

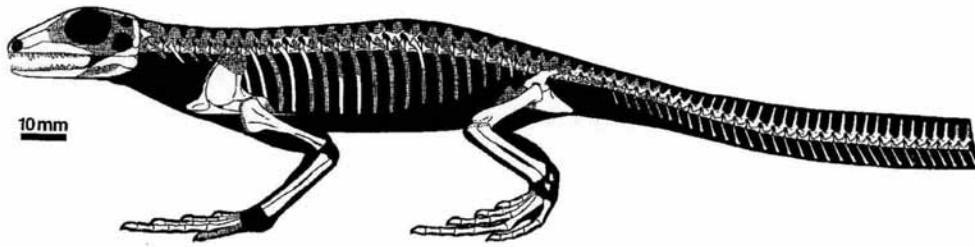
A NEW DIAPSID REPTILE FROM THE UPPERMOST CARBONIFEROUS (STEPHANIAN) OF KANSAS

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ABSTRACT. Diapsids represent one of the most diverse lineages within Amniota, yet, until recently, their Carboniferous record was restricted to one taxon from a single locality near Garnett, Kansas. Accordingly, diapsids were thought not to have undergone the degree of evolutionary radiation which has been attributed to other Carboniferous amniotes. The description of *Spinoaequalis schultzei* gen. et sp. nov. from Upper Carboniferous deposits at Hamilton Quarry, Kansas, indicates that it is closely related to araeoscelidians and provides the first evidence for the diversification of diapsids within the Carboniferous. In addition, *Spinoaequalis* possesses a suite of autapomorphies, most notably to the tail, which display evidence for the earliest known aquatic specialization among amniotes.

DIAPSIDA is one of the most successful groups of amniotes (Carroll 1988) and includes three of the four orders of extant reptiles (crocodiles, lizards, and snakes), dinosaurs including birds, flying reptiles, many aquatic taxa, and other, lesser known, extinct groups. Although diapsids are represented by a long, rich fossil record, little is known of their early history. Araeoscelidia, universally recognized as containing some of the earliest recognized members within Diapsida (Reisz 1977, 1981; Benton 1985; Carroll 1988; Gauthier *et al.* 1988; Evans 1988; Laurin 1991) is represented by two well known genera *Petrolacosaurus* and *Araeoscelis*, and two poorly known forms *Zarcasaurus* Brinkman *et al.*, 1984 and *Kadaliosaurus* Credner, 1889. These taxa are regarded as being representative of the Bauplan from which advanced diapsids evolved (Reisz 1981; Carroll 1988). In addition, due in part to the homogenous morphology of the known members of this clade, it is considered an interesting side branch in diapsid evolution, but one that did not undergo any significant morphological differentiation during its tenure in the Carboniferous. Consequently, increased diapsid diversity is generally thought to coincide only with the appearance of the specialized eosuchians *Claudiosaurus* and *Coeluosaurus* and neodiapsids in the Upper Permian (Laurin 1991).

Reisz (1988) briefly introduced two new diapsids from the Upper Carboniferous Hamilton Quarry of Kansas. He suggested that one of these diapsids may be closely related to araeosceloids (University of Kansas Vertebrate Palaeontology collection KUV 12484), remarking that the limbs possessed similar propodial/epipodial ratios. He chose, however, not to name or classify the specimen formally, but remarked that the unusual caudal anatomy of this amniote was suggestive of aquatic affinities. Further preparation and detailed inspection of its anatomy has permitted a nearly complete skeletal reconstruction (Text-fig. 1). Furthermore, a brief phylogenetic analysis provides strong evidence that this small reptile is indeed a diapsid and the sister taxon to Araeosceloidea. A detailed comparison with later, better known aquatic reptiles (Russell 1967; Currie 1981a; Frey 1982; deBraga and Carroll 1993) has been undertaken to assess its anatomical potential for aquatic propulsion (Hildebrand 1982).



TEXT-FIG. 1. Reconstruction of *Spinoequalis schultzei* gen. et sp. nov. in lateral view; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian. Shaded area represents missing data.

SYSTEMATIC PALAEOLOGY

DIAPSIDA Osborn, 1903
 ARAEOSCELIDIA Williston, 1913

Emended diagnosis. Diapsid reptiles exhibiting long limbs with propodial/epipodial ratios 1:1; anterior margin of scapula slanted posteriorly; and femoral shaft exceeding width of humeral shaft by 50 per cent.

Genus SPINOEQUALIS gen. nov.

Spinoequalis schultzei sp. nov.

Text-figures 1-5

Derivation of name. From the Latin *spina* (spine) and *aequalis* (symmetry) referring to the equal length of caudal neural and haemal spines; specific designation in honour of Dr Hans-Peter Schultze, in recognition of his work on Palaeozoic vertebrates.

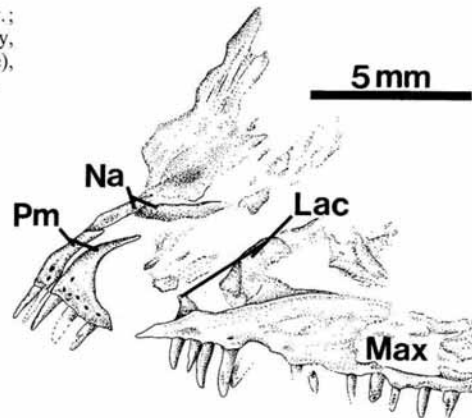
Holotype. KUVF 12484, a nearly complete, articulated, immature individual with a poorly preserved skull, missing the distal portion of the tail. The specimen was collected in three pieces: one containing the snout region, a second containing the rest of the skull and most of the body, and a third piece which contains the hindlimbs, pelvic region, and the preserved portion of the tail.

Type Horizon and Locality. Calhoun Shale, Shawnee Group, Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; Hamilton Quarry near Hamilton, Greenwood County, Kansas.

Diagnosis. A small diapsid reptile distinguished by the following autapomorphies: ventral process of squamosal narrow; trunk ribs holocephalic; caudal neural spines distal to eleventh caudal vertebra elongate, at least 50 per cent. taller than those of proximal caudals; haemal spines are equal in length to the caudal neural spines of same vertebrae; haemal spines increase in length posteriorly; haemal spines with slight distal expansion; caudal centra with a length to height ratio approaching 1:1; caudal neural arches saddle-shaped; transverse processes absent from caudal vertebrae; interclavicle long approaching the length of eight dorsal vertebrae; and acetabulum sub-circular in outline.

