

POSTCRANIAL SKELETON OF *MARILIASUCHUS AMARALI* CARVALHO AND BERTINI, 1999 (MESOEUCROCODYLIA) FROM THE BAURU BASIN, UPPER CRETACEOUS OF BRAZIL



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Abstract. *Mariliasuchus amarali* is a notosuchian crocodylomorph found in the Bauru Basin, São Paulo State, Brazil (Adamantina Formation, Turonian–Santonian). The main trait of *M. amarali* is its robust construction, featuring short, laterally expanded bones. The centra of the vertebrae are amphicoelous. In the ilium, the postacetabular process is ventrally inclined and exceeds the limits of the roof of the acetabulum. *M. amarali* has postcranial morphological characteristics that are very similar to those of *Notosuchus terrestris*, though it also displays traits resembling those of eusuchian crocodyliforms (Crocodyliformes, Eusuchia). The similarity of the appendicular skeleton of *M. amarali* with the recent forms of Eusuchia, leads us to infer that *M. amarali* did not have an erect or semi-erect posture, as proposed for the notosuchian mesoeucrocodylians, but a sprawling type posture and, possibly, had amphibian habits (sharing this characteristic with the extant Eusuchia).

Key words. *Mariliasuchus amarali*. *Crocodyliformes*. Notosuchia. Postcranial skeleton. Bauru Basin. Cretaceous.

Resumen. ESQUELETO POSCRANEANO DE *MARILIASUCHUS AMARALI* CARVALHO Y BERTINI, 1999 (MESOEUCROCODYLIA), DE LA CUENCA DE BAURU, CRETÁCICO SUPERIOR DE BRASIL. *Mariliasuchus amarali* es un crocodilomorfo notosuchi encontrado en la Cuenca Bauru, Estado de São Paulo, Brasil (Formación Adamantina, Turoniano–Santoniano). Esta especie se destaca debido al abundante número de fósiles, excavados en el Municipio de Marília, Estado de São Paulo. La mayor característica de *M. amarali* es su construcción robusta, mostrando huesos cortos y expandidos lateralmente. El centro de las vértebras es anficélico. En el ilium, el proceso postacetabular es ventralmente inclinado y excede los límites del techo del acetábulo. *M. amarali* posee características morfológicas postcranianas que son muy similares a aquéllas de *Notosuchus terrestris*, aunque también muestra rasgos semejantes a los crocodiliformes esuquios (Crocodyliformes, Eusuchia). La similitud del esqueleto apendicular de *M. amarali* con las formas recientes de Eusuchia, llevan a inferir que *M. amarali* no tenía una postura erecta o semi-erecta, como fue propuesto para los notosuchi mesoeucrocodylianos, sino una postura esparrancada y, posiblemente, poseía hábitos anfibios (compartiendo esta característica con los Eusuchia vivientes).

Palabras clave. *Mariliasuchus amarali*. *Crocodyliformes*. Notosuchia. Esqueleto postcranial. Cuenca Bauru. Cretácico.

BRAZIL has a rich fauna of Cretaceous mesoeucrocodylians, represented by fossils found mainly in the Araripe (Santana Formation, Early Cretaceous), Bauru (Adamantina and Marília formations, Upper Cretaceous), and Parnaíba (Itapecuru Formation, Lower Cretaceous) basins.

The Bauru Basin contains a wide diversity of Notosuchia represented by *Sphagesaurus huenei* Price, 1950; *Mariliasuchus amarali* Carvalho and Bertini, 1999; *Adamantinasuchus navae* Nobre and Carvalho, 2006; *Mariliasuchus robustus* Nobre, Carvalho, Vasconcellos and Nava, 2007, and *Armadillosuchus arrudai* Marinho and Carvalho, 2009. All the fossils are found in the Adamantina Formation, in São Paulo State (Price, 1950; Carvalho and Bertini, 1999; Nobre and Carvalho, 2006; Nobre *et al.*, 2007; Marinho and Carvalho, 2009) and their age spans the Turonian–Santonian (Castro

et al., 1999; Dias-Brito *et al.*, 2001). Among the notosuchians from the Bauru Basin, *M. amarali* is remarkable because of its abundance, being represented by several specimens including fragmented postcranial bones, osteoderms, skulls, and nearly complete skeletons.

Among adaptations of *M. amarali*—that it shares with all notosuchids—are skull traits such as lateral orbits, vertical anteriorly located external nostrils, specialized short dentition differentiated into incisiform, caniniform and molariform teeth, and short skull and rostrum (*c.* 12 cm long). Also, its alleged terrestrial habits and possibly omnivorous diet (Nobre *et al.*, 2008).

Carvalho and Bertini (1999) compared the holotype of *M. amarali* with several other notosuchids from South America, Asia, and Africa, including *Notosuchus terrestris*

Woodward, 1896, from the Bajo de la Carpa Formation, Upper Cretaceous of Argentina, which showed the largest number of similarities. Zaher *et al.* (2006) placed *M. amarali* within Notosuchia as a sister group of *Comabuesuchus brachbuccalis* Bonaparte, 1991, from the Upper Cretaceous of Argentina. Based on the skull morphology, Andrade and Bertini (2008) proposed *M. amarali* and *N. terrestris* as sister taxa, supporting the original classification as Notosuchidae. Later, Fiorelli and Calvo (2008) described new findings of *N. terrestris* that included parts of the postcranial skeleton, and placed this species as a sister taxon of *M. amarali*.

The morphological comparisons of notosuchian postcranial skeletons are usually limited, since detailed descriptions of these elements are scarce for Cretaceous mesoeucrocodylians. Pol (2005) described a partially preserved postcranial skeleton of *N. terrestris* and discussed its phylogenetic implications, showing that the postcranial morphology of Crocodyliformes is not conservative and displays many relevant variations. In the last few years, important discoveries in the Upper Cretaceous of Madagascar have revealed a diversified morphology of the postcranial skeleton and its relevant implication for phylogenetic relationships among notosuchian crocodyliforms. Among these species we may highlight *Simosuchus clarki* Buckley, Brochu, Krause and Pol, 2000, with the postcranial skeleton described by Georgi and Krause (2010), Sertich and Groenke (2010) and *Araripesuchus tsangatsangana* Turner, 2006.

The aim of this study is to describe and illustrate the postcranial skeleton of *M. amarali* and compare it with other notosuchian species.

GEOLOGICAL CONTEXT

The Bauru Basin occupies 370,000 km² of the central-southern South American platform, reaching a maximum preserved thickness of 300 meters (Fig. 1). It includes a sequence of siliciclastic rocks of continental origin, comprising two groups, *i.e.*, the Caiuá and Bauru groups (Fernandes and Coimbra 1996). The Caiuá Group includes the Santo Anastácio, Rio Paraná, and Goio Erê formations, comprising sandy deposits accumulated in an eolic environment. The Bauru Group includes the Adamantina, Uberaba, and Marília formations, adding units deposited in fluvial environments and alluvial fans (Fernandes and Coimbra, 1996). According to Batezelli (1998), the outcrops of the Adamantina Formation that border the Peixe River valley, near Marília, São Paulo State, should be called the Araçatuba Formation.

According to Fulfaro *et al.* (1994), the age of these de-

posits ranges between Aptian and Maastrichtian. However, Fulfaro *et al.* (1999) proposed that the Caiuá Group represents an Aptian–Albian deposition occurring in a tectonostratigraphic context very different from that originating the Bauru Group, and consequently in a different basin area — the Caiuá Basin.

The Adamantina Formation, the unit in which the fossils referred to *M. amarali* are found, crops out mostly in the area belonging to the Bauru Basin and is distributed among the states of São Paulo (west), Mato Grosso do Sul (west and south) and in the southern region of Goiás (Fig. 1). This formation comprises fine to very fine sandstone and rosy- to brown-colored silty mudstones, with reddish-brown clay intercalations. It normally lies in massive strata or plane-parallel stratification that alternate in medium- to large-sized layers with cross-stratification (Fernandes and Coimbra, 1996). It was deposited in a braided fluvial system developed in an extensive alluvial plain with ephemeral lakes (Dias-Brito *et al.*, 2001).

The *Mariliasuchus amarali* fossil collection site is located within the Marília Municipality, São Paulo State, on the access road to Doreto farm, 10 km away from the municipal center (GPS coordinates: 22°20'28.14"S–49°56'41.94"W). The outcrop comprises intercalations of fine to very fine reddish sandstone, with reddish-brown mudstone layers and carbonatic levels (Fig. 2).

The main sedimentary structures are small- to medium-sized crossed channeled and tabular stratifications, as well as massive bodies and levels with wavy strata. During the Late Cretaceous, the sediments were deposited in a braided fluvial system, forming small temporary lakes typical of the Adamantina Formation. Bone fragments are frequent throughout the entire outcrop. Most of the strata display *Skolithos*-like vertical excavations, rhizoconcretions, and tubes or excavations produced by arthropods.

The largest concentration of *M. amarali* fossils was found in one of the tabular strata, 2–3 meters above road level and with a lower incidence of bioturbation. This bed overlies an intensely bioturbated bed with microfossils.

SYSTEMATIC PALEONTOLOGY

Order CROCODYLOMORPHA Walker, 1970

Suborder CROCODYLIFORMES Benton and Clark, 1988

Infraorder MESOEUCROCODYLIA
Whetstone and Whybrow, 1983

Genus *Mariliasuchus* Carvalho and Bertini, 1999

Type species. *Mariliasuchus amarali* Carvalho and Bertini, 1999.

