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"JÚLIO DE MESQUITA FILHO"  
Câmpus de São José do Rio Preto

Juan Vítor Ruiz

**A new Sphagesauridae (Crocodyliformes, Notosuchia) from Brazil  
and the evolutionary history of Mesozoic notosuchians**

São José do Rio Preto  
2020

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Dissertação apresentada como parte dos requisitos para obtenção do título de Mestre em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista “Júlio de Mesquita Filho”, Câmpus de São José do Rio Preto.

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“[...] there’s nothing more magical than finding a shiny shell and knowing you’re the first person to have seen it for 150 million years.”  
(ATTENBOROUGH, 2014)

## RESUMO

Sphagesauridae é um grupo de Notosuchia do Cretáceo Superior sul-americano distinguido por mandíbula e dentição extremamente especializadas. No presente estudo, foi descrito um novo Sphagesauridae da Formação Santo Anastácio (Grupo Caiuá, Bacia Bauru), no sudeste do Brasil. O material descrito consiste em um palato parcialmente preservado, neurocrânio, mandíbula e dentição fragmentária. A nova espécie pôde ser atribuída ao gênero *Caipirasuchus* graças à uma região da sínfise mandibular anteroposteriormente longa e lateromedialmente estreita; à presença de cristas apicobasais e esmalte rugoso nos dentes posteriores; à um diastema entre os alvéolos dentários D5 e D6; e à uma linha de forames neurovasculares na superfície lateral do dentário. Foi erigida a espécie *Caipirasuchus attenboroughi* baseado-se em caracteres que a distingue das demais espécies de *Caipirasuchus*, incluindo uma maior divergência no ângulo formado entre as hemimandíbulas (aproximadamente 35°); uma maior inclinação ventrolateral da superfície dos dentários posterior à dentição; uma conexão entre a margem anteroventral da fenestra mandibular externa e o canal meckeliano; e a sutura angular-esplênica em forma de “V”. Foi realizada uma análise filogenética atualizada, que recuperou o clado tradicionalmente conhecido como “notossúquios avançados”, bem como erigido o nome Sphagesauria para este clado. Em uma escala mais ampla, foi recuperado um clado de Notosuchia que inclui Uruguaysuchidae e diversos táxons de Notosuchia considerados “basais” como grupos irmãos consecutivos do clado formado por Sphagesauria + Baurusuchia. Por fim, foi conduzida uma análise biogeográfica, BioGeoBEARS, para melhor entender, em termos temporal e espacial, as cladogêneses implicadas por nossos resultados. Para explicar a distribuição errática dos táxons durante o Cretáceo Inferior e Superior em Gondwana, foi sugerido uma origem barremiana para as formas “derivadas” de Notosuchia. Tal sugestão é corroborada pela hipótese Pan-Gondwana de distribuição de Notosuchia.



**Palavras-chave:** Paleontologia; Vertebrados; Evolução (Biologia).

## ABSTRACT

Sphagesaurids are a group of Late Cretaceous notosuchians from South America distinguished by highly specialized jaws and dentition. In this study, we describe a new sphagesaurid from the Santo Anastácio Formation (Caiuá Group, Bauru Basin), southeast Brazil. The new described remains consist of a partial palate, neurocranium, mandible and fragmentary dentition. The new specimen is assigned to the Genus *Caipirasuchus* due to a lateromedially narrow and anteroposterior long mandibular symphyseal region, the presence of apicobasal ridges and rugose enamel surface in posterior teeth, a diastema between the D5 and D6 alveoli, and a linear row of large neurovascular foramina in the lateral surface of the dentary. The species *Caipirasuchus attenboroughi* was erected based on characters that distinguish it from the other *Caipirasuchus* species, such as a greater divergence angle between the hemimandibles (approximately 35°), a ventrolaterally inclined surface of the dentaries posterior to the toothrow, a connection between the anteroventral margin of the external mandibular fenestra with the floor of the Meckelian canal, and the anterior process of angular in the contacting the splenial, forming a V-shaped suture. An updated phylogenetic analysis was performed, recovering the clade traditionally called “advanced notosuchians” for which the name Sphagesauria was employed. In a broader scale, we recovered a clade of notosuchians that includes uruguaysuchids and an array of other notosuchians as consecutive sister-groups of Sphagesauria + Baurusuchia. A BioGeoBEARS analysis was conducted to understand the timing and place of the cladogenesis implied by our results. It was suggested that the apparent erratic distribution of basal forms of notosuchians in Gondwana landmasses during the Early and Late Cretaceous is a result of a Barremian origin for this clade, which corroborates the Pan-Gondwanan hypothesis for the distribution of notosuchians.

**Keywords:** Paleontology; Vertebrates; Evolution (Biology).

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## LIST OF ABBREVIATIONS AND ACRONYMS

<b>LAPEISA</b>	Laboratório de Paleontologia de Ilha Solteira
<b>Fm.</b>	Formation
<b>DNPM</b>	Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil
<b>TBR</b>	Tree-Bisection-Reconnection
<b>Myr</b>	million year(s)
<b>DEC</b>	Dispersal-Extirpation-Cladogenesis
<b>DIVA</b>	Dispersal–Vicariance Analysis
<b>LRT</b>	likelihood ratio test(s)
<b>AIC</b>	Akaike information criterion(s)
<b>sp. nov.</b>	specie novae
<b>D1-D10</b>	dentary tooth number (varies from 1 to 10)
<b>MZSP-PV</b>	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
<b>CT-scan</b>	computed tomography scan
<b>MPMA</b>	Museu de Paleontologia de Monte Alto, Monte Alto, Brazil
<b>UFRJ DG</b>	Coleção de Paleontologia de Vertebrados da Universidade Federal do Rio de Janeiro no Rio de Janeiro, Rio de Janeiro, Brazil.
<b>MUCP</b>	Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina
<b>MLP</b>	Museo de La Plata, La Plata, Argentina
<b>MACN</b>	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
<b>char.</b>	character
<b>st.</b>	state
<b>DGM</b>	Diretoria de Geologia e Recursos Minerais, Rio de Janeiro, Brazil
<b>MNK PAL</b>	Museo ‘Noel Kempff Mercado,’ Santa Cruz de la Sierra, Bolivia
<b>CPP</b>	Centro de Pesquisas Paleontológicas L. I. Price, Universidade Federal do Triângulo Mineiro (UFTM), Uberaba, Brazil

**RCL** Museu de Ciências Naturais, Pontificia Universidade Católica de Minas Gerais, Brazil

**LPRP** Laboratório de Paleontologia de Ribeirão Preto-USP, Ribeirão Preto, Brazil

**CPPLIP** Centro de Pesquisas Paleontológicas L. I. Price, Universidade Federal do Triângulo Mineiro (UFTM), Uberaba, Brazil

## LIST OF SYMBOLS

<b>km</b>	Kilometer
<b>cm</b>	Centimeter
<b>Ma</b>	Million years ago



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## 1. INTRODUCTION

Notosuchia is a species-rich group of crocodyliforms from Cretaceous deposits, mainly from Gondwana (TURNER; SERTICH, 2010; GODOY *et al.*, 2014; POL *et al.*, 2014; POL; LEARDI, 2015). In the past three decades, a great number of taxa has been discovered from Madagascar (BUCKLEY; BROCHU, 1999; BUCKELY *et al.*, 2000), continental Africa (GOMANI, 1997; SERENO *et al.*, 2003; SERENO; LARSSON, 2009; O'CONNOR *et al.*, 2010) and, especially, South America (BONAPARTE *et al.*, 1991; ORTEGA *et al.*, 2000; CAMPOS, 2001; CARVALHO; CAMPOS; NOBRE, 2005; MARINHO; CARVALHO, 2009; NOVAS *et al.*, 2009; IORI; CARVALHO, 2011; MONTEFELTRO; LARSSON; LANGER, 2011; GODOY *et al.*, 2014; POL *et al.*, 2014; MARTINELLI *et al.*, 2018). The diversity of Notosuchia includes forms predominantly terrestrial (ÖSI, 2013; POL *et al.*, 2014), with a vast array of adaptations, including the shortening of the rostrum and the heterodont dentition, with a reduced number of teeth, related to variable diets, including hypercarnivory, herbivory, omnivory and durophagy (ÖSI, 2013; GODOY *et al.*, 2014; POL *et al.*, 2014; FIORELLI *et al.*, 2016; IORI; CARVALHO, 2018; MELSTROM; IRMIS, 2019).

