporal fenestra, including 'cotylosaurs', anomodontids, turtles, and sauropterygians) and the Diapsida (two temporal fenestrae, including all other reptiles). A refined classification of the Reptilla was worked out by Williston (1917), who recognized reptiles with a complete temporal roofing as the Anapsida, a subclass that in his view included the 'cotylosaurs' and the Chelonia. subsequently, a 'cotylosaur' affinity of turtles became widely accepted, but the precise relationships of turtles within the Anapsida remained controversial.

Jaekel (1915) stressed the anapsid ('stegal') skull structure of early fossil turtles and hypothesized an origin of turtles from the Cotylosauria *sensu* Cope (1880), in particular from pareiasaurs. A pareiasaur ancestry of turtles was later accepted by Gregory (1946), who rejected placodonts as turtle ancestors (a view first proposed by Jaekel, 1902, 1907), and confirmed that turtles must derive from Upper Pennsylvanian of Lower Permian cotylosaurs. Among these, he found turtles more similar to pareiasaurs than to diadectids, as he was the first to identify the acromion process on the lower end of the anterior edge of the scapular blade in pareiasaurs and turtles. A pareiasaur ancestry of turtles was later supported by Parrington (1962) and Ivachnenko (1987).

Olson (1947) suggested grouping the turtles with diadectomorphs, procolophonids, and pareiasaurs in a group he named the Parareptilia. He later (Olson, 1965) redefined the Parareptilia as a group comprising procolophonids and their possible descendants, pareiasaurs, with the diadectids far removed from the origin of the Chelonia. According to his views, turtles may be derived from either the pareiasaurs, or from procolophonids. By contrast, Romer (1964, 1966, 1968) derived turtles from diadectids, noting in particular similarities in palatal structure in the earliest fossil turtle *Proganochelys* and in *Nyctiphruretus*.

An entirely different line of thought on turtle ancestry was initiated by Seeley (1892) with his description of *Eunotosaurus* from the Upper Permian of South Africa. Seeley (1892) referred *Eunotosaurus* to the Mesosauria, but throughout the description stressed the many similarities of postcranial skeletal structure which the new fossil was supposed to share with the Chelonia. In his re-description of the specimen, Watson (1914a: 1020) concluded that "… although our knowledge of *Eunotosaurus* is too small to admit a definite statement to that effect, it is by no means improbable that it is an actual ancestor of the Chelonia." Cox (1969) finally rejected any relationship of turtles with *Eunotosaurus*; the latter was interpreted as an aberrant synapsid by (Lee, 1993a).

Turtle relationships within anapsid reptiles continue to remain controversial to the present day, but their analysis has received new momentum with the application of cladistic techniques. some of the taxa which Olson (1947) had grouped with his parareptiles have since been removed from the Amniota (diadectids), while others (pareiasaurs, procolophonids) have been assigned to a group of problematical status within the Amniota but excluded from a monophyletic Reptilia, and informally called ‘parareptiles’ (Gauthier *et al.*, 1988a). Whereas Gaffney and collaborators (Gaffney & McKenna, 1979; Gaffney & Meylan, 1988; see also Clark & Carroll, 1973) support a sister-group relationship of the Testudines with the Captorhinidae, recent reconsideration of parareptile interrelationships has found turtles to be most closely related either to procolophonids (Reisz & Laurin, 1991, Laurin & Reisz, 1993), or to pareiasaurs (Lee, 1993b, 1995). All of these most recent analysis of turtle interrelationships were predicated upon the assumption that the Testudines are, in fact, anapsids (Fuchs, 1920; Kilias, 1957), and taxa for comparison were chosen accordingly. Comparisons were restricted to Paleozoic taxa, with Araeoscelidia (Reisz *et al.*, 1984) as stem-group diapsids.

All along, however, there have been dissenting voices on the status of turtles as anapsid reptiles. The study of the jaw adductor musculature led Lakjer (1926) to conclude that turtles might be diapsid (see also discussion in Rieppel, 1990). The complete dermal roofing of the temporal region of the skull in some turtles, including the earliest fossil turtle *Proganochelys* (Gaffney, 1990), would, therefore, be secondary, as was, indeed, argued by Goodrich (1916, 1930). Broom (1924) finally placed turtles close to lepidosaurs (i.e. *Sphenodon*) on the basis of the presence of a thyroid fenestra in the pelvis, and of a hooked fifth metatarsal: “Those who regard the structure of the temporal region of the skull as the safest guide to affinity will naturally place the chelonians either with the primitive mammal-like reptiles or the cotylosaurs; those who hold that more reliance can be placed on the structure of the girdles and limbs will be more impressed with the affinities to the primitive diapsids such as *Sphenodon*” (Broom, 1924: 50). Confirming Baur’s (1886) conclusion that turtles and *Sphendon* share remarkable similarities in the structure of the carpus, the discussion of turtle relationships has thus come full circle.

In this paper we present evidence based on cladistic analysis using parsimony that the Testudines may well be related to diapsids, indeed nested within crown-group diapsids rather than within ‘parareptiles’. This result is generated by adding new taxa never before considered in the cladistic analysis of turtle relationships, such as stem-group Sauropterygia, as well as Mesozoic to Recent diapsids.

METHODS

The phylogenetic analysis presented here includes 33 taxa and 168 characters. The in-group taxa include members of taxa recently defined as the monophyletic Reptilia by Laurin & Reisz (1995). The out-group includes six synapsid taxa as well as the anamniotes Seymouriidae and Diadectomorpha. Some of the characters included in this analysis were taken from Rieppel (1994a), Laurin & Reisz (1995), Lee (1993b, 1994, 1995), and deBraga & Reisz (1996), but the vast majority are original to this study and have either never been described before or have been reinterpreted.

Unlike previous attempts to evaluate turtle relationships where most ‘non-anapsid’ clades were collapsed to yield a generalized primitive representative, this practice was minimized here by including as many unique taxa as was feasible. In the case of Synapsida four well established ‘non-therapsid’, monophyletic families were considered along with two therapsid clades. Characters were scored either by personal observation of the material or by consulting the literature (Kemp, 1969, 1982; Jenkins, 1970, 1971; Sigogneau, 1970; Reisz, 1986; Reisz *et al.*, 1992; Modesto, 1995). Diapsida was also split to include as many of the basal representatives of its many clades as was possible. Data for diapsids were taken directly from personal observation of the material by both authors. Finally, Parareptilia was compiled by including all of the most complete, recently described taxa. Information on the Pareiasauria was obtained mainly from Lee (1994, 1995, 1996a, b), whereas data for *Macroleter*, *Owenetta*, and *Procolophon* are taken from deBraga (personal observation and Ph.D unpublished thesis).

No weight was assigned to any character, and reversals and convergence were treated as equally likely evolutionary events. All characters were left unordered. Character optimization was performed using the delayed transformation (DELTRAN) algorithm of PAUP 3.1.1 (Swofford, 1993) which minimizes the number of synapomorphies at any given node. Character polarity was constructed by comparison with outgroup taxa (Seymouriidae, Diadectomorha, and Synapsida). Tree rooting was based on two methods: rooting by outgroup, and rooting on an all zero hypothetical ancestor. Data were compared and although tree lengths were different, the tree topology remained unchanged.

Due to the enormous size of the matrix, the data set was subjected to an heuristic search using the options ‘stepwise addition’ and ‘random search’ with 20 replicates. In each case the results were the same.

RESULTS

Depending on the rooting method either two or four equally parsimonious trees were found. Uisng the generally accepted out-group rooting method two equally parsimonious trees were found (see strict consensus cladogram generated for all trees below [Fig. 1]). The difference between the two trees involves the relative position of archosauromorph taxa and does not affect the position of turtles which remains consistent within Diapsida. The trees have a length of 771 steps and a CI of 0.507 with an RC of 0.348. The ancestor rooting method yields four equally parsimonious trees with lack of resolution only within Archosauromorpha and the relative position between Seymouriidae and Diadectomorpha. The position of turtles and all of the other clades remains unchanged. This set of trees has a length of 772 steps with a CI of 0.506 and an RC of 0.352.

The topology of either set of trees differs significantly from all other published cladistic analyses of turtle relationships in placing turtles within Diapsida. A revised taxonomy of that which was proposed by Laurin & Reisz (1995) is given below to accommodate the changes that have ocurred as a result of this analysis. It is important to note, however, that most of the taxonomic ranks and definitions proposed by Laurin & Reisz (1995) are still valid.

REPTILE TAXONOMY

Our revised indented classification can be summarized as follows:

- Reptilia Linnaeus 1758
  - Parareptilia Olson 1947
    - Millerettidae Watson 1957
    - Ankyramorpha deBraga & Reisz 1996
      - Lanthanosuchoidea Ivachnenko 1980
        - Acleistorhinidae Daly 1969
        - Lanthanosuchidae Efremov 1947
      - Procolophonomorpha Romer 1966
        - *Macroleter* Tverdochlebova & Ivachnenko 1984
      - Procolophonia Seeley 1888
        - Pareiasauria Seeley 1888
          - *Bradysaurus* Watson, 1914b
          - Velosauria Lee 1994
            - *Scutosaurus* Hartmann–Weinberg 1930
            - *Anthodon* Owen 1876
        - Procolophoniformes Lee 1993
          - Procolophonidae Lydekker 1890
          - Owenettidae Broom 1939
- Eureptilia Olson 1947
  - Captorhinidae Case 1911
  - Romeriida Gauthier, Kluge & Rowe 1988a
    - *Paleothyris* Carroll 1969
    - Diapsida Osborn 1903
      - Araeoscelidia Williston 1913
      - Eosuchia Broom 1924
        - *Claudiosaurus* Carroll 1981
        - Neodiapsida Benton 1985
          - Younginiformes Romer 1945
          - Sauria Gauthier 1984
            - Lepidosauromorpha Gauthier *et al.*, 1988c
              - Lepidosauriformes Gauthier *et al.*, 1988c
                - Keuhneosauridae Robinson 1962
                - Lepidosauria Haeckel 1866
                  - Rhynchocephalia Günther 1867
                  - Squamata Merrem 1820
              - Turtles + Sauropterygia unnamed taxon
                - Testudines Linnaeus 1758
                - Sauropterygia Owen 1860
                  - *Placosus* Agassiz 1833
                  - Eosauropterygia Rieppel 1994a
              - Unnamed taxon
                - Choristodera Cope 1876
                - Archosauromorpha von Heune 1946

A very determined attempt to place all of the taxa within established taxonomic units, and to maintain currently accepted definitions, was adhered to whenever possible. Therefore, some clades, which have been previously recognized as of

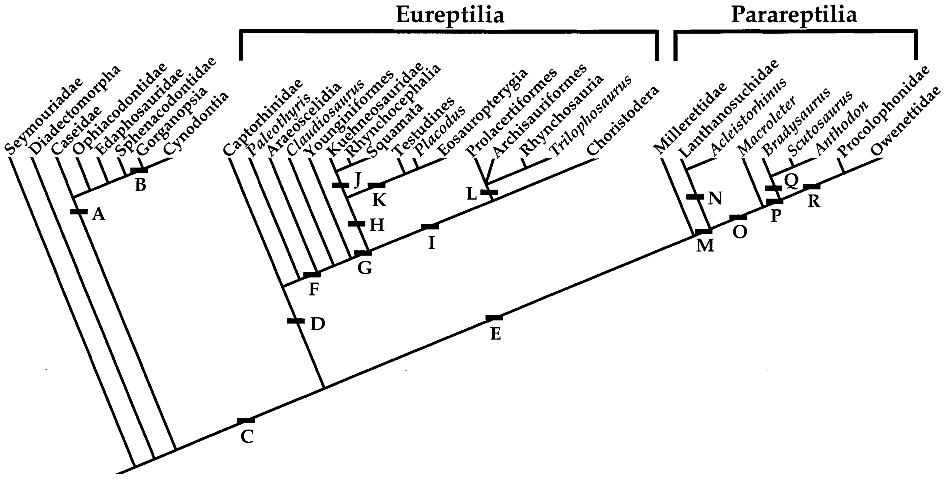

Figure 1. Cladogram of relationships represented by strict consensus tree (note that only some of the nodes are identified/for diagnosis of others refer to text). Note that a diagnosis for Synapsida is provided below although synapsids formed part of the out-group. Although inclusion in the out-group generally precludes clade diagnosis, a diagnosis for synapsids was made possible by including all taxa in the in-group and running the analysis with seymouriids and diadectomorphs as the sole out-group taxa. All of the relationships presented above remained unchanged. Numbers following capital letter (Node I.D.) refer to characters in Appendix 1 and 2. Characters identified with an asterisk imply ambiguity at that node, those characters preceded by a minus sign indicate a reversal, and multistate characters are followed by the derived state in parentheses. A, 24, 32 58, 59*, 90, 117; B, 30(2), −32, 38(2), 41, 53(2), 61, 64, 68, 70, 71(2), 72, 73, 75, 76(2), 78(2), 83(2), 84, 99, 107, 110, 111, 115, 116, 127(2), 131, 133, 137, 138, 140, 141(2), 142, 144, 146, 147, 149(2), 151, 153, 158, 161(2); C, 57, 59(2)*, 74, 84, 126, 158; D, 30*, 36, 41, 53, 120*; E, 13, 20, 82(2), 92, 134, 153; F, 19, 25, 50, 51*, 88, 116, 160; G, 18, 52(2), 53(2), 66, 67*, 68*, 70, 75, 76, 91*, 99, 128, 131, 153, 155; H, 11*, −19, 20, 29*, 42(3)*, 49(2)*, 51(3), 65*, 78(2)*, 89, 107*, 133, 146, 152; I, 1, 4, 6*, 10, −25*, 42(2)*, 49(3)*, 60, 63*, 105, 151; J, 15, 27, 0; K, 8, 64, 80, −116, 121, 123, 143, 158(2)*, −162, −163; L, 11*, 27, 33, 35*, −37*, 136, 149(2); M, 6, 11, 16, 17, 49(2), 83, 86, 91, 106(2), 115; N, 23, 24, 32, 42, 51*, 52, 60(2), 72, −74; O, 55(2), 109*, 117, 120*, 138*, 144*; P, 14, 46*, 56, 76*, 77, 85*, 95, 110*, 130, 137, 149, 158(2), 164; Q, 8, −17, 22, 26, 43, 52, 61, 63, 68*, 68, 72, 73*, 74(2), 79, 80, −83, 97, 111, 112, 118, 126(2), 127(2), 159, 161(2)*, 165, 168; R, −16, 21, 28*, 35, 38*, 42, 65, 69, 78(2), 87, 88*.

equivalent rank (Lepidosauromorpha and Archosauromorpha) no longer share this outcome. Even so, three new taxa have been erected here.

The character discussion that follows will be set in taxonomic order and in order to focus on the problem of turtle relationships and for the sake of brevity only those nodes starting with Reptilia will be discussed in detail. For a more thorough discussion of the composition of Synapsida and of the two anamniote taxa considered in this analysis the reader is asked to refer to the literature as presented above. In addition, although numerous members of Archosauromorpha were included in this analysis the clade has not been diagnosed beyond its most inclusive level (as presented here). The reason for this is due to the inability to resolve the relationship between Prolacertiformes and Archisauriformes and the clade comprising Rhynchosauria and *Trilophosaurus*.

The character numbers given below refer to the numbers in the appendices (Appendix 1 and 2). Ambiguous characters are denoted by an asterisk. A minus sign will denote a reversal, and in the case of a multi-state character, that character will be bound by parentheses. The order of character discussion will be from most primitive condition to most derived state. Characters will be discussed only where they first appear. Each subsequent time where the character is transformed the reader will be referred to the complete character description.

Reptilia Linnaeus 1758

Definition. The most recent common ancestor of diapsids and all its descendants. As described by Laurin & Reisz (1995) Reptilia was erected by Linnaeus (1758) to include testudines, crocodiles, and lepidosaurs. The composition of Reptilia here does not differ in any way from that which was formally defined by Gauthier *et al.* (1988a) and most recently accepted by Laurin & Reisz (1995).

Reptilia is diagnosed by six synapomorphies:

57. Configuration of occiput. In all non-reptiles the occiput is plate-like (0) and contributes to the overall box-like appearance of that region. All reptiles are derived in having a transversely constricted supraoccipital resulting in an open occiput (1).

59(2). Size of posttemporal fenestra.* Posttemporal fenestra are absent (0) in both the anamniote clades considered here. Small posttemporal fenestra (1) where each fenestra occupies much less than one/eighth the transverse width of the occiput are present in all synapsids and in the Lanthanosuchidae. Large posttemporal fenestra (2) which occupy at least one/fifth of the transverse width of the occiput are present in all eureptiles, millerettids, and all members of Procolophonomorpha. This character is ambiguous because the condition cannot be evaluated for *Acleistorhinus*. Therefore state (1) may be an autapomorphy of Synapsida with a convergent occurrence in Lanthanosuchoidea, or it may be a synapomorphy of synapsids and reptiles with a reversal in lanthanosuchoids. By the same token state (2) may be either an autapomorphy of Reptilia with a reversal to state (1) in lanthanosuchoids, or state (2) may be a synapomorphy of synapsids and reptiles with reversals to state (1) in both Synapsida and Lanthanosuchoidea.

74. Presence of suborbital fenestra. A suborbital fenestra in the region where the palatine, pterygoid, and ectopterygoid meet is absent (0) in all non-reptiles where the condition is known. *Placodus*, eosauropterygians and lanthanosuchoids also lack a suborbital fenestra. A suborbital fenestra that is bordered laterally by either the maxilla or the jugal (1) is an autapomorphy of Reptilia with a reversal in Lanthanosuchoidea and within the turtle-suropterygian clade. Exclusion of both the maxilla and the jugal from the lateral border of the suborbital fenestra (2) is an autapomorphy of the clade or a synapomorphy of turtles and sauropterygians with subsequent reversal to state (0) in Sauropterygia. Alternatively, state (0) could represent an autapomorphy of the turtle/sauropterygian clade with the subsequent acquisition of state (2) in turtles.

84. Number of coronoid elements. More than one coronoid (0) is primitive for amniotes. The presence of only one coronoid (1) is an autapomorphy of Reptilia with convergence in the synapsid clade comprised of Gorgonopsia and Cynodontia.

126. Configuration of supinator process. The presence of a large sharply angled supinator process extending anterolaterally from the distal humeral shaft (0) is primitive for amniotes and is retained by all non-reptiles considered here except gorgonopsians and cynodonts. The development of a smaller supinator process that runs confluent with the humeral shaft (1) is an autapomorphy of Reptilia with independent acquisition in gorgonopsians. A further modification where the supinator is reduced to small nubbin or is entirely absent (2) had independently developed in cynodonts, *Trilophosaurus*, Prolacertiformes, *Claudiosaurus*, within araeoscelids, and captorhinids. State (2) is also present in *Procolophon* and Pareiasauria where it may have been acquired independently or where it may be an autapomorphy of Procolophonia with a reversal in *Owenetta*.

158. Number of pedal centralia. The presence of both a lateral and medial pedal centrali (0) is primitive for all non-reptiles considered here except the synapsids Gorgonopsia and Cynodontia. The loss of the medial pedal centrali (1) is an autapomorphy of Reptilia. Loss of both centralia (2) is an autapomorphy of Procolophonia. State (2) may also be an autapomorphy of Lepidosauromorpha with a reversal to state (1) in kuehneosaurs, or it may be a synapomorphy of Testudines and sauropterygians with convergent acquisition in Lepidosauria.

Parareptilia Olson 1947

Definition. The most recent common ancestor of millerettids, Procolophonia and lanthanosuchids, and all their descendants.

Olson (1947) erected Parareptilia and initially included many non-amniote taxa within this group. More recently Gauthier *et al.* (1988a), Laurin & Reisz (1995), and deBraga & Reisz (1996) have more completely diagnosed the clade. The present analysis supports the monophyly of this clade but modified it by excluding Testudines.

This clade is diagnosed by six autapomorphies:

13. Presence of a large anterolateral maxillary foramen. Foramina are common on the labial surface of the maxillary elements but are generally small and of equivalent size to one another (0). This is true for all taxa considered in this analysis except parareptiles where the anterior most foramen is at least twice as large as the remaining foramina (1).

20. Medial extent of contact between prefrontal and palatine. Primitively, the prefrontal and palatine are only slightly in contact if at all (0). This condition is observed in all non-parareptiles except lepidosauromorphs and rhynchosaurs. In the derived state, the palatine forms a broad contact with the palatine ventromedially (1) that is equal to the width of the anterior, orbital extent of the prefrontal. The derived condition has been acquired independently in Parareptilia, Lepidosauromorpha, and Rhynchosauria.

82(2). Position of mandibular joint. Primitively the mandibular joint is even with the occiput (0). This is true of most taxa considered here except those alluded to below. The derived condition is manifested as either a posterior displacement of the jaw articulation relative to the occiput (1) which is an autapomorphy of choristoderans and *Placodus*, and also within some members of Squamata, Eosauropterygia, Archisauriformes and Lanthanosuchidae. The other derived condition is the anterior displacement of the jaw articulation relative to the occiput (2). This condition is a valid autapomorphy of Parareptilia with a reversal to either state (0) or (1) in lanthanosuchids, and an independent acquisition of state (2) in cynodonts, *Trilophosaurus*, some squamates, turtles, and Archisauriformes.

92. Retroarticular process. The absence of a distinct retroarticular process which is defined as any process that disturbs the smooth contour of the posterior edge of the jaw (0) is primitive for amniotes. The derived state is an autapomorphy of Parareptilia with a reversal to the primitive condition in *Acleistorhinus*. The derived state has also developed independently in Eupelycosauria (all synapsids presented here exclusively of Caseidae), and in Neodiapsida.

134. Iliac blade configuration. An elongate posterior process of the iliac blade (0) is primitive for amniotes. A fan-shaped distally expanded iliac blade (1) is an autapomorphy of Parereptilia with independent acquisition in Younginiformes and Testudines. The condition in turtles may reflect a more inclusive synapomorphy with sauropterygians, but the condition is equivocal because the character state cannot be determined for either *Placodus* or eosauropterygians.

153. Distal tarsal V. Primitively the fifth distal tarsal is present (0). Loss of the fifth distal tarsal occurs as independent autapomorphies in Parareptilia, Sauria, and he clade including gorgonopsians and cynodonts.

Millerettidae Watson 1957

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

This taxon is diagnosed by three autapomorphies:

30. Postorbital and supratemporal relationship.* The postorbital and supratemporal remain in contact (0) primitively in the anamniotes Seymouriidae and Diadectomorpha. Contact is also retained in caseids and ophiacodontids and in all ankyramorphs. Loss of contact occurs in all eureptiles where the condition is known (1), within Synapsida in sphenacodontids and edaphosaurids, and the parareptile clade Millerettidae. The supratemporal is entirely absent (2) in gorgonopsians and cynodonts. This character's evolution is ambiguous because state (1) may be a synapomorphy of all Reptilia with a subsequent reversal in Ankyramorpha, or state (1) can be an autapomorphy of Eureptilia with a convergent occurrence in millerettids.

124. Relationship of distal ends of humerus to shaft. Primitively the distal ends of the humerus are robust and each is as wide as one/third the total length of the shaft or greater (0). In the derived state the distal ends of the humerus are reduced and their greatest width measure always less than one/third the total length of the shaft (1). The derived state is a valid autapomorphy of Millerettidae and is independently acquired in Archisauriformes, and in the clade comprised of *Paleothyris* and Diapsida. In the latter grouping the character may reverse independently in Younginiformes and the clade including Choristodera and Archosauromorpha, or it may reverse at the level of Neodiapsida and redevelop (1) in Lepidosauromorpha and Archisauriformes separately.

163. Configuration of manus and pes. Short stout podia where the combined length of the carpus or tarsus exceeds 60% of the length of the fourth digit (0) are common in amniotes primitively. Elongation of the metacarpals and phalanges, so that the carpus or tarsus is never more than 50% of the total length of the fourth digit, resulting in a longer manus or pes (1) was acquired independently in Millerettids, Cynodontia, and Romeriida.

Ankyramorpha deBraga and Reisz 1996

Definition. The most recent common ancestor of Procolophonomorpha and Lanthanosuchoidea and all it descendants (deBraga & Reisz, 1996).

This clade is diagnosed by ten autapomorphies:

6. Dorsal exposure of external nares. Primitively in amniotes the external nares are essentially restricted to lateral margins of the tip of the snout (0); this is often the result of a broad dorsal process of the premaxilla. A reduction in the transverse width of the dorsal process of the premaxilla resulting in a dorsal exposure of the external nares (1) is an autapomorphy of Ankyramorpha. The derived state is found convergently in cynodonts and may either be an autapomorphy of Sauria with independent reversals in lepidosaurs, sauropterygians, and *Trilophosaurus*, or independently acquired in keuhneosaurs, testudines, and the choristoderan-archosauromorph clade.

