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Braincase of *Limnoscelis paludis* Williston

Michael A. Fracasso

(Received 15 October 1986)

Abstract

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Cladistic analysis of many cranial characters, including those of the braincase, indicates that among Paleozoic tetrapods, *Limnoscelis* is most closely related to the diadectomorphs *Tseajaia* and *Diadectes*. The diadectomorphs are primitive reptiles, most closely related to the pelycosaurs.

Key Words

Limnoscelis, braincase, anatomy, systematics, cladistics, Reptilia, Diadectomorpha.

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ISBN No. 0-912532-02-5

Introduction

Limnoscelis paludis has maintained a prominent role in the controversy concerning the origin and early evolution of reptiles. Yet its braincase—comprising several important systematic characters—has never been adequately described. *Limnoscelis* was first described by S. W. Williston in a series of papers during the years 1911–12 (Williston 1911a, 1911b, 1912), and was assigned to the Cotylosauria as a very primitive reptile. The morphologic features of *Limnoscelis* that most influenced Williston's taxonomic assignment are the presence of a rhynchocephalian-type palate consisting of a well-developed free basal articulation and prominent transverse, ventrally directed pterygoid flanges, combined with the absence of the typical labyrinthodont amphibian otic notch. A. S. Romer redescribed *Limnoscelis* in 1946, providing new and ostensibly corrected reconstructions of the skull for areas which had proved difficult for Williston to decipher, in particular the occiput. Romer not only concurred with Williston's earlier diagnosis of *Limnoscelis* as a primitive reptile, but further emphasized that " . . . this form is an exceedingly primitive reptile, definitely advanced over any known amphibian but sufficiently generalized to be regarded as representing the common stem of all lines of reptilian descent" (Romer 1946, Abstract). However, he recognized that the relatively late geologic occurrence of *Limnoscelis* in the Permocarboniferous precluded an actual ancestral role. Romer was not explicit regarding the primitive and unspecialized morphologic features of *Limnoscelis* that he considered significant, but by implication they included the absence of

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temporal fenestrae and the possession of unreduced supratemporal and tabular elements. This combination of features makes *Limnoscelis* appear less specialized and more primitive than its captorhinomorph contemporaries, the protorothyrids (formerly romeriids) and captorhinids.

Debate over the evolutionary significance and problems of the origin of reptiles has intensified in recent years, and following Romer's (1946) explicit advocacy of *Limnoscelis* as an ideal "proxy" ancestor of reptiles, most recent students of this problem have been impelled to address the issue of the relation of *Limnoscelis* to the ancestry and origin of reptiles (Carroll 1969a, 1969b, 1982; Panchen 1972; Lombard and Bolt 1979; Heaton, 1980; Kemp 1980; Reisz and Heaton 1980).

However, despite discoveries of diverse new taxa which have bridged some problematic morphologic gaps, advances in conceptualizations of the micro- and macroevolutionary processes, advances in the principles of biomechanical analysis, and the relatively recent cladistic revolution in systematic philosophy and methodology, there is still no consensus regarding either the low-level systematics of *Limnoscelis* or its potential relation to the problem of the origin of reptiles. The most striking deficiency of all published work concerning *Limnoscelis* has been the unavailability of complete or even accurate anatomical information. Williston and Romer were aware of cranial material from only two specimens: the holotype skull which is complete except for the stapes (YPM 811), and some fragments that presumably belong to a single individual (FMNH 650). Neither author completely described the available cranial material. Both workers focused their studies on the easily visible superficial surfaces of the holotype skull, and both studies contain errors of anatomical interpretation in even well-exposed regions such as the temporal area and occiput. The basicranium was largely covered and the internal cranial cavities completely filled by matrix, so the braincase was hidden in both lateral and dorsal views and has never been fully described. All subsequent workers have relied on Williston's and Romer's published descriptions of the cranial anatomy of *Limnoscelis,* and their results and discussions are necessarily subject to the limitations of the available published data.

I have had access to both the *Limnoscelis* holotype skull (YPM 811) and newly discovered associated cranial elements of *Limnoscelis* collected by Peter Vaughn (UCLA), and have further prepared the holotype cranial material. I have separated the holotype skull into its original 8–10 component blocks that had been cemented together prior to Williston's descriptions, and have mechanically prepared each block to as great a degree as practicable. I can now offer a complete redescription of the *Limnoscelis* braincase that is based largely on the newly prepared holotype skull, and was checked against the extremely well-preserved associated *Limnoscelis* braincase elements collected by Peter Vaughn. Romer had stated, with respect to regions of the skull then inaccessible, "Were we better informed as to the structure of the *Limnoscelis* braincase, palate, and jaw, a number of further definitive reptilian characters could surely be added to this list" (Romer 1946, p. 167). Exposure of these areas has revealed new characters which, although not necessarily reptilian as Romer predicted, are surprisingly unique—particularly the configuration and nature of ossification of the braincase.

Abbreviations

The following institutions are referred to in the text:

CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Harvard University
UCLA	University of California, Los Angeles

YPM Peabody Museum of Natural History, Yale University

Braincase Anatomy

The *Limnoscelis* holotype skull and braincase are extremely well preserved in three dimensions and have been only slightly affected by postdepositional compression. Thorough removal of matrix from the cranial component blocks, combined with cross sections exposed by their separation and minor breaks that occurred during preparation, provides unparalleled information regarding the anatomy of the braincase. Contacts that are indistinct on the skull surface because of weathering or fracturing, or both, are often clearly displayed in cross section. Figures 1 through 7 include restorations of and cross sections through the *Limnoscelis* braincase. Individual elements are described as follows:

Basiparasphenoid The embryologically distinct endochondral basisphenoid and its ventral dermal investiture, the parasphenoid, are tightly apposed and often fused to varying degrees in adult tetrapods. The two elements are indistinguishable and apparently completely fused in *Limnoscelis* as discussed below, and are here treated as a single complex unit which I term the basiparasphenoid.

The basiparasphenoid (Figs. 1–5) is a bipartite element, consisting of a posterior chevron-shaped horizontal plate with its apex pointed anteriorly, and an anterior elongate troughlike extension, the cultriform process. The exposed surfaces of the basiparasphenoid are quite smooth with the exception of a small dense patch of denticles, represented only by their worn bases, that cover the ventral surface of the anterior rostrum of the chevron plate, just posterior to the proximal base of the cultriform process.

The posterior borders of the horizontal chevron plate trend posterolaterally from the midline (Fig. 1), contacting the anterolateral borders of the basioccipital in strongly interdigitate sutures. These sutures terminate at the apices of sharp clefts with unfinished borders. These clefts are situated between the cristae ventrolaterales (tubera basioccipitalia) anteriorly, and the troughlike projections of the fused opisthotic-basioccipital posteriorly. These recesses were probably filled by cartilaginous extensions of the basiparasphenoid and basioccipital in life. Such cartilage probably contributed in small part to the midventral borders of the oblate fenestrae ovales (Fig. 3). The main chevron plate possesses a distinct median longitudinal ridge (Fig. 1) that trends anteriorly and expands to terminate as a thin vertical septum inside the slightly hooded recess formed at the anterior rostrum of the chevron plate, and also extends posteriorly onto the basioccipital.

The lateral borders of the chevron plate project sharply ventrally along their entire lengths as the prominent cristae ventrolaterales. The posterior terminations of the cristae are blunt, unfinished, posterolaterally facing oval surfaces that were undoubtedly capped by cartilage in life. The cristae trend anteromedially from their posterior terminations, smoothly converging at the apex of the chevron plate to form a rounded and thickened hoodlike rostrum. The rostral hood projects posteriorly to slightly overhang the apex of the chevron plate by several millimeters; this forms a very distinct but small posterior recess in the hooded basiparasphenoid rostrum. Similar rostral hoods that have grown posteriorly to a far greater extent are characteristic of *Diadectes* (Olson 1947, described as parasphenoid wings). A rostral hood comparable in development to that of *Limnoscelis* has also been described in *Tseajaia* (Moss 1972). The rostral hood and median septum combine to form a pair of pockets which probably accommodated the paired basicranial portions of the hypaxial muscles.

