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# THE PRIMITIVE REPTILE *LIMNOSCELIS* RESTUDIED.

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**ABSTRACT.** The Permo-Carboniferous reptile *Limnoscelis* is redescribed and compared with amphibian and other reptilian types. It is concluded 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.

## INTRODUCTION.

*LIMNOSCELIS paludis* a reptile from early Permian or late Carboniferous deposits in New Mexico, was described by Williston in 1911; additional data were given in two works of slightly later date (1911a; 1912). This form has received scant attention from later writers. It was obviously a cotylosaur and hence in some sense a "stem reptile." Watson (1917) divided the cotylosaurs into three groups, Seymouriamorpha (primitive), Diadectomorpha (aberrant) and Captorhinomorpha (advanced, without otic notch) and placed *Limnoscelis* in the last group, although recognizing primitive features (1919).

Current concepts and theories of lower tetrapod phylogeny suggest that *Limnoscelis* is worthy of careful consideration in its relations to problems of reptilian origins. Crucial in the matter is the position of *Seymouria* and its allies. Watson (1917, 1919) pointed out the many features in which this redbeds tetrapod bridges the structural gap between amphibians and reptiles and at that time argued that *Seymouria* and its close relatives (particularly *Kotlassia* of the Upper Permian of Russia) should, as the Seymouriamorpha, be considered as the basic reptilian cotylosaur stock. Most later workers, including, for example, the writer (1928), and White (1939) in his recent comprehensive account of *Seymouria* anatomy have adhered to this view.

Recent investigations, however, place a somewhat different light on the situation. Apparent traces of grooves for lateral line organs in *Seymouria* (White, 1939, pp. 326-327) are a strong indication that this form, although not particularly adapted for aquatic life as an adult, had retained an aquatic larval stage and hence probably had an amphibian mode of development (Watson, 1942). Further, as White points out, the otic notch and otic capsule of *Seymouria* are not constructed in a fashion suggestive of reptilian ancestry. Investigation of late Carboniferous and earliest Permian faunas shows the presence there of a number of genera which are apparently related to *Seymouria* and share with it, to a varied degree, the reptile-like features of that form but appear to be rather clearly amphibian in nature. Bystrow's account of *Kotlassia* (1944) yields further data leading in the same direction. *Kotlassia* is a late Permian form which seems clearly related to *Seymouria*. It is, however, much less reptilian in organization, and appears to be degenerate in various features (cf. Watson, 1942, pp. 82-83). This degeneracy is along lines parallel to those seen in the contemporary rhachitomes and stereospondyls, where it is reasonably interpreted as a paedogenetic retention of a permanent amphibian larval life. These facts strongly suggest that in the crucial matter of reproductive processes the Seymouriamorpha were definitely amphibians, although a group which was closely related to the ancestry of the reptiles and may have included their Carboniferous ancestors.

If the seymouriamorphs be removed from the Cotylosauria, where among that group are we to look for our closest approach to a common ancestor of the reptiles? Not, certainly, among the types included in the Diadectomorpha—diadectids, pareiasaurs and procolophonids—for while some of these forms are archaic in many regards, all show specializations which indicate that they represent side branches of the ancestral stock, although unquestionably early and archaic side branches. There remain the Captorhinomorpha. Here our choice is limited. Of the forms which have been included here, *Pantylus* is apparently not a reptile at all, but a lepospondyl (a "microsaur"). The two most typical genera, *Captorhinus* and *Labidosaurus* are obviously advanced and specialized in various features. Apart from a few ill-known genera, there remains for consideration only *Limnoscelis*.

Williston had noted various primitive features, particularly in the postcranial skeleton. Restudy in the light of the possible importance of the genus, and the working out of certain cranial features not interpreted by Williston strongly suggests that *Limnoscelis* may be regarded in most respects as close to an ideal ancestor for most if not all of the reptilian groups.

All the known remains of *Limnoscelis paludis* are from the redbeds of El Cobre Canyon, New Mexico. These beds are included in the Abo formation as currently defined. The exact age determination is difficult (cf. Romer and Price 1940, pp. 28-30). The typical deposits which contain the Abo fauna from the Rio Arriba district appear to be approximately the equivalent of the middle or lower portions of the Wichita group, currently regarded on palaeobotanic and invertebrate evidence as very early Permian in age. The El Cobre beds appear on the evidence of their vertebrate fauna to be somewhat earlier than the typical Abo and might well be late Carboniferous in age.

Except for fragments, I know of no other materials than those described by Williston. These include: (1) the holotype, an articulated skeleton with skull, exhibited in the Peabody Museum of Yale University (No. 811); (2) two incomplete skeletons, Peabody Museum Nos. 809, 819, collected at the same time as the type, formerly in the Peabody Museum collections and now in the Museum of Comparative Zoology; (3) fragmentary materials in the University of Chicago, described by Williston (1912). I wish to thank Director Carl O. Dunbar and former Curator G. Edward Lewis for the privilege of restudying the type, and for their broadly conceived policy regarding exchanges which has enabled us to include the duplicate Yale material in the Harvard study collection of redbeds vertebrates.

*Skull.* The skull (Figs. 1-3) is known only from that of the holotype. This was described by Williston in his original paper, and the description was repeated, in modified form and with additions, in his "American Permian Vertebrates" (1911a). A number of points remained obscure at the time of this description. No further development has since been made of the specimen, but I believe I have been able to determine certain sutures which were not then discerned and (because of recent advances in our knowledge of primitive tetrapods in general) to interpret certain structures once obscure, particularly those of the occipital region.

The skull had been crushed dorso-ventrally, partially disarticulating the cheek region from the skull table. As a result it is difficult to be certain of the position of the cheeks in relation to the table, but attempts at restoration indicate that they were rather more vertically placed and less expanded laterally than would be indicated by Williston's figures (1911, Fig. 1; 1911a, Figs. 3, 6). The separation beween cheek and table took place along a line running forward from the original position of the otic notch toward the orbit, a line of weakness as Watson has noted (1926, p. 218, etc.) in embolomeres. This, however, does not imply that an otic notch was still present here in *Limnoscelis*; this line continues to be a zone of structural weakness even in such moderately advanced reptiles

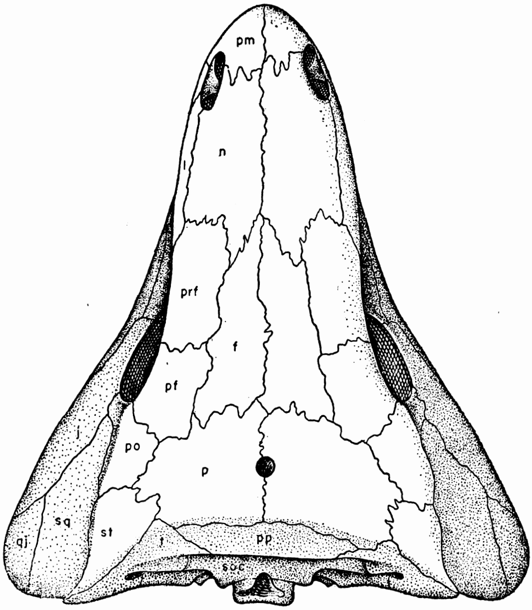

Fig 1. Dorsal view of *Limnoscelis* skull, X 1/3. Abbreviations for this and later figures: *a,* angular; *ar,* articular; *bo,* basioccipital; *c,* coronoid; *d,* dentary; *ec,* ectopterygoid; *eo,* exoccipital; *f,* frontal; *fo,* fenestra ovalis; *it,* intertemporal; *j,* jugal; *l,* lacrimal; *m,* maxilla; *n,* nasal; *on,* original position of otic notch; *op,* opisthotic; *p,* parietal; *pa,* prearticular; *pf,* postfrontal; *pl,* palatine; *pm,* premaxilla; *po,* postorbital; *pp,* postparietal; *ppr,* paroccipital process; *prf,* prefrontal; *ps,* parasphenoid; *pt,* pterygoid; *q,* quadrate; *qj,* quadratojugal; *sa,* surangular; *se,* sphenethmoid; *soc,* supraoccipital; *sp,* splenial; *sq,* squamosal; *st,* supratemporal; *t,* tabular; *v,* vomer.

as the pelycosaurs (*Dimetrodon*, etc.). Whether this line was as sharply marked on the skull in the uncrushed condition as is indicated in Williston's figure is doubtful. Despite the slight increase in depth realized by readjustment of the cheek contours, the skull is (as may be seen in occipital view) unusually low and broad for a reptile.

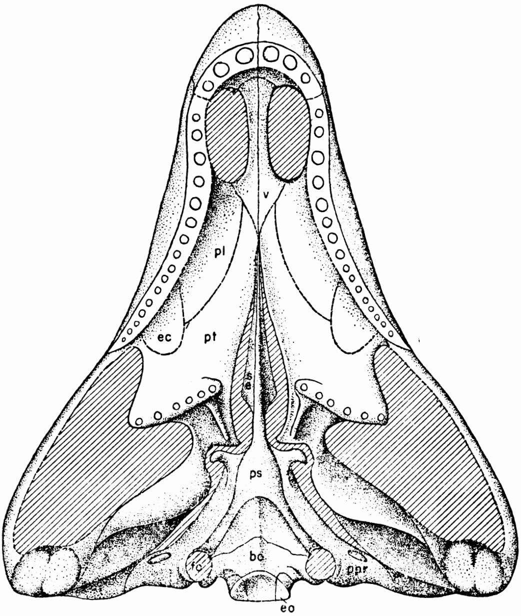

Fig. 2. Ventral view of *Limnoscelis* skull, X 1/3.

In primitive amphibians generally the jaw articulation lies well to the rear of the condyles and occiput, the posterior margin of the suspensorial region slanting well backward in its descent to the articular region. In both amphibians and reptiles many lines show a marked tendency towards a shortening of the jaw and consequent reduction in the length of the cheek region. *Limnoscelis* is already rather advanced in this regard; the articular region is only a short distance behind the occiput and with the closure of the otic notch the posterior margin of the skull is close to a straight line in both dorsal and lateral views.

Reinvestigation of the sutures of the skull roof confirms Williston's determinations in most areas with but minor changes. It would appear that a process of the nasal extended backward on the lateral side of the prefrontal (much as in many pelycosaurs, for example). Inside the lower margin of the external naris there is an area of bone which appears to be a septomaxilla; it is imperfectly preserved on either side, but is more extensive than figured by Williston. The elongation of the narial opening suggests that the septomaxilla possessed a vertical bar subdividing the opening, but there is no proof that such a condition existed.