Stratigraphic and geographic distribution: Adamantina Formation (Turonian–Santonian), Bauru Basin. São Paulo State - Brazil.

***Mariliasuchus amarali* Carvalho and Bertini, 1999**

Figures 3–9

Holotype. Universidade Federal do Rio de Janeiro, Departamento de Geologia, UFRJ-DG 50-R. Nearly complete skull with mandible of a juvenile specimen, preserved with part of the axial and appendicular skeleton articulated to the skull.

Referred specimens. UFRJ-DG 105-R; UFRJ-DG 106-R (Nobre *et al.*, 2008); Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP-PV) 50 and 5, Museu Nacional do Rio de Janeiro, Brazil (MN) 6298-V and 6756-V (Zahert *et al.*, 2006); Museu de Paleontologia e Estratigrafia “Prof. Dr. Paulo Milton Barbosa Landim”, Universidade Estadual Paulista, Rio Claro, Brazil URC R-67, URC R-68 and URC R-69 (Andrade and Bertini, 2008).

Emended diagnosis. Small cranium with a short elevated rostrum. Flat, straight, ornamented cranial roof with rugos-

ity and grooves. The cranium is expanded posteriorly, and anteriorly it presents a strong constriction in the premaxillary region. Semi-vertical external nostrils projecting anteriorly. Large orbits, semi-elliptical in shape and placed semi-laterally in the cranium. Supra-temporal fenestrae large, reaching almost the same size as the orbits and with external openings reaching the caudal limits of the cranial roof. Palatal fenestra located between the palatines and pterygoids. Palatines quadrangular, the caudal portion expanded laterally. Choanae located approximately at cranium mid-length. Incisive foramen between the maxilla and premaxilla. The dentition short and heterodont, not reaching beyond the anterior half of the cranium. The dentition is composed of 3 premaxillary teeth, 5–6 maxillars, and 8–9 in the dentary. The posterior teeth are striated, slightly serrated, with a constriction at the base of the crown and wearing at the apex. The maxillar and premaxillar teeth are conical, pointed, with a hypertrophied tooth in the premaxilla. Anterior mandibular teeth pointed, projecting anteriorly and with wearing at the apex. The ver-

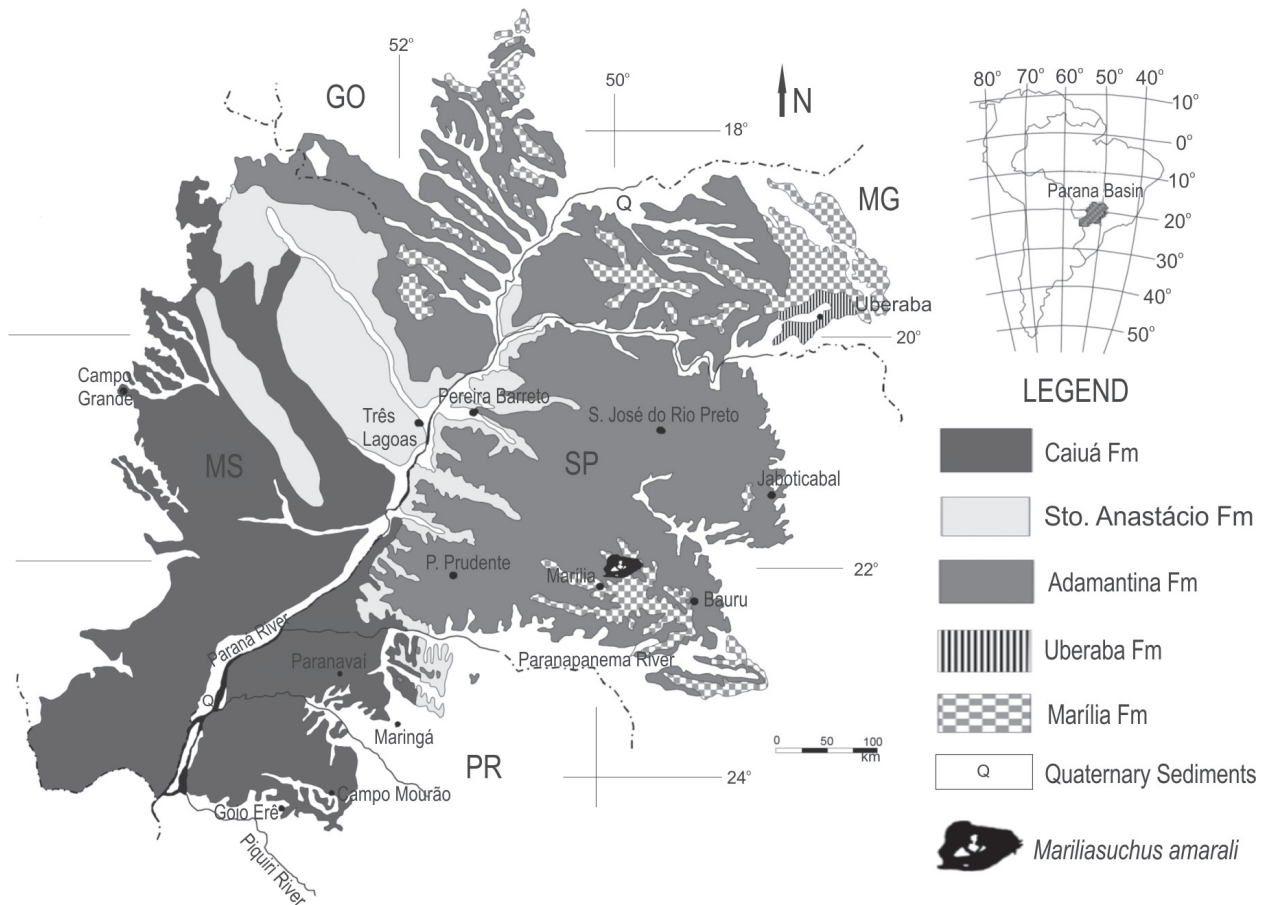


Figure 1. Geological map of the Bauru Basin, modified from Fernandes and Coimbra (1996)/ *Mapa geológico de la Cuenca Bauru, modificado de Fernandes y Coimbra (1996).*

tebral centra are amphicoelous, with two markedly concave articular surfaces. In the cervical vertebrae, the neural spines are dorso-ventrally high and posteriorly curved, and bear an accentuated depression at the base. Three sacral vertebrae are fused to the ilium. The external surface of the osteoderms carries a well-developed antero-posteriorly oriented central crest that is more pronounced along the posterior portion of the osteoderm. Lateral to this central crest, there are several smaller

crests and irregular grooves that gradually decrease towards the osteoderm margin. The scapular blade is slender and greatly expanded at its dorsal end (approximately half of its length), with a particular development of its antero-dorsal region. The ilium is antero-posteriorly expanded, displaying a rectangular shape. The anterior and posterior limbs are robust.

Description of axial skeleton

Specimen UFRJ-DG 105-R has the largest number of preserved vertebrae of all known specimens, *i.e.*, 13 presacral (divided into 6 cervicals and 7 dorsals), 3 sacrals, and 6 caudals. A short series of very small, fragmented vertebrae fused to the matrix can also be found in the anterior part of the tail. Some well-prepared vertebrae display an amphicoelous vertebral centra with an accentuated concavity on the two articular surfaces.

Cervical vertebrae (Fig. 3.1–2). The vertebral centra carry two lateral depressions, *i.e.*, one in a latero-dorsal position and the other in a latero-ventral one. Ventrally, the vertebral centra display a sharp antero-posterior crest between the two latero-ventral depressions. The morphology described above is more evident in the anterior cervical vertebrae, in which the latero-ventral depression is placed more anteriorly. The presence of these crests and depressions confers a triangular aspect to the vertebral centra (in a transverse cross-section).

In lateral view, the neural arch is quadrangular. It is higher than the vertebral centra, reaching one and a half times the height of it in the anterior cervical vertebrae. Dorsally, in the antero-lateral region, the neural arch shows a deep depression or fossa, which becomes more pronounced in the posterior cervical vertebrae.

The zygapophyses are short and project laterally, forming an angle of approximately 45° and 60° with the neural spine and neural arch, respectively. Dorsally, the zygapophyses bulge slightly, with their posterior portion slightly inclined ventrally.

The neural spines of the anterior cervical vertebrae are lower than those of the posterior cervical vertebrae. In the latter, the neural spines are notably high and slightly inclined caudally. The neural spine bases are more antero-posteriorly expanded than the dorsal tip and are subtriangular in lateral view. They are latero-medially thinner anteriorly, acquiring a laminar shape. Their anterior and posterior borders have a groove that starts at the base of the neural spine and runs towards its dorsal portion. The neural spine becomes thicker at the dorsal apex, becoming oval in transverse cross-section.

