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DINOSAURIAN PRECURSORS FROM THE MIDDLE TRIASSIC OF ARGENTINA: *MARASUCHUS LILLOENSIS,* GEN. NOV.

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ABSTRACT—We review the morphology and systematics of *Lagosuchus* from the Middle Triassic Los Chañares Formation. Two species have been named, *Lagosuchus talampayensis* and *L. lilloensis.* The holotype of *Lagosuchus talampayensis* is a fragmentary skeleton that does not exhibit any autapomorphies to distinguish it from contemporary dinosauromorphs, and the genus and species are regarded as nomina dubia. In contrast, the holotype of *Lagosuchus lilloensis* is a well-preserved skeleton that exhibits several distinctive features, allowing reference of additional specimens. We, therefore, designate a new genus, *Marasuchus,* for the species "*Lagosuchus*" *lilloensis.*

Several synapomorphies unite *Marasuchus* and dinosaurs (as Dinosauriformes) to the exclusion of the contemporary dinosauromorph *Lagerpeton* and pterosaurs. These include an antitrochanter on the posterior wall of the acetabulum, an anterior (lesser) trochanter developed as a trochanteric shelf, and a posterior flange on the distal end of the tibia. These dinosauriform synapomorphies in the pelvis and hind-limb persist in dinosaurian descendants with body sizes exceeding that of *Marasuchus* by more than two orders of magnitude.

INTRODUCTION

A. S. Romer's discovery in Argentina of the rich Middle Triassic locality, Los Chañares (Romer, 1967), and his subsequent reports on new archosaurian and synapsid remains represent an important paleontological achievement of his distinguished career. Romer (1972c) and others (Bonaparte, 1975, 1982; Olsen and Sues, 1986) have highlighted the important transitional character of the fauna at Los Chañares with respect to Early and Late Triassic faunas.

Small bipedal archosaurs constitute a significant component of the Los Chañares fauna (Romer, 1971, 1972b; Bonaparte, 1975; Arcucci, 1986, 1987). The significance of these forms and their bearing on dinosaurian origins have been subject to extensive comment in the recent literature (Paul, 1984; Gauthier, 1986; Novas, 1989, 1992; Sereno and Novas, 1990; Sereno, 1991b). Despite this attention, morphological details relevant to their phylogenetic position are poorly known. This paper clarifies the taxonomy and structure of material previously referred to *Lagosuchus talampayensis* and re-examines the evidence for its phylogenetic relationship with Dinosauria.

Institutional abbreviations: **MACN,** Museo Argentino de Ciencias Naturales, Buenos Aires; **MCZ,** Museum of Comparative Zoology, Harvard University, Cambridge; **MLP,** Museo de La Plata, La Plata; **PVL,** Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; **PVSJ,** Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan; **UPLR,** Museo de Paleontología, Universidad Provincial de La Rioja, La Rioja.

Anatomical figures were drawn by P. Sereno with a camera lucida.

SYSTEMATIC HISTORY

Taphonomic and historical factors have complicated the systematic assessment of the vertebrate fauna from the Los Chañares Formation. The vertebrate remains at the locality Los Chañares are frequently concentrated in nodules that contain several taxa. As a consequence, some of the collection numbers referenced by Romer refer to nodules that contain several taxa, rather than individual specimens. In a few instances, specimens have been re-catalogued separately after further preparation of a nodule, and others have been cited incorrectly or without a catalogue number. To further complicate matters, specimens originally cited by Romer in the collections of the Museo de La Plata (MLP) have been re-catalogued into the collections of the Universidad Provincial de La Rioja (UPLR). Thus we begin our re-examination of the Los Chañares ornithodiran *Lagosuchus* with a brief systematic history.

Lagosuchus talampayensis is based on a poorly preserved skeleton cited by Romer (1971:4) as MLP 64–XI–14–11 (in part) and now re-catalogued as UPLR 09. The holotypic skeleton is exposed on a slab that also contains a partial skeleton of the small proterochampsid *Tropidosuchus romeri* Arcucci, 1990, the holotypic skeleton of *Gracilisuchus stipanicicorum* Romer, 1972a, and other disarticulated bones (Fig. 1; Table 1). Romer's (1971:4) diagnosis of *L. talampayensis* does not include any unique features. The accompanying figure of the tarsus and pes (Romer, 1971:

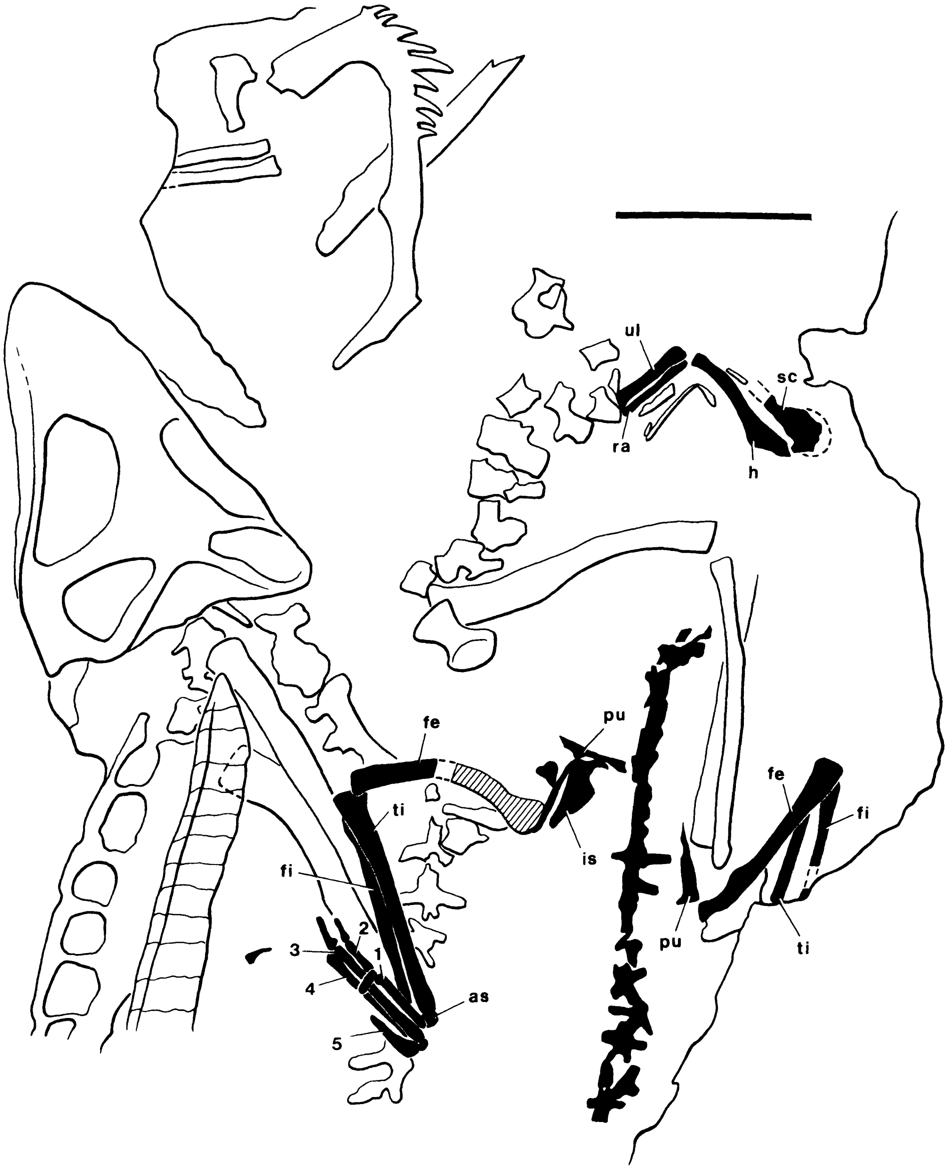

FIGURE 1. Diagram of slab with holotypic skeletons of *Lagosuchus talampayensis* (UPLR 09; solid tone) and *Gracilisuchus stipanicicorum* (left; UPLR 08) and bones of the proterochampsid *Tropidosuchus romeri* (center; UPLR unnumbered; Arcucci, 1990). The slab has been prepared from both sides; the bone configurations shown represent a composite from tracings of upper and lower surfaces of the slab. Cross-hatching indicates broken bone surface. Abbreviations: **1–5**, metatarsals I to V; **as**, astragalus; **fe**, femur; **fi**, fibula; **h**, humerus; **is**, ischium; **pu**, pubis; **ra**, radius; **sc**, scapula; **ti**, tibia; **ul**, ulna. Scale bar equals 5 cm.

fig. 2) is a reconstruction based principally on better preserved materials that were later referred to the same species by Bonaparte (1975). Romer (1971:fig. 3) also figured and referred an unnumbered fragmentary pelvis and proximal femur to *L. talampayensis* (now catalogued as PVL 3871).

Romer (1972b:fig. 2) figured the appendicular portion of the holotype skeleton and referred an additional partial skeleton to *Lagosuchus talampayensis* (cited as MCZ 4116 and now re-catalogued as MCZ 4137). In the same paper, Romer named a second species, *Lagosuchus lilloensis,* differentiated only by its larger size. Romer (1971:figs. 5, 6; unnumbered) figured the left hind-limb and a series of sacral and caudal vertebrae (PVL 3871). This skeleton, however, also includes most of the presacral vertebrae, the left pectoral girdle and forelimb, and the right hind-limb. Romer did not provide a diagnosis for *Lagosuchus lilloensis.* In his review of *L. talampayensis,* Bonaparte (1975:7) considered *L. lilloensis* a junior synonym of *L. talampayensis.* In the same work, Bonaparte referred additional remains tc *L. talampayensis* (PVL 3870, 3872).

SYSTEMATIC PALEONTOLOGY

Systematic Hierarchy:

ARCHOSAURIA Cope, 1869
 ORNITHODIRA Gauthier, 1986
  DINOSAUROMORPHA Benton, 1985
   DINOSAURIFORMES Novas, 1992
    LAGOSUCHUS Romer, 1971

Type Species—*Lagosuchus talampayensis.*
Diagnosis—Same as type species.

LAGOSUCHUS TALAMPAYENSIS Romer, 1971

Romer, 1971:fig. 2 (composite); Romer, 1972b:fig. 3.

Holotype—UPLR 09, fragmentary, semi-articulated postcranial skeleton including the vertebral column from the mid-dorsal to the anterior caudal vertebrae, fragmentary left pectoral girdle and forelimb including the proximal half of the scapula, humerus, radius, and ulna, pelvic girdle and both hind-limbs including the ventral margin of the left ilium, both ischiae and pubes, both femora, partial right and complete left tibiae and fibulae, and left tarsus and pes lacking most of the phalanges.

Locality and Horizon—Southwest part of the Los Chañares locality in the Province of La Rioja, Argentina; Chañares Formation (Ladinian; Stipanicic, 1983). In his field notes (1964–1965), Romer refers to the Los Chañares locality as the "northwest pocket." The nodule containing the holotype of *L. talampayensis* was found in the southwest part of this locality (field number 146, logged as a "tiny skeleton"). The nodule contains several taxa, as described below. Although Romer (1971:4) cited the locality as "2 km north of the mouth of Río Chañares," the exposures of the Los Chañares locality are more accurately located 3 km north of the north branch of the Chañares River and 5 km southwest of the Puerta de Talampaya.

Discussion—The holotype of *L. talampayensis* (Fig. 1) is preserved on a slab with the holotype of *Gracilisuchus stipanicicorum* (UPLR 08) and the remains of the small proterochampsid *Tropidosuchus romeri* (Arcucci, 1990; UPLR unnumbered). Romer (1971:4–6; 1972a:fig. 3) figured the partial forelimb and fragmentary hind-limbs. Apparently, he originally considered a nearby series of vertebrae as part of the holotype (Romer, 1971:5) but later regarded them as caudal vertebrae of *Gracilisuchus* (Romer, 1972b:4). These vertebrae (Fig. 1, center) are clearly too large to belong to the holotype of *L. talampayensis* and represent cervical and dorsal vertebrae of the small proterochampsid *Tropidosuchus romeri.*

Although not mentioned by Romer, the hind-limbs of the holotype are clearly associated with pelvic fragments and a series of 18 small vertebrae, composed of dorsal vertebrae anteriorly and caudal vertebrae posteriorly (Fig. 1). The hind-limbs and fragments of the pelvic girdle are positioned to each side of the presumed sacral region. A partial left forelimb is located at some distance anterior to the vertebrae and is clearly included as part of the holotype by Romer (1971:6; 1972b:3 and fig. 3C). The forelimb is articulated with a partial scapulocoracoid that was not mentioned or figured by Romer. Given its size and location on the slab, the association of the forelimb and scapulocoracoid with the remainder of the holotype is plausible but not without some doubt.