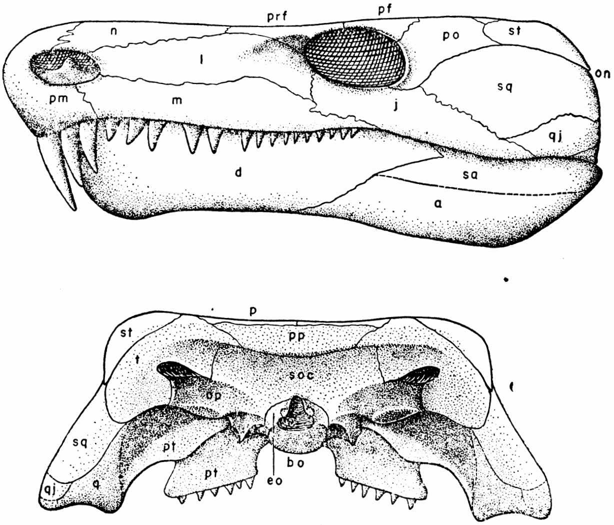

Fig. 3. *Above*, lateral view of *Limnoscelis* skull; *below*, posterior view. X 1/3.

In the skull as preserved there is at the posterior end of the cheek region on either side a crack extending nearly vertically somewhat in advance of and parallel to the posterior margin; this fissure is shown in Williston's figures, especially in his lateral view. Although the details are not clear it seems certain that this break in the dermal bones lies over the anterior (or lateral) edge of the thickened vertical ramus of the quadrate. The sheet of dermal bone covering the region posterior to the break shows no evidence of continuity with the adjacent squamosal and is figured by Williston, following the specimen closely, as a separate structure. It seems, however, impossible to interpret it otherwise than as a broken-off portion of the squamosal which wrapped postero-medially around the ascending ramus of the quadrate in a fashion similar to that seen in primitive tetrapods generally. This situation may be compared with that in forms as far apart as, for example, the primitive amphibian *Palaeogyrinus* (Watson 1926, Fig. 16) and such a pelycosaur as *Dimetrodon* (Romer and Price 1940, pl. 14, upper figure).

In the region of the skull table Williston was able to determine the approximate outlines of the parietals but was in doubt as to other determinations. Restudy with the use of appropriate oils has, I think, enabled me to determine the sutures in this region with reasonable accuracy. The area occupied by the postorbital is essentially that which Williston believed it to have covered. It occupies a position along the back margin of the orbit and extends upward and backward a considerable distance along the lateral margin of the table. Its contact with the supratemporal is short, for the parietal expands laterally in the region of the posterior end of the postorbital.

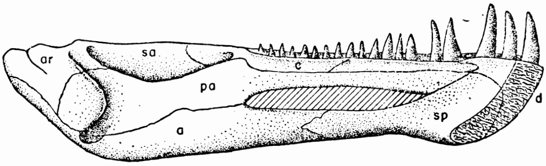

Fig. 4. Internal view of *Limnoscelis* jaw. X 1/3.

The postorbital occupies part of the area in which the intertemporal is found in embolomeres and Seymouriamorpha. The remainder of this area has been preëmpted by the parietal, which thus comes to border the supratemporal anteriorly as well as medially—a construction characteristic of *Limnoscelis* and many other early reptiles, and unknown in amphibians.

The supratemporal, here a well-developed element, is of considerable evolutionary significance. In primitive tetrapods generally it lies in line between the intertemporal area anteriorly and the tabular posteriorly. Here it is essentially in a diagonal position. Its broad antero-medial end is deeply wedged, with a digitate suture, into the postero-lateral corner of the parietal. Thence it extends rather laterally as well as posteriorly to form the posterior part of the lateral margin of the skull table and, tapering as it goes, curves downward to terminate in a slight projection on the skull margin above the posterior end of the squamosal. This distal projection of the supratemporal is paralleled medially by a similar process of the tabular; the structure here appears to be identical with that seen in the pelycosaur *Dimetrodon* (Romer and Price 1940, pls. 6, 10) although the proportions are different.

In *Seymouria*, as shown in White's figure (1939, Fig. 1) the supratemporal has pushed back and down at its tip to attain a position rather comparable to that in *Limnoscelis*. There appears to be a tendency in this direction in embolomeres, but it is masked by the usual development of a pronounced tabular horn.

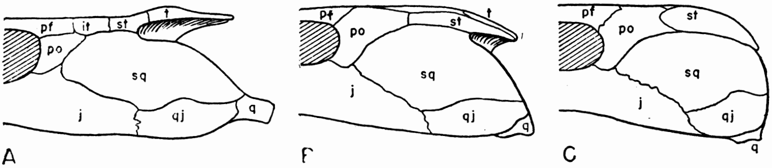

**Fig. 5.** **To illustrate the probable origin of the *Limnoscelis* temporal region. *A*, a primitive amphibian (*Palaeogyrinus* Watson) with a well-developed otic notch; *B*, hypothetical intermediate stage; *C*, *Limnoscelis*. Lateral views of temporal region.**

As discussed in the case of the pelycosaurs, this slight posterior projection may have been associated functionally with ligaments or other structures supporting the eardrum, which must have lain close to the skull margin below this point. Phylogenetically the projection appears to mark the point of closure of the otic notch (Fig. 3, *on*). In certain of the amphibian groups, notably the rhachitomes and stereospondyls, reduction of the notch seems to have proceeded by a gradual lessening in depth from a deep "bay" to a shallow "cove," the anterior margins retaining a rounded contour in the process. In the present case, the otic notch would have begun as a "fissure" type, as seen in embolomeres, and its elimination have occurred not by progressive lessening in depth but by a closing together of the two sides in shear-like fashion, the upper margin closing down upon the lower (Fig. 5). We cannot determine internal structural details in *Limnoscelis*, but in *Dimetrodon* the relations of the squamosal, lateral to the original notch, with the more medial elements argues strongly for this assumption.

In many later reptiles a small dermal element of debated homology is present near the back margin of the skull, usually between parietal and squamosal, often close to the lateral margin of the paroccipital process. This is held by some (as Broom) to be, in most cases at least, homologous with the tabular; by others (Watson, etc.) it is identified as the supratemporal. It is easy to see, from the structure found in *Limnoscelis*, the reason for the difficulty in identification. Here the supratemporal and dorsal portion of the tabular are apposed and similar in many respects. As a guide to the identification of an element in this region in later reptiles, it may be noted that the supratemporal lies essentially lateral to the parietal (or partially wedged into that element) ; the dorsal ramus of the tabular is postero-medial to the corner of the parietal. The supratemporal primitively is purely a roofing element; the tabular in early reptiles (as described below) is mainly developed on the occipital surface. Primitively the tabular is the element in contact with the distal end of the paroccipital process; but the tip of the supraoccipital is close by, and if the tabular were to disappear might readily gain a paroccipital contact. Applying these criteria, the element found in this region in various later reptiles (Figs. 6-8) is in many cases best identified as the supratemporal; but the evidence is in general far from conclusive. There has been a general tendency for the parietal and squamosal to take over in variable fashion the functions and areas of supratemporal and tabular.

The occipital region of the skull is somewhat imperfect and broken and Williston could make little of it. The progress made in recent decades in our knowledge of primitive skull structures in general now permits us, I believe, to interpret this area in reasonable fashion.

Williston's figure of the dorsal surface would indicate that the postparietal (dermal-supraoccipital) and more laterally, the tabular, were rather broadly exposed on the dorsal surface. Actually, however, this area, although showing indications of sculpture and hence of superficial position, is tilted strongly downward, the skull being levelled off here, to lie on a plane intermediate between that of dorsal surface and occiput. We thus have a transitional condition between the typical amphibian and reptilian positions of these elements.

Williston did not determine the sutures here. I believe I have been able to follow the outlines of the postparietal, which appears to be a single median element; I failed to find a median suture. It has a very broad contact with the parietal, almost excluding the tabular from the latter element. Posteriorly and ventrally it constricts, but nevertheless occupies the major part of the levelled area discussed above, and is sharply separated by a pronounced ridge from the occipital area below it.

The postparietal, or dermal supraoccipital, is a paried element in most amphibians, including typical embolomeres and seymouriamorphans. In reptiles it is sometimes reported as a paired structure. Most such cases, however, are doubtful and it is more reasonable to assume that the single condition seen in *Limnoscelis* is a primitive reptilian feature.

The tabular is a well-developed and complex bone, mainly on the occipital surface. It is well preserved on the left side, but is here not so readily distinguishable from the occipital complex; on the right, the tabular has been pushed out of position and broken, but its structure is well displayed. It consists essentially of three processes: a thin dorsal one, which occupies the lateral portion of the levelled area mentioned above, between supratemporal and postparietal and with a short parietal contact; a thickened medial process, essentially cone-shaped, extending inward to terminate in a blunt oval apposed to the lateral process of the supraoccipital; a relatively thin ventrolateral process, which extends downward and outward alongside the distal end of the supratemporal and sheathing the lateral part of the occipital surface—the paroccipital process. The structure is closely comparable to that seen in pelycosaurs (cf. Romer and Price, 1940, pl. 14, upper figure); the thickened medial process is exactly comparable to that seen in primitive pelycosaurs, such as *Ophiacodon* (Romer and Price, 1940, pp. 203-204). As far as I am aware, the tabular in amphibians seldom extends far enough medially on the skull roof to gain a contact with the braincase in the "supraoccipital" region. It does so, however, in *Seymouria* (although the different method of ossification of the braincase confuses the issue), and in this form, as in *Limnoscelis*, the tabular forms the entire dorsal margin of the posttemporal fenestra (White, 1939, p. 334).

Much of the occipital aspect of the skull is capable of interpretation. The occipital condyle is single and flattened dorsally. Most of it is formed by the basioccipital, but laterally a suture is discernible separating basioccipital and exoccipital. This latter element is of normal structure, small in size, and extending upward along the lateral margins of the foramen magnum to terminate in a process on which an articulation for a pro-atlas can be seen. Much of the course of the suture between exoccipital and the supraoccipital and opisthotic can be observed. Owing to the nature and condition of the specimen I failed to determine the foramina expected in this region.

