

A Phylogenetic Perspective on Locomotory Strategies in Early Amniotes¹

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SYNOPSIS. Past approaches to understanding the evolution of locomotory strategies among Paleozoic amniotes (“primitive reptiles” of previous parlance) have been influenced by preservational bias: early occurrences of some amniote taxa were used to polarize the acquisition or development of locomotory structures among the earliest amniotes. Using a phylogeny representing the current consensus in the literature, we investigate the major locomotory strategies that have been posited for Paleozoic amniotes (basal synsapsids on one hand and early reptiles on the other) by optimizing the major locomotory styles identified for these taxa onto the consensus tree, in order to present an overview of the pattern of evolution of locomotory strategies inherited and adopted by various amniote lineages.

INTRODUCTION

Understanding of the earliest amniotes has been a central pursuit of vertebrate paleontologists over the past century (*e.g.*, Case, 1911; Olson, 1947; Parrington, 1958; Vaughn, 1962; Carroll, 1969*a, b*, 1995; Gauthier *et al.*, 1988; Laurin and Reisz, 1997, 1999). Until Reisz (1980, 1986) pointed out that Synapsida should be considered as a basal amniote lineage distinct from reptiles, “origin of amniotes” was synonymous with “origin of reptiles.” The most influential of these earlier studies were those of Carroll (1969*a, b*, 1970) wherein he proposed the morphotype of a hypothetical reptilian ancestor, which he found amongst gephyrostegid anthracosaurian amphibians. Notably, these studies were amongst the last to address the question of amniote origins without a cladistic context. This approach was characterized by a number of factors. First, the earliest known reptiles were assumed to be the most primitive

reptiles. As protorothyridid reptiles (“protorothyrid reptiles” of Carroll, 1969*a, b*, 1970) were known from middle Pennsylvanian sediments (Carroll and Baird, 1972), they were taken as the model of the primitive reptilian morphotype. Second, taxa that departed from the small, gracile, insectivorous bauplan exhibited by protorothyridids were generally considered to be more derived (such as in the case of captorhinid reptiles and many taxa now assigned to Parareptilia) or aberrant (such as in the case of groups lumped into “Cotylosauria”). Last, the “search for a reptilian ancestor” was exactly that, a search for an ancestor. As such, it endeavored to define successively more primitive taxa appropriate to providing a structural origin for reptiles. Although this provided a taxon-to-taxon path without morphological reversals, it also resulted in an ancestral taxon that shared only primitive features with any basal amniote group.

Recent phylogenetic work

By the mid-1970s, the advent of cladistic methods of phylogenetic analysis began to gain popularity in vertebrate paleontological studies. However it was not until the work of Gauthier *et al.* (1988) that the first truly global consideration of early amniote phylogeny utilized that methodology in conjunction with commercially-available microcomputer software (PAUP 2.4) for

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analysis of Paleozoic tetrapod interrelationships. As such, this study became a benchmark for subsequent investigators. Gauthier *et al.* (1988) corroborated earlier phylogenetic work that had focused on more restricted branches of the amniote tree (*e.g.*, Heaton, 1980; Reisz, 1981; Heaton and Reisz, 1986), and they provided the strongest evidence to date for their identification of the closest fossil relatives of amniotes (diadectomorphs and *Solendonsaurus*). More importantly, Gauthier *et al.* (1988) were able to draw attention to several formerly problematic amniote groups by identifying an unsuspected evolutionary radiation of amniotes that had no modern representatives. Interestingly, Gauthier *et al.* (1988) had little faith that their enigmatic assemblage would sustain careful scrutiny by later workers, and christened the group with the informal name “parareptiles.” Reisz and Laurin (1991) later proposed that the closest relatives of turtles were to be found among these “parareptiles” (specifically: procolophonoids), thereby bringing taxonomic legitimacy to the group. However, a detailed analysis did not appear until several years later (Laurin and Reisz, 1995). In the meantime, Lee (1993) also announced that turtles had affinities with “parareptiles,” but regarded pareiasaurs rather than procolophonoids as the closest relatives of testudines, a hypothesis he examined in greater detail in a subsequent publication (Lee, 1995).

The study of Laurin and Reisz (1995) is the second global treatment of early amniote phylogeny. Those authors corroborated the validity of Gauthier *et al.*'s (1988) clade of “parareptiles,” which they recognized officially by giving it Olson's (1947) nomen *Parareptilia*, and they provided strong evidence that procolophonid parareptiles were the closest fossil relatives of turtles. In recognizing turtles as parareptiles, Laurin and Reisz (1995) greatly augmented the taxonomic composition of *Reptilia*. They also identified mesosaurs as the only non-synapsid amniotes to fall outside of this enlarged concept of *Reptilia*, but the addition of new data and a slight modification to their data matrix (Modesto, 1999) results in mesosaurs having the same relative position

among other reptiles as reported by Gauthier *et al.* (1988).

The position of turtles remains hotly contested. Lee (1997) advocated an origin among pareiasaurs, whereas Rieppel and deBraga (1996; see also deBraga and Rieppel, 1997; Rieppel and Reisz, 1999) proposed the more unorthodox hypothesis that turtles are aberrant lepidosauromorph diapsids. The likely phylogenetic position of turtles is not critical to our review, primarily because they make their first appearance only in the Lower Mesozoic. However, the view that turtles are parareptiles is followed here because it appears to be the general consensus, and it allows us to retain the phylogenetic taxonomy that concerns early amniotes and has become established in the recent literature (*e.g.*, deBraga and Reisz, 1996; Modesto, 1999). It should be noted that the larger analysis of deBraga and Rieppel (1997) did not alter the relationships among Paleozoic taxa outlined by Laurin and Reisz (1995).

