A Phylogenetic Analysis of Lepidosauromorpha

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INTRODUCTION

OBJECTIVES OF THIS STUDY

In this paper our primary objective is to analyze phylogenetic relationships within a subtaxon of Sauria, the Lepidosauromorpha (see Addendum, p. 94). Lepidosauromorpha includes the following saurian diapsids: younginiforms, *Paliguana whitei**, *Palaeagama vielhaueri**, *Saurosternon bainii**, kuehneosaurs, rhynchocephalians, and squamates, all of which are defined and diagnosed below according to our usage. For discussion of the use of the "*," see below. The principal problem in discussing the taxa listed above is that the constitution of Rhynchocephalia and Squamata has not been stable, and that the early archosauromorphs and lepidosauromorphs have been lumped in paraphyletic "Eosuchia." As part of our analysis of lepidosauromorphs, we attempt to stabilize the concept of each lepidosauromorph taxon with as rigorous a diagnosis as the nature of the material allows. Our analysis provides a relevant series of outgroups for evaluation of character polarity for phylogenetic analysis within Squamata (Estes et al., 1988).

In order to give our phylogenetic analysis an explicit basis, we first constructed a minimum step cladogram by hand, using the character set given in Appendix I. The polarities are justified in Sections 2 and 3 by outgroup comparison. We then subjected the data matrix in Appendix II to analysis by the PHYSYS program written by J. S. Farris and installed in the California State University CYBER system. The relatively minor differences between the hand cladogram and that of the computer are analyzed in Appendix III. We have tried to be as explicit as possible in our character descriptions and to give as much discussion of variation as is feasible. Nevertheless, in a paper of this size, we have not been able to discuss the homoplasy in various taxa required by our conclusions in as much detail as we would have preferred.

MONOPHYLETIC TAXA AND METATAXA

As phylogenetic systematists our principal objective is to identify monophyletic taxa in the sense of Hennig (1966). Wiley (1981:200) offered a set of criteria for phylogenetic taxonomy, and made the monophyly criterion his Rule 1. A monophyletic taxon is composed of an ancestor and all its descendants at any hierarchical level, from the least inclusive groups of organisms that share an exclusive common ancestry, to the taxon that includes all life. Such taxa are natural, in the sense that they are historical groups sensu Wiley (1981) or complete systems of common ancestry (de Queiroz, 1988). Monophyletic taxa are portions of life that have unique histories concerning such properties as their origin, diversification, and extinction.

Wiley (1981:200) proposed that non-monophyletic groups could be included in a phylogenetic taxonomy "if they are clearly qualified as such." We reject the inclusion of known paraphyletic or polyphyletic taxa because their histories are largely a matter of definition. For example, the origin of the "Eosuchia" is the same as the origin of the Sauria as constituted here, and the diversity and temporal duration of the "Eosuchia" are determined less by evolutionary processes than by the point at which we arbitrarily separate such groups as squamates and archosaurs from the "eosuchians." In his sixth convention, Wiley (1981:213) identified as a problem area the treatment of known para- or polyphyletic groups. In our view, known para- or polyphyletic groups should be abandoned, and should have no place in a phylogenetic taxonomy. We recognize, however, that known paraphyletic groups may need to be mentioned in treatments of the history of taxonomy of certain taxa. For such cases, we recommend that Wiley's sixth convention be modified to limit use of quotation marks to *known* paraphyletic or polyphyletic taxa, because quotation marks are widely used in this context by many systematists ("Eosuchia" as discussed in this paper, is an example).

We permit only one exception to the monophyly convention, the metataxon (Greek, *meta*, near), for taxa for which there is no character evidence supporting *either* monophyly *or* paraphyly.

Metataxa that have previously been given formal names may be provisionally accepted in a phylogenetic taxonomy, but they must be abandoned if additional characters demonstrate nonmonophyly. Because we have used quotation marks to denote known paraphyletic groups we have chosen the asterisk (*) to identify metataxa (e.g., Iguanidae*). The asterisk calls attention to the uncertain status of such taxa and distinguishes them from taxa characterized by synapomorphy as well as from known para- or polyphyletic groups. Metataxa are thus temporarily given the benefit of the doubt, but are formally accepted only until such time as characters are found that subdivide or clarify the relationships of the included organisms. We emphasize, however, that the recognition of subdivisible unresolved groups is arbitrary and that *in no case should such a group be newly named*; the metataxon concept should only be used for unresolved taxa that have *already been given* formal names. Metaspecies (Donoghue, 1985) are metataxa at the least inclusive level, and are identified in the same way as any other metataxon, by the asterisk.

MONOPHYLY OF DIAPSIDA

Romer (1956), like Williston (1925) before him, questioned the monophyly of Diapsida (originally named by Osborn, 1903) because he was uncertain about the origin of the open lower temporal region of squamates; was it the result of emargination from below, or of fenestration and subsequent loss of the lower temporal bar? Nevertheless, Romer (1956) was influenced by workers who presented considerable evidence for the second alternative (e. g. Broom, 1925) and thus included squamates with all non-archosaurian diapsids in the Lepidosauria. The monophyly of Diapsida is now widely accepted (Reisz, 1977, 1981; Gaffney, 1980; Carroll, 1982). Gauthier (1984) provided additional documentation of this monophyly, and divided diapsids into Araeoscelidia and Sauria; the latter taxon was redefined in the spirit of its original definition by McCartney (1802) to include all Archosauromorpha (Huene, 1946, 1948, 1956; n. comb.) and Lepidosauromorpha, rather than applying it to the paraphyletic group "lizards." The Archosauromorpha includes Archosauria, a taxon restricted to the most recent common ancestor of birds and crocodiles and all its descendants (both living and fossil), as well as the following successively more remote outgroups of Archosauria (s. s.): Proterochampsidae, Erythrosuchidae, Proterosuchidae, and the even more remote Protorosauria, Champsosauridae (=Choristodera), *Trilophosaurus*, and Rhynchosauria. Although the precise relationships of the last four taxa within the archosauromorphs are not fully resolved, it is clear that they share some, if not all, of the synapomorphies that distinguish archosaurs from ancestral lepidosaurs, among which are the following:

1. Enlarged premaxilla forming most of tip of snout.
2. Premaxilla with subnarial process extending dorsally up narial margin of maxilla to contact nasal, thereby excluding maxilla and septomaxilla from margin of external naris.
3. Parietal foramen small or absent.
4. Ventral process of squamosal half or less of height of lower temporal fenestra.
5. L-shaped quadratojugal.
6. Posterior process of jugal extends posterior to center of lower temporal fenestra.
7. Broad contact between ectopterygoid and jugal.

8. Bowed posterior margin of skull for passage of middle ear and support of tympanum, and a gracile, imperforate, stapes.
9. Tabulars absent.
10. Enlarged adductor chamber for temporal musculature, as indicated by tall quadrate that extends well below occipital condyle.
11. Parasphenoidal teeth absent.
12. Non-notochordal vertebrae in adults.
13. Transverse processes on trunk vertebrae moderately prominent.
14. Cleithrum absent.
15. Entepicondylar foramen in humerus absent.
16. Medial centrale in manus absent.
17. Complex concavo-convex astragalo-calcanear articulation, and a small, laterally directed, calcanear tubercle (the archosauromorph duplex ankle joint *sensu* Thulborn, 1980).
18. Pedal centrale displaced laterally.
19. Hooked fifth metatarsal, and fifth distal tarsal fails to separate from anlage of fifth digit.

Contrary to long-standing opinion, rhynchosaurs, *Trilophosaurus*, champsosaurs, and protorosaurs are archosauromorphs, and have no close relationship to lepidosaurs (Gow, 1975; Carroll, 1977), thus demonstrating the paraphyly of "Eosuchia." It is possible that coelurosauravids (as constituted by Evans, 1982), thalattosaurs (sensu Romer, 1956; Merriam, 1905; Kuhn-Schnyder, 1952), plesiosaurs (Carroll, 1981), and ichthyosaurs (Tarsitano, 1983) are diapsids. However, coelurosauravids are too poorly known, while thalattosaurs and plesiosaurs, and to an even greater extent ichthyosaurs, are too modified to contribute much to the resolution of the relationships among the basic taxa of this analysis. Indeed, it would be more appropriate to use the evidence presented here to test the possible diapsid affinities of these taxa.

LEPIDOSAUROMORPHS: DIAGNOSES OF LEPIDOSAURS AND THEIR EXTINCT RELATIVES

To facilitate discussion, we accept certain lower-level hypotheses that arise from preliminary analyses of the phylogenetic relationships within younginiforms (Currie, 1982), rhynchocephalians (see below), and squamates (Estes et al., 1988). In the discussion that follows, we emphasize that when we use the terms reptiles, diapsids, saurians, archosauromorphs, archosaurs, lepidosauromorphs, younginiforms, lepidosauriforms, lepidosaurs, kuehneosaurs, rhynchocephalians, and squamates, we refer only to our own concept of these groups (see definitions and diagnoses below and the section Phylogenetic Taxonomy of Amniota); these may or may not be equivalent to concepts of these groups in other studies, but we have followed historical precedent whenever it is consistent with the results of our analysis.

The younginiforms

Younginiformes as constituted by Currie, 1982. Upper Permian to Lower Triassic.

For many years, the concept of the "Eosuchia" has been that group of "primitive lepidosaurians, lacking the specializations of the more progressive members of the subclass" (Romer, 1956:519), or a "mixed bag of diapsid genera sharing only primitive characters" that is ancestral to both archosaurs and lepidosaurs (Evans, 1980:255). Broom (1914:1077) originally defined "Eosuchia" as a suborder of "thecodont reptiles" that retain postparietal and tabular bones, and a non-fenestrated antorbital region of the skull. Few have given further consideration to Broom's claim that *Youngina* is a "thecodont" (but see Gow, 1975) On the contrary, the persistent concept of the relationship of "eosuchians" to other diapsids is better expressed by Broom's (1914:1076) statement that "*Youngina* represents a type more primitive than any previously known, and one which is especially important in that it is very near to the ancestral form." To be included in the "Eosuchia," a species must possess the synapomorphies of the diapsids but lack those of archosaurs and squamates. For the most part, the artificiality of this group has not escaped notice by later authors, and we underscore it here.

Broom erected "Eosuchia" for *Youngina* alone, and this name could be applied to a monophyletic taxon composed of *Youngina* and its close relatives. Nevertheless, "Eosuchia" in current usage is paraphyletic, and we prefer the name Younginiformes of Romer (1945), as constituted by Currie (1982). We consider Younginiformes to include only *Youngina capensis*, *Acerosodontosaurus piveteaui*, and the tangasaurs (Camp, 1945; including *Tangasaurus mennelli*, *Hovasaurus boulei*, *Thadeosaurus colcanapi*, and *Kenyasaurus mariakaniensis* as constituted by Currie, 1982). So delimited, the taxon is monophyletic.

Diagnosis: Based primarily upon the works of Gow (1975) and Currie (1980, 1981a, 1981b, 1982), members of Younginiformes share the following combination of synapomorphies that distinguishes them from all other Diapsida.

1. Relatively elongate and narrow snout (Fig. 1B).
2. Reduction of postfrontal process of parietal and development of a posterior process on postfrontal that separates postorbital from parietal (Fig. 1B).
3. Postorbital extends posterior to the end of the upper temporal fenestra (Fig. 1B).
4. Loss of parasphenoidal teeth (Fig. 2A).
5. Olecranon process and sigmoidal notch of ulna poorly developed in adults (Currie, 1982).

Currie (1980) also characterized *Acerosodontosaurus piveteaui* but did not determine the level of synapomorphy of the characters he discussed. At least two of the characters appear to be synapomorphies of this taxon: the great ventromedial-dorsolateral width of the pubis and the twisted appearance of the radius. *Youngina* has a uniquely modified iliac blade and a single row of middorsal osteoderms (also reported in *Heleosaurus*; this combination of apomorphies has not been reported in any other diapsid (Gow, 1975). Thus, neither *Acerosodontosaurus* nor *Youngina* is likely to be ancestral to tangasaurs (Tangasauridae of Currie, 1982). The name Younginidae Broom (1914) is redundant because it says no more about the known pattern of synapomorphy than does the name *Youngina capensis*.

Compared to *Acerosodontosaurus*, the skull of *Youngina* and the tangasaurs is relatively narrower across the anterior ends of the frontals (Currie, 1980); these two latter taxa also share specialized articulations between the neural arches of the trunk vertebrae (Currie, 1981a), a strongly developed entepicondyle on the humerus in adults, and a radius that is longer than the shaft of the ulna (Currie, 1982). Accordingly, these taxa constitute the younginoids (= Younginoidea of Currie, 1982).

Within younginoids, Currie (1982) has argued that tangasaurs may be distinguished from *Youngina* by the possession of the following synapomorphies:

1. Scapula low in lateral aspect, mainly a ventral element, and subequal to the coracoid in size.
2. Radius 50% - 65% of humerus length and 65% - 75% of tibia length in adults.
3. Fifth distal tarsal not present as a discrete element (if single specimens of *Kenyasaurus* and *Hovasaurus* have been correctly interpreted by, respectively, Harris and Car-

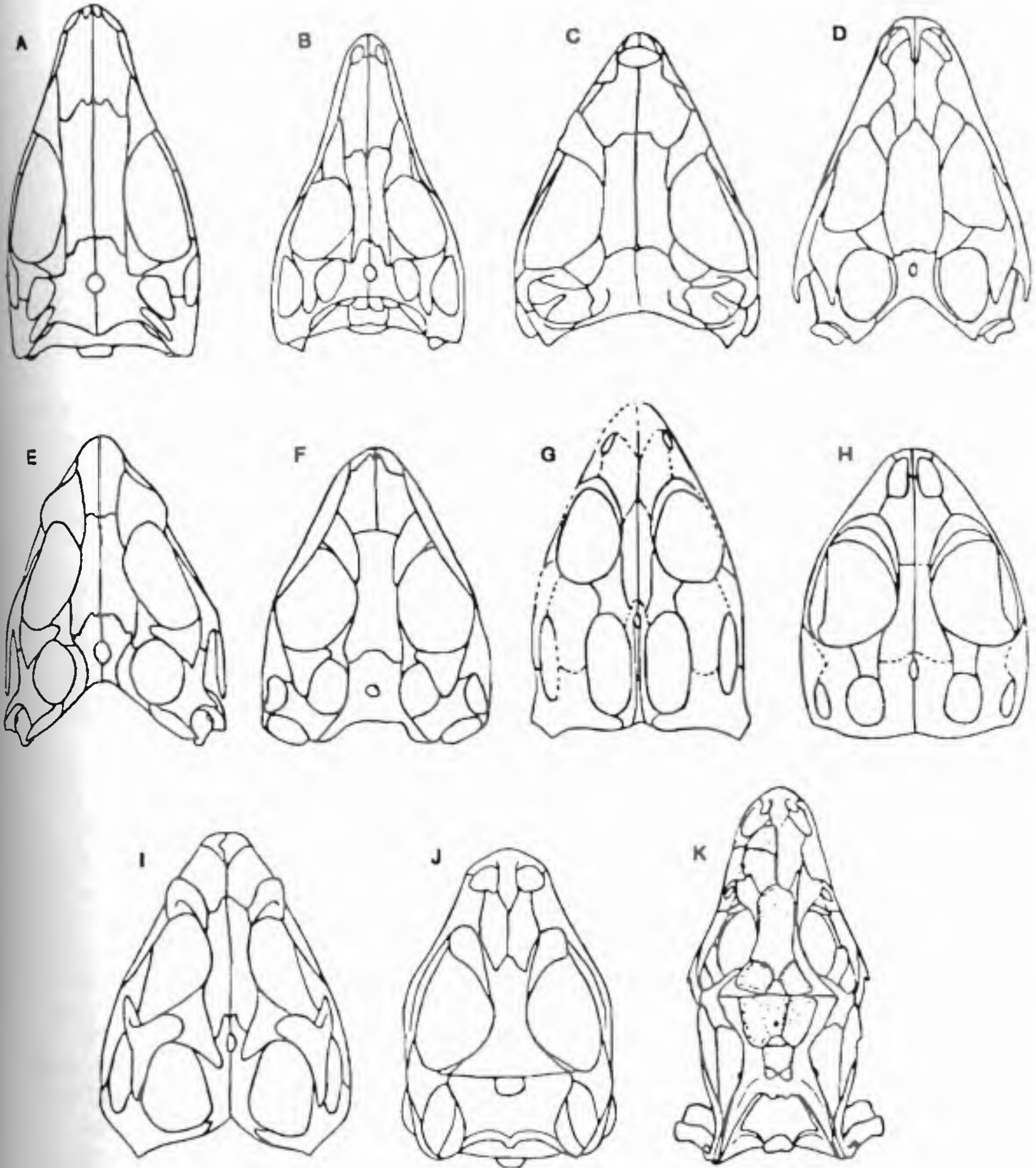

FIGURE 1. Dorsal view of skull. A, *Petrolacosaurus kansensis* (araeoscelidan); B, *Youngina capensis* (younginiform); C, *Kuehneosaurus latus* (kuehneosaur); D, *Gephyrosaurus bridensis* (rhynchocephalian); E, *Clevosaurus hudsoni* (clevosaur); F, *Planocephalosaurus robinsonae* (clevosaur); G, *Sapheosaurus thiollierei* (sapheosaur); H, *Homoeosaurus maximiliani* (homoeosaur); I, *Sphenodon punctatus* (sphenodont); J, *Sceloporus grammicus* (iguanian); K, *Elgaria multicarinata* (autarchoglossan). A after Reisz (1981); B after Carroll (1977); C, D, I after Evans (1980); E after Robinson (1973); F after Fraser (1982); G, H after Cocude-Michel (1963); J after Larsen and Tanner (1974); K after Rieppel (1980).

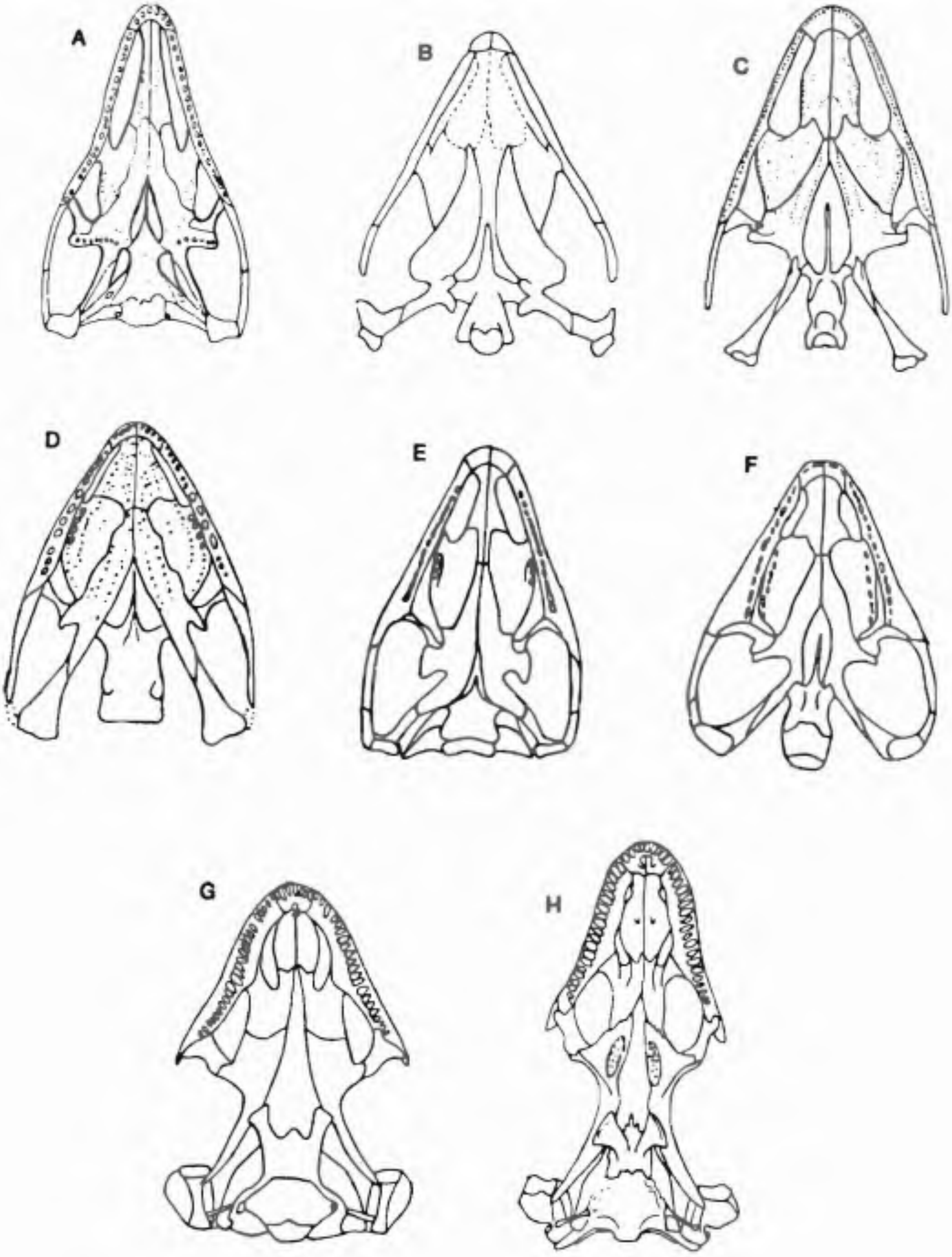

FIGURE 2. Ventral view of skull. A, *Youngina capensis* (younginiform); B, *Kuehneosaurus latus* (kuehneosaur); C, *Gephyrosaurus bridensis* (rhynchocephalian); D, *Planocephalosaurus robinsonae* (clevosaur); E, *Kallimodon cerinensis* (sapheosaur); F, *Sphenodon punctatus* (sphenodont); G, *Sceloporus grammicus* (iguanian); H, *Elgaria multicarinata* (autarchoglossan). A after Carroll (1977); B, C, F after Evans (1980); D after Fraser (1982); E after Cocude-Michel (1963); G after Larsen and Tanner (1974); H after Rieppel (1980).

roll, 1977, and Currie, 1981b, then the fifth distal tarsal fuses to the fourth distal tarsal in adults).

4. Humerus as long or longer than femur in adults.
5. Medial centrale contacts the fourth distal carpal, thus preventing the lateral centrale from contacting the third distal carpal (the available *Youngina* specimens are immature, and *Acerosondontosaurus* is only partly preserved, so some of the characters listed above may later be found to specify more inclusive taxa within younginiforms).

Fig. 11 is a cladogram depicting the phylogenetic relationships within younginiforms; the relationship of younginiforms within lepidosauromorphs appears in Fig. 13.

*Palaeagama vielhaueri** Broom (1926)

Lower Triassic.

Diagnosis: The unique type specimen is a fairly complete but very poorly preserved skull and postcranial skeleton. Based on the descriptions of Carroll (1975a, 1977), we are unable to identify synapomorphies for this taxon, and it is not known to possess any synapomorphies of taxa less inclusive than Lepidosauromorpha. Carroll grouped this taxon with *Saurosternon** and *Paliguana** (see below) but our analysis suggests that this is an overinterpretation. *Palaeagama** is discussed below, following the section on *Saurosternon bainii**, and again in Section 3.

*Paliguana whitei** Broom (1903)

Upper Permian or Lower Triassic.

Diagnosis: The unique type specimen is a partial skull. Based on the descriptions of Carroll (1975a; 1977), we are unable to identify synapomorphies for this taxon. It is discussed below following the section on *Saurosternon bainii** and again further below.

*Saurosternon bainii** Huxley (1868)

Upper Permian.

Diagnosis: The type is a relatively well-preserved and fairly complete postcranial skeleton. Based on the descriptions of Carroll (1975a; 1977), we are unable to identify synapomorphies for this taxon. An additional specimen, Albany Museum 4133, was said by Carroll (1975a:85) to have "few features to differentiate it" from the type specimen of *Saurosternon** except in being about 20% larger. Carroll did not refer this specimen to *Saurosternon**; because the specimen lacks data of any kind, we consider *Saurosternon bainii** to apply only to the type specimen, British Museum (Natural History) no. 1234.

The three specimens listed above as *Paliguana**, *Palaeagama**, and *Saurosternon** constitute Carroll's (1975a; 1977) family "Paliguanidae." Carroll was well aware that no synapomorphies unite these taxa. It is difficult to derive phylogenetically relevant information from comparison of a postcranial skeleton, a isolated skull, and a more complete although poorly preserved specimen; the specimens could either represent the same species or be only distantly related to each other. Nevertheless, Carroll has consistently treated "paliguanids" as if they were monophyletic. The taxon "Paliguanidae" is rejected here and use of any name implying close relationship between *Paliguana**, *Palaeagama** and *Saurosternon** should be avoided. Because these taxa and others like them are based on plesiomorphy, it is not possible to refer other specimens to the taxon in question with any assurance. Such references may or may not be correct; lacking synapomorphies, a decision is impossible.

Kuehneosaurs

Kuehneosauridae and Eolacertilia of Robinson, 1962; non "Eolacertilia" of Carroll 1975a, 1977, Estes, 1983. Upper Triassic.

Diagnosis: Based principally on *Kuehneosaurus latus* and *Icarosaurus siefkeri*, and to a lesser extent on *Kuehneosuchus latissimus*, as described by Robinson (1962; 1967) and Colbert (1970). Seiffert (1973) and Estes (1983) have also considered *Cteniogenys antiquus** to be a possible relative of kuehneosaurs. These references, together with examination of the type of *Icarosaurus* and the analysis offered below, indicate that the following characters are synapomorphies of kuehneosaurs (few if any of these are present in *Cteniogenys antiquus** and we are uncertain as to the relationships of this poorly known lepidosauromorph).

1. External nares confluent on the midline owing to loss of internarial process of premaxilla (Fig. 1C).
2. Parietal foramen on frontoparietal suture (Fig. 1C).
3. Absence (loss? fusion?) of supratemporal (Fig. 1C).
4. Loss of ventral ramus of squamosal (Fig. 3B).
5. Loss of posterior ramus of jugal (Fig. 3B).
6. Absence (loss? fusion?) of quadratojugal (Fig. 3B).
7. Quadrate foramen absent.
8. The distinctive shape and size of the transverse processes and ribs in the midtrunk region, which are thought to have supported a gliding membrane (Colbert, 1970).
9. Non-notochordal trunk vertebrae lacking discrete intercentra.
10. Entepicondylar foramen absent.
11. Elongate gracile limbs.

These synapomorphies indicate that the kuehneosaurs form a monophyletic group. The loss of the lower temporal bar and the presence of a lateral conch on the quadrate were the basis for Robinson's (1962; 1967) conclusion that kuehneosaurs were "lizards." As will be argued below, however, the form of the quadrate characterizes a more inclusive group than squamates alone, and the loss of the lower temporal bar is either convergence or, like the form of the quadrate, it is a synapomorphy of a more inclusive group.

The name Eolacertilia, coined by Robinson (1962) as a higher level group name to include the kuehneosaurs, was made paraphyletic by inclusion of "paliguanids" (Carroll, 1975, 1977, Estes, 1983a). Eolacertilia (sensu Robinson, 1967) is a redundant taxon, carrying no more phylogenetic information than does Kuehneosauridae, and will not be needed until taxa that are closer to kuehneosaurs than to lepidosaurs are discovered.

Rhynchocephalians

Gephyrosaurus bridensis of Evans, 1980 + Sphenodontida of Estes, 1983. Lower Triassic to Recent.

Rhynchocephalians are represented by a single living species, *Sphenodon punctatus*. Like other small reptiles, rhynchocephalians are poorly represented in the fossil record, with fewer than three dozen species referred to this taxon. However, as the photographs in Cocude-Michel's (1963) monograph attest, some rhynchocephalians are among the most completely preserved fossil reptiles. Although the reviews of Cocude-Michel (1963), Kuhn (1969) and Robinson (1973), are important first steps, further analysis of rhynchocephalian anatomy and interrelationships is needed. Consequently, in order to identify rhynchocephalian synapomorphies, we briefly analyze here the

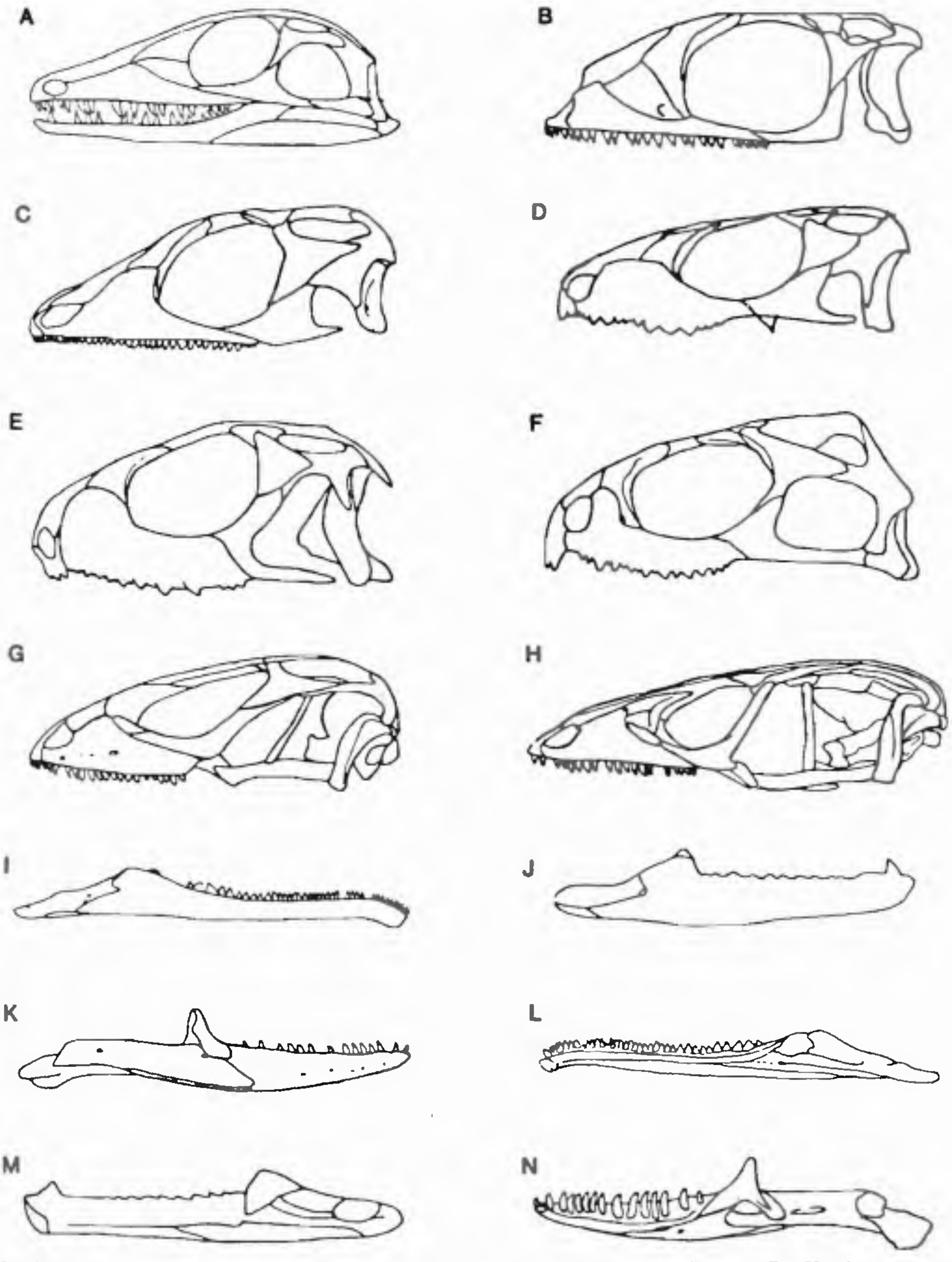

FIGURE 3. Lateral view of skull. A, *Youngina capensis* (younginiform); B, *Kuehneosaurus latus* (kuehneosaur); C, *Gephyrosaurus bridensis* (rhynchocephalian); D, *Planocephalosaurus robinsonae* (clevosaur); E, *Clevosaurus hudsoni* (clevosaur); F, *Sphenodon punctatus* (sphenodont); G, *Sceloporus grammicus* (iguanian); H, *Elgaria multicarinata* (autarchoglossan); J, *Sphenodon punctatus* (sphenodont). Lateral and medial view of mandible. I, L, *Gephyrosaurus bridensis* (rhynchocephalian); J, M, *Sphenodon punctatus* (sphenodont); K, N, *Elgaria multicarinata*. A after Carroll (1977); B after Robinson (1962); C, F, I, J, L, M after Evans (1980); D after Fraser (1982); E after Robinson (1973); G after Larsen and Tanner (1974); H, K, N after Rieppel (1980).

phylogenetic relationships among the major rhynchocephalian groups. The following must be considered preliminary because (1) certain poorly known or equivocal taxa, such as *Pleurosaurus*, *Palacrodon*, *Brachyrhinodon*, and the eilenodonts (= Eilenodontinae of Rasmussen and Callison, 1981), are omitted from the analysis because of the difficulty of determining character states accurately; (2) our sample of rhynchocephalians (aside from what appears in the literature) is limited to five specimens of Recent *Sphenodon*, a cast of a species of the Upper Jurassic *Homoeosaurus*, and fragmentary remains of the Upper Triassic *Clevosaurus* and the Lower Jurassic *Gephyrosaurus*. We have relied heavily on the works of Cocude-Michel (1963), Robinson (1973, 1976), Evans (1980; 1981), and Fraser (1982) for supplementary information.

The long-held belief that rhynchosaurs are rhynchocephalians is not justified. Carroll (1975b) showed that the synapomorphies traditionally thought to ally the rhynchosaurs with the rhynchocephalians, most notably the form of the teeth and snout, are erroneous. Indeed, rhynchosaurs are closer to archosaurs, and rhynchocephalians are closer to squamates (Gauthier 1984; Carroll, 1985). The rhynchocephalians are redefined here to reflect Günther's (1867) original intent that this taxon should encompass *Sphenodon* and its nearest relatives.

Diagnosis: Rhynchocephalia includes the Lower Jurassic species, *Gephyrosaurus bridensis* (Evans, 1980), and its sister taxon, the Lower Triassic to Recent Sphenodontida (see below for diagnosis and included taxa). This conclusion differs from that of Evans (1980, 1981, 1985), who attempted to show that *Gephyrosaurus* and squamates were sister groups. *Gephyrosaurus* and sphenodontidans possess the following synapomorphies, however, that as a group are lacking in all other diapsids:

1. Postfrontal process of parietal reduced, and postfrontal develops a posterior process, thus excluding postorbital from the parietal (Fig. 1D).
2. Postorbital overlaps the dorsal surface of the postfrontal distally, thus imparting a subtrapezoidal outline to the postfrontal when viewed from above (Fig. 1D).
3. The lacrimal is quite reduced and barely exposed in lateral view (Fig. 3C).
4. Enlarged tooth row along maxillary side of palatine (Evans, 1980); palatine broadened laterally, restricting anterior portion of suborbital fenestra (Fig. 2C).
5. Pterygoid process of quadrate extends anterior to the level of the basioccipital tubera (Fig. 2C).
6. Dentary with long posterior process that extends more than half-way between the coronoid eminence and the articular condyle (Fig. 3I).
7. Loss of splenial (Fig. 3L).
8. Strong anteroposterior ridge divides the dorsal surface of the mandibular condyle (Evans, 1980).
9. Length of mandibular condyle equal to width (see fig. 45 in Evans, 1980).

The marginal dentition of *Gephyrosaurus* (Evans, 1980:236-239) is intermediate between the ancestral lepidosaur condition and that of sphenodontidans. Enlarged, conical, posterior teeth and the reduced amount of lateral attachment appear to be additional *Gephyrosaurus*-sphenodontidan (rhynchocephalian) synapomorphies. On the other hand, high tooth number, retention of tooth replacement in the adult, and lack of extreme deposition of attachment bone around the teeth are ancestral lepidosaurian features not seen in any sphenodontidan. *Gephyrosaurus bridensis* is, however, unlikely to be ancestral to any sphenodontidan because it has the following synapomorphies (modified from Evans, 1980):

1. Quadratojugal reduced, may be partly fused to quadrate (Fig. 3C).
2. Loss of the quadratojugal-jugal contact owing to loss of the anterior process of the quadratojugal (Fig. 3C).

3. Frontals fused (Fig. 1D).
4. Parietals fused (Fig. 1D).
5. Dermal rugosities on skull roof (Evans, 1980, figs. 8,9).
6. Loss of supratemporal (Fig. 1D).
7. Restriction of Meckelian fossa by dentary (Fig. 3L).

This combination of synapomorphies is unique, although several of these characters have arisen independently in other lepidosauromorphs (see below). Because there is only a single species with this combination of synapomorphies, there is no need at present for Evans' (1980) redundant higher level category, Gephyrosauridae.

Sphenodontidans (= Sphenodontida of Estes, 1983): Sphenodontidans share the following combination of synapomorphies that are absent in *Gephyrosaurus* and other lepidosauromorphs:

1. Distinctive tooth form and regionalization (Robinson, 1976), including relatively fewer marginal teeth, each of which is relatively large and is fused to the dorsal margin of the jaws, with alternate-sized juvenile dentition anteriorly, and broad-based, somewhat laterally compressed, flanged teeth posteriorly.
2. Prominent coronoid eminence on mandible.
3. Premaxillary teeth replaced by downgrowths of premaxillae, forming paired chisels in all but juvenile individuals.
4. Four or five enlarged teeth at anterior end of palatine tooth row.
5. Palatine further enlarged laterally compared to *Gephyrosaurus* and suborbital fenestra consequently reduced.
6. Loss of lacrimal.
7. Jugal deeply overlaps quadratojugal laterally to extend well posterior to middle of lower temporal fenestra.
8. Jugal contacts squamosal at posteroventral margin of lower temporal fenestra.
9. Narrow quadrate without lateral conch.

For purposes of this analysis, the following informal groups of sphenodontidans are recognized: clevosaurs, *Homoeosaurus*, sapheosaurs and sphenodonts. Synapomorphies for these groups, and the species included within them, are provided below.

Clevosaurs: A group including *Clevosaurus hudsoni* (Robinson, 1973) and *Planocephalosaurus robinsonae* (Fraser, 1982). Although quite different from one another, they possess the following synapomorphies: three or four enlarged, conical teeth in the posterior half of the maxillae, followed by a few very small teeth (Figs. 3D, E); loss of the anterior process of the quadratojugal (Figs. 3D, E); loss of contact between the posterior ramus of the jugal and the ventral ramus of the squamosal at the posteroventral corner of the lower temporal fenestra (Figs. 3D, E).

