

NEW MATERIALS AND REINTERPRETATION OF
LAGERPETON CHANARENSIS ROMER (THECODONTIA,
LAGERPETONIDAE NOV.) FROM THE MIDDLE TRIASSIC
OF LA RIOJA, ARGENTINA*

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INTRODUCTION

Lagerpeton chanarensis forms part of an important Triassic fauna, produced by the lower part of the Ischichuca Formation (Chañares Formation of Romer and Jensen, 1966), Los Chañares locality, La Rioja, Argentina, which corresponds to the Chañarian Reptile Age, correlated with the European Anisian (Bonaparte, 1978, 1982*b*). This faunistic association includes therapsids, both cynodonts and dicynodonts (Romer, 1972*c*; Bonaparte *op. cit.*), and thecodonts pertaining to two suborders (Erythrosuchia and Pseudosuchia, *sensu* Bonaparte, 1982*a*) and five families: Cerritosauridae, Rauisuchidae, Lagosuchidae, Ornithosuchidae and Sphenosuchidae, represented by several genera (Bonaparte, 1978).

The importance of studying this fauna rests in the fact that Middle Triassic thecodonts, particularly from the lower part of this period, represent an important evolutionary moment in the history of archosaurs, since they attempted a great adaptive radiation that was the basis of later evolution of the group. The thecodonts of the Los Chañares fauna had achieved an evolutionary level immediately preliminary to the appearance of adaptive types such as saurischians and ornithischians, which are not recorded until the Upper Triassic, and which dominate the faunas that they comprise until the end of the Mesozoic.

The significance of the Los Chañares fauna increases when it is observed that the worldwide panorama of Middle Triassic thecodonts is particularly restricted.

As to the aforementioned, a better understanding of these Argentine forms can help clarify the systematic and evolutionary interpretation of the group, providing a guide to the

* Original citation: Arcucci, A. 1986. Nuevos materiales y reinterpretación de *Lagerpeton chanarensis* Romer (Thecodontia, Lagerpetonidae nov.) del Triásico Medio de La Rioja, Argentina. *Ameghiniana* 23(3-4):233-242. Translated by Matthew T. Carrano, University of Chicago, February 1997.

acquisition of derived characters in these thecodonts that favored the beginning of archosaur dominance in these Triassic faunas (Bonaparte, 1982b).

The species *Lagerpeton chanarensis* was described by Romer (1971) on the basis of material that consisted only of a hind limb. Next Romer (1972) ascribed an ilium, some long bones and isolated vertebrae to this genus, whose reference is dubious. The material mentioned does not permit systematic interpretation of this species nor connection of it with certainty to other known families, due to the peculiarity of its characteristics. Romer considered it a possible member of the family Scleromochlidae (1972c), comprised only of *Scleromochlus* from the Upper Triassic of England (Woodward, 1907); Bonaparte (1978) commented that *Lagerpeton* could have relationships with *Lagosuchus*, but did not include it in the same family. In more general works it is listed as *Thecodontia incertae sedis* (Krebs, 1976; Cruickshank, 1978b).

MATERIAL

The material used in the description includes the following specimens:

PVL 4619: An incomplete specimen, consisting of a complete pelvis connected to the sacrum; both hind limbs, the left complete, which includes the femur, tibia, fibula, two proximal tarsals, five metatarsals, and all phalanges including the unguals (fig. 1).

PVL 4625: An incomplete specimen (partially enclosed in matrix), with part of the presacral column, sacrum, left half of the pelvis, nine caudal vertebrae, left femur and proximal portion of the tibia.

Both specimens have been deposited in the Colección Paleontología de Vertebrados of the Inst. Miguel Lillo (PVL); they were collected in 1966 by an expedition from Fundación Lillo-CONICET and found in the northeast sector of the town of Rio Los Chañares.

The preparation of material was realized by mechanical methods in the workshop of the aforementioned Sección de Paleontología de Vertebrados by technician Señor Martín Vince.

