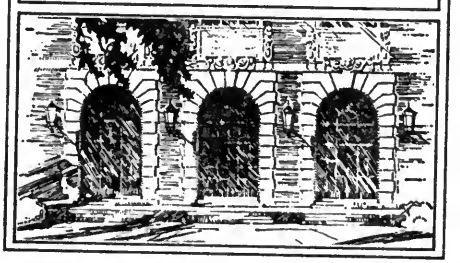

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The Triassic Reptile, *Poposaurus*

EDWIN H. COLBERT

CHAIRMAN, DEPARTMENT OF VERTEBRATE PALEONTOLOGY
THE AMERICAN MUSEUM OF NATURAL HISTORY

INTRODUCTION

The genus *Poposaurus* has for many years been something of an enigma to students of fossil reptiles, a situation that is largely a result of the inadequacy of known materials. At the present time the literature concerning this genus is based upon the single type specimen, which consists of some vertebrae, limb bones and part of a pelvis. The separate bones of the type seem, for the most part, to be fairly definitive, but the sum of the evidence from all of them is rather conflicting. Therefore it is not surprising that published remarks as to the relationships of *Poposaurus* show considerable differences of opinions, with the result that the systematic position of the genus is at the present time undecided.

Poposaurus, fragmentary as the remains may be, is important because it has been commonly regarded as an ornithischian dinosaur of undoubted Triassic age. Whatever may be the taxonomic relationships of this fossil, there certainly is no doubt as to its stratigraphic position; the type was found in the Upper Triassic Popo Agie beds of Wyoming. The genus was named by Mehl (1915b) in a brief description. At that time Mehl did not attempt to make a definitive statement as to the relationships of *Poposaurus*, although he did say that "in some respects it resembles some of the early dinosaurs." He then suggested that *Poposaurus* might be related to *Palaeoctonus*, a genus based upon very fragmentary remains from the Newark beds of eastern North America. It need only be said at this place that *Palaeoctonus*, so far as can be determined upon the basis of known fossils, is probably a phytosaur. Mehl (1915b, p. 522) went on to say that "Everything in the structure of the form so far studied indicates a well-muscled creature light in weight, possibly bipedal in gait occasionally, and most assuredly swift in movement."

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During the years since *Poposaurus* was first described by Mehl various authorities have given some attention to this genus and have tried to place it within the system of reptilian classification. The varying opinions expressed by these authors are summarized below.

In 1921 Nopcsa published a short note devoted to the systematic position of *Poposaurus*. He reviewed the diagnostic characters of the genus as presented by Mehl, and came to the conclusion that *Poposaurus* should be regarded as a primitive orthopod, and should be placed taxonomically among the iguanodonts or the camptosaurs. Thus Nopcsa was the first author definitely to suggest dinosaurian relationships for *Poposaurus*.

A few years later Nopcsa (1928) expressed this view as to the relationships of *Poposaurus* in a formal fashion. He made *Poposaurus* the representative of a new suborder, the Poposauroidea, one of three suborders that constituted his order Orthopoda. (The Orthopoda, as delineated by Nopcsa, is the equivalent of the order generally designated in the literature as the Ornithischia.) Nopcsa defined his suborder Poposauroidea as follows: "Incompletely known; vertebrae biplane; anterior part of ilium expanded downward; bipedal." He recognized within this suborder one family having the same definition as that for the larger taxonomic group.

In Hay's (1930) bibliography of the fossil vertebrates, *Poposaurus* was classified as a theropod dinosaur and placed in the family Anchisauridae. Because of the nature of this publication, no reasons could be given for such an allocation of the genus.

Oskar Kuhn (1937), in his classification of the fossil reptiles, followed the precedent set by Nopcsa ten years earlier by placing *Poposaurus* in a family of its own, within a separate suborder which he called the Poposauria. For the suborder he gave a brief diagnosis which was essentially a paraphrased copy of Nopcsa's earlier diagnosis.

In 1950 von Huene published a paper in which he considered the evidence for the presence of these dinosaurs in rocks of Triassic age. The paper is concerned primarily with tracks discovered in Argentina as indicative of the presence of ornithischians during Triassic times, but in passing he mentions *Poposaurus* as being one of the two genera of supposed ornithischians from the Triassic known from the bones.[1] In this paper he states that *Poposaurus* is "probably" a primitive stegosaurid, but he presents no evidence to uphold this opinion.

[1] In addition to *Poposaurus*, the other supposed Triassic ornithischian dinosaur that has been described is *Geranosaurus*, a South African form. Of the two genera, *Poposaurus* is based upon much the best and most definitive materials.

Finally, within the past few years three important works have appeared, in which the taxonomic relationships of *Poposaurus* are considered. In the first of these, the monumental *Traité de Paléontologie,* edited by Jean Piveteau, the authors of the chapter on dinosaurs, namely Messrs. de Lapparent and Lavocat (1955, p. 795), indicate that *Poposaurus* is a primitive member of the superfamily Iguanodontoidea within the Ornithischia, but they actually do not assign it to a definite position among any of the iguanodont families that they list, perhaps because they are seemingly doubtful as to the value of the evidence. They do say that "*Poposaurus* du Trias inférieur, [*sic*] animal bipède, paraîtrait, en effet, avoir réalisé déjà certaines structures du bassin des Avipelviens." Farther on in this same work (pp. 829–830) they make the following remarks: "Ceux [the ornithopods] qu'on aurait signalés dans le Trias (Huene, 1950) paraissent douteux d'après les documents actuels. Ils ne reposent en effet que sur les éléments suivants:

"1. Pièces du squelette: une petite mandibule, *Geranosaurus* Broom 1911, du Trias supérieur d'Afrique du Sud; ilion, fémur et tibia, *Poposaurus* Mehl 1915, du Trias supérieur du Wyoming.

