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Origins of the higher groups of  
tetrapods: Controversy and consensus

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## 9 Amniote Phylogeny

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The amniotes (reptiles, birds, mammals), which arose during the Carboniferous, represent one of the most prominent vertebrate groups today. Their key innovation, the cleidoic ("closed") egg, has a semipermeable shell (either calcareous or leathery) that allows the embryo to develop outside the mother's body in its own pond of fluid. Water is retained by the shell, and the eggs can be laid on land, unlike the eggs of most amphibians. The cleidoic eggs of amniotes also contain extra-embryonic membranes that function in respiration, feeding, and waste disposal.

The amniotes arose during the Carboniferous period. The oldest described forms date from the early part of the Pennsylvanian (Late Carboniferous), about 300 million years (Myr) ago (Carroll, this volume), although an older reptile from the Mississippian (Early Carboniferous, ca. 340 Myr) of Scotland has been reported (Smithson, 1989). Regrettably, cleidoic eggs have not been found in sediments older than the Early Permian (ca. 270 Myr), and the validity of that specimen has been questioned (Kirsch, 1979). However, the Carboniferous "reptiles" almost certainly are members of the Amniota, because the major amniote lineages arose in the Carboniferous, and they all share very similar egg characters that are unlikely to have arisen independently more than once. Carroll (this volume) gives other arguments in favor of this view.

The closest out-group of the Amniota currently is disputed, as are the

relationships of the major groups within Amniota. These two topics are reviewed here, and a fuller review is given in Benton, 1990.

## THE OUT-GROUPS OF THE AMNIOTA

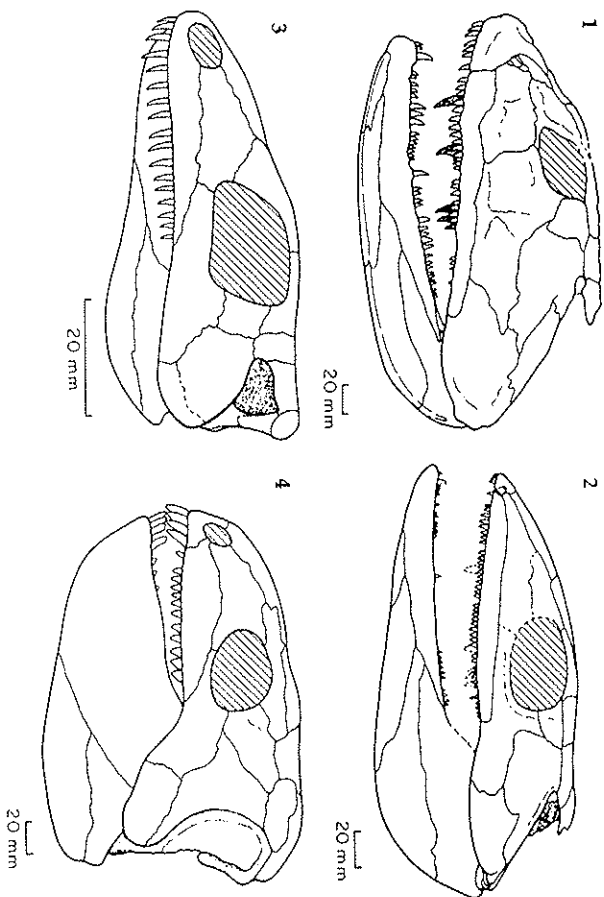
The problem of identifying the sister-group of the Amniota, or indeed the series of out-groups leading to that clade, generally has been tackled under the rubric "the origin of the reptiles." Most authors have accepted for some time that the most reptilelike "amphibians" are the anthracosaurs, or batrachosaurs, of the Carboniferous and Permian. Another amphibian group of that time, the Microsauria, is reptilelike in many respects, but the similarities probably are convergent (Carroll, this volume).

The groups typically classified as amphibians seem to fall into two major groupings (Panchen and Smithson, 1988; Milner, 1988; Panchen, this volume) that cut across the old split into labyrinthodonts and lepospondyls: a batrachomorph clade (i.e., "true" amphibians, including neotridians, colosteids, microsaur, "temnospondyls," and lissamphibians), and a reptiliomorph clade—i.e., those amphibians on the line to the reptiles, as well as all amniotes.

