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from

ORIGINS OF THE HIGHER GROUPS OF TETRAPODS

Controversy and Consensus

Edited by

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To our students of Evolutionary Morphology at
The University of Kansas—past and present.
Thank you.

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11 The Early Radiation of Diapsid Reptiles

Robert L. Carroll and Philip J. Currie

The Diapsida, represented in the modern fauna by *Sphenodon*, lizards, snakes, and crocodiles, encompasses one of the most wide-scale radiations in the history of vertebrates (Fig. 1). Diapsids first appeared in the late Carboniferous but remained rare and showed little diversity until the end of the Paleozoic. During the Late Permian and Triassic, they radiated dramatically, giving rise to a host of lineages including the dinosaurs, pterosaurs, and a variety of secondarily aquatic forms that dominated both the terrestrial and marine environments during the Mesozoic. Many diapsid groups became extinct by the end of the Cretaceous, but lizards and snakes continued to diversify throughout the Cenozoic. Birds are direct descendants of dinosaurs and thus also may be considered within the diapsid radiation. Analysis of any large-scale evolutionary process such as the origin and radiation of the diapsids requires an understanding of the nature of the relationships of the included taxa. Each of the major diapsid groups can be defined readily, but their interrelationships have been subject to continuing dispute. For the past 20 years, cladistics or phylogenetic systematics has been touted widely as an objective and testable procedure for establishing relationships. The emphasis on derived characters and the corresponding need to establish polarities and recognize truly homologous features have given methodological rigor to what Mayr and Simpson previously had considered more of an art than a science.

Despite the clear and logical methodology elaborated by Hennig (1966),

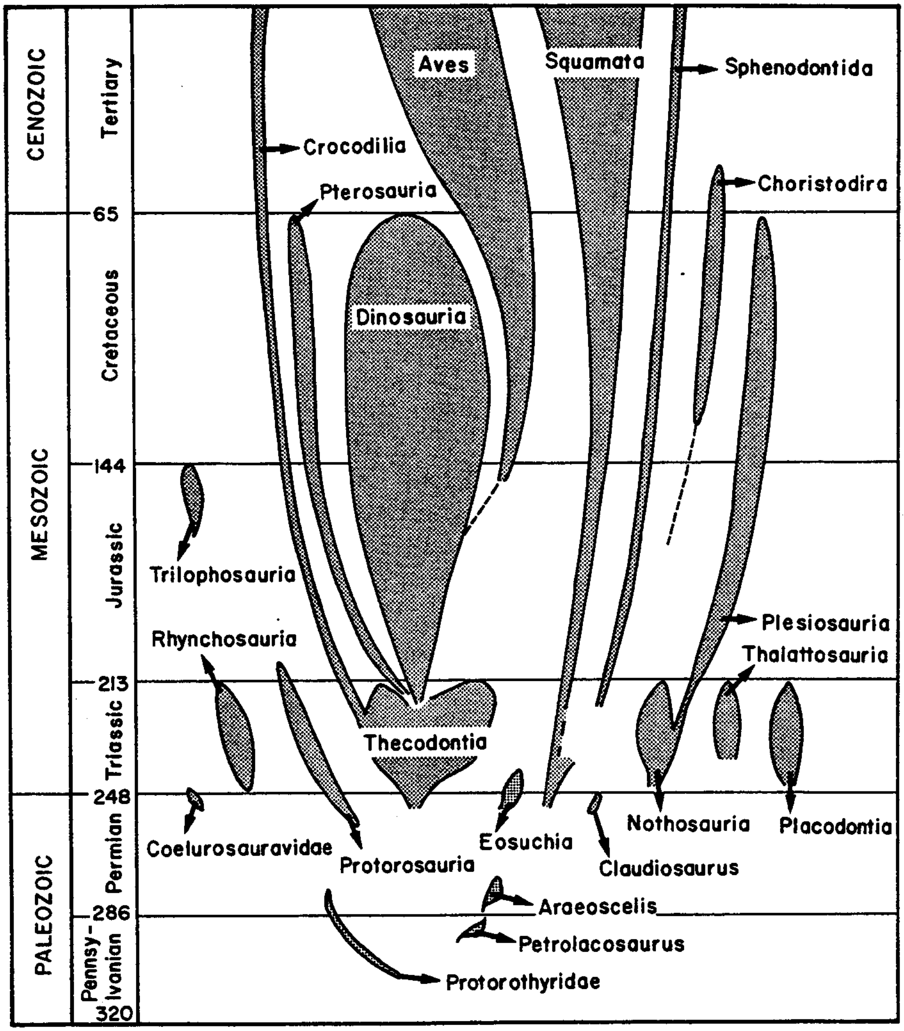


Fig. 1. Temporal distribution of major groups of diapsids.

the application of this methodology has led to some highly contentious phylogenetic conclusions. Examples include the suggestion by Rosen et al. (1981) that lungfish are the sister-group of tetrapods (criticized by Jarvik, 1981; Schultze, 1981; Holmes, 1985; Panchen and Smithson, 1987), Gardiner's proposal (1982) of a sister-group relationship between birds and mammals (disputed by Kemp, 1988; Gauthier et al., 1988), and Løvtrup's phylogeny of the vertebrates (1977). These examples, also noted by Ax (1987), suggest that there may be some general procedural problems in applying Hennig's methodology. These problems should be considered before an effort is made to apply this methodology to the diapsid radiation.

METHODS OF PHYLOGENETIC RECONSTRUCTION

There should be no conflict between the procedures of phylogenetic reconstruction elaborated by Hennig and those used by evolutionary systematists in the school of Simpson and Mayr, because ultimately both are based on fundamental processes of biological evolution. If evolutionary change proceeds in a consistent manner from primitive to derived character-states, the presence of unique derived characters in any two taxa demonstrates that they are more closely related to each other than either is to any other taxon that lacks these characters. Application of this principle requires knowledge of (1) the direction of evolution in order to differentiate derived from primitive characters, and (2) the homology of characters so that similarities resulting from convergence are not mistaken for similarities resulting from common ancestry.

The followers of Hennig and those in the school of Simpson and Mayr differ principally in the way that they establish polarity and homology. Evolutionary systematists rely heavily on the fossil record, whereas cladists emphasize the importance of the modern fauna in developing phylogenetic hypotheses. For an evolutionary systematist, and especially for most paleontologists, the fossil record provides the most direct means of establishing homologies and the polarity of evolutionary change. The direction of evolution can be determined from the relative time of appearance of changing character-states within a monophyletic lineage. Homology can be established on the basis of the presence of the character in question in the immediate common ancestor of the groups being studied. Both can be determined if actual ancestor-descendant relationships can be established. However, if we consider all of organic diversity, knowledge of the fossil record is rarely sufficiently complete to provide this information. Hennig's own research was concentrated on the phylogeny of insects, which have a very incomplete fossil record. Hence, he and his followers have attempted to establish procedures for establishing homology and polarity that are applicable to all groups, even if they lack an adequate fossil record.

Efforts to establish relationships without recourse to the fossil record have figured significantly in cladistic literature. Hennig and his followers have placed emphasis on establishing sister-group relationships, rather than on ancestor-descendant relationships. They also have developed a variety of methods for determining the polarity of evolutionary change and the homology of characters through the study of character distribution among essentially contemporary groups. Homology is judged by essentially probabilistic criteria. According to Patterson (1982), if a large number of other derived features support a sister-group relationship between two groups, then other derived features shared by the two groups are judged to be homologous as well. According to Wiley (1981: 138–139) "homologies can be treated as hypotheses which are tested by other hypotheses of homology and their associated phylogenetic hypotheses." Most of the derived characters found in common in closely related groups would be expected to be homologous, but this method is not capable of establishing which, if any, *specific* characters are homologous, *and* which may be evolved convergently within the groups in question. In contrast, evidence from the fossil record would be expected to be capable of establishing the homology or lack of homology in each character individually.

The most generally used method for establishing polarities in groups without a fossil record is out-group comparison (Kluge, 1977; Wiley, 1981). If particular character-states are common to both the group in question and other related groups (i.e., the out-groups), the character-state is probably primitive. If a character-state is exhibited in one group but is not observed in related groups, the less common occurrence probably represents the derived character-state.

The Importance of Fossils

Ironically, the elaboration of methods of establishing polarity and homology in groups without a fossil record has led to the downplaying of the significance of fossil evidence in groups that do have a significant fossil record.

Wiley (1981), Gaffney (1979), Patterson (1982), and especially Løvtrup (1985) argued that living, rather than fossil, representatives should be emphasized in phylogenetic analysis, even in groups that have a rich fossil record. The primary reason is that living members possess a host of characters that never can be studied in fossils. On the other hand, there are obvious evolutionary reasons why the fossil record should be of greater significance in establishing phylogenetic relationships than even the best known living species.

There is no simple correlation between elapsed time and the amount of evolutionary change, but in general, more changes are likely to have taken place in groups that share only a very distant ancestry than in those that have diverged from a common ancestor more recently. The number of features that result from convergence will almost inevitably increase during evolutionary history, whereas the number of shared characters resulting from common ancestry cannot increase, and may decrease, if synapomorphies are lost or altered. Hence, the likelihood that particular characters are homologous is progressively lower the more distant their common ancestors are in time. The older that groups are geologically, the more hazardous it is to assume that the characters their living members share in common are homologous, and the more difficult it is to establish their relationships on the basis of modern representatives.

It is clear from the writings of Hennig that he considered that the fossil record might provide the ultimate test for phylogenetic hypotheses. For example, he stated (1981:441): "In the preceding chapter I have shown that many of the prerequisites for a really satisfactory account of insect phylogeny are still lacking. The most obvious shortcoming is the almost complete absence of fossils from before the Lower Carboniferous, when a considerable number of insect groups must have arisen according to phylogenetic trees."

Although features of the soft anatomy and physiology may be valuable in establishing hypotheses of relationship in groups without an adequate fossil record, these features have the weakness that they cannot be tested in fossil forms. For example, one may argue that it is more probable that ancestral amniotes had evolved an effective feedback system involving stretch receptors in the axial and appendicular muscles than to assume that this system evolved separately in the ancestors of modern reptiles, birds, and mammals. On the other hand, the presence of this derived condition in modern members of these groups cannot be used to establish that they did share a common ancestor because it is impossible to test whether this system was actually present in any group of Paleozoic tetrapods.

The Prevalence of Convergence

Cladists have based their arguments for the suitability of using modern representatives of groups to establish relationships on the assumption that the majority of similar derived characters are the result of common ancestry and not convergence. According to Kluge (1984), there is no obvious biological basis for assuming that convergence is not a common phenomenon. Surprisingly, no cladists have attempted to demonstrate that convergence is a relatively rare phenomenon.

Because application of the rule of parsimony that governs cladistic analysis depends on the assumption that unique character changes are more common than convergent events, it would be impossible to establish the frequency of convergence through the study of living taxa if it involved more than 50% of the characters being analyzed. On the other hand, detailed knowledge of the fossil record should provide an objective basis for establishing the prevalence of convergence. If the most primitive members of two monophyletic groups are adequately known, it should be possible to establish most of the character changes that occur in their descendants. From them, the relative frequency of unique and convergent character changes can be tabulated. This never can be achieved on the basis of living groups.

Character Selection

Another reason that phylogenies proposed by some cladists may run counter to long-accepted phylogenetic hypotheses is the matter of character selection. Little attention has been paid to how particular characters and taxa are chosen for cladistic analysis. This problem is obscured in many works on Hennigian methodology by the use of hypothetical examples and the use of letters and numbers to represent characters and taxa. Study of the writings of some cladists suggests that the choice of characters is essentially arbitrary. Løvtrup (1985), giving his own examples and citing from other recent papers, listed 22 characters that unite birds and mammals, 14 that establish crocodiles as the sister-group of a combined taxon including birds and mammals, and 16 that unite chelonians and thecodontians. These are chosen from the nearly limitless number of characters exhibited by these groups. The choice of other characters has led previous authors to entirely different interpretations of the relationships of these groups. Clearly, there must be some objective criteria for selecting characters for analysis. One approach would be to use all characters known to change within an assemblage, or some random means of character selection that avoids bias produced by prior assumptions of phylogenetic relationships. This problem is less acute in the case of fossils in which it may be possible to use all characters of the skeletal system.

The problem of character selection strongly influences the application of the rule of parsimony. Parsimony, in the sense of choosing a simple rather than a complex solution for problems, is a general procedure in all science. It has been applied to systematics as a means of choosing between two or more alternate hypotheses of relationship. In general, the hypothesis selected is that which involves the fewest cases of convergence or reversal, or the smallest number of evolutionary steps of any sort. There is, however, no direct evidence that evolution is parsimonious, and convergence may be a common phenomenon. There is another problem with this procedure. It is valid only if the characters considered include all the characters that differ between the groups in question, or some nonbiased sample of these characters. One may say that two groups are related more closely to one another than either is to a third because the first groups are united by 27 shared-derived characters, as opposed to some smaller number supporting the alternate relationships; however, this conclusion is of little significance if there are hundreds of other characters that have not been considered. Parsimony is a practical means of choosing between alternate phylogenetic schemes only if the organisms are basically similar to one another and there is a relatively small number of differences involved, all of which can be analyzed.

It is also necessary to establish some objective means to select the taxa for analysis. This has been "solved" to some extent by cladists who choose to restrict their analysis to living forms (e.g., Løvtrup, 1985). Clearly, such an approach is not justified when the patterns of evolutionary change suggest that the *earliest* known (i.e., fossil) members of monophyletic groups would be much more informative in establishing the pattern of probable relationships.

For nearly 20 years the role of fossils in phylogenetic analysis has been denigrated by many followers of Hennig (but not by Hennig himself). There is now a growing awareness, as illustrated by recent papers by Maisey (1984), Novacek (1986), and Gauthier et al. (1988), that information from the fossil record can contribute substantially to phylogenetic analysis. The following discussion of the relationships of diapsids is intended to demonstrate how Hennig's methodology can be applied to a group with a significant fossil record. At the same time, it serves to test the assumption that convergence is a relatively rare phenomenon and demonstrates the degree to which the use of modern genera is appropriate in evaluating the relationships of the groups to which they belong.

Benton (1985) produced a classification of diapsids that provides an informative contrast to the approach that is attempted here. (See also Evans, 1984; Evans, 1988 and Laurin, 1991 were published too late for evaluation in this review.)

Methodology

In an effort to establish relationships among the major diapsid groups, a relatively simple list of procedures for phylogenetic analysis has been developed. It is intended to be as objective and as free from prior assumptions as possible. The procedures include the following: (1) establishment of the monophyly of the group in question, (2) establishment of the polarities of all characters that vary within the group, (3) recognition of subgroups on the basis of unique apomorphies, (4) determination of derived character-states present in the most primitive members of each monophyletic subgroup, and (5) determination of possible interrelationships on the basis of derived characters shared by the most primitive known members of each subgroup. It would be convenient if this list could be followed in numerical sequence, but, in fact, it has been necessary to work on all categories at once, moving back and forth as information accumulated.

The term *monophyly* is used in this paper to refer to the origin of a group, rather than its subsequent history. For example, the archosaurs are referred to as a monophyletic group on the assumption that they evolved from a single ancestor, without concern for the fact that the term *archosaur* usually is used to the exclusion of their probable descendants, the birds.

Establishment of the Monophyletic Nature of the Group

No dependable classification is possible in the absence of at least a general knowledge of other, related groups. The difficulty of classifying the placoderms, for example, can be attributed at least partially to the fact that their specific relationships to other jawed fish have not been determined (Denison, 1978; Miles and Young, 1977; Goujet, 1984; Gardiner, 1984, 1986). Fortunately, the relationship of diapsids to other early amniotes is well established (Reisz, 1981; Heaton and Reisz, 1986; Carroll, 1982). This knowledge assists in the selection of appropriate out-groups for establishing polarity so that truly unique and derived characters can be used to establish the monophyletic nature of the diapsid subgroups.

Early amniotes are distinguished by the following combination of characters that are derived relative to most other Paleozoic tetrapods: (1) Small adult body size, with highly ossified joint surfaces, carpals, and tarsals. (2) Tooth-bearing transverse flange of pterygoid; loss of fangs on palatal bones. (3) Absence of labyrinthine infolding of teeth. (4) Supraoccipital, a platelike ossification that is movable relative to the skull table. (5) Loss of intertemporal bone and reduction in size of supratemporal, tabular, and postparietal. (6) Stapes with short perforate stem, large footplate, and a dorsal process. (7) Pleurocentra cylindrical and forming the dominant element of the vertebrae, sutured or fused to the arches of all vertebrae except the atlas; intercentra reduced to small crescents but retained throughout the trunk region. (8) Proximal centrale, intermedium, and tibiale co-ossified to form astragalus. In these and other skeletal features, the early representatives of the Paleozoic amniote groups resemble one another closely and apparently diverged from a similar common ancestor not long before their first appearance in the early Pennsylvanian.

Diapsids, in turn, can be differentiated from all members of other early amniote groups by a few features that are derived relative to all other early tetrapods. The most conspicuous traits are the presence of dorsal and lateral temporal openings and a suborbital fenestra. These three cranial characters establish the monophyly of the diapsids. The temporal and suborbital openings may be lost or modified in later species, but all derived patterns can be traced to the primitive condition of the early diapsids.

Reisz (1981) identified some other, less definitive synapomorphies including the possession of well-developed posttemporal fenestrae, a relatively small skull, and a locked tibioastragalar joint. Benton's (1985) objection that these features do not occur in later diapsids or occur in turtles (which do not appear in the fossil record until the late Triassic) is irrelevant in establishing the monophyly of diapsids among early amniotes.

Benton (1985) listed five additional characters of the soft anatomy and development to support the monophyly of diapsids: (1) a Jacobson's organ that develops as a ventromedial outpocketing of the early embryonic nasal cavity; (2) olfactory bulbs anterior to the eyes and linked to the forebrain by the stalklike olfactory tract; (3) one or more nasal conchae in the cavum nasi proprium; (4) a "Huxley's foramen" at the distal end of the extracolumella, surrounded medially by the processus dorsalis and intercalary, and laterally by a laterohyal that links the intercalary to the distal extracolumellar plate; and (5) low levels of urea in the blood. Benton's choice of these characters is based entirely on their presence in living squamates, sphenodontids, birds, and crocodiles (none of which had differentiated in the late Paleozoic) and their absence in modern frogs, salamanders, mammals, and turtles.

