

## A Redescription of the Cranial Anatomy of *Seymouria baylorensis*, the best known Seymouriamorph (Vertebrata: Seymouriamorpha)

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### ABSTRACT

Seymouriamorphs are generally thought to be closely related to amniotes. Preparation of several specimens of *Seymouria baylorensis* from the Lower Permian of Texas requires a reevaluation of the affinities of seymouriamorphs. Contrary to previous reports, *S. baylorensis* has a long cultriform process but lacks mandibular fenestrae, and the transverse flange extends ventrolaterally, as in amniotes, rather than horizontally. The epipterygoid is not fused to the pterygoid. Mature specimens of *S. baylorensis* lack lateral-line canal grooves. In all these respects, *Seymouria* is more similar to amniotes than previously considered, but these similarities do not necessarily imply that seymouriamorphs are closely related to amniotes. The presence of a paired atlantal pleurocentrum and other primitive character states suggest that seymouriamorphs do not belong to the crown group Tetrapoda.

### INTRODUCTION

The origin of amniotes has fascinated generations of paleontologists. Throughout the history of paleontology, several relatives or even groups of relatives of amniotes have been proposed (Watson, 1918; Vaughn, 1962; Carroll, 1970). However, only two groups of vertebrates, diadectomorphs and seymouriamorphs, have been almost universally accepted as representing early relatives of amniotes (Gauthier et al., 1988; Laurin and Reisz, 1995). Diadectomorphs are believed to be the closest relatives of amniotes, and are indeed very similar to the earliest amniotes (Laurin and Reisz, in press; Berman et al., 1992). Seymouriamorphs are generally thought to be closely related to the clade that includes diadectomorphs and amniotes, and differ from the last two taxa by retaining several primitive characters also found in embolomeres and temnospondyls.

Recent phylogenetic analyses of tetrapods suggest that lepospondyls are more closely related to amniotes than to seymouriamorphs (Carroll, 1995; Laurin and Reisz, in press), and seymouriamorphs appear not to be more closely related to amniotes than to lissamphibians (Laurin and Reisz, in press). Instead, seymouriamorphs may be among the last groups to have originated before the evolutionary divergence that led to lissamphibians and amniotes (Laurin and Reisz, in press).

Seymouriamorphs provide clues about the origin of terrestriality in vertebrates. Adult seymouriamorphs appear to have been terrestrial,

and the seymouriamorphs formerly believed to have been more aquatic (*Discosauriscus* Kuhn, 1933, *Utegenia* Kuznetsov and Ivakhnenko, 1981, and *Ariekanerpeton* Ivakhnenko, 1981) are probably represented by immature specimens (Klembara, 1995; Laurin, in press a and b). Embolomeres, early temnospondyls (such as colosteids), loxommatids, *Crassigyrinus* Watson, 1929, and *Ichthyostega* Sæve-Söderbergh, 1932 were probably aquatic or at least semi-aquatic, and terrestrial habits may characterize the clade that includes seymouriamorphs, lepospondyls, lissamphibians, diadectomorphs, and amniotes, according to the phylogenies of Carroll (1995) and Laurin and Reisz (in press).

Although several studies of *Seymouria* Broili, 1904 have recently been published (Berman and Martens 1993; Berman et al., 1987; Olson, 1979 and 1980), their emphasis was on relatively poorly known species of *Seymouria*, and none of them dealt with the best known species of seymouriamorph, *Seymouria baylorensis* Broili, 1904. In addition to being the best known seymouriamorph, this species, along with the poorly known *Kotlassia* Amalitzky, 1921, is one of the few seymouriamorph species represented by fully mature individuals (Klembara, 1995; Laurin, 1995). The last description of the cranial anatomy of *S. baylorensis* was published by White (1939). *Seymouria* is frequently used to polarize characters used in phylogenetic analyses of amniotes (Gauthier et al., 1988; Laurin and Reisz, 1995), and is potentially useful in polarizing characters of a much larger group that also

includes lepospondyls and lissamphibians (Laurin and Reisz, in press). Further preparation of specimens used by White (1939), as well as more recently collected specimens, has revealed some inaccuracies in White's generally excellent description. Advances in our knowledge of other Palaeozoic tetrapods allow us to make more meaningful comparisons than White could. A recent, thorough redescription of *S. baylorensis* is therefore desirable.

Institutional abbreviations: AMNH, American Museum of Natural History; BMS, Buffalo Museum of Science; FMNH, Field Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; TMM, Texas Memorial Museum, the University of Texas at Austin.

Anatomical abbreviations: A. co., anterior coronoid; An, angular; Ar, articular; Bo, basioccipital; Bs, basisphenoid; Co, middle coronoid; D, dentary; D. s., dorsum sellae; E, epipterygoid; Ec, ectopterygoid; Ex, exoccipital; F, frontal; F. o., fenestra ovalis; It, intertemporal; J, jugal; L, lacrimal; M, maxilla; N, nasal; N. V, notch for the fifth cranial nerve; N. VII f, foramen for the facialis branch of the seventh cranial nerve; O, orbitosphenoid; Op, opisthotic; P, parietal; P. co, posterior coronoid; Pa, prearticular; Pal, palatine; Pi. fos., pituitary fossa; Pm, premaxilla; Po, postorbital; Pof, postfrontal; Pop. s. s., sutural surface for the paroccipital process; Pp, postparietal; Prf, prefrontal; Pro, prootic; Ps, parasphenoid; Psp, postsphenial; P.-t. fen., posttemporal fenestra; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; S, stapes; Sa, surangular; Sm, septomaxilla; Sp, splenial; Sq, squamosal; St, supratemporal; T, tabular; V, vomer; V. c. l., notch for the vena capitis lateralis, the stapedial artery, and the hyomandibular branch of the seventh cranial nerve.

#### SYSTEMATIC PALEONTOLOGY

Seymouriamorpha Watson, 1917

Seymouriidae Williston, 1911

*Seymouria* Broili, 1904

**Type species:** *Seymouria baylorensis* Broili, 1904.

**Revised diagnosis:** Seymouriamorph characterized by the following autapomorphies: Pineal foramen smaller than in other seymouriamorphs (less than 4% of the skull length), tabular horn long and bent ventrally (its height is at least 3% of the skull length, measured between the highest point of the dorsal edge of the otic notch and the tip of the horn), mandibular fenestrae absent; and possible absence of bony scales.

*Seymouria baylorensis* Broili, 1904

**Holotype:** AMNH 4342, an incomplete skull.

**Type locality:** West Coffee Creek, near Seymour, Baylor County, Texas, in Clear Fork Group sediments (Leonardian, Lower Permian).

**Referred specimens:** BMS E3500, skull with mandibles; MCZ 1081, a skull lacking most of the palate; MCZ 1083, a string of presacral vertebrae, an ulna, an incomplete right lower jaw, and the left half of a skull lacking the braincase and occiput; MCZ 1084, a fragmentary skull consisting of the posterior portion of the skull table, occiput, parts of the braincase, isolated fragments of the palate and cheek, and a left lower jaw; MCZ 1086, an incomplete skull; TMM 31189-1, a skull with lower jaws lacking the braincase and most of the palate; FMNH UR 458, a poorly preserved skull, three strings of vertebrae including parts of two atlas-axis complexes, two femora, and other fragments of the appendicular skeleton. These are the only specimens used in this study.

**Horizon and locality:** The MCZ and FMNH specimens were found at West Coffee Creek. The BMS specimen was found in the same vicinity, near Seymour, Baylor County, Texas, in Clear Fork Group sediments (Leonardian). TMM 31189-1 comes from the Nocona Formation of the Wichita Group, about 7.5 km east and 4.5 km north of Henrietta, Clay County, Texas.