The supraoccipital is a broad and somewhat concave plate of bone. Dorsally it articulates along a nearly straight suture with the postparietal and (at the lateral ends of this border) with the dorsal process of the tabular. Laterally it articulates with the thickened medial process of that bone. From the lower end of the tabular articulation a curved ridge running medially, ventrally and posteriorly leads to a short area of articulation with the exoccipital lateral to the foramen magnum. This ridge, along which I believe a suture is discernible, appears to represent the line of separation between supraoccipital and opisthotic.

The occipital face of this last element, as a paroccipital process, is a concave area running outward from the ridge referred to and below the medial process of the tabular, to be sheathed laterally by the thin ventral process of the tabular. Whether the two bones are firmly united or whether as in a number of early tetrapods the tip of this process was cartilaginous[1] cannot be determined in the specimen, nor can it be determined whether this process (or its cartilaginous extension) reaches laterally far enough to gain a connection with the squamosal as in most typical reptiles.[2] An area of matrix found above the lateral portion of the paroccipital process and bordered above and laterally by the tabular appears to be the opening of the posttemporal fenestra. The lower margin of the paroccipital process is curved out posteriorly and terminates in a thick, blunt edge—whether natural or due to removal of bone in preparation I cannot say.

The occipital construction described above is that to be expected in a primitive reptile. As the tabular and supratemporal have swung downward laterally, they have carried with them the paroccipital process, formed mainly by the opisthotic. This originally slanted upward and outward to brace the tabular region at the inner margin of the otic notch. In its new position it is in process of gaining a firm connection with the

[1] For example, pelycosaurs (notably *Ophiacodon*) on the one hand and such primitive rhachitomes as *Edops* on the other.

[2] Cf. for example *Dimetrodon*, Romer and Price, 1940, pl. 8.

suspensorial region, thus (as first clearly pointed out by Watson) effectively bracing the region of the jaw articulation on the braincase. Above the paroccipital process, the posttemporal fossa and foramen of a more primitive tetrapod (cf., for example *Edops* in Romer and Witter 1942, Figs. 7, 9) have moved conformably laterally and become reduced in depth to become the posttemporal fenestra: a "window" rather than a pocket *plus* foramen. Above the fenestra the supraoccipital area has (also conformably) expanded laterally to gain a broad lateral contact with the tabular.

More light is needed on the history of the supraoccipital element. This bone is formed in the synotic tectum of the chondrocranium and hence (opposed to the older concepts of the vertebral nature of the skull) is quite unrelated to the other occipital elements; it ossifies in an area connected laterally with those in which proötic and opisthotic are formed. In *Limnoscelis* there appears to be as in later reptiles generally, a large supraoccipital bone. In many of the earlier typical amphibians the supraoccipital region is well ossified but never, as far as I am aware, is there any clear evidence of a discrete supraoccipital bone. In many labyrinthodonts, even including such a presumed close relative of the reptiles as *Seymouria*, this element is apparently absent, leaving a gap filled in life by cartilage; most of the supraoccipital region is definitely ossified by the two otic elements. In *Kotlassia*, however, a supraoccipital is reported; the bone is small and concealed posteriorly by flanges of the postparietal (Bystrow, 1944, p. 387). It is possible that (comparable in history to the actinopterygian supraoccipital) the bone is a new center, developed in the synotic tectum in forms associated with reptilian ancestry.

The occipital region of *Limnoscelis* is essentially a plate-like structure, quite broad and not very deep. A plate-like occiput generally comparable is seen in a number of early and seemingly rather primitive reptiles of various groups and is retained in synapsids, many synaptosaurians and the archosaurs generally. In forms with this type of construction the occiput is of a closed type—the posttemporal fenestrae are small and sometimes lost. In contrast is a type of occiput seen in some advanced cotylosaurs, turtles, ichthyosaurs and especially characteristic of lepidosaurs. There the supraoccipital has a narrow dorsal contact with the skull roof and the paroccipital process is a projecting rod-like structure; between the two there develops a greatly expanded posttemporal fenestra.

In the ventral view of the skull the lateral margins are obscured by the articulated lower jaws. No further development of the anterior part of the palate has been attempted since the time of Williston's description. I have freely restored this region along the lines of the general pattern common to other early reptiles and to the *Seymouria* group and certain embolomeres; a relatively narrow internarial region, formed by the vomers, is a key feature of this pattern. In the specimen the cultriform process of the parasphenoid has been pushed to the right side. Above it on one side is exposed a high, flat bony surface which is obviously the lateral aspect of the sphenethmoid. The opposite side is concealed by matrix so that one cannot be sure whether (as Williston believed) the bone formed a thin vertical plate or whether (as I suspect) the cross-section was that of a thin V, the two lateral surfaces diverging toward the top, in the region exposed, for the inclusion of the anterior part of the brain and the olfactory nerves.[3] The sphenethmoid appears to present a definite posterior margin, as expected, some distance in front of the region of the basal articulation.

Most of the pterygoid region is well preserved, and was described and figured by Williston. The construction is typically reptilian, the so-called rhynchocephalian type of palate common to many early forms of the class, and differs markedly from that of any known amphibian (including seymourians) in the highly developed and toothed flange.[4] Although it is difficult to correct some distortion here, I believe that the interpterygoid vacuities were rather smaller than figured by Williston. There is a well developed movable basal articulation. The posterior portion of the pterygoid is a double sheet of bone. The main quadrate ramus is a large plate, nearly vertical in position, but tilted somewhat medially above, which extends back to overlap the quadrate. Just back of the basal articulation there develops a broad flange extending medially from the base of the quadrate ramus proper. This flange, which has been interpreted as forming the floor of the middle

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[3] As in *Seymouria* (White, 1939, Fig. 9) but higher and narrower.

[4] Situated, one may assume, on the pterygoid rather than on the ectopterygoid, as first stated by Williston. I have not been able to make out any sutures bounding an ectopterygoid, which was presumably small as in early reptiles generally.

ear region, is still highly developed in primitive pelycosaurs, as *Ophiacodon* (Romer and Price, 1940, p. 60, pl. 3), and is represented in vestigial fashion in *Dimetrodon* and various other reptiles by the inturned lower edge of the quadrate ramus and a depression in the concave medial aspect of the bone at the base of this ramus (*ibid.*, pls. 8, 14). In some of the more primitive labyrinthodonts (including seymouriamorphans) the pterygoid may curve inward ventrally partially to floor the middle ear region, and there may be a slight development of a flange anteriorly about a "tympanic excavation" (cf., for example, Romer and Witter, 1942, Fig. 4), but I am not aware of any case in which the flange is as highly developed as in this early reptile. Its development may well be associated with the downward movement of the ear region associated with otic notch elimination.

Details of quadrate structure are not available and the epipterygoid is not visible.

The basicranial region has been described and figured by Williston. The development here, including the presence of basisphenoidal tubera, is that which would be expected in a primitive reptile. The moderate sideways compression of the basisphenoid-parasphenoid region almost exactly splits the difference between the more primitive condition seen in (for example) *Seymouria* (White, 1939, pl. 1, A) and the much more slender structure present here in *Captorhinus* (Price, 1935, pl. 7, B). Well-developed basisphenoidal (or parasphenoidal) tubera appear to be characteristic of primitive reptiles generally. These structures are very seldom developed in known labyrinthodonts, but are known in a few Carboniferous and Permian types, including *Cricotus* and *Seymouria*.

Little can be made out of the lateral walls of the braincase in the general region of the basisphenoid and proötic. Laterally and posteriorly, at the side of the braincase Williston described, with doubt, a bony structure as the stapes. Actually the stapes is absent; this structure is the ventral surface of the paroccipital process, built very much as in *Captorhinus* or primitive pelycosaurs (cf. Price, 1935, pl. 7, B; Romer and Price, 1940, pl. 13, etc.). A strong ridge descending from the anterior margin of the process is the point of attachment of the dorsal process of the stapes (which we may therefore infer to have been constructed much as in the groups just mentioned). At the base of the paroccipital process is the matrix-filled fenestra ovalis. The low latero-dorsal margin is presumably formed by the conjoined proötic and opisthotic. Posteriorly the opisthotic sends down along its margin a strong flange (cf. *Dimetrodon*, Romer and Price, 1940, pls. 13, 14, *op*). Much, at least of the anterior margin is bordered by the parasphenoid. The structure here is highly comparable in most respects to that seen in captorhinids and pelycosaurs. It differs markedly from that in any primitive amphibian as a result of its lower position, which is, of course attributable to the closure of the otic notch and the consequent shift in stapedial position. The pronounced lateral projection of the otic capsule about the fenestra ovalis in *Seymouria* as described by White, is seemingly a specialization hardly to be expected in a reptile ancestor.

The lower jaw is known from the type and a second fragmentary specimen described by Williston. I have nothing to add to his description of the outer surface, but have ventured to make a new figure of the inner aspect (Fig. 4), combined from his figures and data and restudy of the type. The jaw in most respects is of a generalized type. There is a long inframeckelian fenestra, the anterior boundaries of which are uncertain. A strip of coronoid tissue (mislabelled "splenial" by Williston) lies, in primitive reptilian fashion, along the inner margin of the tooth row. It is poorly preserved, the number of elements present cannot be determined nor can it be seen whether or not teeth were present. Because of the presence of two coronoids in certain more advanced reptiles (including pelycosaurs), this number would be expected here. As Williston notes, there is present a powerful process on the inner surface in the region of articular and prearticular. Presumably this was associated with jaw muscle attachment (? pterygoideus, temporalis in part). Similar processes are present in captorhinids and in the primitive pelycosaur *Varanosaurus*, and may have been characteristic of primitive reptiles in general.