Unfortunately, *Planocephalosaurus* presents difficulties with respect to the last two synapomorphies. The referred remains are disarticulated and dissociated. Moreover, although most specimens have an incomplete lower temporal bar, at least some referred specimens display the ancestral sphenodontidan condition in maintaining the squamosal-jugal contact at the posteroventral margin of the lower temporal fenestra. Fraser and Walkden (1983) described *Sigmala sigmala*, another sphenodontid from the same fauna, and indicate that there are at least three others that are undescribed. Until more is known, we will consider the specimens that retain the ancestral condition to be the remains of *Sigmala* or one of the undescribed species. Thus, for purposes of this paper, *Planocephalosaurus* is considered to lack both the anterior process of the quadratojugal and the squamosal-jugal contact.

Homoeosaurus spp.: A genus most recently reviewed by Cocude-Michel (1963) and Kuhn (1969), the species of *Homoeosaurus* are of interest owing to their lizard-like habitus. Compared to sphenodonts and sapheosaurs, *Homoeosaurus* is distinguished by relatively small size, gracile and elongate limbs, and a broad parietal table (Fig. 1H). With the possible exception of the limb proportions, these characters are present in rhynchocephalians ancestrally (Fig. 1D). These characters are, however, confined to juveniles of the sphenodonts and sapheosaurs (e.g., the parietal forms a broad plate in juvenile *Sphenodon*; Howes and Swinnerton, 1901), suggesting that small size of *Homoeosaurus*, and the shape of the parietal table, are manifestations of the same phenomenon. If *Homoeosaurus* is the sister species group of sapheosaurs, as some evidence suggests (see below), then the broad parietal table of *Homoeosaurus* may be a paedomorphic reversal rather than a retained ancestral feature.

Sapheosaurs: A group including *Leptosaurus neptunius*, *Kallimodon cerinensis*, and *Sapheosaurus thiollierei*. These taxa share a broader upper temporal arch (Fig. 1G), an elongate and narrower upper temporal fenestra (Fig. 1G), a postorbital region of the skull that exceeds the length of the preorbital region (Fig. 1G), and laterally compressed caudal vertebral centra (Cocude-Michel, 1963).

Sphenodonts: A group including *Opisthias rarus* and *Sphenodon punctatus*, which are unique among sphenodontidans in having successional, caniniform teeth at the anterior ends of the maxillary and dentary tooth rows. *Sphenodon* has been extensively studied, and it is not justifiable at present to diagnose the sphenodonts on the single character that unites the inadequately known *Opisthias* with *Sphenodon*. So far as they can be compared, *Sphenodon* possesses the following synapomorphies that are absent in *Homoeosaurus*, sapheosaurs, and clevosaurs. Future finds may determine which of these synapomorphies apply to sphenodonts generally, as opposed to *Sphenodon* alone.

Enlarged, relatively broader nasal process of premaxilla (Fig. 1I); loss of jugal-squamosal contact below postorbital (Fig. 3F); diastema between maxillary and premaxillary tooth rows (Fig. 3F); elongate row of teeth on enlarged palatine, the latter nearly closing the suborbital fenestra (Fig. 2F); one vertebra added to presacral vertebral column (Hoffstetter and Gasc, 1969); loss of two (sometimes one) sternal-rib connections, thus yielding eight cervicals, rather than seven, and fourteen poststernal vertebrae, rather than 12 (Hoffstetter and Gasc, 1969); xiphisternum absent; very large, subrectangular supratemporal fenestra (Fig. 1I); loss of posterior process on second sacral rib (Cocude-Michel, 1963).

Homoeosaurus, sapheosaurs, and sphenodonts share the following combination of synapomorphies that distinguishes them from clevosaurs and *Gephyrosaurus*: pattern of tooth wear facets, tooth ultrastructure, and anteroposterior length of the mandibular articulation, all of which indicate development of the propalinal masticatory movements to the degree seen in Recent *Sphenodon* (see Robinson, 1976; Rasmussen and Callison, 1981); parietal foramen nearer to frontoparietal suture (Fig. 1I); quadrate without lateral conch (Robinson, 1973); quadrate straight in lateral view; quadrate reduced so that it does not extend dorsally more than half height of orbit (Fig. 3F); squamosal covers most of quadrate in lateral view (Fig. 3F); enlarged quadrate foramen (Robinson, 1973); loss of retroarticular process (Fig. 3M); short supratemporal process of parietal and long dorsal process of squamosal (Fig. 1G); no discrete supratemporal (fused to squamosal?); greatly enlarged postfrontal extending far posteriorly on parietal (Fig. 1I); except for a few teeth on the vomer in juveniles and the palatine row, all other palatal teeth absent (Fig. 2E); enlarged palatine teeth set parallel to maxillary tooth row (Fig. 2E).

Although the discussion above indicates that sphenodonts, sapheosaurs, and *Homoeosaurus* probably form a monophyletic group, phylogenetic relationships among these three taxa are unclear. Sphenodonts and sapheosaurs share two apomorphic characters, a narrow parietal table (Fig. 1G) and aliform outgrowths on the calcified distal segments of the first eleven poststernal ribs (Cocude-Michel, 1963). Although this character has not been reported in *Homoeosaurus*, the unlikely preservation of calcified cartilage makes the level at which this character is a synapomorphy uncertain. On the other hand, sapheosaurs share two apparent synapomorphies with *Homoeosaurus*: relatively large posterior flanges on the maxillary teeth and long ischial tubera. Because of this conflicting evidence and because the detailed relationships within sphenodontidans are not our primary concern here, we leave the relationships among sphenodonts, sapheosaurs, and *Homoeosaurus* unresolved.

The preceding analysis indicates that rhynchocephalians are readily categorized into a hierarchy of groups nested within groups. However, there is little to be gained from a new taxonomy until more thorough analyses of critical taxa, such as the early Triassic species, *Palacrodon* and *Scharschengia*, and the late Triassic species, such as *Polysphenodon*, *Clevosaurus*, *Planocephalosaurus*, and *Brachyrhinodon* are made, and until more specimens of the late Jurassic eilenodonts and *Opisthias* are available. At this point, we wish only to stress that as members of a monophyletic Rhynchocephalia, sphenodontidans and *Gephyrosaurus* are closer to one another than either of them is to any other lepidosauromorph.

The phylogenetic conclusions of this preliminary analysis of rhynchocephalians are depicted in Fig. 12, and the relationships of that group to other lepidosauromorphs in Fig. 13.

Squamates

Squamata of Oppel, 1811. Late Jurassic to Recent.

"Lizards" are those squamates that lack the synapomorphies of snakes and of amphisbaenians. Therefore, we concern ourselves with squamates, rather than "lacertilians", in the remaining discussion. Because determination of squamate synapomorphies is a primary objective of this analysis, a detailed discussion of these characters appears below.

MORE INCLUSIVE GROUPS OF LEPIDOSAUROMORPHA AND THEIR DIAGNOSTIC CHARACTERS

The basic taxa of this analysis are the younginiforms, *Palaeagama**, *Paliguana**, *Saurosternon**, kuehneosaurs, rhynchocephalians, and squamates, as diagnosed above. These taxa share a combination of synapomorphies in the morphology of the forelimbs and girdles that will be discussed below, and are referred to collectively here as Lepidosauromorpha. As defined here, Lepidosauromorpha is the sister taxon of Archosauromorpha (Huene, 1946, 1949, 1956); these two taxa together constitute Sauria (approximately sensu McCartney 1802, rather than as a synonym of "Lacertilia"). Sauria is itself the sister taxon of Araeoscelidia (Reisz et al., 1984) within Diapsida (Gauthier, 1984).

In the list of characters below, the number of the character in the character list and data matrix (Appendices I and II) is placed in brackets, following the number in this listing. Archosauromorpha and Araeoscelidia are used as first and second nearest outgroups, respectively, to determine character polarities in the following analysis.

LEPIDOSAUROMORPHA

This taxon includes Younginiformes, *Palaeagama**, *Saurosternon**, *Paliguana**, Kuehneosauridae, Rhynchocephalia, and Squamata)

Definition: *Sphenodon* and squamates and all saurians sharing a more recent common ancestor with them than they do with crocodiles and birds.

Diagnosis: 1. [91] The lepidosauromorph sternum. According to Romer (1956), the ancestral condition of the diapsid sternum is retained by Crocodylia (see Romer, 1956, fig. 141). Anteriorly, the cartilaginous sternum forms a broad plate lying between the coracoids on the ventral midline. Behind the coracoids, however, the sternum tapers abruptly to an elongate, rod-like structure supporting four or five ribs. The sternum bifurcates posteriorly to this rod-like structure to form the xiphisterna, which support additional rib extensions (Gladstone and Wakely, 1932). The sternum and its associated ventral rib extensions become calcified or ossified prior to the cessation of growth in living diapsids (see Romer, 1956; pers. obs.). Unfortunately, calcified cartilage is rarely preserved in fossils. Further, extensive calcification usually occurs late in development, thus making it even less likely to be preserved in subadults. More importantly, calcified cartilage is rarely preserved because it macerates quickly in water; in addition, compared to the sternum, the ventral rib extensions are considerably more lightly constructed and less calcified. Consequently, remnants of a calcified sternum are more likely to be found in an associated fossil than are ventral rib extensions. In some groups, such as sauropods and theropods, secondary ossification centers may arise in the anterior portion of the sternum lying between the pectoral girdles (Borsuk-Bialynicka, 1977). In birds other than *Archaeopteryx**, as well as in pterosaurs, the sternum may become greatly enlarged, elaborated, and well ossified for the attachment of the flight musculature. Lepidosauromorphs differ from other diapsids in that the rib-supporting posterior portion of the sternum is formed by two broad plates that fuse to one another prior to the cessation of growth (Broom, 1921; Carroll, 1975a, 1977; Currie, 1981b). This synapomorphy is present in younginiforms, *Saurosternon**, rhynchocephalians, and squamates, but it is not preserved in *Paliguana** or kuehneosaurs. Carroll (1975a) described calcified remnants of the lepidosauromorph sternum in *Palaeagama**. In diapsids, the sternum and its associated ribs become calcified during postnatal development. However, sternal calcification appears to take place at earlier ontogenetic stages in rhynchocephalians and squamates than in crocodiles and birds (pers. obs.). This is probably the case in lepidosauromorphs generally, because calcification (ossification) apparently began relatively early in postnatal development in younginiforms (Currie, 1981b).

2. [114] Fully enclosed ectepicondylar foramen. An ectepicondylar groove is present on the distal end of the humerus in araeoscelidans (Reisz, 1981) and archosauromorphs ancestrally (Gauthier, 1984). Therefore, an ectepicondylar groove is considered to be present in saurians ancestrally. In younginiforms, however, the ectepicondylar groove becomes fully enclosed in bone during postembryonic ontogeny to form an ectepicondylar foramen (Currie, 1981b). The postcranial skeleton is unknown in *Paliguana**, but an ectepicondylar foramen is present in *Saurosternon** and *Palaeagama** (Carroll, 1975a). This foramen is also present in kuehneosaurs (Colbert, 1970) and rhynchocephalians (Evans, 1980), and is generally present in squamates (Lecuru, 1969). Those squamates that lack an ectepicondylar foramen, however, also lack an ectepicondylar groove. The ectepicondylar groove becomes a foramen in the embryo in rhynchocephalians (Howes and Swinnerton, 1901) and in squamates (pers. obs.). Thus, ontogenetic enclosure of the ectepicondylar groove is a synapomorphy of lepidosauromorphs.

3. [106] Medial centrale enlarged to nearly twice size of lateral centrale in manus. In diapsids ancestrally the medial and lateral centralia are subequal in size (Fig. 4A). This character is not preserved in *Paliguana**, *Palaeagama**, and kuehneosaurs. However, in younginiforms (Currie, 1982), *Saurosternon** (Carroll, 1975a), and all squamates and rhynchocephalians that retain an unreduced manus, the medial centrale is as much as twice the size of the lateral centrale (Figs. 4B,C).

LEPIDOSAURIFORMES, new taxon

This taxon includes *Paliguana**, *Saurosternon**, Kuehneosauridae, Rhynchocephalia, and Squamata.

Definition: *Sphenodon* and squamates and all organisms sharing a more recent common ancestor with them than they do with younginiforms.

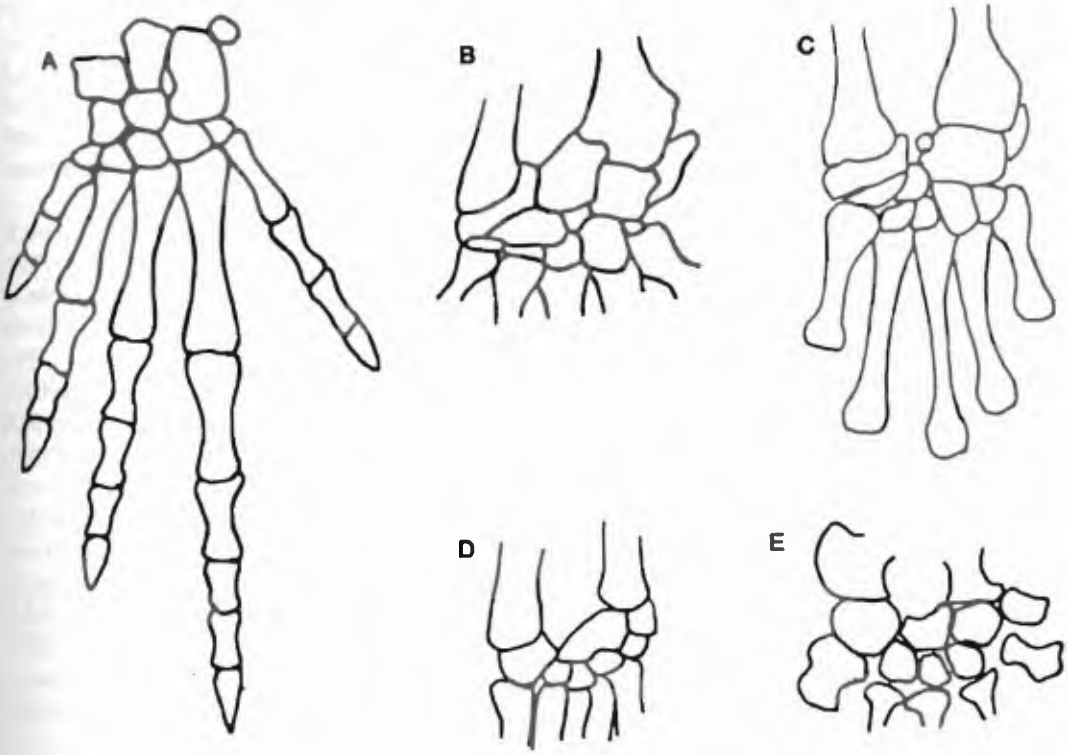

FIGURE 4. Dorsal view of left manus. A, *Petrolacosaurus kansensis* (araeoscelidan); B, *Sphenodon punctatus* (sphenodont); C, *Zonosaurus madagascariensis* (autarchoglossan); D, *Opetiosaurus bucchichi* (autarchoglossan); E, *Clidastes* sp. (autarchoglossan). A after Reisz (1981); B after Carroll (1977) C modified from Carroll (1977); D after Kornhuber (1901); E after Russell (1967).

*Paliguana**, *Saurosternon**, kuehneosaurs, rhynchocephalians, and squamates possess synapomorphies that are absent in younginiforms. Thus, younginiforms, archosauromorphs, and araeoscelidans will be used as successively more remote outgroups in the following analysis. Lepidosauriformes is distinguished from its sister taxon, Younginiformes, by further modifications of the forelimbs and girdles, and the initial modifications associated with the development of a unique ankle joint. To these may be added the modifications of the quadrate and ear region associated with the development of an ear that is sensitive to airborne sound (Carroll, 1977). The form of the quadrate has long been considered a synapomorphy unique to squamates. More recently, however, this assumption has been questioned (Evans, 1980), and we argue below that this synapomorphy applies to all lepidosauromorphs except younginiforms, and not to squamates alone.

In our view, the extinct members of the Lepidosauriformes, i.e., *Paliguana**, *Saurosternon**, and the kuehneosaurs, are too poorly known to be particularly informative. Small sample sizes and poor preservation conspire to leave too many unanswered questions. As is evident in the following list of synapomorphies, their remains clearly indicate that these taxa are closer to rhynchocephalians and squamates than to any other reptiles. We use the name Lepidosauriformes for all lepidosauromorphs that shared a more recent common ancestor with lepidosaurs than they did with younginiforms. Because of the taxonomic instability resulting from new fossil finds, and the uncertainties associated with interpreting their morphology, we do not wish to restrict the name Lepidosauriformes to the above-listed groups alone; equally we do not wish to coin new names for all the more inclusive clades that might appear upon the discovery of new fossils. Therefore, the ultimate diagnosis of Lepidosauriformes will differ from that given below in that it will consist of only the first synapomorphy (ies) to arise in this clade. To emphasize the point that we have made earlier regarding the nature of metaspecies, note that although *Paliguana** and *Saurosternon** share synapomorphies with other taxa at this node, they are themselves undiagnosable by synapomorphies.

Diagnosis: 1. [19] Prominent lateral conch on quadrate for support of tympanum. There is no lateral conch on the quadrate of araeoscelidans (Reisz, 1981), archosauromorphs (including *Prolacerta*, see above), or younginiforms (Gow, 1975). A lateral conch is present on the quadrate of *Paliguana** (Carroll, 1975a), kuehneosaurs (Fig. 3B), and all squamates that retain a tympanum (Evans, 1980). *Sphenodon* lacks both a tympanum and a lateral conch on the quadrate (Fig. 3F). So far as can be determined from the bones, this condition occurs in *Homoeosaurus* and sapheosaurs as well (Figs. 1G,H). In the Triassic sphenodontidans such as *Planocephalosaurus* (Fig. 3D) and *Clevosaurus* (Fig. 3E), however, the quadrate has a poorly developed conch and the lateral margin of the skull is clearly modified for support of a tympanum. As noted above, *Gephyrosaurus* is the sister taxon of all other rhynchocephalians, and this Early Jurassic species has a prominent lateral conch on the quadrate (Fig. 3C). Because rhynchocephalians and squamates are closer to one another than either is to *Paliguana** or kuehneosaurs, a prominent lateral conch on the quadrate is considered to be a synapomorphy of lepidosauriforms. This requires the secondary loss of the quadrate conch and tympanum within sphenodontidans, as has already been suggested by Evans (1980). Perhaps increased specialization for propalinal jaw movements in the sphenodont-homoeosaur-sapheosaur group (Robinson, 1976) may be functionally or developmentally related to the reduced sensitivity of the ear to airborne sound.

The presence of a slender stapes is likely to be correlated with the quadrate conch, because a tympanum seems superfluous without a stapes slender enough to transmit its motion to the inner ear (Carroll, 1977, and references therein). Although there are lepidosaurs with a slender stapes but without a conch or tympanum (i.e., *Sphenodon*), the converse never seems to occur. Aside from the relatively stout stapes retained by younginiforms (Gow, 1975), and the slender stapes known in kuehneosaurs (Evans, 1980), this character is unknown in other extinct lepidosauromorphs.

2. [36] Quadrate bowed in lateral view. The quadrate is not modified for support of a middle and external ear in amniotes ancestrally, nor in reptiles, diapsids, or saurians (Gauthier, 1984). The ancestral condition is also retained by younginiforms (Fig. 3A). Lepidosauriforms differ in that the body of the quadrate is bowed anteriorly for support of the middle ear cavity and the lateral portion of the quadrate is likewise modified to form a conch that supports the tympanum. A bowed quadrate is present in *Paliguana** (Carroll, 1977), kuehneosaurs (Fig. 3B), and in ancestral rhynchocephalians (Fig. 3C) and squamates (Figs. 3G-H). This character may be correlated with the ones preceding and following it; however, examples can be found in which one or more are absent in the presence of the other (e.g., tall quadrate without lateral conch in archosauromorphs; Gauthier, 1984). We therefore treat them separately until the correlation is better documented. A straight quadrate has been developed secondarily in some rhynchocephalians (e.g., *Sphenodon*) and squamates (e.g., chamaeleons).

3. [17] Enlarged adductor chamber and quadrate extends well below occipital condyle. In ancestral saurians the adductor chamber is small and the quadrate does not extend well below the level of the occipital condyle. This condition is seen in araeoscelidans (Reisz, 1981) as well as in amniotes ancestrally (Panchen, 1972), and it is retained in younginiforms (Fig. 3A). In contrast, the adductor chamber is relatively large and the quadrate extends well below the occipital condyle in *Paliguana** (Carroll, 1977), kuehneosaurs (Fig. 3B), and in ancestral rhynchocephalians (Fig. 3D)

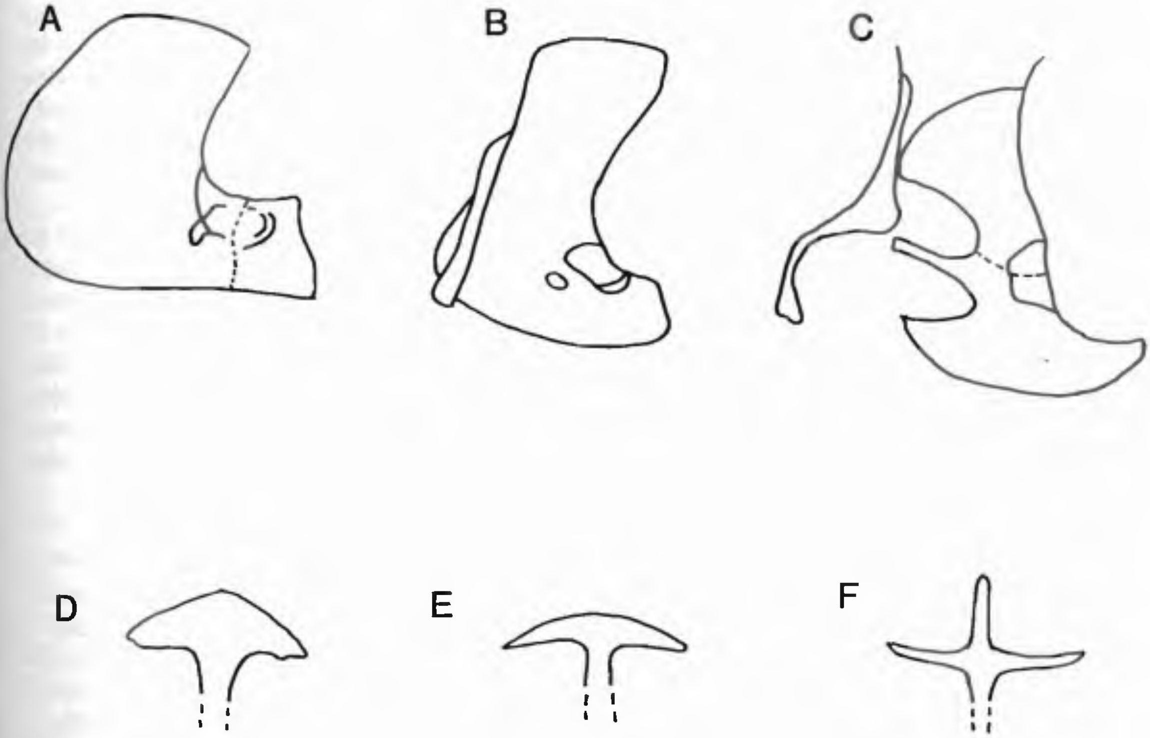

FIGURE 5. Lateral view of scapulocoracoid. A, *Petrolacosaurus kansensis* (araeoscelidan); B, *Gephyrosaurus bridensis* (rhynchocephalian); C, *Lepidophyma flavimaculatum* (autarchoglossan). Ventral view of interclavicle. D, *Youngina capensis* (younginiform); E, *Saurosternon bainii** (lepidosauriform); F, *Lepidophyma smithi* (autarchoglossan). A after Reisz (1981); B, E after Evans (1981); C after Lecuru (1968a); D after Gow (1975).

and squamates (Figs. 3G-H). This character is not preserved in *Saurosternon** and *Palaeagama** (Carroll, 1977, figs. 2 and 3).

4. [72] Prominent retroarticular process of prearticular. A moderately developed retroarticular process is present in saurians ancestrally (Gauthier, 1984; and see Fig. 3A). The retroarticular process is, however, more prominently developed in all lepidosauromorphs that retain a tympanum (Figs. 3L). The synapomorphic condition is present in *Paliguana** (Carroll, 1975a), kuehneosaurs (Robinson, 1962), and in rhynchocephalians (Fig. 3I) and squamates (Fig. 3K) that retain a tympanum. The mandibles are unknown in *Palaeagama** and *Saurosternon**. Although we are not sure of the level at which it arises within lepidosauromorphs, we note that the retroarticular process is formed entirely by the prearticular bone, rather than by the prearticular and articular as in archosauromorphs.

5. [94] Loss of cleithrum. Cleithra are present in diapsids ancestrally (Reisz, 1981). Cleithra are unknown among archosauromorphs (Romer, 1956), but they are present in younginiforms ancestrally (Currie, 1982). The shoulder girdles are not preserved in *Paliguana** and *Palaeagama**. No cleithra are present in *Saurosternon**, kuehneosaurs, rhynchocephalians, or squamates.

6. [93] Gracile interclavicle. The interclavicle is a relatively broad, flat, T- or anchor-shaped element in diapsids ancestrally, judging from the form of the interclavicle in araeoscelidans (Reisz, 1981), the protorosaurian archosauromorph *Prolacerta* (Gow, 1975), and in younginiforms (Fig.

5D). The interclavicle is unknown in *Paliguana** and *Palaeagama**. *Saurosternon** (Fig. 5E), rhynchocephalians (Evans, 1981), and squamates (Fig. 5F) differ from other lepidosauromorphs in that the interclavicle in general, and the lateral processes of the interclavicle in particular, are relatively more slender and lightly constructed. Although the interclavicle is unknown in kuehneosaurs, it is assumed to have been gracile, since a gracile interclavicle is present in *Saurosternon**, which from the standpoint of the postcranial skeleton is the sister taxon of the kuehneosaur-rhynchocephalian-squamate group (see below).

7. [134] The lepidosauriform ankle joint. According to Brinkman (1980), *Saurosternon** is like rhynchocephalians and squamates and unlike other diapsids in that it possesses a process on the ventromedial corner of the fourth distal tarsal that fits under the astragalus somewhat medial to the calcaneal-fourth distal tarsal articulation. This appears to be the initial event in the series of modifications that yields the specialized ankle of squamates (Brinkman, 1980; and see below). The ankle is not preserved in *Palaeagama** and *Paliguana** (Carroll, 1975a), and it has not been described in kuehneosaurs (Evans, 1981). S. Evans (pers. comm.) informs us that on the basis of the dissociated astragalus and calcaneum elements in the British Museum (Natural History), the kuehneosaur ankle is not like that of squamates.

UNNAMED TAXON INCLUDING KUHNEOSAURS, RHYNCHOCEPHALIANS, AND SQUAMATES

Kuehneosaurs and lepidosaurs possess synapomorphies that are apparently lacking in *Paliguana**, *Palaeagama**, and *Saurosternon**. These species, along with the younginiforms, archosauromorphs, and araeoscelidans, are used as successively more remote outgroups in the following analysis. Since much of the kuehneosaur material remains undescribed, it seems advisable not to name this taxon at present. It is clear nevertheless that kuehneosaurs, squamates, and rhynchocephalians possess synapomorphies in the manus and pelvis that distinguish them from *Palaeagama** and *Saurosternon**. Likewise, the members of this unnamed taxon possess synapomorphies in the skull that are lacking in *Paliguana**. It is particularly at this node that the noncomplementary nature of the remains of *Paliguana**, *Palaeagama** and *Saurosternon** are most keenly felt. So far as is known, kuehneosaurs, rhynchocephalians, and squamates share the following combination of synapomorphies that are absent in other lepidosauromorphs.

Diagnosis: 1. [59] Anterolaterally oriented prefrontal-nasal suture. To judge by the condition in araeoscelidans (Fig. 1A), younginiforms (Fig. 1B) and *Paliguana** (Carroll, 1975a), the prefrontal-nasal suture extends anteroposteriorly, parallel to the internasal suture, in ancestral lepidosauromorphs. This character is not preserved in *Palaeagama** and *Saurosternon**. In kuehneosaurs (Fig. 1C) and rhynchocephalians (Fig. 1H), however, the prefrontal-nasal suture is directed anterolaterally, diverging from the internasal suture. The highly modified snout of *Clevosaurus* (Fig. 1E) is considered secondary, because *Planocephalosaurus* is like other sphenodontidans in this regard (Fig. 1F). *Gephyrosaurus* may also be secondarily modified in this respect (Fig. 1D), because Evans (pers. comm. 1984) claims that the seemingly ancestral form of these sutures is accurate, and not an artifact of her reconstruction based on isolated elements. The snout is further transformed in squamates (Fig. 1J), being neither ancestral nor like that of kuehneosaurs and rhynchocephalians. In squamates, as discussed in greater detail below, the nasals are reduced and the facial process of the maxilla is correspondingly enlarged. Based on data discussed below, the snout of squamates is considered a further modification of the ancestral condition of lepidosauriforms.

2. [6] Loss of tabulars. Paired tabular bones are present in araeoscelidans (Reisz, 1981), but they have been lost in all archosauromorphs (see above). Younginiforms (Gow, 1975) and *Paliguana** (Carroll, 1975a), however, retain paired tabular bones. This character is not preserved in *Saurosternon**, and the rear of the skull is too poorly preserved to discriminate between absence

and non-preservation in *Palaeagama** (Carroll, 1975). Thus, tabulars are considered to be present in lepidosauromorphs ancestrally. Tabulars are not reported in kuehneosaurs, and they are absent in all rhynchocephalians and squamates (Robinson, 1967).

3. [5] Loss of postparietals. A pair of small postparietal bones is present in araeoscelidans (Reisz, 1981), and a single postparietal, evidently representing the fusion of the originally paired elements, appears ancestral in archosauromorphs (Gauthier, 1984). The postparietals are retained by younginiforms (Gow, 1975) and *Paliguana** (Carroll, 1977). This character is not preserved either in *Saurosternon** or *Palaeagama**. Accordingly, the bones are considered to have been paired in ancestral lepidosauromorphs. No postparietals have been reported in kuehneosaurs, and they are absent in all squamates and rhynchocephalians (Robinson, 1967).

4. [24] Loss of teeth on transverse flange of pterygoid. Teeth are present ancestrally on the transverse flange of the pterygoid in both archosauromorphs (Gauthier, 1984) and lepidosauromorphs (Fig. 2A). Kuehneosaurs, squamates, and rhynchocephalians have lost the teeth on the transverse flange of the pterygoid (Fig. 2C). This character is not preserved in *Paliguana**, *Palaeagama** and *Saurosternon**, and the synapomorphic condition may apply to a more inclusive group.

5. [33] Paroccipital process of opisthotic contacts quadrate. According to Reisz (1981), Gow (1975), and Carroll (1975a), the distal extremity of the opisthotic remains cartilaginous in diapsids ancestrally. Among lepidosauromorphs, the ancestral condition is retained by younginiforms and *Paliguana** (Carroll, 1977). This character is not preserved in *Saurosternon** and *Palaeagama**. In contrast, the paroccipital process of the opisthotic is fully ossified and contacts the quadrate in kuehneosaurs (Robinson, 1967), and the apomorphic condition obtains throughout posthatching ontogeny in squamates and rhynchocephalians (pers. obs.).

6. [71] Angular reduced and little exposed on lateral face of mandible. The angular is a prominent element in the mandible of araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), and younginiforms (Fig. 3A), for it extends more than one-third of the way up the lateral surface of the mandible. In contrast, the angular extends less than one-third of the way up the lateral surface of the mandible in kuehneosaurs, rhynchocephalians and squamates (e.g., Fig. 3K). This character is not determinable in *Palaeagama**, *Paliguana**, and *Saurosternon**.

7. [97] Humerus robust, but diameter of shaft reduced. Compared to the limbs of early synapsids and captorhinids, amniotes like *Paleothyris** and diapsids share the apomorphy of long and gracile limbs, and this description applies to the humerus as well. Although araeoscelidans have an exceptionally gracile humerus (Reisz, 1981), in saurians ancestrally the element is more like that of *Paleothyris**; it is comparatively robust and thick-shafted relative to its length (Gauthier, 1984). This condition is retained in *Saurosternon** (Carroll, 1977, fig. 10) and in a modified form in younginiforms (Currie, 1981b). The humerus is not preserved in *Paliguana**. Compared to that of *Saurosternon**, the diameter of the shaft of the humerus in kuehneosaurs (Colbert, 1970), rhynchocephalians (Evans, 1981), and especially squamates (see p. 55 below), is reduced relative to the length of that element.

8. [105] Metacarpal IV subequal or slightly shorter than metacarpal III. Because metacarpal IV is longer than III in araeoscelidans (Fig. 4A), archosauromorphs (Gauthier, 1984), and younginiforms (Currie, 1981b), this appears to be the ancestral condition in archosauromorphs and lepidosauromorphs. The manus is not preserved in *Paliguana**, but *Saurosternon** and *Palaeagama** retain the ancestral condition because metacarpal IV is longer and stouter than III (Carroll, 1975a). To judge from the figures of *Icarosaurus* (Colbert, 1970), the fourth metacarpal in kuehneosaurs is subequal to the third in length, thus approaching the condition seen in rhynchocephalians and squamates, in which the fourth metacarpal is shorter than the third (see below).

9. [121] Pelvic girdle fenestrate. As noted by Carroll (1977), the pelvis forms a solid plate in younginiforms, *Saurosternon**, and *Palaeagama**. This is the ancestral condition, because it oc-

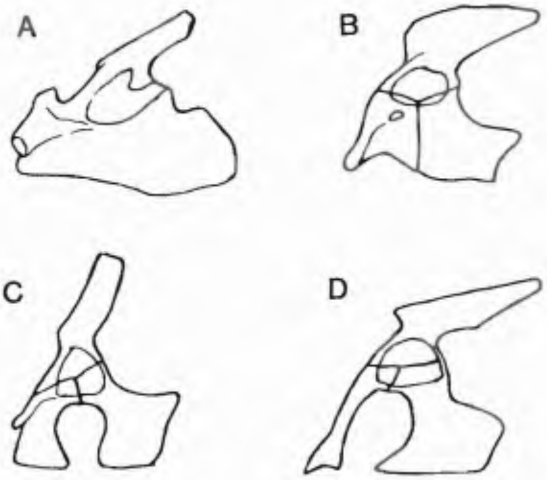

FIGURE 6. Lateral view of pelvic girdle. A, *Petrolacosaurus kansensis* (araeoscelidan); B, *Prolacerta broomi* (archosauromorph); C, *Sphenodon punctatus* (sphenodont); D, *Iguana iguana* (iguanian). A after Reisz (1981); B after Gow (1975); C, D after Romer (1956).

curs in araeoscelidans (Fig. 6A) and in archosauromorphs ancestrally (Fig. 6B). The pelvis is not preserved in *Paliguana**. Kuehneosaurs (Colbert, 1970), rhynchocephalians (Fig. 6C), and squamates (Fig. 6D) are unique among lepidosauromorphs in possessing a fenestrate pelvic girdle. This character is not unique among diapsids, however, because fenestrate pelves have arisen independently in archosaurs and *Askeptosaurus* (Evans, 1981). Nevertheless, the pelvic symphyses of other diapsids are readily distinguished from those of lepidosaurs by numerous morphological details. For example, the pubis in squamates and rhynchocephalians is distinctive in the anteroventral curvature of the anterodorsal face of the element (Carroll, 1977).

LEPIDOSAURIA

This taxon inclues rhynchocephalians and squamates; see Haeckel, 1866.

Definition: The most recent common ancestor of *Sphenodon* and squamates and all of its descendants.

In this section, we argue that squamates and rhynchocephalians are closer to one another than either is to any other lepidosauromorph. Although Haeckel (1866) originally coined the term Lepidosauria for what are here considered to be squamates, his subsequent writings made it clear that he considered *Sphenodon* a closely related form. To preserve his intent, and in order to append maximum information to a widely recognized taxon, we here restrict the name Lepidosauria to the least inclusive taxon of lepidosauromorphs that contains the common ancestor of Rhynchocephalia and Squamata. In the context of extant amniotes, we would emphasize that *Sphenodon* and squamates possess all the above-listed synapomorphies as well as those listed below; one might question whether or not a given fossil is part of this group, but not that lepidosaurs are most closely related among extant amniotes.

To facilitate the following discussion, two primary clades of squamates are recognized, iguanians and autarchoglossans (as used in Gauthier, 1982, this name refers to all other noniguanian squamates, including gekkotans, snakes, and amphisbaenians). Diagnoses for squamate higher taxa are given in Estes et al. (1988). Based on the analysis presented here, the following characters are considered synapomorphies that distinguish lepidosaurs from other amniotes.

Diagnosis: 1. [160] Transverse cloacal slit. The cloacal slit is oriented transversely in lepidosaurs, rather than anteroposteriorly as in other tetrapods (Oppel, 1811; Günther, 1867). We believe that the loss of the amniote penis corresponds to the transformtion of the cloaca in lepidosaurs.

2. [161] Sexual segment of kidney. All tetrapods other than lepidosaurs do not possess a sexual segment of the kidney (Fox, 1977).

3. [162] Tongue notched distally. *Dibamus* is an exception, but other data indicate that this taxon is an autarchoglossan squamate that must have lost the notched tongue (Estes et al., 1988).

4. [163] Small prey secured by tongue. *Sphenodon* and iguanians use the tongue to secure small prey (Gorniak, et al. 1982; pers. obs.), an attribute taken to an extreme in chamaeleons. No autarchoglossan is known to take small prey with the tongue. Minimizing evolutionary events cannot be used to resolve the level of synapomorphy in this case, because two steps are involved whether convergence between iguanians and *Sphenodon* is accepted or if the character is considered to apply to lepidosaurs generally and has become lost secondarily in autarchoglossans. We prefer the latter interpretation because the form and function of the autarchoglossan tongue are in no other sense ancestral (Schwenk, 1988). Indeed, as discussed in Estes et al. (1988), correlated changes in the morphology of the tongue and Jacobson's organ suggest that the autarchoglossan tongue is modified to stress chemoreceptive over prey-capturing qualities, as suggested by Underwood (1971).

5. [164] Ciliary process of eye reduced or absent. At least some degree of development of a ciliary process is present in tetrapods ancestrally. According to Underwood (1970) lepidosaurs are unusual among amniotes in that the ciliary process is reduced or absent.

6. [165] Tendon of nictitans attaches to orbital wall. In reptiles generally, the tendon of the nictitating membrane is attached to the m. pyramidalis, which takes its origin from the surface of the eyeball. In lepidosaurs, however, the tendon is transferred to the m. retractor bulbi and the interorbital septum (Underwood, 1970).