SYSTEMATIC DESCRIPTION

Order **THECODONTIA** Owen, 1859

Suborder **PSEUDOSUCHIA** Zittel, 1887

(**sensu** Bonaparte 1982a)

Family **LAGERPETONIDAE** nov.

DEFINITION: Reptiles of small size (one hind limb 25 cm in length), with very marked locomotor specializations. Last presacral vertebrae with anteriorly-oriented neural spines. Sacrum with two vertebrae, with the last presacral in the process of sacralization. Closed acetabulum, vertical ilium with well-defined preacetabular projection; pubis short and wide; ischium longer than pubis and with an extensive ventral lamina. Hollow femur shorter than tibia, as in *Lagosuchus*. Tibia transversely extended in its distal region, with the ventral process on the anterior border, differing from other thecodonts. Advanced mesotarsal tarsus, similar to *Lagosuchus* and *Trialestes*, but with a more developed ascending process of the astragalus and barely distinguishable calcaneal tubercle. Two distal tarsals that could be fused. Elongate metatarsals. Metatarsal IV longer than the others. Metatarsal I short and V very reduced and lacking phalanges.

Genus **LAGERPETON** Romer, 1971

AGE: Chañarian Reptile Age, Middle Triassic.

GEOGRAPHIC DISTRIBUTION: Provincia de La Rioja, Argentina

DIAGNOSIS: The same as for the species, by monotypy.

TYPE SPECIES: *Lagerpeton chanarensis*, Romer, 1971.

HOLOTYPE: PULR 06 (Museo Paleont. Univ. Prov. de La Rioja) formerly Mus. de La Plata 64-XI-14-10. Right hind limb, femur, tibia and incomplete fibula, two proximal tarsals, two distal tarsals and complete pes.

HYPODIGM: The holotype and specimens PVL 4619 and PVL 4625.

EXTENDED DIAGNOSIS: Posterior dorsal vertebrae with anteriorly-oriented neural spines. Sacrum with two vertebrae united to the ilium, the last presacral with signs of being integrated into the sacrum. Ilium with well-defined anterior projection. Well-developed supraacetabular crest as in *Lagosuchus*. Pubis is wide and shorter than the ischium, laminar, and with symphysis restricted to the distal portion. Ischium with extended ventral lamina, very different from *Lagosuchus*. Hind limb long and slender with tibia longer than the femur, and asymmetrical pes as long as the tibia. Tibia with transversely extended distal region and anterior ventral process

opposite that which appears in *Lagosuchus* and other thecodonts. Sigmoid femur with pneumatization and well-developed fourth trochanter. Reduced fibula with developed anterolateral process. Advanced mesotarsal tarsus of dinosauroid type. Astragalus with more developed ascending process than in *Lagosuchus*. Calcaneum without defined tubercle. Two distal tarsals, corresponding to metatarsals III and IV. Metatarsal IV longer than the rest. Metatarsal I short and V reduced, without phalanges.

DESCRIPTION: *Vertebral column*: Eight posterior dorsal vertebrae, two sacrals and six caudals are preserved, all articulated.

The dorsal vertebral bodies have a length of 7 mm. In lateral view they show a strong ventral constriction, which marks a superficial medial concavity that makes the anterior and posterior ends of the body project more ventrally. The total height of the vertebrae is 12 mm, of which half corresponds to the neural spine.

The neural spines of these dorsal vertebrae have the unusual characteristic among thecodonts of showing a strong anterior inclination. This inclination of the vertebrae is shown in some mammals of saltatory habit (Hildebrand, 1974), and indicates a particular muscular and axial tendon arrangement for *Lagerpeton* not previously recorded in thecodonts. The edges of the neural spines become wide dorsally, which suggests strong tendinous insertions at this level. The prezygapophyses do not project strongly from the vertebral body. In contrast, the postzygapophyses are more robust and have wider bases, and are extended further beyond the posterior edge of the body.

With regard to the sacrum, the neural spines of the dorsals show signs of being integrated into the sacrum, since they show two laterally projecting processes which were united to the ilium by means of cartilage. Very probably it is this type of vertebra that Romer (1972*b*) described as the first of a series of three articulated sacrals.

