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Taxonomic reappraisal of the sphagesaurid crocodyliform *Sphagesaurus montealtensis* from the Late Cretaceous Adamantina Formation of São Paulo State, Brazil

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Abstract

Sphagesaurus montealtensis is a sphagesaurid whose original description was based on a comparison with *Sphagesaurus huenei*, the only species of the clade described to that date. Better preparation of the holotype and the discovery of a new specimen have allowed the review of some characteristics and the identification of several synapomorphies of *S. montealtensis* with the genus *Caipirasuchus*: presence of antorbital fenestra; external nares bordered only by the premaxillae; premaxilla with four teeth and one diastema (between the 3rd–4th teeth); one diastema between the 4th premaxillary tooth and the 1st maxillary tooth; dentary with ten teeth and two diastemata (between the 4th–5th and 5th–6th teeth); nasal with a groove parallel to the suture with the frontal bone; nasal long, with an acute anterior margin touching anterolaterally the premaxilla, jugal is a straight bar in the lateral view; frontal is longer than wide; a dorsoventrally expanded and vertically oriented quadrate with a groove separating the medial and lateral condyles; the frontal has a discrete sagittal crest; dentary with six posterior sphagesauriform teeth and four anterior conical teeth, the first three are the smallest of the series and the fourth is slightly laterally compressed. The referral of *S. montealtensis* to the genus *Caipirasuchus*, as *Caipirasuchus montealtensis* comb. nov. is proposed here, based on the new taxonomic observations and the results of a phylogenetic analysis.

Key words: *Caipirasuchus montealtensis*, Sphagesauridae, Bauru Basin

Introduction

The Bauru Basin (Fig. 1) has been a significant source of Cretaceous crocodyliforms, with tens of individuals discovered and approximately twenty formally described species distributed among Notosuchia, Peirosauridae and Trematochampsidae (Price 1945, 1950, 1955, 1959; Carvalho & Bertini 1999; Campos *et al.* 2001, 2011; Carvalho *et al.* 2004, 2005, 2007; Nobre & Carvalho 2006; Nobre *et al.* 2007; Andrade & Bertini 2008; Marinho & Carvalho 2009; Iori & Carvalho 2009, 2011; Nascimento & Zaher 2010; Iori *et al.* 2011; Kellner *et al.* 2011; Montefeltro *et al.* 2011; Iori & Garcia 2012; Marinho *et al.* 2013).

The Crocodyliformes comprise the most diverse group among the tetrapods of the Bauru Basin, with taxa smaller than one meter in length to others exceeding four meters, different feeding habits and the possible occupation of several niches including terrestrial predators, herbivores and omnivores and semi-aquatic predators (Price 1945, 1950, 1955; Carvalho & Bertini 1999; Iori & Carvalho 2009; Marinho & Carvalho 2009; Kellner *et al.* 2011; Iori & Garcia 2012; Marinho *et al.* 2013). This peculiar crocodyliform fauna is important due to its potential correlation with other Gondwanan landmasses and application for paleoclimatic, paleoenvironmental and paleobiogeographic assessments. (Nobre *et al.* 2008; Carvalho *et al.* 2010). Sphagesaurids have a unique dentition and a complex masticatory mechanism, revealing possible herbivorous or omnivorous habits (Pol 2003; Andrade & Bertini 2008; Iori & Carvalho 2011).

The Sphagesauridae is mainly characterized by the presence of obliquely implanted posterior teeth, with triangular crowns, covered by a relatively thick layer of enamel and a denticulate keel (Kuhn 1968; Marinho & Carvalho 2007; Iori *et al.* 2011). Five species have been described so far: *Sphagesaurus huenei* Price, 1950, *Sphagesaurus montealtensis* Andrade & Bertini, 2008, *Armadillosuchus arrudai* Marinho & Carvalho, 2009, *Caipirasuchus paulistanus* Iori & Carvalho, 2011, and *Caryonosuchus pricei* Kellner, Campos, Riff & Andrade, 2011. Marinho & Carvalho (2007) included *Adamantinasuchus navae* Nobre & Carvalho, 2006 within the Sphagesauridae, but that was refuted by Iori *et al.* (2011) based on an analysis of its lower dentition and its distinct masticatory mechanism.

Andrade & Bertini (2008) provided a fairly accurate description of the holotype of *Sphagesaurus montealtensis* (MPMA 15-0001/90). However, some data were incorrectly noted due to the absence of the more distal region of the rostrum and the incomplete preparation of the fossil. Iori *et al.* (2011) reported a new specimen (MPMA 68-0003/12), redescribed some of these characteristics, and suggested a taxonomic revision of the species. In the present study, a taxonomic reappraisal of *S. montealtensis* is performed based on an analysis of the fossil MPMA 15-0001/90 (species holotype), and of a new specimen (MPMA 68-0003/12) and the discovery of large number of synapomorphies of the genus *Caipirasuchus*.

Geological Setting

The fossils analyzed (MPMA 15-0001/90, MPMA 67-0001/00 and MPMA 68-0003/12) here originate from the rural area of the State of São Paulo, in the Bauru Basin (Fig. 1). This basin was formed in the southern center of the South American Platform by thermomechanical subsidence and was filled in a semi-arid to arid climate, between the Coniacian and the Maastrichtian (Dias-Brito *et al.* 2001; Fernandes & Coimbra 1994, 1996, 2000). The studied specimens were found in sandstones of the Adamantina Formation, of Turonian-Santonian age according to micropaleontological and isotopic studies by Dias Brito *et al.* (2001). Other research groups concluded that this unit was Campanian-Maastrichtian in age based in microfossils (Gobbo-Rodrigues 2001), vertebrates (Bertini *et al.* 1993) and radiometric data (Andrade da Silva 2006). The fossils MPMA 15-0001/90 and MPMA 67-0001/00 are from Monte Alto, São Paulo State and were found in rocks composed by very fine, well sorted matrix and well cemented reddish sand containing carbonate nodules and concretions (Iori & Carvalho 2011). The facies features of the extraction layer of the specimen MPMA 68-0003/12, found in Catanduva, São Paulo State, are very similar to those found in Monte Alto; however, the matrix is poorly cemented, and the number of concretions is considerably less.

Institution Abbreviations: DGM, Departamento de Produção Mineral, Rio de Janeiro, Brazil; MPMA, Museu de Paleontologia “Prof. Antonio Celso de Arruda Campos”, Monte Alto, São Paulo, Brazil; RCL, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil); and UFRJ DG, Departamento de Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Systematic Palaeontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone & Whybrow, 1983

Notosuchia Gasparini, 1971

Sphagesauridae Kuhn, 1968

Referred specimens. *Sphagesaurus huenei* (DGM 332-R, DGM 333-R, RCL-100), *Armadillosuchus arrudai* (UFRJ DG 303-R, MPMA 64-0001/04, UFRJ DG 380-R), *Caryonosuchus pricei* (DGM 1411-R), *Caipirasuchus paulistanus* (MPMA 67-0001/00) and *Caipirasuchus montealtensis* comb. nov. (MPMA 15-0001/90, MPMA 68-0003/12)

Diagnosis. The unique character of the Sphagesauridae is the presence of six sphagesauriform teeth in each maxilla and six in each dentary (Iori *et al.* 2011). The sphagesauriform teeth possess long roots (approximately 1.5 times the height of the crown) and short crowns, triangular in shape and covered by a relatively thick layer of enamel with a denticulate keel and longitudinal striae (Kuhn 1968). These teeth are medioposteriorly compressed with the long axis oriented obliquely; the keels display a posterolingual orientation in the maxillary teeth and an anterolabial orientation in the mandibular posterior teeth (Marinho & Carvalho 2007).

Other general characteristics of the sphagesaurids are: the crowns of the premaxillary teeth are circular in cross-section; the premaxilla has at least two teeth: a hypertrophied caniniform tooth and a post-caniniform tooth with a conical crown and circular cross-section; the maxilla has six teeth, all sphagesauriform, that are teardrop-shaped in cross-section and obliquely implanted, except for the last tooth of the series, which may have its major axis transversely oriented to the sagittal axis; the dentary has six posterior sphagesauriform teeth, all obliquely implanted, except for the first tooth of the series, which is anteroposteriorly oriented; the presence of three to four anterior dentary teeth, all conical and bearing apico-basally oriented grooves (Iori *et al.* 2011).