TABLE 1. Measurements (in mm) of the maximum length of centra and long bones in the holotype of *Lagosuchus talampayensis* (UPLR 09). Parentheses indicate estimates.

	Left	Right
Humerus	28.0	—
Radius	18.0	—
Ulna	(18.0)	—
Femur	41.0	40.0
Tibia	46.6	—
Digit I		
Metatarsal I	14.5	—
Phalanx 1	5.9	—
Digit I		
Metatarsal II	22.0	—
Phalanx 1	6.0	—
Digit III		
Metatarsal III	24.0	—
Phalanx 1	6.6	—
Digit IV		
Metatarsal IV	23.6	—
Digit V		
Metatarsal V	12.0	—
Mid–dorsal centrum	5.0	
Anterior caudal centrum	7.0	

The principal systematic questions that must be dealt with regarding *L. talampayensis* include the following: Is it possible to formulate a useful diagnosis for *L. talampayensis* based on the holotype? If so, can we justify reference of additional, better preserved material to this taxon, as suggested by Romer and Bonaparte? After re-examination of the material, we cannot answer these questions affirmatively, and we present our evidence below.

Romer's (1971:4) diagnosis of *L. talampayensis* does not include any autapomorphies but rather lists symplesiomorphies that are shared by all ornithodirans or more inclusive clades. As we discuss below, specimens that were previously referred to *L. talampayensis* are clearly distinct and exhibit several autapomorphies. None of these distinguishing features, however, are preserved in the holotype of *L. talampayensis.* In addition, the scapulocoracoid and forelimb of the holotype are clearly different from those in referred material (Bonaparte, 1975:figs. 8, 9). The proximal scapular blade is straplike in the holotype (Fig. 1; Table 1) but is unusually broad in PVL 3871. Romer (1971) correctly observed that the forelimb is approximately one-half the length of the hind-limb in both the holotype and in PVL 3871, but he failed to note the markedly different proportions within the forelimb (Tables 1, 4). In the holotype, the radius and ulna are, at most, two-thirds the length of the humerus, whereas in PVL 3871 (the only referred specimen preserving both fore- and hind-limbs), the length of the radius, ulna, and humerus are subequal. Furthermore, the ulna of the holotype is very broad distally, unlike PVL 3871.

In summary, the vertebral column, pelvic fragments, and hind-limbs of the holotype of *L. talampayensis* indicate that it pertains to a small bipedal ornithodiran. Diagnostic features (described below) in specimens that were previously referred to this species, however, are not preserved in the holotype, and the scapulocoracoid and the forelimb in the holotype differ from those in referred specimens. It is possible that the scapulocoracoid and forelimb, which Romer clearly included as part of the holotype, are not part of the same individual (Fig. 1), but this cannot be proven.

There are at least three contemporaneous, small ornithodirans in the Los Chañares fauna: *Lagerpeton chanarensis, Pseudolagosuchus major,* and material previously referred to *L. talampayensis* and reviewed below. The holotype of *L. talampayensis* may represent a fourth ornithodiran, or it may only constitute a chimeric combination of more than a single archosaur. In either case, we are unable to determine any diagnostic features in the holotype of *L. talampayensis.* Regrettably, we must consider the well-known genus *Lagosuchus* and the species *talampayensis* as nomina dubia.

MARASUCHUS, gen. nov.

Type Species—*Marasuchus lilloensis* (Romer, 1972b).

Etymology—Generic name refers to the mara, or Patagonian cavy (*Dolichotis*), a saltatory caviomorph rodent that is quite abundant on the plains of the Campo de Talampaya and around the type locality. The mara, which commonly moves with a stotting (four-legged, bouncing) gait, closely resembles long-legged rabbits and hares (Walker, 1975). The name *Marasuchus* (*mara*; *souchos* (Greek), crocodile) thus retains the spirit of Romer's original genus *Lagosuchus* (*lagos* (Greek), rabbit; *souchos* (Greek), crocodile).

MARASUCHUS LILLOENSIS (Romer, 1972b)

Romer, 1971:figs. 2, 3; Romer, 1972b:figs. 5, 6; Bonaparte, 1975:figs. 1–5, 7–16; Arcucci, 1987:fig. 3.3; Novas, 1989:fig. 3.1–3.6; Sereno, 1991b:fig. 9.

Holotype—PVL 3871, partial articulated skeleton including the posterior portion of the vertebral column, from the last dorsal vertebra to the 25th caudal vertebra (Fig. 4; Romer, 1972b:fig. 6), left scapulocoracoid, humerus, radius, and ulna (Bonaparte, 1975: figs. 8, 9), fragmentary right pelvis, left ilium, and left pubis (Figs. 5, 8; Romer, 1971:fig. 3), partial right and left hind-limbs (Figs. 8, 10; Romer, 1972b:fig. 5).

Locality and Horizon—Los Chañares in the Province of La Rioja, Argentina; Chañares Formation (Ladinian; Stipanicic, 1983). The holotype was collected in 1969 by J. F. Bonaparte from the lower section of the Chañares Formation, apparently at Los Chañares. Bonaparte (1975:10) reported that all of the material of *M. lilloensis* that he collected and described was from the "área de Los Chañares, 2 km al SE de la Puerta de Talampaya." As noted above, this site is more accurately located 3 km north of the north branch of the Chañares River and 5 km southwest of the Puerta de Talampaya.

Revised Diagnosis—Dinosauriform archosaur characterized by anterodorsally projecting posterior cervical neural spines (presacral vertebrae 6–9), marked fossa ventral to the transverse processes in the posterior cervicals and anterior dorsal vertebrae (presacral vertebrae 6 through 10 or 12), subtriangular neural spines in mid- and posterior dorsal vertebrae that contact each other anteriorly and posteriorly, mid-caudal centra twice the length of anterior caudal centra, elongate anterior chevrons that are more than three times the length of the first caudal centrum, broad scapular blade, transversely concave distal pubic blade, and transversely narrow fibular articular surface on calcaneum.

Marasuchus lilloensis is a small, carnivorous dinosauriform that is particularly closely related to Dinosauria, sharing with dinosaurs parallelogram-shaped posterior cervical centra, short forelimbs, a partially open acetabulum, an acetabular antitrochanter, a trochanteric shelf on the proximal femur, and a fibular flange on the tibia.

Referred Specimens—PVL 3870, partial skeleton including the maxilla and partial braincase, vertebral column from the atlas to the anterior caudal vertebrae; articulated pelvis and hind-limbs lacking only the distal phalanges and unguals (Figs. 3A, B, D, 6A, 9, 11; Bonaparte, 1975:figs. 1, 2, 5, 7, 10–16); PVL 3872, partial braincase and articulated vertebral column from the atlas to the ninth presacral vertebra (Fig. 2; Bonaparte, 1975:figs. 3, 4); PVL 4670, articulated anterior caudal vertebrae lacking chevrons; PVL 4671, articulated anterior caudal vertebrae with chevrons; PVL 4672, articulated vertebral column from atlas to the seventeenth presacral vertebra.

Discussion—Based solely on its larger size, Romer (1972b:5) named a second species of the genus *Lagosuchus, L. lilloensis.* The holotype of *L. lilloensis* (PVL 3871), however, exhibits several diagnostic characters, which either are not preserved or are at variance with the holotype of *Lagosuchus talampayensis* (see above). These species, therefore, cannot be synonymized, as suggested by Bonaparte (1975), and we transfer the species *L. lilloensis* to the new genus *Marasuchus.*

All but one of the specimens previously referred to *L. talampayensis* can be referred to *Marasuchus lil-*

loensis on the basis of the above diagnosis. The one exception is MCZ 4137, a fragmentary specimen preserving the dorsal and sacral vertebral column and a fragmentary pelvis (Romer, 1972b:fig. 4; Bonaparte, 1975:fig. 6; field number 174, formerly catalogued as MCZ 4116). The neural spines in the dorsal vertebrae of this specimen alternate in shape between subtriangular and rectangular. An alternating pattern in the shape of the neural spines is unknown elsewhere among archosaurs but is quite common among primitive tetrapods (Sumida, 1990). Unlike the spine pattern in primitive tetrapods, however, both spine shapes in this specimen are equal in height. Bonaparte (1975:22) described this condition as "surely pathological," but no part of the column appears abnormal or asymmetrical. Because the anterior dorsal vertebrae, fragmentary ischium, and pubis are similar to the corresponding bones in *M. lilloensis,* the alternating pattern of neural spine shape either constitutes an unusual case of sexual dimorphism or may indicate the presence of an additional closely related taxon.

DESCRIPTION

The following description of the skull and postcranial skeleton of *Marasuchus lilloensis* supplements and emends previous accounts (Romer, 1971, 1972b; Bonaparte, 1975; Arcucci, 1987; Novas, 1989; Sereno, 1991b).

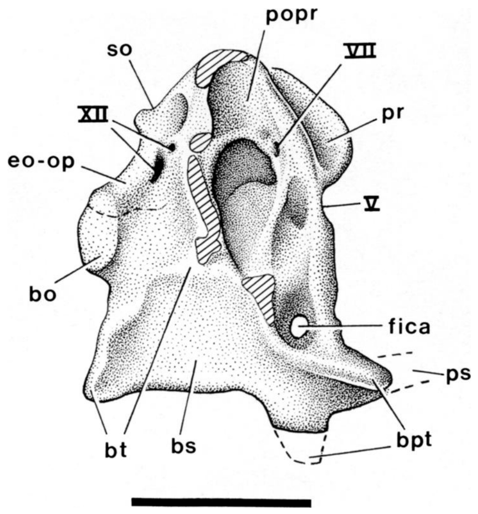

FIGURE 2. Braincase of *Marasuchus lilloensis* (PVL 3872) in ventrolateral view. Cross-hatching indicates broken bone surface. Abbreviations: **V**, **VII**, **XII**, foramina for the respective cranial nerves; **bo**, basioccipital; **bpt**, basipterygoid process; **bs**, basisphenoid; **bt**, basal tubera; **eo-op**, exoccipital-opisthotic; **fica**, foramen for the internal carotid artery; **popr**, paroccipital process; **ps**, parasphenoid; **so**, supraoccipital. Scale bar equals 5 mm.

Cranium

The maxilla and braincase are the only portions of the cranium which are known. The partial maxilla is exposed in medial view and preserves most of the tooth row (PVL 3870). Although an anterior fragment of the maxilla was previously attributed to the premaxilla (Bonaparte, 1975:12, fig. 2), no part of the latter bone appears to be preserved. The anterior margins of the antorbital fenestra are not preserved (contra Bonaparte, 1975:fig. 2), and thus the shape and anterior extension of the fenestra are unknown. The maxilla is compatible in size with the braincase and postcranial remains attributed to the same specimen, but no information was given by Bonaparte (1975) regarding their original association. The braincase is preserved in two individuals (Figs. 2, 3A; Bonaparte, 1975:figs. 1, 3; PVL 3870, 3872), both of which are associated with postcranial material. In PVL 3872, portions of two cranial bones originally associated with the braincase are now lost; these fragments appear to represent the posterior portion of the right squamosal and part of the right postorbital (originally identified as a quadrate; Bonaparte, 1975:fig. 3). Based on associated cervical vertebrae, both braincases seem to represent *M. lilloensis.* They appear quite dissimilar due to abrasion of the basal tubera in PVL 3870 and oblique flattening of PVL 3872, in which the ventral aspect of the braincase is exposed in lateral view (Figs. 2, 3A). In both PVL 3870 and 3872, the borders of the otic openings are broken away, with a large, unnatural opening exposing the spacious middle ear chamber in lateral view (Figs. 2, 3A).

Braincase—The pattern of cranial foramina in *M. lilloensis* conforms to that present in most archosaurs (Figs. 2, 3A). A notch on the anterior margin of the prootic in both specimens constitutes the posterior border of the foramen for cranial nerve V. Located more posteriorly, a small foramen represents the opening for cranial nerve VII (not shown by Bonaparte, 1975:figs. 1, 3). Dorsal to this small foramen, a marked fossa is present. Ventral to the same foramen, a trough passes toward the opening for the internal carotid artery (Fig. 2).

As mentioned above, the otic region is damaged in both specimens. The base of the delicate septum (crista interfenestralis) that divides the fenestra ovalis and jugular foramen in other archosaurs may be preserved in PVL 3872. These openings were previously identified as cranial nerve VII and the fenestra ovalis, respectively (Bonaparte, 1975:fig. 3). As described above, however, the opening for cranial nerve VII is a small foramen located more anteriorly. Two foramina located posterior to the otic openings apparently provided passage for branches of cranial nerve XII. In both specimens, the most posterior of the two foramina is larger.