The key reptiliomorph taxa, according to the cladistic analysis of Panchen and Smithson (1988), are the Loxommatidae, *Crassigyrinus*, the Anthracosauroida, Seymouriamorpha, Diadectomorpha, and Amniota. These taxa all share a basal articulation (where the braincase rotates against the palatal bones), a specialized retractor pit for the eye muscles on the basisphenoid (Panchen and Smithson, 1988), and vertebrae in which the pleurocentrum dominates and the intercentrum is reduced.

If the loxommatids and *Crassigyrinus* are reptiliomorphs, the group arose early in the Mississippian. *Crassigyrinus* (Fig. 1) possesses the reptiliomorph characters noted above, and others—such as the presence of a single convex occipital condyle with a convex atlas articulation, and five digits in the hand (typically four in "true" amphibians)—appear in the anthracosauroids (Fig. 2), seymouriamorphs (Fig. 3), diadectomorphs (Fig. 4), and amniotes.

The seymouriamorphs and diadectomorphs long have been regarded as the closest out-groups to the Amniota, or even as full-fledged reptiles (e.g., Romer, 1945; Heaton, 1980; Carroll, 1982, this volume). It is unclear whether the Seymouriamorpha is the sister-group of the Anthracosauroida (Smithson, 1985), of the Diadectomorpha (Heaton, 1980; Fracasso, 1987), or of the Diadectomorpha and Amniota (Panchen, this volume), as shown in Figure 5. However, the diadectomorphs, such as *Diadectes*



Figs. 1–4. Skulls, in lateral view, of reptiliomorph amphibians. (1) *Crassigyrinus*. (2) The anthracosauroid *Proterogyrinus*. (3) *Seymouria*. (4) *Diadectes*. (From various sources, after Carroll, 1987.)

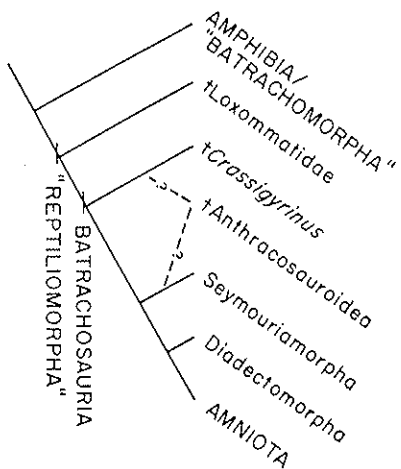


Fig. 5. The phylogeny of the reptiliomorph amphibians. (From information in Panchen and Smithson, 1988, and other sources.)

(Heaton, 1980) or *Limnoscelis* (Fracasso, 1987), are very amniote-like in many ways. Postulated diadectomorph-amniote synapomorphies include (Panchen and Smithson, 1988; Gauthier et al., 1988a) the following: (1) the pterygoid flange directed ventrally and often bearing teeth, (2) the convex occipital condyle fully developed, (3) postparietal and tabular

bones exposed on occiput only, (4) the presence of at least two sacral vertebrae, and (5) the ?presence of an astragalus.<sup>1</sup>

