

# Postcranial skeletons of *Caipirasuchus* (Crocodyliformes, Notosuchia, Sphagesauridae) from the Upper Cretaceous (Turonian–Santonian) of the Bauru Basin, Brazil



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## ABSTRACT

*Caipirasuchus* is a sphagesaurid crocodyliform genus known from Upper Cretaceous rocks (Turonian–Santonian) of the Bauru Basin, Brazil. Although their earlier descriptions were restricted to skull and mandible morphology, three species have been identified. In the present study, the skeletons of three specimens were analyzed from the collection of Prof. Antonio Celso de Arruda Campos Paleontology Museum: *Caipirasuchus montealtensis* (MPMA 68-0003/12), *Caipirasuchus paulistanus* (MPMA 67-0001/00) and *Caipirasuchus* sp. (MPMA 07-0011/00). These specimens are three individuals of a very similar size and have the same postcranial morphology. Analysis of the *Caipirasuchus* skeletons indicate the species were approximately 1.10 m in length and had slender-long bodies and hind limbs twice as long as the forelimbs. Regarding the general postcranial morphology of *Caipirasuchus* results indicate that these were agile animals and used speed as a defense mechanism against predators.

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## 1. Introduction

The lithostratigraphic units in Bauru Basin, Brazil (Fig. 1), contain abundant fossils of distinct Late Cretaceous tetrapods, particularly testudines, crocodylomorphs and dinosaurs. The crocodylomorphs are the most widely studied and diverse group, with dozens of individuals including advanced notosuchians, baurusuchids, peirosaurids and trematochampsids (Price, 1945, 1950, 1955, 1959; Carvalho and Bertini, 1999; Campos et al., 2001, 2011; Carvalho et al., 2004, 2005, 2007; Nobre and Carvalho, 2006; Andrade and Bertini, 2008; Marinho and Carvalho, 2009; Iori and Carvalho, 2009, 2011; Nascimento and Zaher, 2010; Kellner et al., 2011, 2011a; Montefeltro et al., 2011; Iori and Garcia, 2012; Marinho et al., 2013; Godoy, et al., 2014; Pol et al., 2014).

Sphagesaurids are a clade of Late Cretaceous Crocodyliformes known from Adamantina (Bauru Basin, Brazil) and Cajones (Bolivia)

formations. The sphagesaurids are primarily characterized by adapted teeth for herbivory/omnivory and a complex masticatory mechanism (Pol, 2003; Marinho and Carvalho, 2009; Iori and Carvalho, 2011; Iori et al., 2011). Six genera have been formally described: *Sphagesaurus*, *Adamantinasuchus*, *Armadillosuchus*, *Yacarerani*, *Caipirasuchus* and *Caryonosuchus* (Pol, 2003; Nobre and Carvalho, 2006; Andrade and Bertini, 2008; Marinho and Carvalho, 2009; Novas et al., 2009; Iori and Carvalho, 2011; Kellner et al., 2011; Iori et al., 2013).

Descriptive studies of sphagesaurids have focused on cranial material. The information regarding the postcranial structures of sphagesaurids is based on description of the dorsal armor of *Armadillosuchus arrudai* and the *Yacarerani boliviensis* skeleton (Marinho and Carvalho, 2009; Leardi et al., 2015).

A narrower skull and rostrum, and antorbital fenestra are some of the distinctive characteristics of *Caipirasuchus* (Andrade and Bertini, 2008; Iori and Carvalho, 2011; Iori et al., 2013; Pol et al., 2014). To date, three species have been identified: *Caipirasuchus paulistanus* (Iori and Carvalho, 2011); *Caipirasuchus montealtensis* (Andrade and Bertini, 2008; Iori et al., 2013) and *Caipirasuchus stenognathus* (Pol et al., 2014).

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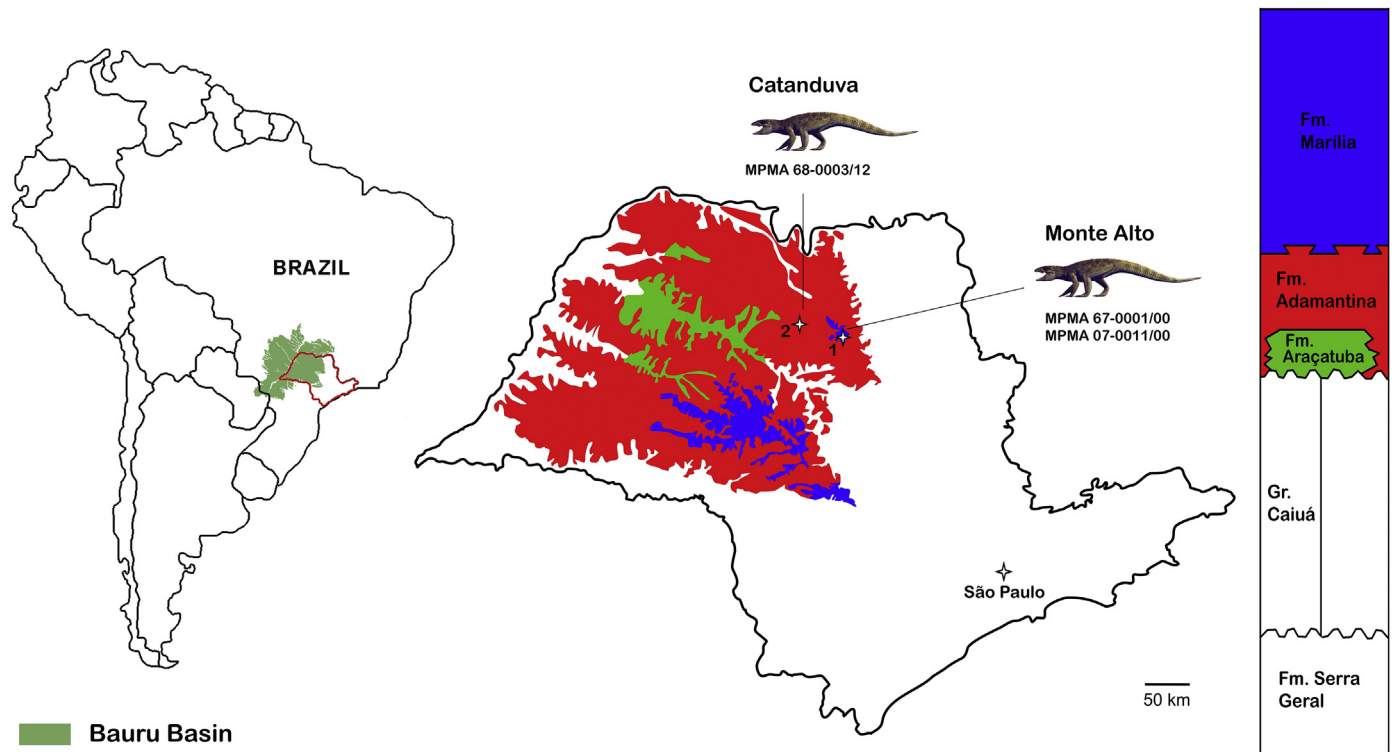


Fig. 1. The Bauru Group in São Paulo State, with the locations of the analyzed specimens: Municipalities of Monte Alto (1) and Catanduva (2). Stratigraphic column of the Bauru Group (modified from Batezelli et al., 2003).

The present paper presents descriptions and analyses of the postcranial remains of three specimens of *Caipirasuchus* (*C. montealtensis*, *C. paulistanus* and *Caipirasuchus* sp.), representing the first detailed description of an axial and appendicular skeleton of a sphagesaurid from the Bauru Basin.