7. [167] Tenon in lower eyelid. A cartilaginous disc, the tenon, is present in lower eyelid of lepidosaurs alone among amniotes (Romer, 1956).

8. [166] Lepidosaur ecdysis. Ecdysis is irregular and piecemeal in amniotes ancestrally, but in lepidosaurs the skin is regularly shed in its entirety (Gans, 1978).

9. [168] Modified middorsal scale row. The middorsal row is considered "modified" if its gross appearance differs from that of the lateral scale rows. So defined, a modified middorsal scale row is present in *Sphenodon*, many iguanians, and in a single group of autarchoglossans, the mosasaurs (Williston, 1899). Etheridge and de Queiroz (1988) considered the modified scale row to be the ancestral condition in iguanians. The detailed shape of the middorsal scale row varies markedly among iguanians, however, from the slightly larger and more projecting middorsal scales of *Dipsosaurus* to the oddly-shaped structures in some chamaeleons to the tail spines of *Amblyrhynchus*. There are also groups in which a middorsal scale row has been lost entirely, such as the sceloporines. In spite of this variation, presence of this character in rhynchocephalians, iguanians, and mosasaurs indicates that it represents the ancestral condition for lepidosaurs; loss of the modified middorsal scale row within autarchoglossans is considered secondary.

The above synapomorphies, which would seldom be preserved in the fossil record, are less useful in determining the relationships of fossil species. Comparative osteology reveals that rhynchocephalians and squamates possess the following combination of synapomorphies that distinguishes them from all amniotes, including kuehneosaurs, *Saurosternon**, *Paliguana**, *Palaeagama**, and younginiforms.

10. [8] Long anterior extent of squamosal, usually extending anterior to level of braincase, and

approaching closely or contacting elongate postorbital ramus of jugal. In archosauromorphs ancestrally and in lepidosauromorphs, the squamosal extends anteriorly approximately halfway over the lower temporal fenestra and is separated from the jugal by a wide gap below the postorbital. The ancestral condition found in araeoscelidans (Reisz, 1981) and archosauromorphs (Gauthier, 1984), and it is retained in younginiforms (Fig. 3A), *Paliguana** (Carroll, 1977), and kuehneosaurs (Fig. 3B). This character is not preserved in *Palaeagama** and *Saurosternon**. Variation among squamates and rhynchocephalians makes this character difficult to interpret. The synapomorphic condition, in which the jugal and squamosal nearly or entirely exclude the postorbital from the lower temporal fenestra, is present in *Gephyrosaurus* (Fig. 3C) and in clevosaurs (Figs. 3D,E), although it is absent in *Sphenodon* (Fig. 3F). Similarly, squamates are variable in this regard. The synapomorphic condition is present in iguanians (Fig. 3G). Except for xantusiids and cordylids, the squamosal is relatively elongate in autarchoglossans (Fig. 3H). However, this character is difficult to interpret in autarchoglossans that have modified the upper temporal arch, including the xantusiids and cordylids noted above. Although obscured by overlap of the postorbital, the synapomorphic condition is present in "aigialosaurs" and mosasaurs (Russell, 1967), and in gekkotans that retain the arches intact (*Bavarisaurus*). Perhaps related to changes in the shape of the postorbital, however, the squamosal is more broadly separated from the jugal in all anguimorphs except xenosaurids, all lacertoids except teiids, and all scincoids except scincids (Estes et al., 1988). Other characters indicate that anguimorphs, lacertoids and scincoids are derived in this regard, and that teiids, xenosaurids and scincids have regained the squamosal-jugal contact secondarily. This character cannot be interpreted in squamates that lack the temporal arches.

11. [1] Reduced lacrimal. Presence of a large lacrimal is ancestral for diapsids, although in most saurians this bone is less prominent than in araeoscelidans (Reisz, 1981). The ancestral condition is retained by younginiforms (Fig. 3A), *Paliguana** (Carroll, 1975), and kuehneosaurs (Fig. 3B), but this character is not preserved in *Palaeagama** and *Saurosternon**. All lepidosaurs possess a synapomorphic condition in which the lacrimal is small and confined to the orbital rim, or it is absent (Figs. 3C,H).

12. [35] Imperforate stapes. The base of the robust stapes bears a foramen for the passage of the stapedial artery in araeoscelidans (Reisz, 1981) and younginiforms (Carroll, 1977). The stapes is more lightly constructed in kuehneosaurs, but is still perforate (Evans, 1980). The stapes of rhynchocephalians is like that of kuehneosaurs in that it is more lightly constructed and elongate than in lepidosauromorphs ancestrally. However, the rhynchocephalian stapes differs in being imperforate in postembryonic developmental stages (Gans, 1978). The stapes is relatively very thin (columelliform) in squamates (pers. obs.). The stapes is imperforate in squamates generally, except in dibamids (Greer, 1976) and some gekkotans (Underwood, 1957). During ontogeny, the position of the stapedial artery changes from being enclosed in the stapes to passing posterior to the stapes in amphisbaenians (Gans and Wever, 1976). We are not certain if the artery lies within the stapes in embryonic *Sphenodon* (Estes et al., 1988, contra Gans, 1978), nor do we have information on this transformation in lepidosaurs other than amphisbaenians. Nevertheless, it appears safe to conclude that the loss of the stapedial foramen during ontogeny is a lepidosaur synapomorphy. Accepting this conclusion requires the secondary acquisition of the perforate stapes in dibamids on one hand, and within gekkotans on the other. The proposed reversals are in keeping with numerous morphological details that point to paedomorphosis in these two groups, which could account for the character discordance that lies at the base of the controversies that surround the relationships of dibamids and gekkotans (see Greer, 1984; Estes et al., 1988).

13. [31] Loss of teeth on the parasphenoid. Teeth are present on this element in diapsids ancestrally, being present in araeoscelidans (Reisz, 1981). If *Heleosaurus* is an archosauromorph (Carroll, 1975b), then the latter group also retains teeth on the parasphenoid ancestrally, although

the element is edentulous in other archosauromorphs (Gow, 1975). Parasphenoidal teeth are absent in younginiforms (Fig. 2A), and their presence or absence is indeterminable in *Paliguana**, *Palaeagama**, and *Saurosternon**. Parasphenoidal teeth are present in kuehneosaurs (Evans, 1980), but they are absent in all rhynchocephalians and squamates (Figs. 2C-H). Lack of knowledge of the distribution of this character leaves the level of synapomorphy ambiguous. In this instance, we will treat the absence of this character in younginiforms as convergence, rather than assume that it applies to lepidosauromorphs generally, with kuehneosaurs subsequently regaining parabasisphenoidal teeth. We accept the former hypothesis until this character can be determined in *Paliguana**, *Saurosternon** and *Palaeagama**.

14. [29] Complete abducens canal and well-developed dorsum sellae. Detailed knowledge of the dorsal surface of the basisphenoid is available for relatively few early diapsids. Grooves in the dorsal surface of the basisphenoid may be present in archosauromorphs such as *Prolacerta* (Gow, 1975). This character is not preserved in *Paliguana**, *Palaeagama**, and *Saurosternon**. According to Evans (1980), however, in *Kuehneosaurus latus* the dorsum sellae is poorly developed, and neither grooves nor canals mark the passage of the abducens nerves in the basisphenoid. In lepidosaurs, however, there are paired canals in the basisphenoid for the passage of the abducens nerves (Evans, 1980). The nerves enter the basisphenoid posterodorsally and emerge from the dorsum sellae anteriorly (Oelrich, 1956). In amphisbaenians, which lack the abducens and other nerves associated with the eye musculature, there are no abducens canals (Gans, 1978). Phylogenetic or functional reduction of the eyes in relation to fossorial habits could account for the absence of the abducens canals in some ophidians as well.

15. [74] Mandibular condyle formed only by articular bone. In ancestral amniotes, the quadrate articulates with the articular medially and the surangular laterally, such that one-fourth to one-third of the mandibular condyle is formed by the surangular bone (Gauthier, 1984). This condition occurs in synapsids (e.g., *Sphenacodon*), Testudines (e.g., *Chelonia*), and archosauromorphs (e.g., *Champsosaurus*). This region is not preserved, or it has not been reported in, extinct lepidosauromorphs. In rhynchocephalians and squamates, however, the surangular forms only the outer rim of the articulation, with the condyle formed by the articular alone. Morphologists have long been mistaken in maintaining that a quadrate-articular attachment is ancestral for amniotes. This reflects the assumption, often perpetuated in textbooks, that "lizards" are relatively unmodified examples of the "primitive" reptilian type. Such treatments generally ignore character transformations within lineages not leading directly to mammals or birds.

16. [75] Teeth attached superficially to jaw. To judge by the condition seen in araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1983), and younginiforms (Gow, 1975), the teeth are set in shallow sockets in the jaw in ancestral lepidosauromorphs (subthecodont). The mode of tooth implantation is unknown in *Paliguana**, *Palaeagama**, and *Saurosternon**. Robinson (1962) and Evans (1980), however, describe the teeth of kuehneosaurs as subpleurodont, being set in shallow depressions. Our observations on *Kuehneosaurus*, however, indicate that the teeth are subthecodont, i.e., lying in shallow depressions. The teeth of rhynchocephalians and squamates are attached superficially to the medial side of the jaw. Superficially attached teeth that undergo normal replacement and are not surrounded by extensive bone of attachment occur widely in squamates and are commonly referred to as pleurodont. Those of sphenodontidans, agamids*, and chamaeleontids are further transformed in that they are generally not replaced and become extensively invested by attachment bone, blurring their individuality (acrodont). Acrodonty and pleurodonty are often defined by the position of the teeth relative to the jaws; acrodont teeth are said to attach apically, while pleurodont teeth attach to the medial surface of the jaws. Unfortunately, under these definitions, the teeth of most agamids* are pleurodont, while those of *Gephyrosaurus* are closer to being acrodont. Because there seems to be general agreement that agamid* teeth are acrodont, and be-

cause those of *Gephyrosaurus* have been described as pleurodont (Evans, 1980), the definition of acrodonty should be based on the general lack of replacement and the investment of the teeth by attachment bone, rather than on the position of the teeth with respect to the jaws. It is inaccurate to describe the teeth of lepidosaurs as either pleurodont or acrodont, as if both were unrelated transformations of some more general mode of implantation, because acrodonty is simply a further modification of pleurodonty. Accepting superficial attachment as the ancestral condition in lepidosaurs requires the shallowly-socketed teeth of ophidians and the more deeply-socketed teeth of mosasaurs to be secondary modifications (Edmund, 1969).

17. [78] Accessory intervertebral articulations (zygosphenes and zygantra). There are no accessory intervertebral articulations in araeoscelidans (Reisz, 1981). Such articulations are also absent in archosauromorphs ancestrally, although accessory articulations have arisen separately in some rauisuchians on the one hand, and in saurischian dinosaurs on the other (Gauthier, 1984). Accessory intervertebral articulations are also absent in younginiforms ancestrally, although younginoids have uniquely modified articulations between the neural spines (Currie, 1981a). Carroll (1975) described zygosphenial joints in *Saurosternon**, although Evans (1981) was unable to confirm his observation, and Carroll (1977:371, fig. 8) did not figure them. As Evans (1981) pointed out, it is difficult to see feebly developed zygosphenial joints in articulated skeletons such as those of *Palaeagama** and *Saurosternon**. The isolated vertebrae of kuehneosaurs lack zygosphenial joints (Colbert, 1970; Evans, 1981). Zygosphenial joints are present in *Gephyrosaurus* and *Sphenodon* (Evans, 1981), and they are thus considered to have been present in the ancestral rhynchocephalian. Among squamates there is considerable variation in this character. Squamate zygosphenial joints may vary from a simple, weakly developed condition, in which the prezygapophysial articular surfaces extend medially onto the neural arch above the spinal cord, to the separately encapsulated and prominently developed structures characteristic of snakes (Hoffstetter and Gasc, 1969; Winchester and Bellairs, 1977). As noted by R. Etheridge (pers. comm.), this character appears to vary with size among iguanians; with some exceptions in taxa that possess such articulations, the larger the lizard the more prominent the zygosphenial joints. This generalization also holds for several groups of autarchoglossans; lacertids, for example, appear to vary in a similar fashion. Compared to iguanians, the exceptions are much more conspicuous in autarchoglossans, because even the smallest snake or gymnophthalmid has prominently developed zygosphenial joints. They are absent in amphisbaenians and the overwhelming majority of anguimorphs, regardless of size (Hoffstetter and Gasc, 1969). Variation in this character makes it difficult to determine the level at which it is a synapomorphy. Nevertheless, zygosphenial joints are present in rhynchocephalians, present or absent in iguanians, and present or absent in autarchoglossans. Accordingly, it is simpler to accept the hypothesis that zygosphenial joints are a lepidosaur synapomorphy, and that they have been lost secondarily in several squamate groups.

18. [80] Caudal autotomy septa present. There are no autotomy septa in the caudal vertebrae of araeoscelidans (Reisz, 1981), or those of archosauromorphs (Gauthier, 1984) and lepidosauromorphs ancestrally. These structures are absent in younginiforms (Currie, 1981), *Saurosternon** (Carroll, 1975a), and kuehneosaurs (Evans, 1981). In *Paliguana** and *Palaeagama** only the nonautotomic base of the tail is preserved. Except for *Homoeosaurus*, all other rhynchocephalians with the tail preserved display intravertebral fracture planes (Howes and Swinnerton, 1901; Cocude-Michel, 1963). Winchester and Bellairs (1977) have recently reviewed the development of this character in a few squamate species. To judge from their examples, it seems that the fragile, regenerable tail that is characteristic of lepidosaurs forms late in development, resulting from a complex series of events yielding an intravertebral septum passing through the caudal ribs, dividing them into unequal portions. The distribution of this character has been reviewed by Etheridge (1967) and Hoffstetter and Gasc (1969). R. Etheridge (pers. comm.) observed a crocodilian that regenerated its

tail after it had been severed through a vertebral centrum. In most taxa (such as crocodilians) that lack autotomy septa and do not normally regenerate the tail, tail loss is accomplished by intervertebral separation. Etheridge therefore suggested that the development of a caudal fracture plane may facilitate regeneration. The issue is complex, however, because amphisbaenians retain fracture planes but do not regenerate the tail (Gans, 1978). Accepting caudal autotomy septa as a synapomorphy of lepidosaurs requires secondary losses among several squamate groups. In some instances, the loss of a fragile tail is intelligible from a functional standpoint, such as in "aigialosaurs" and mosasaurs, in which the tail is used as a sculling organ. In other instances, however, there appear to be no obvious functional explanation for its loss, as in the case of acrodont iguanians. Caudal autotomy septa have arisen independently in mesosaurs and in some captorhinids (Carroll, 1982).

19. [91] Sternum indistinguishably fused during embryogeny. As noted above, the sternal plates are paired for much of postnatal ontogeny in younginiforms, becoming fused to one another only late in post-hatching ontogeny. This character is not preserved in *Paliguana**, *Palaeagama**, and kuehneosaurs. As Carroll (1977) pointed out, the sternal plates are paired in *Saurosternon**, thus indicating the immaturity of the specimen. In squamates and rhynchocephalians the sternal plates are indistinguishably fused to one another in the embryo (Howes and Swinnerton, 1901).

20. [90] Xiphisternum greatly reduced or absent. As noted above, the amniote xiphisternum extends far posteriorly and includes at least five poststernal ribs ancestrally. However, *Sphenodon* lacks a xiphisternum (Günther, 1867), and squamates have a very reduced structure that is usually composed of no more than two ribs (R. Etheridge, pers. comm.; Lecuru, 1968b). For reasons discussed above, this character is seldom determinable in fossils. It seems likely that the reduced xiphisternum is associated with the transformation of the sternum at the level of Lepidosauromorpha; however, because this character is at present determinable only in Recent squamates and *Sphenodon*, we will be conservative in treating it as a synapomorphy of lepidosaurs alone.

21. [115] Ectepicondylar groove transforms into a foramen in embryo. As noted above, there is an ectepicondylar foramen in *Palaeagama**, *Saurosternon**, and kuehneosaurs, but in the absence of earlier ontogenetic stages of these taxa, it cannot yet be determined when enclosure takes place during ontogeny. This character may apply to a more inclusive group. Until more is known, however, it will be considered a synapomorphy of the lepidosaurs, in living members of which the foramen is fully formed in the embryo (Howes and Swinnerton, 1901).

22. [104 & 105] Symmetrical metacarpals. In diapsids ancestrally, the metacarpals increase in size from first to fourth, with metacarpal five being subequal to the first in length (Fig. 4A). In addition, the second, third and fourth metacarpals are stoutest, with the first and fifth being considerably less robustly constructed. *Paliguana** is unknown in this regard, but both *Saurosternon** and *Palaeagama** are ancestral in this respect (Carroll, 1975). In kuehneosaurs most of these relations are maintained, except that metacarpal four is subequal to the third in length (see 3.3.8). In rhynchocephalians and squamates, however, metacarpals two and four are reduced, metacarpal four is shorter than the third, and the first and fifth metacarpals are more stoutly constructed (Fig. 4C); moreover, the first and fifth manal digits are set slightly below the other digits. The metacarpalia are, thus, more symmetrical, a condition that is considered a synapomorphy of Lepidosauria. This character is usually associated with the shortening of the fourth digit, which in most lepidosaurs is not much longer than the third. Archosaurs have an analogous condition, but their hands are otherwise different. In groups that develop webbed hands, such as some tangasaurs and champsosaurs, the metacarpals may be symmetrical. In these groups, however, the entire manus is relatively broader and more symmetrical.

23. [123] Pelvis fused in adults. The ilium, ischium and pubis are fused to one another in adult araeoscelidans (Fig. 6A), as in amniotes ancestrally. However, the pelvic elements remain distinct in all archosauromorphs except for birds other than *Archaeopteryx** (Fig. 6B and Romer,

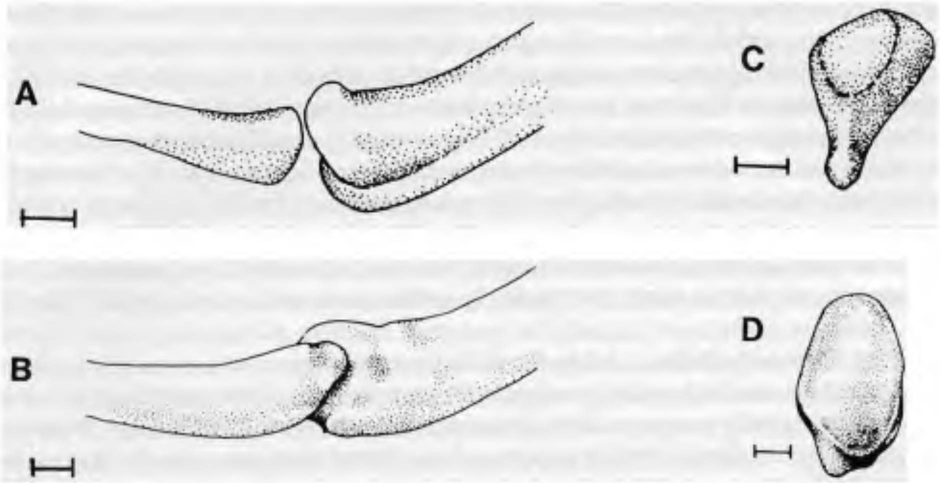

FIGURE 7. Lateral view of right knee (A and B) and distal view of left fibula (C and D). A, *Caiman sclerops* (archosaur); B, *Sauromalus obesus* (iguanian); C, *Sphenodon punctatus* (sphenodont); D, *Tupinambis teguixin* (autarchoglossan).

1956), as well as in younginiforms (Currie, 1981b). Accordingly, an unfused pelvis in the adult is considered a synapomorphy -- via paedomorphosis -- of Sauria. This character is not preserved in *Paliguana**, but in both *Palaeagama** and *Saurosternon** the pelvic elements are separate. Unfortunately, the latter two taxa are represented by single, subadult specimens, thus rendering this character indeterminable. Kuehneosaurs evidently have the ancestral condition because fused pelves have not been reported in *Kuehneosaurus*, which is represented by large samples including adults (Evans, 1981, and pers. comm.). In contrast, in all rhynchocephalians, and in all squamates with unreduced pelves, the ilium, ischium and pubis are indistinguishably coossified in fully mature individuals (pers. obs.). In *Gephyrosaurus*, however, most specimens of pelvic bones are dissociated, suggesting that it may retain the ancestral condition in this respect (S. Evans, pers. comm.). On the contrary, we would suggest that most are not fused because they are not yet fully mature.

24. [116, 120] Ilium forms less than 80-85% of surface area of acetabulum, and iliac blade narrow and more or less steeply inclined posterodorsally. In amniotes ancestrally the iliac blade is relatively small and is steeply inclined posterodorsally, and the ilium forms no more than 60-65% of the surface area of the acetabulum (Gauthier, 1984). This condition is retained in diapsids ancestrally (Reisz, 1981; see Fig. 6B). The ilium is transformed in saurians; it forms 80-85% of the surface area of the acetabulum, and the iliac blade is enlarged, roughly triangular in lateral view, extending to the level of the posterior end of the ischium (Fig. 6B). This condition is present in archosauromorphs (Gauthier, 1984), younginiforms (Currie, 1980), and kuehneosaurs (Evans, 1981), while the ilium is either unknown or too poorly preserved to interpret in *Paliguana**, *Palaeagama**, and *Saurosternon**. In view of this distribution, it appears that an ilium like that seen in Fig. 6B is ancestral for saurians and lepidosauriforms. Accordingly, the relatively thinner (dorsoventrally) and more or less steeply inclined iliac blade, and the reduced contribution of the ilium to the acetabulum that are present in squamates (Fig. 6D) and rhynchocephalians (Fig. 6C), appear to be reversals to the condition seen in amniotes ancestrally. The ilium is relatively elongate posteriorly in lepidosaurs, however, as it is in other lepidosauriforms and saurians.

25. [117] Ilium with pubic flange. A pubic flange is absent on the ilium in saurians and lepidosauromorphs ancestrally, as shown by its absence in archosauromorphs, younginiforms, and kuehneosaurs (see Evans, 1981:112, fig. 34). This character is not preserved in *Paliguana**, *Sau-*

*rosternon**, and *Palaeagama** (Carroll, 1975a). Unlike other lepidosauromorphs, however, rhynchocephalians (Evans, 1981) and squamates (pers. obs.) share a short, flat, more or less pointed flange of the ilium that passes anterodorsally as a lappet over the acetabular junction of the pubis.

26. [119] Anteromedial portion of pubis outturned dorsally. As discussed by Carroll (1977), squamates and rhynchocephalians are unlike other diapsids in sharing a distinctive anteroventral curvature of the anterodorsal face of the pubis.

27. [124] Lepidosaur knee joint. In amniotes ancestrally, the femur and fibula meet end-to-end (Fig. 7A). Rhynchocephalians and squamates share a unique form of the fibular attachment; the flattened and pointed proximal epiphysis of the fibula lies in a vertically oriented, recessed area on the dorsal side of the fibular condyle of the femur (Fig. 7B). In addition, the distal condyles of the femur are subequally developed in saurians ancestrally, whereas in lepidosaurs they are markedly asymmetrical in development, with the tibial condyle being the larger of the two. According to Rewcastle (1980), chamaeleons are unique among Recent squamates in their possession of more symmetrically-developed femoral condyles. Mosasaurs also appear to have more symmetrically-developed condyles. Based on other synapomorphies, and because of their specialized limbs, mosasaurs and chamaeleons are considered to be secondarily derived in this regard. Because the osseous portion of the lepidosaur knee-joint is formed by the femoral and fibular epiphyses, and because the presence of epiphyses in extinct lepidosauromorphs is uncertain (see no. 33 below), it cannot yet be determined if this synapomorphy applies to a more inclusive group than lepidosaurs.

28. [127] Lateral centrale of pes fuses to astragalus in embryo. The lateral pedal centrale is a separate element in diapsids (Fig. 8A) and saurians ancestrally (Gauthier, 1984). This condition occurs in younginiforms (Currie, 1981b) and *Saurosternon** (Fig. 8B), but this region is not preserved in *Paliguana**, *Palaeagama**, or kuehneosaurs. In contrast, the centrale becomes fused to the astragalus in the embryos of squamates (Fig. 8D) and rhynchocephalians (Howes and Swinnerton, 1901; and see Fig. 8C). This synapomorphy may apply to a more inclusive group, but until more is known about this character it will be considered to apply to lepidosaurs only. As noted by Cruickshank (1979) and others, archosaurs also incorporate the centrale into the astragalus in em-

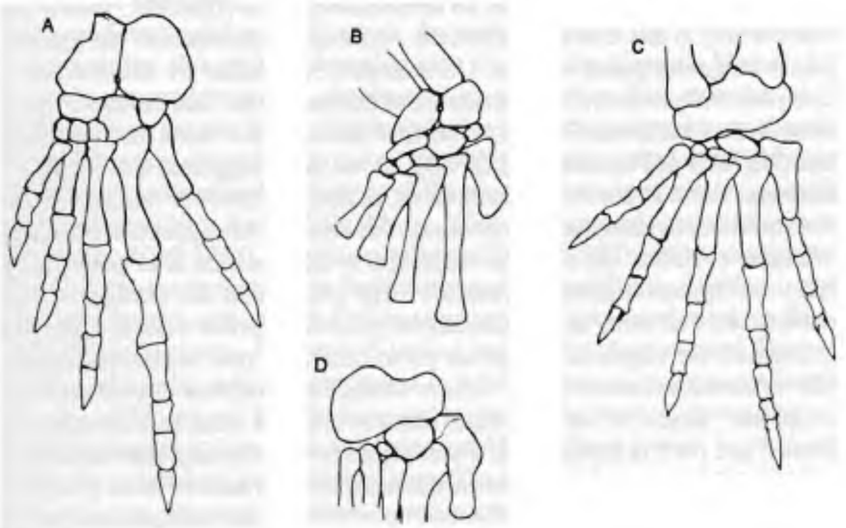

FIGURE 8. Dorsal view of left pes. A, *Petrolacosaurus kansensis* (araeoscelidan); B, *Saurosternon bainii** (lepidosauriform); C, *Sphenodon punctatus* (sphenodont); D, *Iguana iguana* (iguanian). A after Reisz (1981); B, D after Carroll (1977); C after Romer (1956).

bryos. Thus, the loss of a separate pedal centrale early in development is considered to have arisen convergently in archosaurs and lepidosaurs.

29. [126] Astragalus and calcaneum fused prior to attainment of maximum adult size. The astragalus and calcaneum are separate elements in diapsids ancestrally (Fig. 8A). They are separate elements in most archosauromorphs, although they may be fused in some archosaurs, such as pterosaurs, and in birds and some other theropods (Gauthier, 1984). The astragalus and calcaneum are separate elements in younginiforms (Currie, 1982), *Palaeagama**, and *Saurosternon** (Carroll, 1975a), but this region is not preserved in *Paliguana**. The elements are separate in juvenile lepidosaurs, but they fuse to one another prior to the fusion between the scapula and coracoid (O. Rieppel, pers. comm., cites an "adult" *Varanus* in which this fusion does not occur. If accurate as to assessment of age, we expect such variation to be rare). Evans (1981) stated that these elements are paired in kuehneosaurs, but provided no further evidence as to the stage of development represented by the particular specimen observed; it could well be an immature individual in which the fusion had not yet taken place. Until more is known, this synapomorphy will be considered to apply only to squamates and rhynchocephalians. Preliminary observations suggest that coossification between these elements may occur earlier in the ontogeny of squamates than in rhynchocephalians. Mosasaurs appear to be paedomorphic in that fusion of the astragalus and calcaneum, along with other fusions associated with the cessation of growth, are unknown among the numerous fossil representatives of the group (Russell, 1967).

30. [128] Loss of first distal tarsal, thus bringing astragalocalcaneum into contact with first metatarsal. In araeoscelidans (Fig. 8A) and in saurians ancestrally (Gauthier, 1984) the first distal tarsal is ossified and separates the first metatarsal from the astragalus (Fig. 8B). This condition is seen in younginiforms and in *Saurosternon** although this region is not preserved in *Palaeagama**, *Paliguana**, or kuehneosaurs. This character may apply to a more inclusive group, but until more is known, loss of the first distal tarsal is considered a lepidosaur synapomorphy. Among archosauromorphs, the first distal tarsal also fails to ossify in archosaurs (Gauthier, 1984). Thus, the absence of the first distal tarsal in archosaurs and lepidosaurs is considered convergent.

31. [130] Fifth distal tarsal absent. In diapsids a discrete fifth distal tarsal is present ancestrally (Fig. 8A). This element is unknown in all archosauromorphs (Gauthier, 1984). According to Harris and Carroll (1975) and Currie (1981b), the fifth distal tarsal fuses to the fourth during postnatal ontogeny in tangasaur younginiforms. Unfortunately, the ankles are unknown in *Acerosodontosaurus*, *Youngina*, *Paliguana**, *Palaeagama**, and kuehneosaurs. *Saurosternon** does, however, retain a discrete fifth distal tarsal (Fig. 8B). The fifth distal tarsal is not a discrete element in rhynchocephalians (Fig. 8C) and squamates (Fig. 8D). It has been suggested that the fifth distal tarsal either has been lost, fused to the fourth distal tarsal, or fused to the fifth metatarsal. However, the available developmental evidence neither confirms nor denies these hypotheses (Robinson, 1975). Given the available evidence, the simplest resolution to this question is to posit that the "loss" of the fifth distal tarsal applies to saurians generally. The presence of this element in *Saurosternon** would then be explained as either an evolutionary reversal or as further evidence that *Saurosternon** is a subadult in which the suspected fusion has yet to occur. In view of the incomplete data, however, we prefer to consider *Saurosternon** to have retained the ancestral diapsid condition. This requires three separate "losses" of the fifth distal tarsal in diapsids: once in archosauromorphs, once in younginiforms, and once in lepidosaurs. Future finds in development and paleontology may ultimately allow us to determine if "loss" means the same thing in each of these groups.

32. [132] Hooked fifth metatarsal. The fifth metatarsal is not hooked in diapsids ancestrally (Fig. 8A), but the element is apomorphic in saurians ancestrally in that it is short and broad-based (e.g., Fig. 8B). In all archosauromorphs the fifth metatarsal is flattened in the plane of the pes and hooked (i.e., the element extends medially to contact the fourth distal tarsal). This is evidently a case of convergence with the condition seen in lepidosaurs, because among lepidosauromorphs,

younginiforms, *Saurosternon** (Fig. 8B), and kuehneosaurs (Evans, 1985) retain the ancestral saurian condition. This is perhaps why, with the exception of the "hooked" shape, the fifth metatarsals of archosauromorphs and lepidosaurs are otherwise so different. For example, in contrast to the condition in archosauromorphs, the fifth metatarsal in lepidosaurs has medial and lateral plantar tubercles, is inflected about its long axis, and its proximal surface is angulated in a characteristic fashion (see Robinson, 1975, for a more thorough description). *Palaeagama** and *Paliguana** are unknown in this regard.

33. [137] Secondary ossification centers form on ends of all long bones and in several muscle attachments, such as those inserting on retroarticular process, neural arches, basioccipital tubera, posterior end of ilium and several other points on pelvis, as well as in knee and elbow joints. The presence of secondary ossification centers in lepidosaurs has been recognized for many years (e.g., Albrecht, 1883; Dollo, 1884). Moreover, their developmental and histological similarity to those of mammals is also widely recognized (Haines, 1969). Yet there is much speculation and little data relating to their developmental origin and function. Aside from the secondary center associated with the cnemial epiphysis of the tibia in post-*Archaeopteryx** birds, no other diapsids possess this synapomorphy. As in the sternum, calcification within long bone epiphyses begins early in development (Haines, 1969). Subsequent replacement of the calcifications by endochondral ossification takes place in the adult (de Ricqles, 1976). According to Haines (1969), epiphyses are absent in snakes. Because all other data clearly places snakes within the lepidosaurian squamates, those snakes are considered secondarily derived in this regard. The hypothesized reversal in snakes appears to have occurred in mosasaurs as well (Russell, 1967), although epiphyses are present in closely related taxa such as *Pontosaurus lesinensis* (Kornhuber, 1873) and *Opetiosaurus bucchichi* (Kornhuber, 1901). Gross examination may not allow one to discriminate between the long bones of fully adult lepidosaurs and those of other diapsids. To accomplish this would require histological examination, which provides a ready means of distinguishing between the two developmental mechanisms by which the same ends may be achieved in diapsid long bones (Enlow, 1969; Haines, 1969). The easiest and surest means of determining the presence of epiphyses in fossil diapsids depends on finding a specimen with long bones at the stage of development in which endochondral ossification has spread from the metaphysis into the calcified epiphysis, but prior to the complete epiphysial-diaphysial coossification. A good example of this is the olecranon epiphysis that may be seen on the ulna of the sphenodontidan *Kallimodon* (Cocude-Michel, 1963). In this specimen, there is a metaphysial area, represented by a thin line, that separates the fully-formed olecranon process from the diaphysis. In diapsids that do not have epiphyses, the olecranon process on the ulna is readily recognized to be of "normal" derivation when the distal extremity of the process is unfinished, indicating the presence of the usual growth cartilage (e.g., see the olecranon on the ulna of araeoscelidans; Reisz, 1981:44, fig. 20B). Ontogenetic series of archosauromorphs (i.e., *Tanystropheus*; Wild, 1973), and younginiforms (Currie, 1981b) show that epiphyses are certainly lacking in archosauromorphs and lepidosauromorphs ancestrally. Unfortunately, pertinent lepidosauromorphs are not well enough known to be certain of the level at which this character diagnoses a monophyletic group. *Paliguana** lacks a postcranial skeleton, and *Saurosternon** and *Palaeagama** appear to be subadult specimens in which the epiphyses are not ossified. Carroll (1977) and Evans (1981) argued that the form and texture of the ends of the long bones of *Saurosternon** and *Palaeagama** indicate that epiphyses would have been present in adults of these taxa. *Icarosaurus* is represented by a subadult specimen. The form and texture of the diaphysial surfaces, together with the gaps between the long bones, again suggest that epiphyses may have been present in kuehneosaurs as well. Unfortunately, the known elements of *Kuehneosaurus* do not clarify the issue. In this taxon, the referred limb elements are from fully grown adults, so the mode of development is not determinable (S. Evans, pers. comm.). Thus, there appears to be

some reason to suspect that epiphyses are more widely distributed among lepidosauromorphs than has been believed previously. In the absence of unequivocal evidence to the contrary, however, we consider this character a lepidosaurian synapomorphy.

34. [139] Many structures that normally ossify or remain cartilaginous in diapsids tend to calcify well before attainment of maximum adult size in squamates and rhynchocephalians. Among the structures that calcify are the epiphyses, tracheal rings, hyoid apparatus, epicoracoid, suprascapula, hypoischium, sesamoids, sternum, sternal ribs, xiphisternum, inscriptional ribs, and remnants of the interorbital cartilages. This complex is treated as a single character following the suggestion of Haines (1969) that the origin of the calcifications (not ossifications) probably has a common developmental basis. However, some calcifications, such as most sesamoids, may vary in number in lepidosaurs (Rewcastle, 1980). Our observations indicate that at least some of the variation relates to differences in the temporal sequence in which the calcifications appear during ontogeny. Previous workers may have been comparing individuals that differed in stage of development. Preliminary analysis indicates that at least some calcifications may not fit this category; nevertheless, the tendency of cartilages, tendons, ligaments, and sheets of connective tissue to calcify early in postnatal development is considered a synapomorphy of lepidosaurs. This synapomorphy is usually indeterminable in fossils because calcified cartilage disintegrates in macerated specimens (see above).

35. [138] Most of skeleton composed of dense, lamellar, avascular bone of periosteal origin. As described by Enlow (1969) and de Ricqlès (1976), the bones of squamates and rhynchocephalians may be distinguished from those of other amniotes by the fact that the compact bone of periosteal origin is virtually avascular. In addition, there is very little development of cancellous trabeculae in the mid-diaphyses of the long bones. Unfortunately, our knowledge of the distribution of this character is very incomplete. Because it appears to be correlated with small size and associated patterns of growth, we suspect that this character will be found to apply to a more inclusive group within lepidosauromorphs. Nevertheless, until evidence to the contrary is available, we consider it a lepidosaur synapomorphy.

SQUAMATA

Definition: The most recent common ancestor of Iguania and Autarchoglossa, and all of its descendants (see Estes et al., 1988).

In this section, we discuss the synapomorphies of squamates, using rhynchocephalians, kuehneosaurs, *Paliguana**, *Saurosternon**, *Palaeagama**, and younginiforms as successively more remote outgroups. We recognize two principal groups of Squamata, Iguania (Cuvier, 1807) and Autarchoglossa (sensu Gauthier, 1982; includes Autarchoglossa of Camp, 1923, plus gekkotans and snakes; also equivalent to Scincogekkonomorpha of Sukhanov, 1961, 1976, plus snakes and amphisbaenians). Iguania includes those taxa referred to Iguanidae*, Agamidae* and Chamaeleontidae. Iguania, Acrodonta (Agamidae* + Chamaeleontidae), and Chamaeleontidae are readily diagnosible; there is still no positive evidence for either the monophyly or paraphyly of Iguanidae* or Agamidae*; they are therefore considered to be metataxa (see Estes, 1983; Estes et al., 1988; Etheridge and de Queiroz, 1988), and we will not concern ourselves further with iguanian subgroups. As here constituted, all other squamates (including snakes, dibamids, and amphisbaenians) are considered autarchoglossans (see Estes et al., 1988, for subdivision of Autarchoglossa). "Eolacertilia" and "Lacertilia" are paraphyletic, and they will not be used in this discussion.

Compared to extant mammals, turtles, archosaurs, and *Sphenodon*, squamates possess the following synapomorphies of the soft anatomy.

Diagnosis: 1. [169] Presence of discrete m. bursalis. Unlike other amniotes, squamates have developed a discrete m. bursalis, a division of the m. retractor bulbi present generally in tetrapods (Underwood, 1970).

2. [144] Reduced cartilaginous component of anterior braincase and interorbital septum, with large fenestrae and significant membranous component. These regions are largely cartilaginous, with concomitantly smaller membranous components and fenestra, in other amniotes (Bellairs and Kamal, 1981).

3. [135] Interrupted third branchial arch. The third branchial arch is continuous in other amniotes (Kluge, 1983).

4. [170] Femoral and preanal organs present. Femoral and/or inguinal epidermal holocrine follicular glands (terminology of Moody, pers. comm.) are unique to squamates among amniotes (Kluge, 1983).

5. [146] Pallets on ventral surface of tongue tip. Tongue pallets are absent in all amniotes except for squamates (Schwenk, 1988).

6. [159] Paired, evertible hemipenes in males. The amniote penis has been lost in lepidosaurs, and the hemipenes of squamates have long been recognized as diagnostic (e.g., Oppel, 1811).