Description. The specimen was collected originally as three separate sections, and as a result, it cannot be illustrated as a single figure. Therefore, each block is figured separately (Text-figs 2-4). The smallest piece (Text-fig. 2) contains paired premaxillae, a poorly preserved lacrimal, fragments of what are interpreted as the

TEXT-FIG. 2. *Spinoaequalis schultzei* gen. et sp. nov.; KUVV 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian series (Stephanian of Europe), Upper Pennsylvanian; anterior portion of snout.



nasals, and the left maxilla. Of the two larger pieces, one (Text-fig. 3) has suffered damage over much of the exposed surface (corresponding to the specimen's dorsal surface) and has, therefore, been embedded in bioplastic and prepared from its ventral side. Most of the palate, the right maxilla in lateral view, and the medial half of the posterior portion of the left maxilla, the left prefrontal, the paired frontals in ventral view, and a portion of the right parietal are all preserved in this piece. In addition, the block contains what is left of the cheek region and portions of both lower jaws as well as most of the remainder of the skeleton. The second large piece (Text-fig. 4) which contains the remains of the pelvis, a complete left hindlimb and foot, the right foot, and the preserved region of the tail was prepared from the left side and presents the opposite view from that of the other large piece containing most of the skeleton.

The premaxilla presents the typical diapsid configuration, as the dorsal processes of both bones, as preserved, are quite slender (Text-fig. 2). This agrees with the configuration in both *Petrolacosaurus* and *Araeoscelis* as well as in eosuchians (personal observation) and probably represents a diapsid synapomorphy. Captorhinids, *Protorothyris* and *Paleothyris* possess a comparably broad premaxillary dorsal process which occupies nearly the entire dorsal surface of the snout tip (Carroll 1969; Clark and Carroll 1973; Heaton 1979). The tooth-bearing portion of the premaxilla has portions of three teeth preserved, of which the first is a simple, slender peg. Five teeth are described in *Petrolacosaurus* (Reisz 1981), *Araeoscelis* (Reisz et al. 1984), and *Paleothyris* (Carroll 1969). The reduced number in *Spinoaequalis* may be an autapomorphy of this taxon, but the state of preservation of the tooth-bearing region of the premaxilla is not sufficient to draw a definite conclusion.

The maxilla (Text-figs 2, 5) is similar to the configuration in *Paleothyris* and the araeosceloids *Petrolacosaurus* and *Araeoscelis*. There is a caniniform region, but the caniniform teeth are not much larger than the first premaxillary tooth. The teeth are very slender and are quite similar to those in *Petrolacosaurus*.

The plate-like frontals (Text-fig. 5) have a large orbital margin, and are constricted above the orbits. This latter condition is present in araeosceloid and eosuchian diapsids and represents a synapomorphy of these taxa (Laurin and Reisz 1995).

Much of the posterior half of the cheek (Text-fig. 5) is preserved and the posteroventral border of the lower temporal fenestra is discernible. The configuration differs somewhat from that seen in *Petrolacosaurus* in that the post-temporal bar is composed of a slender ventral process of the squamosal and a shorter dorsal process of the quadratojugal. It appears that the lower temporal fenestra is located farther posteriorly, or is relatively larger in *Spinoaequalis* than in *Petrolacosaurus*. However, the posteroventral margin of the lower temporal fenestra has never been established confidently in *Petrolacosaurus* (Reisz 1981, text-fig. 2).

A sliver of bone, visible directly behind the squamosal, may represent the quadrate. However, the preservation of this region of the skull is poor, and this identification is uncertain.

The palate is only partially exposed. The left pterygoid is visible in ventral aspect and is essentially similar to that of araeosceloids except that the transverse flange is not directed anterolaterally and hence retains the primitive transverse orientation (Text-fig. 5). No other palatal elements are visible except for a small portion of the ectopterygoid. The posterior border of the suborbital fenestra can be detected along the anterolateral edge of the ectopterygoid.



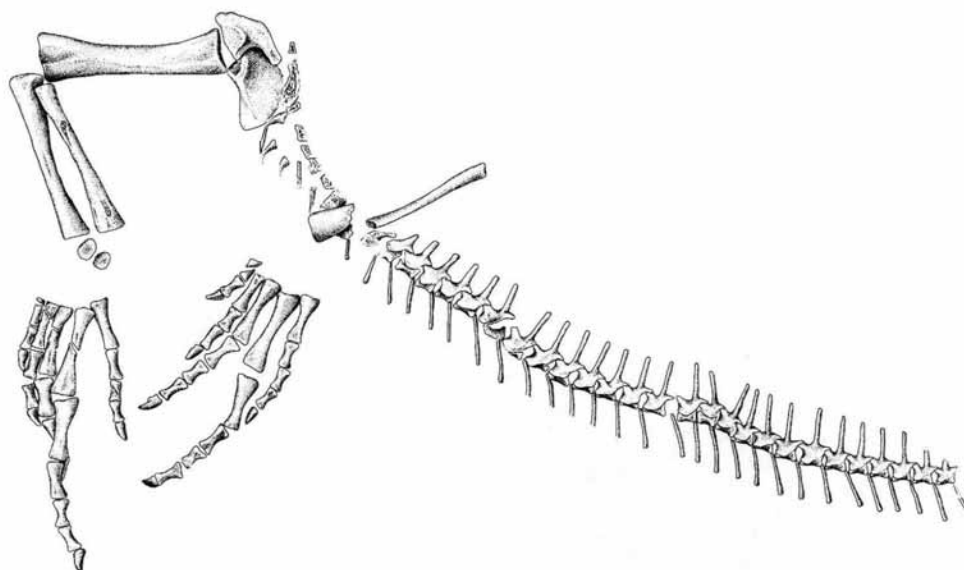
TEXT-FIG. 3. *Spinoaequalis schultzei* gen. et sp. nov.; KUVF 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; ventral aspect of skeleton minus caudal region, $\times 1$.