### 1.1. Abbreviations of institutions:

**MPMA** – Museu de Paleontologia “Prof. Antonio Celso de Arruda Campos”, Monte Alto, São Paulo State, Brazil.

**UFRJ DG** – Departamento de Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro State, Brazil.

## 2. Materials and methods

The three specimens of *Caipirasuchus* analyzed in this study are in the collection of the Paleontology Museum Prof. Antonio Celso de Arruda Campos. They came from Monte Alto municipalities (MPMA 67-0001/00 and MPMA 07-0011/00) and Catanduva (MPMA 68-0003/12), located in the State of São Paulo, Brazil (Fig. 1).

These three specimens of *Caipirasuchus* are very similar in size. The postcranial structures of the specimens are nearly identical in morphology and only differ in bones size. The postcranial skeleton of *Caipirasuchus* was compared to *Armadillosuchus*, *Araripesuchus tsangatsangana*, *Yacarerani*, *Notosuchus*, *Mariliasuchus*, *Simosuchus* and *Baurusuchus albertoi* materials.

## 3. Systematic paleontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Notosuchia Gasparini, 1971

Sphagesauridae Kuhn, 1968 sensu Marinho and Carvalho, 2007

Genus *Caipirasuchus* Iori and Carvalho, 2011

### 3.1. *Caipirasuchus montealtensis* (Andrade and Bertini, 2008)

**Holotype.** MPMA 15-0001/90: Almost complete skull and anterior portion of the mandible.

**Locality and horizon.** Municipality of Monte Alto, São Paulo State, Brazil, in the Adamantina Formation, Bauru Group (Turonian–Santonian of the Bauru Basin).

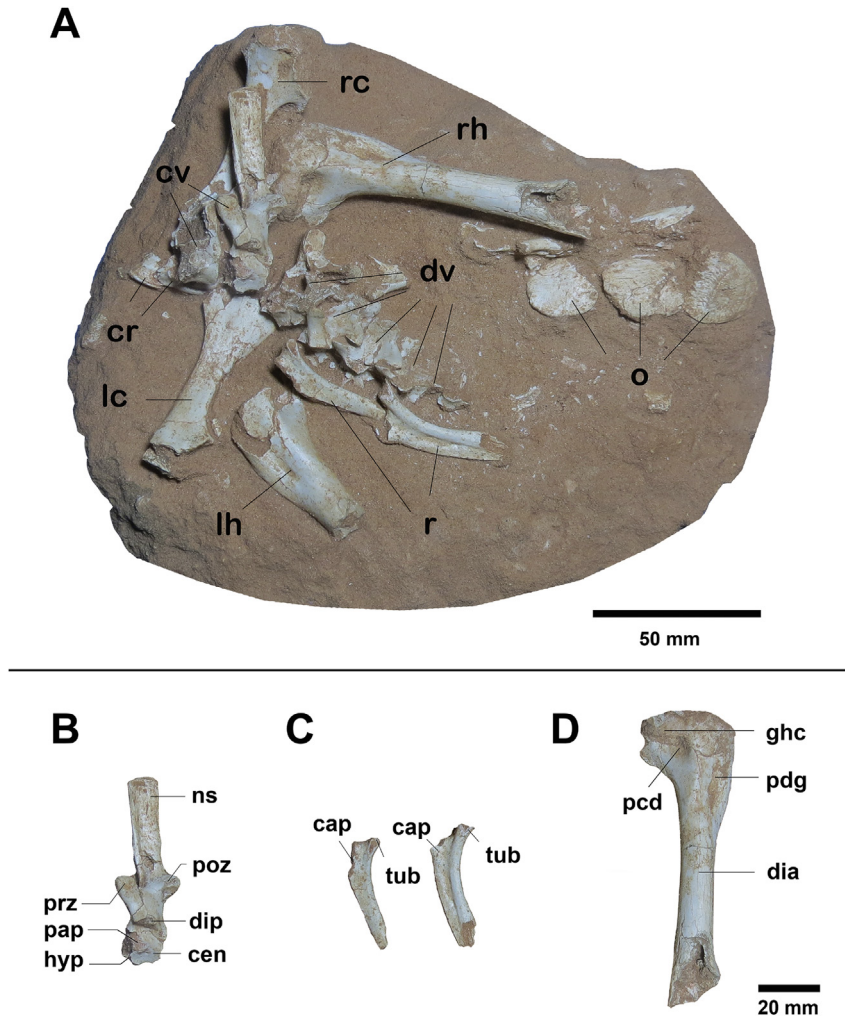
**Referred specimen.** MPMA 68-0003/12: Skull, mandible and part of the postcranial skeleton.

**Locality and horizon.** Municipality of Catanduva, São Paulo State, Brazil, in the Adamantina Formation, Bauru Group (Turonian–Santonian of the Bauru Basin).

#### 3.1.1. Description and comparison

The skeleton of *Caipirasuchus montealtensis* was partially disarticulated as a result of biostratinomic processes, although the displaced bones remained associated. The preserved postcranial elements consist of several osteoderms, both coracoids, the right humerus, the proximal third of the left humerus, two cervical vertebrae and at least four fragmentary dorsal vertebrae and three ribs (Fig. 2). Also, there were preserved a distal articulated series of caudal vertebrae with various osteoderms and hemal arches. Hind limbs are represented by bones such as tarsals, metatarsals and phalanges (Figs. 3 and 4). Some bones were displaced from the set during specimen preparation and were isolated (Figs. 5 and 6).

**Cervical vertebrae.** The last two cervical vertebrae are present, the last one (C8) being better preserved (Figs. 2A and 2B). They are



**Fig. 2.** Anterior postcranial bones of *Caipirasuchus montealtensis* (MPMA 68-0003/12) (A), left lateral view of a cervical vertebra (B), posterior view of the right humerus (C) and left ribs (D) Abbreviations: cap, capitulum; cen, centrum; cr, cervical rib; cv, cervical vertebra; dia, diaphysis; dip, diapophysis; dv, dorsal vertebra; ghc, glenohumeral condyle; hyp, hypapophysis; lc, left coracoid; lh, left humerus; ns, neural spine; o, osteoderm; pap, parapophysis; pcd, posterior circular depression; pdg, posterior deltoid groove; poz, postzygapophysis; prz, prezygapophysis; r, rib; rc, right coracoid; rh, right humerus; tub, tubercle.

relatively short and narrow, their height is 4.5 times their length, and they are 50 mm high. The neural spine has the same height as the rest of the vertebra. The pre- and postzygapophyses are very dorsally displaced, the lateral surface of the prezygapophysis is nearly vertical, and the articular surface is inclined mid-dorsally. The neural canal is wide and has almost the same height as the centrum. The neurocentral suture is very evident. The parapophysis, hypapophysis and lateral portion of diapophysis are eroded.

