# CHAPTER 11

# LOCOMOTOR FEATURES OF TAXA SPANNING THE ORIGIN OF AMNIOTES

**Stuart S. Sumida**

## INTRODUCTION

Analyses of the origin of amniotes has long been tied to advances in "terrestriality." Any analysis involving taxa spanning this transition demands a functional survey of locomotor features. Recently, the study of late Paleozoic tetrapods has entered the realm of experimental analysis and a more rigorous biomechanical approach to osteological remains is becoming more predominant (Lombard and Sumida, 1992). The application of functional interpretations based on experimentally generated models utilizing extant taxa allows more confidence in models of locomotory behavior in basal tetrapods.

Just as important as a functional perspective is a phylogenetic perspective. During the past decade, the use of cladistic analysis in combination with large computer-analyzed databases has provided new hypotheses of relationship for taxa near the origin of amniotes. They provide a phylogenetic framework within which locomotory features may be surveyed. Recent phylogenetic hypotheses have, in some cases, provided novel proposals regarding the arrangement of the

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relationships of late Paleozoic tetrapod taxa. In other cases, older hypotheses that had been discarded previously have been resurrected with new and (presumably) more reliable methods of analysis. The utilization of rigorously documented phylogenetic hypotheses as a framework for functional analysis of primitive tetrapods is important in two regards: (1) It allows the development of hypotheses regarding the evolution of morphological and behavioral traits such as locomotor features, and (2) it alerts us to taxa that must be included in such a survey, taxa that in some cases might have been otherwise omitted.

***Phylogenetic Context***

This study does not attempt to generate a new or alternative hypothesis of the relationships of basal amniotes and their presumptive sister taxa. Rather, it attempts to survey the locomotory features of those taxa, with a phylogenetic hypothesis as the guide for the survey. Over the past three decades a succession of phylogenetic hypotheses have centered on the question of the origin and interrelationsips of amniotes (Carroll, 1969a, 1970; Heaton, 1980; Holmes, 1984; Heaton and Reisz, 1986; Reisz, 1980, 1986; Gauthier *et al.*, 1988; Berman *et al.*, 1992). Of these, later analyses have been revolutionized by the application of cladistic methodology to the generation of such hypotheses. Recently, considerable attention has been paid the discovery of a proposed "earliest amniote", *Westlothiana lizziae*, from the Visean of Scotland. Although Smithson (1989) originally designated *Westlothiana* as the earliest known reptile, more detailed subsequent analyses (Smithson *et al.*, 1994; Carroll, 1995) resulted in an amended diagnosis place it in a position intermediate between more traditionally defined anthracosaurs and amniotes.

The final few years of the twentieth century has witnessed the advent of cladistic analyses generated by powerful computer algorithms utilizing extremely large data sets (Gauthier *et al.*, 1988; Berman *et al.*, 1992; Laurin and Reisz, 1994; Carroll, 1995; Lee, 1995). The studies have been influential in shaping recent understanding of the interrelationships of basal amniotes and provided part of the incentive for this review. Figure 1 is an attempt to synthesize features common to these hypotheses. It does not pretend to reconcile all of the interpretive differences of these studies. A few features are noteworthy: (1) The terms Batrachosauria and

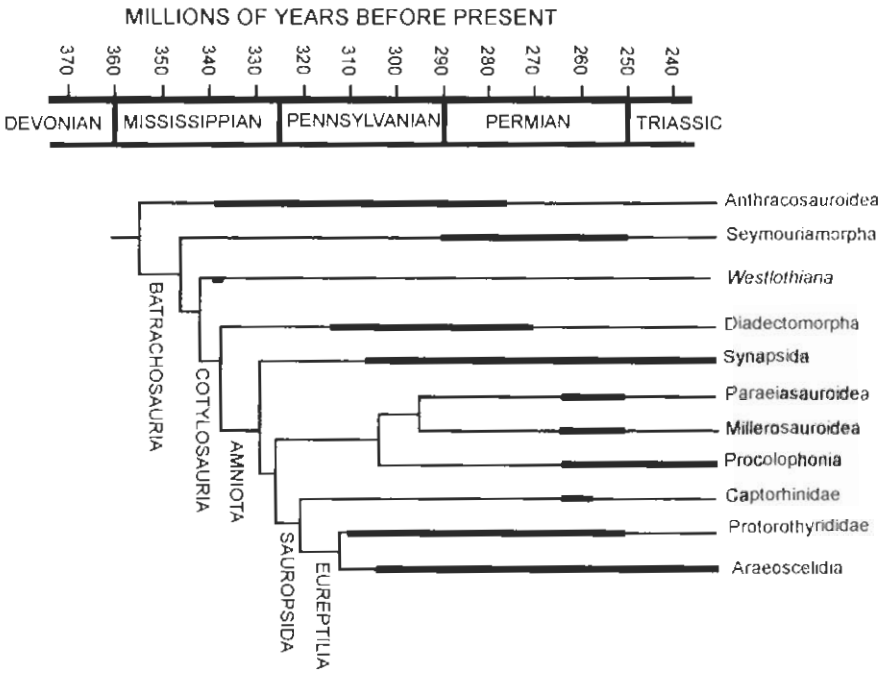



**Figure 1.** Cladogram providing a phylogenetic framework for the features discussed in this study. The cladogram is a synthesis based primarily on the hypotheses of Bolt and Lombard (1992), Lombard and Sumida (1992), Carroll (1995), Laurin and Reisz (this volume) and Lee and Spencer (this volume).

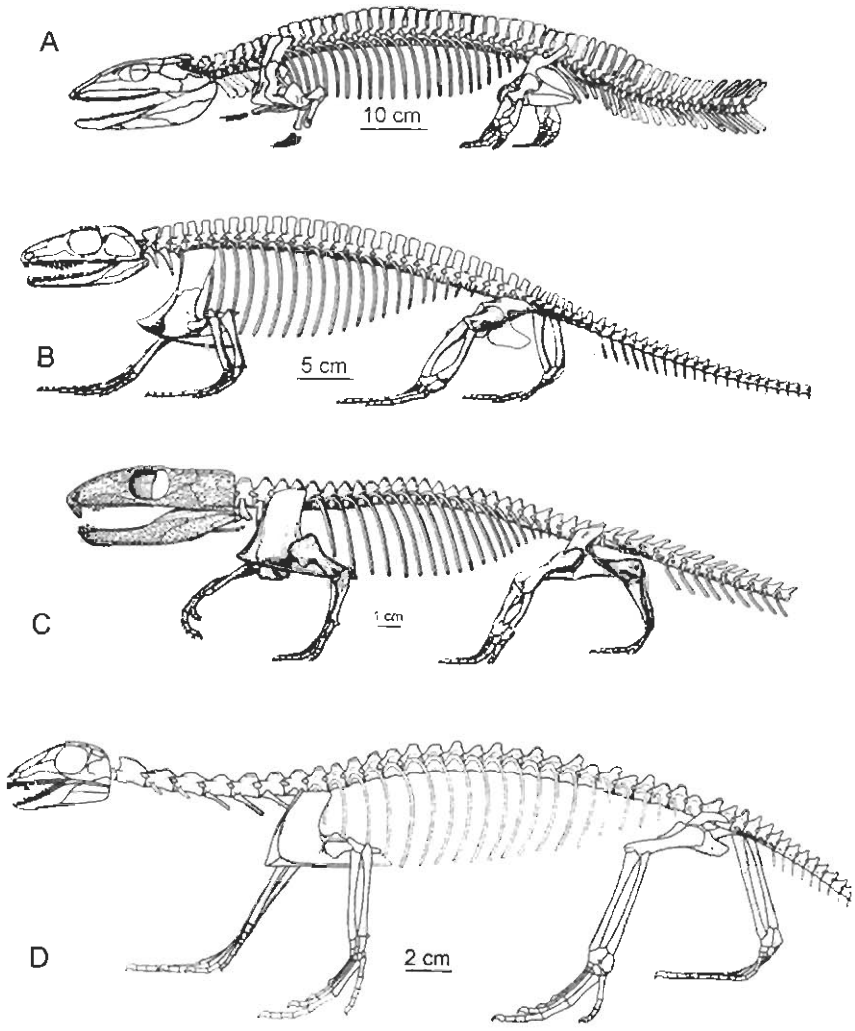
Cotylosauria are those defined by Laurin and Reisz (this volume); (2) the Amniota are characterized in a manner similar to most of the studies cited, though Berman *et al.* (1992) and Lee and Spencer (this volume) have suggested that there is evidence that Diadectomorpha might be realistically considered as amniotes; (3) the Sauropsida are as defined by Lee and Spencer (this volume); (4) the Eureptilia are characterized *sensu* Gauthier *et al.* (1988); and (5) the Paraeiasaurioidea, Millerosauroidea, and Procolophonia have often been grouped as the "Parareptilia" (Olson, 1947; Gauthier, *et al.*, 1988; Lee, 1995; others), however, this group is undergoing aggressive restudy at the time of this writing, and their interrelationships are not interpreted here in a formal taxonomic sense.

***Taxa Considered***

Based on the commonalities of recent phylogenetic studies combined into figure 1, members of the following groups are included in this review: representative basal anthracosaurs, seymouriamorphs, diadectomorphs, pelycosaurian-grade synapsids, basal sauropsids including millerittids and procolophonians, captorhinid reptiles, protorothyridid reptiles, and araeoscelidian reptiles (which include basal diapsid reptiles). Both Gauthier *et al.* (1988) and Laurin and Reisz (1995) have noted the position of mesosaurs near the base of the amniote radiation; however, their adaptation to an aquatic life-style precludes their inclusion here.

Schultze (1987) and Hopson (1991) have argued convincingly that defensible phylogenetic analyses must include, whenever possible, all members of a group being considered. When this is not practical, it is imperative that the basal members of any clade be used in the analysis so as to avoid basing hypotheses of transformation between clades on highly derived, terminal taxa. The latter approach is necessarily taken here. The embolomere *Proterogyrinus* is among the most terrestrial and the most thoroughly described of any anthracosaur (Holmes, 1984). *Seymouria* is easily the best known of seymouriamorphs (Berman *et al.*, 1987). All genera of the Diadectomorpha (*Limnoscelis, Tseajaia, Diadectes*) for which adequate postcranial materials are known are included (Berman and Sumida, 1990; Berman et al, 1992; Sumida *et al.*, 1992). Following Reisz *et al.* (1992), the primitive caseosaurian pelycosaurs *Casea* and *Aerosaurus* and basal eupelycosaurian synapsids are considered. The most primitive captorhinids for which complete postcranial material is known are *Eocaptorhinus*, *Captorhinus*, and *Labidosaurus*; information for this group is a synthesis of data from these genera (Holmes, 1977; Dilkes and Reisz, 1986; Heaton and Reisz, 1980; Sumida, 1989a). Basal procolophonids are probably best represented

**Figure 2.** Left lateral reconstructions of representative late Paleozoic tetrapods. (A) the anthracosauroidian anamniote *Protergyrinus scheeli*, primarily after Holmes (1984); (B) the caseoaurian pelycosaur *Aerosaurus wellesi*, after Langston and Reisz (1981) and Romer and Price (1940); (C) the captorhinid reptile *Eocaptorhinus laticeps*, after Heaton and Reisz (1980); and (D) the araeoscelidian reptile *Araeoscelis gracilis*, after Reisz *et al.* (1984). ➔


A
10 cm
B
5 cm
C
1 cm
D
2 cm

by *Procolophon* (Lee, 1993). *Parieasaurus* is representative of parieasaurs, though the postcranial skeleton in *Bradysaurus* is also well known and utilized here (Boonstra, 1931; Haughton and Boonstra, 1931; Boonstra, 1934). *Milleretta* (Gow, 1972; Thomasen and Carroll, 1981) is utilized here to represent millerettids. The record for postcranial material of protorothyridids is incomplete at best, so data for the group are presented as a synthesis of the best known genera, *Protorothyris* and *Paleothyris* (Clark and Carroll, 1973; Heaton and Reisz, 1986). Araeoscelidian reptiles are represented by *Petrolacosaurus* and *Araeoscelis* (Vaughn, 1955; Reisz, 1981; Reisz *et al.*, 1984). Figures following illustrate particular features of the taxa ennumerated above. Further, whole body reconstructions of representative taxa are illustrated in figure 2.

***Morphology and Methods of Comparison***

Wherever possible, description, discussion, and illustrations are based on actual examination of specimens. There are some groups for which this was problematic, particularly the "parareptiles". In these cases, the literature was necessarily utilized.

Whereas many previous surveys of locomotor capabilities (e.g., Romer, 1922; Holmes; 1980) have focused primarily on the appendicular skeleton, it has been noted that the vertebral column plays an important role in the locomotor behavior of late Paleozoic tetrapods (Olson, 1936a; Holmes, 1989; Sumida, 1987, 1990); thus, structure and regional patterns within the vertebral column are presented. The pectoral and pelvic girdles and long bones of the limbs are each considered in turn. The component bones of the manus and pes are not addressed individually; rather, they are treated as functional wholes.

Although in some cases reconstructions of osteological materials are based on composite studies, as much as possible reconstructions are based on the most complete specimens available. Wherever possible, functional interpretations are based on hypotheses that have been generated by experimental models using extant organisms.

## AXIAL SKELETON

### *General Structure*

The vertebral column of most late Paleozoic tetrapods is composed of multipartite elements with varying degrees of fusion (Fig. 3). In amniotes and their closest sister taxa the vertebral body is composed of two elements: a pleurocentrum that dominates in size and an anteriorly placed intercentrum which is usually reduced to a smaller, crescent-shaped wedge. Laterally directed transverse processes which provide articular surfaces for the ribs vary in size depending on their position; more anteriorly they may span both the neural arch and the centrum, but they are quite small in the most caudal regions of the body. In many of the taxa surveyed here, the neural arches are conspicuously "expanded" or "swollen" giving the outline of the arch a broadly convex appearance. The "swollen" form of the neural arch results in a broadly flared support for the anterior zygapophyses and transverse processes. A neural spine extends from the dorsal midline of the neural arch and is of variable construction in the taxa surveyed.