## THE RELATIONSHIPS OF LIVING AMNIOTE GROUPS

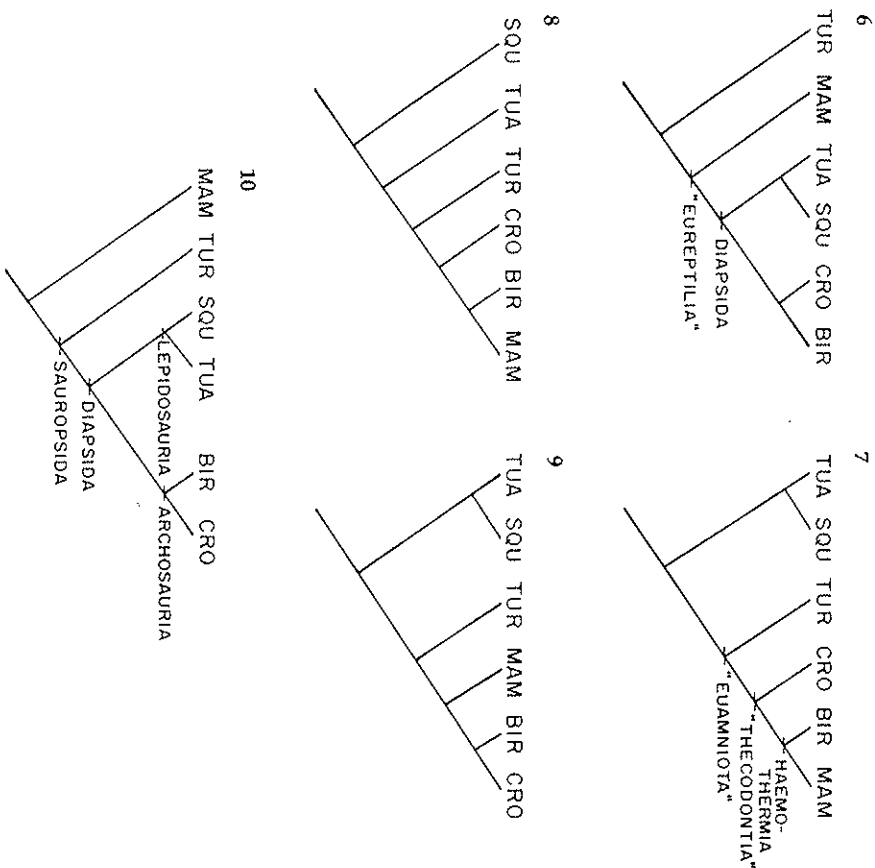
### Morphological Data

Six monophyletic groups (clades) of living amniotes may be assessed for their mutual relationships: turtles (Chelonia or Testudinata), mammals (Mammalia), the tuatara (Sphenodontida), lizards and snakes (Squamata), crocodylians (Crocodylia), and birds (Aves). The turtles are diagnosed by their "shell," a carapace and plastron formed from bone and keratin, as well as other characters (Gaffney and Meylan, 1988). Mammals are diagnosed by possession of hair, mammary glands, and skeletal characters (Kemp, 1988; Rowe, 1988), and the squamates by their skin, paired copulatory organs, kinetic quadratric bone, and other modifications to the skull and skeleton (Evans, 1988; Rieppel, 1988). Crocodylians are diagnosed by their pneumatic posterior skull bones, ear lid, elongate wrist bone, modified pelvis, and numerous other features (Benton and Clark, 1988), and birds by their feathers, furcula (wishbone), fused lower leg bones, reduced tail, and wings (Cracraft, 1988).

A "standard" view of relationships presented by Gaffney (1980) united the tuatara, squamates, crocodylians, and birds as the Diapsida, and paired these with the mammals first and placed turtles as the out-group (Fig. 6). In this arrangement, the tuatara and the squamates form the Lepidosauria, and the crocodylians and the birds the Archosauria. Gaffney argued that the mammals and diapsids share a lower temporal fenestra and a Jacobson's organ in a ventromedial pocket in the roof of the mouth at some stage in ontogeny. The other "traditional" view is that the turtles and diapsids are sister-groups, and that mammals are the out-group to them (see below).

Gardiner (1982) proposed a rather revolutionary cladogram (Fig. 7) in which the Diapsida and the Archosauria were separated, and the birds were the sister-group of the mammals. He listed 28 postulated bird-mammal synapomorphies—i.e., shared characters of the brain case, brain, snout, vertebral column, circulatory system, glands, and physiology (both groups being endothermic)—and an additional 20 characters shared by turtles, crocodylians, birds, and mammals, but not by the tuatara and squamates.

<sup>1</sup>In Amniota and *Diadectes*, there is a single, medial element of the ankle formed by fusion of the tibiale, intermedium, and centrale IV of other forms; it is not clear whether the astragalus of *Diadectes* is homologous to that of amniotes.