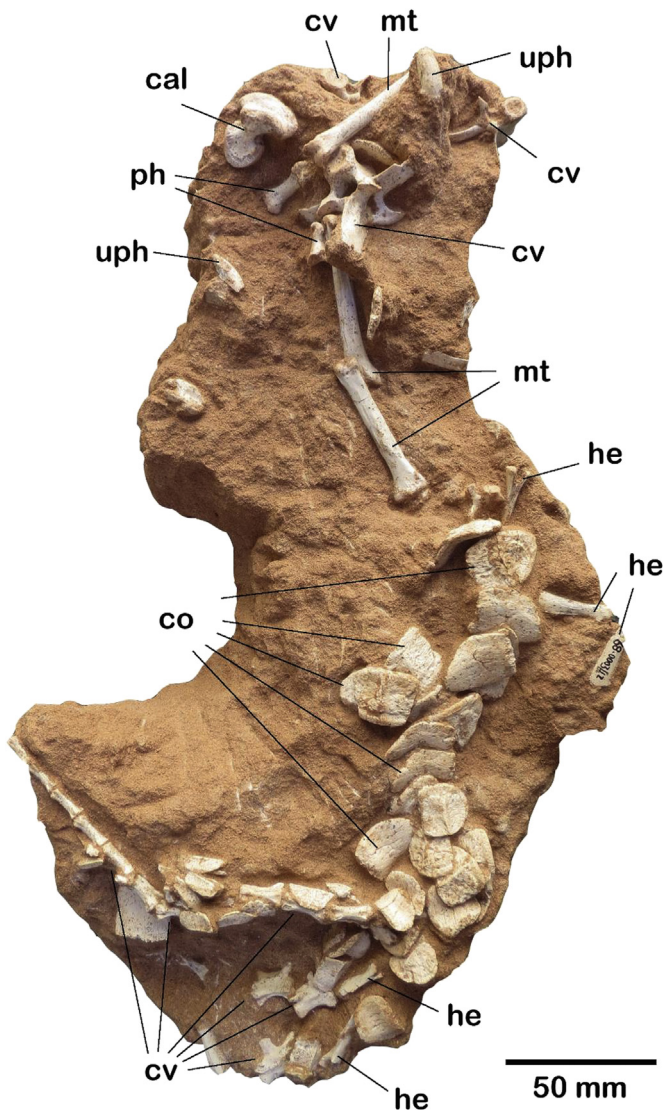
**Dorsal vertebrae.** The remains of five very fragmentary dorsal vertebrae are preserved (Fig. 2). The neural canals are wide. The articular surface of the pre- and postzygapophyses lies nearly along the same horizontal line and alongside the neural canal. The prezygodiapophyseal laminae is present and the neurocentral sutures are opened.

**Caudal vertebrae.** A number of more anterior vertebrae are dispersed in matrix, in addition to a sequence of twelve vertebrae from the tail end (Figs. 3, 4B and 4C). The largest and most anterior preserved vertebra (Fig. 4B) has an anteroposteriorly large neural spine with approximately twice the height of the centrum. The prezygapophysis is near the neural canal, and its articular surface faces the posterior dorsal region. Each transverse process has approximately 1/3 of the vertebral width. The neural canal is wide

and at the dorsal edge is almost as wide as the centrum. The other isolated vertebrae are from the middle caudal's and are similar to the more anterior ones but much smaller. Reduction of the lateral process and neural spine as well as a progressive flattening of the vertebrae are evident. The amphicelic character of few of this vertebra may be observed. The next vertebrae are partially enclosed in the sandstone, and their ventral surfaces and sides parts are exposed. They are also amphicelic, laterally compressed and anteroposteriorly enlarged. The ventral side is slightly curved anteroposteriorly and has two projections marking the transition to the lateral plane. These features become indiscernible in the more posterior vertebrae.

**Cervical ribs.** The cervical ribs are relatively small structures. The proximal portion is robust, approximately half as tall as the vertebral body, and is slightly longer than the vertebra, thus reaching the other cervical ribs (Fig. 2A). The same was observed in *Araripesuchus tsangatsangana*, where the ribs are double-headed and the anterior process of each rib is overlapped by the posterior one of the preceding rib (Turner, 2006). The anterodorsal processes were not preserved.

**Ribs.** The proximal halves of two left ribs can be observed (Figs. 2A and 2C). Both are robust, and the second rib is more



**Fig. 3.** Posterior postcranial bones of *Caipirasuchus montealtensis* (MPMA 68-0003/12). Abbreviations: cal, calcaneus; co, caudal osteoderms; cv, caudal vertebra; he, hemapophysis; mt, metatarsus; ph, phalanx; uph, ungual phalanx.

expanded posteriorly. *Caipirasuchus* do not present pachyostotic ribs like *Armadillosuchus* (Iori, 2013).

**Hemapophyses.** Several hemapophyses are preserved, and almost all of these are disarticulated from the vertebrae (Figs. 3 and 4D). Except for the most posterior ones, which are the same height and width, thus all hemapophyses are similar in appearance and vary only in size. They are flattened laterally and expanded anteroposteriorly, mainly at their most distal portion.

**Coracoids.** Both coracoids are preserved (Fig. 2A) and very similar to *Mariliasuchus*. The distal end is laminar and anteroposteriorly narrower than the proximal end, like *Yacarerani* (Leardi et al., 2015). The lateral surface is slightly convexed, resembling what can be observed in *Notosuchus* (Pol, 2005). They are 65 mm long, and the spatulate distal portion is 20 mm wide and less than 2 mm thick. The main shaft is laminar, unlike *Araripesuchus tsangatsangana*, that presents a long and cylindrical main shaft (Turner, 2006). The glenoid is facing lateroventrally and the bone is dorsally marked by the scapulocoracoid synchondrosis. In lateral view, the coracoid foramen is in the lower region, anteriorly to the glenoid lateral projection; the foramen is constrict, different

from the broad circular foramen observed in *Simosuchus* (Sertich and Groenke, 2010).

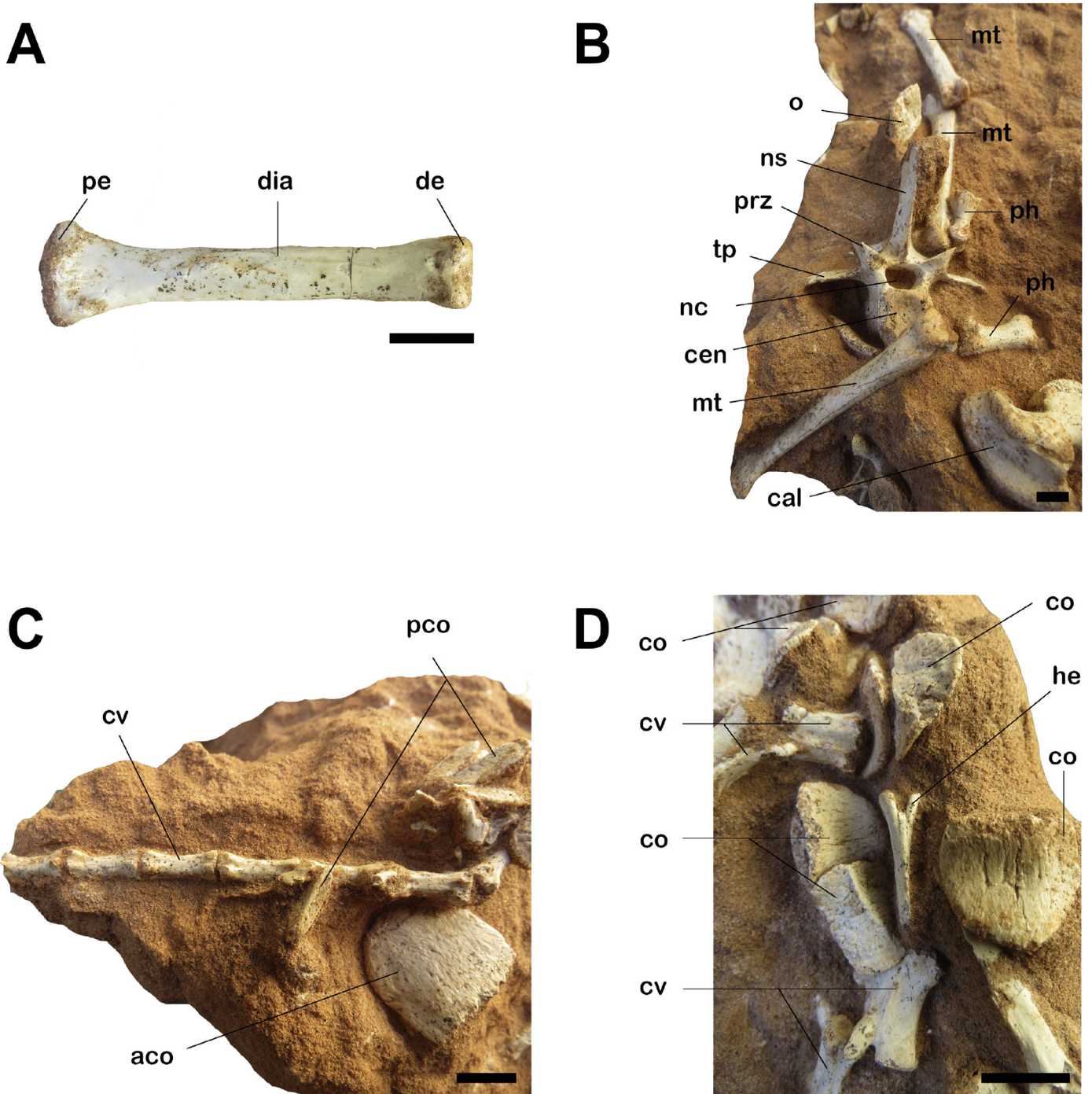
**Humeri.** The right humerus is almost complete (Figs. 2A and 2D), missing only the distal end. In posterior view, it has a long diaphysis and a straight main axis. The proximal end is robust and expanded lateromedially. In the same view, the region of the posterior circular medial depression is concave and as wide as the diaphysis. The deltoid tuberosity is more evident than in MPMA 67-0001/00. In lateral view, the anterior outline presents a 130° angle, where the vertex is the apex of the deltopectoral crest. In general aspect, it is similar to *Mariliasuchus* and *Baurusuchus* humeri, and not as elongated as in *Araripesuchus*, however, it is more gracile than *Armadillosuchus* and *Simosuchus* (Turner, 2006; Nascimento and Zaher, 2010; Sertich and Groenke, 2010; Iori, 2013; Nobre and Carvalho, 2013). The glenohumeral condyle is more medially located, while in *Simosuchus* it aligns with the bone's main shaft. In *Armadillosuchus* (UFRJ DG 303-R), the dimensions of the left humerus show the ratio between the maximum bone width and its length to be almost 1/2, whereas this ratio in *Caipirasuchus* is approximately 1/3 (Iori, 2013).