The braincase and occiput are only incompletely preserved. The exoccipitals are preserved, however, and can be seen as isolated elements. The ventral and lateral borders for the foramen magnum can be seen clearly on the left exoccipital. The posterior margin of the parasphenoid lying behind the overlying posterior half of the lower jaw resembles that of the araeosceloid *Petrolacosaurus* in being concave along its posteriomedial margin. This derived condition may suggest an autapomorphy for Araeoscelidia or perhaps a more inclusive diapsid synapomorphy. This concavity of the parasphenoid exposes the basioccipital to a greater degree than that which is seen in *Paleothyris* (see Carroll 1969, text-fig. 4) or other captorhinomorphs (Clark and Carroll 1973). In these taxa a posteriorly directed flange of the parasphenoid overlies the basioccipital ventrally. A small bone, partially covered by the basioccipital, may represent the opisthotic (Text-fig. 5).

The stapes is a small, robust element (Text-fig. 5) that does not differ in any significant way from the stapes of other early amniotes. The perforating foramen is present and the large footplate suggests a supportive rather than an auditory role for this element in *Spinoaequalis*.

The mandibles are partially preserved, with the nearly complete left jaw ramus exposed medially and the posterior half of the right jaw ramus exposed in lateral view. The generally slender configuration of the lower jaw is quite similar to that found in *Petrolacosaurus*. This slender configuration is certainly the primitive condition for Araeoscelidia, and differs from the much more robust jaws found in *Araeoscelis* (Reisz *et al.* 1984).

Twenty-two presacral vertebrae are visible in *Spinoaequalis* (Text-fig. 3). There is room for an additional four vertebrae within the column making the probable count twenty-six. *Petrolacosaurus* is reconstructed as having twenty-six presacrals (Reisz 1981), but *Araeoscelis* has a long presacral series of twenty-nine vertebrae (Reisz *et al.* 1984). Most of the presacral series in *Spinoaequalis* is exposed only in ventral aspect. Although the bases of the arches can be seen in some of the mid-dorsals and on the axis, little detail can be observed.

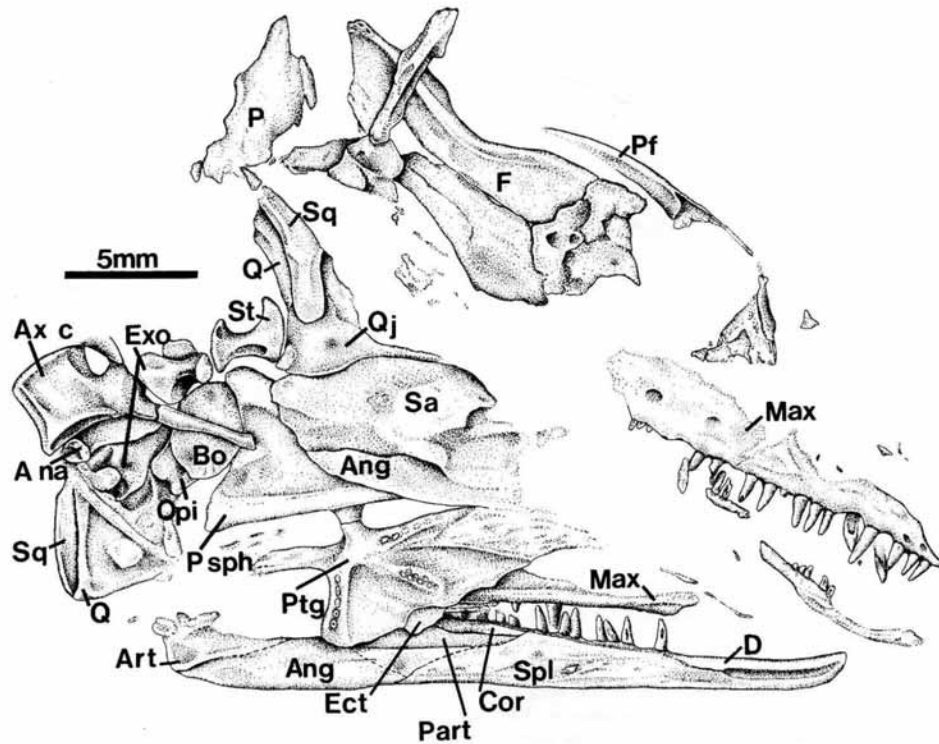


TEXT-FIG. 4. *Spinoaequalis schultzei* gen. sp. nov.; KUVF 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; hindlimb and caudal region, $\times 1.3$.

The atlantal neural arch (Text-figs 3, 5) is preserved but can be seen only in partial internal aspect. Except for the neural spine, the axis is well preserved. The axial centrum is keeled ventrally, but the keel is not as strongly pronounced as in araeosceloids. In addition, unlike all other known araeoscelidians, the cervical centra of *Spinoaequalis* are not appreciably longer than those of the dorsal series. Two cervical ribs are preserved and are associated with the axis and third cervical vertebra. Unfortunately these rib heads are too poorly preserved to determine whether they are dichoccephalic or holocephalic. Articular surfaces for the trunk ribs appear to be composed of a single facet and are located directly below the anterior zygapophysis on the respective neural arch. Holocephalous trunk rib heads would represent an autapomorphy of *Spinoaequalis*. Intercentra are visible throughout the presacral series as in most early amniote groups.

The sacral series is not preserved and the first eight caudals are very poorly preserved (Text-fig. 4). Beyond this region, twenty-six well exposed caudals are present. The remainder of the tail was lost during excavation. In strong contrast to the condition seen in araeosceloids and most other amniotes, where the caudal neural spines get progressively shorter and eventually virtually disappear, along the length of the tail (Reisz 1981, text-fig. 1), the caudal neural spines of *Spinoaequalis* (Text-figs 1, 4) increase in height posteriorly: the spines increase dramatically in height from the tenth caudal (second vertebrae of the last twenty-six) to about the fifteenth and then remain tall, increasing slightly to the twenty-eighth caudal, beyond which there is no noticeable increase in neural spine height for the remainder of the preserved portion of the tail. In addition, in other Permo-Carboniferous amniotes, the haemal spines are generally quite long at the base of the tail, and decrease rapidly in length posteriorly. In most cases the decrease in length is such that distinct haemal spines are absent by the middle of the caudal series. The opposite occurs in *Spinoaequalis*, where the haemal spines are shortest at the base of the tail, and then steadily increase in length posteriorly, remaining long throughout the preserved portion of the tail and matching the height of the neural spines. The haemal spines are slightly expanded distally, but this expansion is only very weakly developed, and does not in any way approach the condition seen in the eosuchian *Hovasaurus* (Currie 1981a). In most other amniotes, including *Petrolacosaurus*, the haemal spines actually taper distally.

