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NEW MATERIALS OF LAGOSUCHUS TALAMPAYENSIS ROMER (THECODONTIA - PSEUDOSUCHIA) AND ITS SIGNIFICANCE ON THE ORIGIN OF THE SAURISCHIA. LOWER CHANARIAN, MIDDLE TRIASSIC OF ARGENTINA

J. F. BONAPARTE

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NEW MATERIALS OF LAGOSUCHUS TALAMPAYENSIS ROMER (THECODONTIA - PSEUDOSUCHIA) AND ITS SIGNIFICANCE ON THE ORIGIN OF THE SAURISCHIA

LOWER CHANARIAN, MIDDLE TRIASSIC OF ARGENTINA*

by JOSÉ F. BONAPARTE
Fundación Miguel Lillo - Career Investigator Member of CONICET

ABSTRACT

On the basis of new remains of *Lagosuchus* that are thoroughly described, including most of the skeleton except the manus, it is assumed that *Lagosuchus* is a form intermediate between Pseudosuchia and Saurischia.

The presacral vertebrae show three morphological zones that may be related to bipedality: 1) the anterior cervicals; 2) short cervico-dorsals; and 3) the posterior dorsals. The pelvis as a whole is advanced, in particular the pubis and acetabular area of the ischium, but the ilium is rather primitive. The hind limb has a longer tibia than femur, and the symmetrical foot is as long as the tibia. The tarsus is of the mesotarsal type. The morphology of the distal area of the tibia and fibula, and the proximal area of the tarsus, suggest a stage transitional between the crurotarsal and mesotarsal conditions. The forelimb is proportionally short, 48% of the hind limb. The humerus is slender, with advanced features in the position of the deltoid crest. The radius and ulna are also slender, the latter with a pronounced olecranon process.

A new family of Pseudosuchia is proposed for this form: Lagosuchidae. Its level of organization is discussed in some detail and the transitional condition of *Lagosuchus* between Pseudosuchia and Saurischia is analyzed. The possible relationships of *Lagosuchus* with Triassic saurischians are discussed according to the information from vertebral zonation, pelvis, hind limb, and disparity of the limbs. It is concluded that *Lagosuchus* is part of a thecodont radiation that probably produced both orders of dinosaurs.

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INTRODUCTION

The composition of the order Thecodontia has been better understood recently with the description of various new forms; especially significant are those from the Middle Triassic of Los Chañares, Argentina, made known by Romer (1971a, 1971b, 1971c, 1972a, 1972b, 1972c, 1972d), in particular because they correspond to a poorly known period in thecodont history.

It is clear that the integration and understanding of the Thecodontia is currently very far from being moderately satisfactory because, in spite of its condition ancestral to the rest of the archosaurs (Saurischia, Ornithischia, Pterosauria and Crocodylia), we have not yet gained sufficiently clear knowledge about the systematic connections of any of these archosaurs with a given group of thecodonts, except the general statement that the suborder Pseudosuchia collects, among its components, forms with a general anatomical plan capable of having originated the remaining archosaurs, notwithstanding the opinion of Krebs (1974). The Lower Triassic *Euparkeria*, in spite of the enormous anatomical distance that separates it from the remaining Archosauria, has been cited many times with reference to the primitive characters of the non-thecodont Archosauria; I follow this, referring to *Euparkeria* for a certain time until enough new forms have been described and studied that more clearly correspond to the ancestral positions of one or another group of saurischians, crocodilians, pterosaurs, etc.

In this sense the analysis and appraisal of new materials of *Lagosuchus talampayensis* Romer (1971b), from Los Chañares, advances the understanding of the origin of the level of organization common to Triassic dinosaurs. The materials described here were produced from the Ischichuca Formation ("Chañares Fm."), La Rioja, Argentina, collected in 1969 during a paleontological expedition organized by the Fundacion-Instituto Miguel Lillo, and financed in large part by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), grant 1217d. Moreover the specimens of *Lagosuchus* now deposited in the Instituto de Antropología de la Universidad Provincial de La Rioja and the Museum of Comparative Zoology of Harvard, USA have been consulted and revised. The Guggenheim Foundation of the United States has made a foreign trip possible for the author, during which he studied the specimens at Harvard.

PRECEDING WORKS

The species *Lagosuchus talampayensis* Romer was originally described (1971b) from incomplete materials of both hind limbs, an incomplete forelimb, and a discontinuous series of vertebrae. The description of the holotype material, figured by Romer in a later work (1972d), was very concise but completed with the consideration of some materials from the collection of the Fundacion-Instituto Miguel Lillo. Thus he could offer a reconstruction of the foot of *Lagosuchus*

(Romer 1971b, fig. 2) showing some details that are reasonably correct. In this same work he illustrated an ilium of *Lagosuchus* that, lamentably, was distorted by post-mortem effects.

In 1972d Romer illustrated the holotype material (Museo de La Plata No. 64-XI-14-11, *partim*) and a series of 11 dorsal vertebrae corresponding to a specimen from the Museum of Comparative Zoology (MCZ 4116), and briefly referred to part of the material described in this work.

Lagosuchus lilloensis Romer, described and figured in the same work (1972d, pp. 5-7, figs. 5 and 6), cannot be separated from *L. talampayensis* by the single argument presented: its 50% larger size. I believe that this species must be considered synonymous with *L. talampayensis.*

The principal characters of *L. talampayensis* cited by Romer are as follows: long and slender hind limb; rather reduced forelimb; femur with clearly projecting articular head that is distinct from the shaft; tibia longer than femur; fused and elongated astragalus and calcaneum, united with the tibia and fibula; digit I short, digit V represented only by a short metatarsal, digits II and IV subequal in metatarsal length, however digit III is the longest of the series.

Romer interpreted *Lagosuchus* as an advanced pseudosuchian thecodont, clearly bipedal, with hind limbs in a vertical position, and whose presence in the Middle Triassic contributed evidence to a possible radiation of thecodonts occurring during the Lower Triassic. The construction of the tarsus (in *Lagosuchus* and *Lagerpeton*) suggests (Romer 1971b, p. 9) that both genera were linked in some way with a radiation towards the dinosaurs, particularly the Coelurosauria, an idea that I think is correct.

CHARACTERS OF THE SPECIES

Order: THECODONTIA
Suborder: PSEUDOSUCHIA
Infraorder: ORNITHOSUCHIA
Family: LAGOSUCHIDAE nov.
Genus: *LAGOSUCHUS* Romer 1971

Type species: *Lagosuchus talampayensis* Romer 1971

Distribution. Lower beds of the Ischichuca Formation ("Chañares Formation"), lower Chañarian, Middle Triassic.

Diagnosis of the genus. Small carnivorous pseudosuchian with three morphological types of presacral vertebrae: anterior cervicals (elongated), cervico-dorsals (short) and posterior dorsals

(elongated); forelimb approximately 47% the length of the hind limb. Pelvis with laterally exposed distal pubis; acetabular region with reductions in the pubis and ischium; ilium of primitive type.

Hind limb with femur shorter than tibia; globular femoral head projects anteromedially; aliform 4th trochanter located on the upper third of the shaft; subcylindrical shaft. Long tibia; articulation of the distal end with characteristics transitional between thecodont (major axis in the axial direction) and saurischian (major axis in the transverse direction) conditions. Mesotarsal-type tarsus, with the astragalus clearly much larger than the calcaneum. Low astragalus, with a dorsal process separating the tibial and fibular facets. Reduced calcaneum with a vestigial calcaneal process. Two distal tarsals, the external with a kind of trochlea to articulate with a fossa of the calcaneum. Long, symmetrical pes; digitigrade condition, with the central digit the longest. Metatarsals I and V of equal length, clearly shorter than the rest.

Slender, elongate humerus with the deltoid crest a certain distance from the proximal end. Radius and ulna also elongate, as in *Pseudhesperosuchus*; ulna with an extensive olecranon process.

Lagosuchus talampayensis Romer 1971
Synonymy: *Lagosuchus lilloensis* Romer 1972

Diagnosis of the species. The same as for the genus.

Holotype. Museo de La Plata No. 64-XI-14-11 (in part), currently in the Instituto de Antropología de la Universidad Provincial de La Rioja, Argentina. Incomplete hind limbs and also one incomplete forelimb.

Hypodigm. In addition to the holotype, the following collection (detailed more later): MCZ 4116 including vertebrae, limb bones and the pelvic girdle; PVL 3870, cranial fragments, vertebral sequence, pelvis and hind limbs; PVL 3871, the holotype of "*Lagosuchus lilloensis*" Romer 1972; PVL 3872, cranial fragments connected to a vertebral series.

Horizon and locality. Lower part of the Ischichuca Formation ("Chañares Formation"), Los Chañares region, 2 km SE of the gateway to Talampaya, Dpto. Gral. Lavalle, La Rioja, Argentina.

Available materials. Holotype: Museo de La Plata No. 64-XI-14-11 (in part), currently in the Instituto de Antropología de la Universidad Provincial de La Rioja. It consists of incomplete hind limbs with the femur, tibia, fibula and pes, and an incomplete forelimb with the humerus, radius and ulna.

MCZ 4116 includes a sequence of 17 presacral vertebrae, most of which are complete and articulated except the last two presacrals; an incomplete sacrum, the incomplete left ilium, a fragment of the pubis, and most of the right femur articulated with the proximal end of the tibia.

PVL 3870 consists of a left maxilla with teeth; a cranial fragment that includes the basioccipital, basisphenoids, exoccipital and opisthotic, connected to an articulated sequence of 9 cervical vertebrae; a sequence of 12 articulated presacral vertebrae; the incomplete sacrum and a series of 15 caudal vertebrae, 3 of which are fused to the sacrum and the rest articulated. The nearly complete pelvis, almost intact on the right side and with little distortion; both complete articulated hind limbs, with the tarsal bones in their original position on the left side; both articulated pedes lacking several phalanges, particularly the unguals.

PVL 3871 the holotype of "*Lagosuchus lilloensis*", consists of a sequence of 29 articulated vertebrae including a dorsal, two sacrals and the remainder caudals; both ilia, and the incomplete right pubis and ischium; both nearly complete articulated hind limbs; the incomplete left scapulocoracoid connected to the complete humerus, and the incomplete radius and ulna.

PVL 3872 is a sequence of 22 articulated vertebrae connected to a cranial fragment that includes part of the right temporal region, the basicranium and the right suspensorium.

DESCRIPTION

The skull. Two cranial fragments are preserved in PVL 3870. One of these corresponds to the basicranium and was found articulated with the anteriormost vertebrae, permitting observation of its left lateral face and part of the posterior region. It consists of the basioccipital, incomplete basisphenoids, prootic, exoccipital, and a large part of the left opisthotic.

There is a large aperture on the lateral face, bordered dorsally by the opisthotic, that encloses the fenestra ovalis, the exit for nerves VII and IX, and the communication with the pituitary fossa. This large opening is bounded ventrally by the basisphenoids, and posteriorly by the basioccipital and exoccipital. The prootic, which borders part of this opening, is the largest ossification of the cranial fragment. There is a depression in its dorsal region corresponding in part to the post-temporal foramen, and an area of contact with the squamosal that extends over the opisthotic. The suture between the prootic and opisthotic is not clear. The topography of the prootic shows pronounced relief on its entire surface. A distinct edge is present dorsally to the fossa that marks the exit of nerve V; a strong step travels over the prootic from its dorsal end near

the opisthotic forward and down up to the anteroventral end, defining a depressed area behind, and an elevated area anteriorly.

The basisphenoids are incomplete, although the sutures with the prootic and basioccipital can be seen. They are missing anteriorly and proximally up to the tuberae of the basioccipital. In posterodorsal view the supraoccipital and opisthotic, or paroccipital process, can be seen, incomplete laterally.

The preserved portion of this cranial fragment measures only 9 mm, from the inferior part of the basisphenoids to the highest part of the opisthotic, from which the posterior cranium would not be more than 20 mm in height.

The rest of the cranial fragment of this specimen corresponds to the left maxilla, exposed in medial view. The inferior border, bearing teeth, is reasonably good except anteriorly and posteriorly where it apparently lacks a short section of bone, although anteriorly there are indications of a premaxillary fragment.

The position of the anterior border of the antorbital opening is relatively clear, and suggests that it was angled anteriorly. The dorsal process of the maxilla is extended anteroposteriorly, relatively low, and extended somewhat backwards, indicating that the skull was relatively low and narrowed anteriorly, in contrast with that of *Gracilisuchus* Romer (1972d) which is relatively tall in this region.

There are 9 teeth preserved and 3 alveoli, by which the minimum number of maxillary teeth is 12. The teeth are conical, relatively robust, laterally compressed and recurved, with some indications of serrated edges. Their appearance is clearly more robust than in *Gracilisuchus* or *Lewisuchus* Romer (1972c), from the same beds and locality.