There are two sacral vertebrae united to the ilium, with square neural spines and lacking wide dorsal borders. The union with the ilium is by means of robust ribs, which are expanded in a fan shape towards their distal region. Moreover, the sacral ribs are connected at their anterior and posterior ends, respectively. The sacral ribs of *Lagerpeton* become inclined in such a way as to form a concave dorsal plane on the sacrum, on both sides of the vertebral bodies. This characteristic distinguishes this sacrum from that of other thecodonts (ornithosuchids and lagosuchids) with sacra that are nearly flat dorsally (Bonaparte, 1975*a*, 1971).

The sacral vertebral bodies are amphiplatyan and become dorsoventrally flattened. There is no fusion of the vertebral bodies, which instead occurs at the level of the zygapophyses. The prezygapophyses are wide laterally and not strongly extended from the body. The

postzygapophyses are shorter than those anteriorly and are limited by a ventral fossa. The transverse processes are short and wide.

The anterior caudal vertebrae have longer bodies ventrally than the presacrals and sacrals. The body has a strong ventral constriction, greater than that seen in the presacrals. The vertebral bodies elongate a certain amount towards the distal region. The neural spines are taller than the vertebral body, and less axially extended than those of the presacrals. In these vertebrae the prezygapophyses are strongly extended from the vertebral body. They have long transverse processes that project from the upper medial part of the body and whose length is equivalent to the height of the vertebra. These processes are less axially extended and flatter. There is a series of 10 articulated caudal vertebrae isolated from the anterior ones in which only the marked ventral fossa can be seen, due to their deterioration.

Pelvic girdle (fig. 2): In specimen PVL 4619 this girdle is found complete with its three elements apparently in their original position.

The ilium is oriented vertically and is lower in the middle part of its blade than at the ends. It has a short, well-defined preacetabular process of angular shape, probably for the origin of the iliotibialis muscle.

Moreover, note the well-developed posterior process of the ilium, typical of most thecodonts, which is equivalent in length to twice the anterior process. The end of this process is situated higher than the anterior part of the ilium. The pubic peduncle is extended anteriorly, and the shorter ischial peduncle is directed posteriorly, which gives an asymmetrical shape to the ventral border of the ilium.

The pubis is short, transversely wide, and curved downwards by a narrow region or neck. In the curved portion note a short, laterally-projecting crest that is the insertion site of the *ambiens* muscle, which functions as the extensor of the limb (Romer, 1972*b*). In its distal part, the pubis is transversely expanded and unites with the opposing bone in a symphysis that is limited to the distal region. Beneath the medial part of the acetabulum note the puboischiatic symphysis, and anterior to this the *thyroid fenestra*, whose borders are somewhat deteriorated.

The ischium of *Lagerpeton* is markedly larger than the pubis, a condition not observed in thecodonts with specialized limbs. It has a border or crest that makes the acetabulum project laterally and posteriorly. In lateral view, this bone is slightly dorsally curved. Distally it presents a dorsoventrally planar and transversely narrow lamina. In its medioventral part the ischium shows a wide lamina of rounded shape, which is united to the opposite ischium by means of a long symphysis. The anterior edge of this ischiatic lamina is united to the posterior border of the pubis approximately at the height of the medial part of the acetabulum, where the lamina reaches its greatest extension.

The acetabulum, formed from the 3 pelvic bones, is closed and laterally-oriented. It has an oval shape, with its major disposition anteroposteriorly. A well marked supraacetabular crest projects from its upper posterior border, which augments the contact surface with the femoral head.

Hind limb (figs. 3, 4 and 5): It is found complete in specimen PVL 4619. Its characteristics match that of the type, since it has long and gracile limbs, with the tibia longer than the femur and the metatarsals elongated.