7. [151] Lacrimal duct extends far anteriorly to become associated with duct of Jacobson's organ. The lacrimal duct is associated with the posterior end of choanal groove in *Sphenodon*, as in amniotes ancestrally (Bellairs and Boyd, 1950).

8. [147] Jacobson's organ completely separate from nasal capsule and develops a fungiform body. Jacobson's organ is typically a simple diverticulum of nasal capsule, and no other tetrapod possesses the squamate fungiform body (Parsons, 1970).

9. [148] Extensive development of sensory epithelium in Jacobson's organ. Squamates are distinctive in the degree of development of the sensory epithelium lining Jacobson's organ (Pratt, 1948).

10. [149] Rotation of Jacobson's organ and associated paraseptal cartilages. Jacobson's organ apparently rotated ninety degrees about its longitudinal axis, placing the paraseptal cartilage medially with the duct of the organ opening ventrally into the oral cavity (Malan, 1946). In *Sphenodon*, the paraseptal cartilage forms a trough-like support for the floor of Jacobson's organ, the duct of which is positioned laterally and opens into the medial wall of the choana.

11. [150] Enlarged lateral nasal gland lodged in cavum conchale. In other reptiles the lateral nasal gland is small and not enclosed in cavum conchale (Malan, 1946; Pratt, 1948).

12. [145] Loss of caruncle. The presence of both an egg tooth and caruncle in amniotes ancestrally (Hill and deBeer, 1949), indicates that squamates, which possess only the former (Edmund, 1969), have lost the latter.

13. [154] Multiple interdigitations of mm. intermandibularis and mandibulohyoideus. These muscles are non-interdigitating in amniotes ancestrally (Camp, 1923; Rieppel, 1978).

14. [156] Complete, rather than partial, separation of m. depressor mandibulae from m. episternocleidomastoideus. These muscles are at least partly confluent in amniotes generally (Rieppel, 1978).

15. [155] Facialis nerve no longer participates in innervation of m. intermandibularis. The n. facialis participates in the innervation of this muscle in amniotes ancestrally (Rieppel, 1978).

16. [157] Fibers of m. clavodeltoideus extend to ventral surface of clavicles. This muscle is typically confined to the dorsal surface of the clavicles (Peterson, 1973).

17. [158] Meniscus in knee joint a single plate pierced by cruciate ligament. The meniscus of the knee generally forms separate lateral and medial crescents on either side of cruciate ligament (Haines, 1942).

18. [143] Prominent perilymphatic sac. The perlymphatic duct does not form a prominent sack in the recessus scalae tympani in amniotes ancestrally (Baird, 1970).

19. [142] Postembryonic position of cochlear duct facing laterally. The cochlear duct faces ventrally in amniotes ancestrally and in the embryos of all squamates (Baird, 1970). The ancestral condition applies to some snakes as well, but this is considered a paedomorphic reversal.

20. [141] Loss of pars tuberalis of adenohypophysis. The pars tuberalis is present is amniotes ancestrally (Wingstrand, 1951).

21. [152] Interhyal either ligamentous or absent. The interhyal is cartilagenous in amniotes ancestrally (de Beer, 1937).

22. [153] Saccular ovaries. Solid ovaries are present in amniotes ancestrally (Porter, 1972).

Most of the abovementioned synapomorphies are not determinable in fossils. The following combination of osteological synapomorphies will, however, separate squamates from rhynchocephalians and from all other lepidosauromorphs as well.

The first two of these relate to the remarkable transformations of the septomaxilla and its associated soft tissue (Malan, 1946). There is clear evidence that these transformations are intimately related both functionally and developmentally (e.g., Bellairs and Boyd, 1950). Thus, as with the case of the tympanum and the lateral conch on the quadrate, these characters are at least partly determinable in fossils.

23. [38] Septomaxilla with posteroventral projection extending towards dorsal surface of vomer to form posterior margin of duct of Jacobson's organ, and anterior and medial margins of duct formed by notch in vomer. These osteological characters are associated with fusion of the sides of the choanal passage to separate the opening of Jacobson's organ from the functional choana in the embryo (Fuchs, 1908).

24. [37] Septomaxilla invests enormously enlarged vestibule to roof Jacobson's organ dorsally and floor nasal passage ventrally. In diapsids the septomaxilla is limited to the posteroventral edge of the fenestra exonarina ancestrally (Gauthier, 1984). According to Malan (1946), the enormous size and posterior prolongation of the vestibule carried the septomaxilla to the interior of the nasal capsule, so that the septomaxilla forms a secondary roof above Jacobson's organ.

25. [62] Premaxillae fused in embryonic developmental stages. Because the premaxillae are paired in younginiforms (Fig. 1B), kuehneosaurs (Fig. 1C), and rhynchocephalians (Fig. 1D), this condition is thought to be ancestral for lepidosaurs. This character cannot be determined in *Paliguana**, *Palaeagama**, or *Saurosternon**. In squamates, however, the premaxillae become fused to one another prior to hatching. Based on other data (Estes et al., 1988), the paired premaxillae present in most gekkotans and scincids are considered to have arisen secondarily and independently.

26. [2] Reduced nasals. In lepidosaurs ancestrally the greatest width of the nasals exceeds that of both nares (= fenestra exonarina). This condition occurs in kuehneosaurs (Fig. 1C) and in rhynchocephalians (Fig. 1F). Neither *Saurosternon** nor *Palaeagama** can be interpreted in this regard. Although the tip of the snout is missing in *Paliguana**, broad nasals are indicated by the preserved impressions of the nasal bones (Carroll, 1977). Younginiforms and *Gephyrosaurus* may be exceptions to this generalization. *Youngina* provides the best known example of the younginiform skull. As is evident from illustrations in Gow (1975), most specimens show varying degrees of postdepositional deformation. Perhaps this accounts for the nasals of *Youngina* being wider (Fig. 1B), or narrower (Gow, 1975), depending on the reconstruction. Nevertheless, the available evidence indicates that younginiforms in general seem to have elongate snouts with concomitantly elongate and narrow nasals. By comparison, araeoscelidans (Fig. 1A), archosauromorphs ancestrally (Gauthier, 1984), and most lepidosauromorphs are relatively short-snouted. Thus, we have interpreted elongate snouts as a younginiform synapomorphy (see diagnosis above). The problem of accurate reconstruction is more acute for *Gephyrosaurus* because its remains are dissociated and disarticulated. In the reconstruction of *Gephyrosaurus* (Fig. 1D) given by Evans (1980), the nasals are relatively narrow compared to those of other rhynchocephalians. This appears to be a unique

attribute of *Gephyrosaurus*, because S. Evans (pers. comm.) assures us that the reconstruction leaves no margin for error in this case. Modification of the snout in most squamates leaves them with relatively smaller and narrower nasals than occur in lepidosauromorphs generally (Fig. 1J). It appears that in squamates the facial process of the maxilla is more prominently developed, thus taking over some of the role of the nasal in roofing the snout. There are, however, several squamates in which this is not the case. Some iguanines among iguanians and polyglyphanodontine teiids among autarchoglossans have relatively broad nasals compared to those of their close relatives; both groups are composed of relatively large lizards. Another class of exceptions to the general case is provided by fossorial autarchoglossan squamates. In these groups, the snout plays an important role in entering the substrate and, like the rest of the skull, it is compact, streamlined and robustly constructed. Although fossorial squamates may have broad nasals, it seems unlikely that this results from simple retention of an ancestral state. Rather, the broad nasals, like virtually every other bone in the skull, are more likely to reflect the constraints imposed by small size and subterranean life. In spite of the cautions noted above, relatively reduced nasals that are not as broad as the distance across the nares are considered a synapomorphy of Squamata.

27. [3] Frontoparietal suture more or less transverse in dorsal view and broader than nasofrontal suture. In lepidosaurs ancestrally the widths of the nasofrontal and frontoparietal sutures are subequal. In addition, the frontoparietal suture is roughly W-shaped, or shaped like an inverted U. The ancestral condition occurs in younginiforms (Fig. 1B), *Paliguana** (Carroll, 1975a), kuehneosaurs (Fig. 1C), and rhynchocephalians (Fig. 1E). This region is not adequately preserved in *Palaeagama**, and the skull is absent in *Saurosternon**. Squamates have long been recognized as unique among reptiles in the shape and width of the frontoparietal suture. Most authors, however, apparently have observed this suture only in articulated skulls, because disarticulated skulls reveal that the frontoparietal suture is seldom straight, particularly ventrally. Nevertheless, the shape of this suture in dorsal view is striking, and this observation has engendered much speculation about its possible role in intracranial mobility. The available experimental evidence speaks against many of the previous interpretations (Smith, 1980), however, and points to the difficulties inherent in determining function from structure alone. Some squamates, such as gymnophthalmids, lacertids, some cordylids, and most mosasaurs, lack straight frontoparietal sutures, although there are exceptions in each group. The most conspicuous exceptions to the general case, however, are the amphisbaenians and ophidians. Although the frontoparietal sutures of ophidians and amphisbaenians are not straight, neither are they ancestral. In the former group, the frontoparietal suture is more nearly U-shaped when viewed from behind (see Estes et al., 1970), and in the latter group, the bones are deeply interdigitated (Gans, 1978). Neither of these conditions can be said to be ancestral (e.g., *Gephyrosaurus*, Fig. 1D; *Kuehneosaurus*, Fig. 1C). More importantly, the evidence presented by Estes et al., 1988) indicates that snakes and amphisbaenians are autarchoglossans, most of which have straight frontoparietal sutures. Because iguanians (Fig. 1J), the sister taxon of autarchoglossans (Fig. 1K), also have straight frontoparietal sutures, this condition is considered synapomorphic for squamates.

28. [63] Parietals fused in embryo. With the exceptions of *Gephyrosaurus* (Fig. 1D) and *Planocephalosaurus* (Fig. 1F), no other lepidosauromorphs save for squamates have fused parietals. Evans (1980) reported finding fused parietals in a specimen of *Sphenodon*, but we are unable to confirm this observation either in the five adults we examined, or in any of those figured or discussed in the literature. *Clevosaurus* (Fig. 1E), the sister taxon of *Planocephalosaurus*, has paired parietals, as do all other extinct sphenodontidans (e.g., Fig. 1H). Paired parietals are also present in all possible outgroups within lepidosauromorphs. Thus, the fused parietals of *Gephyrosaurus* on the one hand, and *Planocephalosaurus* on the other, are considered to have been separately derived. There is, of course, no information about when parietal fusion takes place during ontogeny in

these taxa. The parietal bones may be fused or not in gekkotans and xantusiids. This fact, together with the fused parietals in all other autarchoglossans and iguanians, indicates that fused parietals are a synapomorphy of squamates (e.g., Figs. 1J, K). Although parietal fusion may take place at different times in the ontogeny of some gekkotans and xantusiids, in all other squamates it occurs in the embryo.

29. [14] Supratemporal displaced to a deep position, wrapping around ventral surface, and prominently developed on anterior face, of supratemporal process of parietal. As pointed out by Robinson (1967), in diapsids ancestrally the supratemporal lies in a superficial position posterolateral to the supratemporal process of the parietal (Fig. 1A). Supratemporals are present in younginiforms (Fig. 1B) and *Paliguana** (Carroll, 1977), but their presence cannot be determined in *Palaeagama** and *Saurosternon**. Supratemporals are said to be absent in kuehneosaurs, *Gephyrosaurus*, and all sphenodontidans save for *Clevosaurus*. They are absent in *Sphenodon* and their absence in sapheosaurs and *Homoeosaurus* is probable in view of the large sample of articulated skulls described in the literature and seen by us. Likewise, they are certainly present in the articulated skulls referred to *Clevosaurus*. Evans (1980) and Fraser (1982) reported that supratemporals are absent in kuehneosaurs, *Gephyrosaurus* (the sister taxon of sphenodontidans), and *Planocephalosaurus* (the sister taxon of *Clevosaurus*). S. Evans (pers. comm.) states that in the very well preserved material of both these genera, no facet for a supratemporal is visible and that a single *Gephyrosaurus* specimen of an associated parietal and squamosal lacks an intervening supratemporal. Supratemporals are poor candidates for preservation because they are small bones in lepidosauromorphs and because they are only loosely attached to the remainder of the skull. The history of ideas concerning the presence or absence in *Youngina* of these and other reduced bones (such as tabulars and postparietals) demonstrates that even in the case of articulated skulls these elements may not be preserved. Whether or not these bones are in fact lost in the above groups, it is clear that the size and position of the supratemporal is a squamate synapomorphy. The chief variations seen among squamates are the pronounced development of this element onto the braincase in mosasaurs (Russell, 1967), its posterior displacement on the supratemporal process of the parietal in iguanine iguanians (Etheridge and de Queiroz, 1988), and its elongation and singular role in quadrate suspension in most snakes.

30. [15] Loss of ventral ramus of squamosal. With the exception of *Clevosaurus* (Fig. 3E), kuehneosaurs (Fig. 3B), and squamates (Figs. 3G,H), in all other lepidosauromorphs the squamosal has a prominent descending process that extends to the quadratojugal ventrally (Figs. 1A,F). This character is not preserved in *Palaeagama** or *Saurosternon**. There is a descending squamosal process in *Paliguana**, but poor preservation precludes a conclusion about its ventral extent (see the conflicting reconstructions of Broom, 1903, 1925, and Carroll, 1977). The ventral process of the squamosal is reduced in *Clevosaurus*, but remains well developed in all other rhynchocephalians. The condition in *Clevosaurus* is thus considered convergent, rather than a transitional character bridging the gap between the ancestral condition and that seen in either kuehneosaurs or squamates. Since Robinson (1962), it has been generally agreed that the absence of the descending process of the squamosal in kuehneosaurs is a synapomorphy uniting them with squamates. As argued above, however, rhynchocephalians, not kuehneosaurs, are closest to squamates among lepidosauromorphs. Therefore, the loss of the ventral ramus of the squamosal is considered to have occurred independently in squamates and kuehneosaurs.

31. [16] Quadrate notched or fenestrate above for reception of posteroventral peg-like process of squamosal. As pointed out by Robinson (1967), in diapsids ancestrally the squamosal caps the quadrate dorsally. This condition is also present in younginiforms (Fig. 1A), *Paliguana** (Carroll, 1977), kuehneosaurs (Fig. 1B), and rhynchocephalians (Fig. 1C). This region is not preserved in *Palaeagama** and *Saurosternon**. The squamosal-quadrate articulation is uniquely modified in squa-

mates. Rather than capping the quadrate, the quadrate process of the squamosal is reduced to a peg that abuts the head of the quadrate, usually fitting into a fossa, fenestra, or notch (Robinson, 1967).

32. [12; 21] Quadratojugal and quadrate foramen absent. A quadrate foramen, bound by the quadratojugal laterally and the quadrate medially, is present in lepidosauromorphs ancestrally. This condition occurs in araeoscelidans (Reisz, 1981), archosauromorphs (Gow, 1975), and youngini-forms (Gow, 1975). This character cannot be determined in either *Palaeagama** or *Saurosternon**. *Paliguana** is problematic in this regard. Broom (1903; 1925) concluded that both the quadratojugal and quadrate foramen are present. Carroll (1977), however, considered the quadratojugal to be absent and concluded that the Broom's "quadrate foramen" is an artifact of preparation. R. Reisz (pers. comm. 1987) informs us that the quadrate foramen is in fact present. Kuehneosaurs have lost both the quadratojugal and quadrate foramen, and Robinson (1962) considered this a synapomorphic resemblance to squamates. It is not possible to determine at present if these characters were lost in the common ancestor of the kuehneosaur-lepidosaur group, and reevolved in the rhynchocephalians, or if they were lost independently in kuehneosaurs on the one hand, and in squamates on the other. Until more evidence is available, we posit the latter to have been the case. The anterior process of the quadratojugal forms the posterior part of the lower temporal arch, the loss of which is discussed below.

33. [11] Posterior process of jugal much reduced or absent. As noted in the discussion of rhynchocephalian relationships above, ancestral lepidosauromorphs have a jugal with a prominent process extending posteriorly to contact the quadratojugal below the midline of the lower temporal fenestra. This character is also found in araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), younginiforms (Fig. 1A), and in a modified form in rhynchocephalians (Fig. 1F). This character cannot be determined in *Saurosternon** (Carroll, 1975a). Carroll (1975a) considered the posterior process of the jugal to be absent in *Paliguana** and *Palaeagama**, but Broom (1925) considered it to be present. Because of this discrepancy, we consider this character to be indeterminable in both these taxa. Like the preceding character, this one cannot be optimized by minimizing evolutionary events, because a posterior process of the jugal is absent in kuehneosaurs (Fig. 1B), present in rhynchocephalians, and absent in squamates (Fig. 1H). In keeping with our interpretation of the previous character, we thus consider the posterior process of the jugal to have been lost separately in kuehneosaurs and in squamates, rather than in their common ancestor. A parsimonious resolution of this transformation sequence requires finding taxa that are closer to lepidosaurs than are the kuehneosaurs.

In araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), and lepidosauromorphs ancestrally (Fig. 3A), the posterior process of the jugal met the anterior process of the quadratojugal to form a lower temporal bar. The bar is retained in younginiforms, but as noted above, this character cannot be determined unequivocally in *Palaeagama**, *Paliguana**, or *Saurosternon**. Among the remaining lepidosauromorphs, however, only members of the sphenodont-sapheosaur-*Homoeosaurus* clade have a complete temporal bar; it is absent in kuehneosaurs and squamates and is interrupted posteriorly in clevosaurs and *Gephyrosaurus*.

Acceptance of our proposed hypothesis of relationships necessitates reinterpretation of the evolution of the lower temporal bar in lepidosauromorphs. The absence of this feature has been used to place kuehneosaurs (Robinson, 1967), "paliguanids" (Carroll, 1975a, 1977), and *Gephyrosaurus* (Evans, 1980) closer to squamates than to sphenodontidans. If rhynchocephalians, many of which possess a complete lower temporal bar, are the sister group of squamates, then the bar has either (1) been lost several times convergently within lepidosauromorphs (as suggested by e.g., Evans, 1980) or (2) been lost only once in this group but reevolved within sphenodontidans. We believe that the second hypothesis may be more reasonable. If the lower temporal bar were interrupted only once, only a single reversal is required in the common ancestor of sphenodonts, sapheosaurs, and *Homoeosaurus*. Furthermore, the relationships within Lepidosauria are congruent with an hypothetical transformation series in which a complete lower temporal bar might have reevolved. Squamates would retain the ancestral lepidosaurian condition (based on outgroup comparison with kuehneosaurs) in which the lower temporal bar is absent; *Gephyrosaurus* and clevosaurs, with an enlarged posterior process of the jugal but an incomplete lower temporal bar, would represent intermediate stages in the transformation series. Finally, sphenodonts, sapheosaurs, and *Homoeosaurus* would exhibit the culmination of the transformation series in the reevolution of a complete lower temporal bar.

34. [22] Loss of vomerine teeth. Numerous small teeth are present on the vomers of younginiforms (Fig. 2A) and rhynchocephalians ancestrally (Fig. 2C). This character is not preserved in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a), or in *Kuehneosaurus* (Robinson, 1962). However, what can be seen of the palate in *Icarosaurus* (Colbert, 1970) suggests that the full complement of palatal teeth is present in kuehneosaurs. The presence of vomerine teeth in rhynchocephalians provides further corroboration for the view that vomerine teeth were present in lepidosaurs ancestrally. Aside from the anguine *Pseudopus* and the glyptosaurine sister taxa *Arpadosaurus* and *Melanosaurus* among the anguids, no other squamates have vomerine teeth. All anguine relatives of *Pseudopus* and all glyptosaurine relatives of *Melanosaurus* and *Arpadosaurus* are like other anguids in lacking vomerine teeth. Accordingly, this character is considered apomorphic within both anguines and glyptosaurines (Gauthier, 1982).

35. [26] Pterygoids separated from one another and from vomers by apposition of palatines medially. In lepidosauromorphs ancestrally the pterygoids meet anteriorly and articulate with the vomers, thus separating the palatines on the midline. This condition is found in araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), and younginiforms (Fig. 2A), but is not preserved in *Paliguana**, *Palaeagama** or *Saurosternon** (Carroll, 1975a). What is known of the palate in kuehneosaurs indicates that they retained a pterygoid-vomer contact (Fig. 2B), yet their state of preservation does not allow a definite conclusion on this point. Retention of a pterygoid-vomer articulation in rhynchocephalians indictes that this contact was present in lepidosaurs ancestrally. Squamates have lost the pterygoid-vomer contact by interposition of the palatines on the midline. There are a few exceptions to this generalization. The pterygoids come near to or contact the vomers in polyglyphanodontine teiids (= Adamisauridae, Polyglyphanodontidae and Macrocephalosauridae of Sulimski, 1975; Estes, 1983). In addition, this character may be found in *Shinisaurus* (Xenosauridae), and in occasional specimens of *Teius* (Teiidae) and *Uromastyx* (Agamidae*) (Estes, 1983; pers. obs.). Our knowledge of the position of these taxa among other squamates indicates that these are cases of independent character reversal.

36. [39] Palatine reduced posteromedially, and pterygoid broadly exposed in suborbital fenestra. In lepidosauromorphs ancestrally the palatine has an extensive posteromedial component that closely approaches or contacts the ectopterygoid to exclude, or nearly exclude, the pterygoid from the suborbital fenestra. This condition occurs in araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), and younginiforms (Fig. 2A), but cannot be determined in *Paliguana**, *Palaeagama** or *Saurosternon**. The shape of the palatine is plesiomorphic in kuehneosaurs, but its relation with the ectopterygoid is unknown (Fig. 2B). Rhynchocephalians are plesiomorphic (Figs. 2C-F), but squamates are apomorphic in that the palatine is usually broadly separated from the ectopterygoid medially, and the pterygoid is consequently broadly exposed in the suborbital fenestra (Figs. 2G,H). Some squamates, such as some large iguanine iguanians and several autarchoglossans in which bones about the fenestra are modified (e.g., varanoids), appear to have reversed this character. O. Rieppel (pers. comm.) notes that reversals may occur in some small squamates, particularly fossorial forms with reduced eyes and concomitantly reduced suborbital fenestrae.

37. [60] Choanal fossa on ventral surface of palatine. The anterior margin of the palatine is

emarginate for the passage of the internal choana in lepidosauromorphs ancestrally. This condition occurs in younginiforms (Fig. 2A), kuehneosaurs (Fig. 2B), and rhynchocephalians (Fig. 2C). The palate is not preserved in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a). Squamates are further derived in having a relatively prominent fold in the body of the palatine that forms a fossa overlying the internal nares (Fig. 2H).

38. [20] Reduction of quadrate ramus of pterygoid and pterygoid ramus of quadrate, yielding a loose pterygoid-quadrate attachment formed by fibrous connective tissue. The quadrate and pterygoid overlap one another to form a firm osseous union in lepidosauromorphs ancestrally. This condition is present in younginiforms (Fig. 2B), *Paliguana** (Carroll, 1975a), kuehneosaurs (Fig. 2B), and rhynchocephalians (Fig. 2B), but cannot be determined in *Palaeagama** and *Saurosternon** (Carroll, 1975a). As noted above, rhynchocephalians are derived in having a deeply overlapping pterygoid-quadrate articulation (Fig. 2C). Squamates differ from all other lepidosauromorphs in that the osseous pterygoid-quadrate attachment is replaced by fibrous connective tissue (Robinson, 1967). Although this joint is still formed primarily by fibrous connective tissue, a secondarily developed pterygoid process is present on the quadrate of lacertoids and *Heloderma* (Estes et al., 1988).

39. [34] Paroccipital process expanded distally and takes part in support of quadrate dorsally. The paroccipital process contacts the quadrate in ancestral lepidosaurs, the contact being present in kuehneosaurs, rhynchocephalians, and squamates (see 3.3.5). However, unlike the condition seen in other lepidosaurs, in squamates the paroccipital is expanded distally to play a larger role in supporting the quadrate (Romer, 1956).

40. [35] Stapes very slender. As argued above, a slender stapes is present in lepidosaurs ancestrally. Compared to that of *Sphenodon*, however, the stapes of squamates is even more slender (Romer, 1956). As noted above, stapes are known only in younginiforms and kuehneosaurs among extinct lepidosauromorphs. Many squamates in which the tympanum has been covered, reduced, or lost have enlarged the stapes secondarily. If *Sphenodon* has similarly modified the tympanic region (see p. 30) then it is possible that this synapomorphy applies to Lepidosauria.

41. [28] Columelliform epipterygoid with narrow base that does not contact quadrate. In lepidosauromorphs ancestrally the epipterygoid is broad-based and extends posteriorly to contact the pterygoid process of the quadrate (Romer, 1956). This condition is found in younginiforms (Gow, 1975) and rhynchocephalians (Evans, 1980) but is not preserved in *Paliguana**, *Palaeagama**, *Saurosternon**, and kuehneosaurs (Carroll, 1975; Evans, 1980). Squamates differ from other lepidosauromorphs in that the quadrate-epipterygoid contact has been lost, and the epipterygoid is columelliform. Broom (1914:1076) studied the development of the pterygo-quadrate bar in lepidosaurs, and found that " [in squamates] the lower end of the quadrate is fixed to the lower end of the epipterygoid by a small bar of cartilage almost exactly as in *Sphenodon*."

42. [32] Subdivision of embryonic metotic fissure to form recessus scalae tympani anteriorly and jugular foramen posteriorly; lateral aperture of recessus scalae tympani constitutes an analog of mammalian "fenestra rotunda". In amniotes and lepidosauromorphs ancestrally, there is no subdivision of the fissura metotica and consequently no "fenestra rotunda." The absence of a "fenestra rotunda" is, however, not the same as the absence of a subdivided metotic fissure, because the "fenestra rotunda" may be absent even though the metotic fissure is subdivided in a few squamates (O. Rieppel, pers. comm.). The ancestral condition occurs in araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), younginiforms (Gow, 1975), kuehneosaurs (Robinson, 1962; 1967), and rhynchocephalians (Romer, 1956). This character cannot be determined in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a). Only squamates among diapsids possess this form of "fenestra rotunda," in which a hypertrophied portion of the ampullary region of the otic capsule contacts the basal plate in late embryos, thus subdividing the anterior end of the metotic

fissure (Kamal, 1971; who also notes that the process of subdivision may differ slightly in some snakes). Greer (1984) has recently suggested that because the "fenestra rotunda" is absent in dibamids, they might be the sister taxon of all other squamates. However, serially-sectioned *Dibamus* skulls indicate that dibamids have a subdivided metotic fissure (O. Rieppel, pers. comm.). In any case, dibamids are here considered autarchoglossan squamates (Estes et al., 1988). Because a "fenestra rotunda" of this type is present in all other autarchoglossans, as it is in iguanians, modifications of this region in dibamids must be considered secondary.

43. [30] Vidian canal fully enclosed posterolaterally. According to de Beer (1937) and Evans (1980), the carotid artery and facial nerve of diapsids lie in an open channel along the lateral surface of the basisphenoid or parabasisphenoid before they enter the bone. Completion of the lateral wall of this channel by unossified connective tissue represents the ancestral condition. This condition is present in younginiforms (Gow, 1975), kuehneosaurs (Robinson, 1962), and rhynchocephalians (Save-Soderbergh, 1947; Evans, 1980), but is not determinable in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a). Squamates differ from other lepidosauromorphs in that the lateral wall of the channel ossifies late in embryonic development to form a fully enclosed Vidian canal (Save-Soderbergh, 1947). Rieppel (1979) reported that the highly modified braincase of scolecophidian snakes shows some variation in this regard. Snakes lacking a fully enclosed Vidian canal are here considered to have acquired this character secondarily.

44. [64] Exoccipital fused to opisthotic prior to hatching. In lepidosauromorphs ancestrally the exoccipital fuses to the opisthotic relatively late in development, usually well after sexual maturity. This character relates to the timing of the fusion event in development and is not easily determined in fossils. Without additional data, the presence of a fused exoccipital-opisthotic in an isolated skull shows only that the event has taken place, but not when it occurred. In this instance, however, the converse case may be informative. For example, if a skull is found in which these bones remain separate, then this taxon is plesiomorphic compared with squamates. Thus, younginiforms (Gow, 1975), *Paliguana** (Carroll, 1975a), kuehneosaurs (Evans, 1980), and rhynchocephalians (pers. obs.) are plesiomorphic, because at least some postembryonic specimens referred to these taxa have separate exoccipitals. This character is indeterminable in *Palaeagama** and *Saurosternon** (Carroll, 1975a). In some squamates that we believe for other reasons to be paedomorphic (e.g., *Klauberina* and *Dibamus*), the exoccipital may remain suturally distinct in newly hatched individuals. We have also observed sutural separation of these bones in some late embryos of the skink *Tiliqua*, and O. Rieppel (pers. comm.) has seen it in the lacertid *Podarcis*. *Dibamus* may retain a separate exoccipital until very late in post-hatching development (Greer, 1985). However, because exoccipital-opisthotic fusion takes place in late embryos (rarely in newly hatched individuals) in all other autarchoglossans, and in late embryos in all iguanians, *Dibamus* is considered paedomorphic in this character.

45. [70] Angular reduced, not reaching mandibular condyle. As noted above, the angular is a prominent bone in the mandible of lepidosauromorphs ancestrally. The element extends posteriorly to the level of the mandibular condyle in younginiforms (Fig. 3A) and rhynchocephalians (Fig. 3I). Its posterior extent is indeterminable in *Paliguana**, *Palaeagama**, *Saurosternon**, and kuehneosaurs (Carroll, 1975a; Robinson, 1962). Except for some iguanine iguanians and some teiids, the angular is much reduced in squamates, and it never reaches below the mandibular condyle (Fig. 3K).

46. [69] Coronoid eminence prominent and formed only by uniquely modified coronoid bone. The coronoid eminence is relatively feebly developed in lepidosauromorphs ancestrally (Evans, 1980). Sphenodontidans are distinguished from other rhynchocephalians (*Gephyrosaurus*) by pronounced development of the coronoid eminence (compare Figs. 3I, J). In sphenodontidans, however, the ancestral relations of the elements are maintained; the coronoid eminence is thus

formed by the surangular laterally and the coronoid medially, although the latter is enlarged and projects slightly above the former bone. The ancestral condition, with a low coronoid eminence and a small, subtriangular, medially-placed coronoid bone, is present in araeoscelidans (Reisz, 1981), archosauromorphs (Gauthier, 1984), younginiforms (Gow, 1975), and rhynchocephalians ancestrally (Fig. 3L). This character is indeterminable in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a). Kuehneosaurs are problematic, for although they have a feebly developed coronoid eminence on the mandible, the coronoid bone itself is not present. Since the coronoid bone is small, and it is attached superficially to the mandible in non-squamate lepidosauromorphs, we consider it more likely that the element was not preserved, rather than interpreting the coronoid to have been lost phylogenetically. Squamates are unique in having a very prominent coronoid eminence formed by the coronoid bone alone. The coronoid bone is uniquely modified in that it sits on top of the mandible, often extending laterally to overlap the dentary (Fig. 3K). Further, the coronoid has a prominent posteromedial process that extends down the prearticular to form the anteromedial margin of the mandibular fossa (Fig. 3N). The coronoid has been modified in some squamate groups. In mosasaurs the prominent posteromedial process of the coronoid mentioned above has been lost. Most snakes have greatly reduced or lost the coronoid bone, although *Cylindrophis* (O. Rieppel, pers. comm.), various booids, and to a lesser extent scolecophidians, may retain the element in a less modified form (McDowell and Bogert, 1954). The coronoid sits on top as well as on the medial side of the mandible in snakes and mosasaurs ancestrally, but has no lateral development onto the dentary. Of course, in order to develop the intramandibular mobility characteristic of these groups, the dentary-coronoid overlap would have to be greatly reduced or absent. In several other squamate groups in which the dentary extends far posteriorly, the lateral process of the coronoid may be reduced (e.g., agamids*) or overlapped by the dentary (e.g., xantusiids). Amphisbaenians are like fossorial squamates in general in that the dentary characteristically overrides the coronoid, and some members of this group resemble alethinophidian snakes in the contribution of the surangular to the coronoid eminence. Thus, at least some amphisbaenians and snakes possess mandibles that are anomalously plesiomorphic in this regard.

47. [86] Anterior cervical and posterior trunk ribs single-headed. Ribs from the midtrunk region are single-headed in diapsids ancestrally, with two-headed ribs confined to the anterior cervicals and the most posterior trunk vertebrae (Reisz, 1981). With development of prominent transverse processes in the trunk vertebrae within archosauromorphs, the two-headed structure of the ribs becomes increasingly prominent (Gauthier, 1984). Lepidosauromorphs, however, retain feebly-developed transverse processes and most of their ribs are single-headed. Two-headed cervical ribs are retained by younginiforms (Gow, 1975), kuehneosaurs (which may have a third process; Robinson, 1962), and rhynchocephalians (Evans, 1980). These elements are unknown in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a). As pointed out by Hoffstetter and Gasc (1969), all ribs are single-headed in squamates.

48. [79] Cervical intercentra form prominent hypapophyses. The cervical intercentra may be slightly enlarged compared to others in the column (e.g., *Sphenodon*), but they never form the prominent, blade-like, hypapophyses seen in squamates alone among amniotes (Hoffstetter and Gasc, 1969). The ancestral condition is retained in younginiforms (Gow, 1975), rhynchocephalians (pers. obs.), and (apparently) kuehneosaurs (Evans, 1980). The character is indeterminable in *Paliguana**, *Palaeagama**, and *Saurosternon** (Carroll, 1975a). *Heloderma* appears exceptional among squamates in having reduced these elements secondarily.

49. [171] One vertebra added to cervical series by loss of contact between the rib of the eighth vertebra and the sternum. The more posterior cervicals are not morphologically distinguishable from the anterior trunk vertebrae in many diapsids. Hoffstetter and Gasc (1969) reviewed the various criteria that have been used to determine the number of cervical vertebrae. We agree with their

view that the criterion of sternal rib attachments is the only one that gives uniform results in an objective fashion. Unfortunately, this criterion is useless for the overwhelming majority of fossil specimens. Unless preserved in exquisite detail, such as in some of the Solnhofen *Homoeosaurus* and sapheosaurs (Cocude-Michel, 1963), the connections between the calcified ventral ribs and sternum can rarely be observed in a fossil. By this criterion, living squamates (except chamaeleons) have at least eight cervicals. Because *Sphenodon* also has eight cervicals, we consider this number to have been achieved independently in these two taxa, following the usual interpretation that seven cervicals are present in lepidosaurs and rhynchocephalians ancestrally (Hoffstetter and Gasc, 1969). We must emphasize, however, that in the case of fossils this count can be reliably determined only in some *Homoeosaurus* and sapheosaurs.

50. [87] Sacral and caudal ribs fuse to their respective centra in embryo. The sacral and caudal ribs fuse to their respective centra prior to the attainment of maximum adult size in ancestral saurians (Gauthier, 1984). According to most authors, these elements remain separate in juvenile forms, usually fusing at about the time when the scapulocoracoid coossifies (Currie, 1981b). This is the condition in younginiforms (Currie, 1981b), *Palaeagama** (Carroll, 1975a), and rhynchocephalians (Howes and Swinnerton, 1901). This character is indeterminable in *Paliguana** (Carroll, 1975a). The fusions have already taken place in the available specimens of kuehneosaurs (Colbert, 1970) and *Saurosternon** (Carroll, 1975a), so there is as yet no way to determine when in development they occurred. Squamates are distinguished from other lepidosauromorphs by the fusion of the sacral and caudal ribs to their respective centra prior to hatching.

51. [77] Fusion of neural arches to their respective centra in embryo. The neural arches remain separate from their respective centra until late in development in lepidosauromorphs ancestrally. The ancestral condition has the same distribution among lepidosauromorphs as does the preceding character. Thus, in a specimen in which the scapula and coracoid are separate, the neural arches, and sacral and caudal ribs, are separate from their respective centra. By maximum adult size, however, these suturally united elements fuse to one another. Indeed, the fusions may be correlated events in the development of lepidosauromorphs. In crocodilians, however, caudal rib fusion precedes that between neural arches and centra in the trunk region. Thus, until more is known, we will treat them as different characters. Winchester and Bellairs (1977) have shown that the neuro-central suture is covered by periosteal bone until very late in prejuvenile development in squamates. Xantusiids (e.g., *Lepidophyma*, *Klauberina*) and gekkotans (e.g., *Coleonyx brevis*) are to our knowledge the only squamates in which hatchlings retain a neuro-central suture. Both groups are distinctive among squamates in the degree of paedomorphosis exhibited in their vertebral development.

52. [83] Trunk vertebrae without discrete intercentra. Intercentra are present throughout the vertebral column in lepidosauromorphs ancestrally. Intercentra are present in younginiforms (Gow, 1975), *Palaeagama** and *Saurosternon** (Carroll, 1975a), and in rhynchocephalians aside from *Homoeosaurus* (Evans, 1981). This character is indeterminable in *Paliguana** (Carroll, 1975a). Kuehneosaurs evidently lack discrete intercentra (Evans, 1981). Although intercentra persist in the cervical and caudal regions in all squamates, they are commonly absent in the trunk region (Hoffstetter and Gasc, 1969). Among squamates, discrete intercentra in the trunk region are known only in xantusiids and gekkotans. Contrary to most accounts, we have been unable to find persistent intercentra in the trunk region of xantusiids, with the exception of some juvenile *Xantusia* and *Lepidophyma*. Likewise, trunk intercentra may be present or absent among gekkotans (Kluge, 1983). Because no other autarchoglossans have trunk intercentra, and they are lacking in iguanians, their appearance in some gekkotans and xantusiids is considered another example of paedomorphosis in these groups.

53. [84] Procoelous, non-notochordal vertebrae, with centrum forming conical frustrum. This

character, like the preceding, has been the subject of considerable debate (see review in Hoffstetter and Gasc, 1969; Kluge, 1987). Spool-shaped, notochordal, amphicoelous vertebrae are present in lepidosauromorphs ancestrally. This character is not preserved in *Paliguana** (Carroll, 1975a). The ancestral condition occurs in younginiforms (Currie, 1981b), *Palaeagama**, and *Saurosternon** (Carroll, 1975a), and in rhynchocephalians (Evans, 1981). In kuehneosaurs, the vertebrae are platycoelous and non-notochordal (Robinson, 1962). Some gekkotans appear to possess the ancestral condition and others do not (Moffat, 1973). Some juvenile xantusiids, like some gekkotans, have an "intermediate" condition. In these taxa, spool-shaped centra are retained, but the notochord is obliterated, and there is a poorly-developed procoelous condyle. During posthatching ontogeny, xantusiid vertebral centra transform from being spool-shaped with poorly developed condyles to a conical shape with more prominent condyles (pers. obs.). Once again, except for some xantusiids and gekkotans, all other autarchoglossans are like iguanians in possessing the synapomorphic vertebral form. Accordingly, procoelous vertebrae with conical centra and no notochordal remnants are considered synapomorphic for squamates. Thus, xantusiids and gekkotans display varying degrees of paedomorphosis in their vertebral development (Underwood, 1954; Kluge, 1983).