Dorsal vertebrae (Figs. 3.2 and 4.1–2). There are three preserved anterior dorsal vertebrae articulated to the posterior

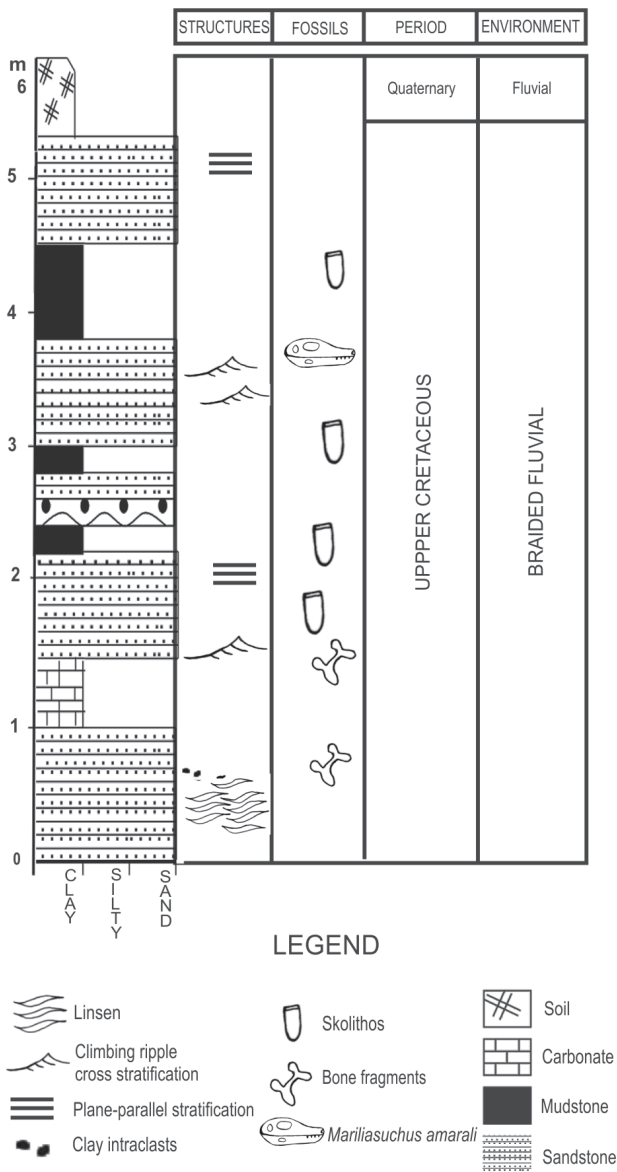


Figure 2. Stratigraphic profile of the outcrop on the left bank of the Peixe River in Fazenda Doreto farm, Marília Municipality, São Paulo State: Upper Cretaceous - Adamantina Formation, Bauru Basin. Location of the holotype of *Mariliasuchus amarali* collected by Carvalho and Bertini (1999)/ Perfil estratigráfico del afloramiento de la margen izquierda del Río Peixe, en la granja Fazenda Doreto, Municipio de Marília, Estado de São Paulo: Cretácico Superior - Formación Adamantina, Cuenca Bauru. Ubicación del holotipo de *Mariliasuchus amarali* colectado por Carvalho y Bertini (1999).

cervical vertebrae, an isolated intermediate dorsal vertebra, and another set of three dorsal vertebrae, which are posterior and connected to the sacral vertebrae.

The first three dorsal vertebrae preserve the vertebral centra, which are triangular in transverse section. The neural arch is lower and smaller than in the cervical vertebrae, showing a quadrangular profile in lateral view. Dorsally, the neural arch exhibits a pit placed in the same region as the cervical vertebrae, albeit less pronounced than in the cervical ones. The neural spines are laminar and rectangular in lateral view.

The fourth preserved dorsal vertebra (Fig. 4) presents a triangular vertebral centrum in transverse section, and two large depressions, placed latero-ventrally in the central portion of the vertebral centrum. The neural arch lacks the depression or dorsal pit occurring in the cervical vertebrae and anterior dorsals. The zygapophyses are not well preserved, but they extend more laterally than in the cervical vertebrae and anterior dorsals. The neural spine is low, latero-medially narrow, and antero-posteriorly long.

The three preserved posterior dorsal vertebrae are con-

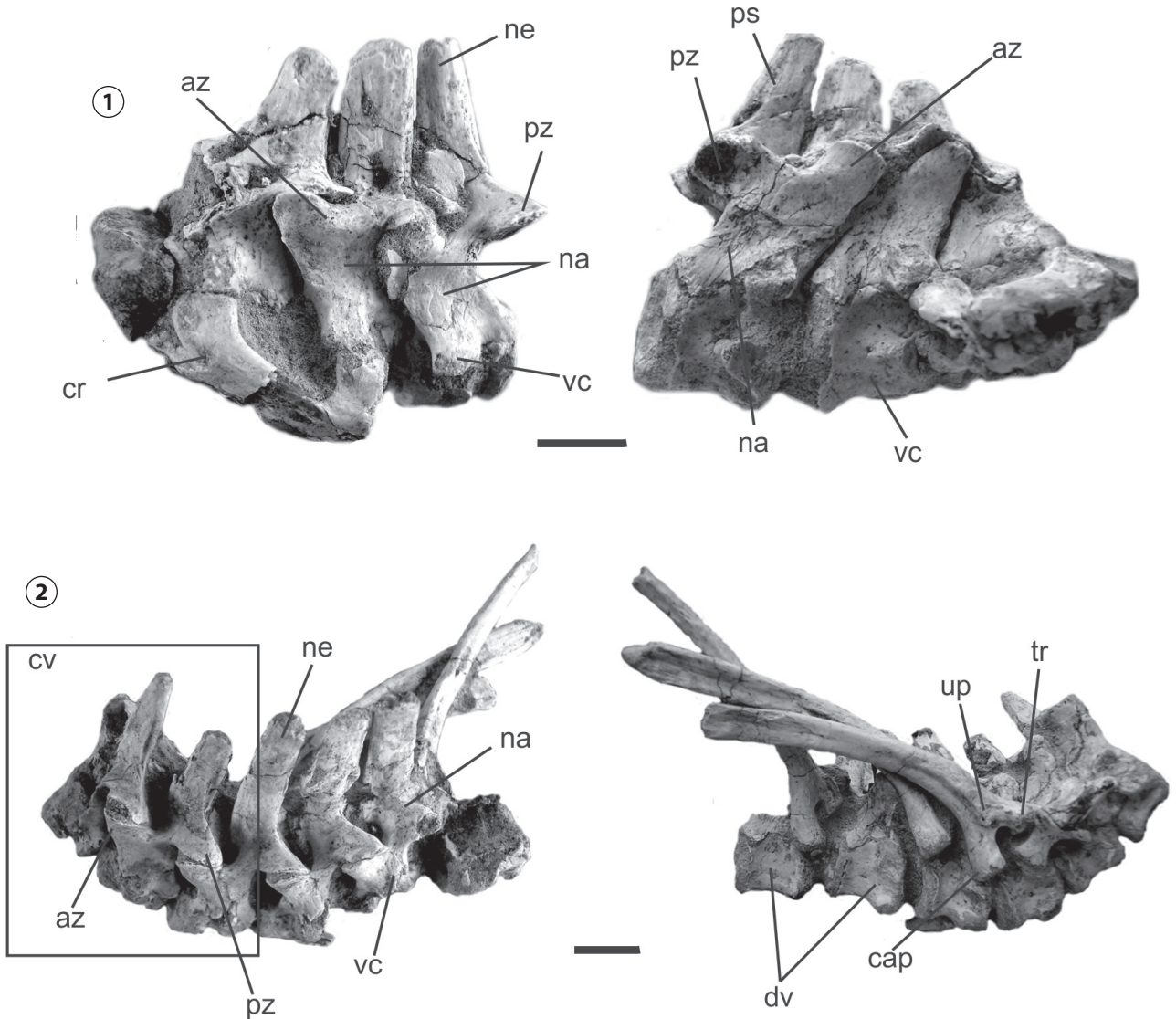


Figure 3. Cervical and dorsal vertebrae of *Mariliasuchus amarali* (UFRJ-DG 105-R). **1**, cervical vertebrae in left and right lateral views; **2**, posterior cervical and anterior dorsal vertebrae in left and right lateral views, including three dorsal ribs. Abbreviations: **az**, anterior zygapophysis; **cap**, capitulum of the rib; **cr**, cervical rib; **cv**, cervical vertebrae; **dv**, dorsal vertebrae; **na**, neural arch; **ne**, neural spine; **ps**, popliteal space; **pz**, postzygapophysis; **tr**, tubercule of the rib; **vc**, vertebral centrum; **up**, uncinat process/ *Vértebras cervicales y dorsales de Mariliasuchus amarali* (UFRJ-DG 105-R). **1**, vertebras cervicales en vista lateral izquierda y derecha; **2**, vértebra cervical posterior y dorsal anterior en vista lateral izquierda y derecha, incluyendo tres costillas dorsales. Abreviaturas: **az**, zigapósis anterior; **cap**, capítulo de la costilla; **cr**, Costilla cervical; **cv**, vértebras cervicales; **dv**, vértebras dorsales; **na**, arco neural; **ne**, espina neural; **ps**, espacio popliteal; **pz**, postzigapósis; **tr**, tubérculo de la costilla; **vc**, centro vertebral; **up**, proceso uncinado. Scale bar/ escala= 1 cm.

nected to each other and to the sacral vertebrae, morphologically different from the preceding elements. Their vertebral centra are rounded, circular to quadrangular in transverse section, with a flat dorsal border. The central portion of the vertebral centra is narrow and the articular surfaces are circular and more expanded than in preceding elements.

Dorso-laterally, the centra have a sinuous suture with the neural arch, which is low and rectangular in lateral view. Ventral to the transverse process and anterior to the zygapophyses is a small but deep pit that—in the last two dorsal vertebrae— seems to be perforated. The rectangular transverse processes are expanded laterally, and posteriorly form

a right angle with the longitudinal axis of the vertebral column.

Sacral vertebrae (Fig. 4). Three sacral vertebrae contact the ilium. The sacral centra are larger and more robust than those of the posterior dorsal and anterior caudal vertebrae. They are more robust than the neural spines of the dorsal and anterior caudal vertebrae, displaying an almost oval shape in transverse cross-section.