Figs. 6-10. The relationships of living amniotes. (6) Gaffney (1980). (7) Gardiner (1982). (8) Löwtrup (1985). (9) Gauthier et al. (1988b), based on living and extinct taxa only. (10) Gauthier et al. (1988b), based on living and extinct taxa. BIR = birds; CRO = crocodylians; MAM = mammals; SQU = squamates; TUA = tuatara; TUR = turtles.

Löwtrup (1985) proposed a third cladogram (Fig. 8), which also involved a breakup of the Diapsida and Archosauria, and the establishment of a bird-mammal clade, the Haemothermia. He also split up the Lepidosauria, making the squamates and the tuatara the most primitive amniote groups.

The views of Gardiner (1982) and Löwtrup (1985) were criticized vigorously by Benton (1985), Gauthier et al. (1988a, b), and Kemp (1988), all of whom found that many of the putative synapomorphies in support of the cladogram in Figures 7 and 8 were nonhomologous, ill-defined, or present in wider groups than at first proposed. The remaining postulated

synapomorphies were said to be heavily outweighed by those in favor of a monophyletic Lepidosauria, Archosauria, and Diapsida, with the mammals and turtles as out-groups (Benton, 1985; Kemp, 1988).

Gauthier et al. (1988b) attempted a thorough analysis of the relationships of living amniotes on the basis of 109 characters. The resulting cladogram (Fig. 9) differs from Gardiner's (Fig. 7) only in the exchange of the positions of the mammals and crocodylians, respectively. However, the amount of agreement of the characters (i.e., their congruence as measured by the Consistency Index was low (C.I. = 0.674). Moreover, the addition of 25 fossil taxa to the analysis and the use of a total of 207 characters of the skull and skeleton yield a very different cladogram (Fig. 10) in which the integrity of the Archosauria and Diapsida is restored. The minimum of at least seven postulated synapomorphies shared by turtles and diapsids in this scheme far outweighs those proposed to unite mammals and diapsids in Figure 6. The turtle-diapsid synapomorphies are as follows: (1) the tabular small or absent; (2) the supratemporal small or absent; (3) a supraoccipital with anterior crista; (4) a suborbital fenestra or foramen in palate; (5) a simple coronoid; (6) the atlas centrum and axis intercentrum fused; and (7) the medial centrale of ankle absent. Gauthier et al. (1988b) argued that the fossils were crucial in establishing their final cladogram of amniote relationships (Fig. 10). Attempts to fit the fossil taxa into a cladogram based solely on modern taxa (e.g., Gardiner, 1982) lead to absurd problems of high levels of parallelism and reversal, as well as major stratigraphic anomalies.

### Molecular Data

Independent lines of evidence for amniote phylogeny have been obtained from studies of amino acid sequences in proteins. These molecular studies are based on the Molecular Clock Hypothesis in some form or another—i.e., the idea that the primary structure of proteins changes in a clocklike, stochastic way. For any particular protein, a rate of substitution per Myr can be established, and this can be used to determine patterns of relationships among taxa; the more distantly related two taxa are, the more differences will be discovered between homologous proteins.

Molecular sequences from a variety of amniotes now are available for the following polypeptides:  $\alpha$ - and  $\beta$ -parvalbumin,  $\alpha$ - and  $\beta$ -hemoglobin, myoglobin, lens  $\alpha$ -crystallin A, fibrinopeptides A and C, cytochrome *c*, and ribonuclease. These have given rise to a number of maximum-parsimony trees. Although the wider relationships of major tetrapod groups are still tentative because of the paucity of nonmammalian sequences, nearly every pairing of mammals, birds, crocodylians, lizards,

snakes, turtles, and amphibians has been found (e.g., Goodman et al., 1985, 1987; Bishop and Friday, 1987, 1988). The arrangements derived from morphological and molecular data are presented below for comparison.