The remaining cranial fragment is from PVL 3872 and also corresponds to the basicranial region, but it offers more information anteriorly because the basisphenoids and opisthotic are more complete, and also preserves a large part of the squamosal and quadrate. This cranial fragment is also connected to the column, in this case 22 vertebrae. In this fragment (fig. 3), which includes both opisthotics, prootics and the complete occipital region (lacking the parietals) - somewhat deformed by dorsolateral compression - note that the opisthotic is ventrally concave in its lateral region, and that it forms a kind of eave over the large lateral basicranial depression, terminating laterally in a point above which is attached the squamosal.

In this the lateral depression, which houses the fenestra ovalis and the exit for nerves VII and IX, coincides morphologically with the previously described cranial fragment, but shows more ossification interiorly.

The basisphenoids are triangular in ventral view, wide in the area of articulation with the basioccipital forming prominent tuberae, and narrow anteriorly from where the prominent,

ventrolaterally projecting basipterygoid processes emerge. The characters of these processes indicate that a mobile articulation existed between the palate and basicranium in this species.

The squamosal, attached to the anterolateral end of the opisthotic, is triradiate, recalling the condition in *Euparkeria* and prosauropods among others, with a thin, ventrally directed extension attached to the quadrate; another relatively short and medially directed, which at the same time borders the upper temporal fenestra and the post-temporal foramen; and the last, broken in this case, directed forwards, which must have attached to the postorbital and bordered the upper and lower temporal fenestrae. Ventrally it presents a large articular cavity for the quadrate.

The quadrate is articulated with the squamosal on its ventral face by means of a poorly developed condyle. It is relatively narrow in lateral view, extends dorsoventrally and curves backwards somewhat, with a well-developed articular condyle for the mandible. The laminar medial face of the quadrate is incomplete, so that its suture with the pterygoids cannot be seen. The connection of both faces of the quadrate forms a strong ridge that covers practically the entire posterior extension of this bone.

These cranial fragments offer little towards obtaining a clear idea of the general morphology of the skull of *Lagosuchus*. The characteristics of both the maxilla and the squamosal and quadrate tend to show that the skull was similar to that of *Euparkeria*, although proportionally lower. At the same time these characters support the interpretation that the skull was proportionally shorter and higher than in the Cerritosauridae (Bonaparte 1971a) such as *Cerritosaurus*, *Chanaresuchus* and *Gualosuchus*. Comparison of the squamosal and quadrate of *Lagosuchus* to that of *Gracilisuchus* Romer (1972b) reveal strong differences, since in this genus from Los Chañares the squamosal is wide laterally and posteriorly, and the quadrate articulates in a more medial plane.

The vertebral column. The remains of the vertebral column in PVL 3870 are very informative, since they articulate with the skull and pelvis, although there is a section of at least 5 missing anterior dorsals; those of MCZ 4116 are somewhat incomplete but allow estimation of the number of presacral vertebrae; and finally those of PVL 3872 offer very fine details on the presacral series.

Among the total presacral vertebral series of *Lagosuchus*, probably 24 or 25, 3 sections can be distinguished as composed of distinct types of vertebrae. These are:

1) the anterior cervicals (up to the 5th vertebra inclusive), which are relatively elongate, slightly tall, with low and axially extended laminar spines.
2) the cervico-dorsals (from 6th to 11th inclusive), which are relatively short and tall, with axially short and forward-directed spines.
3) the dorsals (from 12 or 13 to the last presacral), which are relatively long and low, with axially extended laminar spines.

It is evident that this zonation of the vertebral column represents a standard adaptation of special interest. Although its functional aspects are not analyzed, comparisons are made following the description with its appearance in other Triassic archosaurs.

The preatlas and atlas are well preserved and in their original position in PVL 3872. In dorsal view the arches of the preatlas are laminar, triangular, and have a backwards projection laterally that attaches to the atlas dorsolaterally. Dorsally it is as wide as the atlas and there is an extensive medial suture between them. It was thus preserved in the cited specimen, superimposed on the supraoccipital. In lateral view it is basically flat, with the posterior region laterally convex, well attached to the atlas.

The atlas is similar, generally, to that of *Euparkeria* (Ewer 1965), and apparently more primitive than that of *Riojasuchus* (Bonaparte 1971b). Dorsally it appearance is similar to the preatlas, except that it is less laminar and has a topography on which is manifest a slight prominence axially in which both halves of the atlas unite to form an incipient neural spine. Behind this point extend the relatively extensive and dorsolaterally convex posterior processes, which attach to the atlas.

In lateral view it is also similar to *Euparkeria*, with three distinct processes: one posteriorly that supports the axis; one dorsally that may be called the "spinous atlas" process; and one ventrally that contacts with the odontoids and the atlantal centrum (intercentrum 1). The atlantal centrum is transversely wide, short axially, and subcircular in lateral view. In this view note that, besides the dorsal suture with the atlantal arch, the posterodorsal region articulates with the anteroventral section of the odontoids.

The axis and next 3 cervical vertebrae have markedly compressed vertebral bodies, and provide a ventral keel that nearly disappears in the 6th and subsequent cervicals. The axis neural spine is generally extensive axially but is low. The zygapophyses are well separated from the axial plane and are proportionally large, especially the prezygapophyses. The position of the postzygapophyses does not reach behind the posterior border of the axis body, but are located somewhat more forwards. The zone of the parapophyses and diapophyses are not clear, but seem less pronounced.

The axis body is compressed, less extensive axially, and with anterior and posterior borders that project far laterally, forming edges that unite dorsally to mark the strong depression of the vertebral body. Its general aspect recalls more the characters of *Hesperosuchus* Colbert (1952) than those of *Euparkeria* according to the illustrations of Ewer (1965). Its axial length including the odontoids is 5.5 mm in both available specimens.

3rd, 4th and 5th cervicals. These are basically similar to one another. They are characterized by the anterior position of the prezygapophyses and the wide bony process in which

they culminate. At the same time the postzygapophyses already have a less marked position in the 5th vertebra. The incompletely preserved neural spine must be low, of laminar type, and more extensive axially based on what can be observed. The articular plane of the zygapophysis is oriented downward and medially, approximately as in *Hesperosuchus*.

In the vertebral body, as in the axis, the depressed area is also bounded by clear edges, especially in the dorsal part of this depression. There appear to be vestiges of the parapophysis and diapophysis that are more or less preserved in the 4th vertebra, located in the inferolateral vertebral body.

The proportions of these cervical vertebrae indicate that they are relatively low with more elongate bodies. This is particularly clear if they are compared to the same vertebrae of *Euparkeria* and the ornithosuchids *Gracilisuchus, Ornithosuchus* and *Riojasuchus.* The most extended cervicals of *Lagosuchus* could correspond to the 4th, from which a reduction begins in the following vertebrae that culminates in the 9th. The lengths are 4.3 mm for the 3rd, 5.0 mm for the 4th, and 4.3 mm for the 5th.

6th, 7th, 8th and 9th cervico-dorsals. A very evident change occurs between the previously described group of vertebrae and the four cervico-dorsals. In general these are significantly shorter, in such a way as to reverse the proportions of those more anterior. This is especially noted in the 8th and 9th vertebrae, which are short and high. Vertebra 6 is transitional between the two conditions.

In all of these vertebrae the characteristic that the prezygapophyses are located more forward of the vertebral body and in a relatively high position is maintained. A notable change is already produced in the neural spines, which are laminar and axially extended in the anterior cervicals, but change to axially short and clearly directed forwards while maintaining their short condition. The region for these and the diapophyses is somewhat broken, so the exact positions of these articulations are not clear. Nevertheless it is evident that it has shifted here to a more dorsal position, since in the 7th, 8th and 9th vertebrae it has an edge on the lateral face of the neural arch that gives rise to the transverse process, which is broken but clear in these vertebrae. This edge forms a distinctive cavity below the transverse process, also present in *Euparkeria* (Ewer, 1965, plate 33, fig. 28) although in somewhat more posterior vertebrae. The vertebral body is still excavated laterally in the 8th and 9th, but the dorsal edge has disappeared. The inferior border of these vertebrae does not show vestiges of the ventral keel, as do those more anterior. The measurements are: 4.1 mm for the 6th; 3.6 mm for the 7th; 3.1 mm for the 8th, and 2.6 mm for the 9th.

10th, 11th and 12th vertebrae. These vertebrae increase in length progressively and are transitional in most measurements between the previously described short, high vertebrae and the somewhat more lengthened posterior dorsals. The vertebral bodies become progressively larger going back, and are uniformly compressed. The transverse processes are only slightly prominent but well defined. The parapophyses on the 10th vertebra are located near the suture of the neural arch and the vertebral body, somewhat higher on the 11th, and still higher in the 12th, where they are well-defined and close to the diapophysis. The concavity below the transverse process, bounded by one edge anteriorly and another posteriorly, is maintained with similar features from the 7th vertebra to the 11th; in the 12th the posterior border almost totally disappears, because the aforementioned character is completely modified. In ventral view these vertebrae are uniformly rounded, with both ends projecting laterally. The neural spines are not preserved in their entirety, but it can be noted that they project progressively backwards and are slightly anteroposteriorly extended. The measurements of these three vertebrae are: 3.6 mm for the 10th; 3.6 mm for the 11th, and 3.8 mm for the 12th.

13th to 22nd vertebrae. These vertebrae are relatively uniform. They have transverse processes that are very distinct although poorly developed laterally, with a somewhat anteriorly oriented dorsal plane. In certain vertebrae - the 14th, 15th and 16th in MCZ 4116 - note that the parapophyses and diapophyses are on the end of the transverse process, the first in a slightly more ventral position. The relative position of the transverse process varies slightly. In the 13th and 14th vertebrae it has a more dorsal position that gradually comes from below, located almost in the upper part of the vertebral body up to the 19th and subsequent vertebrae, to the point that in the 22nd it is formed entirely on the anterodorsal border of the body.

The zygapophyses are more separated from one other in these vertebrae than in those described previously, such that the prezygapophyses extend past the anterior border of the body and the postzygapophyses extend past the posterior border; at the same time the articular plane is more horizontal, although with a slight vertical inclination in the axial plane.

The suture between the neural arch and the vertebral body seems more solid, and develops a slight projection in the posterior region.

The neural spine is uniformly wide in these vertebrae, relatively low from the upper border of the postzygapophyseal process, laminar, and with much less separation between one spine and another. Note a dimorphism in MCZ 4116 in the spines of certain vertebrae, that is certainly pathological. The spines of the 14th and 16th vertebrae are approximately half of the axial length of the 15th and 17th vertebrae, which at the same time are abnormally large.

The bodies of these vertebrae are relatively uniform, elongate and low; the anterior and posterior borders are at approximately a right angle with respect to the inferior plane of the body.

Both the relation between the neural spines and the contact between the bodies of this group of vertebrae suggest a relatively rigid connection between them.

Sacral vertebrae. *Lagosuchus* has only two sacral vertebrae, therefore the same primitive condition as *Euparkeria*. There is no fusion evident between them based on the two available sacra, PVL 3870 and MCZ 4116, either between the vertebral bodies or the zygapophyses. The length and volume of these vertebrae are comparable to those of the posterior dorsals, except for the presence of wide, solid sacral ribs that are well fused to the vertebrae and to each other distally. The suture between the transverse processes and the ribs is not clear. Nevertheless, it is clear that the length of the transverse process is greater on the dorsal face than on the ventral. As in *Euparkeria*, the transverse process is located in the anterior region of the first sacral and in the posterior region of the second. The neural spines are of the same type as in the posterior dorsals but are somewhat shorter axially. The sacral vertebrae are posterior in position relative to the ilia. In the two available examples almost the entire body of the 2nd sacral is exposed laterally.

The pectoral girdle. The pectoral girdle is represented only by the somewhat deteriorated left scapula and coracoid from specimen PVL 3871. The scapular blade is relatively wide, with a pronounced dorsal expansion. The supraglenoid structure is little marked; there is no evidence of muscular insertions above the glenoid cavity or near the posterolateral border as in *Ornithosuchus* (Walker, 1964). The acromial process, somewhat broken, projects laterally and is bounded by a depressed area in the anteroventral scapula.

The coracoid is solidly fused to the scapula. It has a lateral projection in its posterior region, corresponding to an area of muscular insertion. The coracoid foramen is relatively large, and located near the edge of the glenoid cavity. This articular cavity has a border on its lateral contour with a principally posterior orientation, indicating that the humerus tended to have little lateral rotation. This characteristic shows more affinities with traits seen in dinosaurs than those in thecodonts, which generally display evidence of lateral rotation of the humerus (Bakker and Galton, 1974).

The forelimb. Of the forelimb, the humerus and almost all of the radius and ulna of the left side are preserved, articulated with the aforementioned scapula and coracoid.