"2. Empreintes de pas: *Anomoepus* Hitchcock, du Trias de la Connecticut Valley; *Rigalites* Huene 1931, du 'Rhétien' d'Argentine. L'attribution de ces empreintes á un Ornithopode demeure possible, mais non certaine."

In the second of the three recent publications, von Huene (1956, p. 556) seemed rather definite as to the taxonomic position of *Poposaurus,* for he regarded it as a member of the family Stegosauridae. In making this assignment, von Huene was reiterating his earlier opinion, expressed in 1950.

In the third of these recent works Romer (1956) presents a very complete and well-considered classification of reptiles down to genera. He does not discuss *Poposaurus,* but in his classification he includes it among the phytosaurs as a synonym of the genus *Lophoprosopus.* Whatever *Poposaurus* may be, it almost certainly is not a phytosaur.

To summarize this discussion, the various opinions as to the relationships of *Poposaurus* may be listed as follows:

Mehl, 1915. "Resembles some of the early dinosaurs."
Nopcsa, 1921. Primitive orthopod.
Nopcsa, 1928. Order Orthopoda; Suborder Poposauroidea; Family Poposauridae.
Hay, 1930. Order Saurischia; Suborder Theropoda; Family Anchisauridae.
Kuhn, 1937. Order Ornithischia; Suborder Poposauria; Family Poposauridae.
von Huene, 1950. Probably a primitive stegosaurid.

de Lapparent and Lavocat, 1955. "Ordre des Avipelviens; Sous-ordre des Orthopodes; Super-famille des Iguanodontoïdés (Ornithopodes)."

von Huene, 1956. Order Ornithischia; Suborder Thyreophora; Family Stegosauridae.

Romer, 1956. Order Thecodontia; Suborder Parasuchia; Family Phytosauridae.

In view of these differing opinions as to the relationships of *Poposaurus*, it is hereby proposed to make a new study of the original materials, to see if a more satisfactory basis can be reached for the classification of this genus. For permission to do this I am greatly indebted to the authorities of Chicago Natural History Museum, and particularly to Drs. Rainer Zangerl and Everett C. Olson, and to Mr. David Techter. Grateful acknowledgments should also be made to Dr. Claude Hibbard of the University of Michigan, for permission to study materials in the collection of the University Museum of Paleontology.

A NEW DESCRIPTION AND AN ANALYSIS OF *POPOSAURUS GRACILIS* MEHL

As it now exists, the type of *Poposaurus gracilis* Mehl consists of the following materials: Chicago Natural History Museum, no. UR 357, two dorsal vertebrae, one caudal vertebra, a left ilium, the proximal portion of a left femur, a right femur, the distal portion of the left tibia, part of the shaft of the right tibia.

In addition to these bones, Mehl mentions in his original description four or possibly five sacral vertebrae, which unfortunately can not be found at the present time. Also, he speaks of two caudal vertebrae, but in the material now available there is only one caudal. Finally, he figures a tibia (labeled in his drawing as the fibula) consisting of two parts, of which at the present time only the distal section is among the type materials.

To confuse the situation still further, there is associated with the type the acetabular portion of a second right ilium, bearing the number UR 358. This is the ilium figured by Lees (1907) in the description of *Paleorhinus bransoni*. The skull of *Paleorhinus bransoni* is numbered CNHM–UC 632.

All of the materials registered under these two numbers, UR 357 and UR 358, presumably were found at a single locality along the Little Popo Agie River, near Lander, in Fremont County, Wyoming. The horizon is the Popo Agie member of the Chugwater formation, of late Triassic age.