The Bauru Basin, in south-central Brazil, possess one of the most important notosuchians diversity in the world. In lithostratigraphic terms, the Bauru Basin is divided, in general, in the Bauru and Caiuá Groups (FERNANDES; COIMBRA, 1996; FERNANDES, 1998). The fossil record of the Bauru Group, especially that from Adamantina Formation, is rich, with more than 20 notosuchians already described (GODOY *et al.*, 2014; MARTINELLI *et al.*, 2018) and represents the most diverse Cretaceous crocodyliform assemblage known (CANDEIRO; MARTINELLI, 2006; RIFF *et al.*, 2012). In contrast, the deposits of Caiuá Group are scarce in records of paleovertebrates, with no crocodyliform described to date.

The accurate dating of both groups of the Bauru Basin plays a critical role in the understanding of the notosuchian evolutionary history. However, the chronostratigraphy of the basin remains under discussion. Some authors points to an older age for the Caiuá Group, placing this unity in Early Cretaceous (FULFARO *et al.*, 1999; DIAS-BRITO *et al.*, 2001; BATEZELLI, 2010, 2015) while a Late Cretaceous age is supported for the Bauru Group (GOBBO-RODRIGUES, 2001). Any temporal inference should be made with caution, especially in the case of the Caiuá Group, which has attracted less attention giving the scarcity of its fossil record (MANZIG *et al.*, 2014; LANGER *et al.*, 2019).

The sphagesaurids (Sphagesauridae, Kuhn, 1968) form a highly specialized group of notosuchians restricted to the Upper Cretaceous deposits in South America (NOVAS *et al.*,

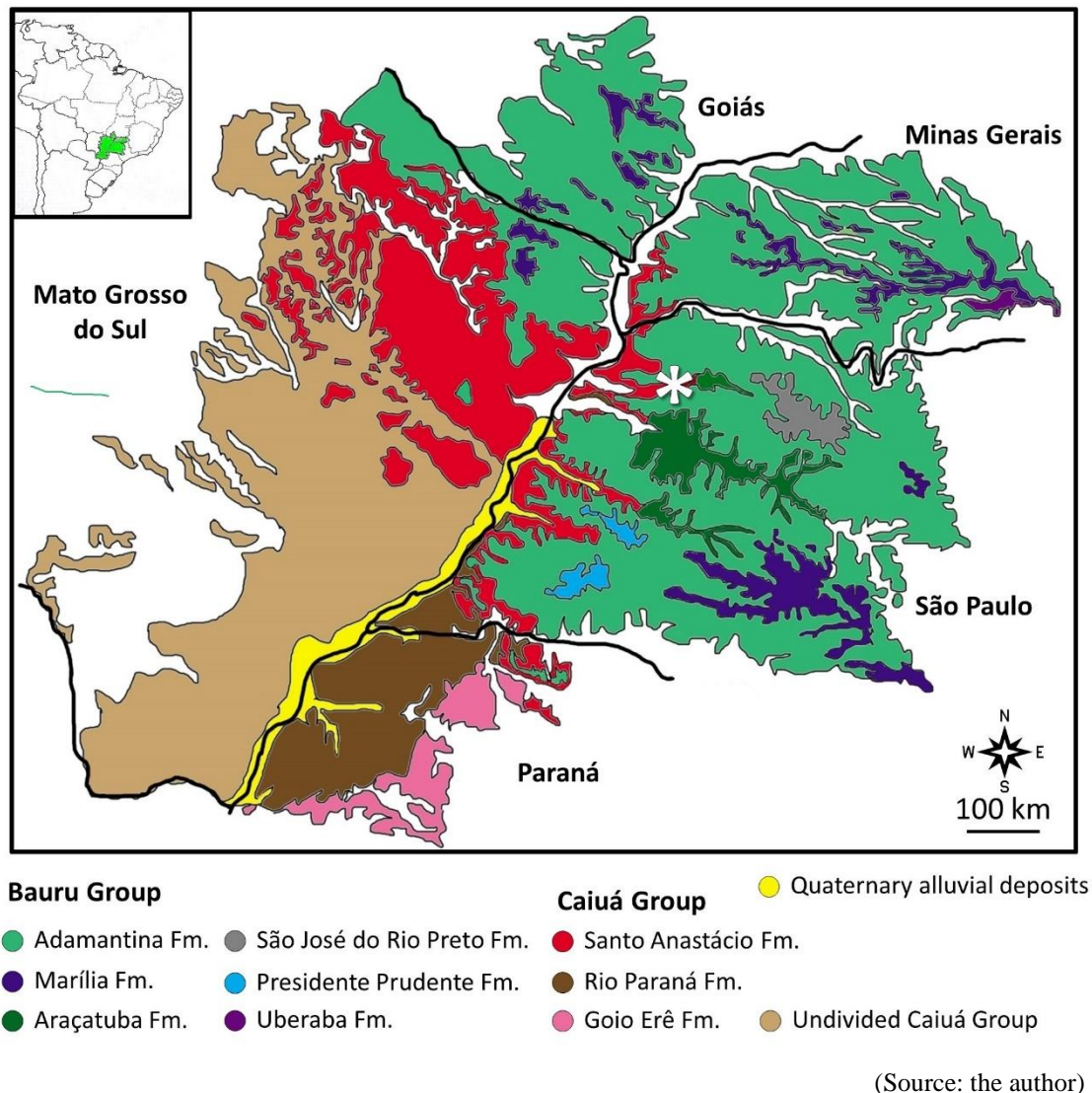
2009; CARVALHO *et al.*, 2010; POL *et al.*, 2014; MARTINELLI *et al.*, 2018). Sphagesaurids are characterized by modified jaws and dentition (POL *et al.*, 2014), including an elongated mandibular symphysis, enlarged neurovascular foramina in the lateral surface of the dentaries, posterior teeth with an oblique orientation in relation to craniomandibular axis and a thick enamel coating, with apicobasal crests and distinct quills on the posterior teeth (MONTEFELTRO, 2013; POL *et al.*, 2014). The past two decades were important for sphagesaurid taxonomy, which now encompasses at least nine species (MARTINELLI *et al.*, 2018). Pol *et al.* (2014) revisited the validity of Sphagesauridae, and divided the group in 3 clades: one formed by medium to large sized species, including *Sphagesaurus huenei* (PRICE, 1950), *Armadillosuchus arrudai* (MARINHO; CARVALHO, 2009) and *Caryonosuchus pricei* (KELLNER *et al.*, 2011a); the second clade formed by the three *Caipirasuchus* species described at that point, *Cai. paulistanus* (IORI; CARVALHO, 2011), *Cai. montealtensis* (IORI *et al.*, 2013) and *Cai. stenognathus* (POL *et al.*, 2014); and a third clade composed by the smaller *Adamantinasuchus navae* (NOBRE; CARVALHO, 2006) and *Yacararani boliviensis* (NOVAS *et al.*, 2009). Additionally, Montefeltro *et al.* (2013) includes the fragmentary *Labidiosuchus amicum* (KELLNER *et al.*, 2011b), as a member of Sphagesauridae, whose affinities are also commented in Pol *et al.* (2014).