**Calcaneum.** The right calcaneum is preserved, and its lateral surface exposed (Figs. 3 and 4B). It is robust and the same as high with the anterior roller expanded anteroposteriorly. The region that separates the calcaneal condyle from the calcaneal tuber is very constricted, like in *Mariliasuchus* and *Yacarerani*, and unlike in *Simosuchus*, which is very robust (Sertich and Groenke, 2010). Leardi et al. (2015) pointed many traits in the calcaneum shared by *Caipirasuchus*: the dorsal surface is concave, the anterior roller is semicircular in lateral view, with an anterodorsally rounded edge and a flat plantar margin; the posteroventral margin of the lateral surface of the tuber has a well-defined tubercle; the plantar surface of the calcaneal tuber has a deep fossa; the posterior surface of the calcaneal tuber has an oblique groove steered dorsolaterally to ventromedially.

**Metatarsals.** Three metatarsals are preserved, and all of these are relatively long and straight (Figs. 3, 4A and 4B), as in specimens MPMA 67-0001/00 and MPMA 07-0011/00. They were preserved disarticulated and scattered, making it difficult to assign their exact positions. The metatarsals are gracile, like in *Yacarerani*, *Araripesuchus*, but they are slightly shorter than those of *Araripesuchus*.

**Phalanges.** Seven of the proximal, medial and distal phalanges are preserved (Figs. 3–5). Similarly to the metatarsals, the phalanges are relatively long; the larger preserved is 20 mm in length and 8 mm width. Three of these phalanges are ungual, narrow and long, displaying nearly flat right lateral and curved left lateral surfaces. The unguals have a very sharp ventral edge end crest as in *Yacarerani*, however, in *Caipirasuchus* these phalanges are relatively lower.

**Osteoderms.** The osteoderms near the humeri are as wide as they are long. The anterior caudal units are subrectangular with the lateromedial being the major axis. Toward the end of the tail, the osteoderms become narrower, anteroposteriorly elongated and with rounded edges. In dorsal view, the subrectangular or sub-rounded osteoderms present two different types of surfaces: a slightly wrinkled subcircular surface with a midline keel and a shallower–flatter surface located anterolaterally to the first one (Fig. 6A). The osteoderm outline is smooth, except for the medial edge, being crenulated. The ventral surface is concave, with marked interwoven pattern of fibers and shallow grooves, and has a small posterodorsal slope in its most caudal portion (Fig. 6B). The medial surface shows crenulation where the paired osteoderms were sutured. The contacts between adjacent anterior and posterior osteoderms are imbricated: the posterior region of one osteoderm is imbricated over the flat dorsal portion of the next osteoderm (Fig. 6C). As the tail becomes slenderer, the wrinkled subcircular surface, imbrication surfaces, and medial crenulations become



**Fig. 4.** *Caipirasuchus montealtensis* (MPMA 68-0003/12). Ventral view of the metatarsus (A), foot bones and caudal vertebra (in anterior view) (B) and caudal bones (C and D): aco, anterior caudal osteoderm; cal, calcaneus; cen, centrum; co, caudal osteoderm; cv, caudal vertebra; de, distal end; dia, diaphysis; he, hemapophysis; mt, metatarsus; nc, vertebral canal; ns, neural spine; o, osteoderm; pco, posterior caudal osteoderm; pe, proximal end; ph, phalanx; prz, prezygapophysis; tp, transverse process.

indistinguishable. The last osteoderms are filiform and are four times longer than wide (Fig. 4C). In *Mariliasuchus* the parasagittal osteoderms are rounded and not imbricated (Nobre and Carvalho, 2013). In *Notosuchus*, each osteoderm is overlapped along the rows by the preceding one (Pol, 2005).

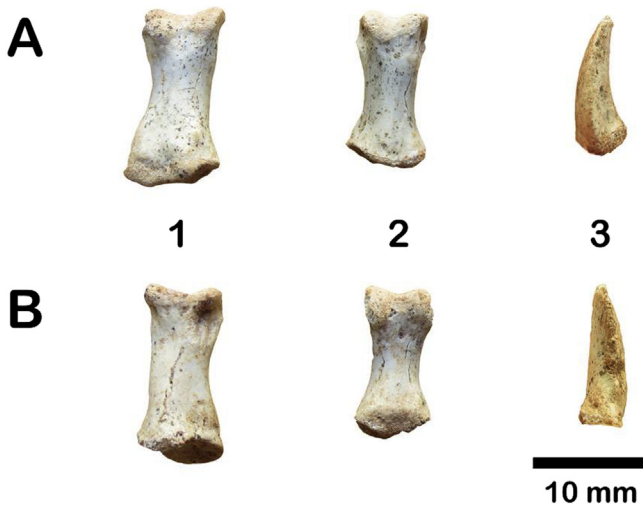
**3.2. *Caipirasuchus paulistanus* (Iori and Carvalho, 2011)**

**Holotype.** MPMA 67-0001/00: the skull, mandible and part of the postcranial skeleton.

**Locality and horizon.** Municipality of Monte Alto, São Paulo State, Brazil, in the Adamantina Formation, Bauru Group (Turonian–Santonian of the Bauru Basin).