The caudal vertebrae also exhibit well developed neural arches with very tall zygapophyses, together formed into a saddle-shaped structure (Text-fig. 4). This unusual appearance is probably the result of the dorsal expansion of the zygapophyseal articulating facets.



TEXT-FIG. 5. *Spinoaequalis schultzei* gen. et sp. nov.; KUV 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian. Magnification of skull region from Text-figure 3.

Transverse processes are absent in *Spinoaequalis* throughout the preserved portion of the tail (ninth to thirty-fourth vertebrae). The combination of rudimentary transverse processes along with tall spines (described above) results in a tail the transverse width of which does not exceed 25 per cent. of its total height.

The caudal centra are unspecialized, but, in combination with the well developed neural arches, result in the combined height of the arch and centrum approaching their antero-posterior length, a condition unknown in any other Carboniferous amniote.

The pectoral components of the appendicular skeleton of *Spinoaequalis* are well preserved (Text-figs 1, 3) and, in most respects, similar to those of araeosceloids. The interclavicle resembles that of *Petrolacosaurus* except that it is relatively longer. Its length occupies seven and one half dorsal vertebrae and is 25 per cent. longer than the humerus. In araeosceloids, such as *Petrolacosaurus* and *Araeoscelis*, the interclavicle is equal to the length of only five and one half dorsal vertebrae and is equal to the humerus in length. The elongate interclavicle may be the result of the juvenile nature of the specimen, for, as demonstrated by Currie (1981a), interclavicular length is negatively allometric relative to dorsal vertebral length.

The clavicles are also preserved and appear unremarkable in comparison with those of other early tetrapods. The scapulocoracoid is ossified as two separate elements. On the left side of the specimen (Text-fig. 3), the anterior-most element supports the glenoid surface along its postero-distal margin. Although the ossification of this region is poor, a large, well developed supraglenoid buttress is visible. This process is similar to that present in araeosceloids and partly conceals the coracoid foramen which lies directly below. The overall size of the scapula (height) is less than that of an araeosceloid of equivalent size. This may be related to its juvenile nature or it may represent an autapomorphy of this taxon. The reconstruction (Text-fig. 1) has been drawn with the scapula possessing typical araeosceloid proportions. Very little else of consequence can be identified.

although the anterior margin of the right scapulocoracoid appears gently convex, so that in a reconstructed individual (Text-fig. 1), this margin would appear to be orientated posteriorly. This configuration is apparent in all araeosceloids (Reisz 1981; Reisz *et al.* 1984) and differs from the tall straight anterior scapular margin present in other Palaeozoic amniotes (Carroll 1969).

The forelimb (Text-fig. 3) is distinguished by its elongate and slender configuration. The distal ends of the limb elements are not preserved and neither are any of the carpal ossifications. An entepicondylar foramen is not visible but a groove located along the postero-distal margin of the humerus presumably represents the proximal limits of this structure. Given the low degree of ossification in other parts of this skeleton, it is likely that the limbs are equally underdeveloped and, therefore, lack ossified ends and their associated structures. The manus is only preserved on the left side and is incomplete, except for the third and fourth digits which have a typically primitive phalangeal count of four and five respectively.

The pelvic girdle has only the right ilium and ischium preserved (Text-fig. 4). The elements are unremarkable and hence differ little from the typical early amniote configuration. The ilium has a strongly developed posteriorly directed iliac blade and contributes to most of the acetabular surface. The ischium forms the remainder of the acetabulum. Unlike *Petrolacosaurus* and other Palaeozoic amniotes, such as *Paleothyris*, the acetabulum is not anteroposteriorly long but nearly circular. This circular configuration was described by Laurin (1991) as an eosuchian synapomorphy. In *Spinoaequalis*, it may simply represent the lack of complete ossification or it may represent a unique condition that may reflect some modification in the motion of the hindlimb.

The hindlimbs are virtually complete, with the right limb best preserved. The femur and crus are nearly equal in length and as such are typical of araeosceloids. The femoral shaft is much more robust (nearly 50 per cent. thicker) than the humeral shaft. This condition is also present in araeosceloids and the eosuchian *Apsisaurus* (Laurin 1991). A robust femur is absent in *Paleothyris* and captorhinids and it may, therefore, represent a diapsid synapomorphy. As in the forelimb, the hindlimb is incompletely ossified. The articulating ends of the limb bones are not preserved and most of the tarsus is missing, with the exception of two small circular structures, best interpreted as the astragalus and calcaneum. The pes is complete and possesses the typically primitive count of 2, 3, 4, 5, 4. As in araeosceloids and unlike other Palaeozoic amniotes, the first metatarsal is much less than half the length of the fourth metatarsal (Text-fig. 3).

DISCUSSION

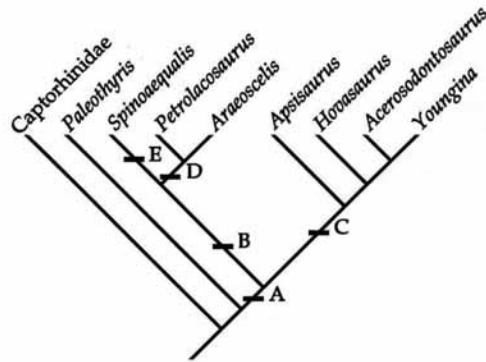
Phylogenetic position

Phylogenetic analysis of *Spinoaequalis* indicates that it is a basal diapsid reptile closely related to the oldest known diapsid, *Petrolacosaurus kansensis*. This phylogenetic interpretation is based on data evaluated below.

A total of nine taxa including two outgroups were used in this analysis. Out-group selection is based on the well established sister-group relationship between captorhinids and *Paleothyris* to Diapsida (Heaton and Reisz 1986; Laurin 1991; Laurin and Reisz 1995). Anatomical data for the out-groups was taken from direct observation and from Carroll (1969) and Heaton (1979). The in-group includes the two best known araeosceloids *Petrolacosaurus* (Reisz 1981) and *Araeoscelis* (Reisz *et al.* 1984), the eosuchians *Apsisaurus* (Laurin 1991) and *Hovasaurus* (Currie 1981a), and the younginiformes *Youngina* (Gow 1975; Carroll 1981; Currie 1981b) and *Acerosodontosaurus* (Currie 1979).