Despite the monophyly of Sphagesauridae been repeatedly confirmed based on independent phylogenetic analysis (MONTEFELTRO; LARSSON; LANGER, 2011; POL *et al.*, 2014; FIORELLI *et al.*, 2016; MARTINELLI *et al.*, 2018), the relationships of sphagesaurids to other notosuchian groups remains under discussion. Recent works suggested that sphagesaurids are deeply nested in the clade “advanced notosuchians” (POL *et al.*, 2014; LEARDI; FIORELLI; GASPARINI, 2015; LEARDI *et al.*, 2015; FIORELLI *et al.*, 2016; MARTINELLI *et al.*, 2018), a group that also includes *Mariliasuchus* (CARVALHO; BERTINI, 1999), *Notosuchus terrestris* (WOODWARD, 1896), and *Morrinhosuchus luziae* (IORI; CARVALHO, 2009). The synapomorphies recovered for this clade also comprise modified jaw conditions, including the parallelism of the mandibular ramus at the symphysis, presence of a fossa in angular that extends along the ventral margin of the mandibular fenestra, and teeth covered by a thick enamel layer (POL *et al.*, 2014). Another set of phylogenetic analyses present Sphagesauridae as sister-group of Baurusuchia (MONTEFELTRO; LARSSON; LANGER, 2011; MONTEFELTRO *et al.*, 2013; GODOY *et al.*, 2014). This alternative scenario is supported by a series of characters, including a highly modified choanal region, with parachoanal fenestrae in the ventral surface of the pterygoid, and the absence of a wall anterior to the opening of the pharyngotympanic tubes. However, the absence of the record

of these clades in older deposits, especially from Lower Cretaceous, makes it difficult to trace the early diversification of these derived forms of notosuchians and the relationship among them.

In 2016, members of the Laboratório de Paleontologia e Evolução de Ilha Solteira (LAPEISA – FEIS/UNESP, Ilha Solteira, São Paulo) found a partially preserved lower jaw and cranial elements of a sphagesaurid during a field work on outcrops of the Santo Anastácio Formation, Caiuá Group, in the municipality of General Salgado, Northwest São Paulo (figure 1). It represents the first crocodyliform known from both the Santo Anastácio Formation and the Caiuá Group, corresponding to a new species of *Caipiraosuchus*, closely related to *Cai. stenognathus* and *Cai. mineirus*

Figure 1. Surface distribution of Bauru Basin rocks. The place of discovery of LAPEISA-0001 is marked with an asterisk. Modified from Fernandes and Ribeiro (2014).



## 2. MATERIAL AND METHODS

### 2.1. Field work and preparation

The fossil was discovered and collected in April, 2016. The field work that resulted in its collection was communicated in advance to Departamento Nacional de Produção Mineral – DNPM (now Agência Nacional de Mineração – ANM), as requested in the ordinance number 4.146 from March 4<sup>th</sup>, 1942. The specimen described here is housed in the permanent collection of LAPEISA, in São Paulo State University, in Ilha Solteira, Brazil. The material was mechanically prepared using pin vise and pneumatic tools at the Laboratório de Paleontologia, Universidade de São Paulo (Ribeirão Preto, Brazil).

## 2.2. Tomography

Portions of the palate and neurocranium of LAPEISA-0001 are still covered by rock-matrix, including the maxilla-palatine contact, the nasopharyngeal duct, the choanal region and the basisphenoid. To access the anatomy of these regions, high resolution computed tomography was performed. The images were acquired by the team of Laboratório de Paleontologia, at the Centro para Documentacao da Biodiversidade of the Universidade de São Paulo (Ribeirão Preto, Brazil). Segmentation was conducted using the software Amira 5.3.3.

## 2.3. Phylogeny

The phylogenetic relationship of the new taxa was investigated using a maximum parsimony analysis of discrete morphologic characters. The specimen LAPEISA-0001 was included in the dataset of Montefeltro *et al.* (2013), which encompass a great diversity of mesoeucrocodylians, including most notosuchians, and a vast sample of cranial and post-cranial characters. The original dataset was expanded, with the inclusion of 9 taxa, (*Agaresuchus fortisiensis*, *Cai. stenognathus*, *Cai. mineirus*, *Caryonosuchus pricei*, *Labidiosuchus amicum*, *Lavocatchampsa sigogneaurussellae*, *Lohuecosuchus megadontos*, *Morrinhosuchus luziae* and *Pakasuchus kapilimai*), and 23 characters (485-507, see *Supplementary*). Among the included characters, fourteen (485-487, 489-491, 493-496, 504-507) are new and nine (488, 492, 497-503) were adapted from Pol *et al.* (2014) data. The final data matrix includes 100 taxa and 507 characters. The resulting matrix was analysed using equally weighted parsimony in TNT 1.5 (GOLOBOFF; FARRIS; NIXON, 2008), with the heuristic search or “traditional search” (10,000 replicates). Tree Bisection Reconnection (TBR) was applied, saving 20 cladograms per round, and random seed was set as 0. The trees were collapsed after each replicate, and a strict consensus constructed. Given the fragmentary nature of *Labidiosuchus*, *Lavocatchampsa*, and *Caryonosuchus*, a second analysis was performed excluding these taxa to evaluate data consistency and avoid polytomies that preclude interpretation of the phylogenetic signal.

## 2.4. Biogeographical analysis

We estimated ancestral areas based on our time-calibrated tree with the R package BioGeoBEARS (MATZKE, 2014). The tree was time-scaled using the package *paleotree* (BAPST, 2012) on R (R CORE TEAM, 2014), based on information from the literature to

define the time-range of each taxa analysed. We used the “mbl” option in which branches are divided equally along the tree and were set to be greater or equal to 1 myr (BRUSATTE *et al.*, 2008). We conducted stratified analysis with two-time bins, Early and Late Cretaceous, using two nested models (M0 and M1; see below) of the two most used biogeographic models, DEC, Dispersal-Extinction Cladogenesis (REE, 2005; REE; SMITH, 2008) and DIVA, Dispersal-Vicariance Analysis (RONQUIST, 1997). The original model settings (M0) were modified (M1) to include  $w$ , a multiplier of the dispersal multiplier matrices (DUPIN *et al.*, 2017) as a free parameter. Additionally, following the approach of Poropat *et al.* (2016), we created “harsh” and “relaxed” versions of the “starting” dispersal multipliers matrices, to evaluate the weight of our assumptions, resulting in three sets of four analyses each. For each set of analyses, we conducted likelihood-ratio tests (LRTs) and weighted Akaike Information Criterion (AICc) to test and choose the best models.

### 3. RESULTS

#### 3.1. Systematic palaeontology

Crocodyliformes Hay, 1930 (by subsequent designation by Clark, 1986)

Mesoeucrocodylia Whetstone and Whybrow, 1983

Notosuchia Gasparini, 1971 (by subsequent designation by Sereno *et al.* 2001)