The femur is notably shorter than the tibia and the ratio between the bones is 86:100. The proximal and distal ends are expanded relative to the shaft, which is markedly sigmoid. The proximal end is a rounded, well-ossified head, projecting anteriomedially. A defined neck between the head and the shaft is not observed, a character that is well developed in some advanced thecodonts (*Riojasuchus*, v. Bonaparte, 1971) and some saurischians. The tibial condyles are well developed and separated by an intercondylar groove. The internal tibial condyle is more medially projecting. The fourth trochanter, which is the insertion site for the caudofemoral musculature (Romer, 1956), can be seen as a strong crest situated on the upper third of the bone, near the femoral head. This is the trochanter that shows the greatest development in both robustness and length. The greater trochanter, on the outer angle of the femoral head, is scarcely noticeable. The lesser trochanter might be represented, in medial view, by a zone of strong rugosities, situated on the opposite edge from the fourth trochanter. Due to a fracture in the shaft, it can be seen that this bone is hollow and has a central cavity filled with matrix, which indicates adaptive tendencies towards lightening of the skeleton.

The tibia is found articulated with the fibula and proximal tarsals, in its original position. The shaft is slender and straight, somewhat curved at its ends. The proximal third of the bone is expanded anteroposteriorly, while it is wider transversely in its articulation with the astragalus, which constitutes a typical dinosauroid character (Bonaparte, 1969, 1975*b*; Bakker and Galton, 1974). The tibia has a strong cnemial crest, limited medially by a very marked depression. The articulation with the fibula, on the upper lateral border, does not extend along the entire length of the border. In dorsal view, the proximal articular surface has a triangular shape with its vertex directed anteriorly, representing the anterior end of the cnemial crest. This articular surface is not horizontal, but inclined laterally. Distally the tibia has an anterior ventral process, clearly different relative to other thecodonts (*Riojasuchus*, *Neoaeosauroides*) and saurischians (Charig, Attridge and Crompton, 1965), which have the so-called "posterior process of the tibia" (Bonaparte, 1971). This change is probably related to structural modifications occurring at the level of the proximal tarsals in *Lagerpeton*.

The fibula is slightly shorter than the tibia and is very reduced in diameter compared to it. Just as the tibia, its proximal and distal portions are displaced in the opposite direction. Proximally it contacts the lateral face of the tibia. The anterior border of the fibula is enlarged near the shaft to form a crest, which corresponds to the anterolateral process of the fibula. This process is found in the majority of pseudosuchians, and in rauisuchids and aetosaurids, but appears shorter and more robust in these than in *Lagerpeton* (Bonaparte, 1971). Ventrally, the fibula is completely in contact with the calcaneum, while its medial border contacts the ascending process of the astragalus. In contrast to what happens with the tibia, it is in posterior view where the fibula reaches its greatest distal projection, and it has a marked concavity on its surface that is supported on the calcaneum.

The proximal tarsals of *Lagerpeton* are firmly articulated together. In the described specimen (PVL 4619), in contrast to the holotype, these two bones are not fused. This difference in the condition of articulation or fusion of the proximal tarsals is not considered diagnostic, since individual differences can cause variations in the ossification of this region.

Both tarsals have a quadrangular shape, the astragalus with great transverse extension and a marked posterior concavity; and the calcaneum almost square and lacking vestiges of the tubercle. The astragalus presents as its principal characteristic the great development of the dorsal process (Bonaparte, 1971), or ascending process (Cruickshank, 1979), which separates the tibial and fibular articular facets and is placed like a CUÑA between these two bones. This tarsus is of advanced mesotarsal type (Chatterjee, 1982), seen in saurischians and ornithischians and in some thecodonts such as *Lagosuchus* and *Trialestes* (Bonaparte, 1975b and 1978; Reig, 1963). The mobility of this type of tarsus is provided by the articulation between the proximal and distal tarsals, and of the latter with the metatarsals, permanently uniting the astragalus and calcaneum rigidly together and to the tibia and fibula.

Note in specimen PVL 4619 two distal tarsals, corresponding in size, morphology and location to those of the holotype, with the difference that here they are fused. The explanation for this difference could be the same mentioned for the proximal tarsals, although it could also be due to variations in preservation. These distal tarsals correspond to metatarsals III and IV and are found fixed to them. The internal distal tarsal is of rectangular shape and dorsally flat, while the external has a conical shape.