### *Dorsal vertebrae*

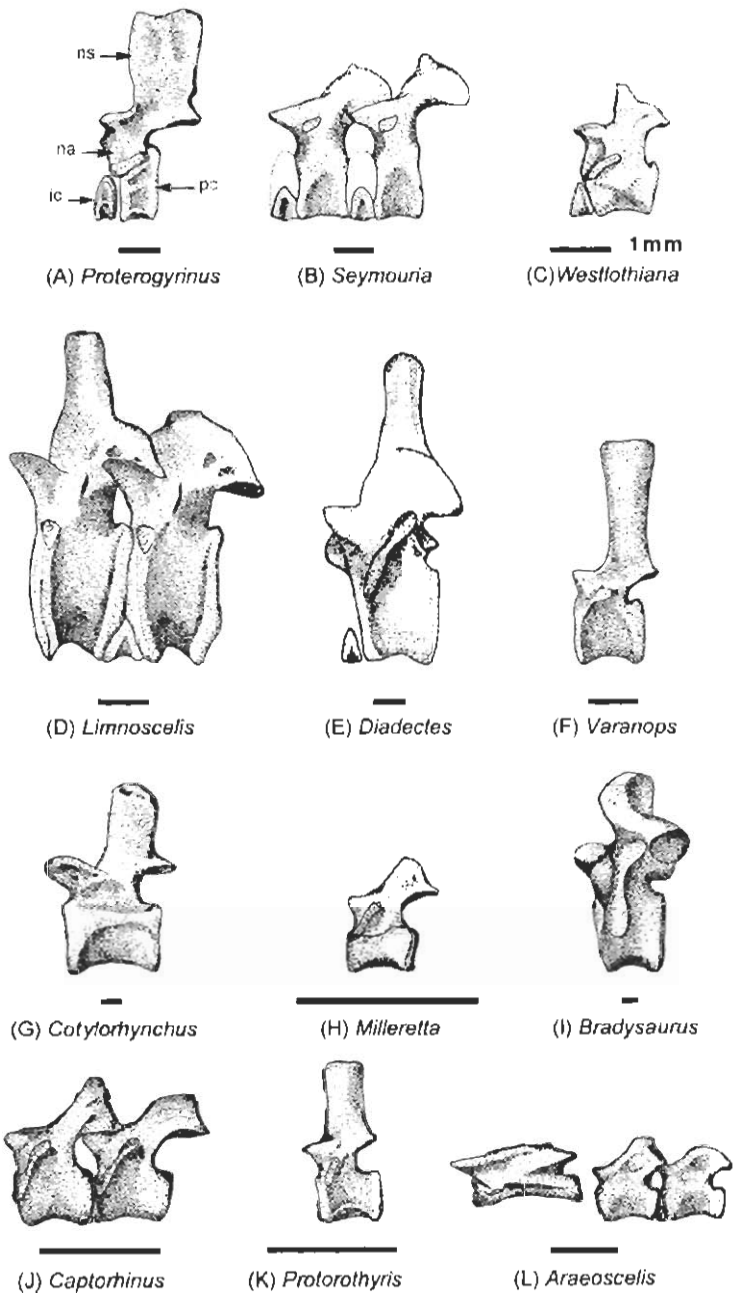
The primitive condition for the taxa surveyed here is exemplified by *Proterogyrinus* (Fig. 3.). The intercenturm is relatively larger than in any of the other taxa examined. It is a single element, U-shaped in anterior and posterior view, but was quite likely larger in life due to the preesence of cartilage. In mature individuals, the pleurocentrum is notochordal and closed though not fused dorsally; in immature specimens the pleurocentrum is open dorsally. The neural arch articulates with the pleurocentrum primarily. It is fused medially and has a tall, quadrangular neural spine. Zygapophyseal facets are set at an angle of approximately 20° to the horizontal. This would imply that movements more complex than simple lateral bending must have been possible. In the event of lateral bending, the angle of the zygapophyseal articulations would have imposed a coupled rotation. (See Holmes, 1989, for a similar analysis of rhachitomous vertebrae.)

In the remainder of taxa examined here, the pleurocentrum is conspicuously larger than the intercentrum. In most taxa other than *Seymouria*, centra are amphicoelous and the intercentrum is reduced to

an almost inconsequential wedge. Although the dorsal vertebrae in most araeoscelidians are generally similar to those of their outgroups, those of the cervical region are conspicuously elongate and help to form a clearly distinguishable "neck" region.

In association with a well-developed pleurocentrum, the neural arch is extremely robust. Seymouriamorphs, diadectomorphs, and most amniotes have a prodigious dorsolateral expansion of the neural arch. On the other hand, *Westlothiana*, protorothyridids, most synapsids, and certain araeoscelidian reptiles do not conform to this pattern. The neural arches in *Westlothiana* are only slightly convex. The neural arches of protorothyridids and some specimens of the the basal diapsid *Petrolacosaurus* are laterally convex. Only one basal synapsid (*Varanosaurus*) exhibits expanded neural arches and this is probably a condition developed convergently (Sumida, 1989b). With this exception, the vertebrae of pelycosaurian-grade synapsids are fairly consistent in their construction. Neural arches are concave, often with depressions or pits that presumably reduced the amount of bone while still retaining adequate structural integrity via an arched construction. Among taxa regarded as "parareptilian", Gow (1972) described the neural arches in millerettids as somewhat broad, but they are not as conspicuously expanded as the neural arches of parieasaurs. Only diadectomorphs have neural arches that are more stoutly and broadly constructed than those of parieasaurs.

**Figure 3.** Left lateral views of single or paired dorsal vertebrae of representative Late Paleozoic tetrapod taxa. (A) The embolomerous anthracosaurian *Proterogyrinus* (primarily after Holmes, 1984); (B) the seymouriamorph *Seymouria*; (C) *Westlothiana*, a tetrapod of uncertain affinities (after Smithson *et al.*, 1994); (D) the diadectomorph *Limnoscelis*; (E) the diadectomorph *Diadectes*; (F) the caseosaurian pelycosaur *Varanops* (primarily after Williston, 1911); (G) the caseosaurian pelycosaur *Cotylorhynchus* (after Stovall *et al.*, 1966); (H) the millerettid *Milleretta* (partially after Gow, 1972); (I) the parieasaur *Bradysaurus* (partially after Boonstra, 1934; Romer, 1956); (J) the captorhinid reptile *Captorhinus*; (K) the protorothyridid reptile *Protorothyris* (partially after Clark and Carroll, 1973; Heaton and Reisz, 1986); (L) cervical (left) and mid-dorsal (right) vertebra of the araeoscelidian reptile *Araeoscelis* (partially after Vaughn, 1955). All scalebars are equivalent to 1 cm except C where it equals 1 mm. Abbreviations: ic, intercentrum; na, neural arch; ns, neural spine; pc, pleurocentrum. ➔


ns
na
ic
pc
1mm
(A) *Proterogyrinus*
(B) *Seymouria*
(C) *Westlothiana*
(D) *Limnoscelis*
(E) *Diadectes*
(F) *Varanops*
(G) *Cotylorhynchus*
(H) *Milleretta*
(I) *Bradysaurus*
(J) *Captorhinus*
(K) *Protorothyris*
(L) *Araeoscelis*

The neural spines in *Proterogyrinus* and most pelycosaurs are laterally compressed and blade like. Those of *Westlothiana*, millerettids, and most of the column in parieasaurs are homogeneously conical. However, in many basal amniotes and their sister groups, there is considerable variability of neural spine structure, both among taxa and within individuals. Neural spines of two general types are found: "tall types" that are approximately conical in shape, and "low types" that are shorter, narrower, and wedge like. In fact, these two spine morphologies often alternate with one another in position through certain regions of the column. In regions of alternation of neural spine height, the zygapophyseal articulations are usually tilted relative to the horizontal plane precluding simple lateral bending.

Neural spine height and width alternate in short stretches of the column of *Seymouria* as well as many specimens of diadectomorphs; however this is never expressed throughout the column. The zygapophyseal articulations are nearly horizontal in most cases; however, they are slightly tilted relative to the horizontal plane in regions of neural spine variability. Representative specimens of the diadectomorphs *Limnoscelis*, *Tseajaia*, and *Diadectes* exhibit alternation of neural spine height. Most diadectomorphs have accessory articulations beyond the central and zygapophyseal contacts.

The neural spines of basal synapsids are uniformly well-developed and quite variable in their morphology among taxa; however, alternation of spine structure is manifested only in the genus *Varanosaurus*. Perhaps notably, *Varanosaurus* is the only pelycosaur that has expanded neural arches and alternation of neural spine morphology as well (Sumida, 1989b). The spines are short in *Aerosaurus* and *Casea*, but show varying degrees of elongation in more derived genera. Unfortunately, vertebral structure is not known for the most basal synapsids, *Oedaleops* and *Eothyris*. Most basal synapsids show a greater degree of zygapophyseal tilt than do seymouriamorphs or diadectomorphs.

The neural spines of millerettids are not particularly well known. Those of pareiasaurs are somewhat better known. They are are stoutly constructed. However, the spines are relatively shorter than those of most diadectids and no examples of alternation of neural spine height are known for any members of the group. One exception to this

is in the cervical region in *Bradysaurus* in which the spine of the third cervical is markedly smaller than that of the axis preceding it and the fourth following it. It may be that the large size of both diadectids and parieasaurs supplanted the need for the functional adaptations associated with alternation of neural spine height.

In most reptilian groups (sensu Gauthier *et al.*, 1988) with swollen neural arches, neural spine morphology inevitably varies. Whenever spine height alternates, zygapophyses diverge from a simply horizontal orientation, taking on a dorsolateral angle from 15 to 25° to the horizontal plane. Although neural arches are narrow and spines do not generally alternate in height in protorothyridids, the presence of a single low-spined cervical (as seen in the parieasaur *Bradysaurus*) is common. Alternation between tall, conical spines with low, narrow, wedge-shaped spines is found in all members of the Captorhinidae for which the vertebral column is adequately known as well as in araeoscelidian reptiles. Expanded neural arches are found in most araeoscelids, and with them alternation of neural spine structure. Reisz (1981) noted that the neural arches in *Petrolacosaurus* were markedly narrower than those of other araeoscelidians and of captorhinids. However, although spine height does not alternate in most specimens, neural spine width does. Some vertebral material clearly associated with crania assignable to *Petrolacosaurus* does have expanded neural arches (Sumida, 1990). Notably, these specimens also demonstrate alternation of neural spine height, though not to the degree seen in other taxa.

The common possession of laterally expanded neural arches, tilted zygapophyses, and alternation of neural spine height appears to represent a related functional complex among taxa at or near the origin of amniotes. Perhaps most importantly, whenever the phenomenon is encountered its greatest expression is near the limb girdles. In the captorhinid reptile *Labidosaurus* it occurs throughout the column, but its most extreme expression is near the limb girdles. The phenomenon is not found throughout the column in *Captorhinus* (Vaughn, 1970; Sumida, 1991) or *Eocaptorhinus* (Dilkes and Reisz, 1986; Sumida, 1991) but it is expressed near both limb girdles in the former and near the pelvic girdle of the latter. Alternation is most prominent in small to moderate sized animals that retain a robust build. In very large taxa,

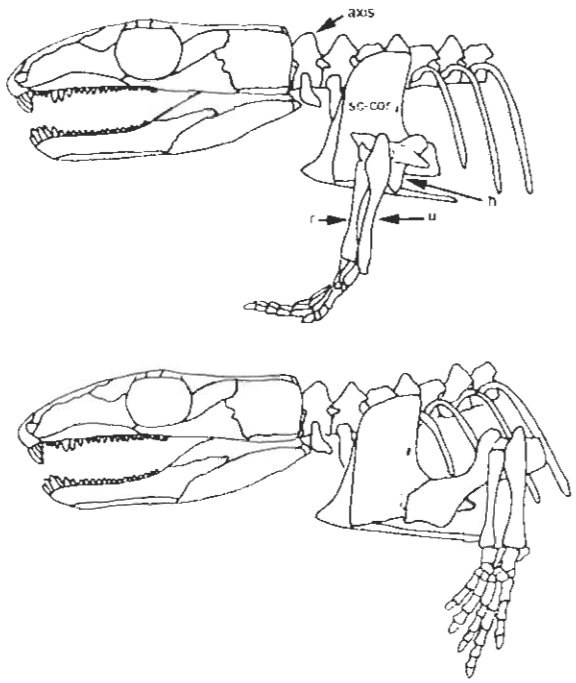



**Figure 4**. Diagrammatic illustration in left lateral view of the forelimb and anterior vertebral column in a captorhinid reptile. (A) Left forelimb in middle of power stroke; (B) left forelimb just out of contact with adjacent vertebral column in extreme dorsiflexion to aid in stabilization and recovery. Abbreviations: axis, axis vertebra; h, humerus; r, radius; sc-cor, scapulocoracoid; u, ulna.

such as diadectids and parieasaurs, only the extremely hypertrophied neural arches remain of the complex. Extremely gracile taxa show evidence of the terminal stages of having abandoned the entire suite of associated characters. Araeoscelidians provide a transitional example of this trend: they are somewhat more gracile than captorhinid reptiles and their neural spine construction does not contrast to the same degree. However, alternation in neural spine height is expressed whenever swollen neural arches are present.

Sumida (1991) suggested that if muscles spanned the interval between tall-type spines, dorsal and lateral vertebral flexion could have been aided. Tilted zygapophyseal articulations in regions of

alternation suggest that lateral flexion would have been necessarily accompanied by axial rotation. The greatest expression of the phenomenon is near limb girdles, so it may have facilitated axial rotation and muscular stabilization of the vertebral column during the recovery stroke of the limb. Figure 4 is a diagrammatic representation of this set of associated movements. Ritter (1993) has demonstrated that epaxial muscles of extant varanid lizards aid in postural stability during locomotion. He further sugests that such action might be characteristic of the Amniota (Ritter, 1995, 1996). The morphological complex associated with alternation of vertebral sturcture could have enhnaced this function significantly in basal amniotes.