In the first sacral vertebra, the vertebral body is subquadrate in ventral view. It is smooth, concave, and its ventral portion is laterally expanded. In ventral view too, the concavity of the second posterior sacral vertebra is shallower;

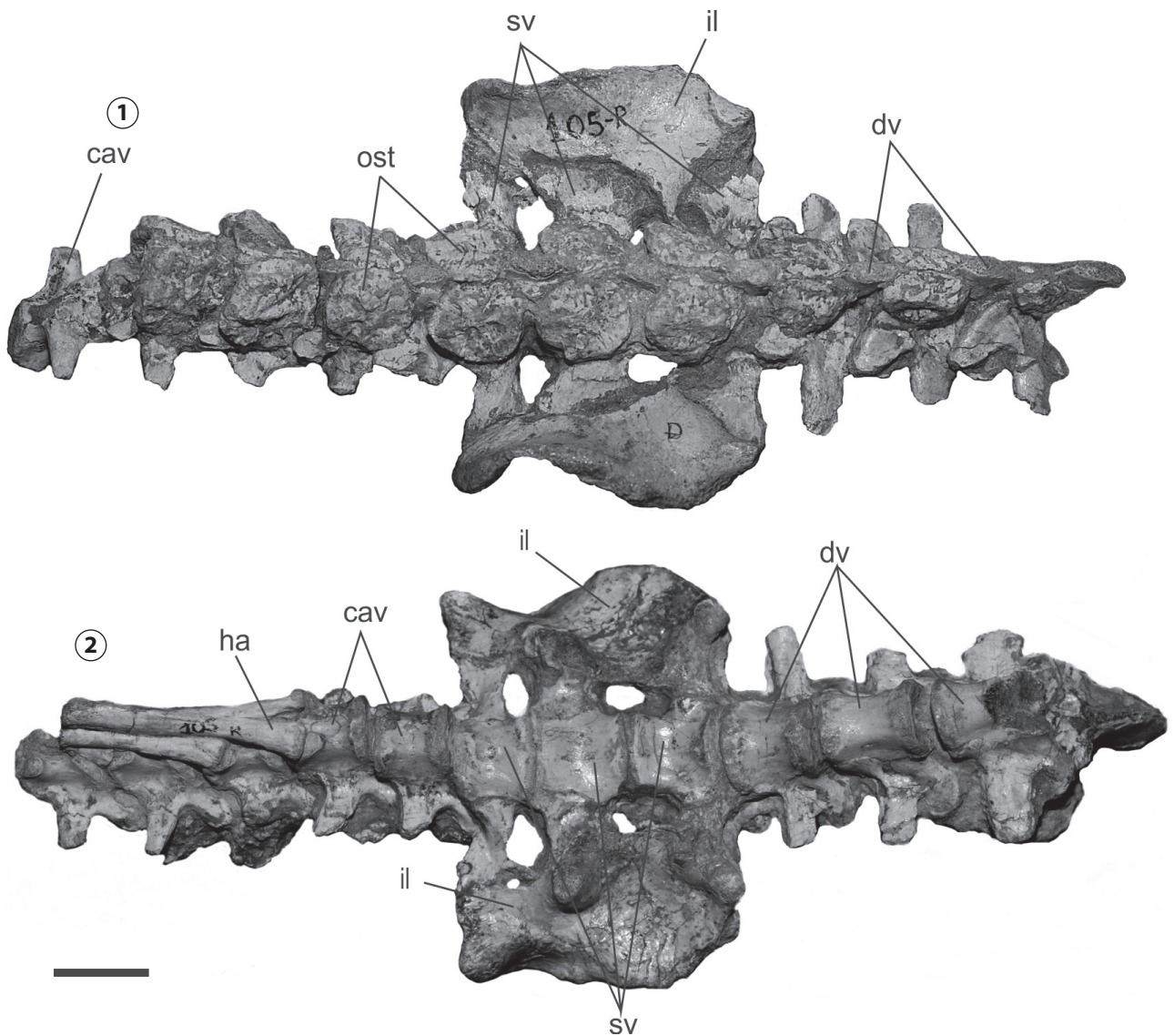


Figure 4. Vertebral column and ilium of *Mariliasuchus amarali* (UFRJ-DG 105-R) in **1**, dorsal and **2**, ventral views. Abbreviations: **dv**, dorsal vertebrae; **ha**, hemal arch; **il**, ilium; **ost**, osteoderm; **cav**, caudal vertebrae; **sv**, sacral vertebrae/ Vertebral column and ilium of *Mariliasuchus amarali* (UFRJ-DG 105-R) en vista **1**, dorsal y **2**, ventral. Abreviaturas: **dv**, vértebra dorsal; **ha**, arco hemal; **il**, ilium; **ost**, osteodermo; **cav**, vértebra caudal; **sv**, vértebra sacral. Scale bar/ escala= 1 cm.

the anterior portion lacks a lateral expansion; in postero-lateral view its contact with the transverse process is excavated.

The transverse processes of the three sacral vertebrae are short provided with a markedly antero-posterior expansion. In dorsal view, the transverse process of the first sacral vertebra is triangular. Posteriorly it has a slight lateral expansion, barely contacting the preacetabular region of the ilium. The transverse process of the second sacral vertebra has a reduced anterior expansion, but is highly expanded posteriorly at its lateral end, contacting the ilium at the level of the acetabulum. In the third vertebra, the transverse process is antero-posteriorly narrower than those of the other sacral vertebrae, it is more laterally expanded and contacts the post-acetabular process of the ilium. It displays a slight posterior expansion at its lateral extremity and, in this region, is dorso-ventrally slender.

Caudal vertebrae (Fig. 4). There are five anterior caudal vertebrae preserved. A progressive change in vertebral morphology can be noticed along the caudal series. The vertebral centrum of the second vertebra is quadrangular in transverse cross-section. Ventrally, the vertebral centrum is slightly concave and, laterally flat along all of its antero-posterior length. The transverse process is small, with a slight lateral expansion, and the neural spine is less robust than in the sacral vertebrae, although it has a more oval outline in transverse cross-section than those of the posterior dorsal vertebrae. The zygapophyses are not preserved.

The centrum of the third vertebra, also quadrangular in transverse cross-section, is ventrally well excavated on its central portion, and laterally flat as the previous vertebra. Posteriorly and ventrally at each side of the ventral depression there are two well-developed protuberances for the articulation of the hemal arches. More ventrally, at each side of the vertebral centra, there are two crests with an antero-posterior orientation.

From the fourth to the sixth caudal vertebra, the vertebral centra decrease in size and their ventral excavation becomes progressively deeper, forming a deep groove. The other vertebrae become medio-laterally narrower and bear a lateral depression. The transverse processes become smaller and narrower antero-posteriorly. The zygapophyses and neural arches are fragmented and covered under the osteoderms by the sedimentary matrix.

Ribs (Fig. 3.2). Three ribs have been preserved attached to the block with the posterior cervical and anterior dorsal vertebrae but they are not in natural articulation. Proximally, they are well preserved but distally they are fragmented. The tubercle and capitulum of the three ribs are preserved and well devel-

oped, measuring from 3 to 7 mm, respectively. They are separated by approximately 3 to 4 mm, measured at the proximal extremity of the tubercles. Antero-dorsally, the uncinat process is a slightly accentuated projection that is more developed proximally and decreases in development by the end of the first third of the rib. Distally, the ribs are blade-shaped, with a wide groove-like antero-posterior depression. Postero-ventrally, the anterior portion of the rib is excavated by a wide groove. **Hemal arches** (Fig. 4.2). There are two preserved Y-shaped hemal branches that are still connected to the fourth and fifth caudal vertebrae. The distal region is very long, and close to the connection point of the two branches, it changes from a quadrangular to a circular transverse cross-section. Further distally, the hemal arches taper and are laminar-shaped, becoming dorso-ventrally expanded.

Pectoral girdle

Scapula (Fig. 5.1). Only the right scapula is preserved. Its length is approximately the same as that of the humerus. The scapular blade is greatly expanded antero-posteriorly, measuring almost half of the scapular length, and with a well-developed antero-dorsal region.

Proximally to the scapular blade there is a constriction, followed by a new robust ventral expansion where the glenoid cavity is placed. There is a crest on the posterior and dorsal border of the glenoid cavity, probably the insertion of the triceps muscle. Immediately dorsal to this crest the posterior border of the scapula is robust, thinning towards the dorsal posterior region. Posteriorly and proximally, it shows a slightly developed medial torsion.

Coracoid (Fig. 5.2). Both coracoids are preserved. They are approximately 0.66 the length of the scapula, reaching a maximum length of 47 mm. The distal and proximal ends are expanded, and the central portion of the bone is narrower and more robust than the proximal and distal ends. The medial surface of the coracoid is concave and the lateral one is convex, with a curvature observed throughout the bone in posterior view.

Proximally, the articular surface for the head of the humerus is flat, and the coracoid foramen is well-developed, located immediately ventral to the articular surface. Ventrally to the proximal portion, the bone narrows and acquires a triangular transverse cross-section. Posteriorly, it expands becoming oval in transverse cross-section. It reaches its maximum expansion at its distal portion. The distal portion is laminar and triangular, with a distal bulge and an expanded anterior corner. The articular facet for the sternum is located along the anterior half of the distal end.