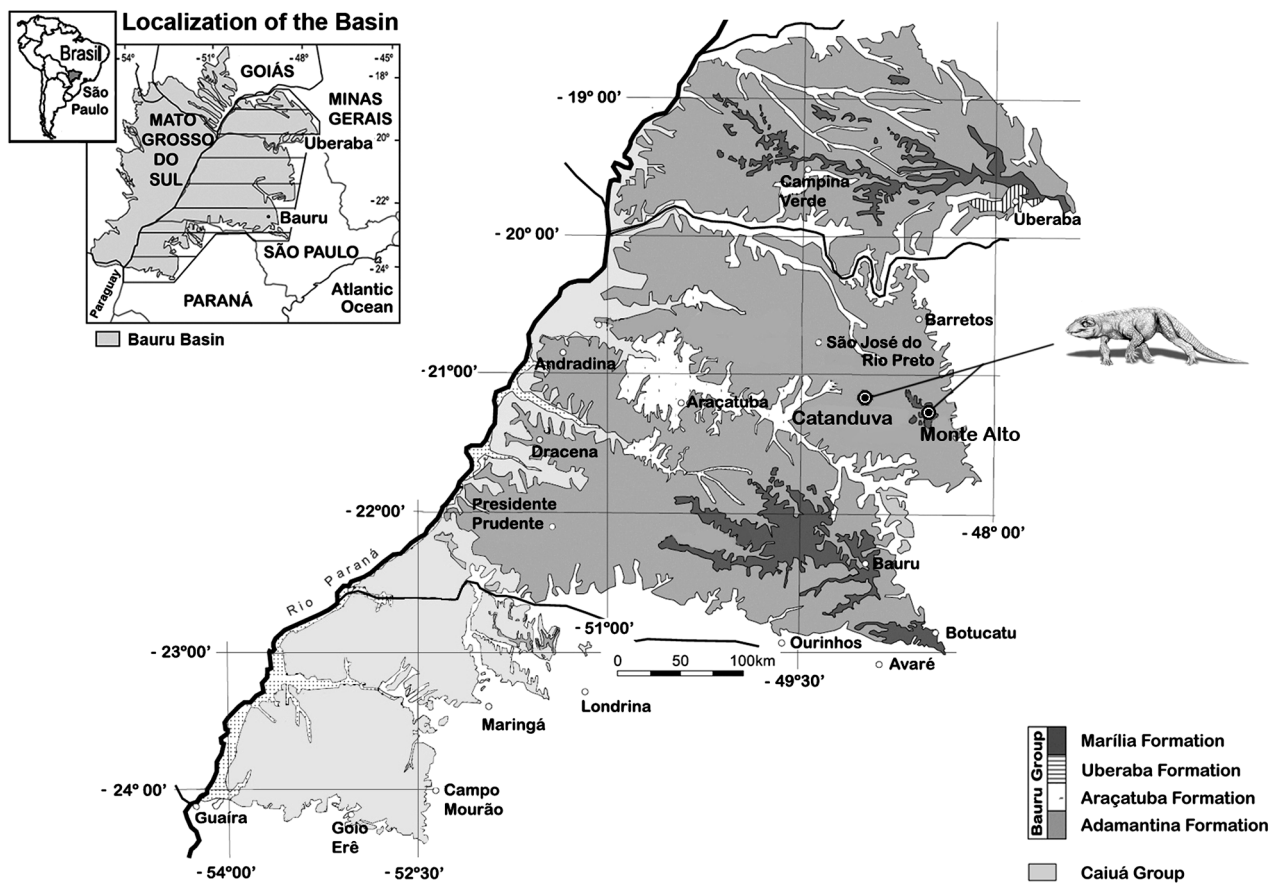


FIGURE 1. Lithostratigraphic map of the eastern part of the Bauru Basin (modified from Fernandes & Coimbra 2000).

Caipirasuchus Iori & Carvalho, 2011

Holotype. MPMA 67-0001/00, a cranium and mandible (Fig. 2, 3, 4) and part of the post-cranium.

Referred specimens. MPMA 15-0001/90, the majority of the cranium and the anterior portion of the mandible (Fig. 5, 6, 7) and MPMA 68-0003/12, a nearly complete cranium and mandible (Fig. 8, 9, 10) and the posterior portion of the post-cranium.

Revised diagnosis for the genus. Sphagesaurid with the following synapomorphies: presence of antorbital fenestra; external nares bordered only by the premaxillae; premaxilla with four teeth and one distema (between the 3rd–4th teeth); one diastema between the 4th premaxillary tooth and the 1st maxillary tooth; dentary with ten teeth and two diastemata (between the 4th–5th and 5th–6th teeth); nasal with a groove parallel to the suture with the frontal bone.

Other set of characters that diagnose the genus are: a long nasal with an acute anterior margin touching anterolaterally the premaxilla, the jugal bone is a straight bar in the lateral view; frontal is longer than wide; a dorsoventrally expanded and vertically oriented quadrate with a groove separating the medial and lateral condyles; the frontal has a discrete sagittal crest; dentary with six posterior sphagesauriform teeth and four anterior conical teeth, the first three are the smallest of the series and the fourth is slightly laterally compressed.

***Caipirasuchus paulistanus* Iori & Carvalho, 2011**

Holotype. MPMA 67-0001/00, a cranium and mandible (Figs. 2, 3, 4) and part of the post-cranium, found in the municipality of Monte Alto, São Paulo State, Brazil.

Revised diagnosis for the species. *Caipirasuchus* is diagnosed by the following autapomorphies: quadrate with the medial condyle extremely elongate ventrally, lower than the ventral edge of the lateral condyle; the rostral lateral wall is vertical with an abrupt transition to the dorsal surface; presence of an oval antorbital fenestra slightly inclined anterodorsally-posteroventrally and lanceolate supraorbital fenestra with its anterior portion more acute than the posterior one.

The pterygoids and ectopterygoids are very high, with the dorsoventral dimension corresponding to approximately sixty percent of the total height of the cranium. The pterygoid medioventral surfaces are smooth.

***Caipirasuchus montealtensis* Andrade & Bertini, 2008 comb. nov.**

Basionym: *Sphagesaurus montealtensis* Andrade & Bertini, 2008.

Holotype: MPMA 15-0001/90, the majority of the cranium and the anterior portion of the mandible (Figs. 5, 6, 7), from the municipality of Monte Alto, São Paulo State, Brazil.

Referred specimen. MPMA 68-0003/12, a nearly complete cranium and mandible (Figs. 8, 9, 10) and a posterior portion of the post-cranium, discovered in the municipality of Catanduva, São Paulo State.

Diagnosis. This species is diagnosed by the autapomorphic presence of a chamber that opens on the mesoventral wall of the pterygoids as a suboval opening. The antorbital fenestrae in this species are small and subcircular.

Remarks. The first studies of MPMA 15-0001/90 considered the general aspect of the cranium, and referred the specimen to the Uruguaysuchidae (Bertini 1993; Bertini & Arruda-Campos 1995; Bertini & Carvalho 1999; Andrade & Bertini 2003). Andrade *et al.* (2006) conducted a study of the choana, and observed several sphagesaurid features. Andrade & Bertini (2008) described the new species, *Sphagesaurus montealtensis*, which showed several synapomorphies with *Sphagesaurus huenei*.

Description. The unique teeth DGM 332-R and DGM 333-R provided the necessary data for the definition of a new genus and species and the diagnosis for the proposal of a new family (Price, 1950; Kuhn; 1968). These “sphagesauriform” teeth (teeth with short triangular crowns covered by a relatively thick enamel layer, with a denticulate keel and longitudinal striae) are unique enough such that a diagnosis can still be applied to all family members; however, an emended diagnosis for the family is adopted here, based on the proposal by Iori *et al.* (2011), which considers a dental pattern observed in all species of the group in addition to the presence of sphagesauriform teeth. This pattern consists of the following: upper dentition where only the premaxillary teeth have a circular cross-section of the crown, while all teeth are sphagesauriform in the maxilla; for a premaxilla with at least two teeth, one hypertrophied caniniform tooth and one post-caniniform tooth with a conical crown and circular cross-section are required; a maxilla with six sphagesauriform, obliquely implanted teeth, except for the most posterior tooth which may present its long axis oriented perpendicularly to the sagittal axis; and dentary with six sphagesauriform posterior teeth, all obliquely implanted, except for the first tooth of the series, which may have its long axis anteroposteriorly oriented.

