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A Saurischian Dinosaur from the Triassic of Brazil

By Edwin H. Colbert[1]

INTRODUCTION

In 1936 an expedition from the Museum of Comparative Zoology of Harvard College, composed of Llewellyn I. Price, now paleontologist in the Divisão de Geologia e Mineralogia, Ministério da Agricultura, Rio de Janeiro, and Theodore E. White, now paleontologist at Dinosaur National Monument in Utah, spent many months making systematic collections of Triassic reptiles from the Santa Maria Formation of Rio Grande do Sul, Brazil. Work was carried on in the vicinity of Santa Maria, where fossiliferous Triassic continental sediments are exposed within city limits as well as some 100 kilometers to the east of this city, particularly in the general region of Candelária. A large and varied collection was obtained and brought back to the Museum of Comparative Zoology for preparation and study.

A few years ago one of the specimens in the collection made by the expedition (M.C.Z. No. 1669), a partial skeleton of an archosaurian reptile, was submitted to me for study. I worked on the specimen, then put it aside for a time. I subsequently went to Brazil, where collections of Triassic reptiles were made in Rio Grande do Sul, in collaboration with Price, and with Carlos de Paula Couto and Fausto Luiz da Souza Cunha, both of the Museu Nacional do Brasil, in Rio de Janeiro.

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This experience gave me firsthand acquaintance with the general stratigraphy and fossil localities of the Triassic beds of Rio Grande do Sul, and specifically with the locality at which the archosaurian skeleton had been found. Since my return from Brazil I have again given attention to this specimen and with greater insight than before. It is described and considered in detail in this paper.

This fossil seems to represent an early saurischian dinosaur, and as such bears upon what we know about the early distribution of dinosaurs (now known also from the Triassic Ischigualasto beds of Argentina) and the age of the Santa Maria sediments.

It seems to be the fate of those who study Triassic reptiles to deal with poorly preserved or incomplete specimens. Such is the case with the present fossil. The pelvis is a structure of particular significance in archosaurian classification and of exceptional importance if a firm decision as to the affinities of the fossil is to be reached. But as luck would have it some parts of the pelvis, particularly the acetabular borders, are eroded or crushed just enough to make it difficult to be sure about their original shape and limits. Even so, the fossil is sufficiently complete to justify its description.

I wish to express my appreciation at this time to the Museum of Comparative Zoology of Harvard College, particularly to Professor Alfred S. Romer, for the opportunity to study the specimen described here. In addition, I wish to acknowledge the advice of various paleontological colleagues who have discussed with me the nature and significance of the fossil. I wish to express appreciation to my Brazilian friends for their courtesies and guidance in the field and in the laboratory. A large measure of thanks is owing to Dr. Frank Westphal of the University of Tübingen for his help.

The drawings for this paper were made by Mrs. Lois Darling, Mr. Michael Insinna, and Miss Jennifer Perrott. The photographs were made by Mr. Chester Tarka.

Fossil Occurrences and Stratigraphic Relationships

The specimen (M.C.Z. No. 1669) was found at a locality a few kilometers to the east of the center of the city of Santa Maria, in a small farm and garden area known as Kilometre 3, or Alemõa. In this area there are eroded gullies or "sangas," which expose red Triassic sediments of the Santa Maria Formation. It was in one of the sangas known as Sanga Grande, or Sanga Baixo, that the specimen was discovered (see fig. 1).

The Santa Maria Formation is approximately 200 meters thick. It

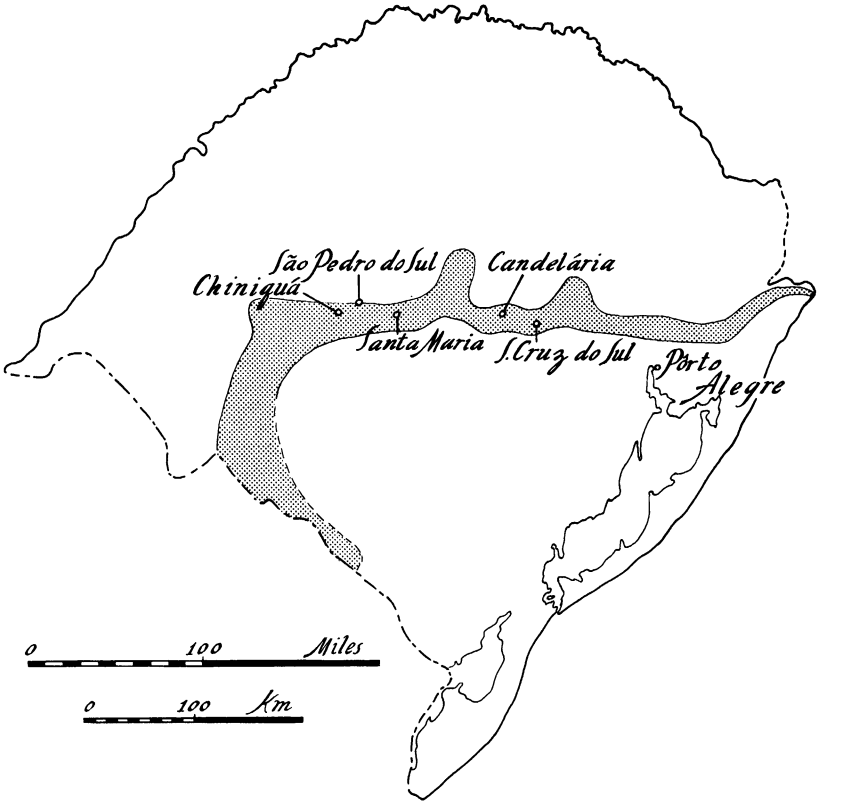

FIG. 1. Outline map of the State of Rio Grande do Sul, Brazil. Triassic exposures are shown by shaded band. Chiniquá (or Xiniquá), Santa Maria, and Candelária are the localities near which Triassic tetrapods have been found in abundance. From the Geologic Map of South America, published by the Geological Society of America, 1950.

may be divided into three parts: a poorly known and rarely exposed basal bed, consisting of sandstones and conglomerates, and gray, feldspathic shales with plant impressions; a middle portion, consisting of bright red sandstones and siltstones bearing bones of reptiles; and an upper portion composed of strongly cross-bedded sandstones of aqueous origin, rose or pinkish in color and containing fossil wood. The bones of the reptiles are found only in the middle part of the Santa Maria Formation, a zone some 30 meters in thickness, the base of which is about 70 meters above the basal beds. This zone is here referred to as the fossiliferous zone.

The sediments at Alemõa, a brilliant orange-red in color, represent the fossiliferous zone of the formation. Countless bones, preserved not only singly but in many cases as associated skeletons, weather out of the sediments in the greatest profusion, and form the visible record of a fauna that must have lived abundantly during Triassic times. Indeed, the abundance of reptilian remains in the Santa Maria Formation as it is exposed within the central portion of Rio Grande do Sul and locally at Alemõa, is comparable with the abundance of contemporaneous reptiles in the Ischigualasto deposits of northern Argentina, about 1400 kilometers to the west. For example, the bottom of the sanga where the specimen under consideration was found is in many places covered by a "pavement," or lag gravel, consisting almost entirely of weathered bone fragments.

It might be assumed from the foregoing that fossils are easy to find and collect in the Santa Maria Formation. Indeed, fossils are not difficult to find, for they are abundantly at hand, but the paleontologist who works in these sediments faces a problem when he tries to assemble a collection of well-preserved, significant specimens, because fossil bones in the Santa Maria beds show a strange type of preservation that makes them difficult to prepare and study. The fossils are in many cases encrusted with a hard layer of iron oxide, and are commonly invaded by mineral matter that causes the bone to break into countless small pieces. These pieces are then forced apart by the accretion of minerals, resulting in a "blowing up" of each bony element. Fortunately, this latter process did not occur in the skeleton described here, but the bones have been broken and crushed, and many parts of the skeleton are missing.

In spite of these difficulties, much has been learned about the Santa Maria fauna, thanks particularly to the field work of von Huene (1929) and of Price (1947). It is now known that the fauna includes a small procolophonid, a large rhynchosaur, several thecodonts, a presumed saurischian dinosaur, some dicynodonts, and a varied series of cynodonts, which have been collected in three principal localities on the outskirts of the city of Santa Maria, in the vicinity of Chiniquá, about 70 kilometers to the west, and in the vicinity of Candelária, to the east.

The associations of the fossils at these three general localities show interesting differences from one another. At Santa Maria rhynchosaurs are abundant, but there are no traces whatsoever of dicynodonts. Cynodonts are very rare. At Chiniquá and at Candelária dicynodonts are frequent, but there are no indications of rhynchosaurs. Cynodonts are well known at Chiniquá and rather abundant at Candelária. Pseudosuchians are present at all three localities, but dinosaurs have not been

found at Candelária.

Why should there be such notable differences in the occurrences of the rhynchosaurs and the dicynodonts at Santa Maria and at the localities to the east and west? It has been suggested that these differences reflect various stratigraphic levels, but that has been difficult to prove. The middle part of the Santa Maria Formation in which the zone of fossil vertebrates is included is similarly developed throughout its various outcrops; it seems to represent an uninterrupted time of sedimentation of continental beds. No marked subdivisions of layers are recognizable in the 30-meter thickness of these sediments. Therefore, it seems not unlikely that the presence of rhynchosaurs and the absence of dicynodonts at Santa Maria, and the opposite occurrences at the other localities may be indications of differences in ecology. But what such differences might have been is a question that cannot be answered using present evidence. It does seem possible that the environment in which the beds at Santa Maria were deposited was unusual, because rhynchosaurs are strange and unusual reptiles. We do not know where and how they lived or what they ate. Perhaps they lived along rivers and dug mollusks for food. Perhaps they lived in wooded uplands, where they fed on husked fruit. However that may be, it is evident that the environment of the Santa Maria rhynchosaur was the environment also inhabited by the dinosaur described below.

DESCRIPTION

STAURIKOSAURUS,[1] NEW GENUS

TYPE SPECIES: *Staurikosaurus pricei,*[2] new species.

DIAGNOSIS: The diagnosis is that given for the species, below.