**Revised diagnosis:** Seymouriamorph characterized by the following autapomorphy: Quadratojugal with ventral projection just in front of the condyle of the quadrate, and with a round process lateral to the condyle.

Differentiated from *S. sanjuanensis* Vaughn, 1966 by the shorter postparietal, the absence or the small size of the posterior process of the lacrimal in the ventral rim of the orbit, and by the presence of a longer and broader anterior process of the jugal extending anterior to the orbit, a jugal-squamosal suture extending posteroventrally rather than ventrally, a broader and less acuminate postorbital, a contribution of the supratemporal to the posteroventral tabular horn, a narrower otic flange of the squamosal, a relatively straight palatine-pterygoid suture, larger, more conical, more robust teeth, a lower tooth count, and a smaller lateral exposure of the articular.

Differentiated from *Discosauriscus* and *Ariekanerpeton* by a longer, narrower skull (length/width ratio above 1.1), posteroventral and anteroventral orbital notches, the broader prefrontal-postfrontal contact, the smaller size of the post-temporal fenestra, narrower palatine and ectopterygoid, a deeper crista ventrolateralis, more prominent sculpturing of the dermal bones of the skull, and greater size.

Differentiated from *Utegenia* by a longer, narrower skull (length/width ratio above 1.1), posteroventral and anteroventral orbital notches, the broader prefrontal-postfrontal contact, the heavy pattern of sculpturing consisting of ridges and pits, the more rectilinear interparietal suture, the greater length of the dorsal ramus of the postparietal, the absence of a contact between postorbital and supratemporal, the greater size of the intertemporal, the edentulous parasphenoid with a narrow cultriform process, a deeper otic notch, a lower presacral count (24 instead of 28) and possibly the absence of dermal scales.

### DESCRIPTION

The skull outline is generally as described by White (1939), but the transverse flange of the pterygoid is visible in lateral view, and the maximal cranial width is at the level of the quadratojugal (fig. 1). White's mistake is understandable because the specimens on which he based his reconstruction have been dorso-ventrally compressed. The orbit is approximately quadrangular with a relatively straight lower edge ending in acute ventral corners and a more rounded dorsal edge (fig. 1). Even though the anteroventral corner of the orbit is the most acute, TMM 31189-1 shows that the anteroventral corner of the orbit would have been much less acute in life than shown by White (1939). The presence of remains of the lateral line system, suggested previously (White, 1939), cannot be unambiguously confirmed, even in the smallest specimens. There is a poorly defined groove on the left postorbital of BMS E3500, but this feature is not visible on the right side of this specimen or on the other specimens. However, the position of this groove just posterior to the orbit coincides with the postorbital ramus of the lateral line system visible in some embolomeres (Holmes, 1989). At most, this poorly defined groove indicates that juveniles may have had a functional lateral line system that was lost in adults. The main difference from White's palatal reconstruction is the presence of a long, narrow cultriform process (fig. 1D, 2). The opening of

the posttemporal fenestra on the occiput can be seen just above the paroccipital process (fig. 1B).

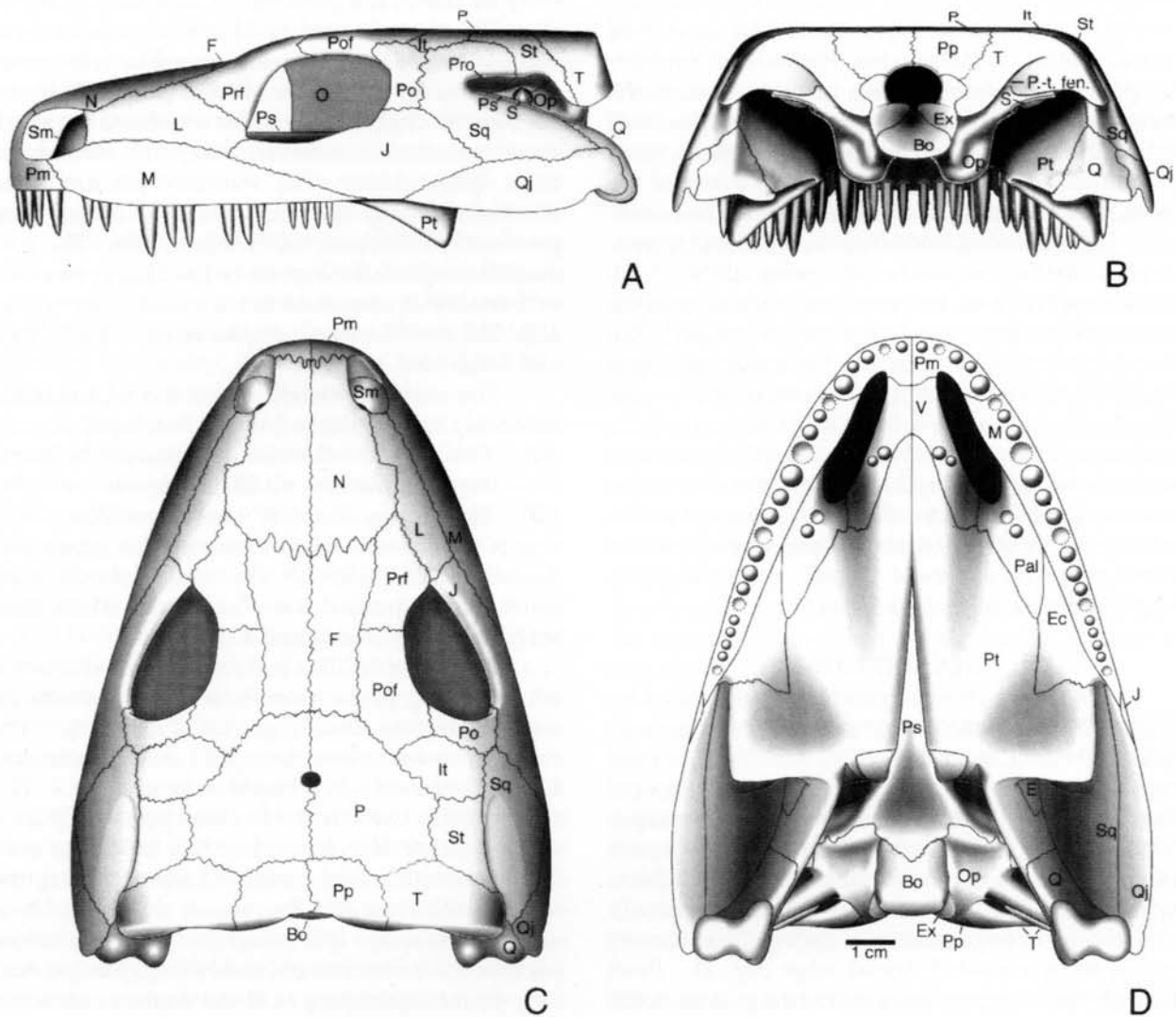
The three processes of the premaxilla have jagged sutures with the nasal, maxilla, and vomer (figs. 1 and 3). The contact with the nasal is by far the most strongly serrated; the serrations are much more numerous than shown in previous reconstructions (White, 1939). The vomerine process is the shortest one (fig. 1D), but is a little longer than previously reconstructed (White, 1939). The premaxilla supports the septomaxilla. There were four or five alveoli, one of which is usually empty (fig. 1D). The alveoli are best displayed in TMM 31189-1 and MCZ 1081.