54. [92] Anterior margin of scapulocoracoid with two emarginations, one in coracoid and one between scapula and coracoid. The scapula and coracoid are not emarginate in araeoscelidans (Fig. 5A), nor in lepidosauromorphs ancestrally (Fig. 5B). The ancestral condition is found in younginiforms (Gow, 1975), kuehneosaurs (Colbert, 1970), and rhynchocephalians (Fig. 5B), and the character is not determinable in *Paliguana** and *Palaeagama** (Carroll, 1975a). Contrary to Carroll (1975a; 1977), the scapulocoracoid of *Saurosternon** is not emarginate anteriorly. In squamates scapulocoracoid emarginations deeply encroach into the body of the element (Fig. 5C). Carroll's specimen drawings (1975a) clearly show that the anterior margin of the scapulocoracoid is straight in *Saurosternon**. In addition, the element Carroll (1977) identifies as a "procoracoid bar," is probably a cervical rib (Estes, 1983). We follow Evans (1981) in considering the scapulocoracoid of *Saurosternon** to be plesiomorphic. With few exceptions, all squamates with unreduced forelimbs have anteriorly emarginate scapulocoracoids (Lecuru, 1968a); the number varies from one (e.g., *Heloderma*) to four (e.g., *Iguana*). Accepting the relationships argued in Estes et al. (1988) suggests that the scapulocoracoid and anterior coracoid emarginations are ancestral for squamates. Thus, more or fewer fenestrae are considered apomorphic within squamates.

55. [95] Clavicle contacts suprascapula. In lepidosauromorphs ancestrally the dorsal end of the clavicle articulates with the scapula. This condition is found in younginiforms (Gow, 1975) and rhynchocephalians (Fig. 5B), but is not determinable in *Paliguana**, *Palaeagama**, *Saurosternon**, and kuehneosaurs (Evans, 1981). With the exception of most agamids*, a few iguanids* (*Polychrus*, *Corythophanes*), and the gekkotan *Uroplatus*, all other squamates with unreduced forelimbs are unique among diapsids in that the clavicle extends dorsally to contact the suprascapular cartilage (Lecuru, 1968b; Fig. 5C).

56. [97] Elongate, gracile limbs. In comparison to rhynchocephalians of equal snout-vent length, squamates have relatively more elongate and lightly constructed limbs. Some squamates, such as *Heloderma* or *Iguana*, may have equally robust limbs, but such animals are invariably much larger than other, similarly proportioned lepidosauromorphs. In addition, the carpals and tarsals are relatively smaller, and the metacarpals and metatarsals are more broadly overlapping and tightly packed proximally. The tibia and fibula approach one another more closely at their respective articulations with the proximal tarsals. The hand is relatively smaller and the radius and ulna are more closely set at their proximal articulations with the humerus and their distal articulations with the proximal carpals. The entire humerus is gracile compared to that of other lepidosauromorphs. Owing to preservation, one can seldom see all these characters in extinct lepidosauromorphs. So far as they are preserved, however, their limbs conform to the proportions and rela-

tions found in Recent *Sphenodon* (pers. obs.). Thus, one usually finds the general proportions of extinct lepidosauromorphs described as being *Sphenodon*-like (e.g., Carroll, 1977). A conspicuous exception is the more squamate-like limb proportions of some species of *Homoeosaurus* (see Rhynchocephalia above) and the kuehneosaurs. The synapomorphies listed above derive from comparison of *Sphenodon* and squamates. So many differences exist that it seems likely that future finds of more completely preserved lepidosauromorphs will allow further hierarchical division of these data.

57. [98] Loss of entepicondylar foramen in humerus. An entepicondylar foramen is present in diapsids ancestrally (Reisz, 1981). Among lepidosauromorphs, only kuehneosaurs and squamates lack this foramen. The presence of an entepicondylar foramen in rhynchocephalians (Evans, 1981) means that this character cannot be evaluated unambiguously. The foramen could have been lost in the kuehneosaur-lepidosaur ancestor, and reevolved in rhynchocephalians. Alternatively, the entepicondylar foramen could have been lost independently in kuehneosaurs on the one hand and squamates on the other. In either case, two evolutionary steps are required, and the decision is thus equivocal. Until more is known, we will consider kuehneosaurs and squamates to have lost this foramen independently.

58. [100] Squamate ulna-ulnare joint. An ulna with a convex distal extremity and a ball-in-socket ulna-ulnare joint are present in diapsids ancestrally (Reisz, 1981). This condition is found in younginiforms (Currie, 1981b) and rhynchocephalians (Fig. 9A). This character cannot be determined in most extinct lepidosauromorphs, either because the region is not preserved (i.e., *Paliguana**) or the specimens are apparently not adults (i.e., *Saurosternon**, *Palaeagama**, *Icarosaurus*). Squamates are unique among diapsids in possessing an enlarged distal epiphysis that is nearly hemispherical in profile and fits into a concomitantly enlarged depression in the ulnare (Fig. 9B).

59. [99] Specialized radius-radiale joint. The distal epiphysis on the radius forms a transversely oriented concavity that articulates with a convex, roller-like surface on the radiale in lepidosauromorphs ancestrally. This condition occurs in younginiforms (Currie, 1981b) and rhynchocephali-

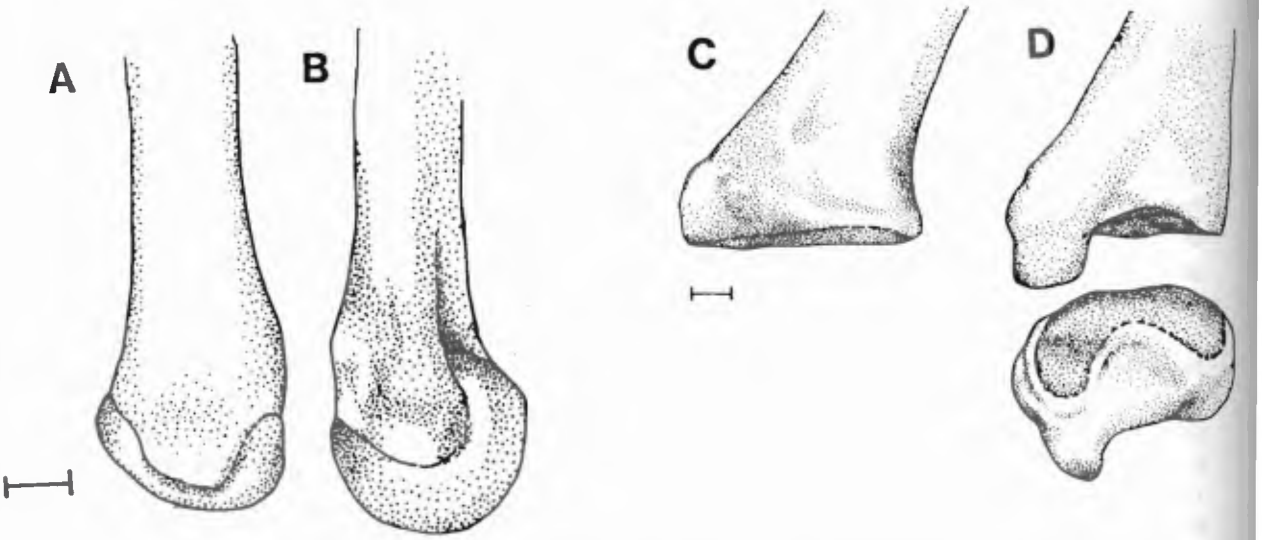

FIGURE 9. Posterior view of distal end of right ulna (A and B), radius (C, D above), and radiale (D below). A, C, *Sphenodon punctatus* (sphenodont); B, *Tupinambis teguixin* (autarchoglossan); D, *Amblyrhynchus cristatus* (iguanian).

ans (Fig. 9C); it is not determinable in *Paliguana**, *Palaeagama**, *Saurosternon**, and kuehneosaurs. Squamates are unique in that they have developed a "styloid" process on the radius; the posteromedial margin of the distal epiphysis of the radius is produced into a bluntly-pointed process lying in a concave depression on the posteromedial surface of the proximal end of the radiale (Fig. 9D).

60. [101] Intermedium reduced or absent in hand. The intermedium is a large element that articulates with the ulna in lepidosauromorphs ancestrally. This is the condition in araeoscelidans (Fig. 4A), younginiforms (Currie, 1981b) and rhynchocephalians (Fig. 4B). As with the previous two characters, this one cannot be determined in many extinct lepidosauromorphs. Among them, only *Saurosternon** has some of the carpals preserved, and Carroll (1975a; 1977) considers its intermedium to be reduced, thus approaching the squamate condition. Since rhynchocephalians also retain the ancestral condition, Carroll's conclusion that *Saurosternon** possesses a reduced intermedium would most reasonably be interpreted as convergence. Unfortunately, the carpals are displaced to some extent and, in keeping with the subadult stage of this fossil, they are poorly ossified. Thus, the position, size, and shape of the "intermedium" cannot be interpreted unambiguously. This apparent case of convergence could as well reflect that the "intermedium" has been misidentified, or that it has not reached its adult size and shape. In view of these ambiguities, we consider this character to be indeterminable in *Saurosternon**. Castañeda and Alvarez (1968, repeated in Renous-Lecuru, 1973) reported a large intermedium in *Bipes*, the only limbed amphisbaenian. Greer and Gans (1984) indicated that this bone is a lateral centrale rather than an intermedium, which is absent. *Opetiosaurus* (Kornhuber, 1901) and mosasaurs (Russell, 1967) are the only other squamates in which a large intermedium has been identified (Russell, 1967). However, the so-called intermedium in this group has the articulations of a lateral centrale distally and an intermedium proximally, and it may thus represent a compound element (see Figs. 4D,E). Until more is known, a greatly reduced or absent intermedium is considered a synapomorphy of squamates (see Fig. 4C).

61. [102] Lateral centrale in hand contacts second distal carpal, thus interrupting contact between medial centrale and third distal carpal. In lepidosauromorphs ancestrally the medial centrale contacts the third distal carpal, thus excluding the lateral centrale from contacting the second distal carpal. This condition occurs in araeoscelidans (Fig. 4A), younginiforms (Currie, 1981b) and rhynchocephalians (Fig. 4B); it is indeterminable in *Paliguana**, *Palaeagama**, *Saurosternon**, and kuehneosaurs. Squamates are unique among lepidosauromorphs in that, relative to the ancestral condition, the lateral centrale is slightly enlarged (or the medial centrale is slightly reduced?) and it contacts the second distal carpal to interrupt the contact between the medial centrale and third distal carpal (Fig. 4C).

62. [103] Modified joint between first metacarpal and wrist. In diapsids ancestrally the first metacarpal contacts the first distal carpal, which in turn contacts the medial centrale and second distal carpal (Fig. 4A). As seen in crocodilians and *Sphenodon*, all metacarpals except the fifth overlap one another proximally in saurians ancestrally (pers. obs.). The ancestral relations of the first metacarpal and first distal carpal are retained in younginiforms (Currie, 1981b) and rhynchocephalians (Fig. 4B). This character is not determinable in *Paliguana**, *Palaeagama**, and kuehneosaurs. The first metacarpal and first distal carpal are preserved in nearly natural association in *Saurosternon** (Carroll, 1975a). As noted above, however, displacement of the more proximal carpals does not allow unambiguous interpretation of the relations of these elements to the remainder of those in the wrist. Following Carroll (1977), we consider the element usually thought of as distal carpal one to be the medial centrale in squamates, and the proximal epiphysis of metacarpal one to be the true first distal carpal. The proximal end of the first metacarpal is thus uniquely modified in squamates; it extends into the row of distal carpals to contact the medial centrale, and the base of the

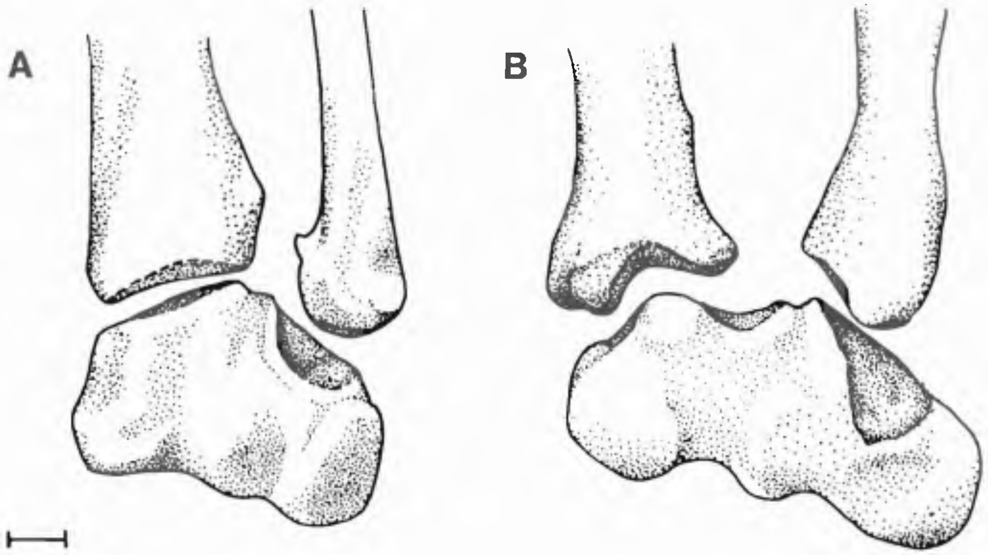

FIGURE 10. Posterior view of left tibio-astragalar joint. A, *Leiolepis belliana* (iguanian); B, *Corucia zebrata* (autarchoglossan).

element is expanded laterally to contact the second distal carpal (Fig. 4C). The form of the joint between the first metacarpal and the wrist allows for some independence of motion between the first and other digits of the hand. At rest, the first manual digit projects medially, and as in saurians generally, the fifth manual digit projects laterally. As a consequence, the outer digits of the squamate hand can extend in opposite directions and converge upon one another when contracted. Presumably, the modifications of the first metacarpal reflect development of some grasping ability in the squamate manus.

63. [121] Pubes in relatively narrow contact at symphysis, and pelvic fenestra consequently enlarged. As noted above, the pelvis is fenestrate in lepidosaurs ancestrally (e.g., kuehneosaurs, Robinson, 1962, 1967; rhynchocephalians, Fig. 6C; squamates, Fig. 6D). Squamates differ from rhynchocephalians and kuehneosaurs, however, in that the pubis is a more lightly constructed element. In particular, the pubes become more gracile distally, so that the pubic symphysis is relatively narrow. Primarily as a result of the modification of the pubis, the pelvic fenestra is relatively larger in squamates than it is in the other members of the kuehneosaur-lepidosaur group.

64. [133] Modification of locked tibio-astragalar joint by loss of ridge and trough articulation. As pointed out by Reisz (1981), the distal extremity of the tibia forms a ridge that fits into a complementary-shaped trough formed between two raised ridges on the proximal surface of the astragalus. Reisz (1981) interpreted this modification as representing a locked joint between the tibia and astragalus, a diapsid synapomorphy. Identification of this character requires fully adult individuals with well-preserved ankles that may be prepared in such a way that this character can be examined. Most of the pertinent fossils cannot be interpreted in this regard. Reisz (1981) noted that this joint is present in araeoscelidans and younginiforms, and we have observed it in *Sphenodon*. Among squamates, however, the tibio-astragalar joint has been modified. No squamate retains the ancestral tibio-astragalar joint intact. Aside from the suppression of the ridge and trough connection, however, that of iguanians is least modified (Fig. 10A). The autarchoglossan tibio-astragalar joint is very different (Fig. 10B; and see Estes et al., 1988). Accordingly, the form of the tibio-astragalar joint retained by iguanians is considered to represent the ancestral squamate condition.

65. [125] Fibular-astragalocalcanear joint involves most of distal end of fibula. In lepidosau-

romorphs ancestrally the fibular-astragalocalcanear joint is confined to a small portion of the distal end of the fibula. This condition is found in araeoscelidans (Reisz, 1981), archosauromorphs (e.g., Sigogneau-Russell and Russell, 1978), younginiforms (Currie, 1981b), and rhynchocephalians (Fig. 7C). The shape of this joint is unknown in *Paliguana**, *Palaeagama**, *Saurosternon**, and kuehneosaurs. The distal epiphysis of the fibula is uniquely modified in squamates. Its shape is such that the fibular-astragalocalcanear joint involves most of the distal end of the fibula (Fig. 7D). The fibular articular surface on the astragalocalcaneum is modified in a complementary fashion, forming a broad, steeply-inclined band on the lateral face of the element.

66. [134] Squamate ankle joint. Synapomorphies in lepidosauromorph ankle morphology have been described above. Brinkman (1980) argued that the squamate ankle differs from the condition in lepidosaurs ancestrally by having developed a complex tongue-in-groove structure at the joint between the astragalocalcaneum and fourth distal tarsal. One of the specializations of the squamate ankle joint is a prominent, dorsally-directed flange on the calcaneum. Another is the extension of the articular surface of the astragalocalcaneum onto the dorsal aspect of the fourth distal tarsal. According to Brinkman (1980), both these modifications are lacking in *Saurosternon**. Based on *Sphenodon* (pers. obs.) and *Gephyrosaurus* (Evans, 1981), it is evident that they are lacking in rhynchocephalians as well. Ankle joints are unknown in *Paliguana** and *Palaeagama**. S. Evans (pers. comm.) indicates that dissociated astragalus and calcaneum elements of kuehneosaurs are plesiomorphic compared with those of squamates.

67. [132] Squamate hooked fifth metatarsal. As described above, lepidosaurs share a number of modifications of the shape of the fifth metatarsal that are lacking in ancestral lepidosauromorphs. This collection of synapomorphies has been described by Robinson (1975), and is usually summarized by the term "hooked fifth metatarsal". As described by Robinson (1975), however, the squamate fifth metatarsal is further specialized, because of the angulation of the proximal head of the element, the prominence of the medial plantar tubercle, and the lateral displacement of the lateral plantar tubercle.

68. [129] Second distal tarsal absent. This bone is a separate element in lepidosauromorphs ancestrally, being present in younginiforms (Currie, 1981b), *Saurosternon** (Fig. 8B), and rhynchocephalians (Fig. 8C). The character is not preserved in *Paliguana**, *Palaeagama**, and kuehneosaurs. In all squamates, however, the second distal tarsal is absent (Fig. 8D).

69. [136] Gastralia absent. Gastralia are present in diapsids ancestrally, being retained by araeoscelidans (Reisz, 1981), younginiforms (Currie, 1981b), *Palaeagama** and *Saurosternon** (Carroll, 1975a), kuehneosaurs (Evans, 1981), and rhynchocephalians (Romer, 1956). Gastralia are retained by archosauromorphs as well, although they have been lost independently within sauropods and birds, and in all ornithischians (Gauthier, 1984). Among lepidosauromorphs, only squamates lack gastralia.

TAXONOMY

CRITERIA USED IN THIS STUDY

In this paper we have documented the successive levels of inclusion for taxa within Lepidosauromorpha. This hierarchy of groups as determined by their nested synapomorphies, and the phylogenetic relationships that may be hypothesized from them, are the principal articles of interest to us here. Although the cladograms (Figs. 11-13) adequately summarize our conclusions, some systematists may prefer a listed taxonomy as well. We provide one here based on criteria given below. These criteria in many ways conflict with those of most traditional taxonomies, as well as the conventions adopted by Wiley (1981), principally because he sought to reconcile the problems of ranking in phylogenetic taxonomy and we explicitly reject the use of ranks for reasons specified below.

1. *No formal categorical ranks are recognized.* Wiley's first convention (1981:200-201) advocated a Linnean hierarchy coupled with some additional terms, although he recognized that there was no biological necessity to do so. Most workers apply formal categorical ranks to taxa, but for reasons discussed below we have provided only an indented taxonomy of Lepidosauromorpha. Wiley offered some practical objections to the use of an indented taxonomy, such as the difficulty of following the sequence if the list spans more than one page. We grant that this may be the case in some instances, but we believe that the points made below override such objections.

Initially, we explored the possibility of providing a ranked taxonomy that would avoid proliferation of names and categorical levels, as suggested by Wiley (1981). However, if we retained the rank of Class for Reptilia as constituted here, the rank then available for Aves approaches the generic level, even with the use of the additional categories that we wanted to avoid. The phyletic sequencing convention discussed by Wiley (1981:206, convention 3) avoids proliferation of names and categories, but leaves many taxa unnamed. Nevertheless, any categorical levels that we used would be subject to considerable revision - and additional proliferation of names - as similar studies of other groups of vertebrates are made. Because extensive revision of vertebrate taxonomy is not a goal of our paper, we have had to look for alternatives.

Beyond these practical matters, there are theoretical reasons for discarding categorical ranks. Most systematists are aware that formal ranks such as Class, Order, or Family are not equivalent across all groups. For example, aside from being monophyletic, it is difficult to discern ways in which the orders Rhynchocephalia and Coleoptera, or the families Felidae and Euphorbiaceae, are equivalent. They differ profoundly in taxonomic and morphologic diversity, as well as in their times of origin. In addition, from the review of Mishler and Donoghue (1982), it is doubtful that currently recognized species and species concepts are equivalent across groups. The lack of equivalency of taxa assigned equal ranks has not prevented some biologists from attributing phylogenetic relevancy to "patterns" in, for example, ordinal or familial diversity through time. Such endeavors probably reveal more about the ill-defined concepts of the ranks Order and Family than about the structure of the biological world.

One could make taxonomic ranks equivalent on the basis of absolute time of origin as suggested by Hennig (1966). This would provide a particularly useful basis for comparison, especially for those interested in examining rate-related processes or biogeographic patterns. Unfortunately, the fossil record provides only minimum estimates of times of origin, and then only for a fraction of the extant biota. One could also rank taxa on the basis of relative divergence times. However, only sister groups would be equivalent; this equivalence would not extend to taxa given the same rank that are not sister groups. For example, in terms of categorical rank in this sense, *Gephyrosaurus* is equivalent to Sphenodontida, just as Iguania is equivalent to Autarchoglossa. However, even if *Gephyrosaurus* and Autarchoglossa were given the same rank, this would not imply equivalence in any phylogenetically meaningful properties.

Discarding categorical ranks does not hamper discussions of the phylogenetic properties of monophyletic taxa. Moreover, no changes in nomenclature are necessary because we preserve rank-associated suffixes and Linnean binomials for the sake of stability. We believe that this approach will have a positive influence on studies of morphologic and taxonomic diversity, and we hope that workers interested in such questions will follow Vrba (1980) by pursuing them in the context of sister taxa rather than taxonomic ranks.

2. *No redundant names are recognized.* In making this decision, we differ from Wiley's second convention (1981:200, 205). Wiley recommended that redundancy be avoided except in the case of the five required Linnean higher categories (Phylum, Class, Order, Family, Genus). Because we reject current concepts of rank, there is no longer a need to retain any redundant names.

As noted above, we are mainly interested in nested patterns of co-occurring synapomorphies and the phylogenetic relationships among taxa that may be hypothesized from them. In this con-

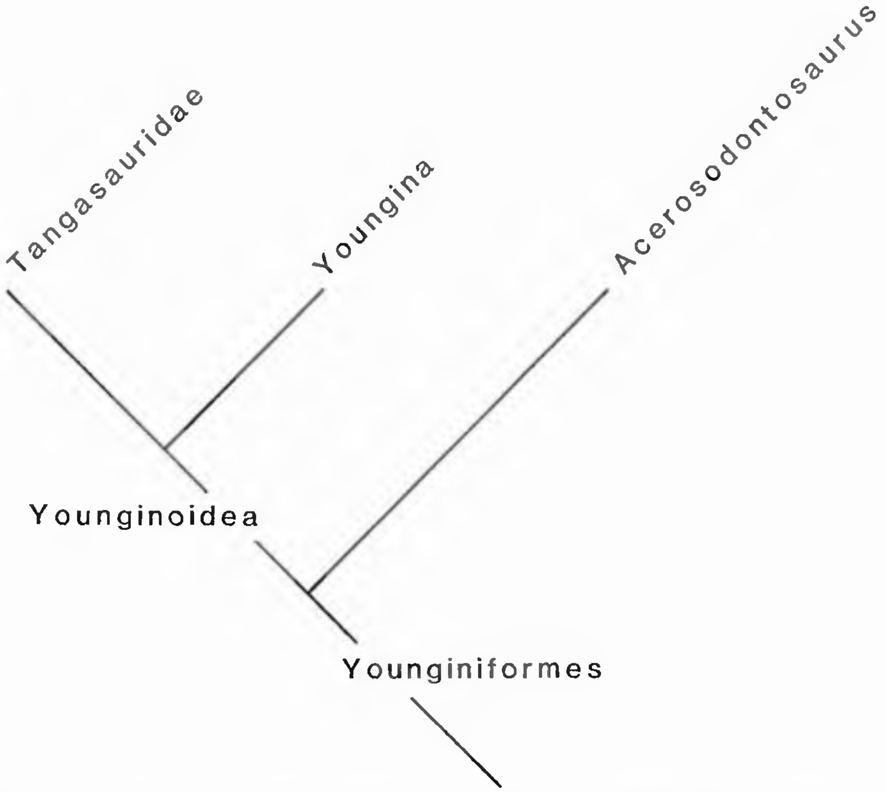

FIGURE 11. Cladogram depicting phylogenetic relationships among Younginiformes as determined by this study.

text, certain taxa now in use are redundant in that they offer no additional information pertinent to this issue. The cladograms in Figs. 11-13 represent our conclusions regarding the hierarchical relationships among the taxa discussed here. Some portions of the cladogram are named and others are not, depending on our knowledge of the relevant taxa. The names used in this work are meant to summarize data pertinent to the issue of monophyly, because it is easier to remember the name of a taxon than it is to remember all the synapomorphies by which it is diagnosed. Similarly, cladograms summarize the hierarchical relationships among monophyletic taxa. From this perspective, neither rank-related suffixes nor additional names at higher categorical levels currently provide phylogenetic information beyond that already summarized in taxon names and cladograms. For example, because *Gephyrosaurus bridensis* is a single taxon, the name Gephyrosauridae is redundant in that it conveys no additional information about relationships that is not already implied by *Gephyrosaurus bridensis*. To continue with this example, in our view the name *Gephyrosaurus bridensis* conveys no more than that this taxon is monophyletic. If we follow the logic of this argument to its natural conclusion, the monophyly of *Gephyrosaurus bridensis* could be conveyed just as easily by either of the terms *bridensis* or *Gephyrosaurus*. For the sake of stability, however, we retain Linnean binomials for the least inclusive taxa that can be diagnosed. In this and our unwillingness to use other redundant categories we differ from Wiley (1981), whose convention 2 extends exemption from redundancy to the five Linnean higher categories Phylum, Class, Order, Family, and Genus.

Thus, in our taxonomy, one need only learn taxonomic names, their synapomorphies, and their hierarchical relationships as expressed in a cladogram (or its equivalent, such as an internested Venn diagram or indented list). Our approach differs from current taxonomic practices only in that no monophyletic groups except for individual species need have more than one name, and rank-related suffixes do not imply equivalence across taxa.

3. *Widely used names are stabilized by restricting them to clades in which at least two branches stemming directly from the basal node are represented by Recent organisms.* Less familiar or new names are used when referring to more inclusive taxa composed of Recent organisms and their extinct sister groups. We believe that it is desirable to give widely used names such as Archosauria and Lepidosauria stable meanings in a phylogenetic context. To this end, we restrict the name Lepidosauria to the common ancestor of *Sphenodon punctatus* and Squamata and all other organisms stemming from that ancestor, and apply the names Lepidosauriformes and Lepidosauromorpha to successively more inclusive taxa composed of lepidosaurs and one or more extinct outgroups.

One virtue of this proposal is that it would provide stable meanings for names that are familiar to the widest possible audience. That is to say, it is unlikely that finds of extinct taxa will have much impact on firmly established hypotheses such as, for example, that *Sphenodon* and squamates are most closely related among extant organisms. Thus, we anticipate that relatively few biologists will have need of the names Lepidosauriformes and Lepidosauromorpha, which convey the more complex structure of relationships with which paleontologists must contend. From the perspective of the neontologist, new finds or interpretations of relationships among extinct lepidosauromorphs should have little impact on the diagnosis and content of Lepidosauria. For example, if some synapomorphies diagnosing Lepidosauria are subsequently found in kuehneosaurs, these characters would still be synapomorphies of extant lepidosaurs relative to extant archosaurs. Moreover, soft anatomical characters diagnostic of lepidosaurs among extant amniotes will very likely never be found in fossils. Thus, we expect that there will always be more synapomorphies summarized by names applied to taxa bracketed by extant members. Indeed, the stability of names so delimited depends on the greater information potentially available at these nodes.

Although one could apply the name Lepidosauria to all taxa that are closer to *Sphenodon* and squamates than to birds and crocodiles (= Archosauria of Gauthier, 1984), we find this alternative less desirable for two reasons. First, in doing so Lepidosauria would offer less phylogenetic information in that it would summarize only three synapomorphies (those diagnosing Lepidosauromorpha) rather than the fifty-four synapomorphies that distinguish *Sphenodon* and squamates from archosaurs. Second, each new extinct outgroup discovered would require that neontologists revise their diagnosis of Lepidosauria, even though the hypothesis that *Sphenodon* and squamates are most closely related among extant organisms would remain unchanged.

The above criterion also has the virtue of clearly distinguishing between the definition of a taxon and its diagnosis. Taxa that are defined by the characters possessed by their members are typological concepts. By defining taxa in terms of ancestry, as we have done, such taxa will be truly phylogenetic concepts (de Queiroz, 1988). Characters, which enable us to recognize taxa, are used to diagnose taxa in phylogenetic taxonomies, but they cannot define them.

Wiley's (1981) third convention employs sequencing in order to minimize the proliferation of taxonomic names and categorical ranks. We find it more convenient to name monophyletic groups, such as Lepidosauriformes, than to list all their included taxa -- *Paliguana**, *Saurosternon**, Kuehneosauridae, Rhynchocephalia, and Squamata -- each time we refer to them. Because we do not recognize categorical ranks, their proliferation is not an issue for us.

Under Wiley's (1981) fourth convention, monophyletic groups in tritomies and polytomies are given equivalent rank and placed sedis mutabilis at the level in the hierarchy at which their rela-

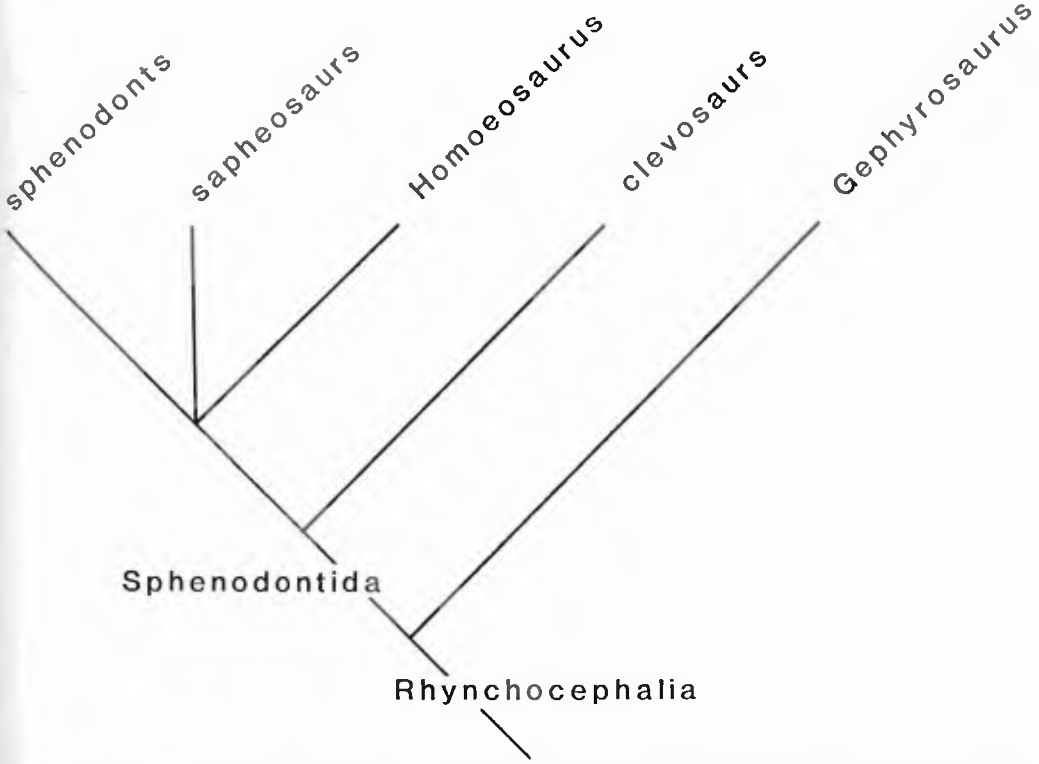

FIGURE 12. Cladogram depicting phylogenetic relationships among rhynchocephalians as determined by this study.

tionships to other taxa are known. Because we use indentation rather than sequencing to convey hierarchical relationships, tritomies and polytomies are indicated by equal indentation, and there is no need to use sedis mutabilis. Sedis mutabilis would be useful in sequenced taxonomies; this convention is by itself, however, sufficient to convey unresolved relationships, and thus there is no need to use equivalent categorical ranks as well.

Following the suggestion in Wiley's (1981) fifth convention, we use incertae sedis for taxa that can be placed in very inclusive clades but whose position within these clades is uncertain. For example, *Palaeagama** has at least some lepidosauromorph synapomorphies, but none of the lepidosauriform synapomorphies can be determined in it. If we merely indented *Palaeagama** equally with Younginiformes and Lepidosauriformes, this might be interpreted as indicating that *Palaeagama** has only one of the three possible relationships: the sister group of Lepidosauriformes, the sister group of Younginiformes, or the sister group of both of these taxa. Because it is also possible that *Palaeagama** is a lepidosauriform, we place it incertae sedis in Lepidosauromorpha.

Wiley (1981) permitted recognition of paraphyletic and polyphyletic taxa as well as those of uncertain status in phylogenetic taxonomies, if they are placed in shutter quotes. Paraphyletic and polyphyletic groups have no place in phylogenetic taxonomies, but we use shutter quotes when referring to such groups in historical discussions. The metataxon (including metaspecies and indicated by *) is used for taxa of uncertain status (see pp. 15-16).

Wiley's (1981) eighth convention deals with the treatment of ancestors. We do not attempt to identify ancestors. However, because an ancestor would always be a species possessing the synap-

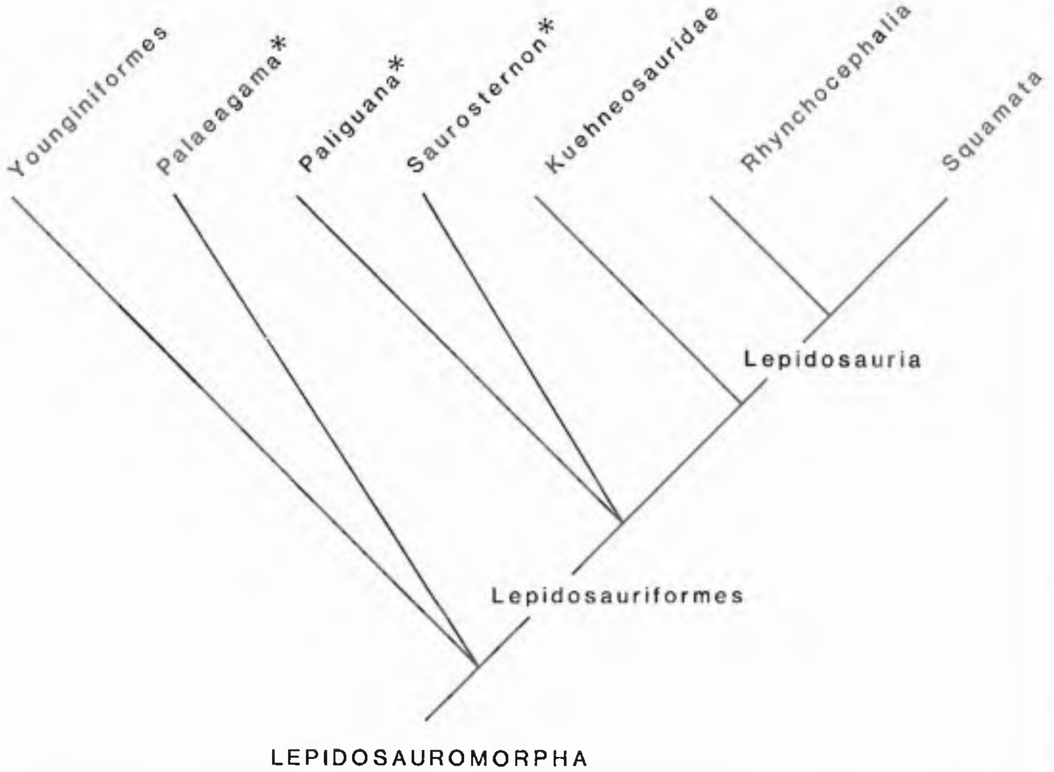

FIGURE 13. Cladogram depicting phylogenetic relationships among lepidosauromorphs as determined by this study.

omorphies of its own monophyletic group but lacking those of its descendant subgroups, an ancestor would always be a metaspecies. This is not to imply that every hypothesized metaspecies is an ancestor, only that as far as morphological data are concerned, there is no reason to rule out this possibility.

Wiley's (1981) last convention deals with the treatment of taxa resulting from hybridization, a subject not of concern to us here.

PHYLOGENETIC TAXONOMY OF AMNIOTA

Paraphyly of "Reptilia" has long been recognized, both by neontologists and paleontologists. Underwood (1957:241) perceptively characterized "Reptilia" as "that motley assortment of all the amniotes which are neither mammals nor birds." Gauthier (1984) argued that extant Amniota consists of two major subtaxa. One of these two taxa is Mammalia; the less widely used name Synapsida was used for a more inclusive taxon containing mammals and all extinct taxa that are closer to mammals than they are to other amniotes. Reptilia was redefined as the other major subgroup of extant amniotes; as a monophyletic taxon it includes birds but not non-mammalian synapsids. Reptilia is restricted here to the most recent common ancestor of turtles, crocodiles, birds, *Sphenodon*, and squamates, and all of its descendants. As might be expected, the relationships of several extinct taxa are unclear. According to Gauthier (1984) and Heaton and Reisz (1986), millerosaurs, mesosaurs, procolophonians, and pareiasaurs appear to be closer to reptiles than to mammals, but they also appear to be outside Reptilia as defined here. There is evidence indicating that some extinct taxa, such as Captorhinidae and several taxa currently included in the "Protorothyridae," are reptiles sensu stricto (Gauthier, 1984; Heaton and Reisz, 1986).