***Atlas-axis complex***

Whereas the dorsal vertebrae of the taxa studied do exhibit some variability, the configuration of the atlas-axis complexes is significantly more conservative (Sumida and Lombard, 1991). The atlas-axis complex (Fig. 5) is a multipartite complex composed of the following elements: paired proatlas, atlantal intercentrum and pleurocentrum, atlantal neural arches, axial intercentrum and pleurocentrum, and axial neural arch. In certain of the taxa the central elements are paired. All elements demonstrate varying degrees of fusion.

The atlantal and axial intercentra abut, precluding exposure of the atlantal pleurocentrum on the ventral side of the axial column. The axial pleurocentrum is a single element that does reach the ventral midline. Among mature seymouriamorphs and all other more derived taxa, the atlantal pleurocentrum is represented by a single ossification. However, it must be noted that immature specimens of *Seymouria* still retain paired pleurocentral components of the atlas (Sumida and Lombard, 1991; Sumida *et al.*, 1992). The atlas-axis complex in *Westlothiana* is not known (Smithson *et al.*, 1994). Diadectomorphs and all of the more traditionally defined amniotes share three features: the possession of atlantal neural spines; fusion of the axial neural arch with a tall, blade-like spine to the axial centrum; and articulation (usually fusion) of the atlantal pleurocentrum with the dorsal aspect of the axial intercentrum.

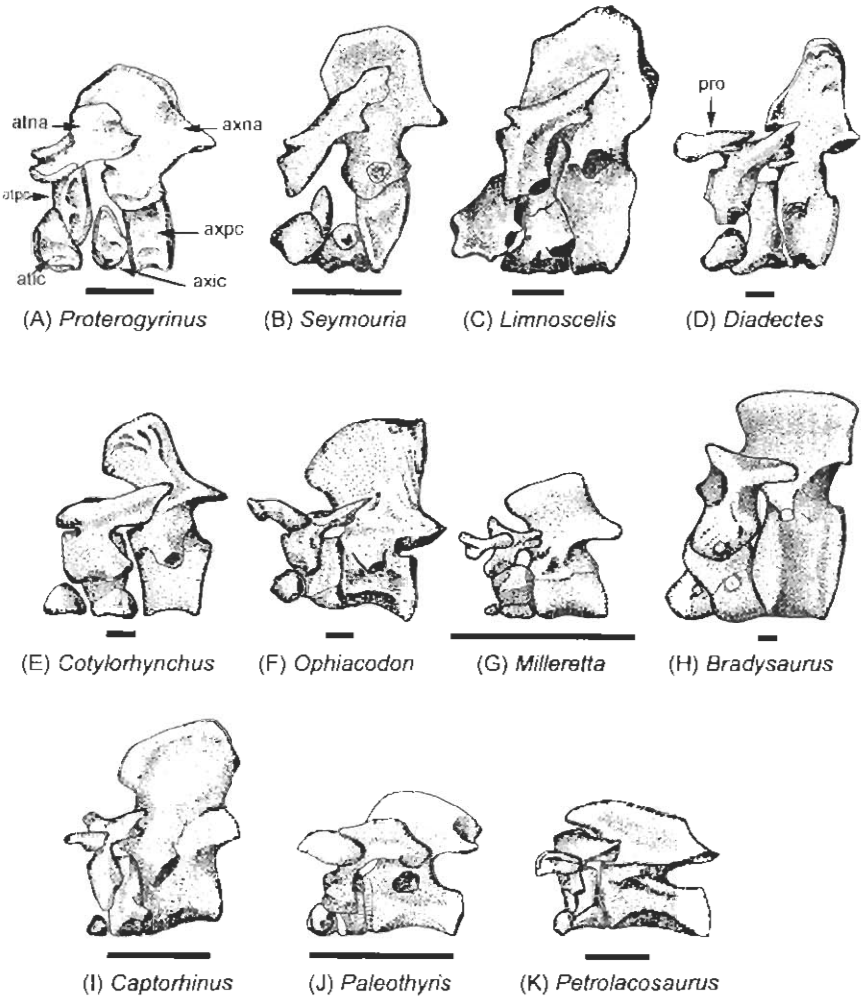
In addition to adaptations to stabilize the column in association with the recovery stroke of the pectoral limb in some of the taxa, there

was likely a need to prevent undue lateral swinging of the head during locomotion. Consolidation of the component elements of the complex and an increase in the stabilizing function of occipital muscles are features of all the taxa considered. This trend is carried to its greatest extreme in diadectomorphs and more traditionally defined amniotes. The fusion of the components of the axis vertebra and the enlargement of its neural spine provided for a larger origin of the obliqus capitus magnus, rectus capitus posterior, and spinalis capitis muscles, as well as the nuchal ligament. Fusion of the atlantal pleurocentrum and axial intercentrum further reduced movement in the complex. The posterior projections of paired atlantal neural arches to either side of the axial neural spine likely restricted movement of the atlas relative to the axis and about the spinal axis in general. This restricted any potential movement to the atlantal pleurocentrum-basioccipital joint. All the muscles originating on the axis inserted onto the skull near the sagittal plane, in a position more suitable for dorso-ventral stabilization than for medio-lateral movement of the atlanto-occipital joint. Contraction of the obliquus capitus magnus would have pulled the skull dorsally and caudally toward the axial neural spine, aiding in holding up the head and stabilizing the joint.

## APPENDICULAR SKELETON

With the conspicuous exception of Holmes (1977, 1980), few since the early work of Romer (1922) have concentrated on both the osteological and muscular components of the basal tetrapod limb.

**Figure 5**. Left lateral views of the atlas-axis complex of taxa near the origin of amniotes. Except where noted, all illustrations are after Sumida *et al.* (1992). (A) The embolomerous anthracosaurian *Proterogyrinus*; (B) the seymouriamorph *Seymouria*; (C) the diadectomorph *Limnoscelis*; (D) the diadectomorph *Diadectes*; (E) the caseosaurian pelycosaur *Cotylorhynchus*; (F) the eupelycosaurian pelycosaur *Ophiacodon*; (G) the millerettid *Milleretta* (partially after Gow, 1972); (H) the parieasaur *Bradysaurus* (partially after Boonstra, 1934); (I) the captorhinid reptile *Captorhinus*; (J) the protorothyridid reptile *Paleothyris*; (K) the araeoscelidian reptile *Petrolacosaurus*. All scalebars are equivalent to 1 cm except G where it equals 0.5 cm. Abbreviations: atic, atlantal intercentrum; atna, atlantal neural arch; atpc, atlantal pleurocentrum; axic, axial intercentrum; axna, axial neural arch; axpc, axial pleurocentrum; pro, proatlas. ➔




(A) *Proterogyrinus* (B) *Seymouria* (C) *Limnoscelis* (D) *Diadectes*

(E) *Cotylorhynchus* (F) *Ophiacodon* (G) *Milleretta* (H) *Bradysaurus*

(I) *Captorhinus* (J) *Paleothyris* (K) *Petrolacosaurus*

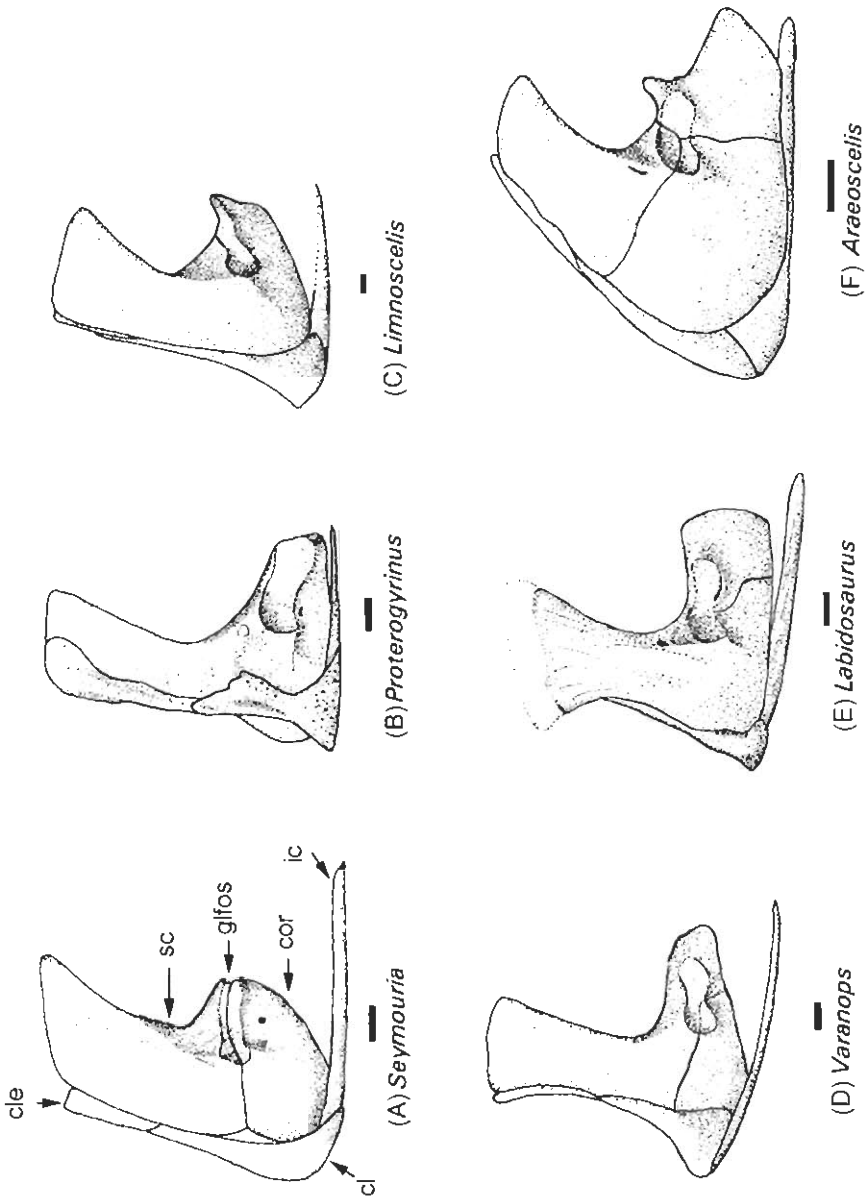
That the appendicular elements supply fewer characters for phylogenetic analyses than do the cranium and lower jaws only compounds this bias. Of the few surveys of tetrapod limb structure that exist, most do not include the more distal antebrachial, crural, and pedal structures; those that do address these areas are generally limited to consideration of single taxa (Romer, 1957; Holmes, 1977, 1980; Sumida, 1989a).

***Pectoral Girdle and Limb***

Heaton's (1980) inability to produce cladistically useful features of the pectoral girdle in his attempt to distinguish among groups of primitive tetrapods highlights the conservative nature of the complex. The pectoral girdle is a multipartite structure incorporating dermal and endochondral elements (Fig. 6). Over time, the endochondral elements have increased in relative mass in the girdle at the expense of the dermal elements. A median, dermal interclavicle is the only unpaired element of the girdle. Paired dermal clavicles and cleithra form the anterior edge of the complex. On each side, a more robust endochondral scapulocoracoid dominates the remainder of the girdle. Primitively, the scapulocoracoid consisted of only dorsal scapular and ventral coracoid ossifications, with the glenoid cavity spanning their articulation. Two coracoid ossifications is a more derived condition. Unfortunately, the pectoral girdle in the potentially intermediate *Westlothiana* is extremely poorly preserved.

The more basal, distinctly anthrocosaurian condition of the pectoral girdle retains significant development of the dermal elements. Robust clavicular elements are retained in all the taxa surveyed here, and Romer (1922) reconstructed this region as a important area of origin for the clavicular head of the deltoid complex; however, its anterior orientation indicates that it probably provided attachment of

**Figure 6.** Left lateral views of the pectoral girdle in taxa near the origin of amniotes. (A) The anthracosaurian *Proterogyrinus* (partially after Holmes, 1984; Romer, 1970); (B) the seymouriamorph *Seymouria* (partially after White, 1939); (C) the diadectomorph *Limnoscelis*; (D) the caseosaurian pelycosaur *Varanops* (partially after Langston and Reisz, 1981); (E) the captorhinid reptile *Labidosaurus*; (F) the araeoscelidian reptile *Araeoscelis* (partially after Vaughn, 1955). Abbreviations: ant cor, anterior coracoid; cl, clavicle; cle, cleithrum; cor, coracoid; icl, interclavicle; post cor, posterior coracoid; s, scapula. All scalebars are equivalent to 1 cm. ➔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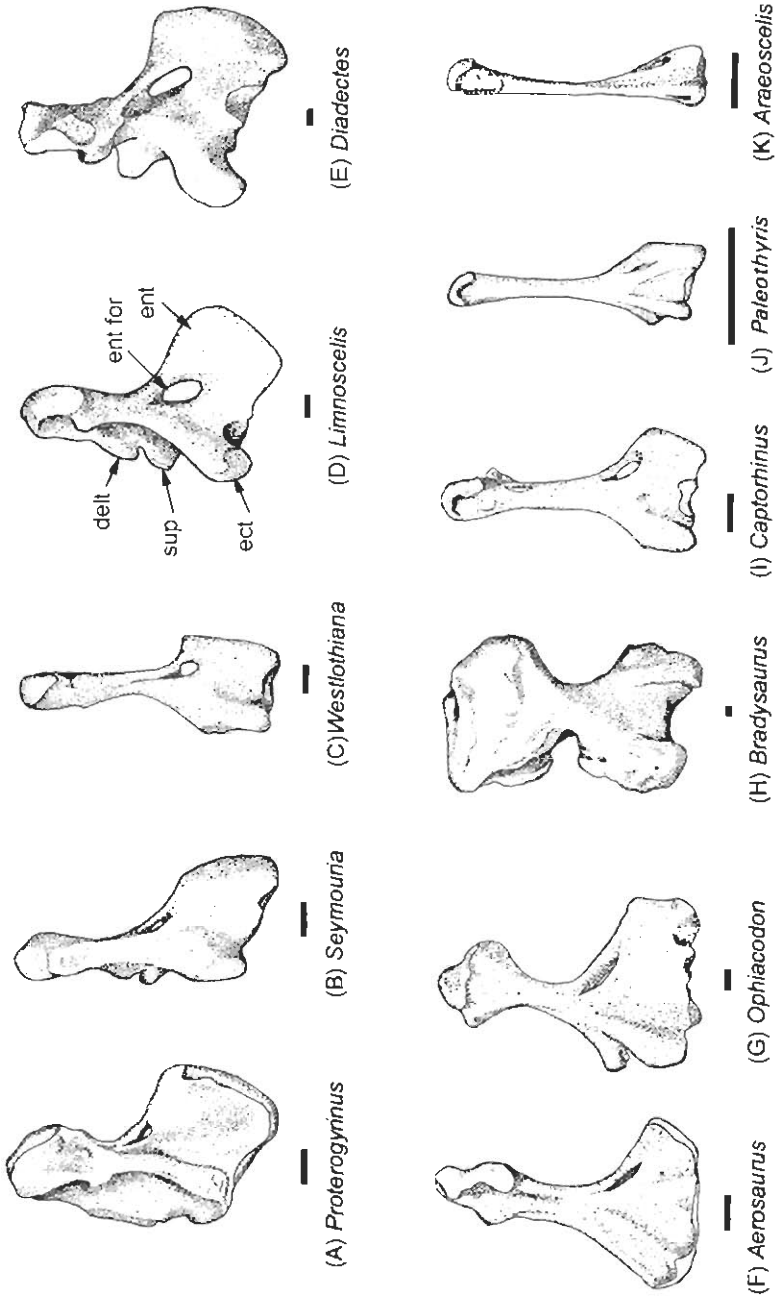
(A) *Seymouria*
(B) *Proterogyrinus*
(C) *Limnoscelis*
(D) *Varanops*
(E) *Labidosaurus*
(F) *Araeoscelis*