Staurikosaurus pricei, new species

TYPE: M.C.Z. No. 1669, a partial skeleton, consisting of the following parts: the two mandibular rami, but not the symphyseal region, the dentaries showing the bases of some teeth in the alveoli; the distal portion of a scapula; the proximal end of the right humerus; 20 presacral vertebrae; three sacral vertebrae; 35 caudal vertebrae; a chevron; various ribs and rib fragments; right and left ilia, pubes and ischia; right and

[1] From staurikos, of a cross, in allusion to the constellation of the Southern Cross; and saurus, lizard.

[2] In honor of Llewellyn Ivor Price, who has made extensive collections and studies of fossil reptiles in Brazil.

left femora, tibiae and fibulae; various fragments, not definitely identified.

HORIZON: Santa Maria Formation, within the fossiliferous zone of the middle part of the formation. Triassic.

LOCALITY: Sanga Grande, or Sanga Baixo, at "Alemõa," or Kilometre 3, on the eastern outskirts of the city of Santa Maria, Rio Grande do Sul, Brazil.

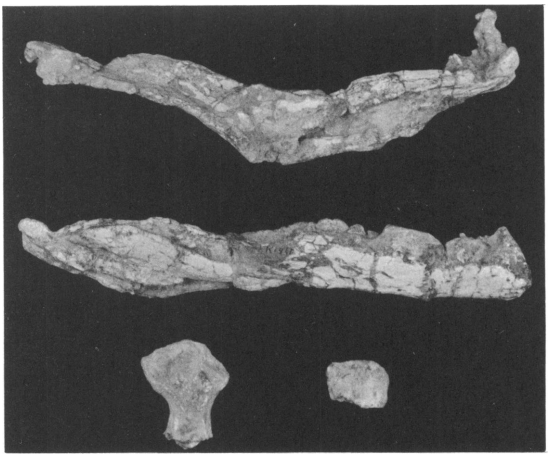

FIG. 2. *Staurikosaurus pricei*, new genus and species. M.C.Z. No. 1669, mandibular rami, distal end of a scapula and proximal portion of a right humerus. ⅓ natural size.

DIAGNOSIS: A bipedal saurischian of small size, with strong hind limbs and small forelimbs. The bones are hollow, but with rather thick walls. The lower jaws are long, about equal to the length of the femur, indicating a skull quite large in relation to the size of the body. The teeth are thecodont. There were probably about 23 to 25 presacral vertebrae (the anterior ones are missing), three sacrals and a long tail with perhaps 40 or more vertebrae. The centra of the vertebrae are platycoelous and constricted in their mid-portions. The vertebrae have strong diapophyses, with buttresses beneath them, and rather short, heavy neural spines. The ilium is deep and short, its iliac crest being abbreviated, and produced posteriorly. The acetabulum is deep within the ilium and its upper margin forms a shelf to take the thrust of the femur against it. The pubis is long, about two-thirds as long as the femur, broad and platelike, and the two pubes are joined along their midlines by a long symphysis. The ischium is broad proximally, but narrows to a rodlike bone in its more distal portions. The bones of the pelvis seemingly do

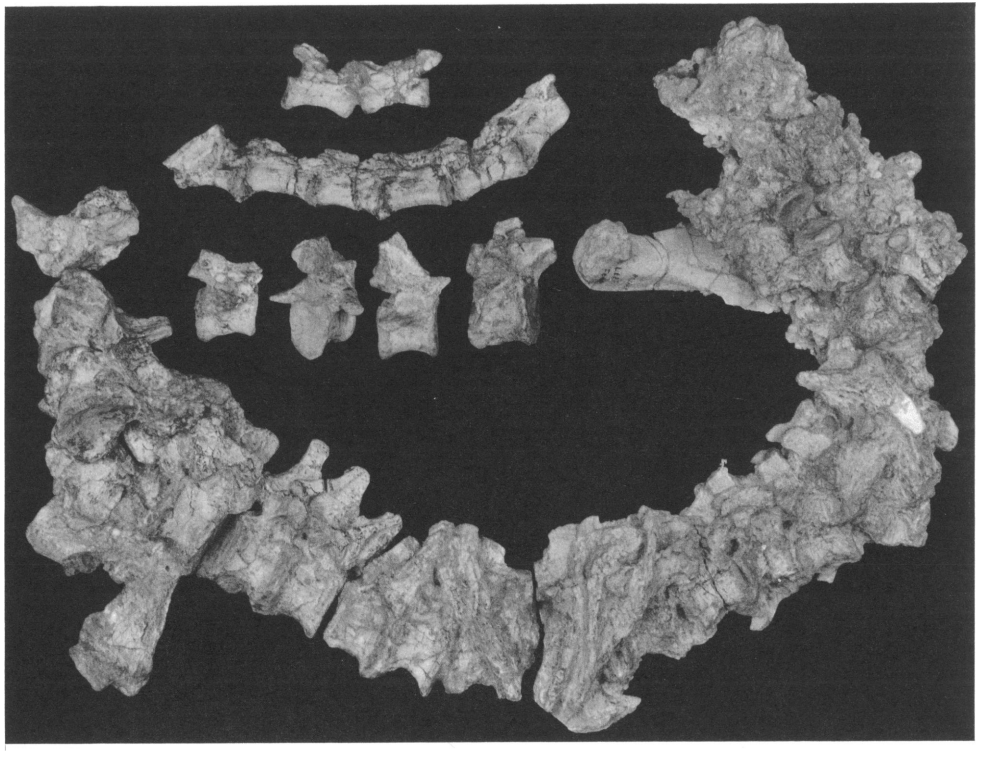

FIG. 3. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669. Twenty presacral, three sacral vertebrae in articulation as discovered; portion of left ilium (left); left femur (right). Above second to fifth caudal vertebrae are some intermediate caudals.

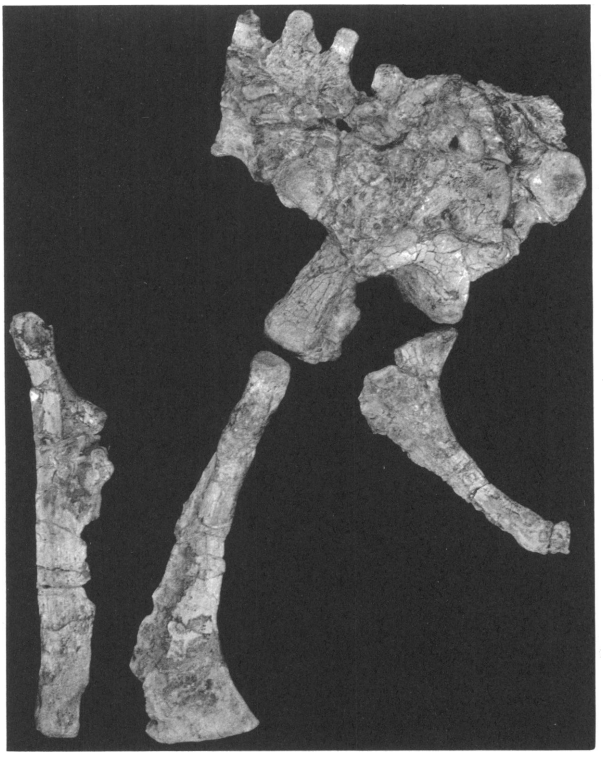

FIG. 4. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, left ilium, ischium, and pubis, external view; right pubis, anterior view. ⅓ natural size.

not unite firmly, but rather are joined by restricted facets, so that the central portion of the acetabulum is open. The femur is a curved, heavy bone, the head strongly set off from the shaft, with no lesser trochanter, but with a strong fourth trochanter. The tibia is strong and the tibia and the fibula are elongated, being slightly longer than the femur. The astragalus and calcaneum are obviously separate, but evidently in life were closely appressed to the limb bones.

Although the skull of *Staurikosaurus* is missing, the two halves of the lower jaw are present and rather complete. They show that this was a large-skulled saurischian, a reptile in which the head was about equal to the femur in length. This would imply that *Staurikosaurus,* which had sharp, thecodont teeth, was a very active predator, a reptile with strong jaws and a wide gape, capable of attacking animals equal to it in size. In this respect it may be compared with various other carnivorous sauris-

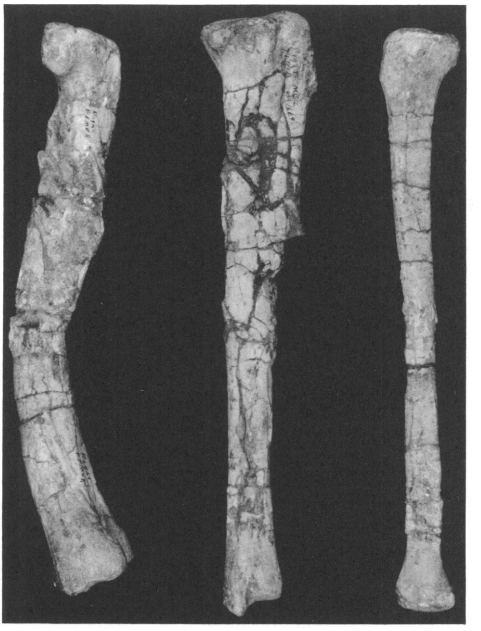

FIG. 5. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, right femur and tibia, internal lateral view; left fibula, external lateral view. ⅓ natural size.

chians of the Triassic, for example with the European genus *Palaeosauriscus.*[1] As for details of the jaws, the two rami are so distorted by crushing that not much can be said about them. The dentaries are thin and rather deep. Behind the dentary, each ramus shows a typical archosaurian fenestra of large size, a large glenoid in the articular, indicative of a strong quadrate, and a well-developed retroarticular process.

[1]*Palaeosaurus* was a name proposed by Riley and Stutchbury in 1836 for a genus of Triassic dinosaurs. This name has been widely used in this context for more than a century, although it is antedated by *Palaeosaurus* Geoffroy, 1833, a Jurassic crocodilian from France. Actually Geoffroy used two spellings of the name in his paper; *Paloesaurus* (p. 48) and *Paloeosaurus* (p. 55). It is obvious that he regarded the second spelling as the correct one, for on page 61 there is a note that reads "Erratum. Au lieu de *Paloesaurus,* en la dernière ligne de la page 48, lisez *Paloeosaurus.*"

Although there is a difference of one letter between the names proposed by Geoffroy (1833) and by Riley and Stutchbury (1836), these names must nonetheless be regarded as homonyms. (International Code, Article 58 [1]).