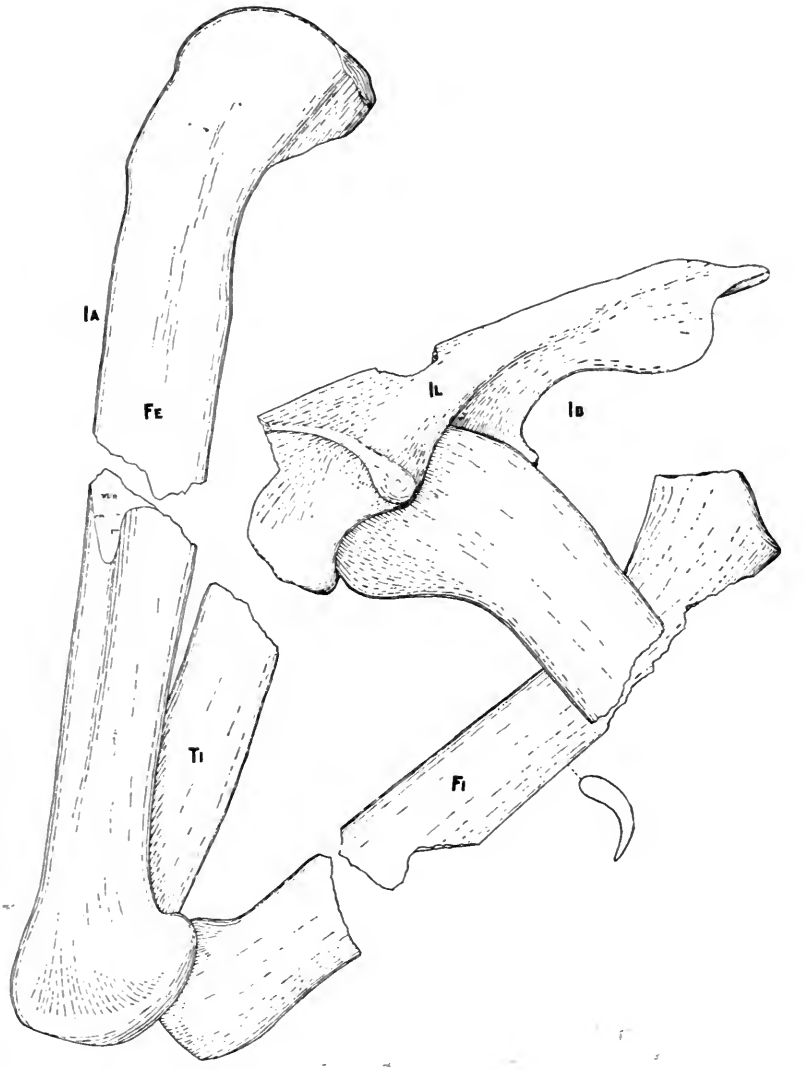

FIG. 30. An original figure of *Poposaurus gracilis* (from Mehl, 1915b). It is here maintained that (a), the femur, the tibia and the bone designated in the original description as a fibula should be identified as of the *right* side, and (b), the ilium and the proximal end of a femur should be assigned to the *left* side. About one-third natural size.

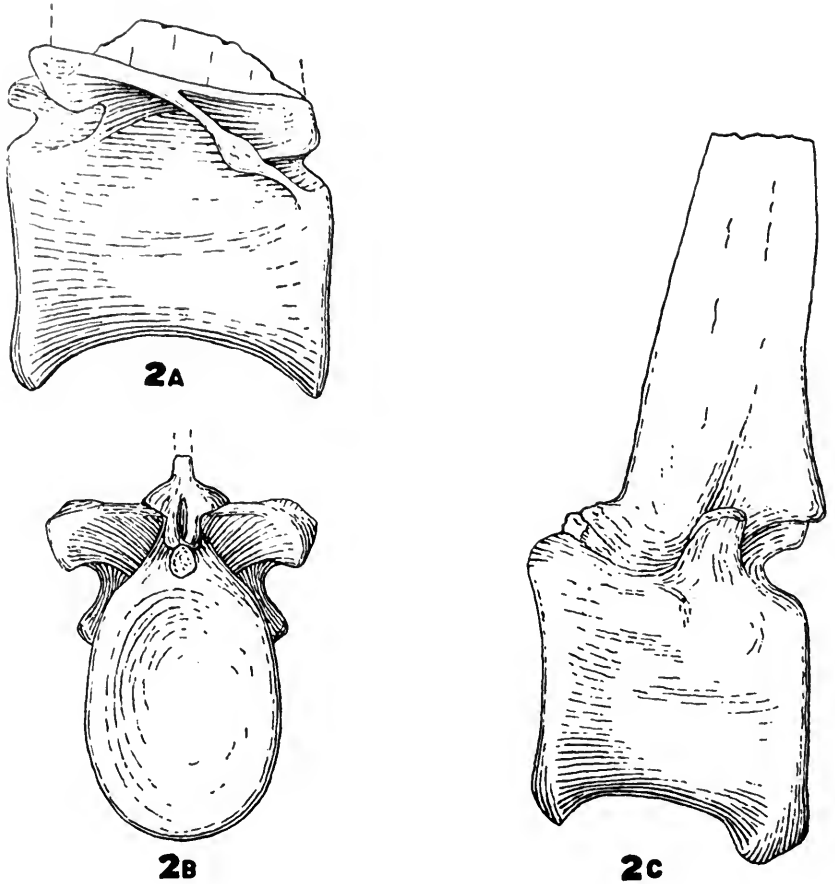

FIG. 31. An original figure of *Poposaurus gracilis* (from Mehl, 1915b). In this figure the spine of the caudal vertebra, as originally preserved, is shown. Slightly smaller than natural size.

THE VERTEBRAE

Mehl's original description of the vertebrae is very complete and accurate. Indeed, some parts of his description constitute the only evidence we have now as to certain features of the structure of the vertebrae in *Poposaurus*, because there has obviously been some breakage of the specimens since the time he described them, with a resultant loss of parts. For example, the posterior zygapophyses of the dorsal vertebra figured by Mehl have since disappeared, and much of the spine of the caudal that he figured is now gone. For easy reference it is here proposed to redescribe the vertebrae, as well

as the other extant parts of the skeleton, thus facilitating the comparisons with which this paper is particularly concerned.

The two dorsal vertebrae (fig. 32) are somewhat elongated, the single remaining caudal somewhat less so. In all of these vertebrae the faces of the centra are considerably deeper than they are broad, somewhat concave, and in all of them the bodies of the centra are greatly constricted in their mid-portion. This is particularly apparent in the two dorsal vertebrae, which thereby somewhat resemble thecodont vertebrae. It is likely that the effect is exaggerated by lateral crushing.

The neural arch is rather high, and in the dorsal vertebrae the diapophysis is a thin, horizontal plate. According to Mehl (1915b, p. 518), the diapophysis "suddenly thickens below [at its posterior extremity] for the tubercular facet which is separated from the posterior zygapophysis by a deep, rounded sinus." Because of the breakage, alluded to above, this point cannot now be verified. The diapophysis is supported, as Mehl pointed out, by two thin laminae, obliquely directed, diverging from the middle portion of its ventral surface toward the anterior and posterior faces of the centrum. The posteriorly directed lamina ends before reaching the edge of the articular face, but the anterior one runs into a large, thickened protuberance, which carries the capitular facet for the rib. The zygapophyses are close together, the anterior ones facing up and inwardly, the posterior ones obviously down and outwardly. The two anterior zygapophyses of the dorsal vertebra are separated by a narrow gap, which Mehl thought might have accommodated a thin, vertical bony supporting plate, beneath the posterior zygapophyses of the preceding vertebra. In this supposition Mehl was probably mistaken. The narrow gap between the anterior zygapophyses of this vertebra can be compared with the generally broad space between these two facets in most vertebrae. In *Poposaurus* the narrowness of the gap is largely artificial, the result of the transverse crushing to which the vertebra has been subjected.