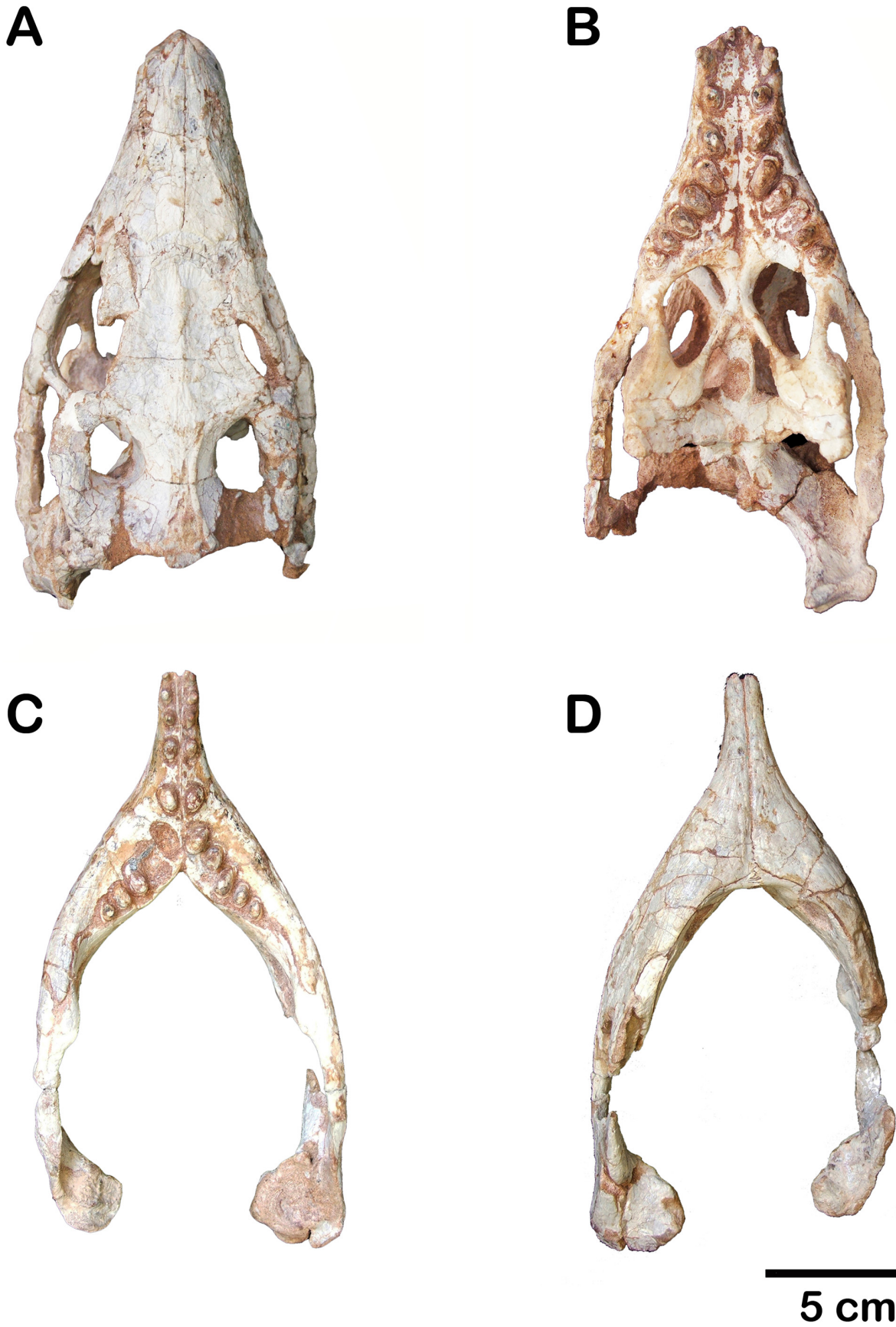


FIGURE 2. Holotype of *Caipirasuchus paulistanus* (MPMA 67-0001/00) Cranium and mandible in dorsal (A and C) and ventral (B and D) views.

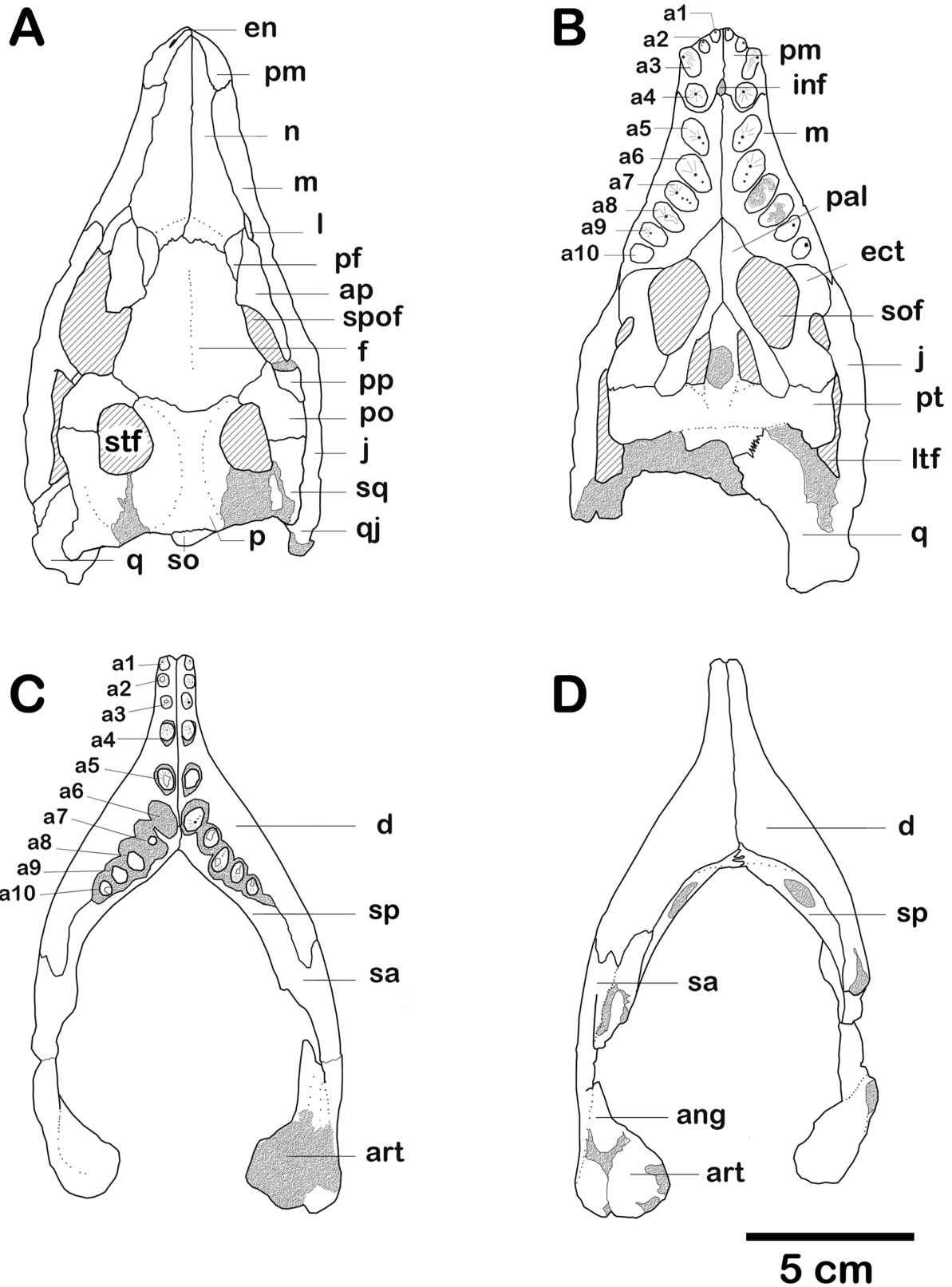


FIGURE 3. Schematic diagram of the holotype of *Caipirasuchus paulistanus* (MPMA 67-0001/00). Cranium and mandible in dorsal (A and C) and ventral (B and D) views. Legend: **a**, alveolus; **ang**, angular; **ap**, anterior palpebral; **art**, articular; **d**, dentary; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **inf**, incisive foramen; **j**, jugal; **l**, lacrimal; **ltf**, laterotemporal fenestra; **m**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pp**, posterior palpebral; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **so**, supraoccipital; **sof**, suborbital fenestra; **sp**, splenial; **spof**, supraorbital fenestra; **sq**, squamosal; **stf**, supratemporal fenestra.

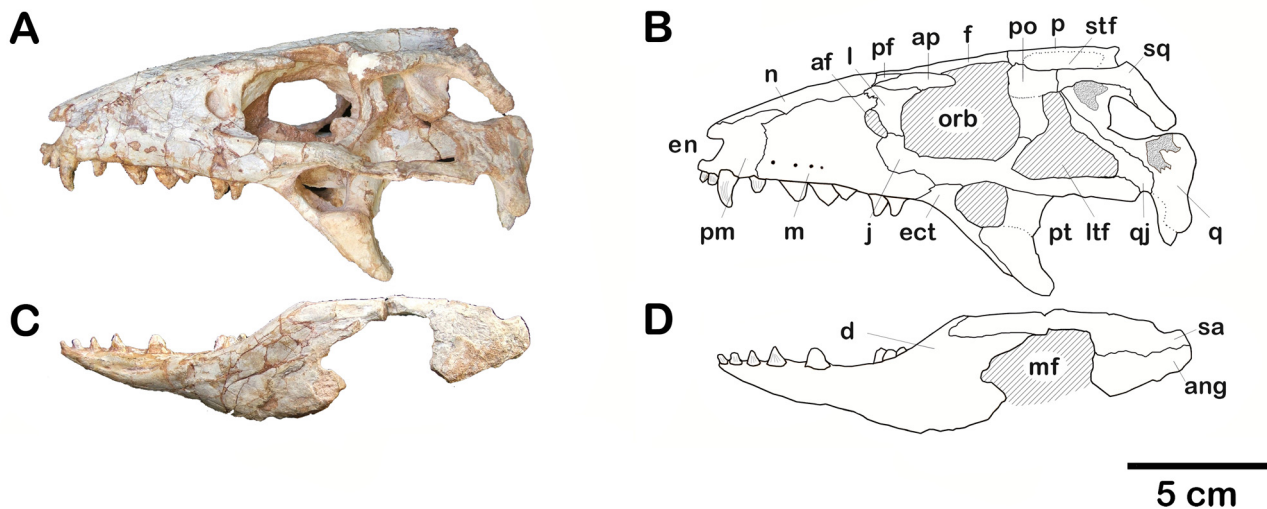


FIGURE 4. Fossil and schematic diagram of the holotype of *Caipirasuchus paulistanus* (MPMA 67-0001/00). Cranium (A and B) and mandible (C and D) in lateral views. Legend: **af**, antorbital fenestra; **ang**, angular; **ap**, anterior palpebral; **d**, dentary; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **j**, jugal; **l**, lacrimal; **ltf**, laterotemporal fenestra; **m**, maxilla; **mf**, mandibular fenestra; **n**, nasal; **orb**, orbit; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sq**, squamosal; **stf**, supratemporal fenestra.