episternal and omohyoid musculature of the neck as well. The cleithrum is reduced to a splint in most amniote taxa. Primitively it is large, extending to the dorsal limit of the girdle in *Proterogyrinus*, *Seymouria*, and diadectomorphs. In amniotes other than synapsids the scapulodeltoid musculature probably originated exclusively from the scapular ossification, whereas in anthroacosaurians it likely spanned the scapula-cleithrum articulation. Pelycosaurs are transitional between these two conditions. *Proterogyrinus*, *Seymouria*, and diadectomorphs share the primitive condition of a broad scapular blade and single coracoid ossification. More derived taxa possess separate anterior and posterior coracoid ossifications.

Whether the coracoid is composed of one or two elements, the configuration of the glenoid fossa is remarkably conservative among tbe taxa surveyed. It is traditionally described as "screw shaped", wherein the articular surface approximates a partially helical strap; the anterior portion of the fossa faces ventrolaterally, the middle almost directly laterally, and the posterior portion dorsolaterally (Fig. 6). It appears that the cartilaginous covering of the articular surfaces of the glenohumeral joint was rather thin (Holmes, 1977; Sumida, 1989a), allowing reasonable hypotheses of movement to be based on the manipulation of bony elements alone. The articular surfaces of the glenoid and humerus are closely congruent, a condition that likely dictated a highly constrained and stereotyped humeral excursion. In forms as disparate as *Seymouria*, the robust parieasaur *Bradysaurus*,

**Figure 7.** Reconstructions of left humeri of taxa near the origin of amniotes in distal, ventral aspect. (A) The anthracosaurian *Proterogyrinus* (from Holmes, 1984); (B) the seymouriamorph *Seymouria*; (C) *Westlothiana* (partially after Smithson *et al.*, 1994); (D) the diadectomorph *Limnoscelis*; (E) the diadectomorph *Diadectes* (partially after Romer, 1956); (F) the caseosaurian pelycosaur *Aerosaurus* (partially after Langston and Reisz, 1981); (G) the primitive eupelycosaur *Ophiacodon*; (H) the parieasaur *Bradysaurus* (after Boonstra, 1934); (I) the captorhinid reptile *Captorhinus*; (J) the protorothyridid reptile *Paleothyris* (partially after Heaton and Reisz, 1986); (K) the araeoscelidian reptile *Petrolacosaurus* (after Reisz, 1981); and (L) the araeoscelidian reptile *Araeoscelis* (partially after Vaughn, 1955). All scalebars equal 1 cm. Abbreviations: delt, deltoid process; ect, ectepicondyle; ent, entepicondyle; ent for, entepicondylar foramen; sup, supinator process. ➔


ent for
ent
delt
sup
ect
(A) Proterogyrinus
(B) Seymouria
(C) Westlothiana
(D) Limnoscelis
(E) Diadectes
(F) Aerosaurus
(G) Ophiacodon
(H) Bradysaurus
(I) Captorhinus
(J) Paleothyris
(K) Araeoscelis

and the comparatively gracile araeoscelidian *Petrolacosaurus*, the screw shaped glenoid is retained.

Romer (1922, 1956) characterized the humerus of Paleozoic tetrapods as essentially tetrahedral, an organizational perspective that has been adopted by nearly all subsequent workers. In simplified terms, the axes of the proximal and distal articular surfaces are at nearly right angles to one another. Figure 7 demonstrates these features and significant structural landmarks. In most forms, the proximal articular surface has a high degree of congruence with the glenoid articulation. The anterior region of the proximal articular surface is concave, matching the ventrolaterally directed convexity of the leading surface of the glenoid. Similarly congruent relationships exist for the more posterior surfaces of the glenoid and humeral head. Jenkins (1971) and Holmes (1977) have shown that the complementary articular surfaces constrain a rotation of the humerus along its long axis as it is retracted. At maximal protraction of the humerus, the humeral concavity at the leading margin of the humeral articular head fits snugly into an anterior glenoid convexity, orienting the distal articular surface cranioventrally. Retraction of the humerus prescribes rotation of the humerus on its long axis, resulting in a ventralward orientation of the distal humeral articulation by the middle of the excursion arc and a posteroventral orientation at the end of the arc. Unfortunately, no extant taxa exhibit a gleno-humeral joint similar to the screw-shaped joint of late Paleozoic tetrapods. However, independent analyses of the forelimb in captorhinids and pelycosaurs (Jenkins, 1971; Holmes, 1977; Sumida, 1989a) have all converged on an interpretation similar to that summarized here.

Skeletal indicators of the muscular role critical in postural support dominate the proximal humerus. Although not clearly defined in *Seymouria* or *Westlothiana*, a well developed process for insertion of the latissimus dorsi is extremely well-developed in diadectomorphs, synapsids, and most basal sauropsids (Fig. 7). Its development in tetrapods with a broad range of body sizes is perhaps indicative of increased importance of the retractor musculature in these taxa generally. Extremely broad surfaces of attachment on the dorsal and ventral surfaces of the proximal humeral head are indicative of significant attachments of the scapulohumeralis and coracobrachialis

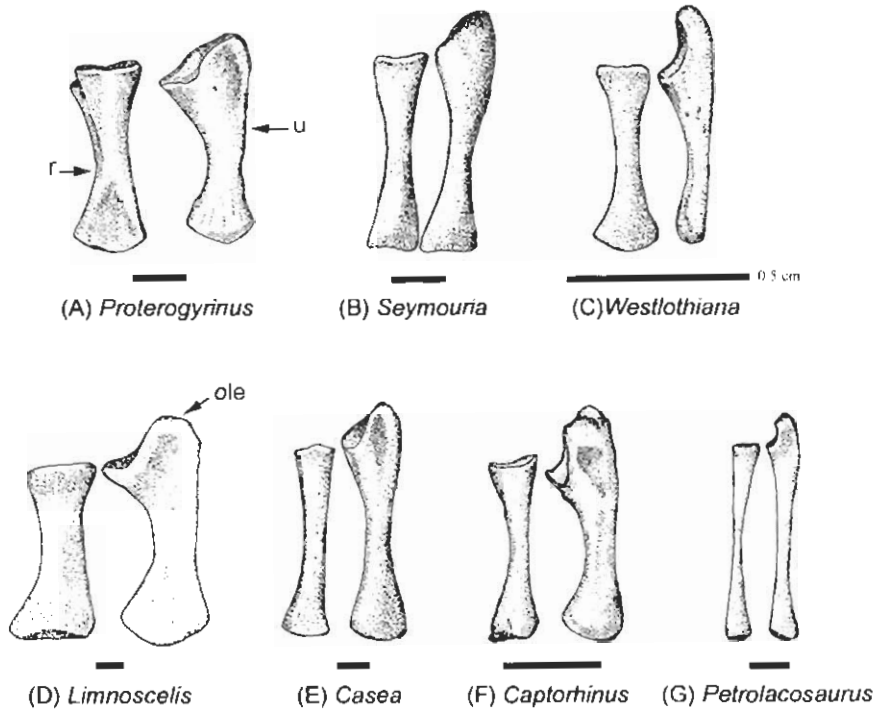



**Figure 8.** Reconstructions of right antebrachial elements of taxa near the origin of amniotes. (A) The anthracosaurian *Proterogyrinus* (from Holmes, 1984); (B) the seymouriamorph *Seymouria*; (C) *Westlothiana* (partially after Smithson *et al.* 1994); (D) the diadectomorph *Limnoscelis*; (E) the caseosaurian pelycosaur *Casea* (after Romer and Price, 1940); (F) the captorhinid reptile *Captorhinus* (from Holmes, 1977); and (G) the araeoscelidian reptile *Petrolacosaurus* (after Reisz, 1981). Elements are shown slightly disarticulated to facilitate viewing of both the radius (left) and ulna (right). All scale bars equal 1 cm except for C where it equals 0.5 cm. Abbreviations: ole, olecranon process; r, radius; u, ulna.

musculature respectively. The deltopectoral crest is robust in all taxa surveyed.

Whereas the proximal and distal articular heads of the humerus are similarly well developed in all taxa considered, the proportions of the intervening humeral shaft reflect the individual body proportions of each taxon. The humeral shaft is extremely short and almost indistinct in the heavy-bodied *Proterogyrinus*, *Seymouria*, diadectomorphs, parieasaurs, large pelycosaurs, and larger

captorhinids. The shaft is slimmer and more elongate in the more gracile *Westlothiana*, protorothyridids, millerettids, protorothyridids, smaller pelycosaurs, small captorhinids, and araeoscelidians. In conjunction with a short humeral shaft, the supinator, entepicondylar, and ectepicondylar processes are robust. The extreme development of these processes provided enormous levers for supinator, flexor, and extensor musculature of the forearm, respectively. Holmes (1977) has suggested that the antebrachium must have been very nearly horizontal at the beginning of the forelimb power stroke, requiring extensive flexor musculature originating from the entepicondyle to maintain postural support during this part of the step cycle. All of the taxa examined here appear to have had such well developed flexor musculature. It is not until diadectomorphs and more derived taxa that the ectepicondyle is better developed, indicating that the contribution of muscular extensors of the antebrachium to propulsion and postural support evolved somewhat later.

Between the entepicondyle and ectepicondyle are an extremely well-developed capitulum and trochlea for radial and ulnar articulations, respectively. Congruence between the distal humerus and antebrachial elements was high, further stereotyping potential movements. The trochlear notch of the ulna is easily recognizable, but the development of a distinct olecranon process that extends well above it is not clearly evident in *Proterogyrinus* or *Seymouria*. An olecranon is present in *Westlothiana* but is not well developed, perhaps because the forelimbs are extremely small size (Smithson *et al.*, 1994). In association with a well-developed olecranon process, the ulnar trochlea is deep and directed anteromedially in diadectomorphs and the Amniota. Manipulation of the components of the elbow joint demonstrates that the anteromedially directed trochlea produces a posterolaterally directed extension of the elbow joint and propulsion. A more efficient lever accommodated the propulsive force delivered by the triceps musculature as the olecranon became more prominent.

In their analysis of the shoulder musculature of varanid lizards Jenkins and Goslow (1983) demonstrated that all three heads of the triceps musculature fired during the middle of propulsive phase. As the firing patterns seen in varanids were broadly similar to those of mammals they characterized as "primitive", they concluded that the

activity patterns must have been inherited from some common ancestor of extant reptiles and mammals. Interpolation of this suggestion into the scenario described previously would suggest that in at least some groups of Paleozoic tetrapods similar firing patterns of the triceps musculature may well have occurred. Jenkins and Goslow (1983) further indicated that the vertebral column of varanids exhibited a lateral convexity toward the support phase at the midpoint of the propulsive phase. Similar orientations of the vertebral column may have existed in captorhinid reptiles (Heaton and Reisz, 1980; Sumida, 1989a) and other late Paleozoic tetrapods (Sumida, 1991). Anteromedial force provided by the triceps and directed by the anteromedially oriented trochlear notch of the ulna may have compensated at least partially for the lateral component of vertebral movement near the propulsive forelimb (Figs. 4 and 9).

The presumed attachment of the radius to the ulna via an interosseous membrane and the potentially free rotation of the radius on the capitulum likely indicates that the movement of the radius was primarily limited somewhat by the movement of the ulna on the humerus. A comparison of the potential movements at the distal end of the antebrachium is more difficult, as knowledge of carpal elements is extremely limited in *Proterogyrinus, Seymouria, Westlothiana*, and diadectomorphs. Without knowledge of the manus in these taxa, an understanding of the possible transformations across the transiton to the amniote condition is not possible. However, a brief description of the condition in representative amniotes (Fig. 10) can lend some insight into certain of their locomotory capabilities. The radiale is essentially a distal extension of the radius, whereas the intermedium and ulnare function together as an extension of the ulna. The distal articular surfaces of these two complexes are in separate planes of the manus, precluding a transverse joint at either of their ends. The most reasonable suggestion remains that of Holmes (1977; supported by Sumida, 1989a): The flat articular surfaces of the bones of the manus were all capable of minimal movements at each joint; summed, this allowed for a moderately flexible forefoot. Although the origin of the pisiform is unclear, diadectids, *Tseajaia*, pelycosaurs, captorhinids, protorothyridids, and araeoscelidians all have a pisiform on the ulnar side of the carpus. It is particularly well developed in captorhinids and

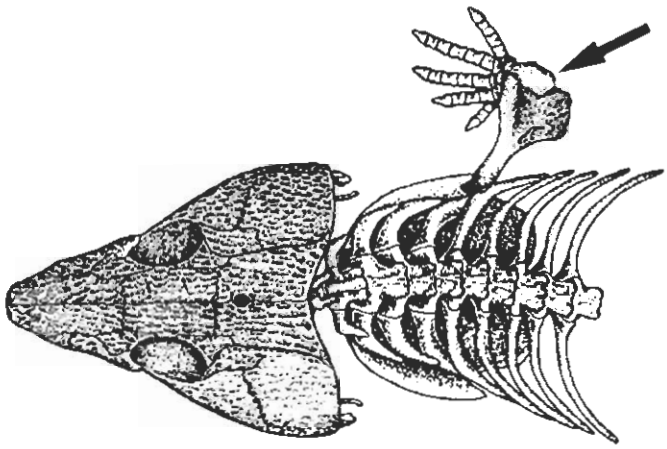


**Figure 9.** Dorsal view of the anterior portion of the vertebral column and the right forelimb near the middle of the support phase in a captorhinid reptile (based partially on Heaton and Reisz, 1980; Holmes, 1977) to aid in demonstrating the direction of force constrained by the anteromedially directed trochlea of the ulna toward the convexity of the laterally bent vertebral column. Arrow represents the direction of force only and is not meant to imply magnitude.

pelycosaurs, providing a stout lever for the flexor carpi ulnaris and extensor carpi ulnaris. This condition is taken to an extreme in the large captorhinid *Labidosaurus*, which also extends the radiale medially in an analogous fashion on the radial side of the carpus.

