CHAPTER 25

Tetrapod phylogeny

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Introduction

Early sarcopterygians were aquatic, but from the latter part of the Carboniferous onward that group has been dominated by terrestrial forms commonly known as the tetrapods. Fig. 1 illustrates relationships among extant Tetrapoda [1–4]. As the cladograms in Figs. 2–20 demonstrate, however, extant groups represent only a small part of the taxonomic and morphologic diversity of Tetrapoda. We hope to convey some appreciation for the broad outlines of tetrapod evolution during its 300+ million year history from late Mississippian to Recent times. In doing so, we summarize trees derived from the distribution of over 972 characters among 83 terminal taxa of Tetrapoda. More than 90% of the terminal taxa we discuss are extinct, but all of the subterminal taxa are represented in the extant biota. This enables us to emphasize the origins of living tetrapod groups while giving due consideration to the diversity and antiquity of the clades of which they are a part.

Our discussion centers on the origins of the major groups of extant tetrapods (Fig. 1). Most biologists study living organisms and are familiar with such groups as frogs, mammals, turtles, crocodilians and birds. More inclusive groups of extant tetrapods, such as Lissamphibia, Amniota and Archosauria, may be less familiar, but they are sufficiently well-known to serve as convenient points of departure. By emphasizing extant taxa we do not mean to endorse the view of Hennig [5], who held that phylogenetic research proceeds first by recognizing groups of Recent species, and then by placing fossils on that cladogram. On the contrary, phylogenetic relationships are best inferred from a simultaneous consideration of all the evidence, regardless of the source [3].

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TETRAPODA
  AMNIOTA
    MAMMALIA
    REPTILIA
      CHELONIA
      SAURIA
        ARCHOSAURIA
          CROCODYLIA
          AVES
        LEPIDOSAURIA
          Sphenodon
          SQUAMATA
  LISSAMPHIBIA
    GYMNOPHIONA
    ANURA
    CAUDATA
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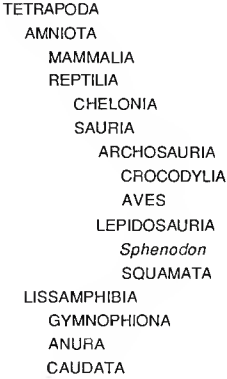
Fig. 1. An indented, unsequenced, phylogenetic taxonomy of Recent Tetrapoda.

Much of what we have to say here is based on materials and methods discussed at length elsewhere [1–4, 6–9]. Our taxonomic scheme differs from the traditional in several ways [2, 3]. For example, we eschew all formal categorical ranks and rely on tree topology to reflect the nested, hierarchical structure of phylogeny. Rank-related suffixes already attached to particular names are retained, but only to conserve the traditional spelling and thus facilitate data retrieval from the literature. We also restrict widely used names to genealogic entities stemming from an ancestor that produced extant sister taxa.

Tetrapod origins

Fig. 2 displays a series of outgroups to Tetrapoda, a name that we restrict to the group composed of the most recent common ancestor of extant lissamphibians and amniotes and all of its descendants [4]. Tetrapods have historically been considered to be those sarcopterygians with four limbs [10]. A morphological gap separates the 'fins' of *Eusthenopteron* from the 'limbs' of ichthyostegalians (i.e., *Ichthyostega, Acanthostega*). The most striking changes involve the distal portions of the paired appendages,


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┌──────────── Panderichthys
│ ┌────────── Ichthyostegalia
│ │  ┌─────── Crassigyrinus
│ │  │
└─┴──┴─────── TETRAPODA
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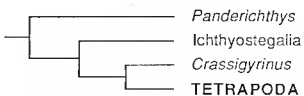
Fig. 2. Cladogram of tetrapod outgroup series. Here, as in the remaining figures, only those names in boldface have living representatives, the rest are composed entirely of extinct taxa. In the former category, upper case lettering denotes taxa whose ancestor produced extant sister groups, and upper and lower case lettering refers to taxa including extant groups plus extinct outgroups.

for example, *Ichthyostega* has toes and *Eusthenopteron* does not [10, 11]. That morphological gap has been used as a convenient marker separating tetrapods from other sarcopterygians. But this is not to say that ichthyostegalians have limbs like those of the ancestor of extant tetrapods. On the contrary, the limbs of ichthyostegalians and, to a lesser extent, *Crassigyrinus* [12], are plesiomorphic compared to those of Tetrapoda (s.s.). The ancestral tetrapod possessed a discrete humeral shaft, lost the primitive canal system in the humerus, had a fully developed shoulder girdle with a prominent scapular blade, and had differentiated proximal tarsals in the foot [4].

We apply Tetrapoda to an extant genealogic entity to make that name more informative and stable, because it then summarizes molecular, behavioral and other less readily fossilized characters, such as 'soft' anatomy, as well as the preservable 'hard' synapomorphies afforded by fossils. The 'soft' characters of Tetrapoda are, admittedly, of little use in assigning extinct taxa to that group. But it is nonetheless reasonable to assume that these characters were present in the ancestral tetrapod and absent in the ancestral choanate. In the case of widely used names we prefer to emphasize what we know – that extant tetrapods shared an ancestor not shared by extant dipnoans – rather than what we do not know – such as whether or not *Crassigyrinus* had differentiated tarsals.