It is extremely unlikely that an extracolumella was present in early diapsids, because the structure and function of the stapes is entirely different from that of any living diapsids. There is no evidence that early diapsids possessed either a tympanum or a middle-ear cavity. It is impossible to establish directly if any of the other soft anatomical and developmental characters cited by Benton were present in *early* diapsids (as defined by the nature of the skull) and not in other early amniotes. They are thus of no utility in testing any phylogenetic hypothesis involving Paleozoic genera.

Establishment of the Polarity of Each Character That Varies within the Group

In order to establish relationships among the diapsids, it is necessary to establish the polarity of all characters that vary within the group. By dealing with *all* variable characters, one can achieve a level of objectivity that would not be possible if characters are selected a priori. A similar approach has been taken by Novacek (1986) in establishing a morphotype for primitive placental groups.

Determination of polarity is a serious problem in itself. Many criteria have been discussed, of which out-group comparison is usually stressed by cladists. To be useful in establishing polarity, the out-group must be a closely related member of the same larger monophyletic assemblage. In the case of the diapsids, the larger monophyletic group is the Amniota, within which protorothyrids and mammal-like reptiles are successively more distantly related sister-groups of diapsids (Heaton and Reisz, 1986).

The most informative out-group for establishing polarity would be the actual ancestors of the group in question. Most followers of Hennig have argued that it is impossible to establish ancestor-descendant relationships, but Wiley (1981:105–107) admitted that it is possible under certain circumstances. Ancestors may be recognized on the basis of the following criteria. An ancestor is a species that can be included within a monophyletic group on the basis of shared derived characters. In addition, the ancestor must (1) retain the primitive character-state for one or more of the morphoclines in which possible descendants possess a more derived condition, *and* (2) lack all apomorphies other than those encountered in the possible descendant forms. The position as putative ancestor can be falsified by the discovery or recognition of such apomorphies.

In the case of early diapsids, the protorothyrid *Paleothyris* (Carroll, 1969) appears to be close to the pattern expected for an ancestor. The only recognized autapomorphy that it possesses is the fusion of the axis intercentrum and the atlas centrum. In the earlier but less well-known genus *Hylonomus,* these bones remain separate. The axis intercentrum and atlas centrum are closely integrated but not fused in the early diapsids. To avoid the apparent circularity of these arguments, one can test the polarity of morphoclines in early diapsids further against the character-states in pelycosaurs and more primitive tetrapods.

Character-states that are present in both *Paleothyris* and early diapsids may be hypothesized as primitive for diapsids as a whole. The most primitive character-states known in diapsids are listed in Appendix I. Most of these are observed in *Petrolacosaurus,* the earliest known genus (Reisz, 1981). In a few characters (indicated in the appendix by an asterisk), *Petrolacosaurus* is derived relative to the state seen in some later diapsids, notably a second genus (*Apsisaurus;* Laurin, 1991) from the Lower Permian of Texas (see also Reisz, 1988). All character-states other than those listed in the left column of Appendix I may be considered derived relative to the condition in the earliest and most primitive diapsids.

Recognition of Subgroups on the Basis of Unique Apomorphies

Numerous subgroups among the early diapsids have been recognized by previous workers. In most cases, they can be diagnosed on the basis of clearly recognizable apomorphies that are unique for each group and widespread within them. Such features as the antorbital fenestra of archosaurs, the streptostylic quadrate of squamates, and the medial narial opening of rhynchosaurs are so clearly unique, obviously derived, and nearly universal in the groups under consideration that they can be used as a preliminary basis for the recognition of the groups. These traits then can be tested for their occurrence elsewhere in this assemblage or their conflict with other characters.

Unique derived features must be present in the earliest members of each group to be useful in their diagnosis. For example, most rhynchosaurs have multiple rows of cheek teeth, and most archosaurs have a lateral mandibular foramen, but these characters cannot be used to establish the monophyly of the groups because they are not present in the earliest known members as established by other criteria. The most conspicuous apomorphies possessed by the diapsid subgroups are listed in Table 1.

As discussed by Hennig (1981), the earliest and most primitive members of a group may have very few derived characters. One would expect to find some taxa in which the diagnostic characters of the group to which they probably belong are poorly developed if present at all. In the case of the diapsids, there are relatively few adequately known forms for which this is a problem. They will be discussed individually.

Most of the long-recognized groups of early diapsids can be defined readily by the autapomorphies listed in Table 1. This analysis has revealed one major change from previous usage. There are no synapomorphies that unite the genera that Romer (1956, 1966) included in the order Eosuchia. In fact, eosuchians must be divided into several distinct taxa. The groups that Romer (1966) classified as the suborders Choristodera and Thalattosauria are each characterized by autapomorphies that distinguish them clearly from all other major diapsid groups. Their phylogenetic positions remain uncertain. The genera that Romer grouped as the Prolacertiformes share unique derived features with *Protorosaurus, Tanystropheus,* and *Tanytrachelos* and are here termed the Protorosauria. Within Romer's Younginiformes, *Palaeagama, Paliguana,* and *Saurosternon* share unique derived characters with the modern lepidosaur groups (Carroll, 1975, 1977). *Heleosaurus* shares several derived features with archosaurs, and *Noteosuchus* with rhynchosaurs. The only genera that share a common anatomical pattern with *Youngina,* on which Broom (1914) based the Eosuchia, are *Acerodontosaurus, Kenyasaurus, Thadeosaurus, Hovasaurus,* and *Tangasaurus* (Currie, 1981a,b, 1982; Currie and Carroll, 1984). The term *Eosuchia* is here confined to these genera. Other recent authors have chosen to abandon the term *Eosuchia* because it has been used in reference to many genera that do not share a close common ancestry.

Most major groups of vertebrates show a similar natural division into a

Table 1. Autapomorphies of diapsid subgroups

Araeoscelida
1. Mammillary processes on neural spines of posterior cervical and anterior dorsal vertebrae
2. Conspicuous process for triceps muscle on posterior coracoid
3. Greatly enlarged lateral and distal pubic tubercles

Coelurosauravidae
1. Squamosal frill
2. Trunk ribs ossified in two segments, forming supports for large gliding membrane

Eosuchia (Younginiformes)
1. Medial centrale interposed between lateral centrale and third distal carpal

Squamata
1. Streptostylic quadrate supporting large tympanum

Sphenodontida
1. Acrodont dentition and particular pattern of limited tooth replacement

Nothosauria
1. Suborbital and interpterygoid vacuities closed with pterygoids meeting along midline as far posteriorly as the occipital condyle
2. Large unossified area between the transversely oriented ventral portions of the clavicles and interclavicle and the elongate, posteromedially directed coracoids

Plesiosauria
1. Pectoral and pelvic girdles greatly expanded ventrally
2. Similar, paddle-shaped hind and forelimbs
3. Ilium not attached to pubis

Protorosauria
1. At least seven very elongate cervical vertebrae
2. Cervical ribs extremely long and slender
3. Tympanum probably supported by squamosal and quadrotojugal

Rhynchosauria
1. Medial narial opening
2. Premaxillae forms overhanging beak
3. Ankylothecodont tooth attachment

Archosauria
1. Antorbital opening

Trilophosauridae
1. No lateral temporal opening
2. Loss of teeth in premaxilla and front of dentary
3. Cheek teeth laterally expanded

Choristodera
1. Elongation of snout with nasal bones fused at midline
2. Prefrontals meeting at midline, separating nasals from frontals
3. Temporal area greatly expanded laterally and extending well posterior to the occipital condyle
4. Internal nares extended posteriorly as grooves in the roof of the palate

Order Thalattosauria
1. Dorsal temporal opening much restricted or entirely closed
2. Jaw articulation far behind level of skull table and occipital condyle
3. Premaxillae elongated and reaching frontals; nasals displaced laterally

Placodontia
1. Trunk vertebrae deeply amphicoelus, but with long transverse processes
2. Closure of lateral temporal opening; quadratojugal forming much of cheek

number of large subgroups—e.g., the orders among placental mammals and Devonian placoderms, and the families of modern birds and bony fish. Presumably, this coherence of natural groups is associated with specific relationships to their physical and biological environments and is perpetuated further by genetic and developmental constraints (Carroll, 1986). For analysis, these monophyletic units may be of any size, from a single genus the phylogenetic position of which is in question, up to (in this study) an entire subclass, the Archosauria, the unity of which is clearly evident on the basis of one or more autapomorphies.

The recognition of such monophyletic subunits at an early stage in cladistic analysis is necessary for the identification of strictly homologous characters. Characters or character-states that evolve within a particular monophyletic group cannot be homologous to characters that evolve within a separate monophyletic group, no matter how similar they may be in structure and function.

For example, the tabular and postparietal are missing in all Recent diapsid groups. However, it can be demonstrated that these losses occurred separately at least twice, and perhaps three or more times within distinct monophyletic subgroups, and thus cannot be homologous traits. This procedure demonstrates that many character-states that seem similar have been achieved convergently. Therefore, it is difficult to establish a reliable phylogeny on the basis of a preliminary analysis of character distribution without first establishing the strict homology of the characters.

Determination of All the Derived Character-States Present in the Most Primitive Members of Each of the Monophyletic Subgroups

The *unique* derived characters that are present in the earliest members of each monophyletic group are of no significance in establishing relationships with other groups. However, each group may possess additional derived features that are shared by other groups which can provide evidence of relationships.

It would seem obvious that only the character-states expressed in the earliest members of each group can be used to establish relationships between groups. Characters evolved *within* a group are of no significance in demonstrating relationships with other groups. This guideline has been ignored by many cladists, however, who typically argue that living members of groups provide much more information than do fossils for establishing relationships. For example, Gardiner (1982) in his discussion of tetrapod phylogeny and Rosen et al. (1981) in their attempt to establish close relationships between lungfish and tetrapods make no effort to demonstrate that the characters that they used were present in the early members of the groups which they discuss. The use of call notes in modern lungfish and salamanders by Rosen et al. to demonstrate the affinities of Paleozoic labyrinthodonts and lungfish was notable.

The importance of establishing the earliest members of monophyletic groups was expressed clearly by Hennig (1981:34) "the task of phylogenetic research is to trace the history of 'modern groups' as far back into the past as possible: this can only be done if we assign to each 'modern group' all the fossils that belong to its ancestral line." This raises a very important procedural question: How do we recognize the earliest member of a monophyletic group? Because of the incompleteness of the fossil record, we have no way of being certain that a particular fossil represents the absolute earliest member of a group. Unless the fossil record of both the group in question and the group that is immediately ancestral to it are known in great detail, ever older "earliest" species might be postulated.

Although we cannot necessarily recognize the earliest member of a group, we can recognize the species with the most primitive suite of character-states. Such a species would belong to what Hennig (1981) referred to as a stem-group. This is an assemblage characterized by the possession of some, but not all, the apomorphies of the typical or modern members of a monophyletic assemblage. The earliest adequately known archosaur, *Chasmatosaurus*, and the earliest known squamate, *Paliguana*, for instance, can be recognized by only one or two of the many features that characterize later members of these groups.

The earliest known member of a group is not necessarily the most primitive morphologically, but in general, species that possess a majority of primitive character-states are also among the earliest forms to appear in the fossil record (Butler, 1982). On the other hand, the early appearance of a species should not, by itself, be taken as evidence for the primitive nature of all its expressed character-states. For example, coelurosauravids (Evans, 1982) are among the earliest diapsids, yet their greatly elongate ribs and peculiar elaboration of the squamosal certainly are not primitive character-states. Paul (1982) commented on the generally close correlation between stratigraphic level and phylogenetic position, and Maisey (1984) recently discussed the close correlation among Mesozoic chondrichthyans.

The derived characters present in the most primitive members of each of the monophyletic groups among the diapsids are listed in Appendices II–VII.

RELATIONSHIPS AMONG DIAPSIDS

Possible interrelationships can now be considered on the basis of derived characters that are shared by the most primitive known members of two or more of the monophyletic subgroups. This is, in fact, simply establishing monophyly at a new level. Again, the characters chosen can be tested against other features to determine congruence.

An important procedure is to begin with the most widespread features that define the largest number of included subgroups. All adequately known diapsids from the Upper Permian and later are united by the following derived characters: (1) strengthening of the temporal bars, (2) downgrowth of the parietals beneath the adductor jaw musculature, (3) exclusion of the lacrimal bone from the narial opening, (4) absence of caniniform maxillary teeth, (5) elimination of the primitive separation between the two coracoids, (6) distal condyles of femur level with each other, (7) caudal ribs straight and fused to centra, and (8) median row of gastralia fused at midline.

Several additional features cited by Benton (1985) as characterizing these diapsids are not present in all early members of this assemblage. For example, in the younginoid eosuchians, the quadrate is not emarginated, as he claimed, or notched posteriorly, nor is the stapes slender by comparison with modern diapsids that have an impedance-matching middle ear. Neither is the retroarticular process well developed, as would be expected in animals such as modern lizards in which this area contributes to support of a tympanum. *Chasmatosaurus*, the earliest adequately known archosaur, does not have a slender sigmoidal femur, nor is the proximal head inflected medially.

Araeoscelida

Two families, the Petrolacosauridae and Araeoscelidae, are more primitive in these features and can be recognized as a distinct monophyletic group by the presence of the autapomorphies cited in Appendix II. These families may be placed in a distinct order, the Araeoscelida (Reisz et al., 1984). Benton suggested that all other adequately known diapsids should be included in a separate taxon, the Neodiapsida.

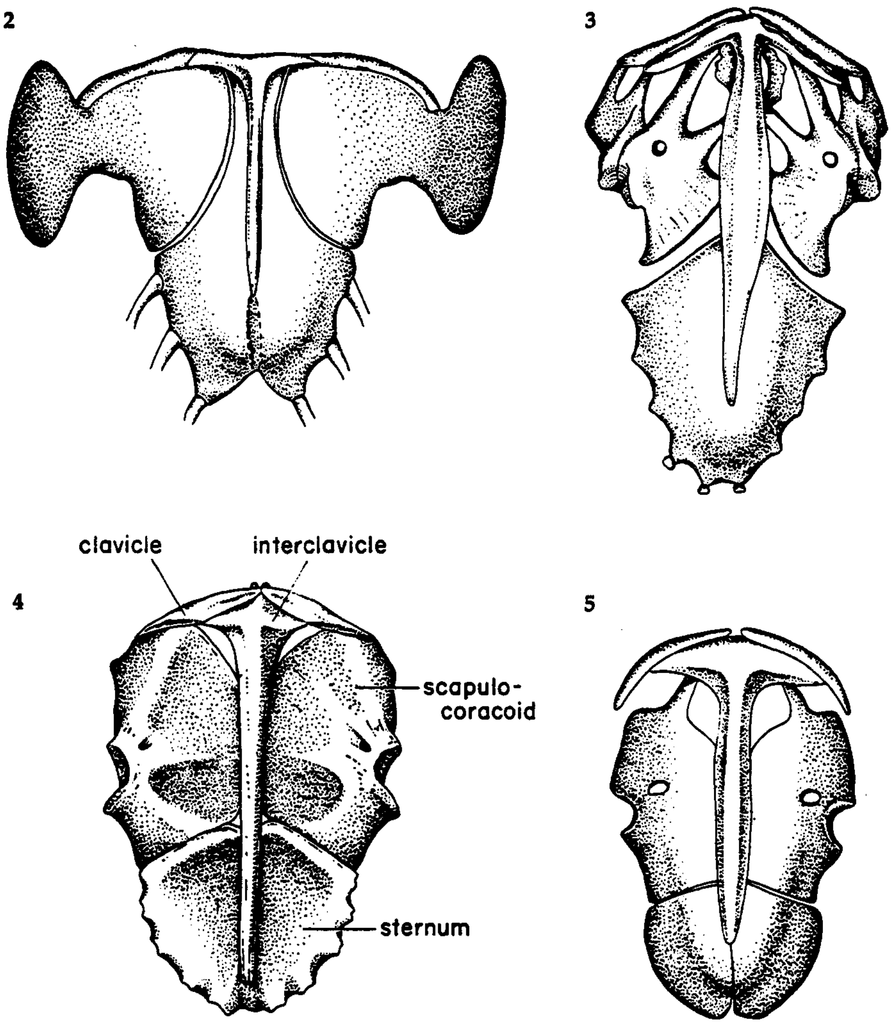
Coelurosauravidae

Five groups of advanced diapsids are recognized by the Late Permian. Most genera belong to two large groups designated by Benton (1985) as the Lepidosauromorpha and the Archosauromorpha. The third is represented by two highly specialized genera, *Weigeltisaurus* from Europe and *Coelurosauravus* [*Daedalosaurus*] from Madagascar (Carroll, 1978; Evans, 1982; Evans and Haubold, 1987). Both are characterized most dramatically by the possession of greatly elongated ribs that almost certainly supported a gliding membrane, as in the modern lizard *Draco*. They lack the synapomorphies that distinguish the lepidosauromorphs and archosauromorphs and retain the following primitive features that are modified by the major groups of advanced diapsids: (1) ribs of atlas vertebra probably retained; (2) large cleithrum; and (3) well-ossified olecranon. Retention of these primitive features probably indicates that the coelurosauravids diverged from the ancestral diapsid lineage prior to the emergence of either the Lepidosauromorpha or the Archosauromorpha.

Lepidosauromorpha

Among the advanced diapsids, the distribution of derived character-states suggests the recognition of two large groups, including all the living genera, the Archosauromorpha and the Lepidosauromorpha. The position of several other groups is more difficult to ascertain. The derived features of these major groups are cited in Appendices III–IV. Benton provided similar character lists, but with little comment on their adaptive significance.

Characters can be used to establish phylogenies without any concern for their biological significance, but an understanding of evolutionary processes is certainly assisted by an appreciation of their function. The different structures of the limbs and girdles in advanced diapsid groups may be associated with divergent patterns of posture and locomotion. Most lepidosauromorphs are relatively small animals whose fossil members are broadly comparable to living lizards and *Sphenodon* in their skeletal anatomy. Presumably, they had a similar sprawling posture and a locomotary pattern based on sinusoidal movement of the trunk. This pattern accentuates that of more primitive tetrapods, but the lepidosauromorphs also are united by specific derived features of the skeleton. The most important of these is the presence of a large sternum (Figs. 2–5), which has specific areas of attachment for the distal ends of the anterior trunk ribs. The basic structure is very similar in modern lizards, *Sphenodon*, and the Permo-Triassic eosuchians (younginiforms). In all, the sternum is a massive median ventral plate, the anterior margins of which articulate with the posterior margin of the scapulocoracoids. Gray (1968) pointed out that the sternum of lizards functions to prevent posterior movement of the scapulocoracoid when the humerus is strongly retracted and forms a surface on which the coracoids can rotate. This rotation moves the glenoid in an extensive horizontal arc that enables the humerus to be extended much farther anteriorly than would be possible from its limited movement within the glenoid. Jenkins and Goslow (1983) provided detailed evidence from X-ray cinematography and electromyography of the range of movement between the coracoids and the sternum in living lizards, and its contribution to locomotion in this group.



