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Phylogeny of the Major Tetrapod Groups: Morphological Data and Divergence Dates

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Summary. The phylogeny of the major groups of tetrapods (amphibians, reptiles, birds, and mammals) has until recently been poorly understood. Cladistic analyses of morphological data are producing new hypotheses concerning the relationships of the major groups, with a focus on the identification of monophyletic groups. Molecular phylogenies support some of these views and dispute others. Geological dates of the major evolutionary branching points are recalculated on the basis of the cladograms and new fossil finds.

Key words: Phylogeny — Tetrapods — Morphology — Cladistics — Divergence — Evolution — Amphibians — Reptiles — Birds — Mammals

Introduction

The standard view of tetrapod evolution is often represented in the form of bushlike phylogenetic trees in which many lines diverge from a rather fuzzy set of common ancestors. These polyphyletic groups (i.e., having several postulated ancestors) have included the mammals, reptiles, amphibians, and many major groups within them, such as the modern amphibians, the diapsid reptiles, dinosaurs, subungulate mammals, and pinnipeds. New systematic techniques, the cladistic analysis of morphologic data, and the computerized analysis (phenetic and cladistic) of molecular information have now led to a remarkable improvement in the resolution of the bushlike phylogenies, although many problems remain to be addressed.

An examination of standard texts may exemplify this increase in resolution. A.S. Romer, in his classic *Vertebrate Paleontology* presents a diagram of the phylogeny of the reptiles (1966, Fig. 156, p. 108) in which 17 separate groups are indicated, and only nine branching points, one basal octotomy, and nine dichotomies (two-way splits). A new phylogeny of the same 17 taxa (Benton 1984a, 1985; Evans 1984; Gauthier et al. 1988a,b) splits up the octotomy into more than eight dichotomies, each associated with particular synapomorphies. There are more than eight, as some of Romer's taxa (Cotylosauria, Eosuchia) are now regarded as paraphyletic (i.e., excluding one or more descendant groups) or even polyphyletic.

Cladistic analysis (Wiley 1981; Ax 1987) entails the reconstruction of patterns of relationships of taxa in the form of dichotomously branching diagrams, or cladograms. These indicate closeness of relationship, or recency of common ancestry, by the relative order of branching points. The cladograms are compiled by means of a character analysis that yields groups based only on shared derived characters (synapomorphies; autapomorphies if the characters pertain to one group). Proponents of cladistics claim greater rigor in their techniques than was exhibited by evolutionary systematics (e.g., Simpson 1961; Mayr 1969), which employed concepts such as ancestor–descendant sequences in reconstructing phylogenetic trees, or phenetics (e.g., Sneath and Sokal 1973), which employs the notion of general similarity.

Molecular data on tetrapod relationships have accumulated over the past 25 years. Protein sequences and DNA sequences are said to record evolutionary change in a more regular, even clocklike, way than does external morphology, so that the

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closeness of relationship of two taxa is measured by the similarity of their homologous proteins by many analysts (Patterson 1987). Others (Bishop and Friday 1987, 1988) use techniques that rely on measures of divergence, but make no assumptions about time-dependent rates of change.

Both cladistics and molecular sequencing have had the effect of increasing the resolution of published phylogenetic trees. Instead of the broad bushlike diagrams seen in most textbooks on vertebrate biology, it has been possible to present largely dichotomous trees that make precise claims about (1) the sister-group relationships, i.e., which group is closest to which; and, (2) the closeness of these relationships, in terms of the relative dates of branching points, or as measures of morphologic or molecular change.

The advantage of the new phylogenies over the earlier versions is not necessarily that they are more *correct* (although that is hoped for!), but that they are more explicit and *testable,* with the characters and their states specified, and they offer greater *predictiveness* (Janvier 1984). Every dichotomy in a cladogram has to be supported by one or more postulated synapomorphies, and it is possible to refute a branching point in a cladogram by demonstrating that the postulated synapomorphies are incorrectly analyzed or are outweighed by more well-founded synapomorphies, which support an alternative cladogram. A multiple branching point, such as that at the base of Romer's Reptilia, is hard to test, as it is more a plea of ignorance than a positive statement. This quality of the testability of cladograms is based more broadly on their predictiveness, i.e., their ability to suggest wider hypotheses in fields such as biogeography and paleontology that may themselves be tested. For example, the postulated order of branching in a cladogram can lead to theories of evolutionary events or biogeographic events that may be assessed by the input of independent studies of geographic distributions, continental drift, and the stratigraphic distribution of fossils. The focus is firmly on the discovery of monophyletic groups (i.e., those that contain all of the descendants of a common ancestor).

At present, cladistic analyses of morphologic data on tetrapod relationships are ahead of molecular studies in terms of the numbers and diversity of taxa that have been studied and in terms of the enumeration of synapomorphies, or homologies, as the basis for phylogenetic reconstruction. However, molecular taxonomists are expanding their data bases rapidly, both in terms of taxa and of proteins and DNA segments analyzed, and they are refining their analytical techniques, so that major advances may be expected.

The purpose of this article is to review the morphological data on the phylogeny of the major tetrapod groups and to highlight problem areas where molecular data may offer resolution. Morphologic data are summarized for all branching points in the figures, but full synapomorphy lists are given only for the major living clades. Available molecular results are compared briefly with the morphologically based phylogenies, and major dates of divergence are calculated for the use of molecular phylogenists.

Monophyly of the Tetrapoda

The Tetrapoda have generally been considered to be a monophyletic group (Gaffney 1979; Rosen et al. 1981; Panchen and Smithson 1987) on the basis of several synapomorphies of the skull, limbs, and limb girdles. These relate to reductions and rearrangements of the skull bones and modifications of swimming fins into load-bearing limbs (Panchen and Smithson 1987):

a) Cheek-plate composed of seven bones in which the jugal and quadratojugal meet broadly, thus excluding squamosal–maxilla contact.
b) Single pair of nasal bones.
c) Fenestra ovalis in the otic capsule on each side of the braincase.
d) Stapes with a canal for the stapedial artery but lacking one for the n. truncus hyomandibularis.
e) Bones of the carpus (and tarsus) have mesial and lateral articulations with other carpal (and tarsal) elements, in addition to proximal and distal ones.
f) Load-bearing digits composed of phalanges in hand and foot.
g) Wrist joint in the forelimb and knee joint in the hindlimb are hinge-joints; ankle joint is rotary.
h) All dermal bones of the pectoral girdle above the supracleithrum are absent.
i) Large scapular blade(?).
j) At least one sacral rib contacts the ilium.
k) Ischia contribute to a median pubo-ischiadic symphysis.

Sister-Group of the Tetrapoda

The ancestor of tetrapods has long been assumed to have been a bony fish belonging to the group Sarcopterygii. This group includes the Dipnoi (lungfishes), the Rhipidistia (extinct forms), and the Actinistia (coelacanths). The Sarcopterygii, including Tetrapoda, show several autapomorphies (Rosen et al. 1981; Panchen and Smithson 1987), such as the

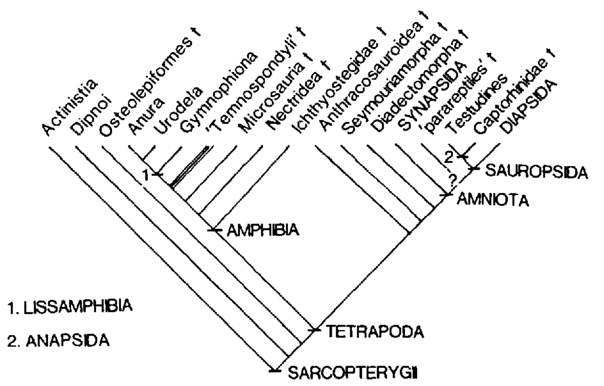

Fig. 1. Cladogram showing postulated relationships of the major groups of tetrapods, and their immediate outgroups, based on recent cladistic analyses of morphological data. Wholly extinct groups are indicated with a dagger (†). Multiple parallel lines indicate paraphyletic groups. See Fig. 2 for a more detailed cladogram of Diapsida and Fig. 3 for Synapsida.

essentially similar pectoral and pelvic fins with several major proximal bones and reduced distal rays and the support of these fins by single strengthened pectoral and pelvic elements, enamel on the teeth, a pulmonary vein, and others.