The caudal vertebra (figs. 31, 32) is somewhat heavier and shorter than the two dorsal vertebrae. It has a rather short, posteriorly placed diapophysis that projects upwardly and laterally from the side of the neural arch. This vertebra originally had a high spine, most of which is now missing. The lower edges of the articular faces on the centrum show facets for chevrons.

The vertebrae of *Poposaurus* show various features that are seen in the vertebrae of primitive dinosaurs. The rather elongated, spool-

FIG. 32. The three type vertebrae of *Poposaurus gracilis* as now preserved; CNHM no. UR 357. A and B, two dorsal vertebrae; C, caudal vertebra. Lateral views, approximately two-thirds natural size.

shaped centra, biconcave at the ends and with constricted mid-portions, are very much like the centra of the early theropods found generally in beds of late Triassic age.

In *Camptosaurus* and *Hypsilophodon*, primitive ornithopods, the dorsal vertebrae are elongated and have concave central faces, but in the middle portions of the centra they show no such constrictions as are seen in *Poposaurus* and in the early theropods.

Another character in which the vertebrae of *Poposaurus* may be compared closely with those of the early theropods is the presence in the dorsal vertebrae of oblique laminae beneath the diapophysis. This feature, so prominent in the Popo Agie specimen, is quite pro-

nounced in all but the most posterior dorsals of the central theropod type, *Coelophysis*, and in the prosauropod, *Plateosaurus*. In contrast, no such laminae or buttresses are to be seen in the primitive ornithopods, *Camptosaurus* and *Hypsilophodon*, or in any of the other early ornithopods for that matter. Neither are they present in the phytosaurs nor generally in the pseudosuchian thecodonts.

The single known caudal vertebra of *Poposaurus* (fig. 32), which is not as elongated from front to back as the dorsals, lacks the oblique laminae or buttresses that are so characteristic of the dorsal vertebrae. The centrum of this vertebra is heavy as compared to the centrum in the dorsals, and is less constricted. These are real differences and are not to be attributed to differential crushing.

In the light of the above comparisons it would appear that the vertebrae of *Poposaurus*, especially the dorsal vertebrae, show close affinities with comparable vertebrae in the primitive theropod dinosaurs. Whether this means that *Poposaurus* should be included among the theropods is not as definite as might be inferred from the anatomy of the vertebrae, because there is now good evidence (as yet unpublished) to indicate that in some of the late Triassic thecodont reptiles the vertebrae had already advanced very far toward the theropod condition, even though the limbs and girdles had retained characteristic thecodont features. The problem as to the relationships of *Poposaurus* must necessarily rest upon all of the known evidence, not only on that of the vertebrae.

THE ILIUM

The ilium of *Poposaurus* (fig. 33) is a very distinctive bone, and at first glance one would suppose that it might give an immediate clue as to the relationships of this Triassic reptilian genus. The trouble is that the ilium, as represented by the almost complete bone described by Mehl, and in addition by the partial specimen which was not included in the type description but which nevertheless would seem to have been found with or near the type, is rather different from any other known reptilian ilium of Triassic age, or of later age for that matter. Therefore comparisons are difficult.

It should be pointed out at the beginning that the interpretation of the ilium in *Poposaurus* has been complicated through the years by an initial misconception as to its position. Mehl described this bone as a right ilium, supposing the long iliac blade to be a preacetabular portion. This in turn led subsequent authors to compare the blade of the ilium in *Poposaurus* with the elongated preacetabular

portion of the ilium characteristic of many ornithischian dinosaurs; indeed, the general tendency to place *Poposaurus* among the Ornithischia may be attributed in large part to the identification of the ilium as belonging to the right side of the pelvis.

It is here maintained that the ilium of *Poposaurus* belongs to the left side of the pelvis. According to this interpretation the long blade becomes postacetabular, homologous with the postacetabular part of the ilium as seen in various archosaurians, among them the theropod saurischians. The preacetabular part of the ilium, according to this view, is quite short, as is frequent in primitive archosaurians, including again the theropods.

There are various reasons for thinking that the ilium of *Poposaurus* comes from the left rather than the right side of the pelvis. For example, there is a definite rugosity along the medial surface of the long iliac blade, indicating an articulation with the sacrum. Such an attachment would be found only on a postacetabular iliac blade in the archosaurian reptiles; a preacetabular blade would be largely free, as indeed it is in the theropods, in which the preacetabular section is short, and as it is in the various ornithischians, in many of which this part of the pelvis is long. Again, of the two articulations on the dinosaurian ilium, one for the pubis and one for the ischium, the latter is commonly strongly convex, almost hemispherical in shape. In *Poposaurus* an articular surface of this type is beneath the long iliac blade, which is presumptive evidence that the blade is a posterior blade, and hence that this is the left ilium.

Finally there is the evidence of the femur. The proximal portion of the femur that articulates with the type ilium is clearly that of a left one. Its form is somewhat obscured by crushing, but the opposite femur is in good shape and it is clearly a right femur not a left one as indicated by Mehl. This is shown by the configuration of the proximal portion of this latter bone, which corresponds in every way with the same section of a right femur of a phytosaur and of a theropod dinosaur.

To return to the description, it may be helpful to consider the bone empirically, without reference to the ilia of other reptiles. It is an unusually elongated and rather low ilium, its anteroposterior measurement about 250 millimeters, its height approximately 80 millimeters. These proportions can be considered as approximately correct, for the bone appears to have suffered very little distortion during the process of fossilization.