We recognize two main groups within Tetrapoda (Fig. 3), Amphibia for extant lissamphibians and their extinct allies and Anthracosauria for extant amniotes and their extinct relatives [4]. The relationships of Nectridea, Aïstopoda and Microsauria to the extant groups are not clear (Fig. 3). Amphibia is restricted to Loxommatidae and its sister group, Temnospondyli (Fig. 3; and see below), by removing early anthracosaurs and the tetrapod outgroups *Crassigyrinus* and Ichthyostegalia.

Amniote origins

Fig. 4 summarizes the early diversification of Anthracosauria [4]. Many of the characters elucidating relationships among early anthracosaurs, such as modifications in the vertebral column, girdles and limbs, together with changes in the dentition and palate, reflect an increasing reliance on patterns of locomotion and prey manipulation suited more to terrestrial settings [4, 13]. Several characters less likely to be observed
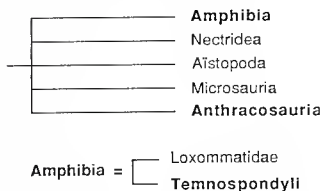
Fig. 3. Cladograms of major groups of Tetrapoda, and initial divergence within Amphibia.

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┌──────────── Anthracosauroideae
─┤   ┌──────── Seymouriamorpha
 └───┤  ┌───── Diadectomorpha
     └──┤
        └───── AMNIOTA
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Fig. 4. Cladogram depicting relationship of Amniota among Anthracosauria.

in the fossil record, such as a cleidoic egg and internal fertilization, are diagnostic of Amniota among extant Tetrapoda, although they may have originated earlier within Anthracosauria. Nevertheless, amniotes can be diagnosed among their extinct relatives by such characters as a caniniform maxillary tooth, appearance of two coracoid ossifications in the shoulder girdle, an astragalus in the ankle joint, and loss of fish-like bony scales from the dorsal surface of the body [4].

Early amniotes

Fig. 5 depicts relationships among the earliest amniotes. Two groups are readily recognized, Synapsida for mammals and their extinct allies, and Reptilia for turtles and saurians and their extinct relatives. Reptilia was initially coined for what are usually thought of as 'lower' tetrapods; it included amphibians as well as amniotes aside from mammals and birds. Amphibians and early anthracosaurs were subsequently removed, so that Reptilia referred to non-avian and non-mammalian amniotes only. The name was brought into the phylogenetic system by removing extinct relatives of mammals, known as 'therapsids' and 'pelycosaurs', from Reptilia, and including birds within it [1–4, 6, 8].

Synapsida is diagnosed by synapomorphies such as a lower temporal fenestra and sloping occiput, and extant Reptilia by phi keratins, uricotely and the dorsoventricular ridge of the telencephalon [3]. Both synapsids and reptiles are known from as early as the mid-Pennsylvanian [3]. The relationships of the later and more modified amniotes of the Permian, the pareiasaurs, millerettids, procolophonians and mesosaurs, are not clear. Several skeletal characters diagnose Reptilia [3], and at least some of these, such as loss of the medial pedal centrale and a small suborbital fenestra, have been reported in some of these Permian forms. This evidence suggests that they are more closely related to reptiles than to mammals [4, 14]. Thus, although it is reasonable to assume that the 'soft' characters mentioned above were absent in the ancestral

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┌──────────── Synapsida
─┤   ┌──────── Pareiasauria
 │   ├──────── Millerettidae
 └───┤
     ├──────── Procolophonia
  ┌──┤
  │  ├──────── Mesosauria
  └──┤
     └──────── REPTILIA
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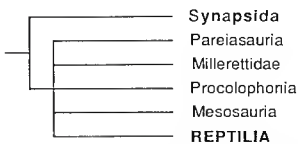
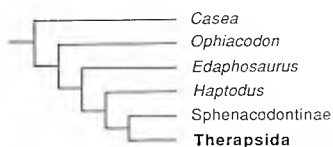Fig. 5. Cladogram depicting initial diversification of Amniota.

Fig. 6. Cladogram depicting selected early divergences within Synapsida.

amniote, but present in the ancestral reptile, we cannot be certain of the level at which they can be considered diagnostic.

Synapsid evolution

Fig. 6 displays relationships among early synapsids [3, 8], whose included taxa have been reviewed recently in considerable detail [15]. In traditional classifications early synapsids are united as paraphyletic 'pelycosaurs', a group considered to have gone extinct shortly after giving rise to paraphyletic 'therapsids', which in turn went extinct just after giving rise to mammals. The term Therapsida is brought into the phylogenetic system by including mammals within it. The same could be done for 'Pelycosauria' by including therapsids, in which case it would be synonymous with Synapsida, the name widely preferred for the taxon including 'pelycosaurs', 'therapsids' and mammals. Synapsid history was long held to be characterized by rampant convergence in the evolution of mammal-like locomotor, masticatory and acoustic systems. It is, however, revealing that few of the previous claims of convergence can be supported when synapsids are placed in a taxonomy based exclusively on common ancestry [3, 8, 16]. The history of synapsid classification illustrates how using overall similarity to infer phylogenetic relationships, and the paraphyletic groups that method so often specifies, invariably impede attempts to reconstruct the history of life.