In most of the taxa surveyed, the fourth digit of the manus is the largest (Fig. 10), however only protorothyridids (Fig. 10C) and araeoscelidians (Fig. 10D) exhibit a dramatically longer fourth digit (Vaughn, 1955; Carroll, 1969b; Reisz, 1981; Heaton and Reisz, 1986). Thus, models dependent on rotation of the manus and pushoff via the elongate fourth digit (e.g. Rewcastle, 1981) are not applicable to basal amniotes and their presumptive sistergroups. More realistically, the model is applicable only to protorothyridids, araeoscelidians and their derivatives.

### *Pelvic Girdle and Limb*

The structure of the pelvic girdle (Fig. 11) is more conservative than that of the pectoral girdle: Dorsal ilia articulate with sacral

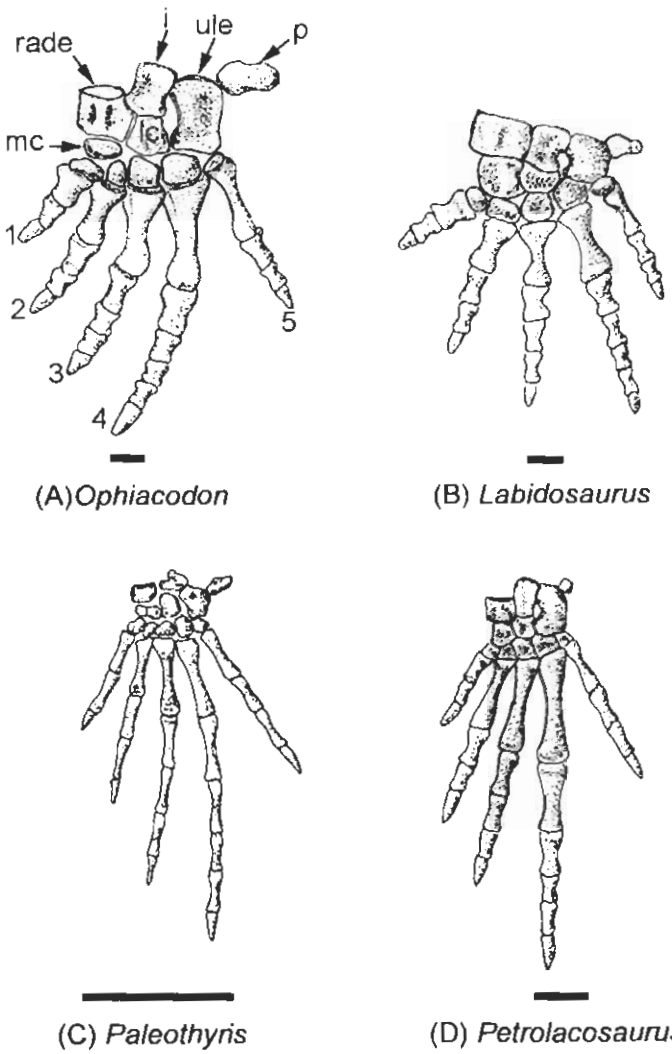


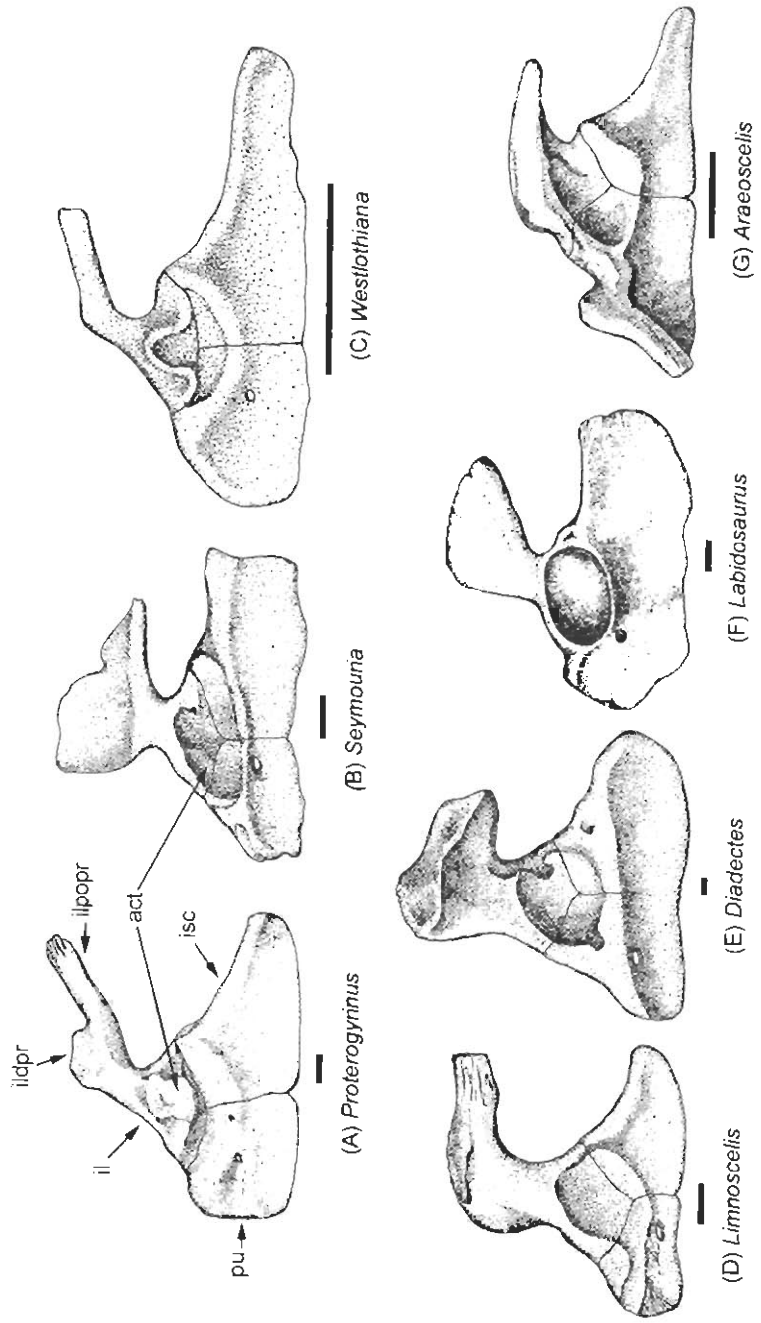

**Figure 10**. Reconstructions in dorsal view of left manus of basal amniotes. (A) The basal eupelyocosaurian pelycosaur *Ophiacodon* (partially after Romer and Price, 1940); (B) the captorhinid reptile *Labidosaurus*; (C) the protorothyridid reptile *Paleothyris* (after Carroll, 1969b); and (D) the araeoscelidian reptile *Petrolacosaurus* (after Reisz, 1981). In some cases, reconstructions presented here are based on the right manus, but all are presented in left view to facilitate comparison. All scalebars equal 1 cm. Abbreviations: i, intermedium; lc, lateral centrale; mc, medial centrale; p, pisiform; rade, radiale; ule, ulnare; 1-5, first to fifth digits.

vertebrae in varying numbers, often depending on the size of the animal, and quadrangular, plate-like pubic and ischial elements meet one another in the ventral midline. Substantive differences are found primarily in the degree of development of processes of the ilium.

Primitively, as in *Proterogyrinus* and (presumably) *Westlothiana*, the ilium has distinct dorsal and posterior processes. The dorsal process articulated medially with the sacral ribs and laterally served as the origin of the iliofemoralis. Romer (1922, 1956) suggested that the posterior process was a point of origin for tail musculature useful in aquatic locomotion. However, in his detailed analysis of *Proterogyrinus*, Holmes (1984) took issue with this interpretation, pointing out that extant, terrestrial taxa retain similar processes. It is likely that the iliofibularis muscle arose from the posterior process, whereas the iliotibialis probably arose from a ridge running ventral to the junction between the two processes. The processes remain distinguishable and both are robust in *Seymouria*. In diadectomorphs, basal synapsids, parieasaurs, and other reptiles the two processes have essentially consolidated into a single iliac blade. Although this probably did not affect the origins of the iliofemoralis and iliofibularis muscles significantly, it effectively moved the origin of the iliotibialis away from the hip joint, providing it a somewhat greater mechanical advantage in extension of the knee joint. Parieasaurs are unique in having a prodigious anterior extension of the iliac blade, one that is probably associated with the development of as many as four sacral ribs for support in this heavy-bodied group.

Some debate has centered around the function of an externally directed "shelf" of the ilium in diadectomorphs, a feature Heaton (1980) recognized as a synapomorphy of the group. Romer (1922,

**Figure 11.** Reconstructions of the pelvic girdle in taxa near the origin of amniotes. (A) The anthracosaurian *Proterogyrinus* (after Holmes, 1984); (B) the seymouriamorph amphibian *Seymouria* (partially after White, 1939); (C) *Westlothiana* (after Smithson *et al.*, 1994); (D) the diadectomorph *Limnoscelis* (after Berman and Sumida, 1991); (E) the diadectomorph *Diadectes* (after Romer 1922, 1956); (F) the captorhinid reptile *Labidosaurus* (after Sumida, 1989a); and (G) the araeoscelidian reptile *Araeoscelis* (after Vaughn, 1955). All scalebars equal 1 cm. Abbreviations: act, acetabulum; il, ilium; ildpr, dorsal process of ilium; ilpopr, posterior process of ilium; isc, ischium; pu, pubis. ➔


ildpr
ilpopr
act
isc
il
pu
(A) Proterogyrinus
(B) Seymouria
(C) Westlothiana
(D) Limnoscelis
(E) Diadectes
(F) Labidosaurus
(G) Araeoscelis

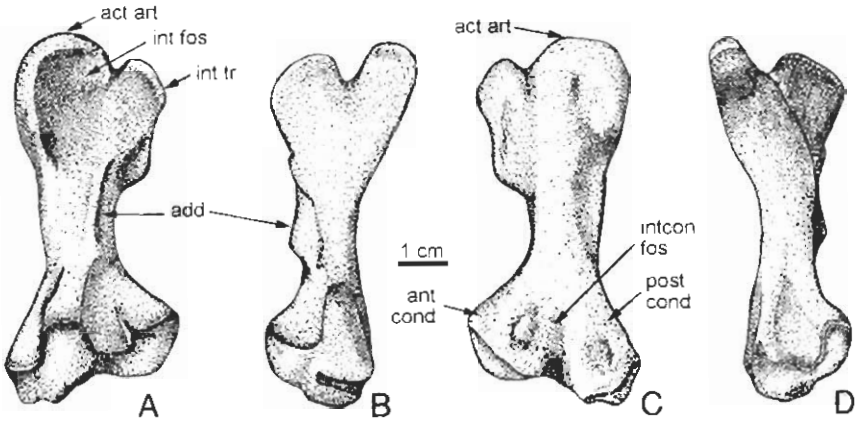



**Figure 12.** Reconstructions of left femur of the captorhinid reptile *Labidosaurus hamatus* illustrating important processes and landmarks. (A) Ventral view; (B) anterior view; (C) dorsal view; and (D) posterior view. Proximal end of the femur is toward the top of the page in all illustrations. Abbreviations: act art, acetabular articulation; add, adductor crest; ant cond, anterior condyle; intcon fos, intercondylar fossa; int fos, intertrochanteric fossa; int tr, intrnal trochanter; post cond, posterior condyle.

1956) and Olson (1936b) suggested that this represented a "rebuilding" of the iliac blade in diadectomorphs and a transitional stage between amphibians and reptiles in which the epaxial muscles were segregated to the dorsal aspect of the sacroiliac articulation. This implies that the lateral iliac shelf of diadectomorphs is homologous to the iliac blade of more derived tetrapods. Epaxial musculature appears to have been restricted to the medial side of the iliac blade in reptiles (Sumida, 1989a), but the potential form of their insertion into the iliac shelf of diadectomorphs is not clear. In pointing out the existence of a similar shelf in the temnospondyl amphibian *Eryops* Olson (1936b) speculated that it may have served as an expansion of the area of origin for the iliofemoralis muscle (Olson, 1936b).

The acetabulum is markedly conservative in its construction in all taxa surveyed (Fig. 11). It is unremarkable for the most part,

smoothly concave and almost circular in outline, with a slight pinching of the recess near its dorsal limit in some taxa. Apparently, it allowed significant potential movement of the femoral head. The proximal head of the femur (Figs. 12 and 13) itself is not nearly as complex as that of the humerus. It is broadly curved and smoothly convex in all taxa examined here. The articular surface is roughly pitted in *Proterogyrinus* and *Seymouria*. Smithson *et al.* (1994) described the proximal articular surface of the femur in *Westlothiana* as more similar to that of protorothyridids than that of *Proterogyrinus*. Smithson *et al.* (1994) illustrate it as more poorly ossified as those of basal reptiles, however this could be an artifact of preservation. In fact, *Westlothiana* is more similar to diadectomorphs and primitive amniotes in the possession of a well developed internal trochanter. The internal trochanter is relatively very large in *Limnoscelis* and *Diadectes*, and distinct in synapsids and basal reptiles. Even the more gracile araeoscelidians display clear evidence of the internal trochanter (Vaughn, 1955; Reisz, 1981).