Therefore Kuhn (1959) was correct in proposing *Palaeosauriscus,* to replace *Palaeosaurus* Riley and Stutchbury, 1836. Kuhn also indicated that the family name should be changed from Palaeosauridae to Palaeosauriscidae.

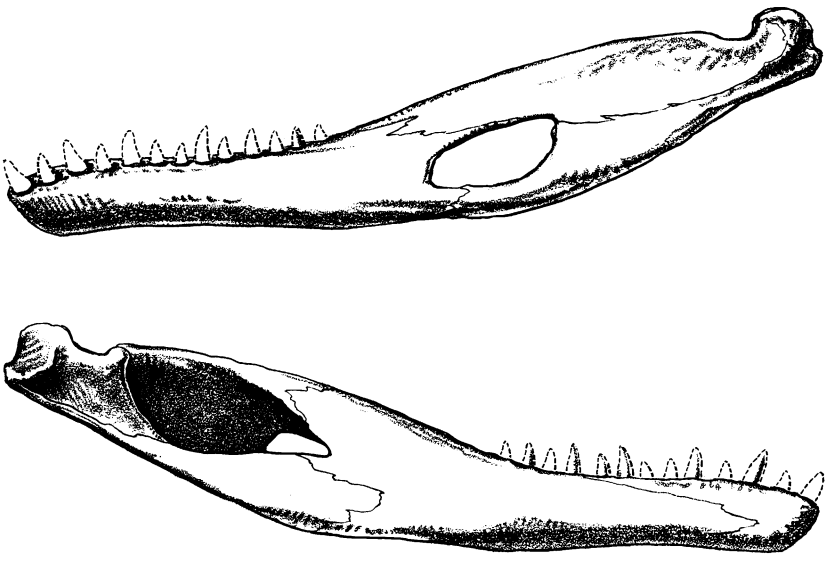

FIG. 6. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, restoration of left mandibular ramus. External lateral view above, internal view below. ½ natural size.

A great part of the vertebral column is preserved in this specimen, but unfortunately the anterior part of the column is missing, so that it is impossible to know the exact number of presacral vertebrae. Presumably there were between 23 and 25 presacrals. Certainly there are three sacral vertebrae in the fossil from Santa Maria, as is characteristic for primitive saurischians. The tail is very long, with 35 caudal vertebrae preserved, and there must have been more, perhaps as many as 10 in addition to those at hand.

The vertebrae are platycoelous, the ends of the centra being expanded to form large intervertebral articulations, their middle being constricted. Thus the vertebral centra have the spool-like or hourglass shape common among archosaurians. It should be said that the centra are somewhat shorter in comparison with their vertical dimensions than is the case in *Spondylosoma,* a supposed saurischian genus described by von Huene (1935–1942) from the Santa Maria beds at Chiniquá, to the west of Santa Maria. The diapophyses or transverse processes are stout but not widely extended, and beneath them in the presacral series are strong ridges or buttresses diverging down obliquely fore and aft on each side, to join the centrum at the juncture with the base of the neural spine. These buttresses consti-

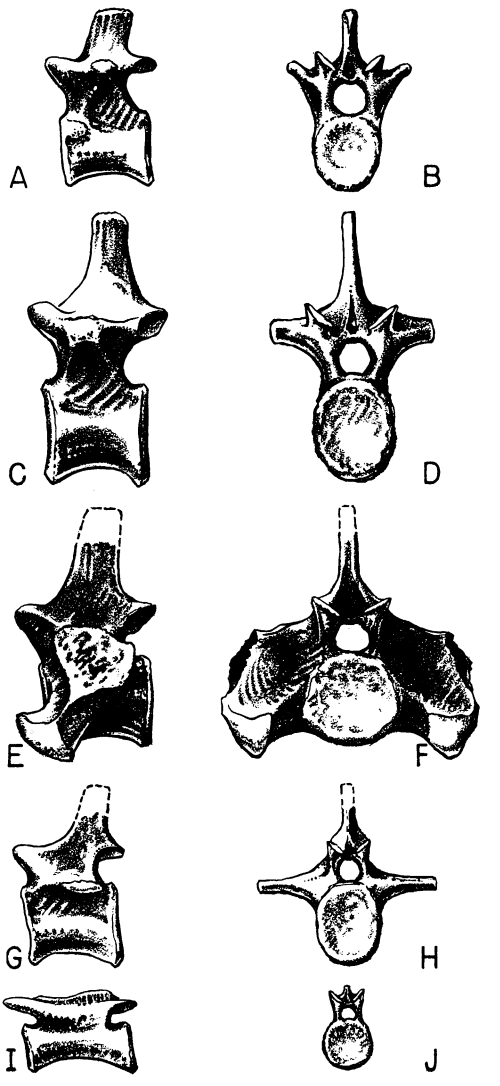

FIG. 7. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, selected vertebrae. A, left lateral view, and B, anterior view of ninth presacral; C and D, similar views of twenty-second presacral; E and F, similar views of second sacral; G and H, similar views of fifth caudal; I and J, similar views of eighteenth caudal. All ½ natural size.

tute a feature quite characteristic of primitive saurischians. The neural arches are rather high in the presacral vertebrae, although the neural

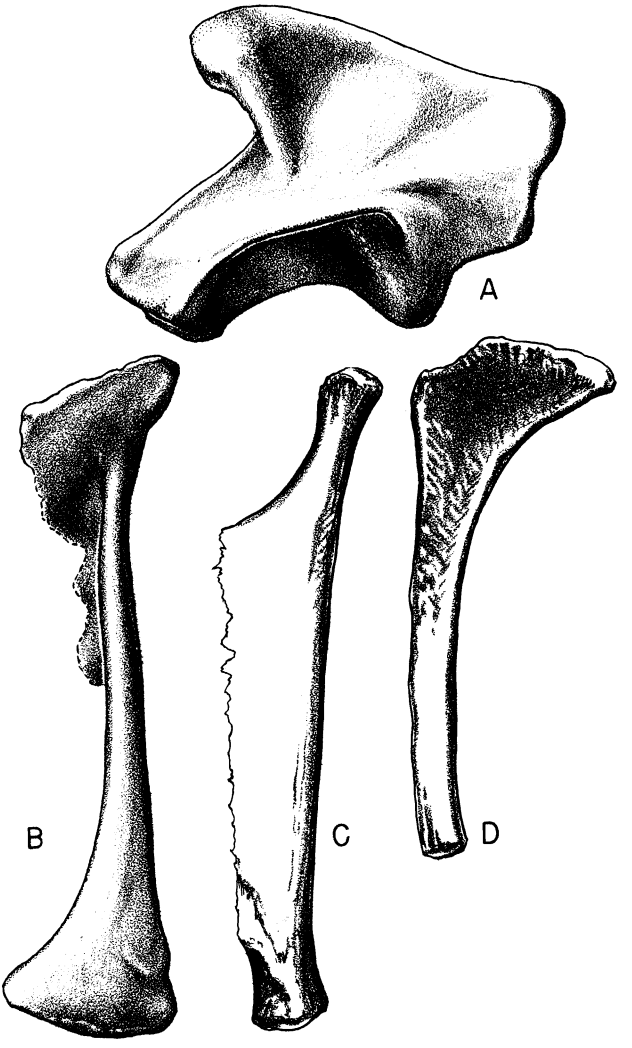

FIG. 8. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, pelvis. A, left ilium, lateral view; B, left pubis, lateral view; C, left pubis, anterior view; D, left ischium, lateral view. All ½ natural size.

spine itself is of modest dimensions. The zygopophyses are obliquely inclined. As might be expected, the presacrals of *Staurikosaurus* increase in size from front to rear.

The three sacrals are very heavy, and have expanded connections with the ilia. The anterior caudals are also heavy, but the bones of the tail

soon begin to become elongated, so that from about the sixth caudal back the vertebrae become increasingly rodlike. A small chevron is among the preserved materials of *Staurikosaurus.*

Some of the ribs are preserved in part in this fossil. They need no particular description.

Of the forelimb, only the proximal part of a humerus is preserved.

Perhaps the most crucial and diagnostic part of the specimen is the pelvis, because, lacking the skull, it constitutes the prime evidence as to the relationships of the genus.

In a recent paper (Colbert, 1963) I have pointed out that there seem to be two basic types of saurischian pelves, one with a relatively short, deep ilium, which may be designated as the brachyiliac type, and the other with an elongated ilium, which may be designated as the dolichoiliac type. Other differences go along with these particular contrasts in the structure and proportions of the ilium. For example, the ilium in the brachyiliac type of pelvis terminates in front in a short process or point and has a relatively large acetabulum. The pubes are broad, and although they may be flared distally they generally do not show an anteroposteriorly enlarged "foot." Furthermore each pubis often has a large thyroid fenestra. The ischium, platelike proximally, is narrow distally. By way of contrast, the dolichoiliac type of pelvis shows an ilium with a much expanded and rounded anterior portion and a prolongation of its posterior part, and it has a relatively small acetabulum; the pubes are relatively narrow and are expanded distally so that they may terminate in knobs or often in a large foot, there is no thyroid fenestra in the proximal portion of each pubis; and the ischia are narrow, often rodlike bones, with little proximal expansion. It was suggested (Colbert, 1963) that the brachyiliac type of pelvis, showing many resemblances to the pelvis of thecodont reptiles, is the more primitive of the two, and that the dolichoiliac pelvis is a derived form, even though it appears at an early stage in the history of saurischian evolution.