The basiparasphenoid of *Limnoscelis* is completely exposed in the left lateral view (Fig. 3), whereas the right side of the braincase is obscured by the close articulation of the pterygoid quadrate ramus and quadrate pterygoid lamella posterior to the basal articulation. The left crista ventrolateralis

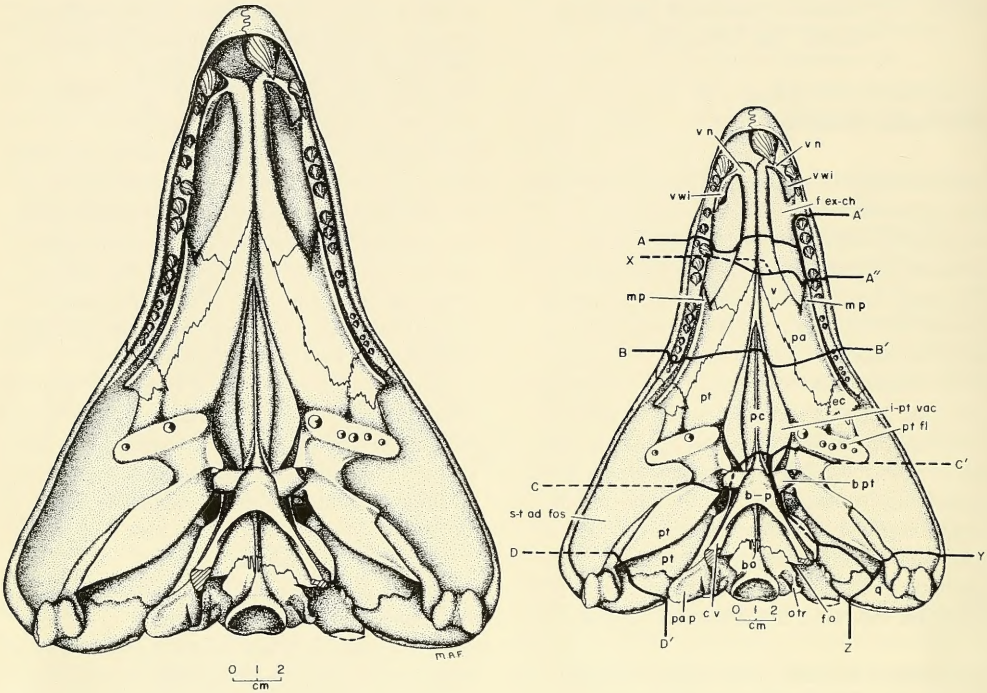

Fig. 1

Braincase and skull of *Limnoscelis paludis* in ventral view, based on restoration of the holotype specimen. Capital letters and heavy dashed or solid lines indicate the locations of cross sections.

Abbreviations for Figs. 1–8: ant = anterior; arc fl = arcuate flange; art d pr st = articular knob for stapes dorsal process; art fac t = articular facet for tabular medial cone; art q = articular area for quadrate; bo = basioccipital; b pt = basipterygoid process; b-p = basiparasphenoid; c pa = crista parotica; c v = crista ventrolateralis; d s = dorsum sellae; ec = ectopterygoid; eth m = ethmosphenoid moiety; ex = exoccipital; f ex-ch = fenestra exochoanalis; f h = hypoglossal foramen (XII); f m = foramen magnum; f o = fenestra ovalis; f p q = foramen paraquadratum proprium; gr vcl, h r = groove of vena capitis lateralis and hyoid ramus of facial nerve (VII); i-pt vac = interpterygoid vacuity; m p = maxillary process; not = notochord; o = otic; op = opisthotic; otoc m = otoccipital moiety; o tr = otic trough; olf tr = olfactory tract (I); p = parietal; pa = palatine; pc = processus cultriformis; pp = postparietal; pro = prootic; ps = parasphenoid; pt = pterygoid; pt fl = pterygoid flange; pa p = paroccipital process; ps = parasphenoid; q = quadrate; qj = quadratojugal; se t = sella turcica; sph = sphenethmoid; st = supratemporal; syn = synotic; s-t ad fos = subtemporal adductor fossa; s o = supraoccipital; s s = solum supraseptale; s-c c h = horizontal semicircular canal; tr n = trigeminal notch (V); t c = tabular cone; t dp = tabular dorsal plate; t oc = tabular occipital plate; ut = utriculus; v = vomer; v n = vomerine neck; v wi = vomerine wing.

rises posteriorly to contribute to the formation of the lateral wall of the braincase anterior to the fenestra ovalis. Further posteriorly, the dorsal border of the crista is an unfinished smooth edge which forms the anteroventral border of the fenestra ovalis. The anterior dorsal border of the crista trends straight forward in contact with the anterior ventral border of the "otic" ossification, before curving sharply dorsally to terminate as the dorsal edge of the posterior base of the dorsum sellae. The posterior base of the

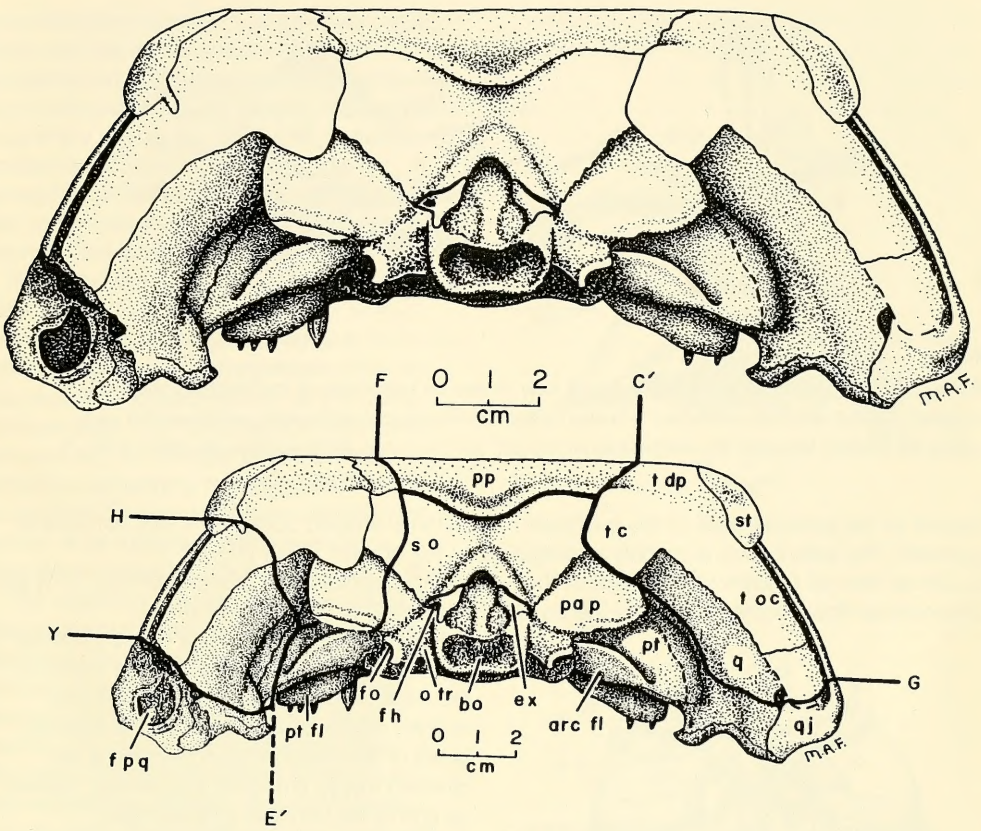

Fig. 2
Braincase and skull of *Limnoscelis paludis* in occipital view, based on restoration of the holotype specimen. Capital letters and heavy solid lines indicate the locations of cross sections. Abbreviations are listed in Fig. 1.

dorsum sellae is an oval surface which is tightly apposed to the anterior border of the "otic" ossification along a sharp contact in lateral view. The basiparasphenoid and otic junction that is both ventral to this sharp contact and anterior to the fenestra ovalis is not abrupt. It is rather a distinct, feebly ossified zone of varying width (Fig. 3). Although the adult braincase is unquestionably joined as a single solid unit, this continuous, rather L-shaped contact between the basiparasphenoid anteriorly and the otic posteriorly is very reminiscent of the primitive rhipidistian divided neurocranium.

The dorsum sellae in dorsal view (Fig. 5) is composed of left and right halves that are completely separated in the midline. A similar division is described in *Ophiacodon* (Romer and Price 1940). Unlike *Ophiacodon,* the dorsum sellae of *Limnoscelis* is obviously continuous with the basiparasphenoid and is not associated with the otic region (prootic of *Ophiacodon*). The finished dorsal border of the basiparasphenoid anterior to the dorsum sellae curves sharply ventrally and again dorsally in a smooth, U-shaped concave arc in lateral view (Fig. 2). The base of this arc lies dorsal to the base of the basipterygoid process, and the anterior border of the arc merges smoothly into the posterior dorsal

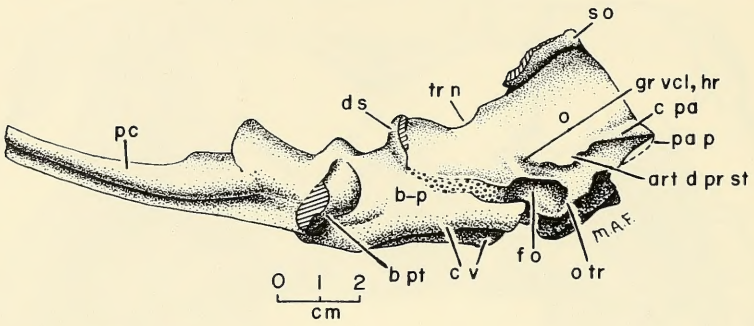

Fig. 3
Braincase of *Limnoscelis paludis* in left lateral view, based on restoration of the holotype specimen. Hatched pattern denotes unfinished or broken areas; coarse stipple represents poorly ossified zone along the contact between the basiparasphenoid and otic elements. Abbreviations are listed in Fig. 1.

border of the proximal base of the cultriform process. The sella turcica is partially exposed in dorsal view as a distinct depression in the neurocranial floor situated medial to the bases of the U-shaped dorsal arcs and just anterior to the dorsum sellae (Fig. 5).

