
Morphology of the Atlas-Axis Complex of the Late Palaeozoic Tetrapod Suborders
Diadectomorpha and Seymouriamorpha

Author(s): Stuart S. Sumida, R. Eric Lombard and David S Berman

Reviewed work(s):

Source: *Philosophical Transactions: Biological Sciences*, Vol. 336, No. 1277 (May 29, 1992), pp. 259-273

Published by: [The Royal Society](#)

Stable URL: <http://www.jstor.org/stable/55893>

Accessed: 30/12/2012 19:52

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The Royal Society is collaborating with JSTOR to digitize, preserve and extend access to *Philosophical Transactions: Biological Sciences*.

<http://www.jstor.org>

Morphology of the atlas–axis complex of the late Palaeozoic tetrapod suborders Diadectomorpha and Seymouriamorpha

STUART S. SUMIDA¹, R. ERIC LOMBARD¹ AND DAVID S BERMAN²

¹*Department of Organismal Biology and Anatomy, The University of Chicago, 1025 East 57th Street, Chicago, Illinois 60637, U.S.A.*

²*Section of Vertebrate Paleontology, The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, U.S.A.*

CONTENTS

	PAGE
1. Introduction	259
2. Abbreviations	260
(a) Abbreviations used in text	260
(b) Abbreviations used in figures	260
3. Materials and methods	260
(a) Seymouriamorpha	260
(b) Diadectomorpha	261
4. Morphological description	261
(a) <i>Diadectes</i>	261
(b) <i>Desmatodon</i>	262
(c) <i>Diasparactus</i>	262
(d) <i>Limnoscelis</i>	263
(e) <i>Tseajaia</i>	265
(f) <i>Seymouria</i>	266
5. Discussion	269
(a) Atlanto-axial features of major groups	269
(b) Diadectomorpha and basal amniotes	270
(c) Transformations of the atlas–axis complex	270
References	272

SUMMARY

The atlas–axis complexes of the better-known genera of the Permo-Pennsylvanian tetrapod suborder Diadectomorpha are described and compared with those of other late Palaeozoic tetrapods. One new synapomorphy of the Diadectomorpha is identified: a large, anteriorly directed, midventral, projection of the axial intercentrum that articulates with a midventral furrow on the posterior margin of the atlantal intercentrum. Within the Diadectomorpha diadectids are apomorphic in possessing a large, anteriorly tapering axial neural spine, that accounts for approximately 40% of the total height of the axis; *Limnoscelis* is apomorphic in having divided parapophyseal facets of the atlantal intercentrum and anteriorly directed ventral processes of the atlantal intercentrum. Relative to the atlas–axis complex in the more primitive amphibian suborder Seymouriamorpha, that of diadectomorphs and other basal amniotes share two derived features: the atlantal pleurocentrum is fused to the dorsal surface of the axial intercentrum, except in *Tseajaia* where the elements are not fused but are positioned similarly; and the axial pleurocentrum and neural arch are fused in all observable stages of ontogeny. Reinterpretation of the atlantal neural arch in *Seymouria* indicates that it does not possess neural spines, a feature it shares with the Diadectomorpha and basal amniotes.

1. INTRODUCTION

The Permo-Pennsylvanian tetrapod suborder Diadectomorpha includes three families: the Diadectidae, known from numerous specimens from the southwestern, south-central, and eastern regions of the United

States; and the Limnoscelidae and Tseajaiidae, both known primarily from deposits of the North American Colorado Plateau. The present composition of the Diadectomorpha was established by Heaton (1980), and although there has been some dispute regarding the characters Heaton used to define the group

(Holmes 1984), his designation of its constituent taxa has been generally accepted.

The Diadectomorpha has been variously classified during the past century. Whereas most authors agree that the most appropriate phylogenetic placement of the Diadectomorpha is near the origin of amniotes, there has been considerable debate as to whether the Diadectomorpha should be included in the Amniota (Watson 1917; Romer 1946, 1956; Fracasso 1983, 1987), or not (Romer 1964; Heaton 1980; Gauthier *et al.* 1988; Panchen and Smithson 1988; Carroll 1988). Recently, Berman *et al.* (1992) demonstrated that characters of the temporal and occipital regions of the skull supported monophyly of the Diadectomorpha, corroborating Heaton's (1980) hypothesis. Characters defined in that study also suggested that the Diadectomorpha might be best included within the Amniota (*sensu* Gauthier *et al.* 1988) as the sister group to synapsids. More data will be necessary before such an assignment may be made with confidence, but, clearly, understanding the morphology of the group is important regarding insights into the origin of amniotes.

A series of phylogenetic analyses of advanced batrachosaurian amphibians and primitive amniotes presented during the past decade (Heaton & Reisz 1986; Gauthier *et al.* 1988; Panchen & Smithson 1988; Berman *et al.* 1992) have clarified considerably the relationships of tetrapods related to the origin of amniotes. The more broadly scaled studies (Panchen & Smithson 1988; Gauthier *et al.* 1988) have acknowledged the importance of characters of the atlas-axis complex in phylogenetic analyses of these groups. However, until recently little information has been available on the atlas-axis complex of members of the Diadectomorpha. Only interpretations of the condition in *Diadectes* have been incorporated in previous surveys of atlanto-axial structures among late Palaeozoic tetrapods (Olson 1936; Evans 1939). Further, Sumida & Lombard (1991) have pointed out errors in the interpretation of *Diadectes* in the most extensive of these surveys (Evans 1939).

Using well-preserved materials of *Diadectes*, Sumida & Lombard (1991) provided a detailed description of the complex in that genus, and a scenario of atlanto-axial transformations in the evolution of anthracosaurian amphibians and the origin of amniotes. To date, however, *Diadectes* is the only diadectomorph for which a complete characterization of the atlas-axis complex is available. Berman *et al.* (1992) clarified certain cranial features of diadectomorphs. During the course of these two studies representative materials of the atlas-axis complex of all families and nearly all the well-known genera of the Diadectomorpha were located and prepared. Consequently, a comprehensive description of the atlas-axis complex throughout the group is now possible.

Reexamination of specimens of the seymouriamorph amphibian *Seymouria* also allows a more complete restoration of the atlas-axis complex than is available in previous studies (White 1939; Watson 1951; Berman *et al.* 1987). Berman *et al.* (1987) provided the most accurate description to date for

Seymouria, focusing on *S. sanjuanensis*. Comparison with materials included in that study and specimens in the collections of the Field Museum of Natural History indicate minor reinterpretation of the complex is appropriate. Complete examples and attendant reconstructions of the atlas-axis complexes in both *S. sanjuanensis* and *S. baylorensis* provide a more confident basis of outgroup comparison with the complex in diadectomorphs.

2. ABBREVIATIONS

(a) Abbreviations used in text

The following institutional acronyms preceding specimen numbers are used in the text: AMNH, American Museum of Natural History, New York, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UCLA VP, University of California, Los Angeles, Vertebrate Paleontology Collections; UCMP, Museum of Paleontology, University of California, Berkeley; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

(b) Abbreviations used in figures

The following abbreviations are used in reference to anatomical structures in the figures: ATI, atlantal intercentrum; ATN, atlantal neural arch; ATP, atlantal pleurocentrum; ATR, atlantal rib; AX, axis (axial neural arch plus axial pleurocentrum); AXI, axial intercentrum; AXI-ATP, axial intercentrum plus atlantal pleurocentrum; AXN, axial neural arch and neural spine; AXP, axial pleurocentrum; AXR, axial rib; PRO, proatlas; PS3, third presacral vertebra.

3. MATERIALS AND METHODS

The geological conventions regarding Lower Permian deposits of north-central Texas used in this paper are those proposed by Hentz (1988). Hook (1989) has provided a key to formational equivalents earlier proposed by Plummer & Moore (1921) and Romer (1974). Formational equivalents for New Mexico specimens are summarized in Berman *et al.* (1987). Methods of illustration and reconstruction are similar to those outlined by Sumida & Lombard (1991).

Elements of the atlas-axis complex utilized in this study have been obtained from a variety of more complete specimens. They include the following.

(a) *Seymouriamorpha*

Seymouria baylorensis: FMNH 6138, anterior portion of vertebral column; Lower Permian, Clear Fork Group undivided, Baylor County, Texas. FMNH UR458, two anterior strings of vertebrae from two different individuals; Lower Permian, Clear Fork Group undivided, Middle Coffee Creek, '*Labidosaurus*

pocket', Baylor County, Texas. *Seymouria sanjuanensis*: CM 28559, complete articulated vertebral column and portion of pelvic girdle; Permo-Pennsylvanian, Cutler Formation, Rio Arriba County, New Mexico. CM 38022, nearly complete articulated skeleton missing parts of fore- and hind-limbs and part of tail; Permo-Pennsylvanian, Cutler Formation, Rio Arriba County, New Mexico.

(b) *Diadectomorpha*

Limnoscelis paludis: YPM 811, complete articulated skeleton; Upper Pennsylvanian, Cutler Formation, El Cobre Canyon, Rio Arriba County, New Mexico. *Limnoscelis dynatis*: CM 47653, disarticulated remains of a single individual; Upper Pennsylvanian, Sangre de Cristo Formation, Fremont County, Colorado. *Tseajaia campi*: UCMP 4225/59012, complete skeleton; Lower Permian, Organ Rock Shale, San Juan County, Utah. *Tseajaia* sp.: CM 38033, nearly complete skeleton; Permo-Pennsylvanian, Cutler Formation, near Arroyo del Agua, Rio Arriba County, New Mexico. CM 38042, nearly complete skeleton; Permo-Pennsylvanian, Cutler Formation, near Arroyo del Agua, Rio Arriba County, New Mexico. *Desmatodon hesperis*: CM 47665 (formerly UCLA VP 1465), partial disarticulated skeleton of a single individual; Upper Pennsylvanian, Sangre de Cristo Formation, Fremont County, Colorado. *Diadectes sideropelicus*: FMNH UR27, skull, presacral column, and pectoral girdle; Lower Permian, Petrolia Formation, Archer County, Texas. *Diadectes* sp.: FMNH UC1075, nearly complete skeleton; Lower Permian, Clear Fork Group undivided, Baylor County, Texas. *Diasparactus zenos*: FMNH UC679, partial skull and nearly complete postcranial skeleton; Upper Pennsylvanian, Cutler Formation, El Cobre Canyon, Rio Arriba County, New Mexico.