TABLE 1. An indented, unsequenced classification of the Lepidosauromorpha.

- Amniota
  - Synapsida (= "pelycosaurs," "therapsids," and Mammalia)
  - Reptilia
    - Anapsida
    - Diapsida
      - Araeoscelidia
      - Sauria
        - Archosauromorpha (for included taxa see Gauthier, 1984)
        - Lepidosauromorpha
          - incertae sedis: *Palaeagama vielhaueri**
          - Younginiformes
            - *Acerosodontosaurus piveteaui*
            - Younginoidea
              - *Youngina capensis*
              - Tangasauridae
                - *Kenyasaurus mariakaniensis*
                - *Thadeosaurus colcanapi*
                - *Tangasaurus menelli*
                - *Hovasaurus boulei*
          - Lepidosauriformes, new taxon
            - *Paliguana whitei**
            - *Saurosternon bainii**
            - unnamed taxon
              - Kuehneosauridae
                - *Kuehneosaurus latus*
                - *Kuehneosuchus latissimus*
                - *Icarosaurus siefkeri*
              - Lepidosauria
                - Rhynchocephalia
                  - *Gephyrosaurus bridensis*
                  - Sphenodontida
                    - clevosaurs
                      - *Clevosaurus hudsoni*
                      - *Planocephalosaurus robinsonae*
                    - unnamed taxon
                      - *Homoeosaurus* spp.
                      - sapheosaurs
                        - *Leptosaurus neptunius*
                        - *Kallimodon cerinensis*
                        - *Sapheosaurus thiollierei*
                      - sphenodonts
                        - *Opisthias rarus*
                        - *Sphenodon punctatus*
                - Squamata (see Estes et al., 1988)

Reptilia as defined here includes two major subtaxa, Anapsida and Diapsida. Formerly paraphyletic, Anapsida is here restricted to Testudines, and all other reptiles that are closer to turtles than they are to diapsids. Following Gaffney and McKenna (1979) and Gaffney (1980), Captorhinidae and Testudines are considered sister groups and both are thus included in a monophyletic Anapsida. Testudines includes extant Chelonia (= the least inclusive taxon encompassing the most recent common ancestor of extant pleurodires and cryptodires), and all other extinct taxa that are closer to chelonians than they are to captorhinids. Diapsida includes two main subtaxa, the extinct Araeoscelidia and the extant Sauria. One could restrict the name Diapsida to what we are here calling Sauria, but the former name was coined for fossils and was meant to signify that they were "two-arched reptiles"; although araeoscelidans are not saurians, they are definitely two-arched and are thus appropriately considered diapsids. In contrast to the term Diapsida, Sauria was originally based on extant organisms, in this case crocodiles and "lizards." Moreover, at least some pre- and post-Darwinian anatomists noted that both birds and snake-like forms were either built on the saurian plan or were saurian derivatives. Sauria cannot be used for the paraphyletic group usually thought of as "lizards", and we have applied this name to the monophyletic taxon that most closely approximates the original content of Sauria (i.e., the original "Sauria" plus snakes and birds). Sauria is composed of Archosauromorpha, which includes Archosauria, and Lepidosauromorpha, which includes Lepidosauria. Bearing the recommendations and qualifications discussed above in mind, we offer an indented but unsequenced taxonomy (Table 1), which emphasizes the relationships within Lepidosauromorpha in the context of their phylogenetic position within amniotes.

This taxonomy depicts the more complex relationships of interest to paleontologists, or neontologists studying the origins of extant lepidosaurs. For most questions posed by comparative biologists, however, the following taxonomy is adequate.

- Amniota
  - Mammalia
  - Reptilia
    - Chelonia
    - Sauria
      - Archosauria
        - Aves
        - Crocodylia
      - Lepidosauria
        - *Sphenodon punctatus*
        - Squamata

CONCLUSIONS

1. Lepidosauromorpha (see Addendum, p. 95) is a group of diapsid reptiles that includes extant *Sphenodon* and Squamata. Diagnoses of monophyletic groups of lepidosauromorphs and their phylogenetic relationships are the primary foci of this paper. The phylogenetic arrangement was accomplished initially by hand, and checked by subjecting the data matrix for 171 characters to computer algorithms in the PHYSYS package (see Appendix III). Both hand and computer results were consistent.

2. Diapsida includes Araeoscelidia and its sister group, the Sauria, which includes all other diapsid reptiles. As used here, Sauria approximates the original concept of McCartney (1802), who included in it crocodiles as well as squamates (see p. 65). We recommend that Sauria not be used as a synonym of paraphyletic "Lacertilia." Sauria as constituted here includes two clades, Archo-

sauromorpha (Huene, 1946, 1949; sensu Gauthier, 1984) and Lepidosauromorpha. Archosauromorpha includes Archosauria (the least inclusive taxon encompassing the immediate common ancestor of birds and crocodiles) and its extinct relatives. Lepidosauromorpha includes Lepidosauria (the least inclusive taxon encompassing the immediate common ancestor of squamates and *Sphenodon*) and its extinct relatives, viz., kuehneosaurs, *Paliguana**, *Saurosternon**, *Palaeagama**, and Younginiformes.

3. "Eosuchia" is a paraphyletic taxon that is rejected here; its contents and usage have varied significantly since Broom (1914) coined this redundant term for *Youngina capensis*.

4. Lepidosauromorpha includes the monophyletic taxa Younginiformes, Kuehneosauridae, Rhynchocephalia, and Squamata, as well as three metataxa *Palaeagama**, *Paliguana**, and *Saurosternon**. It is diagnosed by three synapomorphies: (1) a sternum formed of two broad plates that fuse to each other prior to the cessation of growth, (2) a fully enclosed ectepicondylar foramen in the humerus, and (3) a medial centrale in the manus that is nearly twice the size of the lateral centrale.

5. Following Currie (1982), we recognize Younginiformes on the basis of five synapomorphies. This taxon includes *Acerosodontosaurus piveteaui* and Younginoidea. The younginioids *Youngina capensis* and Tangasauridae are diagnosed by 4 synapomorphies. Tangasaurs are diagnosed by 5 synapomorphies, and include *Tangasaurus mennelli*, *Hovasaurus boulei*, *Thadeosaurus colcanapi*, and *Kenyasaurus mariakaniensis*.

6. *Palaeagama vielhaueri**, *Paliguana whitei**, and *Saurosternon bainii** are not diagnosible; we have referred to such taxa here as metataxa, and use the asterisk (*) to call attention to this circumstance (Donoghue, 1985). Carroll (1975a, 1977) joined these three metaspecies in a family "Paliguanidae." *Palaeagama** is poorly preserved and currently has no synapomorphies allowing reference to any taxon within Lepidosauromorpha. Accordingly, *Palaeagama** is placed incertae sedis in Lepidosauromorpha. The other two taxa are based on non-comparable specimens; there is thus no basis for considering them closely related and we reject the name "Paliguanidae." Both *Paliguana** and *Saurosternon** possess synapomorphies placing them closer to kuehneosaurs and lepidosaurs than to *Palaeagama** or younginiforms.

7. Seven synapomorphies join *Paliguana whitei**, *Saurosternon bainii**, kuehneosaurs, rhynchocephalians, and squamates. These taxa are included in Lepidosauriformes, new taxon, which is the sister group of Younginiformes. The synapomorphies reflect modification of the forelimbs and girdles, development of initial states of a characteristic ankle joint, and initial stages in the development of an ear sensitive to airborne sound.

8. Another taxon including kuehneosaurs, rhynchocephalians, and squamates is diagnosed by nine synapomorphies. Because much of the known kuehneosaur material has not yet been described, we refrain from naming this group.

9. Both Rhynchocephalia and Squamata include living representatives and together these taxa are equivalent to Lepidosauria of Haeckel (1866 and later papers). Lepidosauria is diagnosed by 35 synapomorphies. Considering only those taxa delimited by extant forms, lepidosaurs possess 54 synapomorphies enabling us to distinguish them from archosaurs.

10. Nine synapomorphies diagnose Rhynchocephalia, which includes *Gephyrosaurus* and its sister group Sphenodontida. Rhynchosaurs are archosauromorphs, not rhynchocephalian lepidosauromorphs (Gauthier, 1984; Carroll, 1977, 1987).

11. Sphenodontida is diagnosed by nine synapomorphies and includes *Sphenodon* and all rhynchocephalians that are closer to *Sphenodon* than they are to *Gephyrosaurus*. A number of monophyletic sphenodontidan groups are identified: clevosaurs, sapheosaurs, *Homoeosaurus*, and sphenodonts. Thirteen synapomorphies unite the *Homoeosaurus* - sapheosaur - sphenodont group

with respect to clevosaurs, but the former group constitutes an unresolved tritomy. It would be premature to assign taxonomic names to these groups until the Triassic sphenodontidans are described more fully.

12. Squamata is a monophyletic taxon diagnosed by 69 synapomorphies. The group has traditionally been divided into "lizards" and snakes, with amphisbaenians and dibamids sometimes given equivalent status. Phylogenetic relationships within this group are discussed by Estes et al. (1988). We confine ourselves here to recognizing two informal groups of squamates, iguanians (iguanids*, agamids*, and chamaeleons) and autarchoglossans (all other squamates, including amphisbaenians, dibamids, and snakes); see Estes et al., 1988 for subdivision of Autarchoglossa.

13. The phylogenetic conclusions of this analysis are summarized in Figs. 11-13.

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REFERENCES CITED

Adams, E. 1972. Consensus techniques and the comparison of taxonomic trees. Syst. Zool. 21:390-397.

Albrecht, P. 1883. Epiphyses osseuses sur les apophyses epineuses des vertébrés d'un reptile (*Hatteria punctata*, Gray). A. Manceaux, Bruxelles.

Baird, I. 1970. The anatomy of the reptilian ear. Pp. 193-275. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 2 (Morph. B). Academic Press, New York.

Bellairs, A., and J. Boyd. 1950. The lachrymal apparatus in lizards and snakes. II. The anterior part of the lachrymal duct and its relationship with the palate and with the nasal and vomeronasal organs. Proc. Zool. Soc. London 120:269-310.

_________ and A. Kamal. 1981. The chondrocranium and the development of the skull in recent reptiles. Pp. 1-264. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 11 (Morph. F):1-264, Academic Press, New York.

Borsuk-Bialynicka, M. 1977. Results of the Polish-Mongolian Paleontological Expeditions. Part VII. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, Gen. N., Sp. N., from the Upper Cretaceous of Mongolia. Palaeont. Polonica 37:5-64.

Brinkman, D. 1980. Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia: Iguanidae) and other lizards. Canad. J. Zool. 58:277-289.

Broom, R. 1903. On the skull of a true lizard (*Paliguana whitei*) from the Triassic beds of South Africa. Rec. Albany Mus. 1:1-3.

_________. 1914. A new thecodont reptile. Proc. Zool. Soc. London 1914:1072-1077.

_________. 1921. On the structure of the reptilian tarsus. Proc. Zool. Soc. London 1921:143-155.

_________. 1925. On the origin of lizards. Proc. Zool. Soc. London 1926:487-492.

_________. 1926. On a nearly complete skeleton of a new eosuchian reptile (*Palaeagama vielhaueri*, gen. et sp. nov.). Proc. Zool. Soc. London 1926:487-492.

Camp, C. 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist. 48:289-481.

_________. 1945. *Prolacerta* and the protorosaurian reptiles, part II. Amer. J. Sci. 243:84-101.

Carroll, R. 1975a. Permo-Triassic "lizards" from the Karroo. Palaeont. Africana 18:17-87.

_________. 1975b. The early differentiation of diapsid reptiles. Colloq. Internat. C. N. R. S. 218:433-449.

_________. 1977. The origin of lizards. Pp. 359-396. *In* S. Andrews, R. Miles and A. Walker (eds.), Problems in Vertebrate Evolution. Linnean Soc. London, Symp. Ser. 4, Cambridge University Press and Academic Press.

_________. 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. Phil. Trans. Roy. Soc. London 293(B):315-383.

_________. 1982. Early evolution of reptiles. Ann. Rev. Ecol. Syst. 13:87-109.

_________. 1988. Late Paleozoic and Early Mesozoic lepidosauromorphs and their relation to lizard ancestry. Pp. 99-118. *In* R. Estes and G. Pregill, Phylogenetic Relationships of the Lizard Families, Stanford Univ. Press, Stanford, California.

Castañeda, M., and T. Alvarez. 1968. Contribución al conocimiento de la osteología apendicular de *Bipes* (Reptilia: Amphisbaenia). An. Esc. nat. Cienc. biol., Mex. 17:189-223.

Cocude-Michel, M. 1963. Les rhynchocéphales et les sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. Nouv. Arch. Mus. Hist. Nat. Lyon 7:1-187.

Colbert, E. 1970. The Triassic gliding reptile *Icarosaurus*. Bull. Amer. Mus. Nat. Hist. 143:85-142.

Cruickshank, A. 1979. The ankle joint in some early archosaurs. South Afr. J. Sci. 75:168-178.

Currie, P. 1980. A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. Canad. J. Earth Sci. 17:500-511.

_________. 1981a. The vertebrae of *Youngina* (Reptilia: Eosuchia). Canad. J. Earth Sci. 18:815-818.

_________. 1981b. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeont. Africana 24:99-168.

_________. 1982. The osteology and relationships of *Tangasaurus mennelli* Haughton (Reptilia; Eosuchia). Ann. South African Mus. 86:247-265.

__________ and R. Carroll. 1984. Ontogenetic changes in the eosuchian reptile *Thadeosaurus*. J. Vert. Paleont. 4(1):68-84.

Cuvier, G. 1807. Le Regne Animal distribué d'aprés son organization, pour servir de base à l'histoire naturelle des animaux et l'introduction a l'anatomie comparée. Vols. I-III, 8 vols., Paris.

de Beer, G. 1937. The development of the vertebrate skull. Oxford, Clarendon Press, xxiii + 552 pp.

de Queiroz, K. 1988. Systematics and the Darwinian revolution. Philos. Sci. 55(2).

de Ricqlès, A. 1977. On bone histology of fossil and living reptiles, with comments on its functional and evolutionary significance. Pp. 123-150. *In* A. Bellairs and C. Cox (eds.), Morphology and Biology of Reptiles. Linnean Soc. Symp. Ser. 3. Academic Press, London and New York.

Dollo, L. 1884. Sur les epiphyses des lacertiliens. Zool. Anz. 7:65-70 and 80-84.

Donoghue, M. S. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. Bryologist 88(3): 172-181.

Edmund, A. 1969. Dentition. Pp. 117-200. *In* C. Gans, A. Bellairs, and T. Parsons (eds.), Biology of the Reptilia 1 (Morph. A), Academic Press, New York.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic pattern and the evolutionary process. Method and theory in comparative biology. Columbia Univ. Press, N. Y., viii + 349 pp.

Enlow, D. 1969. The bone of reptiles. Pp. 45-80. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 1 (Morph. A), Academic Press, New York.

Estes, R. 1983. Sauria terrestria, Amphisbaenia. Handbuch der Palaoherpetologie, P. Wellnhofer, ed., part 10A, xxii + 249 pp., Gustav Fischer Verlag, Stuttgart.

__________, T. Frazzetta, and E. Williams. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward. I. Cranial Morphology. Bull. Mus. Compar. Zool., Harvard Univ. 140:25-73.

__________, K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within squamate reptiles. Pp. 119-183. *In* R. Estes and G. Pregill, Phylogenetic Relationships of the Lizard Families, Stanford Univ. Press, Stanford, California.

Etheridge, R. 1967. Lizard caudal vertebrae. Copeia 1967(4):699-721.

__________ and K. de Queiroz. 1988. A phylogeny of Iguanidae. Pp. 283-367. *In* R. Estes and G. Pregill, Phylogenetic Relationships of the Lizard Families, Stanford Univ. Press, Stanford, California.

Evans, S. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool. J. Linnean Soc. London 70:203-264.

__________. 1981. The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool. J. Linnean Soc. London 73:81-116.

__________. 1982. The gliding reptiles of the Upper Permian. Zool. J. Linnean Soc. London 76(2):97-123.

__________. 1984. The classification of the Lepidosauria. Zool. J. Linnean Soc. 82:87-100.

Fox, H. 1977. The urinogenital system in reptiles. Pp. 1-157. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 6 (Morph. E), Academic Press, New York.

Fraser, N. 1982. A new rhynchocephalian from the British Upper Trias. Palaeontology 25:709-725.

__________ and G. Walkden. 1983. The ecology of a late Triassic reptile assemblage from Gloucestershire, England. Palaeogeog., Palaeoclimatol., Palaeoecol. 42:341-365.

Fuchs, H. 1908. Untersuchungen über Ontogenie und Phylogenie der Gaumenbildungen bei den Wirbeltieren. Zweite Mitteilung. Über das Munddach der Rhynchocephalen, Saurier, Schlangen, Krokodile und Saüger und den Zusammenhang zwischen Mund- und Nasenhohle bei diesen Tieren. Zeit. Morph. Anthrop. 11:153-248.

Gaffney, E. 1980. Phylogenetic relationships of the major groups of amniotes. Pp. 593-610. *In* A. Panchen (ed.), The Terrestrial Environment and the Origin of Land Vertebrates, Syst. Assoc. Spec. Vol. 15, Academic Press, London and New York.

_________ and M. McKenna. 1979. A late Permian captohinid from Rhodesia. Amer. Mus. Nat. Hist. Novit. #2688:1-15.

Gans, C. 1978. The characteristics and affinities of the Amphisbaenia. Trans. Zool. Soc. London 34:347-416.

_________ and E. Wever, 1976. The ear and hearing in *Sphenodon punctatus*. Proc. Natl. Acad. Sci. 73:4244-4246.

Gauthier, J. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. Contr. Geol. Univ. Wyoming 21(1):7-54.

_________. 1984. A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. thesis, Department of Paleontology, University of California, Berkeley. University Microfilms #85-12825, Ann Arbor, Michigan.

Gladstone, R. and C. Wakeley. 1932. The morphology of the sternum and its relations to the ribs. J. Anat. 66:508-564.

Gorniak, G., H. Rosenberg, and C. Gans. 1982. Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. J. Morphol. 171(3):321-353.

Gow, C. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeont. Africana 18:89-131.

Greer, A. 1976. On the occurrence of a stapedial foramen in living non-gekkonid lepidosaurs. Copeia 1976(3):591-592.

_________. 1985. The relationships of the lizard genera *Anelytropsis* and *Dibamus*. J. Herpetol. 19(1):116-156.

_________ and C. Gans. 1984. The amphisbaenian carpus: how primitive is it? J. Herpetol. 17(4):406.

Günther, A. 1867. Contribution to the anatomy of *Hatteria*. Phil. Trans. Roy. Soc. London 157:595-629.

Haeckel, E. 1866. Generelle Morphologie der Organismen. Allgemeine Grundzuge der organischen Formen-Wissenschaft, mechanisch begrundet durch die von Charles Darwin reformierte Deszendenz-Theorie. II. Allgemeine Entwicklungsgeschichte der Organismen. Kritische Grundzuge der mechanischen Wissenschaft von den entstehenden Formen der Organismen, begrundet durch die Deszendenz-Theorie. Berlin, clx + 462 pp.

Haines, R. 1942. The tetrapod knee joint. J. Anat. 76:270-301.

_________, 1969. Epiphyses and sesamoids. Pp. 81-116. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 1 (Morph. A), Academic Press, New York.

Harris, J. and R. Carroll. 1977. *Kenyasaurus*, a new eosuchian reptile from the early Triassic of Kenya. J. Paleont. 51:139-149.

Heaton, M. and R. Reisz. 1986. Phylogenetic relationships of captorhinomorph reptiles. Can. J. Earth Sci. 23(3):402-418.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Chicago.

Hill, J. and G. de Beer. 1949. The development and structure of the egg-tooth and caruncle in the monotremes and on the occurence of vestiges of the egg-tooth and caruncle in marsupials. Trans. Zool. Soc. London 26:503-544.

Hoffstetter, R. and J. Gasc. 1969. Vertebrae and ribs of modern reptiles. Pp. 201-310. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 1 (Morph. A), Academic Press, New York.

Howes, G. and H. Swinnerton. 1901. On the development of the skeleton of the tuatara, *Sphenodon punctatus*. Trans. Zool. Soc. London 16:1-86.

Huene, F. von. 1946. Die grossen Stamme der Tetrapoden in den geologischen Zeiten. Biolog. Zentralblatt 65(7/12):266-275.

_________. 1948. A short review of the lower tetrapods. Spec. Publ. Roy. Soc. South Africa, Robert Broom Commemorative Vol., pp. 65-106.

_________. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Gustav Fischer Verlag, Jena, 716 pp.

Huxley, T. 1868. On *Saurosternon bainii*, and *Pristerodon mckayi*, two new fossil lacertilian reptiles from South Africa. Geol. Mag. 5:201-205.

Kamal, A. 1971. On the fissura metotica in Squamata. Bull. Zool. Soc. Egypt 23:53-57.

Kluge, A. 1983. Cladistic relationships among gekkonid lizards. Copeia 1983(2):465-475.

__________, 1987. Cladistic relationships among the Gekkonoidea.

Kornhuber, A. 1873. Einen neuen fossilen Saurier aus Lesina. Abh. k. k. geol. Reichs. 5:75-90.

__________. 1901. *Opetiosaurus bucchichi*, eine neue fossile Eidechse aus der unteren Kreide von Lesina in Dalmatien. Abh. k. k. Reichs. 14:1-24.

Kuhn, O. 1969. Proganosauria, Bolosauria, Placodontia, Araeoscelida, Trilophosauria, Weigeltisauria, Millerosauria, Rhynchocephalia, Proterosauria. Handbuch der Paläoherpetologie 9(1-74), Gustav Fischer Verlag, Stuttgart.

Kuhn-Schnyder, E. 1952. *Askeptosaurus italicus* Nopcsa. Abh. Schweiz. palaont. Gesell. 69:1-73.

Larsen, K. and W. Tanner. 1974. Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. Great Basin Naturalist 34:1-41.

Lécuru, S. 1968a. Remarques sur les scapulo-coracoïd des lacertiliens. Ann. Sci. nat. (Zool.) 10(12):475-510.

__________. 1968b. Étude des variations morphologiques du sternum, des clavicules et de l'interclavicule des lacertiliens. Ann. Sci. nat. (Zool.) 10:511-544.

__________. 1969. Étude morphologique de l'humerus des lacertiliens. Ann. Sci. nat. (Zool.) 11:515-558.

Malan, M. 1946. Contributions to the comparative anatomy of the nasal capsule and the organ of Jacobson of the Lacertilia. Ann. Univ. Stellenbosch (A)25:69-137.

Mayr, E. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, Massachusetts.

McCartney, J. 1802. Preface and Table III. *In* G. Cuvier, Lectures on Comparative Anatomy, translated by William Ross. Oriental Press, Wilson and Co., for T. N. Longman and O. Rees, Paternoster Row.

McDowell, S. and C. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. Nat. Hist. 105:1-142.

Merriam, J. 1905. The Thalattosauria, a group of marine reptiles from the Triassic of California. Mem. California Acad. Sci. 5:1-52.

Mishler, B. and M. Donoghue. 1982. Species concepts: a case for pluralism. Syst. Zool. 31(4):491-503.

Moffat, L. 1973. The concept of primitiveness and its bearing on the phylogenetic classification of the Gekkota. Proc. Linnean Soc. New South Wales 97:275-301.

Oelrich, T., 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc. Publ. Mus. Zool., Univ. Michigan 94:1-122.

Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien. München, 87 pp.

Osborn, H. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Mem. Amer. Mus. Nat. Hist. 1(8):449-508.

Panchen, A. 1972. The interrelationships of the earliest tetrapods. Pp. 65-87. *In* K. Joysey and T. Kemp (eds.), Studies in Vertebrate Evolution, Oliver and Boyd, Edinburgh.

Parsons, T. 1970. The nose and Jacobson's organ. Pp. 99-191. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 2 (Morph. B), Academic Press, New York.

Peterson, J. 1973. Adaptations for arboreal locomotion in the shoulder region of lizards. Ph.D. Dissertation, University of Chicago, Department of Anatomy, 584 pp.

Porter, K. R. 1972. Herpetology. Saunders, Philadelphia.

Pratt, C., 1948. The morphology of the ethmoidal region of *Sphenodon* and lizards. Proc. Zool. Soc. London 118:171-201.

Rasmussen, T. and G. Callison. 1979. A new herbivorous sphenodontid (Rhynchocephalia: Reptilia) from the Jurassic of Colorado. J. Zool. London 191:147-170.

Reisz, R. 1977. *Petrolacosaurus*, the oldest known diapsid reptile. Science 196:1091-1093.

__________. 1981. A diapsid reptile from the Pennsylvanian of Kansas. Spec. Publ. Mus. Nat. Hist. Univ. Kansas 7:1-74.

__________, D. Berman, and D. Scott, 1984. The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. J. Vert. Paleont. 4(1):57-67.

Renous-Lécuru, S. 1973. Morphologie comparée du carpe chez les Lepidosauriens actuels (Rhynchocéphales, Lacertiliens, Amphisbéniens). Gegenbaurs Morph. Jahrb. 119:727-766.

Rewcastle, S. 1980. Form and function in lacertilian knee and mesotarsal joints; a contribution to the analysis of sprawling locomotion. J. Zool. London 191:147-170.

Rieppel, O. 1978. The throat musculature of *Sphenodon*, with comments on the primitive character states of the throat muscles in lizards. Anat. Anz. 144:429-440.

__________. 1979. The braincase of *Typhlops* and *Leptotyphlops* (Reptilia: Serpentes). Zool. J. Linnean Soc. London 65:161-176.

__________. 1980. The perilymphatic system of the skull of *Typhlops* and *Acrochordus*, with comments on the origin of snakes. J. Herpetol. 14(1):105-108.

Robinson, P. 1962. Gliding lizards from the Upper Keuper of Great Britain. Proc. Geol. Soc. London 1601:137-146.

__________. 1967. The evolution of the Lacertilia. Colloq. Internat. C. N. R. S. 163:395-407.

__________. 1973. A problematic reptile from the British Upper Trias. J. Geol. Soc. London 129:457-479.

__________. 1975. The functions of the hooked fifth metatarsal in lepidosaurian reptiles. Colloq. Internat. C. N. R. S. 218:461-483.

__________. 1976. How *Sphenodon* and *Uromastyx* grow their teeth and use them. Pp. 43-64. *In* A. Bellairs and B. Cox (eds.), Morphology and Biology of Reptiles. Linnean Soc. London Symp. Ser. 3, Academic Press, London and New York.

Romer, A. 1945. Vertebrate paleontology. 2nd ed., Univ. of Chicago Press, Chicago, vii + 687 pp.

__________. 1956. Osteology of the reptiles. Univ. Chicago Press, xxi + 772 pp.

Russell, D., 1967. Systematics and morphology of American mosasaurs. Peabody Mus. Yale Univ. Bull. 23, vii + 240 pp.

Säve-Söderbergh, G. 1947. Notes on the brain-case in *Sphenodon* and certain Lacertilia. Zoologiska Bidrag. Fran. Uppsala 25:489-516.

Schwenk, K. 1988. A phylogenetic analysis of the lepidosaur tongue. Pp. 569-598. *In* R. Estes and G. Pregill, Phylogenetic Relationships of the Lizard Families, Stanford Univ. Press, Stanford, California.

Seiffert, J. 1973. Upper Jurassic lizards from central Portugal. Mem. Serv. Geol. Portugal 22:1-85.

Sigogneau-Russell, D. and D. Russell. 1978. Étude ostéologique du reptile *Simoedosaurus* (Choristodera). Ann. Paleont. (Vertébrés) 64(1):1-84.

Smith, K. 1980. Mechanical significance of streptostyly in lizards. Nature 283:778-779.

Sukhanov, V. 1961. (Some problems of the phylogeny and systematics of Lacertilia). Zool. Zhur. 40:73-83.

Sulimski, A. 1975. Macrocephalosauridae and Polyglyphanodontidae (Sauria) from the Late Cretaceous of Mongolia. Pal. Polonica 33:25-102.

Tarsitano, S. 1983. A case for the diapsid origin of ichthyosaurs. Neues Jahrb. Geol. Paläont. 1983(1):59-64.

Underwood, G. 1954. On the classification and evolution of geckos. Proc. Zool. Soc. London 124:469-492.

__________. 1957. On lizards of the family Pygopodidae, a contribution to the morphology and phylogeny of the Squamata. J. Morphol. 100:207-268.

__________. 1970. The eye. Pp. 1-98. *In* C. Gans and T. Parsons (eds.), The Biology of the Reptilia 2 (Morph. B), Academic Press, New York.

__________. 1971. A modern appreciation of Camp's "Classification of the Lizards". Introduction to reprint of Camp, C., Classification of the Lizards, Facsim. Reprint Herpetol., Soc. Stud. Amphib. Rept., pp. viii-xvii.

Vrba, E. 1980. Evolution, species and fossils: how does life evolve? S. Afr. J. Sci. 76:60-84.

Wild, R. 1973. Die Triasfauna der Tessiner Kalkalpen XXIII. *Tanystropheus longobardicus* (Bassani) (neue Ergebnisse). Schweiz. Palaont. Abh. 95:1-162.

Wiley, E. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley, New York, 439 pp.

Williston, S. 1899. Some additional characters of mosasaurs. Kansas Univ. Quart. 8(1A):39-41.

__________. 1925. The osteology of reptiles. Cambridge, 300pp.

Winchester, L. and A. de'Bellairs. 1977. Aspects of vertebral development in lizards and snakes. J. Zool. London 181:495-525.

Wingstrand, K. G. 1951. The structure and development of the avian pituitary. Gleerup, Lund.

APPENDICES

In order to support our contention that the phylogenetic hypothesis presented in this paper is the most parsimonious explanation for the distribution of apomorphic characters among Lepidosauromorpha, we present below the results of a computer based analysis of this group. Appendix I is a list of characters used to determine relationships within Lepidosauromorpha, indicating ancestral and apomorphic conditions for each character. Appendix II is a data matrix giving the distribution of different character states among thirteen taxa of lepidosauromorphs for each character in Appendix I. Appendix III gives the results of a computer based phylogenetic analysis of the data in Appendices I and II, and compares these results with our proposed hypothesis.

APPENDIX I

Characters Used To Determine Relationships Among Lepidosauromorphs

Polarities of these characters are based on outgroup comparisons with archosauromorphs and araeoscelidans, or as discussed in the text above. For each character below, zero denotes the ancestral condition for lepidosauromorphs and other integers indicate apomorphic conditions. In cases where a character with more than two states seems to represent a unidirectional transformation series, successively more derived states are indicated by successively larger integers (e.g., 0 - 1 - 2). The order of these states is inferred from the morphological series (plus outgroup comparison), which is hypothesized to represent an evolutionary sequence of character states. In cases where the apomorphic states of a character with more than one such state appear to have transformed independently from the ancestral condition, the character in question is separated into two or more characters. The characters are organized by skeletal region as they appear in the data matrix (Appendix II). Each character also has a position in the text corresponding to its level of universality, i.e. organization into successively inclusive statements applicable to each group. This position is indicated in one of two ways, described below.

Characters that diagnose major nodes discussed in the section on diagnoses of more inclusive lepidosauromorphan groups (p. 27) have page numbers in brackets that refer to their position in the text. Characters that delimit kuehneosaurs, and subgroups of younginiforms and rhynchocephalians, appear in the section on diagnoses of lepidosaurs and their extinct relatives (p. 17 et seq.) in the diagnoses of these groups and are identified by the following abbreviations or combinations of these abbreviations: Ac = *Acerosodontosaurus*; Ce = clevosaurs; Ho = *Homoeosaurus*; HSS = *Homoeosaurus*-sapheosaur-sphenodont group; Ge = *Gephyrosaurus*; Ku = kuehneosaurs; Rh = rhynchocephalians; Sa = sapheosaurs; Sp = sphenodontidans; Sd = sphenodonts; Ta = tangasaurs; Yd = younginoids; Yf = younginiforms; Yo = *Youngina;* these also appear in the brackets.

I. SKULL

1. Lacrimal large, with extensive exposure on the cheek (0); small, confined to the orbital rim (1); or absent (2). [36; Rh; Sp].
2. Greatest width of nasals exceeds greatest width of both nares (0); is less than the latter (1). [46].
3. Frontoparietal suture more or less W-shaped, subequal to or narrower than the nasofrontal suture in width (0); suture more or less straight, broader than nasofrontal suture (1). [47].
4. Parietal foramen within parietal (0); on frontoparietal border or within frontal (1). [Ku].
5. Postparietals present (0); absent (1). [33].
6. Tabulars present (0); absent (1). [32].
7. Postorbital overlain by postfrontal (0); postfrontal overlain by postorbital (1). [Rh].
8. Squamosal extends anteriorly halfway or less over lower temporal fenestra and is widely separated from jugal by postorbital (0); squamosal extends more than halfway over lower temporal fenestra and comes close to, or contacts, jugal below postorbital (1). [35].
9. Anterior process of quadratojugal present (0); absent (1). [Ce; Ge].
10. Posterior process of jugal extends about halfway back (or less) below lower temporal fenestra (0); extends more than half way back below lower temporal fenestra (1). [Sp]

11. Posterior process of jugal large, extending half way back or more below lower temporal fenestra (0); process small or absent (1). [49; Ku].

12. Quadratojugal present as a separate element at some time during post-embryonic ontogeny (0); never present as a separate element during post-embryonic ontogeny (1). [49; Ku; Sq].

13. Supratemporal present (0); fused or lost (1). [Ge; Ku; HSS].

14. Supratemporal lies superficially (0); supratemporal lies deep, wrapping around ventral surface of supratemporal process of parietal (1) (modified from Robinson, 1967). [48].

15. Ventral process of squamosal present (0); absent (1). [48; Ku].

16. Ventral hollow of squamosal caps dorsal head of quadrate (0); ventral hollow of squamosal absent, a ventral peg of squamosal fits into a notch or hole in dorsal surface of quadrate (1) (Robinson, 1967). [48].

17. Adductor chamber small, quadrate does not extend well below level of occipital condyle (0); enlarged adductor chamber, and quadrate extends well below occipital condyle (1). [30; HSS].

18. Nares paired (0); confluent (1). [Ku].

19. Quadrate narrow in posterior view (0); wide in posterior view, forming a lateral conch (1). [30; HSS].

20. Quadrate overlaps pterygoid laterally to form a fixed connection between the two bones (0); no overlap and no fixed connection exists between the two bones (1). [51].

21. Quadrate foramen present (0); absent (1). [49].

22. Vomerine teeth numerous (0); few or absent (1). [50].

23. Lateral row of enlarged palatine teeth absent (0); lateral tooth row present on palatine, converging posterad (1); anterior four or five teeth of lateral palatine tooth row enlarged relative to others (2); lateral palatine tooth row parallels maxillary tooth row (3); parallel palatine tooth row elongated posteriorly (4). [Rh; Sp; HSS; Sd].

24. Teeth on transverse flange of pterygoid present (0); absent (1) (Carroll, 1988). [33].

25. Palatal teeth present in addition to palatine row (0); except for palatine row, palatal teeth absent (1). [HSS].

26. Pterygoids and vomers in contact medially (0); not in contact medially (1). [50].

27. Pterygoid processes of quadrates long, extending anteriorly to level of sphenoccipital tubercles or beyond (0); processes short, not extending anteriorly to level of sphenoccipital tubercles (1). [Rh].

28. Epipterygoid expanded ventrally, contacting quadrate (0); epipterygoid narrow ventrally, columelliform, not contacting quadrate (1). [51].

29. Abducens canal absent or incomplete (0); present and complete (1). [37].

30. Vidian canal open posterolaterally to form channel on basisphenoid or parabasisphenoid (0); channel fully enclosed by bone (1). [52].

31. Parasphenoid teeth present (0); absent (1). [36; Yf].

32. Metotic fissure not subdivided, recessus scalae tympani absent (0); metotic fissure subdivided to form recessus scalae tympani anteriorly and jugular foramen posteriorly; lateral aperture of recessus forms "fenestra rotunda" (1). [51].

33. Paroccipital process does not extend laterally to contact quadrate (0); process contacts quadrate (1). [33].

34. Paroccipital process not expanded distally (0); expanded distally (1). [51].

35. Stapes thick, perforated for passage of stapedial artery in adults (0); stapes relatively thinner, imperforate in adults (1); stapes columelliform, usually imperforate in adults (2). [36; 51].

36. Quadrate straight in lateral view (0); bowed (1). [30].

37. Septomaxilla limited to posteroventral edge of fenestra exonarina, thus forming bony side wall and part of floor of nasal capsule (0); septomaxilla covers enormously enlarged vestibule to roof Jacobson's organ dorsally and floor nasal capsule ventrally (1) (Malan, 1946). [46].

38. No posteroventral process of septomaxilla (0); process present, forming posterior margin of duct of Jacobson's organ (1). [46].

39. Prominent posterior process of palatine approaches or contacts ectopterygoid to nearly or completely exclude pterygoid from suborbital fenestra (0); posterior process of palatine reduced, pterygoid consequently broadly included in suborbital fenestra (1). [50].

40. Squamosal does not cover most of quadrate in lateral view (0); covers most of quadrate in lateral view (1). [HSS].

41. Postorbital contacting parietal (0); separated from parietal (1). [Yf; Rh].

42. Posterior process of postorbital does not reach to posterior end of upper temporal fenestra (0); process extends beyond posterior margin of upper temporal fenestra (1). [Yf].

43. Upper temporal fenestra broad, suboval to round (0); upper temporal fenestra elongate and narrower (1) (Cocude-Michel, 1963). [Sa].

44. Postorbital region of skull shorter than preorbital region (0); equal to or longer than preorbital region (1) (Cocude-Michel, 1963). [Sa].

45. Upper temporal arch not broad (0); upper temporal arch broad (1) (Cocude-Michel, 1963). [Sa].

46. Supratemporal process of parietal long and dorsal process of squamosal short (0); supratemporal process of parietal short and dorsal process of squamosal long (1). [HSS].

47. Parietal table broad in fully grown individuals (0); narrow (1). [HSS; Ho].

48. Postfrontal not enlarged (0); greatly enlarged (1). [Sd; Ho].

49. Palatine not broadened laterally, suborbital fenestra large and suboval (0); palatine broadened laterally, suborbital fenestra constricted anteriorly (1); palatine further broadened laterally, suborbital fenestra further constricted (2); lateral margin of palatine parallel to medial border of maxilla, suborbital fenestra nearly closed (3). [Rh; HSS; Sd].