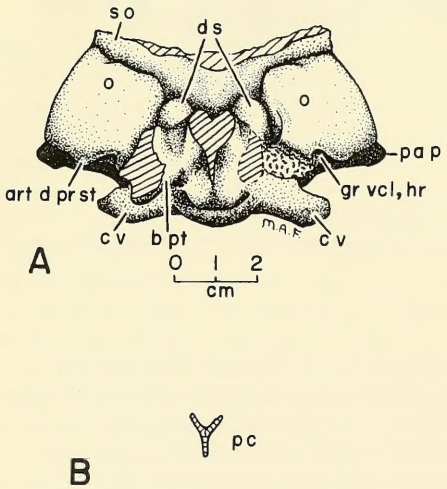

Fig. 4
A. Braincase of *Limnoscelis paludis* in anterior view across transect C-C′ (Fig. 1), based on restoration of the holotype specimen. Hatched pattern denotes unfinished or broken areas; irregular stipple represents poorly ossified zone between the basiparasphenoid and otic elements. *B.* Cultriform process of *Limnoscelis paludis* viewed in transverse section through transect B-B′ (Fig. 1). Abbreviations are listed in Fig. 1.

The basipterygoid processes (Figs. 3–5) are prominent stout pegs that project anteroventrally, just posterior to the proximal base of the cultriform process. The bases of the basipterygoid processes are oval and inclined slightly anteroventrally. The articular faces of the basipterygoid processes are directed mainly anteriorly and partially dorsally as unfinished concave oval surfaces, undoubtedly capped by cartilage in life. These articular surfaces project into the conical recesses of the palatopterygoid arches, which are formed nearly entirely by the pterygoids with slight dorsal contributions from the epipterygoids. The basal articulation of *Limnoscelis* is free and was potentially mobile in life.

The left basipterygoid process has been broken from the basiparasphenoid at its base, revealing the basiparasphenoid in partial frontal section. A line of suture or contact between the basisphenoid and parasphenoid is often visible in articular view or in cross section through the base of the basipterygoid process in fossil tetrapods in which both elements are distinct (for example, *Eryops* illustrated in Sawin 1941, pls. 7–10). The basisphenoid forms the core of the basipterygoid process and the parasphenoid forms only its outer sheath. However, no such division is present externally or in the basal

cross section exposed in *Limnoscelis,* nor is there any trace of a division between basisphenoid and parasphenoid dorsal to the basal articulation on the laterally exposed left wall of the braincase. I conclude from this evidence, as stated earlier, that the basisphenoid and parasphenoid in *Limnoscelis* are completely fused into a single composite element, the basiparasphenoid.

The cultriform process, exposed in lateral view along its entire length (Fig. 3), is an anteroposteriorly elongate troughlike structure whose posterior base merges smoothly into the rounded, hooded rostrum of the main chevron plate (Fig. 1). Its anterior termination projects slightly ventrally between the anteriorly converging medial borders of the pterygoids. The trough is open dorsally and is widest at its midpoint, and possesses a prominent midventral longitudinal keel.

The cultriform process is also exposed in two transverse cross sections (Fig. 4). The posterior basal region of the cultriform process is a stout solid bar with a distinct heartshaped outline in transverse cross section (Fig. 4A). The dorsal lateral lobes of the heart differentiate sharply anteriorly into the well-defined, dorsally divergent lateral trough walls. These walls and the prominent ventral keel impart a distinct Y-shaped outline to anterior transverse cross sections through the trough (Fig. 4B). The trough depth initially decreases sharply just anterior to the solid proximal base, and then decreases gradually anteriorly. The ventral keel of the sphenethmoid plate is diamond-shaped in transverse cross section, and rests snugly inside the cultriform process trough just anterior to its proximal base.

A partial basiparasphenoid found by P. Vaughn in association with other *Limnoscelis* cranial elements (UCLA field number C-70-10) has also been examined, and conforms with the above description.

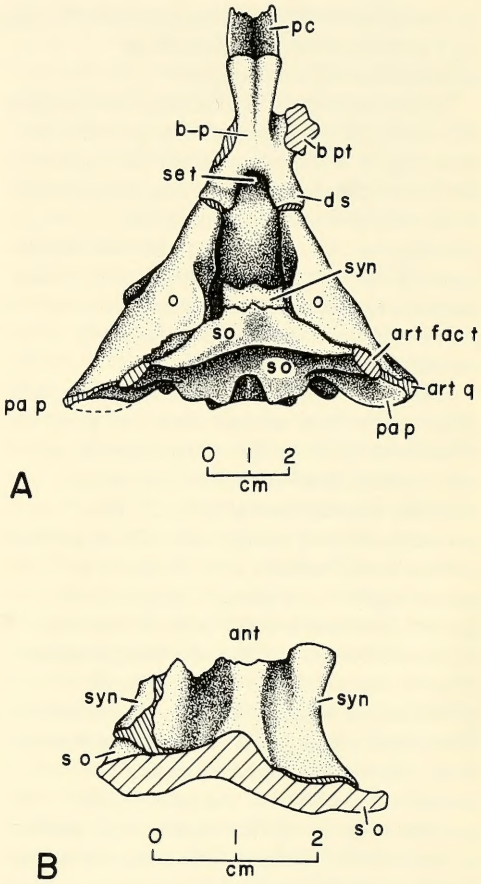

Fig. 5
A. Braincase of *Limnoscelis paludis* in dorsal view, left basipterygoid process removed, based on restoration of the holotype specimen. Hatched pattern denotes unfinished cartilaginous zones and articular areas. *B.* Synotic-supraoccipital complex of *Limnoscelis paludis* in ventral view across transect F-C′ (Fig. 2). Hatched pattern denotes unfinished or broken areas. Abbreviations are listed in Fig. 1.

Otic The otic region of the *Limnoscelis* neurocranium is ossified on each side as a single massive unit of complex form, which I term the otic element (Figs. 2–5, 7D, E). Unlike that of most tetrapods, it is not further divided into discrete prootic and opisthotic elements. Description of the otic is facilitated by roughly dividing it into an anterodorsal prootic region and a posteroventral opisthotic region, separated by the crista parotica. The left otic is well exposed in lateral, dorsal, ventral, and occipital views. The right otic is exposed in ventral, occipital, and limited dorsal view, but

is obscured laterally by close apposition of the right palatoquadrate because of postdepositional compression.

The prootic region is a broadly convex plate with a roughly flask-shaped outline in lateral view (Fig. 3). It possesses a fusiform outline in the frontal plane, being thickest just posterior to its midpoint where it invests the membranous labyrinth of the inner ear, and tapering both anteriorly and posteriorly. It also displays triangular outline in the transverse plane, with the thickened base situated ventrally.

The anterior border of the left prootic region (neck of the flask) dorsally abuts the posterior base of the dorsum sella sharply across an oval surface, visible in lateral view as a vertically oriented contact (Fig. 3). This contact continues straight ventrally as a rather diffuse, feebly ossified zone, before the prootic region turns sharply posteriorly to contact the dorsolateral border of the crista ventrolateralis along a likewise feebly ossified zone. It then continues further straight posteriorly as the rounded and finished lateral free-edged corner of the crista parotica, and finally terminates posteriorly as the ventral-lateral corner of the paroccipital process (Figs. 2, 3). The most anterior portion of the finished ventral prootic edge forms the dorsal border of the fenestra ovalis. Immediately posterior to this, a short rounded protuberance projects ventrally as a distinct knoblike process. This process is the point of attachment of a ligamentous dorsal process of the stapes. A shallow, oblique, anterodorsally directed groove crosses the crista parotica immediately posterior to the dorsal border of the fenestra ovalis and anterior to the articular knob for the stapes dorsal process. This groove marks the course of the vena capitis lateralis and the hyoid ramus of the facial nerve (VII), as presumably did corresponding grooves in pelycosaurs (Romer and Price 1940) and captorhinids (Heaton 1979).