Within Sarcopterygii, the closest relations of the Tetrapoda have classically been assumed to lie within the extinct Rhipidistia, with coelacanths as the closest living outgroup. Rosen et al. (1981) argued that the sister-group of the Tetrapoda is the Dipnoi on the basis of 20 postulated synapomorphies. These were reviewed and generally rejected by Panchen and Smithson (1987) on the following grounds: 10 are regarded as nonhomologous in lungfishes and tetrapods, 4 are not known in key fossil taxa, 2 have an uncertain distribution within Dipnoi and Tetrapoda, 2 appear to apply to a larger inclusive group, and 1 is redundant, leaving only 1 of the 20 as possibly valid.

Panchen and Smithson (1987) present a strong case that the extinct Osteolepiformes (a rhipidistian group) are the sister-group of Tetrapoda on the basis of 10 postulated synapomorphies. The Dipnoi are seen as probably the closest living outgroup to the Tetrapoda, with the Actinistia as second-closest living outgroup (Fig. 1). These relationships are still under discussion, however, by morphologists and paleontologists. Janvier (1986), Schultze (1986), and Long (1989) arrange the fossil sarcopterygian groups rather differently in their cladograms. Further, Schultze (1986) and Long (1989) argue that the Actinistia, rather than the Dipnoi, are the closest living outgroup to the Tetrapoda, although this hypothesis is considered by many (e.g., Forey 1986; Panchen and Smithson 1987) to be poorly supported.

The Amphibia

The Amphibia (frogs, salamanders, limbless caecilians, and fossil temnospondyls, anthracosaurs, and lepospondyls) are clearly a paraphyletic group, if it is assumed to include the ancestor of the reptiles, birds, and mammals (the Amniota). It has long been recognized that certain extinct reptiliomorph amphibians, such as the seymouriamorphs and diadectomorphs closely approach the amniote condition. Hence, it was no surprise when cladistic analyses of living and extinct amphibians (Gaffney 1979; Gardiner 1982, 1983; Løvtrup 1985; Clack and Holmes 1988; Milner 1988; Panchen and Smithson 1988) divided them into a clade containing the living amphibian groups (the Lissamphibia), as well as some extinct forms, and a clade containing the reptiliomorph forms and the Amniota (Fig. 1).

The origins of the Lissamphibia have long been regarded as problematic. The apparently fundamental differences between frogs, salamanders, and caecilians, and the absence of intermediate fossil forms, led many systematists to postulate independent origins. However, it has become clear since the 1950s that the Lissamphibia do share several skeletal synapomorphies that are absent in extinct amphibians (Rage and Janvier 1982; Gardiner 1983; Milner 1988): the specialized teeth (bicuspid, pedicellate), the absence of certain cranial elements (supratemporal, jugal, tabular, postparietal), the paired occipital condyles, and the very short straight ribs, amongst others. Further, within the Lissamphibia, the frogs and salamanders appear to be sister-groups on the basis of up to nine synapomorphies that are absent in the caecilians (Gardiner 1982, 1983; Rage and Janvier 1982; Milner 1988).

The closest outgroups of the Lissamphibia fall within the paraphyletic group Temnospondyli. Carboniferous and Permian taxa such as *Doleserpeton, Amphibamus,* and *Trematops* are successively more distant outgroups (Milner 1988). These show reduction in certain cranial elements, pedicellate teeth (*Doleserpeton*), reduced ribs (*Amphibamus, Doleserpeton*), and other synapomorphies that suggest an approach to the lissamphibian condition.

Outgroups of the lissamphibian–temnospondyl clade include the extinct Microsauria and, tentatively, the Nectridea and the Ichthyostegidae. On the basis of the cladistic analysis by Panchen and Smithson (1988), the microsaurs and nectrideans do not approach the Lissamphibia as closely morphologically as has hitherto been assumed by some (Gardiner 1982, 1983; Løvtrup 1985). The Devonian *Ichthyostega* is generally regarded as one of the oldest-known and most primitive tetrapods and has often been placed as sister-group to all other tetrapods (Gaffney 1979; Gardiner 1982). The new placement within a more narrowly defined Amphibia (Fig. 1) is based on the postulated synapomorphies of a shallow platybasic skull and an immobile basal articulation (no potentially mobile joint between the cheek and the skull table) (Panchen and Smithson 1988), but this view is still highly controversial.

The reptiliomorph amphibians form progressively closer outgroups to the Amniota in the following sequence: Loxommatoidea, *Crassigyrinus*, Anthracosauroidea, Seymouriamorpha (or the latter two united as Anthracosauria), and Diadectomorpha, according to recent analyses (Panchen and Smithson 1988). The Diadectomorpha are regarded as the closest sister-group to the amniotes on the basis of the possession of a pterygoid flange, and (?) an astragalus and calcaneum (Panchen and Smithson 1988), as well as other possible synapomorphies (Gauthier et al. 1988a).

The new cladograms of amphibians (Fig. 1) bear little relation to standard classifications. The subclasses Labyrinthodontia and Lepospondyli are paraphyletic and polyphyletic, respectively; the ichthyostegids may not be the sister-group of all other tetrapods; and the anthracosaur/amniote line includes several primitive forms that had hitherto been excluded.

The Amniota

The reptiles, birds, and mammals together form the group Amniota. This group is generally assumed to be monophyletic (Gaffney 1979; Gardiner 1982; Benton 1985; Løvtrup 1985; Evans 1988; Panchen and Smithson 1988), although it has been suggested (Panchen 1972; Kemp 1980) that it might have had a diphyletic origin, based on the differences between the earliest synapsids and the other early reptiles. The amniotes share many hard-part synapomorphies, which exclude other tetrapods (Gauthier et al. 1988a,b), in addition to the diagnostic cleidoic egg and its extraembryonic membranes:

a) Intertemporal bone is absent, so that the postorbital contacts the parietal and (usually) the supratemporal.
b) Squamosal participates in the margin of the posttemporal fenestra.
c) Large exoccipitals meet medially above the basioccipital and below the foramen magnum.
d) Occipital condyle is hemispherical and well ossified in adults.
e) Distinct caniniform maxillary tooth.
f) Axis slopes dorsally.
g) Cleithrum does not cap the scapula.
h) Three scapulocoracoid ossifications (a scapula plus two coracoid bones).
i) Ossified dorsal scales are absent.
j) Gastralia (abdominal ribs) are closely appressed, often with a small overlapping V-shaped midline structure.