The monophyly of Therapsida and its early phylogeny (Fig. 7) is one of the best-supported and thoroughly documented portions of amniote phylogeny [16]. At least 30 synapomorphies diagnose the skeleton of Therapsida, including such strikingly mammal-like modifications as an external acoustic meatus of the squamosal, an incised angular (ectotympanic), a long canine tooth, as well as the initial modifications of the postcranial skeleton that enable an erect posture and a narrow-tracked gait [3,
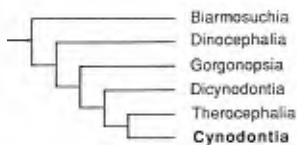

Fig. 7. Cladogram depicting early phylogeny of Therapsida.

8]. The postcranial modifications appear to have facilitated breathing while running, subsequently leading to an elevated basal metabolic rate and the evolution of endothermic homeothermy in later therapsids [17].

The Permo-Triassic record of therapsids in South Africa provides a particularly complete series of forms connecting earlier and later synapsids. That record is crucial to understanding how the highly derived extant synapsids, the mammals, relate to other amniotes [3]. Without that portion of the synapsid record, mammals appear to be the sister group of archosaurs [3] (see below). But when all the evidence is included in the analysis, and not just that fraction available in extant forms, mammals and other synapsids are the sister group to all other amniotes [3]. No single fossil was necessary to recovering the correct tree for Amniota. On the contrary, any one of a broad range of synapsid fossils from *Edaphosaurus* to *Exaeretodon* (Figs. 6–8) would be sufficient to enable recovery of the phylogeny derived from all the evidence [3].

Fig. 8 depicts the phylogeny of Cynodontia [3, 8]. One might not easily recognize the mammalian aspect of an early synapsid such as the fin-backed *Dimetrodon*, but even early Mesozoic cynodonts are sufficiently similar in general habitus to their extant relatives to be unmistakably related. So striking are the resemblances in the dentitions from which many late Triassic cynodonts are known that they were long considered the earliest mammals. A few of these Triassic forms, in particular the morganucodontids, are more completely known, and when all skeletal characters are evaluated, rather than the dentitions alone, then Morganucodontidae is the sister group to Mammalia. Thus, the dental characters used to assign some Triassic cynodonts to Mammalia appear plesiomorphic at this level of analysis, and the fossil evidence of Mammalia dates only as far back as the mid-Jurassic [3, 8, 9].

Early reptiles

Reptilia includes the most recent common ancestor of turtles and saurians and all of its descendants [2–4]. Two major groups are recognized within Reptilia, Anapsida and Diapsida (Fig. 9). The traditional 'Anapsida' was applied to amniotes with unfenestrated skulls, a plesiomorphic resemblance. The paraphyly of that grouping has been demonstrated elsewhere [4]. Suffice it to say that certain 'anapsids', such as pareiasaurs, procolophonians, millerettids and mesosaurs, diverged prior to the origin of
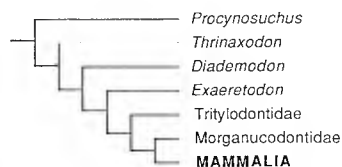

Fig. 8. Cladogram depicting phylogeny of Cynodontia.

Reptilia, whereas other 'anapsids', such as *Paleothyris*, are closer to diapsids than are captorhinids or turtles [4, 14].

Testudines and Captorhinidae are sister taxa (Fig. 9), and the name Anapsida has been restricted to them [2–4, 18]. Because of their overall primitiveness, the early Permian captorhinids play an important role in elucidating the position among amniotes of the highly modified extant turtles [3, 4].

Chelonians aside from *Proganochelys* have traditionally been divided into two groups, the pleurodires and cryptodires. These groups can be diagnosed by different positions for the jaw muscle trochlea [19], but only if one is willing to accept that neither system could have been ancestral to the other. A new taxon, the recently described *Kayentachelys* from the Lower Jurassic of North America [20], suggests otherwise. It was described as an early cryptodire based on its trochlear system, but it has other characters, such as palatal teeth, in which it is plesiomorphic with respect to all extant pleurodires and cryptodires [20, 21]. *Kayentachelys* is here considered to have diverged prior to the origin of extant Chelonia within Testudines (Fig. 10), and the 'cryptodire' trochlear system thus appears diagnostic for a more inclusive group containing all turtles aside from *Proganochelys* [21].

Paleothyris is one of the oldest known amniote fossils (Westphalian D, mid-Pennsylvanian). It was thought to represent an ancestral type from which all other amniotes can be derived [22]. As Fig. 9 indicates, however, *Paleothyris* is the sister group of Diapsida, not Amniota [4, 14]. *Paleothyris* is a romeriid reptile, a group that includes diapsids and other reptiles more closely related to diapsids than to turtles [4, 14]. Like other early romeriids, *Paleothyris*, araeoscelidians and early saurians tended to be lightly constructed and long-limbed, suggesting that their common ancestor was an agile carnivore. The phylogenetic position of *Paleothyris* indicates that cladogenic events marking the divergence of such amniotes as anapsids, procolophonians and synapsids had taken place even earlier in the Carboniferous. However, representatives of these taxa before mid-Pennsylvanian times are unknown; we have yet to find a truly archaic amniote.
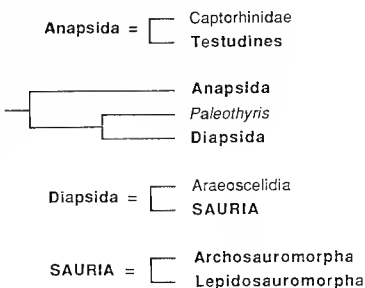

Fig. 9. Cladograms depicting early divergences within Reptilia, including the major groups of Anapsida, Diapsida and Sauria. Romeriida contains diapsids plus all other reptiles that are closer to them than to anapsids.