50. Nasal process of premaxilla narrow (0); broad (1). [Sd].

51. No fangs on dentary and maxilla (0); successional fangs at anterior ends of maxilla and dentary (1). [Sd].

52. No diastema between premaxillary and maxillary tooth rows (0); a large diastema present (1). [Sd].

53. Upper temporal fenestra oval and small (0); very large and subrectangular (1) (Cocude-Michel, 1963). [Sd].

54. Quadrate foramen small (0); large (1) (Cocude-Michel, 1963). [HSS].

55. No premaxillary chisels (0); premaxillae grow downward to form two chisel-shaped structures in post-embryonic ontogeny (Robinson, 1973). [Sp].

56. Maxillary teeth not flanged (0); posterior flange present (1); teeth with prominent posterior flange (2) (Cocude-Michel, 1963). [Sp; Ho].

57. Posterior maxillary teeth not enlarged (0); four enlarged conical flanged teeth followed by three tiny teeth (1) (Robinson, 1973; Fraser, 1982). [Ce].

58. Jugal does not contact squamosal below lower temporal fenestra (0); jugal contacts squamosal below lower temporal fenestra (1). [Sp].

59. Prefrontal-nasal suture parallel with midline (0); anteriorly, suture divergent laterad (1). [32; Ge].

60. Choanal fossa on palatine absent (0); present (1). [51].

61. Snout comparatively broader and shorter (0); longer and narrower (1). [Yf].

62. Premaxillae paired in fully grown individuals (0); fused prior to hatching (1). [46].

63. Parietals paired in fully grown individuals (0); fused prior to hatching (1). [47].

64. Exoccipitals fused to opisthotic in fully grown individuals (0); fused prior to hatching (1). [52].

65. Frontals paired (0); fused (1). [Ge].

II. LOWER JAW

66. Dentary extends posteriorly to level of coronoid eminence or slightly beyond (0); extends posteriorly more than halfway between coronoid eminence and articular condyle (1). [Rh].

67. Splenial present (0); absent (1). [Rh].

68. Meckel's groove open (0); restricted or covered by dentary (1). [Ge].

69. Coronoid eminence formed by coronoid medially and surangular laterally (0); formed primarily by coronoid (dentary may also participate) (1). [52; Sp].

70. Angular extends posteriorly to articular condyle (0); angular does not extend posteriorly to articular condyle (1). [52].

71. Angular extends more than one-third of the way up lateral surface of mandible (0); extends less than one-third of the way up lateral surface of mandible (1). [33].

72. Retroarticular process relatively small (0); large (1). [31].

73. Retroarticular process present (0); absent (1). [HSS].

74. Outer one-third to one-half of articular condyle formed by surangular (0); articular condyle formed entirely by articular, surangular forming only its outer rim (1). [37].

75. Teeth set in shallow sockets or depressions (subthecodont or subpleurodont) (0); superficially attached to medial surface of jaw (pleurodont) (1); superficially attached with tooth replacement reduced or lacking (acrodont) (2). [37; Sp].

76. Articular condyle wider than long, anteroposterior ridge small or absent (0); condyle as long as wide, strong anteroposterior ridge present (1); condyle longer than wide, anteroposterior ridge present (2) (Evans, 1980). [Rh; Sp].

III. VERTEBRAL COLUMN AND RIBS

77. Neural arches fuse to their respective centra in post-embryonic development (0); fuse in the embryo (1). [54].

78. Zygosphenes and zygantra absent (0); present (1). [38].

79. Intercentra of cervical vertebrae relatively flat ventrally (0); keeled ventrally to form specialized hypapophyses (1) (Hoffstetter and Gasc, 1969). [53].

80. Autotomy septa of caudal vertebrae absent (0); present (1). [38].

81. Trunk vertebrae without accessory articulations between neural spines (0); accessory articulations present (1). [Yd].

82. Caudal vertebral centra round or oval in cross-section (0); compressed laterally (1) (Cocude-Michel, 1963). [Sa].

83. Intercentra present on trunk vertebrae (0); absent (1). [54; Ku].

84. Vertebrae amphicoelous (0); procoelous (1). [55].

85. Transverse processes not elongated (0); extremely elongated (1). [Ku].

86. One or more cervical ribs bear two distinct heads (bicipital, dichocephalous) (0); all ribs single headed (unicipital, holocephalous) (1) (Hoffstetter and Gasc, 1969). [53].

87. Sacral and caudal ribs fuse to their respective centra in post-embryonic development (0); fuse in embryonic development (1). [54].

88. Posterior process on second sacral rib present (0); absent (1). [Sd].

89. No aliform outgrowths on distal rib segments (0); aliform outgrowths present (1) (Cocude-Michel, 1963). [HSS].

IV. SHOULDER GIRDLE

90. Xiphisternum relatively large (0); small (1); absent (2). [39; Sd].

91. Rib-bearing portion of sternum a single rod (0); this region of sternum enlarged and formed of two plates that remain paired until nearly maximum adult size (1); paired sternal plates fuse in embryo (2) (Carroll, 1977). [27; 39].

92. Anterior margin of scapulocoracoid without fenestrae or emarginations (0); fenestrae or emarginations present (1). [55].

93. Interclavicle robust (0); gracile (1). [31].

94. Cleithrum present (0); absent (1) (Evans, 1981). [31].

95. Clavicles contact scapula (0); clavicles contact suprascapula (1) (Lécuru, 1968b). [55].

V. FORELIMB

96. Radius not twisted (0); twisted (1) (Currie, 1980). [Ac].

97. Humerus shaft thick, robust (0); humerus robust, shaft reduced in thickness (1); humerus gracile (2) [33; 55; Ho].

98. Entepicondylar foramen of humerus present (0); absent (1). [56].

99. Prominent posteromedial process of distal epiphyses of radius absent (0); present (1). [56].

100. Distal end of ulna gently convex (0); nearly hemispherical, its articulation socket with ulnare concomitantly more prominently developed (1). [56].

101. Intermedium large, contacts ulna (0); small or absent, fails to contact ulna (1). [57].

102. Lateral centrale of manus fails to contact second distal carpal (0); both bones in contact (1). [57].

103. First distal carpal a separate bony element (0); fused to first metacarpal (1). (Carroll, 1977). [57].

104. First and fifth metacarpals relatively thin compared to second, third and fourth (0); first and fifth metacarpals relatively thick; second, third and fourth gracile (1). [39].

105. Fourth metacarpal longer than third (0); third and fourth metacarpals subequal in length (1); fourth metacarpal shorter than third (2). [33; 39].

106. Medial and lateral centrale in hand subequal in size (0); medial centrale as much as twice as large as lateral centrale (1). [28].

107. Olecranon process and sigmoidal notch of ulna well developed in all but juvenile individuals (0); process and sigmoidal notch poorly developed in fully grown individuals (1). [Yf].

108. Shafts of radius and ulna subequal in length (0); shaft of radius longer than shaft of ulna (1). [Yd].

109. Humeral entepicondyle not strongly developed in fully grown individuals (0); strongly developed in fully grown individuals (1). [Yd].

110. In fully grown individuals humerus shorter than femur (0); as long or longer than femur (1). [Ta].

111. Medial centrale does not contact fourth distal carpal, lateral centrale contacts third distal carpal (0); medial centrale contacts fourth distal carpal, thus excluding lateral centrale from contacting third distal carpal (1). [Ta].

112. Scapula larger than coracoid and mainly developed dorsally (0); scapula low, mainly developed ventrally, and subequal to coracoid in size (1). [Ta].

113. In fully grown individuals, radius is 80% length of humerus and 60% length of tibia (0); radius is 50-60% length of humerus and 65-70% length of tibia (1). [Ta].

114. Ectepicondylar groove in humerus present throughout ontogeny (0); foramen formed at some point in ontogeny (1). [28].

115. Ectepicondylar foramen formed in post-embryonic ontogeny (0); foramen formed in the embryo (1). [39].

VI. PELVIC GIRDLE

116. Ilium includes 80-85% of acetabulum (0); ilium includes 60-65% of acetabulum (1). [40].

117. Pubic flange on ilium absent (0); present (1). [40].

118. Iliac blade long (0); short (1) (Gow, 1975). [Yo].

119. Anteromedial portion of pubis not outturned dorsally (0); outturned dorsally (1) (Carroll, 1977). [41].

120. Dorsal edge of ilium essentially horizontal (0); more steeply inclined (1). [40].

121. Pelvic girdle forms a solid plate (0); pelvic girdle with relatively small thyroid fenestra and broad pubic symphysis (1); pelvic girdle with large fenestra and narrow pubic symphysis (2). [33; 58].

122. Ischial tubera short (0); long (1) (Cocude-Michel, 1963). [HSS].

123. In fully grown individuals, pelvic elements separate (0); fused (1). [39].

VII. HIND LIMB

124. Fibula and femur articulate end to end, distal femoral condyles symmetrical (0); fibula sits in a recess on lateral margin of distal end of femur, distal femoral condyles markedly asymmetrical (1). [41].

125. Articular surface of fibula where it articulates with astragalocalcaneum restricted to a small portion of distal end of fibula (0); articular surface covers most of distal end of fibula (1). [58].

126. Astragalus and calcaneum separate throughout ontogeny (0); fused prior to fusion of scapula and coracoid (1). [42].

127. Lateral centrale of pes present as a distinct element throughout ontogeny (0); fused to astragalus in embryo (1). [41].

128. First distal tarsal present (0); absent (1). [42].

129. Second distal tarsal present (0); absent (1). [59].

130. Fifth distal tarsal present as a discrete element at some stage of post-embryonic ontogeny (0); absent or fused to another element in the embryo (1). [42; Ta].

131. Fourth and fifth distal tarsals separate (0); fused during post-embryonic ontogeny (1). [Ta].

132. Fifth metatarsal straight (0); hooked, inflected, angulated proximally and with medial and lateral plantar tubercles (1); modified proximal head and enlarged medial plantar tubercle (2) (Robinson, 1975). [42; 59].

133. Ridge on distal extremity of tibia for astragalar articulation (0); no ridge present (1) (Reisz, 1981). [58].

134. No tongue and groove articulation at fourth distal tarsal/astragalocalcaneal joint (0); process on fourth distal tarsal extends under astragalus to form partial tongue and groove articulation (1); complex tongue and groove ankle joint present (2). [32; 59].

VIII. MISCELLANEOUS OSTEOLOGICAL CHARACTERS

135. Complete third branchial arch (0); interrupted third branchial arch (1) (Camp, 1923; Kluge, 1983). [45].

136. Gastralia present (0); absent (1). [59].

137. Bony epiphyses absent (0); present (1) (Carroll, 1977). [43].

138. Bone with both cancellous and vascular components (0); most of skeleton composed of dense lamellar avascular bone of periosteal origin (1) (Enlow, 1969). [44].

139. Few connective tissue calcifications present (0); calcification of many tendons, sheets of connective tissue; ligaments, sesamoids, and cartilage occurs prior to full maturity (1). [44].

140. A single row of mid-dorsal osteoderms absent (0); present (1) (Gow, 1975). [Yo].

IX. CHARACTERS FROM SOFT ANATOMY

141. Pars tuberalis of adenohypophysis present (0); absent (1) (Wingstrand, 1951). [46].

142. Cochlear duct faces ventrally in adult (0); laterally in adult (1) (Baird, 1970). [46].

143. No prominent perilymphatic sac within recessus scalae tympani absent (0); sac present (1) (Baird, 1970). [46].

144. Extensive development of cartilage in anterior braincase and interorbital septum, membranous fenestrae in this region consequently small (0); reduced cartilaginous component of anterior braincase and interorbital septum, membranous fenestrae in this region consequently large (1) (Bellairs and Kamal, 1981). [45].

145. Caruncle present, egg tooth absent (0); caruncle absent, egg tooth present (1). [45].

146. Pallets on ventral surface of tongue tip absent (0); present (1) (Schwenk, 1988). [45].

147. Jacobson's organ a diverticulum of nasal capsule, fungiform body absent (0); Jacobson's organ entirely separate from nasal capsule, fungiform body present (1) (Pratt, 1948). [45].

148. Sensory epithelium of Jacobson's organ weakly developed (0); sensory epithelium extensive (1) (Pratt, 1948). [45].

149. Paraseptal cartilage forms a trough-like support for floor of Jacobson's organ, the duct of which is lateral, opening into medial wall of choana (0); Jacobson's organ apparently rotated ninety degrees about its longitudinal axis, paraseptal cartilage medially located and duct of Jacobson's organ opens ventrally directly into organ cavity (1) (Malan, 1946). [45].

150. Lateral nasal gland small, not enclosed in cavum conchale (0); gland enlarged, enclosed in cavum conchale (1) (Pratt, 1948). [45].

151. Lacrimal duct extends anteriorly to end of choanal groove (0); extends anteriorly to region of duct of Jacobson's organ (1) (Bellairs and Boyd, 1950; Parsons, 1970). [45].

152. Interhyal cartilaginous (0); ligamentous or absent (1) (de Beer, 1937). [46].

153. Ovaries solid (0); saccular (1) (Porter, 1972). [46].

154. Mm. intermandibularis and mandibulohyoideus not interdigitating (0); multiple interdigitations present (1) (Camp, 1923; Rieppel, 1978). [45].

155. M. intermandibularis innervated by both mylohyoid and facial nerves (0); innervated only by mylohyoid nerve (1) (Rieppel, 1978). [45].

156. M. depressor mandibulae and m. episternocleidomastoideus not completely separated (0); completely separated (1) (Rieppel, 1978). [45].

157. M. clavodeltoideus confined to dorsal surface of clavicle (0); at least some fibers extend onto ventral surface of clavicle (1) (Peterson, 1973). [45].

158. Meniscus of knee joint formed by separate lateral and medial crescents on either side of cruciate ligament (0); meniscus formed by a single plate that is pierced by cruciate ligament (1) (Haines, 1942). [45].

159. Paired copulatory organs absent (0); paired, evertible hemipenes present in males (1) (Oppel, 1811). [45].

160. Cloacal slit anteroposteriorly oriented (0); cloacal slit transverse (1) (Günther, 1867). [35].

161. Kidney without sexual segment (0); sexual segment present (1) (Fox, 1977). [35].

162. Tongue not notched distally (0); notched distally (1) (Schwenk, 1988). [35].

163. Tongue not used to secure small prey (0); used to secure small prey (1) (Gorniak et al., 1982). [35].

164. Ciliary process present (0); reduced or absent (1) (Underwood, 1970). [35].

165. Tendon of m. nictitans attached to m. pyramidalis, the latter taking origin on surface of eyeball (0); tendon attaches to m. retractor bulbi muscle and interorbital septum (1) (Underwood, 1970). [35].

166. Skin not regularly shed in its entirety (0); regularly shed in its entirety (1) (Gans, 1978). [35].

167. No cartilaginous disc (tenon) in lower eyelid (0); present (1) (Romer, 1956). [35].

168. No modified mid-dorsal scale row (0); modified mid-dorsal scale row (1). [35].

169. Two divisions of m. retractor bulbi (0); lateral division becomes m. bursalis (1) (Underwood, 1970). [44].

170. Femoral and preanal organs absent (0); present (1) (Kluge, 1983). [45].

171. Based on calcified ventral rib attachments, seven cervical vertebrae present (0); based on loss of contact between rib of eighth vertebra and sternum, eight cervical vertebrae present (1). [53].

APPENDIX II

Taxon/Character Matrix

This matrix gives the condition of each character in Appendix I for thirteen taxa of Lepidosauromorpha. The character state codes are the same as those in Appendix I with two additional codes. A question mark indicates that the region of the body bearing the character in question has not been preserved; the letter "N" indicates that the taxon cannot be scored for the character in question even though the region is preserved. Characters 13 and 14 are examples of the second case. When the supratemporal is absent, it cannot be determined whether this is a transformation of the condition in which the supratemporal lies superficially or the one in which it lies deep. Thus, those taxa lacking a supratemporal must be scored "N" for character 14, position of the supratemporal.

Abbreviations are as follows, given in the same order as in the columns below: Tan = tangasaurs; You = *Youngina;* Ace = *Acerosodontosaurus*; Pig = *Paliguana*; Pag = *Palaeagama*; Sau = *Saurosternon;* Kue = kuehneosaurs; Sph = sphenodonts; Hom = homoeosaurs; Sap = sapheosaurs, Cle = clevosaurs; Gep = *Gephyrosaurus*; Squ = squamates.

	Tan	You	Ace	Pig	Pag	Sau	Kue	Sph	Hom	Sap	Cle	Gep	Squ
1	0	0	0	0	?	?	0	2	2	2	2	1	1
2	1	1	?	0	?	?	0	0	0	0	0	1?	1
3	0	0	0	0	?	?	0	0	0	0	0	0	1
4	0	0	?	0	0	?	1	0	0	0	0	0	0/1
5	0	0	?	0	?	?	1	1	1	1	1	1	1
6	0	0	?	0	?	?	1	1	1	1	1	1	1
7	0	0	0	?	0	?	0	1	1	1	1	1	0
8	0	0	0	0	?	?	0	1/0	1	1	1	1	1/0
9	0	0	0	?	?	?	N	0	0	0	1	1	N
10	0	0	0	?	?	?	0	1	1	1	1	0	0
11	0	0	0	?	?	?	1	0	0	0	0	0	1
12	0	0	0	?	?	?	1	0	0	0	0	0	1
13	0	0	?	?	?	?	1	1	1	1	0	1?	0
14	0	0	?	?	?	?	N	N	N	N	0	N?	1
15	0	0	0	0	?	?	1	0	0	0	0	0	1
16	0	0	0	0	?	?	0	0	0	0	0	0	1
17	0	0	0	1	?	?	1	0	0	0	1	1	1
18	?	0	?	?	?	?	1	0	0	0	0	0	0
19	0	0	0	1	?	?	1	0	0	0	0	1	1
20	0	0	?	0	?	?	0	0	0	0	0	0	1
21	0	0	?	?	?	?	1	0	0	0	0	0	1
22	0	0	?	?	?	?	?	1	1	1	0	0	1
23	0	0	?	?	?	?	0	4	3	3	2	1	0
24	0	0	?	?	?	?	1	1	1	1	1	1	1
25	0	0	?	?	?	?	0	1	1	1	0	0	0
26	0	0	?	?	?	?	0	0	0	0	0	0	1
27	0	0	?	0	?	?	0	1	1	1	1	1	0
28	0	0	?	?	?	?	?	0	0	0	?	0	1
29	?	0	?	?	?	?	0	1	?	?	1	1	1
30	?	0	?	?	?	?	0	0	?	?	0	0	1

	Tan	You	Ace	Pig	Pag	Sau	Kue	Sph	Hom	Sap	Cle	Gep	Squ
31	1	1	?	?	?	?	0	1	1	1	1	1	1
32	0	?	0	?	?	0	0	0	0	0	0	0	1
33	0	0	?	0	?	?	1	1	1	1	1	1	1
34	0	0	?	0	?	?	0	0	0	0	0	0	1
35	0	0	?	?	?	?	0	1	?	?	?	?	2
36	0	0	0	1	?	?	1	0	0	0	1	1	1
37	?	?	?	?	?	?	?	0	0	0	0	?	1
38	?	?	?	?	?	?	?	0	?	?	?	?	1
39	0	0	?	?	?	?	0	0	0	0	0	0	1
40	0	0	0	0	0	?	0	1	1	1	0	0	0
41	1	1	1	?	?	?	0	1	1	1	1	1	0/1
42	1	1	1	0	?	?	0	0	0	0	0	0	0
43	0	0	?	0	?	?	0	0	0	1	0	0	0
44	0	0	?	?	?	?	0	0	0	1	0	0	0
45	0	0	0	0	?	?	0	0	0	1	0	0	0
46	0	0	0	0	?	?	0	1	1	1	0	0	0
47	0	0	0	0	0	?	0	1	0	1	0	0	0
48	0	0	0	0	0	?	0	1	1	1	0	0	0
49	0	0	?	?	?	?	0	3	2	2	2	1	0
50	0	0	?	?	?	?	0	1	0	0	0	0	0
51	0	0	?	?	?	?	0	1	0	0	0	0	0
52	0	0	?	?	?	?	0	1	?	0	0	0	0
53	0	0	?	0	?	?	0	1	0	0	0	0	0
54	0	0	?	?	?	?	N	1	?	?	0	0	N
55	0	0	?	?	?	?	0	1	1	1	1	0	0
56	0	0	0	0	0	?	0	1	2	2	1	0	0
57	0	0	0	?	?	?	0	0	0	0	1	0	0
58	0	0	0	?	?	?	0	1	1	1	0	0	0
59	0	0	?	0	?	?	1	1	1	1	1	1	1
60	0	0	?	?	?	?	0	0	0	0	0	0	1
61	1	1	?	0	0	?	0	0	0	0	0	0	0
62	?	0	?	?	?	?	0	0	0	0	0	0	1/0
63	0	0	0	0	0	?	0	0	0	0	0/1	1	1/0
64	0	0	?	0	?	?	0	0	?	?	0	0	1/0
65	0	0	0	0	0	?	0	0	0	0	0/1	1	0/1
66	0	0	?	0	?	?	0	1	1	1	1	1	0/1
67	0	0	0	?	?	?	0	1	1	1	1	1	0/1
68	?	?	?	?	?	?	0	0	0	0	0	1	0/1
69	0	0	0	?	?	?	?	0	0	0	0	0	1
70	0	0	0	?	?	?	0	0	0	0	0	0	1
71	0	0	?	?	?	?	1	1	1	1	1	1	1
72	0	0	0	1	?	?	1	0	0	0	1	1	1
73	0	0	0	0	?	?	0	1	1	1	0	0	0
74	?	0	?	?	?	?	?	1	?	?	?	1	1
75	0	0	0	?	?	?	0	2	2	2	2	1	1/2

	Tan	You	Ace	Pig	Pag	Sau	Kue	Sph	Hom	Sap	Cle	Gep	Squ
76	?	?	0	?	?	?	?	2	2	2	?	1	0
77	0	0	0	?	?	?	?	0	?	?	?	0?	1
78	0	0	0	?	?	?	?	1	?	?	?	1	1/0
79	0	0	?	?	?	?	0	0	0	0	?	0	1
80	0	0	?	?	?	0	0	1	1	1	?	1	1/0
81	1	1	0	?	0	0	0	0	0	0	?	0	0
82	0/1	0	0	?	0	0	0	0	0	1	?	0	0
83	0	0	0	?	0	0	1	0	0	0	?	0	1/0
84	0	0	0	?	0	0	0	0	0	0	?	0	1/0
85	0	0	0	?	0	0	1	0	0	0	?	0	0
86	0	0	?	?	?	?	0	0	0	0	0	0	1
87	0	0	0	?	0	?	?	0	?	?	?	?	1
88	0/1	0	?	?	?	?	1	1	0	0	?	0	0/1
89	?	?	?	?	?	?	?	1	0	1	?	?	0
90	?	?	?	?	?	?	?	2	?	?	?	?	1
91	1	?	?	?	?	1	?	2	2	2	?	?	2
92	0	0	?	?	?	0	0	0	0	0	?	0	1
93	0	0	?	?	?	1	?	1	1	1	?	1	1
94	0	0	?	?	?	1	?	1	1	1	?	1	1
95	0	0	?	?	?	0	?	0	0	0	?	0	1/0
96	0	0	1	?	0?	0	0	0	0	0	?	?	0
97	0	0	0	?	0	0	2	1	2	1	?	1	2
98	0	0	0	?	?	0	1	0	0	0	?	0	1
99	0	0	0	?	?	?	?	0	0	0	?	?	1
100	0	0	0	?	?	?	?	0	0	0	?	?	1
101	0	0	0	?	?	1?	?	0	0	0	?	?	1
102	0	?	0	?	?	?	?	0	0	0	?	?	1
103	0	0	0	?	?	0	?	0	0	0	?	?	1
104	0	0	0	?	0	0	0	1	1	1	?	?	1
105	0/2	0	0	?	0	0	1	2	2	2	?	?	2
106	1	1	1	?	?	1	?	1	1	1	?	?	1
107	1	1	1	?	?	?	0	0	0	0	?	0	0
108	1	1	0	?	0	0	0	0	0	0	?	?	0
109	1	1	0	?	0	0	0	0	0	0	?	0	0
110	1	0	0	?	0	0	0	0	0	0	?	0	0
111	1	?	0	?	?	?	?	0	0	0	?	?	0
112	1	0	?	?	?	0	0	0	0	0	?	0	0
113	1	0	0	?	0	0	0	0	0	0	?	?	0
114	1	1?	?	?	1	1	1	1	1	1	?	1	1/N
115	0	0	?	?	?	?	?	1	?	?	?	?	1
116	0	0	0	?	?	?	0	1	1	1	?	1	1
117	0	0	0	?	?	?	0	1	?	?	?	1	1
118	0	1	0	?	?	?	0	0	0	0	?	0	0
119	0	0	0	?	?	?	?	1	1	1	?	1	1
120	0	0	0	?	?	?	0	1	1	1	?	1	1

	Tan	You	Ace	Pig	Pag	Sau	Kue	Sph	Hom	Sap	Cle	Gep	Squ
121	0	0	0	?	0	0	1	1	1	1	?	1	2
122	0	0	0	?	0	0	0	0	1	1	?	0	0
123	0	0	?	?	?	?	0?	1	1	1	?	1	1
124	0	0	0	?	?	?	?	1	1	1	?	1	1
125	0	?	?	?	?	?	?	0	0	0	?	?	1
126	0	?	?	?	?	0	?	1	1	1	?	1	1
127	0	?	?	?	?	0	?	1	1	1	?	1	1
128	0	?	?	?	?	0	?	1	1	1	?	?	1
129	0	?	?	?	?	0	?	0	0	0	?	?	1
130	0/1	?	?	?	?	0	?	1	1	1	?	1	1
131	1	?	?	?	?	0	?	?	?	?	?	?	?
132	0	0	?	?	?	0	0	1	1	1	?	1	2
133	0	?	?	?	?	?	?	0	?	?	?	?	1
134	0	0	?	?	?	1	?	1	1	1	?	1	2
135	?	?	?	?	?	?	?	0	?	?	?	?	1/0
136	0	0	0	?	0	0	0	0	0	0	?	0	1
137	0	0	0	?	?	?	?	1	1	1	?	1	1
138	?	?	?	?	?	?	?	1	?	?	?	?	1
139	?	?	?	?	?	?	?	1	?	?	?	?	1
140	0	1	0	?	0?	0	0	0	0	0	?	?	0
141	?	?	?	?	?	?	?	0	?	?	?	?	1
142	?	?	?	?	?	?	?	0	?	?	?	?	1
143	?	?	?	?	?	?	?	0	?	?	?	?	1
144	?	?	?	?	?	?	?	0	?	?	?	?	1
145	?	?	?	?	?	?	?	0	?	?	?	?	1
146	?	?	?	?	?	?	?	0	?	?	?	?	1
147	?	?	?	?	?	?	?	0	?	?	?	?	1
148	?	?	?	?	?	?	?	0	?	?	?	?	1
149	?	?	?	?	?	?	?	0	?	?	?	?	1
150	?	?	?	?	?	?	?	0	?	?	?	?	1
151	?	?	?	?	?	?	?	0	?	?	?	?	1
152	?	?	?	?	?	?	?	0	?	?	?	?	1
153	?	?	?	?	?	?	?	0	?	?	?	?	1
154	?	?	?	?	?	?	?	0	?	?	?	?	1
155	?	?	?	?	?	?	?	0	?	?	?	?	1
156	?	?	?	?	?	?	?	0	?	?	?	?	1
157	?	?	?	?	?	?	?	0	?	?	?	?	1
158	?	?	?	?	?	?	?	0	?	?	?	?	1
159	?	?	?	?	?	?	?	0	?	?	?	?	1
160	?	?	?	?	?	?	?	1	?	?	?	?	1
161	?	?	?	?	?	?	?	1	?	?	?	?	1
162	?	?	?	?	?	?	?	1	?	?	?	?	1
163	?	?	?	?	?	?	?	1	?	?	?	?	1
164	?	?	?	?	?	?	?	1	?	?	?	?	1
165	?	?	?	?	?	?	?	1	?	?	?	?	1

	Tan	You	Ace	Pig	Pag	Sau	Kue	Sph	Hom	Sap	Cle	Gep	Squ
166	?	?	?	?	?	?	?	1	?	?	?	?	1
167	?	?	?	?	?	?	?	1	?	?	?	?	1
168	?	?	?	?	?	?	?	1	?	?	?	?	1
169	?	?	?	?	?	?	?	0	?	?	?	?	1
170	?	?	?	?	?	?	?	0	?	?	?	?	1/0
171	?	?	?	?	?	?	?	1	0?	0?	?	?	1

APPENDIX III

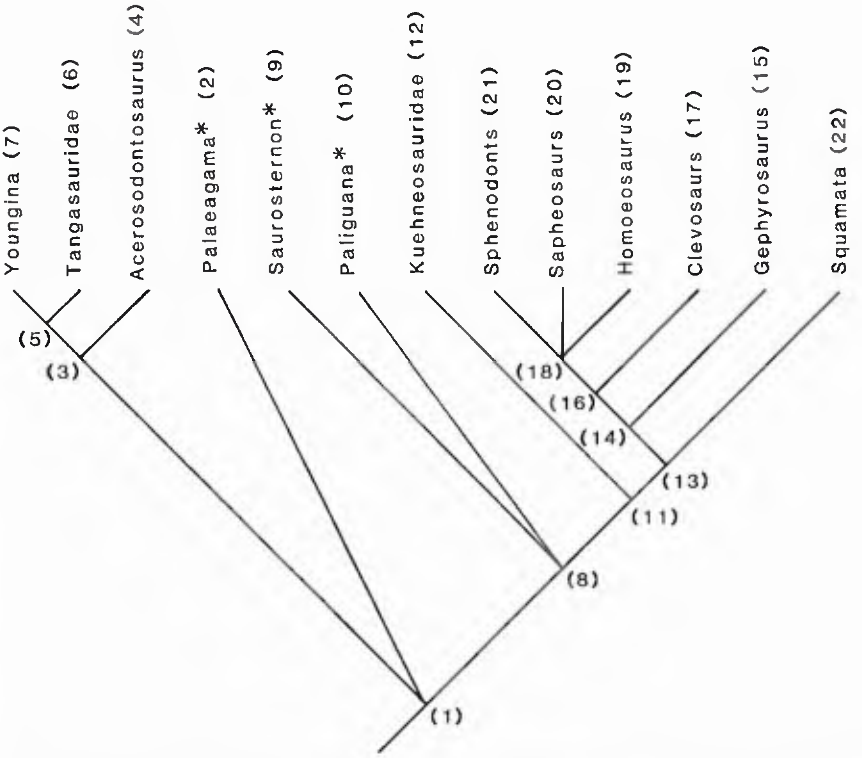
Results of a Computer-Based Phylogenetic Analysis of the Data in Appendices I and II

We analyzed the data in Appendices I and II using the Wagner program in the PHYSYS package for computer assessment of phylogenetic relationships written by J. S. Farris and installed in the California State University CYBER system. Both "?" and "N" character state scores were entered as missing data. Characters that varied within basic taxa were assigned the first of the two or more states listed in Appendix II. Numbers here follow those in Appendices I and II. Characters of soft anatomy (numbers 141-171) were not included in this analysis. These characters serve to support the monophyly of both Lepidosauria and Squamata among other living organisms, but they are of little use in placing many of the fossils we discuss. For example, extant archosauromorphs enable us to infer that the apomorphic conditions were not present in Sauria ancestrally. It is equally parsimonious to accept that the apomorphic resemblances in soft anatomical characters shared by Recent *Sphenodon* and squamates were present in their most recent common ancestor. Because of missing data, however, we cannot determine the level at which these characters arose within lepidosauromorphs prior to the origin of lepidosaurs. In such cases we are inclined to place the characters at the level at which they can be observed (i.e., Lepidosauria), although we recognize that they may apply to more inclusive groups of lepidosauromorphs.

Wagner analysis yielded twenty-eight cladograms of equal length. They differed from one another and from our proposed hypothesis (see text and Fig. 13) only in the relative positions of the three metataxa, *Palaeagama**, *Paliguana**, and *Saurosternon**, and in the relationships among sphenodonts, sapheosaurs, and *Homoeosaurus*. Character discordance accounts for the unresolved relationships among *Homoeosaurus*, sapheosaurs, and sphenodonts, but missing data in the metataxa are responsible for most of the cladograms.

In all twenty-eight cladograms, *Paliguana** and *Saurosternon** formed a monophyletic group with kuehneosaurs plus lepidosaurs, although their precise relationships to the kuehneosaur-lepidosaur clade were variable. *Palaeagama** was more variable in its position, either forming one branch of an unresolved trichotomy with younginoids and *Acerosodontosaurus*, occuring at an unresolved position at the basal node of the cladogram, or taking various positions within a clade consisting of itself, *Paliguana**, *Saurosternon**, and kuehneosaurs plus lepidosaurs, although never within the last group. Sphenodonts, sapheosaurs, and *Homoeosaurus* consistently form a clade, but sapheosaurs are sometimes the sister group of sphenodonts, and other times the sister group of *Homoeosaurus*.

The twenty-eight alternative cladograms were distilled to form a single consensus cladogram (Appendix Fig. 1) using the Adams program in PHYSYS (see Adams, 1972). The following list gives the synapomorphies of the terminal and subterminal nodes (hypothesized clades except in the case of metataxa indicated by *) of the Adams consensus cladogram as determined by the Diagnose program in PHYSYS. Numbers of nodes in this list correspond with those on the consensus cladogram (Appendix Fig. 1). In addition to listing synapomorphies, we also indicate all required convergences and character reversals. The distribution of some characters is such that parsimony will not allow an unambiguous historical interpretation. We discuss briefly those cases in which our interpretations of character optimization differ from those of PHYSYS (viz., Ferris optimization), although we are aware that such decisions are arbitrary.



APPENDIX FIGURE 1. Consensus cladogram of lepidosauromorph relationships as determined by the Adams option in the PHYSYS program. Numbers at nodes are the same as the numbers of nodes discussed in Appendix 3.

NODE 1: LEPIDOSAUROMORPHA

31(1), R in kuehneosaurs (node 12); 90(1); 91(1); 106(1); 114(1); 138(1); 139(1).

In addition to the three characters that we consider synapomorphies of Lepidosauromorpha [91(1), 106(1), 114(1)], the computer analysis places four other characters at this node. The apomorphic condition of the first (31) occurs in tangasaurs, *Youngina*, and lepidosaurs, but the ancestral condition occurs in kuehneosaurs. The character is not preserved in the remaining taxa. Given the relationships proposed here, it is equally parsimonious to consider the apomorphic condition of this character to be a synapomorphy of lepidosauromorphs that has reversed in kuehneosaurs, as the computer analysis does, or to consider this condition to have arisen convergently in lepidosaurs on one hand and in younginiforms on the other, as we have done. Both hypotheses of character evolution require one instance in which we must compromise our initial assessment of homology. Knowledge about the condition of this character in the taxa for which it is currently lacking would help to clarify the situation.

Like the characters of soft anatomy, characters 90, 138 and 139 have been determined only in living lepidosauromorphs. The apomorphic condition of all three characters occurs in both *Sphenodon* and squamates. Thus, provided that the similarity between these taxa is truly homologous (synapomorphous), these similarities are minimally synapomorphies of Lepidosauria, as we have hypothesized, but they may indeed characterize a larger monophyletic group, as the computer analysis suggests.

NODE 2: *Palaeagama**

Both analyses revealed that *Palaeagama** does not possess any apomorphic characters applying to clades smaller than the entire Lepidosauromorpha (Appendix II). Therefore, the position of *Palaeagama** is unresolved, and there is no reason to interpret any of its ancestral features as apomorphic reversals. It is for these reasons that we have identified this taxon as a metataxon and marked it with an asterisk; all that can be said about this fossil is that it is a lepidosauromorph.

While it is possible that *Palaeagama** lacks the synapomorphies of subsets of lepidosauromorphs because it belonged to the evolutionary species that was ancestral to all other lepidosauromorphs, the ambiguity posed by this fossil is more likely to have resulted from its poor state of preservation.

We are able to determine the condition of only 28 out of our 140 osteological characters in *Palaeagama**. Furthermore, none of these 28 characters link this fossil with either Lepidosauriformes or Younginiformes.

The poor preservation of *Palaeagama** explains its variable position in the 28 cladograms resulting from the Wagner analysis and its unresolved position in the Adams consensus cladogram (Appendix Fig. 1). The problem arises not only because all of the lepidosauriform and younginiform synapomorphies are undeterminable in *Palaeagama**, but also because those few characters that can be examined in this fossil are either equally plesiomorphic or not determinable in *Paliguana**, *Saurosternon**, and at least one of the two most inclusive clades within Younginiformes. In other words, any known synapomorphies that might place *Paliguana**, *Saurosternon**, or even Younginiformes closer to kuehneosaurs and lepidosaurs than to *Palaeagama** cannot be determined in the latter. Thus, not one of the following hypotheses about the relationships of *Palaeagama** can be refuted by the available data: the sister group of all other lepidosaurs, the sister group of Younginiformes, the sister group of Lepidosauriformes; the sister group of *Paliguana** - kuehneosaurs - lepidosaurs, the sister group of *Saurosternon** - kuehneosaurs - lepidosaurs, the sister group of kuehneosaurs - lepidosaurs, the sister group of *Paliguana** - *Saurosternon**, the sister group of *Paliguana**, or the sister group of *Saurosternon**. The poor state of preservation of *Palaeagama** makes this fossil amenable to many different hypotheses about its phylogenetic relationships. None of these alternatives is supported by any evidence, and we have chosen to be conservative regarding its position among lepidosauromorphs.

NODE 3: YOUNGINIFORMES

41(1), C in rhynchocephalians (node 14); 42(1); 107(1).

The synapomorphies placed at this node by the computer analysis were all characters that we used to diagnose Younginiformes in the text. In addition, we considered two other characters to be synapomorphies of this group: absence of teeth on the parasphenoid [31(1)] and a relatively narrow and elongate snout [61(1)]. As noted above (node 1), our interpretation of convergence and the computer's interpretation of acquisition and reversal in character 31 are equally parsimonious. A choice between these two hypotheses of character evolution might be made, however, if data were obtained for lepidosauromorph taxa outside the younginiform and the kuehneosaur-lepidosaur clades. The difference between the computer optimization of character 61 and our own is reversed from the situation in characters 138 and 139 (node 1). This time we boldly hypothesize that the synapomorphy applies to all Younginiformes, even though it is not preserved in *Acerosodontosaurus*; the computer optimization conservatively restricts this synapomorphy to the clade consisting of tangasaurs and *Youngina*, the only younginiforms in which it is known to occur.

NODE 4: *Acerosodontosaurus*

96(1).