Although basal anthracosaurs and batrachosaurs surely possessed the puboischiofemoralis internus muscle, the bony markers of its attachment are best seen in *Westlothiana* and more derived taxa. Romer (1922) proposed that the puboischiofemoralis internus in reptiles retains the ancestral functions of protraction and elevation of the femur. All taxa surveyed have an extremely deep intertrochanteric fossa, evidence of the continuing importance of the insertion of the puboischiofemoralis externus as an adductor of the hip joint for postural support. *Seymouria* and heavy-bodied parieasaurs show the most extreme development of the intertrochanteric fossa.

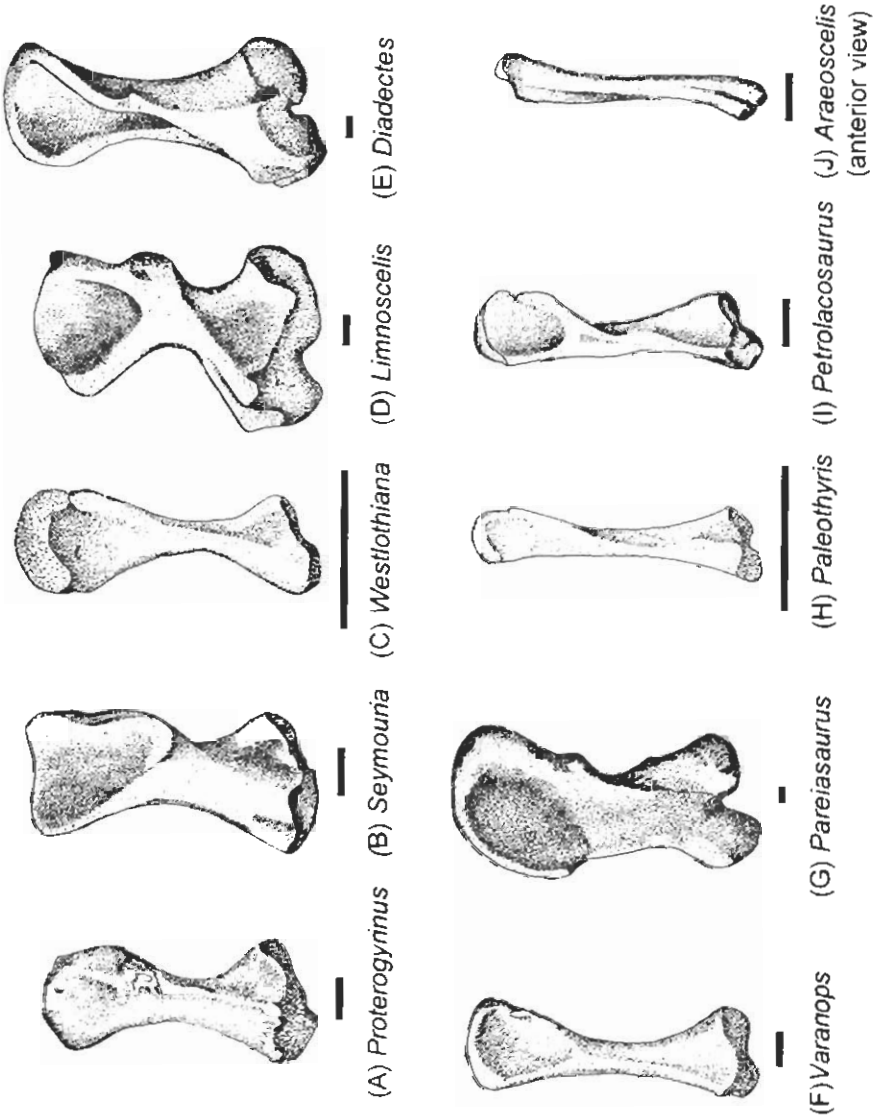
All the taxa surveyed possess a well developed adductor crest on the ventral surface of the femur (Fig. 13). Those with a prominent internal trochanter have refined the crest into a prominent, sharp ridge with a pronounced rugosity for attachment of the caudofemoralis muscle. Contrary to the interpretation of Romer (1922), it appears that the caudofemoralis was a muscle of significant mass in basal amniotes, and possibly their sister groups. Numerous studies of extant reptiles (Snyder, 1954; Rewcastle, 1981; Gatesy, 1990) have confirmed the importance of the caudofemoralis in femoral retraction; given the osteological evidence for its robust presence, the suggestion that it was

similarly important in basal amniotes is quite reasonable. In taxa with extremely short femoral shafts the adductor crest runs in a markedly oblique angle from proximal to distal, probably to allow as long an insertion of the adductor musculature as possible. As the shaft becomes more distinct in more derived taxa the adductor crest nearly parallels the long axis of the femur.

The femur in *Araeoscelis* (Fig. 13J) (Vaughn, 1955; Reisz *et al.*, 1984) is distinctly sigmoid, a condition found in other taxa (tentatively) assigned to the family Araeoscelidae [*Kadaliosaurus* (Credner, 1889); *Zarcasaurus* (Brinkman *et al.*, 1984)]. In their studies on extant mammals, Bertram and Biewener (1988) suggested that although bone curvature may augment stress during loading, it serves to greatly increase loading predictability. This requirement may have been met in the strongly sigmoid curvature of the femur in araeoselids, a more lightly built and presumably agile group.

The distal end of the femur is divided into distinct anterior and posterior condyles in all taxa surveyed (Figs. 12 and13). The anterior femoral condyle reaches further distally in strict dorsal or ventral view. The majority of the distal femoral articulation accommodates the tibia (Fig. 15). Holmes (1984) noted that in *Proterogyrinus* there is little ventral exposure of the femoral articulation, whereas the proximal tibial articulation is rather flat, indicative of the need to keep the knee joint somewhat below the level of the acetabulum to allow the crus to be directed toward the substrate. The articular surfaces of the knee joint are not well ossified in *Seymouria* or *Westlothiana*, precluding speculation about its orientation. In diadectomorphs and basal amniotes, a prominent ridge may be seen traversing the proximal head

**Figure 13.** Reconstructions of the left femur in taxa near the origin of amniotes. (A) the anthracosaurian *Proterogyrinus* (after Holmes, 1984); (B) the seymouriamorph *Seymouria* (partially after White, 1939 and Romer, 1956); (C) *Westlothiana* (partially after Smithson *et al.*, 1994); (D) the diadectomorph *Limnoscelis* (partially after Romer, 1956; Berman and Sumida, 1991); (E) the diadectomorph *Diadectes* (after Romer, 1956); (F) the caseosaurian pelycosaur *Varanops*; (G) the pareiasaurian *Pareiasaurus* (after Romer, 1956); (H) the protorothyridid reptile *Paleothyris* (partially after Carroll, 1969c); (I) the araeoscelidian reptile *Petrolacosaurus* (from Reisz, 1981); and (J) the araeoscelidian reptile *Araeoscelis*, anterior view (after Vaughn, 1955 and Romer, 1956). All scalebars equal 1 cm. ➔


(A) Proterogyrinus
(B) Seymouria
(C) Westlothiana
(D) Limnoscelis
(E) Diadectes
(F) Varanops
(G) Pareiasaurus
(H) Paleothyris
(I) Petrolacosaurus
(J) Araeoscelis
(anterior view)

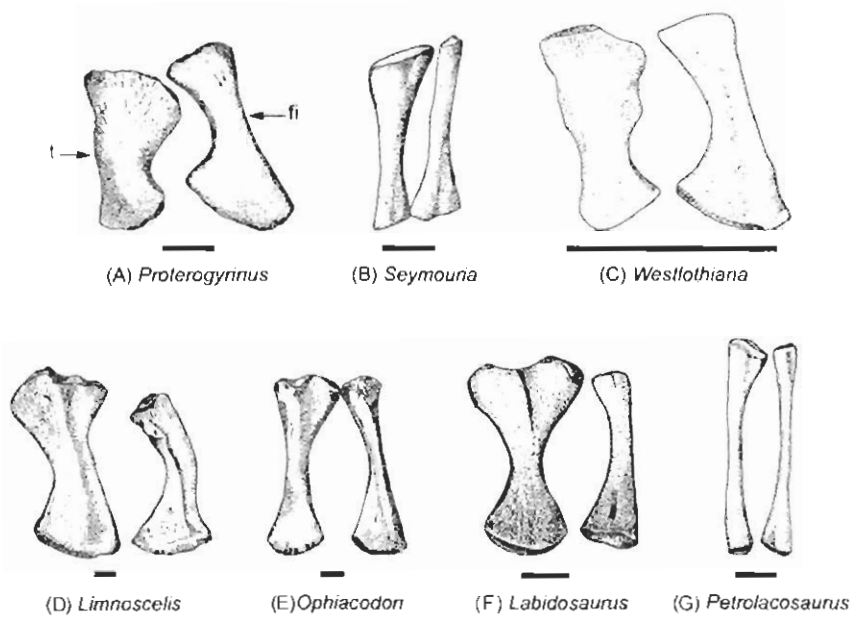



**Figure 14.** Reconstructions of left crural elements of taxa near the origin of amniotes in dorsal (preaxial) view. (A) The anthracosauroidian *Proterogyrinus* (after Holmes, 1984); (B) the seymouriamorph *Seymouria*; (C) *Westlothiana* (partially after Smithson *et al.* 1994); (D) the diadectomorph *Limnoscelis*; (E) the eupelycosaurian pelycosaur *Ophiacodon* (after Romer and Price, 1940); (F) the captorhinid reptile *Labidosaurus* (after Sumida, 1989a); and (G) the araeoscelidian reptile *Petrolacosaurus* (after Reisz, 1981). Elements are shown slightly disarticulated to facilitate viewing of both the tibia and fibula. All scalebars equal 1 cm. Abbreviations: fi, fibula; t, tibia.

of the tibia, dividing it into a larger anteromedial surface and a somewhat smaller posterolateral surface. Articulation of well preserved materials represented by pelycosaurs and the captorhinids *Labidosaurus* and *Captorhinus* indicates that the ridge lay against the inner edge of the posterolateral femoral condyle and in line with the intercondylar fossa (Fig. 15). Based on this scheme of articulation, the crus is estimated to have laid at an angle of approximately 75 to 80° to the femoral axis (Holmes, 1977; Sumida, 1989a). Because the acetabular articulation was relatively free, it is not possible to determine whether the femur angled slightly ventrally (instead of

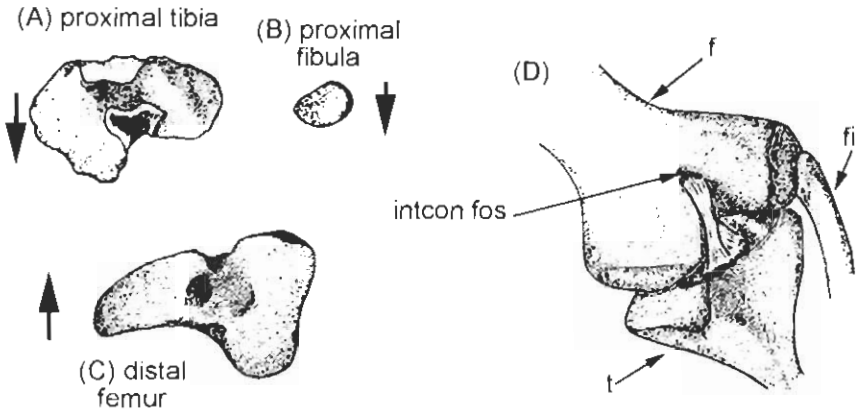



**Figure 15.** Articular surfaces of the left knee joint of the captorhinid reptile *Labidosaurus hamatus*. (A) Proximal surface of tibia; (B) proximal surface of fibula; (C) distal surface of femur; and (D) reconstruction of hyperflexed knee joint to demonstrate position of reconstructed cruciate ligaments. Large arrows indicate the dorsal direction. Abbreviations as in Figs. 12 and 14.

directly lateral), if the crus was positioned at an angle other than 90° to the substrate, or if there was a combination of the two.

Tibial length is approximately half that of the femur in *Proterogyrinus* and *Westlothiana*. This measure approaches 65 to 75% in *Seymouria* and other more derived taxa except for araeoscelidians, where the measures are approximately subequal. Distinguishing muscle scars on crural elements with confidence is extremely difficult. Some taxa have a well developed cnemial crest on the tibia, but its presence may be a function of size of the animal. In most cases, the tibia is more robust than the fibula. Among diadectomorphs plus amniotes, the tibia is conspicuously more robust and longer than the fibula. However, in clearly anamniote batrachosaurs the fibula approaches the tibia in size and is, in fact, longer than the tibia in *Proterogyrinus* and *Westlothiana*.