I have not had the opportunity to examine well-preserved sections of the teeth. Williston states that they show "a deeply infolded dentinal structure," *i. e.*, they have preserved to some degree the labyrinthine structure of the ancestral reptiles. There is little data on tooth replacement but the teeth may be assumed to have shown the waves of replacement of alternating series characteristic of primitive tetrapods in general. The exaggeration in size of the upper incisor teeth in *Limnoscelis* (suggestive of the captorhinid condition) is presumably a minor specialization. There is some indication of a peak in size of teeth in the anterior part of the maxillary series. This trend is, of course, one which leads in synapsids to the development of canines of a mammalian type; but a tendency for this sort

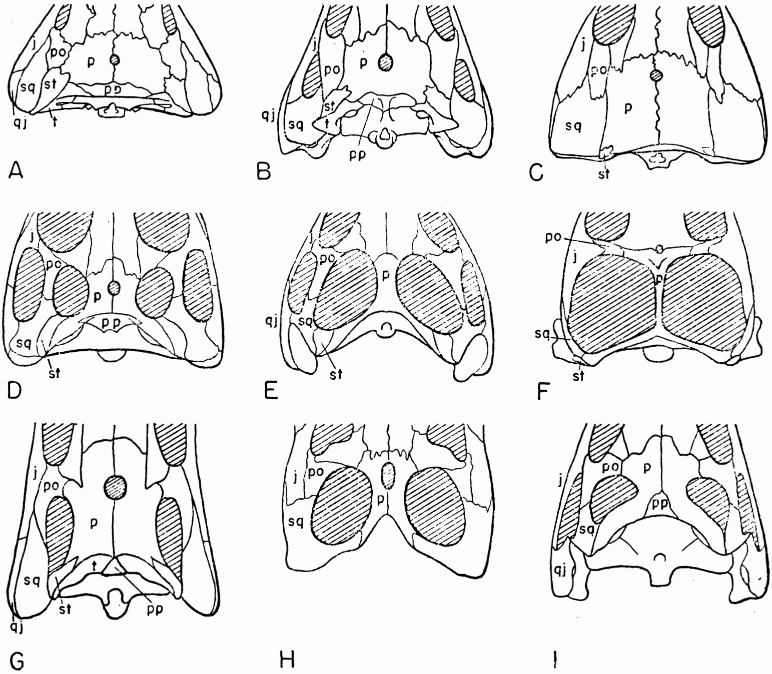

Fig. 6. Dorsal views of posterior portion of skulls of various reptiles. *A*, *Limnoscelis*; *B*, the primitive pelycosaur *Varanosaurus* (after Romer and Price); *C*, the advanced cotylosaur *Captorhinus* (after Price, unpublished); *D*, the eosuchian *Youngina* (after Broom and Watson); *E*, the early rhynchocephalian *Mesosuchus* (after Broom); *F*, the lizard *Conolophus*; *G*, the synaptosaurian *Araeoscelis* (after Williston, Broom and specimens); *H*, the placodont *Placodus* (after Broili); *I*, the thecodont *Euparkeria* (after Broom).

of development is seen, as well, even in rhachitomous amphibians.

*Skull—comparisons.* We shall here discuss the relationships of *Limnoscelis* as deduced from its skull structure, with particular reference to those features of the posterior part of the skull which we have seen to be diagnostic of *Limnoscelis* and which appear to be characteristic of ancestral reptiles. As noted in a later section, the postcranial skeleton indicates that *Limnoscelis* is a very primitive reptile distinctly advanced over amphibian types but sufficiently generalized to have given rise to any of the varied groups of later reptiles. The cranial morphology is in agreement with this conclusion. In Figures 6-8 I have given sketches of the posterior part of the skull in various reptiles for purposes of comparison.

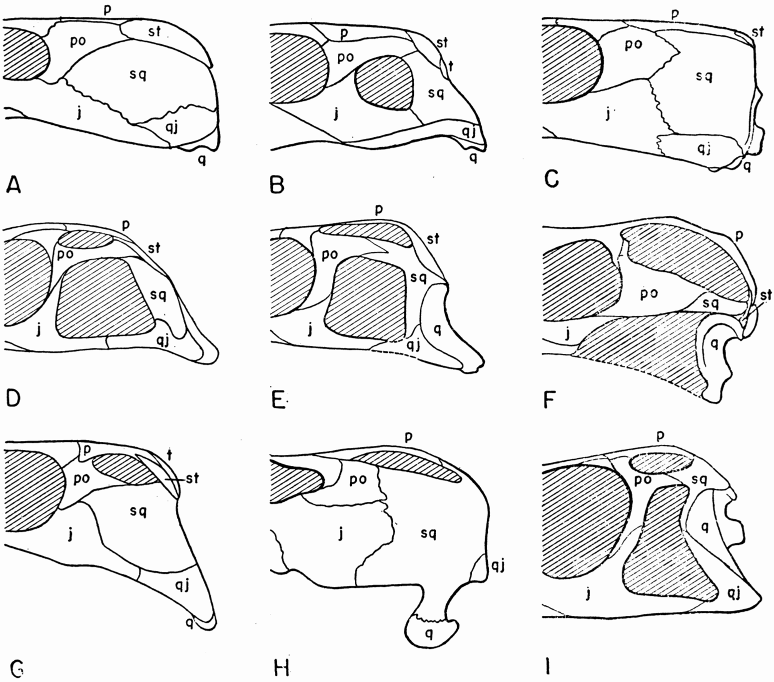

Fig. 7. Lateral views of the skulls shown in Figure 6.

It is generally agreed that the reptiles have arisen from labyrinthodont amphibians, and Watson has ably argued that the embolomerous labyrinthodonts show a general structural pattern antecedent to that of reptiles. In agreement with this conclusion are many features in the skull structure of *Limnoscelis*, such as the arrangement of much of the pattern of the dermal skull roof and palate; in many regards *Limnoscelis* is directly comparable to such primitive types as *Palaeogyrinus*, etc.

*Seymouria* is generally held to be, even if not a reptile, at least a form closely related to reptilian ancestry. As noted elsewhere, study of the postcranial skeleton gives strong support to this conclusion. But as concerns cranial morphology, *Seymouria* shows few points indicating particularly close affinity with reptiles. We have noted above certain features of the supratemporal and tabulars suggestive of relationship to reptiles, and White points out a few other reptile-like characters. As that author notes, however, the *Seymouria* skull is in general of amphibian rather than reptilian type. There is, for example, no development of the reptilian type of pterygoid flange; amphibian palatal fangs persist; the intertemporal bone is still present; the otic and occipital ossifications are quite different in pattern from those of reptiles, etc. Further, as White points out, the otic notch and otic capsule are highly specialized in directions quite other than those which were present in the line of reptilian ancestry. Presumably the reptilian ancestor was a seymouriamorphan of some sort; but *Seymouria* itself is far from being that form. Nor do we know as yet any amphibian of the seymouriamorph type which definitely shows "proto-reptilian" skull characteristics.

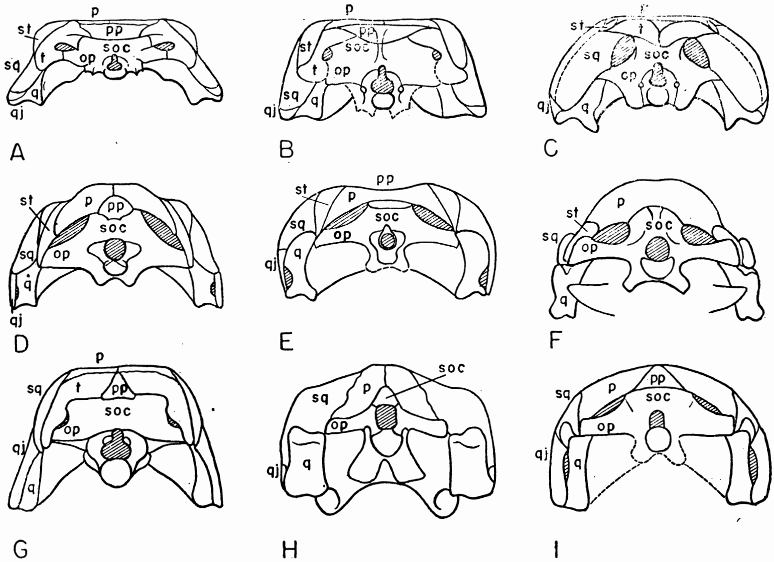

Fig. 8. Occipital views of the skulls shown in Figure 6.

Typical reptilian features of *Limnoscelis* have been noted in our description. They include: occupation by the postorbital and parietal of the area of the former intertemporal area; the posterior shifting of the supratemporal as described above; closure of the otic notch by downward folding of supratemporal and tabular on to the squamosal; partial elimination of tabular and postparietal from the skull roof and concomitant expansion of these elements—particularly the tabular—on the occipital surface; downward rotation of the paroccipital processes and their tabular articulations to brace the suspensorial region; development of the pterygoid flange on the palatal surface. 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.

We have noted in our description of the *Limnoscelis* skull a number of other characters found in this genus and one or more other early reptilian types. We have refrained from adding them to the list just presented because there is little evidence that they were present in the ancestry of all reptiles. While the evidence leads us reasonably to assume that *Limnoscelis* is a member of a truly ancestral reptilian group, it would be presumptuous to claim that it lies exactly at the base of the entire class, and hence inadvisable to claim that it is completely generalized in every feature of skull structure.

Given our present knowledge of *Limnoscelis* structure we can recognize in certain forms already known, members of the same group. *Romeria* and *Protorothyris* are small cotylosaurs described by Price (1937). *Romeria* resembles *Limnoscelis* in general skull shape and dentition; *Protorothyris* is more elongate and with a "premature" development of a large canine. The general pattern of the dermal bones is a primitive one and agrees in most respects with that of *Limnoscelis*, most significantly in the nature of the supratemporal—wedged, as in that genus, into the postero-lateral corner of the parietal. The potential phylogenetic significance of these forms was recognized by Price, but because we knew little of the structure of the supratemporal region in *Limnoscelis*, it was impossible to realize the close relationship which they appear to have to that genus. Both forms, however, are more advanced than *Limnoscelis* in the reduction of the supratemporal to a point where contact with the postorbital has been lost.

It is perhaps significant that these two genera are from the lower formations of the Wichita group in Texas and thus may be of approximately the same age as *Limnoscelis*.

I am unable to recognize among described forms from the Pennsylvanian any other genera definitely assignable to the *Limnoscelis* group. This type of reptile would be expected in the Pennsylvanian. It is not impossible that certain doubtful forms of that age such as "*Eosauravus*" may have been related, but since the *Limnoscelis* postcranial skeleton is similar to that of both seymouriamorph amphibians and diadectid cotylosaurs, definitive criteria are difficult to obtain.[5] This is also true in the case of *Solenodonsaurus* of Nýřan (Broili, 1924; Pearson, 1924), which has been referred to the Seymouriamorpha. As far as is known, the characters present would permit of assignment either to that group or to primitive cotylosaurs, and the evidence concerning truly definitive features of skull table or occiput is inadequate. On the whole, however, the skull contours strongly suggest relationship to *Limnoscelis*.