#### Myoglobin

[[[[Turtle] Lizard] Crocodylian] | Bird [Mammal]]]]

OR

[[[[Turtle] Crocodylian] Lizard] | Bird [Mammal]]]]

#### $\beta$ -Hemoglobin

[Snake [Crocodylian [Bird [Mammal]]]]

OR

[Mammal [Snake [Crocodylian [Bird]]]]

OR

[Snake [Mammal [Bird [Crocodylian]]]]

#### $\alpha$ -Hemoglobin

[Crocodylian [Bird [Mammal]]]]

#### Lens $\alpha$ -crystallin A

[Mammal [Crocodylian [Lizard [Bird]]]]

OR

[Mammal [Lizard [Crocodylian [Bird]]]]

#### Cytochrome *c*

[Bird [Snake [Mammal]]]]

#### "Standard Morphological"

[[Turtle [[Lizard [Snake]]] [Crocodylian [Bird]]]] Mammal]

The majority of these protein-based phylogenetic trees hypothesizes a sister-group relationship between birds and mammals, in apparent support of the morphological views of Gardiner (1982) and Løvtrup (1985). In addition, where relevant sequences are available, turtles often are associated with squamates (lizards and snakes) to form a clade separate from crocodylians or birds. Some authors have accepted these results at face value, whereas others have urged caution until more nonmammalian sequences become available. It has been noted that the relative difference in parsimony values between the most parsimonious tree or trees, and any of a large number of other patterns, often is very small. Further, the structures of some of the polypeptides, such as the hemoglobins and myoglobins, might be correlated functionally with, for example, the endothermy of birds and mammals, and some of their similarities might be convergent or the result of resistance to mutation (Bishop and Friday, 1988).

## THE RELATIONSHIPS OF EARLY AMNIOTES

If the cladogram in Figure 10 is accepted as the best current solution, where do the extinct Carboniferous and Permian amniotes fit in?

### Carboniferous Amniotes

Basically, there are three families of early reptiles known thus far from the Carboniferous—the Protorothyrididae, Petrolacosauridae, and Ophiacodontidae. Each of these has a skull pattern that seems to place it in a different major amniote lineage. Thus, *Paleothyris* (Fig. 11), a typical protorothyridid, has an *anapsid* skull; that is, there are no temporal openings behind the orbit. *Petrolacosaurus*, on the other hand, has a typical *diapsid* skull (Fig. 12), with two temporal openings, and *Ophiacodon* has a *synapsid* skull (Fig. 13), with only the lower temporal opening present.

The relationships of the Petrolacosauridae and Ophiacodontidae would seem to be clear, with the former being close to the origin of the great clade Diapsida, and the Ophiacodontidae being close to the origin of the Synapsida, which includes the mammals (Fig. 14). The anapsid skull of the protorothyridids is the primitive pattern for amniotes and also is characteristic of amphibians and fishes; thus, this character cannot be used as a synapomorphy to link protorothyridids with the only living anapsid amniotes, the turtles. In fact, the protorothyridids seem to be an

