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Caipirasuchus paulistanus, a new sphagesaurid (Crocodylomorpha, Mesoeucrocodylia) from the Adamantina Formation (Upper Cretaceous, Turonian-Santonian), Bauru Basin, Brazil

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ARTICLE

CAIPIRASUCHUS PAULISTANUS, A NEW SPHAGESAURID (CROCODYLOMORPHA, MESOEUCROCODYLIA) FROM THE ADAMANTINA FORMATION (UPPER CRETACEOUS, TURONIAN–SANTONIAN), BAURU BASIN, BRAZIL

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ABSTRACT—A skull and mandible of a new species of notosuchian, *Caipirasuchus paulistanus*, belonging to the Sphagesauridae, were discovered in the rocks of the Adamantina Formation (Bauru Basin: Late Cretaceous). The main autapomorphies are external naris bordered only by premaxillae; very high pterygoids and ectopterygoids; palatines contacting maxillae by a cuneiform process; well-developed oval antorbital fenestra; premaxilla with four teeth; dentary with ten teeth and two diastemata; and one diastema in the premaxilla and another between the fourth alveolus of the premaxilla and the first of the maxilla. Morphological analysis and experimental data suggest an animal with a powerful bite and a dentition with specific regions of action, one adapted to apprehension and the other to food processing.

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INTRODUCTION

The Bauru Basin is located in the south-central region of the South American platform (Fig. 1) and had an arid or semi-arid climate between the Coniacian and the Maastrichtian (Fernandes and Coimbra, 2000). Dias-Brito et al. (2001) suggested, based on micropaleontological studies, that there were two intervals of sedimentation (Turonian–Santonian and Maastrichtian). The Cretaceous sequence is a reddish continental package of sandstones, siltstones, and mudstones, exhibiting levels with calcretes, and deposited in several paleoenvironmental contexts, including aeolian, alluvial, fluvial, and lacustrine (Fernandes and Coimbra, 1994, 1996; Dias-Brito et al., 2001; Batezelli et al., 2003, 2005). This new crocodylomorph was collected in Monte Alto County, São Paulo State, Brazil. Two lithostratigraphic units occur in this region: the Adamantina and Marília formations. The specimen was discovered in the Adamantina Formation, which displays thick strata of fine sandstone.

The Bauru Basin has yielded a large number of crocodyliform species. In the Monte Alto region alone three families have been found: Peirosauridae, Sphagesauridae, and Baurusuchidae (Carvalho et al., 2007; Andrade and Bertini, 2008; Pinheiro et al., 2008). Sphagesauridae includes *Sphagesaurus huenei* Price, 1950, *Adamantinasuchus navae* Nobre and Carvalho, 2006, *Sphagesaurus montealtensis* Andrade and Bertini, 2008, and *Armadillosuchus arrudai* Marinho and Carvalho, 2009.

Sphagesaurus huenei is based on two teeth with unique features for a reptile, specifically long roots and short crowns coated with coarse enamel and with one prominent keel and longitudinal striations (Price, 1950). Kuhn (1968) named the family Sphagesauridae based on this species. Pol (2003) redescribed *S. huenei* from new material, an almost complete skull and part of a mandible.

The diagnosis of sphagesaurids was reviewed by Marinho and Carvalho (2007) and *Adamantinasuchus navae* was included in this family. *Adamantinasuchus navae* had a peculiar dentition: the maxillary teeth present a smooth labial surface and the lingual surface bears small denticles and longitudinal grooves (Nobre and Carvalho, 2006). Andrade and Bertini (2008) described *Sphagesaurus montealtensis*, which exhibits a dentition very similar to that of *S. huenei*, but differs in other traits, such as the presence of an antorbital fenestra.

Armadillosuchus arrudai is a sphagesaurid described by Marinho and Carvalho (2009), whose most peculiar feature is heavy body armor composed of a rigid shield and mobile banded section. *Yacarerani boliviensis* Novas, Pais, Pol, Carvalho, Scanferla, Mones, and Riglo, 2009, is a notosuchian from Bolivia with a posterior dentition similar to that observed in *Adamantinasuchus navae*.

This study presents a morphological description and phylogenetic analysis of a new notosuchian from the Bauru Basin. The new species herein described displays several synapomorphies with *Sphagesaurus huenei* and *S. montealtensis*, and its dental morphology supports its inclusion in the Sphagesauridae. The main autapomorphies are external naris bordered only by the premaxillae; well-developed and oval antorbital fenestra; and premaxilla with four teeth and dentary with ten teeth. The fossil is very well preserved, and morphological analysis allows many aspects of the animal's feeding to be inferred. The new species expands the already great diversity of Cretaceous crocodyliforms from the Bauru Basin, reinforcing the decisive importance of the group in the regional ecosystem at that time.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
SPHAGESAURIDAE Kuhn, 1968
CAIPIRASUCHUS PAULISTANUS, gen. nov. et sp. nov.
(Figs. 2–3)

Etymology—The generic name *Caipirasuchus* is derived from the terms 'Caipira' and 'souchus.' *Caipira* was what the indigenous people of the countryside of São Paulo State called the first settlers of the region. Today, the term refers to the rural inhabitants of the Brazilian states, being in widespread use in the State

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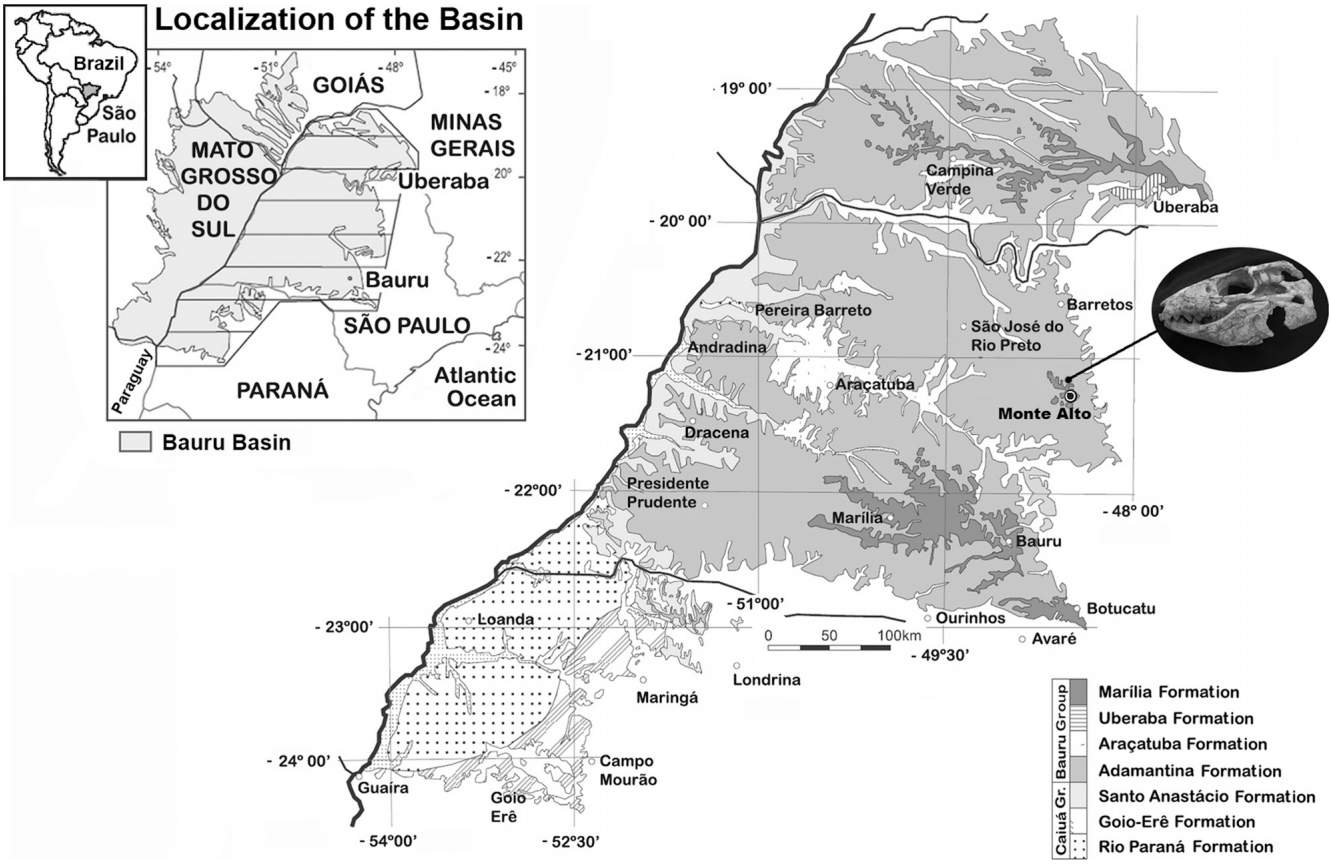