The variation in the teeth number in sphagesaurids occurs in the pre-caniniform teeth of the upper dentition and the anterior teeth of the lower dentition. *Sphagesaurus* shows an edentulous region between the caniniforms, as indicated for *Caryonosuchus pricei* (Pol 2003; Kellner *et al.* 2011). *Armadillosuchus* has one pre-caniniform tooth in each premaxilla (Iori *et al.* 2011), while *Caipirasuchus* exhibits two. In the lower dentition, *Caipirasuchus* exhibits four anterior teeth (pre-sphagesauriform) in each dentary, while *Sphagesaurus*, *Caryonosuchus* and *Armadillosuchus* display three teeth (Pol 2003; Marinho & Carvalho 2009, Iori & Carvalho 2011, Kellner *et al.* 2011).

In the holotype of *Caipirasuchus montealtensis* comb. nov. (MPMA 15-0001/90), the most anterior region of the rostrum is broken. Andrade & Bertini (2008) stated that the lost pre-maxillary region below the external nostril would be too shallow to support more teeth and posited an edentulous region between the caniniforms for the specimen, as is observed in *Sphagesaurus huenei*; however, Iori *et al.* (2011) noted that the left premaxilla, in the medial view, exhibits an alveolus in a longitudinal section located anteromedially to the caniniform alveolus, indicating a more numerous premaxillary dentition. Andrade & Bertini (2008) indicated that the first post-caniniform tooth of the *Caipirasuchus montealtensis* comb. nov. was an obliquely implanted maxillary tooth, but the premaxilla extends beyond the first post-caniniform tooth, which is a conical tooth with a circular cross-section. In larger sphagesaurids, such as *Sphagesaurus* and *Armadillosuchus*, it is possible to observe a posterior process of the premaxilla involving the first post-caniniform tooth, a structure that occurs in all members of the family; however, in smaller sphagesaurids, this projection is very narrow and delicate and can become difficult to identify. The *Caipirasuchus montealtensis* comb. nov. specimens had only the lateral and medial portions of this process preserved, indicating that the first post-caniniform alveolus opens in the premaxilla. Andrade & Bertini (2008) indicated a mandible with nine teeth in each dentary for the fossil MPMA 15-0001/90, with eight preserved pairs of teeth and one assumed pair, which would be procumbent and in the distal region of the mandible. The MPMA 68-0003/12 specimen had all maxillary teeth preserved and implanted; however, all premaxillary alveoli were empty, only the right caniniform was preserved, the right dentary had eight preserved teeth and the left dentary had six preserved teeth. Even with several missing teeth, it is possible to determine that the dentition of *Caipirasuchus montealtensis* comb. nov. was composed with the same number of teeth as *C. paulistanus*, which has a premaxilla with four teeth, a maxilla with six teeth and a dentary with ten teeth. The shape and arrangement of the teeth are also similar in both species: the premaxilla exhibits two small teeth followed by one hypertrophied caniniform and one conical tooth, all with circular cross-sections and marked by longitudinal striae; the first three teeth of the dentary are small, conical, have a circular cross-section and have dorsally faced crowns; the fourth tooth is also conical, with a slightly oval cross-section and longitudinal striae; and the maxillary teeth and the last six teeth of the dentary follow the pattern observed for the entire family.

In general aspects, *Caipirasuchus paulistanus* and *Caipirasuchus montealtensis* comb. nov. have very similar crania and mandibles, and the bone arrangement is almost identical. The crania are narrow, with triangular shapes in the dorsal view, have a very peculiar ornamentation, are oreinirostral and have lateral orbits. It has been observed that in *C. paulistanus*, the cranium and mandible are higher than in *Caipirasuchus montealtensis* comb. nov., a characteristic that is mainly due to the arrangement of the ectopterygoid, palatine and pterygoid bones, the latter of which are very distinct between species.

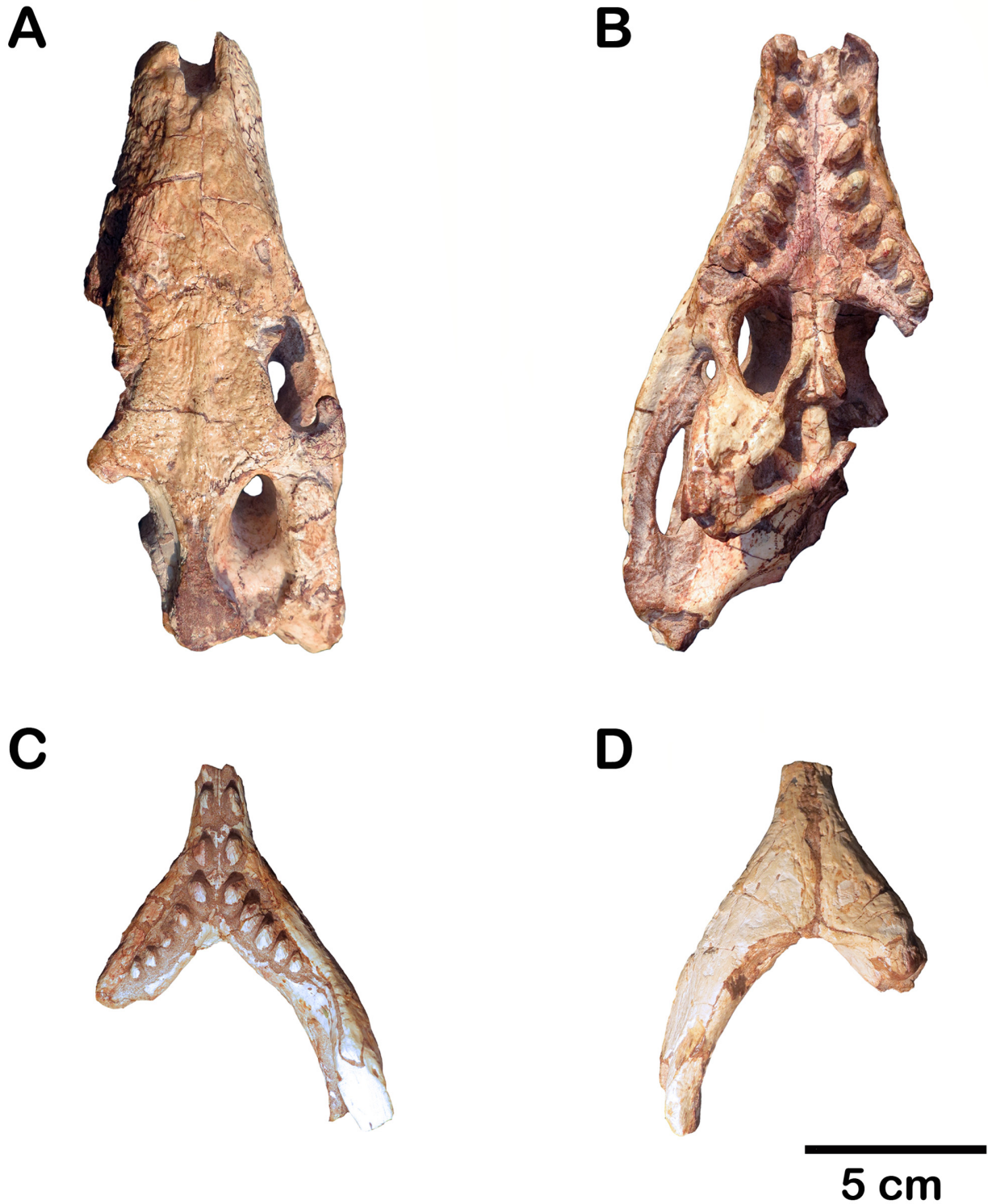


FIGURE 5. Holotype of *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov. (MPMA 15-0001/90). Cranium and mandible in dorsal (A and C) and ventral (B and D) views.