Within the Amniota, relationships are more problematic (Fig. 1). The three major taxa are Synapsida (including mammals), Testudines (turtles), and Diapsida (lizards, snakes, crocodilians, dinosaurs, birds), although the monophyly of the Diapsida has been denied by some (e.g., Romer 1966; Gardiner 1982; Løvtrup 1985); see below. There are three possible groupings of these three major taxa, of which two have gained some recent support: sister-group relationships of the Synapsida and Diapsida, as the Eureptilia, with Testudines as the outgroup (Gaffney 1980), and sister-group relationship of the Testudines and Diapsida, as the Sauropsida, with Synapsida as the outgroup (Gaffney and Meylan 1988; Gauthier et al. 1988a,b; Kemp 1988c).

Gaffney (1980) argued that the Synapsida and Diapsida at some stage in ontogeny share two synapomorphies: a lower temporal fenestra and a Jacobson's organ in a ventromedial pocket. However, these are apparently exceeded by at least seven postulated synapomorphies of Testudines + Diapsida (Sauropsida) (Heaton and Reisz 1986; Gauthier et al. 1988a,b):

a) Tabular is small or absent.
b) Supratemporal is small or absent.
c) Supraoccipital has an anterior crista.
d) Suborbital fenestra or foramen in the palate.
e) Single coronoid.
f) Atlas centrum and axis intercentrum are fused.
g) Medial centrale of the ankle is absent.

The Haemothermia

Some authors (Gardiner 1982; Løvtrup 1985) have argued recently that the Aves are the sister-group of the Mammalia, forming a larger clade, termed the Haemothermia. If this view is correct, then the Archosauria, the Diapsida, and possibly also the Synapsida are not monophyletic, on the basis of 28 postulated mammal–bird synapomorphies. These views have been strongly criticized (Benton 1985; Gauthier 1986; Benton and Clark 1988; Gauthier et al. 1988b; Kemp 1988c), and the morphologic support for such a hypothesis turns out to be weak. Of the 28 characters, Kemp (1988c) argued that 11 are present also in crocodilians, or some other amniotes, seven seem to be nonhomologous in birds and mammals, and two cannot be compared with crocodilians.

However, the morphologic synapomorphies apparently in favor of a mammal–bird clade, and a mammal–bird–crocodilian clade, still seem rather startling. In a careful reanalysis of the controversial Gardiner (1982) and Løvtrup (1985) data, Gauthier et al. (1988b) found clear support for an arrangement of modern amniote taxa as follows: (lepidosaurs(turtles(mammals(crocodilians(birds))))).

In other words, by ignoring all fossil data scrupulously and using some 109 morphologic characters of the five major modern amniote clades, they found a pairing of crocodilians and birds (i.e., the Archosauria), but a close alliance of these with the mammals, and a split of the Diapsida. The addition of data on 207 skeletal characters from 29 diverse groups of well-preserved fossil amniotes restored a more traditional cladogram: (mammals(turtles(lepidosaurs(crocodilians(birds))))), with the integrity of the Diapsida reaffirmed and the mammals clearly distanced from extant reptiles and birds.

Why should the fossil data be used? First, the fossils fill major morphologic gaps. A modern mammal and a modern bird are very different from each other and very hard to compare in detail. Extensive transformation series of fossil taxa exist that lead back from modern mammals, through primitive forms and mammal-like reptiles, to the oldest reptiles, whereas similar series of fossil forms lead back from *Archaeopteryx* through various theropod dinosaurs and early more generalized archosaurs and diapsids.

Second, the fossil taxa often allow uncertain polarities to be determined. The closest outgroups of modern amniotes are the Lissamphibia and the Dipnoi, and it is hard to compare specific characters with them in many cases, or to be sure that they show the primitive state: frogs and lungfishes are themselves highly derived organisms. It is much easier to compare modern birds with *Archaeopteryx* and the dinosaurs, or modern mammals with extinct relatives, than with lizards, snakes, frogs, or lungfishes!

Third, many modern groups are so derived that it is impossible to score many of their morphologic characters. For example, Gauthier et al. (1988b) found that modern turtles were so modified in comparison with other tetrapods that 19% of the data set of characters could not be scored: how can one determine the tooth shapes, distributions, implantation patterns, and orientations when modern turtles lack teeth? The inclusion of fossil turtles and close relatives in the analysis allowed these characters to be scored for Testudines as a whole, as the first turtles still had teeth.

Note here that the temporal information available from fossils is not being used here. The idea that the order of the known fossils in the rocks equals the order of the evolution of characters and the order of branching points in a phylogeny is not adhered to because of possible missing fossils. The importance of fossil taxa in reconstructing tetrapod phylogeny is that they show unique character combinations not seen in any living form. They fill gaps in morphological character space and allow polarities to be better determined and missing character states to be scored.

A more important question is, why do morphological data on living forms and indeed some molecular data (see below) point clearly to a very different tree from that based on all living and fossil taxa? Why do modern mammals and birds seem to converge? The morphological characters they share (Gauthier et al. 1988b) concern a broad range of parts of the body:

a) Endothermy.
b) Incubation of eggs.
c) Smooth erector muscles at the base of hairs or feathers.
d) Hairs or feathers are induced by special groups of cells.
e) Single aortic trunk.
f) Thick compact myocardium and increase in the number of coronary arteries.
g) Auriculoventricular node.
h) Ependymal cells in early stages of neural development.
i) Adventitious cartilage.
j) Vascularized islets of the pancreas.
k) Compact glandular pineal organ.
l) Macula densa in the kidney.
m) Loop of Henle in the kidney.
n) Scroll-like turbinals in the nasal cavity.
o) Calcite otoliths.
p) Three meninges of the brain.
q) Enlarged elaborated cerebellum.
r) Completely co-ossified atlas.
s) Inturned head of the femur.
t) Supra-acetabular buttress on the ilium.

Fossil, and other, data cast doubt on many of these as synapomorphies (i.e., homologies). Gauthier et al. (1988b) regard 6 of the 20 characters as unlikely to be homologies for anatomical, physiological, or embryological reasons (a, e, k–n), whereas 1 (k) cannot be determined in close outgroups, and hence its polarity is hard to determine, and 3 others (r–t) are contradicted by fossil evidence. Nevertheless, the morphological evidence for Haemothermia seems hard to dispute other than by fossil data and the parsimony criterion: the sheer weight of numbers of well-preserved fossil taxa that do not fit in with the idea of a phylogenetic split of birds and mammals after the division of other amniote groups, and the sheer weight of contradictory skeletal synapomorphies of these fossil taxa. Gauthier et al. (1988b) note that as many as 64% of their hard-part synapomorphies are in fact incongruent with the cladogram based on all taxa, fossil and extant, and that this level of homoplasy (convergence, parallelism) may be general.

Many of the characters of Haemothermia are related to the endothermy and high activity levels shared by birds and mammals (a–g, n, p, q, s, t), and this may be a significant adaptive reason for convergent evolution of a broad range of characters not seen in the ectothermic fishes, amphibians, and reptiles.

The Parareptiles and the Anapsida

Certain primitive amniotes, the extinct pareiasaurs, millerettids, procolophonians, mesosaurids, and captorhinids, which were often classed as the Cotylosauria have long been hard to place phylogenetically (Romer 1966; Heaton and Reisz 1986), as so few potential synapomorphies have been discovered uniting any pair of taxa, and those that have been found tend to produce contradictory groupings (Carroll 1982). However, a consensus is beginning to emerge.