4. MORPHOLOGICAL DESCRIPTION

Through the work of Olson (1947) three North American genera are currently recognized as belonging to the Diadectidae: the common and well-known *Diadectes*, and the considerably rarer *Desmatodon* and *Diasparactus*. As Sumida & Lombard (1991) have recently provided a detailed description of the atlas-axis complex in *Diadectes*, its condition may now serve as a basis of comparison with other members of the Diadectomorpha. The following summary is derived primarily from that work. Left lateral and ventral reconstructions are provided in figure 1; illustrations of the atlas-axis complex in *Diadectes*, as well as its individual elements, may be found in Sumida & Lombard (1991).

(a) *Diadectes*

The atlas-axis complex in *Diadectes* (figure 1) is composed of seven elements: a paired proatlas, right and left atlantal neural arches, an atlantal intercentrum, a composite element formed from the fusion of the atlantal pleurocentrum and axial intercentrum,

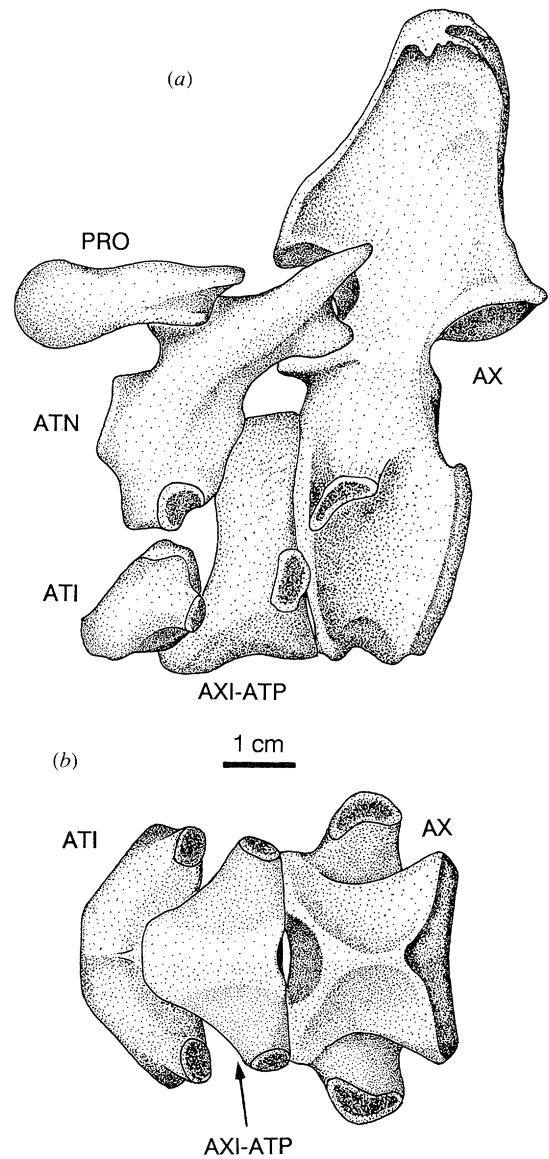


Figure 1. Reconstruction of atlas-axis complex in *Diadectes*: (a) left lateral view; (b) ventral view. Based on FMNH UR27 and FMNH UC1075.

and a well-developed axis formed from the fused axial neural arch and pleurocentrum.

Each proatlas is a slightly curved, kidney-shaped element traversing the gap between a facet on the skull just lateral to the foramen magnum and the atlantal neural arch. A short, blunt, posteriorly directed epiphysis extends beyond the posterior margin of the articulation with the atlantal neural arch.

The atlantal intercentrum is a robust, crescentic wedge in end view, with a wedge-shaped lateral outline. A deep, midventral furrow on its posterior surface received an anteriorly projecting process of the axial intercentrum. The anteroventral margin projects forward to articulate with the anteroventrally sloping surface of the occipital condyle. The very short parapophyses angle posteroventrally for attachment of the capitula of the atlantal ribs.

The atlantal pleurocentrum is fused to the dorsal surface of the axial intercentrum in *Diadectes*, effec-

tively excluding the pleurocentrum from exposure on the ventral margin of the vertebral column. No line of fusion remains to mark the exact limits of the two elements. However, the more ventral position of the axial intercentrum is confirmed by parapophyseal facets for the capitula of the axial ribs. The dorsal extent of the intercentral component cannot be determined exactly, but it may have reached as far dorsally as the ventral level of the notochord. This interpretation is suggested by the position of the dorsal limit of the parapophyses just above the ventral edge of the notochordal pit (Sumida & Lombard 1991, figure 2.4). The most obvious feature of the composite element is its robust, bluntly rounded, anteriorly directed process-like extension in the ventral midline that gives it a triangular outline in ventral view. The process articulates snugly in the midventral furrow of the atlantal intercentrum. The pleurocentral portion of the element gives it an oval shape in anterior view, its width approximately 80% its height. A deep notochordal pit is retained, although it is not perforate.

The atlantal neural arch is paired with no midline fusion. Each consists of a ventral subrectangular plate surmounted by a longitudinally oriented process bearing the anterior and posterior zygapophyses. The latter facet is only slightly tilted. As in the proatlas, an epiphysis extends posteriorly beyond the zygapophyseal articulation. The atlantal epiphysis, however, is larger and directed more posteriorly. There is no atlantal neural spine.

The axis in *Diadectes* is larger than any other vertebrae of the cervical region. The centrum is spool-shaped, although beveled anteriorly and posteriorly for articulation with respective intercentra, and possesses a midventral keel. Transverse processes for articulation with the tubercula of axial ribs are stoutly buttressed. The axial neural arch and pedicel are not swollen or expanded as in more posterior vertebrae, however, they support a neural spine that is more robustly developed than any succeeding cervicals. Laterally it has the shape of a subtriangular wedge. It narrows in transverse thickness anteriorly to a sharp edge, with the posterior surface of the spine having a broad surface of parallel furrows, presumably for muscular and ligamentous attachments.

(b) *Desmatodon*

Early description of the rare diadectid *Desmatodon hollandi* (Case 1908; Romer 1952) was based on only fragmentary jaw materials (CM 1938) from the late Pennsylvanian age Conemaugh Group of eastern Pennsylvania. Vaughn (1969, 1972) described *Desmatodon hesperis* on the basis of a much more complete (although still fragmentary) individual from the late Pennsylvanian Sangre de Cristo Formation of central Colorado. However, atlanto-axial material had not been identified for the genus at that time. Although not described by Vaughn in his initial study, a left atlantal neural arch (CM 47658) (figure 2) was found in association with the holotype, which bears great similarity to that in *Diadectes*. It is approximately two-thirds the size of that in *Diadectes*, a measure in

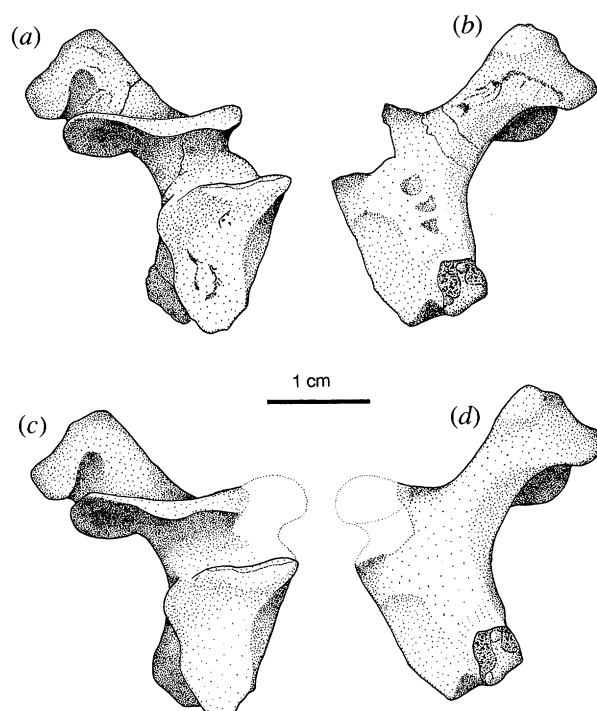


Figure 2. CM 47658, *Desmatodon hesperis*, left atlantal neural arch: (a, b) medial and lateral views; (c, d) reconstruction of left atlantal neural arch in medial and lateral views.

agreement with its slightly smaller cranial size (Vaughn 1969, 1972).

As in *Diadectes*, the atlantal neural arch is composed of a ventral subrectangular plate that supports the longitudinally oriented wall of the neural canal. The atlantal diapophysis is only faintly expressed at the posteroventral corner of the rectangular plate as a subcircular facet. The medial surface of the ventral rectangular plate is nearly completely occupied by a broadly teardrop-shaped articular surface for the atlantal pleurocentrum. The posterior zygapophysis is well preserved, and its distinctly concave articular surface faces medioventrally. Although the articular facet of the posterior zygapophysis is not visible in any of the specimens of *Diadectes* examined, the slightly convex nature of the articular facets of the axial anterior zygapophyses would indicate a condition similar to that in *Desmatodon*. No midline neural spine is present, but a well-developed epiphysis is. Unlike the tapered condition in *Diadectes*, the distal end of the epiphysis in *Desmatodon* is more robust with an angular, spatulate terminus. A broad, subtriangular process extends from its dorsal surface. In medial view, a shallow depression sets off the distal end of the epiphysis. As in *Diadectes*, the transverse outline of the neural canal formed by the atlantal elements is horizontally oval.

An isolated fragment of bone also found in association with CM 47658 may represent an atlantal intercentrum, but it is poorly preserved and lacks surface detail.