Figs. 2–5. Sterna of lepidosauromorphs. (2) *Sphenodon*. (3) *Iguana*. (4) *Hovasaurus*. (5) *Saurosternum*, attributed to the Paliguanidae. (Modified from Carroll, 1987.)

The term *sternum* has been applied to ventromedial ossifications in the thoracic region in birds, mammals, and archosauromorphs, but the structure and function of these elements differ significantly in each group and there is no evidence for their homology. There certainly is no evidence for the presence of a sternum in early members of the archosauromorph assemblage. Hence, the nature of the sternum in primitive lepidosauromorphs provides very strong evidence for the monophyly of this assemblage.

Possibly associated with the differences in their pattern of locomotion, the transverse processes of the trunk vertebrae are shorter and the rib heads single in lepidosauromorphs, whereas the transverse process of archosauromorphs tend to become more elongate than in primitive diapsids, and the ribs are clearly double headed.

The limbs of primitive lepidosauromorphs do not differ greatly from those of more primitive diapsids. However, the neck region is distinctive in having cervical vertebrae 3–5 noticeably shorter than those of the anterior trunk region.

The presence of accessory vertebral articulations in early lepidosauromorphs was noted by Benton (1985) and Currie (1982). Because these areas of articulation vary in position and their degree of expression increases with size, they are not convenient taxonomic indicators.

Eosuchians (Younginiformes)

Among the lepidosauromorphs, the eosuchians (younginiforms) retain a suite of primitive character-states relative to sphenodontids and squamates that suggest that they might occupy a position ancestral to the modern orders. All adequately known eosuchians possess at least one autapomorphy not present in modern lepidosaurs. The medial centrale is interposed between the lateral centrale and the third distal carpal (Fig. 6). This character seems to be sufficient to establish the monophyly of the known eosuchians, excluding the poorly known genus *Galesphyrus* (Carroll, 1976b), which retains the primitive pattern of the wrist in common with early diapsids, squamates, and sphenodontids. Other characters cited by Benton seem less important in establishing the monophyly of the eosuchians. The large size of the entepicondyle of the humerus is characteristic of tangasaurids but has not been demonstrated clearly in *Youngina*. The shape of the neural spines changes during ontogeny and in relationship to adult size, and thus is not a clear-cut difference that can be used for phylogenetic analysis.

Although primitive characters in themselves do not demonstrate the monophyly of a group, they are, in fact, the most conspicuous aspects of eosuchians. The group retains a complete lower temporal bar, and the quadrate, although exposed posteriorly, is not obviously emarginated for support of a tympanum. The retroarticular process is barely evident. The stapes remains massive and angled posteroventrally, as in primitive amniotes. The structure of the stapes, articular, and quadrate provides no evidence for an impedance-matching function of the middle ear.

Aside from the structure of the carpus, eosuchians have no conspicuous derived features of the skeleton that would preclude them from having been ancestral to sphenodontids and squamates.

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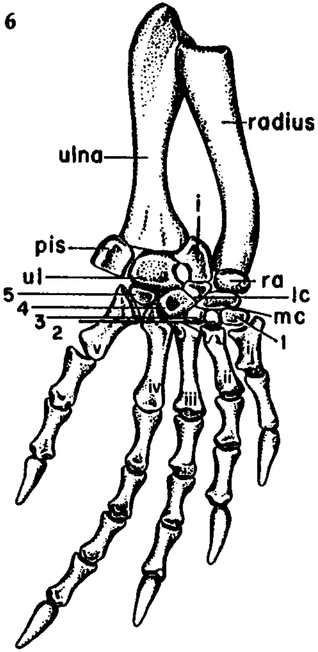
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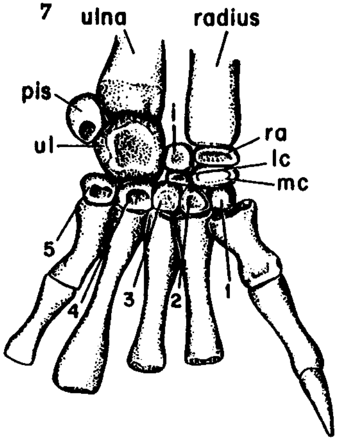
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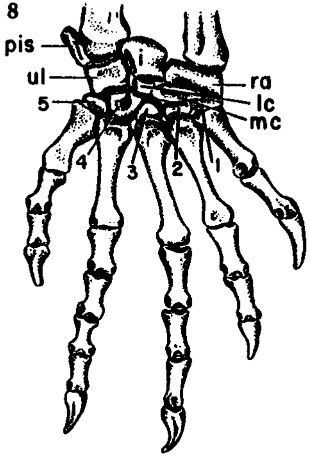
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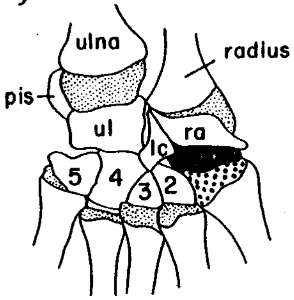

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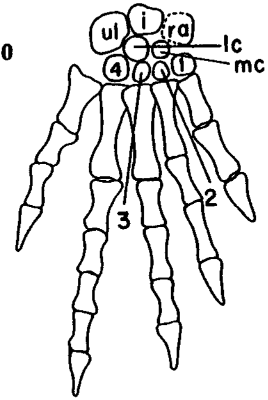


Figs. 6–10. Carpals of diapsids. (6) Lower forelimb of the eosuchian *Thadeosaurus.* (7) Carpus of the putative early lizard *Saurosternon.* (8) Carpus of *Sphenodon.* (9) Carpus of *Iguana.* Epiphyseal ossifications are identified by fine dots. Bone shown by coarse dots might be the epiphysis of the first digit or the first distral carpal. Dark element is the medial centrale. The intermedium is lost. (10) Carpus and manus of the archosauromorph *Protorosaurus,* restored on the basis of illustrations in Meyer (1856). See Appendix VIII for key to abbreviations. (Modified from Carroll, 1987.)

Lepidosauria

Benton (1985) compiled a substantial list of features that unite the Sphenodontida and Squamata within the Lepidosauria, but these are based primarily on the advanced members of these groups. He did not specifically consider the early members, which would be expected to demonstrate the most primitive character-states expressed within each group. Many of the features he cited might have been achieved independently within each group.

Sphenodontida

Benton distinguished sphenodontids on the basis of a large number of derived characters present in a variety of Triassic and Jurassic forms as well as the living genus *Sphenodon*. In fact, primitive character-states of many of these features are observed among the earliest genera, suggesting that the derived condition has been achieved within the group rather than being characteristic of the earliest representatives (Fraser, 1982, 1986). The following list retains the original numbering of Benton (1985):

1. "Lacrimal absent." This is true of all known sphenodontids.
2. "Parietals narrow and reduced to two nearly vertical back-to-back plates with ventro-lateral flanges that contact the supraoccipital." Broad parietals (a primitive condition) are present in the Triassic genera *Planocephalosaurus* and *Polysphenodon*, as well as in *Homeosaurus* from the late Jurassic.
3. "Supratemporal absent." A supratemporal was reported in *Clevosaurus* from the Upper Triassic (Robinson, 1973).
4. "Quadrate not emarginated." No early sphenodontid is known that definitely lacks an emarginated quadrate. In both *Clevosaurus* and *Planocephalosaurus*, the quadrate (perhaps incorporating the quadratojugal) bears a lateral conch that broadly resembles the structure that supports a tympanum in modern lizards. The likelihood of a tympanum being present is further indicated by the presence of a well-developed retroarticular process in these genera. *Sphenodon*, which has a long slender stapes like that of most lizards, might have secondarily lost the impedance-matching function of the middle ear (Wu, 1988).
5. "Teeth acrodont." In all early genera that are definitely identified as sphenodontids, most of the teeth are acrodont, although some genera have been reported to have pleurodont teeth (Fraser, 1986).
6. "One to three fused teeth on the premaxilla which are longer than the maxillary teeth and give a 'beaked' appearance to the skull." *Planocephalosaurus* has five small conical teeth in the premaxilla, closely resembling the pattern in primitive lepidosauromorphs.

7. "Tiny juvenile teeth at the front of the maxilla and dentary." These are evident in many early sphenodontids.
8. "Tooth replacement occurs by addition at the back of the maxilla and dentary." Apparently, this is true of all sphenodontids.
9. "A single row of large teeth on the palatine which are separated from the maxillary teeth by a deep groove." *Planocephalosaurus*, like more primitive diapsids, has several rows of palatal teeth, although the lateral palatine row is the largest.
10. "The dentary teeth fit tightly into the maxilla-palatine groove and the propalinal jaw action polishes the teeth and bone in a uniform way." Tooth occlusion in *Clevosaurus* and *Planocephalosaurus* occurs by vertical jaw movements. These genera do not show evidence for propalinal movement. Vertical tooth occlusion seems to be a feature of most, if not all, early sphenodontids. Propalinal movement is a specialization of the modern genus *Sphenodon*.
11. "No teeth on the palate except for the palatine row." (See number 9.)
12. "Splenial absent." This bone has not been reported in any genera, but it could easily be lost during fossilization. A splenial might have been retained in the closely related family Pleurosauridae (Carroll, 1985).
13. "Broad mandibular symphysis formed entirely by the dentary." Not a clear-cut feature.
14. "Dentary runs well back, forming most of the lateral side of the lower jaw." To this can be added the distinct feature of a high coronoid process of the dentary, supported medially by a well-developed coronoid bone.
15. "Large mandibular foramen bounded by the dentary and surangular." This is not illustrated in Fraser's (1986) reconstruction of *Planocephalosaurus*, but this foramen can be seen in his Figure 2 of Plate 70 of this genus. A notch for this foramen is also apparent in Fraser and Walkden's illustration of *Clevosaurus* (1983).

Several other derived features of early sphenodontids were noted by other authors. In common with most, if not all, other members of the order, the prefrontal of *Planocephalosaurus* extends to the palatine. *Planocephalosaurus* also has a specialized tail-break mechanism, as have other terrestrial sphenodontids. All sphenodonts and early pleurosaurs have a large quadratojugal foramen.

The polarity of another important feature of sphenodontids cannot be established on the basis of evidence currently available. *Sphenodon* has a well-developed lower temporal bar. This feature has long been accepted as primitive for sphenodontids. However, several early forms, including *Clevosaurus* and *Planocephalosaurus*, have an incomplete lower temporal bar. Two possibilities present themselves. The reduction of the lower temporal bar may be a specialization evolved within sphenodontids from a primitive diapsid condition. Alternatively, the open condition might have been retained from their immediate ancestors and the complete bar re-elaborated within some members of the group. Only direct evidence from the immediate ancestors of the group will answer this question with assurance.

In contrast with the condition in lizards, the reduction in the lower temporal bar in early sphenodontids is not associated with mobility of the quadrate, which remains firmly attached to the quadrate ramus of the pterygoid in *Planocephalosaurus* and *Clevosaurus*. Rieppel and Gronowski (1981) associated reduction of the lower temporal bar with elaboration of the lateral portion of the adductor jaw musculature. At least among the pleurosaurs, there seems to be a progressive reduction of the bar (Carroll, 1985). In *Sphenodon, Polysphenodon,* and *Brachyrhinodon,* the lower temporal bar is arched laterally away from the lower jaw. This seems an alternate way of accommodating an enlarged adductor musculature, thus suggesting that a complete lower bar was primitive for the group. Whiteside (1986), in contrast, presented other evidence that suggests that the temporal bar was incomplete in the earliest sphenodontids and their immediate ancestors.

Gephyrosauridae

Gephyrosaurus, from the Lower Jurassic of Great Britain, shares a number of derived features with both squamates and sphenodontids, thereby leaving little question of its assignment to the Lepidosauria (Evans, 1980, 1981).

Benton (1985) considered the following features to be indicative of a sister-group relationship of gephyrosaurids with the Squamata: (1) fused parietal and frontal, (2) reduced lower temporal bar, (3) quadrate notched with well-rounded conch, (4) articular fused to the prearticular, (5) all ribs holocephalous, and (6) sacral ribs fused indistinguishably to sacral vertebrae. Three of these features are also characteristic of early sphenodontids—the reduced lower temporal bar, the quadrate notch, and the fusion of the articular to the prearticular. Solid attachment of the sacral ribs to the centra is observed in mature eosuchians and cannot be considered a unique feature of any advanced group of lepidosaurs. Not all the ribs are holocephalous. Those in the cervical region, as in both sphenodontids and lizards, clearly are double headed. The trunk ribs are single headed in all three groups.

The frontals and/or the parietals are fused along the midline in a variety of squamates, but this is not the case in *Paliguana* (see below), which may be the most primitive lizard. The nature of the foot, the presence of a thyroid fenestra, and specialized caudal autonomy are shared with squamates and sphenodontids.

The presence of separate epiphyseal ossifications and a quadrate conch may be common to all lepidosaurs. The absence of a sternal ossification may be attributed to the nature of preservation.

No features of *Gephyrosaurus* are shared uniquely with the early squamates. However, two features—the contact of the prefrontal with the palatine and the elaboration of a row of large palatine denticles—are otherwise unique to the Sphenodontida, suggesting a sister-group relationship with that order. *Gephyrosaurus* may be a relict of an early stage in the evolution of sphenodontids, in which case the stem-group of the order might be characterized by many fewer derived characters than were listed by Benton.

Squamata

Benton (1985) recognized 23 derived characters of the skeleton as being unique to squamates. It is clear from his list that he has drawn most of the features from the modern lizard groups, known no earlier than the late Jurassic, by which time all the modern infraorders had differentiated. Hennig (1981) argued that it is important to trace taxonomic groups back to the earliest members, although the latter may be recognized by only few of the derived characters that distinguish living species.

The Late Permian or Early Triassic genus *Paliguana* is known only from an isolated skull (Carroll, 1977, 1988). It has several important characters that otherwise are unique to the modern lizard groups. These include (1) presence of a streptostylic quadrate, supported dorsally by the squamosal; (2) a distinctive lateral conch of quadrate, similar to the surface that in modern lizards supports a tympanum (early sphenodontids also have a conch, but it is formed partially by a vestige of the quadratojugal, which does not have this position in squamates); and (3) absence of the lower temporal bar. If *Paliguana* is a lizard, as suggested by these shared derived characters, the other cranial features cited by Benton must have evolved within the early squamates.

Saurosternon, known only from a headless skeleton from the Late Permian or Early Triassic of southern Africa, also was assigned to the squamates. The features that suggest this assignment—the small size of the intermedium, possible fenestration of the scapula, and fusion of the atlas neural arch—are not clearly visible in the specimen. The probable elaboration of separate epiphyseal ossification, the very short fifth metatarsal, and the development of a mesotarsal joint are characters shared by both squamates and sphenodontids. *Saurosternon* can be associated with the lepidosaurs with some assurance, although its assignment to the Squamata may be questioned.

If one accepts *Paliguana* as an early squamate and *Saurosternon* as an early lepidosaur, the following derived characters define the Lepidosauria: (1) an impedance-matching middle ear (evidenced by a lateral conch of the quadrate or quadrate-quadratojugal complex, a slender stapes, and a conspicuous retro-articular process), (2) separate epiphyseal ossifications, (3) short fifth metatarsal, and (4) incipiently mesotarsal foot joint.

If the presence of a lower temporal bar and the solid attachment of the quadrate were primitive features of sphenodontids, the conditions seen in *Paliguana* are derived and indicate that lizards and sphenodontids must have diverged by the Late Permian. If this is the case, the following derived features shared by advanced lizards and sphenodontids, but not by *Paliguana* (or *Saiiropternon* and *Palaeagama*, if these three genera are closely related), must have been achieved by convergence: (1) postparietal and tabular lost, (2) thyroid fenestration of the pelvis, (3) fusion of the astragalus and calcaneum, (4) loss or fusion of the centrale pes, (5) loss of Distal Tarsals 1 and 5, and (6) hooking of the fifth metatarsal.

On the other hand, if the presence of a complete lower temporal bar in some sphenodontids is not primitive for that group but derived from a pattern like that of squamates, sphenodontids might have evolved from animals such as *Paliguana*. If this were the case, *Paliguana* and other members of the Paliguanidae may belong to a stem- or sister-group of advanced lepidosaurs. If this were true, the characters listed above might have been achieved within a single lineage that includes the immediate common ancestors of the sphenodontids and the modern lizard orders. Whiteside (1986) argued that lizards and sphenodontids might have diverged as late as the Middle Triassic. This problem can only be resolved by the discovery of well-preserved lepidosaurs from the Early Triassic.

Kuehneosauridae

Most authors have placed the kuehneosaurids among the primitive squamates. Benton (1985), in contrast, placed them in Neodiapsida *incertae sedis*, arguing that they share at least seven synapomorphies with archosauromorphs. This disagreement shows the difficulty of establishing relationships on the basis of characters the homology of which is not adequately known. Benton listed the following characters as synapomorphies with archosauromorphs: (1) absence of tabulars, (2) vertebrae nonnotochordal, (3) transverse processes of vertebrae projecting laterally, (4) absence of cleithrum, and (5) absence of entepicondylar foramen. All of these features are also encountered among lepidosauromorphs, although they are not found in the most primitive members of this group. All but the great width of the transverse processes are found in Upper Jurassic squamates. Another feature that is shared by kuehneosaurids and some archosauromorphs and that is not seen in other lepidosauromorphs is the confluence of the external nares; this feature is known in rhynchosaurs and crocodiles among the primitive archosauromorphs (as well as in champsosaurs, of doubtful phylogenetic position). None of these groups is likely to have a sister-group relationship with kuehneosaurs on the basis of the majority of other skeletal traits. The configuration of the other bones making up the nasal region in rhynchosaurs, crocodiles, and champsosaurs makes it extremely unlikely that confluent external narial openings are a homologous character. The great elongation of the transverse processes in kuehneosaurids is certainly related to the elaboration of the ribs to support a gliding membrane and is no basis for suggesting homology with the pattern in archosaurs. This condition also is achieved separately in plesiosaurs (see below). Thus, doubt is cast on all the characters used by Benton to suggest affinities between kuehneosaurids and archosauromorphs.