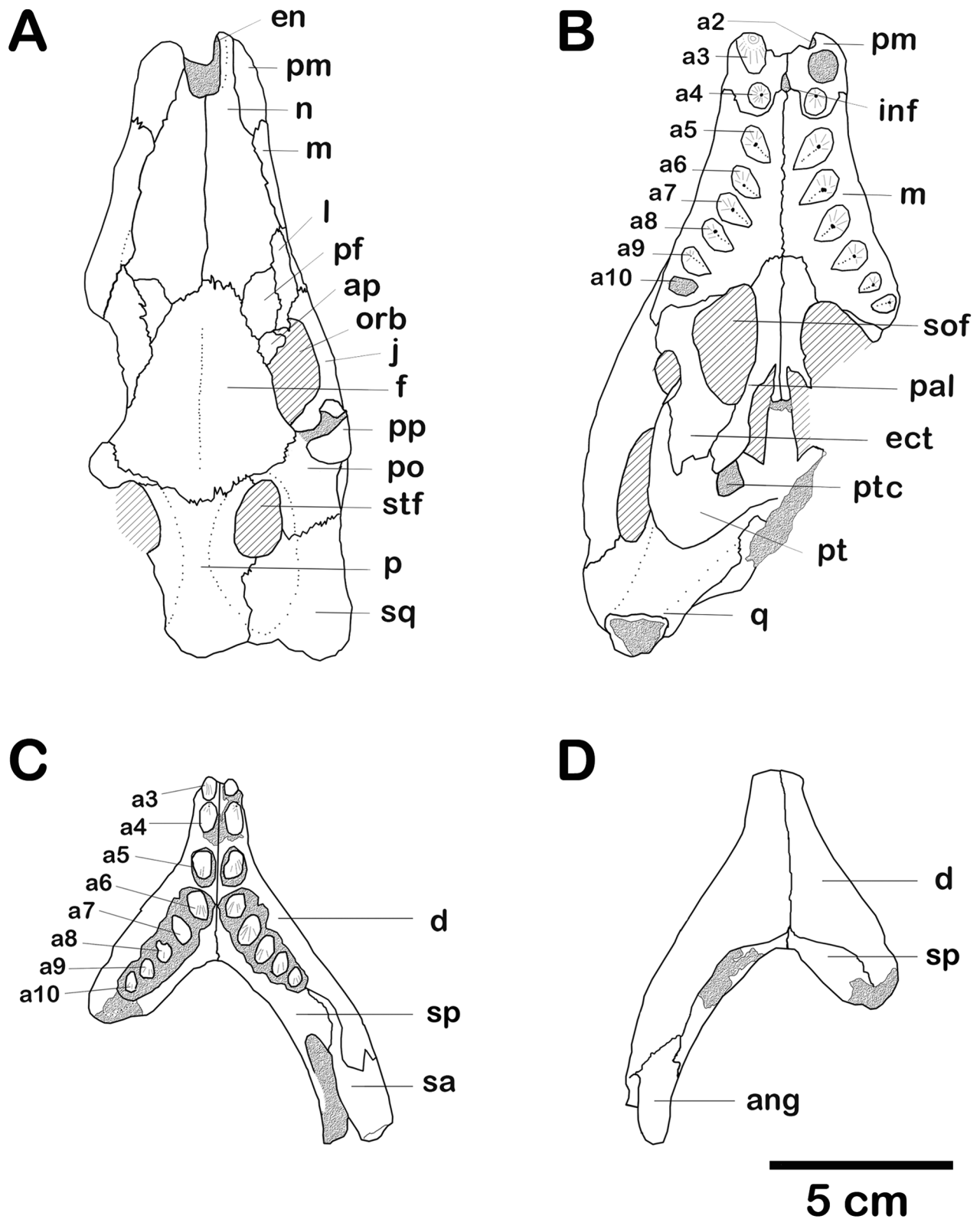


FIGURE 6. Schematic diagram of the holotype of *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov. (MPMA 15-0001/90). Cranium and mandible in dorsal (**A** and **C**) and ventral (**B** and **D**) views. Legend: **a**, alveolus; **ang**, angular; **ap**, anterior palpebral; **d**, dentary; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **inf**, incisive foramen; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **orb**, orbit; **p**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pp**, posterior palpebral; **pt**, pterygoid; **ptc**, pterygoid chamber; **q**, quadrate; **sa**, surangular; **sof**, suborbital fenestra; **sp**, splenial; **sq**, squamosal; **stf**, supratemporal fenestra.

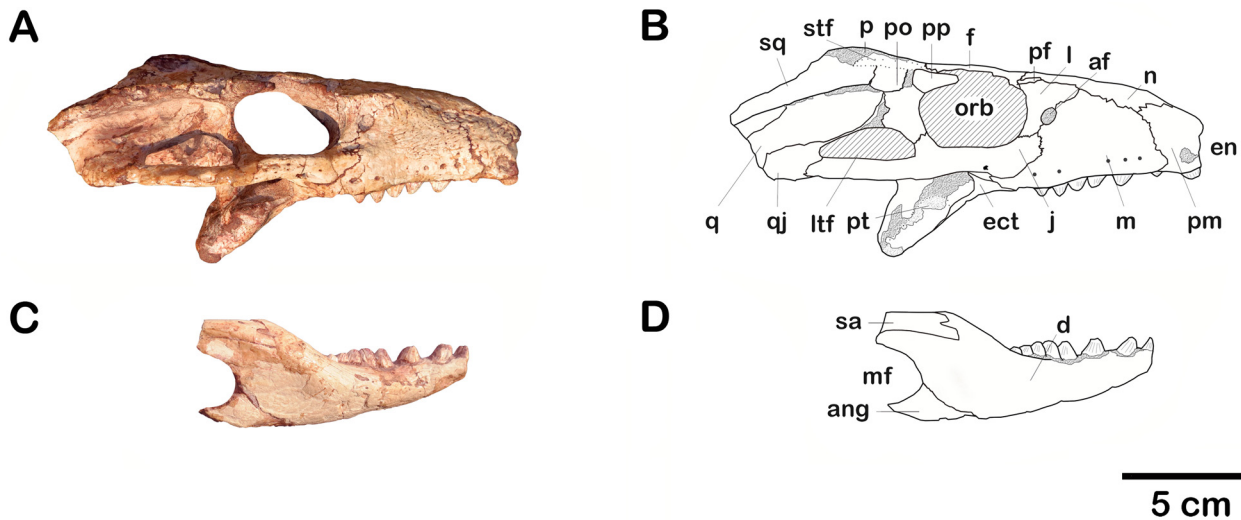


FIGURE 7. Fossil and schematic draw of the holotype of *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov. (MPMA 15-0001/90). Cranium (A and B) and mandible (C and D) in lateral views. Legend: **af**, antorbital fenestra; **ang**, angular; **d**, dentary; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **j**, jugal; **l**, lacrimal; **ltf**, laterotemporal fenestra; **m**, maxilla; **mf**, mandibular fenestra; **n**, nasal; **orb**, orbit; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pp**, posterior palpebral; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sq**, squamosal; **stf**, supratemporal fenestra.

Armadillosuchus, *Sphagesaurus* and *Caryonosuchus* are large sphagesaurids, with crania exceeding 250 mm in total length, while the *Caipirasuchus* crania do not grow over 180 mm in length. Regarding the general shape of the cranium, *Caipirasuchus* displays a longer rostrum and a more lanceolate dorsal outline, while in *Armadillosuchus* and *Sphagesaurus* the rostral regions are shorter and the transition between the rostrum and the posterior portion of the cranium is less smooth. *Caipirasuchus* displays a rostrum that makes up almost half the total cranium length and is relatively more narrow and longer than in *Sphagesaurus* and *Armadillosuchus*. In *C. paulistanus* the rostral narrowing is greater, more gradual and homogenous; the lateral and dorsal planes are nearly flat surfaces and the connection between both planes is marked by a conspicuous edge, while *C. montealtensis* comb. nov. shows a dorsolateral plane, making the transition between the lateral and dorsal planes, in addition to a lateral intumescence on the jugal line. *Caipirasuchus* has long nasal, separate from the external nostril; in *C. paulistanus* they are more anteriorly narrow and are only found on the dorsal and lateral surfaces, with the latter being in contact with the premaxilla and the maxilla (Iori & Carvalho 2011), while in *Caipirasuchus montealtensis* comb. nov. these contacts occur on the dorsolateral surface.

Sphagesaurids present a cranial ornamentation pattern, marked by irregular wrinkles and striae, which is present in almost the entire length of the cranium and lateral of the rostrum and jugal. Laterally, the region near the alveolar margin is smooth and marked by several neurovascular foramina (Andrade & Bertini 2008; Pol 2003; Kellner *et al.* 2011; Iori & Carvalho 2011). Kellner *et al.* (2011) indicated the existence of semicircular grooves in *Caryonosuchus*, and ornamentations with such features are observed in *Caipirasuchus montealtensis* comb. nov. (MPMA 68-0003/12) in the squamosal region preceding the supratemporal fenestra. The medial portions of the parietal and the dorsal surface of the supraoccipital of the *Caipirasuchus* are highly ornamented. Moreover, the genus displays a small concavity on the posteromedial parietal region, a longitudinal crest in the frontal and a grooved region in the nasals that precedes and is parallel to the nasofrontal suture.