The pelvis of *Staurikosaurus* obviously is of the brachyiliac type. Its ilium is short and deep. Indeed, its length is only slightly greater than its depth, in contrast to the typical dolichoiliac ilium, the length of which is commonly two or three times its depth. Moreover, the acetabulum in *Staurikosaurus* is very large, and there is a long peduncle for articulation with the pubis, which extends considerably anterior to the anterior point of the iliac crest, another feature characteristic of the brachyiliac type of pelvis. In the present specimen the acetabulum forms a deep lunette within the lower half of the ilium, and the upper part of this socket has an overhanging rim, well designed to receive the upward

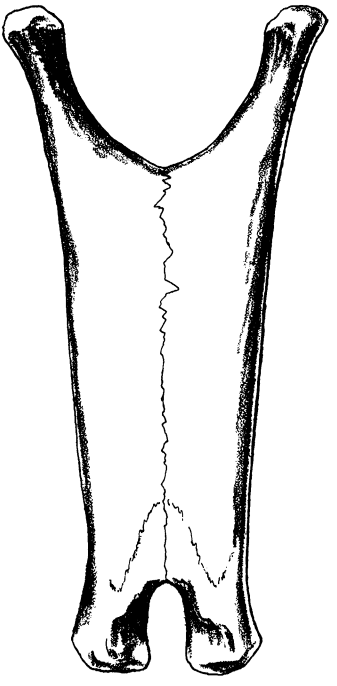

FIG. 9. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, restored pubes in anterior view. ½ natural size.

thrust from the head of the femur. This adaptation in *Staurikosaurus* is patently part of a design for strongly bipedal locomotion. The inner surface of the upper portion of the acetabulum is restricted, with a thin, arched edge that does not extend to the lower pelvic bones. Thus the acetabulum is open, as is typical of the saurischians. The acetabular opening is, however, somewhat restricted, as is the case in certain other primitive saurischian dinosaurs, and not openly rounded as is the case in more advanced forms.

The pubis is long—about three-fourths the length of the femur—and broad, and the two pubes meet in a long symphysis. Together they form a broad, platelike structure. The proximal end of the pubis is "twisted" at about 90 degrees to the main portion of the bone, as is typical of the brachyiliac saurischian pelvis and of the thecodont pelvis, and there is a distinct head for articulation with the anterior peduncle of the ilium. The proximal portion of the pubis is expanded. This section of both bones is partly broken, so that it is not possible to determine with certainty whether or not there was a thyroid fenestra. The pubis is anteroposteriorly flared distally.

The ischium, rather platelike proximally, rapidly thins as it extends

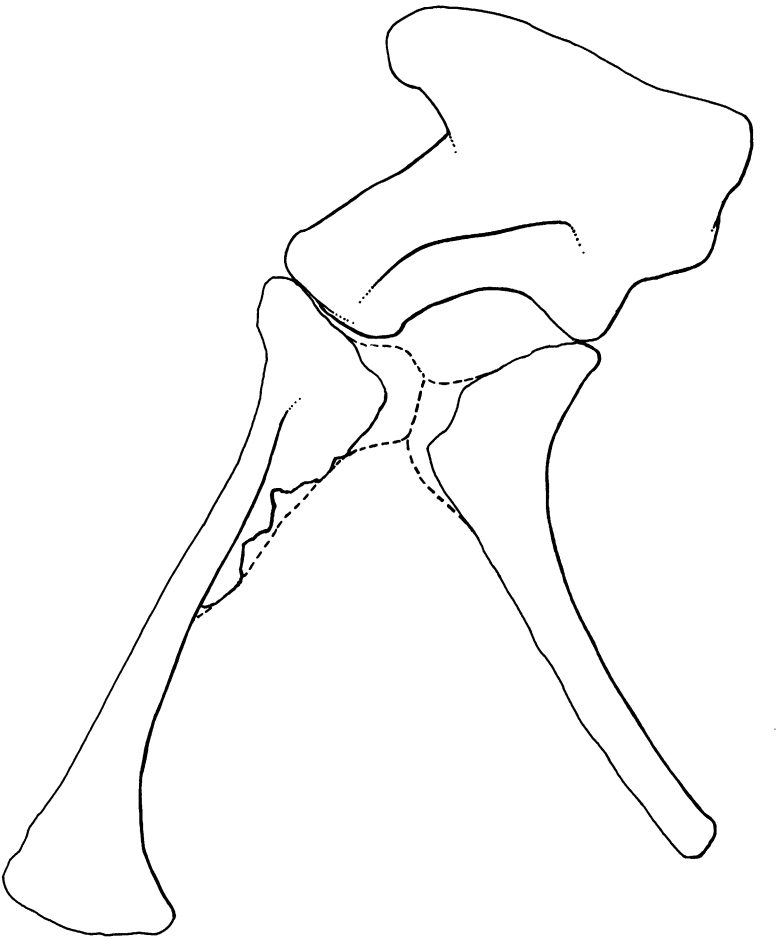

FIG. 10. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669. Restoration of pelvis in lateral view. ½ natural size.

back, so that throughout much of its length it forms a narrow blade. The distal portion is missing, so the precise length of the bone cannot be determined. It probably was considerably shorter than the pubis.

The femur of *Staurikosaurus* is a long, curved bone, with a well-developed head, set off strongly from the axis of the shaft. Here, as in the case of the pelvis, we see a distinct adaptation for bipedal locomotion. The curvature of the femur is convex anteriorly and is quite pronounced. It is very similar to the curvature of this bone in other

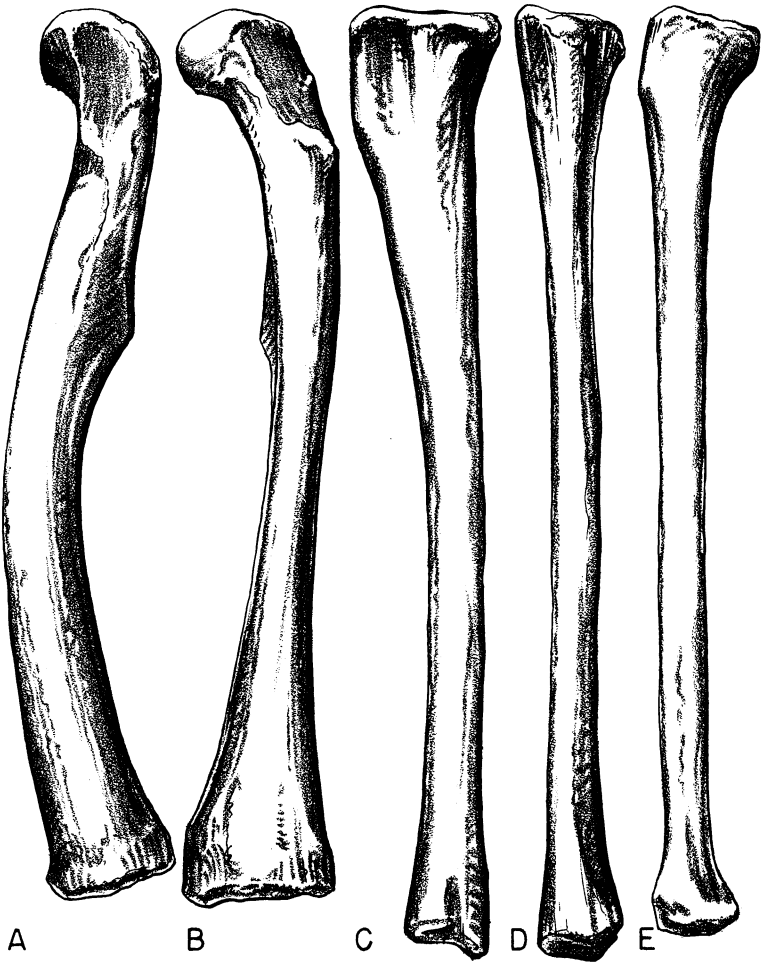

FIG. 11. *Staurikosaurus pricei,* new genus and species. M.C.Z. No. 1669, elements of the hind limb. A, left femur, lateral view; B, left femur, anterior view; C, left tibia, lateral view; D, left tibia, anterior view; E, left fibula, lateral view. All ½ natural size.

bipedal saurischians. There is a strong fourth trochanter located one-third of the length of the femur from its proximal end. Distally this bone is expanded into two condyles for articulation with the tibia, the inner one of which is the larger.

The tibia is a straight, rather slender bone, slightly longer than the femur. It has a prominent cnemial crest. The distal surface of the bone

is characterized by the smooth, somewhat helical surface for close articulation with the tibiale or astragalus, and thus the posterior part of the distal surface is projected down below the anterior portion. Medially there is a groove, running up a short distance on the inner surface of the tibia and making a notch into the inner margin of the articulating surface. This form of distal articulation of the tibia is quite characteristic for many of the saurischian dinosaurs, and is well developed in various Triassic genera, such as *Teratosaurus* and other related forms. It indicates a closely appressed tibiale, again an adaptation for bipedalism.

The fibula is a slender bone, expanded proximally for articulation with the outer condyle of the femur, distally for articulation with a narrow fibulare.

Unfortunately, the pes is missing in this specimen, so it is not possible to say anything about the nature of the tarsus. The form of the distal end of the tibia seems to indicate, however, that *Staurikosaurus* was characterized by a mid-tarsal joint.

From these remarks it is obvious that *Staurikosaurus* was a reptile strongly adapted for bipedalism. What are its relationships?

Comparisons

In the first place, how can we be sure that *Staurikosaurus* is not a pseudosuchian thecodont? This question is raised because it has frequently been maintained that the Santa Maria sediments are of Middle Triassic age, which if true, might preclude the presence of dinosaurs in these rocks. Here we encounter a problem of phylogeny not uncommon in the fossil record. In the present instance it is this: Where do the advanced pseudosuchians end and the primitive saurischians begin? What is the line of demarcation between the two groups?

It is not an easy line to determine, because as so often happens with ancestor and descendant relationships as seen in the fossil record, there is a great deal of gradation between the taxa involved. This has been recognized by various authors with regard to thecodonts and saurischians, and has been emphasized by Romer in the following remarks:

"The development of the bipedal saurischians is a logical resultant of the evolution of typical bipedal thecodonts. The morphological 'boundary' between the two orders in the Triassic (in which period saurischians, in contrast to their ornithischian cousins, were already abundant) is far from clear, and it is further possible that the saurischians are polyphyletic, derived from two or more related thecodont lines."

(Romer, 1956, p. 609).

Von Huene (1956) also has given attention in recent years to the intergradation between pseudosuchian thecodonts and saurischians, and after detailed comparisons of the characters that distinguish these two groups of reptiles has come to the conclusion that in only two respects are such characters mutually exclusive. First, in the pseudosuchians as in other thecodonts the dermal elements of the shoulder girdle, the clavicles and interclavicle, are present, whereas in the saurischians these bones are almost always completely absent. Second, in the thecodonts including the pseudosuchians, the acetabulum of the pelvis is closed, whereas in the saurischians it is open.