The pointed basal tubera are best preserved in PVL 3872 (Fig. 2). The basipterygoid processes are relatively short compared to the length of the braincase and project anteroventrally and laterally.

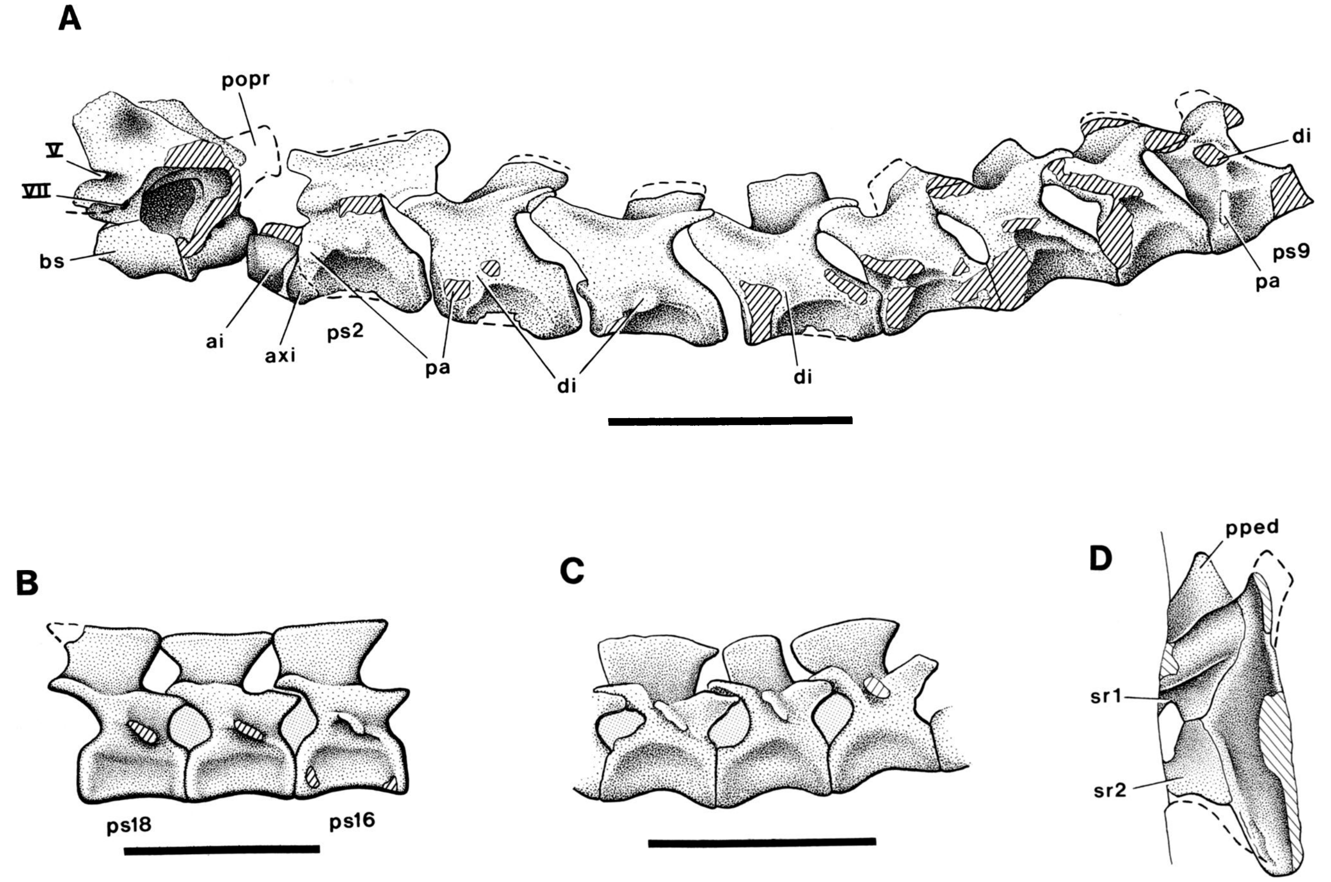

FIGURE 3. Braincase and vertebrae of *Marasuchus lilloensis.* **A**, left lateral view of articulated braincase and anterior nine presacral vertebrae (PVL 3870). **B**, right lateral view of presacral vertebrae 16 to 18 (PVL 3870). **C**, right lateral view of mid-dorsal vertebrae of ?*Marasuchus lilloensis* (MCZ 4137). **D**, dorsal view of right sacral ribs and ilium (PVL 3870). Cross-hatching indicates broken bone surface. Abbreviations: **ai**, axial intercentrum; **axi**, atlantal intercentrum; **bs**, basisphenoid; **di**, diapophysis; **pa**, parapophysis; **popr**, paraoccipital process; **pped**, pubic peduncle; **ps2-18**, presacral vertebrae 2 to 18; **sr1-2**, sacral ribs 1 and 2. Scale bars equal 1 cm, with scale bar in **B** also applicable to **D**.

Vertebral Column

The entire vertebral column except the distal caudal vertebrae are represented in the holotype and referred materials of *M. lilloensis.* The junction between neck and trunk is probably between the ninth and eleventh presacral vertebrae, based on the rapid elevation of the parapophysis across these vertebrae from the neural arch to the centrum. In the following description, however, we do not attempt to divide the presacral column arbitrarily into cervical and dorsal series.

Presacral Vertebrae—In *M. lilloensis* and other ornithodirans, the first three postaxial centra (presacral vertebrae 3–5) are each at least 30 percent longer than the shortest centrum at the base of the neck (presacral vertebra 9 or 10; Fig. 3; Bonaparte, 1975:fig. 5; Sereno, 1991b:34–35, table 1) and also exceed significantly the length of the mid-dorsal centra (presacral vertebrae 14–18). In other archosaurs, these lengths are subequal. In the first 10 presacral centra, the anterior centrum face is dorsally offset from the posterior face, which results in a parallelogram-shaped centrum in lateral view. The degree of offset of the anterior face decreases from the axis to the 10th presacral vertebra and is absent in the 11th presacral vertebra (Fig. 3A; PVL 3870, 3872, 4672; Sereno, 1991b:23–24).

The axial diapophysis is developed as a low prominence just above the neurocentral suture (Fig. 3A). In the presacral series, the diapophysis is not developed as a distinct process until the sixth vertebra, where it has shifted to a central position on the neural arch. A distinct excavation, or hollow, appears on the neural arch under the diapophysis at this point (Fig. 3A). The hollow is present from the sixth to the twelfth presacral vertebra (PVL 3870, 3871, 3872, 4672).

The position of the parapophysis in the presacral series is best preserved in PVL 4672 and confirmed, in part, by PVL 3870 and 3871. The parapophysis is positioned low on the anterior rim of the centrum in the third presacral vertebra and gradually shifts dor-

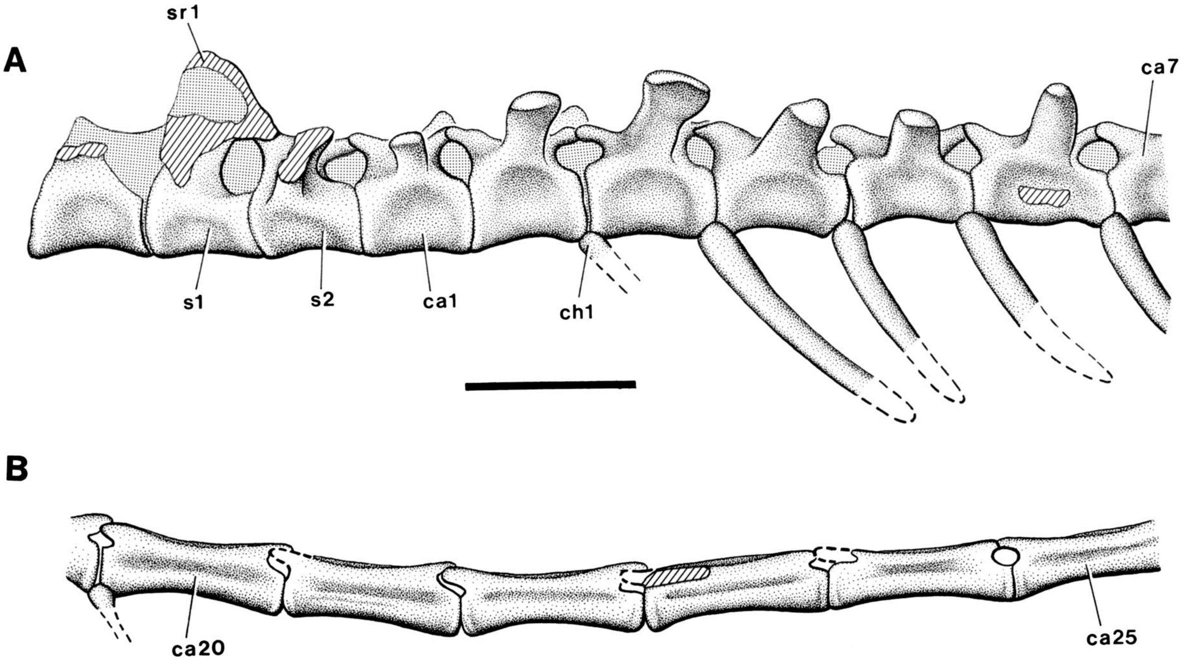

FIGURE 4. Caudal vertebrae and chevrons of *Marasuchus lilloensis* (PVL 3871). Cross-hatching indicates broken bone surface. **A**, left lateral view of anterior caudal vertebrae and chevrons. **B**, left lateral view of mid-caudal vertebrae. Abbreviations: **ca1-25**, caudal vertebrae 1 to 25; **ch1**, first chevron; **s1-2**, sacral vertebrae 1 and 2; **sr1**, first sacral rib. Scale bar equals 1 cm.

sally to the level of the neurocentral suture by the ninth presacral vertebra (Fig. 3A). From the 10th to the 11th presacral vertebrae, the parapophysis shifts dorsally more abruptly. In PVL 3872, for example, the parapophysis in the 10th presacral vertebra is positioned on the neurocentral suture, whereas in the 12th presacral vertebra, it is already at the base of the transverse process (presacral 11 is damaged). In PVL 4672, the parapophysis in the ninth presacral vertebra is situated on the neurocentral suture with a low bony crest extending to the diapophysis; in the tenth presacral vertebra, the parapophysis has moved to the base of the transverse process. This rapid shift from the base of the neural arch to the transverse process between the ninth to the eleventh presacral vertebrae also occurs in many other archosaurs, such as the proterochampsids *Gualosuchus* (PVL 4576) and *Chanaresuchus* (PVL 4575).

The neural spines change shape along the presacral column in *M. lilloensis* (Fig. 3A). In the third and fourth presacral vertebrae, the neural spines are low and broad and project posterodorsally. The fifth presacral has an erect, subquadrate spine. In the sixth to the ninth presacral vertebrae, the neural spine is shorter anteroposteriorly and projects slightly anterodorsally. The neural spines in the 10th to the 12th presacral vertebrae are transitional to the first inverted triangular neural spine in the thirteenth presacral vertebra (PVL 3872). The triangular spines, which may contact one another at anterior and posterior extremities (Fig. 3B), occur along most of the presacral column and are diagnostic for *M. lilloensis*.

Sacral Vertebrae—There are two sacral vertebrae in *M. lilloensis* (Figs. 3D, 4A, 5B, 6D). The sacral centra and ribs are preserved in articulation in PVL 3870 (Fig. 3D) and PVL 3871 (Figs. 4A, 5B). The sacral centra are tightly articulated or fused. The first sacral rib flares distally into a broad process, the anterior margin of which is elevated and inclined anterodorsally (Figs. 3D, 6D). This upturned portion of the first sacral rib buttresses the preacetabular process, a condition similar to that in *Lagerpeton* (PVL 4619, 4625). The second sacral rib flares into a broad plate before attaching to the postacetabular process (Figs. 3D, 6D). The sacral ribs attach high on the ilium, dorsal to the acetabulum and ischial and pubic peduncles (Figs. 5B, 6D).