Fifty characters (Appendices 1 and 2) are used in the present analysis, most of which are taken from Laurin (1991) and Laurin and Reisz (1995). However, some of the characters (character numbers below refer to those in Appendices 1 and 2) have been reinterpreted (nos 33, 42) and a few are original (nos 1, 13, 38, 44, 45, 46, 47, 49). The analysis was performed on a Macintosh Quadra 800 computer using the branch-and-bound algorithm of PAUP 3.1.1, which finds the most parsimonious trees (Swofford 1993). All characters were left unordered and subjected to DELTRAN optimization, which tends to minimize synapomorphies at any given node.

Only one most parsimonious tree (Text-fig. 6) was found requiring seventy steps to resolve and with a consistency index of 0.742 excluding uninformative characters. The cladistic analysis supports the monophyly of Diapsida and the nested sister-group relationship between *Spinoaequalis* and Araeosceloidea to Eosuchia (Younginiformes), as most recently defined by Laurin (1991) and



TEXT-FIG. 6. Cladogram of basal diapsid interrelationships. Ambiguous characters are denoted by an asterisk, reversals by a minus sign, and in the case of a multi-state character, the derived state is placed in parentheses. Nodes assigned a letter in the figure are followed here by the character numbers referred to in Appendix 1: Node A (Diapsida) 1, 5, 7, 12, -16*(1), 17, 24, 37 and 41; Node B (Araeoscelidia) 27, 33 and 38*; Node C (Eosuchia) 13, 32 and 39; Node D (Araeosceloidea) 15, 18*, 19, 20, 21*, 22*, 28*, 36* and 40*; and Node E (*Spinoaequalis schultzei*) 11, 23, 25, 35, 44, 45, 46, 47, 48, 49 and 50.

Laurin and Reisz (1995). In addition, the sister-group relationship between *Spinoaequalis* and Araeosceloidea, coupled with their shared derived appendicular anatomy, allows for the re-establishment of the higher taxon Araeoscelidia (Williston 1913) to accommodate these Palaeozoic diapsid taxa.

For brevity we will not discuss all of the character states diagnosing the various nodes, but, as a result of the addition of *Spinoaequalis*, will consider only those changes that have revised the diagnosis or resolved critical issues of ambiguity for Diapsida and Araeosceloidea. Given the highly specialized anatomy of *Spinoaequalis*, a more detailed discussion of the specific autapomorphies diagnosing this taxon will be considered in the section on lifestyle interpretation.

Diapsida is universally recognized as a monophyletic group but some specific issues concerning character optimization have been problematic. Reisz *et al.* (1984) determined that the presence of a lower temporal fenestra was ambiguous for Diapsida and could have evolved twice. This interpretation was based on the absence of a lower temporal fenestra in *Araeoscelis*. However, the presence of a lower temporal fenestra in *Spinoaequalis* confirms, for the first time, the derived character as an unambiguous synapomorphy for Diapsida with a reversal in *Araeoscelis*.

Araeosceloidea, as most recently defined by Laurin (1991), is diagnosed by eight autapomorphies (numbers preceding character refer to character number in Appendix 1): 18 – dorsal and sacral neural arches shallowly excavated; 19 – cervical centra with sharp ventrally placed keel; 20 – cervical centra elongate; 21 – mammillary processes present on dorsal neural spines; 22 – accessory processes on cervical ribs present; 28 – enlarged coracoid process for triceps musculature; 33 – propodial/epipodial ratios 1:1, 36 – paired, large pubic tubercles present. One additional unambiguous autapomorphy has been more recently recorded by Laurin and Reisz (1995): 15 – transverse flange of pterygoid orientated anterolaterally. Therefore, until the present study, a total of nine autapomorphies diagnosed the clade. Of the nine autapomorphies only one (no. 5 above) was ambiguous.

The present analysis supports the monophyly of Araeosceloidea but revises the diagnosis by excluding one character (no. 33) and creating ambiguity for five of the remaining eight characters: nos 18, 21, 22, 28, and 36. This ambiguity arises due to the incomplete preservation of *Spinoaequalis* which precludes character state determination for the five characters. Therefore, from the original literature, only three unambiguous characters (nos 15, 19, and 20) remain to diagnose Araeosceloidea. One additional character (no. 40) is added as a result of this present analysis, but it is ambiguous. The higher level taxon Araeoscelidia, as resurrected here, is now diagnosed by three characters, only one (no. 38) being ambiguous: 27 – scapular blade slanted posteriorly; 33 – propodial/epipodial ratios 1:1; and 38 – femoral shaft width exceeds width of humeral shaft by 50 per cent. The ambiguity for character no. 38 stems from its presence in the derived state in the eosuchian *Apsisaurus*. The character may have arisen independently in araeoscelidians and

Apsisaurus or it may be a diapsid synapomorphy with a reversal in Neodiapsida. Of the three characters, nos 27 and 38 are new to this study and no. 33 is a former araeosceloid synapomorphy.

The confident identification of *Spinoaequalis* as an araeoscelidian has obviously affected the identification, if not the composition, of diapsids and araeoscelidians. In addition, the presence of *Spinoaequalis* along with an additional as yet undescribed diapsid from the same locality (Reisz 1988), suggests that diapsids were more diverse in the Pennsylvanian than was previously believed. These finds alter the prevailing view that diapsids diversified only around the Permo-Triassic boundary. Instead, diapsid evolutionary radiation may have been well under way during the Carboniferous, very soon after the appearance of its first recognized member.

Lifestyle interpretation

The Hamilton quarry of south-eastern Kansas represents a palaeovalley where rapid sediment deposition occurred in a marine setting (Feldman *et al.* 1993). The fauna is dominated by aquatic vertebrates, including hundreds of superbly preserved small acanthodian fish. Only a handful of fully terrestrial amniote specimens have been found, and most of them are fragmentary and disarticulated, suggesting that their presence is the result of postmortem displacement (Feldman *et al.* 1993). In strong contrast, the delicately constructed skeleton of *Spinoaequalis* has been preserved in articulation. The unfinished articulating surfaces of the long bones, the lack of tarsal and carpal ossification, and the exploded nature of the cranium attest to the immaturity and delicacy of this specimen, suggesting that this individual was not subjected to postmortem transport, but may have been a member of this community. Therefore, the possibility that *Spinoaequalis* represents an aquatic, or at the very least a semi-aquatic, amniote must be considered. The juvenile nature of the specimen makes evaluation of certain parts of the skeleton, for example some of the appendicular components, difficult. However, there is extensive evidence for aquatic affinities in the tail: 1, caudal neural and haemal spines increase in length posteriorly; 2, distal expansion of haemal spines, presumably to strengthen and resist tensile forces applied by powerful lateral flexors of tail; 3, loss of transverse processes throughout most of caudal series; 4, saddle-shaped neural arches with tall zygapophyses to restrict dorso-ventral flexion of tail and hence improve its sculling efficiency; and 5, vertebral bodies (centrum and neural arch) anteroposteriorly compressed, resulting in a length to height ratio approaching 1:1. Most of the features described above are common to aquatic diapsids as documented in the available literature (Russell 1967; Currie 1981a; Carroll 1988; Carroll and deBraga 1992; deBraga and Carroll 1993) and will be briefly discussed below.