Several recent studies have examined the interrelationships of tetrapods in global analyses and are crucial to considerations of the origins of locomotory features in amniotes. Parenthetically, it is important to point out that although the above survey of studies of reptilian origins appears critical of Carroll's (1969*a, b*, 1970) work, he has more recently adopted a phylogenetic systematic approach wherein his proposed hypotheses of relationship amongst basal amniotes differ significantly from his earlier work. In one such study (Carroll, 1995), he suggested lepospondyls as closer relatives of amniotes than such reptiliomorph amniotes as seymouriamorphs and anthracosaurs, a view supported by Laurin and Reisz (1997) and Laurin (1998).

A cladogram summarizing the current consensus of the interrelationships of Paleozoic amniotes and their nearest relatives is shown in Figure 1. By mapping character-state distributions onto this phylogenetic framework, functional hypotheses and scenarios for taxa spanning the amphibian to amniote transition may be tested. In this review we examine the major locomotory strategies exhibited by basal amniotes and

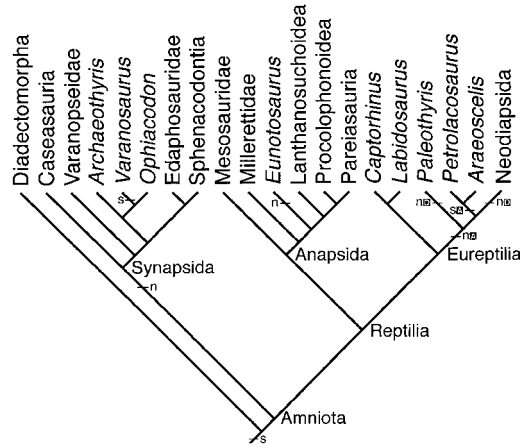


FIG. 1. Consensus of cotylosaurian phylogeny drawn from Gauthier *et al.* (1988), Laurin and Reisz (1995), deBraga and Reisz (1996), and Modesto (2000). Primary vertebral forms (s, swollen and expanded neural arches; n, narrow neural arches) are placed on branches they first appear on this cladogram; alternative scenarios within Eureptilia result from accelerated (A) or delayed (D) transformation options and are indicated by reverse image capital letters. See Laurin and Reisz (1995) and Modesto (2000) for stratigraphic distributions for most of these taxa. See Figure 6 for justification of plesiomorphic state for Amniota.

their anamniote sister taxon Diadectomorpha.

PHYLOGENETIC CONTEXT: AMNIOTE OUTGROUPS AND BASAL AMNIOTES

Schultze (1987) and Hopson (1991) have argued convincingly that defensible phylogenetic analyses must include, whenever possible, all members of a group being considered. If this is impractical, it is imperative that basal members of any clade be employed in an analysis in order to avoid biasing hypotheses of transformation between clades on highly derived, terminal taxa. By logical extension, a consideration of functional transformations must also include such basal taxa. Thus, we begin our functional survey by examining locomotory features in basal amniotes, as well as basal representatives of the tetrapod clades closest to amniotes as a necessary prerequisite for establishing ancestral locomotory abilities in Amniota. Although the interrelationships of more distant “reptiliomorph” taxa continues to be debated, the Diadectomorpha have been confirmed as the sister group of am-

niotes in a variety of recent studies and reviews (Gauthier *et al.*, 1988; Lombard and Sumida, 1992; Laurin and Reisz, 1997). Berman *et al.* (1992) even went so far as to suggest that diadectomorphs share a more recent common ancestor with synapsids than with any other tetrapod group, making them *de facto* amniotes. Diadectomorphs are known from the Permo-Carboniferous of both Europe and North America (Berman *et al.*, 1997).

In general morphology the diadectomorph postcranial skeleton suggests a high degree of terrestriality (Sumida, 1997). The best preserved forms possess highly expanded neural arches that range about three to four times the diameter of the centrum in transverse width (Sumida, 1990). The arches can be described as “swollen” in that their dorsal surfaces are conspicuously convex when viewed from anterior or posterior aspects. The great breadth of the arches, together with the approximately horizontal orientation of the zygapophyseal facets, suggest strongly that the diadectomorph vertebral column primarily facilitated lateral bending during locomotion. Diadectomorphs feature accessory intervertebral articulations that would have further restricted movements of the vertebral column to the horizontal plane. Apart from some lepospondyls (microsaurs), diadectomorphs are the only anamniotes known to exhibit alternation of neural spine height and structure (Sumida, 1990). (Seymouriamorphs exhibit such alternation, but it is extremely inconsistent in pattern.) Although the inclination of the zygapophyseal surfaces is at a slight angle to the horizontal plane in regions of alternation, it is not so extremely expressed as to suggest that diadectomorphs engaged in other than predominantly lateral bending during locomotion.

The appendicular elements are robustly constructed. Propodials (humeri and femora) lack shafts and have massive proximal and distal heads. Epipodial segments measure 70% or greater that of humeri and femora. The diadectomorph manus and pes are short and broad with stout digits. Together, the axial and appendicular skeletons suggest that although appendicular elements are relatively longer and better developed

than in anamniotes (Sumida, 1997), the locomotory strategy of these animals continued to accentuate the plesiomorphic, transverse undulatory action of the vertebral column.

Synapsids

Paleozoic synapsids have been the focus of many large-scale treatments over the past century and their anatomy and interrelationships are well known (Romer and Price, 1940; Reisz, 1986). We concentrate here on the basal, non-therapsid synapsids, known colloquially as “pelycosaurs.” These early synapsids span a temporal range from the Late Carboniferous through to the Late Permian. The overwhelming majority of “pelycosaurs” are from North American and European deposits; a single species is known from southern Africa. Although an amphibious habitus is thought to have arisen in one group, Ophiacodontidae, most early synapsids are regarded generally to have been highly terrestrial animals. Narrow neural arches are found in the overwhelming majority of taxa. Although the term “narrow” is never defined in phylogenetic studies that use neural arch width as a phylogenetic character, the term here is applied to arches whose zygapophyses do not extend laterally beyond the vertebral centrum. The sole synapsid in which narrow arches are absent is the small ophiacodontid *Varanosaurus*, where they are expanded transversely and feature horizontal zygapophyseal articulating facets. The degree of dorsolateral expansion of the neural arches in *Varanosaurus* is not as great as that in diadectomorphs (Sumida, 1990); nonetheless, these two features of the dorsal neural arches suggest that undulatory movements of the vertebral column were emphasized during locomotion in this form (Sumida, 1989). Considering that *Varanosaurus* is nested deeply within Synapsida (Fig. 1), its locomotory strategy is best regarded as a derived for synapsids.