That portion of the acetabulum contained within the ilium is large and deep, and the lower surface shows that it was broadly perforated. At the anterior and posterior extremities of the iliac portion of the acetabulum are the two articular facets, one between the ilium and the pubis in front, and one between the ilium and the ischium at the back. Both of these facets are strongly rugose, and the posterior one for the ischium is rather hemispherical in shape, as has been mentioned above. It is quite evident that the ilium was in contact with the other two bones of the pelvis only at these two points.

From the thickened anteroventral section of the ilium which was in contact with the pubis, a shelf or ledge extends up and back, to form a broad roof over the upper portion of the acetabulum—an adaptation to receive the upward thrust of the femur. The strong development of this feature in the ilium indicates that *Poposaurus* was almost certainly a bipedal reptile in which the weight of the body was pivoted at the articulation between femur and pelvis. Midway between the front and the back the border of this dorsal shelf over the acetabulum is extended out and down to give it added width in this region. On its dorsal surface there is a large, expanded, rugose knob, very probably to accommodate the origin of the ilio-femoralis muscle, from which a strong ridge curves up and forward to the small preacetabular process of the ilium. The ridge is quite high, so that it forms a curved wall separating the forward part of the ilium from the much larger, posterior portion. There is a depression in the bone just in front of the ridge, so that the surface of the ilium above the anterior part of the acetabulum takes the form of a large and rather deep fossa. The structure of the supra-acetabular portion of the ilium in *Poposaurus* is not to be homologized in the least with the antitrochanter of the ornithischian dinosaurs, this latter feature being a folding over of the superior iliac border.

The postacetabular part of the ilium is much elongated. In its posterior part the surface is expanded by a downward growth of the bone in this region to form a sort of flat blade, and as a result the lower border of the ilium sweeps down in a decided curve, back of the acetabulum. The ilium terminates, however, in a sharp point.

This postacetabular portion of the ilium carries on its surface a strong ridge that arises from the surface of the bone near the posterior border of the acetabulum and continues back in a flattened curve to the posterior part of the iliac blade. In its mid-portion this ridge is strong and rugose. Owing to the development of this ridge the

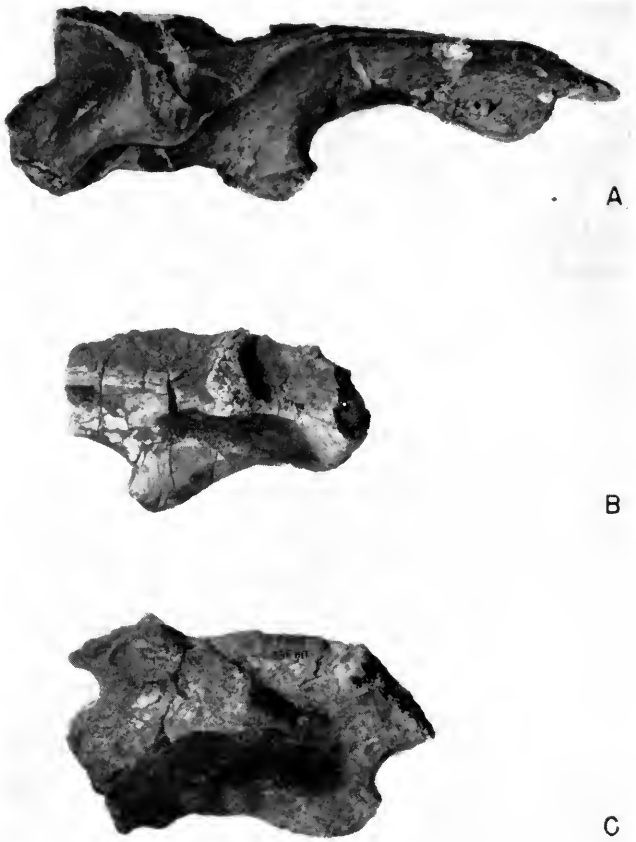

FIG. 33. Three ilia of *Poposaurus gracilis*. A, left ilium of type specimen, CNHM no. UR 357. B, fragment of right ilium from the Dockum beds of Texas, University of Michigan, Museum of Paleontology, no. 11748. C, fragment of large left ilium found near type specimen, CNHM no. UR 358. All external lateral views, approximately one-third natural size.

upper surface of the iliac spine forms a flattened and moderately broad surface.

What does this analysis and interpretation of the ilium of *Poposaurus* show with regard to the relationships of the genus? In the first place, this is certainly an ilium with a perforate acetabulum, a short preacetabular portion, and a long posterior blade. Of the possible Triassic orders that might be considered for the reception of the bone, the Protorosauria, the Thecodontia and the Therapsida may be immediately excluded. In none of these is the acetabulum per-

forated; in all there is a conservative retention of the primitive reptilian structure of this portion of the pelvis. Moreover, in none of these orders is the posterior blade of the ilium produced into a long, low blade such as is characteristic of *Poposaurus*.

This leaves the dinosaurs to be considered. If the identification of the ilium in question as coming from the left side be accepted, then this bone hardly can be attributed to the Ornithischia, in all members of which order there is considerable elongation of the iliac blade anteriorly. As for the Saurischia, the ilium is deep in the sauropods. Only in the primitive theropods is the ilium frequently long and shallow, with the preacetabular portion relatively short and the postacetabular portion elongated as a blade-like structure. Thus, on the basis of general resemblances, the ilium in *Poposaurus* would seem to have various features in common with the same bone in some of the early theropod dinosaurs.

Even here the comparisons are not particularly close. In the early coelurosaurian theropods, such as *Procompsognathus* or *Coelophysis*, the ilium, though long and relatively low, is nevertheless expanded in its anterior portion much more than is the case in *Poposaurus*. Indeed, the only close comparison with *Poposaurus* in this respect is to be seen in the strange pelvis from the Dockum formation of Texas, described by Case as the pelvis of a phytosaur (which it almost certainly is not). In this pelvis the preacetabular portion of the iliac blade is in the form of a very short, anteriorly projecting spine, as was seemingly the case in *Poposaurus*. Otherwise the ilium of this pelvis is in most respects quite different from the same bone in *Poposaurus*.