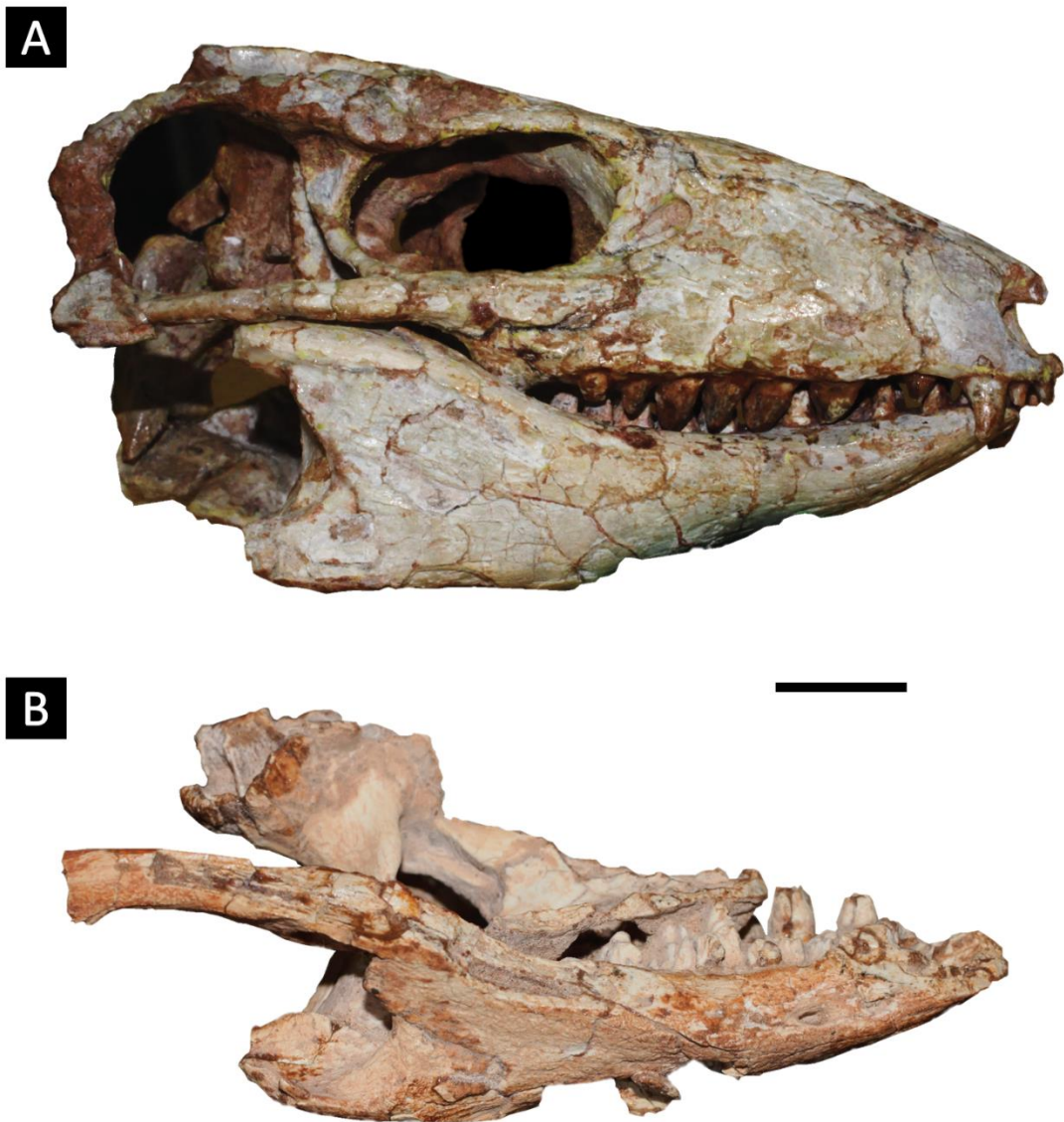
Sphagesauridae Khun, 1968

*Caipirasuchus* Iori and Carvalho, 2011

*Type species: Caipirasuchus paulistanus* Iori and Carvalho, 2011 (figure 2)

*Caipirasuchus attenboroughi* sp. nov. (figure 2)

Figure 2. The holotypes of a) *Caipirasuchus paulistanus* MPMA 67- 0001/00 (IORI; CARVALHO, 2011); and b) *Cai. Attenborough* sp. novae (LAPEISA-0001). Scale bar = 2 cm.



(Source: the author)

**Derivation of name:** the specific name was given in honour to Sir David Attenborough, a palaeontology enthusiastic and fossil collector that sparked in many minds the interest in Life on Earth, past and present, including the first author of this study.

**Holotype:** LAPEISA-0001 includes part of the secondary palate, neurocranium, an almost complete lower jaw with nine preserved tooth-crowns.

**Type locality:** SP highway 463, km 111, municipality of General Salgado, northwest of São Paulo state, Brazil (20°36'9.88"S, 50°30'50.19"W).



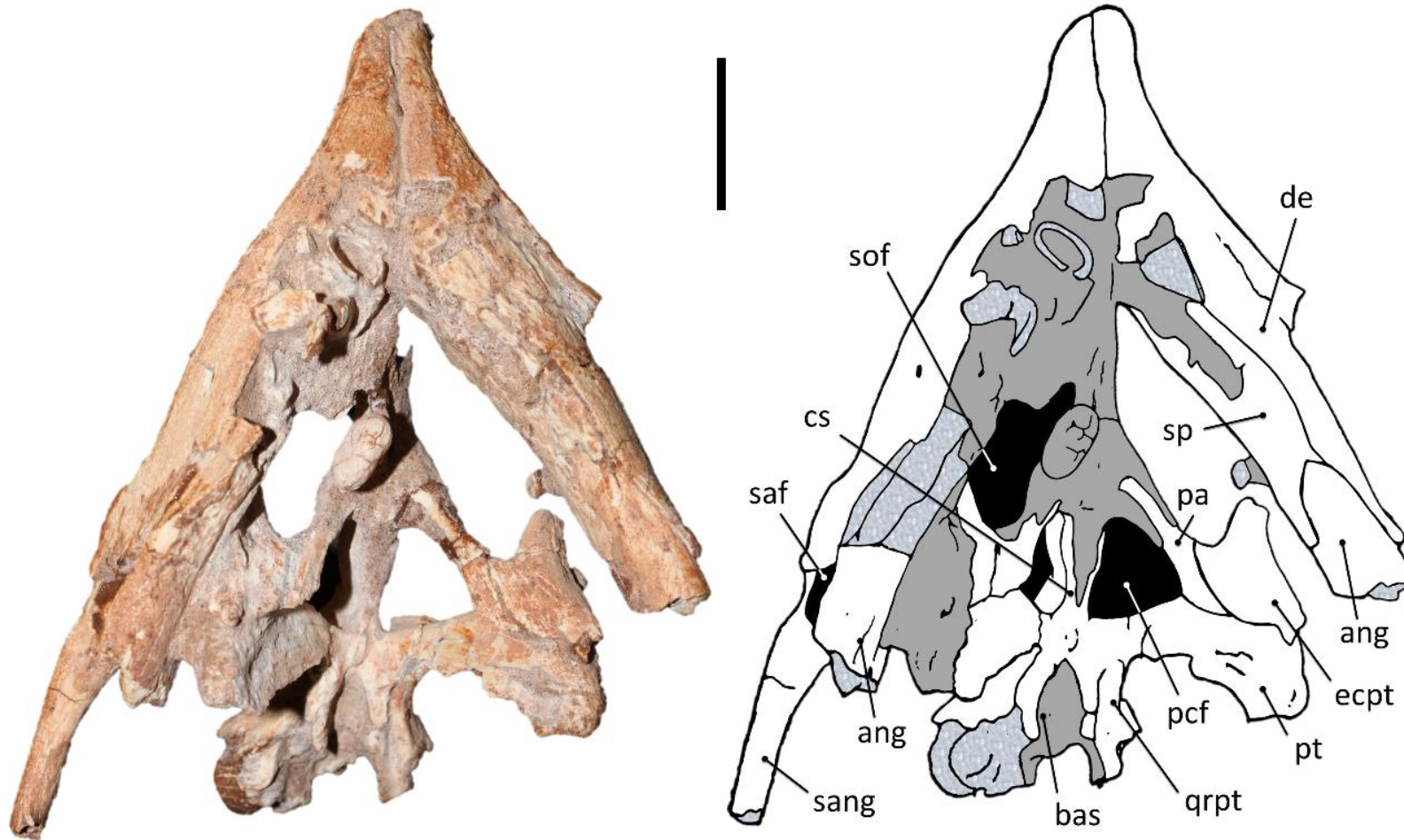
**Stratigraphic horizon:** Santo Anastácio Formation, Caiuá Group, Bauru Basin (Turonian-Campanian, possibly Aptian-Albian, see *Discussion*).

**Diagnosis:** small sized sphagesaurid that differs from other *Caipirasuchus* by having the unique combination of characters (autapomorphies marked with an asterisk): presence of maxillopalatine fenestrae; intermediary exposed area of the ventral surface at the distal portion of the palatines; posterior vertex of the suborbital fenestra enclosed only by ectopterygoid; presence of a groove in the anterior portion of the choanal septum; slender proximal region of the pterygoids at contact with the neurocranium; surface of ventral face of the pterygoids flanges flat and smooth; basisphenoid ventral surface continued anteriorly by the choana; well-developed crest in quadrate parallel to the exoccipital contact\*; absence of foramina in the basioccipital ventrally to the occipital condyle; mandibular rami diverging 35° from each other at the portion between the symphyseal region and the mandibular fenestra\*; mandibular rami continuously diverging to the level of posterior half of the mandibular fenestra\*; lateral surface of the dentaries posterior to the toothrow inclined ventrolaterally\*; enlarged foramen intermandibularis oralis; the anteroventral margin of the external mandibular fenestra gently merges with the floor of the Meckelian canal\*; anterior process of angular in the contact with the splenial\*; coronoid tuberosities disposed posteriorly to the surangular-dentary suture; reduced ventral coronoid tuberosities than the ascending medial process of the angular; diastema between D5 and D6 formed by the dentary and the splenial;