In all narrow-arched synapsids the articulating facets are tilted throughout the column. In caseids and ophiacodontids they are tilted an average of 30 degrees to the horizontal, whereas in edaphosaurids and sphenacodonts the facets are tilted even fur-

ther, averaging 40 degrees (Reisz, 1986). The great angulation of the zygapophyseal facets in these taxa suggests that, in addition to the plesiomorphic side-to-side movement, rotation of the vertebral column was a general feature of locomotory action in synapsids. Tall neural spines are also a characteristic of early synapsids. In basal taxa (caseosaurs, varanopseids) the dorsoventral measures of the spines are only a little greater than their anteroposterior length. In the more crownward forms, the height of the spines is at least twice their length; in edaphosaurids and some sphenacodontids the neural spines are greatly elongated and form “sails” on the back of the animal. The function of such “sails” has been the subject of much speculation and modeling with thermodynamic control the favored hypothesized function (Haack, 1986). The possible role of the relatively shorter spines of closely related forms has not been explored. The tall neural spines of early synapsids, which in life would have been connected to neighboring spines by equally tall interspinous ligaments, may have served to prevent hyper-rotation of the vertebral column during locomotion.

The appendicular skeleton of basal synapsids is markedly less robust in construction than that of diadectomorphs. The relative sizes of the propodial and epipodial elements are essentially the same as in those anamniotes. The manus and pes are short, broad structures in large-bodied taxa, particularly caseids, ophiacodontids and large sphenacodontids, but they appear longer and more gracile in taxa at the smaller end of the size spectrum (*e.g.*, *Varanops*, *Haptodus*). The variance in the general build of the manus and pes is presumably due to scaling with respect to the wide range in body sizes seen among synapsids. Data from the axial skeleton suggest that synapsids adopted a locomotory strategy that incorporated a substantial degree of rotary action into vertebral column. Why synapsids acquired this modification of general vertebral movement is not entirely clear, but it could be related to the slightly more elongated nature of the vertebral column as compared to diadectomorphs and such reptiles as captorhinids (Reisz, 1986). *Vara-*

nosaurus represents an exception to this strategy in its independent adoption of the pattern described for diadectomorphs. The latter have relatively shorter bodies, yet the vertebral column in *Varanosaurus* does not appear to be relatively shorter than that of other synapsids (Sumida, 1989). Accordingly, the role of vertebral rotation in synapsid locomotion might be better investigated in terms of its effect on limb extension and recovery. This is a postulate that is beyond the scope of this review; however, it is interesting to note that Ritter (1996) has pointed out that lateral rotatory movement plays an important role in limb recovery mechanics in a variety of extant lepidosaurs.

Eureptilia

Whereas the Protorothyrididae was once considered the basal stock for all amniotes (e.g., Carroll, 1969a, b, 1970) a series of studies (Heaton and Reisz, 1986; Lombard and Sumida, 1992; Laurin and Reisz, 1995; Sumida, 1997) now indicate that it is nested well within the Eureptilia (*sensu* Gauthier *et al.*, 1988). Eureptilia includes the Captorhinidae, Protorothyrididae, Araeoscelidia, and Neodiapsida, with the latter two taxa forming the clade Diapsida.

The postcranial skeletons of captorhinid reptiles demonstrate clearly terrestrial features. In general, their axial and appendicular skeletons are robustly constructed. Vertebral neural arches are “swollen” and expanded laterally beyond the lateral margins of the centrum, though not to the degree seen in diadectomorphs. Whereas the neural arches may measure as much as four times the width of the centrum in diadectomorphs, those of captorhinids usually measure approximately 1.2 to 2 times the width of the centrum. Greater relative measures of the neural arch are associated with a more caudad position in the presacral column. Virtually all genera of captorhinids for which adequate materials are known demonstrate alternation of neural spine height and structure. Sumida (1990) pointed out that in this group zygapophyseal angle is greater in regions of alternation; however, the angulation is still significantly less than in narrow-arched synapsids, protorothyridids, and ar-

aeoscelidians (including basal diapsids). In regions of the captorhinid column where alternation is either absent or muted, zygapophyseal surfaces are nearly parallel to the horizontal plane. Despite the minor regional occurrence of zygapophyseal tilting in regions of extreme neural spine alternation, captorhinids still appear to have retained a plesiomorphic pattern dominated by lateral undulatory movement of the vertebral column.

Although not as large as those of pelycosaurian-grade synapsids, the appendicular elements of captorhinids demonstrate comparable development of markers of muscular development in propodial and epipodial segments. Particularly well-developed structures common to captorhinids, diadectomorphs, and synapsids include the insertion for the latissimus dorsi, the humeral entepicondyle for antebrachial flexors, and an extremely well developed olecranon process for attachment of triceps musculature (Sumida, 1997). Although not as large as most diadectomorphs, it is noteworthy that certain larger captorhinids such as *Labidosaurus*, *Labidosaurikos*, and other moradisaurine captorhinids do demonstrate diadectomorph-like proportions.