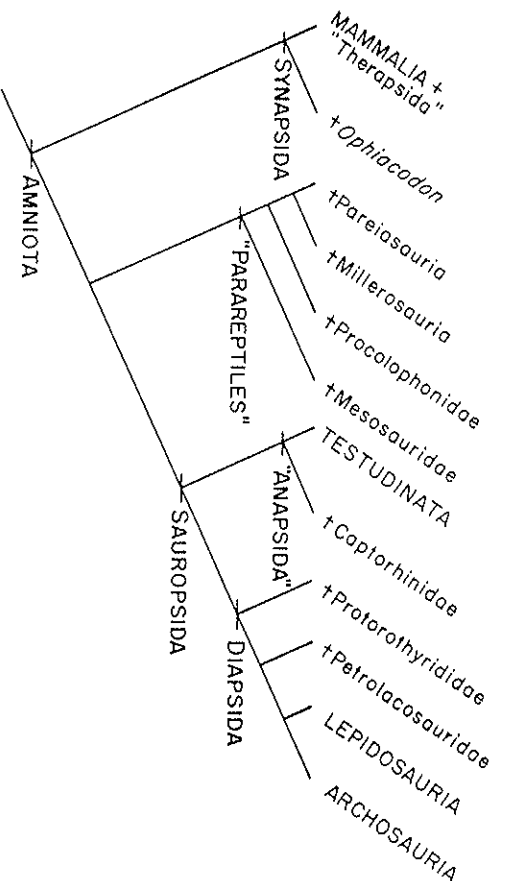
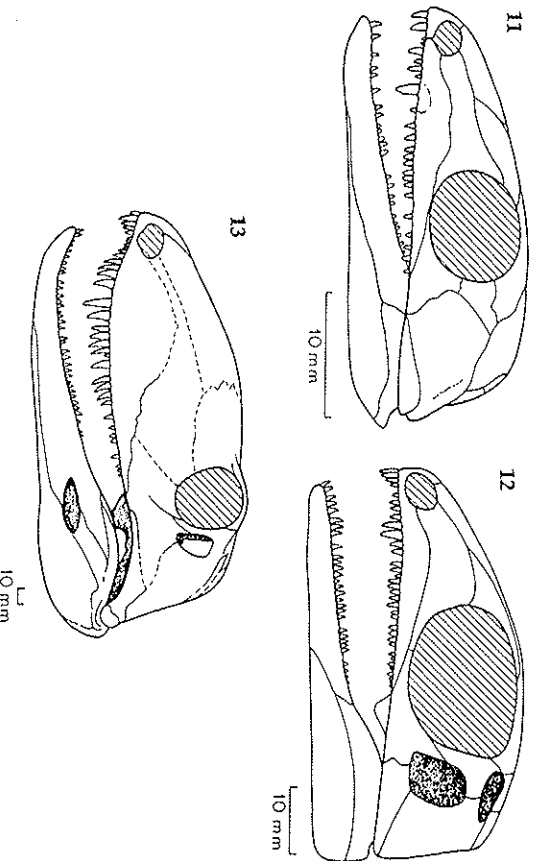


Fig. 14. The phylogeny of the major early amniote groups. (From information in Heaton and Reisz, 1986; Caffney and Meylan, 1988; Gauthier et al., 1988a, b; and other sources.)

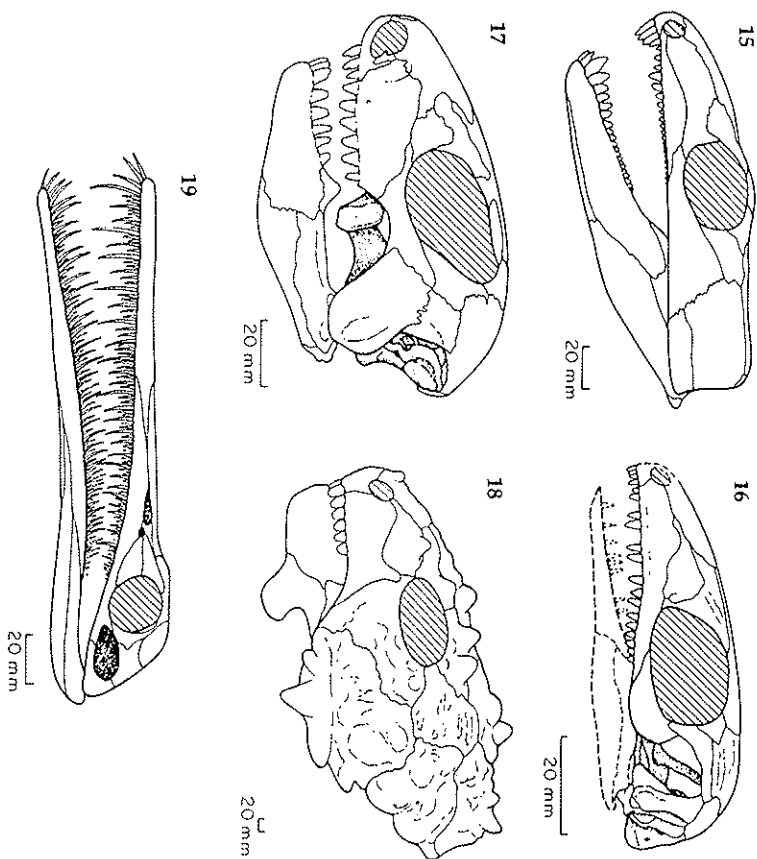
out-group of the diapsids on the basis of several postulated synapomorphies (Heaton and Reisz, 1986)—(1) a short postorbital region of the skull, (2) keels on the underside of the anterior presacral pleurocentra, (3) slender limbs, and (4) long, slender feet.