Among the five species of sphagesaurids described, the bone arrangement of the cranium is very similar, and the interspecies variations occur in the general shape of the cranium, the dental distribution and the presence or absence of certain structures. Some specific characters are observed in some members of the family, such as the rostral tubercles of *Caryonosuchus* and the presence of a cervical shield in *Armadillosuchus* (Kellner *et al.* 2011; Marinho & Carvalho 2009). *Caipirasuchus* exhibits antorbital fenestrae, unlike *Sphagesaurus huenei* and *Armadillosuchus* (Pol 2003; Marinho & Carvalho 2009); in *C. paulistanus*, this fenestra is oval, dorsal-ventrally elongated and is bordered slightly by the jugal in its lower edge, while, in *Caipirasuchus montealtensis* comb. nov., this fenestra is small, circular and bordered only by the lacrimal and the maxilla. The chamber in the pterygoid was only observed in *Caipirasuchus montealtensis* comb. nov. (Iori & Carvalho 2011, Iori *et al.* 2012).

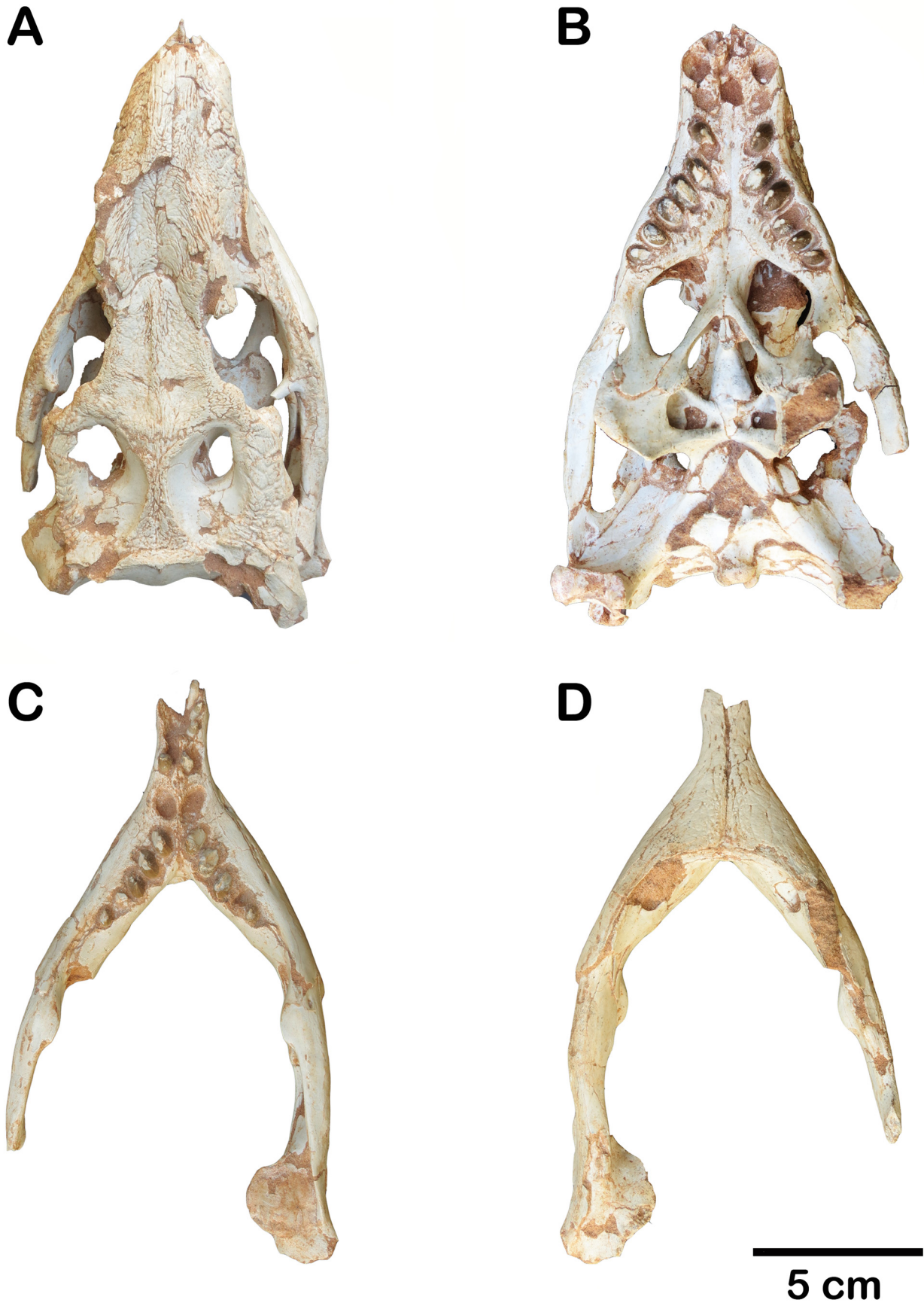


FIGURE 8. The referred specimen of *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov. (MPMA 68-0003/12). Cranium and mandible in dorsal (**A** and **C**) and ventral (**B** and **D**) views.

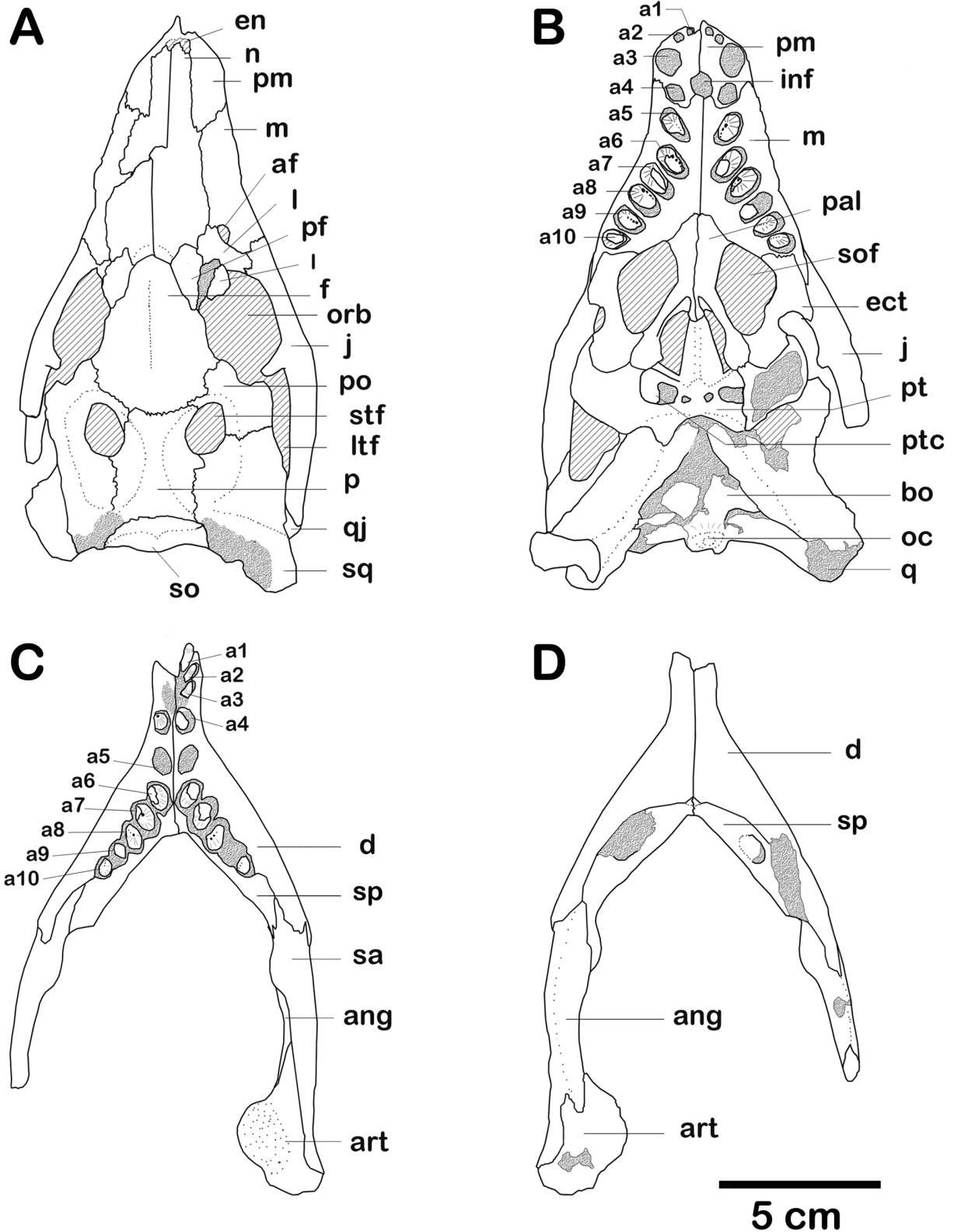


FIGURE 9. Schematic diagram of the referred specimen of *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov (MPMA 68-0003/12). Cranium and mandible in dorsal (**A** and **C**) and ventral (**B** and **D**) views. Legend: **a**, alveolus; **af**, antorbital fenestra; **ang**, angular; **art**, articular; **bo**, basioccipital; **d**, dentary; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **inf**, incisive foramen; **j**, jugal; **l**, lacrimal; **ltf**, laterotemporal fenestra; **m**, maxilla; **n**, nasal; **oc**, occipital condyle; **orb**, orbit; **p**, parietal; **pal**, palatine; **pm**, premaxilla; **pf**, prefrontal; **po**, postorbital; **pt**, pterygoid; **ptc**, pterygoid chamber; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **so**, supraoccipital; **sof**, suborbital fenestra; **sp**, splenial; **sq**, squamosal; **stf**, supratemporal fenestra.