Of araeoscelidians and protorothyridids, only certain members of the former share vertebral features and proportions in common with captorhinids. Araeoscelidians are characterized by elongate “cervical” vertebrae, but those of the mid-dorsal region are extremely similar to the laterally expanded dorsal vertebrae of captorhinids. The araeoscelids *Araeoscelis* and *Zarcasaurus* and at least one specimen of the primitive diapsid *Petrolacosaurus* (University of Kansas Vertebrate Paleontology Collections specimen 33605) possess expanded neural arches and alternation of neural spine structure. As in captorhinids, there is minimal tilt to the zygapophyseal surfaces, and when present is usually less than 15 degrees in *Araeoscelis* and *Zarcasaurus* (Sumida, 1990), and less than 10 degrees in *Petrolacosaurus* (Reisz, 1981). Whereas some specimens of *Petrolacosaurus* retain moderately swollen neural arches, most examples depart from the pattern of conical neural spines alternating with tall narrow ones

to being consistently elongate and nearly quadrangular in section. This condition recalls the approximate shape of the neural spines of basal synapsids, but they are relatively smaller when compared that group.

All araeoscelidians for which data are available possess appendicular skeletons that are significantly more lightly built than those of any of the taxa described herein. Epipodials and propodials are elongate with well-defined shafts and, when present, proximal and distal processes are not as robustly developed. The femur is conspicuously sigmoidal. Manual and pedal elements are similarly gracile and elongate. As in certain extant lepidosaurians, the fourth digit of the manus and pes is significantly more elongate than the others, a condition suggestive of rotation of podal elements to allow enhanced lateral pushoff (Sumida, 1997). Basal araeoscelidians appear to have been an early experiment as a small, gracile, lizard-like organism. However, their vertebral structure appears to have retained the primitive undulatory movement of the axial column.

Other than basal synapsids, protorothyrids are the only basal group of amniotes to possess conspicuously narrow neural arches. In concert with this, their zygapophyseal articulations are inclined between 30 and 40 degrees (Carroll, 1969*a, c*), yet their neural spines are relatively less tall than in pelycosaurs. Appendicular elements of protorothyrids are also more gracile in construction than those of diadectomorphs, captorhinids, or parareptiles. Only mesosaurs and araeoscelidians demonstrate more lightly built limbs than protorothyrids. As in araeoscelidians, manual and pedal construction of protorothyrids is gracile and the fourth digit of both is conspicuously elongate. Protorothyrids appear to have developed a gracile, lizard-like habitus that included significant axial rotation.

Anapsid reptiles

In concert with the ongoing debate on turtle origins, the clade of basal reptiles comprising parareptiles and mesosaurs, and now known as Anapsida (*sensu* Gauthier *et al.*, 1988; see Modesto, 1999), has received much attention in recent systematic studies

and there is considerable disagreement concerning the interrelationships of the constituent taxa. If we disregard the phylogenetic position of turtles, the remaining disagreement does not bear on this review, inasmuch the postcrania of the group of contention, Lanthanosuchidae, are not known in adequate detail (Ivakhnenko, 1980). The vast majority of anapsids are restricted to the Permian, with only the procolophonids surviving into the succeeding Mesozoic. The most basal anapsids were limited to southern distributions in the Pangean supercontinent, but some advanced lineages were restricted to northern portions of Pangea, whereas the more crownward taxa, specifically procolophonoids and pareiasaurs, separately attained cosmopolitan distributions (Modesto, 2000).

Among the three major Paleozoic amniote groups, Anapsida is remarkable for a broad scale of locomotory adaptations. The most basal anapsids, the mesosaurs, are oldest known fully aquatic reptiles. The enigmatic *Eumotosaurus africanus* is characterized by a semi-rigid, turtle-like rib cage (Gow and de Klerk, 1997), one which presumably necessitated a tortoise-like fashion of walking. The large, ponderous pareiasaurs also possessed a relatively short trunk, but featured the most upright limb postures of any Paleozoic reptile group. However, most anapsids evinced a sprawling, lizard-like stance, and their skeletons are highly indicative of terrestriality. As in diadectomorphs, the neural arches of the vast majority of anapsids are expanded transversely and are conspicuously "swollen." However, the neural arches are never wider than they are long, except in pareiasaurs (Figs. 2, 3), where they become as greatly expanded as in diadectomorphs, a convergence suggestive of the scaling effect of large body size. Zygapophyseal facets are oriented roughly horizontally, which together with the great breadth of the arches suggest strongly that lateral bending was the primary movement of the vertebral column during locomotion, an interpretation that applies to the terrestrial forms and the aquatic mesosaurs equally. In the latter, however, accessory intervertebral articulations are also present, which would have

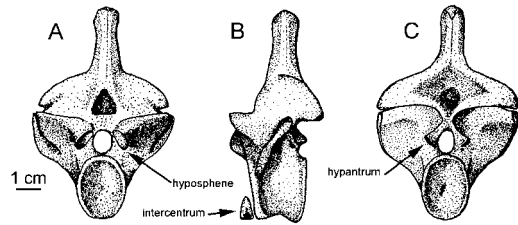


FIG. 2. Single dorsal vertebra of the Late Paleozoic tetrapod *Diadectes* demonstrating “swollen” construction of the neural arch. (A) cranial, (B) left lateral, and (C) caudal views of a single dorsal vertebra.

further restricted the mesosaurid vertebral column to movements in the horizontal plane (Modesto, 1999). The single exception to the presence of expanded, swollen