FIGURE 1. Lithostratigraphic map of the eastern part of the Bauru Basin (modified from Fernandes and Coimbra, 2000).

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of São Paulo and some regions of the neighboring states, covering almost all of the Bauru Basin. The term *souchus* is the Greek word for crocodile. The specific name *paulistanus* is derived from 'paulista,' the designation for the residents of São Paulo State, where the specimen was discovered.

Locality and Stratigraphic Context—Six kilometers from Monte Alto, on the São Francisco Farm (21°13′15.5″S and 48°30′41.6″W), in Homem de Mello, the rural area of Monte Alto County, São Paulo State, southeastern Brazil (Fig. 1). Bauru Basin, Adamantina Formation, Upper Cretaceous (Turonian–Santonian).

Holotype—MPMA 67-0001/00 (Museu de Paleontologia de Monte de Alto). Skull and mandible (Figs. 2–3).

Diagnosis—External naris bordered only by the premaxillae; very high pterygoids and ectopterygoids; palatines contacting the maxillae by a cuneiform projection; well-developed and oval antorbital fenestra; premaxilla with four teeth; a small projection of the maxilla visible dorsally; dentary with two diastemata—with corresponding diastemata in the upper jaw, one in the premaxilla and another between the fourth premaxillary and first maxillary alveoli; supraorbital fenestra lance-shaped; long nasals with acute anterior edge anterolaterally touching the projection from the premaxilla; jugal is a straight bar in lateral view; quadrate is dorsoventrally expanded and oriented, quadrate condyle for the articular faces ventrally rather than posteroventrally; frontal is longer than wide and has a slight crest on the midline; dentary with ten teeth each with dorsally directed apex, the first two conical and the smallest in the series, with progressive lateral flattening from the third to the fourth tooth; the fifth through tenth dentary teeth each have a triangular crown, an transversely elliptical cross-section, and a carina on the anterolabial surface.

DESCRIPTION

The skull and mandible are almost complete and undeformed. All the bones of the snout and palate are preserved. The basicranium is represented only the left exoccipital. The complete dentition consisted of 40 teeth (8 premaxillary, 12 maxillary, and 20 mandibular), but only 37 are preserved; the fourth left maxillary tooth lacks its crown; the sixth and seventh alveoli of the left dentary are empty.

Skull

The skull is high and narrow. In dorsal view, it has a triangular shape. It exhibits subdued ornamentation, with some irregular grooves and furrows observed mainly on the maxilla. The snout tapers gradually and represents almost half of the length of the skull. The orbits are laterally disposed. The teeth are heterodont.

Premaxilla—In lateral view, it is quadrangular and displays an almost imperceptible intumescence in the region of the hypertrophied tooth and also a small anterodorsal projection. Posterodorsally, it contacts the nasal, and its anterior edge borders the whole external naris.

In ventral view, a parabolic projection of the posterior extremity invades the maxilla and surrounds the fourth tooth. It exhibits sagittally the incisive foramen, which is bounded by the contacts between the premaxillae and maxillae. The lateral edge follows the line of the maxilla; it extends straight anteriorly to lie adjacent

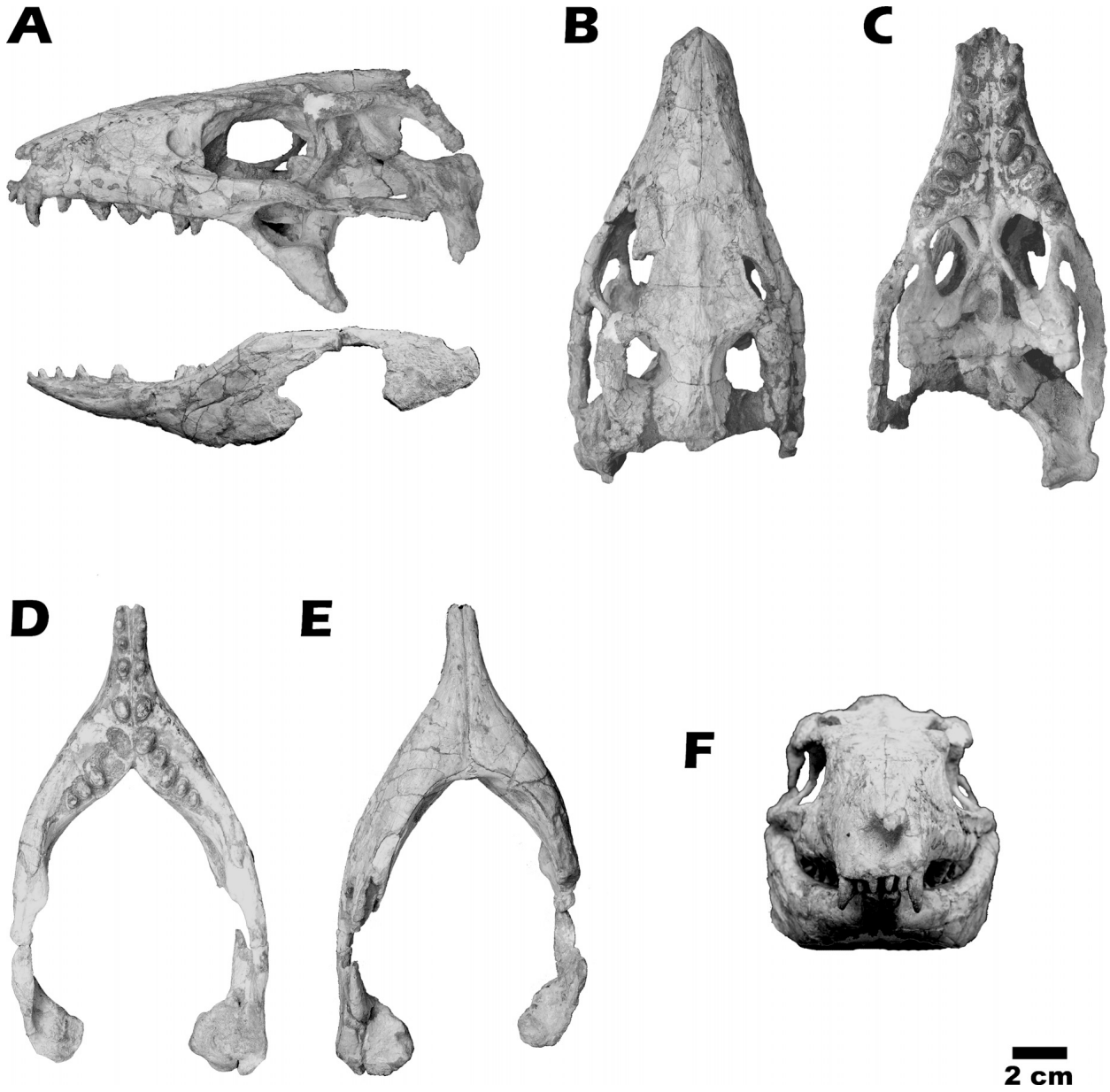

FIGURE 2. *Caipirasuchus paulistanus*. (**A**) Skull and mandible in lateral view; (**B**) skull in dorsal view; (**C**) skull in ventral view; (**D**) mandible in dorsal view; (**E**) mandible in ventral view; (**F**) skull and mandible in occlusion in frontal view.