(c) *Diasparactus*

The genus *Diasparactus* was originally described on

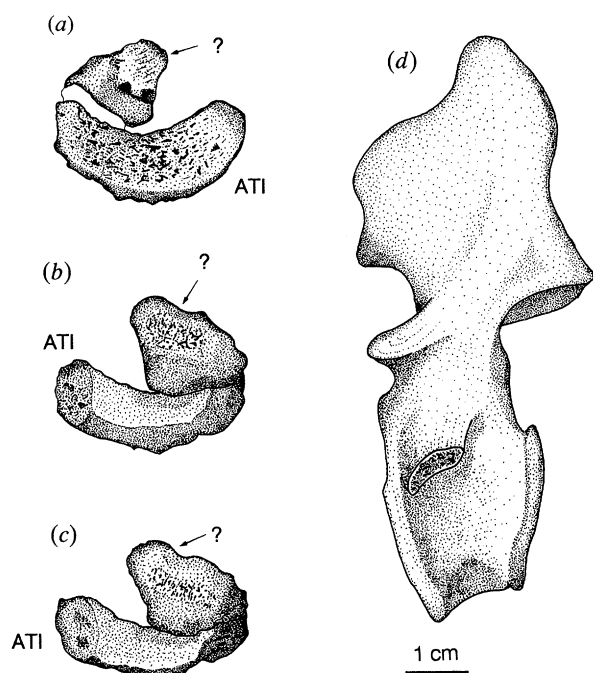


Figure 3. FMNH UC679, *Diasparactus zenos*: (a–c) atlantal intercentrum in anterior, posterior, and posterodorsal views; (d) axis in left lateral view. Illustration in (d) is somewhat simplified.

the basis of four isolated vertebrae (AMNH 4794) (Case 1910) from Permo-Pennsylvanian sediments of the Cutler Formation of El Cobre Canyon in northern New Mexico. Although generic identity based on the holotype is questionable, Case & Williston (1913) later assigned a more complete specimen, FMNH UC679, to the genus. Olson (1947) noted that features of the skull and vertebrae of FMNH UC679 are similar to those in *Diadectes*, but he confirmed the generic distinction of FMNH UC679 within the Diadectidae on the basis of the unique, elongate neural spines of the dorsal vertebrae.

Case & Williston (1913) maintained that the atlantal and axial intercentra, as well as the entire axis were preserved in FMNH UC679. However, only the atlantal intercentrum and the axis can be identified with confidence in the completely prepared specimen (figure 3). As preserved, the atlantal intercentrum was lodged on the underside of the skull near the ventral edge of the occipital condyle, and is visible only in ventral and posterior aspects. A fragment of bone (labelled ? in figure 3 lies just posterior to it and is probably what Case & Williston believed to be the axial intercentrum. However, it is too incomplete to provide an unambiguous identification. The axis is essentially complete.

The atlantal intercentrum in *Diasparactus* is quite similar to that in *Diadectes*. Just as in *Diadectes*, there is a midsagittal depression on its posterior surface. The associated fragment of bone is appressed to the posterolateral corner of the atlantal intercentrum. Its approximately triangular shape suggests the anterior midventral projection of the axial intercentrum in *Diadectes*, but this interpretation could only be offered tentatively at best. However, the median depression of

the posterior face of the atlantal intercentrum makes it reasonable to assume that the axial intercentrum in *Diasparactus* also possessed an anteriorly directed midventral process as in *Diadectes*.

In most respects the axis is similar to that in *Diadectes*. None the less, certain features of the axis in *Diasparactus* allow it to be distinguished from that in *Diadectes*: (i) the ventral margin of the axial centrum angles anteroventrally; (ii) the neural spine has a relatively larger lateral surface; (iii) the anterior half is blade-like and considerably more rectangular, much like the condition in a variety of primitive pelycosaurian grade synapsids (Sumida 1989); and (iv) there is no flat, anteriorly facing surface at the anterior base of the neural spine (Sumida & Lombard 1991, figure 2.11) or knob-like processes at the apex of the spine. Posteriorly, the neural spine expands laterally, providing a broad area on its posterior surface for attachment for epaxial structures.

(d) *Limnoscelis*

A series of studies dating back to the early part of this century (Williston 1911a, b, 1912; Romer 1946; Fracasso 1983, 1987; Berman & Sumida 1990) has given a reasonably complete picture of skeleton of *Limnoscelis*. However, the atlas-axis complex of the type species *L. paludis* was not prepared until the present study. A second species, *L. dynatis*, has recently been described (Berman & Sumida 1990), and an associated left atlantal neural arch not identified at that time is described here. A number of other genera have been provisionally assigned to the Limnoscelidae, but none include atlas-axis material (see Berman & Sumida (1990) for a review of references).

(i) *Limnoscelis paludis*

The only mention of the atlas-axis complex in previous studies of *Limnoscelis paludis* (YPM 811) was restricted to a brief tabulation of the elements visible in dorsal view of the skeleton (Williston 1912). The complex has now been separated from closely associated elements of the skeleton and thorough preparation has revealed a nearly complete atlas-axis complex: right and left atlantal neural arches, an atlantal intercentrum, a fused composite of the atlantal pleurocentrum and axial intercentrum, and fused axial neural arch and pleurocentrum. The elements are preserved in nearly their natural positions, save the absence of the proatlases (figure 4).

Fracasso (1983) proposed that a bit of bone preserved in articulation with the right exoccipital of YPM 811 appeared to be the right proatlas. However, this bone is very poorly preserved and although difficult to interpret, the occiput does not bear obvious facets for articulation with a proatlas. The anterior zygapophyses on the atlantal neural arches are the only evidence of the presence of a proatlas in *Limnoscelis*.

The atlantal intercentrum provides most of the features of the atlas-axis complex in *Limnoscelis* that distinguishes it from those of other diadectomorphs. As in other diadectomorphs, the main body of the

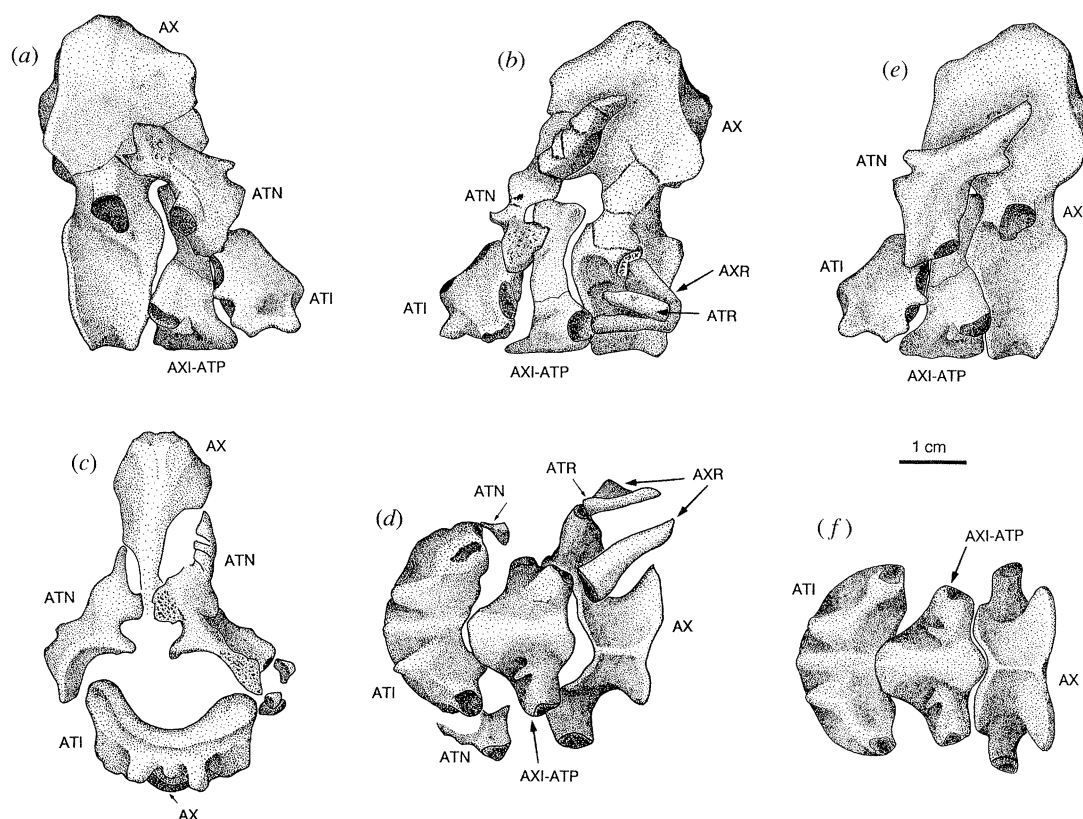


Figure 4. YPM 811, *Limnoscelis paludis*: (a–d) atlas–axis complex in right lateral, left lateral, anterior, and ventral views; (e, f) reconstruction of atlas–axis complex in left lateral and ventral views.

atlantal intercentrum is a blocky, crescentic wedge with a moderately developed midventral ridge. A pair of conspicuous processes project directly anteriorly and slightly ventrally on either side of the ventral midline (figure 4c, d, f). Each process terminates in a blunt point. A posterolaterally oriented ridge connects the base of the processes to the anterior edges of the atlantal parapophyses. The parapophyses in *Limnoscelis* are unique in that they quite clearly are composed of two separate facets (figure 4a, b, e). The possibility that the more dorsal facet represents the atlantal diapophysis is denied by the presence of a distinct diapophysis on the atlantal neural arch. Divided parapophyseal facets on the atlantal intercentrum are unknown in other Palaeozoic tetrapods and, therefore, appear to be unique to *Limnoscelis*. Unfortunately, the head of the atlantal rib is not preserved. Only a fragment of what may be a portion of the shaft of the left atlantal rib remains.

The atlantal neural arches are typical of those found in other late Palaeozoic tetrapods. The right atlantal arch is essentially complete, whereas a portion of the ventral body of the left arch has spalled off and the left atlantal epipophysis has been broken into several pieces. The atlantal neural arches are not fused at the midline and lack neural spines, but do support well-developed epipophyses (figure 4a, b). Although slightly worn in YPM 811, the epipophyses appear to be very similar to those in *Diadectes*. The postero-medial margin of the ventral body of the arch, which presumably articulated with the atlantal pleurocentrum, projects slightly posteriorly and is visible in lateral view as a rounded edge.

As in *Diadectes*, the atlantal pleurocentrum fuses to the dorsal surface of the axial intercentrum in *Limnoscelis* and, therefore, is widely excluded from exposure on the ventral margin of the vertebral column. However, unlike *Diadectes* the lateral line of fusion between the two elements remains visible. The sutural line angles posterodorsally to approximately the dorsal level of the notochordal canal of the axial vertebra. Ventrally, an anteriorly directed, midventral process of the axial intercentrum duplicates the condition in *Diadectes*. A small process directed anteriorly from the base of the right axial parapophysis is undoubtedly a serial homolog of the similar but larger processes of the atlantal intercentrum (figure 4e). Although a similar process is not visible on the left side of the axial intercentrum, it may have been broken away and an assumption of its presence may be reasonable.