Caudal Vertebrae—One of the most unusual characteristics of *M. lilloensis* is the long tail composed of proportionately long caudal vertebrae (Fig. 4; Tables 2, 3). Contrary to Romer (1972b:5), *M. lilloensis* does not have a "normal thecodont type" tail. Centrum length gradually increases along the caudal series as far distally as the 25th caudal vertebra (Tables 2, 3; PVL 3870, 3871, 4670, 4671). Given the usual complement of caudal vertebrae (40 to 50), the complete tail in *M. lilloensis* would have been at least one third longer than preserved in PVL 3871 (Fig. 13). Midway along the tail, centrum length is approximately twice that of the first caudal vertebra, despite considerable decrease in the diameter of the articular faces (Fig. 4B). Among

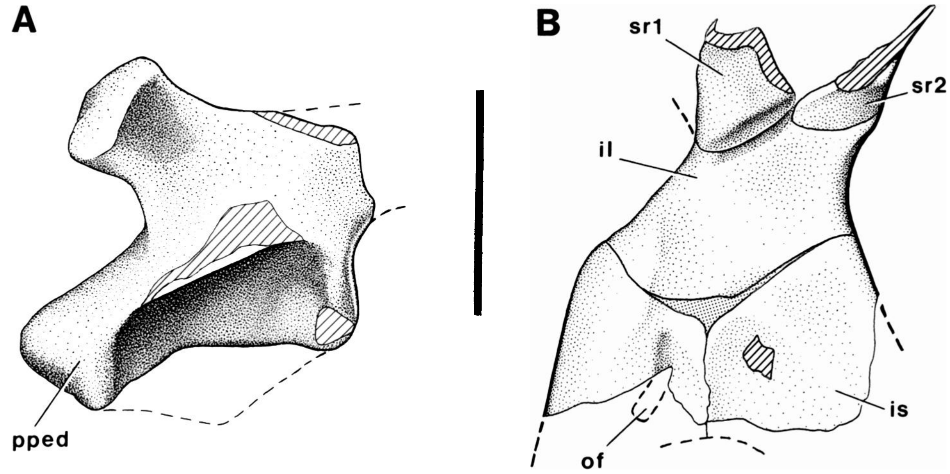

FIGURE 5. Pelvic girdle of *Marasuchus lilloensis*. **A**, left lateral view of left ilium (PVL 3871). **B**, medial view of acetabular region of right pelvic girdle with right sacral ribs (PVL 3871). Cross-hatching indicates broken bone surface, and even stippling indicates matrix. Abbreviations: **il**, ilium; **is**, ischium; **of**, obturator foramen; **pped**, pubic peduncle; **srl-2**, sacral ribs 1 and 2. Scale bar equals 1 cm.

ornithodirans, only basal pterosaurs have such elongate mid-caudal vertebrae.

Transverse processes are present only in anterior caudal vertebrae. In the first and second caudal vertebrae, the transverse processes are short, reaching maximum length in the third caudal vertebra. Distal to this vertebra, the transverse processes decrease in length. In PVL 3871, they are reduced to rounded prominences in the 16th caudal vertebra and are absent in successive caudal vertebrae. In the largest individual (PVL 4671), the transverse processes occur as prominences from caudal 11 to 19.

The neural spines decrease in height along the caudal series from a low spine anteriorly to a low crest in the 15th caudal vertebra (Fig. 4A). Neural spines are absent by caudal 17 or 18. Short pre- and postzygapophyses extend just beyond the centrum faces on all preserved caudal vertebrae. The zygapophyseal articulation is steeply inclined in anterior caudal vertebrae and is oriented vertically in mid-caudal vertebrae.

The first chevron occurs between the third and fourth caudal vertebrae (Fig. 4A), and the last occurs between the 19th and the 22nd caudal vertebrae (Fig. 4B; PVL 3871, 4691). The anterior three chevrons are remarkably long, with a maximum length at least three times the length of the first caudal centrum. In other archosaurs, the length of the anterior chevrons is less than twice the length of the first caudal centrum (e.g., *Chanaresuchus,* PVL 4575, 4647). In *Gracilisuchus* (PVL 4597), a notable exception, the second chevron is also three times the length of the first caudal centrum.

Pectoral Girdle and Forelimb

The **scapulocoracoid** in *M. lilloensis* has an unusually broad scapular blade (PVL 3871; Bonaparte, 1975:fig. 8). Because the entire anterior margin of the blade is broken, its proportions may have been slightly broader. The blade is fractured at mid-length. Slight offset

TABLE 2. Measurements (in mm) of anterior and mid-caudal vertebrae of *Marasuchus lilloensis* (PVL 3871).

Caudal	Centrum length	Caudal	Centrum length
1	5.9	13	8.7
2	6.2	14	9.4
3	6.1	15	9.8
4	6.9	16	9.6
5	7.2	17	9.6
6	7.4	18	10.1
7	7.5	19	10.4
8	7.6	20	10.9
9	7.7	21	10.8
10	8.0	22	11.1
11	8.3	23	11.3
12	8.5	24	11.3
		25	11.5

TABLE 3. Measurements (in mm) of the anterior caudal vertebrae and chevrons of *Marasuchus lilloensis* (PVL 4671). Parentheses indicate estimates.

Caudal	Centrum length	Neural spine length	Chevron length
1	6.9	—	—
2	8.7	—	—
3	8.5	7.5	24.4
4	8.7	6.1	(25.0)
5	8.8	7.5	(24.3)
6	9.0	—	16.5
7	9.3	5.3	(12.5)

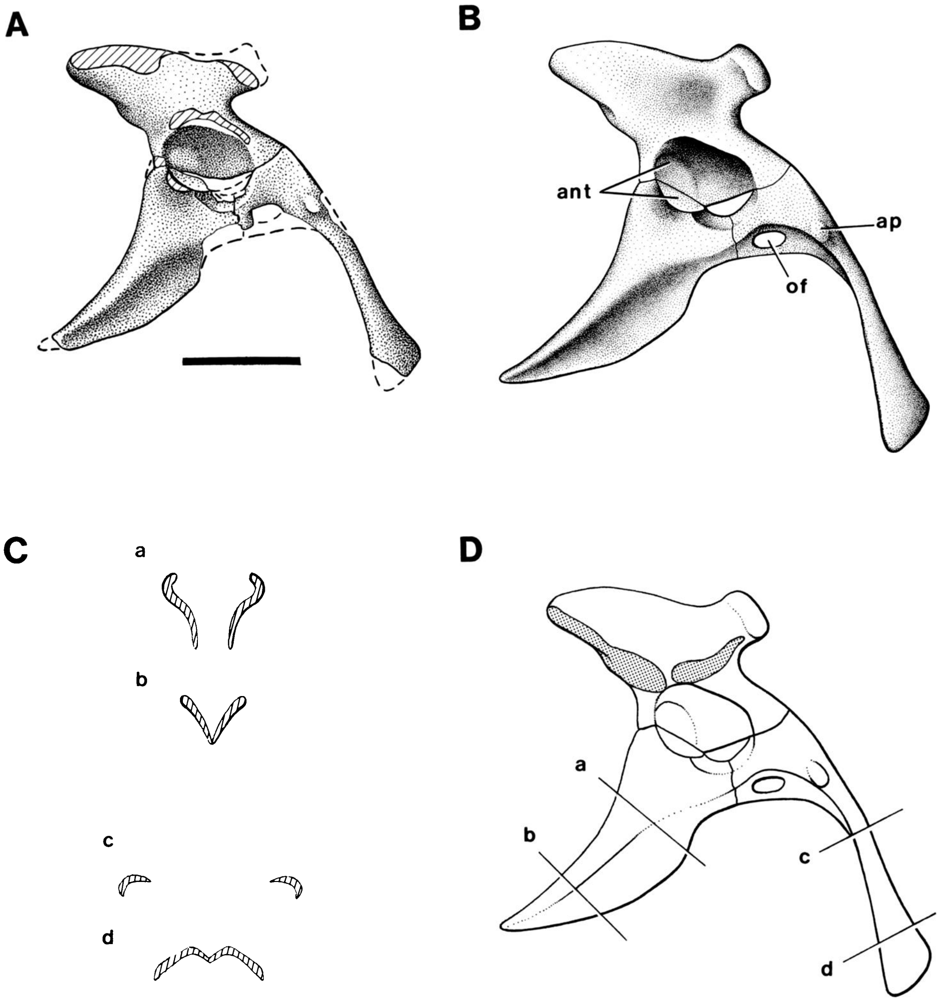

FIGURE 6. Pelvic girdle of *Marasuchus lilloensis.* **A**, right lateral view of right pelvic girdle (PVL 3870), with cross-hatching indicating broken bone surfaces. **B**, reconstruction of pelvic girdle in right lateral view. **C**, cross-sections of pubes and ischiae as shown in **D**, with anterior toward top of page. **D**, reconstruction of pelvic girdle in right lateral view with attachment surfaces of sacral ribs 1 and 2 on the medial side of the ilium indicated by stipple. Abbreviations: **ant**, antitrochanter; **ap**, ambiens process; **of**, obturator foramen. Scale bar equals 1 cm.

of the opposing margins at this fracture suggests that approximately 1 mm of the blade is missing.

The shaft of the **humerus** is very slender, and the distal condyles are not transversely expanded (Bonaparte, 1975:fig. 9). A shallow radial fossa is present above the medial condyle. The **ulna** and **radius** are extremely slender and probably equal the humerus in length, very different proportions than occur in the holotype of *L. talampayensis* (Tables 1, 4).

Pelvic Girdle

The pelvic girdle (Fig. 6; PVL 3870, 3871) is proportionately tall, with a maximum width across the iliac blades approximately one-half the height from the distal margin of the pubis to the top of the ilium. The pelvic girdle, thus, is twice as deep as it is broad.

Ilium—The short, subrectangular preacetabular process is directed anterodorsally and curves laterally to a swollen distal margin that appears to have been capped by cartilage (Figs. 5, 6A, B, D, 8). The shape and orientation of the process, best preserved in PVL 3871 (Fig. 5A), are remarkably similar to those in *Herrerasaurus* (Reig, 1963; Novas, 1994). Previously, the preacetabular process was shown as short and pointed (Bonaparte, 1975:fig. 10); this misinterpretation was based on the broken process in PVL 3870 (Fig. 6A). The postacetabular process is subtriangular with a slightly thickened posteroventral margin. There is no development of a brevis fossa or lateral groove on the postacetabular process similar to that in *Herrerasaurus* or other dinosaurs.

The acetabular fossa is large relative to the head of the femur (Figs. 6, 8A). A strong supraacetabular crest

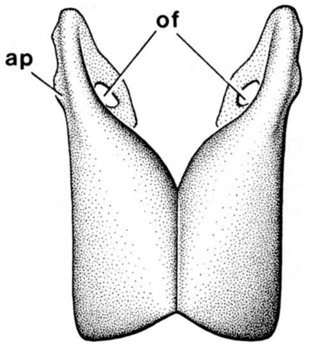

FIGURE 7. Reconstruction of pubes of *Marasuchus lilloensis* in anterior view (based on PVL 3870). Abbreviations: **ap**, ambiens process; **of**, obturator foramen.

overhangs the acetabulum, obscuring the dorsal portion of the fossa in lateral view (Fig. 6B). The most prominent portion of the crest occurs at the base of the pubic peduncle. A triangular apron of the ilium backs the dorsal two-thirds of the fossa (Figs. 5B, 6B). A narrow semicircular gap is present between the apron of the ilium and the ischium and pubis. This gap extends from the anterior end of the antitrochanter on the ischium to the junction between the pubic peduncle of the ilium and the pubis (Fig. 6B). The gap thus separates the ilium from that part of the ischial acetabular margin that appears to be nonarticular. A subtle, raised surface on the posterior portion of the iliac acetabulum forms the dorsal half of an acetabular antitrochanter (Figs. 5A, 6A, B, D), which articulates against the greater trochanter of the femur, as preserved in articulation in PVL 3871 (Fig. 8A).

Ischium—The ischium is shorter than the pubis (Figs. 5B, 6, 8A). Throughout its length, the ischium is platelike and lacks the rod-shaped shaft or thickened dorsal margin that characterizes most dinosaurs. In its proximal half, the dorsal margin of the blade is inturned (Fig. 6C), giving the appearance of a thickened dorsal margin. In its distal half, the blades are gently concave and arch toward the midline, with the thin ventral margin joined with its opposite in symphysis (Fig. 6C).