The pareiasaurs, millerettids, procolophonians, and mesosaurids have been tentatively grouped by Gauthier et al. (1988a) in a clade informally termed the parareptiles on the basis of the shared loss of the maxillary caniniform tooth and the loss of the supraglenoid foramen in the scapulocoracoid. These authors suggest, however, that the parareptile clade may not withstand testing by further morphological character analysis. The parareptiles, if valid, appear to be the sister-group of the Sauropsida (Fig. 1).

The Captorhinidae have been rather more confidently placed within the Sauropsida as sister-group to the Testudines (Gaffney 1980; Heaton and Reisz 1986; Gaffney and Meylan 1988), and this clade has been termed the Anapsida (Gauthier et al. 1988a). Autapomorphies of the Anapsida include:

a) Medial process on the jugal.
b) Ectopterygoid absent.
c) Tabular absent (paralleled in some other groups).
d) Foramen orbito-nasale in the snout region.

The living anapsids, the Testudines, are readily characterized by numerous autapomorphies, and no one has ever doubted their monophyly (Gaffney and Meylan 1988). Obvious autapomorphies include the bony carapace and plastron, the strengthened skull, and the absence of teeth, among many others.

The Diapsida

The diapsids (lizards, snakes, crocodilians, birds, and extinct dinosaurs, pterosaurs, and others) form a major amniote clade. They share four skeletal synapomorphies (Evans 1984, 1988; Benton 1985; Gauthier et al. 1988a):

a) Two temporal fenestrae (hence diapsid).
b) Suborbital fenestra in the palate is well developed.
c) Cervical vertebrae are longer than mid-dorsals.
d) Ridge and groove tibio-astragalar joint.

A major clade within the diapsids that includes all extant forms is known as the Neodiapsida. There are several early diapsid groups, such as the Araeoscelidia, which form a series of outgroups to the neodiapsids. The Neodiapsida is divided into two major groups (Fig. 2), the Archosauromorpha and the Lepidosauromorpha, each associated with several synapomorphies of the skull and skeleton.

The Archosauromorpha include the Archosauria, plus the extinct rhynchosaurs, thalattosaurs, and prolacertiforms as major outgroups. These forms all share a complex concave–convex ankle joint, as well as other seemingly clearcut features, so that the former association of rhynchosaurs and prolacertiforms with the lizards and snakes seems to be unfounded.

The archosaurs have long been recognized as a clade. They all share such hard-part synapomorphies as (Benton 1985, 1989b; Gauthier 1986; Benton and Clark 1988; Evans 1988):

a) Antorbital fenestra.
b) Postfrontal is reduced.
c) Postparietals are fused or absent.
d) Posterior border of the lower temporal fenestra is bowed.
e) Laterosphenoid ossification in the braincase.
f) Teeth are laterally compressed.
g) Intercentra are absent in the trunk vertebrae.
h) Ectepicondylar foramen in the humerus is absent.
i) Fourth trochanter on the femur.

There were a number of extinct archosaur lineages (the basal thecodontians, the dinosaurs, the pterosaurs), which form a major clade (Fig. 2). Their primary division is into a crocodilian line (Crocodylotarsi) and a bird line (Ornithosuchia). Some primitive archosaurs, such as the proterosuchids, form outgroups to these. This split of the thecodontians into two main advanced lines is very different from traditional views that favored either a complex unresolved bushlike phylogenetic tree of Triassic archosaurs (e.g., Romer 1966) or a very different tree

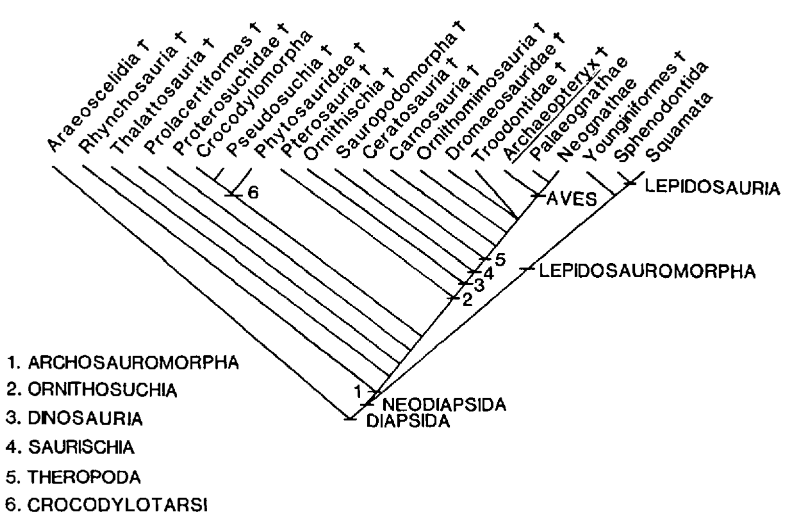

Fig. 2. Cladogram showing postulated relationships of the major groups of Diapsida.

in which dinosaurs had a polyphyletic ancestry and pterosaurs and birds were distanced from them (e.g., Bonaparte 1982; Chatterjee 1982).

The Crocodylotarsi (Fig. 2) include the aquatic phytosaurs and the terrestrial pseudosuchians, both extinct, as well as the crocodilians themselves; the latter have had a long and diverse history and a series of radiations not represented in the few living forms. The crocodylotarsans share a crocodile-normal ankle (peg on astragalus and socket on calcaneum), as well as other synapomorphies.

The Ornithosuchia (Fig. 2) have a variety of autapomorphies, such as the upright posture, and all of the anatomical changes that were entailed in bringing the limbs directly beneath the body. A basal outgroup is characterized by a crocodile-reversed ankle (peg on calcaneum and socket on astragalus), whereas most ornithosuchians have an advanced mesotarsal ankle (no pegs or sockets and no rotation between astragalus and calcaneum). This latter group includes the pterosaurs and the dinosaurs, regarded by certain taxonomists (Gauthier 1986; Benton and Clark 1988; Benton 1990) as sister-groups largely on the basis of characters of the hindlimb. The dinosaurs are probably a monophyletic group, despite traditional views to the contrary, and the three classical subgroups appear to be true clades: they are the Ornithischia, Sauropodomorpha, and Theropoda, the latter two forming a monophyletic Saurischia. The theropods, carnivorous dinosaurs that include the moderately sized ceratosaurs, the larger carnosaurs, and the ostrich-like ornithomimosaurs, appear to include the birds as well. *Archaeopteryx,* the earliest bird, has the skeleton of a small advanced theropod, such as a dromaeosaurid or a troodontid, with the addition of feathers and elongated forelimbs.

The theropod placement of Aves is still highly controversial (e.g., Hecht et al. 1985) but apparently better supported by synapomorphies at present than the alternative theories of a sister-group relationship with certain crocodilomorphs or with unnamed basal archosaurs.

The Aves (birds) show numerous autapomorphies (Cracraft 1986, 1988; Gauthier 1986):

a) Feathers.
b) Robust furcula (wishbone).
c) Calcaneum and astragalus are completely fused in the adult.
d) Distal tarsals are partially fused to the metatarsals.
e) Metatarsals are fused proximally.
f) Pubis is moderately retroverted.
g) Scapulocoracoid fusion is absent.
h) Postorbital bone is reduced or absent.
i) Quadratojugal–squamosal articulation is lost.
j) Joint between the squamosal and the occipital complex is fused.
k) Fewer than 25 caudal vertebrae.
l) Forelimbs are rotated, which allows them to fold against the body.