As in all other diadectomorphs, the axis is the most stoutly developed element of the cervical region. The centrum has a shallow but distinctly pinched ventral keel. The beveled ends of the centrum reflect the articulations with associated intercentra. The transverse processes project well beyond the lateral limits of the centrum. Anterior zygapophyses appear to be very similar to those in *Diadectes* and *Diasparactus*, but the posterior zygapophyses are too poorly preserved permit detailed comparisons. The axial neural spine is an extremely large, blade-like structure, most similar to that in *Diasparactus*. As in other diadectomorphs, the anterior edge of the neural spine is narrow, but posteriorly the spine expands laterally. This gives the spine a triangular outline in horizontal section. The posterior face of the spine is divided by a tripartite set

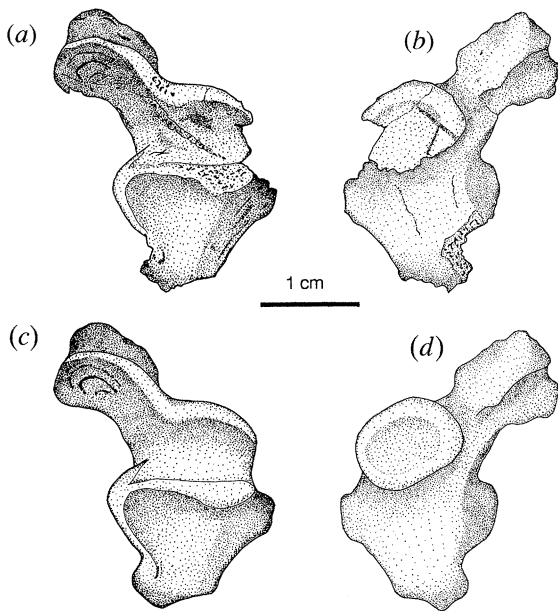


Figure 5. CM 47653, *Limnoscelis dynatis*, left atlantal neural arch: (a, b) medial and lateral views; (c, d) reconstruction in medial and lateral aspects.

of vertical parallel ridges that demarcate two deep furrows.

(ii) *Limnoscelis dynatis*

Only a left atlantal neural arch (figure 5) can be attributed to *Limnoscelis dynatis* (CM 47653). In most

features it is similar to that in *L. paludis*, but disarticulation from other elements allows description of the medial aspect of the atlantal arch. The facet of the medially directed posterior zygapophysis exhibits concentric growth lines similar to the condition common to those typically seen in dorsal vertebrae of *Limnoscelis* and *Diadectes* (Sumida 1990). In medial view the posterior margin of the ventral body of the neural arch appears as a distinctly concave, ear-like projection. The epiphysis in *L. dynatis* is more bluntly rounded than that in *L. paludis*.

(e) *Tseajaia*

Until recently the monospecific Tseajaiidae had been known from only a single complete specimen, UCMP V4225/59012 from the Lower Permian, Organ Rock Shale of San Juan County in southeastern Utah. Although the specimen preserves most of the atlas-axis complex (figure 6d), it was not described in detail by Vaughn (1964) in his preliminary analysis of the genus. In a subsequent description of the specimen, Moss (1972) did include an analysis of the atlas-axis complex; but certain errors in his characterization and reconstruction have become apparent upon additional preparation during the course of this study. Further, specimens recently collected in the Lower Permian Cutler Formation of Rio Arriba County, New Mexico, add to the available knowledge of this extremely rare genus.

Moss (1972) recognized eight components of the

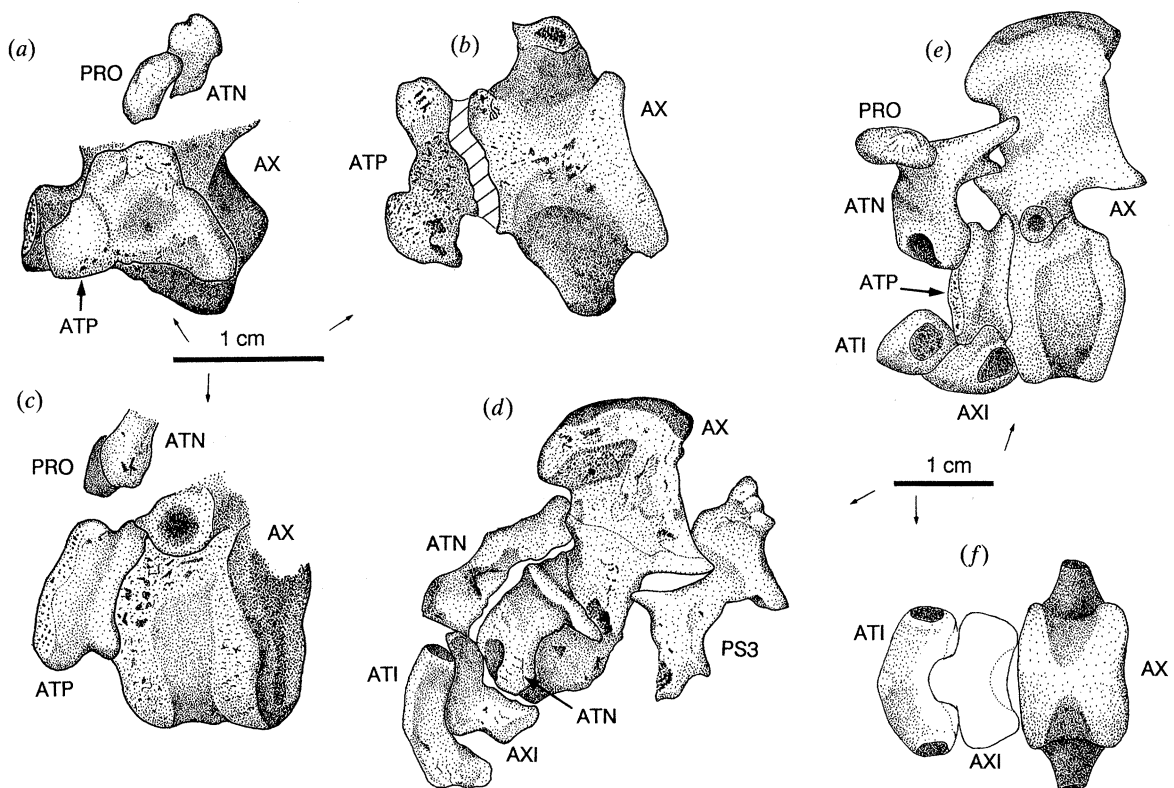


Figure 6. Atlas-axis complex in *Tseajaia*: (a-c) CM 38033, *Tseajaia* sp., components of the atlas-axis complex as preserved in anterior, left lateral, and ventral views; (d) UCMP 4225/59012, holotype, *Tseajaia campi*, as preserved in primarily left lateral aspect; (e, f) reconstruction of the atlas-axis complex in *Tseajaia* based on UCMP 4225/59012 and CM 38033, left lateral and ventral views. Extremely recalcitrant matrix does not permit ventral view of the axial intercentrum and only an outline reconstruction is presented here.

complex in *Tseajaia*: an atlantal intercentrum, paired atlantal neural arches, an atlantal pleurocentrum, an axial intercentrum, and a fused axial pleurocentrum plus neural arch. He assumed the presence of a paired proatlas. Eight elements are also recognized in this study, but not in the configuration as proposed by Moss (1972).

Clearly preserved proatlantal elements cannot be found in the holotype, however, the left proatlas remains in CM 38033 (figure 6a). It is oval to subrectangular in outline and slightly bowed laterally. A small, rounded process toward its posterior end may be serially homologous to the epipophysis of the atlantal neural arch.

The atlantal intercentrum is exposed primarily in anterodorsal view in the holotype (figure 6d). This orientation clearly displays the crescentic nature typical of those in other diadectomorphs and a variety of other advanced batrachosaurian amphibians and primitive amniotes. The anterior edge thins to a narrow lip. However, limited knowledge of the occiput in *Tseajaia* (Berman *et al.* 1992) precludes comment on the joint between the atlantal intercentrum and occipital condyle. Distinctly developed parapophyseal facets project laterally from either side of the element.

Although somewhat weathered, both atlantal neural arch halves are preserved in UCMP V4225/59012. Moss (1972, figure 6a, b), however, misinterpreted the right atlantal neural arch half in medial view as the left arch half in lateral view. Additionally, he misidentified the left atlantal neural arch half as the atlantal pleurocentrum. The left atlantal neural arch half is identifiable by the presence of the diapophysis at its anteroventral corner, which is expressed as a shallow notch. Post-mortem crushing and disarticulation in the holotype prevents detailed description of the atlantal pedicel. Zygapophyseal articulations are not well preserved. What Moss identified as a posterior zygapophysis is the epipophysis of the right atlantal neural arch, and although partially hidden by the axial neural spine, it appears to have the form of a short, pointed structure. What appears to be the left epipophysis has been broken and pushed laterally.

The atlas-axis complex in the holotype is applied closely to the underlying pectoral girdle, and the absence of the atlantal pleurocentrum suggests that it was not preserved. However, it is present in CM 38033 (figure 6a–c), where it is tightly articulated along the upper two-thirds of the anterior face of the axial centrum. Most of its surface is unfinished, suggesting that it may have been the last of the elements of the complex to ossify, not unlike the condition proposed for *Seymouria* by Berman *et al.* (1987). The ends of the lateral surfaces of the atlantal pleurocentrum are flared somewhat outward as rounded ridges, giving it a slightly constricted appearance in lateral view. The body of the element widens considerably ventrally, so that in anterior view it has a somewhat triangular outline, with the base forming a rather flat, horizontal sutural surface for the axial intercentrum.

The axial intercentrum is only partially exposed in the holotype (figure 6d) due to the overlying atlantal intercentrum and extremely recalcitrant matrix. However, it does confirm the presence of a broad, bluntly pointed, anteriorly directed midsagittal process-like extension of its anterior surface for articulation with the atlantal intercentrum. The process is not as large as those in *Diadectes* or *Limnoscelis*. The axial parapophyses face almost directly laterally. The close contact between the axial and atlantal intercentra would have prevented exposure of the atlantal pleurocentrum on the ventral aspect of the vertebral column (figure 6e, f).