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to the third tooth. After this, it becomes curved, joining the other premaxilla and giving the skull a slightly rounded anterior extremity.

The premaxilla has four teeth. The first and second teeth are the smallest, each being less than 5 mm in length, and are conical with discrete longitudinal striations. The third tooth is hypertrophied, measuring about 12 mm in length, and is conical, with a slight apical inclination to the distal edge, and is also longitudinally striated. The longitudinal striations in the first to third teeth cover the whole crown. The fourth tooth is also conical, with a large base in relation to its height, but without superficial structures. There are two diastemata along the superior alveoli, one between the fourth and third alveoli of the premaxilla and another, a little larger, between the fourth alveolus of the premaxilla and the first of the maxilla.

External Naris—It is disposed vertically, opens anterolaterally and is bordered by the premaxillae only.

Incisive Foramen—This is a small opening on the sagittal line of the ventral skull surface, delimited anterolaterally by the premaxillae and posteriorly by the maxillae.

Maxilla—It is high laterally, nearly quadrangular and displays neurovascular foramina. The anterior margin contacts only the premaxilla and does not reach the margin of the external naris. It dorsally contacts the nasal and, posteriorly, the jugal and lacrimal. It forms most of the anterior border of the antorbital fenestra. In ventral view, it exhibits an invaginated contact with the projection of the premaxilla. The posterior extremity contacts the palatine, participates in the anterior border of the palatal fenestra, and touches the ectopterygoid. Six teeth are obliquely disposed in relation to the sagittal axis. They are elliptical in

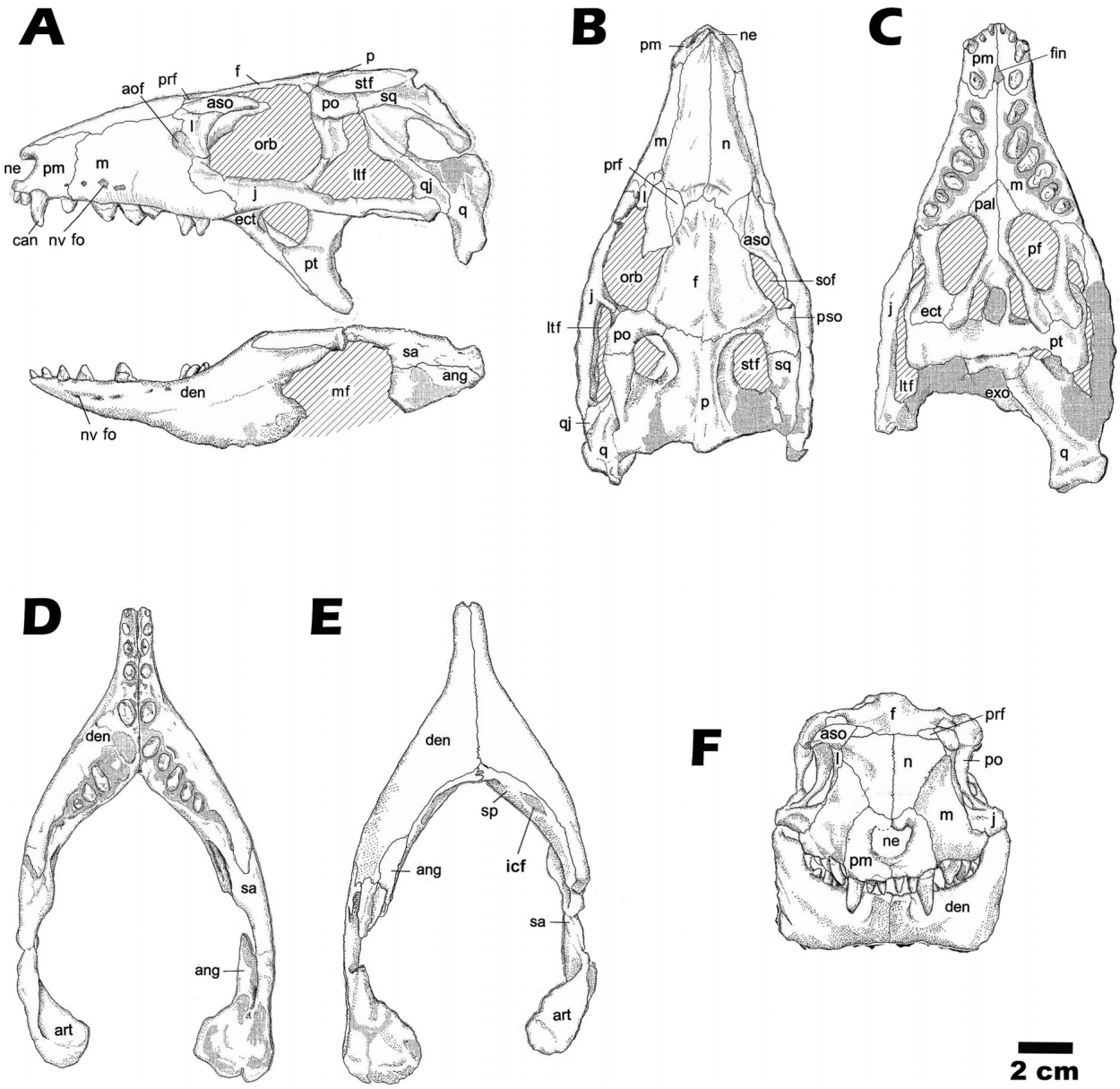

FIGURE 3. Schematic drawing of *Caipirasuchus paulistanus*. (**A**) Skull and mandible in lateral view; (**B**) skull in dorsal view; (**C**) skull in ventral view; (**D**) mandible in dorsal view; (**E**) mandible in ventral view; (**F**) skull and mandible in occlusion in frontal view. **Abbreviations**: **ang**, angular; **aof**, antorbital fenestra; **art**, articular; **aso**, anterior supraorbital; **can**, caniniform tooth; **den**, dentary; **ect**, ectopterygoid; **exo**, exoccipital; **f**, frontal; **fin**, incisive foramen; **icf**, intermandibular caudal foramen; **j**, jugal; **l**, lacrimal; **ltf**, laterotemporal fenestra; **m**, maxilla; **mf**, mandibular fenestra; **n**, nasal; **ne**, external naris; **nv fo**, neurovascular foramina; **orb**, orbit; **p**, parietal; **pal**, palatine; **pf**, palatal fenestra; **pm**, premaxilla; **prf**, prefrontal; **po**, postorbital; **pso**, posterior supraorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sof**, supraorbital fenestra; **sp**, splenial; **sq**, squamosal; **stf**, supratemporal fenestra.