*Limnoscelis* is frequently brigaded with the captorhinid cotylosaurs in a suborder (or order) Captorhinomorpha, characterized primarily by the absence of an otic notch. It is obvious, however, that *Captorhinus* and its larger ally *Labidosaurus* differ markedly from *Limnoscelis*. In some features, such as the multiplicity of marginal teeth, we are dealing with specializations. In other regards the captorhinids appear to be structurally advanced forms, although derivable from a limnoscelid type. The posterior margin of the skull is practically a straight line, with the jaws considerably shortened. Although it is frequently overlooked, there is a trace of the projection which marked the point of closure of the otic notch in *Limnoscelis*. It lies at the tip of the tiny supratemporal, at a point where this bone is in contact with a posterior dermal element possibly homologous with the tabular. However this point is much higher up on the skull than in *Limnoscelis*, and far removed from the paroccipital process. Parietal and squamosal are broadly in contact; a small nubbin of bone wedged into the postero-lateral corner of the parietal is a reduced supratemporal. Neither postparietal nor tabular appears on the skull roof, which is marked off sharply from the nearly vertical occiput. Along the upper rim of the occipital surface there is found a pair of dermal elements usually considered to be paired postparietals; they may, however, be

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[5] The presence of but two proximal tarsals in "*Eosauravus*" is perhaps significant.

equally well interpreted as remains of the tabulars which have moved medially in preserving contact with the narrowed supraoccipital.

Price (1935) has noted the essentially rhynchocephalian nature of the braincase of *Captorhinus.* Particularly notable in this regard is the occipital face. The occiput is no longer a plate. The supraoccipital region has become quite narrow, the paroccipital a distinct rod-like structure which braces the suspensorium directly without intervention of a tabular. A specialization not found in any other group is the development by the squamosal of a strong flange which covers the lateral margin of the occipital region and functionally replaces, in part, the tabular.

With broad separation of supraoccipital and paroccipital, a broad posttemporal fenestra has developed. This type of development of the occiput is one found in number of later reptilian orders, particularly the lepidosaurs, and it may be suggested that, although technically cotylosaurs, the captorhinids may be related to the ancestry of these diapsids.[6] The type of development of the dermal bones of the occipital surface, together with dental specialization indicates, however, that the captorhinids do not lie directly on the ancestral line of the Lepidosauria.

*Limnoscelis* appears to be a very primitive cotylosaur, the captorhinids very advanced forms. It may perhaps be advisable to separate the two types subordinally, and to consider the primitive genus and its relatives as constituting the suborder Limnoscelidomorpha.

That *Limnoscelis* is in almost every regard an ideal ancestor for the pelycosaurs and, through them, for therapsids and mammals is self-evident. In the description of the skull I have in various instances drawn upon known pelycosaur structural features to interpret those of *Limnoscelis.* The resemblances are particularly close with the Ophiacodontia, the most primitive suborder of the pelycosaurs; primitive sphenacodontoids and edaphosauroids are also structurally close in many regards. The elongation of the skull in *Ophiacodon* somewhat obscures the similarities but in the case of such more generalized ophiacodontoids as *Eothyris* or even *Varanosaurus* little is needed

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[6] The fact that *Captorhinus* (Price, 1940) has a structure of the caudal vertebrae facilitating a tail-break in the fashion of rhynchocephalians and primitive lizards 'may well be significant.

except the development of a small temporal opening to transform a cotylosaur into a pelycosaur. Such features as the development of the supratemporal and tabular are almost identical. In contrast to various other reptilian groups, the occiput tends to retain in synapsids the plate-like structure of *Limnoscelis*, although there is some tendency (in *Dimetrodon*, for example) for the development of rod-like paroccipitals.

It has become increasingly apparent in recent years that the lizards and rhynchocephalians are closely related to one another, and the writer has revived the old term Lepidosauria as a subclass designation for these forms and their common ancestors. These ancestors are a Triassic group of small diapsids, currently termed the Eosuchia,[7] of which *Youngina* and its relatives are typical. In these forms we find a series of reptiles which, although advanced in many features including a diapsid construction of the temporal region, can be readily derived, as regards cranial structures from the type seen in *Limnoscelis*, with *Captorhinus* showing intermediate conditions in certain regards. In the temporal region there persists a "supernumerary" element interpreted as either supratemporal or tabular. Taking into consideration the fact that the upper temporal opening has appeared in the area which in *Limnoscelis* was occupied by the outer portion of the parietal, the position of this element is closely comparable to that of the *Limnoscelis* supratemporal. In *Youngina* the tabular, it appears, has vanished; the parietal has taken over part of the area it once occupied and farther laterally and ventrally the supratemporal alone now extends into the area between squamosal and paroccipital process where formerly both supratemporal and tabular terminated. As seen on the occipital surface, the postparietal has persisted. The occipital complex is no longer platelike but has developed in a fashion comparable to that of *Captorhinus* on the one hand, and rhynchocephalians on the other, with a narrow supraoccipital, discrete paroccipital bars, and large posttemporal openings.

In typical rhynchocephalians both supratemporal and postparietal have disappeared; squamosal and parietal have taken over the areas which they once occupied. In the primitive genus

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[7] Camp, in a recent valuable discussion of this group (1945) has transferred to it the term Protorosauria, generally applied to primitive reptiles of the synaptosaurian type—*Araeoscelis*, etc. I cannot agree with him in this transfer and hope to discuss the matter at another time.

*Mesosuchus* (Broom, 1925) however, the supratemporal is still present as in eosuchians and a small postparietal is said to be present as well. As we have noted, the rhynchocephalian braincase (including the occiput) is very similar to that of both *Captorhinus* and the eosuchians.

Current belief tends strongly toward a derivation of lizards from primitive diapsids of the eosuchian type, *Prolacerta* and other genera showing almost diagrammatically intermediate conditions in the loss of the temporal bar. Here the upper temporal opening is widely expanded, but a small "extra" dermal element is present in the angle between squamosal, paroccipital, and parietal. Broom has pointed out on various occasions (1924, 1925, etc.) that this element is very similar in its relations to the ventral portion of the primitive tabular, and were other lepidosaurians unknown, one would be strongly inclined to accept his conclusion on the matter. However, consideration of more primitive and seemingly transitional stages tends to the belief that the bone is the supratemporal. The occiput of the lizards shows again the "rhynchocephalian" type of braincase construction present in captorhinids, eosuchians and rhynchocephalians.

In the *Youngina* group the region of the tip of the supratemporal tends to project somewhat from the contour of the skull roof, as was the case in *Limnoscelis.* Below this point more advanced lepidosaurs develop a prominent otic notch, bounded anteriorly by the curved quadrate; this structure is most highly developed in the Squamata. Analogous or homologous developments of a secondary notch here are seen in archosaurs, turtles and even the diadectomorph cotylosaurs; this type of structure has surely developed more than once among reptiles. In the case of the lepidosaurs, we are certainly dealing with an otic notch, but one surely developed as a secondary structure.

Although the evidence is far from conclusive, the writer believes *Araeoscelis* of the early Permian and its close relatives (*Ophiodeirus*, *Kadaliosaurus*) to be representative of a group leading not only to some curious Triassic types (*Tanystropheus*, etc.) but also to the nothosaurs, placodonts and plesiosaurs, and has brigaded all these forms in the subclass Synaptosauria; the presence of a single upper temporal opening is a diagnostic feature. Despite the fact that *Araeoscelis* and *Ophiodeirus* are small and consequently very slenderly built forms, their basic structures are derivable without too great difficulty from those seen in *Limnoscelis*. The temporal opening has developed in the area along the postorbital-parietal contact, and has left posterior to it a supratemporal very similar in type to that of *Limnoscelis*. In neither *Araeoscelis* nor *Ophiodeirus* is the occiput satisfactorily displayed, but its general structure seems clear. Both postparietal and tabulars are well developed on the occipital surface. As in *Limnoscelis*, and in contrast to the types considered above, the occiput is persistently a plate-like structure, with small posttemporal openings and with a broad contact between the occiput and the skull roof.

Among the sauropterygians, this solid construction of the occiput continues to be present in nothosaurs and placodonts although there is a tendency for the supraoccipital to constrict dorsally and for the paroccipitals, concordantly, to develop in discrete fashion. In the plesiosaurs, however, there has been specialization in occipital development and a formation (seemingly secondarily) of large posttemporal openings. In most sauropterygians supratemporal, tabular and postparietals have all disappeared, leaving the enlarged squamosal and the parietal as the only dermal elements in the temporal and occipital areas.

Whether the great group of archosaurian reptiles evolved independently from primitive reptilian types or arose from eosuchian diapsids is uncertain. The evidence from the temporal and occipital region suggests the former. *Euparkeria* and *Chasmatosaurus*, Lower Triassic thecodonts, are among the oldest of archosaurs. They show (despite some specializations in the latter genus) a construction which appears to be primitive for the group. In contrast to contemporary lepidosaurians, supratemporal and tabular have already disappeared,[8] although a postparietal remains; the parietal has in great measure supplanted the tabular in position and function. In the occiput the supraoccipital is persistently broad (in strong contrast to lepidosaurs) and the posttemporal fenestrae little developed. The broad and solid construction of the occiput seen here persists in most later archosaur types. In *Euparkeria* the squamosal projects strongly backward at the point once occupied by the projecting tips of supratemporal and

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[8] Camp (1930), notes, however, tabulars welded into the upper part of the occiput in phytosaurs.

tabular. Below this point archosaurs, like lepidosaurs, tend to develop to a variable degree a secondary otic notch. As in other forms, from diadectids to lizards, in which this lateral type of notch is present, its development is associated with an anterior movement of the jaw articulation.