11. Ascending process of maxilla. Primitively the maxilla is a low element throughout its length (0). The development of a tall anterodorsal (ascending) process which effectively doubles the height of the maxilla (1) is an autapomorphy of Ankyramorpha. The derived condition appears convergently among Synapsida in Caseidae and in the clade comprised of Gorgonopsia, Cynodontia, and Sphenacodontidae. The derived character may also either be an autapomorphy of Sauria with a reversal in Choristodera and within Prolacertiformes, or an autapomorphy of Lepidosauromorpha and the clade including Rhynchosauria, *Trilophosaurus*, and Archisauriformes.

16. Maxilla/quadratojugal relationship. In all taxa considered here except for Ankyramorpha the maxilla and quadratojugal never come into contact on the posterolateral (cheek) surface of the skull (0). Contact between both elements (1) is an autapomorphy of ankyramorphs with subsequent reversal in Procolophoniformes.

17. Lacrimal morphology. Primitively the lacrimal is a large element that extends from the orbit anteriorly to form the posterior border of the external nares (0). A reduction in the length of the lacrimal causing it to be excluded from the posterior border of the nares (1) represents separate autapomorphies for Ankyramorpha, with a subsequent reversal in Pareiasauria, Eosuchia, and the clade including Gorgonopsia, Cynodontia, and Sphenacodontidae. A secondary derivation involving the extreme reduction of the anteroposterior length of the lacrimal so that its height greatly exceeds its length (2) is developed independently in Cynodontia, Lepidosauria, and Sauropterygia.

49(2). Position of pineal foramen. Primitively the pineal foramen is located in the middle of the parietal (0). Displacement of the foramen either posteriorly (1) or anteriorly (2), or complete loss of the foramen (3) is of common occurrence in amniotes. State (1) is either an autapomorphy of Eupelycosauria or of Synapsida. The ambiguity occurs because caseids posses an anteriorly displaced pineal foramen state (2). Cynodonts have also independently acquired state (2). State (2) is a valid autapomorphy of Ankyramorpha, however, although lanthanosuchids are polymorphic with *Lanthanosuchus* preserving the primitive condition and *Lanthaniscus* possessing the anteriorly displaced (2) foramen. The evolution of this character in Sauria is confusing because of the rampant polymorphism that occurs within its members. The anteriorly displaced foramen (2) may be an autapomorphy of Lepidosauromorpha with reversal to either the primitive condition (0) as in some Rhynchocephalia and Squamata, or reversal to state (1) as in some members of Eosauropterygia. However, the evolutionary sequence is further confused by the fact that some squamates and all turtles have lost the pineal foramen (3), a condition that is also possible, although intuitively unlikely, is that loss of pineal foramen is a saurian autapomorphy with later independent redevelopment in those taxa that possess it. In this scenario a reversal to state (2) would represent two independent acquisitions of the pineal foramen in Lepidosauriformes and Sauropterygia.

83. Coronoid process morphology. A very low coronoid process that runs confluent with the dorsal margin of the lower jaw is primitive for amniotes. A distinct coronoid process where the coronoid rises sharply above the dorsal margin of the lower jaw and is equivalent to at least half the total depth of the jaw at its deepest point (1) is an autapomorphy of Ankyramorpha. Within this clade pareiasaures have reverted to the primitive condition. Additionally, state (1) may also either be an autapomorphy of Neodiapsida with reversal in Choristodera, Keuhneosauridae, Testudines, and within members of Eosauropterygia, Archisauriformes, and Prolacertiformes, or it may be independently acquired in Younginiformes, Lepidosauria, and the clade including Rhynchosauria and *Trilophosaurus*. A separate derived condition where the dentary contributes to the coronoid eminence (2) is an autapomorphy of the clade including gorgonopsians and cynodonts.

86. Surangular morphology. The length of the surangular or its lateral exposure is greater in amniotes primitively, so that it extends anteriorly beyond the coronoid eminence (0). Reduction in the anterior extent of the surangular so that it terminates prior to reaching the coronoid eminence (1) is an autapomorphy of Ankyramorpha and has developed convergently in Eosuchia, with reversals in *Trilophosaurus*, Kuehneosauridae, and within Squamata; and in Cynodontia.

91. Prearticular morphology. Primitively the prearticular extends anteriorly beyond the anterior limit of the coronoid in medial view (0). Reduction in the anterior extent of the prearticular so that it terminates at the coronoid eminence (1) is a valid autapomorphy of Ankyramorphia. The derived state also appears convergently in Edaphosauridae and may either be an autapomorphy of Neodiapsida or the less inclusive Sauria. The ambiguity here stems from the unknown condition for this character in Younginiformes.

106(2). Trunk neural arch morphology. Primitively as in seymouriids and diadectomorphs the neural arches of the trunk region are swollen and produce heavy buttresses which support the zygapophyses (0). Narrowing of the arches (1) occurs in most amniotes and is probably a valid amniote autapomorphy with possible reversal in captorhinids. However, another modification from the primitive state results in swollen arches but with very narrow zygapophyseal support buttresses (2). The latter condition is a valid autapomorphy of Ankyramorpha.

115. Interclavicle morphology. Primitively the interclavicle is rhomboidal in shape (0). A T-shaped interclavicle with broad transverse bars (1) is an autapomorphy of Ankyramorpha. This derived condition is also convergently developed in Eosuchia, with a reversal in Prolacertiformes, and in the clade including gorgonopsians and cynodonts. A further derived state where the interclavicle has a very slender transverse bar (2) may be an autapomorphy of Lepidosauria or of the more inclusive Lepidosauriformes. The ambiguity arises because the character cannot be coded for kuehneosaurs.

Lanthanosuchoidea Ivachnenko 1980

Definition. The most recent common ancestor of *Lanthanosuchus*, *Lanthaniscus*, and *Acleistorhinus*.

This taxon is diagnosed by nine autapomorphies:

23. Frontal configuration. Primitively the anterior margins of the frontals form a transverse suture with the nasals anteriorly (0). In the derived state the anterior margins of the frontals slope forward at an oblique angle forming a V-shaped suture with the nasals (1). The derived condition is an autapomorphy of Lanthanosuchoidea and it has evolved convergently in Prolacertiformes and *Trilophosaurus* among eureptiles. The character may also either be a synapomorphy uniting therapsids (Gorgonopsia and Cynodontia) with the sphenacodontids with a subsequent reversal within Cynodontia, or it may have evolved independently in both sphenacodontids and gorgonopsians.

24. *Frontal lateral margins*. Primitively the lateral margins of the frontals run along an uninterrupted parasaggital course (0). In the derived state the frontals develop a distinct lateral lappet (process) that projects out from the frontal margins at an abrupt 70° to 90° angle (1). These lateral lappets effectively separate the prefrontal and postfrontal above the orbital margin. This derived state is an autapomorphy of Lanthanosuchoidea which has separately evolved in Synapsida.

32. *Postorbital morphology*. Primitively the postorbital is relatively short (0) and does not reach the level of the posterior margin of the skull table (parietal). The derived condition manifests itself as an elongation of the postorbital posteriorly so that it reaches the level of the posterior margin of the parietal (1). The derived state is an autapomorphy of Lanthanosuchoidea with independent occurrence in Eosuchia and Synapsida.

42. *Quadratojugal morphology*. The quadratojugal is present as a large horizontal element (0) in the posteroventral corner of the skull of amniotes primitively. In one of its derived forms the quadratojugal presents itself as a vertical element that is taller than long (1). This tall configuration is an autapomorphy of Lanthanosuchoidea independently acquired in Testudines and Procolophoniformes. A reduction in the overall size of the quadratojugal so that it is restricted to the condylar region (2) is an autapomorphy of the clade comprised of Edaphosauridae, Sphenacodontidae, and Therapsida. State (2) may also either be an autapomorphy of Eosuchia with subsequent reveral to state (0) in Younginiformes and *Trilophosaurus*, and a reversal back to state (1) in Testudines, and within Eosauropterygia, Prolacertiformes, and Choristodera; or independently acquired in *Claudiosaurus*, Rhynchocephalia, and perhaps as a synapomorphy of the archosauromorph-choristoderan clade. The latter scenario is ambiguous because of the polymorphism exhibited in both Choristodera and Prolacertiformes. Loss of the quadratojugal completely (3) is likely an autapomorphy of Lepidosauromorpha with reversals to state (2) in Rhynchocephalia and within some members of Eosauropterygia, and state (1) in Testudines.

51. Elements contributing to lower temporal fossa*. Primitively the lower temporal fossa is absent (0). It is present and the quadratojugal contributes to its posteroventral margin (1) either as independently evolved autapomorphies of Lanthanosuchoidea, *Macroleter*, Diapsida, with subsequent reversals in Testudines and *Trilophosaurus*, and Caseidae; or state (1) is an autapomorphy of Amniota with a subsequent reversal in Eureptilia, redevelopment in Diapsida and again lost in *Trilophosaurus*, within araeoscelidians in *Araeoscelis*, within eosauropterygians in *Placodus*, and turtles; and also lost within parareptiles in Procolophonia. A modification from state (1) occurs when the quadratojugal is excluded from the margins of the lower temporal fossa (2). This state is best interpreted as an autapomorphy of Eupelycosauria. A further derived state where the lower temporal fossa is opened ventrally (3) is an autapomorphy of Lepidosauromorpha, and a reversal (0) in Testudines. State (3) is also independently acquired in Prolacertiformes and *Claudiosaurus*.

52. Postparietal morphology. Primitively the postparietals are present as paired elements (0). Fusion of the elements (1) so that only one is visible is an autapomorphy of the Lanthanosuchoidea which is independently acquired in Diadectomorpha, within synapsids in Eupelycosauria, Captorhinidae, and Pareiasauria. A further modification where the postparietal is lost entirely (2) is an autapomorphy of Sauria independently acquired in *Procolophon*.

60(2). Paraccipital process morphology. Primitively the paroccipital processes extend laterally and contact the cheek or skull table (0). In one derived form the paroccipital processes are directed posteriorly (1). This is an autapomorphy of the Choristodera–Archosauromorpha clade. Yet another modification occurs where the paroccipital processes are directed dorsally forming a very oblique (45°) angle with the region of the occipital condyle, where the processes take their origin, and extending to the ventral surface of the skull table (2). This state (2) is an autapomorphy of Lanthanosuchoidea.

72. Palate mobility. In amniotes primitively the palate retains some mobility at the basicranial articulation (0). Complete loss of kineticism (1) is an autapomorphy of Lanthanosuchoidea and it has developed convergently in Pareiasauria and Therapsida. It may also be an autapomorphy of the Testudines-Sauropterygia clade or diagnose a less inclusive clade the Sauropterygia. The ambiguity here stems from the polymorphism exhibited within Testudines.

−74. Suborbital fenestra. See discussion for Reptilia above.

Acleistorhinidae Daly 1969

Definition. The most recent common ancestor of *Acleistorhinus pteroticus*.

This taxon is diagnosed by four autapomorphies:

31. Postorbital/parietal contact. Primitively amniotes retain a contact between the postorbital and parietal on the dorsal surface of the skull (0). Loss of a visible contact on the skull surface between the postorbital and parietal (1) is an autapomorphy of *Acleistorhinus*. The derived state has been independently acquired as an autapomorphy of Eosuchia with subsequent reversals in keuhneosaurs, turtles, and choristoderans.

41. Quadrate anterior process. A long anterior process of the quadrate so that it extends along the quadrate ramus of the pterygoid to reach the level of the transverse flange of the pterygoid (0) is primitive for amnoites. Reduction in the length of the anterior process of the quadrate so that it occupies less than 55% of the length of the quadrate ramus of the pterygoid (1) is an autapomorphy of *Acleistorhinus*. This character has developed convergently in Therapsida and Eureptilia. In the latter a character reversal may represent an autapomorphy of the Testudines–Sauropterygia clade or it may diagnose the less inclusive clade Testudines. The ambiguity here stems from the inability to code for this character in either Eosauropterygia or *Placodus*.

62. Exoccipital morphology. Primitively the exoccipital bones meet below the foramen magnum (0). Separation of the exoccipitals below the foramen magnum by the basioccipital (1) is an autapomorphy of *Acleistorhinus.* The derived condition manifests itself as independently acquired autapomorphies of the *Paleothyris*/Diapsida (Romeriida) clade and of the clade comprised of Edaphosauridae, Sphenacodontidae, and Therapsida. within the former a character reversal occurs in Testudines, Rhynchosauria, and within Squamata. Polymorphism is also present within procolophonids.

−92. Retroarticular process. See diagnosis for Parareptilia above.

Lanthanosuchidae Efremov 1946

Definition. The most recent common ancestor of *Lanthanosuchus* and *Lanthaniscus.*

This taxon is diagnosed by nine autapomorphies:

12. Maxillary horns. In all amniotes primitively the maxilla lacks any evidence of a horny boss immediately behind the external nares (0). The development of a distinctive boss on the maxilla immediately behind the external nares (1) is an autapomorphy of lanthanosuchids which has evolved convergently in *Scutosaurus.*

19. Skull proportions. Primitively the skull of amniotes has a ratio where the preorbital and postorbital lengths of the skull are equal (0) when the ratios are taken between snout tip and posterior limit of occiput. An increase in the preorbital skull length so that it exceeds the postorbital length (1) is an autapomorphy of lanthanosuchids. The character also evolved independently in Eupelycosauria and Diapsida. Within diapsids a reversal occurs in Lepidosauromorpha and within Archosauromorpha in rhynchosaurs. A separate derived state where the postorbital length of the skull exceeds the preorbital length (2) represents cases of independently acquired autapomorphies in Choristodera and *Placodus.*

26. Frontal ratio. The ratio between the length and the width of the frontal is primitively 4:1 (0). A reduction in the length of the frontal so that its length does not exceed two times its width (1) is an autapomorphy of lanthanosuchids. This character has evolved convergently in Pareiasauria and may either represent an autapomorphy of the Testudines–Sauropterygia clade with a reversal in Eosauropterygia, or it evolved independently in Testudines and *Placodus.*

43. Quadratojugal ornamentation. Primitively the quadratojugal when present is confluent with the cheek and is not ornate in any manner (0). An ornamented quadratojugal so that dermal protuberances project from its surface (1) is an autapomorphy of lanthanosuchids. Pareisaurs have developed this derived feature independently and so have some procolophonids.

−59. Posttemporal fenestra size.* See discussion for Reptilia above.

76. Palatal process of pterygoid.* See diagnosis of Ankyramorpha above.

−82(0,1). Mandibular joint.* See diagnosis of Paraptilia above.

88. Splenial morphology.* Primitively the spenial enters the jaw symphysis. Reduction in the anterior length of the splenial so that it is excluded from the jaw symphysis (1) may be an autapomorphy of Lanthanosuchidae. Alternatively the character may be an autapomorphy of Ankyramorpha. Ambiguity stems from the fact that the character cannot be coded for either *Macroleter* or *Acleistorhinus.* The derived state may also be an autapomorphy of Seymouriidae and is an unambiguous autapomorphy of Diapsida with reversals in Rhynchosauria and *Placodus.*

95. Caniniform teeth. Prmitively caniniform teeth are present (0) in amniotes. Loss of a distinct caniniform region (1) is an autapomorphy of lanthanosuchids. This character has developed independently in Procolophonia, Eosuchia, and Edaphosauridae.

Proclophonomorpha Romer 1964

Definition. The most recent common ancestor of *Macroleter*, pareiasaurs, Procolophoniformes, and all their descendants.

This taxon was emended by Lee (1995) to include nycteroleterids, procolophonids (both Permian and Triassic forms), *Sclerosaurus*, and his pareiasaur-turtle clade. However, due to the fact that the only two detailed descriptions (von Heune, 1902 and Rieth, 1932) are in disagreement and the only known specimen has been lost, *Sclerosaurus* has been excluded from the present study.

This taxon is diagnosed by six autapomorphies:

55(2). Tabular morphology. Primitively the tabular is present and is restricted to the dorsal half of the skull. Its effective dimensions are those of an element that is wider than tall (0). In one derived form the tabular is elongate ventrally so that its length greatly exceeds its width (1). Yet another derived condition is the complete loss of the tabular (2). State (2) is an autapomorphy of Procolophonomorpha with two cases of independent acquisition in captorhinids and eosuchians. State (1) is an autapomorphy of eupelycosaurs.

109. Number of sacral vertebrae.* Primitively amniotes possess two sacral vertebrae (0). The development of at least one additional sacral (1) occurs independently in synapsids in the clade comprised of edaphosaurids, sphenacodontids, cynodonts, and gorgonopsians, in sauropterygians, and in ankyramorphs. The character is ambiguous for Procolophonomorpha because the condition cannot be coded for lanthanosuchoids. It may, therefore, diagnose the more inclusive clade Ankyramorpha.

117. Scapula morphology. Primitively, the scapula is a broad element so that its height, measured from the base of the glenoid dorsally toward its highest point, does not exceed its anteroposterior length, measured from its anteroventral margin to its scapular height exceeds its length by three to four times (1). This character is an autapomorphy of Procolophonomorpha and it has been developed independently in Synapsida and *Trilophosaurus*. A further derived condition where the scapula develops a cylindrical dorsal process (2) represents an autapomorphy of *Anthodon* and may either diagnose the turtle suropterygian clade with a reversal in *Placodus*, or it may have developed independently in both turtles and eosauropterygians.

120. Number of coracoid ossifications.* The presence of one coracoid ossification (0) is considered primitive for tetrapods. The development of two coracoid ossifications (1) may be an autapomorphy of Procolophonomorpha with independent acquisition in Eureptilia and a subsequent reversal in Eosuchia. Alternatively the character may represent an autapomorphy of Reptilia with two independent reversals in millerettids and eosuchians. The ambiguity results because the character cannot be coded in lanthanosuchoids.

138. Acetabular buttress.* A very weakly developed acetabular buttress (0) is present primitively in amniotes. A large acetabular buttress (1) is developed independently in the gorgonopsian/cynodont clade, in Testudines, and in Ankyramorpha. The character is ambiguous for Procolophonormorpha because the condition cannot be determined for lanthanosuchoids. Therefore, the derived character may diagnose the more inclusive clade Ankyramorpha.

*144**. *Size of anterior femoral condyle.* In relation to the posterior condyle of the femur, the anterior condyle is large (0) primitively. Reduction of the anterior femoral condyle so that it is equal to the posterior condyle in distal extent (1) is an autapomorphy of Eosuchia and the clade comprised of Gorgonopsia and Cynodontia. The character is ambiguous for Procolophonomorpha because the derived condition cannot be determined in millerettids nor lanthanosuchids. It may, therefore, diagnose the more inclusive Parareptilia.

Macroleter Tverdochlebova & Ivachnekno 1984

Definition. This taxon represents a currently undescribed, but nearly complete articulated skeleton, as well as details from the literature (Ivachnenko, 1987).

This taxon is diagnosed by six autapomorphies:

*25**. *Frontal configuration.* Primitively, the frontals of amniotes from a transverse suture posteriorly with the parietal (0). In the derived form the frontals develop posterolateral processes which wrap around the anterolateral margins of the parietal (1). Optimization of this character is ambiguous because it could have evolved independently in *Macroleter* and Procolophoniformes. The derived condition has also evolved independently in ophiacondontids and gorgonopsians among Synapsida, and may either represent an autapomorphy of Diapsida with a reversal in squamates, turtles, and the clade comprised of Archosauromorpha and choristoderans, or alternatively it may represent a diapsid autapomorphy with a reversal in Sauria ad then redeveloped in kuehneosaurs and sauropterygians.

*28**. *Orbit shape.* Primitively the orbit of most amniotes is a circle with its anteroposterior and dorsoventral dimensions equalling one another (0). In procolophonomorphs the orbit is elongate so that its anteroposterior length is at least half as long as its dorsoventral height (1). This character is ambiguous because pareiasaurs retain the primitive configuration. Therefore, the derived state can either be an autapomorphy of Procolophonomorpha with a reversal in Pareiasauria or it has developed independently in *Macroleter* and Procolophoniformes.

*38**. *Quadrate posterior margin.* The posterior margin of the quadrate is straight in the vertical plane (0) in amniotes primitively. A derived condition occurs when the posterior margin is deeply excavated so that it is strongly concave (1). This character is ambiguous for *Macroleter* because within procolophonomorphs pareiasaurs retain the primitive condition (0). State (1), however, is a valid autapomorphy of Neodiapsida. Another derived state occurs where the quadrate is reduced and its posterior exposure is restricted to a very fine sliver of bone (2). State (2) is an autapomorphy of therapsids.

*51**. *Lower temporal fossa.* See discussion for Lanthanosuchoidea above.

*109**. *Osteoderms.* See discussion for Lanthanosuchidae above.

162. Limb length. Primitively the limbs of most amniotes are short and stout so that the width of the distal ends of the humerus are greater than $\frac{1}{3}$ the total length of the entire bone (0). Elongate limbs so that the maximal width of the distal ends are less than $\frac{1}{3}$ the length of the entire bone (1) is an autapomorphy of *Macroleter*. The derived state has evolved convergently in *Owenetta*, cynodonts, and the clade comprised of *Paleothyris* and diapsids. In the latter a reversal has occurred separately in *Claudiosaurus*, and the clade including turtles and sauropterygians.

Procolophonia Seeley 1888

Definition. The most recent common ancestor of Pareiasauria and Procolophoniformes and all their descendents.

This taxon is modified from Laurin and Reisz (1995) in that Testudines has been excluded from the present definition.

This taxon is diagnosed by 14 autapomorphies:

14. Maxillary length. Primitively the maxilla is long posteriorly and reaches the posterior limit of the orbital margin (0). In the derived condition the posterior extent of the maxilla is reduced so that it does not reach beyond mid-orbit (1). This character is an autapomorphy of Procolophonia which has evolved independently in eupelycosaurs, kuehneosaurs, *Placodus*, and choristoderans. The character may also diagnose Eureptilia with independent reversals in *Paleothyris*, and Neodiapsida, and subsequent redevelopment in keuhneosaurs, *Placodus*, and choristoderans, or it may represent independent evolution in all those eruptiles that possess it (captorhinids, araeosceloids, *Claudiosaurus*, choristoderans, *Placodus*, and keuhneosaurs).

46. Stapedial dorsal process*. Primitively the dorsal process of the stapes is well ossified and forms a distinct structure (0). The derived form manifests itself as a reduction of the dorsal process so that the stapedial shaft retains a uniform outline throughout its length (1). The ambiguity of this character stems from the fact that the stapes in *Macroleter* is not known. Therefore, this character may diagnose the more inclusive taxon Procolophonomorpha. The derived condition is also present in cynodonts and may be an autapomorphy of Eosuchia, or diagnose the less inclusive Neodiapsida. The ambiguity results from the fact that the condition cannot be scored in *Claudiosaurus*.

56. Supraoccipital morphology. Primitively the supraoccipital is a broad plate-like element that occupies most of the posterodorsal half of the occipital skull surface (0). A reduction in the width of this element so that its width and height are subequal and the development of a raised median ridge (1) represents an autapomorphy of Procolophonia. This character has also developed convergently in the clade comprised of rhynchosaurs and *Trilophosaurus*, as well as Testudines, and may be an autapomorphy of Lepidosauria. Ambiguity arises here because squamates are polymorphic.

75. Cultriform process. In most amniotes the cultriform process is long exceeding the length of the anteroposterior length of the parasphenoid/basioccipital complex (0). Reduction in the length of the cultriform process so that it is shorter than the parasphenoid/basioccipital complex (1) is an autapomorphy of Procolophonia. This character has also evolved independently in therapsids and in saurians. In the latter it has undergone a reversal in Prolacertiformes.

76(1). Palatal process of the pterygoid*. Primitively the palatal processes of the pterygoid extend forward past the anterior margin of the palatine (0). Reduction of the palatal process of the pterygoid so that the bone terminates prior to reaching the anterior limit of the palatine (1) may be an autapomorphy of Ankyramorpha with subsequent reversal in *Acleistorhinus*. The ambiguity stems from the unknown condition, for this character in *Macroleter*. Therefore, the derived condition may be an autapomorphy of Procolophonomorpha and Lanthanosuchidae respectively. The character also appears convergently in *Paleothyris* and may be either an autapomorphy of Sauria with reversals in Prolacertiformes, Rhynchosauria, and *Trilophosaurus*, or independently acquired in Lepidosauromorpha, Choristodera, and Archisauriformes. The derived state is also found as an autapomorphy of the edaphosaurid, sphenacodontid, therapsid clade. A further derivation where the palatal process of the pterygoid forms a transverse contact with the palatine (2) represents independent autapomorphies of Therapsida and *Placodus*.