The pes of *Lagerpeton* is long due to elongation of the metatarsals, and narrow, with the digits arranged parallel to one another. It shows a strong reduction of digits I and V, and an elongation of digit IV (Romer, 1972a). Its total length, including the unguis phalanges, is similar to that of the tibia. No appreciable differences are observed between the diameters of the metatarsals. Metatarsal V is reduced to a rudiment of conical shape. The unguis phalanges are curved and with sharp ends in the form of claws. The most notable characteristic of the pes of

this thecodont is its asymmetrical character (Romer, 1971) relative to an axis passing through digit III. This asymmetry has been observed in other thecodonts, such as *Chanaresuchus* (Romer, 1972a), although not associated with an elongate pes and such a specialized hind limb. This peculiarity makes the functional interpretation of the pedal adaptations of this genus difficult.

COMPARISONS: Comparisons of *Lagerpeton* were principally with other thecodonts referred to the suborders Proterosuchia, Erythrosuchia and Pseudosuchia, excepting groups with marked divergent specializations such as Aetosauria and Phytosauria.

The vertebrae of *Lagerpeton* show a basic morphologic type seen in primitive archosaurs such as *Chasmatosaurus* (Charig, 1976). They also show general similarities with those of *Euparkeria* and *Ticinosuchus* (Ewer, 1965; Krebs, 1976); nevertheless, there are differences in the height and inclination of the neural spines. There are marked differences with the short, tall vertebrae of advanced pseudosuchians such as *Riojasuchus* (Bonaparte, 1972). The anterior inclination of the neural spines of the last presacral vertebrae of *Lagerpeton* constitutes a derived feature, not observed in any other thecodont, which reveals an advanced grade of specialization in the vertebral column.

The sacrum, with only two vertebrae, represents the primitive condition for the order, present in *Proterosuchus*, *Erythrosuchus* and *Euparkeria* (Cruickshank, 1978a, Ewer, *op. cit.*). An advance with respect to this condition is evident in the matter of the last presacral vertebra, which shows signs of having been integrated into the sacrum.

The obviously primitive pelvis of *Lagerpeton* is robust and almost as wide as tall, as in proterosuchians and erythrosuchians, as distinguished from the pelves of raiisuchids and some bipedal reptiles, such as coelurosaurs and carnosours (Bonaparte, 1984), which are taller than wide. However, the ilium in this genus is different from that of other primitive thecodonts due to the marked anterior extension of its iliac blade. It is oriented vertically, as in the majority of pseudosuchians, without adopting the horizontal position of the ilium of raiisuchids and aetosaurs (Bonaparte, 1984). It has a strong supraacetabular crest, very similar to that of *Lagosuchus* (Bonaparte, 1975b). The pubis of *Lagerpeton* is short and robust, similar to that of *Erythrosuchus* and *Euparkeria* (Cruickshank, 1978a; Ewer, 1965).

The pubic symphysis is restricted to the distal region, with a short laminar portion, not extended like that of *Gracilisuchus* and *Ornithosuchus*. In the pubis neither the elongation nor the widening characteristic of carnosours (*Herrerasaurus*, Benedetto, 1973) is apparent, although it is outlined somewhat in *Lagosuchus* (Bonaparte, 1975b) and thus constitutes a derived character.

The ischium is similar to that of proterosuchians and some erythrosuchians such as *Chanaresuchus* (Romer, 1972a) in the development of a wide ventral lamina, distinguishing it from the typical cylindrical ischia of rauisuchids. Moreover, the ischium is characterized by being longer than the pubis, a feature that is also observed in primitive thecodonts (proterosuchians and erythrosuchians) and more clearly in *Euparkeria* (Ewer, 1965).

The acetabulum is closed, not demonstrating any indications of fenestration as seen in advanced forms such as *Lagosuchus*, *Ornithosuchus* and *Scleromochlus* (Bonaparte, 1975b; Walker, 1964; Woodward, 1907).