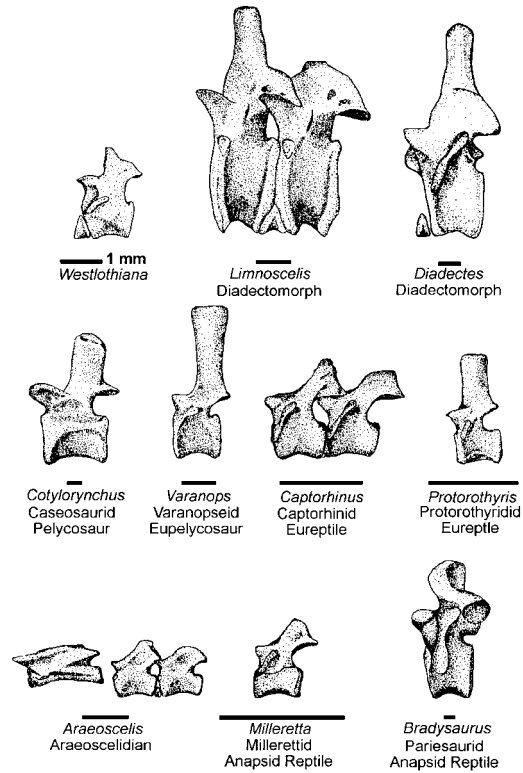


FIG. 3. Reconstructions in left lateral view of single or paired dorsal vertebrae of representative Late Paleozoic tetrapod taxa. All vertebral bodies are drawn to approximately the same size to facilitate proportional comparison of structures. Accompanying bar scales all equal 1 cm except where noted. In each case, generic name is accompanied by a higher order taxonomic description to facilitate systematic consideration of the element. (Partially after Sumida, 1997.)

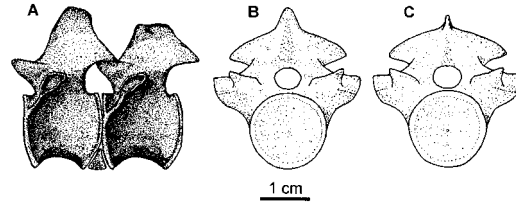


FIG. 4. Dorsal vertebral structure in the ophiacodontid eupelycosaur *Varanosaurus*, the only synapsid to demonstrate expanded neural arches and alternation of neural spine height and structure. (A) left lateral view of two articulate dorsal vertebrae. (B) anterior view of typical dorsal vertebra with large (tall) neural spine morph. (C) anterior view of typical dorsal vertebra with small (low) neural spine morph. (Modified from Sumida, 1990.)

neural arches, and thus the inferred exaggerated lateral flexure of the vertebral column during locomotion, is *Eunotosaurus*, which features a reduced number of anteroposteriorly elongated trunk vertebrae (that articulate with the anteroposteriorly expanded trunk ribs, which in turn form the carapace-like rib cage: Gow and de Klerk, 1997). The serial anatomy of the dorsal spines is not well established for most anapsid groups, but subtle alternation of neural spine height is displayed by posterior-most dorsal vertebrae in tall-spined specimens of *Mesosaurus* (Modesto, 1996).

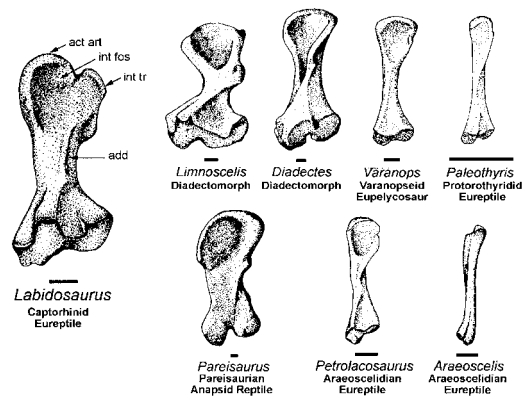


FIG. 5. Reconstructions in dorsal view of the left femur of representative Late Paleozoic tetrapod taxa. All femoral bodies are drawn to approximately the same length to facilitate proportional comparison of structures. In each case, generic name is accompanied by a higher order taxonomic description to facilitate systematic consideration of the element. Accompanying bar scales all equal 1 cm. (Partially after Sumida, 1997.)

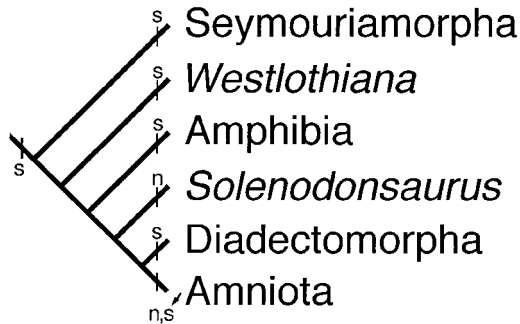


FIG. 6. Justification for interpreting the presence of expanded, swollen neural arches and the locomotory strategy they imply as the ancestral condition for amniotes. Assuming Amniota is polymorphic with regards to the presence of swollen neural arches (s) or narrow arches (n), optimization using five successive outgroups suggests that it is more parsimonious to regard swollen neural arches as the primitive condition for amniotes. Arrow indicates the morphology that is decisive for Amniota in accordance with the distribution of the two states on this tree. Tree topology following Laurin and Reisz (1999).

The appendicular skeleton in general is more gracile than that seen in synapsids and diadectomorphs. Pareiasaurs are the sole exception. Their appendicular elements evince the robustness seen in diadectomorphs. The relative lengths of the propodials and epipodials in anapsids are approximately the same as in other cotylosaurs (*sensu* Gauthier *et al.*, 1988), except in the mesosaurian pectoral limb, where the latter elements are reduced to half the length of the former, a reduction common to aquatic reptiles that employ the tail as a sculling organ. The manus and pes are generally short and broad but are comprised of elements more gracile than the diadectomorphs. The locomotory apparatus as a whole suggests that, as with diadectomorphs, anapsids perpetuated the plesiomorphic undulatory action of the vertebral column. The two derived locomotory strategies that evolved within Anapsida are the presumably turtle-like locomotion of *Eunotosaurus africanus*, where sprawling limbs propelled a semi-rigid body, and the semi-erect stance and gait of pareiasaurs.