77. Transverse flange of pterygoid. Primitively the transverse flange of the pterygoid is deflected posterolaterally (0). A modification so that the transverse flange is directed anterolaterally (1) is an autapomorphy of Procolophonia. This character may also represent an autapomorphy of Diapsida with a reversal at Neodiapsida and then redevelopment in Squamata, *Trilophosaurus*, and within members of Testudines and Rhynchosauria. Alternatively it may have evolved independently in araeosceloids, *Claudiosaurus*, and all of those diapsid taxa discussed above.

85. Meckelian fossa configuration.* Exposure of the Meckelian fossa primarily medially (0) is a primitive feature for amniotes. Dorsal expansion on the medial surface of the jaw by the prearticular results in a closing off of the Meckelian fossa medially (1). This character may be a valid autapomorphy for Ankyramorpha, but unfortunately the medial surface of the jaws are not adequately known in *Macroleter*, *Acleistorhinus*, or lanthanosuchids. The derived character may, therefore, diagnose the more inclusive clade Procolophonomorpha. The derived condition is also found in eureptiles and may either represent autapomorphies of Archosauromorpha and Lepidosauria with a reveral in Eosauropterygia, or it may have developed independently in lepidosaurs in Testudines and *Placodus*, and in archosaurs in the clade including Rhynchosauria and *Trilophosaurus*.

95. Caniniform teeth. Amniotes have a distinct region of caniniform teeth (0) primitively. This region where the anterior maxillary teeth increase in length to about the middle of the tooth row and then diminish in length posteriorly has been lost so that there is no detectable increase in length beyond the anterior most maxillary tooth (1). This character is an autapomorphy of Procolophonia with cases of independent acquisition in lanthanosuchids, edaphosaurids, and eosuchians.

110. Caudal lateral projections.* Lateral projections on the caudal vertebrae (transverse processes) are generally absent beyond the fifth caudal vertebrae (0) in amniotes primitively. Development of caudal projections (transverse processes) beyond the fifth caudal was suggested by Lee (1993b) to be an autapomorphy of pareiasaurs plus turtles. Presently it is interpreted as an ambiguous autapomorphy of Procolophinia, but due to the inability to code for this character in millerettids, *Macroleter*, and lanthanosuchoids, this character could diagnose the more inclusive clade Procolophonomorpha. The derived character has also evolved convergently in therapsids and in neodiapsids with a subsequent reversal in eosauropterygians.

130. Olecranon morphology. A large well developed olecranon so that it extends above the ulnar condylar region (0) is primitive for amniotes. Reduction of the olecranon so that it is restricted to rising no higher than the condylar region or is entirely absent (1) is an autapomorphy of Procolophonia. The derived character is also present in cynodonts and in eosuchians. Within Eosuchia there are independent reversals in *Trilophosaurus* and in Lepidosauriformes in rhynchosaurs and within squamates. The inability to code for this character in keuhneosaurs results in the ambiguity at Lepidosauriformes.

137. Acetabulum morphology. Primitively the acetabulum is oval so that its height is never more than $\frac{3}{4}$ of the total length (0). In the derived state the height and length are sub-equal (1). This character is an autapomorphy of Procolophonia with independent acquisition in therapsids and Eosuchia. In eosuchians there is one case of reversal in testudines.

149. Astragalus/calcaneum morphology. In amniotes primitively the astragalus and the calcaneum are never fused in the adult and very often are loosely sutured (0). In the derived state the astragalus and the calcaneum have fused in the adult although the sutural line may still be seen (1). This character is an autapomorphy of Procolophonia with two cases of independent acquisition Lepidosauria and Testudines respectively. A further derivation where the astragalus and the calcaneum develop a distinct hinge between one another (2) has developed independently in Archosauromorpha and Therapsida respectively.

158(2). Number of pedal centrali. See discussion for Reptilia above.

164. Ungual size. Primitively the unguals are always shorter than the penultimate phalange (0). A great increase in the length of the unguals so that they exceed the length of the penultimate phalange by at least 50% (1) is an autapomorphy of Procolophonia. This character has also evolved independently in rhynchosaurs and within turtles.

Pareisauria Seeley 1888

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

This clade is diagnosed by 26 autapomorphies.

8. Choana morphology. Primitively the choana run parallel to the lingual margin of the maxilla (0). In the derived state the choana curve posteromedially so that the long axis would form an angle of about 45° with the medial surface of the maxilla (1). This derived state is an autapomorpohy of pareiasaurs which has arisen independently in gorgonopsians, rhynchosaurs, and the clade including Testudines and Sauropterygia. Hiding of the choana from palatal view (2) occurs in cynodonts.

−17. Lacrimal morphology. See discussion for Ankyramorpha above.

22. Frontal contribution to orbit. Primitively in amniotes the frontal contributes to the orbital margin (0). Exclusion of the frontal from the orbital margin so that the prefrontal and postfrontal are in contact (1) is an autapomorphy of pareisaurs. This character has evolved independently in *Trilophosaurus*, *Placodus*, cynodonts, and within members of Squamata and Testudines.

26. Frontal ratio. See discussion for Lanthanosuchidae above.

43. Quadratojugal ornamentation. See discussion for Lanthanosuchidae above.

52. Postparietal morphology. See discussion for Lanthanosuchoidea above.

61. Paroccipital process size. Primitively, the paroccipital processes are rod-shaped (0) and are not tightly sutured to the cheek. In the derived form the paroccipital processes become greatly lengthened anteroposteriorly so that dimension exceeds the dorsoventral dimension by at least $\frac{1}{3}$ (1). This condition represents an autapomorphy of pareiasaurs. The derived state has also evolved convergently in Therapsida, Testudines, and within Archosauromorpha.

63. Basioccipital/basisphenoid contact. Primitively the basioccipital and basisphenoid are not in contact dorsally and, therefore, a distinctive gap is present in this region (0). The derived state results in a fusion of the two elements dorsally eliminating the gap (1). This character is an autapomorphy of pareiasaurs. It has also evolved independently in eupelycosaurs, athough it may diagnose a more inclusive clade including ophiacondontids. The derived state is also found in Testudines and in the choristoderan-archosauromorph clade. In either of these two clades the derived state could diagnose more inclusive clades, notably Romeriida, but the inability to code for this character in most diapsid taxa considered here makes its evolution in these clades ambiguous.

66. Opisthotic/cheek contact.* In amniotes primitively the opisthotic is not sutured to the cheek medially (0). Development of a strong non-mobile suture between the opisthotic and the cheek represents three cases of independent development in eupelycosaurs, saurians, with separate reversals in *Placodus* and Prolacertiformes, and possibly procolophonomorphs in *Owenetta.* The ambiguity in this clade arises because the condition cannot be scored for *Macroleter.*

68. Medial wall of inner ear. Primitively the medial wall of the inner ear is unossified (0) in amniotes. A fully ossified medial wall of the inner ear (1) is an autapomorphy of Pareiasauria. This character has also evolved convergently in Therapsida and may also be an autapomorphy of Sauria. The ambiguity for this clade rests on the fact that the condition for this character is not known in *Paleothyris* or all diapsids below the Sauria. The character may, therefore, be an autapomorphy for Romeriida instead.

72. Palate morphology. See dicsussion for Lanthanosuchoidea above.

73(1). Interpterygoid vacuity.* The shape of the interpterygoid vacuity is generally v-shaped (0) in amniotes primitively. A medial inflection of the palatal processes of the pterygoid results in a cresentric interpterygoid vacuity (1). This character may represent an autapomorphy of Procolophonia with a reversal in *Owenatta*, or it may have developed independently in pareiasaurs and *Procolophon.* State (1) is also an autapomorphy of therapsids. A further derivation of the interpterygoid vacuity occurs when it is completely lost (2) due to consolidation of the palate. This character (2) is an autapomorphy of Sauropterygia.

74(2). Suborbital fenestra. See discussion for Reptilia above.

79. Ventral deflection of transverse flange. According to Lee (1995) the primitive configuration for the transverse flange of the pterygoid is represented by a mediolateral projection from the main body of the pterygoid which has its tooth bearing ridge lie in the same plane as the marginal dentition (0). In this way the transverse flange is not visible when the skull is viewed in lateral aspect. In the derived condition the transverse flange has been expanded ventrally so that it extends below the distal limit of the marginal dentition (1). This derived state is an autapomorphy of pareiasaurs which has evolved convergently in edaphosaurids and in eosuchians. within Eosuchia three instances of independent reversals have occurred in Squamata, *Placodus*, and Choristodera.

80. Angle of external edge of transverse flange. Lee (1994) described this character as the distance from the lateral edge of the transverse flange to the inside of the cheek. He did not, however, quantify the character properly. The present interpretation resolves the issue by quantifying the character with respect to the angle formed between the lateral and forward directed components of the flange and its relationship to the parasagittal axis of the skull. Primitively the transverse flange is directed laterally at an angle of nearly 90° and forms an acute angle where it turns sharply anteriorly (0). In some derived states the transverse flange (char. # 77 this analysis) is directed anterolaterally (Reisz & Laurin, 1991) but the angle formed between the lateral and forward directed portions of the transverse flange remains sharp. In the derived state the transverse flange is directed anteriorly at an angle of less than 45° to the parasagittal axis and the lateral and forward portions of the transverse flange merge smoothly forming a curved anterolateral margin (1). This character is an autapomorphy of Pareiasauria that has evolved convergently in choristoderans, *Trilophosaurus*, squamates, and the clade comprised of Testudines plus Sauropterygia. —*83. Coronoid process morphology.* See discussion for Ankyramorpha above.

97. Presacral vertebral count. It has been generally accepted that the primitive vertebral count exceeds 20 vertebrae (0) usually between 24 and 26. Reduction in the presacral count so that there are never more than 20 vertebrae and sometimes even fewer (1) is an autapomorphy of pareiasaurs which has evolved independently in turtles.

111. Caudal rib morphology. Primitively the caudal ribs of amniotes are curved posteriorly so that they form an inverted L-shape (0). Straight ribs which extend perpendicular to the long axis of the tail (1) is an autapomorphy of pareiasaurs which has developed convergently in Therapsida and Eosuchia respectively.

112. Chevron position. The position of the haemal arches (chevrons) in relation to the caudal centra is intercentral (0) in amniotes primitively. In the derived condition the position of the haemal arch has moved so that it is located on a vertebral pedicel present on the anteroventral surface of caudal centra (1). This derived state is an autapomorphy of pareiasaurs which has evolved convergently in turtles and within some squamates.

118. Acromion process. Primitively the acromion process is absent (0) is amniotes. A well developed anterolateral process which is laterally compressed (blade-like) (1) is an autapomorphy of pareiasaurs. Lee believed that this process was homologous with the turtle acromion, but the turtle acromion is not only not similar in shape but it is also not in the same position. In fact, Lee (1994, 1996a) argued for a relationship between the acromion of pareiasaurs and turtles and the clavicle. In his reinterpretation of the shoulder girdle of *Proganochelys*, (*contra* Gaffney, 1990) Lee has argued that the more vertically oriented scapula would result in the acromion reaching the dorsal process of the epiplastron (clavicle). Following his argument further one is told that the exclusion of the clavicle from making contact with the anterior border of the scapula and instead restricted to making contact with the acromion process is then a synapomorphy of turtles and pareiasaurs. We disagree with this interpretation (Fig. 2). First of all, Lee's reinterpretation of the shoulder girdle is questionable, given that some well preserved specimens of *Proganochelys* show that Gaffney's (1990) reconstruction is accurate (Reisz, pers. comm.). Secondly, the turtle acromion is a conical structure (in lateral aspect) tapering to a fine point distally and is strongly deflected ventrally. In addition, the acromion is in line with the single coracoid in *Proganochelys* and arises from the medial edge of the scapular blade and not the lateral edge as in pareiasaurs (2) [Gaffney, 1990]. Furthermore, developmentally the acromion of extant turtles ossifies as a separate element, not as part of the scapula (Rieppel, 1993a). Because of this ventral position, directly in

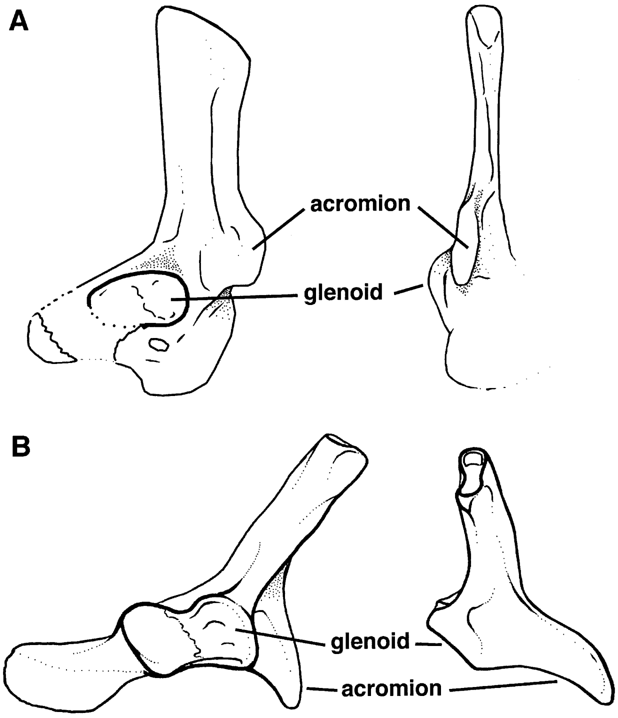

Figure 2. Scapulocoracoids in right lateral and anterior views. A, *Anthodon*. B, *Proganochelys*. Illustrations reveal the relationship of the glenoid to the acromion as well as the relative position of the acromion to the scapular blade and the its position relative to the coracoid. Note that the acromion in *Anthodon* (A) is rectangular in lateral view compared with the broadly triangular, lateral exposure in *Proganochelys*. The position of the acromion along the anterior margin of the scapular blade in *Anthodon* also differs significantly from that of *Proganochelys*. In the former the process is directed forward and associated with the lateral edge of the scapular blade. In the latter the process is deflected anteroventrally and is associated with the medial edge of the scapular blade. Finally, the position of the acromion with respect to the coracoid plate differs in that in *Anthodon* it is located well above the long axis of the coracoid plate and its ventral limit terminates prior to reaching the ventral margin of the glenoid surface, whereas in *Proganochelys* the acromion is in line with the single coracoid and is deflected well below the ventral margin of the glenoid. A, partially redrawn after Lee (1996a). B, after Gaffney (1990).

front of the single coracoid, the turtle acromion may indeed be the modified anterior coracoid. Lee (1996a) rejected this possibility outright as not being congruent with his pareiasaur–turtle sister–group scenario. This argument, however, is circular because it bases the homology of the structure on the phylogeny, yet his phylogeny utilizes the presence of the acromion as a synapomorphy contributing to the diagnosis of his Pareiasauria, therefore, implying homology *a priori*.

Presently the fact that pareiasaurs possess both coracoids, and the possibility that the turtle acromion may be the anterior coracoid, coupled with the great morphological differences in the acromion of turtles and pareiasaurs, and the questionable phylogenetic relationship between both taxa homology of this character is rejected.

*126(2)**. *Supinator process morphology*. See discussion for Reptilia above.

127(2). *Ectepicondylar groove*. Primitively the ectepicondyle is well developed and a distinct groove is present that separates the ectepicondylar process from the distal part of the humeral shaft (0). In a derived form the ectepicondyle remains and the remnant of the groove is left as a small opening on the anterodistal end of the humerus (1). This derived state represents independent autapomorphies of *Procolophon*, *Claudiosaurus*, and Archisauriformes. State one is also found within Eosauropterygia. another modification where the distal opening (ectepicondylar foramen) is completely enclosed in bone (2) represents an autapomorphy of pareiasaurs. State (2) has also evolved independently in rhynchosaurs and within squamates. State (2) has also evolved independently within Testudines, Choristodera, and Younginiformes.

159. Fifth pedal digit morphology. Primitively the fifth pedal digit is longer than the first (0). In the derived state the fifth pedal digit is reduced so that it is shorter than the first and also much more gracile as well (1). This character has developed as independent autapomorphies in pareiasaurs, turtles, and cynodonts.

*161(2)**. *Pedal phalangeal formula.* Primitively the pedal phalangeal formula is 2 3 4 5 4 [3] (0). One derived state has resulted in the loss of one phalange in digit four so that the count is 2 3 4 4 3 (1). Yet another modification results in a phalangeal formula of 2 3 3 4 3 [or less] (2). This character is ambiguous for Pareiasauria because we cannot determine, based on the taxa selected here, which state either (1) or (2) evolved in the common ancestor of Procolophonia. State (2) is, however, an unambiguous autapomorphy of Therapsida and Testudines respectively.

165(1). Body osteoderms. Osteoderms are primitively absent (0) in amniotes. Osteoderms that are sparsely located along the dorsal body surface (1) have developed independently in Pareiasauria and Archisauriformes. The development of a row of osteoderms covering most of the back (2) has developed as an autopomorphy of *Anthodon* with convergence in *Placodus*. In Testudines the origin of the carapace has created some confusion as to its possible homology with body osteoderms. Burke (1989) and Lee (1994) believe the condition to be homologous and we have followed this interpretation here. Therefore, state (2) may represent an autapomorphy of the clade including Testudines and Sauropterygia, or it may have evolved independently in both. Ambiguity arises here because eosauropterygians are primitive in lacking body osteoderms.

168. Gastralia. Primitively gastralia are present (0) in amniotes. Loss of gastralia (1) is an autapomorphy of pareiasaurs which has also evolved convergently in two other clades. In synapsids the character may diagnose Cynodontia or the more inclusive taxon Therapsida. In Lepidosauriformes the derived state may either diagnose that clade with a reversal in rhynchosaurs, or it may have developed independently in keuhneosaurs and squamates.

Bradysaurus Watson 1914b

Definition. The most recent common ancestor of *Bradysaurus seeleyi.* The genus here is interpreted as monospecific because Lee (1994) placed the only other recognized species *Bradysaurus baini* as falling closer to his Velosauria, therefore, making the genus paraphyletic.

This taxon is diagnosed by one autapomorphy:

135. Iliac blade anterior expansion.* Primitively the iliac blade is only slightly expanded anteriorly with the posterior iliac process being at least twice as long (0). In the derived state the posterior process is virtually absent, but the anterior process is greatly expanded into a blade-like structure that extends forward beyond the anterior limit of the pubis (1). This character may represent an autapomorphy of Bradysaurus *seeleyi*. The ambiguity arises because the derived state is also present in *Scutosaurus*, whereas the primitive condition may diagnose the more inclusive Pareiasauria. In addition the derived state has also evolved convergently in cynodonts.

Velosauria Lee (1994)

Definition. The most recent common ancestor of Therischia and Pumiliopareiasauria and all their descendants (Lee, 1994). The two taxa represented by this clade include all pareiasaurs except for the following genera: *Bradysaurus*, *Embrithosaurus*, and *Deltavjatia*.

This taxon is diagnosed by four autapomorphies:

64. Parasphenoid constriction. Primitively the parasphenoid is a relatively long element with its overall length measured from the basipterygoid process to its posterior most extent exceeding the dimension of the narrowest transverse width by at least 40% (0). In the derived condition the parasphenoid is compressed into a nearly square element where its length is never more than 20% of its narrowest transverse width (1). This character is an autapomorphy of Velosauria which has evolved independently in *Claudiosaurus*, Archisauriformes, Therapsida, and the clade comprised of Testudines and Sauropterygia.

113. Cleithrum*. In amniotes primitively the cleithrum is present (0). Loss of the cleithrum (1) may represent an autapomorphy of velosaurids with convergent occurrence in procolophonids, cynodonts, and Eosuchia. However, the inability to code for this character in owenettids makes it ambiguous at this node, and it may instead diagnose the more inclusive Procolophonia.

141(1). Femoral trochanter major. Primitively the trochanter major is absent (0). Development of a trochanter has apparently evolved many times within amniotes. In one state the trochanter is present but is deflected distally from the proximal head of the femur (1). This condition is found in Velosauria. Another manifestation of the trochanter can be observed in Therapsida where the trochanter is developed as a pyramidal structure high up on the femoral shaft nearly in line with the femoral head (2). Finally in Archisauriformes the trochanter major is similar in morphology to that which is present in therapsids but differs in its position in being located at mid-shaft (3).

167. Bony studs on limbs. Bony studs or dermal armour on the limbs is absent in amniotes primitively (0). The presence of conical studs on limbs (1) was interpreted by Lee (1994) as an autapomorphy uniting some pareiasaurs with turtles. The derived state here is interpreted as an autapomorphy of Velosauria with independent acquisition in Testudines.

Anthodon Owen 1876

Definition. The most recent common ancestor of *Anthodon serrarius* and *Anthodon pricei*.

This taxon is diagnosed by four autapomorphies:

117(2). Scapula morphology. See discussion for Procolophonomorpha above.

123. Humeral torsion. Primitively the humeral ends are set off at nearly right angles to one another or at best the proximal end is set of at a 45° angle with respect to the distal end resulting in a twisted appearance (0). In the derived condition the humeral ends become nearly aligned so that the proximal and distal ends are twisted, with respect to one another, by no more than 20° (1). This derived state represents an autapomorphy of *Anthodon* which has evolved independently in Cynodontia, Squamata, and the clade comprised of Testudines and Sauropterygia.

165(2). Body osteoderms. See discussion for Pareiasauria above.

166. Osteodermal ridges.* This character is difficult to interpret with regard to its evolutionary history because it must be scored with a question mark (?) for all taxa lacking osteoderms. However, among all those taxa that have been interpreted as possessing osteoderms most lack any sort of discrete pattern associated with the ossification (0). The appearance of fine regularly spaced radiating ridges from the centre of the osteoderm (1) is interpreted as a possible autapomorphy of *Anthodon.* The ambiguity arises because a second derived state where the radiating ridges are coarse and irregularly spaced (2) occurs in *Scutosaurus* among the taxa considered here. Therefore, the ancestral state cannot be determined for Velosauria and either state (1) or (2) may be primitive for the clade or independently acquired in each.

Scutosaurus Hartmann–Weinberg 1930

Definition. The most recent common ancestor of *Scutosaurus* (Lee 1994).

This taxon is diagnosed by four autapomorphies:

12. Maxillary horn. See discussion for Lanthanosuchidae above.

98. Number of caudal vertebrae.* Lee (1994) has interpreted the number of caudal vertebrae to be at least 25 (0) primitively. In the derived state there are never more than 20 caudals (1). This character may be an autapomorphy of *Scutosaurus* which has evolved convergently in Testudines. The ambiguity for this node arises because the character state cannot be determined for *Anthodon.*

135. Iliac blade anterior expansion.* See discussion for *Bradysaurus* above.

166(2). Osteodermal ridges.* See discussion for *Anthodon* above.

Procolophoniformes Lee 1993b

Definition. The most recent common ancestor of Procolophonidae and Owenettidae and all their descendants.

This taxon is diagnosed by 12 autapomorphies:

−16. Maxilla/quadratojugal relationship. See discussion for Ankyramorpha above.

21. Prefrontal morphology. Primitively the medial surface of the prefrontal has a smooth border (0). In the derived condition the medial surface of the prefrontal develops a bulbous process (1). The derived state is an autapomorphy of Procolophinoformes.

25. Frontal morphology.* See discussion for *Macroleter* above.

28. Orbital shape. See discussion for Macroleter* above.

35. Squamosal lateral exposure. Primitively the squamosal is plate-like and descends ventrally to reach the level of the ventral, orbital margin (0). In one derived form the squamosal retains its generally plate-like appearance but is reduced ventrally and terminates prior to reaching the ventral, orbital margin (1). This condition is an autapomorphy of Procolophoniforms and has evolved convergently within Sauria. In these taxa the derived state may have either evolved separately in Testudines and *Placodus*, and in the clade comprised of Rhynchosauria, *Trilophosaurus*, and Archisauriformes, or it may have evolved within Sauria. The ambiguity here stems from the development of a rod-like squamosal without a ventral process (2) which has evolved in keuhneosaurs, squamates, and Prolaceriformes. State (2) may represent independent development in those taxa considered above or it may be an autapomorphy of Sauria with subsequent development of state (1) in those saurian taxa that possess it. Nevertheless the evolution of this character within Sauria is best considered equivocal.

38. Quadrate morphology.* See discussion for *Macroleter* above.

42(1). Quadratojugal morphology. See discussion for Lanthanosuchoidea above.

65. Ventral braincase tubera. The braincase of amniotes primitively lacks distinct ventrolateral tubera on its ventral surface (0). In one derived state tubera develop on the ventral surface of the basioccipital (1). This condition is an autapomorphy of Procolophoniformes which has evolved convergently within Sauria. In this taxon, the derived state may either represent an autapomorphy of Sauria with independent loss in Rhynchosauria and Choristodera, or it may have developed as an autapomorphy of Lepidosauromorpha with independent development in *Trilophosaurus*, and Prolacertiformes. A further modification of this character where the tubera are developed as large processes on the basisphenoid (2) represents an autapomorphy of Eupelycosauria.