The humerus is slender and proportionally long, with the deltoid crest some distance from the proximal end. The internal tuberosity is slightly prominent and the humeral head well-defined dorsally and ventrally. The shaft is narrow, subcircular in midshaft cross-section, and flattened distally. There is a well-developed trochlear articulation on its distal end for the radius and ulna, with the medial part (for the ulna) of greater size and projecting more ventrally. On the ventral

face, the trochlea ends proximally in a deep depression to accommodate the anterodorsal edge of the radius during maximal flexion.

The humerus of *Lagosuchus talampayensis* is quite distinct from that of *Euparkeria,* in the clear definition of the humeral head, the more distal position of the deltoid crest, and the slenderness and narrowness of its construction. It is clear that *Lagosuchus* is considerably removed from the condition of *Euparkeria*. Among other Pseudosuchia, similar humeral proportions are seen in the Sphenosuchidae (*sensu* Bonaparte 1971b), *e.g. Hesperosuchus* Colbert (1952) and *Pseudhesperosuchus* Bonaparte (1971b), except that in these pseudosuchians the deltoid crest is pendant, almost appendicular, while that of *Lagosuchus* is squarer and more distally located.

Among Triassic saurischians the humerus of *Coelophysis* sp. (seen in a half-prepared specimen in the Museum of Comparative Zoology, USA) shows comparable proportions to those described, and a favorable comparison can also be made with the humerus of *Syntarsus rhodesiensis* Raath (1969).

The radius and ulna were found articulated with the humerus. They are incomplete distally but a minimal length reconstruction indicates that the ulna is slightly longer than the humerus, a feature that is also reported in some Sphenosuchidae, *e.g. Hesperosuchus*. Both bones are very fragile and slender, and the ulna has a marked olecranon process.

In this specimen, PVL 3871, the measurements of the hind and forelimbs are as follows:

femur: 56 mm	humerus: 39 mm (fig. 19)
tibia plus astragalus: 73 mm	radius: approximately 33 mm
pes: 61 mm	ulna: approximately 37 mm
	manus: unknown; ?20 mm

These measurements demonstrate that the hind limb measures 190 mm and the forelimb, although the manus is unknown, is about 92 mm, which signifies a disparity of 48%; in other words the forelimb is approximately 48% the length of the hind limb.

The pelvic girdle. PVL 3870 shows the nearly complete pelvis, fused to the sacrum. The left side shows defects of ossification in the suture between the pubis and ischium, and partially in the ilium, but the right side is very well preserved. MCZ 4116 has a large part of the right ilium and a portion of the right pubis. The ilium described and figured by Romer (1971b, fig. 3) and restored on the basis of a fragment of that bone from the left side (PVL 3871) in reality is not aberrant at all, as Romer supposed. Prof. Romer merely did not discern that the incomplete ilium preserves adhesions of the two proximally incomplete sacral ribs on the internal face, which were interpreted

as "...internal to the normal external blade, (there lies) a broad trough, comparable to that seen in ophiacodonts...". In reality this ilium, or actually both incomplete ilia of this specimen, are of the normal type for *Lagosuchus*. I note that Romer observed and cited the incomplete ilium of this genus from MCZ 4116 and illustrated the vertebral series that accompanies it (1972d, p. 4 and fig. 4), but do not reproduce it, to give better information on this bone of *Lagosuchus*.

The proportions of the pelvic bones clearly indicate a more advanced level than *Euparkeria*, particularly the length and morphology of the pubis. On the other hand it more closely resembles the proportions of the pelvis of the ornithosuchid *Gracilisuchus*, although there are clear differences in its organization, as seen below.

The ilium. The general proportions of this bone are similar to those of some ornithosuchid (*Gracilisuchus*), rauisuchid (*Saurosuchus*), and phytosaurid thecodonts, and particularly to those of some prosauropods such as *Plateosaurus* and *Riojasaurus*, but with the difference that the acetabulum of *Lagosuchus* is closed. The relatively common iliac morphology among diverse prosauropods and thecodonts indicates that this part of the pelvis is highly conserved among these groups, while the changes occurring in the pubis and ischium are much more distinct.

The iliac blade of *Lagosuchus* is extended axially, and concave in the same direction on its lateral face. In truth this face is also concave between the dorsal border and the supraacetabular crest. The upper contour is more or less convex, with the anterior and posterior ends somewhat lower than the middle. The anterior edge of the iliac blade in PVL 3871 ends in a strong anterior process or protuberance, apparently for a muscular insertion. This part of the ilium is mostly behind the anterior end of the pubic peduncle; in other words the iliac blade possesses practically no preacetabular process. On the other hand, the postacetabular portion is extended and represents approximately 50% of the surface. The posterior border of the ilium forms a continuous curve from the ischial peduncle, interrupted only by a process coming from the attachment or suture between the ilium and the posterior part of the 2nd sacral rib.

The medial wall of the acetabulum does not show signs of reduction in the region corresponding to the ilium, since it retains the primitive angled condition between the edges of contact with the pubis and ischium, as seen in most thecodonts except *Ornithosuchus* and *Riojasuchus*. Nevertheless, in PVL 3870 the opening of the acetabulum has started, although it is intermediate in reduction of the pubis and ischium.

The acetabulum is deep, and bordered anteriorly and dorsally by a pronounced supraacetabular crest that forms a kind of extended overhang with its concave inferior face. The deepest point is in the dorsal region, approximately in the middle of this overhang. On the other hand, the region in which the supraacetabular crest shows its greatest lateral projection is somewhat more forward. The posterior region of the acetabulum is lacking this pronounced border

and is instead rounded, possibly to accommodate the area of the greater trochanter during maximal flexion.

The pubic peduncle is considerably larger than the ischial peduncle and its forward and downward orientation matches the orientation of the pubis. The ischial peduncle is oriented more or less vertically (in the supposed quadrupedal posture of the animal).

It is not possible to describe the medial face of the ilium in any detail, since it is incomplete in the two specimens in which it can be observed, MCZ 4116 and PVL 3871. Nevertheless, note that the medial side of the acetabulum is convex, and that deep furrows exist above the acetabulum for the sacral ribs.

Both articulated ilia are positioned vertically relative to the sacrum, according to what is seen in the two specimens, differing from *Euparkeria*, as illustrated by Ewer (1965, fig. 12), in which both ilia converge above.

The ischium. This bone is well preserved in PVL 3870 and does not show any noticeable effects of crushing. It is proportionally shorter than the pubis. In quadrupedal posture the orientation of the ischium would be about 55°-60° relative to the horizontal plane, and directed back and ventrally. In this position the proximal region of the posterior border is oriented almost vertically near its suture with the ilium. Distally this edge is oriented somewhat back and below, forming a wide curve with the vertically positioned proximal region.

The ischial symphysis is limited to the distalmost region, from which they separate progressively to approach a more lateral plane and the previous fossa to the suture with the pubis.

The lateral region of the ischium is relatively flat proximally except for the projection of the inferior border of the acetabular part. In contrast, the remaining 2/3 shows the posterior border well projecting laterally, which continues the laterally concave and laminar symphysial region. The acetabular portion is reduced and separated from the region of union with the pubis by a depression, which I call the acetabular fossa of the ischium. As can be seen in fig. 10, the ischium, the same as the pubis, has a kind of well-defined peduncle for its connection with the pubis, as is the case in some carnivorous saurischians like *Coelophysis.*

It is clear that the ischium of *Lagosuchus* shows notable advances over *Euparkeria*, especially in its elaborated proximal region where an acetabular area, an intermediate zone (acetabular fossa) and an ischiopubic peduncle are distinguished. Not only these characters are more advanced than in the remaining thecodonts. Ahead their possible significance is discussed.

On the other hand, the rest of the ischium is relatively primitive, although more advanced than in *Euparkeria*, lacking the reduction of the medioventral lamina that is especially reduced in the Rauisuchidae, advanced Ornithosuchidae, and Prosauropoda.

The pubis. Both pubes are preserved in their original position in PVL 3870. In PVL 3871 they are also preserved in the area of the symphysis, although a little incomplete. In MCZ 4116 the incomplete right pubis exists in ventral view, associated with the pelvis, and the major part of the left pubis is found articulated with a fragment of ilium on the same slab, close to a skull of cf. *Gracilisuchus.*

The pubis of *Lagosuchus* is long, with a strong transverse reduction in its proximal half, and twisted distally in such a way that the distal end projects dorsolaterally, a very distinct condition from *Euparkeria* or *Gracilisuchus* in which the pubis has a flat, anterodorsally oriented surface throughout its length.

In lateral view the proximal region is relatively dorsoventrally extended, its thickness diminishing rapidly to a point somewhat more distally than the supposed process for the ambiens muscle. The torsion of the pubis begins from the distal end, which brings the dorsal border to a more ventral position than the symphysis.

The acetabular portion of the pubis is reduced, and is indicated by a rounded edge in PVL 3870, while in MCZ 4116 it seems to be somewhat more prominent, although its preservation is poor. In these two specimens there is an opening of the acetabulum between the pubis and ilium that, in the first, most probably is original and was covered by cartilage when the animal was alive. This opening is repeated in PVL 3781 and confirms the existence of an incipient opening in the acetabulum of *Lagosuchus*.

The connection with the ischium is reduced and occurs midway from a well-defined puboischial peduncle. The position of the thyroid fenestra is indicated by a very laterally positioned fossa below the acetabular portion.

In anterior view, note that the pubic symphysis is relatively short and limited distally. In PVL 3870 it is somewhat shorter that is suggested by the left pubis of MCZ 4116; in other words, perhaps there are appreciable differences or individual variations. From the most proximal point of the symphysis a slender, vertically oriented bony lamina continues forward, forming an essentially right angle with the anterodorsal plane of the pubis. This lamina is divergent in the axial plane and appears to connect with the main body of each pubis. It is possible that this bony lamina has a major medial extension, or that cartilaginous tissues continue from it and widen the symphysis.

The ambiens processes are evident in anterior view, as is the limited transverse thickness of each pubis in its proximal region.

The lateral view of the pubis of *Lagosuchus* is very suggestive of possible relationships with the saurischian Herrerasauridae, in particular the incipient distal torsion that is notably more marked in *Staurikosaurus* Colbert (1970) and that culminates in *Herrerasaurus* Reig (1963) by almost forming a true foot. Its proportions are also supportive of its possible relationship with herrerasaurids, but the characters of the puboischial connection are, according to what is seen in the

preserved materials, more advanced than in *Herrerasaurus*, since the puboischial suture is much greater in this genus. In the case of *Lagosuchus* it remains to be seen if the preserved puboischial suture represents the original condition as the available specimens show it, or if, on the contrary, the bony laminae in this region are not sufficiently ossified to be preserved due to the small size of the animal, which I believe is less probable. Nevertheless the specialized condition of the pubis is clear from diverse characters, independent of the lack of ossification.

Comments on the pelvis. The pelvis of *Lagosuchus* is notable for the mosaic of advanced and primitive characters that it shows, which is a good indication of its transitional nature. The ilium is clearly of thecodont type, except for the distinct supraacetabular border. The ischium possesses advanced characters proximally, with an acetabular area in which are distinguished: the acetabular region proper, an acetabular fossa, and an ischiopubic peduncle; however the rest of the ischium is very primitive, generally agreeing with the characters of other Middle Triassic thecodonts, or even somewhat more primitive.

The pubis is the most specialized part of the pelvis of *Lagosuchus*, in stark contrast with the condition of the ilium. In fact the pubis seems more specialized than in prosauropods, which in truth retain an archaic pubis similar to that of ornithosuchids or *Stagonosuchus* (Rauisuchidae). Except for this it seems probable that the pubis as well as the rest of the pelvis of *Lagosuchus* could reasonably be considered very close to that of herrerasaurids. Eventually, in a distinct line of evolution its morphology could possibly be related to the type of pelvis of Triassic Coelurosauria such as *Coelophysis.*

As to the possible relationships between *Lagosuchus* and *Euparkeria* in relation to the pelvis, I believe that the morphological distance between both forms is not in accordance with the temporal distance that separates them. It is thought that there were euparkeriids more advanced in pelvic organization during the end of the Lower Triassic.

The hind limb. The hind limb of *Lagosuchus* is very well represented, since practically complete hind limbs are found in specimens PVL 3870 and PVL 3871.

Femur. In PVL 3870 both femora are very well preserved, with minimum deformation; likewise they are preserved in PVL 3871, although the effects of deformation are more evident here. The femora cited and figured by Romer (1972d, figs. 3 and 5) are: one somewhat smaller and another somewhat larger than those of PVL 3870 described below. In reality Romer did not describe the femur of *Lagosuchus* in any of his works on this genus (1971b; 1972d).

The femur is somewhat shorter than the tibia, 42 mm and 49 mm respectively; in other words the ratio is 85.7:100. The construction of the femur is very light and it is long, principally

cylindrical and thin-walled. In dorsal view it is straighter, with a slight curvature towards the medial plane in the upper third that produces a moderate projection of the femoral head. In this view the fourth trochanter is clearly exposed since it projects medially. Note a moderate medial expansion of the distal end of the femur.