It is unfortunate that the oldest chelonian skull material, as *Triassochelys*, is from the Upper Triassic, by which period enough time has elapsed for profound changes to have occurred in chelonian skull morphology as well as in body structure. In *Triassochelys* the skull is solidly roofed, implying a direct cotylosaurian ancestry; but one cannot exclude the theory (advocated particularly by Broom) that the solid roof is secondary, as a protective device for a nonretractile head. There appears to have been a supratemporal of large size in *Triassochelys*, but neither tabular nor postparietal is reported. The occiput in *Triassochelys* is in a stage of development analogous to that seen in *Captorhinus* and lepidosaurs; there is a rather narrow supraoccipital, a widely opened posttemporal fenestra, and a strong paroccipital process which in later turtles obtains so powerful an attachment to the suspensorium that the dermal roof may be eliminated without detriment to jaw support. Below the paroccipital region, *Triassochelys* and all later turtles show the presence of a highly specialized type of otic notch which may have developed parallel to the somewhat comparable lizard structure or may be of more ancient (cotylosaurian?) origin. There are numerous points of specialization in other features of the chelonian skull and palate, but in no case are the structures such that they cannot have come from those present in a *Limnoscelis*-like form.

Even more isolated structurally than the chelonians are the ichthyosaurs. When they first appear in mid-Triassic days, they are already extremely specialized in skull as well as postcranial skeleton. The braincase, although much modified, was built somewhat along the captorhinid pattern, with powerful paroccipital processes (tilted rather dorsally, however), a relatively narrow supraoccipital, and large posttemporal vacuities; there is no expansion of dermal elements on the occiput. As seen in lateral view there are two dermal elements in the cheek above the quadratojugal and below the single dorsally-placed temporal opening. The lower is frequently termed supratemporal but unless (improbably) a neomorph, must be a squamosal, although a singularly modest one in its degree of development. The upper element frequently (but surely erroneously) termed squamosal, appears in lateral view comparable to a supratemporal and may indeed be that element; however, it is widely developed along the upper and lateral margins of the occiput, and in its position and connections combines curiously many of the attributes of tabular and squamosal as well as supratemporal. In the features mentioned as well as many others, the ichthyosaurs have diverged markedly from the pattern of any other known reptilian type. It is possible to derive an ichthyosaur skull from that of a form of the *Limnoscelis* type, but the jump is a long one, and there are no transitional stages. We may at least comfort ourselves with the negative statement that there is, at any rate, no other known type from which derivation can be more readily made.[9]

The one type of skull found among reptiles which may possibly have been derived from a stage below that of *Limnoscelis* is found in those cotylosaurs which Watson (1914, 1917) has grouped as the Diadectomorpha—the diadectids, pareiasaurs and procolophonids. Although the three families certainly do not form a direct line of descent, we need not here question the assumption of their relationship (cf. Watson, 1914, p. 173) nor concern ourselves with the geologicaly later families[10] but shall concentrate our attention on the Diadectidae as the oldest group and as presenting the essential features of the diadectomorph type. The diadectids were in existence before the close of the Pennsylvanian and thus are among the oldest of known

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[9] Von Huene (1937) has argued for the direct descent of ichthyosaurs from embolomerous amphibians. I do not, however, feel that his evidence is at all conclusive. For example, the absence of a toothed pterygoid flange in ichthyosaurs does not argue for direct derivation from embolomeres in which the flange had not developed, for many other reptiles, from turtles to therapsids, have also lost this structure of ancestral reptiles; double-headed caudal ribs are present in such primitive reptiles as pelycosaurs as well as in embolomeres and ichthyosaurs; etc.

[10] The "advanced" type of occiput seen in pareiasaurs and *Procolophon* suggests their independent origin from cotylosaurs which may have lacked an otic notch and have been as advanced as captorhinids in braincase structure. *Milleretta* [*Millerina*] (Broom, 1938) is suggestive of a form, perhaps on the captorhinomorph level, in which a secondary notch is in process of formation, but whether leading to notched cotylosaurs or (as Broom suggests) to some diapsid group, is difficult to say. The procolophonids recently described from the Permian of Russia by Efremov (1940; cf. Watson, 1942) suggest that the exaggerated notch of that group is a late phylogenetic as well as late ontogenetic development. Certain features of the Russian procolophonids are, however, extremely puzzling, particularly the purely amphibian aspect of the occiput as figured by Efremov.

reptiles. They were then highly specialized in dentition and other cranial structures and hence may reasonably be assumed to have diverged from the reptilian stem at an extremely early stage. The diadectids appear to have been nature's first major "experiment" in the development of herbivorous tetrapods, and in connection with such a diet have evolved marked cranial specializations, including a very peculiar dentition and a shortened jaw. Behind and above the jaw is a highly developed otic notch. The quadrate is a powerful bone, set transversely in the skull; it curves backward above the margin of the notch to articulate, apparently rather freely, at its tip with a socket on the lateral surface of the paroccipital region. Watson (1914, p. 172, etc.) has pointed out that by shortening, the jaw has obtained a powerful and advantageous vertical bracing on the skull roof and braincase, not present in ancestral amphibians. He believes that the diadectids have evolved this system of support directly from a condition in which the primitive notch was still present, rather than prior to its closure in typical reptiles. In Figure 9 A, B, E, I have diagrammatically indicated the method of formation of the diadectid notch in accordance with Watson's ideas. Under this hypothesis, of course, *Limnoscelis* is too advanced a form to have been an ancestor of the diadectomorphs.

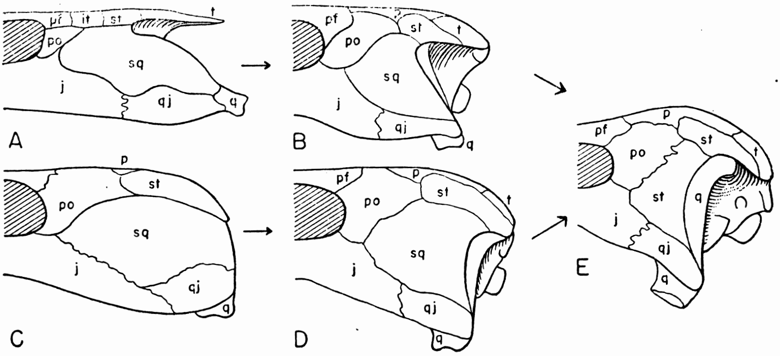

Fig. 9. Diagrams to illustrate two possible methods of formation of the type of otic notch seen in *Diadectes* (*E*). *A-B-E*, on the hypothesis that the notch is directly derived from a primitive amphibian condition, as seen in *Palaeogyrinus* (*A*). *C-D-E*, on the hypothesis that the diadectid notch is a secondary formation from the *Limnoscelis* condition (*C*). *B*, *D*, hypothetical intermediate stages.

I do not, however, feel certain that the diadectid otic notch evolved directly from that of primitive amphibians. Watson assumes that the desirability of vertical support for the jaw articulation was the evolutionary force responsible for jaw shortening. But it may be pointed out that various other reptile groups particularly herbivores, have found it mechanically advantageous to shorten the length of the jaw and move the articulation forward. In some cases, such as are clearly seen in many lizards or in various dinosaurs, the shortening has occurred subsequent to the elimination of the original otic notch and the attainment of satisfactory suspensorial support. In both lizards and dinosaurs the quadrate is powerfully developed and curves backward at its dorsal end to articulate with the postero-lateral corner of the braincase (paroccipital region), as in *Diadectes.* There is in many cases among these later reptiles a marked development of a diadectid-like notch behind the quadrate. Since structural features similar to those in diadectids can develop in forms which had long since lost the original otic notch, I see no reason why the diadectids cannot have evolved in similar fashion, as diagramatically shown in Figure 9, C, D, E.

It may be noted that diadectid skulls show a number of significant structural features not known at present below the *Limnoscelis* evolutionary stage. These include the characteristic reptilian arrangement of the postorbital, supratemporal and tabular; the seemingly significant downward curvature of the last two elements; the very solidly built occipital plate; and the associated horizontal (and very powerful) lateral expansion of this plate. We have noted in *Diadectes* the peculiar hook-shaped development of the dorsal end of the quadrate, which curves back to articulate with the end of a laterally projecting paroccipital. I find it difficult to understand, on the assumption that the diadectid notch is essentially primitive, why the quadrate and paroccipital go out of their way (so to speak) to articulate at a point far from the direct line between occiput and quadrate. It is only understandable if we assume that this condition, almost exactly duplicated in the lizards, is due to a new development of an otic notch and the retention of a quadrate-braincase connection developed at the *Limnoscelis* stage.

*Post-cranial skeleton.* The vertebral structure of *Limnoscelis* is that of a typical cotylosaur, with broadly expanded neural arches and horizontal zygapophysial surfaces. I have been reluctant to believe that this type of arch, not present in either typical labyrinthodonts, on the one hand, or more advanced reptiles on the other, was actually the ancestral reptilian structure. It seems, however, impossible to escape this conclusion. Primitive pelycosaurs, particularly *Varanosaurus* (*Poecilospondylus*) show traces of this broad-arched condition, as Watson pointed out; the mesosaurs likewise possess it, despite the many specializations of that early group. Presumably this broad-arched condition arose at some early date among seymouriamorphans or other early amphibian relatives of the reptiles.

The presacral vertebral count of 26 is a reasonable one for an ancestral reptile. Intercentra are well developed, but reduced from the condition seen in *Seymouria.* The ribs are in general of a primitive ancestral reptilian pattern, running without interruption well back into the caudal series. Somewhat as in *Seymouria* and diadectids the sacrum is transitional in development between a one-ribbed and two-ribbed condition; even among the pelycosaurs, *Ophiacodon* shows a similar structure.

The ribs, as preserved, are "holocephalous," with the heads expanded in the anterior trunk region but not subdivided into capitular and tubercular areas; here, as I believe to have been the case in ophiacodont pelycosaurs (Romer and Price 1940, pp. 110-111), it is probable that the cartilaginous proximal tip of the rib was subdivided into two parts, separated by a small notch for the vertebral artery. As in primitive reptiles generally the articular area of the rib contracts in width in the more posterior part of the trunk, the capitular articulation shifting upward and backward from the intercentrum toward and to a point on the centrum below the transverse process.

The distal portions of the ribs are, as in general in early tetrapods, expanded in the region of the shoulder girdle for the attachment of the levator and serratus anterior muscles supporting the scapular blade. I suspect that the structure described by Williston (1911a, p. 36, Fig. 11a) as a hyoid element is actually a rib of this type. The major sacral rib is a thick, broad, short, shovel-shaped structure, concave along its outer surface and applied closely to the convex inner surface of the anterior part of the iliac blade. Those of *Seymouria* on the one hand and *Ophiacodon* on the other are similarly built.