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transverse cross-section and possess triangular crowns. Some of the teeth have the enamel layer preserved, exhibiting longitudinal striations and a denticulate carina in the posterolingual surface. The fifth and sixth teeth are the smallest. The first teeth are aligned parallel to the sagittal plane; the others are grouped along a line inclined to the sagittal axis; the second tooth is at the intersection point of these two lines.

Neurovascular Foramina—They are small openings, laterally disposed, observed approximately 7 mm above the lateral ventral margin of the rostrum. On the left side, there are five foramina, four in the maxilla and one in the premaxilla.

Palatine—There are two distinct parts to the palatine. The anterior half is more robust and linked to the other palatine, and both form a 'V'-shaped process between the maxillae. Posteriorly, the palatines are thin rods, separated from each other, which expand slightly at their posterior-most extents, contacting the pterygoids and ectopterygoids. The palatines appear to contact processes of the pterygoids where they diverge, but this is not clear.

Palatal Fenestra—This is delimited medially by the palatine, laterally by the pterygoid, and anteriorly by the maxilla. It is ellipsoid in shape and is posteroventrally projected on an inclined

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surface, forming an angle of approximately 135° in relation to the ventral surface of the maxilla.

Pterygoid—This is nearly vertical and is higher than wide. Anteroventrally, it contacts the ectopterygoid and palatine. Posterodorsally, it touches the quadrate. The posterior process is moderately triangular in lateral view.

Ectopterygoid—This bone is strongly flexed posteroventrally, at about 135° to the ventral surface of the palate. The proximal extremity is wider than high; it lays on the pterygoid and medially contacts the palatine. Its medial portion is cylindrical. In lateral view, the dorsal tip expands radially, contacting the maxilla anteriorly and the jugal dorsally.

Nasal—The nasal is an elongate bone, constituting nearly half of the length of the skull. The left nasal displays more evident sutures, mainly at the proximal edge. Externally, it exhibits two surfaces, dorsal and lateral. The lateral surface contacts the maxilla and premaxilla. The premaxilla, maxilla, and lacrimal contact the nasal ventrally. The anterior edge touches a small process from the premaxilla anterolaterally and, therefore, does not contribute to the border of the naris. The anterior tip of the nasal is tapered: it gradually widens posteriorly, reaching the maximum width next at the lacrimal contact, where it is 3 times as wide as at the premaxilla. Posteriorly, it is pointed in a cuneiform projection posteromedially, which contacts the frontal and, posterolaterally, the prefrontal. Posteriorly its dorsal surface is depressed, beginning a few millimeters in front of the contact with frontal; anteriorly this depression is well marked by an evident line parallel to the frontonasal suture.

Anterior Supraorbital—The anterior extremity lays on the lacrimal and has a sharp contact with the nasal. It touches the frontal laterally and this contact is very small. From this contact it tapers, forming a bar that projects toward the posterior supraorbital. In dorsal view, it displays a triangular shape with the larger border laterally.

Posterior Supraorbital—This is a small rounded bone in contact with the postorbital and the anterior supraorbital.

Supraorbital Fenestra—In dorsal view, it appears to have a lance-like shape. Posteriorly, it is delimited by the posterior supraorbital and moderately by the postorbital, medially by the frontal, and laterally by the anterior supraorbital.

Lacrimal—The lacrimal is exposed on the lateral surface of the skull and internally in the orbital wall. Dorsally, it is covered by the contact with the anterior supraorbital. It possesses an anteroventral depression constituting part of the antorbital fenestra. Ventrally, it contacts the jugal, and has, above the antorbital fenestra, a small quadrangular projection contacting the nasal and the maxilla.

Antorbital Fenestra—This opening is elliptical. Dorsoanteriorly, it is bordered by the maxilla, where the antorbital fossa is deeper. The posterior edge is formed by the lacrimal, which is oriented diagonally, entering into the fenestra and contacting the maxilla. Ventrally, it is delimited by the jugal, which has a small projection posterodorsally.

Jugal—It is extremely thin, becoming wider anteriorly, and contacts the maxilla, lacrimal, and ectopterygoid. It exhibits a slight depression anterodorsally, next to the antorbital fenestra in the ventral border of which it moderately participates. The contact with the quadratojugal is not well defined. It ventrally bounds the major part of the orbit and the jugal bar also contributes to the postorbital bar.

Orbit—The orbit has a diameter approximately one quarter the length of the skull. It is oval in outline and of medium size. It is oriented laterally, bounded by the jugal, postorbital, posterior supraorbital, and anterior supraorbital bones.

Laterotemporal Fenestra—This is completely preserved only on the left side. It is triangular in outline, limited by the postorbital bar, jugal, quadratojugal, and, possibly, the quadrate.

Prefrontal—The left prefrontal is very well preserved. It has a semi-lunate shape, exhibiting a parabolic contour medially that contacts the nasal. Posteriorly, it contacts the frontal and, laterally, the posterior supraorbital.

Frontal—The frontal is longer than wide and exhibits a discrete crest sagittally. Anterolaterally it contacts the nasal, prefrontal, and has a point contact with the anterior supraorbital. It displays a smooth edge laterally, bordering the supraorbital fenestra. The proximal tip contacts, through well-preserved sutures, the postorbital and parietal.

Parietal—Anteriorly, it contacts the frontal and, laterally, the postorbital. The junction with the squamosal is not preserved. Medially, it exhibits a small semicircular crest bordering the concavity of the supratemporal fenestra.

Supratemporal Fenestra—This is rounded, with its medial border delimited by the parietal, which is higher than the anterior and lateral borders. The postorbital borders the fenestra anteriorly and the squamosal delimits it laterally.

Squamosal—Both squamosals are incomplete, but the left is better preserved. The anterior portion contacts the postorbital. It displays a discrete lateral projection.

Quadrate—Only the left quadrate is preserved. The contact with the quadratojugal and its participation in the laterotemporal fenestra are not evident. It is a tall bone and the facet of articulation with the articular is positioned ventrally. The quadrate shaft projects ventrally. Dorsomedially, it contacts the exoccipital. The contact with the pterygoid is very robust; it is well consolidated and located anteroventrally.

Mandible

The mandible is nearly complete. In lateral view, it is slender anteriorly, but deeper around the mandibular fenestra. Dorsally, from the surangular-dentary contact, the curvature is very marked to the position of the ninth tooth; posterior to this, its border remains straight to its posterior-most tip. The ventral margin remains straight from the mandibular fenestra region to the position of the ninth tooth; after this point, the margin has a slight inclination, which proceeds to the anterior edge of the mandible, displaying an acute angle with the dorsal border. Neurovascular foramina are disposed laterally in the first anterior half of the dentary. In ventral view, it shows a very narrow and almost angular (not rounded) anterior extremity.

Dentary—All of the teeth have dorsally oriented apices. The first six teeth gradually increase in size posteriorly. They are arranged in a line parallel to the sagittal axis; the outer teeth, besides the sixth, are arranged on a line diagonal to this axis. The first two teeth are conical and are the smallest in the series, with progressive lateral flattening from the third to fourth tooth; from the fifth to the tenth, all of the teeth have a triangular crown and an elliptical transverse cross-section; the carina is on the anterolabial surface. The sixth, seventh, and eighth teeth are the same size, whereas the ninth and the tenth are, respectively, smaller. The sixth to tenth teeth are situated adjacent to the internal margin of the dentary and are obliquely inclined to the sagittal axis. When articulated, the dentaries in dorsal view are 'Y'-shaped.