### 3.2. Comparative description

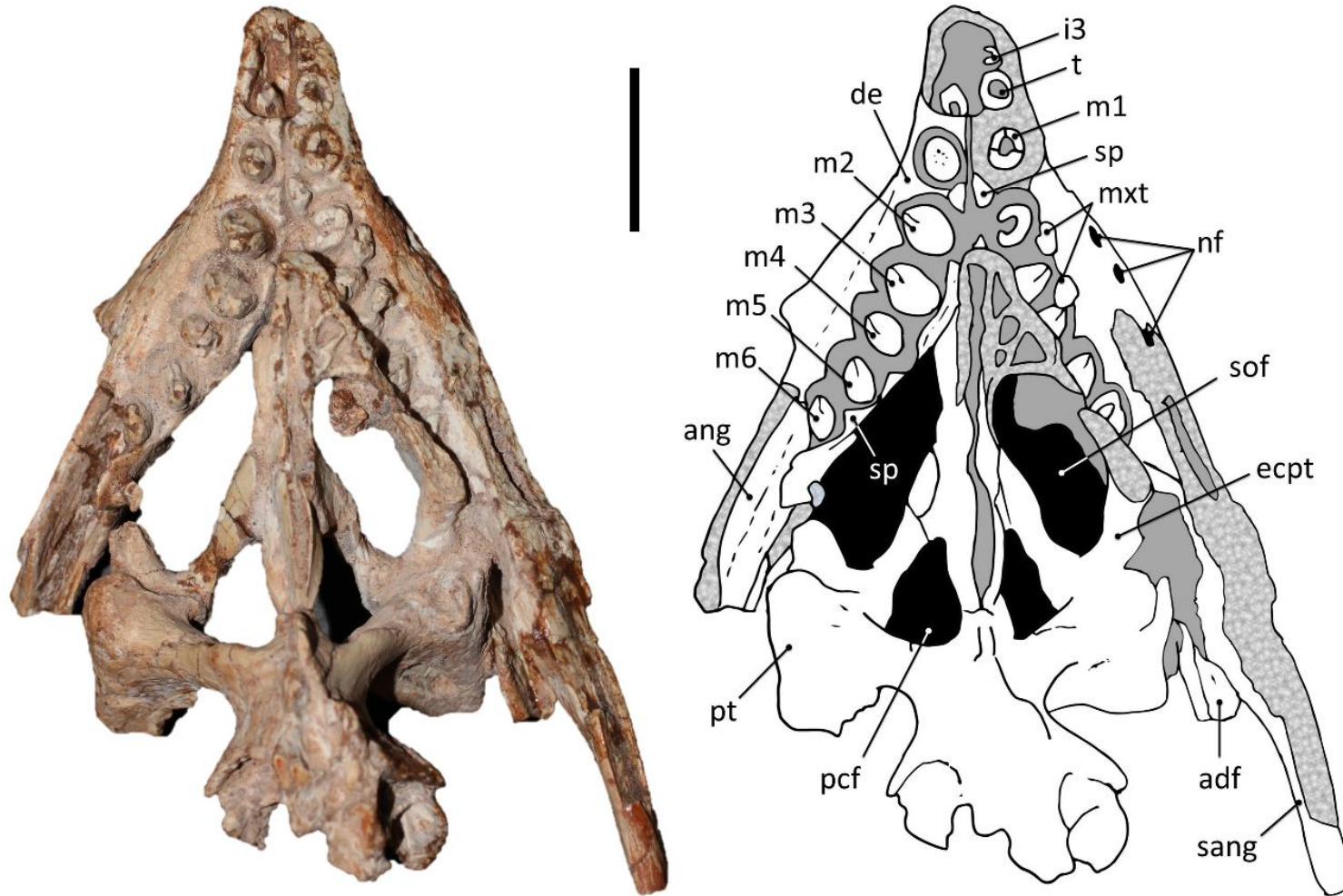
LAPEISA-0001 corresponds to partial secondary palate and the neurocranium (figure 3), an almost complete mandible, six tooth crowns preserved in the left mandibular ramus and four teeth fragments from the maxillary dentition (figure 4), two of them preserved laterally to the right lower jaw and two isolated from the remaining elements. The crowns of D6-D8 and D10 in the right mandibular ramus are broken, but D9 is almost complete. The bones preserved do not show signs of taphonomic deformation and the general shape of the bone are assumed as genuine. However, LAPEISA-0001 has a flattened surface on the anterodorsal portion of the mandibular symphyseal region caused by a bulldozer, so most of its dorsal and anterior surfaces are lost, including the incisiform teeth. A similar damage is also present on the posterodorsal region of the right mandibular ramus.

Figure 3. Ventral view of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001). The dark grey light greys indicate presence of rock matrix and broken surfaces, respectively. **ang.:** angular; **bas.:** basisphenoid; **cs.:** choanal septum; **de:** dentary; **ecpt.:** ectopterygoid; **pa.:** palatine; **pcf.:** parachoanal fenestra; **pt.:** pterygoid; **qrpt.:** quadrate ramus of pterygoid; **saf.:** shallow anterior fossa of the surangular; **sang.:** surangular; **sof.:** suborbital fenestra; **sp.:** splenial. Scale bar = 2 cm.



(Source: the author)

Figure 4. Dorsal view view of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001). The dark and light greys indicate presence of rock matrix and broken surfaces, respectively. **adf.**: adductor fossa of the angular; **ang.**: angular; **de.**: dentary; **ecpt.**: ectopterygoid; **i3:** incisiviform 3; **m1 to m6:** molariforms; **mxt.**: fragments of the maxillary teeth; **nf.**: neurovascular foramina; **pcf.**: parachoanal fenestra; **pt.**: pterygoid; **sang.**: surangular; **sof.**: suborbital fenestra; **sp.**: splenial; **t.**: transitionary tooth. Scale bar = 2 cm.



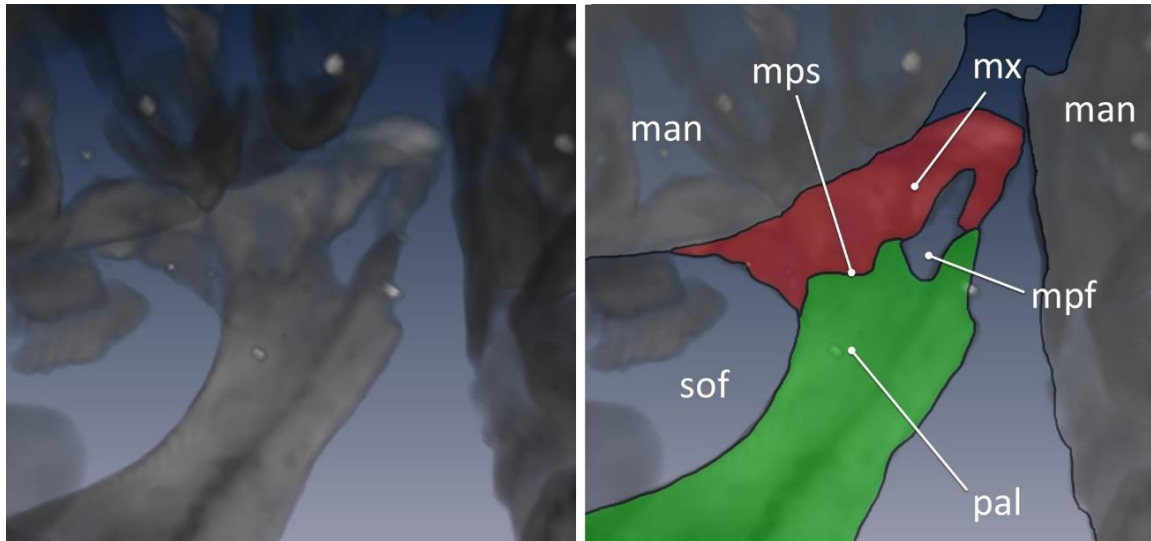
(Source: the author)

LAPEISA-0001 presents a partially preserved secondary palate, with the right infraorbital fenestra, right maxillopalatine fenestra, the choanal groove and both pterygoid flanges (figure 3). Also, part of the neurocranium is preserved, including the quadrate ramus of pterygoids, basisphenoid and part of the basioccipital, quadrate and exoccipital in the region surrounding the triple contact of these bones.