The maxilla extends under the septomaxilla anteriorly and contacts the quadratojugal posteriorly. This contact is hidden by the jugal in lateral view (fig. 1A), but it is visible in palatal view (fig. 1D). There were about 17 tooth positions, about five of which were usually empty (this is best displayed in TMM 31189-1). The tips of the teeth of all the available specimens are broken; therefore, their length can only be estimated (fig. 1).

The septomaxilla consists of a curved sheet of bone forming part of a cone whose apex was located above the nasal (figs. 1A, C and 3A). The suture between the septomaxilla and the premaxilla and maxilla is simple and curved. The septomaxilla contacts the lacrimal posteriorly by a vertical, serrated suture. In MCZ 1081 (the only specimen with a well preserved septomaxilla), the septomaxilla contacts the vomer medially. It is uncertain whether it is an artifact of preservation, because the vomer has obviously been pushed dorsally in this specimen, or if the contact existed in life. It is likely that the septomaxilla contacted the median septum. Therefore, air would have probably had to pass dorsal to the septomaxilla to reach the choana, as White argued. This may imply that the external naris was dorsal, as White (1939) suggested, but it could also mean that air had to go through a relatively complex channel between the external naris and the mouth. No septomaxillary foramen was present. The only openings through which nerves or blood vessels could have exited the nasal capsule would have been the choana and the external naris. However, the latter opening appears to have extended posterodorsally between the nasal and the septomaxilla (fig. 1A).

The frontal is sutured to the orbitosphenoid ventrally and is thickened at this contact.

The prefrontal is a complex element composed of dorsal and lateral exposures and a broad orbital flange extending medially from the orbital rim.



**Figure 1.** Reconstruction of the skull of *Seymouria baylorensis* in A, left lateral view; B, occipital view; C, dorsal view; D, palatal view (based on BMS E3500, MCZ 1081, and MCZ 1083). The tips of the teeth were not preserved and had to be inferred. The position of the stapes is hypothetical. The dermal sculpturing and the palatal denticles have been omitted in all the reconstructions.

White (1939) inferred that the latter process was directed obliquely anteromedially into the orbit, but undistorted specimens (TMM 31189-1 and BMS E3500) show that it is oriented in a more or less transverse plane. Its contact with the palatine is fairly extensive and is located just medial and ventral to the lacrimal foramen. It is similar to the ventral prefrontal flange found in several temnospondyls (Bolt, 1974). The contact of the postfrontal with the prefrontal is wide, unlike the narrow contact in smaller seymouriamorphs.

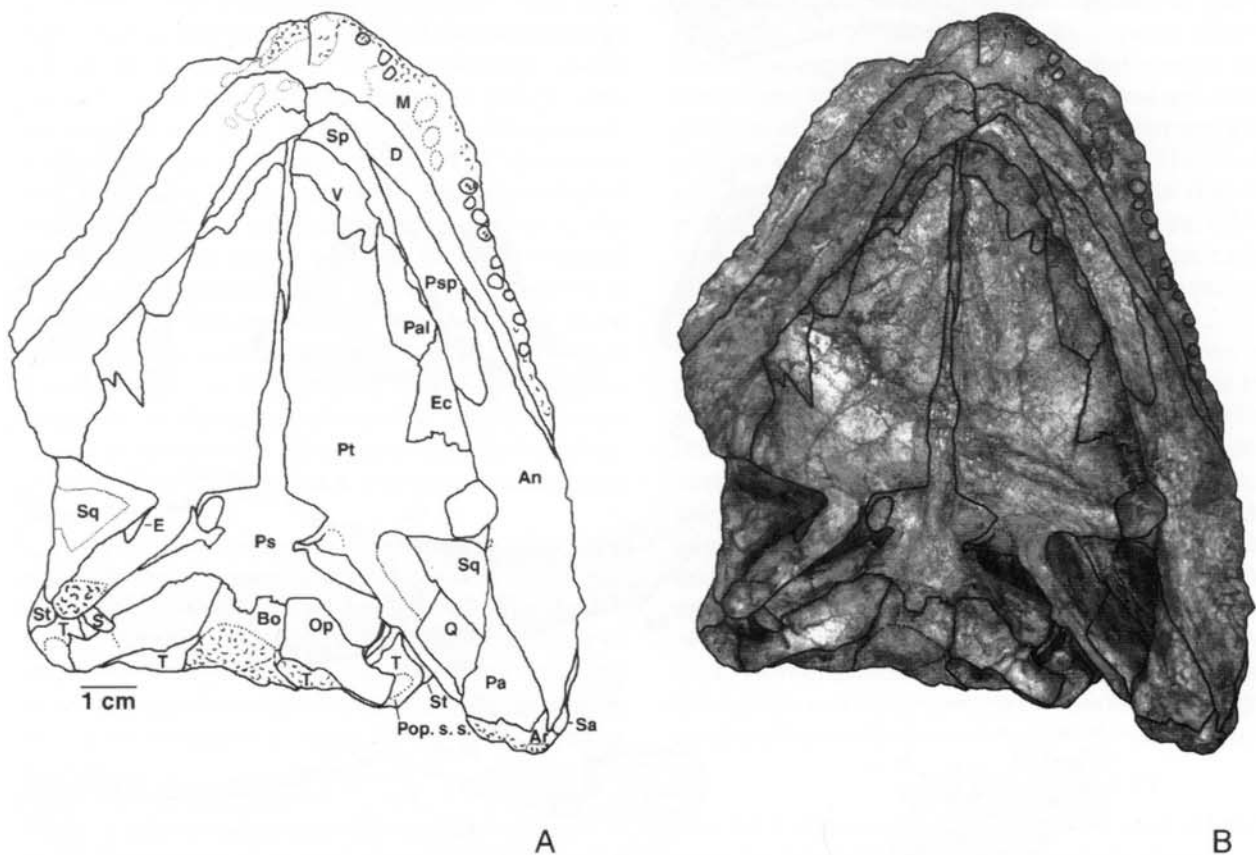
The dorsal surface of the parietal is fairly flat, and it is visible almost exclusively in dorsal view (fig. 1C). Its ventral surface bears a thick ridge in the midline, behind the pineal foramen. This ridge is visible in all specimens in which this area is exposed, but it is especially well developed in TMM 31189-1.

The otic flange (as we may call any smooth flange contributing to the formation of the otic notch) of the supratemporal is oriented ventrally at a right angle to the skull table. The otic flange of the supratemporal is wide anteriorly but tapers