The problem of classifying the kuehneosaurids demonstrates how important it is to establish the specific homology of characters before they can be used as evidence for phylogeny reconstruction. For example, the tabular, postparietal, and supratemporal may be considered homologous bones in all tetrapods, but their loss is not necessarily a homologous process in different lineages. The absence of the tabular and postparietal in modern squamates, sphenodontids, crocodiles, and kuehneosaurs can be considered homologous only if that loss occurred in the immediate common ancestors of all these groups. That can be established only on the basis of the fossil record of probable common ancestors. Even the presence of a large number of derived characters in common with other groups, as in the case of the kuehneosaurids, can lead to contradictory phylogenetic conclusions, only one of which could possibly be correct. Clearly, parsimony is of no use in establishing relationships on the basis of characters whose homology has not been established.

The most important character that might link kuehneosaurids with lepidosauromorphs, the presence of a sternum, cannot be established in *Icarosaurus* because of the position in which the specimen was preserved (Colbert, 1970). It is doubtful that a sternum would be preserved in the fissure-filling deposits from which material of *Kuehneosaurus* has been described. None has been reported in *Planocephalosaurus*, for example, although this animal is unquestionably a sphenodontid. Sterna are known in the articulated Upper Jurassic specimens of sphenodontids from Solenhofen. The prefrontal does appear to enter the margin of the upper temporal opening in *Kuehneosaurus*, as restored by Robinson (1962). As in other lizards, the dorsal ribs are single headed. One undeniable squamate feature exhibited by *Kuehneosaurus* is the configuration of the quadrate, which suggests both streptostyly and support of a lizardlike tympanum. A quadrate of this pattern is known only among lepidosaurs, and never among archosauromorphs.

Sauropterygians

Two major groups of Mesozoic aquatic reptiles, the nothosaurs and plesiosaurs, are readily characterized by autapomorphies (Appendix IV). They can be united in a single large assemblage on the basis of the unique configuration of the shoulder girdle, in which the scapula is superficial to the clavicular blade—a reversal of the usual relationship between these bones. This supports the long-held view that they could be classified in a common group, the Sauropterygia, on the basis of the similar manner of specialization for aquatic locomotion, the presence of a dorsal temporal opening, and an emarginated cheek with a fixed quadrate.

The relationship of sauropterygians with other reptiles has long been controversial. They were once assigned to a separate subclass, the Synaptosauria (together with the placodonts). Kuhn-Schnyder (1962) argued that nothosaurs and plesiosaurs could be derived from primitive diapsids by the loss of the lower temporal bar. This idea was dismissed by Romer (1971) but was elaborated further by Carroll (1981). The problem of resolving these alternate hypotheses is that there are no clear-cut synapomorphies uniting sauropterygians with the major diapsid groups. Without earlier, more primitive fossils, their phylogenetic position cannot be established unequivocally.

Claudiosaurus (Carroll, 1981) from the Upper Permian of Madagascar combines features of primitive lepidosauromorphs and primitive sauropterygians. *Claudiosaurus* resembles eosuchians in a host of primitive features and specifically shares the derived lepidosauromorph features of the entrance of the postfrontal into the margin of the upper temporal opening and short transverse processes with holocephalous trunk ribs. *Claudiosaurus* also can be included within the Lepidosauromorpha on the basis of the presence of a large sternum. This bone is not calcified as in eosuchians and lepidosaurs; instead, it is preserved as an impression between the coracoids and the ventral gastralia in several well-preserved specimens. The carpus of *Claudiosaurus* resembles that of eosuchians, except for its retention of the primitive pattern of contact between the lateral central and the third distal carpal. Except for the elongation of the neck, a common feature in secondarily aquatic reptiles, there are no derived characters in common with any archosauromorphs. *Claudiosaurus* shares with nothosaurs and plesiosaurs the loss of the lower temporal bar and the restriction of the palatal vacuities.

At least some nothosaurs have a quadrate with an emarginated posterior margin, a character shared with lepidosaurs, but they lack the other features by which that group is recognized. The stapes is missing in plesiosaurs (Brown, 1981); there is no evidence for an impedance-matching middle ear in that group. If *Claudiosaurus* is a member of the sister-group of sauropterygians, an impedance-matching ear must be assumed to have evolved separately in nothosaurs and lepidosaurs. Separate epiphyseal ossifications are absent in *Claudiosaurus* and sauropterygians; they are unlikely to have been lost, as must be hypothesized if they shared a common ancestry with lepidosaurs. Sauropterygians, including *Claudiosaurus*, are thought to have diverged from the stem-group of lepidosauromorphs before either eosuchian or lepidosaurs.

Consideration of the sauropterygians reveals a methodological weakness in the procedures discussed here. Concentration on the character-states of the most primitive members of each group is based on the assumption that all relationships can be traced to the earliest members of major groups. This may be a common evolutionary pattern, to judge by the radiation of placental mammals and advanced teleosts in the Late Cretaceous and Early Tertiary and the radiation of placoderms and primitive chondrichthyans in the Late Silurian and Early Devonian. On the other hand, this methodology makes it difficult to recognize successive divergences within a particular assemblage. For example, two major groups of mammalian aquatic carnivores, the odobenoids and phocids, evolved from within separate advanced families of the Order Carnivora, long after the initial radiation of the order (Tedford, 1976). Plesiosaurs and nothosaurs can be placed within a larger monophyletic assemblage, the Sauropterygia, by cladistic analysis, but this does not reveal the specific nature of their relationships. Nothosaurs are characterized by unique derived features of the palate and pectoral girdle, but it is possible (or even probable) that these features have undergone evolutionary modification toward the pattern of plesiosaurs among taxa that retain many nothosaurian characters. This conclusion cannot be established using all nothosaurs for comparison with primitive plesiosaurs, but it can be detected if comparison is made with one particular genus among the nothosaurs, *Pistosaurus* (Sues, 1987a). This genus was long classified as a nothosaur on the basis of general skeletal similarities, but Edinger (1935) noted that the palate was not closed, as in typical nothosaurs, and that the nasal bones were much reduced. The pectoral girdle may be somewhat modified toward the pattern of plesiosaurs but retains definitive features of nothosaurs.

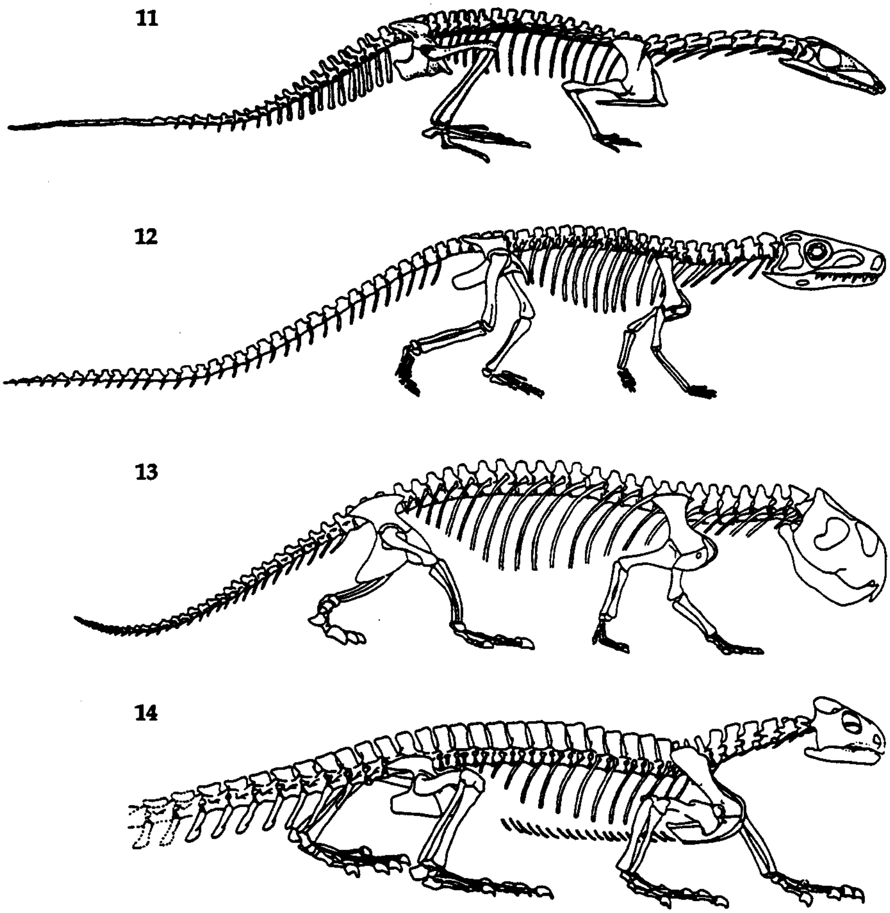
Pistosaurus may be considered a member of the stem-group of plesiosaurs with which it shares the loss of the entepicondylar foramen, the great reduction of the nasal bones, and the incipient development of large, platelike coracoids. All of these features are clearly derived relative to the most primitive nothosaurs, suggesting that *Pistosaurus*, and hence plesiosaurs as a group, evolved from within the nothosaurs, rather than having a typical sister-group relationship (divergent evolution from a common ancestral stock). It can be argued that the open nature of the palate in *Pistosaurus* and plesiosaurs is a primitive, rather than a derived, feature, which implies separation of these groups prior to the elaboration of the definitive nothosaur character states. In contrast, specialization of other aspects of the skull and the pectoral girdle implies divergence of plesiosaurs from a nothosaur pattern, rather than from a common ancestral stock.

If one follows the latter interpretation, nothosaurs would be considered a paraphyletic group in cladistic terminology. With or without the inclusion of *Pistosaurus*, nothosaurs nevertheless are a clearly defined group on the basis of specializations of the appendicular skeleton for aquatic locomotion that are distinct from the pattern of plesiosaurs (Carroll and Gaskill, 1985).

Archosauromorpha

With minor exceptions, those advanced diapsids that are not included in the Lepidosauromorpha can be included in a second large assemblage, the Archosauromorpha. The archosauromorphs embrace the archosaurs (represented during the Upper Permian and Lower Triassic by the proterosuchian thecodontians), rhynchosaurs, protorosaurs, and trilophosaurids (Figs. 11–14). In contrast with lepidosauromorphs, they are generally large and tend toward a more upright posture; the limbs would have moved in a more fore-and-aft direction. This is reflected initially in changes in the structure of the rear limb. All groups of archosauromorphs known in the Upper Permian and Lower Triassic are characterized by a foot structure in which the astragalus and calcaneum articulate with one another so that the feet can face more nearly forward throughout the stride. The fifth distal tarsal is lost, and the fifth metatarsal is inflected medially to articulate with the fourth distal tarsal (Figs. 15–18) (Characters 1–3).

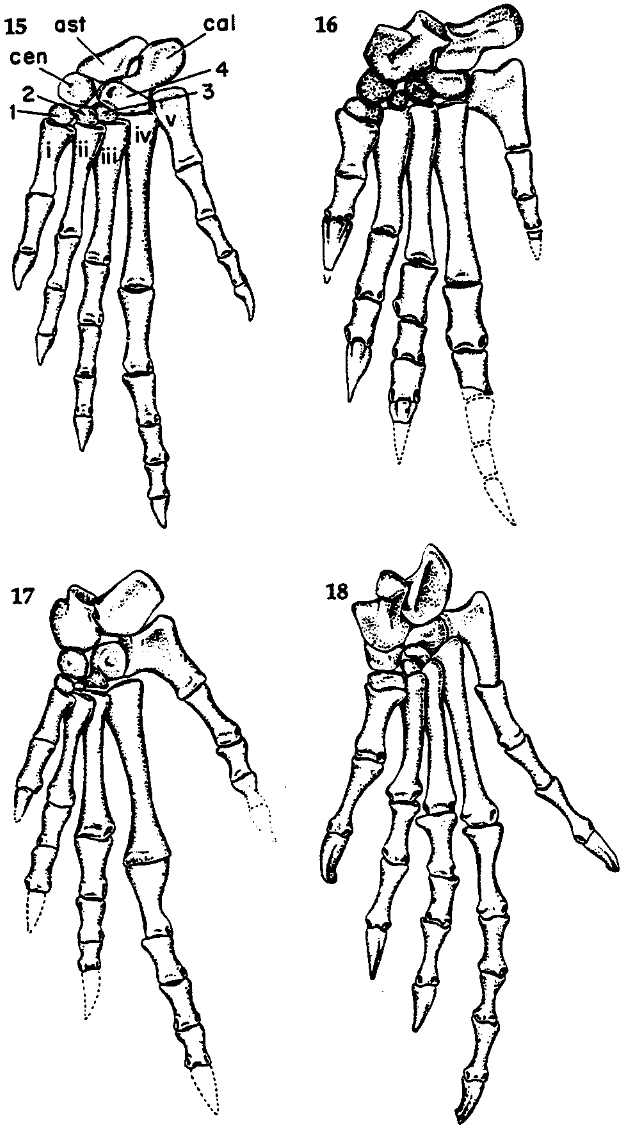
Lepidosaurs also evolved a hooked fifth metatarsal, but in that group it is not known until the late Triassic and is associated with a much different pattern of the proximal tarsals, which become fused with one another. Benton (1985) pointed out that the fifth metatarsal of archosauromorphs lacks the plantar tubercles that characterize that bone in lepidosaurs. Goodrich (1916) noted that turtles also have a hooked fifth metatarsal, but it is clear from the distribution of many other derived traits that the hooking of the bone evolved separately in lepidosauromorphs, archosauromorphs, and Chelonia. Although similar in both structure and function and ultimately derived from the same element in primitive amniotes, the hooked fifth metatarsal should not be considered a homol-



Figs. 11–14. Skeletons of primitive archosauromorph diapsids. (11) The protorosaur *Prolacerta*, approximately 1 m long (modified from Gow, 1975). (12) The archosaur *Euparkeria*, approximately 0.5 m long (modified from Ewer, 1965). (13) The rhynchosaur *Paradapedon*, approximately 1.5 m long (modified from Chatterjee, 1974). (14) *Trilophosaurus*, approximately 2 m long (modified from Gregory, 1945).

ogous structure in these three groups. Specialization of this bone also may have proceeded separately in squamates and sphenodontids.

Because of the basically different pattern of the skull and/or dentitions among early archosaurs, rhynchosaurs, protorosaurs, and trilophosaurids, it may be difficult to accept these features of the tarsus as truly synapomorphous. Despite the near identity of the tarsus in the three groups, it is possible that this pattern developed convergently. This hypothesis seems less likely, however, if we consider the character transformation within each of the groups. Although the earliest and otherwise



Figs. 15–18. Tarsus and foot of primitive archosauromorphs. (15) Tarsus of *Protorosaurus* (restored on the basis of illustrations in Meyer, 1856). (16) The primitive archosaur *Chasmatosaurus* (modified from Cruickshank, 1972). (17) The early rhynchosaur *Noteosuchus* (modified from Carroll, 1976a). (18) *Trilophosaurus* (modified from Gregory, 1945).

most primitive member of each of these groups exhibits a common pattern, later members of all adequately known groups show progressive divergence. Little more than a change in proportions and a loss of distal elements occur among the protorosaurs (Wild, 1974). The rhynchosaurs show a progressive integration of the centrale with the more proximal tarsals, and a partial fusion into a single unit (Carroll, 1976a). The archosaurs show a variety of derived patterns, but all could have evolved from that of the earliest genus (Brinkman, 1981).

Benton (1983, 1985) listed many other synapomorphies of early archosauromorphs. If one includes only the derived characters of the most primitive members of all the groups, the list continues as follows: (4) presence of a lateral tuber on the calcaneum (only incipiently developed in *Protorosaurus* from the Upper Permian), (5) loss of the tabular, (6) stapes without a foramen, (7) vertebrae not notochordal, (8) transverse process on dorsal vertebrae extends beyond level of zygapophyses, (9) cleithrum absent, (10) no entepicondylar foramen, and (11) loss of pisiform. Items 2, 3, 5, 6, 7, 9, and 10 also occur within the lepidosauromorph lineage but evolve there long after these features appear in the early archosauromorphs.

Benton (1985) listed the absence of a foramen in the carpus between the ulnare and intermedium as characteristic of archosauromorphs. However, a foramen between two carpal bones is retained in *Noteosuchus, Trilophosaurus,* and *Protorosaurus.* In the fossils of these genera, the elements are disarticulated; thus, it is not certain which bones are represented, but a perforating foramen definitely is retained. The surrounding bones were probably in a pattern little different from that of the eosuchian *Acerosodontosaurus* (Currie, 1980). The carpus is poorly ossified in *Chasmatosaurus* (the earliest adequately known archosaur), and none of the elements can be identified by their shape.

An item not included at this level by Benton, but which is probably common to all archosauromorphs, is the more extensive ossification of the braincase (Character 12). The basioccipital and basisphenoid are contiguous, whereas they are separated by an unossified gap in primitive diapsids, and the basisphenoid and prootic are united anterolateral to the dorsal sellae.

Benton suggested that the trilophosaurids, rhynchosaurs, archosaurs, and protorosaurs (Prolacertiformes) are progressively more derived groups within the archosauromorph assemblage. He considered trilophosaurids to be the sister-group of other archosauromorphs on the basis of the primitive configuration of the premaxilla and quadratojugal. Most of the cranial sutures were fused in the specimens examined by Gregory (1945) in his comprehensive description of *Trilophosaurus.* In material examined by Parks (1969), the premaxilla extends behind the narial opening to meet the nasal in the manner of other archosauromorphs. The configuration of the quadratojugal is equivocal. The postfrontal enters the margin of the upper temporal opening, a feature considered characteristic of lepidosauromorphs, but this also occurs in some early rhynchosaurs.