**Suborbital fenestra:** The general shape of the suborbital fenestra is obscured by the fragmentary nature of the specimen. However, it is more similar to the elongated fenestra of *Cai. mineirus* than that of *Cai. paulistanus* and *Cai. montealtensis*, in which the greatest lateromedial axis is about two thirds of the anteroposterior axis. As in the other Sphagesauria (“advanced notosuchians”, see results) *Comahuesuchus* and baurusuchids, the pterygoids do not border the suborbital fenestra (POL *et al.*, 2014). In ventral view, the palatines form the medial margin of the fenestra, while the ectopterygoid participates in the posterior margin and the posterior half of the lateral margin of the fenestra. The participation of the palatines in the posterior vertex of the suborbital fenestra is variable in Sphagesauria. In LAPEISA-0001, *Cai. mineirus*, *Cai. montealtensis*, *Mariliasuchus amaralis* (UFRJ DG 106-R), *Notosuchus*, *Morrinhosuchus* and baurusuchids, the palatines do not border the posterior vertex of the suborbital fenestra, while in *Cai. paulistanus*, *Yacarerani* and *Comahuesuchus*, the vertex is located in the contact between palatines and ectopterygoid. In at least one specimen of *Mariliasuchus* (MZUSP-PV 50) and in *Caipirasuchus stenognathus* (MZUSP-PV 139), each one of the fenestrae has one of the conditions (see *Pterygoids*). The nasopharyngeal duct of LAPEISA-0001 is wider than in *Cai. paulistanus*, *Cai. montealtensis* and *Cai. mineirus*, similar to that of *Cai. stenognathus*, based on the relation of its anteroposterior length (from the anterior vertex of the suborbital fenestra to the choanal groove) and its width at the narrowest point.

**Choanal groove:** the Sphagesauria have a unique and complex choanal region. In all taxa in which this region is preserved (all four species of *Caipirasuchus*, *Sphagesaurus*, *Yacarerani*, *Mariliasuchus amarali* and *Notosuchus*), the choana presents a posteriorly directed opening, placed at the vertex formed by the medial contact between the palatines at the posterior region of the palatine bar. In LAPEISA-0001 this region is covered by sediments, but same chonal arrangement is revealed by the ct-scan images (fig. 5).

Figure. 5. CT-Scan detailing the secondary palate of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001), in ventral view. **man.:** mandible; **mpf.:** maxillopalatine fenestra; **mpps.:** maxilla-palatine suture; **mx.:** maxila; **pal.:** palatine; **sof.:** suborbital fenestra



(Source: the author)

Posterior to the choana, LAPEISA-0001 has a pair of large, broad, and roughly triangular openings, that are equivalent to the parachoanal fenestra (*sensu* MONTEFELTRO; LARSSON; LANGER, 2011), which usually appears as a single large, triangular fenestra in Sphagesauria and baurusuchids (POL, 2003; ANDRADE; BERTINI, 2008a; MONTEFELTRO; LARSSON; LANGER, 2011; GODOY *et al.*, 2014). The parachoanal fenestra faces anteroventrally along its anterior portion, and posteroventrally on its posterior portion, at the level of the pterygoid flange. In LAPEISA-0001, the anterolateral margin of the parachoanal fenestra, as well as the anterior portion of the medial margin, is formed by the palatines, while the pterygoids enclose it medially via the choanal septum, and posteriorly via the anterior margin of the pterygoids wings, as in *Cai. stenognathus*, *Cai. mineirus* and *Cai. montealtensis* (MPMA 68-0003 12). That condition present in most *Caipirasuchus* differs from the large anteromedially surface of pterygoids that surrounds partially or most of the choanal groove (*sensu* POL *et al.*, 2014) as in sebecids, mahajangasuchids, peirosaurids (*Montealtosuchus*, *Lomasuchus*, *Hamadasuchus*, *Barreirosuchus*), *Araripesuchus* and *Anatosuchus*.

The stout choanal septum forms the medial region of the choanal groove and tapers in its posterior third. LAPEISA-0001 presents a longitudinal groove at the anterior portion of the ventral surface of the choanal septum. The same groove is present in *Caipirasuchus stenognathus* and *Cai. mineirus*, which is absent in *Cai. paulistanus* and *Cai. montealtensis*. As in the other *Caipirasuchus* species, the pterygoid comprises most of the choanal septum, with the palatines participating only in the anterior portion of the choanal groove.



LAPEISA-0001 does not have any sign of the the parachoanal fossae (*sensu* MONTEFELTRO; LARSSON; LANGER, 2011) on the ventral surface of the pterygoids, differently from baurusuchids, sebecids and some sphagesaurids (*Sphagesaurus* and *Cai. montealtensis* MPMA 15-0001 90; MPMA 68-0003 12).

**Maxilla:** only a small portion of the right maxilla is preserved, forming the anterior margin of the suborbital fenestra and contacting the palatine medially (figure 5). The contact between the maxilla and palatine is marked by an elongated maxillopalatine fenestra (*sensu* ANDRADE; BERTINI, 2008b). Among Sphagesauria, the maxillopalatine fenestra is present in *Cai. stenognathus* (POL *et al.*, 2014), *Cai. mineirus* (MARTINELLI *et al.*, 2018), *Mariliasuchus amarali* (URC R-67, URC R-68, UFRJ 106-R; MZSP-PV 50; ANDRADE *et al.*, 2006; ZAHER *et al.*, 2006; ANDRADE; BERTINI, 2008b) and *Notosuchus* (MACN-PV-RN 1038; ANDRADE; BERTINI, 2008b; BARRIOS *et al.*, 2018). In LAPEISA-0001, the maxilla forms the anterolateral margin of the maxillopalatine fenestra, enclosing most of it as in *Cai. stenognathus* and *Notosuchus*. In contrast, the maxillopalatine fenestrae of *Cai. mineirus* and *Mariliasuchus* are formed mostly by the palatines.

**Palatines:** both palatines are mostly accessible in the ct-scan images. It contacts the maxilla anteriorly, via a posterolaterally to anteromedially directed suture that forms a triangular shaped surface in ventral view. The palatines enclose the posterior margin of the maxillopalatine fenestra.

The medial surface of palatines is similar to that of other *Caipirasuchus*, forming the long and narrow interfenestral bar between the suborbital fenestrae. The palatines flat ventral surface form the floor of the nasopharyngeal duct. The longer interfenestral bar present in all species of *Caipirasuchus* is also similar to the condition present in *Sphagesaurus huenei*, while this structure in *Yacarerani*, *Mariliasuchus* and *Notosuchus* is stouter. In baurusuchids, the ventral floor of the nasopharyngeal is longer and narrower than the sphagesaurids (POL *et al.*, 2014), and in *Comahuesuchus* and *Pakasuchus*, although poorly preserved, there is a longer interfenestral bar, but wider than in the species of *Caipirasuchus*.

The posterior region of the palatines diverges laterally in two symmetrical posterolaterally directed palatine bars (*sensu* ZAHER *et al.*, 2006) that separate the suborbital fenestrae from the choanal groove. The distal portion of the palatine bars contacts the medial edge of the ectopterygoid at the posterior corner of the suborbital fenestra, but do not form its posterior vertex. The distal tip of the palatine bars reaches the contact between ectopterygoid and pterygoid forming a triple contact at the ventromedial portion of the pterygoid flanges. The ventral surface of the palatines near the contact with the ectopterygoid in LAPEISA-0001 is

similar to *Cai. stenognathus* and with intermediary morphology between what is present in *Cai. paulistanus* and *Cai. montealtensis*, and the extremely reduced exposed surface present in *Cai. mineirus*.

The posterior region of palatines of LAPEISA-0001, positioned medially within the choanal groove, is only accessible in the ct-scan images. Its ventral surface is marked by a longitudinal groove. At its posterior end, the palatines become narrower, forming the anterior margin of the choanal openings, including the choanal septum, and attaching to the pterygoid posteriorly.

**Ectopterygoids:** the preserved portion of the ectopterygoids in LAPEISA-0001 is limited to the posteroventral process which forms a bar that encloses the posterolateral margin of the suborbital fenestra, and its portion overlaying the pterygoid flanges. On the right side, the participation of the ectopterygoid in the lateral margin of the suborbital fenestra is preserved only on its posterior portion, so the exact configuration of the anterior process of ectopterygoid is not assessible in this specimen.