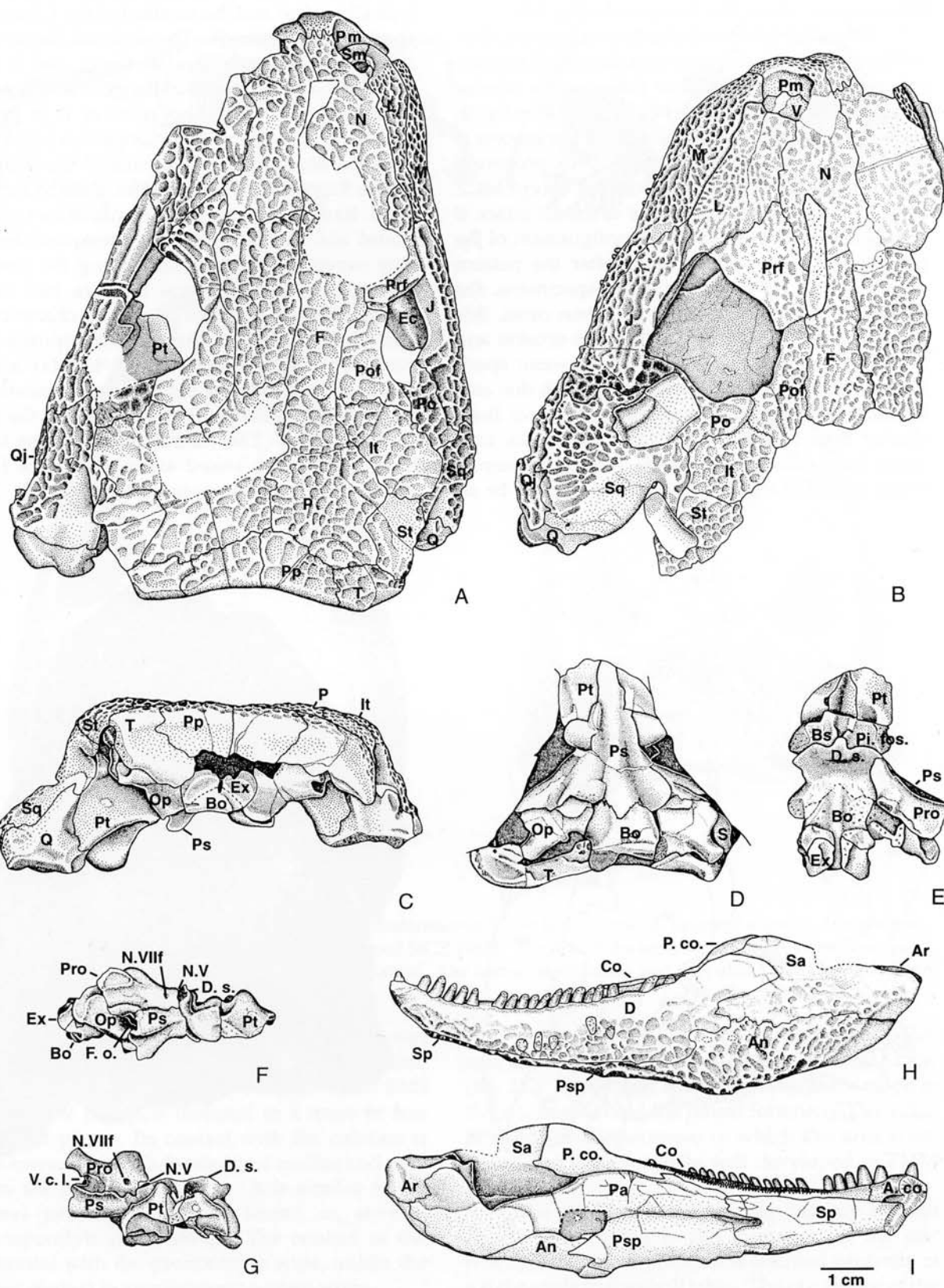
abruptly in width shortly before merging into the tabular horn, where the flange ends (fig. 1A).

The tabular is divided into a sculptured, dorsal flange and a smooth, occipital flange. The posterolateral corner of the dorsal flange of the tabular forms over half of a long, thick, ventrolaterally directed process. The other portion of the process is composed of the supratemporal. This process is somewhat damaged in all specimens except MCZ 1081, in which the right process is almost intact, if somewhat bent ventrally. The configuration of the process has been reconstructed after the pattern seen in MCZ 1081. In the other specimens, the process is distinctly shorter. In some cases, this difference can be clearly attributed to erosion and other preservational artifacts, but in some specimens such as TMM 31189-1, even though this area is damaged, the process appears to have been shorter than in MCZ 1081. This difference may result from sexual dimorphism, it may represent a more primitive condition, or it could even be an

ontogenetic phenomenon (TMM 31189-1 is the geologically oldest and the smallest of the *S. baylorensis* specimens examined). The occipital flange of the tabular consists of a medial flange and a lateral flange. The lateral occipital flange braces the paroccipital process and covers most of it in occipital view (fig. 1B). The medial flange is sutured to the occipital flange of the postparietal medially, and covers the posttemporal fenestra, thereby constricting it. Its anterior surface is sutured to the opisthotic dorsal and medial to the post-temporal fenestra. Any nerve or blood vessel leaving the braincase through the posttemporal fenestra had to pass posterolaterally through a narrow channel. The posterior wall of this channel is composed of the medial occipital flange of the tabular and the opisthotic, whereas the anterior wall consists of the lateral occipital flange of the tabular and the paroccipital process. The ventral surface of the tabular bears a complex, raised articular surface for the distal tip of the paroccipital process (fig. 2). White



**Figure 2.** Skull of a large specimen of *Seymouria baylorensis* (BMS E3500). A, Labeled line drawing. B, Edited photograph.



interpreted this surface as a canal for the dorsal process of the stapes and the dorsal end of the hyoid arch (White, 1939: fig.4). The specimens that he studied were apparently not fully mature and had a relatively short paroccipital process, but the larger, more mature BMS E3500 shows that the paroccipital process reached at least the medial end of this articular surface (fig. 2). A cartilaginous extension of the paroccipital process presumably extended to the lateral edge of this articular surface. Therefore, the association between this area and a presumed cartilaginous dorsal process of the stapes (for which there is no evidence), while not strictly impossible, is not supported by these new observations.

The postparietal is a complex bone composed of a dorsal flange, an occipital flange, and a ventromedial process. In TMM 31189-1, the suture between the occipital flanges of the postparietal and tabular extends ventromedially. This configuration is also visible in MCZ 1081 (fig. 3C) and MCZ 1086, and it is used in the new reconstruction (fig. 1B). However, in BMS E3500, the same suture extends ventrally to the level of the exoccipital. This configuration is only visible on the left side and may be abnormal or an artifact. The morphology of the ventral tip of the occipital flange is poorly preserved and can only be estimated by comparison with specimens of *S. sanjuanensis*. The ventromedial process is analogous to the supraoccipital of amniotes, and it roofs the braincase medial to the opisthotic. The lateral edge of the ventromedial process is separated from the dorsal flange by a deep recess, and its surface is marked by more foramina than that of the dorsal flange. However, it is not exposed on the occiput, unlike the supraoccipital of cotylosaurs, because the occipital flange covers it posteriorly. This area was illustrated by White (1939: fig. 4), and his interpretations appear to be correct.

The jugal is a robust element with a triangular cross-section; it expands ventromedially and ventrolaterally from its thin orbital rim. In TMM 31189-1, BMS E3500 and MCZ 1981, the jugal appears to reach the ventral edge of the cheek and hide the maxillary-quadratojugal contact laterally, as shown in the reconstruction (fig. 1A). In MCZ 1983, a

narrow portion of the contact between the maxilla and the quadratojugal is visible in lateral view below the jugal, but this may result from distortion. White (1939) may have based his reconstruction on this specimen; he shows a narrow contact between the maxilla and the quadratojugal laterally.

The quadratojugal is a long and narrow element in lateral view, but an examination of the medial surface of the cheek shows that it is broad medially. The quadratojugal overlaps the squamosal and the jugal medially, it barely reaches the ectopterygoid anteriorly, and it covers the lateral surface of the quadrate (fig. 1D). A small, smooth rounded flange of the quadratojugal covers part of the lateral condyle of the quadrate. The rest of the lateral surface of the quadratojugal is sculptured like most of the other dermal cranial bones.

The transverse flange of the pterygoid extends ventrolaterally from the basicranial area, as in amniotes, limnoscelids (Fracasso, 1983), and diadectids (Berman et al., 1992), and is very thick along its posterior and lateral edges. However, it lacks the row of large teeth found in limnoscelids and in several early amniotes. The quadrate ramus lacks a tympanic (or arcuate) flange; its ventral edge is blunt and expands anteriorly where it merges into the palatal and transverse flanges. A deep emargination of the pterygoid receives the basiptyergoid process of the basisphenoid (fig. 1D). The shape and size of this articular surface indicates that the parasphenoid was in the plane of the palate rather than dorsal to it, as in amniotes. The basicranial articulation of *Seymouria* was probably akinetic, but it was not fused.