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┌──────────── Proganochelys
│   ┌──────── Kayentachelys
│   │
└───┤   ┌──── CHELONIA
    └───┤
        └────
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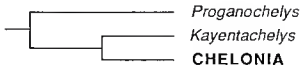
Fig. 10. Cladogram depicting early phylogeny of Testudines.

Early saurians

Diapsida includes the late Pennsylvanian to early Permian araeoscelidians, and the saurians of the late Permian to Recent (Fig. 9). Sauria includes two main groups, Lepidosauromorpha for extant lepidosaurs and their extinct relatives and Archosauromorpha for archosaurs and related extinct forms (Fig. 9). It is not yet clear if the relationships of such specialized diapsids as the glider *Coelurosauravus*, or the aquatic plesiosaurs, lie within or outside of Sauria [2].

With a few exceptions, such as some mosasaurs and snakes, lepidosaurs are small and insectivorous [23, 24]. Their small size and lightly constructed skeletons contribute to their generally poor fossil record. The monophyly of Lepidosauria is well supported when it is restricted to Rhynchocephalia and Squamata [2]. Although represented today only by *Sphenodon*, rhynchocephalians are common in the Triassic and Jurassic, and squamates are more abundant from the late Jurassic on. Gekkotans from the late Jurassic are among the earliest known squamates [25]. Given their position in squamate phylogeny, it is clear that the primary squamate clades, Iguania and Scleroglossa, had already diverged by that time [26]. Lizards do not form one group of squamates and snakes another; snakes are part of Scleroglossa, which includes both lizard-like forms, such as geckos and lacertids, and snake-like forms, such as dibamids and amphisbaenians [26]. Missing data complicate our understanding of the early history of Lepidosauria (Fig. 11). The bodiless *Paliguana*, the headless *Saurosternon*, and the gliding kuehneosaurs appear to be early forms that diverged prior to the origin of Lepidosauria [2]. Both character discordance and missing data obscure relationships of Younginiformes. Current data place it within Lepidosauromorpha [2], but that position is not well supported.

The early archosauromorphs in Fig. 12 tend to be larger carnivores and herbivores and thus more completely known. The larger-scale relationships are now fairly stable [1, 27, 28], but many details of the early history of archosauromorphs are obscure be-

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┌──────────── Younginiformes
│   ┌──────── Palaeagama
│   │   ┌──── Paliguana
└───┤   │
    └───┤   ┌ Saurosternon
        └───┤   ┌ Kuehneosauridae
            └───┤
                └ LEPIDOSAURIA
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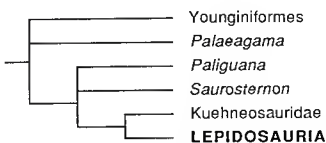
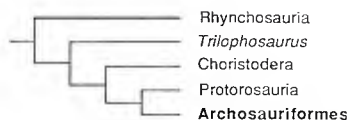Fig. 11. Cladogram depicting early diversification of Lepidosauromorpha.

Fig. 12. Cladogram depicting early diversification of Archosauromorpha.

cause the better known forms occur unusually late and are highly modified. The presence of the archosauriform *Archosaurus* in the late Permian indicates that the initial diversification of Archosauromorpha took place prior to the end of the Paleozoic. Relatively unmodified examples of herbivorous rhynchosaurs and insectivorous/carnivorous protorosaurs are known from the early Triassic [27]. However, the derived late Triassic representatives of these groups are more completely known. The specialized herbivore *Trilophosaurus* is also known only from the late Triassic, and the aquatic, piscivorous choristoderans are unknown from sediments prior to the early Cretaceous [1].

Fig. 13 depicts relationships among early Archosauriformes. Even the earliest members of that group, the aquatic proterosuchids, display a suite of cranial modifications that mark their macropredaceous habits [1]. These include tooth form and implantation, an enlarged adductor chamber, and an elaboration of the cranial musculature as suggested by the morphology of the antorbital and mandibular fenestrae. These and other changes in the skull point to the ability to secure, subdue and ingest larger prey.

The development of macropredaceous habits in archosauriforms was enhanced further by modifications in the postcranial skeleton that enabled a narrow-tracked gait and erect stance, and thus the ability to breathe while running [17]. Most of these postcranial features were absent in the earliest archosauriforms [29]. But the full suite of adaptations, including a four-chambered heart, muscular diaphragm and multicameral lungs, enlarged cerebellum, and the requisite musculo-skeletal novelties [30], were in place by the origin of Archosauria at the end of the early Triassic [3]. As noted above, contemporaneous therapsids solved the problem of breathing while running in an analogous fashion. Indeed, most of the characters that appear to ally post-Triassic therapsids with archosauromorphs are convergences related to the locomotor system [3].
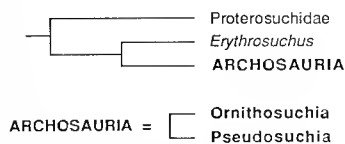

Fig. 13. Cladograms depicting selected divergences within Archosauriformes, and the two main groups of Archosauria.