In medial view it is sigmoid, with a wide backward curvature down from the fourth trochanter, and a shorter but more marked forward curvature limited to the upper third and ending at the femoral head.

The head of the femur is very well ossified and shows a fairly clearly delimited articular area, especially anteromedially. Apparently this area comprised the major part of the proximal region, including a large part of the greater trochanter. In proximal view the femoral head has an ovoid shape, with the major axis directed principally anteroposteriorly and the minor axis transverse to the anterior. The anterior edge is rounded and corresponds to the articular area, while the posterior edge is more angled and formed by the greater trochanter. The orientation of the femoral head is principally dorsal and slightly towards the medial plane, so that the angle that the femur presents relative to the axial plane of the sacrum must be 20° to 30°, and the movement between the positions of maximal extension and flexion would presumably cover 150°. In the position of maximal extension the anterior border of the supraacetabular crest is "accommodated" in the curvature below the femoral head; in the position of maximal flexion the posterior border of the trochanter is "accommodated" in the depression of the posterior acetabular border.

The greater trochanter is less distinct proximally, although it is differentiated from the head of the femur by a groove on the medial face of the femur. The posterior border of the greater trochanter is angled and prolonged distally below the lesser trochanter.

The lesser trochanter is very well preserved in the left femur of PVL 3870. It is located on the lateral face very near the posterior border, somewhat above the fourth trochanter. It is conspicuous, relatively extended along the axial length of the femur, and with numerous rugosities, but does not have the projecting proximal border as is the case in prosauropods, and clearly defined in Triassic coelurosaurs and certain advanced thecodonts such as *Ornithosuchus* and *Riojasuchus.*

The 4th trochanter is entirely within the upper third of the femur. Its projection is completely medial and aliform. The medial border of the trochanter is very blunt, with marks for ligamentous insertion. Its anterior face is concave, producing a depression between the trochanter and the shaft, a character repeated more weakly on the posterior face.

The distal end shows a marked medial expansion and the most ventral point corresponds to the external and anterior border of the external or fibular condyle, which follows a certain angle for the union between the femur and tibia in anterior view. The anterior surface of the distal end is convex, with a barely perceptible supracondylar depression that is exaggerated on the right femur

by postmortem effects. The articular area for the tibia reaches the anterior face, a character that is clearly seen on the left femur.

There is an intercondylar depression in the posterior region of this section of the femur, with a certain dorsal extension that separates both tibial condyles. The internal tibial condyle is more angular in cross-section and extends medially, while the external tibial condyle is blunter, more voluminous, and projects backward. The fibular condyle forms the lateral projection of the end of the femur.

According to these observations on the right femur, articulated with the tibia and fibula, the internal tibial condyle is directly superimposed on the posteromedial border of the tibia, the external tibial condyle places its posterior end between the tibia and fibula, and the fibular condyle is on the fibula. In this way the fibula articulates on the lateral face of the external tibial condyle and on the distal face of the fibular condyle.

The shaft of the femur is generally very constant in its width and subcircular condition. There is a great difference in this aspect with the condition in *Euparkeria*. Below the head of the femur the cross-section of the shaft is oval, with the posterior region narrower than the anterior. At this level the distal projection of the greater trochanter seems to separate areas of muscular origin on the medial and lateral faces of the femur. At the femoral midshaft the cross-section is more or less circular, with a slight posterior protuberance that corresponds to a small but clear border that runs distally from the proximity of the 4th trochanter, near the medial plane, in the direction of the fibular condyle, although it disappears above. Evidently this border separates clearly distinct muscular areas, perhaps for the flexor and extensor muscles.

Another character of interest on the femur is the long, distally directed depression that begins at the height of the upper part of the 4th trochanter, and that disappears medially a little below the same. This depression is bounded laterally by a tall, very rounded border, corresponding to the dorsal face of the femur.

Tibia and fibula. These are present in the two limbs of specimens PVL 3870 and 3871. In MCZ 4116 there is a proximal fragment articulated with the right femur. Romer figured the complete left tibia and fibula, and the incomplete elements of the right side of the holotype. As indicated above, the tibia (without astragalus)-femur ratio is 100:85.7 respectively.

The tibia is proportionally slender, and practically straight in anterior and lateral views, although apparently the distal end projects somewhat forwards, since a similar slight curvature is noted in the various available tibiae. In lateral view a moderate proximal expansion is present, with a slight posterior projection. The fibular process or condyle is prominent, forming a very wide articular area with the femur, triangular in contour, and with the major axis oriented anteroposteriorly. The tibial shaft is weakly compressed mediolaterally.

In PVL 3870 the distal end shows the following characteristics in relation to the surface of the union with the astragalus: in the left tibia the anteroposterior axis is slightly greater than the transverse, 4.1 mm and 3.2 mm respectively; on the other hand in the right tibia these values are inverted, 2.7 mm and 4.1 mm. In the tibia of PVL 3871 that can be measured, the anteroposterior axis is 4.6 mm and the transverse 3.9 mm. Some deformation exists in the three in different ways and perhaps the original condition includes very similar values for both axes. This character is important in that it signifies the transition between the original condition typical of thecodonts, in which the major axis is in the anteroposterior direction, and the condition of dinosaurs, in which the major axis is transverse. This modification must be the result of the increased immobility between the astragalus and tibia that occurred during the thecodont-dinosaur transition, and also of the increased width of the astragalus at the expense of the calcaneum.

In lateral view note that the inferior end of the tibia reaches its most ventral point on the posterior border as in other thecodonts, *e.g. Riojasuchus, Neoaetosauroides*, etc. In posterior view note that the distal end (in all the available specimens it is united to the astragalus) has the form of an inverted L. Therefore there is an extensive area of contact with the astragalus whose axis, somewhat major, is anteroposterior and represents the typical condition present in most thecodonts, and a second area of contact (in reality a continuation of the anterior) oriented transversely that recalls the condition in herrerasaurids and prosauropods. It seems clear that the transverse area of contact with the astragalus is a specialized development of *Lagosuchus* that would represent an intermediate condition between that of thecodonts and dinosaurs. In anterior view note that the transverse expansion cited of the distal end is also manifest above in the shaft up to 8 mm from the inferior border.

The fibula is much more fragile, with the central and lower portions of the shaft essentially cylindrical and the upper half much flatter, although with a slightly convex lateral face. In anterior view it is almost straight, with a slight condylar expansion on the distal end. In lateral view note the proximal expansion that projects basically backwards.

The distal end of the right fibula of PVL 3870 is very well preserved and shows that its articulation has a more or less oval contour, with the major axis anteroposterior, and convex lateral and medial edges. The posterior end reaches the distalmost point of the fibula and its blunt, rugose aspect suggests that it would be a site for strong muscular insertions. The articular surface is concave and much flatter anteriorly, with a lower anterior border towards the posterior part.

Astragalus and calcaneum. According to indications of preservation in the holotype and specimens PVL 3870 and 3871, these tarsal bones were firmly united to the tibia and fibula. Moreover both their morphological characters and the great size disparity between them suggest that *Lagosuchus* had a tarsal articulation of the mesotarsal type seen in dinosaurs, and not the

typical crurotarsal condition present in nearly all advanced thecodonts and crocodilians. Nevertheless, the tarsus of *Lagosuchus* shows various primitive traits, and demonstrates that the mesotarsal condition is derived from the crurotarsal condition.

In anterior view the conjoined astragalus and calcaneum are relatively low and transversely wide, with notable dominance of the space occupied by the astragalus. Therefore note that of the 7.5 mm total width presented by these bones in PVL 3870, only 2 mm correspond to the calcaneum. Generally in thecodonts these characters are different since in *Euparkeria*, according to personal data taken from specimen 6049 in the South African Museum, the total width is 12 mm of which 4 mm corresponds to the calcaneum; in *Riojasuchus* the total width is 52 mm of which the calcaneum occupies 2 mm; and in *Neoaetosauroides* the total width is 50 mm with the calcaneum occupying 19 mm.

In anterior view, the astragalus shows a slight dorsal edge that separates the tibial and fibular articular planes from the rest of the anterior face, and that articulates with metatarsals I, II and III in maximal flexion. There is a dorsal process in the proximal region that separates the articular surfaces for the tibia and fibula, and is similar to the astragalus of thecodonts but less developed dorsally and more extended backwards. Both the tibial and fibular articular facets are relatively flat in anterior view and located at the same level.

In medial view the astragalus is low, trapezoidal in contour, and has an anterior side that is essentially vertical and higher than the posterior, which is inclined down and backward. The most ventral, and at the same time the most anterior, point of the astragalus corresponds the anteromedial angle, as in the ornithischian *Pisanosaurus* Casamiquela (1967), but less pronounced.

In posterior view the astragalus is lower, superimposed on the calcaneum laterally, and presents a dorsolaterally oriented fibular facet. These characters are common in thecodonts, with the difference that in *Lagosuchus* the astragalus is lower. The lateral view, which is smaller than the medial view, shows a dorsal area for articulation or union with the fibula, and a downward- and medially inclined ventral area with some concavities and convexities for its contact (union or articulation) with the calcaneum.

In distal view the astragalus shows characters typical of dinosaurs: the medial region is wider than the lateral, with the greatest anteroposterior extension near the medial border; the posterior border is rounded and straighter, while that of the anterior has a less round border but is anteriorly concave. Finally, the anteroposterior diameter is laterally reduced, and there is a small, marked depression for the calcaneum. All these ventral region characters are very similar to those in Herrerasauridae and Prosauropoda, and basically distinct from those in Thecodontia.

The calcaneum is preserved in the left limbs of specimens PVL 3870 and 3871: it is evident that it was not fused to the astragalus, as indicated by Romer (1971b, p. 4). It is proportionally reduced in size. In anterior view it has a more or less triangular shape with the vertex above, and

note that the astragalus is recurved medially. In posterior view it is transversely wider (as in the majority of thecodonts) and situated below the astragalus. In this posterior view note clearly the posterior prolongation of the lateral face in the form of a calcaneal process, and the depression that separates it from the rest of the calcaneum.

In lateral view its contour is very oval and irregular, with a more or less flat surface and rugosities that correspond to muscular insertions. In ventral view note that the calcaneum and astragalus are in articular position (PVL 3870). The posteroventral region shows a slight prolongation that connects to the astragalus. Laterally this feature forms an angle with the calcaneal process and there is a concave zone in its connection in which must articulate the external distal tarsal.

Distal tarsals. Both distal tarsals are preserved in approximately their original position in the left pes of PVL 3870. The external is directed above metatarsal IV and superimposed slightly on the other distal tarsal, which is near metatarsal III. Tarsal IV (external) is elongate anteroposteriorly, and proportionally narrow transversely except in the anterior region. The narrow dorsal surface is concave from back to front, presenting an elevated posterior border apparently to be accommodated on the posteroventral fossa of the calcaneum forming a true trochlea. Laterally it has a much taller concave articular surfaces from front to back for metatarsal V. This facet is oriented laterally, not posterolaterally as in the thecodonts *Riojasuchus*, *Saurosuchus*, and *Neoaetosauroides.* The condition of this tarsal is very distinct from than seen in thecodonts, and accordingly reflects a distinct relation between the crus and tarsus from these; apparently in *Lagosuchus* the condition is digitigrade, and plantigrade in the remaining thecodonts.

Distal tarsal III is also elongate anteroposteriorly, with a more or less rectangular contour, but wider than distal tarsal IV. Its dorsal face is rounded, convex transversely, and flat in the opposite direction. This tarsal articulates distally with metatarsal III and ventromedially with metatarsal II. Proximally its place of articulation must be on the lateral part of the ventral face of the astragalus, perhaps touching the medial part of the calcaneum.

Metatarsals. 5 complete metatarsals are preserved in the left foot of PVL 3870 very close to the original position. The observations are very well completed by the data (also valuable) from the remaining 3 articulated feet, one from the same specimen and the others from PVL 3871.

The lengths of metatarsals I and V are very similar, and much less than the others. II is somewhat shorter than III and IV, which are practically equal in PVL 3870, and the greatest size of III is in PVL 3871.

The measurements in both specimens are as follows, respectively: mt. I, 14 mm and 21 mm; mt. II, 25 mm and 36 mm; mt. III, 29 mm and 39 mm; mt. IV, 28 mm and 38 mm; and mt. V, 14 mm and ?22 mm.

Metatarsal I is transversely flattened in its proximal half, and more developed dorsoventrally; distally the articular expansion is small. Proximally this metatarsal articulates with the astragalus.

Metatarsal II possesses a more voluminous and robust proximal region than the other metatarsals. Proximolaterally it articulates with distal tarsal III, and on a greater area proximally with the astragalus. The extension is greater than the width of this metatarsal in its proximal region. The distal end shows a notable transverse expansion in the articular region. Above the articulation, on the dorsal face, there is a very marked depression to accommodate the proximodorsal end of the first phalanx in maximal extension.