### Permian Amniotes

The synapsids radiated extensively during the Permian, giving rise to numerous lineages of "pelycosaurs," of which *Ophiacodon* is an example in the Late Carboniferous—Early Permian and therapsids in the Late Permian. These are considered further by Hotton (this volume) and Hopsón (this volume). The diapsids also radiated in the Late Permian, after an unusual and apparent gap during the Early Permian; their later evolution is considered herein by Carroll and Currie (this volume). Several anapsid groups also had their heyday in the Permian, and they are more difficult to place in the phylogenetic scheme. These include the captorhinids (Fig. 15), millerettids (Fig. 16), procolophonids (Fig. 17), pareiasaurs (Fig. 18), and mesosaurs (Fig. 19). Hitherto, the captorhinids generally have been bracketed with the protorothyridids as the Captorhinomorpha, but their shared characters all seem to be plesiomorphous. The millerettids occasionally have been linked with the diapsids, or even with the lizards, but the evidence for this alliance is weak. The other three groups generally have been abandoned to a rag-bag group of basal reptiles, the "Cotylosauria," because they have no particular fea-



Figs. 11–13. Skulls, in lateral view, of Carboniferous amniotes. (11) The protorothyridid *Paleothyris*. (12) *Petrolacosaurus*. (13) *Ophiacodon*. (From various sources, after Carroll, 1987.)



Figs. 15–19. Skulls, in lateral view, of anapsid Permian amniotes. (15) *Captorhinus*. (16) *Milleirosaurus*. (17) *Procolophon*. (18) The pareiasaur *Pareiasaurus*. (19) *Mesosaurus*. (From various sources, after Romer, 1956, and Carroll, 1987.)

tures of the major amniote clades. Carroll (1982, this volume) argued that these five groups cannot be placed readily in a phylogenetic scheme, because they were given off piecemeal from a long-lived protorothyridid stock over a span of about 70 Myr extending from the Late Carboniferous to the Early Permian. He demonstrated that the postulated synapomorphies for any pairing of the five are matched by equally convincing shared derived characters for quite different patterns.

However, some modest progress has been made in attempts to disentangle the relationships of these groups. The captorhinids seem to be the sister-group of the Testudines (Fig. 14) on the basis of four skull characters (Gaffney and Meylan, 1988; Gauthier et al., 1988a): (1) the medial process of jugal absent, (2) the ectopterygoid absent, (3) the tabular absent, and (4) the foramen orbitonasale present.

The remaining four anapsid groups are brigaded tentatively as the "parareptiles" by Gauthier et al. (1988a). Pareiasaurs and millerettids are

regarded as sister-groups because they share reduction in the size of premaxillary teeth (?),<sup>2</sup> fusion of the caudal ribs to the vertebrae (?), and the absence of the supinator process of the humerus. The procolophonids are the postulated out-group of these two groups (Fig. 14) on the basis of the position of the articulation in front of the occiput, and the loss of the caniniform maxillary teeth (cf. Figs. 16–18 with Figs. 11–13, 15). The "parareptiles" as a whole (Fig. 14) are diagnosed (Gauthier et al., 1988a) by the greatly swollen neural arches in trunk vertebrae, the fusion of the caudal ribs to the vertebrae (?reversed in procolophonids), and the loss of the supraglenoid foramen in the scapulocoracoid.

## SUMMARY

The Amniota is a major vertebrate clade that includes reptiles, birds, and mammals. The amniotes arose in the Early Carboniferous, and their subsequent success probably is the result of their possession of the cleidoic egg, which allowed them to become fully terrestrial.

The out-groups of the Amniota include a series of reptiliomorph "amphibians" that acquired various reptilelike synapomorphies. These are best seen in the diadectomorphs, the postulated sister-group of the Amniota.