In the present instance it is not possible to use evidence from the shoulder girdle, because of the lack of materials, but certainly the structure of the pelvis, with its open acetabulum, places *Staurikosaurus* on the side of the saurischians. Is it possible to call upon other evidence from the partial skeleton at hand, to help determine the problem, even though this evidence is not mutually exclusive between the pseudosuchians and the saurischians? The answer is yes, because even though the evidence from individual characters may not be completely conclusive, its sum should be very important in one direction or the other.

Thus, in addition to the character of the acetabulum, which is an all or nothing feature and which does indicate *Staurikosaurus* as of saurischians relationships, there are other gradational characters of the pelvis that may be considered. In the pseudosuchians the ilium is generally comparatively shallow, ending in a sharp point posteriorly. In the brachyiliac saurischians the ilium is deep and is, in general, truncated posteriorly. The ilium in *Staurikosaurus* accords with the brachyiliac saurischians in these respects; essentially it is as deep as it is long and is quite truncated posteriorly.

In the pseudosuchians the ischium is platelike; in the saurischians it is rodlike. In *Staurikosaurus* the ischium, rather expanded proximally, quickly tapers to a slender rod.

The femur in the pseudosuchians is generally longer than the tibia, whereas in the primitive saurischians the opposite is usually the case. In *Staurikosaurus* the femur is shorter than the tibia. Again, the head of the femur is not markedly set off from the shaft in most pseudosuchians, whereas it is in the saurischians. The head of the femur is set off at a distinct angle from the shaft in *Staurikosaurus.* In the pseudosuchians the fourth trochanter of the femur is weak, whereas in the primitive saurischians it is generally strong. In *Staurikosaurus* it is a well-developed feature of the bone. In the pseudosuchians the astragalus

and calcaneum are separate, but in the saurischians these bones are commonly fused and firmly appressed to the tibia-fibula, thus making a mid-tarsal joint. In certain primitive saurischians, however, the astragalus and calcaneum are separate, independent elements, and such seems to be the case in *Staurikosaurus.*

Finally, in the vertebral column, the presacral vertebrae in saurischian dinosaurs commonly show a pair of well-defined buttresses on each vertebra, which originate on the underside of the transverse process and extend down on the side of the neural arch, diverging from each other. Such buttresses are generally not to be seen in the pseudosuchian thecodonts. They are a prominent feature of the vertebrae of *Staurikosaurus.*

In summation, therefore, there are various characters in the skeleton of *Staurikosaurus,* so far as it is known, which reinforce the positive evidence of the pelvis, especially the open acetabulum, as to the saurischian relationships of this genus. The position of *Staurikosaurus* within the Saurischia is the next point to be determined.

The first question is whether or not there is any close relationship between *Staurikosaurus* and *Spondylosoma,* an archosaurian genus described by von Huene (1935–1942) from the Santa Maria Formation, and classified by him as a saurischian. In the original description von Huene (1935–1942) did not assign *Spondylosoma* to any particular position within the Saurischia; subsequently, in 1956, Romer listed it among the Thecodontosauridae, which in turn he regarded as coming within the Prosauropoda. This allocation of the genus has been followed by other authors.

The type of the single species, *Spondylosoma absconditum,* found in the vicinity of Chiniquà, to the west of Santa Maria, consists of the distal portion of a left scapula, the proximal end of a right humerus, the distal end of a left femur, a portion of a left tibia and eight vertebrae. Two rather small, compressed, pointed teeth with serrated edges may belong to this specimen. The vertebrae are small, the largest one is about 43 mm. long. These vertebrae have medially compressed centra with platycoelous articular surfaces, and some of them show very strong buttresses, which, as mentioned above, is typical of many saurischians. These vertebrae, which may be identified as cervicals, are rather elongated, as might be expected in a prosauropod, and all of the vertebrae are proportionally longer than are the vertebrae of *Staurikosaurus.* The scapula is narrow and somewhat expanded at the top and is of saurischian type, whereas the pubis is elongated with a proximal, subdivided facet, also of saurischian type.

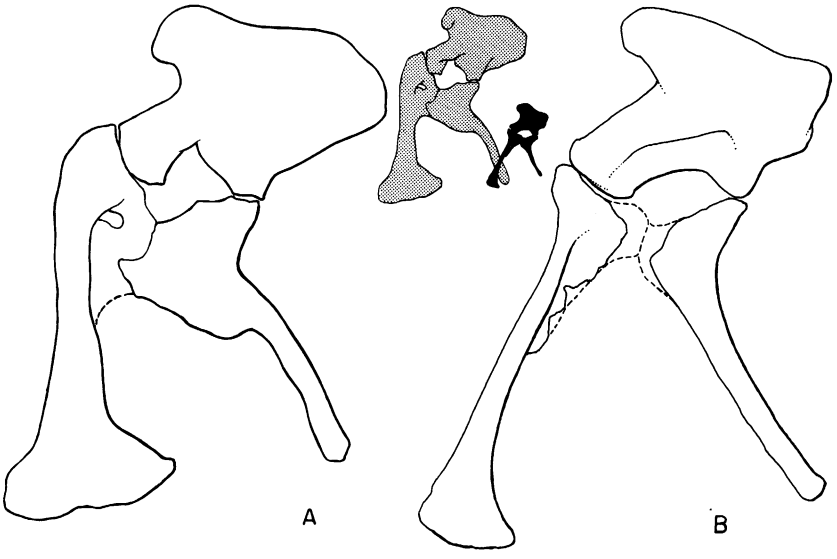

FIG. 12. Comparison of the pelvis, in left lateral view and drawn to unit scale, of A, *Herrerasaurus ischigualastensis* Reig; and B, *Staurikosaurus pricei,* new genus and species. The small shaded drawings show the relative sizes of the pelves to each other.

These several characters indicate the saurischian nature of *Spondylosoma,* and at the same time show it to be something different from *Staurikosaurus.* The proportions of the vertebrae indicate that this small saurischian had a moderately long neck, and possibly a rather small skull, quite in contrast to the proportional development of neck and head in *Staurikosaurus.* Romer was probably correct in placing *Spondylosoma* among the Thecodontosauridae.

A genus that appears to be comparable with *Staurikosaurus* is the saurischian *Herrerasaurus* from the Triassic Ischigualasto beds of Argentina. This form, based on a considerable amount of material, was briefly described by Reig (1963), who figured a portion of a lower jaw, a pelvis, and the elements of the hind limb. *Herrerasaurus* is obviously about twice as large in linear dimensions as is *Staurikosaurus,* but aside from this size differential there are certain resemblances. Although the portion of jaw figured by Reig is far from complete, it is quite evident that the mandible must have been comparatively large, perhaps almost as long as the femur. This is true of *Staurikosaurus.* A large skull is indicated for *Staurikosaurus* as well by the relative shortness of the vertebrae in the anterior portion of the column.

Comparisons of the pelvis are interesting. In both of these genera the ilium is short and deep, with the anterior point of the iliac blade extending no farther forward than the front border of the pubic peduncle, and the posterior part of the blade being relatively short. This part of the bone is much more truncated in *Staurikosaurus* than in *Herrerasaurus,* because the ilium in the latter genus is perhaps somewhat more like that of *Plateosaurus.* In both *Staurikosaurus* and *Herrerasaurus* the pubic peduncle is large and robust, as is characteristic of brachyiliac saurischians. Although it is not possible to be sure from the figure of *Herrerasaurus,* because of breakage indicated in the acetabular portion of the ilium, it nevertheless appears that the acetabular foramen is restricted, as it is in *Staurikosaurus.* That this is so, was confirmed recently by the author, when he visited the Instituto Miguel Lillo at the University in Tucumán, where he examined the type of *Herrerasaurus ischigualastensis.*

In both genera the pubis is very long, in *Herrerasaurus* as long as the tibia, in *Staurikosaurus* somewhat shorter than the tibia, owing to the relatively greater length of the tibia in this latter genus. As perhaps a more accurate ratio, the pubis is essentially twice the height of the ilium in both genera. Reig (1963) described the pubis of *Herrerasaurus* as megalosaurian in form, with a distal foot, widely expanded in an anteroposterior direction. The expansion of the distal extremity of the pubis in *Staurikosaurus* is marked, but it appears to be rather different from that seen in the Jurassic and Cretaceous carnosaurs. In these latter forms the expansion appears to be an enlargement from the knoblike termination of the pubis seen in Triassic coelurosaurians, such as *Coelophysis,* a point that would accord with the derivation of the middle and late Mesozoic true carnosaurians from coelurosaurian ancestors, as advocated by the present author in 1964. In *Staurikosaurus* the development of this "foot" seems to be a more general expansion throughout the lower portion of the bone, and it appears that this may also be true in *Herrerasaurus.*

The ischium shows similarities in both genera, being proximally expanded and distally constricted into a rather rodlike bone.

Resemblances are to be seen in the femur, which in both genera is a bone with a strong anteriorly convex curve, with the head set off at a distinct angle from the shaft, and with a strong fourth trochanter situated well above the median point of the shaft. The tibia of *Herrerasaurus* is shorter than the femur and is relatively stout, that of *Staurikosaurus* is considerably longer than the femur and is slender. The fibula of the former genus likewise is heavier than that of the latter form. These differences reflect adaptations to size and weight; *Herrerasaurus* was a rather