DISCUSSION

Basal amniotes demonstrate two markedly different patterns of vertebral mechan-

ics. Optimization of the two locomotory strategies onto the amniote consensus tree (Fig. 1) suggests that the one accentuating sinusoidal movement of the vertebral column is plesiomorphic for amniotes. Accordingly, the narrow-arched condition of synapsids, *Eunotosaurus*, *Paleothyris* and neodiapsids was acquired independently in these amniote taxa. Our preferred hypothesis is highly sensitive to the position of the successive outgroups to Amniota. We have used the phylogenetic conclusions of Laurin and Reisz (1999), the most recent workers to examine the broader scope of tetrapod interrelationships, to identify outgroup taxa. The relative positions of Amphibia, *Westlothiana*, and Seymouriamorpha as recognized by Laurin and Reisz (1999) are critical to our identification of expanded neural arches as the ancestral condition for amniotes (Figure 6), as character optimization suggests that the narrow arched condition ascribed to *Solenodonsaurus* is an autapomorphy of that taxon (a basal “anthracosaur,” using the prioritized phylogenetic terminology of Laurin and Reisz, 1999).

The alternative to our preferred hypothesis, in which narrow neural arches and the locomotory strategy that they imply is ancestral for amniotes, is supported in a scenario that is marginally less parsimonious (at 6 steps) than the hypothesis advocated here (5 steps). In this alternative hypothesis the evolution of expanded presacral vertebrae in reptiles becomes complicated by ambiguous optimization, leading to the possibility that expanded, swollen neural arches arose independently in anapsids, captorhinids, and araeosceloids. That possibility competes with two equally parsimonious interpretations: (1) that laterally-expanded, swollen neural arches arose in the ancestral reptile and reversed separately in *Paleothyris* and in neodiapsids; or (2) they arose in the ancestral reptile and reversed in the ancestral romeriid (*sensu* Gauthier *et al.*, 1988), only to reappear in the ancestral araeosceloid.

In the more parsimonious interpretation, in which expanded neural arches is the ancestral condition for amniotes, only the last two scenarios must be considered, but only in part, as the only uncertainty lies in

whether narrow arches arose in the ancestral romeriid and reversed in araeosceloids (the accelerated transformation scenario), or whether narrow arches arose separately in *Paleothyris* and neodiapsids (the delayed transformation scenario). It is currently impossible to choose between these latter two evolutionary histories with regards to the evolution of locomotory strategies in romeriid reptiles. However, a rigorous interpretation of the vertebral anatomy of the Early Permian reptile *Thuringothyris mahlendorfae* could shed some light on this problem. A fortuitous cross-section through one presacral vertebra suggests that this taxon was characterized by expanded neural arches (Boy and Martens, 1991). Accordingly, if *Thuringothyris* is indeed a protorothyridid as Boy and Martens (1991) have concluded (there is some question as to the rigor of their phylogenetic analysis), and if it can be demonstrated that the taxon is a basal member of Protorothyrididae, *Thuringothyris* could be decisive in terms of the optimization of the two locomotory strategies onto this part of the amniote tree, for it would support the delayed optimization scenario which suggests that narrow arches arose independently in (some) protorothyridids and in neodiapsids.

Our conclusions contrast with those of earlier workers, primarily Carroll and his co-workers (Carroll, 1969*a, b*; Carroll and Baird, 1972; Clark and Carroll, 1973), who regarded the narrow neural arches of protorothyridids as representing the primitive condition for amniotes. That hypothesis, however, was the logical conclusion of the evolutionary-systematic methodology that was popular with vertebrate paleontologists prior to the advent of phylogenetic systematics. Most taxa that were assigned to Protorothyrididae are Late Carboniferous in age, and this includes the oldest known amniote, *Hylonomus lyelli*. The early appearance of this taxon and other protorothyridids suggested to evolutionary systematists that narrow arches were ancestral for amniotes, and that it followed logically that the expanded, swollen vertebrae of anapsid, captorhinid, and araeosceloid reptiles must have been derived from the narrow-arched condition. Our phylogenetic perspective

suggests that this scenario is less likely than the alternative, in which the condition seen in anapsids, captorhinids, and araeosceloids was inherited from a remote, anamniote ancestor.

Our results have interesting paleobiological implications with regards to the locomotor strategies that were inherited or adopted by various early amniotes. It appears that those amniotes that evolved narrow neural arches and adopted a locomotory strategy that placed less emphasis on lateral undulation of the backbone were highly precocious as far as the fossil record is concerned. During the Carboniferous, which records the first 15 million years of early amniote history, there is only a single amniote taxon (the diapsid genus *Petrolacosaurus* of the Late Stephanian) with expanded neural arches; all other Carboniferous amniotes are assigned either to Protorothyrididae or to Synapsida. Other broad-arched amniotes do not appear for many millions of years. Captorhinids appear during the late Asselian (equivalent to the early or middle Wolfcampian), anapsid reptiles during the Sakmarian (late Wolfcampian), and the synapsid *Varanosaurus* in the Artinskian (Leonardian). In the case of the anapsid reptiles, their late appearance in the fossil record (drawn from the observation that members of their sister group Eureptilia are preserved in Westphalian strata) could be explained by an early history spent in Permo-Carboniferous Gondwana, which records no continental sedimentation until the late Kazanian. That hypothesis is supported by a biogeographic analysis of anapsids using phylogenetic frameworks (Modesto, 2000). The relatively late entry into the amniote record by captorhinids, whose protorothyridid relatives appear in Westphalian sediments, is harder to explain, and the same applies to the synapsid *Varanosaurus*, whose narrow-arched sister taxon *Ophiacodon* appears at the close of the Stephanian.