The origins of birds and crocodilians

Extant Crocodylia and Aves appeared in the late Cretaceous, but the separate archosaur lineages leading to them diverged much earlier, in the latter part of the early Triassic. Archosauria can be divided into two main groups, birds and their extinct relatives in Ornithosuchia, and crocodilians and allies in Pseudosuchia [6] (Fig. 13). The early history of Ornithosuchia is complicated by our incomplete knowledge of some forms, such as *Lagosuchus* and *Herrerasaurus*, and the specialized morphology of others, such as the volant pterosaurs. Elaboration of the locomotor system played a central role in the history of both major groups of archosaurs [30]. But it was among the erect and bipedal ornithosuchians, which twice took to the air in powered flight [31], that lateral undulation was most thoroughly suppressed, and the role of the trunk in forced-draft ventilation enhanced, facilitating evolution of endothermic homeothermy in later ornithosuchians [17].

Perhaps the most familiar ornithosuchians are the dinosaurs, including extant birds. Even the earliest dinosaurs are easily recognized by the bird-like appearance of their skeletons [6]. That is to say, early dinosaurs were bipedal cursors with enlarged pelves, long and gracile hindlimbs, and functionally digitigrade and tridactyl feet. The importance of the forelimbs in terrestrial locomotion was reduced and, at least in early dinosaurs, the forelimbs were as well suited to grasping and manipulating food as to bearing weight. In addition, their vertebral columns display a characteristic regionalization involving a mobile and S-shaped neck, a shortened and stiffened trunk, an enlarged sacrum, and a tail modified to enhance its role as a dynamic stabilizer. Several of these characters antedate the origin of dinosaurs [6, 32, 33]. Some of the same modifications diagnosing dinosaurs, or their structural antecedents, are present in some other ornithosuchians, such as Ornithosuchidae, and to a greater extent in Pterosauria and *Lagosuchus*, and especially in *Herrerasaurus* [1, 6].

The presence of some dinosaur characters in non-dinosaurian archosaurs called 'thecodonts' led to the hypothesis of polyphyletic origins for Dinosauria [29]. Recent work [6] shows that some 'thecodonts' diverged prior to the split between crocodilians
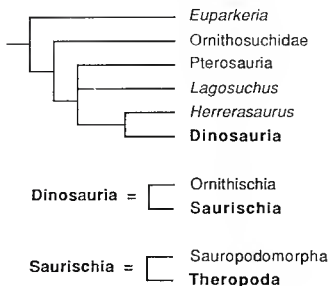

Fig. 14. Cladograms depicting early phylogeny of Ornithosuchia, and the major groups of Dinosauria and Saurischia.

and birds (Fig. 13), while others are either closer to birds (Fig. 14) or closer to croco-dilians (Fig. 17). Once again, a paraphyletic taxon, in this case the 'Thecodontia', rather than rampant convergence, was the source of the problem [6].

Dinosauria includes two major clades, the extinct Ornithischia and extant Saur-ischia, the latter represented by two main groups, extinct Sauropodomorpha and ex-tant Theropoda (Fig. 14). Saurischia was defined on the basis of plesiomorphic resem-blances in the pelvis – they were the dinosaurs that were not ornithischians – but several characters in the skull, vertebral column, and hands indicate its monophyly [6]. The diverse ornithischians were an important group of medium- to large-sized herbivores such as the well-known *Stegosaurus*, *Triceratops* and *Iguanodon* [34]. The long-necked and stout-limbed sauropodomorph saurischians were another important group of Mesozoic herbivores. Sauropodomorpha includes the largest dinosaurs, such as the gigantic sauropods *Supersaurus* and *Ultrasaurus*. Bakker [35] recently reviewed possible ecological roles of ornithischians and sauropodomorphs in the context of their Mesozoic communities.

Early theropod saurischians retained the carnivorous habits of their predecessors, but improved upon them with the addition of raptorial forelimbs specialized for seiz-ing prey [6]. The initial diversification of Theropoda (Fig. 15) is marked by the ac-quisition of increasingly bird-like attributes, especially in the limbs and girdles [6]. Ceratosaurs dominate the record of the group in the late Triassic, with even more bird-like theropods predominating from the late Jurassic on. *Compsognathus* appears to be the sister taxon of a group that includes the huge carnosaurs with diminutive fore-limbs, such as *Tyrannosaurus*, as well as the coelurosaurs, or birds and their extinct rel-atives. Unlike that group of three-fingered and stiff-tailed theropods, *Compsognathus* re-tains the four-fingered hands and less modified tail of ceratosaurs.

The coelurosaurs in Fig. 16 represent extant birds and a selection of their extinct outgroups. Only a handful of early coelurosaurs are known from more than scraps of a few individuals. The same can be said for the fossil record of their surviving relatives among Aves. Nevertheless, what is known of the coelurosaur record in the Mesozoic indicates that many modifications previously associated with flight, such as a fused bony sternum, a furculum, long forelimbs with bird-like wrists, together with the basic elements of the flight stroke, evolved in a predatory context prior to the origin of flight [6, 36].

No one doubts that extant dinosaurs are endothermic homeotherms, but the origin of this suite of characters within Dinosauria has been the subject of some dispute [35]. Evidence from bone histology indicates that even the earliest dinosaurs were able to
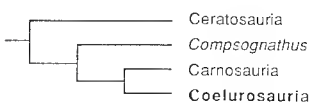

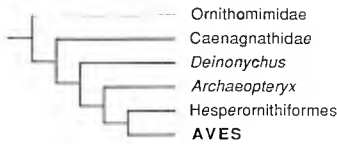Fig. 15. Cladogram depicting early phylogeny of Theropoda.