**3.2.1. Description**

The postcranial skeleton of this specimen is preserved in four groups (Fig. 7). The following structures are preserved: anterior dorsal vertebrae, humerus, shoulder girdle bones, a few forelimb phalanges, a dorso-sacro-caudal vertebrae sequence and their respective osteoderms starting at the posterior half of the animal,

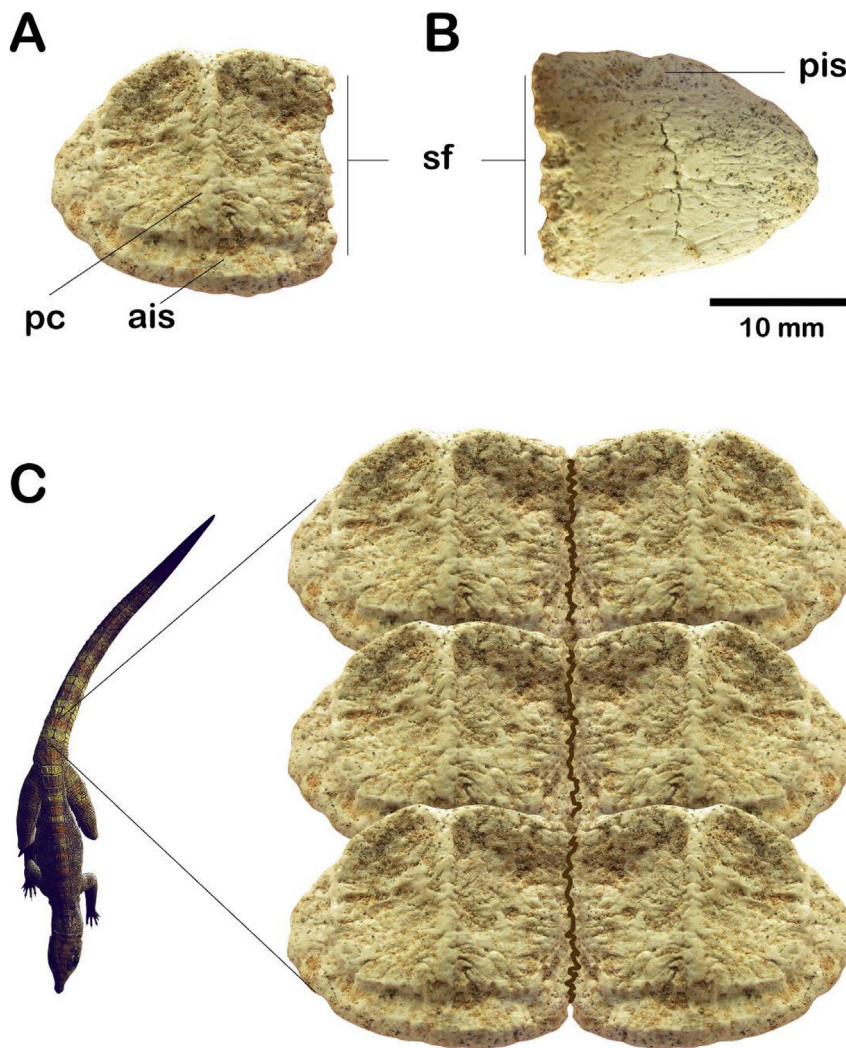


**Fig. 5.** *Caipirasuchus montealtensis* (MPMA 68-0003/12) phalanges in dorsal (A) and ventral (B) views, with a proximal (1), a medial (2) and an ungual (3) phalanx.

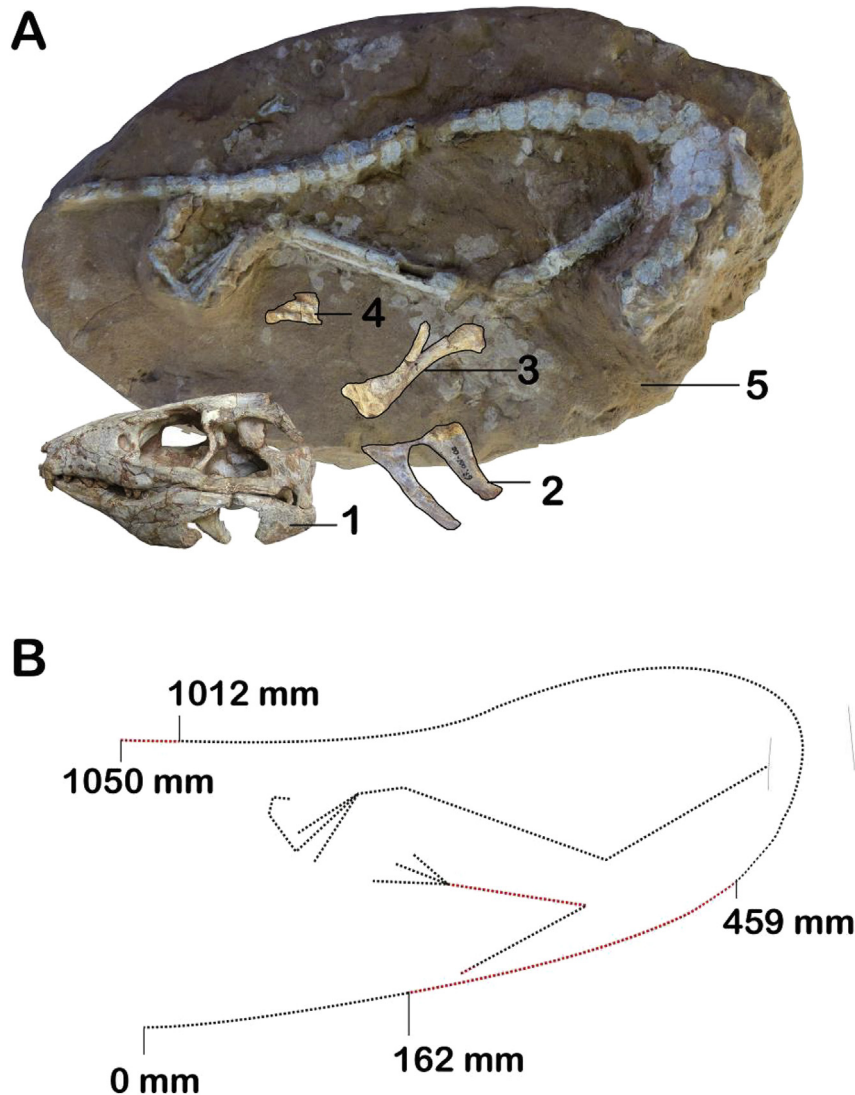
part of the pelvic girdle, a few ribs and the right hind limb. Although the skeleton are articulated, the proximal and distal ends of long bones and its trochanters are not preserved, probably due to some chemical action in diagenetic stage, like the specimen MPMA 07-0011/00.

**Vertebrae and ribs.** Three ribs are exposed and are characterized by a small anteroposterior expansion at the proximal portion. The group of vertebrae (dorsal, sacral and caudal) is completely covered by sediment. The matrix cement makes it impossible to remove it mechanically.

**Forelimb bones.** The right humerus, scapula and coracoid are preserved in a single nodule. The scapula and coracoid are covered by sediment, which precludes a detailed description. The humerus is 85 mm long; in lateral view, it displays slight bending in its distal half (Fig. 8). The trochlear region does not expand laterally and has approximately the same width as the adjacent portion of the diaphysis. A group of seven phalanges from three digits is preserved. The following associations of structures are observed: an isolated ungual phalanx, one sequence of three phalanges, one of them ungual; and another three phalanges sequence (Fig. 8). These



**Fig. 6.** Osteoderm (MPMA 68-0003/12) in dorsal (A) and ventral (B) views. (C) Scheme showing the arrangement of the double row of osteoderms, with a suture between homologous pairs and imbrication between adjacent anterior and posterior osteoderms. Abbreviations: ais, anterior imbrication surface; pc, principal crest; pis, posterior imbrication surface; sf, suturing face.