69. Occipital flange. Amniotes primitively have a smooth curvature of the posterior end of the skull so that there is no excavation below the posterior edge of the parietal or postparietals (0). In the derived state the posterior margin of the skull is excavated so that the parietal or postparietal is embayed (1) forming a distinctive shelf. This derived state is an autapomorphy of Procolophoniformes.

78(2). Dentition on T-flange of pterygoid. Primitively there are three distinct fields of teeth on the pterygoid. One field extends anteriorly along the mid-line, another field extends anterolaterally and onto the palatine, and the third field is directed laterally onto the transverse flange of the pterygoid. In addition, the field of teeth on the third (anterolateral) row is in the form of a broad pavement of teeth or denticles (0). In the derived state the T-flange has lost the denticles and had developed a large distinct row of teeth on a raised ridge (1). State one is interpreted as an autapomorphy for Amniota. A further derivation where the teeth (third row) are completely lost from the T-flange (2) is an autapomorphy of Procolophoniformes. State (2) has also evolved convergently in Therapsida and may represent either an autapomorphy of Sauria with a reversal to state (1) in Choristodera and within Archisauriformes and Prolacertiformes, or an autapomorphy of Lepidosauromorpha and the clade comprised of Rhynchosauria and *Trilophosaurus* respectively.

87. Surangular morphology. Laurin & Reisz (1995) described the absence of a ridge (lateral shelf) on the lateral face of the surangular (0) as primitive for amnoites. In the derived state a distinct ridge extends from just behind the coronoid to the level of the condyle (1). The derived condition is an autapomorphy of Procolophoniformes that has developed independently in Squamata. Testudines, and Rhynchosauria.

88(1). Splenial morphology.* See discussion for Ankyramorpha above.

Procolophonidae Lydekker 1890

Definition. The most recent common ancestor of *Anomoiodon*, *Burtensia*, *Candelaria*, *Contritosaurs*, *Eumetabolodon*, *Hypsognathus*, *Kapes*, *Koiloskiosaurs*, *Leptopleuron*, *Macrophon*, *Microphon*, *Microthelodon*, *Myocephalus*, *Myognathus*, *Neoprocolophon*, *Orenburgia*, *Paoteodon*, *Procolophon*, and *Thelegnathus* and all their descendants (Laurin & Reisz, 1995).

This taxon is diagnosed by 11 autapomorphies:

45. Stapes morphology.* Primitively the stapes of amniotes is a robust element (0) that functions in a supportive role rather than in an auditory function. The development of a rod-like stapes (1) so that its greatest length exceeds its greatest width by at least four times may be an autapomorphy of Procolophonidae. The ambiguity arises because the stapes in owenettids is not known. Therefore, this character may diagnose the more inclusive clade Procolophoniformes.

52(2). Postparietal morphology. See discussion for Lanthanosuchoidea above.

66. Opisthotic/cheek relationship.* See discussion for Pareiasauria above.

73. Interpterygoid vacuity.* See discussion for Pareiasauria above.

103. Cervical centra morphology. Primitively the cervical centra are smoothly rounded (0). In *Procolophon* and all other procolophonids where the condition could be coded the cervical and anterior dorsal centra have developed a keeled ventral ridge (1). This character is, therefore, an autapomorphy for Procolophonidae which has evolved independently in Eupeolycosauria and Romeriida.

113. Cleithrum.* See discussion for Velosauria above.

126(2). Supinator process.* See discussion for Reptilia above.

127(1). Ectepicondylar groove. See discussion for Pareiasauria above.

150(1). Relationship of distal tarsal IV to astragalus. Primitively the astragalus and distal tarsal IV only abut against one another (0). In the derived state the astragalus and distal tarsal IV develop a broad, well defined articulation between both elements (1). This condition is well developed in any large mature procolophonid and is clealry evident in the SAM specimen of *Procolophon.* State (1) may also represent either an autapomorphy of Lepidosauromorpha wth a reversal in sauropterygians, or it may have developed independently in Lepidosauria and Testudines respectively. In addition state (1) is also found in cynodonts. A further derivation occurs in gorgonopsians where both the astragalus and distal tarsal IV form a broad contact but have not developed an articulating surface (2). The evolution of this character (either state 1 or 2) in Therapsida is ambiguous.

160. Metapodial relationship.* The metapodials do not overlap one another proximally (0) in amniotes primitively. An overlap of the proximal head of the metapodials so that nearly half of the surface of an adjacent metapodium is overlain by its neighbour (1) may represent an autapomorphy of Procolophonidae. Ambiguity arises because the character cannot be coded for owenettids.

161(1). Pedal phalangeal formula.* See discussion for Pareiasauria above.

Owenettidae Broom 1939

Definition. The most recent common ancestor of *Barasaurus* and *Owenetta* and all of their descendants.

This taxon is diagnosed by four autapomorphies:

36. Squamosal contribution to posttemporal fenestra. Primitively the posttemporal fenestra when present does not receive any contribution from the squamosal (0). In the derived state the squamosal enters into the dorsolateral border of the posttemporal fenestra (1). The derived condition is an autapomorphy of Owenettidae which has convergently occurred in Eureptilia.

128. Entepicondylar foramen. Primitively the entepicondylar foramen is present (0). Loss of an entepicondylar foramen (1) is a derived character of Owenettidae. The derived condition has also evolved in Sauria with a subsequent reversal in Rhynchosauria and within Eosauropterygia.

−138. Acetabular buttress. See discussion for Procolophonomorpha above.

162. Limb ratios. See discussion for *Macroleter* above.

Eureptilia Olson 1947

Definition. The most recent common ancestor of *Paleothyris*, Captorhinidae, and Diapsida and all their descendants.

This taxon is diagnosed by five autapomorphies:

30. Postorbital/supratemporal relationship.* See discussion for Millerettidae above.

36. Squamosal contribution to posttemporal fenestra. See discussion for Owenettidae above.

41. Quadrate anterior process. See discussion for Acleistorhinidae above.

53. Supratemporal morphology. Primitively the supratemporal is a large element that occupies a large area on the posterolateral corner of the skull (0). In the derived state the supratemporal is greatly reduced and is exposed only as a thin sliver of bone on the posterior most lateral margin of the skull roof (1). This character is an autapomorphy of Eureptilia with independent evolution in the ophiacodontid/eupelycosaur clade. A further modification to the derived state occurs with the complete loss of the supratemporal (2). State (2) has evolved as independent autapomorphies in Sauria and Therapsida respectively.

120. Coracoid ossifications.* See discussion for Procolophonomorpha above.

Captorhinidae Case 1911

Definition. The most recent common ancestor of *Captorhinus*, *Captorhinikos*, *Captordinoides*, *Hecatogomphius*, *Kahneria*, *Labidosaurikos*, *Labidosaurus*, *Moradisaurus*, *Protocaptorhinus*, *Rhiodenticulatus*, *Romeria*, and *Rothianiscus*, and all their descendants (Laurin & Reisz, 1995).

This taxon is diagnosed by six autapomorphies:

14. Maxillary length.* See discussion for Procolophonia above.

52. Postparietal morphology. See discussion for Lanthanosuchoidea above.

55(2). Tabular morphology. See discussion for Procolophonomorpha above.

81(2). Ectopterygoid morphology. Primitively the ectopterygoid is present and lacks any dentition along its surface (0). In edaphosaurids the ectopterygoid develops a large pavement of teeth (1) which is associated with the elaboration of a tooth plate in this taxon. A further modification occurs where the ectopterygoid is lost and replaced by a medial process of the jugal (2). This character is an autapomorphy of

Captorhinidae. A variant on the loss of the ectopterygoid occurs in Testudines where the element is replaced by a lateral process from the pterygoid (3).

−106. Trunk neural arch morphology. See discussion for Ankyramorpha above.

126(2). Supinator process. See discussion for Reptilia above.

Romeriida Gauthier, Kluge & Rowe 1988a

Definition. The most recent common ancestor of *Paleothyris* and Diapsida and all their descendants.

This taxon is diagnosed by five autapomorphies:

62. Exoccipital morphology. See discussion for Acleistorhinidae above.

103. Cervical and anterior dorsal centra morphology. See discussion for Procolophonidae above.

124. Humeral length to distal end ratio. See discussion for Millerettidae above.

162. Limb ratios. Se discussion for *Macroleter* above.

163. Manus and pes morphology. See discussion for Millerettidae above.

Paleothyris Carroll 1969

Definition. The most recent common ancestor of *Paleothyris*. This taxon is diagnosed by one autapomorphy:

76(1). Palatal process of pterygoid. See discussion for Lanthanosuchidae above.

Diapsida Osborn 1903

Definition. The most recent common ancestor of Araeoscelidia, *Claudiosaurus*, Younginiformes, and Sauria and all their descendants.

This taxon is diagnosed by seven autapomorphies:

19(1). Preorbital/postorbital skull ratio. See discussion for Lanthanosuchidae above.

25. Upper temporal fossa. Primitively all amniote taxa lack an upper temporal fossa (0). The development of a distinct opening bordered by the parietal medially, the postorbital/postfrontal laterally, and the squamosal posteriorly (1) is unique to diapsids. Within this clade there has been one case of a reversal in Testudines.

51(1). Lower temporal fossa.* See discussion for Lanthanosuchoidae above.

88. Splenial morphology. See discussion for Lanthanosuchidae above.

116. Mineralized sternum. Primitively amniotes lack a calcified sternum (0). A fully mineralized sternum (1) is an autapomorphy of Diapsida with a subsequent reversal in the testudines/Sauropterygia clade. The derived condition has also evolved independently in Therapsida.

160. Metapodial overlap. See discussion for Procolophonidae above.

Araeoscelidia Williston 1913

Definition. The most recent common ancestor of *Araeoscelis*, *Kadaliosaurus*, *Petrolacosaurus*, *Spineoaequalis*, and *Zarcasaurus*, and all their descendants.

This taxon is diagosed by four autapomorphies:

*14**. *Maxillary length.* See discussion for Procolophonia above.

*77**. *Pterygoid flange orientation.* See discussion for Procolophonia above.

*145**. *Fibula morphology.* Primitively the fibula of amniotes is strongly bowed away from the tibia (0). In the derived state the fibular shaft has become straightened so that it does not bow away from the tibia (1). This character may diagnose Araescelidia with independent evolution in Neodiapsida. Alternatively this character may be an autapomorphy of Diapsida with a reversal in *Claudiosaurus* and rhynchocephalians. The ambiguity arises because the character cannot be coded for keuhneosaurs.

*157**. *Ratio of metatarsal I to metatarsal IV.* Primitively the first metatarsal is much greater than 50% of the total length of the fourth metatarsal (0). In the derived state the first metatarsal is greatly shortened so that it never exceeds 50% of the total length of the fourth metatarsal (1). This character may either be an autapomorphy of Araeoscelidia with independent evolution in Younginiformes, Rhynchocephalia, and the clade comprised of Rhynchosauria and *Trilophosaurus*, or an autapomorphy of Diapsida with independent reversals in the Testudines/Sauropterygia clade, Archisauriformes, and *Claudiosaurus*. The ambiguity arises because the character cannot be coded for keuhneosaurs.

Eosuchia Broom 1924

Definition. The most recent common ancestor of *Claudiosaurus*, Younginiformes, and Sauria and all their descendants.

This taxon is diagnosed by 22 autapomorphies:

17(1). Lacrimal morphology. See discussion for Ankyramorpha above.

31. Postorbital/parietal relationship. See discussion for Acleistorhinidae above.

32. Postorbital morphology. See discussion for Lanthanosuchoidea above.

48. Parietal shelf. Primitively the parietal is not excavated or embayed on its lateral margins for the adductor jaw musculature (0). In the derived condition the parietal is embayed along its lateral margins to accommodate the dorsal migration of the adductor jaw musculature (1). This character is an autapomorphy of Eosuchia with a reversal in Testudines. Recently (Laurin, 1991) the development of the adductor shelf has been interpreted as an autopomorphy of Neodiapsida, but the presence of the derived condition in *Claudiosaurus* requires that the diagnosis be amended here.

55(2). Tubular morphology. See discussion for Procolophonomorpha above.

79. Transverse flange orientation. See discussion for Pareiasauria above.

86. Surangular morphology. See discussion for Ankyramorpha above.

95. Caniniform dentition. See discussion for Lanthanosuchidae above.

102. Atlantal ribs. Primitively amniotes possess well ossified atlantal ribs (0). Loss of atlantal ribs (1) represents an autapomorphy of Eosuchia.

111. Caudal rib morphology. See discussion for Pareiasauria above.

113. Cleithrum. See discussion for Procolophoniformes above.

114. Clavicle morphology. In primitive amniotes the clavicles are broad and blade-like with their anteroposterior dimension (length) exceeding the dorsoventral dimension (depth) by at least 50% (0). In the derived condition the clavicles are much more gracile and nearly rod-like so that the length to depth ratio approaches 1:1 (1). The derived character is an autapomorphy of Eosuchia with reversals in Testudines, and within Squamata, and Eosauropterygia.

115(1). Interclavicle morphology. See discussion for Ankyramorpha above.

119. Supraglenoid buttress. A very large buttress above the glenoid (0) is indicative of amniotes primitively. Loss of the supraglenoid buttress (1) is an autapomorphy of Eosuchia.

−120. Coracoid ossifications. See discussion for Reptilia above.

125. Humeral distal articulating facets. Primitively the humerus possesses a distinct trochlea and capitellum for articulation with the ulna and radius respectively (0). In the derived condition the articulating facets on the humerus become less well pronounced and instead develop as a low double condyle (1). The derived character is an autapomorphy of Eosuchia with reversals in keuhneosaurs, within rhynchocephalians, and within Archisauriformes.

130. Olecranon morphology. See discussion for Procolophonia above.

132. Metacarpal IV to III ratio. Primitively the fourth metacarpal is longer than the third (0). In the derived condition metacarpal IV is either equal or shorter in comparison to metacarpal III (1). This character is an autopomorphy of Eosuchia with a subsequent reversal in the rhynchosaur/*Trilophosaurus* clade and within some members of Testudines.

137. Acetabulum morphology. See discussion for Procolophonia above.

139. Femoral shaft morphology. Primitively the shaft of the femur is straight and robust (0). In the derived state the femur is lender and sigmoidally curved (1). This character is an autapomorphy of Eosuchia with a subsequent reversal in Testudines.

142(1). Intertrochanteric fossa morphology. In primitive amniotes the intertrochanteric fossa is well defined as a deep excavation spanning the proximoventral region of the femur resulting in a concave area that is nearly one half as deep as it is wide (0). One derived configuration results in the reduction of this concavity so that the depth is never more than one quarter of the total width (1). A further modification results in the complete loss of the concavity (2). State (1) is an autapomorphy of Eosuchia with reversals in Testudines and within Eosauropterygia. State (1) has also evolved independently in Therapsida. State (2) manifests itself only within some members of Archisauriformes.

144. Anterior femoral condyle. See discussion for Procolophonomorpha above.

Claudiosaurus Carroll 1981

Definition. The most recent common ancestor of *Claudiosaurus.*

This taxon is diagnosed by 12 autapomorphies:

14. Maxillary length.* See discussion for Procolophonia above.

15. Maxilla contribution to orbit. Primitively the maxilla is excluded from the orbital margin (0). Inclusion of the maxilla into the orbital margin (1) is an autapomorphy of *Claudiosaurus.* The derived state has also evolved independently as an autapomorphy of Lepidosauriformes wth a subsequent reversal within some members of Squamata. The derived character is also found within some members of Testudines, Eosauropterygia, Archisauriformes and Prolacertiformes.

42(2). Quadratojugal morphology.* See discussion for Lanthanosuchoidea above.

51(3). Lower temporal fossa. See discussion for Lanthanosuchoidea above.

64. Parasphenoid constriction. See discussion for Velosauria above.

77. Pterygoid flange orientation.* See discussion for Procolophonia above.

105. Cervical rib morphology. Primitively the cervical ribs of amniotes have a uniform outline throughout their length (0). In the derived state the cervical ribs develop an anterior process that is present just below the rib head (1). The presence of an anterior process is an autapomorphy of *Claudiosaurus*, which has evolved independently in Sauropterygia and in the clade comprised of Archosauromorpha and Choristodera. within the latter a reversal has occurred in Rhynchosauria.

122. Humeral epicondyles. The distal process of the humerus (epicondyles) are generally well developed in amniotes (0). This results in the typical humeral configuration where the distal end is at least twice as broad as the humeral shaft. In some instances the epicondyles are greatly reduced (1) so that the distal end of the humerus is only slightly broader than the shaft. The derived condition is an autapomorphy of *Claudiosaurus*, that may also represent an autapomorphy of the Testudines/Sauropterygia clade. The ambiguity at this node results from the polymorphic states for both turtles and squamates.

126(2). Supinator process. See discussion for Reptilia above.

127(1). Ectepicondylar groove. See discussion for Pareiasauria above.

143. Femoral distal condyles. In amniotes primitively the distal end of the femur possesses two prominent condyles for articulation with the crus (0). A reduction in the distal projection of the condyles so that they are almost indistinguishable from the distal end of the femur (1) is an autapomorphy of *Claudiosaurus*. The derived state has also evolved independently in Choristodera, Cynodontia, and the clade including Testudines and Sauropterygia.

−162. Limb morphology. See discussion for *Macroleter* above.

Neodiapsida Benton 1985

Definition. The most recent common ancestor of Younginiformes and Sauria and all their descendants.

This taxon is diagnosed by eight autapomorphies:

38. Quadrate morphology. See discussion for *Macroleter* above.

39. Quadrate lateral exposure. Primitively the quadrate is covered laterally by the squamosal and the quadratojugal (0). In the derived condition the quadrate is exposed in lateral view along most of its length (1). This character is an autapomorphy of Neodiapsida.

45. Stapes morphology.* See discussion for Proclophonidae above.

46. Dorsal process of stapes.* See discussion for Procolophonia above.

92. Retroarticular process. See discussion for Parareptilia above.

110. Caudal lateral projections (transverse processes). See discussion for Procolophonia above.

145. Fibula morphology.* See discussion for Araeoscledia above.

154. Metatarsal V morphology. Primitively the fifth metatarsal is long and slender and appears much like all of the other metatarsals (0). In the derived state the fifth metatarsal is shortened and develops a broad base so that anatomically it is quite distinct from the other metatarsals (1). This modification results as an autapomorphy of Neodiapsida with a subsequent reversal in Sauropterygia.

Younginiformes Romer 1945

Definition. The most recent common ancestor of *Youngina*, *Acerosodontoaurus*, and *Hovasaurus*, and all their descendants.

This taxon is diagnosed by five autapomorphies:

29. Postfrontal contribution to upper temporal fenestra.* Primitively in those taxa where an upper temporal fenestra is present the postfrontal is excluded from the fenestra margin (0). In the derived state the postfrontal contributes to the anterolateral margin of the upper temporal fenestra (1). This character may either diagnose Younginiformes with independent evolution in Lepidosauromorpha, or it is an autapomorphy of Neodiapsida with a subsequent reversal in the archosauromorph/choristoderan clade.

83. Distinct coronoid process.* See discussion for Ankyramorpha above.

−124. Humeral ends/humeral length ratio.* See discussion for Millerettidae above.

134(1). Iliac blade morphology. See discussion for Parareptilia above.

157. Metatarsal I to IV ratio.* See discussion for Araeoscelidia above.

Sauria Gauthier 1984

Definition. The most recent common ancestor of Choristodera, Archosauromorpha and Lepidosauromorpha and all their descendants.

This taxon is diagosed by 14 autapomorphies:

18. Lacrimal duct. Primitively the lacrimal duct is enclosed by the lacrimal only (0). In the derived state the lacrimal duct is partially bordered by the maxilla (1). This character is an autapomorphy of Sauria with independent reversals within members of Testudines and Archisauriformes.

52(2). Postparietal morphology. See discussion for Lanthanosuchoidea above.

53(2). Supratemporal morphology. See discussion for Eureptilia above.

66. Opisthotic/cheek contact. See discussion for Pareiasauria above.

67. Prootic/parietal contact.* Primitively the prootic and the parietal do not come into contact (0). The derived condition manifests itself as a sutured contact between prootic and parietal which contributes to the formation of a solid braincase wall (1). This character is ambiguous at this level because the character cannot be coded in *Paleothyris*, nor in any diapsid below Sauria. Lee (1995) had argued that this character was also present in pareiasaurs, and hence a testudine/pareiasaur synapomorphy, but closer inspection reveals that the prootic in pareiasaurs is in contact with the ventral process of the supraoccipital and not the parietal.

68. Medial wall of inner ear.* See discussion for Pareiasauria above.

70. Sphenethmoid ossification. Primitively the sphenethmoid is present in all amniotes as an ossified extension of the pila antotica which surrounds the anterior end of the braincase and is sheathed below by the cultriform process of the parasphenoid (0). Loss of the sphenethmoid ossification (1) is an autapomorphy of Sauria with convergent development in Therapsida.

There has been some confusion surrounding the homology of this element and the pleurosphenoid in the recent literature. Lee (1994, 1995) citing Gaffney's (1990) description of *Proganochelys* interpreted an interorbital element in the brain case of pareiasaurs as the pleurosphenoid. In actual fact the element described by Gaffney

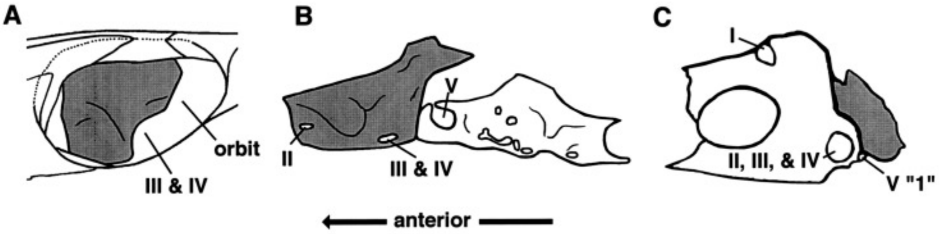

Figure 3. Braincases in lateral view. A, *Captorhinus*. B, *Embrithosaurus*. C, *Uria*. Shaded areas in A and B represent the primitive amniote sphenethmoid. The shaded area in C represents the pleurosphenoid. Note that cranial nerves II, III, and IV do not penetrate the pleurosphenoid (C), whereas they are located well within the body of the sphenethmoid (A, B). In addition, the trigeminal nerve (V) exits the braincase directly anterior to the pleurosphenoid. This contrasts sharply with the relationship of the trigeminal to the sphenethmoid where it exits the braincase directly behind its posterior most margin. A, drawn from Oklahoma Museum specimen (PMNH, 52329); B, redrawn from Lee (1993b, 1995); and C, redrawn from Zusi (1993).

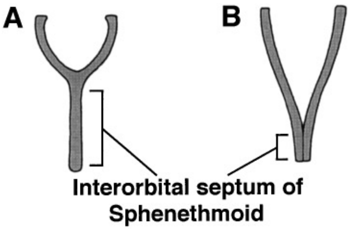

Figure 4. Cross section of sphenethmoid. A, anterior-most region of element. B, posterior-most region (dorsum sellae). Note the V-shaped configuration of the element posteriorly compared to the Y-shaped appearance associated with the region of the interorbital septum. Partially reconstructed after Holmes (1984).

can be none other than the posterior end of the sphenethmoid. This is clear, based on the relationship of the element to the large trigeminal (V) foramen and to the dorsum sellae (Fig. 3). The confusion arises because the pleurosphenoid arises developmentally from the same region as the sphenethmoid, the region of the dorsum sellae. The difference between the two elements can only be assessed by the relationship of the cranial nerves that penetrate the respective elements. The pleurosphenoid is always perforated by or at the very least forms part of the border of two foramina, the V cranial nerve posteriorly and a foramen for the III and IV cranial nerves anteriorly (Zusi, 1993). Conversely, the sphenethmoid is always pierced by a foramen for cranial nerve II anteriorly and has a concavity if not a complete foramen for cranial nerves III and IV posteriorly. In essence, the sphenethmoid and pleurosphenoid are separate ossifications of the orbital cartilages, with the former representing an anterior ossification often observable as an interorbital septum and the latter a more posterior ossification which is in contact with the prootic. Using these criteria the ossification in pareiasaurs and *Proganochelys* must represent the primitive retention of the sphenethmoid. Lee has also used the shape of the element as an indication that pareiasaurs possess a true pleurosphenoid. However, the typical Y-shaped cross-section of the sphenethmoid is only apparent if one looks in the interorbital region (Fig. 4). The farther posteriorly that the cross-section is taken the more likely the sphenethmoid is to appear as a V-shaped structure (Holmes, 1984) which superficially appears like the paired pleurosphenoid ossifications. In fact, if the section is taken just anterior to the dorsum sellae the sphenethmoid can very easily be confused for the pleurosphenoid.