The dorsal border of the prootic region (Figs. 3, 5) is a rounded, largely unfinished edge which trends roughly posterodorsolaterally from its contact with the dorsum sella, toward the supraoccipital. The most anterior portion of this border is a gently rounded concavity, the trigeminal notch, that marks the point of exit of the trigeminal nerve (V) as presumably does a corresponding concavity in pelycosaurs (Romer and Price 1940) and captorhinids (Heaton 1979). The dorsal prootic border, posterior to the level of the thickened zone of the osseous labyrinth, terminates against the internal surface of the supraoccipital over a broadly apposed area which is marked dorsally by a scarfed feather edge. The posterior prootic border trends posteroventrolaterally from the posterodorsal corner, and its dorsal region is largely hidden by the tightly apposed supraoccipital posteriorly and nearly apposed quadrate plate laterally. I cannot determine whether the dorsal posterior edge of the prootic contributes internally to the oval surface of contact between the supraoccipital and tabular medial cone. The ventral portion of the posterior prootic border is an unfinished free edge that forms the laterodorsal border of the paroccipital process, and terminates ventrally at the posterior lateral corner of the paroccipital process.

There are no discrete foramina apparent on the fully exposed lateral wall of the left prootic region. The blood vessels and nerves expected in this area probably passed through the feebly ossified zone between the basiparasphenoid and prootic.

The opisthotic region (Figs. 1–3), ventral to the crista parotica, is a complex form composed of a posterodorsolaterally directed, tapered pyramidal paroccipital process with broadly concave faces, and a posteroventrolaterally directed stout troughlike process which forms the posterior border of the fenestra ovalis. Each paroccipital process is a broadly concave, roughly rhombic, anterodorsally sloping plate in occipital view (Fig. 2), with distinct dorsolateral and ventrolateral unfinished edges that meet to form a nearly right-angled posterolateral corner, which marks the posterior termination of the crista parotica. The unfinished dorso- and ventrolateral free edges were probably continued in cartilage to contact the

ventral edges of the tabular cone and medialdorsal surface of the quadrate, respectively. The dorsomedial border of each paroccipital process contacts the ventrolateral border of the supraoccipital in an irregular suture along a raised ridge, which slopes posteromedially toward the lateral corner of the exoccipital (Fig. 2). The ventromedial border of each paroccipital process is also marked by a ridge which slopes dorsomedially toward the lateral corner of the exoccipital. The posterolaterally directed opisthotic troughs are present just anterior to, and project ventrally below, these ridges.

The longitudinal axes of the stout troughlike projections are oriented posteroventrolaterally. Each open trough faces anterolaterally and its terminal unfinished, curved free edge forms the concave arcuate posterior border of the large oblate fenestra ovalis. The unfinished free edges of each trough were probably capped by cartilage. The proximal base of each trough merges with the ventral edge of the paroccipital process along a low ridge, as described above. The anteromedially directed convex trough bases flatten proximally and merge into a flat-based recess between the trough base and the raised edges of the occipital condyle; this recess is U-shaped in frontal section.

Romer and Price (1940) described remarkably similar troughs in *Dimetrodon* as ventral projections of the opisthotics and distinct from the basioccipital (pls. 13, 14 and fig. 10C, "OP," in Romer and Price 1940). Opisthotic troughs are also present but greatly expanded laterally in *Seymouria* (White 1939) and likewise distinct from the basioccipital. The troughs appear to be continuous with the basioccipital in *Limnoscelis,* as there is no evidence of sutures or other separation between the trough bases and the basioccipital. It seems likely that the opisthotics and basioccipital have fused in this region in *Limnoscelis.*

The left otic is exposed in a single section by an oblique transverso-sagittal break at the level of the osseous labyrinth, just anterior and medial to the paroccipital process (Fig. 7). The otic has a robust rhombic outline in this oblique section. The otic-supraoccipital contact is visible as a distinct, irregular anterodorsally inclined suture. The outermost edge of the horizontal semicircular canal is exposed as a sharply defined matrix-filled cast. A poorly defined matrix-filled void, probably a section through the utriculus, is partially exposed just dorsal to the semicircular canal.

The plane of the horizontal semicircular canal is oriented sharply anterodorsally at a nearly 45° angle with respect to the parallel planes of the skull table and basioccipital plate. The longitudinal axis of the occipital condyle also trends sharply anterodorsally at a nearly 45° angle with respect to the plane of the basioccipital plate. These relations suggest that the skull articulated with the vertebral column such that the snout was oriented downward at a nearly 45° angle to horizontal, contrary to previous restorations. This orientation would allow the axis of the occipital condyle to parallel that of the horizontally oriented vertebral column and provide the condyle with a tight fit against the atlas centra, and would also restore the plane of the horizontal semicircular canal to a horizontal orientation.

There is no visible indication of either a suture or textural difference between the dorsal and ventral portions of the otic in this exposed section, even though the section passes through both the prootic and opisthotic regions of the otic. This supports my inference that the otic is a single ossification in *Limnoscelis.* The internal texture of the otic is uniformly coarsely cancellous throughout this section across the osseous labyrinth.

Sphenethmoid The sphenethmoid (Fig. 6) is a median longitudinal plate which is ventrally thickened and dorsally bifurcate. The ventral thickening forms a longitudinal keel that rests snugly in the trough of the basiparasphenoid cultriform process. The dorsal bifurcations form a pair of dorsolaterally directed wings, the solum supraseptale, which abut against the underside of the skull roof. The entire structure possesses a distinct

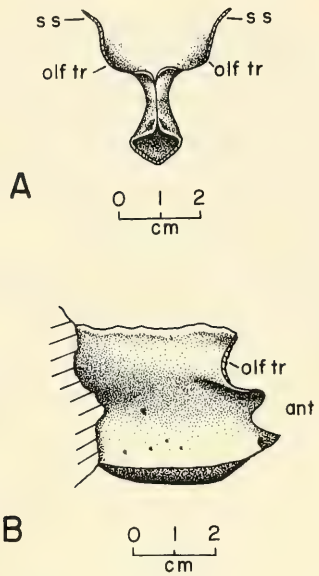

Fig. 6
Sphenethmoid of *Limnoscelis paludis* in anterior view (*A*) and right lateral view (*B*), based on restoration of holotype specimen. Hatched pattern denotes unfinished borders and areas covered by matrix. Abbreviations are listed in Fig. 1.

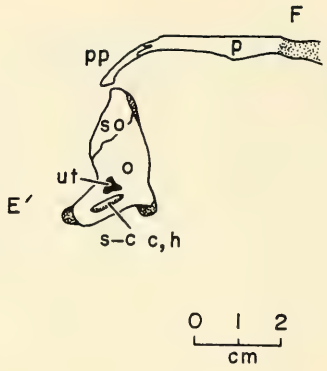

Fig. 7
Left otic, supraoccipital, and posterior skull table of *Limnoscelis paludis* viewed looking laterally across transect F-E′ (Fig. 2). Abbreviations are listed in Fig. 1.

Y-shaped outline in transverse section. The exposed lateral surfaces of the sphenethmoid are locally pierced by several minute foramina.

The ventral keel is rhomboid in transverse section, and most robust at its midlength. It possesses unfinished anteroventral borders whose edges in lateral view trend anterodorsally before converging in the midline as the sharp-edged anterior border of the interorbital septum. The area enclosed below these unfinished edges is matrix-filled, raising the possibility that the keel may enclose an open channel for an indeterminate portion of its length. The cultriform process extends anteriorly beyond the unfinished anterior limits of the sphenethmoid, so it seems probable that the sphenethmoid was continued anteriorly by cartilage for a comparable distance.

The anterior border of the short interorbital septum above the ventral keel is a sharp-edged, concave arc in lateral view, before bifurcating sharply to form the paired anterior borders of the solum supraseptale. The anterior borders of the solum supraseptale are unfinished free edges that diverge dorsolaterally from the interorbital septum to abut against the ventral surfaces of the frontals and parietals. A single prominent convex-outward bulge exists ventrally along the anterior border of each solum supraseptale. The bulges are semicircular in outline and their axes are directed anterolaterally. The bulges are located at the level of the anterodorsal borders of the orbits in lateral view, and probably represent the areas of exit of the olfactory tracts (cranial nerve I) from the ossified portion of the sphenethmoid. Corresponding structures in the anterodorsal region of the sphenethmoid that are described as grooves or channels carrying branches of the olfactory nerve (I) exist in *Anthracosaurus* (Panchen 1977) and pelycosaurs (Romer and Price 1940).

The dorsal lateral borders of the solum supraseptale trend straight posteriorly as unfinished free edges closely apposed against the undersides of the frontals and parietals. The anterodorsal border of the left solum supraseptale is tightly wedged into a lateral longitudinal groove in the underside of the left frontal, whereas the unfinished dorsal border

of the right solum supraseptale has been displaced ventral to its area of articulation because of postdepositional rotation and slight compression of the entire sphenethmoid about its longitudinal axis.

The posterior borders of the sphenethmoid are not exposed, but they appear to terminate at a level just anterior to the parietal foramen.

The interorbital septum thickens posteriorly toward its midlength from its sharp-edged anterior border. It is uncertain whether a single discrete thick median septum exists here, or whether the interorbital septum in this area is actually a composite of two tightly apposed but distinct lateral plates.