Both our analysis and that of the computer interpreted the twisted radius of *Acerosodontosaurus* to be a synapomorphy of this taxon. We are currently unable to provide adequate justification for the polarity of our second hypothesized synapomorphy of *Acerosodontosaurus*, the dorsomedially-ventrolaterally widened pubis, and have, therefore, omitted it from our character list (Appendix I).

NODE 5: YOUNGINOIDEA (Tangasauridae plus *Youngina*)

2(1), C in *Gephyrosaurus* (node 15) and squamates (node 22); 61(1); 81(1); 108(1); 109(1).

Three synapomorphies, 81(1), 108(1), and 109(1), were placed at this node both by us and by the computer analysis. One of the two remaining synapomorphies of younginoids recognized by the computer analysis [61(1)] has already been discussed (node 3). The other, narrow nasals [2(1)], is not included in the text as a younginoid synapomorphy, although it is encompassed in character 61(1), the long, narrow snout. In any case, we admit that the superficial apomorphic similarity in the nasals of squamates and younginoids must be attributed to convergence. In the text we chose to withhold judgement on the condition of the nasals in *Gephyrosaurus*. If this taxon is also considered to possess narrow nasals, then this condition must also be convergent on that seen in younginoids, although not necessarily on that in squamates.

NODE 6: TANGASAURIDAE

110(1); 111(1); 112(1); 113(1); 131(1).

The list of tangasaur synapomorphies given by the computer analysis is identical to the list given in the text.

NODE 7: *Youngina*

118(1); 140(1).

The synapomorphies of *Youngina* listed by the computer analysis are identical to those given in the text.

NODE 8: LEPIDOSAURIFORMES (including *Paliguana**, *Saurosternon**, Kuehneosauridae, Rhynchocephalia, and Squamata)

17(1), R in the sphenodont-sapheosaur-*Homoeosaurus* clade (node 18); 19(1); R in sphenodontidans (node 16); 24(1); 36(1), R in the sphenodont-sapheosaur-*Homoeosaurus* clade (node 18); 71(1); 72(1), R in the sphenodont-sapheosaur-*Homoeosaurus* clade (node 18); 74(1); 78(1); 93(1); 94(1); 115(1); 124(1); 134(1); 137(1).

All seven of the lepidosauriform synapomorphies given in the text [17(1), 19(1), 36(1), 72(1), 93(1), 94(1), 134(1)] are also recognized by the computer analysis, which places seven additional synapomorphies at this node [24(1), 71(1), 74(1), 78(1), 115(1), 124(1), 137(1)]. Not one of these additional synapomorphies, however, can be determined in *Paliguana** or *Saurosternon** (or in *Palaeagama**), and most of them cannot be determined in one or more other members of the hypothesized clade. While the computer analysis is bold in listing these characters as synapomorphies of the largest possible clade, we prefer to restrict them to subsets of this clade in which their occurrence can be documented. We realize, however, that some or all of these characters may later be found to be synapomorphies of more inclusive groups.

Incomplete fossil material is responsible for the lack of full resolution at this node. Although seven of the characters listed above cannot be determined either in *Paliguana** or *Saurosternon** (24, 71, 74, 78, 115, 124, 137), each of these taxa shares apomorphic characters with kuehneosaurs and lepidosaurs that are absent in Younginiformes. Unfortunately, these two sets of synapomorphies are completely non-overlapping, for no comparable parts of the organisms are preserved: *Paliguana** is represented by a skull, *Saurosternon** only by the postcranial skeleton. Thus, it is impossible to know which of these characters are synapomorphies of the entire Lepidosauriformes (node 8) and which ones (if any) link only one of the two Permo-Triassic fossils with the kuehneosaurs and lepidosaurs. The trichotomy cannot be resolved with the present data.

NODE 9: *Saurosternon**

101(1?), C in squamates (node 22).

Although in the text we considered *Saurosternon** to lack diagnostic apomorphies, the computer analysis objectively recognizes a single diagnostic apomorphy for this fossil: the reduced size of the intermedium. We considered this character to be indeterminable in *Saurosternon**; however, in the data matrix (Appendix II), we questionably assigned state I to this taxon for the size of the intermedium. Carroll (1975, 1977, 1985) used the reduced intermedium of *Saurosternon** as evidence for a close relationship between "paliguanids" and "lizards" (squamates). Numerous characters suggested a sister group relationship between rhynchocephalians and squamates, rather than between *Saurosternon** and squamates. We thus concluded that even if Carroll were correct in his morphological interpretation, a reduced intermedium in *Saurosternon** and squamates would more reasonably be interpreted as convergence, because rhynchocephalians are plesiomorphic in this regard. The computer analysis supports our conclusion.

NODE 10: *Paliguana**

We are not aware of any diagnostic apomorphies in *Paliguana**, and the results of the computer analysis require no convergences or character reversals to be apomorphies at this node. This lack of diagnostic apomorphies is our reason for designating *Paliguana** as a metataxon and marking it with an asterisk (see p. 16).

NODE 11: UNNAMED GROUP (including Kuehneosauridae, Rhynchocephalia, and Squamata)

5(1); 6(1); 33(1); 59(1); 97(1); 105(1); 121(1).

Seven characters [5(1), 6(1), 33(1), 59(1), 97(1), 105(1), 121(1)] are common to both the list of synapomorphies of this monophyletic group given in the text and that given by the computer analysis. In addition, we recognize one synapomorphy for this group that is not recognized by the computer analysis [24(1)]. We consider this character, the loss of teeth on the transverse flange of the pterygoid, to be a synapomorphy of this clade, while the computer analysis uses it for a more inclusive group. Because this character is not determinable in all of the additional taxa in the more inclusive group, both hypotheses are consistent with available data. The hypothesis offered by the computer analysis is bolder; we have been conservative in considering the synapomorphy to apply only to that group in which its presence can be adequately documented.

NODE 12: KUEHNEOSAURIDAE.

4(1); 11(1), C in squamates (node 22); 12(1), C in squamates (node 22); 13(1), C in *Gephyrosaurus* (node 15) and in the sphenodont-sapheosaur-*Homoeosaurus* clade (node 18); 15(1), C in squamates (node 22); 18(1); 21(1), C in squamates (node 22); 31(0), state 1 originates in lepidosauromorphs (node 1), R in kuehneosaurs; 83(1), C in squamates (node 22); 85(1); 88(1), C in sphenodonts (node 21); 97(2), C in *Homoeosaurus* (node 19) and squamates (node 22); 98(1), C in squamates (node 22).

All eleven of the kuehneosaur synapomorphies listed in the text are also listed at this level by the computer analysis, but the latter recognizes two additional synapomorphies at this node. One, presence or absence of teeth on the parasphenoid (character 31), has already been discussed (see node 1). The other, presence or absence of posterior processes on the second sacral ribs (character 88) appears to be highly homoplastic at this level of analysis. The processes are absent in many squamates (pers. obs.) and in the younginiform *Hovasaurus* (Currie, 1981b) so that when variation within the basic taxa is considered our phylogenetic hypothesis requires a minimum of two instances of convergence in addition to that between kuehneosaurs and sphenodonts.

It is noteworthy that morphological equivalents of seven of the twelve kuehneosaur synapomorphies are also present in squamates. Acceptance of the phylogenetic hypothesis offered here necessitates that these be considered either (1) convergent, or (2) synapomorphies of a larger clade (node 11) that have subsequently reversed within rhynchocephalians. At present there is no way to choose between these two hypotheses, and both our own analysis and that of the computer have opted for the more conservative hypothesis of convergence (more conservative in the sense that the questionable synapomorphies apply to less inclusive groups).

The exclusive apomorphic similarity between kuehneosaurs and squamates is evidence contrary to our proposed hypothesis of a sister group relationship between squamates and rhynchocephalians;

however, anyone who rejects the sister group relationship between rhynchocephalians and squamates in favor of one between kuehneosaurs and squamates must confront an even larger body of contrary evidence: the apomorphic similarities between rhynchocephalians and squamates that are absent in kuehneosaurs (see node 13).

NODE 13: LEPIDOSAURIA

1(1); 8(1); 29(1); 35(1); 75(1); 80(1); 91(2); 104(1); 105(2); 117(1); 119(1); 120(1); 123(1); 126(1); 127(1); 128(1); 130(1); 132(1).

The eighteen osteological synapomorphies of lepidosaurs recognized by the computer analysis are all used as part of the diagnosis of Lepidosauria in the text [character 22 includes both 104(1) and 105(2)]. In addition, we list nine other synapomorphies [31(1); 74(1); 78(1); 90(1); 115(1); 124(1); 137(1); 138(1); 139(1)] at this node. Because data are lacking in certain critical taxa, it is impossible to determine the precise limits of the monophyletic group characterized by each of these nine synapomorphies. The computer analysis boldly attributes them to the largest possible group, assuming that they are present in taxa for which data are lacking. Thus, when data are lacking in all taxa outside Lepidosauria (characters 90, 138 and 139) the computer analysis considers the synapomorphy to characterize all lepidosauromorphs (node 1). Likewise, when data are lacking in *Paliguana**, *Saurosternon**, and kuehneosaurs (characters 74, 78, 115, 124, 137), the computer analysis considers the synapomorphy to apply to Lepidosauriformes (node 8). In contrast, we conservatively attribute these synapomorphies only to monophyletic groups in which their presence can be documented in members of both or all branches stemming from the basal node in the clade.

The situation in character 31 is slightly different and is discussed under node 1. Missing data in *Palaeagama** are discussed under node 2.

NODE 14: RHYNCHOCEPHALIA

7(1); 23(1); 27(1); 41(1), C in younginiforms (node 3); 66(1); 67(1); 76(1).

All of the synapomorphies of Rhynchocephalia recognized by the computer analysis occur in the diagnosis given in the text. In addition, we consider a small lacrimal that is barely exposed in lateral view to be a synapomorphy of this group. Both squamates and rhynchocephalians have a small lacrimal [character 1(1), node 13], but that of *Gephyrosaurus* is smaller than is the lacrimal of many squamates (it is absent in other rhynchocephalians). Of course, the lacrimal of some squamates may also be reduced or even absent, as in sphenodontidans [character 1(2), node 16]; we consider this to be convergent.

NODE 15: *Gephyrosaurus*

2(1?), C in squamates (node 22) and in younginoids (node 5); 9(1), C in clevosaurs (node 17); 13(1), C in kuehneosaurs (node 12) and in the sphenodont-sapheosaur-*Homoeosaurus* clade (node 18); 63(1), C in squamates (node 22); 65(1); 68(1).

Five of the six synapomorphies that the computer analysis gives for *Gephyrosaurus* are also given in the text [9(1), 13(1), 63(1), 65(1), 68(1)]. The computer analysis places one additional synapomorphy at this node, narrow nasals [2(1)]. *Gephyrosaurus* has been reconstructed with relatively small nasals (Evans, 1980), but we remain uncertain on this point because the skull parts are disarticulated and dissociated. Squamates have reduced nasals, and thus we scored *Gephyrosaurus* "1?" in the data matrix in order to bias the results in favor of a sister group relationship between *Gephyrosaurus* and squamates, instead of our proposed hypothesis. In spite of this bias, our hypothesis of a sister group relationship between *Gephyrosaurus* and sphenodontidans has more character support. Thus, if *Gephyrosaurus* actually has reduced nasals, this apomorphic resemblance to squamates must be considered convergent.

We listed one synapomorphy for *Gephyrosaurus* in the text that was not recognized by the computer analysis. This character, reduction of the quadratojugal and its partial fusion to the quadrate, does not appear in our character list (Appendix I) or data matrix (Appendix II), although it could be represented by an intermediate state in character 12. This would again be a shared apomorphic simi-

Lacrimal absent
jugal long
quadrate narrow
parallel subdental pos
tooth row elongate
palatine broadened
55 premax. chisels
55 maxillary teeth
5 posterior flange
acrodont

larity between *Gephyrosaurus* and squamates, but would still be considered convergent because of the many characters linking *Gephyrosaurus* and Sphenodontida.

NODE 16: SPHENODONTIDA

1(2); 10(1); 19(0), state 1 originates at the lepidosauriform node (node 8) and reverses in sphenodontidans; 23(2); 49(1); 55(1); 56(1); 75(2).

All eight of the sphenodontidan synapomorphies listed by the computer analysis are given in the text [1(2), 10(1), 19(0), 23(2), 49(1); 55(1); 56(1), 75(2)]. We consider two additional characters to be sphenodontidan synapomorphies. Using only the taxa considered in this analysis, this position is not justified for the first character, the contact between the jugal and squamosal below the lower temporal fenestra [58(1)]. This character is present in the sphenodont-sapheosaur-*Homoeosaurus* group. However, it is absent in sphenodontidans in which the lower temporal arch is modified, viz., clevosaurs and the sphenodontidan sister group, *Gephyrosaurus*. Our conclusion in this regard stems from a preliminary analysis of other Triassic rhynchocephalians that were not considered in this work (see pp. 25-27 and 96-98). Some of these taxa have this character and they appear to be either the sister group of clevosaurs or the sister group of all the sphenodontidans considered in this analysis. Although it is absent from the character list (Appendix I) and data matrix (Appendix II), we consider a prominent coronoid eminence to be another synapomorphy of sphenodontidans. Because the sphenodontidan coronoid eminence retains the ancestral relations of coronoid and surangular, it is not to be confused with the similarly tall coronoid eminence of squamates, which is formed by the coronoid bone alone [character 69(1), node 22].

NODE 17: CLEVOSAURS

9(1), C in *Gephyrosaurus* (node 15); 57(1).

The two characters that the computer places at this node are also listed as synapomorphies of clevosaurs in the text. We recognize an additional synapomorphy for this group: loss of contact between the posterior ramus of the jugal and the ventral ramus of the squamosal at the posteroventral corner of the lower temporal fenestra [character 58(0)]. Our hypothesis is not the most parsimonious one given the data in Appendix II. It relies on the hypothesis that certain Triassic rhynchocephalians not included in the analysis, but retaining the ancestral condition, are not more closely related to sphenodonts, sapheosaurs, or *Homoeosaurus* than they are to clevosaurs.

NODE 18: UNNAMED TAXON (including sphenodontids, sapheosaurs, and *Homoeosaurus*)

13(1), C in kuehneosaurs (node 12) and in *Gephyrosaurus* (node 15); 17(0), for which state 1 originates in lepidosauriforms (node 8) and reverses at node 18; 22(1), C in squamates (node 22); 23(3); 25(1); 36(0), for which state 1 originates in lepidosauriforms (node 8) and R at node 18; 40(1); 46(1); 48(1); 54(1); 58(1); 72(0), for which state 1 originates in lepidosauriforms (node 8) and reverses at node 18; 73(1); 76(2).

Thirteen of the 14 characters listed by the computer analysis as synapomorphies at this node are treated likewise in the text [13(1), 17(0), 22(1), 23(1), 25(1), 36(0), 40(1), 46(1), 48(1), 54(1), 72(0), 73(1), 76(2)]. In the text, we place two additional synapomorphies here: 19(0) and one not included in the character list. Although we give only 14 characters in the text (the tally above would suggest that we give 14 + 2 or 16), two pairs in the first group are redundant: when the retroarticular process is absent [73(1)] it cannot also be large (72), and when all palatal teeth are absent except for the palatine row [25(1)], vomerine teeth must be absent [22(1)]. Character 58(1), placed here by the computer analysis but not by us, is discussed under Sphenodontida (node 16). Of the two other synapomorphies placed at this node in the text but not by the computer analysis, one [19(0)] is redundant with a character already listed as a synapomorphy here [54(1)], and the other (parietal foramen near frontoparietal suture) is not included in the character list.

NODE 19: *Homoeosaurus*

56(2), C in sapheosaurs (node 20); 97(2), C in kuehneosaurs (node 12) and squamates (node 22); 122(1), C in sapheosaurs (node 20).

One character is common to both the *Homoeosaurus* synapomorphy list generated by the computer analysis and that given in the text [97(2)]. The additional character given in the text, small size, is not included in the character list or the data matrix (Appendices I and II). The two characters given by the computer analysis but not listed in the text [56(2), 122(1)] are discussed under sapheosaurs (node 20).

NODE 20: SAPHEOSAURS

43(1); 44(1); 45(1) 47(1), C in sphenodonts (node 21); 56(2), C in *Homoeosaurus* (node 19); 82(1); 89(1), C in sphenodonts (node 21); 122(1), C in *Homoeosaurus*.

All of the sapheosaur synapomorphies given in the text are included in the computer generated synapomorphy list for the same taxon [43(1), 44(1), 45(1), 82(1)]. The four additional characters are placed as synapomorphies at this node because the relationships among *Homoeosaurus*, sapheosaurs, and sphenodonts are unresolved. Two of these characters, narrow parietal table [47(1)] and aliform outgrowths on the distal rib segments [89(1)] suggest a sister group relationship between sapheosaurs and sphenodonts, but the other two, prominent posterior flange on maxillary teeth [56(2)] and long ischial tubera [122(1)] suggest a sister group relationship between sapheosaurs and *Homoeosaurus*.

If either of these two relationships is hypothesized, then two of the four synapomorphies apply to a more inclusive group than sapheosaurs alone. The status of the remaining two characters as sapheosaur synapomorphies, however, is ambiguous. These characters must be homoplastic, because they are incongruent with the other two and thus with the relationships suggested by them. The precise nature of this homoplasy is unclear. No matter which phylogenetic hypothesis is adopted, the two incongruent characters may be convergent in sapheosaurs and in the taxon (either sphenodonts or *Homoeosaurus*) that is not its sister group (in which case they would be synapomorphies of sapheosaurs). Alternatively, the characters may be synapomorphies of the entire sapheosaur-sphenodont-*Homoeosaurus* clade that have reversed in the sister group of sapheosaurs. Thus, either two, one or none of these four characters can reasonably be considered sapheosaur synapomorphies, but the decision as to which characters these are must await an hypothesis of relationships among sapheosaurs, sphenodonts, and *Homoeosaurus*.

NODE 21: SPHENODONTS

23(4); 47(1), C in sapheosaurs (node 20); 49(2); 50(1); 51(1); 52(1); 53(1); 54(1); 88(1), C in kuehneosaurs (node 12); 89(1), C in sapheosaurs (node 20); 90(2).

Eight of the 11 sphenodont synapomorphies given by the computer are also listed in the text [23(4), 49(2), 50(1), 51(1), 52(1), 53(1), 88(1), 90(2)]. We place three additional synapomorphies that are not included in the character list (number of cervical vertebrae, number of presacral vertebrae, jugal and squamosal fail to contact below postorbital). The computer also recognizes three sphenodont synapomorphies that we do not. Two of these, characters 47(1) and 89(1), are discussed under sapheosaurs (node 20). The third, an enlarged quadratojugal foramen [54(1)] is present in *Sphenodon*, but is indeterminable in sapheosaurs and *Homoeosaurus*. We boldly hypothesize that it applies to all three taxa, because it is related to reduction of the quadrate and its lateral conch (character 40), which appears characteristic of all three taxa.

NODE 22: SQUAMATA

2(1), C in *Gephyrosaurus* (node 15) and younginoids (node 5); 3(1); 11(1), C in kuehneosaurs (node 12); 12(1), C in kuehneosaurs (node 12); 14(1); 15(1), C in kuehneosaurs (node 12); 16(1); 20(1); 21(1), C in kuehneosaurs (node 12); 22(1), C in the sapheosaur-sphenodont-*Homoeosaurus* clade (node 18); 26(1), 28(1); 30(1); 32(1); 34(1); 35(1); 37(1); 38(1); 39(1); 60(1); 62(1); 63(1), C in *Gephyrosaurus* (node 15); 64(1); 69(1); 70(1); 77(1); 79(1); 83(1), C in kuehneosaurs (node 12); 84(1); 86(1); 87(1); 92(1); 95(1); 97(2), C in kuehneosaurs (node 12) and *Homoeosaurus* (node 19);

98(1), C in kuehneosaurs (node 12); 99(1); 100(1); 101(1), C in *Saurosternon** (node 9); 102(1); 103(1); 121(2); 125(1); 129(1); 132(2); 133(1); 134(2); 135(1); 136(1).

All 48 characters listed as squamate synapomorphies by the computer analysis are also listed as such in the text, where one additional synapomorphy is given [171(1)]. There are only 47 squamate osteological characters in the text, but two of the 49 characters given by the computer analysis are listed under one text number [12(1) and 21(1)] while another is described in the text section on soft anatomy [Sect. 3.5.3; 135(1) in Appendix 1], suggesting that 50 characters are involved. The one additional character given in the text, eight cervical vertebrae [171(1)], is omitted from the character list above (bringing the tally back to 49). Since determination of the number of cervical vertebrae requires knowledge of the sternal attachment of the cartilaginous ventral rib extensions, which are rarely preserved, we listed this as a character from soft anatomy and omitted it from the computer analysis. *Sphenodon* and squamates have eight cervicals, but Jurassic sphenodontidans have only seven. We have followed those workers who claim that the presence of seven cervicals is plesiomorphic (e.g., Hoffstetter and Gasc, 1969), but we must emphasize that this character is indeterminable in most fossil lepidosauromorphs.

ADDENDUM

Several years have passed since this manuscript was first submitted for publication. In the interim, we have gathered additional evidence, and several works have been published relevant to the early history of Lepidosauria. We will take this opportunity to briefly summarize this new information.

Recently published hypotheses concerning the Permo-Triassic diversification of Sauria (or Neodiapsida of Benton, 1985) developed by S. E. Evans (1984) and M. J. Benton (1982, 1983, 1984, 1985) are broadly concordant with our own. A consensus has emerged that there are two groups of saurians; one includes lepidosaurs and their extinct relatives (Lepidosauromorpha) and the other contains archosaurs and their extinct relatives (Archosauromorpha). We differ in our opinion as to the precise relations of some taxa within Lepidosauromorpha, but most differences stem from process assumptions inherent in character optimization. Some characters are so distributed on the most parsimonious tree that their phylogenetic histories cannot be determined without reference to process assumptions, such as the frequency of convergence versus reversal in evolution (Maddison et al., 1984). The optimization, or placement on a tree, of such characters will not affect the topology of the most parsimonious tree (except in certain cases involving missing data). Nevertheless, optimization can affect the amount of character support at any given node, as well as the interpretation of the history of character transformation.

Among extant amniotes, the monophyly of Lepidosauria and Squamata is well founded. We would now add the following characters to the diagnosis of Lepidosauria. Although the precise level of synapomorphy for these characters may not be known, they nonetheless provide some level of resolution in questions of relationships within Lepidosauromorpha.

1. Prefrontal - palatine brace. These bones are not in contact with one another in saurians and lepidosauromorphs ancestrally. Firm sutural connection between the prefrontal and palatine may be related to the reduced role of the lacrimal in supporting this region of the skull.

2. Splenial not involved in mandibular symphysis. The ancestral condition is retained in archosauromorphs and the derived condition applies to all lepidosaurs. Lack of information in nonlepidosaur lepidosauromorphs precludes a firm decision regarding the point at which this synapomorphy arose.

Studies in progress by one of us (JAG) and T. Rowe are reviewing the amniote atlas-axis complex; the following lepidosaur synapomorphies have been discovered.

3. Reduction or loss of proatlas. The proatlas is absent in all squamates (see below), and rhynchocephalians have only small elements compared to those of other amniotes. Assuming that the

small elements of rhynchocephalians are transitional to the absence in squamates, reduction and loss of the proatlas can be considered synapomorphic.

4. Characteristic articular surface of axis. The form of the atlantal-axial articulation is unique to lepidosaurs among saurians (e.g., Fraser and Walkden, 1984, plate 53, figs. 1,2). The ancestral condition is retained by archosauromorphs, but missing data in early lepidosauromorphs does not allow more precise placement for this and the following character.

5. Centrum 1 and 2, and intercentrum 2, fuse at cessation of growth. Centrum 1 and intercentrum 2 are fused in all adult reptiles. Lepidosaurs are diagnosed by the fusion of both of these to the axis in the adult.

Finally, Gauthier, Kluge, and Rowe (1988) have identified additional lepidosaur synapomorphies during their analysis of amniote phylogeny.

6. Absence of thick calcareous shell with pores and paired tertiary egg membranes (Hill, 1933; Packard et al., 1977).

7. Little albumen in egg at laying (Packard et al., 1977)

8. Ornithuric (rather than hippuric) acid primary product of benzoic acid conjugation (Jordan et al., 1980).

9. Adrenal gland suspended in gonadal mesentary (Gabe, 1970).

10. Thymus not lobed (Bockman, 1970).

11. Intercarotid anastimosis absent (Wingstrand, 1951).

12. Sinus cavernosus absent (Wingstrand, 1951).

13. Scales formed by superimposed, rather than alternating, alpha and beta keratin layers (Maderson, 1972).

The diagnosis of the kuehneosaur-lepidosaur group should also be emended to include the maxilla having replaced the jugal on the ventrolateral border of the orbit. In addition, character 8 in Appendix I, jugal-squamosal contact on the supratemporal arch, should be removed from the diagnosis of Lepidosauria. It is definitely present in *Icarosaurus*, but cannot be determined in the disarticulated *Kuehneosaurus*, and we prefer to add character 8 to the diagnosis of the kuehneosaur-lepidosaur group.

We also recommend the addition of the following characters to the diagnosis of Squamata.

1. Proatlas absent. This element is absent in all squamates (Hoffstetter and Gasc, 1969).

2. Fusion of parasphenoid to basisphenoid in embryo (except in some xantusiids). A separate parasphenoid is retained in nearly full grown *Sphenodon*, but this element fuses with the basisphenoid in squamate embryos (except in some xantusiids; pers. obs.). *Sphenodon* is presumed to have retained the ancestral condition. We must point out, however, that the condition of this character is unknown in most saurians, and that the squamate condition is found in at least some archosauromorphs.

3. Atlantal neural arches broadly in contact and provide extensive cover for neural canal dorsally. The arches cover only the dorsolateral surfaces of the neural canal and are only in narrow contact dorsally in saurians ancestrally (T. Rowe, pers. comm. 1987).

4. Atlantal neural arches fuse to intercentrum 1 at cessation of growth. The arches remain separate from the intercentrum in saurians ancestrally (Gauthier and Rowe, ms).

5. Two rows of subdigital scales (Etheridge and de Queiroz, 1988).

Largely because of new information from Triassic sphenodontidans discussed below, the history of two characters, the entry of the postfrontal into the supratemporal fenestra, and the morphology of the jugal and quadratojugal in the lower temporal bar, appear equivocal. Regardless of which hypothesis of relationships is preferred, these characters must have had complex histories. The latter bone in particular has figured prominently in discussions of lepidosaur systematics. There is a growing body of evidence that the lower temporal arch may have reevolved within Sphenodontida. The arch is composed of a large, unfused quadratojugal with a short anterior process and a long posterior jugal process that contacts both the quadratojugal and squamosal in most Jurassic and later sphenodontidans. Although its detailed construction is diagnostic, the simple presence of this arch has long been assumed to be plesiomorphic. It may have reevolved as a result of enhancement of the propalinal shearing mastication characteristic of this group (Whiteside, 1986). The matter is not clear, however, in that several taxa from the base of Rhynchocephalia appear to display both conditions within the same species (Whiteside, 1986). The history of the lower temporal bar is likely to remain ambiguous until articulated skulls of more examples of Permian non-lepidosaur lepidosauriforms are found (see further discussion below).

Our understanding of rhynchocephalian phylogeny has changed substantially during the last few years. It is clear that the hypothesis proposed above must be refined and reevaluated in light of a larger body of evidence provided by several newly described rhynchocephalians from the late Triassic of England (Fraser and Walkden, 1984; Fraser, 1986; Whiteside, 1986), a review of the morphology of *Polysphenodon* and pleurosaurs (Carroll, 1985), and our own studies of late Jurassic sphenodontids such as *Pleurosaurus*, *Sapheosaurus*, *Kallimodon*, and *Homoeosaurus*. We cannot provide a detailed analysis at this time, but certain changes in our hypothesis are worthy of a brief review.

I. We would add to the diagnosis of Rhynchocephalia: (1) the small size of the atlantal neural arches, and (2) the large size atlantal intercentrum (T. Rowe, pers. comm. 1987). Also, because Hill and deBeer (1949) argued that both a dentinal egg tooth and horny caruncle are present in amniotes ancestrally, *Sphenodon* (and other rhynchocephalians?) can be diagnosed by having lost the former character.

II. *Gephyrosaurus* still appears to be the sister group of all other rhynchocephalians. But new information from other early members of this group, in particular *Diphyodontosaurus*, affect the diagnoses of both taxa. Evans (1985a) and Whiteside (1986) suggest that *Gephyrosaurus* displays a retarded rate of replacement at the posterior ends of the marginal tooth rows; this feature appears diagnostic of Rhynchocephalia. We argued that the marginal dentition of *Gephyrosaurus* is in several ways intermediate between that of lepidosaurs ancestrally and that seen in sphendontidans. Whiteside (1986) has argued further that the tooth-form and replacement pattern of *Diphyodontosaurus* is intermediate between that of *Gephyrosaurus* and Sphenodontida. We listed seven characters in the diagnosis of *Gephyrosaurus*. However, the morphology of *Diphyodontosaurus* suggests that characters 1 and 7 may be diagnostic of all Rynchocephalia, characters 2 and 6 are equivocal and, assuming that the fused frontals and parietals referred to *Diphyodontosaurus* in fact belong to *Planocephalosaurus* (see below), the diagnostic content of characters 3 and 4 is also ambiguous. Firmer conclusions must await the find of articulated specimens of early sphenodontidans.

III. Tooth morphs provide evidence for at least six rhynchocephalians from the Triassic fissures of southwest England (Fraser, 1986; Whiteside, 1986). Referral of non-tooth-bearing bones to these taxa relies mainly on size and relative abundance, because all elements are disarticulated. Under these circumstances it is difficult to evaluate certain cases of character discordance. For example, the form of the teeth, dentary, premaxilla, and maxilla confidently referable to *Diphyodontosaurus* indicate that it diverged from other rhynchocephalians after *Gephyrosaurus*, but before *Planocephalosaurus* (Whiteside, 1986). In contrast, the morphology of the less confidently referred frontal, parietal, and prefrontal suggest that *Diphyodontosaurus* and *Planocephalosaurus*) are sister taxa (Whiteside, 1986). Both cannot be true, but are these and other cases of apparent character discordance in early rhynchocephalians the result of homoplasy or of simple mixing of elements belonging to these sympatric taxa?

IV. Using only the morphology of the tooth-bearing bones, *Diphyodontosaurus* appears to be closer to sphenodontidans than is *Gephyrosaurus*. Whiteside (1986) noted that the posterior marginal teeth of *Diphyodontosaurus* may be described as in character 1 in our diagnosis of Sphenodontida. In terms of the maxillary and dentary tooth rows as a whole, our description in character 1 still applies to Sphenodontida. Whiteside (1986) also concluded that *Diphyodontosaurus* is like Sphenodontida and unlike *Gephyrosaurus* in that they share fewer than 8 premaxillary teeth and a reduced or absent subdental gutter; his illustrations of the maxilla (e.g., Whiteside, 1981, fig. 7) demonstrate that it possesses the sphenodontidan-like posterolateral process above the posterior end of the maxillary tooth row. Sphendontidan characters 2, 4, 5, and perhaps 6 remain at this level. Whiteside (1986) and Fraser (1986) would add that sphenodontidans also have fewer than five premaxillary teeth, that the dentary overreaches Meckel's canal anteriorly, and that there is a prominent lip below the tooth row on the lateral face of the dentary. Their figures also indicate that an inset posterior maxillary tooth row, taller posterior end of the maxilla, and striated maxillary teeth arose at this level as well. Of the remaining characters, 7 and 8 are difficult to assess for reasons noted above, and character 9 appears to diagnose a group of sphendontids excluding *Planocephalosaurus* but including *Clevosaurus*. A shearing bite appears to have been fully developed at this point in rhynchocephalian phylogeny (Whiteside, 1986).

V. We proposed a sister group status for *Planocephalosaurus* and *Clevosaurus*, but the evidence in Fraser (1986) and Whiteside (1986) indicates that we were mistaken. In addition to character 9 just discussed, five characters suggest that *Clevosaurus, Sigmala, Polysphenodon*, pleurosaurs, and the homoeosaur-sphenodont group are most closely related. They have an extensive dorsal overlap of the postorbital onto the postfrontal, fewer than four premaxillary teeth in juveniles that are subsequently replaced by the chisel-like structures in adults, and flanges on the palatine teeth and a reduction of the palatal dentition not involved in the shearing apparatus. Based on Carroll's (1985) description of *Polysphenodon* and *Palaeopleurosaurus*, and our observations of Jurassic pleurosaurs and homoeosaurs, a laterally bowed lower temporal arch arose in this group (see Carroll, 1985, for a contrary view). The clevosaur group is now restricted to *C. hudsoni* and *C. minor* (Fraser and Walkden, 1983) and, on the basis of an extensive jugal - maxilla suture, perhaps *Sigmala* as well.

VI. Pleurosaurs appear to be closer to the homoeosaur-sphenodont group than they are to other sphenodontidans. Pleurosaurs have most of the synapomorphies of the group composed of sphenodonts and homoeosaurs (including sapheosaurs; see below). These include; the absence of non-shearing palatal dentition, extensive propalinal masticatory movements, a narrow parietal, a parietal foramen near the frontoparietal suture, a short, unbowed quadrate that is covered laterally by the squamosal and shows no trace of a tympanic conch, a large quadratojugal and quadrate foramen, short supratemporal processes of the parietal and concomitantly long dorsal process of the squamosal (formed by a fused supratemporal?), an elongate and narrow upper temporal fenestra (reversed in *Homoeosaurus*), and an enlarged postorbital region of the skull.

VII. Homoeosaurs and sphenodonts appear most closely related in that the retroarticular process is absent, the postfrontal is enlarged, and the palatal teeth diverge less from the posterior maxillary teeth. Our diagnosis of sapheosaurs is problematic, but they share long ischial tubera with *Homoeosaurus*. In addition, our observations indicate that *Kallimodon* and *Homoeosaurus* are sister groups; we will refer to sapheosaurs and *Homoeosaurus* (probably including *Euposaurus*) as homoeosaurs. *Kallimodon* is less modified than the small-sized and long-limbed *Homoeosaurus*, but both share the apomorphies of absence of caudal autotomy and of postcervical intercentra in the trunk. Moreover, the parietals of *Kallimodon* are intermediate between the narrow elements of post-Triassic sphenodontidans and the broad parietal table of *Homoeosaurus*, confirming our suspicion of paedomorphic reversal in the latter taxon. The history of the prominently flanged posterior maxillary teeth is unclear; such teeth are present in *Clevosaurus* but not *Sigmala*, and they are present in pleurosaurs and homoeosaurs but not sphenodonts.

To conclude our consideration of new evidence in lepidosaur phylogeny, we must discuss two taxa from the early Triassic of South Africa that have been suggested to be "lizards," *Colubrifer campi* (Carroll, 1982) and *Lacertulus bipes* (Carroll and Thompson, 1982). Both appear to be small diapsids but neither taxon exhibits characters diagnostic of Squamata. *Colubrifer* lacks a conch on the quadrate (pers. obs.), indicating that it lies outside of Lepidosauriformes. Absence of teeth on the transverse process of the pterygoid could, however, indicate that *Colubrifer* might be closer to Lepidosauriformes than to Younginiformes. Unfortunately, either because of missing data or plesiomorphy, there is no clear indication that this specimen is referable either to Sauria or Lepidosauromorpha. *Lacertulus* is also represented by a single, partial skeleton. The short and stout fifth metatarsal indicates that it is part of Sauria, but little else can be said regarding its relationships within that taxon.

Finally, *Niphosaurus kermacki* is the most fragmentary of the newly described diapsids (Evans, 1985). Nevertheless, this specimen from the late Permian of South Africa displays one diagnostic character of the kuehneosaur-lepidosaur group, the exclusion of the jugal from the suborbital rim by the maxilla (Evans, 1985, fig. 2). It also appears to lack a jugal posterior process, but the level of synapomorphy of this character remains unclear; the apomorphic condition could provide evidence for relationship either to squamates or kuehneosaurs, or to a more inclusive group.

ADDENDUM LITERATURE CITATIONS

Benton, M. 1982. The Diapsida: a revolution in reptile relationships. Nature 296:306-307.

__________. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. Phil. Trans. Roy. Soc., London, B, 302:605-717.

__________. 1984. The relationships and early evolution of the Diapsida. Pp. 575-596. *In* M.W.J. Ferguson (ed.), The Structure, Development and Evolution of Reptiles. Linnean Soc. London, Symp. Ser., Cambridge University Press and Academic Press.

__________. 1985. Classification and phylogeny of the diapsid reptiles. Zool. J. Linnean Soc. 84:97-164.

Bockman, D. 1970. The thymus. Pp. 111-133. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 3 (Morph. C). Academic Press, New York.

Carroll, R. 1982. A short limbed lizard from the *Lystrosaurus* Zone (Lower Triassic) of South Africa. J. Paleont. 56:183-190.

__________. 1985. A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeontographica 189:1-28.

__________ and P. Thompson, 1982. A bipedal lizardlike reptile from the Karroo. J. Paleont. 56:1-10.

Evans, S. 1985a. Tooth replacement in the Lower Jurassic lepidosaur *Gephyrosaurus bridensis*. N. Jb. Geol. Palaont. Mh. 1985(7):411-420.

__________. 1985b. A new diapsid reptile from the Upper Permian of South Africa. N. Jb. Geol. Palaont. Mh. 1985(2):87-99.

Fraser, N. 1986. New Triassic sphenodontids from south west England and a review of their classification. Palaeontology 29(1):165-186.

Fraser, N. and G. Walkden. 1984. The postcranial skeleton of the Upper Triassic sphenodontid *Planocephalosaurus robinsonae*. Palaeontology 27(3):575-596.

Gabe, M. 1970. The adrenal. Pp. 263-318. *In* C. Gans and T. Parsons (eds.), Biology of the Reptilia 3 (Morph. C). Academic Press, New York.

Gauthier, J., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4(2).

Hill, J. 1933. V. The development of the Monotremata. Part II. The structure of the egg-shell. Trans. Zool. Soc. London 24:443-456.

Jordan, T., J. Smith, and L. Vaughan. 1980. Benzoic acid conjugation in Tuatara. Biochem. Syst. Ecol. 8:101-103.

Maderson, P. 1972. When? Why? and How?: Some speculations on the evolution of the vertebrate integument. Amer. Zool. 12:159-171.

Maddison, W., M. Donoghue, and D. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83-103.

Packard, G., C. Tracy, and J. Roth. 1977. The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. Biol. Rev. 52:1-105.

Whiteside, D. 1986. The head skeleton of the Rhaetian sphenodontid *Diphyodontosaurus avonensis* gen. et sp. nov. and the modernizing of a living fossil. Phil. Trans. Roy. Soc. London B, 312(1156):379-430.