The presence of the strong, forwardly curving ridge extending from the mid-portion of the acetabulum to the anterior tip of the iliac blade, the long, posterior iliac blade, expanded in its posterior portion and terminating in a point, and the development on this posterior iliac blade of a dorsal, flattened shelf, are all characters that cannot be closely matched among the ilia of any other theropods, or of any other known Triassic or later Mesozoic reptiles, for that matter. In certain respects the configuration of the back portion of the iliac blade in *Poposaurus* shows some resemblances to the same region in *Coelophysis*, but comparisons are only of the most general nature.

The one close comparison between the ilium of *Poposaurus* and this bone in other early theropods is in the form of the acetabulum itself. Here, in the configuration of the lower acetabular border, in

the shape of the pubic and ischial facets, and in the lateral extension of the ilium to form a deep socket for the reception of the head of the femur, the resemblances to the primitive theropods, such as *Coelophysis*, are notable.

On the basis of these considerations it would seem that perhaps the most valid interpretation of the ilium in *Poposaurus* is to regard it as a specialized theropod type, derived from a very early theropod in which the preacetabular portion of the iliac blade had not advanced appreciably beyond the thecodont condition. The acetabulum itself is rather characteristically theropod in form. In the postacetabular portion of the pelvis there has been strong specialization, with the development of the long, blade-like structure of rather complex form, very possibly in part as an adaptation for the origin of strong ilio-fibularis and ilio-tibialis muscles.

THE FEMUR

If the proximal and distal ends of one femur were truly associated, as Mehl indicates in his figure of *Poposaurus*, then this reptile had a rather long straight femur. The probabilities are strongly in favor of such an association, but there is always the faint possibility that there has been a mixture of bones in this Popo Agie material—a possibility that must be kept in mind. It is here assumed, however, that the materials all belong to a single animal, and the description will be made upon the basis of this assumption.

As mentioned before, Mehl indicated the proximal fragment associated with the ilium as from the right side, and the two pieces comprising an essentially complete femur as from the left side. And as also mentioned above, this is almost certainly wrong; the relationships of right and left should be reversed.

The head and the proximal end of the femur in *Poposaurus* are rather unspecialized (fig. 34). The head, although directed medially, is not set off from the shaft of the bone by a decided neck; rather, there is a gradual curve from the shaft to the head of the femur, much as is the case in the thecodont archosaurians. Moreover, there is no well-defined great trochanter at the proximal end of the femur in this reptile. Consequently, the upper end of the femur has a decided thecodont appearance, being not unlike the same portion of the phytosaurian femur in this respect.

On the other hand, the middle and lower portions of the femur are definitely specialized. The lower segment of the right femur as

preserved in the type indicates that in this reptile the shaft of the femur was fairly straight. Perhaps this relatively straight shaft influenced some students favorably toward the idea that *Poposaurus* shows ornithischian characters, for it must be admitted that there is a certain resemblance to the hadrosaurian dinosaurs in this respect.

This resemblance to the ornithischian dinosaurs, and particularly to the hadrosaurs, is strengthened by the shape of the distal condyles of the femur in *Poposaurus*, for in this reptile from the Triassic of Wyoming the posterior curve of the internal condyle swings up to terminate in a sort of "hook." A hook-shaped condyle like this is seen in many ornithischians, particularly the hadrosaurs, but it should be noted that in these dinosaurs the condyle having this shape is the *outer* one. The inner condyle in the hadrosaurs does not show such extreme curvature of its back portion. By way of contrast, some of the saurischians, particularly the more advanced carnosaurs, show a somewhat hook-shaped *inner* condyle of the femur.

Another interesting feature of the femur of *Poposaurus* is the presence of what appears to be a trochanter on the inner side of the shaft and in about its mid-portion. If this feature is real, and not the result of crushing, it is almost surely a fourth trochanter, comparable to the fourth trochanter as developed on the shaft of the femur in various theropods, but in them generally somewhat higher on the bone than it is in *Poposaurus*. Also, this process may be compared with the fourth trochanter in the ornithischian dinosaurs. Generally speaking, the trochanter is larger and more prominent in the ornithischians than it is in the theropods, and than seems to be the case in *Poposaurus*. Moreover, the fourth trochanter in the bipedal ornithischians is commonly "pendent," with a downwardly directed point which serves as an origin for a tendon to the lower leg.

What is the evidence of the femur as to the relationships of *Poposaurus?* Although the evidence is somewhat mixed, showing a primitive proximal region combined with various specializations in the rest of the bone, on the whole it indicates relationships with the theropods.

BONES OF THE LOWER LEG

Associated with the right femur of *Poposaurus* are two bones which Mehl designated as the left tibia and fibula, respectively. The end of the so-called fibula nearest to the right femur has since disappeared, but the remainder of the bone, the major portion, is still among the type materials. The bone that Mehl labeled the tibia is only a portion of the shaft.

Both of these bones are large. It seems quite probable that the bone designated as the tibia by Mehl is the right tibia, associated with the femur. The other bone is almost certainly too robust to have been the fibula, as labeled by Mehl. More probably this is the other tibia, perhaps, as indicated in Mehl's figure, with its proximal end away from the femur and its rounded distal end next to the femur. The end of the large section now at hand is badly crushed and flattened, so nothing definitive can be said with regard to its characters. It should be noted that this bone, as originally figured by Mehl, would seem to have been appreciably shorter than the femur.

Because of the crushed and fragmentary nature of these two bones they are of little value in helping to determine the relationships of *Poposaurus*.