Benton recognized a sister-group relationship between the protorosaurs and archosaurs because of the possession of the following features: (1) long snout and narrow skull, (2) nasal longer than frontal, (3) posttemporal fenestra small or absent, (4) recurved teeth, (5) extensive participation of the parasphenoid/basisphenoid in the side wall of the braincase, and (6) long, thin, tapering cervical ribs with two or three heads and an anterior dorsal process. None of these characters is convincing. The first two features, both aspects of skull proportion, do not greatly differ from those of *Youngina* and might be primitive for what Benton referred to as neodiapsids.

The posttemporal fossae (Character 3, above) in *Prolacerta*, the earliest member of these groups in which the occiput can be reconstructed (Camp, 1945; Robinson, 1962; Gow, 1975) are not significantly smaller than those of eosuchians and early lepidosaurs. The posttemporal fossae are small in *Chasmatosaurus* and other early archosaurs, but this feature cannot be used to unite this group with protorosaurs.

Recurved teeth (Character 4, above) are a common feature of carnivorous reptiles and are very strongly developed in *Heleosaurus* (Carroll, 1976c), which might be close to the base of the archosauromorph assemblage. Otherwise, the dentition is highly specialized in rhynchosaurs and trilophosaurids; this suggests that the condition in archosaurs and protorosaurs may be primitive for the Archosauromorpha, rather than a synapomorphy of these two groups. The nature of the braincase is not known in the Upper Permian genus *Protorosaurus*. The differences between the structure of the braincase in archosauromorphs and lepidosauromorphs is more significant than that between primitive members of the archosauromorph groups and is not considered to be an effective character for differentiation taxa at this level.

The ribs (Character 6, above) are distinctive in protorosaurs, but the configuration of the heads of the anterior ribs in the early archosaur *Chasmatosaurus* are quite similar to those of the lepidosauromorph *Claudiosaurus* and primitive nothosaurs (Carroll and Gaskill, 1985), champsosaurs, and thalattosaurs (see below). In all these groups, the configuration of the ribs may be associated with the great length of the cervical vertebrae and may not be indicative of close taxonomic affinities.

If *Chasmatosaurus* is accepted as the most primitive archosaur, the only adequately documented apomorphy of this group is the presence of an antorbital fenestra (Charig and Sues, 1976). The configuration of the orbit in the shape of an inverted triangle also occurs in the early genera *Euparkeria* and *Erythrosuchus* but might not be expressed clearly in smaller, more primitive genera. Benton listed the possession of a fifth trochanter on the femur, but this does not apply to *Chasmatosaurus*. The relatively small number of synapomorphies shared between *Chasmatosaurus* and later archosaurs is characteristic of members of a stem-group.

Chasmatosaurus is specialized in having a down-turned premaxilla. Benton cited this as a character shared with *Prolacerta*, but it is not so figured in any restorations of the latter genus, nor does this feature occur in the earlier protorosaur, *Protorosaurus*.

The haemal arches are long in both *Prolacerta* and *Chasmatosaurus*, and expanded distally. *Protorosaurus*, however, has haemal arches of normal proportions. Close affinities between *Chasmatosaurus* and *Prolacerta* to the exclusion of other protorosaurs would require that *Chasmatosaurus* had undergone several significant evolutionary reversals, including the redevelopment of a lower temporal bar and shortening of the length of the cervical vertebrae.

Benton suggested the alliance of *Malerisaurus* (Chatterjee, 1980, 1986) with the Protorosauria on the basis of the elongated cervical vertebrae and the presumed loss of the temporal bar. The nature of the lower temporal bar is uncertain, but the quadratojugal is illustrated as a large platelike bone, in sharp contrast with that of all adequately known protorosaurs. The cervical vertebrae, although somewhat elongated, actually resemble those of *Trilophosaurus*, rather than those of *Protorosaurus*. The centra are sharply angled, which would have resulted in a permanently arched, elevated neck. Chatterjee (1980) described the fifth metatarsal as not hooked, but the head is considerably expanded and may have functioned as a hooked element. *Malerisaurus* does not fit clearly with any of the better known groups of archosauromorphs and its specific affinities remain uncertain.

There is ample evidence for the union of the four major groups of archosauromorphs within a single, monophyletic assemblage, but much less evidence for their specific interrelationships. None of the groups is obviously close to the point of origin of any of the others. Most of the characters evident in the earliest members of these groups are autapomorphies, suggestive of rapid and marked divergence. A few characters can be used to support special affinities among these groups, but their significance is uncertain. Primitive archosaurs and protorosaurs have a median postparietal, rather than paired bones. This condition is unique among diapsids and may indicate that archosaurs and protorosaurs are related more closely to one another than either is to rhynchosaurs and trilophosaurids. Primitive archosaurs and protorosaurs also retain teeth on the transverse flange on the pterygoid. In both rhynchosaurs and

Trilophosaurus, the postfrontal enters the margin of the upper temporal opening. This feature is common to lepidosauromorphs, but the taxonomic significance of its appearance in the archosauromorphs is not known.

Heleosaurus, from the Upper Permian of southern Africa, was suggested as an archosaur ancestor by Carroll (1976c) on the basis of the presence of dermal armor of a pattern vaguely similar to that of thecodonts, and the nature of the teeth (laterally compressed, recurved, and serrated). Other features of archosauromorphs, as opposed to lepidosauromorphs, are the presence of six elongate cervical vertebrae and the absence of a sternum, which would almost certainly be evident in an eosuchian preserved in this manner.

Unfortunately, most of the definitive features of archosauromorphs cannot be determined. Neither the carpus or tarsus is present, nor is the dorsal portion of the skull, which would reveal the presence of an antorbital fenestra and dorsal process of the quadratojugal behind the ventral temporal opening. *Heleosaurus* is a plausible member of the sister-group of later archosauromorphs, but its phylogenetic position is too uncertain for it to be used to establish polarity of character transformation in that group.

Mesozoic Diapsids Not Related to Either the Lepidosauromorpha or the Archosauromorpha

All living diapsids and the majority of Mesozoic forms can be classified among either the Archosauromorpha or the Lepidosauromorpha. A few Mesozoic groups cannot be assigned at present to either taxon. They may have evolved directly from primitive stem diapsids or have diverged so greatly from one of the two major groups that their correct affinities cannot be established without additional fossils.

The Choristodera, Thalattosauria, and Placodontia all lack the key features by which either lepidosauromorphs or archosauromorphs are recognized. None shows either the specialization of the tarsus common to archosauromorphs or the presence of a sternum that is characteristic of lepidosauromorphs. Because both of these features are associated specifically with effective terrestrial locomotion, it is conceivable that they have been lost in these groups, all of which are secondarily aquatic. However, in the absence of other evidence to support their affinities with either of these groups, it seems more parsimonious to assume that these features are primitively absent. If this is the case, all of these groups may have evolved separately from the stem diapsids. Early members of all three groups also lack thyroid fenestration of the pelvis, indicating that they must have diverged from the base of the derived groups, if not from stem diapsids.

Choristodera

Champsosaurs (order Choristodera) were relatively common forms in the Upper Cretaceous and Lower Tertiary of North America (Erickson, 1972) and Europe (Sigogneau-Russell and Russell, 1978). Incomplete remains have also been reported from the Lower Cretaceous of Mongolia (Sigogneau-Russell and Efimov, 1984) and the Jurassic of Europe and North America (Evans, 1990). Most champsosaurs are similar in size and proportions to crocodiles and apparently had similarly semiaquatic habits. The Lower Cretaceous fossils contribute little to our understanding of their affinities. Aside from their autapomorphies, other derived traits of champsosaurs resemble those of both archosauromorphs and lepidosauromorphs (Appendix VII). Champsosaurs, however, lack any of the key features that define either group.

In addition to the derived features, it is important to consider some primitive features that indicate derivation from a relative primitive level of diapsid evolution. Champsosaurs lack the thyroid fenestra and retain denticles on the palate, including those on the transverse flange of the pterygoid, which are lost in all other diapsid groups before the Cretaceous. There is no retroarticular process, and the dermal elements of the shoulder girdle are massive and primitive. The radius resembles that of eosuchians, but the humerus is similar in shape to that of protorosaurs and lacks an enclosed ectepicondylar foramen in most genera. Most trunk ribs are holocephalous, but the anterior ribs are partially separated. Presumably this group has evolved separately from other diapsids since the Late Permian or Early Triassic.

If only the most primitive members of other major groups are compared, Cretaceous and Tertiary champsosaurs share most derived features with the archosauromorphs: (1) thecodont implantation of marginal teeth, (2) more than five cervical vertebrate, (3) loss of notochordal canal of vertebrate, (4) loss of trunk intercentra, (5) loss of cleithrum, (6) loss of entepicondylar foramen, (7) loss of pisiform, (8) three fused sacral vertebrae, and (9) hooked fifth metatarsal. On the other hand, all of these characters are also encountered among one or more advanced members of the lepidosauromorph assemblage (specifically, advanced squamates) except for the fusion of the sacral vertebrae.

Several features of champsosaurs are shared with other aquatic forms: (1) thecodont implantation of teeth, (2) long neck, (3) lack of fusion between centrum and neural arch, (4) reduced ossification of the carpals and tarsals, (5) pachyostotic ribs, and (6) short epipodials.

Champsosaurs demonstrate the difficulty of trying to establish relationships on the basis of particular isolated traits, rather than considering the organism as a whole. In the case of this group, it should be admitted that they are highly specialized diapsids with no obvious features that unite them with any particular ancestral group. The only way to ascertain their relationship with more certainty is to discover fossils of intermediate morphology that may link them with some particular group of more primitive diapsids.

Further evidence of the affinities of the Choristodera has recently been provided by the discovery of fossils from the Middle Jurassic of England belonging to the genus *Cteniogenys* (Evans, 1990). Remains of this genus are completely disarticulated and represent animals much smaller than the better known Cretaceous genera, but share with them 19 derived characters. *Cteniogenys* exhibits 10 derived characters in common with primitive archosauromorphs, but several of the derived characters shared by protorosaurs, rhynchosaurs, and archosaurs retain a more plesiomorphic condition, suggesting that the Choristodera were the first group to diverge from the base of the archosauromorph radiation.

Thalattosauria

The Thalattosauria encompasses an assemblage of secondarily aquatic genera from the Middle and Upper Triassic. They are united by striking specializations of the skull (Appendix VII) (Figs. 19–22). Three families are recognized, each represented by one or two genera: Thalattosauridae from the Upper Triassic of western North America (Merriam, 1905), Claraziidae (Peyer, 1936), and Askeptosauridae (Kuhn, 1952) from the Middle Triassic of Switzerland. The families are clearly distinct from one another and none is uniformly more primitive or close to the pattern expected of a common ancestor, although *Askeptosaurus* retains more primitive characters than either *Clarazia* or *Thalattosaurus*, which Rieppel (1987) considered to form the more derived sister-group.

All cranial features can be derived from those of either *Prolacerta* or *Youngina*, but the postcranial skeleton has character-states that are more primitive than those of early members of either the Archosauromorpha or Lepidosauromorpha. There is no evidence of archosauromorph specialization of the tarsus or fifth metatarsal, nor is there evidence for the presence of a lepidosauromorph sternum. The transverse processes of the trunk vertebrae are not as reduced as in early lepidosauromorphs, nor is the maxilla excluded from the margin of the external nares as in most archosauromorphs. *Clarazia* is primitive in retaining a solid, platelike pelvis, but a thyroid fenestra is developed in *Askeptosaurus*.

Placodontia

Placodonts have long been associated with the aquatic nothosaurs and plesiosaurs, on the basis of vaguely similar specializations toward an aquatic way of life and the presence of a conspicuous dorsal temporal opening. In a recent discussion of the skull of *Placodus*, Sues (1987b)

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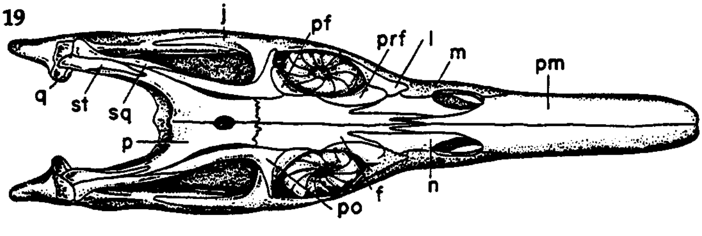

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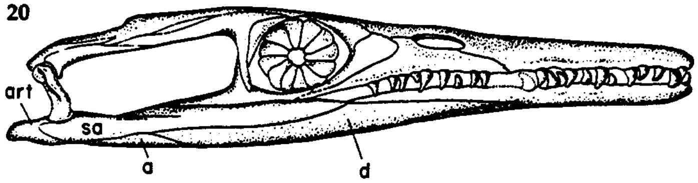

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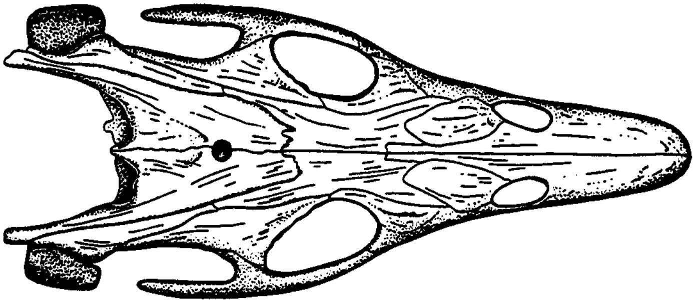

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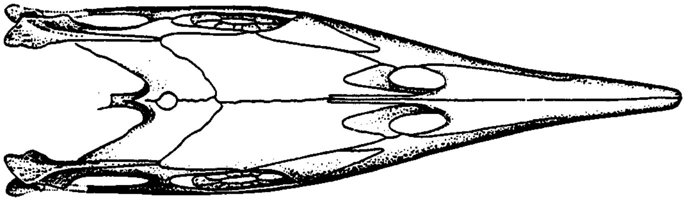

Fig. 19–22. Skulls of thalattosaurs. (19) Dorsal view of the skull of *Askeptosaurus* (modified from Kuhn-Schnyder, 1952). (20) Lateral view of *Askeptosaurus*. (21) Dorsal view of the skull of *Clarazia* (modified from Rieppel, 1987). (22) Dorsal view of the skull of *Thalattosaurus* (modified from Merriam, 1905).

pointed out that there are no specific shared derived characters that unite placodonts with sauropterygians. Rather, he placed them as Diapsida *incertae sedis*.

The most complete knowledge of the group is provided by *Placodus*. This is a relatively primitive genus within the order but already highly specialized relative to other diapsids (Drevermann, 1933). Some more primitive features are evident in *Helveticosaurus*, but this genus is not well known and is divergent in other features, notably the presence of more than 40 presacral vertebrae; thus, it is difficult to justify its use as an example of primitive placodonts (Peyer, 1955). A striking feature that unites *Helveticosaurus* with the better-known placodonts is the configuration of the vertebrae, which are unique among diapsids. As in some archosaurs and plesiosaurs, the transverse processes are greatly elongated, but they accompany centra that are conspicuously amphicoelous and notochordal. The pedicles of the arches are very high.

Helveticosaurus also resembles *Placodus* in possessing very long, spatulate anterior teeth, but it definitely lacks the large, flattened cheek teeth that otherwise characterize most placodonts. The shoulder girdle is unlike those of nothosaurs and plesiosaurs in the small size and oval configuration of the coracoids. In *Helveticosaurus*, the interclavicle is primitive in retaining a long, robust stem. Peyer (1955) reconstructed the relationships of the clavicle and interclavicle according to the pattern of *Placodus*, in which the interclavicle is largely superficial to the clavicular blades, but this cannot be unequivocally established from the specimen. The interclavicle has clearly demarcated recesses for the clavicular blades, as in primitive amniotes. Unfortunately, it is not possible to establish whether the bone is preserved in dorsal or ventral view. If in dorsal view, *Helveticosaurus* shows a derived condition, as in *Placodus* and nothosaurs, but, if the bone is seen in ventral view, the pattern resembles that of primitive reptiles (confirmed by Rieppel, 1989:133).

Placodonts do not have the reversed relationship of the base of the scapula and clavicular blade that characterizes nothosaurs and plesiosaurs. As illustrated by *Placodus*, placodonts have a number of derived features shared by both lepidosauromorphs and archosauromorphs, but placodonts cannot be associated convincingly with either group. The possession of numerous primitive character states suggests that placodonts might have diverged separately from the stem diapsids. They possess neither the specializations of the foot that are characteristic of archosauromorphs, nor any evidence of the sternum of lepidosauromorphs. There is little development of a thyroid fenestration, and the opisthotic is not suturally attached to the cheek. As in lepidosauromorphs, the postfrontal enters the margin of the upper temporal opening, but this also occurs in early rhynchosaurs.

It is conceivable that placodonts diverged from the lepidosauromorphs at about the level of *Claudiosaurus*, with which they share the restriction of the suborbital fenestra, and the extension of the pterygoids to the midline, closing the interpterygoid vacuities. The palate differs from that of nothosaurs in the expansion of the palatine at the expense of the pterygoid. The absence of a sternum occurs in other aquatic groups and is not strong evidence for affinities with sauropterygians.

Rieppel (1989) recently reviewed the anatomy and taxonomic position of *Helveticosaurus*. He concluded that there was no strong evidence of close affinity with the placodonts. Depending on how characters were analyzed, *Helveticosaurus* shares approximately the same number of derived states with lepidosauromorphs and archosauromorphs. Rieppel considered that classification of *Helveticosaurus* within the Archosauromorpha should be considered tentative for the time being. He concluded by stating: "The question must again be raised whether this rather high degree of character incongruence is due to an as yet unsatisfactory characterization of the two major subgroups of diapsid reptiles, or whether it does in fact reflect a high degree of convergence in early diapsid reptiles."

DISCUSSION

The relationships discussed in this paper are summarized in a cladogram (Fig. 23) keyed to the characters that support the affinities of the various groups. Despite the relatively complete knowledge of the skeleton in representatives of most of the groups, many relationships remain incompletely resolved. In particular, the affinities of the Choristodera, Thalattosauria, and Placodontia, and the interrelationships of the several archosauromorph groups cannot be convincingly established. In these cases, we lack sufficient knowledge of early members of these groups which might show characters lost in the descendants that would permit them to be placed in a specific phylogenetic position. As noted by Hennig (1981), the earliest members of derived groups may be differentiated by only rather trivial features that may be lost in their descendants.

The remaining diapsids may be grouped in three categories—the stem diapsids, including the Araeoscelida and coelurosauravids; the Archosauromorpha; and the Lepidosauromorpha. These conclusions do not differ greatly from those reached by Benton (1985), but they are accomplished by a much different approach to character analysis.