75. Cultriform process length. See discussion for Procolophonia above.

91. Prearticular morphology.* See discussion for Ankyramorpha above.

99. Vertebral centra. Primitively amniotes have amphicoelous vertebrae which are perforated by the notochord (0). Exclusion of the notochord from the vertebral centra (1) is an autapomorphy of Sauria with a subsequent reversal in *Placodus*. The derived state has also evolved convergently in Therapsida.

128. Entepicondylar foramen. See discussion for Owenettidae above.

131. Perforating foramen. The manual perforating foramen is present (0) in amniotes primitively. Loss of the perforating foramen (1) is an autapomorphy of Sauria with a reversal in *Trilophosaurus*. The derived state has also evolved independently in Therapsida.

153. Distal tarsal V. See discussion for Parareptilia above.

155. Metatarsal V morphology. A straight metatarsal V (0) is characteristic of amnoites primitively. In the derived state there is a hooking of the proximal end of the fifth metatarsal so that its articulating facet lies nearly at a right angle to the long shaft of the element (1). This character is an autapomorphy of Sauria with a reversal in Sauropterygia and within some members of Prolacertiformes. The derived state has also developed independently in cynodonts.

Lepidosauromorpha Gauthier *et al.* 1988c

Definition. The most recent common ancestor of Testudines, Sauropterygia, and Lepidosauriformes and all their descendants. This taxon has been emended from its traditional composition by the inclusion of Testudines as the sister taxon to Sauropterygia.

This taxon is diagnosed by 15 autapomorphies:

11. Ascending process of maxilla.* See discussion for Ankyramorpha above.

−*19(0). Preorbital/postorbital skull ratios.* See discussion for Lanthanosuchidae above.

20. Prefrontal palatine contact. See discussion for Parareptilia above.

29. Postfrontal contribution to upper temporal fenestra.* See discussion for Younginiformes above.

42(3). Quadratojugal morphology.* See discussion for Lanthanosuchoidea above.

49(2). Pineal foramen.* See discussion for Ankyramorpha above.

51(3). Lower temporal fossa. See discussion for Lanthanosuchoidea above.

65(1). Ventral braincase tubera.* See discussion for Procolophoniformes above.

76. Palatal process of pterygoid.* See discussion for Proclophonia above.

78(2). Transverse flange of pterygoid dentition.* See discussion for Procolophoniformes above.

89(1). Lateral exposure of angular. Primitively the angular is exposed along $\frac{1}{3}$ of the lateral face of the posterior part of the jaw (0). In the derived condition this lateral exposure is reduced to narrow sliver (1) or the angular is completely excluded from the lateral surface of the lower jaw (2). State (1) is an autapomorphy of Lepidosauromorpha with one case of convergence in Rhynchosauria. State (2) is an autapomorophy of Cynodontia.

107. Dorsal intercentra.* In primitive amniotes the intercentra are retained throughout the vertebral column (0). Loss of intercentra throughout the vertebral column (1) may be an autapomorphy of Lepidosauromorpha with independent acquisition in Choristodera, or it may be an autapomorphy of Sauria with a subsequent reversal in Archosauromorpha. The derived state has also evolved convergently in Therapsida.

133. Thyroid fenestra. In amniotes primitively the pelvis is a tightly sutured unfenestrated, plate-like element with only the presence of the small obturator foramen (0). The development of a large fenestra between the ilium dorsally, the pubis anteroventrally, and the ischium posteroventrally (1) is an autapomorphy of Lepidosauromorpha which has evolved independently in Therapsida and within some members of Prolacertiformes.

146. Perforating artery of pes. In its primitive state the perforating artery of the pes passes through a foramen located between the astragalus and the calcaneum (0). Proximal migration of the artery so that it passes between the tibia and fibula and above the proximal tarsal elements with the subsequent loss of the perforating foramen (1) is an autapomorphy of Lepidosauromorpha. The derived condition has evolved convergently in Therapsida and in Rhynchosauria.

152. Distal tarsal I. Primitively the first distal tarsal is present as a discrete element (0). Loss of distal tarsal I (1) is an autapomorphy of Lepidosauromorpha. Within lepidosauromorphs some rhynchocephalians and testudines have re-acquired the first distal tarsal. In additon loss of the first distal tarsal has also evolved independently in some members of Archisauriformes and Prolacertiformes.

Lepidosauriformes Gauthier *et al.* 1988c

Definition. The most recent common ancestor of Keuhneosauridae, Rhynchocephalia, and Squamata and all their descendants.

This taxon is diagnosed by three autapomorphies:

15. Orbital exposure of maxilla. Primitively the maxilla is excluded from the lateral margin of the orbit (0). Inclusion of the maxilla into the lateral margin of the orbit (1) is an autapomorphy of Lepidosauriformes with independent acquisition in *Claudiosaurus* and within some members of Testudines, Eosauropterygia, Archisauriformes, and Prolacertiformes. Additionally some squamates have reversed to the primitive state.

27. Frontal morphology. The frontals in amniotes primitively are parallelogram in shape (0). Mid-length constriction resulting in an hourglass shape (1) is an autapomorphy of Lepidosauriformes. The derived condition is also found within some members of Testudines and Eosauropterygia among the Lepidosauromorpha. The character is also an autapomorphy of Archosauromorpha with a case of independent reversal within some Rhynchosauria.

40. Quadrate lateral conch. Primitively the quadrate is often hidden from lateral view. When it is exposed it retains a smooth lateral border (0) in most taxa. The development of a distinct ridge which extends along the vertical axis of the anterolateral border of the quadrate resulting in a distinctive conch (1) is an autapomorphy of Lepidosauriformes.

Keuhneosauridae Robinson 1962

Definition. The most recent common ancestor of *Cteniogenys*, *Icarosaurus*, *Keuhneosaurus*, *Keyhneosuchus*, *Perparvus*, and *Rhabdopelix* and all their descendants.

This taxon is diagnosed by 11 autapomorphies:

6. External nares exposure.* See discussion for Ankyramorpha above.

7. External nares. In all amniotes primitively the external nares are separated by an internarial bar (0). Loss of the internarial bar of the premaxilla has occurred independently in keuhneosaurs, rhynchosaurs, and choristoderans.

14. Maxillary length. See discussion for Procolophonia above.

−31. Postorbital/parietal relationship. See discussion for Acleistorhinidae above.

35(2). Squamosal lateral exposure.* See discussion for Procolophoniformes above.

−86. Surangular morphology. See discussion for Ankyramorpha above.

104. Cervical intercentra.* Primitively the cervical vertebrae of amniotes retain intercentra (0). Loss of cervical intercentra (1) may be an autapomorphy of Keuhneosauridae with independent evolution in Sauropterygia. Alternatively it may be an autapomorphy of Lepidosauromorpha with a reversal in Lepidosauria and within some members of Testudines.

108. Transverse process of dorsal vertebrae. The transverse processes of the dorsal vertebrae, in most amniotes, are short and do not extend beyond the lateral limit of the zygapophyseal articulations (0). In the derived condition the transverse processes of the dorsal vertebrae are elongate and extend at least past the lateral limit of the zygapophyseal articulations and often to a great degree (1). This character is an autapomorphy of kuehneosaurs which has evolved independently in *Placodus* and Archisauriformes.

−125. Distal humeral articulating facets. See discussion for Eosuchia above.

129(2). Radius/ulna ratio. In amniotes primitively the radius is shorter than the ulna (0). An increase in the length of the radius so that it is longer than the ulna (1) or both elements are of equal length (2) has occurred within saurians. State (1) has evolved within some members of Eosauropterygia, Prolacertiformes, and Younginiformes. State (2) is best interpreted as an autapomorphy of keuhneosaurs with convergent acquisition in sauropterygians and choristoderans and within Prolacertiformes.

168. Gastralia.* See discussion for Pareiasauria above.

Lepidosauria Haeckel 1866

Definition. The most recent common ancestor of Rhynchocephalia and Squamata and all their descendants.

This taxon is diagnosed by nine autapomorphies:

17(2). Lacrimal morphology. See discussion for Ankyramorpha above.

83(1). Coronoid process.* See discussion for Ankyramorpha above.

94. Tooth implantation. Primitively the teeth in amniotes are implanted in deep sockets (0). A loosely attached pleurodont configuration (1) is an autapomorphy of Lepidosauria. A further modification where the teeth are ankylosed to the jaws (2) may represent an autapomorphy uniting rhynchosaurs with *Triliphosaurus*.

115(2). Interclavicle morphology.* See discussion for Ankyramorpha above.

147. Tibia/astragalus articulation.* Primitively in amniotes the astragalus and tibia articulate via a very loose fitting joint (0). Development of a tight fitting well defined joint between both elements (1) may be an autapomorphy of Lepidosauria with independent acquisition in Testudines, Rhynchosauria, and Archisauriformes, or it may represent an autapomorphy of Sauria with cases of independent reversal in Sauropterygia, *Triliphosaurus*, and Prolacertiformes. In addition, the derived state is an unambiguous autapomorphy of Therapsida.

149(1). Astragalus/calcaneum relationship. See discussion for Procolophonia above.

150(1). Distal tarsal IV/astragalus articulation.* See discussion for Procolophonidae above.

156. Fifth metatarsal plantar morphology. Primitively in all taxa even those possessing a hooked fifth metatarsal there is no indication of any additional epiphyseal ossifications on the body of the element (0). The development of a plantar tubercle (epiphyseal ossification) on the fifth metatarsal (1) is an autapomorphy of Lepidosauria.

158(2). Number of pedal centralia.* See discussion for Reptilia above.

Rhynchocephalia Günther 1867

Definition. The most recent common ancestor of *Asiacephalosaurus*, *Brachyrhinodon*, *Clevosaurus*, *Dianosaurus*, *Eilenosaurus*, *Gephyrosaurus*, *Homeosaurus*, *Kallimodon*, *Leptosaurus*, *Meyasaurus*, *Monjurosuchus*, *Opisthias*, *Pelecymale*, *Polysphendon*, *Planodephalosaurus*, *Raojugalosaurus*, *Sapheosaurus*, *Sigmala*, *Sphenodon*, and *Toxolophosaurus* (Carroll, 1988; Gauthier *et al.*, 1988c; and Wu, 1991).

This taxon is diagnosed by nine autapomorphies:

33. Jugal morphology. Primitively the jugal has a short posterior process which extends only as far as the middle of the cheek region (0). An elongate posterior process of the jugal so that it reaches the posterior edge of the skull (1) is an autapomorphy of Rhynchocephalia. This character has also evolved convergently in edaphosaurs and in Archosauromorpha.

−42(2). Quadratojugal morphology. See discussion for Lanthanosuchoidea above.

56. Supraoccipital morphology.* See discussion for Procolophonia above.

101. Accessory vertebral articulations.* In amniotes primitively the vertebrae lack any type of accessory vertebral articulation such as zygosphere or zygantra (0). The development of zygosphene or zygantra (0) may represent an autapomorphy of Rhynchocephalia. The ambiguity here arises because squamates are scored as polymorphic for this trait. Therefore, this character may diagnose the more inclusive taxon Lepidosauria with independent loss within all of the squamates exhibiting the primitive state. The derived character also manifests itself independently in cynodonts and eosauropterygians.

127(2). Ectepicondylar groove.* See discussion for Pareiasauria above.

−128. Entepicondylar foramen. See discussion for Owenettidae above.

−130. Olecranon morphology.* See discussion for Procolophonia above.

−145. Fibua morphology.* See discussion for Araeoscelidia above.

157. Metatarsal I to IV ratio.* See discussion for Araeoscelidia above.

Squamata Merrem 1820

Definition. Ths most recent common ancestor of Eolacertilia, Iguania, Gekkota, Scincomorpha, Anguimorpha, and Serpentes, and all their descendants (Carroll, 1988; Estes *et al.*, 1988).

This taxon is diagnosed by nine autapomorphies:

−*25**. *Frontal morphology.* See discussion for *Macroleter* above.

*35(2)**. *Squamosal lateral exposure.* See discussion for Procolophoniformes above.

−*37. Occipital flange of squamosal.* Primitively in anamniotes the occipital flange of the squamosal is not well developed (0). In Amniota the squamosal develops a distinct posterolateral flange which wraps around the back of the skull (1). A reversal of the anamniote condition occurs as an autapomorphy of Squamata with an independent reversal in Eosauropterygia. The reversal may also represent an autapomorphy of the choristoderan/archosauromorph clade or it may diagnose the less inclusive clade Archosauromorpha. The ambiguity arises because the character cannot be determined in Choristodera.

77. Pterygoid flange orientation. See discussion for Procolophonia above.

−*79. Ventral extent of pterygoid flange.* See discussion for Pareiasauria above.

80. Angle of external edge of transverse flange. See discussion for Pareiasauria above.

87. Surangular lateral shelf. See discussion for Procolophiniformes above.

123. Humeral torsion. See discussion for *Anthodon* above.

*168**. *Gastralia.* See discussion for Pareiasauria above.

Turtles + Sauropterygia (un-named taxon)

Definition. The most recent common ancestor of Testudines, *Placodus*, and Eosauropterygia and all their descendants.

This taxon is diagnosed by ten autapomorphies:

8(1). Choana configuration. See discussion for Pareiasauria.

64. Parasphenoid constriction. See discussion for Velosauria above.

80. Angle of external edge of transverse flange. See discussion for Pareiasauria above.

−*116. Mineralized sternum.* See discussion for Diapsida above.

121. Coracoid foramen. Primitively the coracoid foramen is enclosed by the coracoid only (0). Inclusion of the scapula into the border of the coracoid foramen (1) is an autapomorphy of the Testudines/Sauropterygia clade.

123. Humeral torsion. See discussion for *Anthodon* above.

143. Femoral condyles for crus. See discussion for *Claudiosaurus* above.

*158(2)**. *Number of pedal centralia.* See discussion for Reptilia above.

−*162. Limb morphology.* See discussion for *Macroleter* above.

−*163. Morphology of podia.* See discussion for Millerettidae above.

Testudines Linnaeus 1758

Definition. The most recent common ancestor of *Proganochelys*, *Australochelys*, and Casichelydia and all their descendants.

This taxon is diagnosed by 41 autapomorphies:

3. Premaxillary dentition. Primitively all tetrapods have premaxillary teeth (0). Loss of teeth (1) is an autapomorphy of Testudines with one case of independent acquisition in the putative clade comprised of Rhynchosauria and *Trilophosaurus.*

6. External nares exposure.* See discussion for Ankyramorpha above.

—*25*. Frontal morphology.* See discussion for *Macroleter* above.

26. Frontal length/width ratio.* See discussion for Lanthanosuchidae above.

—*31. Postorbital/parietal relationship.* See discussion for Acleistorhinidae above.

—*32*. Postorbital morphology.* See discussion for Lanthanosuchoidea above.

35(1). Squamosal lateral exposure.* See discussion for Procolophoniformes above.

—*41*. Quadrate anterior process.* See discussion for Acleistorhinidae above.

—*42(1). Quadratojugal morphology.* See discussion for Lanthanosuchoidea above.

—*48. Parietal embayment for adductor musculature.* See discussion for Eosuchia above.

49(3). Pineal foramen.* See discussion for Ankyramorpha above.

—*50. Upper temporal fossa.* See discussion for Diapsida above.

—*51(0). Lower temporal fossa.* See discussion for Lanthanosuchoidea above.

56. Supraoccipital morphology. See discussion for Procolophonia above.

61. Paroccipital process morphology. See discussion for Pareiasauria above.

—*62. Exoccipital relationship to foramen magnum.* See discussion for Acleistorhinidae above.

63. Bacioccipital/basisphenoid relationship.* See discussion for Pareiasauria above.

74(2). Suborbital fenestra.* See discussion for Reptilia above.

81(3). Ectopterygoid. See discussion for Captorhinidae above.

85. Meckelian fossa.* See discussion for Procolophonia above.

87. Surangular lateral shelf. See discussion for Procolophoniformes above.

97. Presacral vertebral count. See discussion for Pareiasauria above.

98. Caudal vertebral count. See discussion for *Scutosaurus* above.

112. Chevron position. See discussion for Pareiasauria above.

—*114. Clavicle morphology.* See discussion for Eosuchia above.

117(2). Scapula morphology.* See discussion for Procolophonomorpha above.

118(2). Acromion process. See discussion for Pareiasauria above.

134. Iliac blade configuration.* See discussion for Parareptilia above.

—*137. Acetabulum morphology.* See discussion for Procolophonia above.

138. Acetabular buttress. See discussion for Procolophonomorpha above.

—*139. Femoral shaft configration.* See discussion for Eosuchia above.

140. Femoral fourth trochanter. Primitively the femora of amniotes possess a distinctive ridge of process (4th trochanter) on the proximoventral surface of the femur (0). Loss of the fourth trochanter (1) is an autapomorphy of Testudines which has evolved independently in Therapsida and in the putative clade comprised of Rhynchosauria and *Trilophosaurus.*

141(1). Trochanter major. See discussion for Velosauria above.

—*142(0). Intertrochanteric fossa.* See discussion for Eosuchia above.

147. Tibia/astragalus relationship.* See discussion for Lepidosauria above.

149(1). Astragalus/calcaneum relationship. See discussion for Procolophonia above.

150(1). Distal tarsal IV/astragalus relationship.* See discussion for Proclophonidae above.

159. Fifth pedal digit. See discussion for Pareiasauria above.

161(2). Pedal phalangeal formula. See discussion for Pareiasauria above.

*165(2)**. *Body osteoderms*. See discussion for Lanthanosuchidae above.

167. *Bony studs on limbs*. See discussion for Velosauria above.

Sauropterygia Owen 1869

Definition. The most recent common ancestor of *Placodus*, Eosauropterygia and all their descendants.

This taxon is diagnosed by 11 autapomorphies:

1. *Premaxillary size*. Primitively the premaxilla is restricted to the anterior tip of the snout with its posterior extent being limited by the length of the dorsal process (0). In the derived state the premaxilla is increased in overall size so that much of the anterior half of the snout is composed of the premaxilla (1). This character is an autapomorphy of sauropterygians with independent acquisition in cynodonts and in the clade comprised of Choristodera and Archosauromorpha.

17(2). *Lacrimal morphology*. See discussion for Ankyramorpha above.

*72**. *Palate kinesis*. See discussion for Lanthanosuchoidea above.

73(2). *Interpterygoid vacuity*. See discussion for Pareiasauria above.

−*74(0)**. *Suborbtal fenestra*. See discussion for Reptilia above.

*104**. *Cervical intercentra*. See discussion for Keuhneosauridae above.

105. *Cervical ribs*. See discussion for *Claudiosaurus* above.

109. *Number of sacral vertebrae*. See discussion for Procolophonomorpha above.

*129(2)**. *Radius/ulna ratio*. See discussion for Keuhneosauridae above.

−*154*. *Metatarsal V length*. See discussion for Neodiapsida above.

−*155*. *Metatarsal V morphology*. See discussion for Sauria above.

Placodus Agassiz 1833

Definition. The most recent common ancestor of *Placodus*.

This taxon is diagnosed by 18 autapomorphies:

9(1). *Nasal morphology*. Primitively the nasals are paired elements (0) in amniotes. fusion of both elements (1) is an autapomorphy of *Placodus* which has evolved convergently in Choristodera and some Squamata. Complete loss of the nasals (3) has also evolved in some squamates.

14. *Maxillary length*. See discussion for Procolophonia above.

19(2). *Preorbital/postorbital skull ratios*. See discussion for Lanthanosuchidae above.

22. *Frontal contribution to orbit*. See discussion for Pareiasauria above.

*26**. *Frontal length/width ratio*. See discussion for Lanthanosuchidea above.

−*32**. *Postorbital posterior extent*. See discussion for Lanthanosuchoidea above.

*35(1)**. *Squamosal lateral exposure*. See discussion for Procolophoniformes above.

−*66*. *Opisthotic/cheek contact*. See discussion for Pareiasauria above.

76(2). *Palatal process of pterygoid*. See discussion for Lanthanosuchidae above.

−*79*. *Transverse flange ventral extent*. See discussion for Pareiasauria above.

*82(1)**. *Mandibular joint*. See discussion for Parareptilia above.

*83(1)**. *Coronoid process*. See discussion for Ankyramorpha above.

*85**. *Meckelian fossa*. See discussion for Procolophonia above.

−*88(0)*. *Splenial morphology*. See discussion for Lanthanosuchidae above.

−*99. Vertebral centra*. See discussion for Sauria above.

108. Dorsal transverse processes. See discussion for Keuhneosauridae above.

122. Humeral epicondyles*. See discussion for *Claudiosaurus* above.

165(2). Body osteoderms*. See discussion for Lanthanosuchidae above.

Eosauropterygia Rieppel 1994a

Definition. The most recent common ancestor of *Corosaurus*, Pachypleurosauroidea, Eusauropterygia and all their descendants (Rieppel, 1994a).

This taxon is diagnosed by four autapomorphies:

−*37. Squamosal occipital flange*. See discussion for Squamata above.

101. Accessory vertebral articulations. See discussion for Rhynchocephalia above.

−*110*. Caudal lateral projections*. See discussion for Procolophonia above.

117(2). Scapula morphology*. See discussion for Procolophonomorpha above.

Choristodera + Archosauromorpha (unnamed taxon)

Definition. The most recent common ancestor of Choristodera and Archosauromorpha and all their descendants.

This taxon is diagnosed by 11 autapomorphies:

1. Pemaxilla morphology. See discussion for Sauropterygia above.

4. Premaxillary posterior process. Primitively the premaxilla lacks a postnarial process (0). In the derived state the premaxilla has developed a bony process that rises posterodorsally excluding the maxilla from the posterior margin of the external nares (1). This character is an autapomorphy of the Choristodera-Archosauromorpha clade. The derived state has also manifested itself within some members of Squamata, Testudines, and Eosauropterygia.

6. External nares exposure*. See discussion for Ankyramorpha above.

10. Nasal/frontal ratio. Primitively the greatest length of the nasal is equal to or shorter than the greatest length of the frontal (0). An increase in the length of the nasal so that it exceeds the frontal length by at least 25% (1) is an autapomorphy of the Choristodera–Archosauromorpha clade which has also evolved convergently in eupelycosaurs.

−*25*. Frontal configuration posteriorly*. See discussion for *Macroleter* above.

42(2). Quadratojugal morphology*. See discussion for Lanthanosuchoidea above.

49(3). Pineal foramen*. See discussion for Ankyramorpha above.

60(1). Posttemporal fossa. See discussion for Lanthanosuchoidea above.

63. Basioccipital/basisphenoid relationship*. See discussion for Pareiasauria above.

105. Cervical ribs. See discussion for *Claudiosaurus* above.

151. Calcaneal tuber. Primitively the calcaneum has a uniformly, smooth outline (0). The development of a distinct tuberosity on its posterolateral margin (1) is an autapomorphy of the Choristodera–Archosauromorpha clade. This character has also developed convergently in the clade comprised of Cynodontia and Gorgonopsia.

Choristodera Cope 1876

Definition. The most recent common ancestor of *Champsosaurus*, *Cteniogenys*, *Simoeodosaurus*, and *Tchoiria* and all their descendants (Evans & Hecht, 1993).

This taxon is diagnosed by 14 autapomorphies:

7. External narial openings. See discussion for Keuhneosauridae above.

9(1). Nasal morphology. See discussion for *Placodus* above.

14. Maxillary length. See discussion for Procolophonia above.

19(2). Preorbital/postorbital skull ratio. See discussion for Lanthanosuchidae above.

−31. Postorbital/parietal contact. See discussion for Acleistorhinidae above.

47(1). Parietal skull table. Primitively the parietal is a broad element (0). Medial constriction of the parietal (1) is an autapomorphy of Choristodera which has evolved independently within some members of Archisauriformes, Eosauropterygia, Squamata, and Rhynchocephalia. A further derivation where a pronounced saggital crest is developed (2) is an autapomorphy of Cynodontia and the clade comprised of Rhynchosauria and *Trilophosaurus*.

−79. Transverse flange ventral extent. See discussion for Pareiasauria above.

80. Angle of external edge of transverse flange. See discussion for Pareiasauria above.

82(1). Mandibular joint position. See discussion for Parareptilia above.