There has been much dispute over the relationships of living amniotes, occasioned by the fact that many soft-part anatomical, physiological, and molecular data seem to ally birds closely with mammals. However, the balance of evidence strongly favors a monophyletic Lepidosauria (tuatara, lizards, snakes), Archosauria (crocodilians, birds), Diapsida (lepidosaurs, archosaurs), and Sauropsida (turtles, diapsids), with the Synapsida (mammals plus extinct relatives) as the sister-group of the Sauropsida (reviewed in more detail in Benton, 1990).

The Carboniferous and Permian amniotes can be accommodated within this cladogram (Fig. 20), and it becomes clear that all three amniote lineages are present in the Pennsylvanian (the Diapsida with *Pentlacosauridae*, the Synapsida with *Ophiacodontidae*) or the Early Permian (the Anapsida [turtles, etc.] with *Captorhinidae*). Other Permian amniotes fall on the diapsid or synapsid line, or in a fourth postulated lineage, the "parareptiles," which died out in the Late Triassic (the last procolophonid). The relationships of the "parareptiles" still are problematic, because each of the four groups is quite distinctive, and yet none of them shows any convincing synapomorphies with another clade.

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<sup>2</sup> = polarity uncertain.

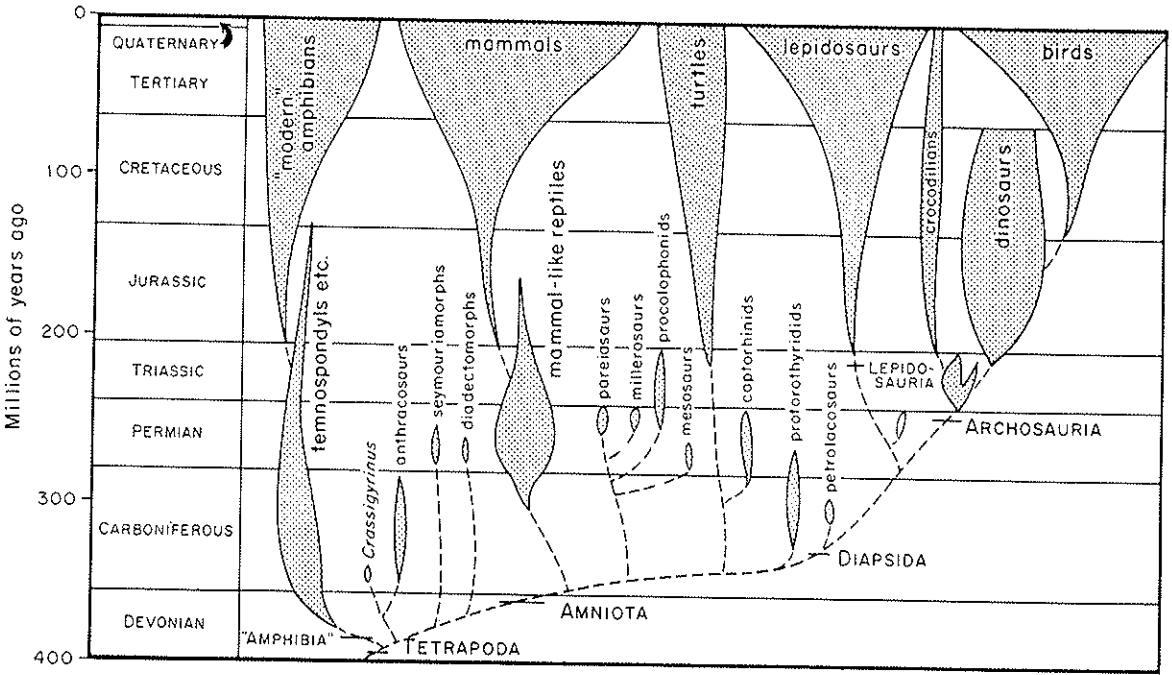


Fig. 20. Phylogeny of the early amniotes during Carboniferous and Permian times, based on the cladogram in Figure 14, with the addition of stratigraphic and diversity data from Carroll (1987) and other sources.

Amniote Phylogeny

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