The epiptyergoid is suturally distinct from the pterygoid and located on the lateral surface of the pterygoid, as in many tetrapods (fig. 2). White (1939) had interpreted a broad, transverse, vertical flange located above the basicranial area as the dorsal process of the epiptyergoid of "*Conodectes favosus*" (a junior synonym of *Seymouria baylorensis*), and this interpretation first appeared plausible because a similar flange was found in other seymouriamorphs (Laurin, 1995, in press b). However, further preparation of BMS E3500 revealed the presence of an epiptyergoid lateral to the pterygoid and suturally distinct from it. This configura-

**Figure 3.** Specimen drawings of *Seymouria baylorensis*. A, Skull of MCZ 1081 in dorsal view. B, Partial skull of MCZ 1083 in dorsal view. This skull is dorso-ventrally crushed, causing the sides of the snout and cheek to be more exposed than in an undistorted specimen. C, Occiput of MCZ 1081. Part of the braincase is visible through the damaged left tabular horn. D, E, F, G, Braincase of MCZ 1081 in ventral view (*in situ*), dorsal view, right lateral view, and anterior view respectively. Much of the cultriform process is missing, and the left otic capsule is not drawn because it is attached to the skull roof. H, I, Left lower jaw of MCZ 1083 in lateral and medial views, respectively.

tion is found in many tetrapods, but the presence of a transverse, vertical flange of the pterygoid dorsal to the basicranial area is an autapomorphy of seymouriamorphs.

The ectopterygoid is tightly sutured to the jugal and quadratojugal posterolaterally (fig. 1D). Its shape is variable. In MCZ 1083 it is a small, rectangular element posterolateral to the palatine. The suture between the ectopterygoid and the pterygoid is linear, as reconstructed by White (1939). In BMS E3500, the posteromedial corner of the ectopterygoid forms an acute angle wedged between the transverse flange and the palatine flange of the pterygoid. This is the configuration reconstructed here (fig. 1D).

The cultriform process is much longer than described by White (1939) and extends almost to the level of the palatine tusks (fig. 1D), although an undetermined portion of its anterior tip may have been hidden by the pterygoid in life. It is very slender and well preserved only in BMS E3500 (fig. 2), a specimen not available to White. Dorsally, the cultriform process is grooved and it probably supported the orbitosphenoid. This dorsal portion of the cultriform process seems to be the structure that White (1939) called the presphenoid. The parasphenoid extends posterolaterally toward the anteroventral rim of the fenestra ovalis (figs. 1D and 3D-G). This portion of the parasphenoid is located between the opisthotic and the prootic and is unique to seymouriamorphs (Laurin, in press b).

The dorsum sellae is high and has an anterior median ridge (fig. 3E). Anteriorly, this ridge becomes paired and encloses the pituitary fossa. The pituitary fossa is narrow posteriorly and widens anteriorly, where it is confluent with the space medial to the orbitosphenoid. The basisphenoid does not extend anteriorly beyond the pituitary fossa and ends abruptly at this level (fig. 3E). The articular facets of the basiptyergoid process are restricted to the tip and anterior surface of the process and are well demarcated from the rest of the surface covered by periosteal bone (fig. 3E).

Only remnants of the orbitosphenoid can be seen on TMM 31189-1 and on MCZ 1081. Therefore, I have been unable to determine if it is a paired orbitosphenoid or a median, Y-shaped sphenethmoid as is found in amniotes. The preserved fragments extend along the ventral surface of the skull roof from the level of the anterior portion of the parietal anteriorly along about two-thirds of the frontal. The orbitosphenoid widens anteriorly.

The braincase was beautifully illustrated by White (1939), and his reconstructions and descrip-

tion were essentially correct. Therefore, a new reconstruction of the braincase is not given here (except reconstructions of the braincase *in situ* in fig. 1B, D). The following description emphasizes specimens illustrated for the first time (fig. 3).

The exact shape of the occipital condyle can only be guessed because it is not completely ossified in any of the available specimens. However, White's reconstruction of the condyle seems to have been based on MCZ 1081, which is not completely ossified and is not the largest specimen available. Accordingly, the new reconstruction (fig. 1B) shows the probable shape of a more fully ossified condyle. A deep notochordal pit is present in MCZ 1081 and may have been retained throughout ontogeny, as in embolomeres and some diadectomorphs. The condyle was oval and transversely broad. The suture between the basioccipital and the exoccipital is clear on the lateral surface of the braincase (fig. 3F), but only its approximate location can be deciphered on the occipital surface because much of this area is covered by cancellous bone. The basioccipital forms the anterior part of a paired process bordering the notochordal canal (fig. 1B, and 3E). The posterior two-thirds of this process is composed of the exoccipital. The dorsal surface of the basioccipital bears a strong ridge anterior to the exoccipital (fig. 3E). This may be the structure that White (1939) identified as the ossified anterior end of the notochordal sheath.

The otic capsule is a complex structure consisting of a broad, posterodorsally slanting paroccipital process and a slightly shorter, ventral cylindrical otic tube. The prootic forms the anterodorsal half of the paroccipital process (fig. 3D-G). The opisthotic forms the posterior half of the paroccipital process and the otic tube, while the parasphenoid is restricted to the anterior half of the otic tube. The reconstruction of the braincase drawn by White reflects the specimens that he studied, but the larger, presumably more mature BMS E3500 shows that the paroccipital process was longer in mature individuals.

The stapes, present in several specimens (MCZ 1081, MCZ 1084, MCZ 1086, and BMS E3500) is a small, distally tapering rod. It differs from the braincase elements in its smooth and shiny surface. Its thick proximal end seems to fit loosely into the fenestra ovalis, but it is not expanded into a distinct footplate. Its orientation can only be guessed, because the stapes was not tightly sutured to any of the surrounding elements. Therefore, it has moved to some extent in all the available specimens. However, it seems likely that the narrow end was di-

rected toward the tympanum. To what extent the ossified portion of the stapes was enclosed in the otic tube (as described by White) is not known, but its position outside the otic tube in all the specimens suggests that it did not fit very deeply into the tube and probably reached the vicinity of the ear drum distally.

The lower jaw is preserved in several specimens, but MCZ 1083 is by far the most informative because it is well preserved, complete, and free from the skull. This jaw formed the basis of White's (1939) reconstruction, but a new description is appropriate because new specimens provide important additional information.

The articular bears two oval, shallow articular surfaces for the condyles of the quadrate. The medial cotyle is shorter and narrower than the lateral one. The ridge between the cotyles extends anteriorly and about 30° lateral to the long axis of the lower jaw (measured between the articular and the symphysis). The articular is a massive bone and extends ventrally to the bottom of the lower jaw, but no farther anteriorly than the level of its articular surfaces. Even in mature specimens, the retroarticular process is small and poorly defined. It is located slightly dorsal, lateral and posterior to the point where the articular, the prearticular and the angular meet (fig. 3I).

White reconstructed a mandibular fenestra between the prearticular, the angular and the postsplenial because he saw a hole in this area in the mandible of MCZ 1083, but broken edges suggest that this structure is an artifact. The same area is preserved in BMS E3500 and TMM 31189-1. A break in BMS E3500 indicates that several bones overlapped each other in this area. Furthermore, an examination of TMM 31189-1 shows that no foramen was present between the prearticular, the angular and the postsplenial. White also drew a foramen just anterior to the prearticular, between the splenial and the postsplenial. Further preparation of MCZ 1083 shows only a deep depression in this area, and examination of TMM 31189-1 reveals that this too is probably an artifact.