Perhaps the most important conclusion reached by this study is the apparent frequency of convergence. If the monophyletic groups have been identified correctly and the polarity of character transformations interpreted correctly, a great number of similar derived character-states

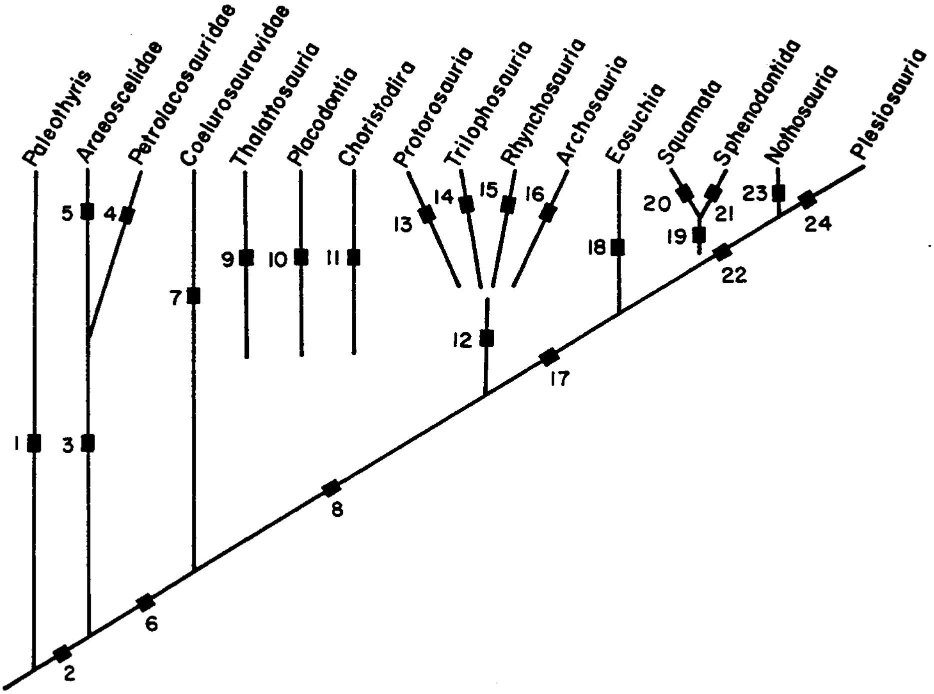

Fig. 23. Cladogram showing hypothesized relationships among major diapsid groups. Derived characters are as follows. (1) Fusion of atlas centrum and axis intercentrum. (2) Dorsal and lateral temporal openings and suborbital fenestra. (3) Six cervical vertebrae, 2–6 much longer than trunk centra; mammillary processes on neural spines; conspicuous triceps process on coracoid; enlarged lateral and distal public tubercles; and epipodials nearly equal in length to propodials. (4) Conspicuous ischiadic notch. (5) Nine cervials, 29 presacral vertebrae; fusion of axial intercentrum to atlantal centrum; cheek teeth enlarged; and ectepicondylar foramen. (6) Strengthening of temporal bars; downgrowth of the parietal beneath the adductor jaw musculature; exclusion of the lacrimal bone from the narial opening; absence of caniniform maxillary teeth; elimination of the primitive separation between the two coracoids; acetabulum rounded, without distinct supra-acetabular buttress; tibial and fibular condyles of femur in same plane; caudal ribs fused to centra; medial rows of gastralia fused at midline. (7) Trunk ribs ossified in two segments, forming support for gliding membrane; squamosal frill; trunk vertebrae elongate; and loss of dorsal intercentra. (8) Ribs of atlas vertebra lost (exceptions exist); cleithrum reduced; olecranon reduced; and caudal ribs extend straight laterally. (9) Dorsal temporal opening much restricted; premaxillae elongated and reaching frontals, nasals displaced laterally; posterior margin of skull table deeply emarginated; and occiput lying well forward relative to quadrate suspension. (10) Vertebrae with elongate transverse processes, but deeply amphicoelous centra; loss of lateral temporal opening; quadratojugal forms much of cheek; anterior teeth spatulate and procumbent; quadrate fitting into a socket formed by squamosal and quadratojugal; and prefrontal and postfrontal separate frontal from orbital margin. (11) Elongation of snout with nasal bones fused at midline; prefrontals meeting at midline separating nasals from frontals; temporal area greatly expanded laterally and extending well posterior to the occipital condyle; and internal nares extended posteriorly as grooves in the roof of the palate. (12) Astragalus and calcaneum articulating with one another; fifth distal tarsal lost; fifth metatarsal hooked; presence of a lateral tuber on the calcaneum; loss of tabular; stapes without a foramen; vertebrae not notochordal; transverse

evolved in separate monophyletic groups. This can be demonstrated most readily in well-established groups such as the Lepidosauromorpha and the Archosauromorpha. If genera such as the younginoids are recognized correctly as primitive lepidosauromorphs, and *Protorosaurus* and *Chasmatosaurus* are primitive archosauromorphs, then a host of characters recognized in later members of both groups must have evolved convergently. A conservative list includes the following: (1) closure of upper temporal opening, (2) loss of tabular, (3) loss of postparietal, (4) loss of supratemporal, (5) loss of pineal opening, (6) reduction or loss of lacrimal, (7) loss of teeth from transverse flange of pterygoid, (8) fusion of bones along the midline of the skull (premaxillae, nasals, frontals, parietals, and/or vomers), (9) reduction or loss of lower temporal bar, (10) extension of opisthotic to cheek, (11) development of thecodont implantation, (12) ossification of area of pleurosphenoid or laterosphenoid, (13) loss of stapedial foramen, (14) development of an impedance-matching middle ear, (15) elaboration of retroarticular process, (16) development of procoely, (17) loss of notochordal perforation, (18) elongation of neck, (19) loss of trunk intercentra, (20) elongation of transverse processes of trunk vertebrae, (21) loss of entepicondylar foramen, (22) development of thyroid fenestration, (23) loss or fusion of centrale in pes, (24) loss of Distal Tarsals 1 and 5, (25) hooking of fifth metatarsal, (26) reduction of phalangeal count, and (27) elaboration of dermal armor.

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process on dorsal vertebrae extending beyond level of zygapophyses; cleithrum absent; no entepicondylar foramen; and loss of pisiform. (13) Seven very elongate cervical vertebrae; cervical ribs very thin; and loss of lower temporal bar. (14) No lateral temporal opening; loss of teeth in premaxilla and front of dentary; cheek teeth laterally expanded; extensive fusion of dermal bones in the adult; and cervical vertebrae angled and procoelous. (15) Ankylothecodont tooth implantation; median narial opening; and overhanging premaxillae. (16) Antorbital fenestrae. (17) Cervical Centra 3–5 shorter than trunk centra; reduced length of transverse processes of trunk vertebrae; trunk ribs holocephalous; and large, ossified sternum with which coracoids articulate. (18) Medial centrale interposed between lateral centrale and Distal Carpal 3. (19) Epiphyses elaborated as specialized joint surfaces; incipient mesotarsal joint; and lateral conch of quadrate supporting tympanum. (20) Quadrate streptostylic; loss of lower temporal bar; loss of ventral process of squamosal; and intermedium much reduced. (21) Acrodont attachment of at least some of the marginal teeth; enlargement of the lateral row of palatine teeth; precise occlusion of marginal teeth; tooth replacement of acrodont teeth occurs by addition at back of maxilla and dentary; dentary characterized by its great posterior extension, coronoid process and mandibular foramen; prefrontal forms solid articulation with dorsal surface of palatine; very large quadratojugal foramen; and prominent posterior process of ischium. (22) Ventral portion of scapula superficial to blade of clavicle; loss of lower temporal bar, without development of streptostyly; and reduction of palatal fenestra. (23) Suborbital and interpterygoid vacuities closed, with pterygoids meeting along midline as far posteriorly as the occipital condyle; and large unossified area between the transversely oriented ventral portions of the clavicle and the elongate, posteromedially directed coracoids. (24) Loss of stapes; pectoral and pelvic girdles greatly expanded ventrally; and hind and forelimbs with similar paddle shape.

These characters are all considered to exemplify convergence, because it would be difficult, if not impossible, to determine whether or not they evolved from the same or a distinct ancestral pattern if we knew only the descendant forms. Other characters might be cited as examples of convergence, but they are not really comparable in the context of the remainder of the anatomy. The medial narial openings of kuehneosaurids and crocodiles clearly are different structurally, as well as having evolved separately. The structures that are called sterna in dinosaurs, birds, mammals, and lepidosauromorphs are functionally and structurally distinct, as well as being nonhomologous, and it may be questioned as to whether they should be considered as examples of convergence at any level.

Many other cases of convergence appear to have occurred among the early diapsids, but their demonstration rests on hypotheses of relationships that are not so clearly established. If *Saurosternon* is a primitive squamate, many of the features of the postcranial skeleton that characterize Triassic and Jurassic lizards and sphenodontids must have evolved separately—development of thyroid fenestration, fusion of centrale, fusion of astragalus and calcaneum, loss of Distal Tarsals 1 and 5, and hooking of fifth metatarsal.

Whatever the specific relationships of the placodonts, Thalattosauria, and Choristodera, the presence of some primitive features suggest that they evolved from near the base of the radiation of advanced diapsids. This implies that many of their derived similarities also were achieved convergently.

Accepting that the conclusions regarding the monophyly of groups and the polarity of character change have been correctly assessed, we find that there are relatively few cases of reversals compared with the frequency of convergence. If the pisiform is actually lost in the ancestors of archosaurs, then it must have re-evolved in the earliest crocodiles. This bone may simply have been poorly ossified in early archosaurs, but there is no evidence for it elsewhere in this assemblage. Early crocodiles exhibit an antorbital fenestra, but it is lost in later forms, showing a reversal from the primitive archosaur condition. In contrast with most other early diapsids, *Araeoscelis* and *Trilophosaurus* lack a lateral temporal opening. If these genera are diapsids, as indicated by all other features of the skeleton, this character has reversed to a pre-diapsid pattern. Temporal openings also are closed among several groups of dinosaurs and within the Squamata, although this is accompanied by so many other changes in the skull that it may not be proper to think of these changes as reversals. If sauropterygians evolved from primitive lepidosauromorphs, the sternum must have been lost in the process—a reversal to a more primitive character state. Advanced archosaur groups loose the hooking of the fifth metatarsal that evolved in early archosauromorphs. The impedance-matching ear is lost in many modern lepidosauromorph groups.

It is difficult to quantify objectively the relative number of changes that can be referred to as convergences and reversals, but convergence appears to be much more common. There is no justification for presuming that convergences and reversals are equally likely events, as has been assumed by many authors who make use of numerical procedures for establishing phylogenies.

What is clearly evident is that convergence is a *much* more common phenomenon than is the origin of strictly unique features. If this is the case, statistical arguments, based on parsimony, are very unlikely to provide correct phylogenies in groups with long evolutionary histories.

The problem of phylogenetic analysis is not how to establish possible relationships from a host of characters whose possibility of convergence or uniqueness is difficult to establish, but how to recognize the specific homology of each character. Clearly this cannot be done statistically, but can be achieved only by a knowledge of the actual evolutionary history of the species in question. This can be established only on the basis of the fossil record.

SUMMARY AND CONCLUSIONS

Establishing relationships among diapsid reptiles provides an informative mode for extending cladistic methodology to groups with a good fossil record. Cladistic methods were elaborated initially to deal with groups without an adequate fossil record, but their basis in fundamental evolutionary processes should make them even more effective when applied to groups in which there is more direct evidence of the specific homology of traits and the polarity of character transformation.

Phylogenetic analysis of the early diapsids was undertaken employing the following procedures: (1) establishment of the monophyletic nature of the entire group; (2) establishment of the polarity of all characters that vary within the group; (3) recognition of subgroups on the basis of unique apomorphies; and (4) determination of the derived character-states present in the most primitive members of each of the monophyletic subgroups. Relationships were recognized on the basis of derived characters shared by the most primitive known members of each group.

This procedure differs significantly from that practiced by most cladists in that it emphasizes the significance of the earliest members of each group, rather than their living representatives, for establishing relationships. The earliest members of any group would be expected to share the greatest number of uniquely derived characters with their sister-group, and to show the least amount of convergence. The longer the period of time since the divergence of two groups, the greater the possibility for the loss of original synapomorphies and the accumulation of characters achieved by convergence.

Recognition of subgroups on the basis of unique derived characters at an early stage in analysis demonstrated that many derived characters have evolved convergently in two or more groups. Of 142 character transformations that can be systematically treated, 43 or approximately 30%, appear to have occurred uniquely in a single lineage. Ninety-nine, or approximately 70%, exhibit convergence. Approximately 20 additional characters exhibit less clear-cut or less well-established patterns of change (see Appendix I). These particular numbers are not significant, for they would change depending on how characters are defined and how exhaustively character changes are followed among more derived archosauromorphs and lepidosauromorphs. The general pattern is clear, however. Convergence, as evidenced by the fossil record, is a very important phenomenon among diapsids. It is not possible to establish reliable relationships on the basis of character distribution without knowing the homologous nature of the characters in question. Homology can be established on the basis of the fossil record, by the discovery of the character in the common ancestors of the groups in question. Homology of particular characters cannot be judged accurately on the basis of the distribution of other characters.

On the basis of analysis of character-states in the most primitive known members of each major subgroup of early diapsids, this assemblage may be divided into two major groups with living representatives and several entirely extinct groups. The archosauromorphs include the following subgroups: archosaurs, rhynchosaurs, protorosaurs, and trilophosaurids. Lepidosauromorphs include eosuchians, lepidosaurs (paliguanids, kuehneosaurids, advanced lizards and snakes, sphenodontids), and the sauropterygians (nothosaurs and plesiosaurs). The Araeoscelida is the sister-group of all other diapsids, and the coelurosauravids may belong to the sister-group of the common ancestors of archosauromorphs and lepidosauromorphs. The positions of the Choristodera, Thalattosauria, and Placodontia remain uncertain. They may have evolved separately from the stem diapsids.

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APPENDIX I. Distribution of character-states in diapsids. Primitive character-states shown by *Petrolacosaurus* (Reisz, 1981) and *Apsisaurus* (Laurin, 1991) (indicated by *). The protorothyrid *Paleothyris* is the primary basis of out-group comparison to establish polarity. Ar = Araeoscelida; Co = Coelurosauridae, Eo = Eosuchia; Sq = Squamata; Sph = Sphenodontida; No = Nothosauria; Ple = Plesiosauria; Pro = Protorosauria; Rhy = Rhynchosauria; Arch = Archosauria; Tri = Trilophosauridae; Ch = Choristodera; Th = Thalattosauria; Pla = Placondontia.

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
SKULL		
1. Upper temporal opening	1a. Loss of upper temporal opening	Some Sq, some Arch, some Th, some Pla
2. Lateral temporal opening	2a. Loss of lateral temporal opening	*Araeoscelis*, Tri, some Arch
3. Suborbital fenestra	3a. Loss of suborbital fenestra	No
4. Temporal bars flattened in plane of skull	4a. Temporal bars rounded and thickened	All groups other than Ar
5. Parietal flat, without ventral processes medial to the upper temporal opening	5a. Ventral process medial to upper temporal opening	All groups other than Ar
6. Lower temporal bar complete	6a. Reduction or loss of lower	Co, Sq, some Sph, No, Ple, Pro
7. Retention of all bones present in the skull of primitive amniotes, including paired postparietals, tabulars, and supratemporals	7a. Fusion of postparietal	Primitive Pro, primitive Arch
	7b. Loss of postparietal	Advanced Sq, Sph, No, Ple, advanced Pro, Rhy, advanced Arch, Tri, Ch, Th, Pla
	7c. Loss of tabular	Advanced Sq, Sph, No, Ple, Pro, Arch, Tri, Ch, Th, Pla

The appendixes have not been updated since they were originally submitted and corrected in 1988.