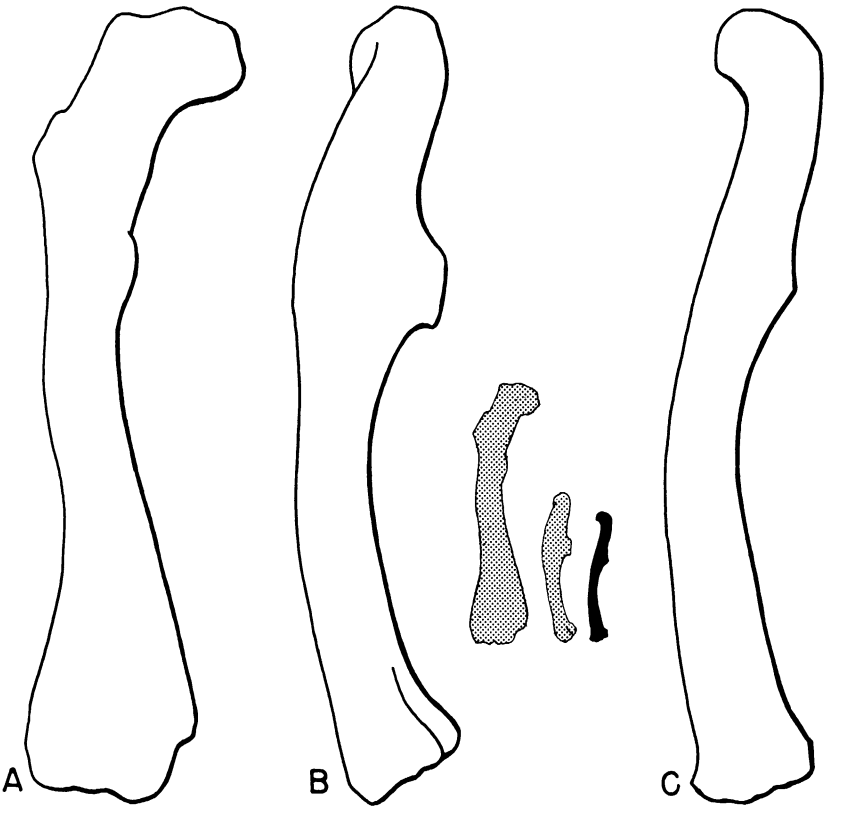

FIG. 13. Comparison of left femora, drawn to unit scale, in A, *Herrerasaurus ischigualastensis* Reig; B, *Ischisaurus cattoi* Reig; and C, *Staurikosaurus pricei,* new genus and species. The small shaded drawings show the relative sizes of the three femora.

large reptile, *Staurikosaurus* by comparison was a small, lightly built animal. In *Herrerasaurus* the astragalus and calcaneum are separate bones, and it appears that the same was probably true in *Staurikosaurus.* No comparisons can be made of the feet in the two genera here under consideration.

The resemblances that have been outlined are those between two primitive saurischians, probably not far removed from their common ancestor. The differences are those between two saurischians adapted along separate lines, the one toward considerable size, the other toward a much smaller and lighter structure. One may suppose that *Herrerasaurus* was a ponderous carnivore, *Staurikosaurus* an agile predator. The important point

TABLE 1

MEASUREMENTS (IN MILLIMETERS), RATIOS AND INDICES

	Staurikosaurus pricei M.C.Z. No. 1669	*Herrerasaurus ischigualestensis* From Reig	*Ischisaurus cattoi* From Reig	*Spondylosoma absconditum* From von Huene
Estimated length of mandible	215	300±10	225±10	
Length of femur	229	473	286	
Length of tibia	246	411	280	
Ratio: femur to tibia	93	87	115	
Length of ilium	98	238		
Height of ilium	94	180		
Index: height to length	96	76		
Length of pubis	171	409		
Ratio: pubis to femur	75	87		
Length of ischium	136[a]	330		
Length of centrum anterior presacrum	24	43		32
Height of centrum	17			24
Index: height to length	71			75
Length of centrum				
Second sacral	29	57		37

[a] As restored.

to be made is that in spite of the differences that point to early stages of adaptive radiation, the resemblances show these two dinosaurs to be more or less at the same grade of evolutionary development and therefore probably more or less of the same age.

Reig (1963) did not classify *Herrerasaurus* within the Saurischia; Rozhdestvensky and Tatarinov have recently (1964) placed it within the Gryponichidae, which they regarded as the equivalent of von Huene's (1956) Palaeosauridae. These same authors have placed *Ischisaurus,* another saurischian genus described by Reig in the same paper with *Herrerasaurus,* in the Gryponichidae as well. Unfortunately for the purposes of comparisons Reig figured only the femur and humerus of *Ischisaurus,* although he indicated the existence of a considerable amount of material for the type of this genus at hand. It may be possible that *Ischisaurus* resembles *Staurikosaurus* even more closely than does *Herrerasaurus.* The femora in the two genera are similar in the curvature of the shaft, in the general position of the head, and in the location and size of the fourth trochanter. Here, again, we see a saurischian at a stage of evolution and probably of geologic age close to *Staurikosaurus.*

A comparison of *Staurikosaurus* with the European genus *Palaeosauriscus,* is essentially a repetition of comparisons with *Herrerasaurus,* for these two latter genera seem to be closely related, as implied by Rozhdestvensky and Tatarinov (1964). They resemble each other in size. In the general form of the pelvis the two genera may be compared, although the ilium of *Herrerasaurus* is relatively deeper and not so pointed posteriorly, whereas the pubis is not distally expanded in *Palaeosauriscus.* It is fair to say that *Herrerasaurus* and *Palaeosauriscus* are at closely comparable stages of phylogenetic development, perhaps of age, and in these respects *Staurikosaurus* may be compared with them.

Taxonomic Position

In the light of these comparisons where is *Staurikosaurus* to be placed within the taxonomy of the saurischians? In 1964 the present writer suggested that all Triassic saurischians should be included within two suborders: the Theropoda, including coelurosaurians; and the Palaeopoda, including palaeosaurians and plateosaurians. It is proposed to adhere to this arrangement in the present discussion.

Staurikosaurus, a brachyiliac saurischian, certainly comes within the Palaeopoda, as does *Herrerasaurus.* Its more precise allocation within the palaeopods involves various possibilities. Generally speaking, the small size, the evident relatively large skull and rather short vertebrae,

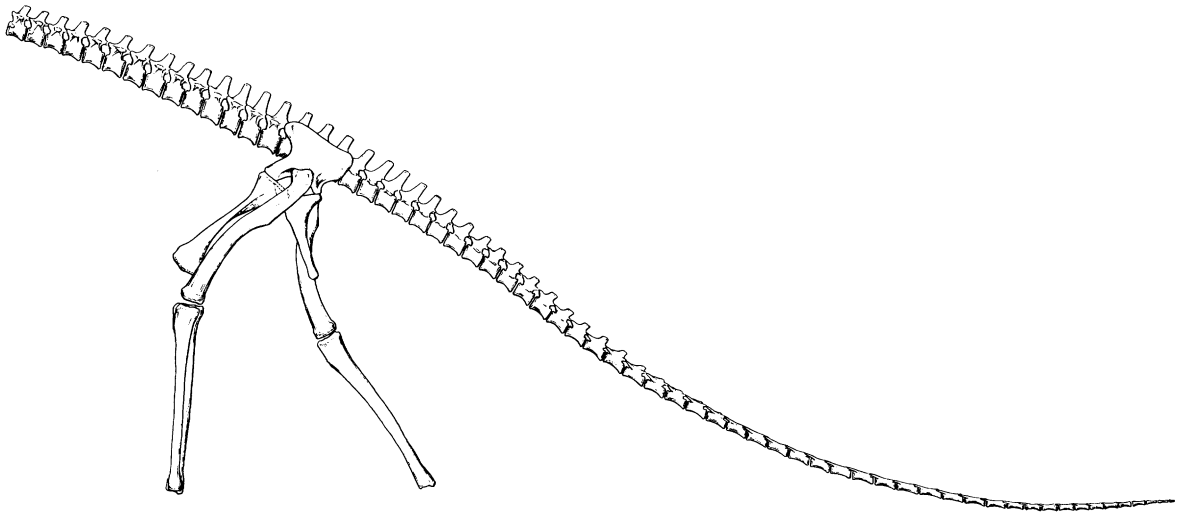

FIG. 14. *Staurikosaurus pricei,* new genus and species. Incomplete posterior section of articulated skeleton in left lateral view. $\frac{1}{10}$ natural size.

as well as the strongly developed bipedalism and elongated lower limb that characterize this genus, are features that point to its position within the infraorder here designated as the Teratosauria, the brachyiliac carnivores of the Triassic, rather than within the infraorder Plateosauria, the palaeopods trending in the direction of the later sauropods.

Kuhn in 1959 quite properly replaced the name *Palaeosaurus* with *Palaeosauriscus.* From this it follows that the widely used family name Palaeosauridae is to be replaced by Palaeosauriscidae. Here this series of substitutions stops. There is no rule requiring that names of higher categories be based on family names. We do not therefore have to use a name such as Palaeosauriscia, which, as a spoken word, might be mistaken for some combination utilizing the name of the order Saurischia. It is here suggested that the infraorder, designated as Palaeosauria (see Colbert, 1964), be changed as follows:

TERATOSAURIA, NEW NAME

The Teratosauria as here recognized includes perhaps three families: the Ammosauridae, Palaeosauriscidae, and Teratosauridae. The Ammosauridae is characterized by rather elongated vertebrae, and a relatively short, broad pubis, which characters would seem to exclude *Staurikosaurus* from its confines. *Palaeosauriscus,* which is typical of the Palaeosauriscidae also has somewhat elongated vertebrae, but these are perhaps more nearly comparable with the vertebrae of *Staurikosaurus* than those of *Ammosaurus.* Moreover, *Palaeosauriscus* has an elongated, rather narrow pubis, which accords with the nature of this bone in *Staurikosaurus.* In the Teratosauridae the pubis is also long and narrow, but these dinosaurs are large with a large skull in which the teeth are elongated and dagger-like. From what is seen of the jaw of *Staurikosaurus* it appears that although the skull in this genus was probably rather large, the teeth were probably relatively small, pointed, and straight, which again brings it into line with *Palaeosauriscus.* For these reasons, therefore, *Staurikosaurus* is here classified within the Palaeosauriscidae.

Spondylosoma, it will be recalled, was placed by Romer (1956) within the Thecodontosauridae, one of the three families of the infraorder Plateosauria (the other two being the Plateosauridae and the Melanorosauridae) according to the present classification. The known characters of *Spondylosoma* justify its retention in this position; it is small, as is typical of members of this family, and it shows elongation of the neck vertebrae and other characters that align it with those palaeopods that show affinities to the predecessors of the sauropods. *Herrerasaurus* was

placed by Rozhdestvensky and Tatarinov (1964) in the Thecodontosauridae. This saurischian is one of the larger Triassic dinosaurs, and its obviously large skull and large teeth, indicated in the lower jaw, as well as the weight of the hind limb, relatively short tibia, and broad foot, are characters that might justify the placing of *Herrerasaurus* in the Teratosauridae.

Ischisaurus, a small dinosaur, from what is known shows certain resemblances to *Staurikosaurus* and might belong, like the latter, in the Palaeosauriscidae rather than in the Thecodontosauridae, where it was placed by Rozhdestvensky and Tatarinov (1964). As for still another dinosaurian genus *Triassolestes,* described by Reig (1963), it certainly appears to be a podokesaurid, as maintained by that author.