With respect to the hind limb, due to the combination of adaptations that it presents, *Lagerpeton* shows great similarities with some clearly primitive thecodonts and others with dinosauroid characteristics or uncertain affinities, such as *Scleromochlus*. Both the femur and tibia show characters typical of advanced thecodonts (*Lagosuchus*, Bonaparte, 1975b) and bipedal, cursorial dinosaurs (*Coelophysus*, Colbert, 1964; *Deinonychus*, Ostrom, 1969). The indicators of pneumaticity observed in the femur of *Lagerpeton* are very similar to those present in forms such as *Lagosuchus* and some carnosaurs (*Piatnitzkysaurus*, Bonaparte, pers. comm.), although in the latter the pneumatic cavities extend to other parts of the skeleton.

The tibia of *Lagerpeton* has other derived features, such as the fact that its distal end is transversely expanded, which is not observed in any other thecodont, and until now constituted a clearly dinosauroid character (Bonaparte, 1975b).

With respect to the proximal tarsals, *Lagerpeton* has an advanced mesotarsal type of tarsus, only comparable to that observed in *Lagosuchus* and *Trialestes* among thecodonts, although distinguishable in others (Bonaparte, 1978).

This tarsal type differs notably from the crurotarsal or crocodiloid type shown in almost all the other pseudosuchians. This condition is derived with respect to proterosuchians, and was achieved very early in the Triassic, since Lower Triassic erythrosuchians (*Erythrosuchus*) have only two distal tarsals, probably derived from the four distal tarsals and intermedium of more primitive thecodonts (Cruickshank, 1978a).

The pes also shows a combination of primitive and derived characters. Among the primitive features is the asymmetrical pattern of the pes, a condition comparable to that of reptiles as primitive as eosuchians (*Youngina*, Hughes, 1963) and *Proterosuchus*, also observed in some forms of extant lepidosaurs, such as iguanids and varanids, which are plantigrade, and some occasionally bipedal forms such as *Basiliscus* (Snyder, 1954). Among thecodonts, the development of an asymmetrical pedal pattern is present in *Chanaresuchus* (Romer, 1972a), a genus associated with *Lagerpeton* in the Los Chañares fauna, but in this case it is not combined with elongation of the tibia and metatarsals, nor with the mesotarsal tarsus. The reduction of digit V to only a metatarsal is a tendency observed in pseudosuchians (*Gracilisuchus*,

Riojasuchus and *Lagosuchus*, Bonaparte, 1975a and b), although it occurs in greater or lesser form in other groups, such as cerritosaurids (Romer, 1971).

In *Lagerpeton*, the shortened* metatarsal of more primitive thecodonts is not present, although it persists in some Upper Triassic groups such as rauisuchids, aetosaurs and phytosaurs (Krebs, 1976). The long, clawed digits of *Lagerpeton*, arranged in parallel, contrast strongly with the robust, divergent digits of erythrosuchians (Cruickshank, 1978a), or those with short phalangeal series like those of *Scleromochlus* (Woodward, 1907).

DISCUSSION AND CONCLUSIONS

From the above comparison some concepts about the characters present in *Lagerpeton* can be summarized (see comparative table).

The morphology of the last dorsal vertebrae of *Lagerpeton* (length of vertebral body, anterior inclination of neural spines) indicate adaptive tendencies for increased movement of the vertebral column, supposedly related to locomotion, which have not been observed in other thecodonts and undoubtedly represent derived characters.

The hind limb of *Lagerpeton* shows numerous apomorphic characters: short femur, longer tibia with anteriorly-directed ventral process, mesotarsal-type tarsus; while in the pes, in spite of the derived character of metatarsal elongation, note a clear asymmetry of the type seen in proterosuchians, which do not have adaptive tendencies for bipedalism.

Moreover, *Lagerpeton* shows many important characters in the organization of the pelvis, comparable to those of a more primitive thecodont family: proterosuchids. These markedly primitive characters are: laminar ischium longer than the pubis, with a more developed ventral lamina of convex shape, pubis short and robust, with less defined symphysis.