Measurements of *Poposaurus gracilis* Mehl
(Type, CNHM–UR 357)

	MM.
Dorsal vertebra, length of centrum	57
Dorsal vertebra, ant. articular surface, transverse	32
Dorsal vertebra, ant. articular surface, vertical	40
Caudal vertebra, length of centrum	50
Caudal vertebra, post. articular surface, transverse	38
Caudal vertebra, post. articular surface, vertical	48
Ilium, length	251
Ilium, height	80
Femur, approximate length	480

CONCLUSIONS

A careful assessment of the bones that comprise the type of *Poposaurus gracilis* shows that this Triassic reptile combines various anatomical characters that, taken together, make it a particularly baffling problem in taxonomy. In some characters, such as the features of the dorsal vertebrae, of the acetabular region, and to a large degree of the femur, *Poposaurus* shows definite theropod resemblances. In others, such as the general aspects of the ilium, *Poposaurus* is quite unlike any other known reptile. Other characters, such as the features of the lower leg bones, are indeterminate. After consideration of the various characters that are involved, it is here suggested that *Poposaurus* is a theropod dinosaur.

As to its larger relationships within the suborder, the known characters would seem to indicate that *Poposaurus* is a carnosaur. It is moderately large for a Triassic reptile and the bones are thick-walled, as one would expect in the carnosaurs. The form of the vertebrae is

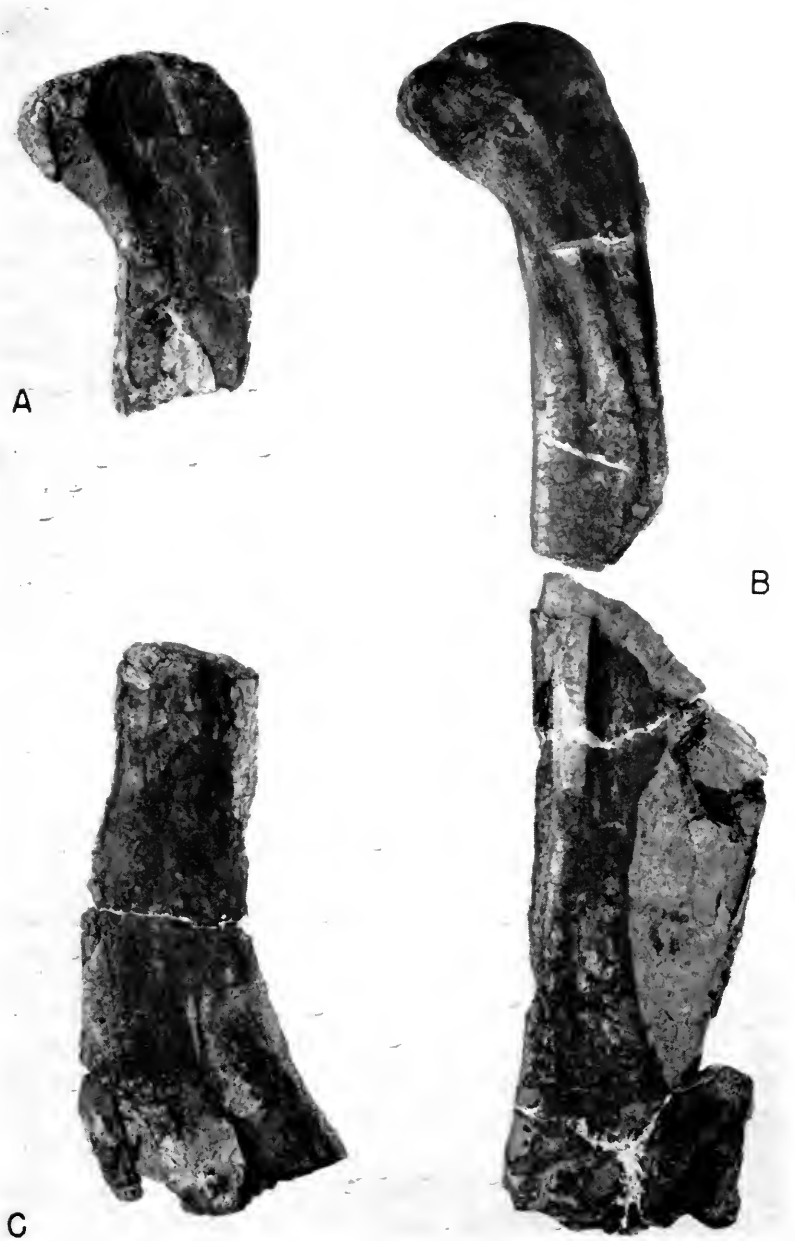

FIG. 34. Type limb bones of *Poposaurus gracilis*. CNHM no. UR 357. A, proximal end of left femur, external lateral view. B, proximal and distal sections of right femur, internal lateral view. C, distal section of right tibia. All approximately one-third natural size.

what might be expected in a primitive carnosaur. The ilium seemingly has a small anterior process, which would be characteristic for a primitive carnosaur but not for a coelurosaur. There is a reasonably large acetabular foramen. The straight femur, longer than the tibia, is a carnosaur feature that is in contrast to the coelurosaurs.

Where then should the genus be placed within the carnosaurs? Its relationships are probably closest to such Triassic carnosaurs as the Paleosauridae and the Zanclodontidae, but the form of the ilium is so unlike that of any known archosaurian ilium, and the ilium is such a basic feature in the interpretation of these reptiles, that the assignment of *Poposaurus* to a separate family is here suggested as the best solution to the problem under the present circumstances.