Archaeopteryx is the basal avian taxon, followed by some other extinct forms as outgroups to the major clades. Living birds fall into two groups (Fig. 2), the Palaeognathae (flightless ratites and tinamous) and the Neognathae (all other birds). These two modern groups share the loss of teeth and various other synapomorphies with each other, and each clade appears to be well supplied with a variety of anatomical autapomorphies (Cracraft 1988). Contrary views have been expressed that the Palaeognathae at least is a nonmonophyletic group, but these arguments are currently not convincing.

The lepidosauromorph branch (Fig. 2) of the Neodiapsida includes the extinct younginiforms as basal outgroup, together with a few other less certainly placed taxa. The majority of lepidosauro-

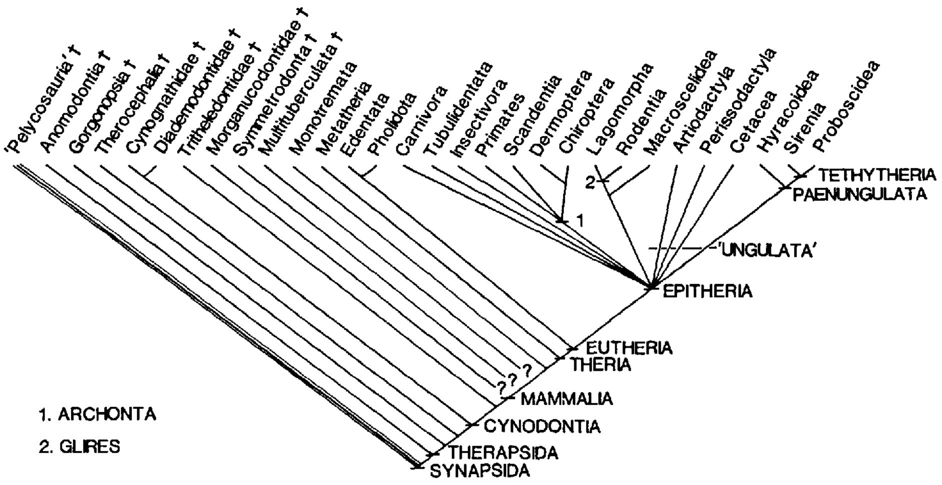

Fig. 3. Cladogram showing postulated relationships of the major groups of Synapsida. The sequence of basal mammalian groups is based on Kemp (1988b) rather than Rowe (1988).

morphs, however, are placed in the Lepidosauria, a major clade that has a number of autapomorphies (Evans 1984, 1988; Gauthier et al. 1988c):

a) Lacrimal is restricted to the orbital margin.
b) Squamosal extends well over the lower temporal fenestra.
c) Complete abducens canal and well-developed dorsum sellae.
d) Slender stapes, imperforate in adults.
e) Teeth are attached superficially to the jaws (pleurocoelous).
f) Parasphenoid teeth are absent(?).
g) Accessory facets (zygosphene/zygantrum) on the neural arches(?).
h) Caudal autotomy.
i) Ossified epiphyses with discrete centers(?).
j) Paired sternal plates fuse in the embryo.
k) First and fifth metacarpals are thicker than the second and fourth.
l) Third metacarpal is longer than the fourth.
m) Dorsal edge of the ilium is steeply inclined.
n) Ilium has a strong pubic flange.
o) Anteromedial portion of the pubis is turned out dorsally.
p) Pelvic elements fuse in adults.
q) Astragalus and calcaneum fuse in the juvenile.
r) Lateral pes centrale is fused to the astragalus.
s) First distal tarsal is absent, and first metatarsal meets the astragalocalcaneum.
t) Fifth distal tarsal is absent or fused.
u) Fifth metatarsal is hooked in two planes.

The living lepidosaurs include lizards, snakes, amphisbaenids, and the tuatara, *Sphenodon.* This last animal has long been regarded as the most primitive lepidosaur, a well-known living fossil, and indeed the Sphenodontida are sister-group to the other two. Because the snakes arose from within the lizard clade, the Sauria (Lacertilia) must be regarded as paraphyletic. Several large-scale cladistic analyses of lizards and snakes (together, the Squamata) are now available (Estes et al. 1988; Gauthier et al. 1988c; Rieppel 1988a,b).

The Synapsida

The synapsids, the extinct mammal-like reptiles and the mammals, are the second major amniote clade. They share a number of synapomorphies in comparison with other amniotes (Kemp 1982, 1988a; Hopson and Barghusen 1986; Reisz 1986; Gauthier et al. 1988a):

a) Postorbital is narrowly separated from the posterior end of the skull.
b) Postparietals are fused.
c) Lower temporal fenestra only.
d) Occiput slopes anterodorsally.
e) Septomaxilla has a broad base and a dorsal process.
f) Medial process of the jugal is sutured to the pterygoid.

The diverse mammal-like reptile groups form a long series of outgroups to the Mammalia, and a few of the major taxa are indicated (Fig. 3). The earliest synapsids are included in the paraphyletic group Pelycosauria, which consists of outgroups to the majority of synapsids, the Therapsida. The therapsids share a large number of synapomorphies (Kemp 1982, 1988a; Hopson and Barghusen 1986), many of which are mammal-like, such as the forward movement of the jaw joint, the enlargement of the reflected lamina on the angular, the incorporation of the squamosal into the structure of the external ear, and the enlargement of the canine teeth. The anomodonts, gorgonopsians, and therocephalians, three important outgroups to the advanced therapsids, show the acquisition of further mammal-like synapomorphies.

The advanced therapsids, the cynodonts, gave rise to several lineages that are regarded as outgroups to the Mammalia (Kemp 1982, 1983, 1988a; Hopson and Barghusen 1986). Only three are shown here (Fig. 3), the carnivorous Cynognathidae, the herbivorous Diademodontidae, and the insectivorous Tritheledontidae (Ictidosauria). The synapomorphies associated with branching points between the basal cynodonts and the mammals include several that track the loss of the postdentary bones in the lower jaw and the incorporation of one (articular) into the middle ear, the shift of the jaw joint from a quadrate–articular joint to a squamosal–dentary joint, further differentiation of the teeth, the combination of the orbit and lower temporal fenestra into a single structure with a zygomatic arch beneath, and the braincase bones expanded to form parts of the dorsal and lateral skull roof, amongst others. The tritheledonts are generally accepted as a close outgroup of the mammals, but there is still much controversy over the relationships of the other higher cynodonts (Kemp 1983, 1988a; Hopson and Barghusen 1986).

The Mammalia are generally defined at the level in the cladogram between Tritheledontidae and Morganucodontidae, although there has been discussion over where the line should be drawn (see below). This position allows the Mammalia to be recognized by the following synapomorphies (Kemp 1983, 1988b), although some depend on resolution of the relationships of certain higher cynodonts:

a) Squamosal glenoid–dentary condyle as the sole jaw joint.
b) Differentiation of the cheek teeth into premolars (replaced once) and molars (not replaced).
c) Double-rooted molars that are aligned longitudinally.
d) Molars have well-developed wear facets.
e) Quadrate has an elongate stapedial process (crus longus of the incus).
f) Anterior lamina forms the side wall to the cavum epiptericum.
g) Floor to the cavum epiptericum lies below the primary exit of the seventh cranial nerve.

These hard-part characters may all be determined in well-preserved fossil specimens. Other, perhaps better-known, mammalian synapomorphies such as hair, milk, and mammary glands, and extensive parental care may have appeared at this point in the cladogram, but they can only be said with certainty to pertain to the most recent common ancestor of living mammals, the node corresponding to Monotremata + Theria (Fig. 3). Indeed, Rowe (1988) names taxa above this node as Mammalia, and the extinct outgroups traditionally called mammals are placed in the broader clade Mammaliaformes.