Forelimb

Humerus (Fig. 6.1). Only the right humerus of UFRJ-DG 105-R is preserved. It is robust with an expanded proximal end, cylindrical diaphysis, and a slightly expanded distal end (when compared to the proximal expansion). In lateral view, the humerus is sigmoidal, with the proximal extremity projected posteriorly and the distal one anteriorly. The maximum length is 75 mm, and the proximal end is 25 mm in latero-medial orientation. The diaphysis is 22 mm long and has a diameter of 9.5 mm at its central portion. In anterior and posterior views, the proximal end is triangular, with a straight articular surface. Posteriorly and distal to the head of the humerus there are two concavities. One is deep, oval, and located

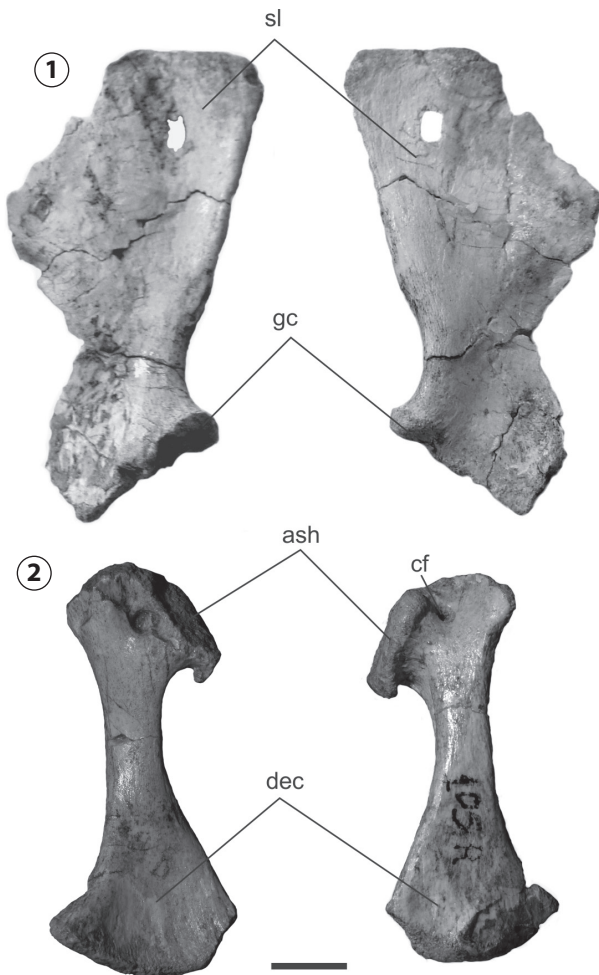


Figure 5. *Mariliasuchus amarali* (UFRJ-DG 105-R); **1**, right scapula in medial and lateral views; **2**, right coracoid in medial and lateral views. Abbreviations: **ash**, articular surface of the humerus; **cf**, coracoid foramen; **dec**, distal expansion of the coracoid; **gc**, glenoid cavity; **sl**, scapular lamina/ *Mariliasuchus amarali* (UFRJ-DG 105-R); **1**, escápula derecha en vista medial y lateral; **2**, coracoides derecho en vista medial y lateral. Abreviaturas: **ash**, superficie articular del húmero; **cf**, forámen coracoides; **dec**, expansión distal del coracoides; **gc**, cavidad glenoidea; **sl**, lámina escapular. Scale bar/ escala= 1cm.

right below the gleno-humeral condyle (the articular surface at the central portion of the proximal end). This depression is for insertion of the scapulohumeralis muscle. The second concavity—for the insertion of the triceps brachii muscle—is proximo-distally long and located laterally on the posterior surface of the humerus at the level of the deltopectoral crest.

The deltopectoral crest begins gradually at the proximal end of the humerus and develops progressively, reaching its maximum development at the first third of the humerus and then decreasing in development towards the diaphysis. In lateral view, the deltopectoral crest has a triangular shape with a well-developed base (proximal portion), extending from approximately 32 mm in length, and has a height of 7 mm. Lateral to the crest, the anterior surface of the humerus bears a shallow, proximo-distally elongated depression running as a groove along the entire length of the crest. The anterior surface is gently concave medially to the deltopectoral crest.

The distal end is quadrangular in cross-section and bears two well-developed condyles. Posteriorly, between the lateral and medial condyles, the humerus bears a concavity that extends towards the beginning of the diaphysis.

Radius (Fig. 6.2). The right radius is preserved. The bone is narrow and smaller than the ulna and is cylindrical throughout the whole length of the diaphysis. The proximal end is expanded latero-medially, triangular in posterior and anterior views. The proximal articular surface is concave on its central portion, in contrast to the lateral and medial corners that are projected above this concavity. The proximal half of the diaphysis is slightly arched antero-posteriorly and the distal portion of the diaphysis is straight. The distal end of the radius is less expanded than the proximal one. Posteriorly, it shows long concavity on the distal contact region with the ulna.

Ulna (Fig. 6.3). The ulna is more robust than the radius and has a diaphysis oval in cross-section. The proximal end is widely expanded antero-posteriorly, delimiting two concavities in this region, *i.e.*, a lateral one and medial one. The proximal articular surface is badly preserved, although it is possible to notice a concavity in the region that articulates with the medial condyle of the humerus and a convexity that articulates with the intercondylar surface of the humerus.

The diaphysis of the ulna is latero-medially compressed throughout its length, with an oval cross-section. The distal end has an antero-posteriorly long articular surface, which is concave and turned medially.

Pelvic girdle

Ilium (Fig. 7.1–7.3). The right and left ilia are preserved,

strongly attached to the sacral vertebrae through sediment that cannot be removed. The ilium is robust and antero-posteriorly expanded, rectangular in lateral view. Anteriorly in dorsal view, the iliac crest is thicker and more laterally projected than in the rest of the bone. Posteriorly, along the post-acetabular region, the crest is more slender and projects dorsally. The dorsal margin of the ilium has a sinuous outline along its entire antero-posterior length. In this region, or

along this lateral sinuous line, the surface of the bone bears small rugosities on the dorsal surface of the iliac crest.

The acetabulum is deep and occupies the anterior and ventral half of the ilium. Dorsally to the acetabular fossa there is a protuberance responsible for the sinuous shape of the bone visible in lateral view.

Ischium (Fig. 7.4). The right and left ischia are well preserved. Proximally, the two articular projections for the ilium and pubis form an open angle of *c.* 120°. The anterior right articulation for the ilium is broken. The posterior right articulation is rounded, well-developed, displaying a flat, slightly excavated articular surface with a ventrally placed pubis. Below these articular projections the bone is progressively laminar and wide, becoming a slender blade that appears antero-posteriorly expanded with a strong postero-ventral projection.

Pubis (Fig. 7.5). Both bones are preserved, but the right element is better preserved than the left one. Proximally, the articular surface for the ischium is flat and oval to semi-triangular. Distal to the proximal end, the bone becomes cylindrical and expands progressively in an antero-posterior direction towards its distal end. In the distal region, the pubis is laminar and has a rounded distal border. The lateral surface of the bone is convex and the medial surface is concave.

Hindlimb

Femur (Fig. 8.1). The right and left femora are preserved. The head of the femur expands medially and is laterally compressed, with an antero-posteriorly rounded articular surface that projects medially toward the acetabulum.

Distal to the head, the femoral neck is slightly constricted, expanding medially at the level of the fourth trochanter, which bulges medially as a prominent rugosity and renders this portion of the bone very robust. The fourth trochanter is located at the proximal third of the total length of the bone. The center of the fourth trochanter bears a crest that is more conspicuous than the rest of the trochanter surface; this crest runs towards the diaphysis. The rugosities and the crest of the fourth trochanter produce a gently quadrangular to oval transverse cross-section of the diaphysis. The femoral shaft becomes cylindrical only along its distal portion. Only a slight curvature can be observed along the distal portion of the diaphysis, posteriorly projecting towards the distal end of the femur.

The distal end is slightly deformed, preventing accurate measurement. This region is laterally expanded and has two well-developed tibial condyles. The internal (medial) condyle is smaller than the external (lateral) one. Anteriorly, between the two condyles, there is a deep, short groove for the passage of the