The ischial acetabular margin provides important evidence regarding the phylogenetic relationships of *M. lilloensis.* As noted by Bonaparte (1975:30, 59), the ischial acetabular margin is differentiated into posterior articular and anterior nonarticular portions (Fig. 6B). The articular portion forms a laterally projecting, semicircular surface that constitutes the ventral half of the antitrochanter, which articulates against the greater trochanter of the femur (Figs. 6B, 8A). Anterior to this surface, the margin of the ischium is recessed ventrally

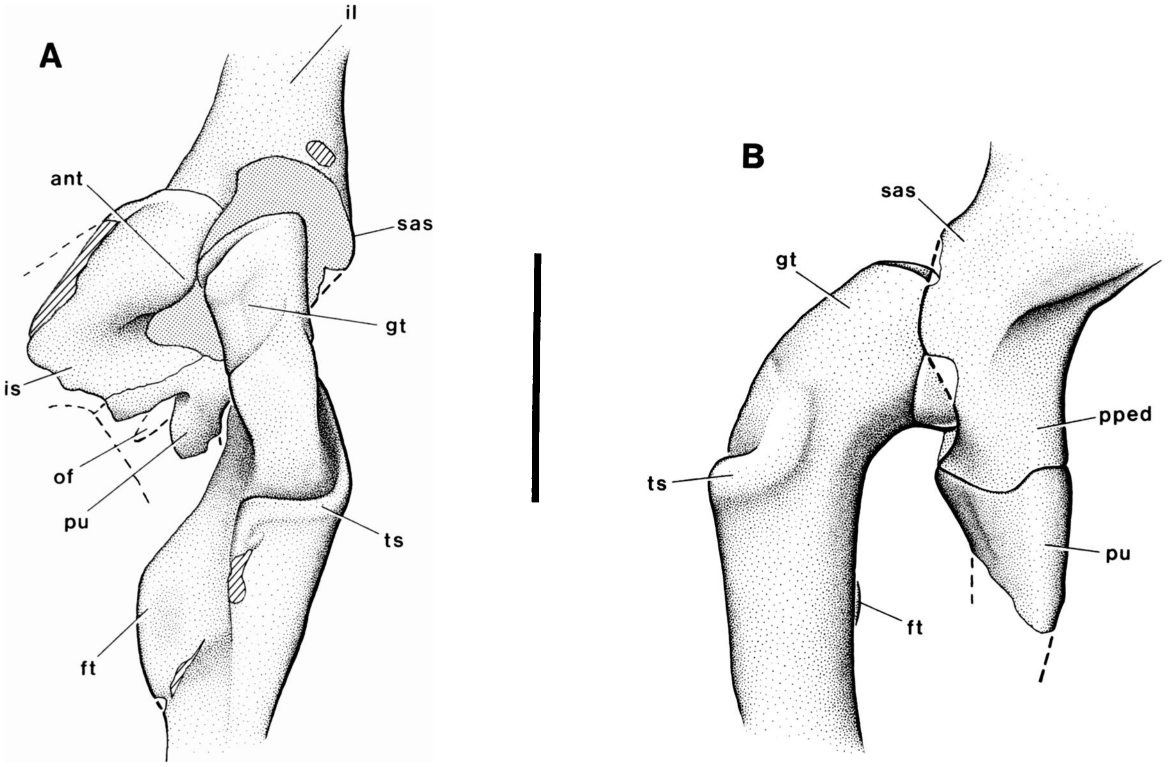

FIGURE 8. Right acetabulum and proximal femur of *Marasuchus lilloensis* (PVL 3871). **A**, posterolateral view; **B**, anterior (slightly lateral) view. Cross-hatching indicates broken bone surface, and even stipple indicates matrix. Abbreviations: **ant**, antitrochanter; **ft**, fourth trochanter; **gt**, greater trochanter; **il**, ilium; **is**, ischium; **of**, obturator foramen; **pped**, pubic peduncle; **pu**, pubis; **sas**, supraacetabular shelf; **ts**, trochanteric shelf. Scale bar equals 1 cm.

and could not have articulated directly with the femur. This portion of the acetabular margin is gently concave transversely and anteroposteriorly and is separated from the ilium by a narrow gap in the wall of the acetabulum.

Pubis—The iliac peduncle of the pubis is broad anteroposteriorly and, as in many dinosaurs, has a gently concave articular surface for the opposing pubic peduncle of the ilium (Figs. 5B, 6–8). The ischial peduncle of the pubis is incomplete ventrally in available specimens. The dorsal margin of the obturator foramen is preserved in both PVL 3870 and 3871, and the contact between the pubis and ischium ventral to the acetabulum would have been more substantial than is preserved (Figs. 5B, 6A, B). Previously, the pubis was figured without an obturator foramen, and the broken pubic peduncle was considered an advanced dinosaurian feature (Bonaparte, 1975:fig. 10). The acetabular margin is transversely narrow and faces slightly laterally.

In anterior view, the transverse width across the pubes narrows slightly from the proximal to distal ends (Fig. 7). Near the proximal end, a knoblike ambiens process is present on its lateral side (Figs. 6B, 7). The pubic blade is plate-like throughout its length, with no development of a rodlike proximal shaft or thickened lateral margins (Fig. 6C). Likewise, there is no distal thickening of the blade or development of a pubic foot, as occurs in *Herrerasaurus* and some other theropods. Each blade is anteriorly convex, with maximum convexity shifting from the midline of the blade proximally to the medial corner distally (Fig. 7). The conjoined blades, therefore, are W-shaped in cross-section at mid-length (Fig. 6C).

Hind-limb

Femur—The head of the femur is egg-shaped in proximal view, with the broader end projecting into the acetabulum (Figs. 8, 9, 10A, B). Two depressions, or grooves, are present on the proximal end that pass along the medial side of the head (Fig. 9). The first is a narrow groove for the ligamentum capitus femoris located on the medial margin of the head. The second is a broader, shallow depression (Fig. 9:gr) that separates the low medial trochanter of the head proper from the greater trochanter. The proximal articular surface of the head extends distally, following this depression a short distance on the medial side of the femoral head. A similar depression and distal extension of the articular surface are present on the femoral head in *Herrerasaurus* (Novas, 1993) and most other dinosaurs (e.g., *Syntarsus,* Rowe, 1989:fig. 4C, E) but are absent in *Lagerpeton* (Sereno and Arcucci, 1994) and pterosaurs (Wellnhofer, 1978). As in *Herrerasaurus* and other dinosaurs, the smooth, cartilage-covered articular surface of the head, which is clearly delimited from the shaft, extends onto the ventral aspect of the inturned portion of the head (Figs. 8B, 9A:arrow).

In PVL 3871, the greater trochanter is marked by a low ridge that angles posterodistally across the lateral surface of the trochanter (Fig. 8A). Other irregular rugosities mark the lateral aspect of the greater trochanter in the smaller specimen (PVL 3870). Farther distally, a bulbous trochanteric shelf curves from the anterolateral side of the shaft, where it is vertically oriented, across the lateral side of the shaft and down the posterior margin (Fig. 8). The trochanteric shelf is sharply delineated with a shallow trough inside. In form and position, it is very similar to the trochanteric shelf in *Herrerasaurus* (Novas, 1994) and *Staurikosaurus.* In PVL 3870, the trochanteric ridge is broken away, and the rugosities mentioned above on the greater trochanter were previously described as the lesser trochanter (Bonaparte, 1975).

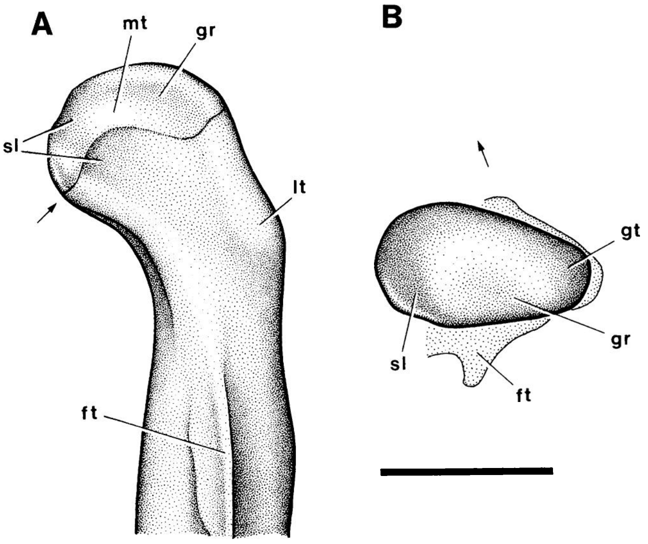

FIGURE 9. Proximal end of right femur of *Marasuchus lilloensis* (PVL 3870). **A**, posteromedial view, with arrow pointing to the medial margin of the articular surface of the femoral head. **B**, proximal view, with arrow pointing anterior when the femur is held in natural articulation in the acetabulum. Abbreviations: **ft**, fourth trochanter; **gt**, greater trochanter; **gr**, groove; **lt**, lesser trochanter; **mt**, medial tuberosity; **sl**, sulcus for the ligamentum capitis femoris. Scale bar equals 5 mm.

The femoral shaft has a sigmoid curve in lateral view, with the head and trochanters curving anteriorly and the remainder of the femur gently arched, or bowed, anteriorly. Bowing of the shaft is easily affected by postmortem torsion or crushing. The fourth trochanter is developed as a symmetrical, aliform process. It projects from the posteromedial side of the shaft, when the axis through the distal condyles is oriented transversely, as best preserved in PVL 3871 (Fig. 9).

The distal ends of available femora have suffered distortion and crushing of the distal articular surface. The partially exposed distal end of the left femur in PVL 3870 may be the least distorted, and a reconstruction of the distal end is based on all specimens (Fig.

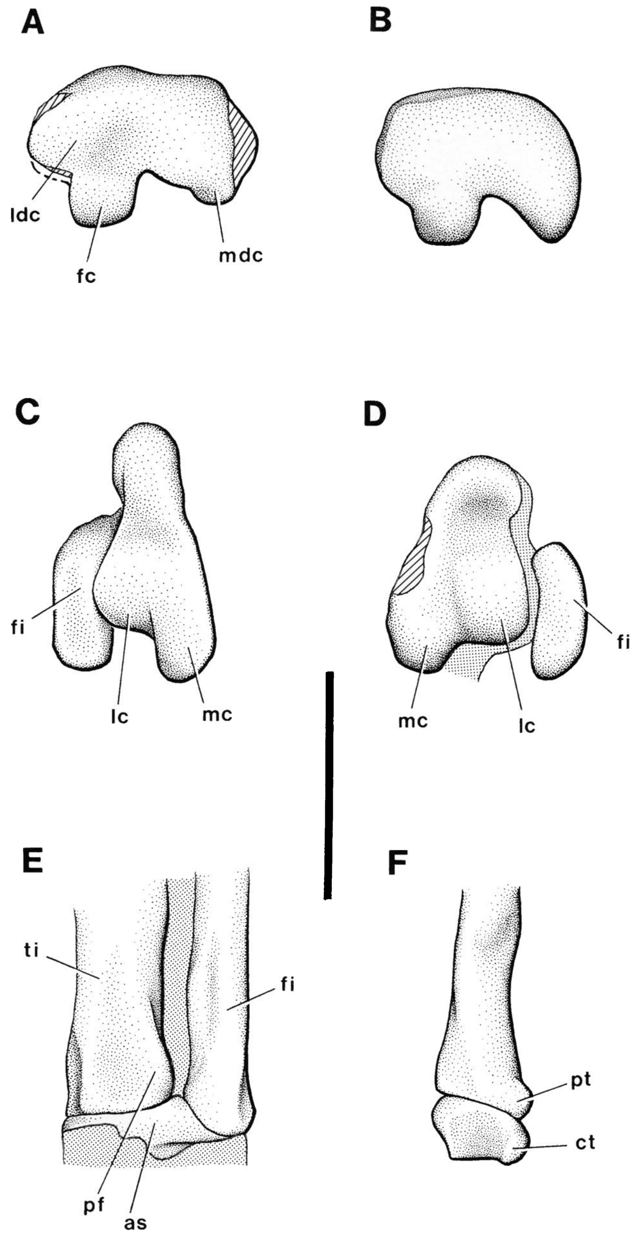

FIGURE 10. Hind-limb of *Marasuchus lilloensis* (PVL 3871). **A**, distal end of right femur in distal view. **B**, reconstruction of distal end of right femur (based on PVL 3870 and 3871). **C**, proximal end of left tibia and fibula in proximal view. **D**, proximal end of right tibia and fibula in proximal view. **E**, distal end of right tibia and fibula in posterior view. **F**, left fibula and calcaneum in lateral view. Cross-hatching indicates broken bone surface, and even stippling indicates matrix. Abbreviations: **as**, astragalus; **ct**, calcaneal tuber; **fc**, fibular condyle; **fi**, fibula; **lc**, lateral condyle; **ldc**, lateral distal condyle; **mc**, medial condyle; **mdc**, medial distal condyle; **pf**, posteromedial flange; **pt**, posterior tuber; **ti**, tibia. Scale bar equals 1 cm.

10B). The medial distal condyle is subtriangular, and the lateral distal condyle continues posteriorly as a subrectangular fibular condyle (labelled in reverse by Bonaparte [1975:fig.12]). The posterior portion of the lateral distal condyle also articulates with the fibula.