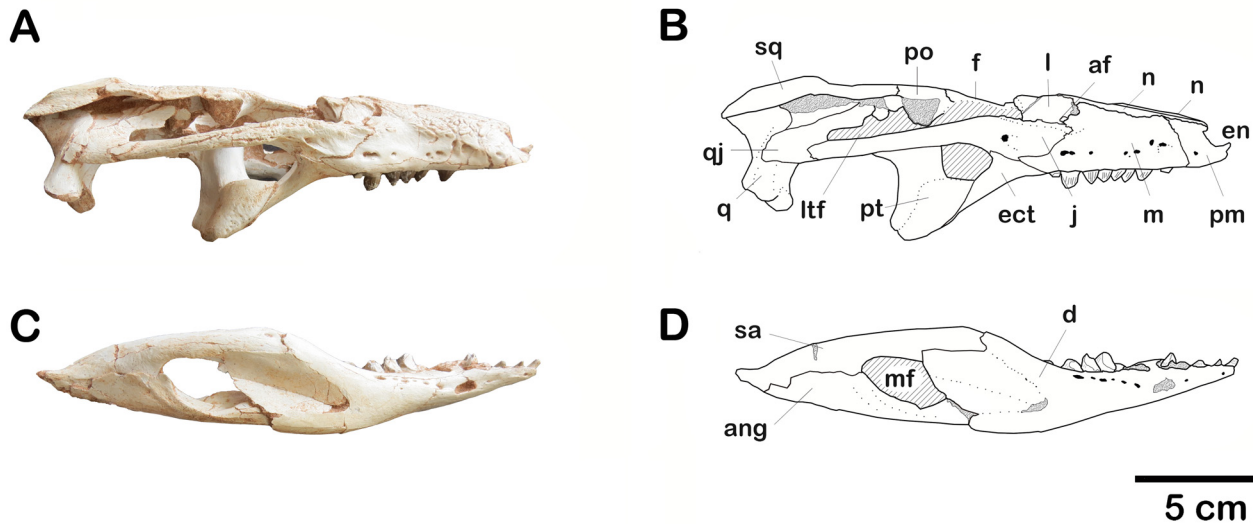


FIGURE 10. Fossil and schematic diagram of the referred specimen of *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov. (MPMA 68-0003/12). Cranium (**A** and **B**) and mandible (**C** and **D**) in lateral views. Legend: **af**, antorbital fenestra; **ang**, angular; **d**, dentary; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **j**, jugal; **l**, lacrimal; **ltf**, laterotemporal fenestra; **m**, maxilla; **mf**, mandibular fenestra; **n**, nasal; **pm**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sq**, squamosal.

Only the holotype of *C. paulistanus* had completely preserved palpebrals. In both specimens of *Caipirasuchus montealtensis* comb. nov., only a small fragment of the anterior palpebrals was preserved; however, it is possible to observe a smooth region in the lateral margin of the frontal in specimen 68-0003/12, which indicates that there could have been a fenestra bordered by the frontal and the palpebrals, as with *C. paulistanus*.

Caipirasuchus paulistanus exhibits an external nostril bordered only by the premaxillae; an anterodorsal process of the maxilla makes contact with the nasal, excluding them from the external nostril margin. In *Sphagesaurus huenei*, the nasals participate in the margin slightly. Andrade & Bertini (2008) propose that the same would happen with the MPMA 15-0001/90 specimen; however, this region is not preserved in this fossil. *Caipirasuchus montealtensis* comb. nov. (MPMA 68-0003/12) shows a remnant of the anterodorsal process of the premaxilla, which most likely also excludes the nasal from the external nostril margin because the distal portions of the nasals exhibit suture marks. An anteroventral process of the premaxilla is also observed in *Caipirasuchus montealtensis* comb. nov. (MPMA 68-0003/12), as indicated by Pol (2003) for *S. huenei*. The presence of the anterior processes of the premaxillae in sphagesaurids allows us to consider the possible existence of an internarial bar in members of the family, as occurs in most Notosuchia.

The fossils of *Armadillosuchus*, *Caryonosuchus* and *Sphagesaurus* do not have preserved choanae, while the specimens of the genus *Caipirasuchus* have these regions almost intact, with fossil MPMA 68-0003/12 of *Caipirasuchus montealtensis* comb. nov. being the best preserved. The proximal halves of the palatines border the nasopharyngeal duct, laterally and ventrally. The opening of this duct is located at the beginning of the lateral deflection of the palatines. A small medial process of the palatine extends from this point and contacts a large anterior process of the pterygoid, forming a tubular structure, noted by Andrade & Bertini (2008) as an interchoanal septum. A fenestra is formed laterally to this bar, bounded by the deflected bar of the palatine and by the pterygoid. *Caipirasuchus* presents the internal nostril opening caudally, unlike most of the crocodylomorphs, where the choana opens ventrally. The medial regions of the pterygoids differ greatly among the species of *Caipirasuchus*. In *C. paulistanus*, these regions are smooth and closed, while *C. montealtensis* comb. nov. displays a chamber opening in this bone. This opening is wide and occupies approximately half of the medioventral surface of the pterygoid. The chamber occupies the entire distal portion of the pterygoid; a foramen opens dorsally in the pterygoid chamber. There may be a pneumatic connection between the nasopharyngeal duct, the interchoanal septum and the chamber of the pterygoid.

The main autapomorphies of the genus *Caipirasuchus* are as follows: the presence of an antorbital fenestra, an external nostril bordered only by the premaxillae and a premaxilla with four teeth. Structurally, *C. paulistanus* has a higher cranium and a narrower rostrum, whereas *Caipirasuchus montealtensis* comb. nov. exhibited a lower

cranium and mandible, providing a more robust aspect to this taxon. The cranial roof of specimen MPMA 68-0003/12 collapsed during fossilization, but some morphometric data could still be measured. It was noted that both specimens of *Caipirasuchus montealtensis* comb. nov. showed similar measurements and differed from *C. paulistanus* by presenting the following characteristics: a larger rostral width at the line of the caniniforms; a lower mandibular height, both in the anterior region of the mandibular fenestra and at the highest point of the symphysis; and, in *C. paulistanus*, the distal ends of the ectopterygoids and proximal ends of the pterygoids project more ventrally than in *Caipirasuchus montealtensis* comb. nov. (Fig. 11). This projection results in a more acute angle formed between the mandible plane and the suborbital fenestrae plane in *C. paulistanus* compared to that in *Caipirasuchus montealtensis* comb. nov. (135° for *C. paulistanus* and approximately 147° for *Caipirasuchus montealtensis* comb. nov.) (Iori & Carvalho 2011). The most striking aspect that differentiates these two species is the pterygoid chamber, which is present in *Caipirasuchus montealtensis* comb. nov. and absent in *C. paulistanus*.