The differential lengths of the tibia and fibula (Fig. 14) have clear implications for the cruro-pedal articulation. The tarsus in *Seymouria* is poorly known; however, reconstructions for those in

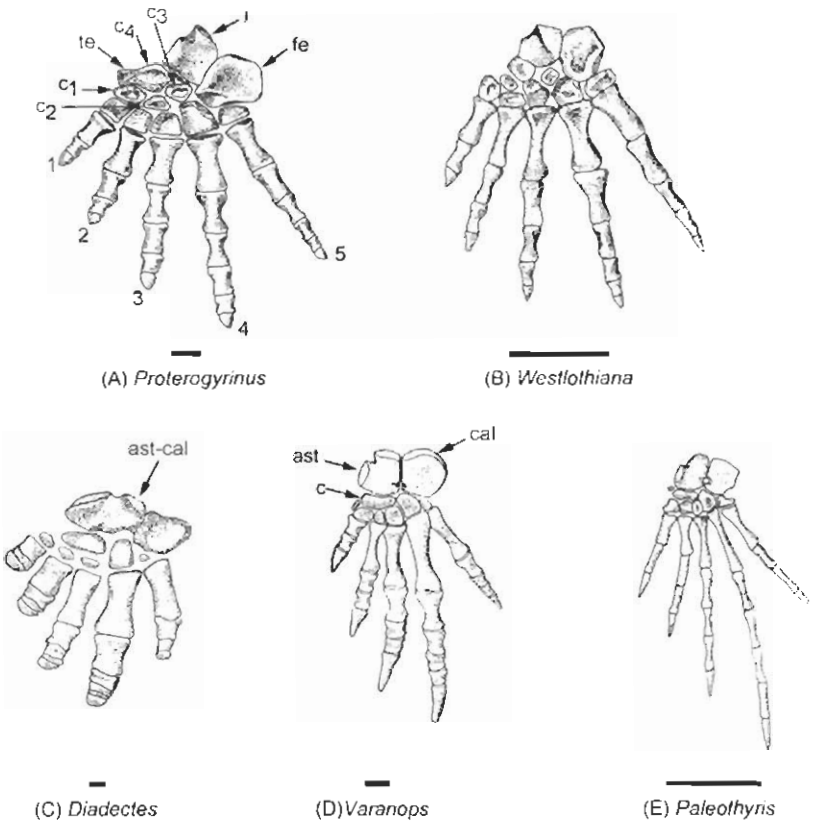


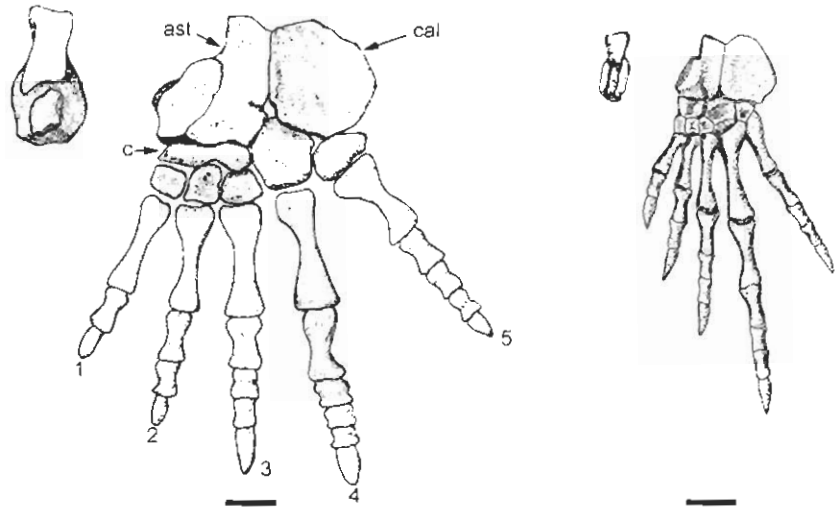

**Figure 16.** Reconstructions of the left pes in taxa near the origin of amniotes. All are in dorsal view except for B which is in ventral view. (A) The anthracosaurian *Proterogyrinus* (after Holmes, 1984); (B) *Westlothiana* (after Smithson *et al.*, 1994); (C) the diadectomorph *Diadectes* (after Romer and Byrne, 1931; Romer, 1944); (D) the caseosaurian pelycosaur *Varanops*; and (E) the protorothyridid reptile *Paleothyris* (after Carroll, 1969b). All scalebars equal one centimeter. Abbreviations: ast, astragalus; ast-cal, fused astragalus-calcaneus; c, centrale; cal, calcaneus; $c_{1-5}$; first to fifth centralia; fe, fibulare; i, intermedium; te, tibiale; 1-5, first to fifth digits.

*Proterogyrinus* and *Westlothiana* are available (Holmes, 1984; Smithson, *et al.*, 1994). More primitively, the fibula articulates with a distinct fibulare and intermedium. It appears that this might be the case in *Seymouria*, but poor preservation makes accurate

determination difficult. In *Proterogyrinus* the tibia articulates with the intermedium and an element that Holmes (1984) restored as a fused tibiale plus fourth centrale. Smithson *et al.* (1994) restored the distal articulation of the tibia in *Westlothiana* with the intermedium and tibiale only. In no instance is there an articular plane that completely traverses the foot either at the proximal end of the tarsus or within it. The only complete transverse "joint" of the foot is between distal tarsal elements and the metatarsals.

Considerable argument has surrounded the homologies of the "astragalus" in amniotes. Rieppel (1993) suggested that the amniote astragalus is a neomorph that resulted from ontogenetic repatterning and that it is not homologous to the tibiale plus intermedium (Peabody, 1951). As a group very near the origin of amniotes, the Diadectomorpha would be a logical choice for information regarding this question. However, the group provides only confusing or autapomorphic features. The tarsus is poorly known in *Limnoscelis*. Independent tibiale, intermedium, and fibulare are known but poorly preserved in *Tseajaia*. In some (Romer, 1944; Rieppel, 1993) but not all (Romer and Byrne, 1931) specimens of *Diadectes* (Fig. 16) all three elements appear to be fused into a single "astragalo-calcaneal" element, apparently unique to the genus. Difficulties in understanding the homologies of tarsal elements make a diagnosis of the transformations of the ankle joint difficult, allowing a comparison of potential movements but not encouraging speculation on the homologies of joint articulations.

In amniotes in which these elements can be identified with confidence , the proximal tarsus (Figs. 16 and 17) has consolidated as an L-shaped astragalus and an approximately oval calcaneum. The fibula articulates with both the astragulus and the calcaneum, whereas the tibia articulates with the astragalus only and at a level distinct from that of the fibula. Most araeoscelidians have a unique articulation between the astragalus and tibia in which a distinct ridge of the tibia is set firmly into a trough of the astragalus, essentially creating a "locked" tibiotarsal joint (Vaughn, 1955; Reisz, 1981) (Fig. 17). More generally, the interposition of the fourth distal tarsal prevents the distal astragalo-calcaneal surfaces from defining a midtarsal joint in basal amniotes. As in the anamniotes surveyed in this study, the only




(A) *Labidosaurus* (B) *Petrolacosaurus*

**Figure 17.** Articular surfaces of the left pes in (A) the captorhinid reptile *Labidosaurus* and (B) the araeoscelidian reptile *Petrolacosaurus*. Both are accompanied by a medial view of the astragalus to demonstrate the unique tongue and groove surface for the locking tibio-talar joint in *Petrolacosaurus* (after Reisz, 1981). Scalebars equal 1 cm. Abbreviations as in Fig. 16.

mesotarsal joint appears to be between distal tarsals and metatarsal elements. Although amniotes retain an intrapedal joint, the proximal tarsus may have been a less flexible mosaic of bones. This is taken to an extreme in araeoscelidians.

Digits of the pes are extensions of the flexible foot. As in the manus, the fourth digit is usually longer than the others in most of the taxa analyzed here but not remarkably so. Schaeffer (1941) suggested that the flexible mosaic of the tarsus in basal reptiles was similar to that in salamanders in which the foot is oriented anteriorly and the entire flexible mosaic was used in a progressive propulsion. Brinkman (1980, 1981) reiterated this view in his examinations of extant iguanid lizards. Rewcastle (1981) proposed that the condition of an extremely elongate fourth digit and the resulting mode of locomotion in iguanid lizards was a reasonable model for "primitive reptilian locomotion". It appears that only the more advanced protorothyridids and

araeoscelidians exhibit a phalangeal morphology consistent with Rewcastle's (1981) hypothesis. Thus, Rewcastle's model may be correct, but perhaps at a position within the Reptilia as opposed to a condition characteristic of all amniotes.

## STRUCTURAL SUMMARY

The preceding survey demonstrates that there is no clear and distinct transitional point in locomotor features between anamniote and amniote "sides" of the transition. Rather, there is a continuum of changes. Following is a summary of that continuum of changes mapped onto the hybrid hypothesis of relationships presented in Figure 1.

***All Taxa Considered***

- In all of the taxa considered the pleurocentrum is the dominant element of the vertebral centrum, possibly facilitating stiffening the vertebral column to aid in terrestrial support.
- The abutment of the atlantal intercentrum and axial intercentrum preclude exposure of the atlantal pleurocentrum on the ventral side of the vertebral column.
- The configuration of the gleno-humeral articulation is extremely conservative; the glenoid is screw shaped and the humeral head has high congruence, stereotyping considerably the movements at that joint.
- The humerus may be described generally as tetrahedral, although this feature is considerably streamlined in more derived, gracile forms.
- The manus is a flexible mosaic of bones, though it becomes less so in diadectomorphs and amniotes.
- The pelvic girdle is composed of three fused bones on each side, ilium, ischium, and pubis. The acetabulum is a concave depression at the intersection of these bones and is relatively conservative throughout the taxa included in this survey.
- The concave acetabulum received a smoothly convex femoral head in an articulation that was less constrained that the glenohumeral articulation.

- A deep intertrochanteric fossa of the proximal femoral head underscores the importance of the puboischiofemoralis externus as a postural support muscle.
- A well developed adductor crest underscores the importance of associated postural support muscles to all taxa surveyed here.

***Batrachosauria***

- In seymouriamorphs and the majority of sister taxa, the neural arches become extremely robust or "swollen," one example of the use of an arched construction to lend structural integrity to the supporting function of the vertebral column. This condition is lost in *Westlothiana* (although it retains convexly bowed neural arches), most synapsids, protorothyridids, and certain araeoscelids.
- The dorsal and posterior processes of the iliac blade no longer exist as separate entities. This may have moved the origin of the iliotibialis muscle further from the hip joint, enhancing its function in extension of the knee.

**Westlothiana** + ***Diadectomorpha*** + ***Amniota***

- Although the puboischiofemoralis internus muscle certainly existed in more primitive taxa, its insertion on a visible and well-developed internal trochanter is first noted here.
- A pronounced rugosity for the attachment of the caudofemoralis musculature demonstrates the importance of that muscle as the largest retractor of the femur.

***Cotylosauria (Diadectomorpha + Traditionally Defined Amniota)***

- Variability in the construction of neural spines is present, though relatively irregular and inconsistent in seymouriamorphs. It is first seen as a column-long phenomenon in at least some specimens of diadectomorphs.
- A number of features of the atlas-axis complex point to stabilization of the head: fusion of the axial neural arch and centrum, fusion of the atlantal pleurocentrum to the dorsal aspect of the axial intercentrum, and bracketing of the axial neural spine by posteriorly directed atlantal neural arches.
- A well-developed insertion for the latissimus dorsi muscle is more obvious, although this may be a reflection of size.

- Extreme development of the entepicondyle suggests that flexor musculature of the antebrachium becomes more important in support at the initiation of the contact phase of the forelimb.
- The olecranon process is distinctly larger, suggestive of the increasing importance of the triceps musculature in extension of the elbow and propulsion by the forelimb.
- The anteromedial orientation of the ulna helps to compensate for the lateral component of force generated by the vertebral column as the triceps fires at the midpoint of the propulsive arc of the forelimb.
- A pisiform bone on the ulnar side of the manus may provide for a slightly more efficient lever of the extensor carpi radialis and flexor carpi radialis muscles.
- Tibial length increases beyond half that of the femur, typically measuring 70% or more that of the femur.

***Amniota (Synapsida + "Parareptilia" + Eureptilia)***

- The scapular blade is narrower than in basal outgroups.
- The humeral shaft becomes markedly more distinct, although the heavy-bodied parieasaurs are an exception. This condition is also found in *Westlothiana*, though it may be convergent due to the extremely small size of its limbs.
- A ridge traversing the proximal tibial head increases the congruence of fit with the distal femoral articular surface.
- A true astragalus develops in association with a consolidation of the tarsus and the tarsus becomes a less flexible mosaic of bones.

***Sauropsida ("Parareptilia" + Eureptilia)***

- The cleithrum is reduced to a splint, consolidating the scapulodeltoid musculature on the scapular blade; basal pelycosuarian-grade synapsids present an intermediate condition in this regard.

***Eureptilia (Captorhinidae + Protorothyrididae + Araeoscelidia)***

- Alternation of neural spine height and structure (accompanied by mediolaterally tilted zygapophyses) is refined as a phenomenon most commonly located near the limb girdles. The condition likely allowed muscular control of the vertebral column to aid in stabilization of the trunk and in the recovery stroke of limbs.

***Protorothyrididae + Araeoscelidia***

- The expanded neural arch diminishes in conjunction with the more lightly built, gracile form of the skeleton. Because some specimens of araeoscelidians retain expanded neural arches, protorothyridids may be autapomorphic for this character, a condition developed convergently with synapsids and *Westlothiana*. In conjunction with this, alternation of neural spine height is not seen in groups lacking expanded neural arches.
- The manus is narrower and more lightly built and the fourth digit is significantly longer than the others. A high degree of rotation of the manus and pushoff via the elongate digit may have evolved in this group.
- As in the manus, the pes is narrower and more lightly built than in outgroups and the fourth digit is considerably longer than the others. Rotation of the pes and pushoff via the elongate digit (as in iguanid lizards) may have evolved in this group.

***Araeoscelidia (Basal Diapsida)***

- Araeoscelidians are characterized by extremely elongate cervical vertebrae. The head is small and light, resulting in a definitive neck region.
- The femur is slightly sigmoid in shape, allowing greater load predictability.
- In conjunction with the more gracile form of the skeleton, the tibia and femur are nearly equal in length.
- In most, a "locked" tibiotarsal joint lends even more stiffness and structural integrity to the ankle joint.

## DISCUSSION AND SPECULATION

As suggested at the beginning of this survey, this study is not intended to define synapomorphies of successively nested taxa. Rather, it has demonstrated that the traditionally accepted notion of a transition to a relatively more "terrestrially adapted" amniote is not appropriate. The anamniote sister groups to the Amniota are also clearly terrestrial taxa.

Anthracosauroids and seymouriamorphs share many locomotor features with amniotes. The primitive tetrapod *Westlothiana* combines

a mosaic of primitive and derived features of both the axial and appendicular skeleton. This is not surprising, as its cranial morphology presents a similarly complex admixture of features. In their analysis of its phylogenetic placement, Smithson *et al.* (1994) were forced to redefine the Amniota if it were to be included, or to designate *Westlothiana* as an amniote stem taxon. In either case, the condition of *Westlothiana* further demonstrates that there are few defining boundaries between anamniotes and amniotes, at least based on postcranial features.