The unusual configuration of the neural and haemal spines has been alluded to above, but the significance of this arrangement is that, among tetrapods, only aquatic or semi-aquatic organisms possess the characteristic increase in both neural and haemal spine height from base to at least mid-caudal length (deBraga and Carroll 1993). In addition, distal expansion of the haemal spines is also common to taxa that have been interpreted as having an aquatic or semi-aquatic lifestyle including, in addition to the amniote *Hovasaurus*, the anamniote *Archeria* (Holmes 1989). The haemal spine expansion in *Spinoaequalis*, although not as strongly developed as in *Hovasaurus* (Currie 1981a), certainly exhibits an incipient condition that further supports the suggestion that the tail was modified to enable an aquatic existence.

The absence of transverse processes beyond the most proximal portion of the tail (usually around the tenth caudal vertebrae) is well documented for aquatic taxa such as mosasaurs (deBraga and Carroll 1993) and *Hovasaurus* (Currie 1981a). Transverse processes are also absent in *Spinoaequalis*, whereas they remain well developed in non-aquatic amniotes throughout most of the caudal series. The loss of transverse processes is probably the result of the need to compress the tail so that it might function more effectively as a sculling organ.

The unusual saddle-shaped neural arches result from the elaboration of tall zygapophyses. Presumably, this zygapophyseal configuration would tend to resist flexion along the dorso-ventral axis of the tail, thereby improving its effectiveness as a sculling organ. In aquatic taxa, tall, well-developed zygapophyses are generally present only on the anterior-most caudals, where much of the muscular stress would be imparted during lateral flexion of the tail (Russell 1967; Carroll and

deBraga 1992; deBraga and Carroll 1993). In aquatic reptiles, such as *Hovasaurus* (Currie 1981a) and mosasaurs, the absence of well developed zygapophyses beyond the most proximal region of the tail coincides with the presence of anteroposteriorly-expanded neural spine bases. These accessory articulations serve to resist vertebral dislocation in the absence of functional zygapophyses. The absence, in *Spinoaequalis*, of accessory articulations may explain the need to maintain well-developed zygapophyses beyond the most proximal region of the tail. As in crocodiles (Frey 1982), it is possible that modifications to the caudal musculature may have also served to stabilize the tail.

The absence of functional zygapophyses may also serve to reduce the transverse width of the tail in many aquatic taxa. Aigialosaurs and mosasaurs lose all functional zygapophyses beyond the pygal series (Russell 1967; Carroll and deBraga 1992; deBraga and Carroll 1993). The retention of zygapophyses in *Spinoaequalis* may present a paradox initially, but the configuration of the zygapophyses (transversely narrow) and the absence of transverse processes does not interfere with lateral compression of the tail. As mentioned above, the loss of transverse processes in *Spinoaequalis* results in a tail that is only 25 per cent. as wide as it is tall. These ratios are similar to those of other aquatic taxa (personal observation) and differ from the configuration in non-aquatic amniotes where the tail is much broader, with the width approaching 50 per cent. of its height.

The last caudal modification present in *Spinoaequalis* is the antero-posterior compression of the caudal centra. The result is a vertebral body which is as tall as it is long. This differs from the pattern in most Palaeozoic amniotes (except in aquatic taxa) where the antero-posterior length of the caudal vertebrae, excluding spines, is always greater than its height (deBraga and Carroll 1993).

There is very little doubt that the tail of *Spinoaequalis* possesses all of the necessary refinements required of an aquatic or semi-aquatic animal. However, it is surprising that, unlike most other aquatic amniotes, *Spinoaequalis* does not appear to have any significant modifications to the limb girdles and retains typically terrestrial long, slender limbs.

In *Hovasaurus* (Currie 1981a) and other aquatic taxa (Russell 1967; Carroll and deBraga 1992) the scapula has a low aspect. This modification is interpreted as an aid in lowering the centre of gravity in an aquatic animal. This is required so that stability in the water can be maintained. Slight reduction in scapular height has been identified in the lizard *Aigialosaurus* (Carroll and deBraga 1992), although it does not possess any other typically aquatic appendicular characteristics. The poor ossification of the scapular blade in *Spinoaequalis* precludes confirmation of whether scapular reduction is an aquatic characteristic or simply an indicator of immaturity.

Some aquatic diapsids do have long limbs, most notably the hindlimbs of *Hovasaurus* (Currie 1981a). However, the limbs of *Hovasaurus* are modified in that the manus, and to an even greater extent the pes, possess digits that are nearly of equal length. This is apparent when comparing digits III-V of *Hovasaurus* with the same digits in *Petrolacosaurus*, *Spinoaequalis*, or most other Palaeozoic amniotes. In *Hovasaurus* digit III is 80 per cent. of the length of digit IV. This ratio is only slightly greater than that present in *Petrolacosaurus* and *Spinoaequalis*. (75 per cent.). However, the ratio between the fifth digit and the fourth is quite noticeably different when comparing *Hovasaurus* and the latter taxa. In *Hovasaurus*, as in many other aquatic taxa, the hands and feet are modified into paddles and, accordingly, the digits are subequal in length. The fifth digit of the pes in *Hovasaurus* has increased in length to such an extent that it exceeds the length of the third digit and approaches (exceeding 80 per cent.) the total length of the fourth (Currie 1981a). In *Spinoaequalis*, the fifth digit retains the characteristic terrestrial ratio where it is always shorter than the third digit and only slightly greater than one-half the length of the fourth digit.