**Fig. 7.** *Caipirasuchus paulistanus* (MPMA 67-0001/00) skeleton (A). Skull and mandible (1); set with two left ribs (2); right humerus, coracoid and scapula (3); set with incomplete sequences of phalanges from three fingers (4); and main sample with osteoderm sequence, right hind limb and pelvic girdle (5). (B) Skeleton length, with measured (black) and estimated (red) dimensions.

bones are approximately half of the sizes corresponding hind limb phalanges size.

**Pelvic girdle.** Only the two ilia can be observed, which are quite robust (Figs. 9A, 9C and 9D). In dorsal view, the maximum width between the ilia does not exceed 70 mm. The iliac crests do not protrude much laterally and this provided the animal relatively narrow hips.

**Hind limb bones.** In this specimen, most of the right hind limb, which is articulated to the pelvic girdle, is preserved (Fig. 9A). The bones are heavily damaged but allowed some biometric data. In length, the femur is approximately 100 mm, the tibia and fibula are approximately 110 mm, and the metatarsals are approximately 50 mm. The sequence of phalanges of the second digit is preserved and measures approximately 60 mm long (Fig. 9B). The tibia, fibula and metatarsals are quite elongated, gracile and straight.

**Osteoderms.** Most of a double row of osteoderms is preserved in this specimen. This sequence starts near the dorsal region and ends nearly at the end of the tail (Fig. 9A). Similarly to the specimen MPMA 07-0011/00, most of the osteoderms are rounded and become more elongated in the last third of the tail. Most caudal

paramedian osteoderms are preserved, except for the 10th and those posterior to the 24th pair; the three sacral and the last five dorsal pairs are also preserved.

### 3.3. *Caipirasuchus* sp.

**Specimen.** MPMA 07-0011/00: Partial skull, mandible, a series of paramedian osteoderms, vertebrae and appendicular bones.

**Locality and horizon.** Municipality of Monte Alto, São Paulo State, Brazil, in the Adamantina Formation, Bauru Group (Turonian–Santonian of the Bauru Basin).

#### 3.3.1. Description

The postcranial bones of this specimen are distributed among four blocks (Fig. 10). Were observed two series of osteoderms, hind and forelimb bones, caudal vertebrae.

**Caudal vertebrae.** The distal caudal vertebrae are preserved. Almost all of the vertebrae are covered by their respective

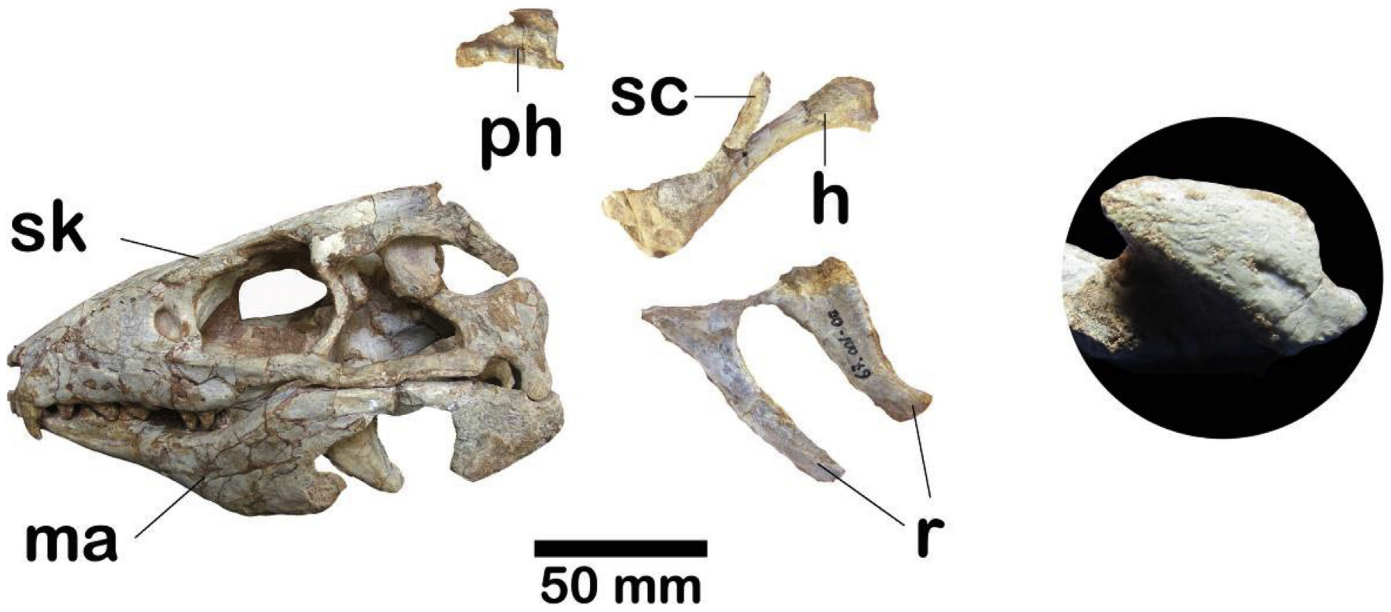


Fig. 8. Preserved parts of the anterior half of a *Caipirasuchus paulistanus* (MPMA 67-0001/00) skeleton. In detail, lateral view of the unguis phalanx. Abbreviations: sc, scapula; sk, skull; h, humerus; ma, mandible; ph, phalanges; r, rib.