Metatarsal III articulates proximally with the internal distal tarsal. Its transverse width is less than metatarsal II, and closer to that of metatarsal IV. Its dorsoventral width is somewhat less than that of II, but its ventral face is more robust. In dorsal view metatarsals III and IV present a slightly outward-projecting proximal region. Distally mt. III is relatively strong, and greater in dorsoventral width than II and IV. Especially in PVL 3871, mt. III is clearly the thickest and longest of the series.

Metatarsal IV articulates proximally with the external distal tarsal for half of the greater part of the surface, and eventually with the distolateral border of the internal distal tarsal. The cross-section of the proximal region is triangular, with the medial side attached to metatarsal III in such a way that there is a large space between the ventral region of this metatarsal and mt. V. Distally it is somewhat more reduced than mt. III.

Metatarsal V is almost in its original position in the right foot, and somewhat moved in the left of PVL 3870. A slight expansion begins from approximately the center of this metatarsal that culminates proximally in a laminar, oval form, with convex dorsolateral and concave ventral surfaces, and a ventrally projecting external border. The proximal region of this metatarsal is of the type possessed by *Herrerasaurus* and Prosauropoda, distinct from metatarsal V, in contrast to that seen in Rauisuchidae, Aetosauria, *Euparkeria* and Ornithosuchidae.

The metatarsals of *Lagosuchus* are, as a group, elongate, fragile, apparently bound tightly together, and conforming to a symmetrical foot with reduction of metatarsals I and V, and mt. III more developed than the rest. Its arrangement suggests that *Lagosuchus* was a good runner.

Phalanges. The phalanges of *Lagosuchus* are proportionally elongate and more slender. The proximal phalanx of digit I is preserved, and does not show evidence of reduction. Digit III has 3 phalanges preserved in the right foot of both specimens, lacking the ungual. They are elongate

but with marked expansions in the articular region, and considerably longer than those of digit IV, which confirm that digit III was the longest and most robust.

Digit IV shows 3 phalanges in the left foot of PVL 3870 and 4 in the left foot of PVL 3871, which are clearly more slender than in digit III. Metatarsal V has no associated phalanges although its distal end shows a very clear articular area. It is possible that the digital formula of *Lagosuchus* was the same as in the majority of thecodonts: 2-3-4-5-2.

COMPARISON

The comparison of *Lagosuchus* with other known thecodonts, already known from the Lower, Middle or Upper Triassic, shows, as seen below, that this genus from Argentina possesses distinct characters of such significance that it is necessary to recognize a new family of thecodonts for its systematic placement.

Thecodonts of Los Chañares. Romer described thecodonts from the same locality that produced *Lagosuchus*. *Luperosuchus* Romer (1971a) is a form of considerable size whose systematic position in the family Rauisuchidae is satisfactory, in spite of the fact that the type material is represented only be a large part of the lateral half of the cranium. *Luperosuchus* and the other rauisuchids were relatively large carnivorous thecodonts, with crocodilian-type tarsal bones (known in *Ticinosuchus, Prestosuchus, Rauisuchus, Saurosuchus*, etc.), in other words with a crurotarsal articulation, and, among other differences, with the femur longer than the tibia. These two characters are sufficient to demonstrate the important differences between *Lagosuchus* and Rauisuchidae.

Romer described two new genera from Los Chañares: *Chanaresuchus* and *Gualosuchus* Romer (1971c). These forms show a primitive organization of the three pelvic bones, especially the pubis, which is very short and wide, completely distinct from those of *Lagosuchus*. In reality all the proportions and morphology of the foot, tarsus, tibia, fibula, and femur are completely distinct from those of *Lagosuchus*. In a previous work (Bonaparte 1971a) *Chanaresuchus, Gualosuchus* and *Cerritosaurus* were grouped in the family Cerritosauridae.

Gracilisuchus Romer (1972b) is an interesting and primitive ornithosuchid whose fundamental difference with *Lagosuchus* consists of the characters of the tarsus, of crurotarsal type in *Gracilisuchus* and mesotarsal in *Lagosuchus*, besides the important differences in the pubis and the proportions between the femur and tibia. It is evident that *Lagosuchus* has a more advanced locomotor organization than its contemporary neighbor *Gracilisuchus.*

Lewisuchus Romer (1972c) is known in incomplete form. There is a fragment of cranium and mandibles with good morphological details, 17 articulated vertebrae from the axis, two

scapulocoracoids, two incomplete humeri, etc. The possibilities for comparison with *Lagosuchus* are restricted; nevertheless it can be observed that the cervical and anterior dorsal vertebrae of the two forms show very clearly different characters, especially in the morphology of the 6th through 11th vertebrae, which in *Lagosuchus* are short, tall, and with short forward-directed neural spines. None of these features exist in *Lewisuchus*, since the same vertebrae have different functions in the two genera. On the other hand the humerus and femur of *Lewisuchus* also coincide in being very distinct from those of *Lagosuchus*.

Finally *Lagerpeton* Romer (1971b), also from Los Chañares, shows very clear generic differences, although evidently it is nearer to *Lagosuchus* than the previously mentioned forms. Both genera possess similar proportions between the femur and tibia, and the mesotarsal condition is present in both, but there are very peculiar conditions in the proportions of the metatarsals of *Lagerpeton* (see Romer 1971b, figs. 1 and 2) that clearly justify the generic status of this form. It is also possible that *Lagerpeton* has three sacral vertebrae (Romer 1972d, fig. 1, H.) in place of the two possessed by *Lagosuchus*.

In summary, the differences between *Lagosuchus* and the other Los Chañares thecodonts correspond to family level differences, except perhaps with *Lagerpeton.*

T**hecodonts of the Lower Triassic**. The thecodonts of the Lower Triassic: Ehrmayin Series of China; *Lystrosaurus* Zone and *Cynognathus* Zone of South Africa; Zones V and VI of the USSR; Panchet Formation of India, including in part the suborder Proterosuchia and the family Euparkeriidae, which is the most primitive in the suborder Pseudosuchia. The members of Proterosuchia of the Lower Triassic are characterized by the primitive organization of the pes, pelvic girdle or hind limb, such that the difference between them and *Lagosuchus* is very clear and does not require comment. There are also notable differences with the family Euparkeriidae but of a lesser grade. Between them the distinct morphology of the pubis and the proximal ischium, the distinct organization of the tarsus, etc., all indicate that *Lagosuchus* is notably more advanced than the members of this family, *Euparkeria*, and other assigned to this such as *Wangisuchus* Young (1964) and *Turfanosuchus* Young (1973).

Thecodonts of the Middle Triassic. Apart from those of Los Chañares there are few thecodonts known from this section of the Triassic. The majority of these correspond to the family Rauisuchidae, with forms from East Africa such as *Stagonosuchus* and *Mandasuchus*, from Europe such as *Ticinosuchus*, and from Brazil such as *Rauisuchus* and *Prestosuchus*. This family apparently dominated in the Middle Triassic, with representatives from the Lower Triassic (*Fenhosuchus* Young, 1964) to the Upper Triassic (*Saurosuchus* Reig, 1959 from Ischigualasto and *Fasolasuchus* Bonaparte, MS., from the Los Colorados Formation). The various genera of this

family are in general large carnivorous thecodonts, walking in a quadrupedal habit, already having the tarsus with crurotarsal articulation and the tibia much shorter than the femur. These characters alone are enough to separate the Rauisuchidae from *Lagosuchus*.

Other Middle Triassic thecodonts such as *Pallisteria* and *Teleocrater* Charig (1967) from East Africa, or *Ctenosauriscus* Krebs (1969) from Europe, each one representing a particular family, are too poorly known for now to make some valid comparison with *Lagosuchus*, except that all of them are much larger in size and that *Ctenosauriscus* has hypertrophied neural spines.

Finally, the Middle Triassic thecodonts of Brazil not included in Rauisuchidae are: the aforementioned *Cerritosaurus* belonging to the same family as *Chanaresuchus* and *Gualosuchus*; I have considered (Bonaparte 1972c) other Brazilian forms as assigned to uncertain families, such as *Hoplitosuchus, Procerosuchus* and *Rhadinosuchus* described by Huene (1942) that where it is possible to compare are distinct from *Lagosuchus*, of notably larger size.

Thecodonts of the Upper Triassic. The thecodonts of this part of the Triassic include those of the Ischigualasto Formation, corresponding to the suborders Phytosauria, Aetosauria, Pseudosuchia and the descendants of Proterosuchia (Proterochampsidae and Rauisuchidae). It is not necessary to comment on the differences between the first two suborders and *Lagosuchus*, since they are totally distinct adaptive lineages. The same is true for Proterochampsidae and Rauisuchidae, easily separable from *Lagosuchus* at the familial level, especially by the characteristics of the hind limb.

For their part the Pseudosuchia of the Upper Triassic are represented by a variety of forms grouped into the families Ornithosuchidae, Scleromochlidae, Sphenosuchidae?, Triassolestidae?, and forms like *Erpetosuchus* that possibly should be placed in their own family.

The Ornithosuchidae possess a crocodilian-type tarsus, a laminar and anterodorsally exposed pubis, and do not show zonation in the presacral vertebrae as seen in *Lagosuchus*, as entirely conforms to very clear differences.

The family Scleromochlidae, according to its sole genus *Scleromochlus*, presents some suggestive affinities, particularly the proportionally long limbs. Nevertheless, differences with *Lagosuchus* are indicated, which can be seen in relation to the characters of the presacral vertebrae and the condition of the sacrum, with 4 vertebrae in *Scleromochlus* (Huene, 1956, fig. 489). Moreover, the tarsus of *Scleromochlus*, which I had the opportunity to observe in Newcastle, England, thanks to the kindness of Dr. Alick Walker, is of crurotarsal, or crocodilian, type.

The family Sphenosuchidae is composed, in my opinion, of *Sphenosuchus, Hesperosuchus, Pseudhesperosuchus*, and doubtfully *Saltoposuchus*. The hind limb bones of the genera *Hesperosuchus* and *Pseudhesperosuchus* are known, which show that the femur has a very prominent 4th trochanter, in place of the well-defined aliform trochanter of *Lagosuchus*. Moreover

the proportions between the tibia and femur are distinct, since in these genera the tibia is shorter or the same length as the femur, different from *Lagosuchus* in which the same is much longer than the femur. Another important distinctive character between Sphenosuchidae and *Lagosuchus* is seen in the coracoids which show a notable posteromedial prolongation in *Sphenosuchus* and the remaining cited genera, which does not exist in *Lagosuchus*.

Triassolestidae Bonaparte (1971c) from the Ischigualasto Formation is known only by the cranial remains described by Reig (1963), and by some bones of the forelimb (Bonaparte 1971c), but a practically complete undescribed skeleton exists, produced from the same beds. The pelvis of Triassolestidae has a long and robust ischium, very distinct from that of *Lagosuchus*, the femur does not possess an aliform 4th trochanter and is longer than the tibia, and the cervical vertebrae are very elongate; in other words a series of characters that clearly differentiate it from *Lagosuchus*.

Finally, the only maxillary remains of *Lagosuchus* permit difference to be seen with *Erpetosuchus* Newton (1894) from Elgin, Scotland. This peculiar pseudosuchian has a very restricted number of teeth in the anterior part of the maxilla, only 4, while *Lagosuchus* has a maxilla without apparent reduction in the number of teeth, since in the preserved fragment it has 9 teeth and 3 empty alveoli. It is indubitable that *Erpetosuchus* was a specialized form as to the characters of its dentition, while *Lagosuchus* has generalized features in the disposition and number of these.

In summary, especially for the mixed characters of the pelvis with the primitive ilium, advanced pubis, and ischium also with mixed characters, and in particular by the features of the tarsus and its mesotarsal condition, *Lagosuchus* is basically distinct from members of the various thecodont families, such that a particular family is proposed for its systematic placement: **Lagosuchidae** nov.

DEFINITION OF LAGOSUCHIDAE

Carnivorous dinosaurian pseudosuchians. 3 morphological types are distinguished in the presacral vertebrae: the anterior cervicals, cervico-dorsals, and posterior dorsals, a condition that, combined with the traits of the hind limbs, suggests mainly bipedal progression. Extreme disparity between the fore and hind limbs. Advanced pelvis, with a long, specialized pubis with reduction in the proximoventral area and a defined peduncle for contact with the ischium; dorsolaterally exposed distal end of the pubis; primitive ilium with pronounced supraacetabular crest; proximal region of the ischium with an acetabular area, a depressed area, and a well-defined peduncle for articulation with the pubis; distal end of the ischium poorly specialized; acetabulum with incipient opening via slight reduction in the acetabular regions of the pubis and ischium. Sacrum with two vertebrae. Femur shorter than the tibia, with an aliform 4th trochanter and an anteromedially directed femoral head. Two areas for articulation with the astragalus are distinguished on the distal end of the tibia,

one directed anteroposteriorly and another transversely. Tarsus of dinosaurian type, with reduced calcaneum, vestigial calcaneal process, astragalus and calcaneum not fused together and connected to the tibia and fibula; mesotarsal condition.