The middle coronoid, the anterior half of the posterior coronoid, and the posterior half of the anterior coronoid are covered in a shagreen of denticles. The lateral surface of the dentary is sculptured except just below the marginal tooth row and around the coronoid process. It bears 25 to 26 alveoli, about 6 of which are empty.

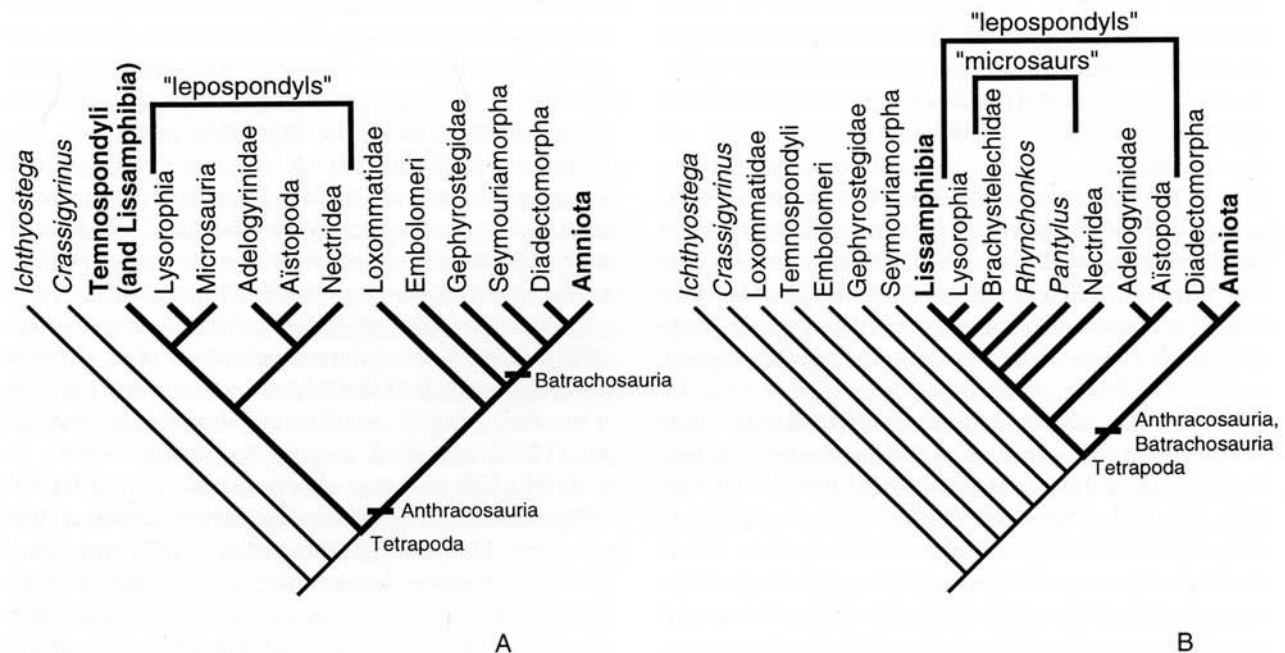
The previous description of the postcranium of *Seymouria baylorensis* (White, 1939) was essentially correct. Only a few comments on the atlas-

axis complex are warranted. White (1939) stated that the atlantal pleurocentrum (that he called the odontoid) was a single bone, but he quoted his entire description of the atlas-axis complex from Watson (1918). Unfortunately, Watson appears to have misinterpreted the atlas-axis complex. The element that he identified as the atlantal intercentrum corresponds to the axial intercentrum, and his "odontoid" may be the axial pleurocentrum. These new identifications are supported by comparisons with more recent illustrations of the atlas-axis complex of *S. baylorensis* (Sumida et al., 1992). If these new interpretations are correct, there is no evidence that the atlantal pleurocentrum was a median (single) ossification. Indeed, Berman et al. (1987) reported a paired pleurocentrum in FMNH 6138, and my observations on FMNH UR 458 enable me to confirm the paired nature of this element. However, Berman et al. (1987) suggested that the atlantal pleurocentrum of *Seymouria* ossified late in ontogeny because it is not mineralized in the known specimens of *S. sanjuanensis*. Sumida et al. (1992) went further and accepted Watson's (1918) statement that the atlantal pleurocentrum was median but suggested that this condition was reached late in ontogeny. Such a scenario is possible, but considering the inconsistencies in Watson's reconstruction of the atlas-axis complex of *Seymouria* and the presence of a paired atlantal pleurocentrum in all the specimens of *S. baylorensis* that have been studied recently (including FMNH UR 458, a large, adult or subadult individual), the atlantal pleurocentrum was probably paired in this species and in other seymouriamorphs. The atlantal pleurocentrum is poorly known in other seymouriamorphs, but it may also be paired in *Ariekanerpeton* (Laurin, in press b).

## DISCUSSION

### Previous work on *S. baylorensis*

Considering that it was published more than half a century ago, White's (1939) description of *S. baylorensis* is remarkably accurate. Most of the inaccuracies in his description would have been impossible to correct using only the specimens that were available to him. The corrections that required information from other specimens include the less acute angle of the orbit, the contribution of the jugal to the ventral edge of the skull, the presence of a long cultriform process, the ventrolateral orientation of the transverse flange of the pterygoid, the absence of mandibular fenestrae, and the paired atlantal pleurocentrum.



**Figure 4.** Tetrapod phylogenies. A, The widely accepted phylogeny of tetrapods (modified from Lombard and Sumida, 1992). B, The new phylogeny, based on a computer-assisted analysis of a matrix composed of 38 taxa and 157 characters. This tree is a simplified version of the phylogeny of Laurin and Reisz (in press); many of the terminal taxa shown here are represented by a sample of lower taxa in Laurin and Reisz (in press). Extant taxa are in bold type. According to this new phylogeny, seymouriamorphs are no longer part of Tetrapoda (drawn in bold lines), Anthracosauria, and Batrachosauria. "Lepospondyls" and "microsaurs", as currently recognized, are paraphyletic groups.

### Ontogenetic problems in seymouriamorphs

Comparisons between various genera of seymouriamorphs are hampered by ontogenetic considerations. *Seymouria* and *Kotlassia* seem to be the only seymouriamorphs represented by fully mature individuals. This probably explains why *Kotlassia* was usually believed to be a seymouriid; a recent phylogenetic analysis of seymouriamorphs suggests that *Discosauriscus* and *Ariekanerpeton* are more closely related to *Seymouria* than to *Kotlassia* (Laurin, in press a). Other seymouriamorphs such as *Discosauriscus*, *Ariekanerpeton*, and *Utegenia* are only known from larval and small to mid-sized postmetamorphic specimens (Klembara, 1995). Therefore, some of the differences used to differentiate *S. baylorensis* from *Discosauriscus* and *Ariekanerpeton* in the revised diagnosis must be used with caution, and not all the new anatomical features of *S. baylorensis* can be used in the diagnosis. For instance, the presence of a vertical transverse flange of the pterygoid located above the basicranial area does not distinguish *Seymouria* from other seymouriamorphs, because this flange was also observed in *Ariekanerpeton* (but misinterpreted as part

of the epipterygoid) and is probably diagnostic of seymouriamorphs (Laurin, in press b). Anatomical data on larger specimens of *Ariekanerpeton* and *Discosauriscus* are needed for a revision of seymouriamorph systematics. Unfortunately, mature specimens of these two genera are not available.