As in all other diadectomorphs, the axis is the largest and most robustly constructed element of the cervical series. In the holotype the centrum is visible in lateral view only, whereas in CM 38033 its ventral surface is also exposed, revealing a sharp, midventral keel. Both the anterior and posterior ventral margins of the centrum are bevelled to accommodate intercentra. The centrum is deeply amphicoelous. The pedicels and transverse processes are extremely worn in both UCMP V4225/59012 and CM 38033. The transverse processes, however, appear to have been well developed, but their actual extent cannot be determined with the materials available. Although much of the surface bone has spalled off, the axial neural spine in *Tseajaia* is best seen in the holotype. It is large and blade-like in lateral view. Its convex dorsal margin extends beyond the anterior margin of the neural arch. Other features of the spine are typical of other diadectomorphs: the spine is subtriangular in dorsal outline tapering to an anterior apex; it has a broad posterior surface that served for the attachment of epaxial ligaments and musculature; and it was likely embraced on either side by the atlantal epipophyses.

(f) *Seymouria*

The Seymouriamorpha are generally considered to be more primitive than either the Diadectomorpha or the basal members of any amniote clade (Romer 1966; Gauthier *et al.* 1988; Berman *et al.* 1992). Heaton (1980) included the Russian families Nycteroleteridae and Kotlassiidae and the predominantly North American Seymouriidae in the Seymouriamorpha. Other than an isolated atlantal neural arch, no atlanto-axial material is known from the holotype of *Kotlassia* (Bystrow 1944). Bystrow's (1944) description of the atlas-axis complex in other specimens of *Kotlassia* are consistent with that of a temnospondyl amphibian. The possibility of such a designation has been advanced by Smithson (1982) and Holmes (1984) regarding certain of the cranial material attributed to the genus. Of the Nycteroleteridae, postcranial remains are known for *Nyctiphruetus* (Efremov 1938, 1940), but they were not available for examination. The North American seymouriid genus *Seymouria* is represented by numerous specimens and is taken here to be representative of the Seymouriamorpha.

Of the known species in the genus *Seymouria*, well-preserved atlas-axis materials are available for *S. baylorensis* (FMNH 6138 and FMNH UC458) and

S. sanjuanensis (CM 28559 and CM 38022). Earlier descriptions of the atlas-axis complex in *S. baylorensis* by White (1939) and Watson (1918, 1951) were recently revised by Berman *et al.* (1987), who demonstrated significant errors in those reconstructions in the course of their examination of *S. sanjuanensis*. Only minor changes to the work of Berman *et al.* (1987) are noted here.

(i) *Seymouria sanjuanensis*

Although *Seymouria sanjuanensis* (figure 7a, b) was first described by Vaughn (1966), Berman *et al.* (1987) provided the first description of its atlas-axis complex. Their materials came from Lower Permian Organ Rock Shale of the Cutler Group, southeastern Utah, and the Lower Permian Cutler Formation of north-central New Mexico respectively.

The atlantal intercentrum is a typically crescentic wedge. Although worn, bilateral processes are visible on the posterolateral aspects of the element. These low, rounded processes appear to be similar in position to those in *Limnoscelis*, but are not nearly as acuminate nor as large in proportion to the rest of the element. The processes are directed anteriorly, and therefore it is unlikely that they could be interpreted as costal facets. The parapophyseal facets are distinct and face posteriorly, laterally, and ventrally. As reconstructed here, the atlantal intercentrum is placed more dorsally than that proposed by Berman *et al.* (1987).

No atlantal pleurocentrum is known for *Seymouria sanjuanensis*, prompting Berman *et al.* (1987) to hypothesize that the specimens they examined may have been immature and that the element was probably represented by cartilage. As the atlantal and axial intercentra articulated closely with one another,

the atlantal pleurocentrum could not have reached the ventral aspect of the vertebral column.

Berman *et al.* (1987) described each half of the atlantal neural arch in *Seymouria sanjuanensis* as having a 'prominent spine that projects dorsally across the anterolateral surface of the axial spine.' The spine is considerably larger and more dorsally directed than those processes interpreted as epipophyses in diadectomorphs (Sumida & Lombard 1991). The modified reconstruction presented here proposes that the process was directed more posteriorly, reaching the level of the posterolateral corner of the axial neural spine. This orientation brings the anterior and posterior zygapophyses closer to the horizontal plane. The anterior zygapophysis is weakly developed, but its presence does indicate the existence of a proatlas in life. Diapophyses are not discernable.

The axial intercentrum is quite robust, rivalling the atlantal intercentrum in size. The ventrolateral margins of the axial intercentrum are also marked by low, rounded processes that are presumed to be serially homologous with those of the atlantal intercentrum. As in *Limnoscelis*, a bony ridge runs between them and the axial parapophyses. The short parapophyses of the axial intercentrum are distinct, and are directed posteriorly, laterally, and ventrally.

The pleurocentrum and neural arch of the axis are not fused in available specimens of *Seymouria sanjuanensis*, a condition that may also reflect immaturity (Berman *et al.* 1987). The centrum is strongly wedge-shaped in lateral view, pinched between the axial and third intercentra, with only a narrow entrance into the ventral margin of the column. The transverse processes project well beyond the pedicels of the neural arch. The axial neural arch and spine are the largest of the cervical series.

(ii) *Seymouria baylorensis*

Descriptions and reconstructions of the atlas-axis complex in *Seymouria baylorensis* have been made by Watson (1918) and White (1939). All of the specimens they used, as well as those examined in this study, were recovered from the Lower Permian Clear Fork Group of Baylor County, Texas. The atlas-axis complex in *S. baylorensis* (figure 7c, d) is similar in most respects to that in *S. sanjuanensis*, however, certain features appear to distinguish the two species.

Whereas the atlantal intercentrum of *Seymouria baylorensis* is extremely similar to that of *S. sanjuanensis*, the atlantal neural arch is different. The posterodorsally directed processes of the atlantal neural arch are clearly shorter, extending to approximately the middle of the axial neural spine rather than its crest. They are also less gracile in build, with a heavier, more angular terminus. Contrary to the interpretations of Watson (1918, 1954), the epipophyses did not come into contact with each other in the midline. White (1939) erroneously described the atlantal neural arch halves as having a tall, blade-like neural spine.

An atlantal pleurocentrum is clearly present in FMNH 6138. It is a narrow oval in lateral outline. Berman *et al.* (1987) pointed out that its presence in FMNH 6138 was probably a reflection of the larger

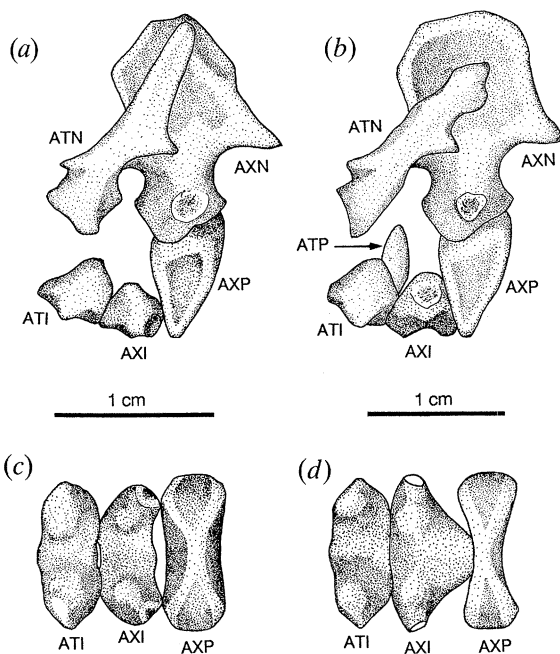


Figure 7. Reconstructions of atlas-axis complexes in *Seymouria*: (a, c) *Seymouria sanjuanensis*, left lateral and ventral views based on CM 28599 and CM 38022; (b, d) *Seymouria baylorensis*, left lateral and ventral views based on FMNH 6138 and FMNH UR458.