In the light of the above, it is suggested in the present paper that the Triassic dinosaurs of South America show the following taxonomic relationships:

Order Saurischia
- Suborder Theropoda
  - Infraorder Coelurosauria
    - Family Podokesauridae
      - *Triassolestes romeri* Reig—Ischigualasto, Argentina.
- Suborder Palaeopoda
  - Infraorder Teratosauria, new name
    - Family Palaeosauriscidae
      - *Staurikosaurus pricei,* new genus and species—Santa Maria, Brazil.
      - *Ischisaurus cattoi* Reig—Ischigualasto, Argentina.
    - Family Teratosauridae
      - *Herrerasaurus ischigualastensis* Reig—Ischigualasto, Argentina.
  - Infraorder Plateosauria
    - Family Thecodontosauridae
      - *Spondylosoma absconditum* von Huene—Santa Maria, Brazil.

At best the above arrangement is tentative, and awaits the refinements of further work on more materials. Indeed, the classification of Triassic saurischians as proposed by the present author, as well as previous classifications by other authors, leaves much to be desired. So many of the Triassic forms are known from fragmentary materials, that the delineation of diagnostic characters for families is incomplete. One of the problems is that all of the brachyiliac saurischians of the Triassic are closely related. The several families that have been set up for these dinosaurs are, if valid, the branches of a phylogeny in the early stages of its development; consequently their resemblances to one another are many and their differences are comparatively slight. This must be kept in mind. We are here looking at early dinosaurian history not far

removed from its thecodont ancestry.

Age and Correlations

The occurrences of *Staurikosaurus* as well as of *Spondylosoma* in the Santa Maria beds are of particular significance, as they may bear upon the age and the correlation of these sediments. The same can be said for the dinosaur genera *Herrerasaurus, Ischisaurus,* and *Triassolestes* described by Reig (1963), and their bearing upon the age of Ischigualasto Formation of Argentina.

The Santa Maria Formation has been regarded either as of Middle Triassic or Late Triassic age. Those who equate this formation with the middle portion of the Triassic sequence generally state that it probably comes within the topmost part of this Triassic division; those who equate it with the upper part of the Triassic generally, state that it belongs to the lowermost division of the Keuper. The difference between the two views is not great, yet it should be reexamined. It is here maintained that the Santa Maria beds of Brazil and the Ischigualasto beds of Argentina must be considered together, because there hardly can be much doubt but that the sediments in the two regions and their similar faunas, represent closely related, if not contemporaneous, widespread phases of Triassic history in the southern portion of South America.[1]

Romer has for a number of years been a strong proponent of a Middle Triassic age for these beds, as expressed in various publications, most recently in 1966. Bonaparte, rather tentatively supported a Middle Triassic age in 1960 for both the Santa Maria and Ischigualasto formations, and more definitely for the Ischigualasto beds in 1962. He defined these sediments as "Mesotriassic." (But see below.) A similar view was maintained by Reig (1963, p. 4) for the Ischigualasto beds, thus: "Rhynchosaurs, Therapsids and Rauischid Thecodonts make the fauna Middle Triassic in age, but the other elements seem to indicate that we are dealing with a fauna of the uppermost Middle Triassic."

The idea that the Santa Maria beds should be placed in the Upper Triassic was set forth as long ago as 1933 by von Huene, who stated that these sediments (which he called the Rio do Rasto beds) are of Carnian

[1] It should be noted, however, that Bonaparte on the chronology of Triassic formations in Argentina implied that the Ischigualasto Formation may be slightly younger than the Santa Maria Formation. "Present knowledge indicates that the cynodonts from Ischigualasto are a little younger than those from Brasil. . . ." (Bonaparte, 1966b, p. 7). And on page 8: "In several genera of the fauna of the Ischigualasto Formation, then, we find some advances over related Brasilian genera."

or Late Triassic age. This opinion was followed by Couto (1943). Price (1947) placed the Santa Maria Formation in the Upper Triassic, more or less as an equivalent of the Stormberg beds of South Africa. Frenguelli placed the Argentine beds in the Keuper in 1948, whereas Groeber and Stipanicic in 1952, and Stipanicic in various papers since then, regarded them as of Norian age. Caster (1952) also placed the Ischigualasto Formation in the Upper Triassic but was more equivocal about the Santa Maria Formation, indicating it covered a considerable time sequence, from the final stages of the Early Triassic through the Late Triassic. Zingano and Cauduro (1959) also judged the Santa Maria beds to be the equivalent of the Stormberg, citing the opinions of von Huene, Price, and Mackenzie Gordon. These authors in addition called attention to work on plants and arthropods by Pinto (1956) that would correlate the Santa Maria with the Molteno of South Africa, the "Série Cacheuta" of Argentina, and the Wianamatta of Australia. It may be added that the Molteno, hitherto placed in the Middle Triassic, perhaps because it comes between the unequivocal Lower Triassic *Cynognathus* zone and the unequivocal Upper Triassic Red Beds Formation, possibly belongs, as indicated by recent studies, in the lower portion of the Upper Triassic. Cox, 1965, recognizing the difficulty of making unequivocal age assignments for the South American Triassic formations, suggested upon the basis of his review of the evidence, that the Santa Maria Formation might be of Ladinian age, antedating slightly the Carnian Ischigualasto Formation. Finally, Bonaparte now (1966a and 1966b) regards the Ischigualasto Formation as having Upper Triassic affinities, placing it at the Carnian level in the Triassic sequence. Whether this automatically raises the Santa Maria Formation to a similar level is a moot point. If the Ischigualasto fauna is slightly more advanced than the Santa Maria, as intimated by Bonaparte, then this latter assemblage might be of late Middle Triassic (Ladinian) affinities. In addition to the workers listed above, the present author has advocated a possible Upper Triassic position for the Santa Maria Formation and its included fossils.

So far as the vertebrate fauna is concerned, the differences in opinions as to the age and correlation of the Santa Maria and the more or less equivalent Ischigualasto Formation are brought about to a large degree by what might be called a "mixture" of elements in the fauna. How does one evaluate related faunas that contain procolophonids, therapsids, rhynchosaurs, pseudosuchians, and saurischian dinosaurs? In this context the new, progressive elements in such faunas generally are, in my opinion, of greater value than long established conservative forms. Many animals can and do persist as holdovers into later faunal assemblages, but they are

not necessarily the forms most crucial to the dating of these later faunas, a fact that should be kept in mind.

Candelaria, a representative of one of the long-lived groups within the Santa Maria fauna, is a conservative genus as compared with other Triassic procolophonids, such as the forms described from the German Buntsandstein, and especially those Triassic genera from the Elgin sandstone of Scotland and the Newark beds of North America. By reason of its long, bradytelic heritage, it is not definitive in this connection.

The several therapsids, representing the other long-lived group in the Santa Maria fauna, are of much more significance in this regard. As for the dicynodonts, there is no reason why they might not represent persisting members of a group that lived through the extent of Triassic time, especially since some dicynodont genera obviously were long lived. Certainly the presence of the gigantic *Stahleckeria* in the Santa Maria fauna is closely paralleled by the presence of the gigantic *Placerias* in the Upper Triassic Chinle and Newark faunas of North America. The other Santa Maria therapsids are cynodonts, which seemingly constitute a close link with the Lower and especially the Middle Triassic cynodonts of southern Africa, notably with certain genera in the Manda and Molteno formations. These resemblances are fortified by the presence in the Argentinian Ischigualasto sediments of numerous broad-toothed or "gomphodont" cynodonts, which Bonaparte (1966a and 1966b), as we have seen, considers as being slightly younger than the cynodonts of Brazil.

This brings us to the groups of Triassic origin, among which the rhynchosaurs are particularly characteristic, and, as we now know, of worldwide distribution. These reptiles probably reached their widest development in late Triassic times, although Romer (1962) has envisaged them as constituting a group reaching its greatest adaptive radiation within the Middle Triassic. Of the known genera, however, *Hyperodapedon* occurs in the Keuper of Europe, whereas *Paradapedon* is found in the Maleri beds, certainly of Keuper age, in India. (Recently a new and as yet undescribed rhynchosaur has been discovered in the Upper Triassic Newark sediments of Nova Scotia.) *Mesosuchus* and *Howesia* are in the Lower Triassic *Cynognathus* zone of Africa and *Eifelosaurus* (questionably included here) occurs in the European Buntsandstein. This leaves as Middle Triassic rhynchosaurs (excepting the Santa Maria genus, *Scaphonyx*) *Rhynchosaurus* from England, in sediments recently determined as of Middle Triassic (Ladinian) affinities rather than as of Keuper age (as had been considered), and *Stenaulorhynchus* from the Manda beds of Africa. Perhaps *Scaphonyx* is also of Middle Triassic affinities, but its

morphological features are undoubtedly much closer to the Upper Triassic *Hyperodapedon,* than to those of *Stenaulorhynchus.* On the face of such evidence, therefore, the Santa Maria rhynchosaur seems to come within the Upper rather than the Middle Triassic.

We now come to the dinosaurs, which should be carefully considered because these reptiles, both saurischians and ornithischians, are considered to have originated in late Triassic times. Certainly in the type Triassic of southern Germany there are no positively identified dinosaurs below the Lettenkeuper, the base of the Upper Triassic in that area. This fact deserves close attention, because our concepts of Triassic correlations should, in the last analysis, be based upon the succession of the Triassic in the type region. The difficulty of the type Triassic is that it consists of a lower and an upper division of continental facies, separated by a marine middle division. Consequently we are not able to define a true Middle Triassic continental fauna in the type region, although the fossil remains of various land-living types are found here and there in the Muschelkalk, evidently the remnants of animals that were washed from the land into marine near-shore facies. Such facies are especially marked in the Triassic of Württemberg, in decided contrast to regions farther to the north and east. Thus we obtain a glimpse of Middle Triassic land-living tetrapods in the region where the Triassic was first studied and defined.