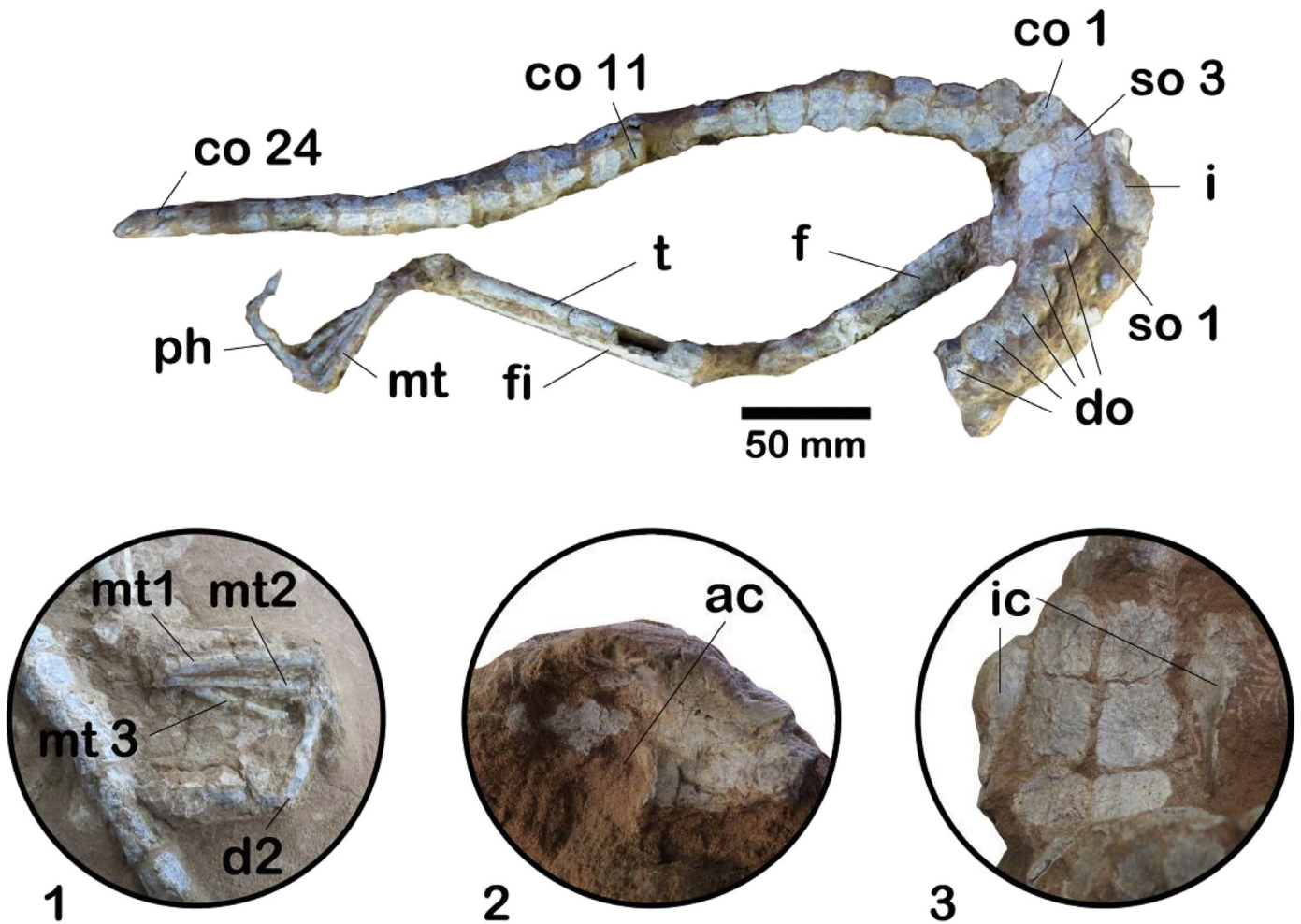
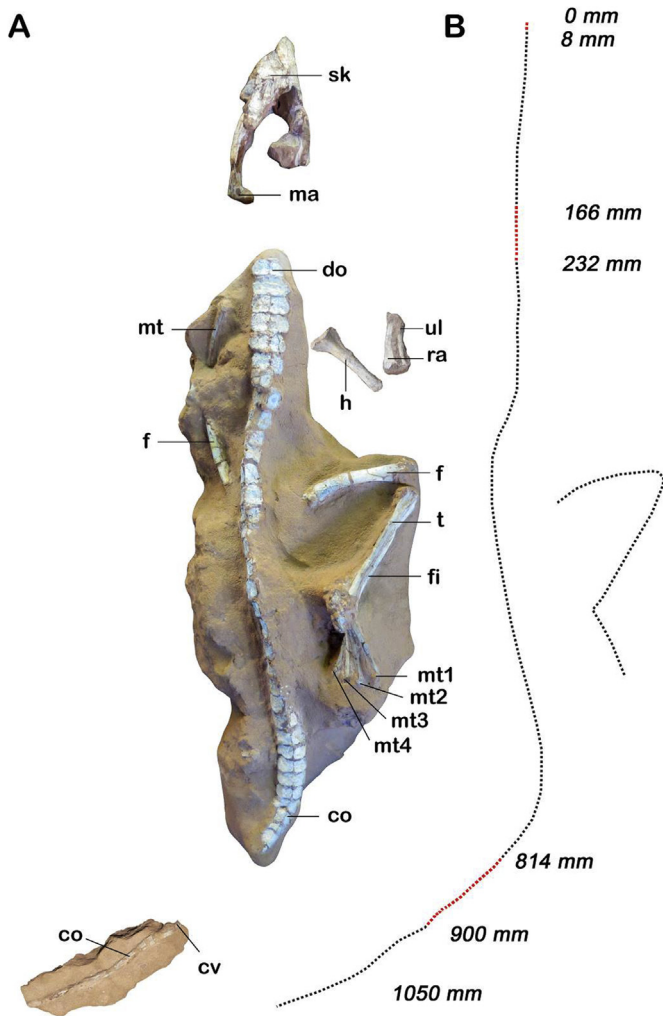


Fig. 9. Preserved parts of the posterior half of a *Caipirasuchus paulistanus* (MPMA 67-0001/00) skeleton. Details: right foot (1); left lateral view of the ilium (2) and dorsal view of the pelvis (3). Abbreviations: ac, acetabulum; co, caudal osteoderm; d, digit; do, dorsal osteoderm; f, femur; fi, fibula; i, ilium; ic, iliac crests; mt, metatarsus; ph, phalanx; so, sacral osteoderm; t, tibia.





**Fig. 10.** Dorsal view of a *Caipirasuchus* sp. (MPMA 07-0011/00) skeleton (A). Abbreviations: cv, caudal vertebra; co, caudal osteoderm; do, dorsal osteoderm; f, femur; fi, fibula; h, humerus; ma, mandible; mt, metatarsus; sk, skull; ra, radius; t, tibia; u, ulna. (B) Skeleton length, with measured dimensions in black and estimated dimensions in red.

osteoderms. The tail of the animal tapered greatly toward the distal end, and its most posterior diameter did not exceed 5 mm.

**Forelimb bones.** The right humerus, radius and ulna are preserved. The humerus is isolated and is partially covered by matrix. The diaphysis is 65 mm long, straight, and its proximal region is greatly expanded. The radius and ulna are encrusted by a carbonate nodule, but it is possible to measure the diaphyses, which do not seem to exceed 50 mm in length.

**Hind limb bones.** One isolated fragment of diaphysis of the right femur and a putative isolated metatarsal are preserved. The following bones are preserved and articulated: left femur, tibia, fibula, tarsals and metatarsals. The fossils were not fully prepared mechanically, thus making difficult to observe several traits of anatomic relevance, particularly in the tarsal region. The proximal ends of the femora are not preserved, in contrast with the humerus. The femoral diaphysis is straight, approximately 90 mm long and robust, with a diameter of approximately 10 mm at its central portion. The tibia and fibula have straight main axes; they are very narrow and elongated, approximately 110 mm long, and their diameters are approximately half of the femur's. The metatarsals are equally straight, narrow and long and with a length of approximately 50 mm.

**Osteoderms.** A sequence containing 35 left osteoderms is preserved, mostly with their counterparts on the right side also preserved. These osteoderms are imbricated and consist of a double row that was arranged dorsally along the midline of the animal. The lateral border of the osteoderms show a rounded outlines and the osteoderms bear a small medial keel facing anterodorsally. The distal osteoderms at the end of the tail is not well preserved, but these dermal components are more elongated anteroposteriorly than those of the most anterior part of the animal.

#### 4. Estimated body size of *Caipirasuchus*

The exact dimensions of individuals cannot be measured because none of the *Caipirasuchus* specimens included a completely preserved individual. However, their proportions were estimated based on the analyses of the three individuals.

In most of the crocodyliforms there is a double row of osteoderms distributed parasagittally along the back of the animal, lateral to the neural spines. Thus, there is a connection between the number and size of osteoderms and the number and size of vertebrae. These elements were used to estimate the body's length of *Caipirasuchus*, taking into account that the number of vertebrae is approximately the one observed in *Baurusuchus albertoi* (atlas, axis, 6 cervicals, 16 dorsals, 3 sacrals and the first 35 caudal vertebrae) that was missing only the last caudal vertebrae (Nascimento and Zaher, 2010).

The preserved length of the fossil MPMA 67-0001/00 (holotype of *Caipirasuchus paulistanus*) is 705 mm long (sincrano = 162 mm, sequence 12th dorsal pairs – 24th caudal pairs osteoderms = 543 mm). *Caipirasuchus montealtensis* (MPMA 68-0003/12) possess the last two cervical and the first five dorsal vertebrae preserved, the sequence is 75 mm long. *Caipirasuchus* sp. (MPMA 07-0011/00) besides a preserved sequence of 35 osteoderms (530 mm), displays the sequence of 10 final caudal osteoderms (150 mm). The complementary sequences of the three individuals measures 930 mm (disregarding the varying sizes of individuals) with the sequences of missing vertebrae (1st–6th cervical and 1st–11th dorsal), the specimens would surpass one meter long.