Neurovascular Foramina—These are observed in groups of three, on the lateral surface of the dentary, approximately 5 mm below the laterodorsal border of the mandible, in the region of the fourth and fifth teeth.

Splenial—This is tall and in its more anterior region participates in the mandibular symphysis.

Intermandibular Caudal Foramen—This is rounded and located in the splenial, in the ventral half of the internal surface of the mandible, next to the contact with the dentary.

Surangular—The dorsal margin is slightly convex from the contact with the articular to the contact with the dentary. Ventrally,

it touches the angular, partially borders the mandibular fenestra and joins the dentary.

Angular—The contact with the articular and dentary are not well defined, but the angular dorsally contacts the surangular.

Mandibular Fenestra—This is oval in outline and is located in the posterior half of the mandible. It is delimited anteriorly by the dentary, posterdorsally by the surangular, and posteroventrally by the angular.

DISCUSSION

Comparisons

Caipirasuchus paulistanus exhibits two distinct regions with remarkable traits: the anterior half of the head is tapered in all planes and the rostrum is relatively long in relation to those of other notosuchians, whereas the posterior half is very tall, mainly in the region of the mandibular fenestra and the ectopterygoid and pterygoid bones. *Caipirasuchus* shares some synapomorphies with the genera *Sphagesaurus* and *Armadillosuchus*. The morphologic patterns and disposition of teeth in *Caipirasuchus* are similar to those found in *Sphagesaurus* and *Armadillosuchus*. The three genera display a relatively thick enamel layer in the teeth of the maxilla, longitudinal striations on the anterolabial face, and a keel on the posterolingual face. These teeth are disposed obliquely to the longitudinal axis of the skull (Price, 1950; Pol, 2003; Andrade and Bertini, 2008; Marinho and Carvalho, 2009).

Caipirasuchus paulistanus has 40 teeth, with 4 teeth in each premaxilla, 6 in each maxilla, and 20 in the mandible. The anterior teeth are conical and the posterior crowns triangular. This dental distribution is the same as that observed in *Yacarerani boliviensis* (Novas et al., 2009). In *Caipirasuchus paulistanus* the first two premaxillary teeth are small, conical, and located anteriorly. The third tooth is hypertrophied and the fourth is slightly compressed labiolingually. These characteristics are distinctly different from those observed in *Sphagesaurus huenei* Price, 1950, which has an edentulous anterior region of the skull and only two teeth in the premaxilla (Pol, 2003).

Andrade and Bertini (2008) described *Sphagesaurus montealtensis*, whose skull anteriorly is similar to that of *S. huenei*, besides having one tooth in the premaxilla and seven teeth in the maxilla. After better preparation of the holotype, a different distribution of teeth was observed, with six in the maxilla and at least two in the premaxilla; the anterior region seems to support more teeth. *Chimaerasuchus paradoxus* Wu, Sues, and Sun, 1995, and *Yacarerani boliviensis* present procumbent teeth in the premaxilla, a trait not found in *Caipirasuchus paulistanus* (Wu and Sues, 1996; Novas et al., 2009). *Caipirasuchus paulistanus* has six teeth in the maxilla, all with triangular crowns and oblique implantation, as in *Sphagesaurus*, *Notosuchus*, and *Yacarerani*, whereas *Adamantinasuchus navae* possesses seven maxillary teeth (Pol, 2003; Nobre and Carvalho, 2006; Lecuona and Pol, 2008).

A circular perforation between the second tooth of the premaxilla and the first maxillary tooth can be observed in *Sphagesaurus huenei*. Such a structure does not occur in *Caipirasuchus paulistanus*. *Caipirasuchus paulistanus* shares an incisive foramen between the premaxillae and maxillae with *Sphagesaurus*. This structure was also seen in *S. montealtensis* after sediment was removed. Two diastemata occur in the superior dental region of *Caipirasuchus paulistanus*, one between the third and fourth alveoli of the premaxilla and another between the fourth alveolus of the premaxilla and the first of the maxilla. *Sphagesaurus montealtensis* has two similar diastemata isolating the last alveolus of the premaxilla, whereas in *Sphagesaurus huenei*, all the teeth are juxtaposed.

Caipirasuchus paulistanus has posterior teeth with keels, each tooth bearing only a single denticulate keel. *Adamantinasuchus navae* and *Yacarerani boliviensis* bear three rows in each maxillary tooth (Nobre and Carvalho, 2006; Novas et al., 2009). *Caipirasuchus paulistanus* does not have multicusped teeth, whereas *Candidodon itapecuruense* Carvalho and Campos, 1988, has true heterodonty, with conical, spatulate caniniform and molariform teeth (and a spatulate central cusp surrounded by denticles in the base of the crown). The pattern of molariform teeth in *C. itapecuruense* is very similar to that in *Malawisuchus mwakasyungutiensis* Gomani, 1997. Multicusped teeth also occur in *Chimaerasuchus paradoxus*, *Simosuchus clarki* Buckley, Brochu, Krause, and Pol, 2000, *Uruguaysuchus aznarezi* Rusconi, 1933, and *Uruguaysuchus terrai* Rusconi, 1933 (Rusconi, 1933; Wu and Sues, 1996; Gomani, 1997; Buckley et al., 2000; Nobre and Carvalho, 2002). *Uruguaysuchus* and *Simosuchus* share the same pattern in the shape of the multicusped teeth. They are spatulate and strongly compressed laterally with longitudinally oriented cusps, besides having a very evident constriction at the base of the crown (Buckley et al., 2000).

The dentitions of *Araripesuchus*, *Anatosuchus*, *Morrinhosuchus*, and *Pakasuchus* are quite distinct from that of *Caipirasuchus paulistanus*. *Araripesuchus* has two types of teeth (a conical one and another expanded anteroposteriorly, with two denticulate keels) besides a hypertrophied tooth in the maxilla. *Pakasuchus kapilimai* O'Connor, Sertich, Stevens, Roberts, Gottfried, Hieronymus, Jinnah, Ridgely, Ngasala, and Temba, 2010, possesses caniniform, premolariform, and molariform teeth; a more peculiar trait is in the large molariforms, which possess two parallel crests oriented rostrocaudally and separated by a longitudinal trough. *Anatosuchus minor* Sereno, Sidor, Larsson, and Gado, 2003, has a relatively numerous dentition in relation to other notosuchians (46 pairs of teeth), with the teeth of the maxilla slightly curved to the back and possessing an anterior keel, without serrations. *Morrinhosuchus luziae* Iori and Carvalho, 2009, retains only the posterior teeth in the preserved dentary, with globular crowns and circular cross-sections (Price, 1959; Carvalho and Bertini, 1999; Ortega et al., 2000; Pol and Apesteguia, 2005; Sereno et al., 2003; Iori and Carvalho, 2009; Sereno and Larsson, 2009; O'Connor et al., 2010).

Caipirasuchus paulistanus displays four pairs of teeth in the mandibular bodies and six in the symphysis. Thus, there are 10 pairs of teeth in the mandible. Andrade and Bertini (2008) described nine pairs of teeth in *Sphagesaurus montealtensis*, the first five pairs being in the symphysis and the other four in the mandibular bodies. The mandible in *S. montealtensis* is incomplete, but the preserved part displays a very similar pattern to that in the mandible of *Caipirasuchus paulistanus*, including the thin shape and the disposition of the teeth and diastemata, but *Caipirasuchus paulistanus* has a taller mandible, especially in the region of the mandibular fenestra. As for the mandible of *Sphagesaurus huenei*, only the more distal part of the dentary, with the first four teeth, has been preserved and, like *Caipirasuchus paulistanus*, the first three teeth are conical and increase in size following an anteroposterior orientation.