The posteroventral bar of the ectopterygoids in LAPEISA-0001 is broad with a subcircular cross section. This condition is similar to that of *Caipirasuchus stenognathus*, while in *Cai. mineirus*, *Cai. paulistanus* (MPMA 67-0001/00) and *Cai. montealtensis* (MPMA 15-0001/90, MPMA 68-0003/12), the ectopterygoid bar is more gracile and flatter. Posterior to the bar, the ectopterygoid expands lateromedially, contacting the posterior end of the palatine bar medially and the pterygoid posteriorly. This expanded surface of the ectopterygoid overlaps the pterygoid ventral surface, forming the ectopterygoid flange. The ectopterygoid-palatine contact in both sides, it is present a small process of the ectopterygoid anteriorly directed forming the entire posterior vertex of the suborbital fenestra. This condition is also present in both ectopterygoids in *Cai. mineirus*, *Cai. montealtensis* and *Mariliasuchus*, while in *Cai. stenognathus*, this feature is present in only one side, which is regarded as preservation bias (POL *et al.*, 2014). In *Cai. paulitanus*, *Yacararani* and *Comahuesuchus*, the palatine also participates in the posterior vertex of the suborbital fenestral, while in *Mariliasuchus*, both conditions are present. In *Notosuchus*, *Morrinhosuchus* and baurusuchids, the ectopterygoids forms a larger part of the posterior portion of the palatine bars.

**Pterygoids:** the pterygoids are completely fused in a single median element which, for the descriptive purpose, is divided in three distinct regions: an anterior portion, a pair of lateroventrally projecting flanges and the dorsal portion. The anterior portion of the pterygoid borders the posterior margin of the parachoanal fenestrae. Their projecting flanges compose the pterygoid wings. The dorsal portion firmly attaches to the neurocranium, contacts the

latersphenoid and quadrate anteriorly, and the pterygoid process of the quadrate posterolaterally.

The anterior process of pterygoids has a great participation in the lateral and posterior edges of the parachoanal fenestrae, enclosing it posteriorly through the anterior margin of the pterygoid flanges, and medially through the choanal septum (see *Choanal groove*). In *Caipirasuchus* the separation between the parachoanal fenestrae is formed by the anterior projection of pterygoids for most of (LAPEISA-0001, *Cai. stenognathus*, *Cai. mineirus*, *Cai. montealtensis*) or entirely (*Cai. paulistanus*). The ventral surface of the choanal septum in LAPEISA-0001 tapers on its posterior third, and bears a longitudinal groove on its anterior surface, a condition shared by *Cai. stenognathus* and *Cai. mineirus*, and distinct from *Cai. paulistanus* and *Cai. montealtensis*. However, the narrow posterior third in *Cai. stenognathus* and *Cai. mineirus* is more laminar than in LAPEISA-0001, which has a slightly more developed ventral surface.

The pterygoid flanges are lateroventrally directed, with a narrower proximal region at the contact with the neurocranium, as in *Caipirasuchus montealtensis*, *Cai. stenognathus*, and *Cai. mineirus*. The attachment of the pterygoid flange on the neurocranium is behind the posterior margin of the choana in LAPEISA-0001, and the base of the flange is anteroposteriorly narrow, expanding gradually from that point to the ventral tip of the flange. Among the *Caipirasuchus* species, the condition present in LAPEISA-0001 is different only from *Cai. paulistanus* (MPMA 67-0001 00), in which the proximal region of the flange is stouter. In ventral view, the form and orientation of the pterygoids flanges varies among Sphagesauria. LAPEISA-0001, *Caipirasuchus montealtensis*, *Cai. mineirus*, *Cai. stenognathus*, *Sphagesaurus*, *Mariliasuchus* and *Notosuchus*, share the same condition in which the lateroventral orientation of the pterygoid flanges is approximately of 90° to the longitudinal axis of the skull, and with a restricted proximal region. *Morrinhosuchus* presents a similar condition to *Cai. paulistanus*, with a broader base but also oriented in approximately 90°. *Yacararani* shows a more posteromedially oriented flanges at approximately 45° to the longitudinal axis of the skull, and the same width throughout its length.

The ventral surface of the pterygoid flange in LAPEISA-0001 is flat and smooth, lacking the parachoanal fossae present in *Cai. montealtensis* (MPMA 15-0001/90; MPMA 68-0003/12) and the slight depression present in *Cai. stenognathus* and *Cai. mineirus*. The presence of a parachoanal fossa and similar structures is variable in sphagesaurids, baurusuchids and sebecids, and probably represent multiple acquisitions in the evolutionary history of these taxa (POL *et al.*, 2014). Apart the Sphagesauria, this feature is also present in *Stratiosotusuchus*,



*Pissarrachampsa*, *Aplestosuchus*, *Sebecus querejazus* and *Lorosuchus* (ANDRADE; BERTINI; PINHEIRO, 2006; MONTEFELTRO; LARSSON; LANGER, 2011; POL *et al.*, 2014; GODOY *et al.*, 2014). DIAS *et al.*, (2019) indicated that the parachoanal fenestra in *Cai. montealtensis* (MPMA-68.0003/12, MPMA-68.0004/12) is a complex structure that includes a secondary chamber, connected to the internal nares and assumed to have an important role in vocalization. In LAPEISA-0001 and *Cai. paulistanus*, this second chamber is absent.

Although the posterior border of both flanges is not completely preserved in LAPEISA-0001, the laminar nature of this region is confirmed. In its lateral border, the lamina becomes thicker due to pneumatic diverticula, as in other *Caipirasuchus* and baurusuchids (MONTEFELTRO; LARSSON; LANGER, 2011). In the anterior region of the ventral surface of the flanges, the pterygoid contacts the ectopterygoid laterally and the palatine medially. A small pedicel forms a platform that supports the posterior ends of the ectopterygoids and the palatine bars, a trait found in all other *Caipirasuchus* (notably enlarged in *Cai. stenognathus*), as well in *Yacarerani*, *Mariliasuchus* and *Notosuchus* (POL *et al.*, 2014).

The anterodorsal face of the pterygoid flanges bears a marked crest that extends lateroventrally along the flange, from its top to about half of its length. Dorsally to this crest, the surface of the pterygoid is flat at the level of the posterior margin of the parachoanal fenestra. This structure is absent in *Mariliasuchus* (UFRJ 105-R) and appears to be absent in *Cai. paulistanus* (MPMA 67-0001/00) and *Notosuchus* (MUCP-147, MLP-64-IV-16-5).

Posterior to the flanges, in ventral view, the pterygoids extend posterodorsally, contacting the quadrate and attaching to the basisphenoid. As in other sphagesaurids and *Mariliasuchus*, the quadrate process of pterygoid of LAPEISA-0001 is reduced due to the long pterygoid process of the quadrate. In other notosuchians, such as baurusuchids, sebecids, peirosaurids, mahajangasuchids, *Araripesuchus*, *Uruguaysuchus*, *Simosuchus*, *Malawisuchus* and *Morrinhosuchus*, the quadrate process of the pterygoid extends posteriorly, up to the level of the lateral pharyngotympanic tube (POL *et al.*, 2014).