The composition and phylogenetic placement of the Diadectomorpha has long been a subject of debate. Most investigators suggest that the Diadectomorpha shares a more recent common ancestor with amniotes than with any other group (e.g. Heaton, 1980; Gauthier t al., 1988; Laurin and Reisz, 1995, also this volume). On the other hand, Berman *et al.* (1992) and Lee and Spencer (this volume) advocate the inclusion of the Diadectomorpha within the Amniota. Hopefully, further study of these groups will resolve these interpretive differences. Meanwhile, it is worthwhile noting that diadectomorphs plus amniotes (Cotylosauria, *sensu* Heaton, 1980) share more locomotor features than any other transitional node in this study. The difficulty in determining where to draw the line between "amphibians" and "amniotes" underscores the blurry nature of the transition between the groups when locomotor features are considered.

One postcranial feature that does appear to support amniote monophyly is the presence of an astragalus. Perhaps significantly, locomotor differences between synapsids and sauropsids appear to minimal. The heavy-bodied pariesaurs are admittedly specialized in their development of proportionally robust supporting structures, but other osteological features are not substantively different. Reptiles on the other hand demonstrate the greatest suite of common features next to the diadectomorphs + amniotes. This may be a result, in part, of the strong emphasis given to that group in recent years. When large thorough studies (e.g. Lee, 1993, 1995; Laurin and Reisz, 1995) of the "parareptilian" (basal sauropsid) groups are integrated into our knowledge of amniote phylogeny, a concomitant understanding of locomotory capabilities may also result.

The close relationship of protorothyridids and araeoscelidians is now strongly supported (Heaton and Reisz, 1986; Berman *et al.*, 1992; Smithson *et al.*, 1994), a close relationship that appears to be reflected in the similarity of locomotor features surveyed here. Together, they will likely provide important out-group data for the analysis of more derived reptilian groups.

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## LITERATURE CITED

Berman, D. S, R. R. Reisz, and D. A. Eberth. 1987. *Seymouria sanjuanensis* (Amphibia, Batrachosauria) from the Lower Permian Cutler Formation of north-central New Mexico and the occurrence of sexual dimorphism in that genus questioned. *Canadian Journal of Earth Sciences*, 24:1769-1784.

Berman, D. S, and S. S. Sumida. 1990. A new species of *Limnoscelis* (Amphibia, Diadectomorpha) from the Late Pennsylvanian Sangre de Cristo Formation of central Colorado. *Annals of Carnegie Museum*, 59:303-341.

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. *Journal of Paleontology*, 66:481-499.

Bertram, J. E. A., and A. A. Biewener. 1988. Bone curvature: sacrificing strength for load predictability? *Journal of Theoretical Biology*, 131:75-92.

Bolt, J. R., and R. E. Lombard. 1992. Nature and quality of the fossil evidence for otic evolution in early tetrapods. Pages 377-403 in: *Evolutionary Biology*

*of Hearing* (A. Popper, D. Webster, and R. R. Fay, eds.). New York: Springer-Verlag.

Boonstra, L. D. 1931. Parieasaurian studies. Part VII.–On the hindlimb of two little-known parieasaurian genera: *Anthodon* and *Parieasaurus*. *Annals of the South African Museum*, 28:429-503.

Boonstra, L. D. 1934. Parieasaurian studies. Part XI.–The vertebral column and ribs. *Annals of the South African Museum*, 31:49-68.

Brinkman, D. 1980. Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia; Iguanidae) and other lizards. *Canadian Journal of Zoology*, 58:277-289.

Brinkman, D. 1981. The hindlimb step cycle of *Iguana* and primitive reptiles. *Journal of Zoology*, London, 181:91-103.

Brinkman, D., D. S Berman, and D. A. Eberth. 1984. A new araeoscelid reptile, *Zarcasaurus tanyderus*, from the Cutler Formation (Lower Permian) of north-central New Mexico. *New Mexico Geology*, 6:34-39.

Carroll, R. L. 1969a. Origin of reptiles. Pages 1-44 in: *Biology of the Reptilia, Volume 1, Morphology* (C. Gans, A. d'A. Bellairs, and T. S. Parsons, eds.), New York: Academic Press..

Carroll, 1969b. Problems of the origin of reptiles. *Biological Reviews*, 44:393-432.

Carroll, 1969c. A middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology*, 43:151-170.

Carroll, R. L. 1970. The ancestry of reptiles. *Philosophical Transactions of the Royal Society of London* B, 257:267-308.

Carroll, R. L. 1995. Problems of the phylogenetic analysis of paleozoic choanates. *Bulletin of the Museum of Natural Historiy, Paris*, 17:389-445.

Clark, J., and R. L. Carroll. 1973. Romeriid reptiles from the Lower Permian. *Bulletin of the Museum of Comparative Zoology*, 144:353-407.

Credner, H. 1889. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. VIII. Theil. *Kadaliosaurus priscus* Cred. *Zeitschrift deutsche geologische Gesellschaft*, 41:319-342.

Dilkes, D. W., and R. R. Reisz. 1986. The axial skeleton of the Early Permian reptile *Eocaptorhinus laticeps* (Williston). *Canadian Journal of Earth Sciences*, 23:1288-1296.

Gatesy, S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology*, 16:170-186.

Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. The early evolution of the Amniota. Pages 103-155 in: *The Phylogeny and Classification of the Tetra-pods, Volume 1, Amphibians, Reptiles, Birds*, Systematics Association Special Volume No. 35A (M. J. Benton, ed.). Oxford: Clarendon Press.

Gow, C. E. 1972. The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). *Journal of Zoology*, London, 167:219-264.

Haughton, S. H., and L.D. Boonstra. 1931. Parieasaurian Studies. Part VI.–The osteology and myology of the locomotor apparatus. A–Hind limb. *Annals of the South African Museum*, 28:297-366.

Heaton, M. J. 1980. The Cotylosauria: a reconsideration of a group of archaic tetrapods. Pages 497-551 *in: The Terrestrial Environment and the Origin of Land Vertebrates*, Systematics Association Special Volume No. 15 (A. L. Panchen, ed.). London: Academic Press.

Heaton, M. J., and R. R. Reisz. 1980. A skeletal reconstruction of the Early Permian captorhinid reptile *Eocaptorhinus laticeps* (Williston). *Journal of Paleontology*, 54:136-143.

Heaton, M. J., and R. R. Reisz. 1986. Phylogenetic relationships of captorhinomorph reptiles. *Canadian Journal of Earth Sciences*, 23:402-418.

Holmes, R. 1977. The osteology and musculature of the pectoral limb of small captorhinids. *Journal of Morphology*, 152:101-140.

Holmes, R. 1980. *Proterogyrinus schelli* and the early evolution of the labyrinthodont pectoral limb. Pages 351-376 in: *The Terrestrial Environment and the Origin of Land Vertebrates* (A. L. Panchen, ed.), Systematics Association Special Volume No. 15, London: Academic Press.

Holmes, R. 1984. The Carboniferous amphibian *Proterogyrinus scheelei* Romer, and the early evolution of tetrapods. *Philosophical Transactions of the Royal Society of London* B, 306:431-527.

Holmes, R. 1989. Functional interpretations of vertebral structure in Paleozoic amphibians. *Historical Biology*, 2:111-124.

Hopson, J. A. 1991. Systematics of the non-mammalian Synapsida and implications of evolution in synapsids. Pages 635-693 *in: The Origin of Higher Groups of Tetrapods: Controversy and Consensus* (H.-P. Schultze and L. Trueb, eds.). Ithaca: Cornell University Press.

Jenkins, F. A. 1971. The postcranial skeleton of African cynodonts. *Bulletin of the Peabody Museum of Natural History*, 36:1-216.

Jenkins, F. A., and G. E. Goslow. 1983. The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exanthematicus*). *Journal of Morphology*, 175:195-216.

Langston, W., and R. R. Reisz. 1981. *Aerosaurus wellesi*, new species, a varanopseid mammal-like reptile (Synapsida: Pelycosauria) from the Lower Permian of New Mexico. *Journal of Vertebrate Paleontology*, 1:73-96.

Laurin, M., and R. R. Reisz. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, 113:165-223.

Lee, M. S. Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science*, 261:1716-1720.

Lee, M. S. Y. 1995. Historical burden in systematics and the interrelationships of 'parareptiles'. *Biological Reviews*, 70:459-547.

Lombard, R. E., and S. S. Sumida. 1992. Recent progress in understanding early tetrapods. *American Zoologist*, 32:609-622.

Olson, E. C. 1936a. The dorsal axial musculature of certain primitive Permian tetrapods. *Journal of Morphology*, 59:265-311.

Olson, E. C. 1936b. The ilio-sacral attachment of *Eryops*. *Journal of Paleontology*, 10:648-651.

Olson, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana: Geology*, 11:3-53.

Peabody, F. 1951. The origin of the astragalus of reptiles. *Evolution*, 5:339-344.

Reisz, R. R. 1980. The Pelycosauria: a review of the phylogenetic relationships. Pages 553-592 in: *The Terrestrial Environment and the Origin of Land Vertebrates*, Systematics Association Special Volume No. 15 (A. L. Panchen, ed.). London: Academic Press.

Reisz, R. R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Special Publication of the Museum of Natural History*, No. 7, 74 pages.

Reisz, R. R. 1986. Pelycosauria. *Handbuch der Palaeoherpetologie*, 17:1-102.

Reisz, R. R., D. S Berman, and D. Scott. 1984. The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. *Journal of Vertebrate Paleontology*, 4:57-67.

Reisz, R. R., D. S Berman, and D. Scott. 1992. The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the Early Permian of Texas. *Zoological Journal of the Linnean Society*, 104:127-184.

Rewcastle, S. C. 1981. Stance and gait in tetrapods: an evolutionary scenario. Pages 239-267 in: *Vertebrate Locomotion* (M. H. Day, ed.), Zoological Society of London Symposium No. 48, London: Academic Press.

Rieppel, O. 1993. Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *Journal of Vertebrate Paleontology*, 13:31-47.

Ritter, D. A. 1993. Epaxial muscle function during lizard locomotion. *American Zoologist*, 33:25A.

Ritter, D. A. 1995. Axial muscle function during lizard locomotion. *American Zoologist*, 35:146A.

Romer, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History*, 46:517-606.

Romer, A. S. 1944. The Permian cotylosaur *Diadectes tenuitectes*. *American Journal of Science*, 242:139-144.

Romer, A. S. 1956. *The Osteology of the Reptiles*. Chicago: The University of Chicago Press.

Romer, A. S. 1957. The appendicular skeleton of the Permian embolomerous amphibian, *Archeria*. *Contributions, Museum of Geology, University of Michigan*, 13:103-159.

Romer, A. S. 1970. A new anthrocosaurian labyrinthodont, *Proterogyrinus scheelei*, from the Lower Carboniferous. *Kirtlandia*, No. 10, 16. pp.

Romer, A. S., and F. Byrne. 1931. The pes of *Diadectes*: notes on the primitive tetrapod limb. *Palaeobiologica*, 4:25-48.

Romer, A. S., and L. W. Price. 1940. *Review of the Pelycosauria*. Geological Society of America Special Paper, No. 28, 538 pages.

Schaeffer, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bulletin of the American Museum of Natural History*, 78:395-472.

Schultze, H.-P. 1987. Dipnoans as sarcopterygians. Pages 39-74 in: *The Biology and Evolution of Lungfishes* (W. E. Bemis, W. W. Burggren, and N. E. Kemp, eds.). New York: Alan R. Liss.

Smithson, T. R. 1989. The earliest known reptile. *Nature*, 314:676-678.

Smithson, T. R., R. L. Carroll, R. L. Panchen, and S. M. Andrews. 1994. *Westlothiana lizziae* from the Visean of East Kirkton, West Lothian, Scotland, and the amniote stem. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 84:383-412.

Snyder, R. C. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *American Journal of Anatomy*, 95:1-36.

Stovall, J. W., L. I. Price, and A. S. Romer. 1966. The postcranial skeleton of the giant Permian pelycosaur *Cotylorhynchus romeri*. *Bulletin of the Museum of Comparative Zoology*, 135:1-30.

Sumida, S. S. 1987. Two different forms in the vertebral column of *Labidosaurus* (Captorhinomorpha, Captorhinidae). *Journal of Paleontology*, 61:155-167.

Sumida, S. S. 1989a. The appendicular skeleton of the early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. *Journal of Vertebrate Paleontology*, 9:295-313.

Sumida, S. S. 1989b. Reiuterpretation of vertebral structure in the early Permian pelycosaur *Varanosaurus acutirostris* (Amniota, Synapsida). *Journal of Vertebrate Paleontology*, 9:419-426.

Sumida, S. S. 1991. Vertebral morphology, alternation of neural spine height, and structure in Permo-Carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. *University of California Publications in Zoology*, 122:1-133.

Sumida, S. S., and R. E. Lombard. 1991. The atlas-axis complex in the late Paleozoic genus *Diadectes* and the characteristics of the atlas-axis complex across the amphibian to amniote transition. *Journal of Paleontology*, 65:973-983.

Sumida, S. S., R. E. Lombard, and D. S Berman. 1992. Morphology of the atlas-axis complex of the late Palaeozoic tetrapod suborders Diadectomorpha and Seymouriamorpha. *Philosophical Transactions of the Royal Society of London*, 336:259-273.

Vaughn, P. P. 1955. The Permian reptile *Araeoscelis* restudied. *Bulletin of the Museum of Comparative Zoology*, 113:305-467.

Vaughn, P. P. 1970. Alternation of neural spine height in certain Permian tetrapods. *Bulletin of the Southern California Academy of Sciences*, 164:1-30.

White, T. E. 1939. Osteology of *Seymouria baylorensis* Broili. *Bulletin of the Museum of Comparative Zoology*, 85:325-409.

Williston, S. W. 1911. *American Permian Vertebrates*. Chicago: The University of Chicago Press.