Long and fragile metatarsals, especially I and V which are somewhat more than half the length of metatarsal III, with the pes of symmetrical type.

LEVEL OF ORGANIZATION OF LAGOSUCHIDAE

There is not doubt that *Lagosuchus* is of special phylogenetic interest because the various characters of its skeletal organization show transitional traits between Pseudosuchia and Saurischia. I call attention to, among other things, the fact that this Middle Triassic thecodont possessed a hind limb and pubis with specialized characters of the condition of some Triassic saurischians, much more so than any other thecodont known from the Upper Triassic.

The vertebral column. Here we see that *Lagosuchus* has developed 3 perfectly distinguishable zones in the presacral vertebrae.
Therefore we have:

1) a model of cervical vertebrae up to the 5th inclusive, which are relatively elongate, slightly tall, with more or less extended laminar spines;
2) another vertebral model in the cervico-dorsal vertebrae, from the 6th to 11th, which are relatively short and tall, with axially short and forward-directed spines;
3) another vertebral model in the posterior dorsals from the 12th or 13th to the last presacral, which are relatively long and low, with axially extended laminar spines.

It is clear that this zonation of the vertebral column corresponds to a determining function. In our opinion the development of a bipedal habit would be one of the primary factors that conditioned this, especially producing a curvature above the anterior part of the neck, much more exemplified in *Deinonychus* Ostrom (1969).

Among the various suborders of Thecodontia a comparable case is encountered only in Pseudosuchia. In *Euparkeria* Ewer (1965) the beginning of an incipient zonation is present, manifest in the shortening of the vertebral centra at the top of the pectoral girdle and elongation in the dorsal posterior region, accompanied by some differences in the morphology and orientation of the vertebral spines. Without going into great detail, it is evident that *Euparkeria* occupies an ancestral condition with respect to the zonation of the presacral vertebrae.

Among Ornithosuchidae that we possess good evidence of the column are *Gracilisuchus* (Middle Triassic), *Ornithosuchus* and *Riojasuchus* (Upper Triassic). In all of them the previously noted characteristics of the zonation of the column are practically nonexistent, less notable than in

Euparkeria. It could be indicated that bipedalism would be an occasional habit in Ornithosuchidae, as has been noted in recent crocodiles (J. Lucas in Charig, 1972) which also possess the cited zonation in the vertebral column.

Among the Sphenosuchidae there is evidence of the vertebral series, incomplete in *Hesperosuchus* Colbert (1952) and more complete in *Pseudhesperosuchus* Bonaparte (1971b). Although the skeletal reconstruction of *Hesperosuchus* (Colbert, op. cit, fig. 34) shows that the 8th through 13th vertebrae inclusive are shorter than the anterior cervicals and posterior dorsals, the available materials are not very clear in this respect. In *Pseudhesperosuchus* the 2nd, 3rd, and 4th cervical vertebrae are longer than the rest, which are at the same time of large size.

Among the Triassic dinosaurs in which this feature of zonation of the column can be compared are Prosauropoda, Coelurosauria and, somewhat doubtfully, Herrerasauridae. Known prosauropods invariably have a long neck, as is the case in *Plateosaurus* Huene (1907), *Efraasia* Galton (1973) or *Riojasaurus* Bonaparte (1971b), of which excellent materials are known. There are short vertebrae in the transition between the cervicals and dorsals as is the case in *Lagosuchus*, although with distinct characteristics, since the shorter vertebral segments of prosauropods correspond approximately to the 10th through 14th vertebrae; in other words this zone of the vertebral column is located further back in Prosauropoda than in *Lagosuchus*, although it retains a similar function in enabling neck elevation.

Among Coelurosauria, *Coelophysis* is a genus represented by very complete materials, and it can be taken as a representative of the family Podokesauridae, including *Procompsognathus*, with respect to the zonation of the column. *Coelophysis* has elongate cervical vertebrae, and it shows somewhat short first dorsals between the 10th and 14th inclusive, recalling the condition in *Lagosuchus*, although with the difference than in this latter the zone is between the 6th and 11th vertebrae. In the reconstruction of *Procompsognathus* illustrated by Huene (1921), the sector comprised between the 10th and 14th vertebrae inclusive shows shorter vertebral segments, with similar characteristics to *Coelophysis.*

Of the family Herrerasauridae Benedetto (1973), the available evidence indicates that *Herrerasaurus* had a short neck, and that a "cervico-dorsal" vertebra of this genus, illustrated by the cited author in fig. 1, shows it to be short and tall. In *Staurikosaurus* from the Middle Triassic of Brazil, according to a reinterpretation of the existing material done by Galton, that he had the kindness to share with us, one observes a region of short vertebrae with small spines in the transition between the cervicals and dorsals, clearly comparable to that seen in *Lagosuchus*.

In summary, from this comparison it follows that the zonation of the vertebral column in *Lagosuchus* is a specialized character present in diverse Triassic saurischians, which reflects special adaptations for accomplishing increased movement and positioning of the neck with respect to the dorsal region of the column. Limiting these considerations to saurischians with short necks

(Carnosauria), it is evident that this zonal differentiation of the presacral vertebral sequence, very clear in *Deinonychus* (Ostrom, 1969), would be an adaptation concomitant with bipedal posture and predatory requirements. Apparently these adaptive characteristics were clearly initiated in *Lagosuchus*.

Sacrum. The sacrum of *Lagosuchus* is constituted only of two vertebrae, which signifies a thecodont-type level of organization, with the explanation that certain advanced thecodonts like *Riojasuchus* and *Ornithosuchus* had exceeded the original number of 2, incorporating a third into the constitution of the sacrum. Nevertheless the suggestion of Galton (1973, p. 235 and fig. 16A), who notes the possibility that the prosauropod *Efraasia* had only two sacral vertebrae, is interesting.

Pelvis. The pelvis of *Lagosuchus* is very indicative of the transitional condition of this thecodont between two very distinct levels of organization, the thecodont type and the saurischian type.

The ilium is typical of a thecodont, comparable to Rauisuchidae, Euparkeriidae or Phytosauridae. On the other hand the pubis shows a completely distinct level of specialization from the ilium. Its advanced features - such as the reduction of the proximoventral region with the disappearance of the obturator fenestra and consequent reduction of the puboischial contact, the torsion of the distal end that tends to expose it laterally, forming an incipient "foot", and the reduction of the pubic symphysis - are characters present only in coelurosaurian saurischians and in Herrerasauridae, in other words of a more advanced type than Prosauropoda.

The ischium presents a proximal region with very advanced characters, in which an acetabular area, a peduncle for its union with the pubis, and a depressed area between these features can be differentiated. The reduction in the area of the union of the ischium and pubis is notable.

The proximal region of the ischium is similar to that of the thecodont *Ornithosuchus*, in my opinion more advanced than that of the primitive saurischian *Herrerasaurus* and of Prosauropoda, since it ischiopubic contact is much greater in these latter. At the same time, the ischium of *Coelophysis* is somewhat more advanced in its proximal region than in *Lagosuchus*.

The medial and distal region of the ischium is frankly primitive, with a ventral laminar projection that does not exist in *Herrerasaurus*, Prosauropoda, *Coelophysis*, not even in some thecodonts like *Ornithosuchus*, Rauisuchidae, etc.

In summary, the pelvis of *Lagosuchus* has a typically thecodont ilium, a pubis of saurischian-carnosaurian type, an ischium with the proximal region with characters of saurischian

type (or advanced pseudosuchian) and the medial and distal region of primitive pseudosuchian type.

Hind limb. a) Femur: the very cylindrical shaft, the features of the 4th trochanter, the ossification and anteromedial projection of the femoral head, as well as the fact that the femur is shorter than the tibia, are characters that define it as corresponding to a very advanced pseudosuchian or primitive saurischian like the Herrerasauridae or eventually *Coelophysis.* The prosauropods invariably show a more specialized femur, above all by the medial projection of the femoral head, which does not exist in *Lagosuchus*.

b) Tibia and fibula: It is evident that the tibia and fibula of *Lagosuchus* are specialized since, besides being proportionally fragile and long, they are longer than the femur. One of the few thecodonts with these characters is *Lagerpeton* Romer (1971b) from Los Chañares and *Scleromochlus* Woodward (1907) of Scotland.

In general the ratio between the length of the tibia and femur in pseudosuchians indicates than both segments were of similar length in advanced forms like *Hesperosuchus, Saltoposuchus*, or more frequently the tibia was shorter than the femur (Ornithosuchidae, Rauisuchidae).

On the other hand, Triassic and post-Triassic Coelurosauria had, in general, a tibia longer than the femur, a character that has been considered an indication of locomotor specialization.

The distal end of the tibia of *Lagosuchus* presents transitive characters between the typical thecodont condition and that of dinosaurs. In thecodonts the major axis of the distal tibial articulation is oriented anteroposteriorly, while in dinosaurs, both saurischians and ornithischians, the distal end of the tibia has the form of an L, with one axis oriented anteroposteriorly and another transversely. The stage represented by *Lagosuchus* corresponds, in my opinion, to an intermediate condition between that present in both groups of archosaurs. In this character of the tibia, *Lagosuchus* is more advanced than Thecodontia, and somewhat more primitive than Saurischia and Ornithischia.

c) Tarsus: The tarsus of *Lagosuchus* is morphologically and functionally of the type possessed by saurischians and ornithischians, although with somewhat the same characteristics. It differs completely from that known among pseudosuchians, which invariably are of crocodilian type, the crurotarsal condition, except in *Lagerpeton* and *Triassolestes* (Bonaparte 1971c). In other words the level of organization of the tarsus of *Lagosuchus* is of the type possessed by dinosaurs.

d) Pes: The pes has an evident symmetry around digit III, although metatarsal IV is not much shorter. Metatarsals I and V are reduced, and of similar length and width. Another advanced

character of the foot is that metatarsals II, III and IV are long, slender, and preserved in a parallel position, presumably in contact between them, at least in their proximal half.

In an interesting analysis on the evolution of the pelvis and hind limb in archosaurs, Charig (1972) pointed out that in the advanced, digitigrade forms the length of the phalangeal series is equal or slightly greater than the metatarsals, a character that *Lagosuchus* possesses in digit III and eventually in IV, although not in II.

The pes of *Lagosuchus* is obviously more advanced and more illustrative of the digitigrade, bipedal, and cursorial condition than that of Ornithosuchidae and Rauisuchidae. The arguments of Charig (1972) in which the general structure coincides satisfactorily with the characters of *Lagosuchus*, in such a way that the pes separately indicates well the advanced locomotor organization of *Lagosuchus*.

e) Disparity of the limbs: the ratio of length between the fore and hind limbs of *Lagosuchus* is 1:2.4, very approximately, since the length of the manus is not known. In *Coelophysis* the same ratio is approximately 1:2; in *Dilophosaurus* it is approximately 1:2.5; in the ornithosuchid *Riojasuchus* 1:1.5; and in *Ornithosuchus* approximately 1:1.8. In other words *Lagosuchus* presents a notable disparity between both limbs that is in agreement with its supposed bipedal posture, a suggested by the anatomy of the hind limb. In Diagram 1 the result of this analysis is diagrammed, in relation to the general scheme of the level of organization in Thecodontia and Saurischia.

IS LAGOSUCHUS A THECODONT OR A SAURISCHIAN?

The transitional condition of *Lagosuchus* between thecodonts and saurischians presents the opportunity, for the first time, to analyze and define preliminarily what the anatomical modifications were that occurred between the two groups, and especially how this happened according to the evidence presented by *Lagosuchus*. Recently Bakker and Galton (1974) and Charig (1972) have shown various characters that differentiate between Thecodontia and Dinosauria (*sensu* Bakker and Galton) and explained their functional implications, which support the clear distinction between these archosaurian reptiles. However *Lagosuchus* cannot be placed in either group without suggesting contradictions, (for example, the mesotarsal condition if it is placed among Thecodontia, or the sacrum or ilium if among Saurischia). In this manner I note that presently we do not have enough information or preceding works in the paleontological literature with respect to transitional characters between these clearly distinguished groups. Therefore I think that the study of *Lagosuchus* is a good opportunity to incorporate information and concepts that distinguish an advanced thecodont from a primitive dinosaur.

Following this intention I am confronted with similar problems to those raised in the attempt to define or distinguish more advanced cynodonts from more primitive mammals.

Clearly the information provided by this genus from Los Chañares allows us to clarify the concepts of transition between thecodonts and dinosaurs somewhat, but I understand that the theme is incomplete and will only be explained by new studies and discoveries that are brought to light in the future.