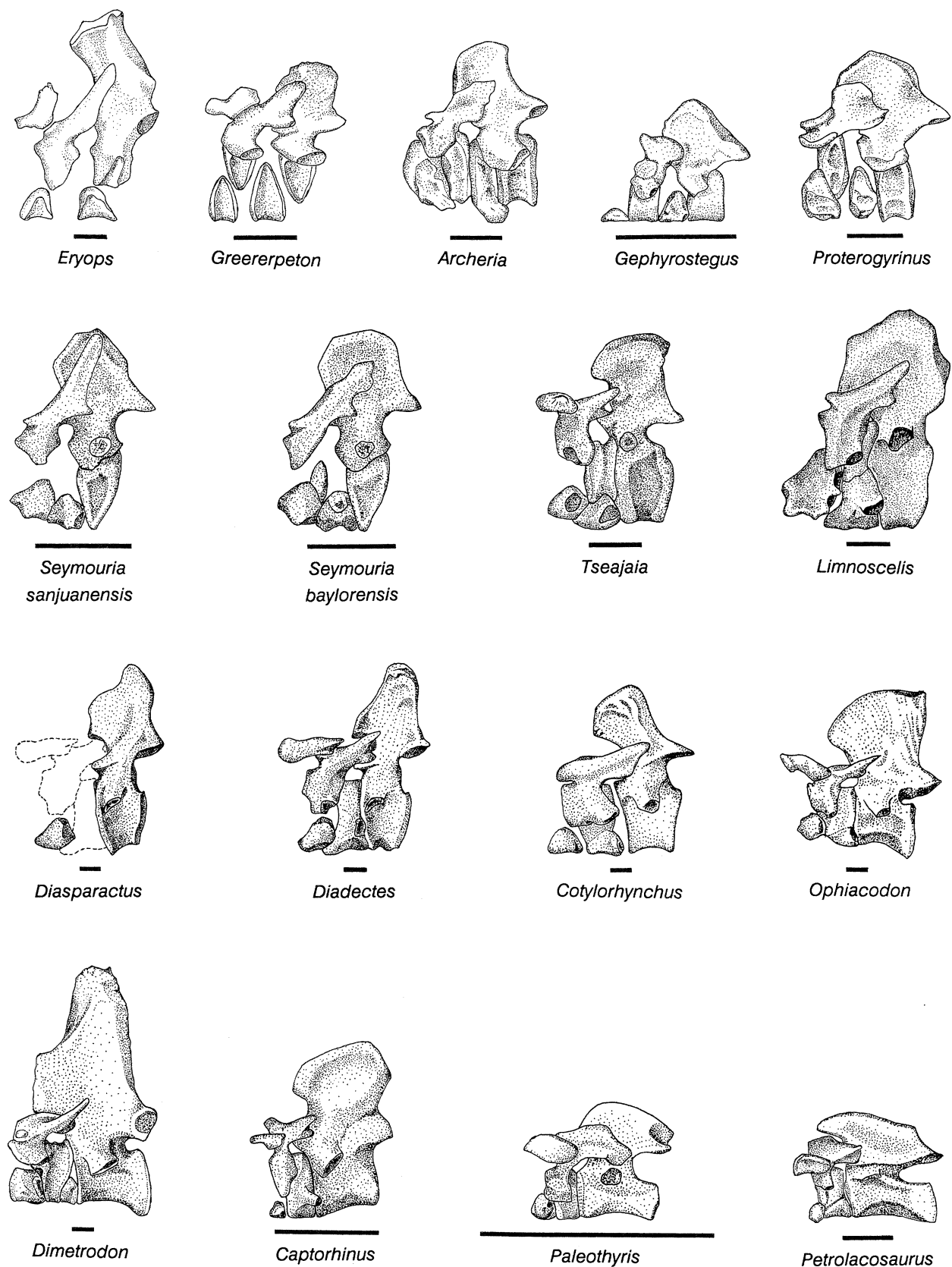


Figure 8. Atlas-axis complexes of late Palaeozoic tetrapods in left lateral view. All examples are drawn to approximately the same antero-posterior lengths to facilitate comparison. Temnospondyl amphibians *Eryops*, *Greererpeton*, and *Archeria* after Moulton (1974), Godfrey (1989), and Holmes (1989) respectively; anthracosaurian amphibians *Gephyrostegus* and *Proterogyrinus* after Carroll (1970) and Holmes (1984) respectively; caseosaurian pelycosaur *Cotylorhynchus* after Stovall *et al.* (1966); primitive eupelycosaurian pelycosaur *Ophiacodon* after Romer & Price (1940); advanced eupelycosaurian pelycosaur *Dimetrodon* after Romer & Price (1940); captorhinid reptile *Captorhinus* after Sumida (1990); protorothyridid reptile *Paleothyris* after Carroll (1969); diapsid reptile *Petrolacosaurus* after Reisz (1981). All bar scales equal to 1 cm.

size and greater maturity of the specimen. They further proposed that complete ossification of the atlantal pleurocentrum as a single element likely occurred late in life in *Seymouria*. Watson (1918) and White (1939, fig. 13) also recorded the presence of an atlantal pleurocentrum as a singly ossified element in *S. baylorensis*. Their specimens were also large and mature, and, therefore, consistent with the conclusion of Berman *et al.* (1987). In no case is the atlantal pleurocentrum known to fuse with the axial intercentrum in *S. baylorensis*. The atlantal pleurocentrum is wedged between the atlantal and axial intercentra, which clearly abut one another, thereby preventing exposure of the atlantal pleurocentrum on the ventral side of the column. This condition is in contrast to that displayed in diadectomorphs and primitive amniotes wherein the atlantal pleurocentrum is positioned directly dorsal to the axial intercentrum (figure 8).

The axial intercentrum of *Seymouria baylorensis* has well-developed ventrolateral processes as in *S. sanjuanensis*. In *S. baylorensis* the axial intercentrum differs in that its posteroventral margin is developed into a stout, posteriorly projecting, triangular process. Watson (1918, figure 8) speculated that such structure existed by way of a hypothetical reconstruction, and White (1939, figure 12) illustrated it similarly. Neither commented on the condition however. The posteriorly directed process appears to provide some congruence to the articulation with the axial pleurocentrum.

The axial centrum and neural arch do not fuse in any of the specimens examined, although White (1939) noted that in only one extremely mature individual did they appear to fuse. White (1939) incorrectly described the axial neural spine as longitudinally narrow but considerably expanded transversely. Specimens studied by Watson (1918) did not include the axial neural spine, and he mistakenly predicted that it would be similar to those of following vertebrae. The axial neural spine is actually unique relative to those of the other cervical vertebrae. It is robust, with the largest anteroposterior dimension of any cervical vertebra. The axial neural spine of *S. baylorensis* has a more rectangular outline than that of *S. sanjuanensis*.

5. DISCUSSION

Phylogenetic hypotheses generated by recent work on the cranial structure of members of the Diadectomorpha and Seymouriamorpha (Berman *et al.* 1987, 1992) provide a context for a discussion of the more complete atlanto-axial data for these groups. This information bears on the features of the individual members of the Diadectomorpha and Seymouriamorpha, taxonomy of the Diadectomorpha, and the evolution of the atlas-axis complex in derived anhracosaur and early amniotes.

(a) Atlanto-axial features of major groups

Sumida & Lombard (1991) characterized the atlas-axis complex in the genus *Diadectes* as including: paired, well-developed proatlases and atlantal neural

arches, lack of atlantal neural spines, an extremely robust atlantal intercentrum, fusion of the atlantal pleurocentrum to the dorsal aspect of the axial intercentrum, a large anteriorly directed, midventral projection of the axial intercentrum, exclusion of the atlantal pleurocentrum from exposure on the ventral surface of the vertebral column, fusion of the axial neural arch and centrum, and a robustly developed axial neural spine. The above survey indicates that all but one of the diadectomorph taxa for which the complex is known conform to this description. The single exception is the lack of fusion between the atlantal pleurocentrum and axial intercentrum in *Tseajaia*. The relative placement of these elements in *Tseajaia*, however, is identical to that in *Limnoscelis* and *Diadectes*. Characteristics of the atlantal neural arch of *Limnoscelis dynatis* and *Desmatodon hesperis* and of the atlantal intercentrum and the axis in *Diasparactus* also conform to this general model.

Berman *et al.* (1992) noted that sutural characters of the temporal and occipital regions of the skull support a monophyletic origin of the Diadectomorpha. The distinctive process projecting anteriorly from the ventral midline of the axial intercentrum can now also be considered a diadectomorph synapomorphy. This feature does not occur in any other tetrapod taxon in which the atlas-axis complex is known (figures 8, 9), and clearly supports monophyly of the Diadectomorpha.

Within the Diadectomorpha some taxa exhibit distinguishing features of the atlas-axis complex. Paired facets of the atlantal parapophysis in *Limnoscelis* appear to be unique among Palaeozoic tetrapods. Additionally, the atlantal intercentrum in *Limnoscelis* possesses acuminate, anteriorly directed processes on either side of the ventral midline. Similar processes are also present on the axial intercentrum. Although similar processes appear on the atlantal intercentrum in *Seymouria*, they are not nearly as well-developed. Members of the Diadectidae are characterized by an extremely large axial neural spine that accounts for approximately 40% of the total height of the vertebra. *Diasparactus* may be distinguished from *Diadectes* by the more rectangular, blade-like structure of its axial neural spine.

Unlike the Diadectomorpha, it is not possible to characterize the Seymouriamorpha on the basis of features from the atlas-axis complex. None the less, a clearer picture of the complex in the genus *Seymouria* is now available. Contrary to previous interpretations, the atlantal neural arches do not bear neural spines. The position of the spine-like processes relative to the axial neural spine indicates that they are better interpreted as well-developed epipophyses. The atlantal pleurocentrum in *Seymouria* appears to have ossified late in ontogeny. When present, as in mature specimens of *S. baylorensis*, the atlantal pleurocentrum is prevented from reaching the ventral surface of the vertebral column by a close, broad articulation between the atlantal and axial intercentra. Further, it is wedged between these two elements rather than positioned dorsal to the axial intercentrum, as in diadectomorphs and other primitive amniotes.

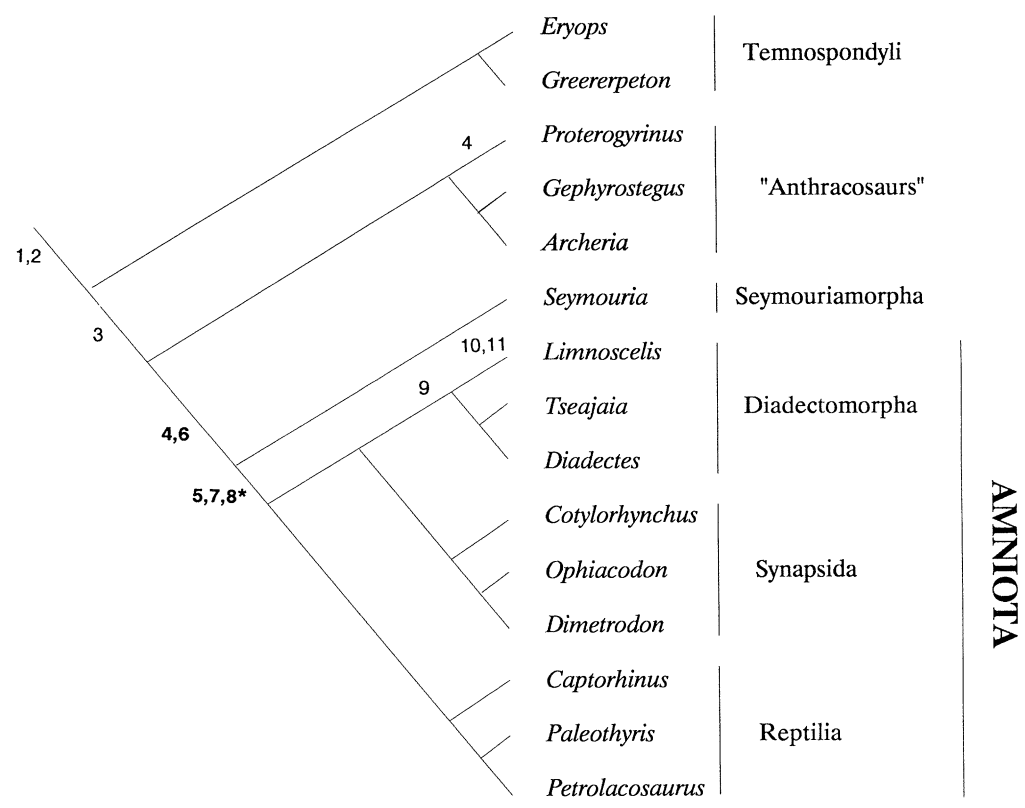


Figure 9. Character transformations of the atlas-axis complex among selected late Palaeozoic tetrapod genera. The hypothesis of relationships of higher order groups is based primarily on Gauthier *et al.* (1988), Panchen & Smithson (1988), Sumida & Lombard (1991), and Berman *et al.* (1992). Numbers indicate distribution of derived states for those numbered characters summarized in table 1 and whose taxon-character-state distributions are given in table 2. * = reversed in *Dimetrodon* and other spenacodontid pelycosaurs.