### Seymouriamorph affinities and classification

A recent phylogenetic analysis requires a drastic change in the classification of seymouriamorphs (Laurin and Reisz, in press). In previous studies (Laurin, 1995, in press a and b), seymouriamorphs were classified within the higher taxa Tetrapoda Goodrich, 1930 and Batrachosauria Efremov, 1946. According to the principles of priority of phylogenetic definitions (de Queiroz and Gauthier, 1990, 1992, and 1994), the definitions of Tetrapoda and Batrachosauria given by Gauthier et al. (1988, 1989) have priority.

Gauthier et al. (1989) defined Tetrapoda as the crown group of terrestrial vertebrates (a crown group is a clade that includes the last common ancestor of all the living members of a group, and

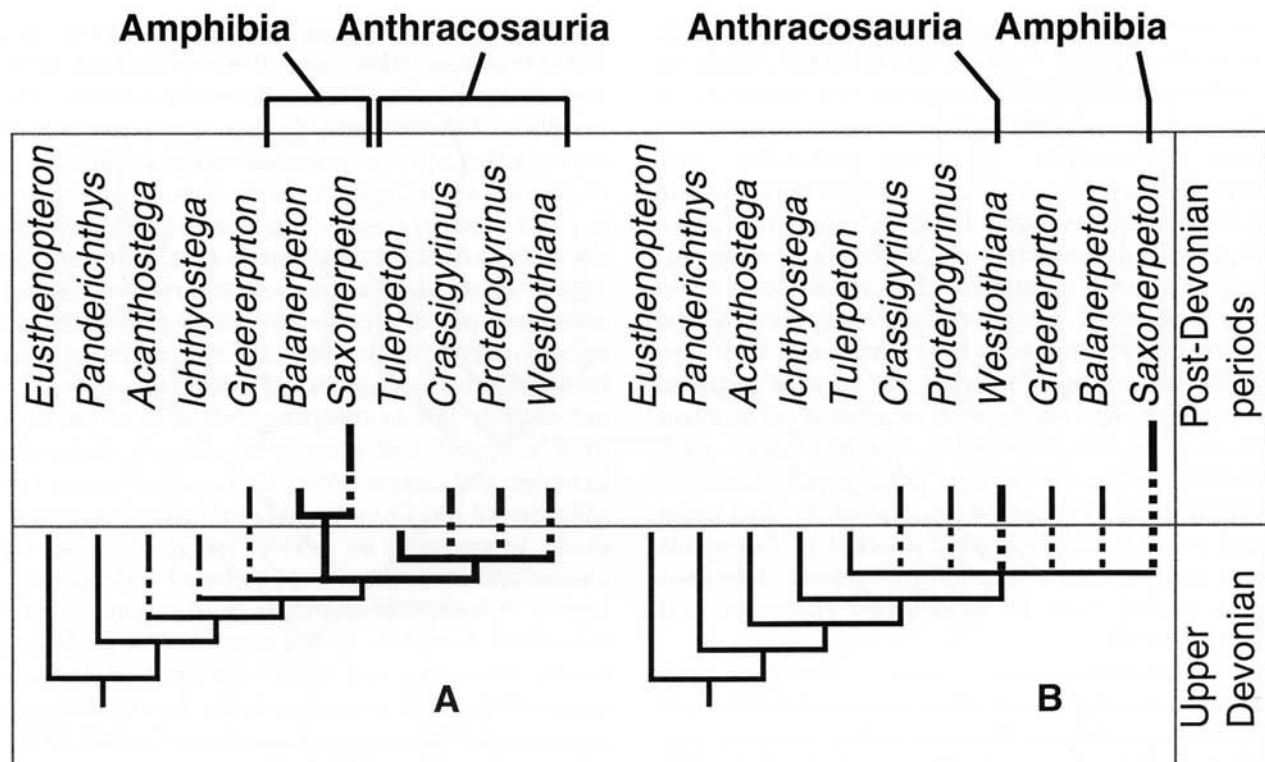
all its descendants). As such, Tetrapoda explicitly excluded some limbed vertebrates, such as *Ichthyostega* (fig. 4A). Applying the definition of Tetrapoda suggested by Gauthier et al. (1989) to the new phylogeny (fig. 4B) indicates that seymouriamorphs are not members of Tetrapoda (and hence they should not be called tetrapods, because only members of Tetrapoda deserve this epithet). This conclusion differs drastically from the established usage of Tetrapoda, because this taxon was erected to include vertebrates with four limbs (as opposed to fins). As such, it included lissamphibians, amniotes, their presumed relatives (such as seymouriamorphs), and vertebrates, such as *Ichthyostega*, not thought to be closely related to lissamphibians or amniotes. However, this older and more widely accepted concept of Tetrapoda was never given a formal phylogenetic definition and should now be abandoned (Lebedev and Coates, 1995).

Batrachosauria was erected for seymouriamorphs and other presumed relatives of amniotes, and this is the most widely accepted concept of Batrachosauria (Boy and Bandel, 1973; Berman et al., 1987; Laurin, 1995). However, the first phylogenetic definition of this taxon clearly stated that it included extant amniotes and all other anthracosaurs that are more closely related to amniotes than to embolomeres (Gauthier et al., 1988). The definition of Anthracosauria S  ve-S  derbergh, 1934 as all taxa that are more closely related to amniotes than to lissamphibians (Gauthier et al., 1988), and the new phylogeny of terrestrial vertebrates (Laurin and Reisz, in press) indicate that Batrachosauria is redundant with Anthracosauria because all anthracosaurs are more closely related to amniotes than to embolomeres (fig. 4B). Therefore, Batrachosauria is declared a junior synonym of Anthracosauria according to the principle of page priority (the first phylogenetic definitions of these taxa were published by Gauthier et al., 1988, but Anthracosauria was defined first), and Batrachosauria should not be used unless it is given a new phylogenetic definition. Seymouriamorphs were previously considered to be anthracosaurs, but according to the phylogenetic definition of Anthracosauria, this classification is no longer acceptable because seymouriamorphs are not more closely related to amniotes than to lissamphibians (fig. 4B).

Lebedev and Coates (1995) recently argued that Tetrapoda originated in the Devonian and that *Tulerpeton* Lebedev 1984, *Crassigyrinus*, the embolomere *Proterogyrinus* Romer, 1970, and

*Westlothiana* Smithson and Rolfe, 1990 are anthracosaurs (they use the equivalent term Reptiliomorpha Panchen and Smithson 1988). The results of Lebedev and Coates (1995) imply that seymouriamorphs are also anthracosaurs, and these results are in conflict with mine (Laurin and Reisz, in press). Since Lebedev and Coates (1995) provide the only published data matrix that includes presumed relatives of amniotes (anthracosaurs) and presumed relatives of lissamphibians (amphibians sensu Gauthier et al., 1989), their view deserves to be considered carefully. It is difficult and perhaps not entirely fair to compare both studies because their methods and aims were slightly different; Lebedev and Coates (1995) attempted to assess the affinities of the Devonian taxon *Tulerpeton*, previously interpreted as a stem-tetrapod, whereas Laurin and Reisz (in press) produced a global phylogeny of tetrapods and their close relatives. Furthermore, Lebedev and Coates (1995) included mostly Devonian and Mississippian taxa in their analysis (the only exception is the Lower Permian lepospondyl *Saxonerpeton* Carroll and Gaskill, 1978), whereas Laurin and Reisz (in press) included Devonian to extant taxa. The absence of amniotes and lissamphibians from the analysis of Lebedev and Coates (1995) requires assumptions about the anthracosaur or amphibian status of at least some of the included taxa, and for the purpose of this discussion, we will assume that *Westlothiana* is an anthracosaur and that *Saxonerpeton* is an amphibian.