Caipirasuchus paulistanus has all the teeth of the mandible dorsally (vertically) oriented without procumbent teeth, whereas *Adamantinasuchus navae*, *Yacarerani boliviensis*, *Armadillosuchus arrudai*, *Comahuesuchus brachybuccallis* Bonaparte, 1991, *Mariliasuchus amarali* Carvalho and Bertini, 1999, *Mariliasuchus robustus* Nobre, Carvalho, Vasconcellos, and Nava, 2007, and *Araripesuchus rattoides* Sereno and Larsson, 2009, all display anteriorly directed anterior teeth in the mandible (Carvalho and Bertini, 1999; Martinelli, 2003; Nobre and Carvalho, 2006, Nobre et al., 2007; Marinho and Carvalho, 2009; Novas et al., 2009; Sereno and Larsson, 2009).

The mandibular symphysis in *Caipirasuchus paulistanus* is relatively long and the ventral exposure of the splenial is very modest, occurring only in the region of the mandibular symphysis, whereas *Simosuchus* exhibits a very short symphysis and *Notosuchus*, *Araripesuchus*, and *Baurusuchus* possess an

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extensive ventral exposure of the splenial (Buckley et al., 2000; Ortega et al., 2000; Kley et al., 2010).

The main singular feature of *Caipirasuchus paulistanus* occurs in the premaxilla. This bone has a small projection anterodorsally, which resides above the external naris, excluding the nasals from the narial border. Therefore, the external naris is bordered only by the premaxillae. *Simosuchus* presents a dorsolateral projection in the premaxilla entering between maxilla and nasal, whereas in *Caipirasuchus* this dorsal projection extends anteromedially and contacts the anterior portion of the nasal (Kley et al., 2010). This pattern of sutures around the naris observed in *Caipirasuchus paulistanus* is unique for Notosuchia; however, it occurs in many other crocodyliform lineages, especially those with elongate rostra.

The snout in *Caipirasuchus paulistanus* is oreinorostral and without any constriction, furrow, or depression in dorsal aspect between the bones. This differs from *Anatosuchus*, whose maxilla is laterally expanded, and *Mariliasuchus*, which displays a constriction, giving the premaxilla a bulbous aspect. An opening or notch in the premaxilla-maxilla contact is observed in *Comahuesuchus*, *Malawisuchus*, *Uruguaysuchus*, *Morrinhosuchus*, and *Araripesuchus gomesii* Price, 1959 (Rusconi, 1933; Price, 1959; Carvalho and Bertini, 1999; Gomani, 1997; Martinelli, 2003, Sereno et al., 2003; Nobre et al., 2007; Iori and Carvalho, 2009).

The genus *Sphagesaurus* has a slight anteroposterior projection in the maxilla and premaxilla in line with the jugal, as well as a slight depression in the region of the contact between the nasal-maxillary suture and the premaxilla. These structures do not occur in *Caipirasuchus paulistanus* (Pol, 2003; Andrade and Bertini, 2008). *Sphagesaurus* displays a triangular depression in the preorbital region; this structure does not exist in *Caipirasuchus paulistanus*, which in this region is slightly concave dorsoventrally, and shows an antorbital fenestra that is well developed, elongate, and oval. This opening is small and circular in *S. montealtensis*, about half as large as in *Caipirasuchus paulistanus*. *Sphagesaurus huenei* does not have an antorbital fenestra (Pol, 2003; Andrade and Bertini, 2008).

The lacrimal in *Caipirasuchus paulistanus* displays an anterior dorsal projection that is co-linear with the anterior margin of the antorbital fenestra, whereas in *S. montealtensis* this projection surpasses the antorbital fenestra. In lateral view, *Caipirasuchus paulistanus* shows the jugal as an anteroposteriorly straight bar without any lateral projection, unlike *Simosuchus clarki*, with its curved and posteriorly downward-projected jugal, *Adamantinasuchus navae*, whose jugal has a laterally projected crest and is arched in the central portion of the bone, and *Yacarerani boliviensis*, which has a laterally projecting prong in the jugal that is also dorsoventrally flattened (Buckley et al., 2000; Nobre and Carvalho, 2006, Novas et al., 2009).

In dorsal view, the skull of *Caipirasuchus paulistanus* has a triangular outline, similar to those of *Araripesuchus gomesii*, *Araripesuchus buitreraensis* Pol and Apesteguia, 2005, *Araripesuchus patagonicus* Ortega, Gasparini, Buscalioni, and Calvo, 2000, *Candidodon itapecuruense*, *Uruguaysuchus aznarezi*, *U. terrai*, *Malawisuchus mwakasyungutiensis*, *Sphagesaurus huenei*, and *S. montealtensis*.

Caipirasuchus paulistanus has long narrow nasals, like those of *Anatosuchus minor*, which become anteriorly pointed, and similar to those of *Malawisuchus mwakasyungutiensis*. They are different from those of *Notosuchus terrestris*, whose nasals are short and wide, and *Yacarerani boliviensis*, which displays rostrally expanded nasals above the external naris. *Comahuesuchus*, *Malawisuchus*, and *Simosuchus* exhibit a short nasal-maxilla contact, whereas in *Caipirasuchus paulistanus* this contact is very long. The nasal posteromedially contacts a projection of the frontal in *Caipirasuchus paulistanus*. This is distinct, for instance, from *M. mwakasyungutiensis*, in which this contact only occurs posteriorly (Gomani, 1997; Carvalho and Bertini, 1999; Martinelli, 2003; Sereno et al., 2003; Novas et al., 2009).

In *Caipirasuchus paulistanus*, the frontal contacts the postorbital posterolaterally, whereas in *A. minor* this contact is completely lateral. The frontal in *Caipirasuchus paulistanus* exhibits a longitudinal crest, whereas in *C. itapecuruense* this bone is flat (Nobre and Carvalho, 2002; Sereno et al., 2003). In *Caipirasuchus paulistanus*, the contact between the supraorbital bones (anterior and posterior) is not significant and a fenestra is formed, bordered by the supraorbital, frontal, and postorbital, whereas in *Araripesuchus* the supraorbital bones do not touch. In *Simosuchus clarki*, these bones are large and display a wide contact without any space between them (Buckley et al., 2000; Ortega et al., 2000).

Caipirasuchus paulistanus has the pterygoid bordering the palatal fenestra posterolaterally and contacting the palatine medially, a trait shared with *Comahuesuchus brachibucallis* and differing from *Notosuchus terrestris*, whose ectopterygoid borders the palatal fenestra posteriorly and posterolaterally, and contacts the palatine through an anteromedial projection (Martinelli, 2003). The distal tips of the ectopterygoid and the proximal tips of the pterygoid project more ventrally in *Caipirasuchus paulistanus* than in *S. montealtensis*. This projection imparts to *Caipirasuchus paulistanus* a more acute angle between the ventral plane of the maxilla and that of the palatal fenestra (135° in *Caipirasuchus paulistanus* and approximately 147° in *S. montealtensis*).