None of the expected foramina which are present in the lateral sphenethmoid walls of many osteolepids and primitive tetrapods can be recognized in *Limnoscelis,* although several minute perforations are visible on the right side. The optic foramina (II) are conspicuously absent, and are either incised into the hidden posterior borders of the sphenethmoid or exited posteriorly through the open unossified zone between the sphenethmoid and anterior border of the basiparasphenoid.

Synotic The synotic (Fig. 5) is a small median wedge-shaped element situated posterodorsally between the otic capsules. Its dorsal surface is tightly apposed against the overlying anteroventral surface of the supraoccipital. The anterior border of the synotic is a rough, unfinished free edge which was probably continued anteriorly by cartilage. The synotic is several millimeters thick at its preserved anterior border and tapers posteriorly to a featheredge in a scarf contact with the overlying supraoccipital. A small portion of the posterior synotic border has broken off on the right side and clearly reveals the finished ventral surface of the supraoccipital above the finished ventral surface of the synotic, proving the existence of two discrete ossifications in this area *contra* Heaton (1980). The lateral synotic borders are smooth, finished concave arcs.

The ventral surface of the synotic anteriorly forms a well-developed median longitudinal ridge which is bordered laterally by two well-defined grooves or channels. These structures decrease in amplitude posteriorly as the synotic thins, so that the posterior border simply undulates over the contours of the overlying ventral supraoccipital surface. A median synotic ridge, although less well defined, is also expressed posteroventrally on the ventral surface of the supraoccipital. The lateral grooves may mark the course of the occipital arteries, as do grooves in similar positions in the neurocranium of *Eusthenopteron* (Jarvik 1980, vol. 1, figs. 86, 88).

Basioccipital The basioccipital (Figs. 1, 2) is a roughly triangular plate with a prominent median posterior knoblike projection, the occipital condyle. The horizontal anterior plate of the basioccipital possesses a distinct median ventral longitudinal ridge continuing from the basiparasphenoid, which posteriorly deepens and bifurcates dorsolaterally in a smooth arc to form the raised rim of the occipital condyle. The exposed surfaces of the basioccipital are otherwise quite smooth.

The anterior borders of the basioccipital trend posterolaterally from the apex of its median ridge in contact with the posterior borders of the basiparasphenoid as described previously. These sutures terminate posterolaterally at the apices of deep, V-shaped clefts with unfinished edges, situated between the cristae ventrolaterales anteriorly and the otic-basioccipital troughlike projections posteriorly. Cartilaginous extensions of the basioccipital into these clefts probably contributed in small part to the formation of the posteroventral borders of the oblate fenestrae ovales. Posterior to the clefts, the basioccipital has fused with the opisthotic region and both contribute to the troughlike projections that border the fenestrae ovales posteriorly, as described previously. The U-shaped recess between each trough base and the raised lateral border of the occipital condyle probably marks the approximate line of junction between the basioccipital and opisthotic region.

The occipital condyle (Figs. 1, 2) is a massive structure with a nearly circular cross

section except for its dorsal rim, which is broadly depressed ventrally at its midpoint. Its longitudinal axis is angled approximately 45° ventral to the plane of the anterior basioccipital plate. The articular surface of the occipital condyle is weathered and presently slightly concave, and there is little doubt that it was also concave in life. The laterodorsal rims of the occipital condyle underlie the reduced exoccipitals, which do not enter into the articular surface of the condyle. The middorsal rim of the condyle forms the concave, broad-based ventral boundary of the foramen magnum. The middorsal rim also bears a low but distinct median longitudinal ridge which broadens as it disappears from view inside the foramen magnum.

Exoccipital The exoccipitals (Fig. 2) are small triangular elements wedged between the supraoccipital above and the basioccipital below, and form the ventrolateral margins of the foramen magnum. The exposed surfaces of both exoccipitals are weathered and the ventral region of the right exoccipital is hidden by a small overlying element, probably the right proatlas. Each exoccipital possesses a smooth surface texture. A small, oval matrix-filled foramen exists just inside the ventrolateral apex of the left exoccipital and is completely enclosed within the element. This is probably an exit for the hypoglossal nerve (XII). The corresponding area of the right exoccipital is hidden by the proatlas.

The medial border of each exoccipital slopes ventrolaterally from its dorsal apex as a finished free edge which forms the ventrolateral border of the foramen magnum. The lateral border also slopes ventrolaterally from the dorsal apex, nearly contacting the medioventral border of the supraoccipital along a straight edge. This line of close apposition is presently matrix-filled, but was probably originally filled by cartilage except for a small open foramen through which passed the vagus nerve (X). The ventral edge of each exoccipital contacts the basioccipital in an irregular suture. The ventral region of each exoccipital is also closely apposed to the anterior surface of the proatlas, which is present in articulation on the right side of the specimen. However, no well-defined facet for proatlas articulation is visible on the left exoccipital.

The exoccipitals of *Limnoscelis* are greatly reduced in size relative to their stout, columnar configuration in taxa such as *Eryops* (Sawin 1941), *Seymouria* (White 1939), *Eocaptorhinus* (Heaton 1979), and *Ophiacodon* (Romer and Price 1940). The exoccipitals in *Eryops, Seymouria,* and *Ophiacodon* also contribute substantially to the lateral or laterodorsal areas of the occipital condyle, whereas in *Limnoscelis* the exoccipitals simply rest on the basioccipital dorsal and dorsolateral to the large occipital condyle and do not contribute to its formation.

Supraoccipital The supraoccipital (Figs. 2, 5, 7D, E) is a transversely elongate, median, bowtie-shaped plate which is slightly curved in a concave direction in the frontal plane relative to the skull table. It is the cornerstone of the solid, closed occiput. Its midventral border is strongly incised as a concave arcuate finished edge which forms the narrowed dorsal border of the egg-shaped foramen magnum. Primitive posttemporal fenestrae, as defined by participation of the supraoccipital in their median borders (Fracasso 1983, p. 305–11), are absent. The exposed surface is weathered and exhibits a coarse spongy texture.

The dorsal border of the supraoccipital is hidden by the overlap and overhang of the median postparietal along a smooth, gently convex arc (Fig. 2). The dorsal lateral edges of the supraoccipital abut the dorsal medial bases of the tabular cones along linear, tightly apposed contacts. Posterodorsal displacement of the right tabular displays the articular surfaces of both the tabular cone and supraoccipital. The articular facet of the supraoccipital is a roughly triangular area that closely matches the dorsal area of the tabular cone against which it is normally tightly apposed. The ventral lateral edges of the supraoccipital contact the dorsal edges of the paroccipital processes in irregular sutures along the apices of low ridges (Fig. 2). The

lateral ventral borders of the supraoccipital slope dorsomedially and are slightly separated from the dorsal lateral borders of the exoccipitals by matrix-filled gaps, as noted previously.

The supraoccipital is exposed in two cross sections (Figs. 5B, 7). Figure 5B illustrates the supraoccipital in a frontal section that parallels the arcuate postparietal-supraoccipital overlap. The ventral finished lip of the postparietal is not visible in this figure, but the amount of postparietal overhang is indicated by matrix which separates the two elements in the counterpart section. The supraoccipital is thickened centrally, which I interpret as a midventral longitudinal ridge. The anterodorsal extremity of the supraoccipital curves sharply anteriorly at a nearly right angle to the almost vertical occipital plate, to closely parallel the undersides of the overlying parietals. This area of the supraoccipital is underlain by the tightly apposed, ossified synotic.

The supraoccipital is exposed laterally in a sagittal section passing through the left otic capsule (Fig. 7). The supraoccipital is tightly sutured to the otic along an anterodorsally sloping contact, and thus has a wedge shape in this section.

Systematic Implications

The tetrapod braincase is a complex structure yielding many systematic characters. However, until now, the braincase of *Limnoscelis* has been both incompletely described and incorrectly interpreted in part. These shortcomings have limited its value as a potential indicator of phyletic relationships among Paleozoic tetrapods. Description of anatomical features not previously exposed, reinterpretation of structures that were problematic, and application of cladistic character analysis (Fracasso 1983, p. 208–43) has facilitated the evaluation of braincase characters that help to elucidate the phyletic relations of *Limnoscelis* with other Paleozoic tetrapods. The following synopses of selected character analyses that pertain to the braincase are presented in rough order of their increasingly derived expression in *Limnoscelis*. Morphocline polarities were determined by using osteolepiform fishes as the out-group of tetrapods (Fracasso 1983, p. 218–21).

Braincase Character Analyses

Basal Articulation The basal articulation of *Limnoscelis* (Figs. 1, 3–5) is unquestionably mobile and was probably a synovial joint in life (Fracasso 1983). Since the osteolepiform basal articulation was also mobile (Thomson 1967; Jarvik 1980), this state must be considered primitive with respect to tetrapods and of low value in assessing the relation of *Limnoscelis* to other tetrapods.