Within the genus *Seymouria*, *S. baylorensis* may be distinguished from *S. sanjuanensis* by the possession of a posteriorly directed process on the ventral midline of the axial intercentrum and relatively shorter postero-dorsal processes of the atlantal neural arch. The presence of an ossified atlantal pleurocentrum in *S. baylorensis* and its absence in *S. sanjuanensis* may only be a reflection of differing ontogenetic stages, and is probably not a reliable distinguishing character.

(b) *Diadectomorpha* and basal amniotes

On the basis of temporo-occipital characters, Berman *et al.* (1992) demonstrated that the Diadectomorpha could be considered to share a more recent common ancestor with pelycosaurian grade synapsids than with any other taxon. This hypothesis would place the diadectomorphs within the Amniota. Correspondingly, diadectomorphs and basal amniotes share features of the atlas-axis complex (figure 9). Large posterodorsally directed processes of the atlantal neural arches are not present. In both the axial centrum and neural arch are fused in all observable stages of ontogeny. In addition, with the exception of *Tseajaia*, the atlantal pleurocentrum is fused to the dorsal surface of the axial intercentrum. The condition in *Tseajaia* differs only in that the elements are unfused. In contrast, in *Seymouria* and other more primitive taxa atlantal pleurocentrum is wedged between the atlantal and axial intercentra (figure 8).

Lack of fusion could be interpreted as a condition distinct from that in other diadectomorphs, indicating the retention of a primitive condition similar to that in *Seymouria*. Alternatively, if fusion of the atlantal pleurocentrum and axial intercentrum is considered a synapomorphy of the Diadectomorpha, the condition in *Tseajaia* might be reasonably interpreted as a reversal.

The distribution of the character states discussed above is consistent with two different hypotheses of relationship between the Diadectomorpha and other basal amniotes: one (Berman *et al.* 1992) unites the Diadectomorpha and the Synapsida in a single clade of the Amniota (figure 9), whereas the other more commonly suggested proposal places the Diadectomorpha as a primitive sister group to the Amniota (see, for example, Heaton 1980; Gauthier *et al.* 1988). Berman *et al.* (1992) have acknowledged the need for additional data before more confident hypotheses of the interrelationships of the Diadectomorpha may be proposed. However, for the purposes of analysis of the transformations of the atlas-axis complex, their hypothesis is utilized here. We acknowledge that features of the atlas-axis complex alone are not sufficient to define diadectomorphs as amniotes with respect to reproduction.

(c) *Transformations of the atlas-axis complex*

It is not possible to construct a hypothesis of

Table 1. *Characters of the atlas-axis complex and their states*

(The numbers of the characters correspond to those listed in figure 9 and table 2. The designation of the primitive or ancestral state as 0 and the derived state as 1 correspond to those in Sumida & Lombard (1991) and in the text. Citations indicate the first cladistic description of the character.)

Character 1.	Differentiated atlas-axis complex (Gauthier <i>et al.</i> 1989)
0.	Present
1.	Absent
Character 2.	Axial neural spine (Sumida & Lombard 1991)
0.	Paired halves
1.	Fused along dorsal midline
Character 3.	Structure of axial pleurocentrum (Sumida & Lombard 1991)
0.	Composed of paired elements
1.	Single element that reaches ventral midline
Character 4.	Relationship of atlantal and axial intercentra to atlantal pleurocentrum (Reisz 1980)
0.	Atlantal pleurocentrum separates atlantal and axial intercentra to reach ventral midline of column
1.	Atlantal and axial intercentra articulate to exclude atlantal pleurocentrum from ventral midline of column
Character 5.	Processes of atlantal neural spines (this paper, modified from Sumida & Lombard (1991))
0.	Large, posterodorsally directed processes
1.	Small epiphyses
Character 6.	Atlantal pleurocentrum (Sumida & Lombard 1991)
0.	Composed of paired elements
1.	Single ossified element in mature individuals
Character 7.	Fusion of axial neural arch and pleurocentrum (Gauthier <i>et al.</i> 1988)
0.	Unfused
1.	Fused
Character 8.	Relationship of atlantal pleurocentrum to axial intercentrum (Reisz 1980)
0.	Atlantal pleurocentrum contacts or is narrowly separated from anterior surface of axial intercentrum
1.	Atlantal pleurocentrum articulates with, or is fused to, dorsal surface of axial intercentrum
Character 9.	Anteriorly directed, midventral process of axial intercentrum (Sumida & Lombard 1991)
0.	Absent
1.	Present
Character 10.	Facets of atlantal parapophysis (this paper)
0.	Single
1.	Paired
Character 11.	Ventral processes of atlantal intercentrum (this paper)
0.	Absent
1.	Present

phylogenetic relationships based solely on characters of the atlas-axis complex. However, it is possible to propose a series of transformations that illustrate the evolution of the complex among late Palaeozoic

tetrapods based on reasonably well-known examples (figure 8). Figure 9 is a synthesis of current, commonly accepted hypotheses of relationship as represented by individual genera. Sumida & Lombard (1991) proposed a list of nine characters useful in describing changes in the atlas-axis complex among Late Palaeozoic tetrapods near the origin of amniotes. Two features unique to *Limnoscelis* are added here. Together, these characters and their states are discussed below and summarized in tables 1 and 2. Finally, the levels at which the derived states of each character are observed are labeled in figure 9. *Limnoscelis*, *Tseajaia*, and the taxa illustrated in figure 8 may now be interpolated into that scenario.

The possession of a differentiated atlas-axis complex and fusion of the axial neural spine into a single element remain features of all of the taxa involved in the analysis, including the temnospondyl amphibians *Eryops* and *Greererpeton*. Anthracosauroids and all other more derived taxa may be characterized by fusion of the paired halves of the axial pleurocentrum into a single element that reaches the ventral midline of the column.

Articulation between the atlantal and axial intercentra to exclude the atlantal pleurocentrum from exposure on the ventral surface of the vertebral is a feature of the Seymouriamorpha and Amniota. No postcranial material is known for the genus *Nycteroleter*, the only nycteroleterid seymouriamorph (Efremov 1938, 1940). The atlantal pleurocentrum is also excluded from the ventral surface of the vertebral column in the anthracosauroid amphibian *Proterogyrinus* (Holmes 1984). Sumida & Lombard (1991) noted that it shares this character with *Seymouria* and *Diadectes* plus amniotes. If *Proterogyrinus* is considered to be among the more derived members of the Anthracosauria (see, for example, Holmes 1984), it

Table 2. *Distribution of character-states among taxa described in the text, illustrated in figure 8, and included in cladogram of figure 9*
(Description of characters and their states are given in the text and summarized in table 1.)

characters	1	2	3	4	5	6	7	8	9	10	11
taxon	character-states										
<i>Eryops</i>	1	1	0	0	0	0	0	0	0	0	0
<i>Greererpeton</i>	1	1	0	0	0	0	0	0	0	0	0
<i>Proterogyrinus</i>	1	1	1	1	0	0	0	0	0	0	0
<i>Gephyrostegus</i>	1	1	1	0	0	0	0	0(?)	0	0	0
<i>Archeria</i>	1	1	1	0	0	0	0	0	0	0	0
<i>Seymouria</i>	1	1	1	1	0	1	0	0	0	0	0
<i>Limnoscelis</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Tseajaia</i>	1	1	1	1	1	1	1	1	1	0	0
<i>Diadectes</i>	1	1	1	1	1	1	1	1	1	0	0
<i>Cotylorhynchus</i>	1	1	1	1	1	1	1	1	0	0	0
<i>Ophiacodon</i>	1	1	1	1	1	1	1	1	0	0	0
<i>Dimetrodon</i>	1	1	1	0	1	1	1	1	0	0	0
<i>Captorhinus</i>	1	1	1	1	1	1	1	1	0	0	0
<i>Paleothyris</i>	1	1	1	1	1	1	1	1	0	0	0
<i>Petrolacosaurus</i>	1	1	1	1	1	1	1	1	0	0	0

may be reasonable to interpret its possession of that derived state as convergent on that in more advanced terrestrial forms like seymouriamorphs and basal amniotes. If, however, the Proterogyrinidae is interpreted as the most primitive of embolomorous anthracosauroids (see, for example, Clack 1987), the condition in other embolomeres could be considered as a reversal.

Sumida & Lombard (1991) considered the ossification of the atlantal pleurocentrum into a single element in mature individuals as characteristic of seymouriamorphs and amniotes. Reanalysis of the atlas-axis complex in *Seymouria* has not altered this interpretation.

Loss of atlantal neural spines was considered by Sumida & Lombard (1991) as a feature distinguishing diadectomorphs and amniotes from seymouriamorphs and other more primitive amphibian taxa. Reinterpretation of the atlantal neural arch in *Seymouria* has not altered this hypothesis. The considerably smaller processes of the atlantal neural arch in diadectomorphs and other amniotes is termed a diapophysis here, however use of such a term for the large posterodorsal processes in amphibians is deferred until a more thorough determination of the potential homology between these structures may be made.

As discussed above, amniotes (here including the Diadectomorpha) may be characterized by: (i) fusion of the axial centrum and neural arch; (ii) reduction of large posterodorsally directed processes of the atlantal neural arch; and (iii) position of the atlantal pleurocentrum directly dorsal to the axial intercentrum. In addition, with the exception of *Tseajaia*, (iv) the atlantal pleurocentrum and axial intercentrum fuse. Within the Amniota the Diadectomorpha may be clearly distinguished by the possession of an anteriorly directed, midventral process of the axial intercentrum.

The authors are indebted the following persons for the loan of specimens under their care and for permission to prepare certain of those materials: Dr J. Bolt, Field Museum of Natural History; Dr J. Ostrom, Yale Peabody Museum of Natural History; Dr K. Padian, University of California Museum of Paleontology, Berkeley. Special acknowledgment is extended to Ms A. Henrici for her careful and thorough preparation of much of the material. The *Limnoscelis dynatis* and *Desmatodon hesperis* specimens from the late Pennsylvanian Sangre de Cristo Formation are part of a larger collection of late Palaeozoic vertebrates collected by Dr P. Vaughn and generously donated to the Carnegie Museum of Natural History. Ms E. Rega translated the German literature. Early versions of this manuscript were read by Dr R. Reisz, Ms C. Bush, and Mr C. Solomon. Their comments and suggestions are greatly appreciated. Support for this study was provided by the National Science Foundation through grant BSR 90-04171 (to D.S.B.).