The evidence presented here seems to pose a contradiction. The tail of *Spinoaequalis* certainly exhibits typically aquatic features and yet most features of the limbs suggest a fully terrestrial lifestyle. This apparent conflict has been noted also in the Cretaceous lizard *Aigialosaurus* (Carroll and deBraga 1992). This taxon possesses a typically terrestrial morphology with only slight modifications to the tail, most notably compression of the vertebral centra. These modifications are even less striking than those present in *Spinoaequalis* (the neural and haemal spines are not greatly elongated in *Aigialosaurus*), yet show a progressive pattern of modification which is only completely

manifested in their fully aquatic relatives the mosasaurs. The modifications present in *Spinoaequalis*, although not convincingly representative of a fully aquatic animal, are certainly incipient for that lifestyle and offer a rare glimpse of a 'transitory' organism.

CONCLUSIONS

The evidence presented above demonstrates that from both phylogenetic and biological points of view, diapsids were diversifying during the Palaeozoic. *Spinoaequalis* clearly represents an initial attempt at occupying an aquatic habitus not expressed by any other known Carboniferous amniote. It is noteworthy to consider that for a very long time aquatic amniotes are represented only by diapsid reptiles. Aquatic turtles do not make their appearance until the Mesozoic and synapsids (whales) do not invade the seas until the Cenozoic. It is likely that some aspect of both the anatomy and the physiology of diapsids imparts to them a selective advantage in invading the aquatic medium. Seymour (1982) demonstrated the energetically efficient means of aquatic locomotion among living diapsid reptiles. The typical sinusoidal motion present in diapsids is advantageous for aquatic locomotion. Diapsids were not only the first amniotes apparently to return to the water, they have continued to do so repeatedly and in greater number.

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REFERENCES

- BENTON, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, **84**, 97–164.
- BRINKMAN, D. B., BERMAN, D. S. and EBERTH, D. E. 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. 1969. A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology*, **43**, 151–170.
- 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London, Series B*, **293**, 315–383.
- 1988. *Vertebrate paleontology and evolution*. W. H. Freeman, New York, 698 pp.
- and deBRAGA, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, **12**, 66–86.
- CLARK, J. and CARROLL, R. L. 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 Rotliegenden des Plauen'schen Grundes bei Dresden. Teil. VIII. *Kadaliosaurus priscus*. *Zeitschrift der Deutschen Geologische Gesellschaft*, **41**, 319–342.
- CURRIE, P. J. 1979. A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. *Canadian Journal of Earth Sciences*, **17**, 500–511.
- 1981a. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. *Palaeontologia Africana*, **24**, 99–168.
- 1981b. The vertebrae of *Youngina* (Reptilia: Eosuchia). *Canadian Journal of Earth Sciences*, **18**, 815–818.
- deBRAGA, M. and CARROLL, R. L. 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes. *Evolutionary Biology*, **27**, 245–322.
- EVANS, S. E. 1988. The early history and relationships of the Diapsida. 221–260. In BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Volume 1: Amphibians, reptiles, birds*. Clarendon Press, Oxford, 377 pp.
- FELDMAN, H. R., ARCHER, A. W., KVALE, E. P., CUNNINGHAM, C. R., MAPLES, C. G. and WEST, R. R. 1993. A tidal model of Carboniferous Konservat-Lagerstätten Formation. *Palaios*, **8**, 485–498.
- FREY, E. 1982. Ecology, locomotion and tail muscle anatomy of crocodiles. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **164**, 194–199.

- GAUTHIER, J. A., KLUGE, A. G. and ROWE, T. 1988. The early evolution of the Amniota. 103–155. In BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Volume 1: Amphibians, reptiles, birds*. Clarendon Press, Oxford, 377 pp.
- GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana*, **18**, 89–131.
- HEATON, M. J. 1979. Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian of Oklahoma and Texas. *Bulletin of the Oklahoma Geological Survey*, **127**, 1–84.
- and REISZ, R. R. 1986. Phylogenetic relationships of captorhinomorph reptiles. *Canadian Journal of Earth Sciences*, **23**, 402–418.
- HILDEBRAND, M. 1982. *Analysis of vertebrate structure*. John Wiley and Sons, New York, 654 pp.
- HOLMES, R. B. 1989. The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca* Cope. *Palaeontographica Abteilung A*, **207**, 161–206.
- LAURIN, M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society*, **101**, 59–95.
- and REISZ, R. R. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, **113**, 165–223.
- OSBORN, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs from the American Museum of Natural History*, **1**, 265–270.
- REISZ, R. R. 1977. *Petrolacosaurus*, the oldest known diapsid reptile. *Science*, **196**, 1091–1093.
- 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Special Publication of the Museum of Natural History, University of Kansas*, **7**, 1–74.
- 1988. Two small reptiles from a Late Pennsylvanian quarry near Hamilton, Kansas. *Regional geology and paleontology of Upper Paleozoic Hamilton quarry area*. Kansas Geological Survey, Guidebook Series, **6**, 189–194.
- BERMAN, D. S. and SCOTT, D. 1984. The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. *Journal of Vertebrate Paleontology*, **4**, 57–67.
- RUSSELL, D. A. 1967. Systematics and morphology of American mosasaurs. *Bulletin of the Peabody Museum of Natural History*, **23**, 1–237.
- SEYMOUR, R. S. 1982. Physiological adaptations to aquatic life. 1–51. In GANS, C. and POUGH, H. (eds). *Biology of the Reptilia, Volume 13*. Academic Press, New York, 345 pp.
- SWOFFORD, D. L. 1993. *PAUP: Phylogenetic analysis using Parsimony; version 3.1.1*. Champaign: Illinois Natural History Museum.
- WILLISTON, S. W. 1913. An ancestral lizard from the Permian of Texas. *Science*, **38**, 825–826.

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ABBREVIATIONS USED IN THE TEXT-FIGURES

Ana	atlantal neural arch	Na	nasal
Ang	angular	Opi	opisthotic
Art	articular	Psph	parasphenoid
Axc	axial centrum	Part	prearticular
Bo	basiooccipital	Pm	premaxilla
Cor	coronoid	Ptg	pterygoid
D	dentary	Q	quadrate
Ect	ectopterygoid	Qj	quadratojugal
Exo	exoccipital	Sa	surangular
F	frontal	Spl	splenic
Lac	lacrimal	St	stapes
Max	maxilla	Sq	squamosal

APPENDIX 1

Description of characters used in the phylogenetic analysis. Characters are ordered anatomically. A zero in parentheses denotes the primitive condition whereas a number one or two in parentheses represents the derived state.