Martin Schmidt (1928), in his compendium "Die Lebewelt unserer Trias" indicated four dinosaurs as having been found in the Muschelkalk. These are *Teratosaurus* (?) *schutzi,* from the Upper Muschelkalk, but with the locality data not definite; *Zanclodon silesiacus,* from the very bottom of the Muschelkalk, from the Wellenkalk; *Thecodontosaurus primus,* from the Wellenkalk; and *Thecodontosaurus latespinatus,* supposedly from the Upper Muschelkalk, but without definite locality data. Brief evaluations of these occurrences are presented below, based not only upon analysis of the several cases made by the present author, but also upon careful investigation by Frank Westphal (personal correspondence). In short, the several occurrences may be summarized as follows.

Zanclodon schutzi, subsequently assigned to the genus *Teratosaurus* was described by E. Fraas in 1910, on the basis of a single tooth, said to come from the uppermost Muschelkalk (Trigonodus Dolomit) from the surroundings of Schwäbisch Hall, Württemberg. The stratigraphic information on this tooth is very equivocal indeed. Fraas seemingly based his stratigraphic allocation of the single tooth that constitutes the type upon the nature of the rock matrix adhering to it. "So ist kein Zweifel über das Lager, aus welchem er stammt und ein Irrtum ausgeschlossen." But

von Huene (1956) considered the stratigraphic position of the specimen doubtful, saying that it came "eventuell aus dem allerhöchsten Muschelkalk von Schwäbisch Hall." Moreover, the nature of the specimen itself is so uncertain that no valid identification of it can be made. Von Huene suggested that it might properly be placed in the genus *Tanystrophaeus.*

Therefore *Zanclodon schutzi* can be eliminated from any serious consideration on the grounds of the virtual impossibility of making a valid identification of the type and the uncertainty of its stratigraphic position.

Zanclodon silesiacus, also based upon a single tooth, was described by Jaekel in 1910. The horizon is given as the Lower Muschelkalk, and the locality is Upper Silesia. In the case of this specimen there is no particular doubt as to the validity of the stratigraphic and geographic data. But the systematic assignment of the fossil can be, and has been, subject to doubt. A single archosaurian tooth, such as this, can rarely be of much value for the purpose of a generic identification, or even for assignment on a higher taxonomic level. This was recognized not only by von Huene (1956) but also by O. Kuhn, 1965, who stated that the fossil "kann ein Theropode sein, aber auch ein thecodontier oder Prolacertilier."

Zanclodon silesiacus, because of the uncertainty as to which order of reptiles it may belong, can be eliminated from consideration here.

Thecodontosaurus primus was described by von Huene (1908) on the evidence of two incomplete vertebrae, found in the Lower Muschelkalk, near Gogolin, Upper Silesia. There is no reason to doubt the stratigraphic position of the fossils, which as von Huene pointed out, probably floated into their burial position from some higher ground. But as in the case of the species considered above, there is considerable doubt as to the taxonomic identification of the fossils. They may be dinosaurian, but they can perfectly well be pseudosuchian vertebrae, and most probably are.

Therefore *Thecodontosaurus primus* is an equivocal species, and has no sound value in any consideration as to the lower limits at which dinosaurs have been found.

Thecodontosaurus latespinatus was also described by von Huene (1908) on the evidence of a series of vertebrae, said by him to come from the *semipartitus* zone at the very top of the Upper Muschelkalk at Laineck near Bayreuth, from the *nodosus* beds, also high in the Muschelkalk near Göttingen, from the upper Bonebed on the border between the Muschelkalk and the Lettenkeuper at Oelmühle near Crailsheim, and from the *semipartitus* zone of Blainville near Lunéville. If these occur-

rences can be accepted, they would place one dinosaur, at least, high in the Middle Triassic of Germany. But there may be some doubt as to the validity of some of these records.

Aside from the problem of stratigraphic assignments, there has been considerable doubt expressed as to the identification of any of these materials as dinosaurian. O. Kuhn in 1965 remarked of this species that it is "eine ganz unsichere Form, die wohl gestrichen werden muss; wahrscheinlich besteht Identität mit *Tanystrophaeus conspicuus*." The resemblances to *Tanystrophaeus* were noted by von Huene (1908) in his original description, and this has been confirmed by Westphal (personal correspondence). It seems to me that the only specimens described by von Huene that might show any possible indication of being saurischian are the vertebrae figured in plate XCI, figures 3, 4, and 7 of his monograph of 1908. These all allegedly come from the *semipartitus* zone at the very top of the Muschelkalk, two from Bayreuth, one from Blainville near Lunéville. But at best their identification is open to question.

Thecodontosaurus latespinatus is, like the other forms previously considered, a species of uncertain position, therefore valueless for determining the lowest occurrences of dinosaurs in the stratigraphic record.

Thus the evidence for saurischian dinosaurs below the Lettenkeuper of Germany evaporates when subjected to close scrutiny, and the presence of such dinosaurs in the area of the type Triassic prior to the advent of the Late Triassic history is still to be proved.

This brings us, finally, to the pseudosuchians. In connection with the type Triassic, there should be mentioned the description by Krebs, 1963, of the skeleton of *Ticinosuchus ferox,* found in the Anisian beds of southern Switzerland. Here we see a good, fully terrestrial tetrapod from the type Middle Triassic of Central Europe, and are given a clue as to what a land-living Middle Triassic reptile from the type sequence is like, not what it ought to be like.

Ticinosuchus obviously is closely related to *Prestosuchus,* a pseudosuchian described by von Huene from the Santa Maria Formation. So close are the relationships of these two genera that, as Krebs has argued, they can both be placed within the same family, the Rauisuchidae, as defined by von Huene in 1956. This does not necessarily mean that the two genera are of correlative age; it seems probable that *Prestosuchus* may be a persistent type, later in age than *Ticinosuchus.* But the evident relationship of the pseudosuchian from the Santa Maria Formation with the genus from the Middle Triassic sediments of Switzerland suggests that their time separation may not be great. *Ticinosuchus* is of Anisian age; *Prestosuchus* may be of Ladinian age. It is interesting to note that

TABLE 2
SUGGESTED CORRELATION OF CERTAIN SOUTH AMERICAN TRIASSIC FORMATIONS

		Alpine stages	Germanic section	South Germany	Brazil	Argentina
Triassic	Upper	Rhaetian	Keuper	Rät		
		Norian				Los Colorados
		Carnian				Ischigualasto
		Ladinian		Lettenkohle	Santa Maria	Los Rastros
	Middle	Ladinian	Muschelkalk	Haupt Muschel-kalk		
				Anhydrit Gruppe		
		Anisian		Wellen-kalk		

Bonaparte considered certain pseudosuchians from the Ischigualasto Formation, which he placed at about a Carnian position, to "represent anatomical advances over the Brasilian and African rauisuchids, comparable to the position noted in the cynodonts" (1966, p. 7).

In a final analysis the temporal position of the Santa Maria Formation, as indicated by the fossil vertebrates, seems to come down to a choice between the evidence of the cynodonts and the pseudosuchians on the one hand, which favors a possible late Middle Triassic or Ladinian age, as against the evidence of the rhynchosaurs and the dinosaurs on the other hand, which favors a possible Upper Triassic or Carnian age. (The procolophonids and the dicynodonts are here considered as being of less significance for dating than the other elements in the fauna.) The cynodonts and the pseudosuchians in the Santa Maria fauna certainly indicate what such Middle Triassic reptiles ought to be

like, although they might be persistent forms into the lowest phases of the Upper Triassic, as suggested for the cynodonts, at least, by the recent discovery of a cynodont very much like a Manda form, from the Newark beds of Nova Scotia. The rhynchosaurs and dinosaurs are certainly typical Upper Triassic forms, although they might be pioneer types coming in at the final stages of Middle Triassic history. The procolophonid and the dicynodonts might be in either stage of this portion of Triassic time.

If the Santa Maria Formation is of Ladinian age, then we see the appearance of dinosaurs in this part of the world prior to their known appearance elsewhere. This may be true, especially in view of the evidence, as expressed by Bonaparte, that the cynodonts and the pseudosuchians of the Santa Maria seem to be slightly more primitive than these same reptiles in the Upper Triassic Ischigualasto Formation.

But is it not equally possible, even though the fauna of the Santa Maria Formation is slightly more primitive in some of its aspects than the fauna of the Ischigualasto Formation, that these two assemblages might nevertheless be of Upper Triassic affinities? Why could not the Santa Maria fauna, with the dinosaurs *Staurikosaurus* and *Spondylosoma,* the rather advanced rhynchosaur *Scaphonyx,* and persistent cynodonts and pseudosuchians, be only slightly older than the Ischigualasto fauna that contains the dinosaurs *Herrerasaurus, Ischisaurus,* and *Triassolestes,* the rhynchosaur *Scaphonyx,* and persistent cynodonts and somewhat advanced pseudosuchians? Why could not both faunas come within the confines of the basal part of the Upper Triassic with the Santa Maria fauna representing the beginning of Late Triassic tetrapod history in South America, and the Ischigualasto fauna representing the continuation of that history into the later phases of Carnian time? Certainly there is enough geologic time available within the basal portion of Late Triassic time to accommodate both these faunas in succession.

CONCLUSIONS

Staurikosaurus pricei, from the Santa Maria Formation of Rio Grande do Sul, Brazil, is here identified and described as an early saurischian dinosaur. It may be considered one of the various reptiles that ushered in the beginning of Late Triassic history in this part of South America. It occurs in association with traversodontid cynodonts, dicynodonts, and pseudosuchians that give to the Santa Maria fauna a general Middle Triassic appearance, yet the presence of this dinosaur, together with the saurischian genus *Spondylosoma,* as well as with an advanced rhynchosaur,

Scaphonyx, lends a distinct Upper Triassic aspect to the fauna. Although the evidence, as based upon the morphological development of its various constituent elements, indicates that the Carnian Ischigualasto fauna of Argentina is slightly later than the Santa Maria fauna, which with some justice might then place this latter fauna within the Middle Triassic Ladinian time stage, it is here suggested that the differences between various genera in the two faunas are of such slight import that both assemblages can very logically be placed within the lower or Carnian phase of the Upper Triassic. Such an assignment, which accords with the presence of dinosaurs and a specialized rhynchosaur in the faunas, is here suggested as being more appropriate than an assignment of the Santa Maria assemblage to the late Middle Triassic on the basis of genera representing evolutionary lines persisting from earlier stages of Triassic history.

Thus the Santa Maria fauna represents an early phase in the world-wide spread of the Late Triassic tetrapod faunas, which are particularly characterized by the presence within them of primitive saurischian dinosaurs.

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