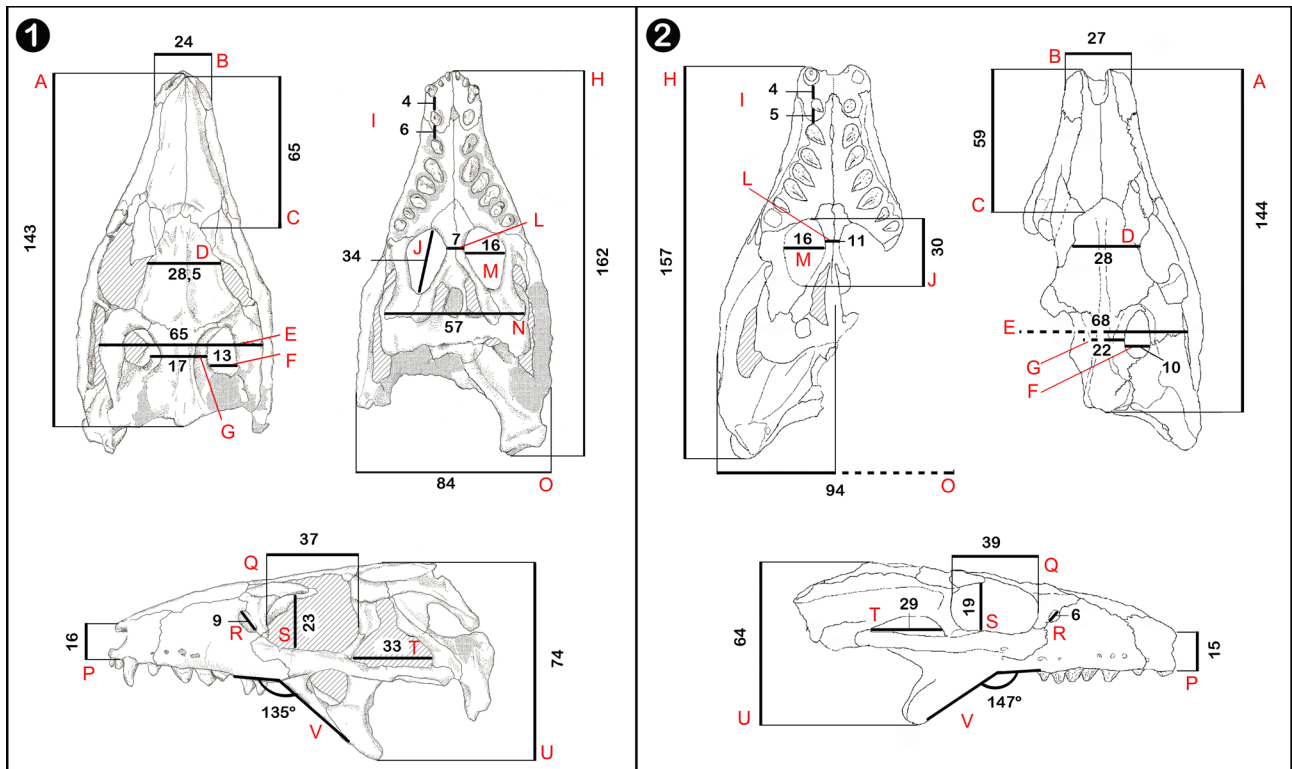


FIGURE 11. Cranial dimensions in millimeters of *Caipirasuchus paulistanus* (MPMA 67-0001/00) in (1) and of *Caipirasuchus montealtensis* comb. nov. (MPMA 15-0001/90) in (2). Legend: **A**—maximum dorsal length of the cranium; **B**—cranium width in the region of caniniform teeth; **C**—maximum nasal length; **D**—minimum distance between the supraorbital fenestrae; **E**—maximum width of cranial roof; **F**—width of supraorbital fenestra; **G**—minimum distance between supraorbital fenestrae; **H**—maximum length of the cranium; **I**—lengths of diastemata; **J**—dimension of suborbital fenestra; **L**—minimum distance between suborbital fenestrae; **M**—width of suborbital fenestra; **N**—distance between the external faces of ectopterygoids; **O**—maximum width of the cranium; **P**—minimum height of the cranium; **Q**—maximum orbital length; **R**—maximum dimension of antorbital fenestra; **S**—orbital height; **T**—maximum length of laterotemporal fenestra; **U**—maximum cranium height; **V**—angle between the ventral maxillary plane and the palatal fenestra plane. Schematic drawings extracted from Andrade & Bertini (2008) and Iori & Carvalho (2011).

The holotype of *C. paulistanus* did not have the dorsal region of the articular preserved, but, in the MPMA 68-0003/12 specimen of *Caipirasuchus montealtensis* comb. nov., an anteroposteriorly expanded protuberance in the articular region with the quadrate was observed, which allows anteroposterior sliding of the mandible. This arrangement in the craniomandibular articulation must be present in the other sphagesaurids because it would contribute to the propalinal movement noted in several studies with members of the family (Pol 2003; Marinho & Carvalho 2009; Iori & Carvalho 2011).

Iori & Carvalho (2011) presented a phylogenetic analysis, where *Sphagesaurus montealtensis* (*Caipirasuchus montealtensis* comb. nov.) appears to be a sister species to *Armadillosuchus*; however, in that study, the data used were from a holotype (MPMA 15-0001/90) with an incomplete cranium and mandible. In the present study, a

different specimen (MPMA 68-0003/12) was used to provide data on the cranial and post-cranial characters that were not preserved in the previous holotype. The results indicate that *Caipirasuchus paulistanus* and *Caipirasuchus montealtensis* comb. nov. are sister species among Sphagesauridae, corroborating what is proposed in the present study.

Phylogenetic analysis

The new relationships were tested with a phylogenetic analysis. This analysis and the kinship relationships in Sphagesauridae were carried out using the TNT software (Goloboff *et al.* 2008). A strict consensus of the 17 most parsimonious trees obtained (CI [consistency index] = 0.34; RI [retention index] = 0.66; tree length = 833 steps) is presented here. A survey of previously published characters was used (Novas *et al.* 2009), with the addition of 7 taxa: *Caipirasuchus paulistanus*, *Caipirasuchus montealtensis* comb. nov., *Armadillosuchus arrudai*, *Caryonosuchus pricei*, *Morrinhosuchus luziae* Iori & Carvalho, 2009, *Barreirosuchus franciscoi* Iori & Garcia, 2011 and *Gondwanasuchus scabrosus* Marinho, Iori, Carvalho & Vasconcellos, 2013. The matrix is composed of 234 characters and 59 taxa, comprising 58 crocodylomorphs and one outgroup taxon (*Gracilisuchus stipanicicorum*).

The analysis shows Sphagesauridae is a monophyletic group within Notosuchia. *Caipirasuchus paulistanus* and *Caipirasuchus montealtensis* comb. nov. appear as sister species, corroborating what has been proposed for these taxa (Figure 12).

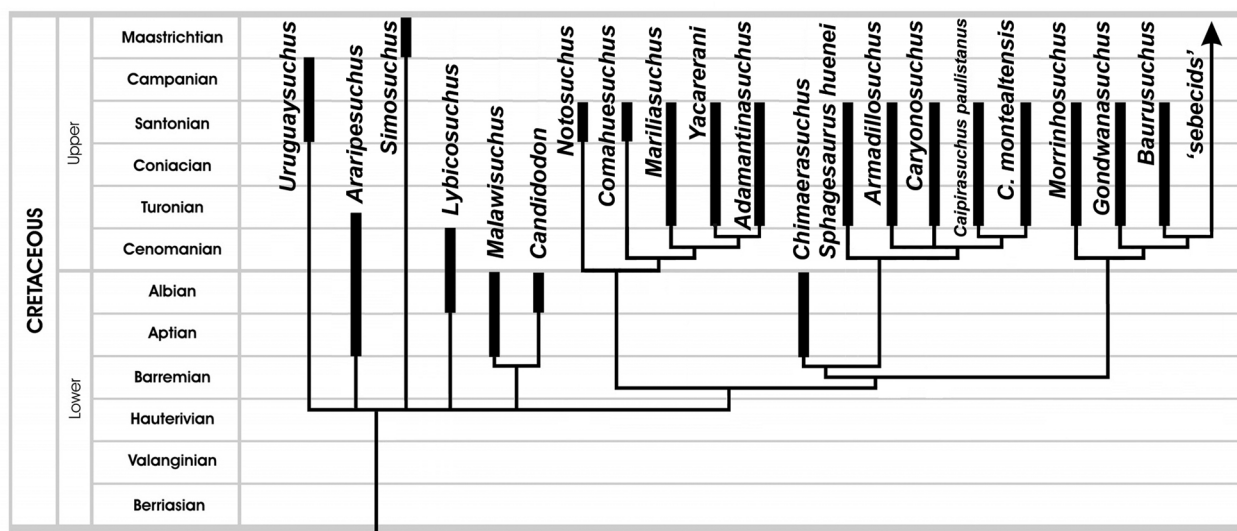


FIGURE 12. The strict consensus of the 17 most parsimonious trees obtained (CI = 0.34; RI = 0.66; tree length = 833 steps). The analysis shows Sphagesauridae as a monophyletic group within Notosuchia, with *Caipirasuchus paulistanus* and *Caipirasuchus montealtensis* (Andrade & Bertini, 2008) comb. nov. as sister species (modified from Novas *et al.* 2009).

The cladistic analysis shows Notosuchia with an oblique posterior dentition, occurring in two regions of the phylogenetic tree. The first cluster includes *Notosuchus*, *Mariliasuchus*, *Adamantinasuchus* and *Yacarerani*. The second cluster is composed by the sphagesaurids—*Sphagesaurus huenei*, *Caipirasuchus paulistanus*, *Caipirasuchus montealtensis* comb. nov., *Armadillosuchus* and *Caryonosuchus*, which form the monophyletic clade with *Chimaerasuchus* as a sister group.

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