Advanced thecodonts. The distinction between primitive thecodonts and dinosaurs is very clear, particularly from the organization of the pelvis and hind limbs, and especially taking into account the Proterosuchia (Erythrosuchidae and its descendants Rauisuchidae; and Proterosuchidae and its descendants Cerritosauridae and Proterochampsidae), Aetosauria and Phytosauria.

In these groups there are primitive characters that are directly or indirectly ancestral to Saurischia and Ornithischia, such as the sacrum with two vertebrae, the pelvis with a closed acetabulum, the short pubis and ischium (except in Rauisuchidae), the primitive femur lacking a medial projection, with poor definition of the femoral head, and lacking a lesser trochanter; the tibia and fibula shorter than the femur; the primitive tarsus; the humerus generally with an ectepicondylar foramen, etc.

However the more advanced thecodonts, grouped in the suborder Pseudosuchia (particularly Ornithosuchidae), show dinosaurian characters in the pelvis with an incipient acetabular fenestration, extended pubis, reduced ischium, and other characters of the femur such as the definition of the femoral head that shows a neck, and the development of the lesser trochanter (Walker, 1964; Bonaparte, 1971b). In other thecodonts such as *Triassolestes* (undescribed materials) from the Ischigualasto Formation, the tarsus shows dinosaurian characters in the reduction of the calcaneum and the traits of the astragalus (Bonaparte, 1971c). Also in *Triassolestes* the humerus is more similar to the type shown in dinosaurs, which in general have the deltoid crest located more distally than in thecodonts (Bakker and Galton, 1974).

It is clear that these dinosaurian characters in Upper Triassic thecodonts are the result of a parallel evolution between them and dinosaurs, in such a way that the distinction between the two groups is not always clear (v. gr. Walker, 1964). Since we know this now, one of the clearer differences between advanced thecodonts and primitive dinosaurs is manifest in the perforate acetabulum, incipient in one and well-defined in the other; the limited development of the lesser trochanter that contrasts with its good definition in dinosaurs; and the tarsal condition, which is crurotarsal in thecodonts, with a crocodilian astragalus and calcaneum (except *Triassolestes, Lagosuchus* and *Lagerpeton*), and mesotarsal in dinosaurs.

Primitive dinosaurs. The more primitive dinosaurs are the Middle and Upper Triassic Saurischia, from upper Chañarian (approximately Ladinian), Ischigualastian (approximately Carnian), and Coloradian (approximately Norian) ages, represented in South America and other continents by Prosauropoda, Coelurosauria and Carnosauria, if the Herrerasauridae of Argentina and Brazil and *Dilophosaurus wetherilli* Camp (1954) of Arizona are referred to this latter infraorder.

The Triassic Ornithischia - *Pisanosaurus* Casamiquela (1967), *Fabrosaurus* Ginsburg (1964) and Thulborn (1972), and *Heterodontosaurus* Crompton and Charig (1962) - show more distinct advances with respect to the rest of the Triassic dinosaurs, especially in the organization of the pelvis and hind limb, and in the development of a herbivorous-type dentition (Bonaparte, in press), such that it does not appear to be useful to consider them in an analysis of primitive forms of dinosaurs in relation to the thecodont-dinosaur transition.

The Triassic Coelurosauria show more specialized traits than the Prosauropoda and herrerasaurids in the greater number of sacral vertebrae, the tibia longer than the femur, the anterior projection of the ilium and the specializations of the pes and manus.

As Bakker and Galton (1974) clearly pointed out "...the postcranial anatomy of prosauropod grade seems to be the primitive condition of dinosaurs...", except, it can be noted, that the elongate and fragile cervical vertebrae represent a specialization concomitant with the size reduction of the skull.

The Herrerasauridae, *Staurikosaurus* Colbert (1970) and *Herrerasaurus* Reig (1963), are the most primitive saurischians in many aspects of their organization (and the fossil record), since they have maintained the carnivorous habit of their ancestors, although they possess a more specialized pubis than the Prosauropoda.

In summary, the more primitive characters of herrerasaurids and prosauropods are integrated together (artificially) with generalized traits in order to compare them with the characters of *Lagosuchus*, and presented in the following table:

habits: carnivorous (Herrerasauridae) - quadrupedal (Prosauropoda)

presacral vertebrae: with three distinct morphological zones

neck: short (Herrerasauridae)

sacrum: 3 vertebrae

ilium: without anterior projection

acetabulum: open

pubis: laminar, exposed dorsally (Prosauropoda)

femur: lesser trochanter poorly developed (Herrerasauridae)

tibia: shorter than the femur (Prosauropoda)

tarsus: mesotarsal condition; separate astragalus and calcaneum

Lagosuchus talampayensis agrees with 6 of the 10 characters indicated in this combination of primitive prosauropod and herrerasaurid traits. Of the remaining 4, 2 are more advanced in *Lagosuchus* (the pubic characters and the tibia-femur ratio), and the other 2 are clearly more primitive (the number of sacral vertebrae and the open acetabulum). In our opinion these features of the Los Chañares species reflect a primitive condition in the organization of the pelvis, that, adding to the also primitive character in the distal part of the ischium and the peculiar morphology of the distal tibia, makes us consider *Lagosuchus* as an advanced thecodont having the condition of primitive saurischians.

I believe that the alternative, to consider it a primitive dinosaur, is not justified, since for this we must ignore the diagnostic value of such definitive characters of the advanced level of locomotor organization as the sacrum with 3 or more vertebrae, associated with the perforation of the acetabulum, and the peculiar morphology of the distal end of the tibia of dinosaurs (with a transversely disposed major axis).

Therefore it seems more reasonable to retain this species from Los Chañares among the Pseudosuchia, in a lineage ancestral to dinosaurs, which would confirm the clearly stated idea that they originated in the Pseudosuchia. Recently Krebs (1974) held that "...the Pseudosuchia, which are not ancestors to later archosaurs...", an idea that seems ambiguous since I endorse that the Pseudosuchia, from the interpretations of various paleontologists from 1950 up to the most recent works, always includes the direct ancestors of Crocodilia, Saurischia, and eventually indirectly Ornithischia and Pterosauria. In our opinion the Pseudosuchia *sensu* Romer (1972) and Bonaparte (in press) combines various lineages that can be clearly considered ancestral to Crocodilia, Saurischia, and Ornithischia.

In Diagram 2 I have diagrammed the relative position of *Lagosuchus talampayensis* among the levels of organization of Thecodontia and Saurischia.

Our systematic interpretation of *Lagosuchus talampayensis* is that it is a thecodont with various dinosaurian characters. Obviously this thecodont has developed a series of characters close to saurischians, and because of this I think that the evolutionary grade of Saurischia was crossed by diverse thecodonts in some anatomical features, or many as is the case in *Lagosuchus*, without managing to attain this level completely. Further below are cited the advanced characters shared by specialized thecodonts and primitive saurischians and, aside, those of primitive saurischians.

Advanced characters shared by thecodonts and saurischians

habits: bipedal; digitigrade

presacral vertebrae: with 3 distinct morphological zones

pubis: long, exposed dorsally or dorsolaterally, with reductions in the proximoventral region

femur: subspherical head with neck, projecting anteromedially; with well-developed lesser and 4th trochanters

tarsus: reduction of the calcaneum; mesotarsal condition

metatarsals: elongate, approximately symmetrical around III

scapulocoracoid: glenoid cavity directed principally backwards

humerus: deltoid crest a clear distance from the proximal end; well-defined humeral head and internal tuberosity

Distinct characters of primitive saurischians

acetabulum: clearly open

tibia: transversely disposed area of contact with the astragalus and posterior descending process

This brief analysis and listing of specialized characters shown in some thecodonts and also in primitive saurischians, plus the enumeration of a pair of characters suitable to saurischians (and ornithischians), presents the opportunity to define or distinguish a thecodont of advanced locomotor habit from a primitive dinosaur. In truth the distinction between the two is limited to the distinct grade of locomotor organization and concomitant characters.

Order Thecodontia

(advanced thecodont)

Carnivorous habits, quadrupedal or bipedal; presacral vertebrae with 3 distinct morphological zones; pelvis with advanced characters but with closed acetabulum; femur with well-defined head projecting from the shaft but with little development of the 4th and lesser trochanters. Distal end of the tibia with anteroposteriorly directed articulation and both sides forming an angle without posterior descending process. Crurotarsal- or mesotarsal-type tarsus with reduced calcaneum. Metatarsus elongate; foot symmetrical around III.

Scapula with glenoid cavity directed at a variable angle up to projecting backwards. Humerus with well-defined head and internal

Order Saurischia

(primitive dinosaur)

Carnivorous habits, quadrupedal or bipedal; presacral vertebrae with 3 distinct morphological zones. Pelvis with relatively primitive characters but with open acetabulum. Femur with head well defined from the shaft and projecting anteromedially; with good development of the 4th and internal trochanters. Distal end of the tibia with transversely-directed contact with the astragalus and posterior descending process. Mesotarsal-type tarsus. Metatarsals elongate or not, symmetrical or not. Scapula with glenoid cavity directed backwards; humerus invariably with the deltoid crest a marked distance from the proximal end.

Carpus not crocodilian. Variable disparity

tuberosity; and the deltoid crest located a clear distance from the proximal end. Crocodilian (*Pseudhesperosuchus*) or non-crocodilian (*Riojasuchus*) carpus. Variable disparity between the limbs.

THE POSSIBLE RELATIONSHIP OF LAGOSUCHUS WITH TRIASSIC SAURISCHIA

The comparison of various characters of *Lagosuchus*, such as the zonation of the presacral vertebrae, the principal traits of the pelvis and hind limb, and the disparate ratio between the limbs, with Euparkeriidae and Ornithosuchidae on one hand and Prosauropoda, Herrerasauridae and Coelurosauria on the other, provides some argument towards interpreting the phylogenetic relationships of this Los Chañares form. The ideas obtained are gratifying in the following diagram, on which I comment.

Zonation of the presacral region of the vertebral column. In this character, it seems clear that *Euparkeria* occupies an ancestral position since there are indications of zonation, with somewhat shorter vertebrae at the height of the pectoral girdle, with slight modifications in the morphology and orientation of the spines. From the level of *Euparkeria*, a level more suitably called Euparkeriidae, a radiation is shown and documented by Middle Triassic pseudosuchians (Ornithosuchidae, Lagosuchidae, *Lewisuchus*). One of the lineages of this radiation gave rise to Ornithosuchidae, which shows no major advances relative to this character. The other lineage of this radiation includes *Lagosuchus*, whose probable origin in Euparkeriidae, in relation to this character, is no obstacle to permit it being at the same time ancestral to Herrerasauridae and eventually Prosauropoda and Coelurosauria.

Characters of the pelvis. In the comparative analysis of the pelvis I also encountered justification to describe at least two distinct lineages from *Euparkeria*. One of these is shown in Ornithosuchidae by the persistence of a laminar, wide, anterodorsally exposed pubis. The other lineage, from *Lagosuchus*, shows a substantial modification in the pubis which has a laterally exposed distal end, since it ceases being laminar and transversely wide.

The pelvis of Herrerasauridae, with an open acetabulum, can be strongly considered to have originated from the type present in *Lagosuchus*, with a nearly closed acetabulum but with notable

similarity in the pubis. With little morphological evidence I infer that the pelvis of Coelurosauria also could have originated from the type present in *Lagosuchus*.

I believe that the pelvis of Prosauropoda could be derived from a type intermediate between that of Euparkeriidae and *Lagosuchus*, which is not distinct from that of the primitive Ornithosuchidae of Los Chañares *Gracilisuchus stipanicicorum*, with a laminar pubis.

Characters of the hind limb. For this phylogenetic intent following the characters of the hind limb I have paid special attention to the tarsal characters, pedal morphology, and the femur-tibia ratio. The crurotarsal condition of Euparkeriidae and Ornithosuchidae contrasts with the mesotarsal condition of the remaining groups under consideration, which does not invalidate the relation between the two because I do not share the opinion of Krebs (1965, 1974) with respect to the lack of phylogenetic relationship between them, and agree with Schaeffer (1941) and Charig (1972) that transition between the two types is perfectly possible, particularly from the "less elaborated" condition shown in *Euparkeria*. The characters of the tarsus and distal end of the tibia in *Lagosuchus*, although of mesotarsal condition, in part confirm this transition.

Besides the condition of the tarsus, note that the length of the femur is constantly greater than the tibia in Euparkeriidae and Ornithosuchidae, in spite of some ornithosuchids like *Riojasuchus* that accomplish notable femoral specializations.

In *Lagosuchus* note the contrast offered by two aspects of the hind limb; one is the transitive condition of the distal end of the tibia between the thecodont and dinosaurian types, a condition surpassed by all Triassic dinosaurs; and the other, the feature of locomotor specialization that shows the ratio of lengths of the pes, tibia and femur to be comparable only to those of some Coelurosauria.