Synotic and Supraoccipital Heaton (1980) has recently clarified the distinct nature and potential phylogenetic utility of the oft-confused tetrapod synotic and supraoccipital ossifications. He notes that the otic capsules may be bridged in early ontogeny by a cartilaginous dorsal tectum synoticum. The combined unit thus formed is separated by the fissura metotica from the more posterior pilae ascendens of the occipital arch, which may also be bridged dorsally by a cartilaginous tectum posterior. The tectum synoticum and tectum posterior may each become ossified as discrete elements: the synotic and supraoccipital, respectively. Both elements are present in osteolepids and are roughly separated in the adult neurocranium by the fissura occipitalis lateralis (Heaton 1980; see Jarvik 1980, vol. 1, figs. 86, 88, 97; and vol. 2, fig. 42), and both are also present in some tetrapods, including the anthracosaur *Palaeoherpeton* (Panchen 1964; Heaton 1980) and *Limnoscelis,* where a distinct suture is visible between the tightly apposed synotic and supraoccipital (*contra* Heaton 1980; see descriptions in preceding text). An unossified synotic may have been present in *Dimetrodon* also, because the anterior border of the supraoccipital beneath the skull table is marked by an unfinished, subrectangular recess at the level of the overlying parietal-postparietal suture. This

recess probably accommodated a reduced, cartilaginous synotic in life (personal examination of MCZ 1347, *Dimetrodon limbatus*). Heaton (1980) suggests, as an aid to identification of single elements in the dorsal occipital area of the neurocranium, that the supraoccipital usually exhibits a distinct lateral sutural contact with the prootic and exoccipital, whereas the synotic-prootic contact is generally fused.

Since discrete synotic and supraoccipital elements are present in osteolepiforms, their existence must be considered primitive relative to tetrapods, and their presence in *Limnoscelis* is of limited systematic value.

Sphenethmoid. The osteolepid neurocranium is sharply divided into two discrete components: an anterior sphenethmoid moiety and a posterior otoccipital moeity, separated by the fissura preoticalis. Neither of these units is further differentiated into discrete component ossifications. The paired basipterygoid articular facets develop at the posteroventrolateral corners of the sphenethmoid unit, which is anteroventrally underlain by the poorly differentiated parasphenoid cultriform process. The neurocranial region overlying the cultriform process, anterior to the basipterygoid facets, corresponds to the discrete tetrapod sphenethmoid. The lateral walls of the osteolepid sphenethmoid region diverge directly dorsolaterally from their narrow midventral longitudinal axis, thus imparting a distinctive V- or U-shaped outline in transverse section. This morphology must be considered primitive with respect to tetrapods based on outgroup comparison.

The sphenethmoid of *Limnoscelis* exists as a median vertical plate, the interorbital septum, which is bifurcate dorsally to form a pair of solum supraseptales. This imparts a distinctive Y- or T-shaped outline in transverse section. This morphology is derived with respect to the primitive tetrapod state, and is shared with *Anthracosaurus,* captorhinids, diadectids, eogyrinids, *Ophiacodon,* and possibly *Tseajaia* among a group of selected Paleozoic tetrapods (Fracasso 1983).

The single vertical interorbital septum of these taxa may have been derived as a ventral downgrowth of the longitudinal base of the primitive tetrapod V-shaped sphenethmoid, or from convergence of the lateral walls of the primitive V-shaped sphenethmoid which proceeded dorsally from the ventral longitudinal base. The available evidence is insufficient to determine which of these alternatives, if not both, occurred in any given taxon.

Parasphenoid Plate and the Neurocranial Division The structural unity or division of the neurocranium into two discrete units, and the strongly correlated morphology of the parasphenoid posterior plate, have both been considered important systematic characters by many workers. The neurocranium of osteolepids and ichthyostegids is divided by a transverse fissure, the fissura preoticalis, into anterior ethmosphenoid and posterior otoccipital moieties (Thomson 1967; Jarvik 1980, vol. 1; disputed in *Ichthyostega* by Rosen, Forey, Gardiner, and Patterson 1981, p. 165). The parasphenoid in both taxa is restricted as a ventral investiture of the orbitotemporal region of the ethmosphenoid (Jarvik 1980, vol. 1). The parasphenoid is widest posteriorly where it develops laterodorsal walls which rise to sheathe the ventral surface of the basipterygoid processes. It gradually tapers anteriorly to a narrow, gutterlike trough which floors the interorbital wall (Jarvik 1980, vol. 1). The posterior ventral surface of the parasphenoid is scarred by two lateral pockets marking the insertion areas of the paired subcranial muscles (basicranial muscle #3; Jarvik 1980, vol. 1, figs. 93, 94; vol. 2, figs. 41, 42), which span the fissura preoticalis and originate on the otoccipital. These pockets are deepest and best defined anteromedially, where they are separated by a very low, rounded median ridge. This gross parasphenoid morphology in combination with a divided neurocranium is primitive with respect to tetrapods based on

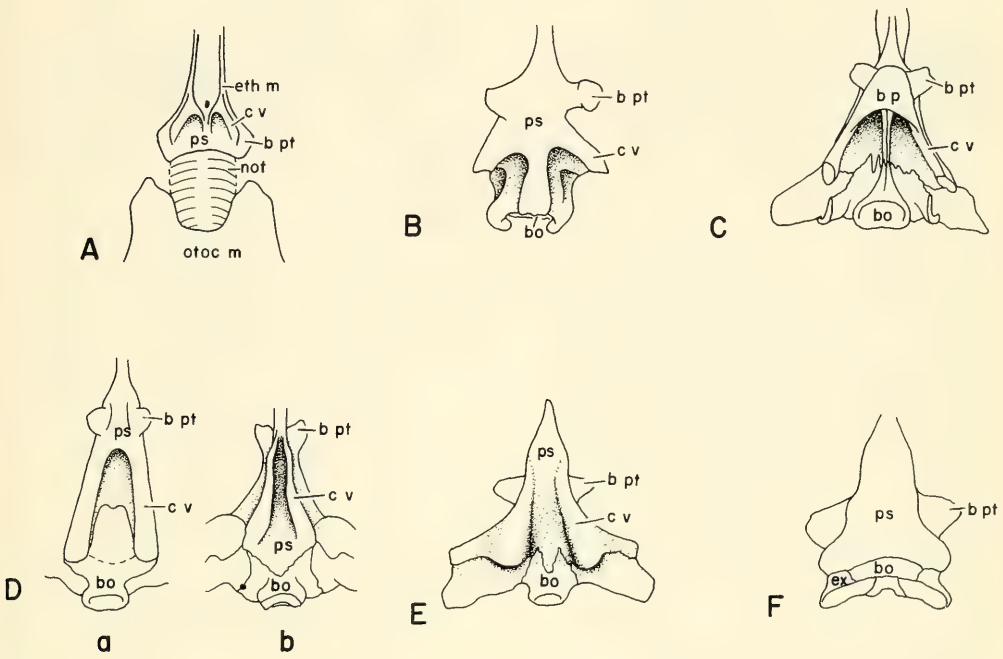

Fig. 8

Basicranial morphotypes of representative Paleozoic fish and tetrapods. *A.* State TA, *Eusthenopteron,* after Jarvik (1980). *B.* State TB, *Greererpeton* (personal examination of cast of CM 11089). *C.* State TB-1, *Limnoscelis paludis. D.* State TB-2; a) *Ophiacodon,* after Romer and Price (1940), and b) *Eocaptorhinus,* after Heaton (1979). *E.* State TB-3, *Seymouria,* after White (1939). *F.* State TB-4, *Eryops,* after Sawin (1941). Abbreviations are listed in Fig. 1.

outgroup comparison, and for convenience has been coded State TA (Fig. 8A).

The neurocranium of all known tetrapods with the possible exception of ichthyostegids has been consolidated by the obliteration of the fissura preoticalis and development of sutural contacts between the primary neurocranial elements and their dermal investitures. Notably, the posterior border of the parasphenoid has migrated posteriorly through the position of the ancestral fissura preoticalis so that the body of the parasphenoid now sheathes the otic region of the originally posterior otoccipital moiety. The parasphenoid can be subdivided into a narrow anterior cultriform process and a wide posterior plate, separated by a definite constriction just anterior to the basipterygoid processes. The posterior plate of *Greererpeton* retains a pair of excavations posteriorly which are separated by a low, rounded and ill-defined median ridge, but whose lateral borders are more pronounced as a pair of weakly developed cristae ventrolaterales. These areas now represent the points of insertion of the basicranial portion of the trunk axial musculature. Although the morphology of the muscle scars is nearly identical to those of *Eusthenopteron,* the posterior migration of the parasphenoid and obliteration of the fissura preoticalis suggests that this insertion area has been pirated by the basicranial portion of the 6th or more posterior myomeres, because myomeres 3, 4, and 5 had spanned the fissura preoticalis (Jarvik 1980, vol. 1 and 2) which no longer exists. This parasphenoid morphology is derived with respect to the primitive state and

has been coded State TB (Fig. 8B). Subsequent changes in morphology of the parasphenoid plate have proceeded in several directions, depending on the increased development or eventual loss of the basicranial portion of the trunk axial musculature.