REFERENCES

Berman, D.S., Reisz, R.R. & Eberth, D.A. 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. *Can. J. Earth Sci.* **24**, 1769–1784.
Berman, D.S. & Sumida, S.S. 1990 *Limnoscelis dynatis*, a new

species (Amphibia, Diadectomorpha) from the Late Pennsylvanian Sangre de Cristo Formation of Central Colorado. *Annls Carnegie Mus.* **9**, 303–341.
Berman, D.S., Sumida, S.S. & Lombard, R.E. 1992 Reinterpretation of sutural patterns of the temporal and occipital regions in *Diadectes* and the relationships of diadectomorphs. *J. Paleont.* **66**. (In the Press.)
Bystrow, A.P. 1944 *Kotlassia prima* Amalitzky. *Bull. geol. Soc. Am.* **55**, 379–416.
Carroll, R.L. 1969 A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *J. Paleont.* **43**, 151–170.
Carroll, R.L. 1970 The ancestry of reptiles. *Phil. Trans. R. Soc. Lond. B* **257**, 267–308.
Carroll, R.L. 1988 *Vertebrate paleontology and evolution*. (698 pages.) New York; W. H. Freeman and Sons.
Case, E.C. 1908 Description of vertebrate fossils from the vicinity of Pittsburgh, Pennsylvania. *Annls Carnegie Mus.* **4**, 234–241.
Case, E.C. 1910 New or little known reptiles and amphibians from the Permian (?) of Texas. *Bull. Am. Mus. nat. Hist.* **28**, 163–181.
Case, E.C. & Williston, S.W. 1913 Description of a nearly complete skeleton of *Diasparactus zenos*. In *Permo-Carboniferous vertebrates from New Mexico*. (ed. C. Case, S. W. Williston & M. G. Mehl), pp. 17–53. Carnegie Institute of Washington Publication 181.
Clack, J.A. 1987 *Pholiderpeton scutigerum* Huxley, an amphibian from the Yorkshire coal measures. *Phil. Trans. R. Soc. Lond. B* **318**, 1–107.
Efremov, J.A. 1938 On some new Permian reptiles of the U.S.S.R. *Dokl. Acad. Sci. S.S.S.R.* **19**, 771–776.
Efremov, J.A. 1940 Die Mesen-Fauna der permische Reptilien. *Neues Jb. Min., Geol., Palaeont.* **84**, 379–466.
Evans, F.G. 1939 The morphology and functional evolution of the atlas-axis complex from fish to mammals. *Annls New York Acad. Sci.* **39**, 29–104.
Fracasso, M.A. 1983 Cranial osteology, functional morphology, systematics and paleoenvironment of *Limnoscelis paludis* Williston. (624 pages.) Ph.D. dissertation, Yale University.
Fracasso, M.A. 1987 Braincase of *Limnoscelis paludis* Williston. *Postilla* **201**, 1–22.
Gauthier, J.A., Kluge, A.G. & Rowe, T. 1988 The early evolution of the Amniota. In *The phylogeny and classification of tetrapods*, vol. 1: (Amphibians, reptiles, birds) (Systematics Association special volume No. 35A) (ed. M. J. Benton), pp. 103–155. Oxford: Clarendon Press.
Godfrey, S.J. 1989 The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. *Phil. Trans. R. Soc. Lond. B* **323**, 75–133.
Heaton, M.J. 1980 The Cotylosauria: a reconsideration of a group of archaic tetrapods. In *The terrestrial environment and the origin of land vertebrates*. (Systematics Association special volume No. 15) (ed. A. L. Panchen), pp. 497–551. London and New York: Academic Press
Heaton, M.J. & Reisz, R.R. 1986 Phylogenetic relationships of captorhinomorph reptiles. *Can. J. Earth Sci.* **23**, 402–418.
Hentz, T.F. 1988 Lithostratigraphy and paleoenvironments of upper Paleozoic red beds, North-Central Texas: Bowie (new) and Wichita (revised) Groups. *Univ. Texas, Austin, Bur. Economic Geol. Report of Investigations*. **170**, 1–55.
Holmes, R. 1984 The Carboniferous amphibian *Proterogyrinus scheeli* Romer, and the early evolution of tetrapods. *Phil. Trans. R. Soc. Lond. B* **306**, 431–527.
Holmes, R. 1989 The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca* Cope. *Palaeontographica* **207**, 161–206.

- Hook, R.W. 1989 Stratigraphic distribution of tetrapods in the Bowie and Wichita Groups, Permo-Carboniferous of North-Central Texas. In *Permo-Carboniferous vertebrate paleontology, lithostratigraphy, and depositional environments of north-central Texas*. (ed. R. W. Hook), pp. 47–53. Field Trip Guidebook No. 2, 49th Annual Meeting of the Society of Vertebrate Paleontology, Austin, Texas.
- Moss, J.L. 1972 The morphology and phylogenetic relationships of the Lower Permian tetrapod *Tseajaia campi* Vaughn (Amphibia: Seymouriamorpha). *Univ. Calif. Publ. geol. Sci.* **98**, 1–72.
- Moulton, J.M. 1974 A description of the vertebral column of *Eryops* based on the notes and drawings of A. S. Romer. *Breviora* no. 428, 44 pages.
- Olson, E.C. 1936 The dorsal axial musculature of certain primitive Permian tetrapods. *J. Morph.* **59**, 265–311.
- Olson, E.C. 1947 The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana: Geol.* **11**, 3–53.
- Panchen, A.L. & Smithson, T.R. 1988 The relationships of the earliest tetrapods. In *The phylogeny and classification of tetrapods*, vol. 1 (*Amphibians, reptiles, birds*) (Systematics Association special volume No. 35A) (ed. M. J. Benton), p. 1–32. Oxford: Clarendon Press.
- Plummer, F.B. & Moore, R.C. 1921 Stratigraphy of the Pennsylvanian formations of North-central Texas. *Univ. Texas Bull.* **2132**, 1–237.
- Reisz, R.R. 1980 The Pelycosauria: a review of phylogenetic relationships. In *The terrestrial environment and the origin of land vertebrates* (Systematics Association special volume No. 15) (ed. A. L. Panchen), pp. 553–592. London and New York: Academic Press.
- Reisz, R.R. 1981 A diapsid reptile from the Pennsylvanian of Kansas. *Spec. Publs Mus. nat. Hist. Kansas* no. 7, 74 pages.
- Romer, A.S. 1946 The primitive reptile *Limnoscelis* restudied. *Am. J. Sci.* **244**, 149–188.
- Romer, A.S. 1952 Late Pennsylvanian and early Permian vertebrates from the Pittsburgh-West Virginia region. *Annls Carnegie Mus.* **33**, 47–110.
- Romer, A.S. 1956 *Osteology of the Reptiles*. (776 pages.) University of Chicago Press.
- Romer, A.S. 1964 *Diadectes* an amphibian? *Copeia* **4**, 718–719.
- Romer, A.S. 1966 *Vertebrate Paleontology*, (468 pages.) University of Chicago Press.
- Romer, A.S. 1974 Stratigraphy of the Permian Wichita redbeds of Texas. *Breviora* no. 427, 31 pages.
- Romer A.S. & Price, L.I. 1940 Review of the Pelycosauria. *Spec. Pap. geol. Soc. Am.* no. 28, 538 pages.
- Smithson, T.R. 1982 The cranial morphology of *Greererpeton burkmorani* Romer (Amphibia: Temnospondyli). *Zool. J. Linn. Soc.* **76**, 29–90.
- Stovall, J.W., Price, L.I. & Romer A.S. 1966 The postcranial skeleton of the giant Permian pelycosaur *Cotylorhynchus romeri*. *Bull. Mus. comp. Zool.* **135**, 1–30.
- Sumida, S.S. 1989 Reinterpretation of vertebral structure in the Early Permian pelycosaur *Varanosaurus acutirostris* (Amniota, Synapsida). *J. vert. Paleont.* **9**, 451–458.
- Sumida, S.S. 1990 Vertebral morphology, alternation of neural spine height, and structure in Permo-Carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. *Univ. Calif. Publ. Zool.* **122**, 1–133.
- Sumida, S.S. & Lombard, R.E. 1991 The atlas-axis complex in the Late Paleozoic diadectomorph amphibian *Diadectes* and the characteristics of the atlas-axis complex across the amphibian to amniote transition. *J. Paleont.* **65**, 973–983.
- Vaughn, P.P. 1964 Vertebrates from the Organ Rock Shale of the Cutler Group, Permian of Monument Valley and vicinity, Utah and Arizona. *J. Paleont.* **38**, 567–583.
- Vaughn, P.P. 1969 Upper Pennsylvanian vertebrates from the Sangre de Cristo Formation of central Colorado. *Los Angeles Co. Mus. Nat. Hist. Contr. Sci.* no. 164, 28 pages.
- Vaughn, P.P. 1972 More vertebrates, including a new microsauro, from the Upper Pennsylvanian of Central Colorado. *Los Angeles Co. Mus. Nat. Hist. Contr. Sci.* no. 223, 30 pages.
- Watson, D.M.S. 1917 A sketch classification of the pre-Jurassic tetrapod vertebrates. *Proc. zool. Soc. Lond.* **1917**, 167–186.
- Watson, D.M.S. 1918 On *Seymouria*, the most primitive known reptile. *Proc. zool. Soc. Lond.* pp. 267–301.
- Watson, D.M.S. 1954 *Paleontology and Modern Biology*. (216 pages.) New Haven: Yale University Press.
- White, T.E. 1939 Osteology of *Seymouria baylorensis* Broili. *Bull. Mus. comp. Zool.* **85**, 332–409.
- Williston, S.W. 1911a A new family of reptiles from the Permian of New Mexico. *Am. J. Sci.* **31**, 378–398.
- Williston, S.W. 1911b *American Permian Vertebrates*. (145 pages.) University of Chicago Press.
- Williston, S.W. 1912 Restoration of *Limnoscelis*, a cotylosaur reptile from New Mexico. *Am. J. Sci.* **34**, 457–468.

Received 11 November 1991; accepted 16 December 1991