100(1). Vertebral morphology. Primitively the vertebrae of amniotes are amphicoelous (0). Development of platycoelous vertebrae (1) is an autapomorphy of Choristodera. This condition has also evolved independently within some members of Eosauropterygia, Prolacertiformes, and in *Trilophosaurus*. Other vertebral centra-morphologies are not elaborated here for they have no evolutionary significance at the level of this analysis. However, the most common arrangement, which appears numerous times among amniotes, is represented by a proceolous (2) condition. This condition is found within some members of Squamata and Archisauriformes.

107. Dorsal intercentra*. See discussion for Lepidosauromorpha above.

−124. Humeral ends/humeral length ratio*. See discussion for Millerettidae above.

129(2). Radius/ulna ratio. See discussion for Keuhneosauridae above.

143. Distal femoral condyles. See discussion for *Claudiosaurus* above.

Archosauromorpha Heune 1946

Definition. The most recent common ancestor Prolacertiformes, Archisauriformes, Rhynchosauria, *Trilophosaurus*, and all their descendants.

This taxon is diagnosed by seven autapomorphies:

11. Maxilla ascending process*. See discussion for Ankyramorpha above.

27. Frontal configuration. See discussion for Lepidosauriformes above.

33. Jugal posterior extent. See discussion for Rhynchocephalia above.

35. Squamosal lateral exposure*. See discussion for Procolophoniformes above.

−37. Occipital flange of the squamosal*. See discussion for Squamata above.

136. Pubic tubercle. Primitively if a public tubercle is present it is small and directed anteriorly from the dorsolateral margin of the pubis (0). Modification in the orientation of the tubercle occurs when the process is greatly enlarged and deflected ventrally (1) [Benton & Clark, 1988]. The derived state is an autapomorphy of Archosauromorpha.

149(2). Astragalus/calcaneum relationship. See discussion for Procolophonia above.

DISCUSSION

Testing for congruence

The present analysis, albeit represented by a larger data base than previous phylogenetic analyses involving Testudines, does not necessarily represent a more accurate *de facto* representation of turtle origins when compared to other recent interpretations (Laurin & Reisz, 1995; Lee, 1994, 1995, 1996a). In fact, it can be argued that the phylogenetic hypothesis presented here is yet another indication of how poorly understood the issue of turtle origins are. This analysis does have some advantages over the others in that it has benefited from two detailed works which have contributed immensely to the present body of knowledge detailing turtle evolution (Laurin & Reisz, 1995; Lee, 1995). Most of the characters described in detail in the previous analyses were incorporated into this analysis and with few exceptions the coding presented by the previous authors was adhered to. In cases where the present authors disagreed with an earlier interpretation of the character, that character is discussed in detail in the taxonomic section above.

The only significant, methodological advantage between this analysis and previous ones is in testing for congruence between developmental data and the morphological data set. The *a priori* assumption here is that the present phylogeny is congruent with the evolution or distribution of developmental data. Lack of congruence would fail to support the present analysis whereas congruence would fail to reject the null hypothesis. Failure in the case of the latter would not result in an absolute acceptance of the present phylogeny, but it would for the first time present an analysis that has been subjected to and evaluated using additional data to assess its thesis.

Granted that in order to use developmental data only living taxa could be considered, but this is sufficient because rejection, or lack of support for the present phylogeny, would manifest itself quite readily using only living groups. This premise is based on the fact that for turtles to be the sister-taxon to sauropterygians they must by definition be nested within Sauria. Furthermore, turtles must share a closer sister-group relationship to (living) lepidosauromorphs than the latter would with archosauromorphs. Therefore, in order to reject or fail to support the present phylogeny it would be necessary only to show that lepidosauromorphs share more developmental characteristics in common with archosauromorphs than with turtles. Alternatively the present phylogeny would be supported if turtles would share more in common with lepidosauromorphs. Polarity for these characters was established by direct comparison with mammals. Presence of a particular trait in a mammal delineates the primitive condition.

(I) The presence of a triradiate jugal in the earliest stages of ossification is primitive for amniotes as both extant mammals (deBeer, 1937) and crocodiles (Rieppel, 1993b) retain this condition. In squamates the jugal is instead semi-lunate and lacks the posterior process entirely (Rieppel, 1992a). As far as other lepidosaurs are concerned the presence of a triradiate jugal in the mature *Sphenodon* may be misleading because basal members of the clade lacked a lower temporal bar which resulted in the great reduction of the posterior process of the jugal (Wu, 1991). Furthermore, developmental studies of *Sphenodon* show a semi-lunate jugal throughout most of its development with the posterior process appearing late in development (Howes & Swinnerton, 1901; deBeer, 1937).

In turtles the jugal has a semi-lunate shape (Rieppel, 1993a, 1995) and appears very much like the structure that is found in extant lepidosaurs. Comparison with fossil taxa is difficult because although the jugal may appear triradiate in mature specimens there is presently no way of establishing what the developmental sequence was like.

(II) The development of the interclavicle and clavicles of extant diapsids and turtles has been examined most recently by Rieppel (1992a, 1993a,b, 1995) and the conclusions were that the gracile cruciforme interclavicle (entoplastron in Testudines) is developmentally identical when comparing squamates and turtles. In crocodiles, although the interclavicle is gracile it does not develop the slender transverse bar at its proximal end and is, therefore, not cruciforme. Non-mammalian synapsids have a broad interclavicle with a rhomboidal anterior process and extant mammals have lost the interclavicle except for monotremes which possess a very distinctive element that is roughly T-shaped except that its posterior process is quite broad.

(III) Ontogenetic development of the carpus. Primitively the carpus ossifies in the following sequence as exemplified by the mammal *Mus* (Shubin & Alberch, 1986): ulnare ossifies first followed by the intermedium and then the fourth distal carpal or radiale. The remainder of the carpus then develops in a quick order which is sometimes difficult to denote. However, the first three elements described above always follow that developmental sequence.

Within extant reptiles, recent work by Rieppel (1992a,b,c, 1993a,b, 1994b) has outlined a very precise and consistent developmental sequence for the ossification of the carpus. In squamates the sequence of ossification in *Lacerta vivipara* (Rieppel, 1992a), *Cyrtodactylus pubisulcus* (Rieppel, 1992b), and *Lanthanotus borneensis* (Rieppel, 1992c) is virtually identical and in all cases the first element to ossify is the ulnare followed by the fourth distal carpal and only then the intermedium. The 'radiale' described by Rieppel for these taxa is actually derived from the intermedium and is developmentally not a true radiale but a centrale (Shubin & Alberch, 1986; Caldwell, 1994). In the only other lepidosaur where the developmental sequence has been studied, *Sphenodon*, the sequence of ossification is again like that of squamates where the ulnare comes first followed by distal carpal IV.

In crocodiles (Rieppel, 1993b) the ossification sequence is ulnare followed by the radiale, and the pisiforme. In fact in the adult, distal carpal IV may not be fully ossified. This condition contrasts strongly with what is found in lepidosaurs and even mammals, although the early appearance of the radiale and the fact it is truly a radiale (segments from the radius) resembles more closely the mammalian condition than it does the lepidosaur pattern.

Finally, among extant taxa Testudines exhibit the following pattern of ossification of the carpus: distal carpals I–III, followed by the intermedium, centrali III, then distal carpal IV, centrale IV, and finally the ulnare (Rieppel, 1993a). This pattern differs significantly from any other extant reptile in that the most distal elements of the carpus ossify prior to the most proximal elements. However, like the condition in lepidosaurs the radiale never ossifies but its topological position is instead occupied by an enlarged centrale that has developed from budding of the intermedium.

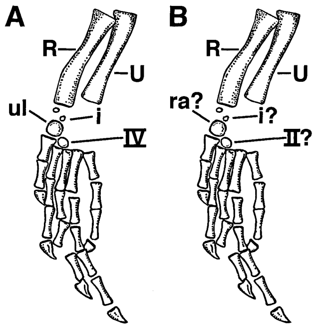

Figure 5. Forelimb of *Thadeosaurus colcanapi* (1908–11). A, figure as drawn by Currie and Carroll (1984). B, figure as reinterpreted for this study. Note that the identification of the ulnare and distal carpal IV are questioned due to their relative position to the elements of the antebrachium and the digits. In the original interpretation (A) the element identified as the ulnare is found in proximity not to the ulna and fourth digit as would be expected, but is instead located directly distal to the radius and proximal to the second digit. Although the position could be accounted for by post-mortem displacement, the possibility that the elements in question represent structures other than those originally interpreted cannot be ruled out.

Among fossil taxa Caldwell (1994) has recently elucidated the developmental sequence for the eosuchian grade diapsids. In *Hovasaurus* the first element to ossify is the ulnare followed by the intermedium and finally distal carpal IV. In *Thadeosaurus* the ulnare appears to be first but only two specimens show this clearly. In one specimen (MNHN 1908-11-4) what has been labelled by Caldwell as the ulnare is located below the radius and proximal to metacarpal II and may not be the ulnare at all (Fig. 5). Furthermore, the sequence of ossification exhibited for another specimen of *Thadeosaurus* (MNHN 1908-11-16) has an element below the radius which Caldwell labeled as the intermedium. However, whenever the intermedium ossifies it does so between the ulna and radius and often closer to the ulna than the radius. This makes sense given that the intermedium develops in concert with the ulnare as a bifurcation product of the ulna. The position of the element that Caldwell refers to as an intermedium is more correctly interpreted as a true radiale. Finally the ossification sequence of *Claudiosaurus* as exemplified by the smallest and by extension the youngest specimen (CM 47508) has four ossifications present and the apparent ossification sequence would be ulnare, intermedium, centrali, and finally distal carpal IV. Among the fossil taxa considered by Caldwell only *Hovasaurus* exhibits a pattern that is found in extant lepidosaurs. However, even in this case the intermedium appears to ossify before the fourth distal carpal. *Thadeosaurus* may retain a true radiale judging by its position in the carpus of the specimens enumerated above and, therefore, would exhibit the primitive condition, and *Claudiosaurus* although not possessing a ‘radiale’ early in ontogeny seems to delay the appearance of the fourth distal carpal when compared to extant lepidosaurs.

(IV) The development of the tarsale proximale or a discrete cartilaginous precursor which ossified into the astralagus and calcaneum is known among extant lepidosaurs and turtles only (Rieppel, 1993b, 1995). In crocodiles the cartilaginous precursors are separate elements which then ossify individually into the astragalus and calcaneum. The condition in mammals is not well known, but in fossil synapsids and reptiles (including parareptiles) the passage of the perforating artery through a foramen between the astragalus and calcaneum precludes the presence of a single cartilaginous precursor in these taxa.

(V) The presence of a hooked fifth metatarsal, and more specifically its development, is another element that has recently been suggested to be homologous between diapsids and turtles (Rieppel, 1995). Ossification of this element is described as being greatly delayed in crocodiles, squamates, and turtles in relation to the rest of the pes. Furthermore, the hooked fifth metatarsal is strongly developed in both turtles and squamates and in these taxa ossification starts in exactly the same region: on the medial preaxial side where the hooked portion of the fifth metatarsal articulates with the lateral postaxial side of the proximal head of the fourth metatarsal. Unfortunately the developmental sequence in mammals is not well known and the pattern exhibited by all fossil taxa has not and possibly will never be determined. We do, however, know that the hooked fifth metatarsal is absent in all non-mammalian synapsids except cynodonts. We also know that a hooked fifth metatarsal is present in all adequately known saurians except sauropterygians where the absence of the hooking is interpreted as a reversal possibly associated with the development of an aquatic lifestyle in these taxa. Nevertheless, although we can identify the evolution of the element within amniotes we cannot determine its developmental pattern in any taxa without extant members. Establishing the ossification pattern in mammals would go a long way to solving the nature of the homology of this element in all those extant taxa that possess it.

From the developmental data at present we can make the following conclusions: (i) of the five developmental sequences evaluated above we know that three (I, III, and IV) of these support a tutrle-lepidosaur sister-group relationship; (ii) the remaining two (II and V) lack sufficient evidence to support or refute the sister-group relationship; and (iii) not one of the sources of data evaluated above presents strong evidence to suggest that turtles and lepisodaurs cannot be sister-taxa. This final assumption is of course based on negative evidence and is, therefore, of dubious value, but it is striking that of the three supporting data sets all are unique to these two taxa. As noted by Rieppel (1995) the development of a semi-lunate jugal (I) and the presence of a single cartilaginous precursor (IV) [tarsale proximale] appear to be valid synapomorphies of turtles and lepidosaurs. Certainly these developmental patterns can be the result of convergence but congruence with the current phylogenetic data set suggests otherwise. In addition the absence of the radiale as a discrete element that segments from the radius in squamates and turtles and its presence in both crocodiles (Müller & Alberch, 1990) and mammals among extant groups (Shubin & Alberch, 1986) and the possibility that it was also present in non-lepidosauromorph fossil diapsids such as *Thadeosaurus* (see discussion above) suggests quite strongly that carpal ossification (III), although sequentially different between turtles and all other amniotes (dispal carpals ossifying before proximal elements in the former), may also be a valid synapomorphy of this putative clade.

Additional soft tissue data (Gauthier *et al.*, 1988b) can also be evaluated. In the largest data set ever accumulated, Gauthier and colleagues reviewed both Gardiner's (1982) and Lövetrup's (1985) data for the relationships of amniotes. In Gauthier *et al.*'s (1988b) assessment 67 soft tissue characters were evaluated. Assuming that their polarization of the data set was correct (using living amphibians to act as the out-group) then the following soft-tissue characters are plausible synapomorphies for the turtle-lepidosauromorph clade (numbers in front of character refer to those used by Gauthier *et al.* [1988b]): (G37) - subclavian arteries displaced cephalad and (A11) -

colour vision. Gauthier *et al.*'s (1988b) data also presents several lepidosauromorph-archosauromorph (their Crocodylia excluding Aves) putative synapomorphies: (G21) - loss of sinus venosus and development of septum sinu-venosi; (G24a) - three turbinals; (G34c) - tendon of nictitans to pyramidalis muscle; (A9) - plasma concentration of urea and uric acid; (A14) - olfactory bulbs; (A20) - position of kidney; and (A25) - Huxley's foramen (see Gauthier *et al.* [1988b] for the character details).

The developmental evidence discussed above is by no means exhaustive but it does nevertheless suggest a possible phylogenetic signal that has often been disregarded as at best heretical and at worst impossible. The soft tissue data is much less convincing and in fact may suggest a much more likely sister-group relationship between lepidosaurs and archosaurs than the former would share with turtles. However, although the soft tissue evidence is weak (only two characters supporting the turtle-lepidosaur relationship compared with seven for the lepidosaur-archosaur relationship) it must still be considered in light of all of the other data and as such serves to add more support to the present phylogenetic hypothesis.

Comparing phylogenies

Recent phylogenetic analyses (Gauthier *et al.*, 1988a; Reisz & Laurin, 1991; Lee, 1993b; Laurin & Reisz, 1995; Lee, 1995) have been constrained by the belief that turtles are 'anapsids' and, therefore, the groups selected for comparison and character polarization have been restricted to those basal (Paleozoic) members of extant amniote taxa. Lee (1995: 462) lamented that previous workers did not consider sufficiently disparate taxa or characters in their analyses:

> The problem with this approach is clear: for instance turtles and pareiasaurs both possess an enlarged foramen palatinum posterius, a shared derived trait that occurs in no other primitive amniote. However, in Gauther *et al.*'s first analysis [1988a], pareiasaurs were not included, hence this character would have been discarded (it would have been an autapomorphy of turtles, and thus phylogenetically uninformative). While pareiasaurs were included in their second analysis [1988b], this chelonian-pareiasaur synapomorphy would again have been ignored, because they did not extensively revise and extend their character set by comparing pareiasaurs directly with the other groups (e.g. turtles), but instead used only the characters included in the first analysis.

Although Lee (1995) was correct in his assessment, it did not preclude him from falling into the same trap. In his analysis of parareptile interrelationships he restricts his analysis to Paleozoic taxa alone, therefore, having a profound effect on the phylogenetic implications for turtle origins. In fact, upon reviewing some of the recent literature on the subject of turtle origins it appears as though a crusade has been launched with one camp exemplified by Laurin and Reisz and the other by Lee. The result is a heated debate that has taken on some rather aggressive tones especially the latest round fired by Lee (see Lee, 1995, addendum p. 545).

Beyond all of the posturing the end result has been positive in that presently the knowledge or data set available for Paleozoic taxa has increased by an order of magnitude not previously believed. There is no question at present that parareptiles are monophyletic and although the exact relationship of some problematic, poorly known taxa such as lanthanosuchids and *Sclerosaurus* may be debatable (Lee, 1995;

Table 1. Bootstrap and support indices for critical nodes. Laurin and Reisz (1995), table 1A, Lee (1995) table 1B

Taxon	Bootstrap value %	Support index (steps needed to collapse node)
A		
Diadecotomorpha	75	2
Amniota	87	4
Sauropsida	80	2
Reptilia	67	1
Parareptilia	96	5
Procolophonia	100	22
Testudinomorpha	82	5
Eureptilia	69	4
Romeriida	59	2
Diapsida	76	5
B		
Nyctiphruretia	91	3
Procolophoniformes	93	4
Owenettidae	90	2
Procolophonoidea	88	3
Hallucicrania	96	5
Pareiasauroidea	83	2
Pareiasauria	100	7

deBraga & Reisz, 1996) the overall picture of the phylogenetic interrelationships of the parareptiles is now well established. The present analysis agrees with both Lee (1995) and Laurin & Reisz (1995) that within Parareptilia pareiasaurs and procolophonoids are more closely related to one another that either is to any other parareptile. Indeed the greatest area of disagreement is the position of Testudines.

Both Lee (1995) and Laurin & Reisz (1995) evaluated their phylogenies by bootstrapping and 'support index' methods (Table 1). In each case the strongest node in their respective phylogenies was the clade that included turtles. Lee's Pareiasauria ('pareiasaurs' [Lee's quotations] plus turtles) required seven steps to collapse the node and the clade was supported by a 100% confidence value for the boot-strapping analysis (Lee, 1995). In the study by Laurin and Reisz their Procolophonia which exhibited the following grouping [pareiasaurs [turtles, procolophonids]] was also supported by a 100% boot-strapping value and required twenty-two extra steps to collapse (Laurin & Reisz, 1995). In addition if we include the number of steps required to collapse their Testudinomorpha (five steps) the nesting of turtles within Procolophonia as the sister taxon to Procolophonidae requires 27 steps to collapse. Although at first glance it appears that Laurin and Reisz's analysis is more strongly supported when compared to Lee (only seven steps required to collapse his Pareiasauria (pareiasaurs plus turtles), it must be recognized that Lee's analysis has by necessity (a phylogenetic analysis of parareptiles in his case compared to Laurin and Reisz's brother amniote phylogeny) broken down the more inclusive Procolophoniformes (equivalent to this paper's and Laurin and Reisz's Procolophonia) into four successive sister clades. If one adds up the number of steps required to collapse each one of the clades nested within Lee's Procolophoniformes (except for Procolophonoidea which diagnoses a monophyletic clade separate from that which gave rise to turtles) then eighteen steps (Procolophoniformes, four steps;

Table 2. Ratio of steps (measured as %) required to collapse critical nodes (here turtles are nested) in comparison to overall tree length

Analysis	Clade steps to collapse	Ratio as % value
Laurin & Reisz, 1995	Parareptilia (5 steps) + Procolophonia (22 steps) + Testudinomorpha (5 steps) = Total (27 steps)	32/323 = 9.9%
Lee, 1995	Procolophoniformes (4 steps) + Hallucicrania (5 steps) + Pareiasauroidea (2 steps) + Pareiasauria (7 steps) = Total (18 steps)	18/80 = 22.5%
Present study	Eureptilia (3 steps) + Diapsida (3 steps) + Eosuchia (3 steps) + Neodiapsida (3 steps) + Sauria (3 steps) + Lepidosauromorpha (3 steps) + Testudines & Sauropterygia (2 steps) = Total (20 steps)	20/771 = 2.6%

Hallucicrania, five steps; Pareiasauroidea, two steps; and Pareiasauria, seven steps) are required to break Lee's phylogeny.

Comparing the ratio of steps required to collapse each of the phylogenies (Laurin & Reisz, 1995; Lee, 1995) to the total number of steps required to resolve the respective trees yields the following result. Laurin and Reisz's analysis requires 32 steps out of the total of 323 steps, required to resolve the tree, for a ratio of 9.9%. Lee's analysis requires 18 steps out of a total of 80 for a ratio of 22.5% (Table 2). In fact, what the results suggest is that Lee's phylogeny and by extension his character selection is more heavily biased toward those characters that will help resolve relationships within Procolophoniformes (Lee's nomenclature) than is Laurin and Reisz's (1995) analysis. This interpretation is also supported by the high confidence limits for Lee's data set (0.80 CI) as well as, to a lesser extent, Laurin and Reisz's (0.669 CI), which are more an indicator of the skewed nature of the characters selected for analyses. Again, this is not surprising because in both cases the most critical parameter under consideration was the phylogenetic position of turtles, and the neting of turtles within Parareptilia had already been accepted on the basis of previous analyses (Reisz & Laurin, 1991; Lee, 1993b). In fact the only real difference between the two trees, aside from the obvious phylogenetic implications, are the number of characters and the number of taxa considered.

Present phylogeny

The approach followed herein differs strongly from previous analyses in its global approach. The position of turtles within Amniota was accepted but its relationship to any of the major amniote clades was left uncertain. Therefore, as many taxa as possible (those taxa with fossil relatives) were incorporated into the analysis. The present analysis was also subjected to both a bootstrap analysis, of which 100 replicates were run using the heuristic algorithm of PAUP 3.1.1. (Swofford, 1993),

Table 3. Bootstrap and support indices for critical nodes. *Note: the exact support index for Amniota was not calculated past ten steps because of computer time constraints

Taxa	Bootstrap value as %	Support index
Amniota	99	over 10 steps*
Synapsida	55	5 steps
Reptilia	48	4 steps
Eureptilia	37	3 steps
Romeriida	38	3 steps
Diapsida	41	3 steps
Eosuchia	47	3 steps
Neodiapsida	41	3 steps
Sauria	43	3 steps
Choristodera +	59	2 steps
Archosauromorpha	61	2 steps
Lepidosauromorpha	39	3 steps
Lepidosauriformes	41	2 steps
Lepidosauria	63	2 steps
Testudines + Sauropterygia	43	2 steps
Sauropterygia	89	2 steps
Parareptilia	53	3 steps
Ankyramorpha	60	3 steps
Lanthanosuchoidea	92	5 steps
Macroleter + Procolophonia	43	3 steps
Procolophonia	60	3 steps
Pareiasauria	91	4 steps
Procolophoniformes	86	3 steps
Velosauria	68	2 steps

and a support index analysis as most recently described by Eernisse and Kluge (1993).

The global nature of the analysis produced the following results: (1) because of the numerous taxa and the large data set (168 characters in all) homoplasy is quite rampant; (2) as a result of the high rate of homoplasy the overall consistency index for the tree was rather low (0.507) when compared to either of the previous two phylogenies discussed above; (3) furthermore, the support index for the nodes and the bootstrap values were also much lower than that which has been published supporting alternative views on turtle relationships (Table 3).

Bootstrap values and support indices for Laurin and Reisz (1995) and Lee (1995) were briefly discussed above (Table 1). Compared to either one of those analyses the present one pales when its bootstrap and support indices are evaluated. For instance, the number of steps required to collapse the clade comprised of Testudines and Sauropterygia is a mere two steps, and the confidence limit for this clade is only 43%. In fact the only clade that requires more than seven steps (Lee's strongest clade) to collapse and is supported by a confidence value of 100% is Therapsida. Only two other clades in the present analysis are supported by bootstrap values that exceed 90% and they are, interestingly, nested within Parareptilia. These clades are Lanthanosuchoidea which is supported by 92% of the randomly generated trees and Pareiasauria which is supported by a 91% confidence value. Surprisingly although both clades yield the highest support values only one (Lanthanosuchoidea) clade has a relatively high, in comparison to the rest of the clades in this analysis, support index (five steps). Pareiasauria collapsed after only two steps. An additional attempt at evaluating the robusticity of this analysis quantitatively was accomplished

TABLE 4. Overall clade strength (taken as an average (%) of all the bootstrap values for all the clades from the respective trees). *Note: both Lee's (1995) and the Laurin and Reisz (1995) data were rerun using a PAUP analysis. Although Laurin and Reisz's results were replicated, Lee's results could not be and the monophyly of his in-group is in question. In fact, the 80 steps required to resolve his tree can be attained only if all of the out-group taxa are excluded from the analysis and replaced by an all zero ancestor. We question this approach, especially given the fact that the monophyly of all the taxa included in his in-group had not previously been established

Analysis	Tree-length	Clade strength %
Laurin and Reisz, 1995*	323 steps	79.1
Lee, 1995*	80 steps*	91.6
Present study	771 steps	59.6

by taking the measure of the 'clade strength' as calculated by taking the average of all the bootstrap values for all the clades in the particular tree. This yielded a value of only 59.6% for the present analysis compared to 79.1% for the Laurin and Reisz (1995) phylogeny and the even more impressive 91.6% for Lee's (1995) analysis (Table 4). In fact, the three values are informative in that they are directly correlated to the homoplasy in each of the phylogenetic hypotheses, with the present analysis exhibiting the greatest homoplasy and Lee's analysis the least.