The basic form of the parasphenoid plate may be retained as described above for State TB. However, the insertion areas of the basicranial trunk axial muscles have expanded and are much more pronounced. The cristae ventrolaterales are prominently developed as the lateral borders of the insertion scars, presumably serving to increase the area of insertion. The cristae ventrolaterales may converge anteriorly near the level of the basipterygoid processes in the form of a single horseshoe-shaped ridge which bounds the paired muscle scars anteriorly as well as laterally. This ridge may develop even further into a pronounced hood, so that the most anterior basicranial insertion sites are recessed ventrally into the body of the parasphenoid beneath the hood. The median ridge separating the paired excavations is strongly developed and quite thin and sharp, presumably narrowed and thus accentuated by the medial expansion of the paired basicranial muscle masses. This morphology is coded State TB-1 (Fig. 8C) and was derived from State TB by expansion of the basicranial muscles and anterior confluence of the cristae ventrolaterales, which is sometimes elaborated as a hood. This is the morphology possessed by *Limnoscelis* and shared with diadectids and *Tseajaia*.

The parasphenoid plate may also possess a pair of low, rounded cristae ventrolaterales which do not necessarily converge anteriorly to bound the basicranial muscle scars. The anterior bounding ridge, if present, never exists as a hooded recess. A median ridge is not present between the cristae ventrolaterales. The loss of the median ridge may have been caused by either a further medial expansion of the basicranial muscle masses to crowd out the already narrowed ridge present in State TB-1, or a lateral shift of the basicranial muscle insertions onto the cristae ventrolaterales, with a concomitant diffusion of their medial defining edges and a de-differentiation of the already weak median ridge present in State TB. This morphology is coded TB-2 (Fig. 8D) and can be derived from either State TB or TB-1 by loss of the median septum between the muscle scars.

A more derived morphology exhibited by *Seymouria* may develop from the above by expansion of the posterior corners of the parasphenoid laterally beyond the cristae ventrolaterales, as wings that floor the likewise laterally expanded otic capsules (State TB-3, Fig. 8E).

The most derived parasphenoid morphology is a simple flat plate, possessed by most rhachitomes. Excavated muscle scars are never present, nor are their correlates, the cristae ventrolaterales or a median ridge, although a very low and ill-defined central depression may be present. This state has been coded State TB-4 (Fig. 8F) and can be derived from any of the above states by loss of the insertion area of the basicranial axial trunk muscles on the parasphenoid.

Fusion of the parasphenoid and basisphenoid in *Limnoscelis* is certainly derived. However, the distribution of this condition among other Paleozoic tetrapods is not known, thus limiting its usefulness for phyletic inferences.

The feebly ossified zone of contact between the *Limnoscelis* basiparasphenoid and otic is reminiscent of the osteolepiform neurocranial division, and is especially interesting because of the putative advanced status of *Limnoscelis* among Paleozoic tetrapods. However, a weakly ossified junction between these elements might be expected during early stages of tetrapod neurocranial consolidation. It therefore seems reasonable to assume that this state is primitive with respect to tetrapods, and thus of limited systematic value.

Occipital Condyle and Exoccipitals

Eusthenopteron does not possess an occipital condyle. Rather, the condylar region ventral to the foramen magnum is completely perforated. It forms a cylindrical ring of

subcircular outline that allows unrestricted passage of the notochord anteriorly, where it abuts directly against the notochordal pit concavity of the ethmosphenoid (Jarvik 1980, vol. 1, fig. 86). This cylindrical tunnel through the otoccipital may be considered in abstract as an infinitely concave occipital condyle. It is bounded in occipital view by the ill-defined precursors of the discrete components of the tetrapod occipital condyle, which are inferred to be serially homologous with components of the vertebrae. These comprise three ossification centers positioned relative to one another as the apices of a triangle; dorsolateral interdorsals (exoccipitals) and a median ventral vertebral arch (basioccipital) (Jarvik 1980, vol. 2, fig. 38). The ring may be complete dorsally between the interdorsals and traversed by a median longitudinal groove for the passage of the basilar artery (Jarvik 1980, vol. 1, fig. 86), or open dorsally so that the foramen magnum and notochordal canal are confluent. These variations are minor, and this basic morphology may be considered primitive with respect to tetrapods. Many derivatives of this primitive morphology occur in tetrapods.

Anthracosaurus, Edops, eogyrinids, *Gephyrostegus, Greererpeton, Seymouria, Tseajaia,* and some diadectids exhibit a more derived state. The basioccipital and exoccipitals are well developed and have expanded medially to either restrict or completely block the notochordal canal. The condyle retains a subcircular or slightly oblate elliptical outline, and the articular face is concave with respect to the occipital plane. The dorsal margin of the condyle between the exoccipitals is commonly incomplete, but may be continuous. This state may be simply derived from the primitive configuration by differentiation and expansion of the now discrete basioccipital and exoccipitals.

The occipital condyle of *Limnoscelis* is further derived. The exoccipitals are greatly reduced, and contribute little or nothing to the condylar articular surface. The condyle retains a subcircular outline, and its articular face is slightly concave and imperforate. This morphology can be derived from the preceding state by reduction of the exoccipitals, or directly from the primitive state by greater relative growth of the basioccipital. It is shared with some captorhinids, and possibly some diadectids and protorothyrids. Other tetrapod occipital condyle morphologies can be derived ultimately from these states (Fracasso 1983, p. 311–15).

Posttemporal Fossae The fossae Bridgeii of osteolepiforms, homologous with the tetrapod posttemporal fossae, are a pair of troughlike excavations in the dorsolateral walls of the neurocranial otoccipital moiety. These excavations open posteriorly onto the occiput, and presumably served as the insertion sites of the anterior axial trunk musculature (Jarvik 1980, vol. 1). Each fossa is exposed in occipital view as a rounded fenestra bordered medially by the dorsal ossified area of the otoccipital moiety (tectum posterior, or tetrapod supraoccipital), ventrally by the crista parotica (paroccipital process of tetrapods), dorsolaterally by the tabular, and dorsomedially by the postparietal. This configuration must be considered primitive with respect to tetrapods based on outgroup comparison, and is coded State HA for convenience. The many variations of this primitive configuration that exist in tetrapods fall into two classes: those taxa in which an ossified supraoccipital is present, and those in which it is absent. Concerning derivation of the *Limnoscelis* configuration, only a selected subset of those morphotypes that possess a supraoccipital is considered. Others are discussed in detail elsewhere (Fracasso 1983, p. 305–11, 419–20).

Some protorothyrids display the primitive configuration, whereas others exhibit a slightly more derived state. Either the tabular has been reduced or the paroccipital process has migrated ventrally, or both, so that the squamosal now enters into the lateral border of the fossa between the paroccipital process and tabular. This configuration is coded State HA-1.

A more derived state is exhibited by other protorothyrids and some early diapsids, wherein the postparietal is reduced and either

retreated or excluded from the dorsomedial border of the fossa. The fossa is bounded by the supraoccipital, paroccipital process, squamosal and tabular. This state is coded HA-2 and can be readily derived from either of the above more primitive states.

Ophiacodon possesses a morphology that is even further derived. The tabular has expanded and extends ventromedially onto the occiput to exclude the postparietal and the supraoccipital from the medial border of the fossa. The fossa is bordered by the tabular, paroccipital process and squamosal. This configuration is coded State HA-6 and can be derived from any of the preceding states.

Limnoscelis possesses an extremely derived occiput in which no posttemporal fossae exist; the occiput is closed dorsal to the paroccipital processes (Fig. 2). However, all of the elements that border the fossae in the taxa described above are present. These include the supraoccipital, paroccipital process, squamosal, tabular, and postparietal. Since the *Limnoscelis* tabular is enlarged rather than reduced, it is likely that this occipital configuration was derived from any of the more primitive states HA, HA-2, or HA-6 by a shift of the anterior axial muscle insertions onto the surface of the occiput, and expansion of one or more of the surrounding bones over the area of the fossa. Similar closed occiputs, designated as State HC, are possessed by *Anthracosaurus,* eogyrinids, *Tseajaia,* diadectids, and possibly *Gephyrostegus.*

Dorsum Sellae A large gap across the midline divides the dorsum sellae of *Limnoscelis* into left and right halves. This derived condition is also exhibited by *Ophiacodon* and other pelycosaurs. However, the *Limnoscelis* dorsum sellae retains a primitive mode of development from the basiparasphenoid, unlike the further derived state of most pelycosaurs wherein the dorsum sellae develops from the prootic. Unfortunately, the distribution of these character states is not generally known in Paleozoic tetrapods; so the systematic utility of these features is limited at present.