Curiously, these primitive traits are found associated with an ilium with a very developed anterior process and a strong supraacetabular crest, which are derived features generally observed at the dinosauroid level of anatomical organization.

In spite of not intervening in the taxon definition, the association of primitive and derived characters in *Lagerpeton* is clear and determinate that the traditional concepts and interpretations of the type of structures related to different types of locomotion in archosaurs (Charig, 1972; Coombs, 1976 and others) must be reconsidered and broadened.

On the other hand, the retention of primitive characters in this genus indicates the relatively recent emergence of its adaptive type (Bonaparte, pers. comm.), and it could well be related to groups such as cerritosaurids (*Chanaresuchus*, *Gualosuchus*), contemporaries in the Los Chañares fauna. This was the basal group for a wide adaptive radiation that involved *Lagerpeton*.

Although certain derived characters, comparable to those of *Lagerpeton*, are also observed in other pseudosuchians such as *Lagosuchus*, it seems probable that these similarities are due to adaptive convergences, more than due to close or ancestor-descendant relationships.

Since this taxon is defined exclusively by its derived characters and these do not permit its inclusion into any of the known pseudosuchian families (Bonaparte, 1982a), the new family Lagerpetonidae is proposed for this genus.

ACKNOWLEDGEMENTS

To Dr. José F. Bonaparte and Dr. Jamie E. Powell, for introduction to the theme and critical reading of the manuscript. To the authorities of the Inst. Miguel Lillo, for having allowed access to material in their collection to accomplish this work. To Sra. Amanda Giordano and Sr. José Pumares (Univ. Prov. de La Rioja), for having facilitated access to material deposited there.

FIGURES

Fig. 1. - **Lagerpeton chanarensis** (PVL 4619). Left lateral view of pelvis, sacrum and complete hind limb.

Fig. 2. - **Lagerpeton chanarensis** (PVL 4619). Left lateral view of pelvis. Scale 1 cm.

Fig. 3. - **Lagerpeton chanarensis** (PVL 4619). Left femur: **A**, lateral view; **B**, medial view. Scale 1 cm.

Fig. 4. - **Lagerpeton chanarensis** (PVL 4619). Left tibia and fibula articulated with the astragalus and calcaneum: **A**, anterior view; **B**, posterior view. Scale 1 cm.

Fig. 5. - **Lagerpeton chanarensis** (PVL 4619). Complete left pes: **A**, anterior view; **B**, lateral view. Scale 1 cm.

COMPARATIVE TABLE

Characters	<i>Chanaresuchus</i>	<i>Lagosuchus</i>	<i>Lagerpeton</i>
1. orientation of neural spines	anterior	straight	posterior
2. number of sacral vertebrae	two	two (one more in sacralization)	two (one more in sacralization)
3. anterior projection of ilium	absent	very poorly developed	well developed
4. supraacetabular crest	absent	well developed	well developed
5. acetabulum	closed	perforate	closed
6. length of ischium	shorter than pubis	shorter than pubis	longer than pubis
7. ischial lamina	very developed	less developed	very developed
8. distal expansion of pubis	absent	present	absent
9. pubic symphysis	less dorsoventrally extended	more dorsoventrally extended	less dorsoventrally extended
10. length of femur	longer than tibia	shorter than tibia	shorter than tibia
11. fourth trochanter	well developed	well developed	well developed
12. femoral head	less developed	well developed	well developed
13. femoral condyles	less ossified	well ossified	well ossified
14. distal portion of tibia	anteroposteriorly extended	intermediate	transversely extended
15. ventral process of tibia	absent	posteriorly projecting	anteriorly projecting
16. anterolateral process of fibula	absent	absent	well developed
17. type of tarsus	crurotarsal	advanced mesotarsal	advanced mesotarsal
18. calcaneal tubercle	present	absent	absent
19. metatarsals	short	elongate	elongate
20. pes	asymmetrical due to enlargement of digit II	symmetrical around digit III	asymmetrical due to elongation of digit IV