Tree lengths are also generally agreed to be indicative of clade strength, so that the shorter the tree the more likely the evolutionary hypothesis being presented, as suggested by parsimony. In this case the tree length (TL) for the cladogram presented here (Fig. 1) is 771 steps. An alternative hypothesis of turtle relationships where turtles are placed as the sister taxon to Pareiasauria results in a TL of 776 steps. Alternatively, placing turtles within Pareiasauria as Lee (1993b, 1994, 1995, 1996b) believes results in the following TL's: as a sister taxon to *Bradysaurus* TL of 782; as the sister taxon to Velosauria TL of 778; as the sister taxon to *Scutosaurus* TL of 778; and finally as the sister taxon to *Anthodon* TL of 775. The last scenario is the one most widely championed by Lee (1994, 1996b) where turtles are nested within his pareiasaurian Carapacia which includes *Nanoparia* and *Anthodon* among others. Although this tree is only four steps longer than the most parsimonious tree (MPT) presented here it is not the only plausible alternative to our phylogenetic grouping. In fact, placing turtles with Lepidosauria also results in a cladogram with a TL of 775.

Obviously, if one considers tree length as the most informative feature of a cladistic analysis then the data supporting a Testudines-Sauropterygia clade represents the shortest or most parsimonious tree. This MPT is four steps less than the next shortest tree which either supports turtles as sister taxa to derived pareiasaurs or as sister taxa to lepidosaurs. However, TL is not the only indicator of phylogenetic robusticity and often other methods to estimate clade strength have been employed including support indices and bootstrapping (see discussion above).

Although the present analysis is not strongly supported by bootstrap analysis the clade of Testudines-Sauropterygia is still found more frequently than any other grouping. Parieasaurs with turtles, for example, are found in only 24% of the trees; Procolophonia with turtles in 21% of the trees; Ankyramorpha with turtes was found in 20% of the trees; Parareptilia plus turtles was found in 18% of the trees; *Macroleter*, Procolophonia, and turtles form a clade in 14% of the trees; Therapsida and turtles form a clade in 12% of the trees, which is much higher than the other proposed parareptile grouping for Procolophoniformes (procolophonids and owenettids) and turtles which is found in only 1% of the trees. Indeed, turtles are found nested within Romeriida in 48% of the trees; within Eosuchia in 47%; within Sauria in 43%; within Diapsida in 41%; within Neodiapsida in 40.5%; and within Lepidosauromorpha in 39% of the total number of trees generated through the bootstrap method. Whether these values are significantly higher than those values for uniting turtles with various members of Pareptilia is unclear. Using strict statistical methodology for supporting data requires a 95% confidence limit. On the basis of this criteria not one of the clades presented here would be supported except for Amniota (Table 3). As noted by Laurin and Reisz (1995), 95% confidence limit for bootstrapping is probably too severe a constraint and we are inclined to agree, but as to what the cut-off point should be is a matter for debate. We propose that each analysis is different and reflects the focus of the particular workers. Therefore, high bootstrap values for a cladogram that has very little homoplasy and a high CI are only indicative of the fact that the characters selected for analysis were sufficiently discrete to resolve the interrelationships between those taxa considered, and furthermore, that most of the taxa under consideration were members of a highly derived monophyletic group (i.e. Lee's Procolophoniformes [1995]). Any deviation from this approach, either by selecting characters that are highly homoplasious or selecting numerous and diverse taxa belonging to many separate clades, or both, would substantially lower the CI and as a result the bootstrap values as well.

The strength of this analysis is, therefore, not reflected in the traditional manner (i.e. high CI, etc.) because it incorporates numerous derived members of the major amniote clades. This differs significantly from the general approach which considers derived taxa only within the in-group and all out-group taxa are then restricted to a few basal members. Hence in both Laurin and Reisz (1995) and to a greater extent in Lee (1995), outgroups for Parareptilia were restricted to constructing primitive states for Synapsida and Diapsida with only a few discrete taxa such as *Paleothyris*, in the case of Laurin and Reisz (1995), being considered. Furthermore, although turtles are known only from the Upper Triasic, all previous analyses restricted taxon selection to mainly Paleozoic members, ignoring the possibiliy that turtles may have shared a more recent common ancestry with clades that are well represented and diverse only in the Triassic (i.e. derived members of Diapsida such as saurians). The effect here is that any possible phylogenetic signal between turtles and any other taxa, that may manifest itself within derived members of a particular clade, is never exposed. Rieppel (1995) has alluded to this *caveat* and has weighed it against the drawbacks of undertaking a wide-ranging (in terms of using derived members of major amniote taxa) global analysis. In effect the risk of reducing the CI for any particular analysis and hence weakening the phylogenetic hypothesis (lower CI and lower bootstrap values), must be considered in face of a problematic clade, of which turtles represent an elegant example.

Turtle origins and the fossil record

Speculation on the origin of turtles has raged on for nearly a century (see introduction above). Most workers have believed that turtles represent a relic of the primitive 'anapsid' condition. There have been dissenting voices over the years but for the most part these views were ignored as being beyond the realm of possibility.

Recently with major analyses focusing on amniote origins (Gauthier *et al.*, 1988a; Laurin & Reisz, 1995) and others focusing specifically on turtle relationships (Reisz & Laurin, 1991; Lee, 1993b) and the origins of parareptiles (Lee, 1994, 1995; deBraga & Reisz, 1996) a consensus has arisen which for the most part supports the origin of turtles from parareptilian stock. The only other recent and contrasting view is held by Rieppel (1994a, 1995) who suggests a plausible diapsid-turtle relationship. However, only Lee (1994) and Laurin and Reisz (1995) have addressed the issue of the fossil record and what it suggests about the plausible relationship between turtles and parareptiles.

Lee's view argues for a paraphyletic Pareiasauria (a view not supported here) from which turtles arose. The nesting of turtles within Pareiasauria is critical for Lee's evolutionary hypothesis because it is the only way that the extreme gap in the fossil record can be minimized. Given that pareiasaurs arise in the lower-most part of the Upper Permian (*Tapinocephalus* zone [Kitching, 1977]), the origin of turtles would have had to take place in the Lower Permian if turtles and pareiasaurs are sister taxa, a time span of over 80 Myr. However, if Lee (1994) is correct and turtles are nested within Pareiasauria as the sister-group to his Fleocyclopsia (including the late Permian pareiasaur *Anthodon*) then turtles need not arise until the very end of the Upper Permian. The difference is significant because in the first evolutionary scenario the gap in the fossil record of turtles is over 80 Myr. Laurin and Reisz (1995) reiterated a similar argument for suggesting that a procolophonid-turtle sister group relationship would be much more congruent with the fossil record than a turtle-captorhinid sister-group relationship as had been proposed by most previous workers (Clark & Carroll, 1973; Gauthier *et al.*, 1988b). Although both Lee (1994) and Laurin and Reisz, (1995) expressed concern over the extensive fossil gap for turtles their arguments that a 40 Myr gap is somehow better than an 80 Myr gap are unconvincing. In fact, if one uses their logic we find that turtles nested within Lepidosauromorpha as the sister-taxon to Sauropterygia offers the least gap in the fossil record and the greatest congruence with the phylogenetic data (see Norell, 1992). Turtles could, therefore, have evolved in the Lower to Middle Triassic, a gap of less than 20 Myr. We are, however, not suggesting that the decrease in the fossil gap is evidence for our evolutionary hypothesis, only that it is supportive.

Can turtles be diapsids?

The possibility that turtles can be nested within Diapsida is intuitively difficult to accept or even consider. Ever since the early part of this century with Williston's (1917) classification of the reptiles and its subsequent entrenchment in the literature, the significance of temporal fenestration as a diagnostic tool has led most workers to exclude turtles from any possibility of having a diapsid origin. However, as mentioned above, there have always been voices of dissent (Lakjer, 1926). Why has it been so hard to consider the possibility that turtles may share a close relationship to diapsids? There is one overriding consideration that is always raised when the heresy yields its ugly head: turtles cannot be diapsids because they retain the 'primitive, anapsid' skull. It is interesting that turtles are interpreted as being 'too primitive', based on skull anatomy, to be considered diapsid relatives yet very often

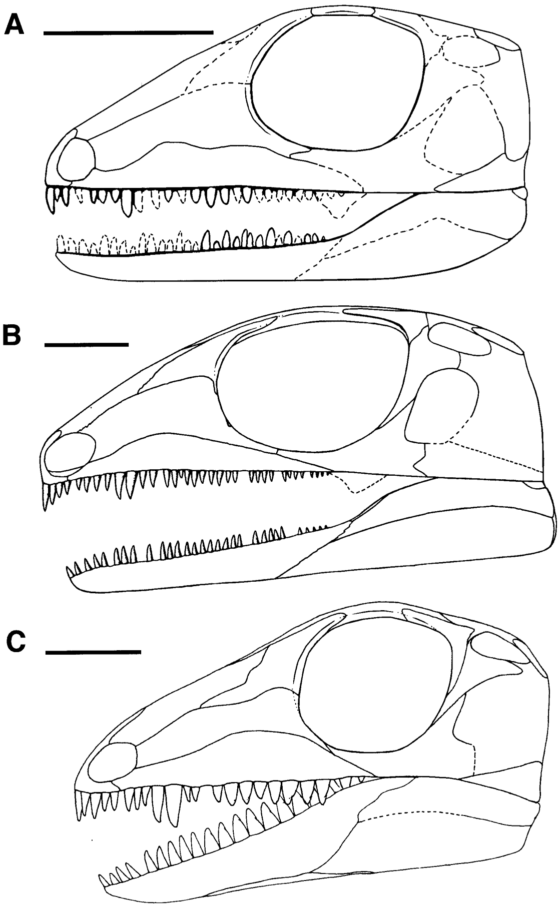

Figure 6. Skull reconstructions of araeosceloid diapsids. A, *Spinoaequalis*, after deBraga and Reisz (1995); B, *Petrolacosaurus*, after Reisz (1981); C, *Araeoscelis*, after Reisz *et al.* (1984). Scale bar = 1 cm.

the difficulty in recognizing turtle origins is blamed on the very specialized (highly-derived) nature of the post-cranium (Zangerl, 1969; Carroll, 1988; Rieppel, 1993a; Burke, 1989).

Temporal fenestration as a tool for identifying genealogy has remained one of the few quantitative, easily identified characters throughout the last century. It is easy to see why this is so—a skull either has fenestra or it does not. Laurin (1991) demonstrated that at least one of the diapsid fenestra, the lower or lateral fenestra, may not have evolved in the common ancestor of diapsids. This interpretation was based on the lack of a lateral temporal fenestra in one (*Araeoscelis*, Fig. 6C) [Reisz *et al.*, 1984] of the two well known araeosceloids available at the time of his study. More recently deBraga and Reisz (1995) identified another araeosceloid (*Spinoaequalis*, Fig. 6A) which possesses a lateral temporal fenestra and, therefore, argued that the presence of two fenestra must have been present in the common ancestor of diapsids. However, if one considers the original material of *Petrolacosaurus* (Fig. 6B) as described and illustrated by Reisz (1981) one can see that the lateral temporal fenestra is smaller in comparison to *Spinoaequalis* (deBraga & Reisz, 1995). Furthermore, the

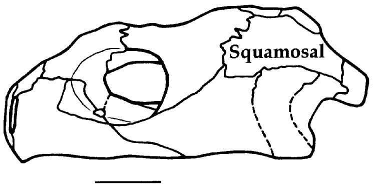

Figure 7. Skull reconstruction of *Proganochelys*, after Gaffney (1990).

anteroventral border of the squamosal in *Petrolacosaurus* is very broad anteroposteriorly compared to the narrow more tapered squamosal of *Spinoaequalis*. These differences were not initially recognized by deBraga and Reisz (1995) but they are clearly present and may shed some light on the evolution of the lateral temporal fenestra. Given that *Spinoaequalis* is the sister taxon to the araeosceloids *Petrolacosaurus* and *Araeoscelis* and that *Spinoaequalis* possesses a larger lateral temporal fenestra and a narrow ventral process of the squamosal relative to what is found in *Petrolacosaurus*, and that the lateral temporal fenestra is entirely absent in *Araeoscelis*, is it possible that we are witnessing the loss of the lateral temporal fenestra in Araeoscelidia. Could this scenario not be repeated for the upper temporal fenestra as well?

If one looks at the architecture of the turtle skull as exemplified by *Proganochelys* (Gaffney, 1990) the most striking feature about the cheek is the very tall quadratojugal. However, what is even more striking is the almost entirely supra-orbital position for the ventral limit of the squamosal. No other ‘anapsid’ skull has this type of squamosal configuration (See Laurin & Reisz, Fig. 6). Indeed, in *Proganochelys* (Fig. 7) the squamosal is embayed ventrally in a manner that would be consistent with the presence of a lateral temporal fenestra. It is possible that the very tall quadratojugal may have expanded dorsally to enclose a fenestra that may have been present in the turtle progenitor. We admit that there is no direct evidence to support this scenario and we have been careful to exclude any of these assumptions from our phylogenetic analysis, but by the same token we believe it does deserve some consideration.

Certainly, the development and subsequent loss of one of the temporal fenestra is demonstrated in at least one diapsid clade (Araeoscelidia) and it must have occurred at least one other time in Eosauropterygia. In addition, the recent identification of lateral temporal fenestra in many members of ‘anapsid’ grade taxa (Hamley & Thulborn, 1993; deBraga & Reisz, 1996) suggest that in at least one case a temporal fenestra is not either difficult to develop nor difficult to lose. In fact, we would suggest that the evolution of the lateral temporal fenestra has been subjected to a great deal of homoplasy and should be evaluated, as it is in this analysis, on the basis of morphology and the relationship of the relevant bones forming its border. This last consideration is necessary to avoid confusion surrounding the evolutionary history of the lateral temporal fenestra in those taxa that possess it. Finally, aside from the issue of temporal fenestration (or lack of), turtles have always been considered to have a very specialized body plan which, as iterated above, has made it difficult to recognize ancestry.

Lee (1995, 1996b) has most recently attempted to recognize and quantify the morphological changes that must have occurred in the evolution of the turtle body plan. Previously, Burke (1989) had suggested that the greatest difficulty in interpreting turtle origins had to deal with the problem of the evolution of the carapace and by extension the peculiar relationship of the rib-cage to the shoulder girdle. Lee (1996b) has proposed a plausible evolutionary scenario from pareiasaur to turtle but has failed to convincingly demonstrate how the shoulder girdle could have become internal to the rib-cage. In fact, if one examines placodonts the relationship of their shoulder girdle to their carapace is much more turtle-like than anything Lee can identify in pareiasaurs. In addition, Lee's most convincing argument is that both pareiasaurs and turtles have stiffened their trunks and, therefore, evolved a limb driven locomotary system. This stiffening of the trunk according to Lee (1996b) developed over time by numerous evolutionaty steps including increased dermal armour, (found in many other taxa including placodonts) and flat expanded ribs (placodonts). In addition to the morphological changes elucidated above and described in detail by Lee (1996b) which have evolved in other taxa independently, this limb driven system has also evolved in at least two other major groups, the placodonts and the plesiosaurs. Therefore, as innovative as Lee's ideas are they are not by any stretch unique among reptiles. In fact, we propose that only a resurrection and indeed expansion of Gregory's (1946) excellent work comparing turtles with pareiasaurs and placodonts would suffice to perhaps resolved the possible homologies of the characters elucidated by Lee.

CONCLUSION

We submit that the present analysis is the first to attempt an evaluation of turtles origins from as broad and unconstrained an evolutionary assumption as is possible. The results of this analysis are far reaching and suggest a very heretical view regarding the origin not only of turtles but by extension the interrelationships within all Reptilia. Indeed, the reptilian crown-group Sauria, which traditionally has included all the living lepidosaurs and archosaurs plus all of their fossil relatives must be redefined to include Testudines. Comparison between the present analysis and the most recent analyses involving turtle origins was undertaken and areas of concern were addressed. Furthermore, a comparison with recent developmental data was undertaken which tended to support the current phylogeny. One of the weaknesses involves the great number of convergences and the rather paradoxical view that although turtles are here defined as diapsids, they lack all of the basal diapsid characters including, most notably, any evidence of temporal fenestration.

Although this study is the first to present a detailed cladistic argument for a turtle-diapsid (sauropterygian) relationship, it is by no means the first to suggest this scenario (Cope, 1892; Jaekel, 1907; Broom, 1924; Lakjer, 1926; Rieppel, 1994a, 1995). We hope that at the very least this study has demonstrated the underlying weaknesses and traps that are manifest when undertaking any phylogenetic analysis where an unusual or highly autapomorphic group is concerned. Certainly, the problem of convergence as an evolutionary reality is very much in evidence here. Many of the extant members of the major amniote clades have developed similar morphological features which probably reflect evolutionary constraints that are present, without a doubt, at the level of the genome (Eernisse & Kluge, 1993).

We do not expect that this study represents the final word on turtle origins, but that it instead hastens further work on the subject. In many ways it is because of the emotional debate that has been undertaken over the last few years and the phenomenal amount of work on the origins of amniotes and parareptiles, and their implications for the origins of turtles, that this study was undertaken at all. May this zeal for unravelling evolutionary puzzles never cease.

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APPENDIX 1

Character list: All characters are unordered. Following the character description the published source for those characters taken from the literature is given along with the original character number. Note that for characters original to this study and those that can be easily evaluated (i.e. loss of an element) a character source is not enumerated.

1. Premaxilla exposure: exposure anterolateral to external nares small restricted to low posterolateral process forming less than one-half the height of the premaxilla (0); posterolateral process tall reaching dorsal process (1). Modified from Rieppel, 1994a, #1.
2. Premaxilla/prefrontal contact: absent (0); present (1).
3. Premaxilla dentition: present (0); absent (1).
4. Premaxilla/external nares relationship: excluded from posterior border of nares (0); contributes to posterior border (1). From Rieppel, 1994a #2.
5. Septomaxilla facial process: absent (0); present (1). From Reisz *et al.*, 1992 #6.
6. External nares exposure: dorsal process of premaxilla broad restricting nares to a lateral exposure (0); dorsal process narrow resulting in dorsal exposure of nares (1).
7. External nares: separated by intranarial bar of premaxilla (0); confluent (1).
8. Choana palatal exposure: parallel medial border of maxilla (0); deflected posteromedially (1); hidden in palatal view (2).
9. Nasals: paired (0); fused (1); lost (2).
10. Nasal/frontal ratio: nasal equal to or shorter than frontal (0); nasal at least one-third longer, or better (1). From Rieppel, 1994a #4.

11. Maxilla ascending process: absent (0); present between orbit and external nares (1). From Laurin and Reisz, 1995 #19.
12. Maxillary horn: absent (0); present directly behind external nares (1). From Lee, 1994 #25.
13. Anterolateral maxillary foramen: absent or if present equal in size to all other foramina (0); present at least twice the diameter of all other foramina (1). From Laurin and Reisz, 1995 #20.
14. Maxilla length: extends to posterior orbital margin (0); does not reach posterior margin of orbit (1).
15. Maxilla orbital exposure: absent (0); present (1). From Lee, 1994 #28.
16. Maxilla/qudratojugal relationship: not in contact (0); in contact (1). From Laurin and Reisz, 1995 #22.
17. Lacrimal morphology: present and contributing to exteral nares (0); present at least as long as tall, but excluded from external nares (1); if present snall, restricted to orbital margin, or absent entirely (2). From Rieppel, 1994a #7.
18. Lacrimal duct: enclosed by lacrimal only (0); lateral border formed by maxilla (1). Modified from Laurin and Reisz, 1995 #10.
19. Skull proportions: preorbital skull length equal to postorbital length (0); preorbital length exceeds postorbital skull length (1); postorbital length exceeds preorbital skull length (2). From Rieppel, 1994a #9.
20. Prefrontal/palatine antorbital contact: narrow forming less than $\frac{1}{3}$ the transverse distance between the orbits (0); contact broad forming at least $\frac{1}{2}$ the distance between the orbits (1). Modified from Laurin and Reisz, 1995 #6 and #7.
21. Bulbous medial process of prefrontal: absent (0); present (1). From Lee, 1995 #22.
22. Frontal orbital contribution: present (0); absent (1). From Laurin and Reisz, 1995 #2.
23. Frontal anterior margins: frontal suture with nasal transverse (0); oblique forming an angle of at least 30° with long axis of the skull (1).
24. Frontal lateral lappet: absent (0); present (1). From Modesto, 1995 #9.
25. Frontal posterolateral processes: absebt (0); present (1). From Rieppel, 1994a #12.
26. Frontal proportions: length exceeds width by at least four times (0); length no greater than twice the width (1). From Lee, 1995 #24.
27. Frontal morphology: parallelogram shaped (0); hour-glass shaped (1).
28. Orbit shape: generally circular (0); anteroposteriorly elongate so that the length exceeds the height by at least 30% (1). Modified from Lee, 1995 #23.
29. Postfrontal contribution to upper temporal fenestra: postfrontal excluded (0); postfrontal included (1). Modified from Rieppel, 1994a #10.
30. Postorbital/supratemporal relationship: in contact (0); not in contact (1); supratemporal absent (1). Modified from Laurin and Reisz, 1995 #12.
31. Postorbital/parietal relationship: in contact (0); contact absent (1).
32. Postorbital posterior extent: terminates prior to reaching posterior limit of parietal (0); extends to at least the posterior limit of the parietal (1).
33. Jugal posterior process: extends posteriorly only to the middle of the cheek (0); reaches nearly the posterior limit of the skull (1).
34. Zygomatic arch configuration: squamosal excluded (0); squamosal included (1).
35. Squamosal lateral exposure: ventral process long, descends to level limit of orbital margin (0); ventral process short, terminates prior to reaching ventral orbital margin (1); ventral process absent or restricted to region above dorsal limit of orbit (2).
36. Squamosal contribution to posttemporal fenestra: absent (0); present (1). From Laurin and Reisz, 1995 #26.
37. Squamosal occipital flange: absent or poorly developed forming only a thin ridge (0); flange well developed forming a broadly exposed lapett (1). Modified from Laurin and Reisz, 1995 #27.
38. Quadrate excavation: absent along posterior edge (0); posterior edge deeply excavated forming a concave region (1); quadrate greatly reduced (2). Modified from Rieppel, 1994a #29.
39. Quadrate exposure laterally: absent (0); present (1). From Rieppel, 1994a #30.
40. Quadrate lateral conch: absent (0); present (1). From Rieppel, 1994a #31.
41. Quadrate anterior process: long, extending forward along its sutural contact with the quadrate process of the pterygoid to nearly reach the level of the transverse flange (0); short, not extending anteriorly beyond 55% the length of the quadrate process of the pterygoid (1).
42. Quadratojugal morphology: present and horizontal dimension exceeds vertical dimension by a factor of at least three (0); present but vertical dimension exceeds horizontal by a factor of at least two (1); present, but greatly reduced and restricted to condylar region (2); absent (3).