Tibia—The proximal end of the tibia is subtriangular, with a bulbous, rounded anterior margin (Fig. 10C; less distorted on the left side of PVL 3871). Although the anterior margin of the proximal end of the tibia is strengthened compared to that in many crurotarsal archosaurs, a discernable cnemial crest is not developed. In *Herrerasaurus* and other basal dinosaurs, in contrast, a groove separates a distinct cnemial crest from the remainder of the proximal articular surface of the tibia (Novas, 1994). In *M. lilloensis,* the medial condyle of the proximal end of the tibia is unusual. It extends far posterior to the lateral condyle, as does the fibula (Fig. 10C, D).

The gently convex articular surface of the distal end is subquadrate with a rounded anteromedial corner (Fig. 12A). In PVL 3870, the distal articular surface is damaged and has previously been described as "L-shaped" (Bonaparte, 1975:fig. 14D, G; Novas, 1989). Unlike the condition in crurotarsal archosaurs, the posterior surface of the distal shaft is flat and oriented in a transverse plane (Fig. 10E, 12A). A vertical groove is present on the lateral side of the distal shaft near the posterolateral corner (Arcucci, 1987; Novas, 1989). Because the groove is located near the posterior margin of the distal shaft, a rudimentary laterally directed flange is developed (Fig. 10E; "posterior process" of Novas, 1989). The groove terminates distally as a notch in the distal articular surface (Fig. 12A) that accommodates the prominent lateral rim of the tibial facet on the astragalus—the precursor of the astragalar ascending process in dinosaurs (Arcucci, 1987; Novas, 1989).

TABLE 4. Measurements (in mm) of the pectoral girdle and forelimb of *Marasuchus lilloensis* (PVL 3871). Parentheses indicate estimates.

Scapula	
Minimum width	6.0
Minimum length	25.0
Humerus	
Maximum length	38.6
Minimum shaft width:	
Mediolateral	1.9
Anteroposterior	2.9
Length from head to deltopectoral crest apex	9.8
Maximum proximal width	(9.0)
Maximum distal width	6.1
Ulna	
Length	(36.0)
Length of olecranon	5.5
Radius	
Length	(31.0)

TABLE 5. Measurements (in mm) of the hind-limb of *Marasuchus lilloensis* (PVL 3870, 3871).

	PVL 3870		PVL 3871	
	Left	Right	Left	Right
Femur				
Maximum length	42.2	43.0	57.5	55.1
Anteroposterior shaft diameter	3.6	3.8	—	—
Head of apex of fourth trochanter	11.5	11.6	16.9	16.7
Maximum width proximal end	5.8	5.7	—	—
Maximum width distal end	6.2	6.6	—	—
Tibia				
Maximum width	50.1	47.6	70.0	70.0
Anteroposterior mid–shaft diameter	3.0	2.7	3.6	—
Proximal end width (anteroposterior)	—	—	10.8	9.8
Distal end width (anteroposterior)	—	—	4.5	—
Distal end width (transverse)	—	—	4.0	—
Fibula				
Maximum length	—	—	70.1	69.7
Anteroposterior shaft diameter	—	2.0	2.7	2.4
Maximum anteroposterior width of proximal end	—	5.0	6.6	5.8
Maximum anteroposterior width of distal end	—	3.7	4.8	—
Astragalus				
Maximum transverse width of distal articular surface	4.7	—	—	—
Digit I				
Metatarsal I	14.1	—	—	—
Phalanx 1	7.3	—	—	—
2	—	—	—	—
Digit II				
Metatarsal II	24.8	—	36.3	—
Phalanx 1	—	7.6	9.3	8.3
2	—	—	—	7.1
3	—	—	—	—
Digit III				
Metatarsal III	28.0	—	40.4	—
Phalanx 1	8.4	8.7	—	11.2
2	6.6	—	—	7.4
3	7.1	—	—	—
4	—	—	—	—
Digit IV				
Metatarsal IV	27.8	—	36.0	—
Phalanx 1	6.8	6.5	—	6.9
2	—	4.3	—	4.7
3	—	—	—	4.5
4	—	—	—	4.4
5	—	—	—	—
Digit V				
Metatarsal V	14.5	—	—	—

The posterolateral flange of the tibia passes posterior to this prominent astragalar crest (Figs. 10E, 11A, C). The form of the distal end of the tibia does not differ significantly from that in *Pseudolagosuchus major* (Arcucci, 1987; Novas, 1989).

Fibula—The proximal end of the fibula is broader than the distal end (Fig. 10C–F), the reverse of the condition among most crurotarsal archosaurs. It is quite large, relative to the proximal end of the tibia, and articulates with the fibular condyle of the femur as well as part of the lateral distal condyle. The fibular shaft is straight. The anterior trochanter is developed as a low crest on the anterior margin of the proximal shaft. This crest is considerably lower than the hypertrophied flange that occurs in *Lagerpeton.*

In distal view, the articular surface is elliptical, with

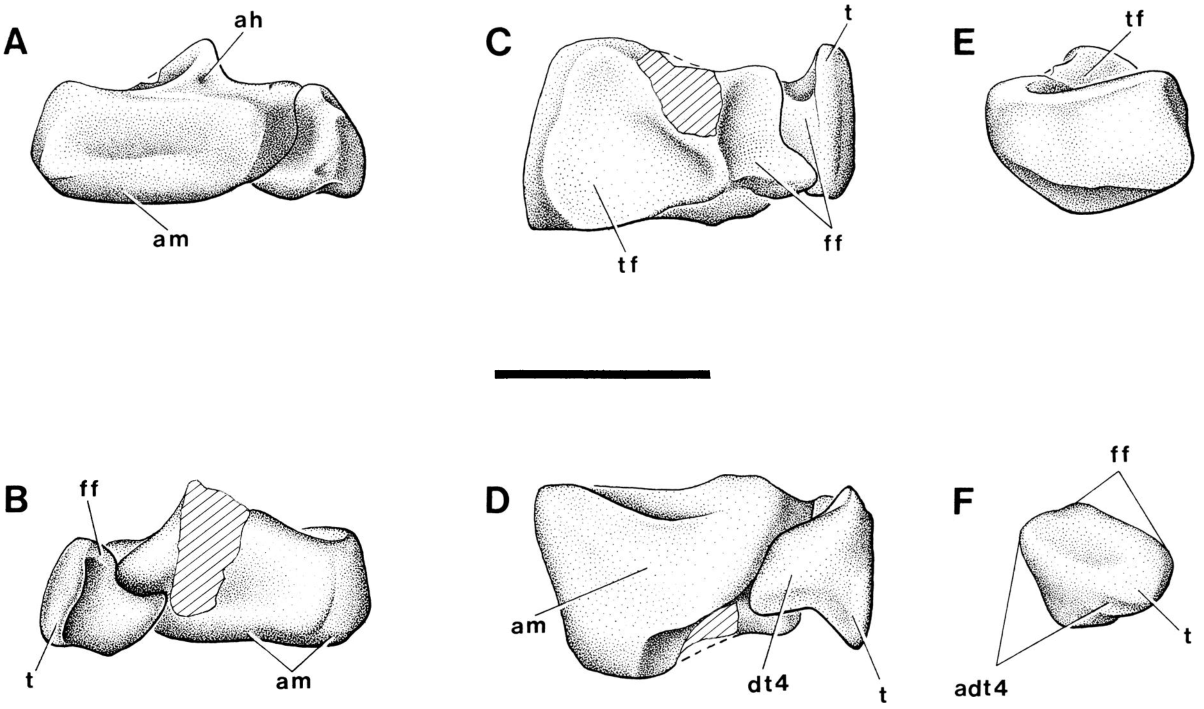

FIGURE 11. Left astragalus and calcaneum of *Marasuchus lilloensis* (PVL 3870; from Sereno, 1991b). **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, ventral view; **E**, medial view; **F**, lateral view of calcaneum. Cross-hatching indicates broken bone surface. Abbreviations: **adt4**, articular surface for distal tarsal 4; **ah**, anterior hollow; **am**, articular surface for metatarsals I and II; **ff**, fibular facet; **t**, tuber; **tf**, tibial facet. Scale bar equals 5 mm.

the principal axis directed anteromedially (Fig. 12A; contra Bonaparte, 1975:38). This oblique orientation closely resembles the condition in basal dinosaurs (e.g., *Herrerasaurus*; Novas, 1994) and crurotarsal archosaurs. The distal end is gently concave anteroposteriorly along its lateral margin, as seen in lateral and distal views (Figs. 10F, 12A). The distal end is also transversely convex and strongly bevelled on its medial side (Figs. 10E, 12A), conforming to the asymmetrical articular facet formed by the astragalus and calcaneum (Fig. 11C). A prominent posterior tuber is present proximal to the calcaneal tuber (Fig. 10F).

Tarsus—The proximal tarsals are best preserved on the left side of PVL 3870 (Fig. 11). The astragalus is complete except for damage on its posterior surface. In anterior view, a vertical, rectangular, nonarticular surface separates the ventral articular surface (am) from the dorsal facets for the crus (Fig. 11A). As in most archosaurs, a vascularized depression (ah) is present above the anterior nonarticular surface (Fig. 11A). Unlike *Lagerpeton* (Sereno and Arcucci, 1994) or *Herrerasaurus* (PVSJ 373), a depression is present between the astragalus and calcaneum in anterior view (Fig. 11A). In posterior view (Fig. 11B), a similar, but gently concave, nonarticular surface is present on the astragalus, suggesting that the cartilaginous articular cap for the ankle joint was restricted to the distal roller surface of the astragalus. The full medial extension of the calcaneum is exposed in this view.

In dorsal view, the astragalus is trapezoidal with a broader anterior side (Fig. 11C). The subtriangular tibial facet is separated from the fibular facet by a wedge-shaped crest that climbs to an apex near the anterior margin. The lower posterior portion of the crest (partially damaged in PVL 3870) articulates in a notch on the distal end of the tibia (Fig. 12A). The form of this crest does not differ significantly from that in *Chanaresuchus* and many crurotarsal archosaurs (Sereno, 1991b). We hesitate, therefore, to refer to this crest as an "ascending process" (Arcucci, 1987; Novas, 1989), a term that may better be restricted to the homologous, but distinctly developed, process in dinosaurs. Lateral to this crest, the astragalus narrows in dorsoventral depth to a thin flange overlying the calcaneum. The concave lateral margin of the flange exposes the fibular facet of the calcaneum.

In ventral view, the distal articular surface of the astragalus is subtriangular (Fig. 11D). The anteromedial corner is prominent and forms an acute angle, as in other dinosauromorphs (Novas, 1989:685; Sereno, 1991b:24–25). The medial side of the astragalus is bevelled for articulation with the medial process of the calcaneum. Although the astragalar articular surface has been shown as a concave "depression" (Novas, 1989:fig. 3.3), the articular surface exposed around the calcaneum is clearly anteroposteriorly convex, as in *Herrerasaurus* (PVSJ 373).

The medial side of the astragalus (Fig. 11E) has a near vertical orientation. The anterior margin is deeper than the more rounded posterior margin, and the dorsal margin is nearly straight.

The relatively small calcaneum is wedge-shaped, with a tapering process that extends ventral to the astragalus (Fig. 11A–C). In dorsal view (Fig. 11C), the articular surface for the fibula is divided into a narrow lateral rim, which is gently convex anteroposteriorly (Figs. 10F, 11C, F), and a flat surface that angles ventromedially under the astragalus (Fig. 11B, C). Thus, only the lateral margin of the fibular surface is weakly convex; the fibular surface does not resemble a "convex pulley" (Novas, 1989:681), as occurs in crurotarsal archosaurs (Sereno, 1991b). In ventral view (Fig. 11D), the convex elliptical surface for articulation with distal tarsal 4 is separated from the calcaneal tuber by a shallow groove (Fig. 11D, F). The tab-shaped calcaneal tuber projects posteriorly (Figs. 10F, 11B–D, F).

The two distal tarsals are very similar in form to those in *Lagerpeton* (PVL 3870; Bonaparte, 1975; Sereno and Arcucci, 1993). The third distal tarsal is subrectangular in proximal view (Bonaparte, 1975:fig. 15). As in *Lagerpeton,* it is situated over metatarsal 3 and overlaps the lateral margin of metatarsal 2. Distal tarsal 4 is divided into a broad anterior plate, which overlaps the lateral margin of distal tarsal 3, and a deep posterior heel, between which is a notch for articulation with metatarsal 5 (Fig. 12B). In PVL 3870 (Bonaparte, 1975: fig. 15C, D), the anterior margin and anteromedial corner of distal tarsal 4 are broken away. The complete distal tarsal 4 is slightly longer anteroposteriorly than distal tarsal 3, as in *Lagerpeton.*

Pes—The shafts of metatarsals I to IV are straight and closely appressed throughout most of their lengths, including metatarsal IV (Fig. 12B). The shaft of metatarsal V angles mediodistally across the posterior aspect of the metatarsus, an orientation that may be natural, as it also occurs in many dinosaurian pedes. The distal ends of metatarsals II to IV have dorsal extensor depressions for the intercondylar processes of their respective proximal phalanges. The unguals of several of the digits are lacking, and the phalangeal formula probably was 2(1)-3(2)-4(3)-5(4)-0 (maximum number of phalanges preserved given in parentheses). There is no evidence for phalanges in digit V (contra Bonaparte, 1975:fig. 16).