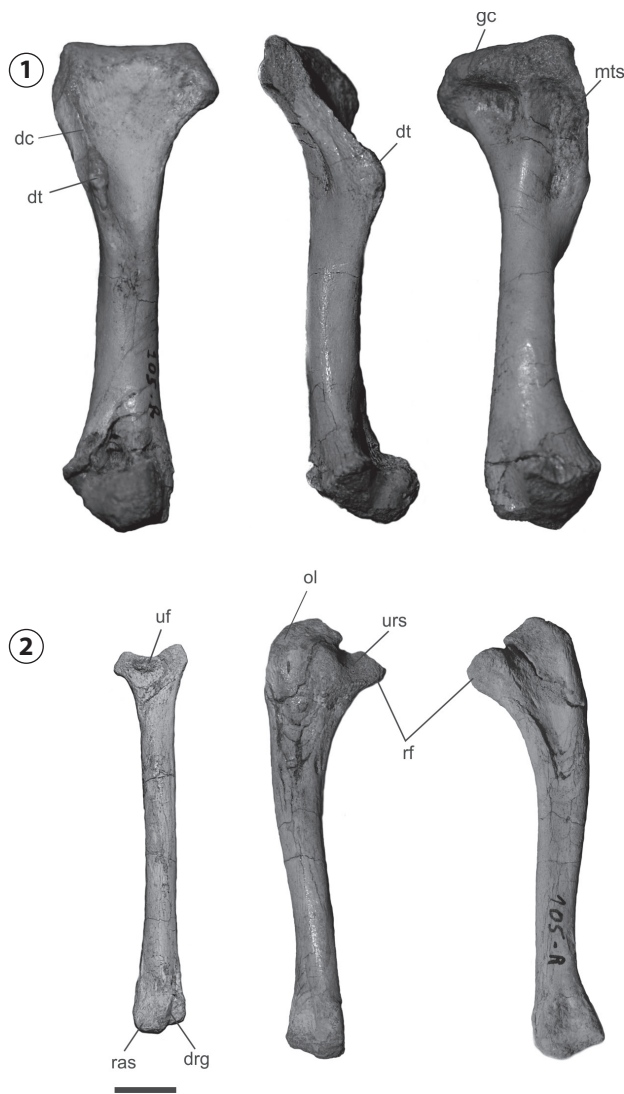


Figure 6. *Mariliasuchus amarali* (UFRJ-DG 105-R); 1, right humerus in anterior, lateral and posterior views; 2, right radius in lateral view; 3, right ulna in lateral and medial views. Abbreviations: **dc**, deltopectoral crest; **drg**, distal radial groove; **dt**, deltopectoral tuberculum; **gc**, glenohumeral condyle; **mts**, medial triceps sulcus; **ol**, olecranon; **ras**, radial articular surface; **rf**, radial facet; **uf**, ulnar facet; **urs**, ulnar radiohumeral surface/ **Mariliasuchus amarali** (UFRJ-DG 105-R); **1**, húmero derecho en vista anterior, lateral y posterior; **2**, radio derecho en vista lateral; **3**, ulna derecha en vista lateral and medial. Abreviaturas: **dc**, cresta deltopectoral; **drg**, surco distal radial; **dt**, tubérculo deltopectoral; **gc**, cóndilo glenohumeral; **mts**, surco medial triceps; **ol**, olécranon; **ras**, superficie radial articular; **rf**, faceta radial; **uf**, faceta ulnar; **urs**, superficie ulnar radiohumeral. Scale bar/ escala= 1cm.



Figure 7. *Mariliasuchus amarali* (UFRJ-DG 105-R); **1**, right ilium in dorsal view; **2**, right and left ilium and sacral vertebrae in ventral views; **3**, right ilium in latero-ventral view; **4**, right ischium in lateral and medial views; **5**, right pubis in latero-dorsal and medio-ventral views. Abbreviations: **af**, acetabular fossa; **asi**, articular surface for to the ilium; **il**, ilium; **ost**, osteoderm; **sv1**, first sacral vertebrae; **sv2**, second sacral vertebrae; **sv3**, third sacral vertebrae/ *Mariliasuchus amarali* (UFRJ-DG 105-R); **1**, *ilium derecho en vista dorsal*; **2**, *ilium derecho e izquierdo y vértebras sacrales en vista ventral*; **3**, *ilium derecho en vista lateroventral*; **4**, *ischium derecho en vista lateral y medial*; **5**, *pubis derecho en vista laterodorsal y medioventral*. Abreviaturas: **af**, *fosa acetabular*; **asi**, *superficie articular para el ilium*; **il**, *ilium*; **ost**, *osteodermo*; **sv1**, *primera vértebra sacral*; **sv2**, *segunda vértebra sacral*; **sv3**, *tercera vértebra sacral*. Scale bar/ escala= 1 cm.

femoral quadriceps muscle. Posteriorly, the intercondylar fossa is deep in comparison to its short longitudinal extension.

Tibia (Fig. 8.2). The right tibia is preserved, but its extremities are slightly deformed by diagenetic processes. The tibia is robust and its extremities are medio-laterally expanded. The diaphysis is cylindrical along almost of its length and is medially bowed, giving the bone a medially-arched shape. The proximal portion is antero-posteriorly flattened and slightly twisted or projected anteriorly. In proximal posterior view, the cnemial crest carries a protuberance. Laterally and medially, there are two depressions that form wide grooves running along each side of the cnemial crest.

The distal portion — in posterior view — shows a concave depression between the lateral and medial condyles. In anterior view it is convex, with the lateral and medial portion projected posteriorly. The articular surface for the astragalus cannot be observed.

Calcaneum (Fig. 8.3). The right and left calcaneum are partially preserved. The anterior medial portion is attached by sedimentary matrix to the astragalus, metatarsals, and tibia.

The calcaneum is laterally compressed and in the medial portion, forming a protuberance posterior to the articulation with the astragalus. Posteriorly, the calcaneum expands dorsally, forming the calcaneal tuber, with a process triangular in medial and lateral views. This process is slightly projected laterally, and posteriorly it shows a straight rectangular profile, with a dorsoventrally oriented central depression.

Ventrally, below the anterior condyle, the calcaneus is flat and in the posterior portion it has a deep fossa with a circular border. This fossa is the deepest depression in the calcaneum. The lateral surface of the calcaneum is flat, showing an anterior and ventrally projected gentle depression that reaches the limits of the ventral fossa.

Metatarsals (Fig. 8.4). The right metatarsals 1 and 2 are preserved attached by sedimentary matrix to the right tibia and right calcaneum. The four left metatarsals are partially preserved, but the first and fourth are incompletely preserved.

The metatarsals are thick and long. The first element is smaller, and the second metatarsal, which is the largest of

the series, is half the length of the tibia. In cross-section, the metatarsals have an oval diaphysis, with the distal end slightly expanded and the proximal ones markedly expanded. Ventrally, the proximal end of the first metatarsal has a small depression. The second metatarsal is markedly expanded proximally, while ventrally it is convex.

The distal ends carry shallow depressions on their dorsal and ventral surfaces. Laterally and medially, each metatarsal has two long and triangular fossae, one on each side. These fossae are deeper close to the articular facet, and shallow out towards the diaphysis. The articulation surface for the phalanx is slightly excavated in its central portion, forming small medial and lateral condyles.

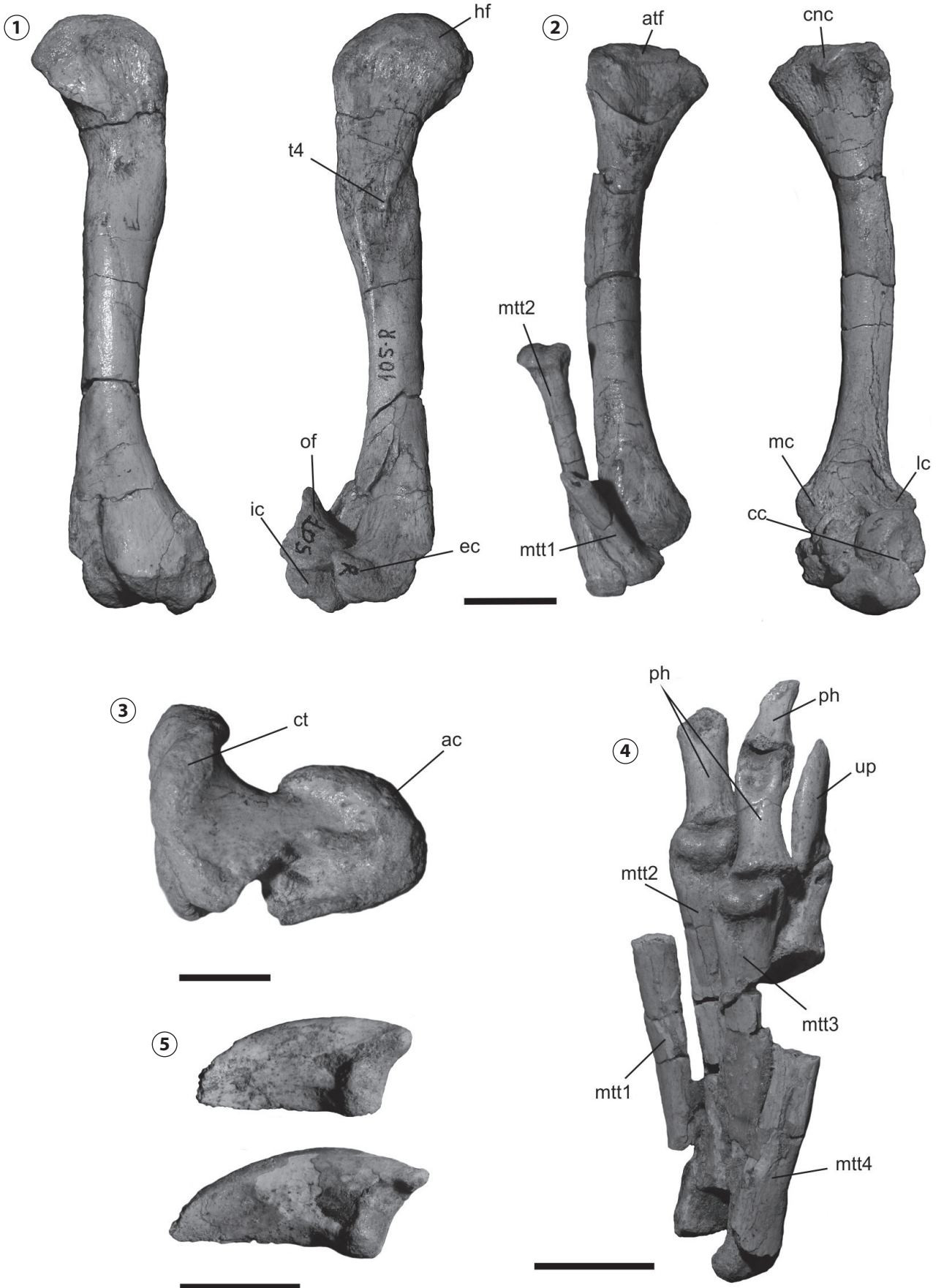
Non-terminal phalanges (Fig. 8.4). The proximal phalanx of right digit 1, proximal and distal left phalanges of digits 2 and 3, and a distal phalanx of digit 4 are preserved. The proximal phalanges of digits 2 and 3 are small, wide, and robust. Their central portion is circular in cross-section. Proximally, the articular surface for the metatarsal is flat to gently concave, expanded, and circular. The distal end lacks a medio-lateral expansion and is quadrangular in cross-section. The ventral surface is covered by sedimentary matrix.