43. Quadratojugal ornamentation: absent (0); present (1).
44. Stapedial shaft: rod-like in cross section (0); blade-like in cross section (1). From Reisz *et al.*, 1992 #41.
45. Stapes morphology: robust with its greatest depth exceeding one-third of its total length (0); slender with the length at least four times the depth (1).
46. Stapedial dorsal process: present as ossified process (0); absent (1). From Laurin and Reisz, 1995 #67.
47. Parietal skull table: broad with the mid-line, transverse, width not less than half of the length measured along the element's midline (0); constricted with the length exceeding the width by at least three times (1); forming saggital crest (2). Modified from Rieppel, 1994a #16.
48. Parietal shelf for adductor musculature: absent (0); present as shallow excavations on the lateral margins of the perietal (1). From deBraga and Reisz, 1995 #6.
49. Pineal foramen position: located in the middle of the body from the parietal (0); displaced posteriorly (1); displaced anteriorly (2); absent (3). From Rieppel, 1994a #15.
50. Upper temporal fenestra: absent (0); present (1).
51. Lower temporal fenestra: absent (0); present quadratojugal included (1); present quadratojugal excluded (2); open ventrally (3).
52. Postparietal: present and paired (0); present but fused (1); absent (2). From Laurin and Reisz, 1995 #4.
53. Supratemporal: present and large with its transverse dimension nearly equal to its parasaggital dimension (0); present but reduced so that its transverse dimension is less than half of its parasaggital dimension (1); absent (2).
54. Intertemporal: present (0); absent (1).
55. Tabular: present but restricted to dorsal region of occiput (0); present but ventrally elongate descending to lvel of occipital condyle (1); absent (2).
56. Supraoccipital: plate-like with no saggital crest (0); body of supraocciptal constricted at midline forming saggital crest (1). Modified from Laurin and Reisz, 1995 #55.
57. Occiput configuration: broad and plate-like forming broad sutural contact with the tabular dorsolaterally (0); open with only slight contact, if any, with tubular (1).
58. Angle of occiput: oriented primarily vertically (0); tilted or sloping anteriorly at an angle of about 45° (1). From Romer and Price, 1940.
59. Posttemporal fenestra: absent (0); present but diameter less than half of the diameter of the foramen magnum (1); large posttemporal fenestra with a diameter at least eqqual to that of the foramen magnum (2).
60. Orientation of paroccipital process: extends laterally forming 90° with parasaggital plane (0); paroccipital process deflected posterolaterally at an angle of about 20° from the transverse width of the skull (1); paroccipital process deflected dorsolaterally at an angle of nearly 45° (2).
61. Paroccipital process morphology: slender with anteroposterior dimension not exceeding dorsoventral dimension (0); heavy with anteroposterior dimension at least $\frac{1}{3}$ greater than dorsoventral dimension (1).
62. Exoccipital bones: meet below foramen magnum (0); do not meet (1). From Rieppel, 1994a #28.
63. Basioccipital/basisphenoid relationship: floor of braincase with gap between both elements (0); elements fused to floor brain cavity (1). From Lee, 1993b #A5.
64. Basi/parasphenoid ratio: narrowest transverse width no more than 60% of the maximum length measured from basipterygoid process to posteriomost limit (0); narrowest part (waist) exceeds 80% of the length (1). Modified from Lee, 1994 #12.
65. Ventral braincase tubera: absent (0); present and restricted to basioccipital (1); present, very large, and restricted to basisphenoid (2). Modified from Lee, 1994 #13.
66. Opisthotic/cheek contact: not in contact (0); in contact and tightly sutured (1). From Lee, 1993b #A3.
67. Prootic/parietal contact: absent (0); present (1).
68. Medial wall of inner ear: unossified (0); ossified (1). From Lee, 1993b #A6.
69. Occipital flange: absent (0); present (1). From Lee, 1995 #30.
70. Sphenethmoid: present (0); absent (1).
71. Pleurosphenoid: absent (0); present (1). See node description for Sauria for details.
72. Palate: kinetic (0); akinetic (1). From Rieppel, 1994a #32.
73. Interpterygoid vacuity: anterior end tapers sharply (0); anterior border cresentric (1); absent (2). From Lee, 1994 #18.

74. Suborbital fenestra: absent (0); present but with contribution from either maxilla or jugal along lateral border (1); present, but with both maxilla and jugal excluded from lateral border (2). Modified from Rieppel, 1994a #34.
75. Cultriform process: long, exceeding length of parasphenoid body and reaching forward to the level of the posterior limit of the internal nares (0); short, not reaching the level of the internal nares (1). Modified from Laurin and Reisz, 1995 #52.
76. Palatal process of pterygoid: extends anterior to the anterior limit of the palatine (0); forms oblique suture with palatine but process ends before reaching anterior limit of palatine (1); forms transverse suture with palatine (2).
77. Orientation of transverse flange of pterygoid: directed predominantly laterally (0); oriented in an anterolateral direction (1). From Laurin and Reisz, 1995 #45.
78. Dentition on transverse flange: present as a shagreen of teeth (0); present but with one large distinct row of teeth along the posterior edge of the transverse flange (1); edentulous (2). Modified from Laurin and Reisz, 1995 #46.
79. Ventral extent of transverse flange: extends below maxillary tooth row (0); terminates at level of or above maxillary tooth row (1). From Lee, 1995 #14.
80. Transverse flange lateral margin: posterolateral margin forms sharp edge with anteromedial margin (0); posterolateral margin merges smoothly into anteromedial margin forming a smoothly convex lateral outline (1).
81. Ectopterygoid: present and edentulous (0); present and dentigerous (1); absent replaced by medial process of jugal (2); absent replaced by lateral process of pterygoid (3).
82. Mandibular joint: even with occiput (0); behind occiput (1); anterior to occiput (2). From Rieppel, 1994a #27.
83. Coronoid process: absent (0); present formed by coronoid (1); present formed by dentary (2). Modified from Laurin and Reisz, 1995 #79.
84. Coronoid number: more than one (0); only one coronoid (1). From Laurin and Reisz, 1995 #74.
85. Meckelian fossa: faces mediodorsally (0): faces dorsally due to greatly expanded prearticular (1). From Laurin and Reisz, 1995 #70.
86. Surangular length: extends anterior to coronoid eminence (0); terminates prior to reaching a level of coronoid eminence (1). From Laurin and Reisz, 1995 #72.
87. Surangular lateral shelf: absent (0); present (1). Modified from Laurin and Reisz, 1995 #78.
88. Splenial: enters mandibular symphysis (0); present but excluded from mandibular symphysis (1); entirely absent (2). Modified from Reisz and Laurin, 1991 #7.
89. Angular lateral exposure: exposed along $\frac{1}{3}$ the lateral face of the mandible (0); exposed only as a small sliver along the lateral face (1); absent from lateral aspect (2).
90. Ventral edge of angular: smooth no ventral projection (0); keeled (reflected lamina) (1). From Romer and Price, 1940.
91. Prearticular: extends anterior to coronoid eminence (0); terminates prior to reaching coronoid eminence (1). From Laurin and Reisz, 1995 #75.
92. Retroarticular process: absent (0); present (1). From Rieppel, 1994a #38.
93. Labyrinthine infolding: present (0); absent (1). From Laurin and Reisz, 1995 #68.
94. Tooth implantation: set in deep sockets (); loosely attached to medial surface of jaw (1); ankylosed to jaw (2). Modified from Rieppel, 1994a #42.
95. Caniniform teeth: present (0); absent (1). From Laurin and Reisz, 1995 #24.
96. Single canine tooth: absent (0); present (1). From Laurin and Reisz, 1995 #25.
97. Presacral vertebral number: more than 20 (0); 20 or less (1). From Lee, 1995 #35.
98. Number of caudal vertebrae: 20 or more usually 25 (0); less than 20 (1). From Lee, 1994 #70.
99. Vertebral centra: notochordal (0); non-notochordal (1). From Rieppel, 1994a #48.
100. Vertebral central articulations: amphicoelous (0); platycoelous (1); other (2). From Rieppel, 1994a #49.
101. Accessory vertebral articulations: absent (0); present (1). From Rieppel, 1994a #53.
102. Atlantal ribs: ossified (0); not ossified (1).
103. Cervical central: ventrally smooth or rounded (0); ventrally keeled (1). From Laurin and Reisz, 1995 #87.
104. Cervical intercentra: present (0); absent (1). From Rieppel, 1994a #51.
105. Cervical ribs: without anterior process (0); anterior process present (1). From Rieppel, 1994a #56.
106. Trunk neural arches: swollen with heavy zygapophyseal butress (0); narrow, strongly excavated

neural arch with no heavy butress (1); swollen, but with narrow tall zygapophyseal butress (2). From Laurin and Reisz, 1995 #86.

107. Dorsal intercentra: present (0); absent (1). From Rieppel, 1994a #50.
108. Dorsal transverse processes: short no more than the total transverse width of the neural arch (0); long exceeding the transverse width of the neural arch (1). Modified from Rieppel, 1994a #55.
109. Number of sacral vertebrae: two (0); three or more (1). Modified from Rieppel, 1994a #58.
110. Caudal lateral projections (transverse processes): absent beyond fifth caudal (0); present beyond fifth caudal (1). From Lee, 1993b #A10.
111. Caudal rib shape: L-shaped, curved (0); straight (1). From Lee, 1995 #72.
112. Chevron position: intercentral (0); located on anterior pedicel (1). From Lee, 1993b #A11.
113. Cleithrum: present (0); absent (1).
114. Clavicle: interclavicular process of clavicle broad and blade-like with the maximum anteroposterior length at least $\frac{1}{3}$ of its transverse dimension (0); slender with its anteroposterior length less than $\frac{1}{5}$ of the transverse dimension (1).
115. Interclavicle: anterior end rhomboidal (0); T-shaped but with broad transverse bar with its anteroposterior dimension at least $\frac{1}{4}$ the transverse width of the bar (1); T-shaped but transverse bar slender with its anteroposterior dimension much less than $\frac{1}{4}$ the transverse width (2).
116. Mineralized sternum: absent (0); present (1). From Laurin and Reisz, 1995 #100.
117. Scapula: short and broad with its height not exceeding its width (measured at the level of the glenoid) by more than three times (0); tall and blade-like with its height exceeding the width by at least a factor of four (1); tall and slender nearly cylindrical in cross-section (2). Modified from Lee, 1993b #B2.
118. Acromion process: absent (0); present, blade-like, parallelogram in lateral aspect, and arising from the lateral edge of the scapula (1); present, triangular in lateral aspect, and arising from ventromedial border of scapula (2). Modified from Lee, 1993b #A12.
119. Supraglenoid butress: present (0); absent (1). From Rieppel, 1994a #69.
120. Coracoid ossifications: one (0); two (1). From Rieppel, 1994a #70.
121. Coracoid foramen: enclosed by coracoid only (0); enclosed by coracoid and scapula (1). From Rieppel, 1994a #71.
122. Humeral epicondyles: large, forming distinct processes (0); reduced so that distal end of humerus appears only marginally broader than shaft (1). From Rieppel, 1994a #75.
123. Humeral torsion: proximal and distal ends reduced to no more than 20° (1). Modified from Lee, 1996b #F3.
124. Humeral shaft/distal end ratio: shaft length less than $\frac{1}{3}$ the maximum width of the distal end of the humerus (0); shaft long at least four times the width of the distal end (1).
125. Humeral distal articulations: distinct trochlea and capitellum (0); low double condyle (1).
126. Supinator process: large angled away from humeral shaft (0); large confluent with shaft (1); small or absent (2). Modified from Laurin and Reisz, 1995 #101.
127. Ectepicondylar groove/foramen: foramen absent, but deep groove present along anterior edge of humerus (0); foramen and groove absent, but a small notch present anterodistally (1); completely enclosed foramen present, no deep groove (2). Modified from Laurin and Reisz, 1995 #102.
128. Entepicondylar foramen: present (0); absent (1). From Reisz and Laurin, 1991 #10.
129. Radius/ulna ratio: radius shorter than ulna (0); radius longer than ulna (1); radius and ulna subequal (2). From Rieppel, 1994a #78.
130. Olecranon: large and set off from proximal end of ulna (0); small or entirely absent (1). Modified from Laurin and Reisz, 1995 #105.
131. Perforating foramen of manus: present (0); absent (1).
132. Metacarpal IV/III ratio: fourth longer than third (0); fourth equal to or shorter than third (1).
133. Thyroid fenestra: absent (0); present (1).
134. Posterior process of iliac blade: long, extending posteriorly well past level of acetabulum (0); posterior process reduced, distal end of illium fan-shaped (1). From Laurin and Reisz, 1995 #108.
135. Anterior process of iliac blade: blade not expanded anteriorly with at most only a very small anterior process (0); anterior process large often exceeding dimension of posterior process (1). From Lee, 1994 #97.
136. Pubic tubercle: if present small and directed anteroventrally (0); large and strongly turned ventrally (1). From deBraga and Reisz, 1995 #36.
137. Acetabulum oval (0); circular (1). From Rieppel, 1994a #82.

138. Acetabular process: weakly developed (0); large, overhangs femoral head, appears as triangular lateral extension when viewed from below (1). From Lee, 1993b #A16.
139. Femoral shaft: short and stout (0); sigmoidally curved and slender (1). From Rieppel, 1994a #83.
140. Femoral fourth trochanter: present (0); absent (1).
141. Femoral trochanter major: absent (0); present and deflected distally from the proximal head of the femur (0); pyramidal in shape and nearly in line with the head of the femur (2); similar in shape to state (1) but positioned at mid-shaft length (3). Modified from Lee, 1995 #50.
142. Intertrochanteric fossa: well defined (0); reduced (1); absent (2). From Rieppel, 1994a #84.
143. Distal femoral condyles: large, projecting from distal end of shaft (0); reduced, not projecting beyond distal end of femur (1). From Rieppel, 1994a #85.
144. Anterior femoral condyle: larger, extends distal to posterior condyle (0); anterior condyle reduced and sub-equal or smaller than posterior condyle (1). From Rieppel, 1994a #86.
145. Fibula: bowed away from tibia (0); straight not bowed away (1).
146. Perforating artery of pes: located between astragalus and calcaneum (90); located between distal ends of tibia and fibula (1). From Rieppel, 1994a #87.
147. Tibia/astragalus articulation: loose fitting (0); tightly fitting with well developed articulation (1). Modified from Laurin and Reisz, 1995 #116.
148. Discrete astragalus: absent (0); present (1).
149. Astragalus/calcaneum relationship in adult: never fused (0); fused (1); hinge present (2). Modified form Laurin, 1991 #F8.
150. Astragalus/distal tarsal IV articularion: articulation poorly defined (0); articulation well defined (1); articulation absent (2).
151. Calcaneal tuber: absent (0); present (1). Modified from Laurin, 1991 #F9.
152. Distal tarsal I: present (0); absent (1).
153. Distal tarsal V: present (0); absent (1).
154. Metatarsal V: long and slender with length exceeding the width of the base by at least three times (0); short and broad with base width equivalent to at least twice the length of the element measured along its midline (1). Modified from Rieppel, 1995 #69.
155. Metatarsal V shape: straight (0); hooked (1).
156. Metatarsal V plantar tubercle: absent (0); present (1).
157. Metatarsal I/IV ratio: metatarsal I greater than 50% the length of metatarsal IV (0); Metatarsal I less than 50% the length of metatarsal IV (1). From deBraga and Reisz, 1995 #41.
158. Number of pedal centralia: both lateral and medial centralia present (0); medial pedal centralia lost (1); both centralia lost (2).
159. Fifth pedal digit: longer than first digit (0); shorter and more lightly built than first (1). From Lee, 1993b #A15.
160. Metapodials: not overlapping proximally (0); overlapping (1). From Laurin and Reisz, 1995 #121.
161. Pedal phalangeal formula: 2, 3, 4, 5(4), 4 (0); 2, 3, 4, 4, 3 (1); 2, 3, 3, 4, 3 or less (2). From Laurin and Reisz, 1995 #122.
162. Limbs: short and stout (0); long and slender (1). From Heaton and Reisz, 1986 #K.
163. Manus and pes: short and broad (0); long and slender (1). From Heaton and Reisz, 1986 #L.
164. Ungual size: unguals shorter than phalanges (0); unguals at least 50% longer than penultimate phalanges (1).
165. Body osteoderms: absent (0); present but few restricted to mid-line (1); present but spread all over back (2). From Lee, 1994 #123.
166. Osteodermal ridges: absent (0); fine regular spaced ridges (2); heavy irregularly spaced ridges (3). From Lee, 1994 #125.
167. Osteodermal limb studs: absent (0); present as conical studs (1). From Lee, 1994 #128.
168. Gastralia: present (0); lost (1). From Lee, 1994 #129.

APPENDIX 2

Input data matrix: including 33 taxa and 168 characters (0) denotes primitive state; (1, 2, ... etc.) denotes derived condition; (?) denotes unknown.

```
                             1111111111222222222233333333334444444444555555555

Taxon               1234567890123456789012345678901234567890123456789012345678

------------------------------------------------------------------------------

Seymouriadae        0000000000000000000001000000000000000000000000000000000000

Diadectomorpha      0000000000000000000001000000000000000000000000000001010000

                                          1  1     1                      1

Caseidae            0000000000100000000000010000?00100001000000000002010010001

Ophiacodontidae     000000000100000000100000100 0?0101001000000100001021110001

                                           1

Edaphosauridae      0000?00000000100000?00010000?10011001000020100001021111001

                                      1            1

Sphenacodontidae    0000100001100100101000100000?10101001000020100001021111001

                                           1

Gorganopsia         0000100101100100 1?1?00111000?20001001200120100001021211001

Cynodontia          0000110201100100210001000000?20001001200120?01212021211001

Captorhinidae       0000000000000100000000000000?10000011000100000000001112010

                                                                    2

Paleothyris         00000000000000000?0000000000?10000011000100000000000110010

Millerettidae       ?000000000001 0000?0100000000?10000001000000000000000000010010

                                            1             1           1

Acleistorhinus      00000100001010011?0?00110000?01100001000110000002011010010

Lanthanosuchidae    00000100001110001?1?00110100?00100001000011???000011010010

                                   1                                2

Macroleter          00000100001010011?0?00001001?00000001100000???002010012010

Bradysaurus         0000010100101101000101000100?00000001000001001002001012110

Scutosaurus         0000010100111101000101000100?00000001000001001002001012110
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Anthodon            0000010100101101000101000100?00000001000001001002001012110
Procolophon         000001000010110010011000100 1?00000101100010011002002012110
                                                              1
Owenetta            0000010000101100 1?0?10001001?00000111100010???002000012110
Araeoscelidia       00000000000001000?10000010000100000110001000000000110110010
Claudiosaurus       0000000000?001101?1?00?010000111000110001200??01013?112010
Younginiformes      0000000000000000101000001000111100011110100011010110110010
                                                                          2
Kuehneosauridae     000?0110001001101?0?000010100?01002??1111300??012132212010
Testudines          0010010100100000100100000100?10000111110010011003002012110
                       1          1  12  1    1                         2
Rhynchocephalia     0000000000100010210100000010111110011110120011010122112110
                                          1 1              1      1 2 3 2
Squamata            0000000000000000210100000010110100210111130011010132112010
                       1    1 1   1   1  11       1               1 2   2  1
                            2         2                             3
Choristodera        1001011?11000100112?000000000?01000??110?20011113112212?10
                                                             3
Rhynchosauria       11110111001000001?0100000000011110110110120011213112212110
                                  1           1
Prolacertiformes    1001010001000000 1?1000100010011000210110120011012132112010
                              1  11         1       1        3      3   2
Trilophosaurus      1?11000?00?00?????1?011000100?1??0???110?000?1213102212110
Archisauriformes    1000010001100000100000000010011110110110120011010112112010
                       1         11  11     1                     1 3   2
Placodus            1000000110100100212101001100111000111110?300??012132212010
Eosauropterygia     100000000010?000210?00000000111100010010?200??011132212010
                       1   1      1   1     1 1          1   3    1 2
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                                                           11111111111111111
                  5666666666677777777778888888888999999999900000000001111111
Taxon             9012345678901234567890123456789012345678901234567890123456
----------------------------------------------------------------------------
Seymouriadae      0000000000000000000000000000010000000000000000000000000000
Diadectomorpha    0000000010000000000000000000000000000000000000000000000000
                                           1        1
Caseidae          1000000000000000000100000000000100100000000000010000000000
Ophiacodontidae   1000?000??0000000001000000000000101100100000000100000000000
Edaphosauridae    100110210?000000?1011010000000011110100000000100100100000000
Sphenacodontidae  1001102110000000101000000000000101100100000010010010000000
Gorganopsia       10111121?10121101202000021000001011001001000100110111000 11
Cynodontia        1011112111012110120200022101022101100100101011011011101111
                                                         1
Captorhinidae     2000000000000001000100200100000000100000000000000000000000
                                                                        1
Paleothyris       2001?000??0??00?0101000001?0000000100000000010010000000000
Millerettidae     2000?000?00??001000100020100000001100000000?0001000?0?000?
Acleistorhinus    ?201?000??0??10000010002?1?10?00101000????????????????????
Lanthanosuchidae  12000000??0??1000101000011??01?0?11010??000????200?????01?
                                         1
Macroleter        20?0?00???0??00?0?01000211?10?00111000000000000002001?0?0010
Bradysaurus       2010100101000112111111020111000011101010000?00020011110010
Scutosaurus       2010110101000112111111020111000011101011000?00020011111010
Anthodon          20101101010001121111110201110000111010 1?000?00020011111010
Procolophon       2000001100100011111200021111110011101000000100200 11001010
                     1                                   1
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Owenetta            2000?010??1??001111200021111111001110000?000?0002001?0??01?
                                                        1
Araeoscelidia       2001?000??0??001001100000100010000100000000010010000000001
Claudiosaurus       200??100??0??0010011100001?1010000101000?0011011000010111?
Younginiformes      2001?000??00?0010001100011??0?00?1101000000110010001?00101
                                                                          1 1
Kuehneosauridae     20?1?01???0??001???0?0?001?0??10?1101000100?11?1110?10????
Testudines          20101111110100021102113001111110101???110001100?1001111010
                                11    1    2         1      12   1
Rhynchocephalia     2001?01110010001110210001101011011111000001?10010001101121
                     1       1                              1       1
Squamata            2000001111010001101201001100111001111000100110011001101021
                       1 1      1    1     1  11    1        21          1 1
                                           2
Choristodera        210110011?01??0111010101010?01?01110100011011011100110111?
Rhynchosauria       211010010?01?00210021000111110101112100010011001000110111?
                                      1
Prolacertiformes    21011010??01?0010001100001?1010011101000100?10110001101101
                         1             2    1                2   1  1
Trilophosaurus      211?10111101?0011012110211100??01112100?11011011000?10111?
                                                             2
Archisauriformes    201111?1110110011101100001010100?1101000100?10110101101111
                     1           1     2   11 1              1   1  1
                                           2                 2
Placodus            2001?1101101?120120201011111001011101000000?1111111?1?1110
Eosauropterygia     2001???11101?12010?21100010?0110?11000?0101?11111010101000
                     1               1     11           1    1             11
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Input data matrix (continued)

                  1111111111111111111111111111111111111111111111111111

                  1112222222222333333333344444444445555555555666666666

Taxon             7890123456789012345678901234567890123456789012345678

----------------------------------------------------------------------

Seymouriadae      0000000000000000000000000000000000000000000000000?00

Diadectomorpha    0000000000000000000000000000000000000000000000000?00

Caseidae          1000000000000000000000000000000100000000000000000?00

Ophiacodontidae   0000000000000000000000000000000100000000000000000?00

                  1

Edaphosauridae    10000000000000??0000000000000001?00????0?0???0??0?00

Sphenacodontidae  1000000000000000000000000000000100000000000000000?00

Gorganopsia       1000000001200010100011012101011122101000010020000?0?

Cynodontia        1200?01002200111101011112111011121101010011021100?01

Captorhinidae     0001000002000000000000000000000100000000010000000?00

Paleothyris       0001000101000000000000000000000100000000010001100?00

Millerettidae     00?00?01?1?00?0?0100000000??00?100001000?10?00100?00

Acleistorhinus    ????????????????????????????????????????????????0???

Lanthanosuchidae  0?????0?????????????????????????????????????????0?0?

Macroleter        10?1000001000000010001000001?00100001000010001000?0?

Bradysaurus       11?10000?22001000110110000010001100010000210200 11001

Scutosaurus       11?10000?2200100011011001001000110001000021020011211

Anthodon          21?10010?2200100010011001001000110001000021020012111

Procolophon       10?1000002100100010011000001000111001000020110010000

                        1                                         1

Owenetta          ???10000?10101??0100?0000???0?01?0?????0?????1??0?00

Araeoscelidia     0001000101000000000000000001001000000000110101100?00

                           2
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```
Claudiosaurus       001001011121001010000101?0111000100000000010100100?00
Younginiformes      ?01000000110001010100101?0101100100000100110101100?00
                              2 1
Kuehneosauridae     0010000101012?111?00101?0101???10???????0?10101?00?01
Testudines          22?0101111010110110001011011111111100111002112000201?
                         1    2    1                   1            1
Rhynchocephalia     00100001012000111000101001010111111001111120101100?00
                            1              1           1
Squamata            00100011110100111000101001010111111011111020101100?01
                              2  1         1    1            1
Choristodera        ?01000000110121110?00101001111??10?101110?10?01100?00
                              2
Rhynchosauria       00100000011010110000110110101111120101110110101110?00
                        1
Prolacertiformes    001000000120111110001101?0101100120001100010101100?00
                                2   1                  11  1 1
Trilophosaurus      10100000012010000000110110101100120101110110101100?00
Archisauriformes    00100000101110111000110103101101120101110010101101000
                    1   11  1                21        1
Placodus            00101111110121??1?00101001111?01000110000?01000020?0
Eosauropterygia     201010111100111?1?0010100011010100011000020100000??0
                         1    112          1 1  1
```