The monophyly of the Mammalia has been disputed. However, arguments that there are two lineages—prototheres (i.e., monotremes and most Mesozoic mammals) and therians (marsupials and placentals)—which supposedly arose from separate noncynodont and cynodont ancestors, respectively (e.g., Kermack and Kermack 1984), are hard to support in view of the strength of the arguments for monophyly of the Mammalia, and for close alliance of the Monotremata with the Theria (Kemp 1983, 1988b; Hopson and Barghusen 1986; Rowe 1988).

The Mesozoic mammals, groups such as the morganucodontids, symmetrodonts, multituberculates, and many others (Fig. 3), have been hard to classify phylogenetically (McKenna 1975; Kemp 1982, 1988b; Rowe 1988). They seem to form outgroups to the living groups of mammals, with the Multituberculata as tentatively very close in view of their possession of three ear ossicles. Kemp (1983, 1988b) and others place the multituberculates and other Mesozoic mammals largely as outgroups to the Monotremata + Theria, whereas Rowe (1988) finds that the multituberculates and symmetrodonts are closer outgroups to the Theria than is the Monotremata. However, synapomorphies are hard to determine from often incomplete material, and much further work will be needed to disentangle basal mammalian relationships.

Among living mammals, the monotremes (platypus, echidna) have long been regarded as the most primitive (Fig. 3) because of their retention of the egg-laying habit, the single cloaca, and other features. However, it has become apparent that they are probably the sister-group of the Theria (marsupials + placentals), and not a distant protothere line—an exhaustive review of their anatomy (Kemp 1983; Rowe 1988) has shown so many detailed parallelisms in the braincase, ear, and elsewhere, that these latter must be regarded as synapomorphies.

The marsupials, all of which have the primitive pouch, a pseudovaginal canal, replacement of only the last premolar amongst the cheek teeth, dental enamel with distinct tubercles, and other features (Novacek 1982; Novacek and Wyss 1986; Novacek et al. 1988), share a variety of synapomorphies with the placentals (McKenna 1975; Kemp 1983; Rowe 1988), and the sister-group relationship of these two taxa has rarely been questioned:

a) Anterior lamina is fused to the ventral ramus of the alisphenoid, and the cranial process of the squamosal is expanded.
b) Tympanic membrane is vertical.

c) Tribosphenic molar teeth, with a protocone and a correspondingly enlarged talonid basin.
d) Interclavicle is absent.
e) Procoracoid is absent.
f) Eggshell is absent.

The placental mammals (Eutheria) have also generally been accepted as a clade on the basis of a large number of largely soft-part synapomorphies (McKenna 1975; Novacek et al. 1988):

a) Modified trophoblast and inner cell mass.
b) Chorioallantoic placenta.
c) Prolonged intrauterine gestation.
d) Shell membrane is absent.
e) Seminal vesicle.
f) Mullerian ducts are fused into a median vagina.
g) Ureters pass lateral to derivatives of the Mullerian ducts.
h) Corpus callosum connects cerebral hemispheres.
i) Retinal cones of the eye are simple and lack oil droplets.
j) Optic foramen is distinctly separated from the sphenorbital fissure.
k) Upper molars have narrow stylar shelves.
l) Epipubic bones and pouch are absent.

There are serious problems in elucidating the phylogeny of the Eutheria. It was suggested earlier this century that the Eutheria might split into four or five major clades (Gregory 1910; Simpson 1945)—one for primates, tree shrews, bats, and insectivores; one for rodents and lagomorphs; one for artiodactyls, whales, and carnivores; one for perissodactyls, hyraxes, sirenians, and elephants; and one for edentates and pangolins. This later gave way to the view that the placentals form a polytomous bush from which no precise branching points can be extracted (e.g., Romer 1966; Simpson 1978; Gingerich 1987).

Recent cladistic analyses of placental morphology (McKenna 1975; Novacek 1982; Novacek and Wyss 1986; Shoshani 1986; Novacek et al. 1988; Prothero et al. 1988) have established a few clades within Eutheria, but there is controversy over some and confusion over others. Most authors accept that the basal outgroup within Eutheria is the Edentata (sloths, anteaters) + Pholidota (pangolins). Most also accept the following groupings (Fig. 3):

a) Rodentia + Lagomorpha (rabbits), the Glires, + Macroscelidea (elephant shrews);
b) Chiroptera (bats) + Dermoptera (flying lemurs) + Scandentia (tree shrews) + Primates, the Archonta; and
c) Proboscidea (elephants) + Sirenia (sea cows) + Hyracoidea (hyraxes), the Paenungulata.

The last clade is disputed (Prothero et al. 1988). The Carnivora, Tubulidentata (aardvarks), Insectivora, Artiodactyla (pigs, cattle, deer, etc.), Perissodactyla (horses, tapirs, rhinos), and Cetacea (whales) have proved hard to place. One analysis (Shoshani 1986) has linked the Carnivora to the archontan clade, the Cetacea to the paenungulate clade, and placed the artiodactyls, perissodactyls, and tubulidentates in another. The placement of the last three ungulate groups is particularly contentious. Some analyses (Novacek 1982; Shoshani 1986; Novacek et al. 1988) find no support for an ungulate clade, whereas others (McKenna 1975; Prothero et al. 1988) argue that it is acceptable as a group including artiodactyls, perissodactyls, tubulidentates, cetaceans, and paenungulates. Although the placentals are probably the best-known animals, it has proved hard to resolve their phylogeny from morphological data.

Molecular Results on Tetrapod Phylogeny

It is impossible to compare the large numbers of recently proposed phylogenetic trees for tetrapods, and for mammals and birds in particular, based upon molecular data. Sequences from a variety of tetrapods are now available for the following polypeptides: α- and β-parvalbumin, α- and β-hemoglobin, myoglobin, lens α-crystallin A, fibrinopeptides A and C, cytochrome *c*, and ribonuclease. These have given rise to a number of maximum-parsimony trees (Goodman et al. 1982, 1985, 1987; de Jong et al. 1985; Miyamoto and Goodman 1986; Bishop and Friday 1987, 1988).

The wider relationships of major tetrapod groups are still tentative because of the paucity of nonmammalian sequences: a startling array of pairings of mammals, birds, crocodilians, lizards, snakes, turtles, and amphibians has been found:

α-parvalbumin:
(frog(mammal))
β-parvalbumin:
(snake(frog(turtle)))
α-hemoglobin:
(frog(snake(crocodilian(bird(mammal))))) or
(frog(mammal(snake(crocodilian(bird))))) or
(frog(snake(mammal(bird(crocodilian)))))
β-hemoglobin:
(frog(crocodilian(bird(mammal))))
Myoglobin:
((((turtle)lizard)crocodilian)(bird(mammal))) or
((((turtle)crocodilian)lizard)(bird(mammal)))
Lens α-crystallin A:
(mammal(crocodilian(lizard(bird)))) or
(frog(mammal(lizard(crocodilian(bird)))))
Cytochrome *c*:
(mammal(turtle(bird(lizard(snake)))))
Standard morphologic:
(frog(mammal(turtle((lizard(snake))(crocodilian(bird))))))

The phylogenetic trees derived from myoglobin and β-hemoglobin show a sister-group relationship between birds and mammals, in apparent support of the morphologic evidence for a clade Haemothermia (see above). In addition, where relevant sequences are available, turtles are often associated with squamates (lizards and snakes), forming a clade separate from crocodilians or birds. Some authors have accepted these results at face value, whereas others have urged caution until more nonmammalian sequences become available. Most other polypeptides, however, give phylogenetic trees that are closer to the standard morphologic pattern. 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 is often very small (Benton 1985; Bishop and Friday 1988; Kemp 1988c). 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).