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
	7d. Loss of supratemporal	Some Sq, advanced Sph, No, Ple, advanced Arch, Tri, Ch, Th, Pla
8. No midline fusion of premaxillae, nasals, frontals, parietals, or vomers	8a. Fusion of premaxillae	Advanced squamates, some Arch
	8b. Fusion of nasal	Some Sq, Ch, Pla
	8c. Loss of nasals	Some Sq, Ple
	8d. Fusion of frontals	Some Sq, some Sph, some No, some Arch
	8e. Fusion of parietals	Some Sq, some Sph, advanced Pro, some Rhy, some Arch
	8f. Fusion of vomers	Some Sq, some Ple, some Arch, Pla
9. Conspicuous pineal opening midway in length of parietal	9a. Closure of pineal opening	Some Sq, some Ple, some Rhy, some Arch, Tri, Ch
	9b. Pineal opening between parietal and frontal	Some Sq
10. Postfrontal does not form margin of upper temporal opening	10a. Postfrontal enters margin of upper temporal opening	Eo, Sq, Sph, No, Ple, primitive Rhy, Tri, Pla
11. Postfrontal and postorbital separate ossification	11a. Fusion of postfrontal and postorbital	Some Sq, some Ple, some Arch, some Ch
12. Orbital and narial openings round	12a. Changes in many ways that can not be systematically tabulated	
13. Narial opening paired, anterior position	13a. Medial narial opening	Some Sq, some Arch, Ch
	13b. Narial opening posterior	Some Sq, some Sph, No, Ple, some Arch, Th, Pla
14. No antorbital opening	14a. Antorbital opening	Arch
15. No external mandibular fenestra	15a. External mandibular fenestra	Sph, most Arch
16. Premaxilla not deflected ventrally	16a. Premaxilla deflected	*Chasmatosaurus*, Rhy
17. Premaxilla excluded from posterior margin of external nares by maxilla	17a. Premaxilla forms posterior margin of external nares	? some Sq, Pro, Rhy, Arch, Tri, Ch
18. Quadrate with slender dorsal process, not exposed posteriorly	18a. Quadrate with strong dorsal process, exposed posteriorly	Sq, Sph, No, Ple, Pro, Rhy, Arch, Tri, Th, Pla

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
19. Quadrate firmly supported by pterygoid, squamosal, and quadratojugal	19a. Quadrate movable, streptostylic	Sq, ?Pro, ?Th
20. Posterior margin of cheek not embayed for support of tympanum	20a. Posterior margin of cheek embayed for support of tympanum	Sq, Sph, No, Pro, Rhy, Arch, Tri, Th, Pla
21. Occipital condyle in same transverse plane as jaw articulation	21a. Jaw articulation anterior to occipital condyle	Sq, Sph, some Arch
	21b. Jaw articulation posterior to occipital condyle	Some Sq, advanced No, Ple, some Rhy, some Arch, Tri, Ch, Th, Pla
22. Lacrimal bone extending from orbit to external nares	22a. Lacrimal bone not reaching narial opening	All groups other than Ar
	22b. Lacrimal bone lost	Some Sq, Sph, some No, Ple, some Arch, Pla
23. Quadratojugal essentially horizontal, not extending behind lateral temporal opening	23a. Quadratojugal extending behind lateral temporal opening	Pro, Rhy, Arch, ?Ch
	23b. Quadratojugal lost	Sq, Sph, most No, Ple, advanced Pro
24. Prefrontal does not extend to palatine	24a. Prefrontal reaches palatine	Sph, some Arch, Pla
25. Single row of conical marginal teeth	25a. Multiple rows of marginal teeth	Advanced Rhy, some Arch
	25b. Change of tooth shape	Too diverse to document
26. Tooth implantation subpleurodont	26a. Pleurodont	Advanced Sq
	26b. Acrodont	Some Sq, Sph
	26c. Thecodont implantation	Some Sq, No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
	26d. Ankylothecodont	Rhy
	26e. Loss of teeth from premaxilla and/or end of dentary	Advanced Rhy, some Arch, Tri, some Pla
27. Tooth replacement	27a. Loss of regular replacement	Some Sq, most Sph
28. Approximately 5 teeth in premaxilla	28a. Increase or decrease	Too varied to tabulate
29. Approximately 35 teeth in maxilla	29a. Increase or decrease	Too varied to tabulate
30. Maxillary teeth of positions 6 and 7 enlarged canines	30a. No conspicuous canine teeth	All groups other than Ar

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
31. Three rows of denticles radiating from area of basicranial articulation	31a. Loss of tooth row on transverse flange of pterygoid	Sq, Sph, No, Ple, advanced Pro, Rhy, advanced Arch, Tri, Ch, Th, Pla
	31b. Loss of all palatal teeth	Some Sq, No, Ple, Rhy, some Arch, Tri
	31c. Elaboration of teeth on palatine	Sph, Pla (in quite a different way)
32. Movable basicranial articulation	32a. Loss of basicranial articulation	No, Ple, some Arch
33. Epipterygoid a narrow vertical rod	33a. Epipterygoid widened to form a longitudinal plate	Some No
	33b. Epipterygoid lost	Some Sq, some Arch (not consistently described)
34. Unossified gap between basioccipital and basisphenoid	34a. Basioccipital contiguous with basisphenoid	Pro, Rhy, Arch, Tri, Ch
35. Basisphenoid not in contact with prootic	35a. Basisphenoid reaches prootic	Pro, Rhy, Arch, Tri (not consistently described)
36. Area of pleurosphenoid (or laterosphenoid) not ossified	36a. Pleurosphenoid ossified	Advanced Sq
	36b. Laterosphenoid ossified	Advanced Arch
37. Long tapering cultiform process	37a. Cultiform process short or eliminated	Some Sq, No, Ple, advanced Rhy, advanced Arch, Tri, Ch, Pla
38. No vidian canal	38a. Vidian canal formed between basisphenoid and parasphenoid	Advanced Sq, advanced Arch
39. No fenestra rotundum	39a. Fenestra rotundum	Advanced Sq, advanced Arch
40. Ossified portion of paroccipital process not reaching cheek or top of quadrate	40a. Ossified portion of opisthotic reaching cheek or top of quadrate	Advanced Sq, Sph, advanced No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
41. Large perforate stapes with dorsal process and posteroventrally directed stem	41a. Stapes directed laterally	Sq, Sph, No, Pro, Rhy, Arch, Tri
	41b. Stapes without foramen	Some Sq, No, Pro, Rhy, Arch, Tri
	41c. Loss of stapes	Ple, ?Ch, ?Pla
LOWER JAW		
42. Retention of two splenial bones and one coronoid	42a. Loss of one splenial	Most advanced diapsids (condition not systematically documented)

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
	42b. Loss of both splenials	Some Sq, most if not all Sph
43. No conspicuous coronoid process	43a. Conspicuous coronoid process	Advanced Sq, Sph, some Arch, Pla
44. No retroarticular process	44a. Conspicuous retroarticular	Sq, Sph, No, Ple, Pro, Rhy, Arch, Tri
45. Ceratobranchial I the only ossified element of hyoid apparatus, a long, slender rod	45a. Part of corpus ossified	Crocodiles (condition not documented in most groups)
POSTCRANIAL SKELETON		
46. 25 or 26 presacral vertebrae	46a. Increased number	Some Ar, ?Co, some Sq, some Sph, No, Ple, some Arch, Th, some Pla
47. All vertebral centra amphicoelous and notochordal	47a. Reduced amphicoely to platycoely	Some Sq, No, Ple, Pro, Rhy, Arch, Tri, Ch, Th
	47b. Procoely	Advanced Sq, advanced Arch
48. Intercentra retained throughout trunk	48a. Loss of trunk intercentra	Most Sq, some Sph, No, Ple, Rhy, advanced Arch, Ch, Th, Pla
49. *Five cervical vertebrae	49a. Increased number of cervical vertebrae	Ar, some Sq, some Sph, No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
50. *Cervical vertebrae 3–5 approximately length of the anterior trunk vertebrae	50a. Cervical vertebrae 3–5 shorter than anterior trunk vertebrae	Eo, primitive Sq, Sph, some Rhy, some Arch
	50b. Cervical vertebrae longer than anterior trunk vertebrae	Ar, some Sq, Pro, Arch, Tri
51. Intercentra of atlas and axis separate atlas pleurocentrum from ventral margin of ventral column	51a. Retained in primitive members of most derived groups. Pattern varied in advanced genera but not sufficiently well known for consistent analysis	
52. Proatlas paired	52a. Proatlas lost	Most advanced groups, but not crocodiles and *Sphenodon*. Not consistently described
53. Atlas arch paired and not fused to centrum	53a. Arch fused at midline	Sq
	53b. Arch fused to centrum	Some Arch
	53c. Arch lost	Some Sq, some Arch

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
54. Axis intercentrum suturally attached, but not fused to atlas pleurocentrum	54a. Intercentrum fused to atlas pleurocentrum	Ar, some Arch (pattern not consistently described)
55. *20 or 21 trunk vertebrae	55a. Increased number	Some Ar, some Sq, some Sph, No, Ple, some Arch, Th, some Pla
	55b. Decreased number	*Petrolacosaurus*, *Claudiosaurus*, Pro, Tri, some Arch
56. *Neural spines slender and roughly rectangular in lateral view. Arch and centrum solidly attached	56a. Mammalary processes	Ar
	56b. A variety of other shapes the distribution of which cannot be tabulated conveniently	
	56c. Arches and centra not solidly attached	Some Sph, No, Ple, Ch, Pla
57. Transverse processes of trunk vertebrae extending slightly beyond level of zygaphophyses	57a. Shorter transverse processes	Eo, most Sq, Sph
	57b. Elongate transverse processes	Kuehneosauridae, some No, Ple, Pro, Rhy, Arch, Tri, Pla, some Sq
58. Two sacral vertebrae	58a. Reduction in number of sacral vertebrae	Some Sq
	58b. Additional sacral vertebrae	No, Ple, most Arch, Ch
59. 60–65 caudal vertebrae	59a. Increase or decrease in number	Not consistent enough to tabulate
60. No caudal autotomy	60a. Caudal autotomy	Most advanced Sq, most Sph
61. Haemal arches beginning behind third caudal centrum, slender and progressively reduced in size posteriorly	61a. Change in position of first haemal arch and change in shape	Too varied to tabulate conveniently
62. Ribs articulating with all presacral, sacral, and first 11–12 caudal vertebrae	62a. Loss of anterior cervical ribs	At least atlas rib lost in most groups other than Ar and Co, and some Arch
	62b. Fusion of cervical ribs to transverse processes	Advanced Arch, Pla, some Sq
	62c. Fusion of posterior trunk ribs to vertebrae, or loss	Some Sq, some Arch
	62d. Fusion of caudal ribs to transverse processes	All diapsids other than Ar

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
63. Cervical ribs clearly double-headed	63a. Single-headed cervical ribs	Sq, advanced Ple
	63b. Addition of anterior process	No, Ple, Pro, Arch
64. Heads of trunk ribs separated by narrow constriction	64a. Single-headed trunk ribs	Eo, Sq, Sph, No, Ple, Th
	64b. Clearly double-headed trunk ribs	Some Arch
65. Sacral ribs not fused to either centrum or ilium, widely expanded distally	65a. Sacral ribs fused to centrum and/or ilium	Some Arch
	65b. Sacral ribs not expanded distally	Some Sq, some Sph, No, Ple
66. Caudal ribs sharply recurved to the rear	66a. Straight caudal ribs	All diapsids other than Ar; Co somewhat transitional
67. Cleithrum, clavicle, and interclavicle retain pattern of primitive amniotes	67a. Cleithrum lost	Sq, Sph, Not, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
	67b. Blade of clavicle medial to scapula	No, Ple
	67c. Interclavicle entirely superficial to blade of clavicles	No, Ple, Pla
	67d. Interclavicle absent	Some Sq, advanced Arch
68. No trace of sternal elements	68a. Large medial sternum with which coracoids articulate	Eo, Sq, Sph
	68b. Median rod	Crocodiles
	68c. Paired plates	Some dinosaurs
	68d. Median plate for origin of flight muscles	Pterosaurs
69. Both anterior and posterior coracoids	69a. A single coracoid	All diapsids except Ar
	69b. Scapula and coracoid slow to co-ossify or not co-ossified	Advanced Sq, some Sph, advanced Pro, Arch, No, Ple, Ch, Pla
70. *No conspicuous process for triceps muscle	70a. Conspicuous triceps process	Ar
71. Screw-shaped glenoid	71a. Open glenoid	Sq, Sph, No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
72. Supraglenoid and coracoid foramina	72a. Loss of supraglenoid foramen	Pro, some Sq, Rhy, No, Ple, Ch, Th, Pla
	72b. Loss of coracoid foramen	Some Arch, some Sq
73. No separate epiphyseal ossification	73a. Epiphyseal ossification	Sq, Sph

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
74. Humerus with entepicondylar foramen	74a. Loss of entepicondylar foramen	Advanced Sq, some No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
75. Distinct supinator process	75a. Loss of supinator process	*Araeoscelis*, Co, Eo, Sq, Sph, No, Ple, Rhy, Arch, Tri, Th, Pla (not Ch)
76. Groove for radial nerve not enclosed by bone to form ectepicondylar foramen	76a. Enclosure of ectepicondylar foramen	*Araeoscelis*, Co, Eo, Sq, Sph, No
	76b. Loss of ectepicondylar foramen	Some Sq, No, Ple, Arch, Th, Pla
77. Ulna with clearly defined olecranon and sigmoid notch	77a. Reduction of olecranon and sigmoid notch	Eo, some Sq, some Sph, No, Ple, some Arch, Ch, Th, Pla
78. *Shaft of ulna and radius subequal in length, and shorter than humerus	78a. Ulna and radius subequal to humerus, or longer	Ar, some Sq, Pro, some Arch
	78b. Shaft of radius longer than that of ulna	Eo
79. All primitive elements of amniote carpus retained	79a. Loss of elements	Some Sq, some Sph, No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
80. Perforating foramen surrounded by intermedium, ulnare, and lateral centrale	80a. Loss of perforating foramen	? Co, Sq, Sph, No, Ple, some Pro, some Rhy, Arch, Ch, Th, Pla
81. Medial centrale articulating with third distal tarsal	81a. Medial centrale interposed between lateral centrale and third distal carpal	Eo
82. Proximal ends of metacarpals slightly overlapping	82a. Changes too varied to categorize systematically	
83. Length of metacarpals increase from I–IV; Metacarpal V is intermediate in length between I and II	83a. Changes too varied to categorize systematically	
84. Phalangeal count 2-3-4-5-4	84a. Reduced phalangeal count	Some Sq, some No, some Pro, ?Rhy, Arch, ?Ch, Th
	84b. Hyperphalangy	Some Sq, some No, Ple
85. Unguals sharply pointed and laterally compressed	85a. Reduction and modification of unguals too varied to categorize systematically	

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
86. Puboischiadic plate plate complete, without thyroid fenestra	86a. Thyroid fenestra	Advanced Sq, Sph, No, Ple, advanced Pro, advanced Rhy, advanced Arch, advanced Th
87. Narrow, posteriorly directed iliac blade	87a. Expansion of iliac blade	Co, advanced Rhy, advanced Arch, Tri
	87b. Reduction of iliac blade	Some Sq, No, Ple
88. Ilium in contact with pubis	88a. Ilium loses contact with pubis	Ple, some Arch
89. Supra-acetabular buttress retained	89a. Supra-acetabular buttress lost	All diapsids except Ar, and some No
90. Pubis perforated by obturator foramen	90a. Loss of obturator foramen	Some Arch, Ple
91. Femur with straight shaft and terminal head	91a. Sigmoidal shaft	Eo, Sq, Sph, Pro, Rhy, most Arch, Tri
	91b. Head displaced medially	Advanced Arch
92. Deep intertrochanteric fossa, internal trochanter, but no fourth trochanter	92a. Reduction and/or loss of intertrochanteric fossa and internal trochanter	Some Sq, Not, Ple, advanced Arch, advanced Pla
	92b. Fourth trochanter	Advanced Arch
93. Fibular condyle extending beyond tibial condyle	93a. Condyles in same plane	All diapsids other than Ar
94. *Tibia and fibular substantially shorter than femur	94a. Tibia and fibula as long or longer than femur	Ar, some Sq, Pro, some Arch
95. Astragalus and calcaneum meet along a straight, flat articulating surface that is indented by perforating foramen	95a. Fusion of astragalus and calcaneum	Advanced Sq, Sph
	95b. Specialized articulation between astragalus and calcaneum	Pro, Rhy, Arch, Tri
96. Separate centrale	96a. Fusion of centrale to astragalus	Advanced Sq, Sph
	96b. Loss of centrale	No, Ple, some Pro, advanced Arch, Ch, Th
97. Five distal tarsals	97a. Loss of distal tarsals	Most Sq, Sph, No, Ple, Pro, Rhy, Arch, Tri, Ch, Th, Pla
98. Proximal heads of metatarsals overlapping	98a. Changes too varied to categorize systematically	
99. Length of metatarsals increases from I to IV	99a. Changes too varied to categorize systematically	

APPENDIX I.—*continued*

Primitive diapsid condition	Derived condition	Groups in which derived state is observed
100. Metatarsal V approximately the length of II, not markedly shorter and not hooked	100a. Metatarsal V markedly shorter than II, but not hooked	Paliguanids, some Arch
	100b. Metatarsal V hooked	Advanced Sq, Sph, Pro, Rhy, Arch, Tri, Ch
101. Phalangeal count 2-3-4-5-4	101a. Phalangeal count reduced	Some Sq, some Not, some Arch
	101b. Hyperphalangy	Some No, Ple, some Sq
102. Fifth digit divergent	102a. Fifth digit absent	Some Sq, some Arch
103. Gastralia in chevron pattern, elements not fused at midline	103a. Gastralia fused at midline	All diapsids except Ar
	103b. Gastralia lost	Sq, Arch derivatives
104. No dermal armor	104a. Dermal armor	Some Eo, some Sq, some Arch, some Pla

APPENDIX II. Derived Characters of Early Diapsid Families

A. Synapomorphies Shared by Petrolacosauridae and Araeoscelidae

1. At least six cervical vertebrae; axis and more posterior cervicals much longer than trunk vertebrae
2. Mammillary processes on neural spines of posterior cervical and anterior dorsal vertebrae
3. Conspicuous process for triceps muscle on posterior coracoid
4. Greatly enlarged lateral and distal pubic tubercles
5. Epipodials nearly equal in length to propodials

B. Apomorphy of Petrolacosauridae

1. Conspicuous ischiadic notch

C. Apomorphies of Araeoscelidae

1. Nine cervical, 29 presacral vertebrae
2. Fusion of axial intercentrum to atlantal centrum
3. Secondary closure of lateral temporal opening

4. Cheek teeth enlarged and reduced in number
5. Enclosure of radial nerve to form ectepicondylar foramen

D. Synapomorphies of All Diapsids Other Than the Araeoscelida (these characters have been systematically omitted from the subsequent lists)

1. Strengthening of the temporal bars
2. Downgrowth of the parietals beneath the adductor jaw musculature
3. Exclusion of the lacrimal bone from the narial opening
4. Absence of caniniform maxillary teeth
5. Elimination of the primitive separation between the two coracoids
6. Acetabulum rounded, without distinct supra-acetabular buttress
7. Tibial and fibular condyles of femur in same plane
8. Caudal ribs fused to centra
9. Medial rows of gastralia fused at midline

E. Synapomorphies of Coelurosauravidae

1. Trunk ribs ossified in two segments, forming support for large gliding membrane
2. Squamosal frill
3. Trunk vertebrae elongate
4. Loss of dorsal intercentra

APPENDIX III. Derived Features of Lepidosaurs and Eosuchians, Based on Character-States in the Most Plesiomorphic Genera

AA = autapomorphy of group; M = characters shared by advanced lizard groups and sphenodontids, but not by paliguanids; SL = synapomorphy of lepidosauromorphs; SS = synapomorphies shared by modern squamates and paliguanids; and SSS = synapomorphies shared by squamates, paliguanids, and sphenodontids.