As Lebedev and Coates (1995) explained, their phylogeny is an Adams consensus-tree of the shortest trees (fig. 5A). My initial attempt at finding this tree using PAUP 3.1.1 (Swofford, 1993) failed, and communicating with the junior author provided an explanation: a printer error resulted in a miscoding of character 41 in *Balanerpeton* Milner and Sequeira, 1994. This entry should read "1" rather than "?". A decay analysis was undertaken to evaluate the support for this phylogeny. Anthracosauria requires a single extra step to collapse (fig. 5B), but Tetrapoda (Amphibia plus Anthracosauria) requires four extra steps to collapse. Therefore, the decay analysis suggests that *Tulerpeton* is more closely related to tetrapods than to *Ichthyostega* and *Acanthostega* Jarvik, 1952 (four extra steps are required to find trees incompatible with this hypothesis), but it indicates that evidence for placing *Tulerpeton* in Anthracosauria and Tetrapoda is weak, as some trees requiring a single extra step place *Tulerpeton* elsewhere. A bootstrap analysis yielded similar results; Anthracosauria was found in only 57% of



**Figure 5.** Phylogeny of stem-tetrapods superposed on a coarse geological time scale. A, The Adams consensus-tree found by Lebedev and Coates (1995). According to this phylogeny, Tetrapoda (drawn in bold lines), Anthracosauria, and Amphibia originated in the Devonian. B, The strict consensus-tree of all the trees that require one extra step. Notice that Tetrapoda, Anthracosauria, and Amphibia may be post-Devonian taxa. The terminology of suprageneric taxa follows Gauthier et al. (1988). Dashed lines indicate periods in which the existence of a lineage is not documented.

the 200 bootstrap replicates (using the branch and bound algorithm), but Tetrapoda was found in 98% of the replicates. These results indicate that Tetrapoda may not date back to the Devonian, because if *Tulerpeton* is not an anthracosaur, the oldest known tetrapod dates back to the Mississippian. Furthermore, a single extra step is required to remove *Proterogyrinus* (an embolomere) and *Crassigyrinus* from Anthracosauria (fig. 5B). Therefore, the data published by Lebedev and Coates (1995) provide only weak support for the traditional thesis that embolomeres (and their presumed relatives such as seymouriamorphs) are anthracosaurs. By comparison, the analysis of Laurin and Reisz (in press) is more robust because five extra steps are required to collapse Anthracosauria and eight extra steps are required to collapse Tetrapoda (sensu Gauthier et al., 1988).

Lebedev and Coates (1995) suggested that adaptation to a terrestrial environment took place independently in stem-amniotes and in stem-amphibians because the earliest anthracosaur (*Tulerpeton*, according to their phylogeny) is primitively aquatic (there is no evidence that the ancestors of *Tulerpeton*

had ever been terrestrial). This thesis conflicts with my suggestion that adult seymouriamorphs were terrestrial and that terrestrial habits appeared before Tetrapoda. However, Lebedev and Coates' (1995) argument depends on the identification of *Tulerpeton* as an anthracosaur. Therefore, the theory that terrestrial habits predate the origin of Tetrapoda is at present better supported than the alternative they proposed.

#### Significance of the new anatomical data

In some respects, *Seymouria* appears to be more similar to amniotes than previously thought, but most of these similarities are either convergent autapomorphies of this genus or primitive characters that do not indicate close relationships. *Seymouria* lacks the large mandibular fenestra reminiscent of embolomeres. However, mandibular fenestrae have been reported in other seymouriamorphs such as *Kotlassia* and *Ariekanerpeton* (Bystrow, 1944; Ivakhnenko, 1981). The presence of fenestrae in *Ariekanerpeton*, *Discosauriscus*, and *Utegenia* could also result from incomplete ossification of the mandibular elements,

but this does not explain their presence in *Kotlassia*, which is represented by large specimens. If these reports are accurate, the loss of mandibular fenestrae is probably only an autapomorphy of *Seymouria* and does not indicate close relationships with amniotes.

The presence of a long cultriform process in *S. baylorensis* is a primitive character shared with most other early terrestrial vertebrates. The presence of a long cultriform process has already been noted in *S. sanjuanensis* (Berman and Martens, 1993) and in *Ariekanerpeton* (Laurin, in press b). Therefore, it appears that seymouriamorphs were no different in this respect from most other early terrestrial vertebrates.

The transverse flange of *S. baylorensis* has the same orientation as its homologue found in amniotes, although it lacks the row of large teeth found in some groups of early amniotes. Berman and Martens (1993) believed that the transverse flange of *S. sanjuanensis* was flat, but this observation was based on a dorso-ventrally crushed specimen. The evidence presented here suggests that the transverse flange of *Seymouria* extends ventrolaterally. However, comparisons with several other early vertebrates suggest that whenever a transverse flange is present, it extends ventrolaterally rather than laterally (Laurin and Reisz, in press). Furthermore, the flange is present in more vertebrates than is generally realized. The transverse flange is present in gephyrostegids, in some temnospondyls (such as: *Ecolsonia* Vaughn, 1969; *Tersomius* Case, 1910; *Amphibamus* Cope, 1865), and even in some gymnophiones, such as rhinatrematids. A recent phylogenetic analysis suggests that this character is a synapomorphy of gephyrostegids, Seymouriamorpha, and Tetrapoda that was lost in lepospondyls (Laurin and Reisz, in press). Therefore, the presence of a transverse flange in seymouriamorphs does not imply that they are necessarily closely related to amniotes.

The presence of a distinct epipterygoid is a derived character found in amniotes, most lepospondyls, and a few relatives of tetrapods (seymouriamorphs, *Proterogyrinus*, and the temnospondyl *Tersomius*). The primitive condition of having a fused pterygoid-epipterygoid complex is found in several early vertebrates such as aistopods (Carroll, in press), *Archeria* Case, 1915 (Holmes, 1989), colosteids (Smithson, 1982), and loxommatids (Beaumont, 1977). The presence of a distinct suture between the epipterygoid and the pterygoid may be a synapomorphy of Tetrapoda (Laurin and Reisz, in press) and Seymouriamorpha,

or it may be a synapomorphy of all these taxa and embolomeres. Either optimization implies some convergence and reversals, but this character suggests that seymouriamorphs are closely related to tetrapods.

The paired atlantal pleurocentrum of seymouriamorphs is different from the circular atlantal pleurocentrum found in amniotes, diadectomorphs, and lepospondyls. A paired pleurocentrum undoubtedly represents a primitive condition for terrestrial vertebrates because the atlantal pleurocentrum is paired in osteolepiforms, most temnospondyls, and some embolomeres (such as *Proterogyrinus*). Therefore, the configuration of the atlantal pleurocentrum also suggests that seymouriamorphs fall outside Tetrapoda (fig. 4B).

By themselves, the new observations on the atlantal centrum are not sufficient to warrant removal of Seymouriamorpha from Tetrapoda, but a recent phylogenetic analysis (Laurin and Reisz, in press) indicates that seymouriamorphs retain many other primitive characters lost in tetrapods (fig. 4B). These characters were previously documented in seymouriamorphs (White, 1939), but the new phylogeny provides a new interpretation of their significance. These characters include the presence of an otic notch, an intertemporal, a contact between the pterygoid and the squamosal along the posterior edge of the cheek, vomerine and palatal fangs, three coronoid elements, and labyrinthine infolding of tooth enamel. The new interpretation of these characters, along with the new observations reported above, provide compelling evidence that seymouriamorphs are not closely related to amniotes, and that they are not tetrapods.

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