Based on the construction of the neural arches and alternation of neural spines in most of the taxa surveyed above, Sumida (1990, 1997) suggested that the hypothetical ancestral amniotes did indeed engage in undulatory locomotion. It was further spec-

ulated that the pattern of vertebral neural spine construction and associated transversospinalis musculature of basal amniotes and their immediate anamniote sister taxa must have been active in other functions in addition to undulatory movement. It was suggested that the transversospinalis group also provided postural support ipsilateral to the contact limb during undulatory locomotion. This hypothesis of muscular and locomotor function was, however, based on fossil taxa and was thus not easily testable. Furthermore, it lacked a rigorous phylogenetic context. Given the constraints on the survey, it remained an untested hypothesis. More recently, using electromyographic, kinematic, and denervation studies, Ritter (1995) demonstrated that although vertebral elements may constrain the excursion arcs of the axial column, epaxial musculature did not contribute to actually generating undulatory movement and was instead restricted to the function of postural support. Additional study (Ritter, 1996) further demonstrated that lateral axial bending is a function of the hypaxial musculature, particularly the external oblique and rectus abdominus muscles.

The distribution of this pattern amongst lepidosaurian reptiles and the stabilizing function of the transversospinalis musculature in mammals lead Ritter (1995, 1996) to suggest that this division of labor between epaxial and hypaxial musculature was most parsimoniously interpreted as a basal amniote characteristic. If Ritter is correct, it may be suggested that the preferred hypothesis of vertebral movement patterns summarized above may now be linked to a demonstrated pattern of axial muscular activity. Given the congruence between the most parsimonious pattern of observed and inferred muscular pattern, this suggests that the pattern of undulatory locomotion powered by hypaxial musculature with epaxial musculature acting in postural stability probably extended to Diadectomorpha as well. Such a prediction could not have been made with any confidence without the phylogenetic context outlined above.

This survey of postcranial structure in Late Paleozoic terrestrial tetrapods demonstrates the utility of phylogenetic trees in

generating simple, yet powerful interpretations for patterns of locomotor evolution. A phylogeny generated independent of functional scenarios allows actual testing of alternative hypotheses of the development of locomotor complexes without the introduction of confounding circular arguments. The suggestion of using phylogenies to map or predict the evolution of functional complexes appears relatively straightforward. However, despite the general acceptance of the importance of phylogeny as a context for virtually any evolutionary endeavor or interpretation of character change over time, the search for ancestors based on *a priori* assumptions of locomotor constraint still persists in certain cases (e.g., Feduccia, 1999; Ruben and Jones, 2000; Geist and Feduccia, 2000). Fortunately, the predictive and explanatory ability of cladograms to generate functional predictions independent of *a priori* functional assumptions has rendered such approaches as a distinct minority.

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REFERENCES

- Berman, D. S., S. S. Sumida, and R. E. Lombard. 1992. Reinterpretation of the temporal and occipital regions in *Diadectes* and the relationships of diadectomorphs. *J. Paleont.* 66:481–499.
- Berman, D. S., S. S. Sumida, and R. E. Lombard. 1997. Biogeography of primitive amniotes. In S. S. Sumida and K. L. M. Martin (eds.), *Amniote origins, completing the transition to land*, pp. 85–140. Academic Press, San Diego.
- Boy, J. A. and T. Martens. 1991. Ein neues captorhinomorphes Reptile aus dem thüringischen Rotliegend (Unter-Perm; Ost Deutschland). *Paläontologische Zeitschrift* 65:363–389.