The distal phalanges of digits 2 and 3 are fragmentary. The distal phalanx of the fourth digit is markedly expanded proximally and has a circular articular surface. Distally, it is quadrangular in transverse cross-section, showing small lateral, medial, dorsal, and ventral depressions.

Ungual phalanx (Fig. 8.4–5). Two right unguual phalanges are preserved not articulated with the rest of the skeleton, in addition to the left unguual phalanx of the fourth digit (attached to the sedimentary matrix). They are medio-laterally flattened, especially along their distal portion. Proximally they are robust, with their dorsal portion projected proximally in relation to their plantar portion. They have a strong dorsal curvature with an expanded dorsal surface. The ventral margin is less arched and narrower than the dorsal surface, giving this region an angular shape. One of the unguual phalanges has a medial curvature or torsion along the bone.

Osteoderms (Fig. 9). Two dorsal rows of osteoderms are

Figure 8. *Mariliasuchus amarali* (UFRJ-DG 105-R); **1**, left femur in anterior and postero-medial views; **2**, right tibia in anterior and postero-lateral views, including the metatarsals and calcaneum; **3**, right calcaneum in lateral view; **4**, left set of metatarsals, phalanges and postero-lateral unguual phalanges in dorsal views; **5**, unguual phalanx in lateral and medial views. Abbreviations: **ac**, anterior condyle of the calcaneum, **atf**, articular tibial facet; **cc**, calcaneum; **cnc**, cnemial crest; **ct**, calcaneal tuber; **ec**, external condyle; **hf**, head of the femur; **ic**, internal condyle; **lc**, lateral condyle; **mc**, medial condyle; **mtt**, metatarsals; **of**, osteoderm fragment; **ph**, phalange; **t4**, fourth trochanter; **up**, unguual phalanx/ **Mariliasuchus amarali** (UFRJ-DG 105-R); **1**, fémur izquierdo en vista anterior y postero-medial; **2**, tibia derecha en vista anterior y posterolateral, incluyendo los metatarsales y calcáneo; **3**, calcáneo derecho en vista lateral; **4**, metatarsus izquierdos, falanges y falanges ungueales posterolaterales en vista dorsal; **5**, falange ungueal en vista lateral y medial. Abreviaturas: **ac**, cóndilo anterior del calcáneo, **atf**, faceta articular tibial; **cc**, calcáneo; **cnc**, cresta cnemial; **ct**, tuber del calcáneo; **ec**, cóndilo externo; **hf**, cabeza del fémur; **ic**, cóndilo interno; **lc**, cóndilo lateral; **mc**, cóndilo medial; **mtt**, metatarsales; **of**, fragmento de osteodermo; **ph**, falange; **t4**, cuarto trocánter; **up**, falange ungueal. Scale bar/ escala = 1 cm.



placed laterally at each side of the vertebral neural spines (Fig. 4.1). These osteoderms are rounded to oval and with an ornamented external surface and a smooth, concave ventral surface. The external surface carries a well-developed central crest that is antero-posteriorly oriented and more pronounced along the posterior portion of the osteoderm. Lateral to this central crest, there are several smaller crests and irregular grooves that gradually decrease towards the border of the osteoderm. The osteoderms are in contact with the axial skeleton. No osteoderm imbrication was observed.

DISCUSSION

Anatomical comparisons

Osteoderms. The osteoderms display wide morphological variation within Crocodylomorpha. *M. amarali* has a dorsal row of osteoderms placed laterally at each side of the vertebral neural spines. The external surface of the osteoderms possesses a well-developed central crest oriented antero-posteriorly, flanked by several smaller crests and irregular grooves that fade gradually towards the border of the osteoderm. A similar morphology is present in *N. terrestris*; *Uruguaysuchus aznarezi* Rusconi, 1933 (Guichón Formation, Lower Cretaceous, Aptian, Uruguay); *Malawisuchus mwakasyungutiensis* Gomani, 1997 (Lower Cretaceous, Malawi, Africa) and in basal crocodylomorphs. Differences in the crest position—which can be located laterally or medially—can also be found in basal groups of crocodylomorphs.

In *Candidodon itapecuruense* Carvalho and Campos 1988 (Itapecuru Formation, Parnaíba Basin, Lower Cretaceous, Aptian–Albian, Maranhão, Brazil), and *Araripesuchus gomesii* Price, 1959 (Santana Formation, Membro Romualdo, Araripe Basin, Lower Cretaceous, Aptian–Albian, Piauí, Brazil), the osteoderms are quadrangular with a laterally placed crest (Nobre, 2004). The external ornamentation of the osteoderms is formed by small pits (ornamentation also present in *Uruguaysuchus aznarezi*). In Crocodylia, the ornamentation is mainly of deep well-delimited depressions, which may or may not display a central crest.

Vertebrae. The cervical vertebrae of *M. amarali* and *N. terrestris* are similar. Both species have high, posteriorly curved neural spines with a pronounced depression at their bases. According to Pol (1999, 2005), this depression and the orientation of the zygapophyses, together with the widened and posteriorly curved shape of the neural spine, indicates that *N. terrestris* had the ability to perform dorso-ventral movements.

In *M. amarali* the neural spines are positioned on the posterior half of the neural arches, whereas in *N. terrestris*

they are antero-posteriorly centered on the neural arches. The condition of *M. amarali* is a plesiomorphic trait in relation to that of *N. terrestris* and *Chimaerasuchus paradoxus* Wu, Sues and Sun, 1995 (Wulong Formation, Lower Cretaceous, Aptian–Albian, Hubei, China).

Pectoral girdle. In *M. amarali*, the scapula has a well-developed scapular blade, similar to that in *N. terrestris*, *C. paradoxus*, *S. clarki*, and *A. tsangatsangana*. In contrast, the scapular blade is only slightly developed in *C. itapecuruense*. In *M. amarali* the scapular ridges—that are strongly developed in *A. tsangatsangana*—were not observed. The posterior portion of the scapula is nearly straight in *C. itapecuruense* and *C. paradoxus*, but differs from that of *M. amarali*, which has a strong curvature in the ventral and posterior portion. Fiorelli and Calvo (2008) described a sharp conspicuous constriction between the dorsal and ventral portions of the scapula of *N. terrestris*, a feature also found in *M. amarali*.

The distal portion of the coracoid of *M. amarali* is more expanded than the proximal one, a condition similar to that in *C. paradoxus*, *S. clarki*, and extant crocodyliforms. In *N. terrestris* the ventral portion of the coracoid was described by Pol (2005) and Fiorelli and Calvo (2008) as being poorly expanded and thus different from the coracoid of *M. amarali*. The coracoid is robust in *M. amarali*, presenting a thick diaphysis, differing from *A. tsangatsangana*, a species in which this area is elongated and with a proportionally narrower diaphysis.

Forelimb. In *M. amarali*, *N. terrestris*, *C. paradoxus*, *S. clarki* and *U. aznarezi*, the humerus is notably robust, differing from those of more basal crocodylomorphs such as *Dibothrosuchus elaphros* Simmons, 1965 and protosuchids, in which the humerus is long and slender. An elongated humerus is also found in *C. itapecuruense*, *M. mwakasyungutiensis*, *A. tsangatsangana* and *Anatosuchus minor* Sereno, Sidor, Larsson and Gado, 2003 (the latter of which comes from the Lower Cretaceous Elrhaz Formation, Niger, Africa; Sereno and Larsson, 2009). In eusuchian crocodyliforms the humerus is less robust than in *M. amarali*, *N. terrestris*, *C. paradoxus* and *U. aznarezi*, although it is more robust than in protosuchids.

In *M. amarali* and *N. terrestris*, the humerus also has a strongly sigmoidal profile in lateral view, differing from those of basal crocodylomorphs such as *D. elaphros*. In *C. itapecuruense* and *M. mwakasyungutiensis* the humerus is also less sigmoidal than in *M. amarali* and *N. terrestris*.

In *M. amarali*, *N. terrestris* and *U. aznarezi* the short, latero-medially compressed delto-pectoral crest is slightly developed and does not display a marked medial deflection. There is a long, wide groove-shaped depression on the lateral

border of the deltopectoral crest depression, a trait shared with *N. terrestris*, *M. amarali*, *C. paradoxus* and *U. aznarezi*. In basal crocodylomorphs, such as *D. elaphros* and protosuchids, the delto-pectoral crest is more developed, as is the case of *C. itapecuruense*. In *C. paradoxus* and *C. itapecuruense* the delto-pectoral crest is medially deflected.

In *M. amarali* there is a deep circular depression placed on posterior and proximal surface of the humerus below the articular surface. Pol (2005) described this trait in *N. terrestris* and commented that it would be shared only with *C. paradoxus* and probably with *U. aznarezi*. It appears to occur in *M. amarali* too.