The girdles and limbs are of a general pattern expected in a primitive reptile, and in many regards they are very similar to those of the *Diadectes* group. Their massive build seems to be in part a primitive character, in part related to the fact that *Limnoscelis* is a relatively large form—a smaller relative would presumably have a more slender limb structure.

The ossification of the limb bones is, as Williston notes, very imperfect. There were obviously large unossified areas on the ends of the limb bones, and many of the carpal and tarsal elements appear to have been completely cartilaginous in nature. Since all three of the Yale specimens are of approximately the same size, it is reasonable to believe that they represent adult individuals. In consequence this lack of ossification cannot be attributed to immaturity. It seems certainly indicative, as in the case of other reptiles, of aquatic habits.

In the dermal shoulder girdle the interclavicle and clavicle are of a nature expected in a primitive reptile. The bifurcation of the lower end of the clavicle as illustrated by Williston appears to be present on both clavicles of the type (the only known examples of this bone), and is suggestive of the contours seen here in *Diadectes* (cf. Case 1911, Fig. 26, *a*) in which, however, clavicle and interclavicle are firmly united. The cleithrum is represented by only a vertical strip of bone lying along the anterior margin of the scapula, and lacks the expansion capping the scapula in *Diadectes* and, apparently, in early labyrinthodonts generally (as *Eryops*, *Dendrerpeton*, etc., among the rhachitomes, *Archeria* ["*Cricotus*"] among embolomeres). It is, however, as highly developed as in any more "advanced" reptiles, in which the bone is seldom more than a splint and seldom present at all beyond the early Permian. It may be noted that in the seymouriamorphs, the cleithrum also lacks any marked dorsal expansion.

The development of this portion of the cleithrum appears to be intimately associated with the degree of ossification of the scapular blade. In forms with a capping cleithrum the scapula is generally found to be fully ossified up to a definitive upper margin in contact with the cleithral cap. Presumably in ontogeny upward ossification of the cleithral membrane is synchronous with ossification in the scapular cartilage. One may reasonably assume that if in phylogeny ossification of the upper end of the scapular blade is retarded or abandoned, the cleithrum also tends to restrict its ossification in correlated fashion.

The scapulo-coracoid is of primitive build. The scapular blade is short, but was presumably continued above in cartilage. Williston described the inner opening of a supposed glenoid foramen. As he points out, the retention of this glenoid foramen is a primitive amphibian feature unknown in other reptiles except the diadectids.[11] The supracoracoid foramen is unusually large and opens outward posteriorly rather than laterally and close beneath the glenoid—a primitive, essentially amphibian condition. A vertical fissure in the coracoid plate is interpreted by Williston as a suture between two coracoid elements. If this interpretation is correct, we have here one of the few advanced or specialized features in *Limnoscelis*.

The history of the coracoid elements in early tetrapods needs further clarification. In most fossil amphibians, including embolomeres, there is no evidence of any separate coracoid ossification, but since a separate coracoid is found both in frogs and the quite unrelated nectridian *Diplocaulus*, it may have been present in some early forms, and a coracoid ossification is present in *Seymouria*. In typical Mesozoic and Recent reptiles there is never more than one coracoid, and hence it has been reasonably assumed that a single coracoid was a primitive reptilian condition. Two coracoids are present in the synapsids, but this might be readily assumed to be a secondary condition. Among cotylosaurs, the diadectids appear to have but a single coracoid. But two coracoids are apparently present in all other members of the order—captorhinids, pareiasaurs, procolophonids.

Williston has adequately figured the humerus. Its general build is the tetrahedral type found in almost all early tetrapods with short but stout limbs; it can be closely compared with the humeri of *Seymouria*, on the one hand, and *Diadectes* on the other. There is no development of a shaft region. The presence of an entepicondylar foramen, once thought to be a reptilian feature, is no longer diagnostic, since it is now known in various early amphibians, including not only *Seymouria*, but "*Cricotus*," *Dendrerpeton*, and *Diplocaulus*.[12] The various processes—deltopectoral, supinator, ectepicondylar, entepicon-

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[11] But compare the discussion by White, 1939, pp. 364–366, of nutrient foramina in this position.

[12] Although embolomeres are surely related to the reptilian ancestors, the *Archeria* ("*Cricotus*") humerus shows little resemblance to the reptilian type except for the presence of this foramen.

dylar—are those presumably primitive in tetrapods, since they are present in fairly similar fashion in both redbeds reptiles and forms as far removed from their pedigree as *Eryops*. The high degree of development of the ectepicondyle and its marked projection dorsally from the distal surface of the bone are features in which (as Williston notes) the bone is primitive in nature, and not comparable to that in other reptiles except diadectids. *Seymouria* compares here with *Limnoscelis*. In the absence of a shaft region, the supinator crest is separated by only a notch from the deltopectoral crest; among reptiles only the diadectids are comparable in the retention of this amphibian-like feature.

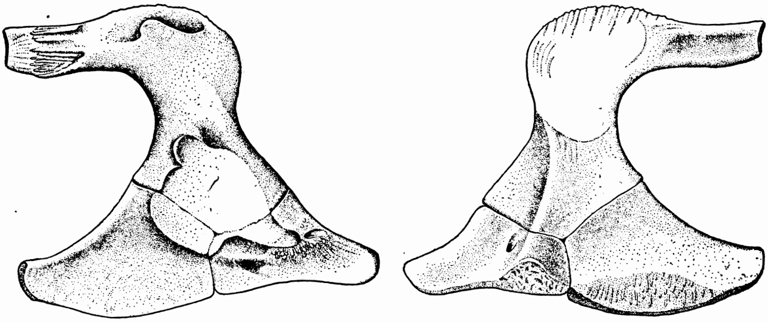

Fig. 10. Pelvis of *Limnoscelis*, right side. *Left*, external view; *right*, internal surface. Composite, approximately ¼ natural size.

The carpus is incompletely preserved and was apparently poorly ossified. As far as it is known, it seems to have been of a type expected in a primitive reptile. The presence of a pisiforme is presumably a reptilian feature.

The metacarpals and phalanges are short and broad, with flattened rather than compressed terminal members, and with the reptilian formula of 2-3-4-5-3—all features found in diadectids, and in *Seymouria* as well. In *Limnoscelis*, as in diadectids but not, apparently in *Seymouria*, toe V is relatively slender and probably set off at an angle from the other digits—a reptilian characteristic.

Pelvic material available to Williston included that of the type specimen and that with No. 809. Further material associated with No. 819, while fragmentary, reveals much significant detail and makes further description and illustration desirable (Fig. 10). The pelvis shows features of a primitive reptilian type. It is comparable in various respects to those found in embolomeres and seymouriamorphans, diadectids, captorhinids and ophiacodontoid pelycosaurs.

The ilium retains the long posterior extension seen in many early amphibians; this was cartilage-tipped and strongly rugose in connection with attachment of caudal tendons and ligaments. The anterior portion of the iliac blade is moderately expanded in the fashion of *Seymouria* and of primitive reptiles in general. I have discussed on various occasions (1922, pp. 559-560; Romer and Price 1940, pp. 126-127, etc.) the process of rotation and in-turning of the upper part of the iliac blade in the development of reptiles. *Limnoscelis*, like *Diadectes* shows an early stage in this process. The type specimen clearly shows the development on the anterior part of the blade of a pocket bounded laterally by a thin, vertical flange of bone. The ilium is comparable to that of *Ophiacodon* (cf. Romer and Price 1940, Fig. 49) except that in that pelycosaur the dorsal pocket faces more medially than in *Limnoscelis* and the flange lateral to it has developed so that its dorsal margin now forms the new definitive dorsal margin of the blade. *Seymouria* is here definitely more primitive for there is no indication of flange development. The inner surface of the iliac blade, somewhat convex in section, shows markings clearly indicating the close application to it of the large sacral rib. The posterior part of the blade is concave externally in vertical section.

The acetabular region in every regard shows a primitive pattern common to most early Permian reptiles and amphibians. The pubis is markedly out-turned anteriorly at its dorsal margin, so that the lateral surface faces strongly downward. Close to the acetabulum the bone is very rugose for muscular or tendinous attachments; there is, however, no indication in the material of the strong lateral process seen particularly in such primitive ophiacodonts as *Clepsydrops* and *Varanosaurus* or in the lizards.

As in primitive tetrapods generally the anterior portion of the internal aspect of the girdle, including much of the pubic region and the adjacent portion of the ilium, forms a triangular surface, its apex on the ilium, its base situated ventrally; this surface faces as much anteriorly as medially and was presumably covered in life by limb muscle origins (puboischio-femoralis internus). This surface is slightly concave, and is pierced by the internal opening of the obturator foramen. In contemporary rhachitomous amphibians the pubis is greatly thickened beneath this area; in *Limnoscelis*, however, due to the fact, noted above, that the lateral pubic face turns sharply inward, the bone here is of modest thickness. Comparable conditions are seen in this region in forms as far apart as the embolomere *Archeria* and *Seymouria* on the one hand, and *Diadectes*, captorhinids and ophiacodontoid pelycosaurs on the other.

The triangular internal surface just described is bounded posteriorly by a marked ridge descending along the inner margin of the ilium onto the posterior part of the pubis. Posterior to this line the inner surface of the girdle was presumably close to the wall of the body cavity (except for the presumed presence of a small ischiotrochanteric muscle at the back margin).

The pelvic symphysis was thin in its most anterior portion; opposite the posterior end of the specialized pubic triangle described above and the ridge descending at this point, the symphysis was greatly thickened and, from the "unfinished" appearance of the surface here, the union was effected by a layer of cartilage. The ischia met each other at a sharp angle and their symphysis was rather deep. The union, however, was apparently a relatively loose one, for the bone has a finished surface; there are numerous vertical striations and ridges which appear to have been apposed to similar structures on the element opposite.

The type of symphysis seen here is foreshadowed to some extent by that seen in *Archeria* and *Seymouria*; a generally comparable structure is present in diadectids, captorhinids and ophiacodontoid cotylosaurs.