- Carroll, R. L. 1969a. Problems of the origin of reptiles. *Biol. Rev.* 44:393–432.
- Carroll, R. L. 1969b. Origin of reptiles. In C. Gans, A. d'A. Bellairs, and T. S. Parsons (eds.), *Biology of the Reptilia*, pp. 1–44. Academic Press, New York.
- Carroll, R. L. 1969c. A middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *J. Paleont.* 43:151–170.
- Carroll, R. L. 1970. The ancestry of reptiles. *Phil. Trans. Roy. Soc. London Ser. B* 257:267–308.
- Carroll, R. L. 1982. Early evolution of reptiles. *Ann. Rev. Ecol. Syst.* 13:87–109.
- Carroll, R. L. 1995. Problems of the phylogenetic analysis of Paleozoic choanates. *Bull. Mus. Natl. Hist. Paris.* 17:389–445.
- Carroll, R. L. and D. Baird. 1972. Carboniferous stem-reptiles of the family Romeriidae. *Bull. Mus. Comp. Zool.* 143:321–364.
- Case, E. C. 1911. A revision of the Cotylosauria of North America. *Publ. Carnegie Inst. Washington*, D.C. No. 415, 122 pp.
- deBraga, M. and R. R. Reisz. 1996. The Early Permian reptile *Acleistorhinus pteroticus* and its phylogenetic position. *J. Vert. Paleont.* 16:384–395.
- deBraga, M. and O. Rieppel. 1997. Reptile phylogeny and the interrelationships of turtles. *Zool. J. Linn. Soc.* 120:281–354.
- Feduccia, A. 1999. *The origin and evolution of birds*. 2nd ed. Yale University Press, New Haven.
- Gauthier, J. A., A. Kluge, and T. Rowe. 1988. The early evolution of the Amniota. In M. J. Benton (ed.), *The phylogeny and classification of the tetrapods*, Vol. 1, *Amphibians, reptiles, birds*, Systematics Association Special Volume No. 35A, pp. 103–155. Clarendon Press, Oxford.
- Geist, N. R. and A. Feduccia. 2000. Gravity-defying behaviors: Identifying models for protoaves. *Amer. Zool.* 40:664–675.
- Gow, C. E. and W. de Klerk. 1997. First record of *Eumotosaurus* (Amniota: Parareptilia) from the Eastern Cape. *Palaeont. Afr.* 34:27–31.
- Haack, S. C. 1986. A thermal model of the sailback pelycosaur. *Paleobiol.* 12:450–458.
- Heaton, M. J. 1980. The Cotylosauria: A reconsideration of a group of archaic tetrapods. In A. L. Panchen (ed.), *The terrestrial environment and the origin of land vertebrates*, Systematics Association Special Volume No. 15, pp. 497–551. Academic Press, New York.
- Heaton, M. J. and R. R. Reisz. 1986. Phylogenetic relationships of captorhinomorph reptiles. *Can. J. Earth Sci.* 23:402–418.
- Hopson, J. A. 1991. Systematics of the non-mammalian Synapsida and implications of evolution in synapsids. In H.-P. Schlitz and L. Trueb (eds.), *The origin of higher groups of tetrapods: Controversy and consensus*, pp. 635–693. Cornell University Press, Ithaca.
- Ivakhnenko, M. F. 1980. Lanthanosuchids from the Permian of the East European platform. *Paleont. J.* 14:80–90.
- Laurin, M. 1998. The importance of global parsimony and historical bias in understanding tetrapod evolution. Part I. Systematics, middle ear evolution, and jaw suspension. *Ann. Sci. Nat.* 1:1–42.
- Laurin, M. and R. R. Reisz. 1995. A reevaluation of early amniote phylogeny. *Zool. J. Linn. Soc.* 113:165–223.
- Laurin, M. and R. R. Reisz. 1997. A new perspective on tetrapod phylogeny. In S. S. Sumida and K. L. M. Martin (eds.), *Amniote origins, completing the transition to land*, pp. 9–59. Academic Press, San Diego.
- Laurin, M. and R. R. Reisz. 1999. A new study of *Solenodonsaurus janenschii*, and a reconsideration of amniote origins and stegocephalian evolution. *Can. J. Earth Sci.* 36:1239–1255.
- Lee, M. S. Y. 1993. The origin of the turtle body plan: Bridging a famous morphological gap. *Science* 261:1616–1620.
- Lee, M. S. Y. 1995. Historical burden in systematics and the interrelationships of “parareptiles.” *Biol. Rev.* 70:459–547.
- Lee, M. S. Y. 1997. Pareiasaur phylogeny and the origin of turtles. *Zool. J. Linn. Soc.* 120:197–280.
- Lombard, R. E. and S. S. Sumida. 1992. Recent progress in understanding early tetrapods. *Amer. Zool.* 32:609–622.
- Modesto, S. P. 1996. The anatomy, relationships, and palaeoecology of *Mesosaurus tenuidens* and *Stereosternum tumidum* (Amniota: Mesosauridae) from the Lower Permian of Gondwana. Unpublished Ph.D. Thesis, University of Toronto.
- Modesto, S. P. 1999. Observations on the structure of the Early Permian reptile *Stereosternum tumidum* Cope. *Palaeont. Afr.* 35:7–19.
- Modesto, S. P. 2000. *Eumotosaurus africanus* and the Gondwanan ancestry of anapsid reptiles. *Palaeont. Afr.* 36. (In press)
- Olson, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana Geol.* 11:1–53.
- Parrington, F. R. 1958. The problem of classification of reptiles. *J. Linn. Soc. (Zool.)* 56:99–115.
- Reisz, R. R. 1980. The Pelycosauria: A review of the phylogenetic relationships. In A. L. Panchen (ed.), *The terrestrial environment and the origin of land vertebrates*, Systematics Association Special Volume No. 15, pp. 553–592. Academic Press, New York.
- Reisz, R. R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Sp. Pub. Mus. Nat. Hist. Univ. Kansas* 7:1–74.
- Reisz, R. R. 1986. Pelycosauria. *Handbuch der Paläoherpetologie* 17:1–102. Gustav Fischer Verlag, Stuttgart.
- Reisz, R. R. 1997. The origin and early evolutionary history of amniotes. *Trends Ecol. Evol.* 12:218–222.
- Reisz, R. R. and M. Laurin. 1991. *Owenetta* and the origin of turtles. *Nature* 349:324–326.
- Rieppel, O. and M. deBraga. 1996. Turtles as diapsid reptiles. *Nature* 384:453–455.
- Rieppel, O. and R. R. Reisz. 1999. The origin and early evolution of turtles. *Annu. Rev. Ecol. Syst.* 30:1–22.
- Ritter, D. 1995. Epaxial muscle function during loco-

- motion in a lizard (*Varanus salvator*) and the proposal of a key innovation in the vertebrate musculoskeletal system. *J. Exp. Biol.* 198:2477–2490.
- Ritter, D. 1996. Axial muscle function during lizard locomotion. *J. Exp. Biol.* 199:2499–2510.
- Romer, A. S. and L. I. Price. 1940. Review of the Pelycosauria. *Geol. Soc. Amer. Spec. Papers* 28, 538 pp.
- Ruben, J. and T. D. Jones. 2000. Selective factors in the origin of fur and feathers. *Amer. Zool.* 40:585–598.
- Schultze, H.-P. 1987. Dipnoans as sarcopterygians. In W. E. Bemis, W. W. Burggren, and N. E. Kemp (eds.), *The biology and evolution of lungfishes*, pp. 39–74. Alan R. Liss, New York.
- Sumida, S. S. 1989. Reinterpretation of vertebral structure in the Early Permian pelycosaur *Varanosaurus acutirostris* (Amniota, Synapsida). *J. Vert. Paleont.* 9:419–426.
- Sumida, S. S. 1991. Vertebral morphology, alternation of neural spine height, and structure in Permian–Carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. *Univ. Calif. Publ. Zool.* 122:1–135.
- Sumida, S. S. 1997. Locomotor features of taxa spanning the origin of amniotes. In S. S. Sumida and K. L. M. Martin (eds.), *Amniote origins, completing the transition to land*, pp. 353–398. Academic Press, San Diego.
- Vaughn, P. P. 1962. The Paleozoic microsaur as close relatives of reptiles, again. *Am. Midl. Nat.* 67:79–84.