DISCUSSION

Marasuchus lilloensis

Previous diagnoses of *M. lilloensis* have not listed diagnostic characters (autapomorphies) but rather have included characters that apply to all dinosauriforms, ornithodirans, or more inclusive groups. Romer (1971: 4), for example, lists the long and slender limb proportions, the inturned femoral head, and the fact that digit III is the longest pedal digit. Bonaparte (1975:9) extended this diagnosis by including more symplesiomorphies, such as a femur that is shorter than the tibia, two distal tarsals, and pedal digits I and V that are shorter than digits II–IV. The only character mentioned by Bonaparte (1975:9) that we regard as an autapomorphy of *M. lilloensis* is the posterolateral deflection of the distal pubic blade; ironically, he regarded this character as evidence to unite *M. lilloensis* and some saurischian dinosaurs (Bonaparte, 1975:59, 72; but see character 7 below). Recognizing the lack of autapomorphies in the published descriptions, Gauthier (1986) regarded *L. talampayensis* (including the material we refer to *M. lilloensis*) as a metaspecies.

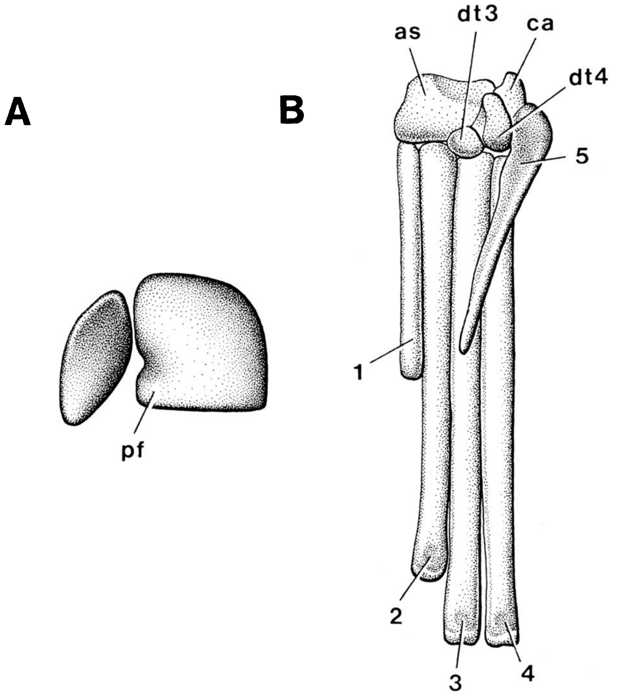

FIGURE 12. Restoration of the distal ends of the crus, tarsus, and metatarsus of *Marasuchus lilloensis* (based on PVL 3870 and 3871). **A**, distal ends of right tibia and fibula in distal view (anterior toward top of page). **B**, proximal tarsals in distal view and distal tarsals and metatarsus in posterior view (from Sereno, 1991b). Abbreviations: **1-5**, metatarsals I to V; **as**, astragalus; **ca**, calcaneum; **dt3-4**, distal tarsals 3 and 4; **fi**, fibula; **pf**, posteromedial flange; **ti**, tibia.

However, *M. lilloensis* exhibits several autapomorphies, and these diagnostic features have helped to identify less complete specimens of this species in material from Los Chañares (characters 1–8; see Appendix for character-state distributions among outgroup taxa). (1) The neural spines in the posterior cervical vertebrae project anterodorsally (Fig. 3A:ps 6–9), a condition that does not occur in *Herrerasaurus* (PVSJ 373), *Staurikosaurus* (Colbert, 1970:fig. 7A, B), pterosaurs (Wellnhofer, 1978; Sereno, 1991b:fig. 20), or crurotarsal archosaurs (e.g., *Riojasuchus,* Bonaparte, 1972). The condition in *Lagerpeton* is unknown. (2) A shallow depression is present ventral to the transverse process in the presacral vertebrae (Fig. 3A). The depression or hollow is present from the sixth to the tenth or twelfth presacral vertebra. A similar depression is not present in basal dinosaurs, pterosaurs, or crurotarsal archosaurs, although the condition in *Lagerpeton* is not known. In *Herrerasaurus* and *Staurikosaurus,* two laminae extend anteroventrally and posteroventrally from the transverse processes in posterior cervical and dorsal vertebrae (Novas, 1994). The intervening fossa under the transverse process resembles the hollow in *M. lilloensis* but is deeper and better defined. (3) The triangular neural spines in mid- and posterior dorsal vertebrae are also diagnostic for *M. lilloensis* (Fig. 3B). The anterior and posterior tips of adjacent spines either contact each other or approach one another very closely, when the vertebral column is held horizontal. A similar condition has not been reported among other archosaurs and is not present in the posterior dorsals of *Lagerpeton* (Sereno and Arcucci, 1994).

One of the most remarkable features in *M. lilloensis* is the length of the tail. (4) Caudal centrum length increases posteriorly such that mid-caudal centra are twice the length of anterior caudal centra (Fig. 4; Table 2). (5) Similarly, and possibly related to the elongate tail, the anterior chevrons are very long, exceeding the first caudal centrum length by three times (Fig. 4; Table 3). In other archosauriforms for which the tail is known (e.g., *Chanaresuchus, Coelophysis*), centrum length in all but the short posteriormost caudal vertebrae rarely differs by more than 20%, and chevron length is approximately twice that of the first caudal centrum. The stiffened tail in basal pterosaurs constitutes an exception; caudal centrum length increases distally to more than twice its initial length (Wild, 1978). The anterior chevrons in *Gracilisuchus* (PVL 4597), likewise, are proportionately as long as in *M. lilloensis* and constitute a rare exception. Mid- and distal caudal vertebrae and anterior chevrons are unknown in *Lagerpeton.*

(6) In *M. lilloensis,* the scapular blade is particularly broad proximally. The minimum width of the proximal scapular blade (6 mm) is one-fourth the length of the scapular blade (25 mm). These broad proportions are diagnostic for *M. lilloensis* and, among other archosaurs, occur only in phytosaurs and some basal crocodylomorphs. (7) In *M. lilloensis,* the lateral portion of the distal pubic blade is deflected posterolaterally, in contrast to the transverse orientation in other basal archosaurs. Bonaparte (1975) considered this condition similar to the posteriorly projecting pubic foot in herrerasaurids and other theropods (Sereno and Novas, 1994). However, the lateral margin of the pubis in *M. lilloensis* is not thickened and does not project posteriorly, as in the pubic foot in theropods. Thus the similarity between the lateral portion of the distal blade in *M. lilloensis* and the thickened, posteriorly directed pubic foot in theropods is not clear and, in any case, would not represent a synapomorphy, given the absence of a pubic foot in ornithischians and sauropodomorphs.

Lastly, (8) the band-shaped lateral margin on the fibular facet of the calcaneum in *M. lilloensis* is also unusual. The fibular facet is flat with a narrow, slightly anteroposteriorly convex band along the lateral margin (Fig. 11C). In *Lagerpeton* (Sereno and Arcucci, 1994) and dinosaurs, the fibular facet is concave with a relatively sharp lateral rim. In *Pseudolagosuchus,* the facet is gently convex without a well-defined lateral rim (Novas, 1989:fig. 3.8). In crurotarsal archosaurs, the facet forms a convex condyle (Sereno, 1991b). The condition in pterosaurs is poorly known because of coossification of the crus and proximal tarsals.

The Dinosauriform Postcranium

Although originally classified as a "pseudosuchian" (Romer, 1972c), *M. lilloensis* has always been considered to share a closer relationship with dinosaurs than with other basal archosaurs. Romer, Bonaparte, and subsequent authors (Gauthier, 1984, 1986; Paul, 1984; Brinkman and Sues, 1987; Novas, 1989; Sereno, 1991b) have identified numerous synapomorphies in support of this hypothesis. *Lagerpeton* and Pterosauria, however, were either excluded from these studies, or pterosaurs were considered part of the ingroup and at least potentially closer to dinosaurs than *M. lilloensis* (Gauthier, 1984, 1986; Gauthier and Padian, 1985). Recent re-examination of basal ornithodirans suggests, to the contrary, that *Lagerpeton* and Pterosauria constitute successive sister-taxa to a more restricted group including *M. lilloensis* and dinosaurs (Sereno and Novas, 1990; Sereno 1991b; Novas, 1992; Sereno and Arcucci, 1994:fig. 6). Much of the character evidence that previously was used to unite *M. lilloensis* and Dinosauria actually supports Ornithodira, a monophyletic group that also includes *Lagerpeton* and pterosaurs.

Novas (1989:685) lists five characters that specifically unite *M. lilloensis* and dinosaurs. One character, the acute anteromedial corner on the astragalus (Novas, 1989:character 4), is also present in *Lagerpeton* (Sereno, 1991b:24–25), and thus characterizes a more inclusive taxon. A second character includes both the reduction and posterolateral deflection of the calcaneal tuber (Novas, 1989:character 7). Absence of the tuber in the outgroups *Lagerpeton* and pterosaurs, however, certainly constitutes reduction, and the deflection of the tuber in outgroups that lack a tuber, of course, cannot be interpreted as either primitive or derived. The tuber in more distant outgroups, such as ornithosuchids, is posteriorly directed. Thus, the posterior orientation of the tuber in *M. lilloensis* and some dinosaurs is of questionable significance as a synapomorphy. A third character, the reduction or absence of a peg-in-socket astragalocalcaneal joint (Novas, 1989: character 5), presumes that a "crocodile-reversed" tarsus is primitive for Ornithodira and that such a condition is present in immediate outgroups to *M. lilloensis* and dinosaurs. Neither presumption, we believe,

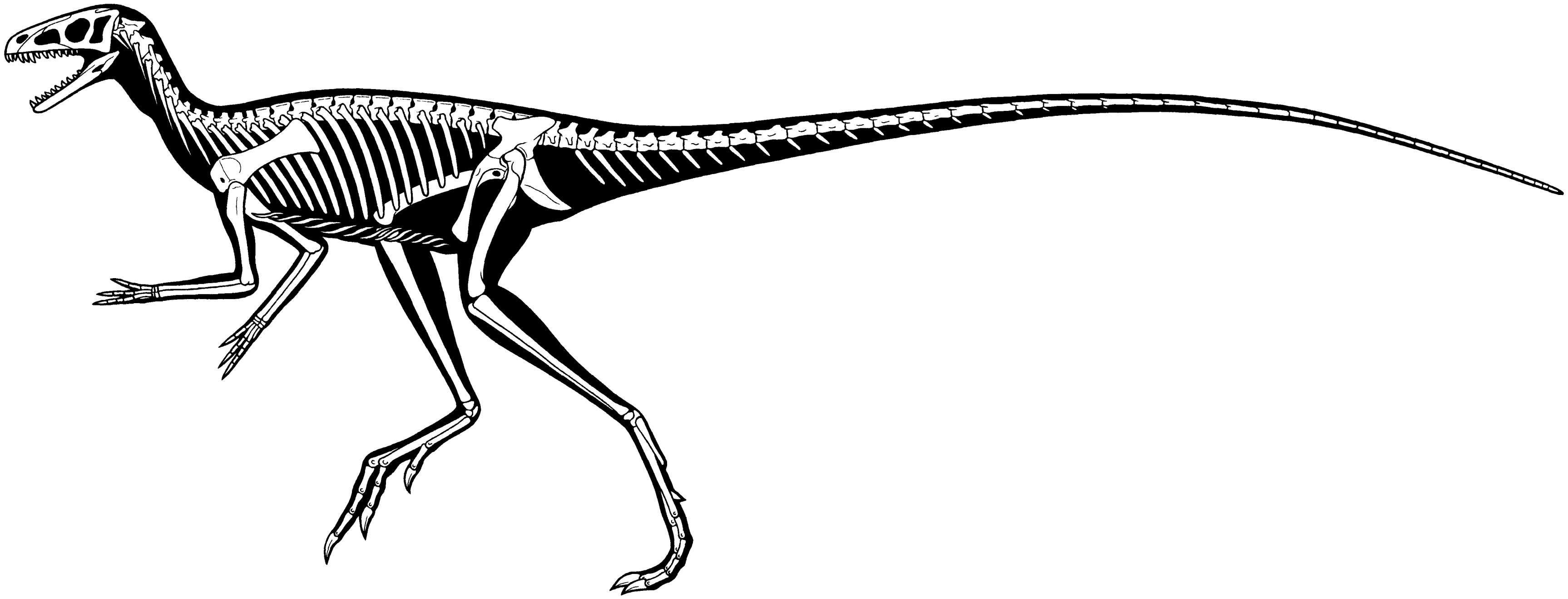

FIGURE 13. Reconstruction of *Marasuchus lilloensis* (based on PVL 3870 and 3871). The skull roof, manus, distal tail, ribs, and gastralia are restored.

is correct (Sereno and Arcucci, 1990; Sereno, 1991b). A fourth character mentioned by Novas (1989:character 3), the development of a posterior flange on the distal end of the tibia, is a synapomorphy uniting *M. lilloensis* and dinosaurs, as discussed below (see character 17). It appears to be the only synapomorphy mentioned in the literature that excludes *Lagerpeton* and pterosaurs, prior to the analysis of Sereno and Novas (1990), Sereno (1991b), and Novas (1992).