In the herrerasaurid *Staurikosaurus* the tibia is somewhat longer than the femur; in *Herrerasaurus* the tibia is somewhat shorter than the femur, but there is a match in femoral morphology and pedal characters such as to suggest a proximity between Herrerasauridae and Lagosuchidae. Because of this the differentiation of herrerasaurids from the Lagosuchidae lineage must have occurred before the level of *Lagosuchus*.

With regard to Coelurosauria, it is perfectly possible to derive these from the type of limb possessed by *Lagosuchus*.

The hind limb of prosauropods presents notable differences from the other groups considered. The asymmetrical structure of the foot contrasts with the condition in *Lagosuchus* and Herrerasauridae; the defined medial projection of the femoral head and the robust femoral architecture, just as the tibia shorter than the femur (a general condition in all prosauropods), supports that prosauropods must have differentiated before achieving the level of *Lagosuchus*.

Ratio between the fore- and hind limbs. The percentage reached by the length of the forelimb relative to the hind indicates, on one hand, a certain constancy between *Euparkeria* and the Ornithosuchidae, and on the other a relative equality between the ratios in *Lagosuchus* and *Coelophysis* such as to suggest a phylogenetic relationship. However the percentages noted among Prosauropoda suggest that the phylogenetic value of this ratio could be very relative or useless if considered alone.

The disparity in the limbs of *Lagosuchus* and other traits of the hind limb clearly indicate relationships with Herrerasauridae and eventually *Coelophysis.* However the relationship with Prosauropoda appears obscure, not only because the disparity is generally less, but also for the notable morphological differences in the hind limb. In other words in the case of Prosauropoda the character of limb disparity is subordinate to the morphological information. As stated above, the variable disparity in the limbs among Prosauropoda, which show very constant anatomical characters throughout their postcranial skeleton, suggests that this disparity could show advances and retreats conditioned by the habits of the various species, and would therefore hold little value in interpreting their phylogenesis.

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José F. Bonaparte
Instituto de Geología
Funación Miguel Lillo
Miguel Lillo 205

S. M. de Tucumán (R. A.).

FIGURE CAPTIONS

Fig. 1. - *Lagosuchus talampayensis* Romer, PVL 3870. Left lateral view of the braincase. Abbrev.: AP, area of contact of the parietal; ASQ, area of contact of the squamosal; BSF, basisphenoids; BOC, basioccipital; EXO, exoccipital; FPOS, area of the post-temporal foramen; LTS, laterosphenoids?; PRO, prootic; V, exit for nerve V; X, exit for nerve X.

Fig. 2. - *Lagosuchus talampayensis* Romer, PVL 3870. Incomplete maxilla and premaxilla in internal view. Dotted lines indicate reconstruction of broken parts. Abbrev.: MX, maxilla; N, external naris; VPO, preorbital vacuity.

Fig. 3. - *Lagosuchus talampayensis* Romer, PVL 3872. Right ventrolateral view of the braincase. Abbreviations as in figure 1 and additionally: CDQ, distal condyle of the quadrate; CPQ, proximal condyle of the quadrate; FO, fenestra ovalis?; PSF, parasphenoids; Q, quadrate; VII, in part occupied by the exit for nerve VII.

Fig. 4. - *Lagosuchus talampayensis* Romer, x 3. A, lateral view of the atlas and preatlas articulated with the axis and skull, respectively; B, dorsal view of the arches of the atlas and preatlas. Abbrev.: AA, atlantal arch; BOC, basioccipital; CA, atlantal centrum; PE, spinous process of the atlas; PRA, preatlantal arch; SOC, supraoccipital.

Fig. 5. - *Lagosuchus talampayensis* Romer, PVL 3870, x 3. A, sequence of 9 cervical vertebrae articulated together and to the cranial fragment illustrated in fig. 2A; B, sequence of 11 articulated dorsal vertebrae.

Fig. 6. - *Lagosuchus talampayensis* Romer, MCZ 4116, approx. x 3. Sequence of presacral vertebrae from the 8th cervical to the 24th? presacral that is connected to the two sacral vertebrae; at the same time united to the right ilium and the proximal part of the femur. Abbrev.: PUB, pubis; AC, acetabulum; FI, facet for the ischium; FEM, femur; S1, S1, sacral ribs 1 and 2.

Fig. 7. - *Lagosuchus talampayensis* Romer. A, the 4th, 9th and 18th vertebrae that caracterize the three morphological zones shown in the presacral vertebral sequence of this species; B, sequence of the 7th to 12th presacral vertebrae that illustrate the morphological change that occurs in this region, and the characters shown that have to do with the torsion of the neck.

Fig. 8. - *Lagosuchus talampayensis* Romer, PVL 3871, x 2. A, lateral view of the left scapula as preserved; B, reconstruction of the same. Abbrev.: ACR, acromial process; PC, lateroposterior process of the coracoid; FC, coracoid foramen.

Fig. 9. - *Lagosuchus talampayensis* Romer, PVL 3871, x 2. A, B, left humerus in dorsal and ventral views, respectively; C, distal portions of the incomplete left radius and ulna in approx. lateral view. Abbrev.: CD, deltoid crest; POL, olecranon process; TI, internal tuberosity.

Fig. 10. - *Lagosuchus talampayensis* Romer, PVL 3870, x 2. Lateral view of the pelvis as preserved, including part of the 2nd sacral vertebra and three caudal vertebral bodies. Missing

portions are reconstructed with dotted lines. Abbrev.: CSUP, supraacetabular crest; EA, acetabular fossa of the ischium; PA, ambiens? process; PP, pubic peduncle.

Fig. 11. - *Lagosuchus talampayensis* Romer, PVL 3870, x 2. A, anterior view of the pelvis in figure 10, also as preserved; B, reconstruction of the same anterior view. Abbrev.: M, matrix; P, plastic; S1 and S2, sacral ribs 1 and 2.

Fig. 12. - *Lagosuchus talampayensis* Romer, PVL 3870, x 2. Right femur in A, ventral view; B, dorsal; and C, medial. Abbrev.: CF, fibular condyle; CL, longitudinal crest; CTE, external tibial condyle; CTI, internal tibial condyle; TRM, greater trochanter; TR4th, fourth trochanter.

Fig. 13. - *Lagosuchus talampayensis* Romer, PVL 3870, x 1.7. A and B, right tibia, fibula, tarsus and pes in medial and lateral views, respectively. C and D, left pes in disal and ventral views, respectively. Abbrev.: AST, astragalus; FIB, fibula; TE, external tarsal; TI, internal tarsal.

Fig. 14. - *Lagosuchus talampayensis* Romer, PVL 3870, x 2. A, anterior view of the distal end of the left tibia and fibula, articulated with the astragalus and calcaneum; B, medial view of the end of the tibia articulated with the astragalus; C, lateral view of the end of the fibula articulated with the calcaneum; D, posterior view of the specimen illustrated in A; E, ventral view of the same; G, posterior view of the distal end of the right tibia and fibula, united with the astragalus; H, ventral view of the same. Abbrev.: AST, astragalus; CAL, calcaneum; F, fibula; PC, calcaneal process; PD, dorsal process of the astragalus; T, tibia.

Fig. 15. - *Lagosuchus talampayensis* Romer, PVL 3870, x 4. A, ventromedial view of the proximal part of right metatarsals 1, 2, and 3 with the internal tarsal in original position. B, ventral view of right metatarsals 3, 4, and 5 with the internal tarsal, also the proximal portion; C, proximal view of the left pes showing metatarsals 1 and 2 and both distal tarsals; D, external view of the external tarsal of the left pes. Abbrev.: TI, internal tarsal; TEXT, external tarsal; MT1, MT2, MT3, MT4, MT5, metatarsals 1 through 5; V, ventral; D, dorsal; (1), areas of muscular insertion.

Fig. 16. - *Lagosuchus talampayensis* Romer, PVL 3870, x 2. Reconstruction of the left pes in dorsal view. Missing phalanges are marked with diagonal lines.

Fig. 17. - *Lagosuchus talampayensis* Romer. Skeletal reconstruction, based on various incomplete specimens. No information exists on the carpus. Bipedal and quadrupedal habits must have been common in *L. talampayensis*, according to the speed of its movement.

Fig. 18. - Some of the major species known from th local fauna of Los Chañares, La Rioja prov. Above, *Probelesodon lewisi* Romer and *Massetognathus pasuali* Romer; center, *Chanaresuchus bonapartei* Romer; below, *Gracilisuchus stipanicicorum* Romer and *Lagosuchus talampayensis* Romer, approx. x 0.10. Taken from Romer and Lewis (1973), Jenkins (1970), Romer (1972a), and Romer (1972b), respectively, except *Lagosuchus*.

Fig. 19. - *Lagosuchus talampayensis* Romer, PVL 3871, x 2. Left femur and humerus, showing the disparate proportions that are shown by these bones.

Diagram 1. Phylogenesis and systematics of Triassic Thecodontia (partial), Saurischia, and Ornithischia, indicating their possible relationships. The provincial ages of the Triassic of South America are indicated.

Diagram 2. Uniting of the principal morphological characters of *Lagosuchus talampayensis* in relation to a "Thecodont level," based on forms such as Proterosuchidae-Ornithosuchidae, and a "Saurischia level," based on the condition of Triassic saurischians. A panorama of relationships is obtained that more clearly fits either level according to the group of traits considered.

Diagram 3. Reproduction of the presacral vertebral sequence of various thecodonts and saurischians, which permits visualization of the existence of only two distinct "lineages": a) *Gracilisuchus-Ornithosuchus-Riojasuchus*; b) *Lagosuchus-Staurikosaurus*-Prosauropoda-*Coelophysis*, supposed to have originated in Euparkeriidae.

Diagram 4. Phylogenetic relationships according to the evidence shown by features of the pelvis. The *Lagosuchus-Staurkosaurus-Herrerasaurus* lineage is obvious; the *Lagosuchus*-Coelurosauria connection is probable, and the relationships of Prosauropoda are uncertain because of the persistence of the laminar pubis.

Diagram 5. Phylogenetic relationships according to the evidence from the hind limb. The possible Lagosuchus-Coelurosaurus relationship is shown as very possible; the characters of Prosauropoda revel a possible disconnection from the relatively homogeneous *Lagosuchus-Staurkosaurus-Herrerasaurus* group.

Diagram 6. Phylogenetic relationships according to the evidence from the value of the ratio between the fore and hind limbs, expressed as a percentage. On the one hand, there is certain unity between Euparkeriidae and Ornithosuchidae. It is also clear that the proportions of *Lagosuchus* are more marked, which is indicated by other diagrams as inherited by Coelurosauria. Prosauropoda shows that the value of this character should be taken with some caution, since great variation exists among them.

PLATES

PLATE I

Figure 1. - *Lagosuchus talampayensis*, PVL 3870, x 1. Ventrolateral view of the cranial fragment illustrated in fig. 1, united to 9 vertebrae.

Figure 2. - *Lagosuchus talampayensis*, PVL 3870, x 1.6. Medial view of the left maxilla with teeth, probably with a fragment of the premaxilla.

Figure 3. - *Lagosuchus talampayensis*, PVL 3872, x 2. Ventrolateral view of the cranial fragment illustrated in fig. 3, articulated with the three first vertebrae. Note the preatlas and atlas articulated with the axis in their original position.

PLATE II

Figure 1. - *Lagosuchus talampayensis*, PVL 3872, x 0.7. Lateral view of the sequence of 22 vertebrae articulated with the cranial fragment (pl. 1, fig. 3).

Figure 2A. - *Lagosuchus talampayensis*, PVL 3871, x 0.9. Lateral view of the scapula and coracoid and dorsal humerus, radius and ulna of the left side. Radius and ulna incomplete distally.

Figure 2B. - *Lagosuchus talampayensis*, PVL 3871, x 0.9. Anterior view of the opposite side of the same specimen.

PLATE III

Figure 1. - *Lagosuchus talampayensis*, PVL 3870, x 1.8. Right lateral view of the pelvis.

Figure 2. - *Lagosuchus talampayensis*, PVL 3870, x 0.7. Medial view of the left femur, tibia and astragalus.

PLATE IV

Figure 1A. - *Lagosuchus talampayensis*, PVL 3870, x 1.3. Medial view of the right femur.

Figure 1B. - *Lagosuchus talampayensis*, PVL 3870, x 1.3. Dorsal view of the right femur.

Figure 2A. - *Lagosuchus talampayensis*, PVL 3870, x 1.6. Posterior view of the left tibia and fibula united to the astragalus and calcaneum. Note the calcaneal process, and the peculiar morphology of the distal region of the tibia.

Figure 2B. - *Lagosuchus talampayensis*, PVL 3870, x 1.3. Dorsal view of the left pes with the two distal tarsals. Note only the proximodistal portion of met. V.

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