Polypeptide sequences are available now for representatives of all but the smallest of mammalian orders, and these have yielded a large number of phylogenetic trees. Recent analyses generally find that marsupials are the sister-group of a monophyletic Eutheria, and monotremes are usually placed as the sister-group of those two. Among placental mammals, most analyses (Goodman et al. 1985, 1987; Miyamoto and Goodman 1986) pick out five major clades in the following sequence:

a) Edentata as the basal outgroup;
b) Paenungulata and Tubulidentata;
c) Artiodactyla, Perissodactyla, and Cetacea;
d) Glires and Primates; and
e) Chiroptera, Scandentia, Insectivora, Carnivora, and Pholidota.

Earlier studies by the Goodman team, with fewer sequences available, differed in the placement of Insectivora, Carnivora, Rodentia, and Pholidota, and in one, the Artiodactyla was split into two independent clades.

Phylogenies compiled recently from single proteins show some major differences (Shoshani 1986; Novacek and Wyss 1986; McKenna 1987; Wyss et al. 1987; Novacek et al. 1988). For example, some myoglobin data link lagomorphs, rodents, and primates (McKenna 1987). Another analysis of myoglobin data split the lagomorphs into two separate clades. More protein data may help resolve some of these fundamental problems, as there are still major gaps in available nucleotide sequence libraries for nonmammalian tetrapods. However, the tree-making algorithms and their evolutionary assumptions, as well as definitions of molecular synapomorphies, may also have to be further examined (Bishop and Friday 1987, 1988; McKenna 1987; Wyss et al. 1987).

Dates of Divergence of Major Tetrapod Groups

Calculations of dates and absolute rates of divergence in phylogenetic trees depend on one or more fixed points—dates of branching points that can be fixed with some confidence from the fossil record. Such data are available to molecular phylogenists from many sources (Romero-Herrera et al. 1978; Novacek 1982; Goodman et al. 1987; McKenna 1987; Wyss et al. 1987), but the new cladograms of tetrapods, as well as new fossil discoveries and reinterpretations of old ones, have fundamentally altered certain of the fixed points. Revised data are presented here, on the basis of the latest systematic and paleontologic work (Table 1 and Fig. 4).

The data listed in Table 1 are tabulated for the 23 numbered branching points in Fig. 4. In the first column, the name of the clade that corresponds to each branching point is given. Then, primary data for the two evolutionary lines above the branching point are given. The two lines are designated left- and right-hand sides according to the layout of Fig. 4. For each line, three pieces of information are given: its name, the generic name of the oldest representative of that line, and its age, stratigraphically and in millions of years (Myr). These ages are used to give a minimum age of the branching point. As an example, the whole clade represented in Fig. 4, corresponding to branching point 1, is the Sarcopterygii. It is made up of two lines, the Actinistia to the left and an unnamed group (Dipnoi + Rhipidistia + Tetrapoda) to the right. The oldest actinistian is *Dictyonosteus* from the Givetian (GIV), dated about 377 Myr ago. The oldest representative of the dipnoan–rhipidistian–tetrapod line is *Porolepis* from the Siegenian (SIEG), dated about 398 Myr ago. The latter form is the older of the two, and hence provides an absolute minimum date of branching of 398 Myr. This is increased to 405 Myr to allow for another major branching event (no. 2), which also occurred before 398 Myr ago.

The major living tetrapod clades are indicated in Fig. 4, with particular emphasis on the eutherian mammals. The branching points (numbered 1–23) are based on the cladograms (Figs. 1–3). The minimum age of the branching point can be assessed with some confidence, assuming that the oldest fossil in the clade above truly belongs to that clade. It is not possible to assess the maximum age of the

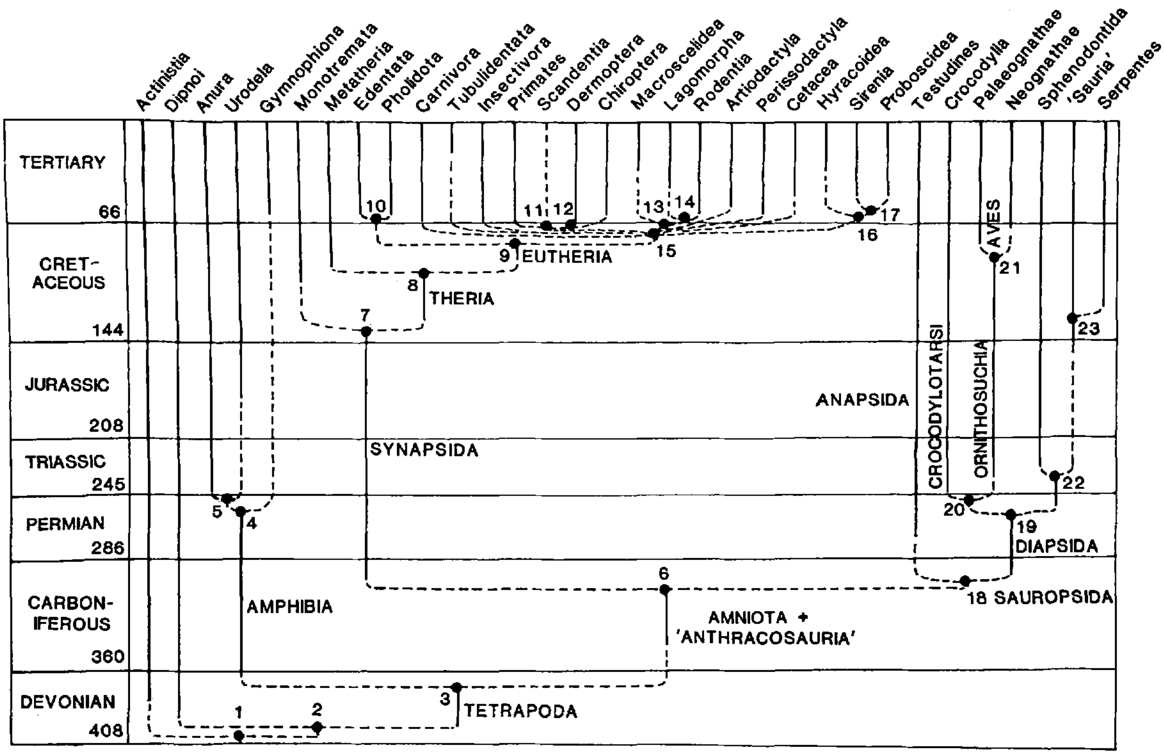

Fig. 4. Phylogenetic tree of the major groups of living tetrapods, based on branching points from the cladograms in Figs. 1–3. The timescale is based on current knowledge of the fossil record, with the dates of branching points based on data in Table 1.