Eosuchians (based on *Youngina* and *Thadeosaurus*)

AA	Medial centrale interposed between lateral centrale and Distal Carpal 3
AA	Reduced ossification of olecranon; radius may exceed shaft of ulna in length
SL	Postfrontal entering margin of upper temporal opening
SL	Cervical Centra 3–5 shorter than trunk centra
SL	Reduced length of transverse processes of trunk vertebrae
SL	Trunk ribs holocephalous
SL	Large, ossified sternum with which coracoids articulate
SL	Quadrate exposed posteriorly (no evidence of support of tympanum)

Paliguanidae (based on *Paliguana, Saurosternon,* and *Palaeagama)*

SL	Postfrontal entering margin of upper temporal opening
SL	Cervical Centra 3–5 shorter than trunk centra
SL	Reduced length of transverse processes of trunk vertebrae
SL	Trunk ribs holocephalous
SL	Large ossified sternum with which coracoids articulate
SSS	Epiphyses elaborated as specialized joint surfaces
SSS	Incipient mesotarsal joint
SSS	Fifth metatarsal much shorter than fourth
SS	Quadrate streptostylic
SS	Loss of lower temporal bar
SS	Loss of ventral process of squamosal
SS	Lateral conch of quadrate supporting tympanum
SS	Intermedium much reduced

Sphenodontida (based on the most primitive pattern of Upper Triassic genera)

AA	Acrodont attachment of at least some of the marginal teeth
AA	Enlargement of the lateral row of palatine teeth
AA	Precise occlusion of marginal teeth
AA	Tiny juvenile teeth at the front of the maxilla and dentary
AA	Tooth replacement of acrodont teeth occurring by addition at the back of the maxilla and dentary
AA	Lacrimal absent
AA	Dentary characterized by its great posterior extension, coronoid process, and mandibular foramen
AA	Prefrontal forming solid articulation with dorsal surface of palatine (condition in crocodiles and placodonts not considered homologous)
AA	Very large quadratojugal foramen
AA	Prominent posterior process of ischium
SL	Postfrontal enters margin of upper temporal opening
SL	Cervical Centra 3–5 shorter than trunk centra
SL	Reduced length of transverse processes of trunk vertebrae
SL	Trunk ribs holocephalous
SL	Large ossified sternum with which coracoids articulate (not known in Triassic sphenodontids, but preserved in Upper Jurassic genera)
SSS	Separate epiphyseal ossifications
SSS	Impedance-matching middle ear
M	Caudal centra specialized for autotomy
M	Thyroid fenestration of pelvis
M	Fusion of astragalus and calcaneum, probably incorporating centrale
M	Loss of Distal Tarsals 1 and 5
M	Fifth metatarsal short and hooked

Kuehneosauridae

AA Greatly elongated trunk ribs
AA Median narial opening (not considered homologous to condition in rhynchosaurs)
AA Scapular blade narrow
SS Quadrate streptostylic and emarginated posteriorly
SL Postfrontal entering margin of upper temporal opening
SL Cervical Centra 3–5 shorter than trunk centra
SL Holocephalous trunk ribs

Characters shared with some archosauromorphs and some lepidosauromorphs

1. Loss of tabular, supratemporal, and postparietal
2. Lower temporal bar lost
3. Conspicuous retroarticular process
4. Elongate transverse processes of trunk vertebrae
5. Vertebrae non-notochordal
6. Loss of entepicondylar foramen
7. Reduced ossification of carpus
8. Thyroid fenestration

Characters of advanced lizards

1. Pineal opening between frontals and parietal

APPENDIX IV. Derived Characteristics of Lizard Groups Known from the Upper Jurassic to the Present

(S) = character shared with sphenodontids; (P) = synapomorphies of paliguanids and modern lizard groups.

Skull

1. Loss of lower temporal bar and ventral ramus of squamosal (P)
2. Absence of fixed connection between quadrate and pterygoid (P)
3. Dorsal end of quadrate enlarged to articulate with squamosal (streptostyly) (P)
4. Quadrate embayed posteriorly for reception of tympanum (P)
5. Light, rodlike stapes (S)
6. Paroccipital process extending to top of quadrate (S)
7. Tabular and postparietal lost (S)
8. Supratemporal expanded distally, lateral to distal end of parietal
9. Transverse hinge between parietals and frontals; one or both bones fused at midline
10. Fenestra rotunda present
11. Vidian canal enclosed by parasphenoid and basisphenoid
12. Coronoid bone extended as long coronoid process (S)
13. Dentition pleurodont or acrodont, exceptionally thecodont (not subpleurodont)
14. Denticles lost from transverse flange of pterygoid (S)

Postcranial Skeleton

1. Except for some members of the Gekkota, centra procoelous; trunk intercentra lost
2. Cervical intercentra specialized as hypopophyses
3. Atlas arch fused medially (?P)
4. Tail-break mechanism, unless secondarily lost (S)
5. Scapulocoracoid with two to four fenestrae (?P)
6. Scapula and coracoid slow to co-ossify, compared with eosuchians (S)
7. Large sternum, the anterior edge of which forms a surface for rotation of the coracoid (S) (P)
8. Bony epiphyses of limb bones form specialized, articulating surfaces (S) (P)
9. Entepicondylar foramen of humerus lost
10. Intermedium of carpus reduced or lost (P)
11. Puboischiadic plate with large thyroid fenestra; no bony connection of pubis and ischium below fenestra (S)
12. Pubis outturned dorsally (S)
13. Astragalus (including centrale) fused to calcaneum (S)
14. Mesotarsal joint formed between proximal tarsals and fourth distal tarsal (S) (P)
15. Usually only one distal tarsal retained
16. Fifth metatarsal much shorter than fourth (S) (P)
17. Fifth metatarsal hooked (S)
18. Gastralia lost

APPENDIX V. Derived Features of Sauropterygians, Based on Character-States in the Most Plesiomorphic Genera

AA = unique derived feature of this group; SA = derived features shared with one or more groups of advanced diapsids; SAL = derived feature shared with some archosauromorphs and some lepidosauromorphs; SL = derived feature shared with lepidosauromorphs; SS = derived feature shared specifically with nothosaurs and plesiosaurs; and SSS = synapomorphy uniquely shared by nothosaurs and plesiosaurs.

Derived Characters of Nothosaurs

AA Suborbital and interpterygoid vacuities closed; pterygoids meet along midline as far posteriorly as the occipital condyle
AA Large unossified area between the transversely oriented ventral portions of the clavicle and the elongate, posteromedially directed coracoids
SA Loss of postparietal, tabular, and supratemporal
SA Quadrate embayed posteriorly

SA	Stapes reduced to a narrow rod
SA	Loss of palatal dentition
SA	Loss of transverse flange of pterygoid
SA	Thecodont implantation of marginal dentition
SA	Posterior position of external nares
SA	Loss of lower temporal bar without development of streptostyly
SA	Reduction or loss of lacrimal
SA	Conspicuous retroarticular process
SA	Loss of trunk intercentra
SA	Centra not notochordal
SA	Arches and centra not co-ossified
SA	Neck elongate (at least 17 cervical vertebrae)
SA	Three or more sacral vertebrae
SA	Cervical ribs with anterior process
SA	Trunk ribs single-headed
SA	Ribs variably pachyostotic
SA	Sacral ribs not expanded distally
SA	Articulating surfaces of limbs, girdles, carpals, tarsals poorly ossified
SA	Loss of cleithrum
SSS	Ventral portion of scapula superficial to blade of clavicle
SA	Interclavicle superficial to clavicle
SA	Epipodials reduced
SA	Thyroid fenestra
SA	Blade of ilium much reduced

Derived Characters of Plesiosaurs (based on superficial observation of Lower Jurassic genera, never described in detail, and Brown, 1981, on Upper Jurassic genera)

AA	Loss of stapes
AA	Pectoral and pelvic girdles greatly expanded ventrally
AA	Similar paddle shape of hind and forelimbs
AA	Ilium not attached to pubis (not considered homologous to condition in crocodiles)
SA	Lower temporal bar lost
SA	Nasals lost
SA	Loss of palatal dentition
SA	Loss of transverse flange of pterygoid
SA	Thecodont implantation of marginal dentition
SA	Opisthotic extending to cheek
SA	Jaw articulation well below tooth row
SA	Conspicuous retroarticular process
SA	Vertebrae non-notochordal
SA	Arches and centra not co-ossified
SA	No trunk intercentra
SA	28 or more cervical vertebrae

SA	Great elongation of transverse processes of trunk vertebrae
SA	Three or more sacral vertebrae
SA	Single-headed trunk ribs
SA	Articulating surfaces of limbs, girdles, carpals, and tarsals poorly defined
SA	Loss of cleithrum
SSS	Ventral portion of scapula superficial to blade of clavicle
SA	Humerus lacking both ectepicondylar and entepicondylar foramina
SA	Epipodials reduced
SA	Hyperphalangy
SA	Thyroid fenestra
SA	Blade of ilium much reduced

Derived Characters of *Claudiosaurus*

SL	Postfrontal borders on upper temporal opening
SS	Loss of lower temporal bar without development of streptostyly
SS	Reduction of suborbital and interpterygoid vacuities
SAL	? Loss of postparietal and tabular
SAL	Eight cervical vertebrae
SL	Short transverse processes on trunk ribs
SS	Partial integration of third sacral rib
SAL	Loss of cleithrum
SAL	Shoulder girdle displaced posteriorly
SL	Cartilaginous sternum
SS	Slight reduction in degree of ossification of carpals and tarsals

APPENDIX VI. Derived Characters of Archosauromorphs, Based on Character-States in the Most Plesiomorphic Genera

AA = autapomorphy of each group *within* archosauromorphs; and SA = synapomorphies uniting archosauromorphs.

Protorosauria (based on *Protorosaurus* and *Prolacerta*)

AA	Seven very elongate cervical vertebrae
AA	Cervical ribs very thin
AA	Loss of lower temporal bar
AA	? Tympanum supported by quadrate, squamosal, and quadratojugal
	Postparietal median (also occurs in early archosaurs)
SA	Tooth implantation subthecodont or thecodont
SA	Premaxilla extending behind external nares
SA	High quadrate
SA	Quadratojugal behind lower temporal opening
SA	Elongate stapes without stapedial foramen

SA	Paroccipital process extends to top of quadrate
SA	Basioccipital and basisphenoid contiguous; basisphenoid reaching prootic
SA	Loss of postparietal and tabular (supratemporal retained)
SA	Prominent retroarticular process
SA	Vertebrae not notochordal
SA	Elongate transverse processes of trunk vertebrae
SA	Cleithrum absent
SA	Pisiform, radiale, and fifth distal carpal lost or slow to ossify
SA	Loss of entepicondylar foramen
SA	Astragalus and calcaneum articulate with one another
SA	Fifth distal tarsal lost
SA	Fifth metatarsal hooked

Rhynchosauria (based on *Noteosuchus, Howesia,* and *Mesosuchus*)

AA	Ankylothecodont tooth implantation
AA	Median narial opening
AA	Overhanging premaxillae (condition in *Chasmatosaurus* not considered homologous)
	Postfrontal entering margin of upper temporal opening
SA	Premaxilla extends behind external nares
SA	High quadrate
SA	Quadratojugal behind lower temporal opening
SA	Elongate stapes without stapedial foramen
SA	Paroccipital process extending to top of quadrate
SA	Basioccipital and basisphenoid contiguous; basisphenoid reaching prootic
SA	Loss of postparietal and tabular (supratemporal retained)
SA	Prominent retroarticular process
SA	Vertebrae not notochordal
SA	Elongate transverse process of trunk vertebrae
SA	Cleithrum absent
SA	Pisiform, radiale, and fifth distal carpal lost or slow to ossify
SA	Loss of entepicondylar foramen
SA	Astragalus and calcaneum articulating
SA	Fifth distal tarsal lost
SA	Fifth metatarsal hooked

Archosaurs (based on *Proterosuchus* [*Chasmatosaurus*])

AA	Antorbital fenestrae
AA	Laterally compressed serrate teeth (also occurs in *Heleosaurus*)
	Postparietal median (also occurs in early Protorosaurs)
SA	Long neck; cervical vertebrae as long or longer than trunk vertebrae
SA	Thecodont implantation
SA	Premaxilla extending behind external nares

SA	High quadrate, presumably supporting large tympanum
SA	Quadratojugal behind lower temporal opening
SA	Paroccipital process extending to top of quadrate
SA	Basioccipital and basisphenoid contiguous; basisphenoid reaching prootic
SA	Tabular lost (supratemporal retained)
SA	Vertebrae not notochordal
SA	Elongate transverse processes
SA	Loss of cleithrum
SA	Loss of entepicondylar foramen
SA	Number of carpals reduced; ?pisiform lost
SA	Astragalus and calcaneum articulating with one another
SA	Heel of calcaneum directed posteriorly
SA	Fifth distal tarsal lost
SA	Fifth metatarsal hooked

Trilophosauridae (based on *Trilophosaurus*)

AA	No lateral temporal opening
AA	Loss of teeth in premaxilla and front of dentary
AA	Cheek teeth laterally expanded
AA	Extensive fusion of dermal bones in the adult
AA	Cervical vertebrae procoelous
SA	Tooth implantation thecodont
	Postfrontal entering margin of upper temporal opening
SA	Premaxilla excluding maxilla from narial opening
SA	High quadrate
	Pineal opening lost
SA	Elongate stapes without stapedial foramen
SA	Paroccipital process extending to top of quadrate
SA	Prominent retroarticular process
SA	Vertebrae not notochordal
SA	Elongate transverse processes
SA	Cleithrum absent
SA	Loss of entepicondylar foramen
SA	?Pisiform lost; radiale and fifth distal carpal lost or slow to ossify
SA	Astragalus and calcaneum articulating with one another
SA	Calcaneal heel
SA	Fifth distal tarsal lost
SA	Fifth metatarsal hooked

Malerisaurus

AA	Articulating surfaces of posterior cervical centra angled at 50°–75° with long axis of centra to provide a fixed curvature of neck
AA	Parietal fused at midline
SA	Premaxilla extending behind external nares
SA	High quadrate

SA	Quadratojugal behind lower temporal opening
SA	Paroccipital process extending to top of quadrate
SA	Basioccipital and basisphenoid contiguous; basisphenoid reaching prootic
SA	Loss of postparietal, tabular, and supratemporal
SA	Prominent retroarticular process
SA	Nine cervical vertebrae; all but atlas elongate
SA	Vertebrae not notochordal
SA	Elongate transverse processes of trunk vertebrae
SA	Cleithrum absent
SA	Loss of entepicondylar foramen
	Head of fifth metatarsal not hooked, but widely expanded

APPENDIX VII. Derived Characters of Groups Whose Phylogenetic Position Is Uncertain

AA = autapomorphies unique to this group; SA = derived similarities with some archosauromorphs; SL = derived similarities with some lepidosauromorphs; SAL = derived similarities with some archosauromorphs and some lepidosauromorphs.

Choristodera (based on the more primitive of
derived character-states described in *Champsosaurus*
and *Simoedosaurus*)

AA	Elongation of snout with nasal bones fused at midline; prefrontals meeting at midline separating nasals from frontals
AA	Temporal area greatly expanded laterally and extending well posterior to occipital condyle
AA	Internal nares extended posteriorly as grooves in the roof of palate
SAL	Loss of postparietal, supratemporal, tabular, and pineal foramen
SA	Basioccipital and basisphenoid form continuous floor of braincase
SAL	External nares medial in position
SAL	Extensive paroccipital process supported by quadrate
SAL	Extremely long jaw symphysis
SAL	Thecodont implantation of marginal teeth
SAL	Nine cervical vertebrae
SA	Three fused sacrals
SL	Reduced ossification of vertebrae, girdles, carpals, and tarsals
SAL	Vertebrae not notochordal
SA	Loss of trunk intercentra and cross-pieces of haemal arches
SL	Ribs pachyostotic
SAL	Loss of cleithrum
SAL	Loss of entepicondylar foramen
SAL	Cervical ribs with anterior processes

SAL	Femur much longer than humerus
SAL	Reduced phalangeal formula
SAL	No pisiform
SL	Short epipodials

Placodontia (based on the more primitive of derived character states observed in *Placodus* and *Helveticosaurus*)

AA	Vertebrae with elongate transverse processes, but deeply amphicoelous centra
AA	Loss of lateral temporal opening; quadratojugal forming much of cheek
AA	Anterior teeth spatulate and procumbent
AA	Quadrate fitting into a socket formed by squamosal and quadratojugal
AA	Prefrontal and postfrontal separating frontal from orbital margin
SAL	Loss of postparietal, supratemporal, and tabular
SAL	Loss of lacrimal
SAL	Nasal fused at midline
SAL	External nares posterior in position (common to many aquatic groups)
SAL	Loss of teeth on pterygoid
SL	Postfrontal entering margin of upper temporal opening
SAL	Quadrate recessed posteriorly, suggesting support of tympanum
SAL	Prefrontal having pillarlike contact with palatine (crocodiles, sphenodontids, and the nothosaur *Simosaurus*)
SL	Closure of interpterygoid vacuity and suborbital fenestra reduced to a slit
	Contact between maxilla and ectopterygoid
SAL	Vomer fused
SL	Cervical centra shorter than those of trunk
SAL	Loss of trunk intercentra
SL	Single-headed trunk ribs
SAL	Loss of cleithrum
SAL	Loss of entepicondylar foramen
SL	Reduced ossification of ends of limb bones, girdles, tarsals, and carpals (common to many aquatic groups)

Thalattosauria (based primarily on *Askeptosaurus* and *Clarazia*)

AA	Dorsal temporal opening much restricted or entirely closed
AA	Premaxillae elongated and reaching frontals; nasals displaced laterally
AA	Posterior margin of skull table deeply emarginated; occiput lying well forward relative to quadrate suspension
SAL	At least 7–8 cervical and 30–32 trunk vertebrae

SAL	External nares posterior in position and close to midline
SAL	Reduction of lower temporal bar
SAL	Loss of tabular and postparietal, but not supratemporal
SA	Loss of trunk intercentra and cross-piece of haemal arches
SAL	Cervical ribs with anterior process
SAL	Loss of cleithrum
SAL	Loss of entepicondylar foramen
SL	Reduced length of epipodials (common to many aquatic groups)
SA	Reduced ossification of carpals and tarsals (common to many aquatic groups)
SAL	Loss of fifth distal tarsal
SAL	Reduction in phalangeal count

APPENDIX VIII. Anatomical Abbreviations Used in the Figures

a = angular; art = articular; ast = astragalus
cal = calcaneum; cen = centrale
d = dentary
f = frontal
i = intermedium
j = jugal
l = lacrimal; lc = lateral centrale
m = maxilla; mc = medial centrale
n = nasal
p = parietal; pf = postfrontal; pis = pisiform; pm = premaxilla; po = postorbital; prf = prefrontal
q = quadrate
ra = radiale
sa = surangular; sq = squamosal; st = supratemporal
ul = ulnare
1–5 = distal carpals or tarsals
I–V = metacarpals or metatarsals

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