The ulna in *M. amarali* is very similar —because of the antero-posterior expansion of the proximal portion— to that of *N. terrestris*, *S. clarki* and *U. aznarezi*. This expansion is also found, albeit not as well-developed, in *C. paradoxus*. The proximal portion of the ulna in *N. terrestris* is strongly compressed laterally, as in *M. amarali*. Such a compression may probably be found in *U. aznarezi*, as suggested by Rusconi's illustrations (Rusconi, 1933). In *C. itapecuruense*, *M. mwakasyungutiensis*, *A. tsangatsangana* and basal crocodylomorphs such as *D. elaphros*, the antero-posterior expansion is less marked, and the proximal end is less compressed laterally.

Another remarkable trait shared among these crocodyli-

forms is the curvature or anterior projection of the proximal portion of the ulna. In *M. amarali*, *N. terrestris*, *U. aznarezi*, and *C. paradoxus*, the proximal portion of the ulna is strongly curved anteriorly, displaying a strong convexity in this region. In basal species of Crocodylomorpha (*D. elaphros*) and in other Cretaceous mesoeucrocodylians (e.g., *C. itapecuruense*, *M. mwakasyungutiensis*), the ulna is anteriorly less curved along its proximal portion.

The diaphysis of the ulna of *Mariliasuchus amarali* is strongly compressed medio-laterally, becoming flat on its medial surface. It is semi-oval in cross-section. The same morphology can be found in *N. terrestris* described by Pol (2005), who remarked that this was a common condition among Crocodyliformes, unlike the basal crocodylomorphs that have a cylindrical diaphysis. In *C. itapecuruense* the diaphysis of the ulna lacks this medio-lateral compression, and is cylindrical in cross-section.

Pelvic girdle. The ilium of *M. amarali* is similar to that in *N. terrestris*, but differs in a few aspects. In both species, the anterior process of the ilium is greatly reduced when compared to basal crocodylomorphs such as “sphenosuchians” and protosuchids. In extant crocodyliforms such as *Alligator*, the anterior process of the ilium is also reduced. In the region of the acetabulum, the ilium is wide. A remarkable antero-posterior development of the post-acetabular

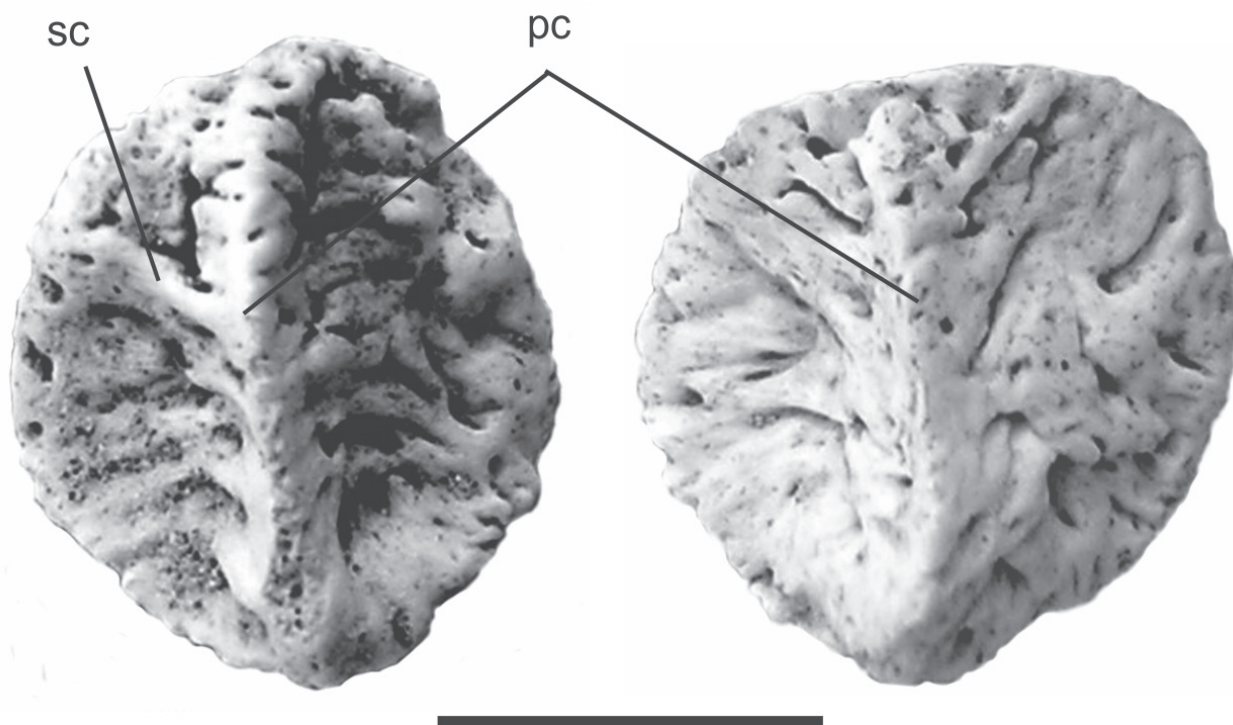


Figure 9. Osteoderms of *Mariliasuchus amarali* (UFRJ-DG 111-R) in dorsal view; Abbreviations: **sc**, secondary crests; **pc**, principal crests/ Osteoderms de *Mariliasuchus amarali* (UFRJ-DG 111-R) en vista dorsal; Abreviaturas: **sc**, crestas secundarias; **pc**, cresta principal. Scale bar/ escala= 1 cm.

process can also be observed in both *M. amarali* and *N. terrestris*; it reaches approximately the same length as the acetabular portion.

Laterally, posterior to the acetabular fossa, the ilium of *M. amarali* is dorsally projected, forming a crest and a concavity in latero-ventral view. This concavity is also found in extant crocodyliforms.

The distal portion of the ischium of *M. amarali* is expanded posteriorly, with no anterior expansion. In basal crocodylomorphs and protosuchids the ischium shows an expansion in the distal anterior portion as well. In extant crocodyliforms (Alligatoridae and Crocodylidae) the distal anterior portion is absent or only slightly developed. Based on these traits, the ischium of *M. amarali* is more similar to those of derived forms of Crocodyliformes.

In extant eusuchians, the acetabular fossa faces laterally, is shallow, and offers little restriction to movement when compared with more basal crocodylomorphs (Parrish, 1987). In *M. amarali* the acetabular fossa, in addition to being shallow, is antero-posteriorly broad, possibly allowing ample movement of the femur.

Hindlimb. In *M. amarali* the femur is robust, as also described for *N. terrestris* by Fiorelli and Calvo (2008) and in *S. clarki*. The head of the femur is greatly compressed in *M. amarali*, a trait also described by Rusconi (1933) for *U. aznarezi*. This lateral compression is found in *A. navae* and *C. itapecuruense*, but is better marked than in *M. amarali*. In *C. itapecuruense*, *A. navae*, *A. tsangatsangana* and *M. mvakasyungutiensis* the femur is less robust than in *M. amarali*.

The femur of *M. amarali* is anteriorly curved along its proximal portion and posteriorly along its distal portion. These curvatures along the diaphysis of the femur of *M. amarali* are similar to those of the femur of eusuchians. In *C. itapecuruense*, *A. navae* and *M. mvakasyungutiensis* the diaphysis of the femur is straighter than in *M. amarali* and eusuchians.

The femoral diaphysis of *M. amarali* is compressed medio-laterally at the level of the fourth trochanter, becoming more cylindrical only along the most distal portion of the diaphysis. In *A. navae* the fourth trochanter is less developed than in *M. amarali*, and this region of the diaphysis is not as compressed as in *M. amarali*, displaying an oval cross-section. At the preserved part of this trochanter in the fragmentary femur of *C. itapecuruense*, this region is more cylindrical than in the species mentioned above.

The metatarsals and phalanges in *M. amarali*, like the rest of the skeleton, have a more robust general aspect simi-

lar to those of extant crocodyliforms. In *C. itapecuruense* the metatarsals are long and slender, and the diaphysis is cylindrical, differing from those of *M. amarali*, which are oval in transverse cross-section.

In *M. amarali* the two preserved unguis phalanges are robust, greatly expanded dorso-ventrally, and with a strongly marked ventral curvature. There is a very fragmentary unguis phalanx in *A. navae* displaying similar traits to those of *M. amarali*. In extant crocodyliforms, the unguis phalanges are narrower and not so curved. In basal crocodylomorphs, such as *Hallopus victor* Marsh, 1881, the unguis phalanges are also slender and less curved dorso-ventrally than in *M. amarali*.

The hindlimbs of all crocodyliforms are evidently longer than the forelimbs (Wellnhofer, 1971). According to Fernández (2009), crocodyliforms with terrestrial habits display greater development of the tibia and fibula than extant forms with amphibious habits. Comparing the hind- and forelimbs of *M. amarali* with those of basal crocodylomorphs with terrestrial habits, we find that *M. amarali* limbs are remarkably robust.

CONCLUSIONS

The morphology of the postcranial skeleton of *M. amarali* differs from other Cretaceous notosuchians such as *C. itapecuruense*, *A. tsangatsangana* and *A. gomesii*, but shares similarities with *N. terrestris* and *S. clarki*. However, *M. amarali* also displays features that resemble the condition of recent forms of Eusuchia.

The morphology of the cervical vertebrae in *M. amarali* indicates the possibility of ample dorsal movements, a characteristic also inferred for *N. terrestris*.

The morphology of the ilium and the acetabular fossa, associated to the robustness and similarity of the appendicular skeleton of *M. amarali* to those of extant eusuchians leads us to infer that *M. amarali* did not have an erect or semi-erect posture, as proposed for other notosuchian mesoeucrocodylians, but, rather a sprawling-type posture, possibly with amphibious habits as extant eusuchians have.

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