1. Dorsal process of premaxilla broad (0) or narrow (1), resulting in dorsal exposure of external nares.
2. Lacrimal large forming posterior border of external nares (0), or reduced and excluded from narial margin (1).
3. Anterodorsal process of maxilla absent (0) or present (1), reaching nasal and dorsal limit of external nares.
4. Caniniform teeth present (0) or absent (1).
5. Lateral margins of frontals straight resulting in a parallelogram shape (0) or lateral margins constricted above orbit (1) creating an hour-glass shape.
6. Dorso-lateral margins of parietal not excavated (0) or excavated (1) for adductor musculature.
7. Upper temporal fenestra absent (0) or present (1).
8. Posterior process of postorbital short, not reaching posterior limit of upper temporal fenestra (0), or long (1), extending beyond posterior border of fenestra.
9. Occipital flange of squamosal present (0) or absent (1).
10. Quadrate not exposed in lateral aspect behind squamosal (0) or exposed (1).
11. Ventral process of squamosal broad with the distal width approaching total height (0) or slender with width much less than total height (1).
12. Lower temporal fenestra absent (0) or present (1).
13. Posterior process of jugal short and relatively broad (0) not reaching beyond mid-point along ventral margin of lower temporal fenestra or long and slender (1) approaching posterior limit of lower temporal fenestra.
14. Paroccipital process not reaching cheek (0) or well ossified and reaching suspensorium (1).
15. Transverse flange of pterygoid orientated transversely or postero-laterally (0) or oriented antero-laterally (1).
16. Ectopterygoid present and large (0), present but small (1) and restricted to lateral margins of palate, or absent (2).
17. Suborbital fenestra absent (0) or present (1).
18. Neural arches or posterior dorsal and sacral vertebrae not excavated (0) along lateral margins or shallowly excavated (1).
19. Ventral surface of cervical and anterior dorsal centra without sharp keel (0) or strongly keeled (1).
20. Cervical vertebrae and remainder of presacral column subequal (0) or cervical vertebrae elongate (1).
21. Neural spines of dorsal vertebrae without dorsolaterally projecting (mammillary) processes (0) or mammillary processes present (1).
22. Anterior margin of cervical ribs without accessory processes (0) or accessory processes present (1).
23. Trunk rib heads dichoccephalic (0) or holocephalic (1).
24. Sternum not mineralized (0) or mineralized (1).
25. Interclavicle equal to not more than the length of six dorsal vertebrae (0) or interclavicle length equal to eight dorsal vertebrae (1).
26. Interclavicle head diamond shaped (0) or T-shaped (1).
27. Anterior margin of scapula straight (0) or slanted posteriorly (1).
28. Coracoid process for triceps musculature small (0) or large (1).
29. Humeral ends robust exceeding one third of total humeral length (0) or humerus gracile (1) with ends less than one third the total length.
30. Entepicondyle of humerus weakly developed (0) or large and strongly developed (1).
31. Radial shaft straight (0) or twisted (1) along its long axis.
32. Olecranon process on ulna present (0) or absent (1).
33. Propodial/epipodial ratios less than one (0) or equal to one (1).
34. Iliac blade with well-developed postero-distal process (0) or expanded into fan-shaped structure dorsally (1).
35. Acetabulum elongate or oval in configuration (0) or circular (1).
36. Pubic tubercles small (0) or large (1).
37. Adductor crest on femoral shaft present (0) or absent (1).
38. Femoral shaft equal to humeral shaft in diameter (0), exceeding humeral shaft diameter by 50 per cent. (1), or humeral shaft diameter exceeds that of femur by 50 per cent. (2).

39. Femur equal to humerus in length (0) or femur at least 10 per cent. longer than humerus (1).
 40. Tibia without distinct ridge (0) for articulation with astragalus or tibia with distinct ridge that fits into astragalar groove (1).
 41. Metatarsal I at least 50 per cent. the length of metatarsal IV (0) or less than 50 per cent. the length (1) of metatarsal IV.
 42. Manus and pes short and broad (0) or long and slender (1).
 43. Metapodials do not overlap proximally (0) or do overlap (1).
 44. Neural spines of proximal caudal vertebrae equal or taller than those of distal portion (0) or proximal caudal vertebrae shortest and increasing in height posteriorly (1).
 45. Haemal spines longer than neural spines of same caudal vertebrae (0) or neural and haemal spines of equal length (1).
 46. Haemal spines tallest at base of tail and decreasing in height posteriorly (0) or haemal spines shortest at base of tail increasing in length posteriorly (1).
 47. Haemal spines not expanded distally (0), slightly expanded distally (1), or greatly expanded distally (2).
 48. Caudal vertebrae (neural arches and centra) longer than tall (0) or length and height subequal (1).
 49. Caudal zygapophyses flat and not expanded dorsally (0), zygapophyses tall (1), or functional zygapophyses absent (2).
 50. Transverse processes present throughout most of caudal series (0) or absent on distal caudals (1).

APPENDIX 2

Data matrix for taxa examined in present analysis. Numbers above taxon names refer to character state numbers from Appendix 1. A question mark represents missing data.

	11111111122222
<u>Taxon</u>	<u>1234567890123456789012345</u>
<i>Captorhinidae</i>	0000000?0000002000000000
<i>Paleothyris</i>	0000000?0000000000000000?
<i>Spinoaequalis</i>	100010??11?011?00??1?1
<i>Petrolacosaurus</i>	1000101000010?111111110?0
<i>Araeoscelis</i>	1000101000000111111111010
<i>Apsisaurus</i>	????????00011??110110?0??
<i>Acerosodontosaurus</i>	?1111?1111111?11000001??
<i>Youngina</i>	1111111111110011000001?0
<i>Hovasaurus</i>	????111111110??00000110
	222233333333334444444445
<u>Taxon</u>	<u>6789012345678901234567890</u>
<i>Captorhinidae</i>	000010000000000000000000
<i>Paleothyris</i>	0001000000000000110??000
<i>Spinoaequalis</i>	01?1000101?110?1111111111
<i>Petrolacosaurus</i>	0111000100111011110000000
<i>Araeoscelis</i>	0111000100111111110000000
<i>Apsisaurus</i>	00010010??0111???????????
<i>Acerosodontosaurus</i>	????111011010??1??1??1???
<i>Youngina</i>	10001110110101??1?0000000
<i>Hovasaurus</i>	10001010000121?1111112121