The femur is of a structural pattern common to all stout-limbed early tetrapods and can be compared in many respects to the femur of various contemporary amphibians and reptiles. The region of the fourth trochanter is greatly elevated; much more so than in any other early reptiles with which I am familiar, although certain edaphosauroid pelycosaurs are fairly comparable; *Eryops* shows a somewhat similar development among contemporary amphibians. The ridge running distally from the fourth trochanter leads to the ventral surface of the internal condyle. This is a feature common to many early reptiles, and may be seen, for example in nearly all the pelycosaur femora (except advanced sphenacodonts) figured by

Romer and Price (1940, Figs. 36, 37). It is not characteristic of rhachitomes, but is found in the embolomere *Archeria* and in *Seymouria*. A readily recognizable feature of the *Limnoscelis* femur is the way in which the fourth trochanter and the ridges leading to it are seen to be turned sharply forward when the bone is viewed ventrally. This is well shown in Williston's figure (1912, Fig. 6). *Seymouria* is highly comparable in this regard (although the orientation of the figure by White 1939, p. 383 is not such as to make this apparent). In other points, as well, the *Seymouria* femur represents the closest known approach to the *Limnoscelis* pattern.

In the tarsus, as in the carpus, imperfect ossification restricts our knowledge of the structure present. As Williston notes, in all three specimens which have the hind leg present, there are two proximal tarsals preserved, and in two of the three cases two small elements, more distal in position and uncertain as to nature, were present. It is obvious that we are dealing with a reptilian rather than an amphibian type of tarsus, and one in strong contrast with that described in *Seymouria* by Watson (1919, pp. 282-284) and White (1939, pp. 384-386). In *Seymouria* three elements are apparently present in the proximal row, including a well developed tibiale; the intermedium is a thin structure which can have had little to do with support of the tibia. In *Limnoscelis* a cartilaginous tibiale may have been present[13] but the two major elements were obviously those preserved—the intermedium (astragalus) and fibulare (calcaneum). The former has a prominent convex rolling surface on its lateral margin which surely bore, as in later reptiles, the main support for the tibia. Despite the cartilaginous nature of their margins, astragalus and calcaneum show distinct evidence of the usual vascular notch between their apposed surfaces.[14]

The pes is comparable in nature and stage of development to the manus; the reptilian formula of 2-3-4-5-4 is present; as usual in early reptiles the pes is moderately larger than the manus. There is no evidence of the reduction of the lateral margin of the pes seen in diadectids.

As indicated by various points in the discussion above, the

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[13] Schaeffer (1941, p. 429) states that three proximal tarsals were present. This, however, is an assumption based on the fact that the lower end of the tibia is very broad.

[14] Structural features of the tarsals are poorly represented in Williston's earlier figure of the limb, and are better seen in figures 19 to 21 of his 1912 paper.

postcranial skeleton of *Limnoscelis* is exceedingly close to the ideal condition which might have been erected for a hypothetical stem reptile. The skeleton is in almost every respect primitive and generalized. This conclusion is strongly supported by the closely comparable structures seen in the diadectids, despite the cranial and dental specializations characteristic of that group. There are few noteworthy differences between *Limnoscelis* and diadectids apart from the skull. The diadectids show a few advanced or aberrant features such as additional vertebral articulations, a slightly more advanced iliac blade, a somewhat reduced femoral trochanteric system, and a few peculiarities in foot structure. *Limnoscelis* is more primitive in these regards and shows (apart from the lack of a cleithral cap in the known material) no specialized features to debar it structurally from morphological ancestry to the diadectid type.

Various comparisons made above have further indicated that *Limnoscelis* can be readily regarded as antecedent in postcranial structures to the captorhinid cotylosaurs and to the synapsid mammal stock. The captorhinid limb and girdle skeleton is somewhat more advanced structurally than that of *Limnoscelis* and the relatively small size of captorhinids is correlated with a relatively slender build of their limbs, but basic changes are few. Among the advanced synapsids—therapsids or even progressive pelycosaurs—we find a postcranial skeleton quite different in nature from that of *Limnoscelis*. But as we descend the synapsid series to primitive pelycosaurs of the ophiacodontoid group, we bridge nearly the whole gap. So similar in postcranial structure to *Limnoscelis* are members of the *Clepsydrops-Varanosaurus-Ophiacodon* type that did we not know the skull of *Limnoscelis* we would probably have placed its skeleton among the ophiacodontoids although recognizing its more primitive position.

It must be emphasized that immediate recognition of resemblances between *Limnoscelis* and captorhinomorphs and pelycosaurs by no means implies that *Limnoscelis* is more closely related to the ancestry of these forms than to other reptiles. Time and size are factors which enter into the comparison. As may be readily seen in the series from *Limnoscelis* through the pelycosaurs to the therapsids, there tends to be a constant change in skeletal structures in the course of early reptilian evolution. The skeleton of an advanced Triassic therapsid shows no great similarity to that of *Limnoscelis*; did we not know the stages intermediate in time and phylogeney, we would not realize the close relationship of the postcranial skeleton of *Limnoscelis* to that evolved in the synapsids. The early Permian reptile fauna consisted almost entirely of cotylosaurs and pelycosaurs; there are few or no remains of recognized members of other major reptilian groups—lepidosaurs, archosaurs, synaptosaurs, chelonians, ichthyosaurs. By the time that these groups first come clearly into the paleontological picture, in the Triassic, so much evolutionary progress had occurred that their axial and appendicular skeletons are not at all closely comparable to those of such an archaic type as *Limnoscelis*. There are, however, no reasons to believe that the skeletal structures present in these later groups have not passed through a *Limnoscelis*-like stage.

With regard to the antecedents of the *Limnoscelis* skeleton, we have noted above many points of comparison between *Limnoscelis* and various amphibian types. There are numerous general structural features and even details of girdle construction quite comparable to those of rhachitomous forms such as *Eryops*. Since it seems certain that the rhachitomes are far removed from reptilian ancestry, many of these features may be assumed (despite the possibility of parallelism) to be common inheritances from early tetrapods. The embolomeres are generally believed to be close to the ancestry of the reptiles. Unfortunately there is little published data on the postcranial skeleton of embolomeres. I hope to publish at another time a description of the postcranial skeleton of *Archeria* ["*Cricotus*"], a genus apparently closely related to *Eogyrinus* (as described by Watson). There are few evidences in the postcranial skeleton of this genus of any particularly close affinity to reptiles; it must be noted however that *Archeria* is a late, very probably specialized, and possibly degenerate embolomere.

The one close approach to *Limnoscelis* postcranial structures seen among any group here regarded as amphibian is in the seymouriamorphans, of which *Seymouria* is best known. Certain of the resemblances, such as the possession of an entepicondylar foramen, may be regarded as the retention in seymourians and reptiles of features present in primitive tetrapods but lost in more typical amphibians. Common features, however, are so numerous that many of them are presumably to be considered as advanced characters attained along a common line of descent. These include, for example, the presence of a long-stemmed interclavicle (absent in other known labyrinthodonts), great similarity in many features of girdle construction; practical identity in major limb elements; presence in seymourians of a five-toed manus and (in *Seymouria*) of a reptilian phalangeal formula; and most especially, the presence in this group of a type of vertebra—with broad, convex neural arches, complete centrum and "reduced" intercentrum—quite unknown in any other amphibian group. The Seymouriamorpha may not have attained the reptilian grade of organization and (as shown by the skull) *Seymouria* may lie off of the line leading to reptiles, but the group is certainly very close to reptilian ancestry.

*Discussion.* We have described above various features of the skull and skeleton of *Limnoscelis* and compared this genus morphologically with amphibian and other reptilian types. In postcranial structure it is highly comparable to seymouriamorphans, and shows relatively little advance over members of that reptile-like amphibian group; in its skull structure, however, it shows features which are characteristic of reptiles; features to which those exhibited in known seymourians are not antecedent. Its anatomy, both cranial and postcranial, is definitely reptilian, but so generalized that *Limnoscelis* can be regarded as a structural ancestor of later major groups within that class.

The time factor, however, indicates that *Limnoscelis* cannot lie precisely at the base of the reptilian phylogenetic tree. The El Cobre beds may well be uppermost Pennsylvanian rather than lower Permian. But, even so, reptilian diversification was already under way at that time; these very beds contain remains of several pelycosaurs, and specialized diadectids are known from deposits at least as early. *Limnoscelis*, despite its primitive character, was then a relict type, presumably a little modified descendant of the actual reptile ancestor of earlier Pennsylvanian days. As noted earlier a few forms of that age may possibly be limnoscelids, but the remains are inadequate.

We know of no Carboniferous amphibian which can be considered a satisfactory ancestor for such a stem reptile as *Limnoscelis*. As indicated by various comparisons in earlier sections, the seymouriamorphans are satisfactory as regards almost every postcranial feature and they, together with the related embolomeres, represent the closest amphibian approach to the *Limnoscelis* skull type. In no known member of the Seymouriamorpha, however, do we find a construction of the post-orbital region of the skull roof of such a nature that the limnoscelid structure could have been readily derived from it. To be desired as an amphibian ancestor of the reptiles is a form built on the general seymouriamorphan pattern, but with the intertemporal absent, the supratemporal posteriorly placed and the otic notch of modest size and of the embolomere type.

The three skeletons of *Limnoscelis* are of approximately the same size and hence presumably represent reasonably mature animals. Despite this, the skeleton is poorly ossified. Carpus and tarsus remained largely unossified; the long bones were obviously capped by considerable masses of cartilage. Here, as in other cases among lower tetrapods, this condition may be reasonably interpreted as indicating an aquatic mode of life. Williston recognized this, but, because of the rather stout limbs and the nonpiscivorous dentition was inclined to believe that *Limnoscelis* spent but part of its life in the water, and (as implied in the name) to class it as a marsh-dweller. We may point out, however, that, as testified by crocodilians and phytosaurs, well-developed limbs are no bar to successful aquatic life and note that the wealth of contemporary amphibians gave good scope to a carnivorous water dweller.

We have elsewhere (Romer and Price 1940, pp. 173-174, 199, etc.) commented on the fact that the oldest and most primitive pelycosaurs show even more conclusive evidence of aquatic habits, and that it seems likely that this was a retention of the ancestral amphibian mode of life rather than a return to water from land. The evidence of *Limnoscelis* combined with that of the pelycosaurs suggests that the earliest reptiles were still essentially aquatic animals, as had been their amphibian ancestors.

It is usually assumed that the development of the amniote egg occurred subsequent to the assumption of a terrestrial existence by the early reptiles and that this development was the final step in their emancipation from the water. Although I shall not develop the point further on this occasion, the evidence cited above suggests that this may have been the reverse of the true situation, and that the reptile egg preceded the adult in its adaptation to purely terrestrial conditions.

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