Table 1. Estimation of dates of branching points of the major clades of extant tetrapods in millions of years (Myr) (time scale is Palmer 1983)

Branch point	Clade name	Left-hand lineage		
			Oldest taxon	Age (Myr)
1	Sarcopterygii	Actinistia	*Dictyonosteus*	GIV (377)
2	–	Dipnoi	*Dipnorhynchus*	SIEG (398)
3	Tetrapoda	Amphibia	*Ichthyostega*	FAM (363)
4	Lissamphibia	Batrachia	*Triadobatrachus*	SCY (242)
5	Batrachia	Anura	*Triadobatrachus*	SCY (242)
6	Amniota	Synapsida	*Archaeothyris*	MOS (300)
7	Mammalia sensu stricto	Monotremata	*Steropodon*	ALB (105)
8	Theria	Metatheria	*Pariadens*	CEN (94)
9	Eutheria	Edentata + Pholidota	*Ernanodon*, etc.	THA (59)
10	–	Edentata	*Ernanodon*, etc.	THA (59)
11	Archonta	Primates	*Purgatorius*	MAA (67)
12	Volitantia	Dermoptera	*Elpidophorus*	DAN (65)
13	Anagalida	Macroscelidea	*Metoldobotes*	RUP (33)
14	Glires	Lagomorpha	*Gobiolagus*, etc.	BRT (42)
15	Epitheria	16 orders	*Purgatorius*	MAA (67)
16	Paenungulata	Hyracoidea	unnamed forms	PRB (38)
17	Tethytheria	Sirenia	*Prorastomus*, etc.	LUT (48)
18	Sauropsida	Anapsida	*Protocaptorhinus*	SAK (272)
19	Neodiapsida	Archosauromorpha	*Protorosaurus*	KAZ (255)
20	Archosauria	Crocodylotarsi	*Stagonosuchus*, etc.	ANS (240)
21	Neornithes	Palaeognathae	*Gobipteryx*	CMP (79)
22	Lepidosauria	Sphenodontida	*Brachyrhinodon*, etc.	CRN (227)
23	–	Sauria	*Dorsetisaurus*, etc.	KIM (154)

The oldest taxon on each side (left and right) of the branching point (see Fig. 4) is given with the stratigraphic stage and the estimated age of the midpoint of that stage, unless more precise age data are available. Data are from various sources (Harland et al. 1967; Benton 1987, 1988, 1989; Carroll 1987, and references therein). The minimum age of the branching point is calculated as just older than the oldest taxon in the two clades above that point and rounded up by 1–4 Myr. All such dates are minima and subject to error, especially where not constrained by branching points close below (these are marked by ?). Abbreviations of stage names: ALB, Albian;

branching point precisely. The maximum dates can be constrained to some extent by the next minimum date of divergence below in the cladogram. However, just as minimum dates of divergence can be pushed down by new fossil discoveries, so too can their constraint on the branching points above.

All that is possible is to assume that the maximum age is not generally more than about 10% more than the minimum age. The main argument in favor of such a view relates to the absence of fossils—the greater the gap between minimum and maximum branching ages, the more missing fossils have to be assumed. Recent paleontologic experience has been that new finds of early representatives of major tetrapod clades do not shift the age of origin back much beyond the expected point. For example, the oldest-known monotremes were until recently only Middle Miocene in age (ca. 14 Myr ago), but the origin of monotremes had to be dated as at least Valanginian (Early Cretaceous; 135 Myr ago) because of the age of the oldest known fossils in the sister-group clade, the Theria. The recent find of an early monotreme in the Albian (105 Myr ago) of Australia (Archer et al. 1985) has extended their range by 90 Myr, but not beyond the expected date of branching. Likewise, the recent find of the oldest marsupial fossil in the Cenomanian (94 Myr ago) of North America (Cifelli and Eaton 1987) has added 15 Myr to their record, but has not pushed the minimum date of divergence of marsupials and placentals further back than had been predicted before.

An even more dramatic case concerns the gymnophionans (caecilian amphibians). Until 1970, no fossils of this group were known at all, but then a Paleocene, and later a Maastrichtian (Late Cretaceous), form were discovered, shifting the age back to 67 Myr ago. Even more recently, an Early Jurassic caecilian has been found, pushing the age back to 195 Myr ago, but not affecting the calculated date of the split between gymnophionans and other lissamphibians of 250(?) Myr ago.

Conclusions

The broad outlines of the phylogeny of the tetrapods are becoming clearer in some areas because of the

Table 1. Continued

	Right-hand lineage		Minimum age (Myr)
	Oldest taxon	Age (Myr)	
Dipnoi + Rhipidistia + Tetrapoda	*Porolepis*	SIEG (398)	405?
Rhipidistia + Tetrapoda	*Porolepis*	SIEG (398)	400?
Amniota + reptiliomorphs	*Eoherpeton*	VIS (342)	365?
Gymnophiona	Unnamed form	PLB (195)	250?
Caudata	*Albanerpeton*	BAJ (180)	245?
Sauropsida	*Hylonomus*	MOS (305)	310?
Theria	*Aegialodon*	VAL (135)	140?
Eutheria	*Gypsonictops*, etc.	CMP (79)	100
Epitheria	*Purgatorius*	MAA (67)	72
Pholidota	*?Amelotabes*	THA (59)	60
Volitantia + Scandentia	*Icaronycteris*	YPR (55)	68
Chiroptera	*Icaronycteris*	YPR (55)	67
Glires	*Franimys*, etc.	THA (59)	62
Rodentia	*Franimys*, etc.	THA (59)	60
16 orders	—		70
Tethytheria	Unnamed forms	YPR (55)	62
Proboscidea	Unnamed forms	YPR (55)	60
Diapsida	*Hylonomus*	MOS (305)	308?
Lepidosauromorpha	*Youngina*	TAT (249)	260?
Ornithosuchia	*Lagosuchus*	CRN (227)	245
Neognathae	Unnamed forms	MAA (70)	80?
Squamata	*Dorsetisaurus*, etc.	KIM (154)	230?
Serpentes	*Lapparentophis*	LCR (121)	125?

ANS, Anisian; BAJ, Bajocian; BRT, Bartonian; CEN, Cenomanian; CMP, Campanian; CRN, Carnian; DAN, Danian; FAM, Famennian; GIV, Givetian; KAS, Kasimovian; KAZ, Kazanian; KIM, Kimmeridgian; LCR, Lower Cretaceous; LUT, Lutetian; MAA, Maastrichtian; PLB, Pliensbachian; RUP, Rupelian; SAK, Sakmarian; SCY, Scythian; SIEG, Siegenian; TAT, Tatarian; THA, Thanetian; VAL, Valanginian; VIS, Visean; YPR, Ypresian application of rigorous new systematic methods. However, some key areas of disagreement still exist, and their implications could be great. If birds and mammals are sister-groups, as some suggest, then these two groups would have diverged as little as 225 Myr ago (Benton 1984b). If, on the other hand, the birds are part of a diapsid clade, and the mammals are part of a synapsid clade, then the date of divergence shifts back to 315 Myr ago or more (Table 1). Such basic factual differences as these can have major implications in our interpretations of rates of morphological and molecular evolution. For example, the new morphologically derived dates of divergence presented here (Fig. 4 and Table 1) appear to support Goodman et al.'s (1987) suggestion that sequence evolution was much faster in the early tetrapod lineage up to the amniote ancestral node (about 310 Myr ago) than in the amniote lines leading to the origins of modern mammals (about 140 Myr ago) and of modern birds (about 80 Myr ago). Further work by morphologists and molecular biologists will doubtless resolve many of these areas of confusion in the phylogeny of tetrapods. Some of the differences may, however, highlight problems with the analytical techniques and problems with our understanding of the relationship of phylogeny and evolutionary processes.

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