The palatal fenestra in *Sphagesaurus montealtensis* is small and situated on a less inclined surface than in *Caipirasuchus paulistanus*. *Caipirasuchus paulistanus* does not have a maxilopalatal fenestra, a structure that occurs in *M. amarali* and *Notosuchus terrestris*. *Caipirasuchus paulistanus* has a vertically directed quadrate that does not project laterally, which differs from *Notosuchus terrestris*, in which this bone is inclined downward and outward (Carvalho and Bertini, 1999).

The skull of *Caipirasuchus paulistanus* is the tallest among the Sphagesauridae, markedly more so than in *Armadillosuchus arrudai*, which has a dorsoventrally flattened skull (in which the skull roof is wide, with the squamosal bones projecting lateroventroposteriorly). The snout of *Armadillosuchus* is proportionally wider than in the other Sphagesauridae (Marinho and Carvalho, 2009).

The diagnosis proposed for Sphagesauridae by Marinho and Carvalho (2007) includes new characters, mainly in relation to the disposition of the teeth. The pattern found in *Caipirasuchus paulistanus* (with mesioposteriorly compressed posterior teeth, with the major axis oriented obliquely; maxillary teeth with one keel positioned posterolingually, whereas in the posterior dentary teeth the keels are positioned anterolabially; the maxillary and anterior dentary teeth with a crown circular in section, and the maxillary teeth and posterior dentary teeth with a triangular cross-section) indicates its inclusion in this family. Nevertheless, other diagnostic traits, such as the laterally expanded and dorsoventrally compressed jugal, and the premaxilla with two or three teeth, do not occur in *Caipirasuchus paulistanus*. Andrade and Bertini (2008) presented a new diagnosis for Sphagesauridae similar to the one for the genus *Sphagesaurus*. This must be revised, mainly in relation to the number of teeth and form of the anterior region of the premaxilla.

Morphological Analysis and Experimental Data

Caipirasuchus has two distinct regions of the skull and mandible, a tapered rostrum, and a very tall posterior part of the skull. The taper of the skull and mandible may be associated with diet, because an anteriorly projected rostrum increases the length of the region for apprehension of the food. The following osteological traits influenced this development: the anteriorly projected dentary and with multiple diastemata, one diastema in

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the premaxilla and another between the fourth alveolus of the premaxilla and the first of the maxilla, the dorsal extent of the premaxilla, long nasals, and the palatines contacting the maxillae by a cuneiform process.

The posterior half of the skull is very tall and the bones involved in jaw muscle attachments are dorsoventrally expanded. The pterygoids and ectopterygoids are ventrally oriented and are almost perpendicular to the cranial roof. This inclination slightly influences the rostral pterygoid muscle length, and makes the region of the skull-mandible articulation deeper. This configuration would increase the length of many of the jaws muscles, primarily the external mandibular adductor and caudal mandibular adductor muscles. The caudal intermandibular foramen is large, which denotes a relatively thick intramandibular muscle in this region. A tall skull and mandible indicates the presence of long muscle fibers and consequently the potential for greater muscle extension and a greater gape.

The bite of the animal was simulated with plasticine, and two regions of action were observed. In the anterior region (with the conical teeth), the mesial-most teeth pierce and seize, acting in prey capture and apprehension. The posterior region (with teeth that have a triangular crown and oblique implantation) were not effective in piercing but had extensive occlusion, so although this region could also assist in apprehension, its main function would be in food processing.

The morphology of the teeth that are obliquely implanted is the same in both the skull and mandible, with differences occurring in the orientation of the carinae. In the maxilla they are posteromesially oriented, whereas in the mandible the carinae are anterolaterally oriented. This arrangement allows an antagonistic action between the carinae of maxillary and mandibular teeth during the propalinal jaw movement that has been reconstructed for sphagesaurids (Pol, 2003; Marinho and Carvalho, 2007). Some lateral movement of the mandible would also be necessary for an effective contact between the carinae.

Phylogenetic Analysis

The phylogenetic relationships of the new species were obtained using TNT (Goloboff et al., 2008). A strict consensus of the 10 most parsimonious trees obtained (CI = 0.35; RI = 0.66; tree length = 801 steps) is presented. The data set used herein was based on a previously published data set (Novas et al., 2009), with the addition of four taxa: *Sphagesaurus montealtensis*, *Armadillosuchus arrudai*, *Morrinhosuchus luziae*, and the new species (Appendix 1). The data set is composed of 234 characters and 55 taxa, comprising 54 crocodylomorph taxa plus an outgroup (*Gracilisuchus stipanicicorum*). Bremer support was calculated using the BREMER.RUN script supplied with TNT.

The following traits support the notosuchian node: ventrally opening notch on the ventral edge of the rostrum at the premaxilla-maxilla contact reduced or absent; presence of posterior peg on the symphysis; quadrate major axis directed ventrally; large and aligned neurovascular foramina present on the lateral maxillary surface; number of sacral vertebrae more than two; all caudal vertebrae amphicoelous or amphyplantian, insertion area for M. pterygoideous posterior extends onto the lateral surface of angular; dentary does not extend posteriorly beneath the mandibular fenestra; and retroarticular process with an extensive rounded, wide, and flat (or slightly concave) surface projecting posteroventrally and facing dorsomedially. The node Sphagesauridae is supported by the absence of the ventrally opening notch on ventral edge of rostrum at premaxilla-maxilla contact and by compressed, obliquely oriented crowns of maxillary teeth.

The cladistic analysis shows notosuchians with posterior teeth disposed obliquely occurring in two regions of the phylogenetic tree (Fig. 4). The first group includes *Notosuchus*, *Mariliasuchus*, *Adamantinasuchus*, and *Yacarerani*. The second is composed by the sphagesaurids—*Sphagesaurus huenei*, *S. montealtensis*, *Armadillosuchus*, and *Caipirasuchus*, which forms a monophyletic clade that is the sister group of *Chimaerasuchus*. Novas et al. (2009) correlated the complex dental patterns within notosuchians as a result of a prior acquisition, the propalinal motion of the mandible. This high dental diversification may have generated parallelism in the oblique implantation of the teeth, which would explain the occurrence of the two groups. Marinho and Carvalho (2007) included *Adamantinasuchus* within the Sphagesauridae, based mainly in the disposition and arrangement of the posterior teeth. The phylogenetic analysis presented here does not confirm this proposal, and *Adamantinasuchus* is found to be positioned closer to the notosuchids.