Fig. 16. Cladogram of selected divergences within Coelurosauria.

grow rapidly to medium and large sizes [37]. This suggests that from the outset of their history dinosaurs possessed a physiological capacity beyond that retained by extant crocodilians, if not the level seen in modern birds [37]. The point in theropod history at which feathers originated, and by extension an avian level of homeothermy, remains unknown. Feathers appear to be absent in *Compsognathus* but they are present in the early bird *Archaeopteryx* [38]. However, we know nothing of the skin in a considerable array of theropods that are more closely related to birds than is *Compsognathus* (Figs. 15, 16).

Pseudosuchia, or extant crocodilians and their extinct relatives [1, 6], has a long and complex history (Figs. 17–19). Members of this group were abundant and diverse during much of the Triassic, but only crocodylomorph pseudosuchians survived the end of that Period [39, 40]. Triassic pseudosuchians include crocodile-like aquatic carnivores, the phytosaurs, heavily armored herbivorous aetosaurs, and a variety of less well-known terrestrial cursors, such as the herbivore *Lotosaurus*, small carnivores such as *Ticinosuchus*, and highly cursorial carnivores such as *Postosuchus* and *Terrestrisuchus* (Fig. 17). The cladograms in Figs. 17, 18 and 19 provide no more than an outline of pseudosuchian phylogeny. The early and mid-Triassic record of Pseudosuchia is particularly incomplete. And their somewhat more extensive late Triassic record is made up either of highly modified forms, particularly aquatic types, or fragmentary remains of some terrestrial taxa.

Crocodylomorphs have long been the top carnivores in fresh water, a position held throughout much of the latter part of the Paleozoic by temnospondyl amphibians, and briefly by phytosaurs during the Triassic. Modern crocodilians are unusual among archosaurs in having negatively allometric limbs [41], but then they are generally suspended by water when not sunning on banks near the water's edge. However, early crocodylomorphs and their outgroups include several long-limbed cursors [1, 30, 39], which suggests that the short limbs and sluggish habits of extant crocodilians may be secondary features associated with their amphibious habits.
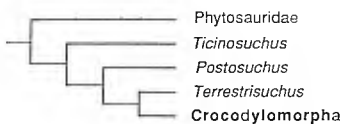

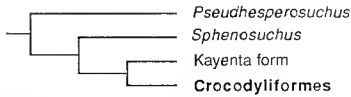Fig. 17. Cladogram of selected early divergences within Pseudosuchia.

Fig. 18. Cladogram of selected early divergences within Crocodylomorpha.

Fig. 19 is a cladogram of selected crocodyliforms spanning the last 180 million years [39, 40]. Most of these taxa are recognizably crocodilian in general aspect, although Crocodylia itself extends back only to the late Cretaceous [39]. The group also contains a number of modified taxa, including secondarily terrestrial carnivores such as *Sebecus* and *Baurusuchus*, and the marine thalattosuchians with reduced armor, paddle-like limbs and fin-like tails [39, 42]. There are numerous fossil crocodyliforms because their preferred environments are well-represented in the fossil record. That record has not yet received the attention it deserves.

The origin of Lissamphibia

Amphibia is composed of extant lissamphibians and all extinct tetrapods that are more closely related to them than they are to amniotes. The earliest divergence within the group is between Loxommatidae and Temnospondyli (Fig. 3). A phylogeny of selected temnospondyls [7] is presented in Fig. 20.

Many of the Paleozoic and Mesozoic temnospondyls, such as *Greererpeton*, *Edops*, and *Eryops*, were large, aquatic or amphibious carnivores. However, the only surviving temnospondyls, the lissamphibians, are generally small and insectivorous. All lissamphibians, not only the saltatory anurans and limbless gymnophiones, but the quadrupedal urodeles as well, are highly modified relative to the ancestral tetrapod.
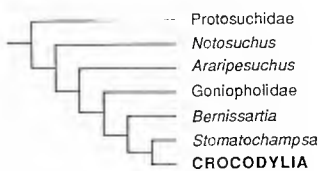

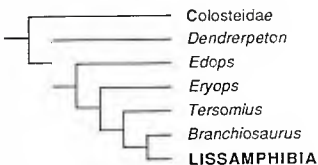Fig. 19. Cladogram of selected divergences within Crocodyliformes.

Fig. 20. Cladogram of selected divergences within Temnospondyli.

Discussion

The phylogenetic and stratigraphic positions of the tetrapod outgroup *Crassigyrinus* (Fig. 2), the colosteid amphibian *Greererpeton* (Fig. 20), and the anthracosauroid anthracosaur *Eoherpeton* (Fig. 4) indicate that the initial diversification of tetrapods had taken place by the late Mississippian. By similar reasoning, all cladogenic events in Figs. 3, 4 and 5, including the divergences between anapsids and romeriids, and *Paleothyris* and diapsids (Fig. 9), had taken place by mid-Pennsylvanian times. This suggests that divergences leading to extant mammals, turtles and saurians occurred over a span of roughly 10 million years. But from the perspective of the present day, those events occurred more than 300 million years ago.