The distance between the iliac crests in the pelvis of *C. paulistanus* is 70 mm. The genus *Caipirasuchus* is characterized by individuals with slender bodies, the maximum width of which exceeds the skull's by only a few centimeters (Fig. 11).

The right hind limb of specimen MPMA 67-0001/00, *Caipirasuchus paulistanus*, is almost completely preserved, except for the proximal and distal ends of its longer bones; the bones are in their original positions, and the stylopodium, zeugopodium and autopodium sequence yields a total length of 420 mm; the autopodium is 150 mm long, and the remaining 270 mm. The limb was fossilized inflected, with a 130° angle between stylopodium and zeugopodium, which results in a height of 240 mm between the hip and autopodium joints.

The three specimens each contain at least one preserved humerus. In *Caipirasuchus paulistanus*, this bone is 85 mm long, the same as in *C. montealtensis*, although in the latter, a small part of the distal portion is broken off. The only specimen with a preserved anterior zeugopodium is MPMA 07-0011/00. The diaphyses of these bones are approximately 55 mm long; these bones, if complete, should be about 85 mm in length, when comparing with the zeugopodium of *Yacarenani* (Leardi et al., 2015). *Caipirasuchus paulistanus* is the only specimen in which few of the forelimb phalanges are preserved, and these are approximately half as long as the hind limb phalanges. The forelimb is much shorter, i.e., approximately half the size of the hind limb's, which ended up in a posteriorly flexed posture (Fig. 11).

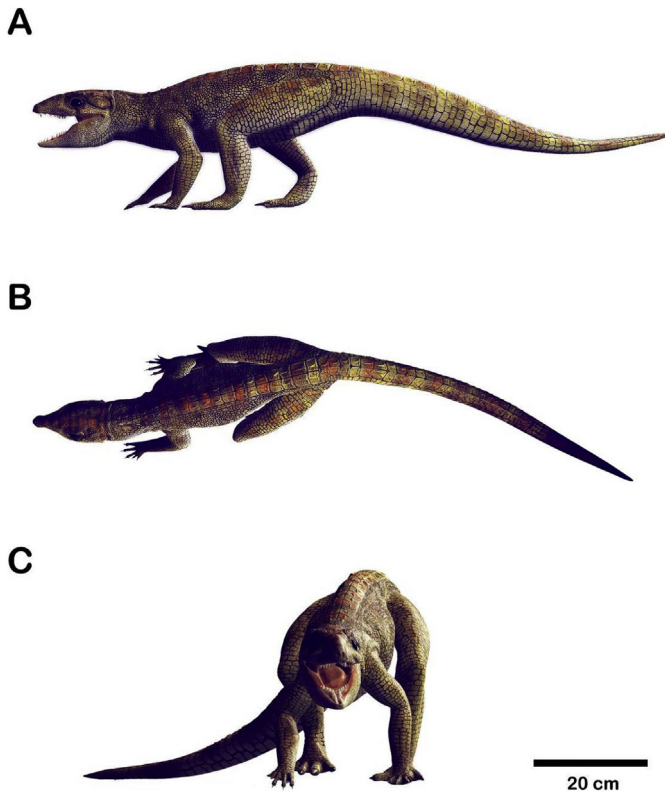


Fig. 11. *Caipirasuchus paulistanus* reconstruction based on the skeleton morphology and measured dimensions. Art by Deverson da Silva (Pepi).

## 5. Discussion

Three individuals of *Caipirasuchus* are preserved, however, more detailed characteristics of the bones can only be observed in the fossil MPMA 68-0003/12, whereas MPMA 67-0001/00 and MPMA 07-0011/00 were used to estimate the size of the animals, as they

do not have the hinge regions of long bones preserved, and delicate parts of the fossil were lost during mechanical preparation.

The appendicular bones of *Caipirasuchus* are long, like *Araripesuchus tsangatsangana*, but less gracile. Humerus and coracoids are very similar to those of *Marillasuchus*, whereas, the femora of the *Caipirasuchus* are relatively longer (Turner, 2006; Nascimento and Zaher, 2010).

The tail of *Caipirasuchus* is long, representing about half of the animal's length, like in *Baurusuchus albertoi*, (Nascimento and Zaher, 2010), and differently of *Simosuchus* (Krause et al., 2010).

The osteoderms are arranged in a double row distributed parasagittally along the back of the *Caipirasuchus*, like in the majority of the Crocodyliformes. Do not presents complex shields as in *Armadillosuchus*, *Simosuchus* and *Montealtosuchus* (Marinho and Carvalho, 2009; Hill, 2010; Tavares et al., 2015).

Sphagesaurids are divided into three groups: *Adamantinasuchus* plus *Yacarerani*, *Caipirasuchus*, and larger species (*Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus*). *Yacarerani* shares many postcranial traits with other notosuchians and differs from eusuchians, like an anteroposteriorly short axial neural spine, a wide scapular blade, a complex radiale-ulnare articulation, and modifications of the facets on the calcaneum (Leardi et al., 2015). The main peculiarity of *Armadillosuchus arrudai* is a cervical armor (firmly sutured osteoderms and a sequence of flexible imbricated bands composed of 6 or 8 osteoderms); the short humerus, pachyostotic ribs and the scapulae with the same width as height indicates the soundness of the skeleton (Marinho and Carvalho, 2009; Iori, 2013).

*Caipirasuchus*, like other sphagesaurids, displays sphagesauriform teeth, which are indicative of an herbivorous and/or omnivorous diet, a habit that reflects occupation of lower trophic levels (Iori et al., 2013). Thus, these animals were food sources for second- or third-order consumers, such as larger theropods and predatory crocodyliforms (Andrade and Bertini, 2008; Marinho and Carvalho, 2009; Carvalho et al., 2010; Iori and Carvalho, 2011; Iori et al., 2011; Godoy et al., 2014). Godoy et al. (2014) described a new baurusuchid with preserved stomach remains that were attributed to bones of a sphagesaurid, which confirms the predation of this group.



Fig. 12. Life scenery of *Caipirasuchus* escaping of the predators. Art by Deverson da Silva (Pepi).

Among the herbivorous/omnivorous forms, two distinct corporal morphology occur in Ziphosuchia, the slender (*Notosuchus* and *Mariliasuchus*, for instance) and the stock (*Armadillosuchus*, *Simosuchus*, etc). The analysis of the structural pattern of the *Caipirasuchus* skeletons reveals specimens that were approximately 1.10 m in length, with slender (long and narrow) bodies and long hind limbs (Fig. 11).

The robustness of the *Armadillosuchus* combined with its protective armor, provided the animal with a strong defense mechanism against predators (Marinho and Carvalho, 2009). *Caryonosuchus pricei* possess a peculiar rostral tuberosities and the conspicuous ornamentation of the skull (Kellner et al., 2011); the tuberosities may represent a defensive feature of the species, i.e., one not used in attacks but rather serving to make the cranial set more robust and resistant, particularly in the region of the nasal bones, which are typically quite thin. These horn-like structures and the dorsal protection in *Armadillosuchus* are analogous to those observed in Ankylosauria (Coombs, 1978; Carpenter, 2004) and represent important protection features.

The body shape of *Caipirasuchus*, i.e., slender, long bodies and hind limbs twice as long as the forelimbs could indicated cursorial habit, in addition a light body could cooperate in gaining speed at opportune times.

## 6. Conclusion

Analysis of postcranial remains of *Caipirasuchus* widen the knowledge about the family osteology, so far little known. The reconstruction of the body structure contributes to a better definition of the Cretaceous Crocodyliformes of Bauru Basin.

*Caipirasuchus* were approximately 1.10 m in length, with slender (long and narrow) bodies and long hind limbs. Differently of the *Armadillosuchus*, which used its bony protection as armor, *Caipirasuchus* must have been agile and thus used its agility to escape from predators (Fig. 12).

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