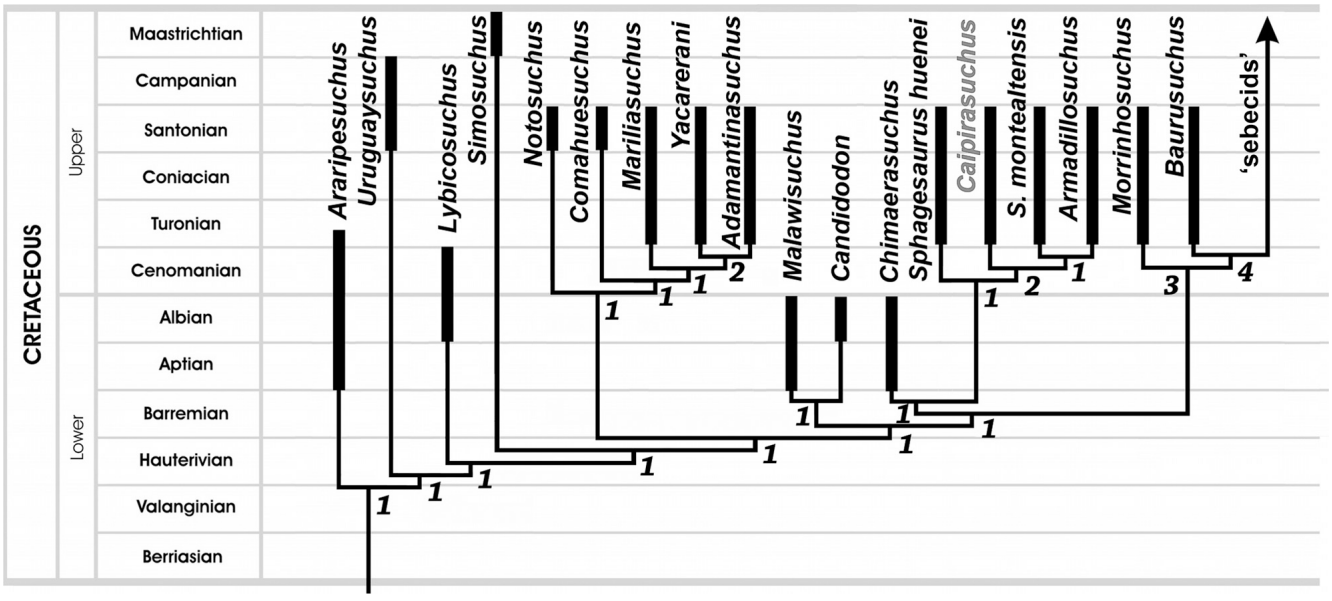

FIGURE 4. Strict consensus of the 10 most parsimonious trees (CI = 0.35; RI = 0.66), each with 801 steps. The phylogenetic relationships obtained show *Caipirasuchus paulistanus* within Notosuchia and among the derived sphagesaurids. Values of Bremer support are shown below the branches (modified from Novas et al., 2009). See Supplementary Data 1 (www.vertpaleo.org/jvp/JVPcontents.html) to see the complete cladogram.

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FIGURE 5. Restoration of the head of *Caipirasuchus paulistanus*.

CONCLUSIONS

The skull and mandible of *Caipirasuchus paulistanus* are the most completely known among the sphagesaurids of the Bauru Basin. The skull has all the bones of the snout and a partial palate and the mandible is almost complete. The holotype of *Caipirasuchus paulistanus* (MPMA 67-0001/00) has been compared with several species attributed to the Notosuchia. It shares many synapomorphies with *Sphagesaurus*, related mainly to tooth morphology and orientation. However, *Caipirasuchus paulistanus* has a taller and more anteriorly tapered skull and mandible, as well as other peculiar characteristics, such as a premaxilla with four teeth, a well-developed antorbital fenestra, and an external naris bordered only by the premaxillae. A cladistic analysis supports the monophyly of the Sphagesauridae including *Caipirasuchus*, *Armadillosuchus*, and both species of *Sphagesaurus*.

The skull and the mandible exhibit two distinct regions: the much-tapered rostrum and the very tall posterior half (Fig. 5). The region of the insertion of the jaw muscles in the skull and mandible is tall, suggesting relatively larger muscles than in related forms, and thus the presence of strong muscles and consequently a powerful bite. The dentition can be divided in two parts, the anterior, used for apprehension, and the posterior, used for processing food.

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APPENDIX 1. The data set used in the phylogenetic analyses was based on a previous published data set (Novas et al., 2009), with the inclusion of the data of the taxa below.

Caipirasuchus paulistanus

```
1 0 0 0 0 0 0 1 0 1 0 1 1 0 ? 1 1 1 0 0 1 1 2
1 1 1 0 0 1 ? 0 ? 1 ? 1 2 2 1 0 0 1 0 0 0 ? ?
? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 2 1 2 1 2
0 0 1 0 1 0 0 1 1 0 0 0 ? ? ? ? ? ? ? ? ? ? ?
? ? 0 ? 0 0 0 0 0 0 1 0 1 1 1 2 ? ? 0 ? ? ? ?
0 ? 0 1 1 1 1 0 ? 1 0 1 1 0 1 0 ? 0 1 1 0 1 1
0 0 ? 0 1 ? ? 0 ? 0 1 1 ? ? ? 0 1 0 0 0 0 0 0
1 0 0 0 ? 1 ? 0 0 1 0 0 0 0 0 ? 0 ? 1 0 1 0 0
0 0 0 1 0 1 1 ? 1 1 0 0 0 1 ? ? 1 0 0 ? 0 ? ?
0 0 0 0 0 0 0 0 1 ? 0 0 ? ? ? 1 1 0 0 1 0 1 1
1 0 0 0
```

Sphagesaurus montealtensis

```
1 0 1 ? 0 0 0 1 0 1 0 0 ? 0 ? 1 1 0 1 0 1 1 2
1 1 1 0 0 1 0 0 ? 1 ? 1 1 2 ? 0 0 1 0 0 0 ? ?
? ? 2 0 ? ? ? ? ? 0 ? ? ? ? ? ? ? 0 ? 1 2 1 2
0 ? ? ? ? 0 ? 1 ? 0 0 0 ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? 1 1 ? ? ? 1 2 ? ? 0 ? ? ? ?
? ? 0 1 1 1 1 ? ? 1 0 1 1 0 1 0 ? 0 1 1 0 1 1
1 0 ? 0 1 ? ? 0 ? 0 ? 1 ? ? ? 0 1 0 0 0 0 0 0
1 0 0 0 ? ? ? 0 0 ? ? 0 0 0 0 ? 0 ? 1 0 ? 0 0
0 0 ? 1 0 1 1 ? 1 1 0 ? ? 1 ? ? 1 0 0 ? 0 ? ?
0 0 0 0 0 0 ? ? ? ? ? 0 ? ? ? 0 1 0 ? 1 0 ? 1
? ? ? ?
```

Armadillosuchus arrudai

```
2 0 1 0 0 0 ? 1 0 ? 1 ? ? 0 ? 1 1 0 1 0 1 1 2
1 1 1 0 0 1 0 0 ? 1 1 1 1 ? ? ? ? ? ? ? ? ? ?
? ? 2 1 ? 1 ? ? ? 0 0 ? ? ? ? ? ? ? 2 1 3 1 ?
? ? ? ? ? ? ? ? ? 1 0 0 0 ? ? ? ? ? ? ? ? ? ?
? ? {012} {01} 2 {01} ? ? {01} ? 1 0 1 2 1 1 ? ?
0 ? ? ? ? ? ? 0 ? 1 1 1 0 ? 1 0 1 ? ? 1 1 1 ?
? 1 0 1 1 1 0 1 ? 1 ? 1 1 ? 0 1 1 ? ? ? 0 1 ?
? ? 0 0 0 1 0 0 0 0 0 0 1 0 ? {01} 0 0 ? ? 1 ? 0
? ? ? ? 0 0 ? ? 1 1 ? ? 1 ? ? 1 ? ? ? 1 ? ? 1
0 ? ? 0 ? ? 0 1 0 0 0 0 ? ? 0 ? ? 0 ? ? ? 0 1
0 0 ? ? ? ? ? ? ? ? ?
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Morrinhosuchus luziae

```
1 ? 1 ? 0 0 ? ? 1 1 ? ? 0 0 ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 2 ? ?
? ? ? ? ? 0 ? 1 ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? 2 ? ? ? ? ? ? ?
? ? 1 1 0 ? ? ? 0 1 0 0 0 0 ? ? ? ? ? 1 ? 0 1
? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? 0 ? 0 0 0 0
? ? ? ? ? ? ? ? ? 0 0 ? 0 ? ? ? ? 0 ? 0 ? ? 0 0
0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? ? ?
0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ?
? ? ? ?
```

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