Questions on that time scale present special problems for systematists relying exclusively on the Recent biota for their data. A molecular systematist interested in relationships among major groups of extant amniotes, for example, would need a molecule that evolved rapidly enough to detect divergences on a scale of considerably less than 10 million years. During the ensuing 300 million years, however, that rate of change would effectively obliterate any information regarding these early divergences retained by that molecule. Lanyon [43] argued that divergence times affect the probability of recovering the correct phylogeny from stochastically evolving characters, such as nucleotide substitutions in nuclear DNA that occur at a generally accepted rate of 10^{-9}. From his graphs, the probability of correctly identifying a synapomorphic nucleotide substitution that arose 300 million years ago during a 10 million year span is almost zero.

An analogous problem confronts the morphologist. Among early amniotes, for example, there are but two basic configurations of the occiput, either vertical, the ancestral condition, or anterodorsally sloping as in early synapsids [3]. But which of these states applies to modern mammals? Their enlarged brains have induced profound changes in occipital morphology; the occiput is neither forward sloping nor is it vertical because it bulges out to accommodate the brain. Several aspects of occipital morphology are important in reconstructing the earliest events in tetrapod phylogeny [3, 4, 14]. Unfortunately, there are no extant tetrapods in which that region of the skull can be said to have retained its original form [3]. In fact, there has not been a tetrapod whose occipital region retains anything like its original morphology since the end of the Triassic, over 180 million years ago [3].

Gauthier et al. [3] examined the attributes that any taxon, whether extinct or extant, must have in order to alter a phylogenetic hypothesis. They observed that the critical taxa have a high ratio of ancestral to derived characters, and referred to such taxa as plesiomorphic sister groups. They noted further that evolutionary history reveals a positive correlation between time and change, which accounts for why a fossil would be expected to approach the ancestral condition more closely than would a living representative of the same clade. Thus, extinct members of an early diverging group can be of greater relevance in phylogenetic inference than are their extant rep-

resentatives, at least under certain conditions. Specifically, fossils are expected to be most important when reconstructing ancient divergences in groups represented by no more than a few, highly modified, survivors [3]. Turtles offer a case in point because they appear to have diverged from other reptiles shortly after the split between reptiles and mammals. In light of the problems outlined above, one might expect that the phylogenetic relationships among turtles, mammals and saurians might be difficult to resolve from the vantage of the present day alone. And that is indeed the case (e.g., Hillis and Dixon, chapter 26 in this volume).

Finally, no extant tetrapod can be considered generally primitive. That extant taxa are a mosaic of ancestral and derived characters is well known; the sprawling posture of lizards might be ancestral with respect to the erect posture of mammals, but then the mammalian vomeronasal organ is plesiomorphic compared to the elaborately modified system of lizards. Some fossils can be considered to be generally primitive; a colosteid, such as *Greererpeton*, is a far more primitive amphibian than is an extant salamander, just as *Eocaptorhinus* is a much better example of a primitive reptile than is a lizard. Indeed, all extant lizards are removed by no less than 180 synapomorphies from the ancestral reptile. That is why it is generally preferable to speak of characters, rather than taxa, as being primitive when referring to all but the earliest members of a clade. Mosaic evolution belies the perspective of the traditional vertebrate anatomy course, which treats most other extant tetrapods as if they were mere stepping stones on the evolutionary path to mammals. We trust our brief review of the major features of tetrapod phylogeny dispels that notion. We also trust that this review clarifies the inadequacy of the traditional division of tetrapods into 'amphibians', 'reptiles', birds and mammals. To retain the former two taxa as traditionally conceived is to deny the concept of evolution its central role in biological taxonomy [44], and to accord special status to the latter two taxa because they are 'so different' from other extant amniotes is to deny the fossil record [3].

Acknowledgements

References

1 Gauthier JA. A cladistic analysis of the higher systematic categories of the Diapsida. No. 85-12825. Ann Arbor: Univ Microfilms Int, 1984.

2 Gauthier JA, Estes RE, de Queiroz K. A phylogenetic analysis of Lepidosauromorpha. In: Estes RE, Pregill GK (Eds.) Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L Camp. Palo Alto: Stanford University Press, 1988; 15–98.

3 Gauthier J, Kluge AG, Rowe T. Amniote phylogeny and the importance of fossils. Cladistics 1988; 4: 105–209.

4 Gauthier J, Kluge AG, Rowe T. The early evolution of Amniota. In: Benton MJ (Ed.) The Phylogeny and Classification of the Tetrapods. I. Amphibians, Reptiles and Birds. Syst Assoc Spec Vol 35A. Oxford: Clarendon Press, 1988; 103–155.

5 Hennig W. Insect Phylogeny. New York: John Wiley, 1981.

6 Gauthier J. Saurischian monophyly and the origin of birds. In: Padian K (Ed.) The Origin of Birds and the Evolution of Flight. M California Acad Sci, 1986; 8: 1–55.

7 de Queiroz K, Cannatella DC. The monophyly and relationships of the Lissamphibia. Am Zool 1987; 27: 60a.

8 Rowe T. Osteological Diagnosis of Mammalia, L. 1758, and its Relationship to Extinct Synapsida. Berkeley: University of California, 1986. PhD Dissertation.

9 Rowe T. Definition, diagnosis and origin of Mammalia. J Vert Paleo 1988; 8: 241–264.

10 Gaffney ES. Tetrapod monophyly: a phylogenetic analysis. Carnegie Mus Nat Hist 1979; 13: 92–105.

11 Jarvik E. Basic Structure and Evolution of Vertebrates (Vols. I, II). London: Academic Press, 1980.

12 Panchen AL. On the amphibian *Crassigyrinus scoticus* Watson from the Carboniferous of Scotland. Phil Trans R Soc London Ser B, 1985; 309: 505–568.