We describe below several synapomorphies that unite *M. lilloensis* and Dinosauria (as Dinosauriformes), using *Lagerpeton,* Pterosauria, and Crurotarsi as successive outgroups (characters 9–17; see Appendix for character-state distributions; Sereno and Arcucci, 1994: fig. 6).

(9) *Presacrals 6–9 with parallelogram-shaped centra* (Fig. 3A: Sereno, 1991b:fig. 20). In dinosauriforms, the strong sigmoid curve in the cervical series is produced by dorsal offset of the anterior face of the centrum in the anterior nine or 10 presacral vertebrae.

(10) *Forelimb one-half or less the length of the hindlimb* (Fig. 13). Synapomorphies 9 and 10 are discussed in detail by Sereno (1991b:23–24, 50). Because the condition in *Lagerpeton* is not known, these synapomorphies may eventually support Dinosauromorpha.

(11) *Opening in acetabular wall between the ilium and pubis* (Fig. 6B). Iliac and pubic contributions to the acetabular wall are separated by a gap. In *M. lilloensis,* the gap begins immediately posterior to the peduncles of the ilium and pubis (Figs. 5B, 6B). All basal dinosaurs exhibit this condition (e.g., *Lesothosaurus,* Sereno, 1991a; *Coelophysis,* Colbert, 1989; *Plateosaurus,* Huene, 1926). In the outgroups *Lagerpeton* and pterosaurs, the acetabulum is closed. In crurotarsal archosaurs, the acetabulum is either closed (e.g., phytosaurs) or open by a narrow gap between the ilium and ischium, but not between the ilium and pubis (e.g., *Ornithosuchus,* Walker, 1964).

(12) *Acetabular antitrochanter* (Fig. 6B). A distinct, raised antitrochanter is present on the posterior side of the acetabulum, on the peduncles of the ilium and ischium in *M. lilloensis* and most dinosaurs. The antitrochanter articulates against the head of the femur and may be related to a trough crossing the head of the femur in *M. lilloensis* (Figs. 8A, 9, gr) and dinosaurs. The ischial antitrochanter occupies the posterior one-half of the acetabular margin; the anterior half is recessed and apparently does not articulate directly with the femur. Bonaparte (1975) first noticed this specialized form of the ischial acetabular margin in *M. lilloensis* and its similarity to that in dinosaurs. *Herrerasaurus* (Reig, 1963; Novas, 1994) and most other dinosaurs show the acetabular antitrochanter and the recessed anterior half of the ischial acetabular margin. In a few dinosaurs such as *Lesothosaurus* (Sereno, 1991a:fig. 10), the differentiation of the ischial portion of the antitrochanter is less pronounced. An acetabular antitrochanter is not developed in *Lagerpeton,* pterosaurs, or crurotarsal archosaurs, with the possible exception of the advanced sphenosuchian *Terrestrisuchus* (Crush, 1984). Some crurotarsal archosaurs appear to have developed an acetabular antitrochanter on the anterior side of the acetabulum, on the pubis and ischium (Sereno, 1991b:32–33).

(13) *Pubis length three times or more acetabular diameter* (Fig. 6B). The pubis is relatively longer in *M. lilloensis* and dinosaurs, as compared to acetabular diameter. Acetabular diameter, rather than femur length, is used for comparison to avoid possible confusion with independent changes in limb proportions. The maximum length of the pubis (from the iliac peduncle to the distal end of the blade) in *M. lilloensis* is more than three times maximum anteroposterior acetabular diameter, as it is in *Herrerasaurus* and other basal dinosaurs. In *Lagerpeton,* pterosaurs, and some crurotarsal archosaurs (e.g., phytosaurs, aetosaurs), this ratio ranges from 1.5 to 2.5. Ornithosuchians and many suchians have independently acquired a relatively longer pubis.

(14) *Extension of the proximal articular surface on the femur under head* (Figs. 8B, 9A, arrow). The articular surface of the femoral head extends around the head and onto its ventral side in *M. lilloensis* and dinosaurs. In *Lagerpeton* (Sereno and Arcucci, 1994), pterosaurs, and most crurotarsal archosaurs (e.g., phytosaurs, *Gracilisuchus*), the articular surface does not extend onto the ventral aspect of the head (when the femoral shaft is oriented vertically). *Riojasuchus,* a notable exception, has a bulbous, rounded femoral articular head (Bonaparte, 1972:fig. 17). The closely related form *Ornithosuchus* (Walker, 1964), however, lacks this condition, and it must have arisen independently.

(15) *Femoral anterior trochanter* (Fig. 8). In dinosauriforms, the femur is characterized by a distinct anterior (lesser) trochanter on the lateral side of the proximal end (Sereno and Novas, 1990; Novas, 1992). Among dinosaurs, the anterior trochanter, which usually takes the form of a tab-shaped process (see below), is ubiquitous in basal dinosaurs and absent in only a few subgroups (e.g., most ankylosaurs, sauropods). A similar discrete process is absent in *Lagerpeton* and has not been reported in pterosaurs.

(16) *Femoral trochanteric shelf* (Fig. 8). In the basal dinosauriforms *Marasuchus* and *Pseudolagosuchus,* the anterior trochanter forms a sigmoid crest, termed the trochanteric shelf, that curves across and then down the shaft of the femur toward the fourth trochanter (Sereno and Novas, 1990; Novas, 1992). The anterior trochanter, however, is absent altogether in dinosauromorph outgroups, and the trochanteric shelf is present only in some dinosaurs. Thus the interpretation of this character as a dinosauriform synapomorphy is equivocal. The shelf is present in *Herrerasaurus* (Novas, 1994) and ceratosaurian theropods (dimorphic; Rowe and Gauthier, 1990) but is absent in tetanuran theropods, sauropodomorphs, and ornithischians. In *Staurikosaurus* (MCZ 1669) and *Pseudolagosuchus* (Novas, 1992), the shelf is present but is developed only as a low sigmoidal prominence.

(17) *Tibia with posterolateral flange* (Figs. 10E, 12A).

In all dinosauriforms, a laterally directed flange is developed on the distal end of the tibia that extends posterior to the cupped tibial facet on the astragalus (Fig. 11C) toward the fibula (Arcucci, 1987; Sereno and Novas, 1990; Novas, 1989, 1992). This posterolateral flange, therefore, must pass over the rim of the original tibial facet on the astragalus (Fig. 11C). In *M. lilloensis,* a groove on the distal end of the tibia separates the flange from the main part of the distal end and accommodates the rim of the original astragalar facet for the tibia. In dinosaurs, the posterior flange is more robust (Novas, 1989). The development of a distinct posterior flange also results in squaring of the distal end of the tibia (Fig. 12A). The distal end of the tibia in dinosauriform outgroups, in contrast, is oval (e.g., *Lagerpeton,* Sereno and Arcucci, 1994), subcircular (pterosaurs; Wellnhofer, 1978), or peanut-shaped (crurotarsal archosaurs) and lacks any development of a posterior flange.

CONCLUSIONS

Two small bipedal archosaurs in the Middle Triassic Los Chañares fauna, *Lagerpeton chanarensis* and *Marasuchus lilloensis,* provide the best available evidence of ornithodirans that predate the Late Triassic radiation of dinosaurs. Comparative analysis of *L. chanarensis, M. lilloensis,* and other ornithodirans strongly suggests that these two contemporary ornithodirans share a more recent common ancestry with dinosaurs (as Dinosauromorpha) than with pterosaurs. Within Dinosauromorpha, *M. lilloensis* and dinosaurs appear to be more closely related (as Dinosauriformes). Several supporting synapomorphies include a gap in the acetabular wall between the ilium and pubis, an antitrochanter on the posterior wall of the acetabulum, extension of the articular surface on the femoral head onto its ventral aspect, and a posterolateral flange on the distal end of the tibia.

These dinosauriform synapomorphies involve novel articular relations and processes for muscle attachments that may indicate modifications in the function of the hind-limb. Although their functional significance remains obscure, these anatomical modifications persist among dinosaurian descendants, many of which attain body sizes more than two orders of magnitude greater than that of *L. chanarensis* and *M. lilloensis.*

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APPENDIX

CHARACTERS AND TAXON-CHARACTER MATRIX

The coding and distribution of 17 characters is shown below for *Marasuchus lilloensis,* basal dinosaurs (*Herrerasaurus ischigualastensis, Coelophysis bauri, Plateosaurus engelhardti, Lesothosaurus diagnosticus*), *Lagerpeton chanarensis,* pterosaurs, and crurotarsal archosaurs. Characters 1–8 are interpreted as autapomorphies of *M. lilloensis* and provide the basis for the revised diagnosis. Characters 9–17 are interpreted as dinosauriform synapomorphies uniting *M. lilloensis* and Dinosauria, with *Lagerpeton chanarensis,* pterosaurs, and crurotarsal archosaurs serving as successive outgroups (Sereno and Novas, 1990; Sereno, 1991b; Sereno and Arcucci, 1994:fig. 6). Character information for basal dinosaurs comes from Colbert (1989), Huene (1926), Novas (1989), Reig (1963), Sereno (1991a, b), and Thulborn (1972).

Marasuchus lilloensis

1. Posterior cervical (ps6–9) neural spine orientation: vertical (0); anterodorsally inclined (1).
2. Posterior cervical (presacral 6 to 10–12) with depression ventral to transverse process: absent (0); present (1).
3. Mid- and posterior dorsal neural spine form: subrectangular (0); subtriangular (1).
4. Caudal centrum length: subequal (0); increasing distally to approximately twice the length of first caudal centrum (1).
5. Anterior chevron length: less than (0), or more than (1), 3 times the length of first caudal centrum.
6. Scapular blade width: minimum blade width less than (0), or more than (1), 25 percent blade length.
7. Distal pubic blade orientation: transverse (0); deflected posterolaterally (1).
8. Band-shaped lateral margin on fibular facet of calcaneum: absent (0); present (1).

Taxon	Character			
	5	10	15	
Marasuchus lilloensis	11111	11111	11111	11
Herrerasaurus ischigualastensis	0000?	0X011	11111	11
Coelophysis bauri	00000	0X011	11111	$\underline{1}$1
Plateosaurus engelhardti	00000	00011	11111	01
Lesothosaurus diagnosticus	??00?	0X??1	11111	01
Lagerpeton chanarensis	??0??	?00??	00000	X0
PTEROSAURIA	000$\underline{1}$0	00000	00000	X0
CRUROTARSI	00000	00000	$\underline{0000}$0	XX

Character–state abbreviations: 0 = plesiomorphic state, 1 = apomorphic state, $\underline{0}$ = plesiomorphic state for clade with some ingroup variation, $\underline{1}$ = apomorphic state for clade with some ingroup variation, ? = not preserved or unknown, X = unknown as a result of transformation.

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9. Centrum shape in presacrals 6–9 (or 10): subrectangular (0); parallelogram-shaped (1).
10. Forelimb/hind-limb ratio: more than 0.5 (0); 0.5 or less (1).
11. Iliac-pubic acetabular wall: closed (0); open (1).
12. Acetabular antitrochanter: absent (0); present (1).
13. Pubis length relative to acetabular diameter: less than 3 times (0); 3 times or more (1).
14. Extension of femoral head articular surface: limited (0); extends under head (1).
15. Femoral anterior trochanter: absent (0); present (1).
16. Femoral trochanteric shelf: absent (0); present (1).
17. Tibial posteromedial flange: absent (0); present (1).