Opisthotic Trough The *Limnoscelis* opisthotic region develops a prominent troughlike projection that borders the fenestra ovalis posteriorly and is apparently continuous with the basioccipital. This troughlike projection is a derived feature and is shared with *Dimetrodon* and *Seymouria,* although the basioccipital does not enter into formation of the trough in either taxon.

Fusion of Ossifications The osteolepiform basisphenoid and parasphenoid are discrete elements, so the fusion of these elements in *Limnoscelis* and most pelycosaurs must be derived with respect to tetrapods. In contrast, the osteolepiform adult otoccipital moiety is a single massive element, so the absence of fully differentiated prootic, opisthotic, and basioccipital regions of *Limnoscelis* might be considered a primitive state. However, adult pelycosaurs possess similarly consolidated neurocrania; yet Romer and Price (1940) noted that the elements are distinct in immature *Ophiacodon* braincases. It is thus possible that the *Limnoscelis* braincase consolidation is a function of ontogenetic age, because fusion of bones with increasing age is common in lower tetrapods. Since the nature of ossification of the juvenile osteolepiform braincase is unknown, the morphocline polarities derived from the outgroup and ontogenetic series may be in conflict. Therefore, the systematic significance of these features is ambiguous without further knowledge of neurocranial ossification in ontogenetic series, and the details of neurocranial differentiation in other taxa.

Synthesis of Cranial Characters

Characters pertaining to the braincase, as analyzed above, are potentially valuable indicators of phylogenetic relationship. However, as many characters as is practical should be incorporated into a phylogenetic analysis, and braincase characters comprise only a small subset of available morphologic

characters. Figure 9 is a condensed version of a cladogram that depicts the phylogenetic relationships of *Limnoscelis* and selected Paleozoic tetrapod and fish taxa. Forty-five cranial characters, including most of the braincase characters discussed above, comprise 211 discrete character states that were incorporated into the original cladogram (Fracasso 1983). The twenty-four taxa of the original cladogram, ranging in rank from genus to order, have been largely grouped into higher ranked taxonomic assemblages in Figure 9. The lower ranked taxa in closest proximity to *Limnoscelis* have been retained to portray the proximate systematic affinities of *Limnoscelis* in greatest detail and to facilitate discussion of the significance of the braincase characters that were analyzed earlier. Parallelism and convergence of character states is very frequent (Table 5 in Fracasso 1983). As a result of widespread convergence, taxa are most often defined by unique combinations of shared-derived character states (Fracasso 1983), which might themselves be considered unique-derived character states of a higher rank. Rarely are any of the taxa defined by single unique-derived character states. The distribution of character states that delineate the higher ranked taxa of the condensed cladogram (Fig. 9) is misleading without an expanded discussion of the distribution of homoplastic states, which is beyond the scope of this manuscript. Therefore, character states have not been posted on the condensed cladogram, and the reader is referred to Fracasso (1983) for a comprehensive discussion. Postcranial characters were not used in the preceding analyses but may be added to future studies, where they will serve as potential falsifiers of the present cladograms.

The sphenethmoid morphology characterized by a Y- or T-shaped cross section is a shared-derived character state that unites *Limnoscelis* with diadectids, *Ophiacodon,* and possibly *Tseajaia,* and is developed convergently in anthracosaurs. A parasphenoid plate with well-developed basicranial muscle insertion sites

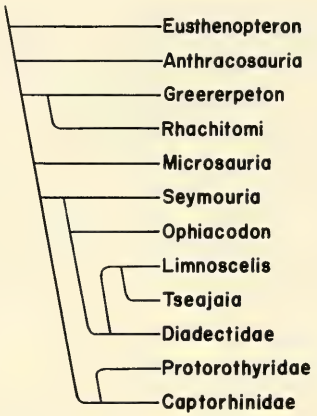

Fig. 9
Cladogram illustrating the phylogenetic relationships of *Limnoscelis paludis* relative to other selected Paleozoic and Recent fish and tetrapod taxa, after Fracasso (1983).

characterized by prominent cristae ventrolaterales, a median ridge, and a pronounced anterior hood (State TB-1) is also a derived character state that is shared by *Limnoscelis, Tseajaia,* and *Diadectes.* The derived occipital condyle of *Limnoscelis,* characterized by greatly reduced exoccipitals and a subcircular, slightly concave occipital condyle formed entirely by the basioccipital, has been developed convergently in some diadectids, protorothyrids, and captorhinids.

The very derived closed occiput of *Limnoscelis,* in which posttemporal fossae are absent but all the elements that normally surround them (supraoccipital, paroccipital process, squamosal, tabular, postparietal) are present, is shared with *Tseajaia* and diadectids and is developed convergently in anthracosaurs. The existence of a divided dorsum sellae, developed from the basiparasphenoid, appears to be unique to *Limnoscelis.* A similarly divided dorsum sellae appears to have developed convergently in *Ophiacodon,* but the parent ossification is the prootic rather than the basiparasphenoid. The prominent troughlike projection of the opisthotic that borders the fenestra ovalis posteriorly in *Limnoscelis* has also developed convergently in *Dimetrodon* and *Seymouria.*

Limnoscelis, Tseajaia, and diadectids form a tightly knit monophyletic group which I designate the Diadectomorpha, *sensu* Heaton (1980). Within the higher order Cotylosauria clade (*sensu* Heaton 1980, but including *Ophiacodon*) comprised of diadectomorphs, *Ophiacodon,* and *Seymouria,* the diadectomorphs are uniquely defined by the possession of a closed occiput (State HC), which also has been developed independently by the anthracosaur clade. The cladogram (Fig. 9) implies that *Seymouria* and diadectomorphs, including *Limnoscelis,* are reptiles, and that microsaurs are the sister-group of reptiles. This conclusion should not be surprising, as many similarities between cotylosaurs, microsaurs, and reptiles have long been recognized, and nearly all cotylosaurian taxa and microsaurs previously have been discussed as possibly close to reptile ancestry (White 1939; Romer 1946, 1950; Olson 1947, 1965; Vaughn 1960, 1962; Carroll and Baird 1968).

The inference that diadectomorphs and *Seymouria* are reptiles follows from four assumptions: 1) the amniote egg is a unique structure, having evolved only once; 2) *Ophiacodon* is a member of a monophyletic pelycosaur clade precursor to mammals; 3) protorothyrids and captorhinids are members of a monophyletic clade precursor to modern reptiles; and 4) the cladogram (Fig. 9) accurately depicts the phylogenetic relationships of the included taxa. Luckett (1977) argued convincingly for a monophyletic origin of the amniote egg, based largely on the complexity and similarity of its structure and development in diverse amniote taxa. Romer and Price (1940), Reisz (1980), and Kemp (1982) have discussed the monophyly of the pelycosaurs and the inclusion of *Ophiacodon* in that clade; the evolution of therapsids from pelycosaurs and the derivation of mammals from therapsids have long been recognized (Kemp 1982). Protorothyrids and captorhinids are generally considered to comprise a monophyletic assemblage (Clark and Carroll 1973; Gaffney and McKenna 1979; Heaton 1979; Carroll 1982), from which all Recent reptiles are ultimately derived (Carroll 1982). The character analyses and method of construction of the original cladogram from which Figure 9 was derived are documented in Fracasso (1983, p. 208–461).

Given the premises listed above, the mammalian and living reptilian amniote clades may be traced backward on the cladogram (Fig. 9) to their point of common origin, which occurs at the base of the *Seymouria-Ophiacodon*-diadectomorph clade. This node represents the latest time at which a unique amniote egg could have evolved, and all taxa situated above this point must be amniotes. Microsaurs are the sister-group of amniotes.

Until now, gephyrostegid anthracosaurs had been considered as the most plausible amphibian lineage to bear a close relationship to reptile ancestry (Carroll 1969a, 1969b, 1970a, 1970b). Anthracosaurs are actually quite distantly removed from reptile ancestry. Gephyrostegids have proved to be misleading because they are primitive members of the relatively primitive anthracosaur clade, and the search for reptile ancestors has traditionally focused on taxa that appear primitive or generalized, or both, so that few or no specializations would preclude them from reptile ancestry. The problem with taxa that survive being culled by the criterion of primitiveness is that they are commonly primitive enough to be the ancestors of anything the researcher wishes them to be (Rosen, Forey, Gardiner, and Patterson 1981). The shift of emphasis to the identification and analysis of shared-derived character states has clarified the phylogenetic relationships of several Paleozoic tetrapod taxa (Fig. 9), has identified diadectomorphs and *Seymouria* as reptiles, and microsaurs as the sister-group of reptiles.

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The Author

Michael A. Fracasso. 6805 Wood Hollow #239, Austin, TX 78731.