13 Heaton MJ. The Cotylosauria: a reconsideration of a group of archaic tetrapods. In: Panchen AL (Ed.) The Terrestrial Environment and the Origin of Land Vertebrates. Syst Assoc Spec Vol 15. London: Academic Press, 1980; 497–551.

14 Heaton MJ, Reisz RR. Phylogenetic relationships of captorhinomorph reptiles. Can J Earth Sci 1986; 23: 402–418.

15 Reisz RR. Pelycosauria. In: Carroll RL, Kuhn O, Tatarinov LP (Eds.) Encyclopedia of Paleoherpetology, Part 17a. Stuttgart: Fisher, 1986; 1–102.

16 Kemp TS. Mammal-like Reptiles and the Origin of Mammals. London: Academic Press, 1982.

17 Carrier DR. The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. Paleobiology 1987; 13: 326–341.

18 Gaffney ES, McKenna MC. A late Permian captorhinid from Rhodesia. Am Mus Novit 1979; 2688: 1–15.

19 Gaffney ES. A phylogeny and classification of the higher categories of turtles. Bull Am Mus Nat Hist 1975; 155: 387–436.

20 Gaffney ES, Hutchison JH, Jenkins FA, Meeker L. Modern turtle origins; the oldest known cryptodire. Science 1987; 237: 289–291.

21 Dryden LS. Paraphyly of the Cryptodira and Phylogenetic Systematics of Turtles. Lawrence: University of Kansas, 1988. MS Thesis.

22 Carroll RL. A middle Pennsylvanian captorhinomorph and the interrelationships of primitive reptiles. J Paleont 1969; 43: 151–170.

23 Pough FH. Lizard energetics and diet. Ecology 1973; 54: 837–844.

24 Carroll RL. The origin of lizards. In: Andrews SH, Miles RS, Walker AD (Eds.) Problems in Vertebrate Evolution. Linnean Soc Symp Ser 4, 1977; 359–396.

25 Estes RE. Sauria terrestria, Amphisbaenia. Encyclopedia of Paleoherpetology 10A. Stuttgart: Gustav Fischer Verlag, 1983.

26 Estes RE, de Queiroz K, Gauthier J. Phylogenetic relationships within Squamata. In: Estes RE, Pregill GK (Eds.) Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp. Palo Alto: Stanford University Press, 1988; 119–281.

27 Benton MJ. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. Phil Trans R Soc London Ser B, 1983; 302: 605–717.

28 Benton MJ. Classification and phylogeny of the diapsid reptiles. Zool J Linnean Soc 1985; 84: 97–164.

29 Charig AJ. Dinosaur monophyly and a new class of vertebrates. A critical review. In: Bellairs Ad'A, Cox CB (Eds.) Morphology and Biology of the Reptiles. London: Academic Press, 1976; 65–104.

30 Parrish JM. Locomotor adaptations in the hindlimb and pelvis of Thecodontia. Hunteria 1986; 1: 1–35.

31 Padian K. The origins and aerodynamics of flight in extinct vertebrates. Palaeontology 1985; 28: 423–433.

32 Bonaparte JM. Nuevas materiales de *Lagosuchus talampayensis* Romer (Thecodontia: Pseudosuchia) en el origen de las Saurischia, Triasico medio de Argentina. Acta Geol Lilloana 1975; 13: 5–90.

33 Bakker RT, Galton PM. Dinosaur monophyly and a new class of vertebrates. Nature 1974; 248: 168–172.

34 Sereno P. Phylogeny of the bird-hipped dinosaurs (order Ornithischia). Natl Geog Res 1986; 2: 234–256.

35 Bakker RT. The Dinosaur Heresies. New York: William Morrow, 1986.

36 Gauthier JA, Padian K. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (Eds.) The Beginnings of Birds: Proceedings International *Archaeopteryx* Conference, Eichstätt 1984. Eichstätt: Freunde des Jura-Museums 1985; 185–197.

37 Reid REH. The histology of dinosaurian bone, and its possible bearing on dinosaurian physiology. In: Ferguson, MWJ (Ed.) The Structure, Development and Evolution of Reptiles: A Festschrift in Honour of Professor A.d'A. Bellairs on the Occasion of his Retirement. Symp Zool Soc London London: Academic Press 1984; 52: 629–663.

38 Ostrom JH. The osteology of *Compsognathus longipes* Wagener. Zitteliana 1978; 4: 73–118.

39 Clark JM. Phylogenetic relationships of the crocodylomorph archosaurs. Chicago: University of Chicago, 1986. PhD Dissertation.

40 Benton MJ, Clark JM. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ (Ed.) The Phylogeny and Classification of the Tetrapods. I, Amphibians, Reptiles and Birds. Syst Assoc Spec Vol 35A. Oxford: Clarendon Press, 1988; 289–332.

41 Dodson P. Functional and ecological aspects of relative growth in *Alligator*. J Zool London, 1975; 175: 315–355.

42 Romer AS. Osteology of the reptiles. Chicago: University of Chicago Press, 1956.

43 Lanyon SM. The stochastic mode of molecular evolution: what consequences for systematic investigations? Auk, 1988; 105: 565–573.

44 de Queiroz K. Systematics and the Darwinian revolution. Phil Sci 1988; 55: 238–259.