Of course *Poposaurus* has already been placed within its own family, the Poposauridae, by Nopcsa, but as a member of the Ornithischia, not the Saurischia. It is here proposed that the family, as based upon its single type genus, be lifted bodily from the one dinosaurian order and be transferred to the other. Thus its taxonomic relationships might be expressed as follows:

Order Saurischia
  Suborder Theropoda
    Infraorder Carnosauria
      Family Poposauridae
        Genus *Poposaurus*
          Species *Poposaurus gracilis* Mehl

By removing *Poposaurus* from the Ornithischia to the Saurischia, the evidence for ornithischian dinosaurs in the Triassic period, already weak, becomes even weaker. Only *Geranosaurus* remains as a supposed Triassic ornithischian known from bones, and as a specimen *Geranosaurus* is even more unsatisfactory than *Poposaurus*. The only other evidence for ornithischians within the Triassic is that of the footprints—and how reliable is such evidence?

THE GEOLOGIC OCCURRENCE OF *POPOSAURUS*

It is stated above that more materials are needed to put our knowledge of *Poposaurus* on a firmer basis than that on which it now rests. If such materials are to be found, it seems likely that they may be discovered in the Dockum beds of Texas as readily or perhaps even more readily than in the Popo Agie sediments of Wyoming.

In the collections of the University of Michigan there is a portion of a right ilium of *Poposaurus* (fig. 33, B) that was found in the Dockum formation near Otis Chalk, in Howard County, Texas. As may be seen from the figure it is very closely comparable to the type ilium, and it certainly indicates an identity of genera if not of species between the Triassic sediments of Wyoming and Texas. When one considers how much more productive the Dockum has been in past years than the Popo Agie, it seems likely that at some time in the future the Texas Triassic may yield the relatively complete skeleton of *Poposaurus* that is so much to be desired.

Certainly this fossil from Texas indicates a close correlation between that portion of the Dockum in which it was found and the Popo Agie. Dr. J. T. Gregory, on the basis of his detailed study of the phytosaurs, feels that the Popo Agie, in which there occur the relatively primitive phytosaurs, *Angistorhinus* and *Palaeorhinus*, is somewhat earlier in age than most other North American Triassic horizons such as the Chinle or the Newark series. *Angistorhinus* is also found in the lower part of the Dockum, and the presence of *Poposaurus* in the Texas sediments broadens the evidence as to the relatively early position within the upper Triassic sequence of this particular horizon.

REFERENCES

Case, Ermine Cowles

1922. New reptiles and stegocephalians from the upper Triassic of western Texas. Publ. Carnegie Inst. Washington, no. 321, pp. 1–84, figs. 1–33, pls. 1–14.

1943. A new form of phytosaur pelvis. Amer. Jour. Sci., **241**, pp. 201–203, 1 fig.

Colbert, Edwin Harris, and Gregory, Joseph T.

1957. Correlation of continental Triassic sediments by vertebrate fossils. Bull. Geol. Soc. Amer., **68**, pp. 1456–1467.

Hay, Oliver Perry

1929. Second bibliography and catalogue of the fossil Vertebrata of North America, vol. I. Publ. Carnegie Inst. Washington, no. 390, viii+916 pp.

1930. Second bibliography and catalogue of the fossil Vertebrata of North America, vol. II. *Ibid.*, xiv+1074 pp.

Huene, Friedrich R. von

1906. Über die Dinosaurier der aussereuropäischen Trias. Geol. Paleont. Abhandl., Jena, Neue Folge, **8**, Heft 2, pp. 1–60, 102 figs., pls. 1–16.

1926. Notes on the age of the continental Triassic beds in North America, with remarks on some fossil vertebrates. Proc. U. S. Nat. Mus., **69**, art. 18, pp. 1–10, 6 figs.

1932. Die Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monogr. Geol. Paleont., (1), **4**, parts 1 and 2, viii+361 pp., 41 figs., 56 pls.

1939. Zur Deutung der Reptilreste vom Popo Agie River. Zentralbl. Min. Geol. Paleont., Abt. B, **1939**, pp. 397–399, 2 figs.

1950. Die Entstehung der Ornithischia schon früh in der Trias. Neues Jahrb. Geol. Paläont., Monatsh., Abt. B, part 2, pp. 53–58.

1956. Paläontologie und Phylogenie der Niederen Tetrapoden. Jena, Gustav Fischer, xii+716 pp.

KUHN, OSKAR

1937. Die fossilen Reptilen. Berlin, Gebrüder Borntraeger, viii+121 pp., 92 figs.

LAPPARENT, ALBERT F. DE, and LAVOCAT, RENÉ

1955. Dinosauriens. *In* PIVETEAU, JEAN, Traité de Paléontologie. Paris, Masson et Cie, tome 5, Amphibiens, Reptiles, Oiseaux, pp. 785–962, figs. 1–156.

LEES, J. H.

1907. The skull of *Paleorhinus*, a Wyoming phytosaur. Jour. Geol., **15**, pp. 121–151, figs. 1–8.

LULL, RICHARD SWANN

1953. Triassic life of the Connecticut Valley. Revised. State of Connecticut, State Geol. Nat. Hist. Surv., Bull. no. 81, pp. 1–331, 168 figs., 12 pls.

MEHL, M. G.

1915a. The Phytosauria of the Trias. Jour. Geol., **23**, pp. 129–165, figs. 1–20.

1915b. *Poposaurus gracilis*, a new reptile from the Triassic of Wyoming. Jour. Geol., **23**, pp. 516–522, figs. 1–2.

NOPCSA, F. VON

1921. Zur systematischen Stellung von *Poposaurus* (Mehl). Zentralbl. Min. Geol. Paleont., p. 348.

1928. The genera of reptiles. Palaeobiologica, **1**, pp. 163–188.

PIVETEAU, JEAN

1955. See LAPPARENT, ALBERT F. DE, and LAVOCAT, RENÉ

ROMER, ALFRED SHERWOOD

1956. Osteology of the reptiles. University of Chicago Press, xxi+772 pp., 248 figs.