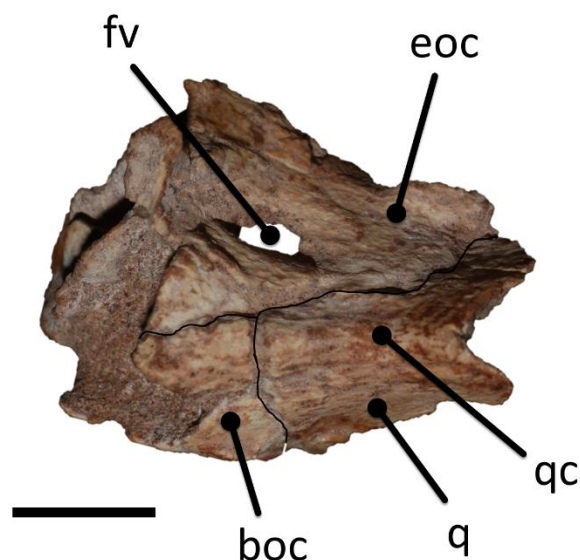
**Basisphenoid:** only the anterior region of the basisphenoid is present and covered with rock matrix. Its general shape is similar to that of *Cai. stenognathus*, which is attached to the pterygoid anteriorly and laterally. Its ventral surface is markedly depressed between a pair of lateral ridges that converge anteriorly. In this configuration, the opening of the medial pharyngeal tube and the pharyngotympanic tubes are within the depression. In addition, this depression forms a continuous canal with the medial surface of the pterygoid. Other sphagesaurids (*Yacarerani*, *Sphagesaurus*, *Armadillosuchus*), have the anatomy of this region similar to the extant crocodylians, in which the openings are at the level with the outer ventral

surface of the neurocranium, as in most notosuchians such as *Mariliasuchus*, *Notosuchus*, *Araripesuchus*, *Uruguaysuchus* and baurusuchids (POL *et al.*, 2014). In LAPEISA-0001, the ct-scan images revealed a collapsed ventral floor, so the openings of the pharyngeal tube and pharyngotympanic tubes are not visible within the depression.

A large ventral exposition of the basisphenoid is a common feature of notosuchians such as in baurusuchids, *Mariliasuchus* and sphagesaurids (MONTEFELTRO; LARSSON; LANGER, 2011; POL *et al.*, 2014). In *Caipirasuchus* in which the region is preserved, including LAPEISA-0001, *Cai. montealtensis*, *Cai. stenognathus* and *Cai. mineirus*, the ventral surface of the basisphenoid has a trapezoidal shaped with a length equal or longer than its width.

**Occipital fragment:** part of the right portion of the occipital region of the neurocranium is preserved in LAPEISA-0001. The fragment is limited to the region near the contact of exoccipital, basioccipital and quadrate (figure 6). The preserved fragment has two main surfaces, a posteroventral face, composed mostly by the ventral portion of exoccipital, with a small participation of the quadrate; and a ventral face, composed by the quadrate and the posterior basioccipital.

Figure 6. Occipital fragment of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001), in ventral view. A dark line indicates the contact between the bones. **boc.:** basioccipital; **eoc.:** exoccipital; **fv.:** *forame vagi*; **q.:** quadrate; **qc.:** quadrate crest. Scale bar = 1 cm.



(Source: the author)

The exoccipital is the main element present in the fragment. The preserved region in LAPEISA-0001 is similar to the posteroventral face of the exoccipital described for *Cai.*

*stenognathus* (POL *et al.*, 2014). In most of mesoeucrocodylians, a ridge, that runs medially from the parasagittal process, divides the exoccipital in a posterodorsal and a posteroventral plane (POL *et al.*, 2014). In LAPEISA-0001, only the portion ventrally to the ridge is preserved, so the participation of the exoccipital in the occipital condyle or in the margin of the foramen magnum cannot be determined. Dorsal to the contact with the basioccipital, there is a large foramen *vagi*, but no further details can be assessed.

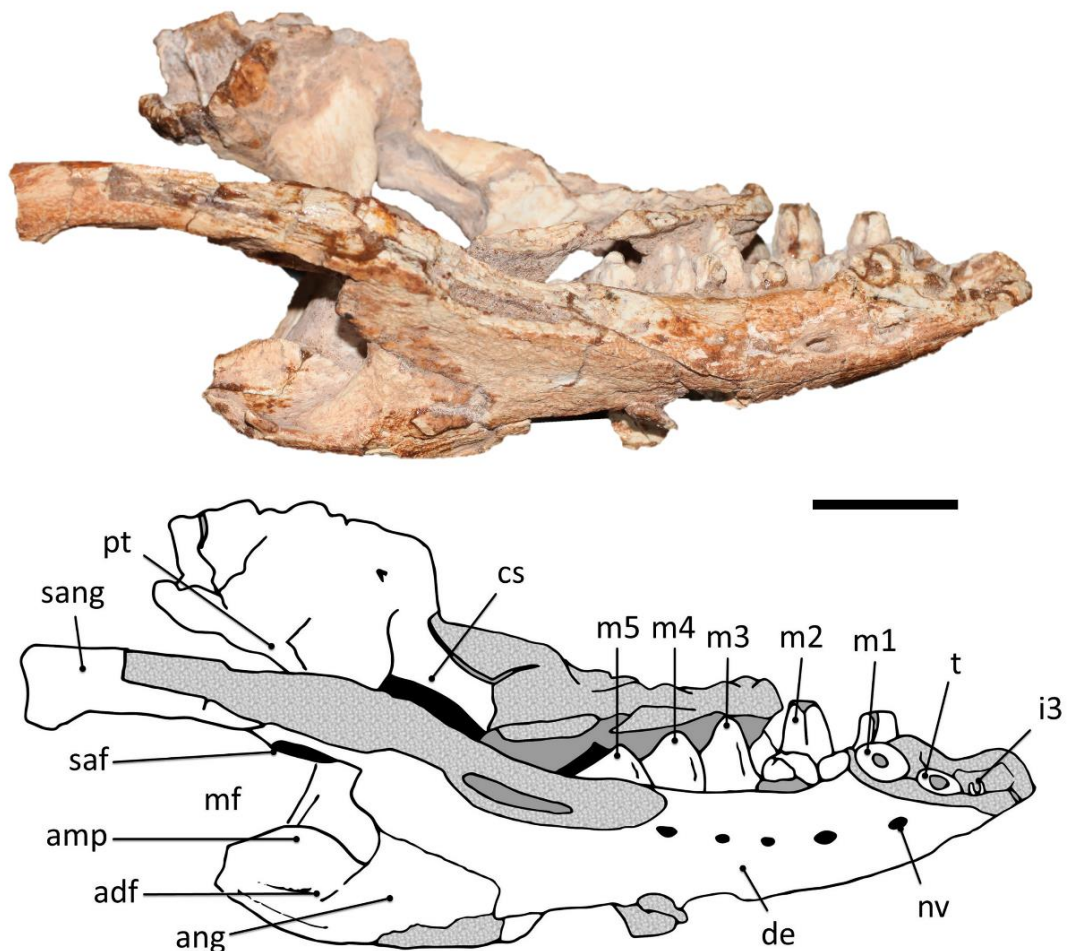
The quadrate projects medially into the paraoccipital process, with an extensive contact with the exoccipital, a condition found in all mesoeucrocodylians (POL *et al.*, 2014). The preserved portion in LAPEISA-0001 corresponds to the medial most portion of the quadrate-exoccipital suture. At this point, the quadrate bears a crest that runs parallel to the suture. This crest is absent in *Cai. stenognathus*, *Cai. mineirus* and *Yacararani*, it is incipient in *Cai. montealtensis* (MPMA 15-0001/90; MPMA 68-0003/12) and *Cai. paulistanus*, and well-developed in LAPEISA-0001, *Sphagesaurus* and *Armadillosuchus* (UFRJ DG 303-R). A similar crest is found in some peirosaurids (*Montealtosuchus*, *Stolokrosuchus*) and *Simosuchus*, but it is more ventrally positioned and distant from the quadrate-exoccipital contact, and therefore considered non-homologous to the crest in sphagesaurids. Medially to this crest, the quadrate contacts the basioccipital. In *Sphagesaurus* and *Armadillosuchus*, the well-developed crest of the quadrate excludes the exoccipital from the occiput, and it is not visible in ventral view, a condition unique among crocodyliforms (ANDRADE; BERTINI, 2008a; POL *et al.*, 2014).

The basioccipital is poorly preserved. Most of its surface is fragmented, exposing the brain cavity. A small fragment of the basioccipital is the only fragment of the occipital condyle, which seems to have a distinct neck, as in other *Caipirasuchus*. However, in contrast with *Cai. stenognathus*, there is no foramen in the ventral surface just beneath the occipital condyle.

**Mandible:** the mandible of LAPEISA-0001 comprises an almost complete symphyseal region and the mandibular rami to the level of the anterior margin of the mandibular fenestra in both sides (figure 7; 8). The posterior part of the ventral surface and the posterior surface of the symphyseal region is not preserved. The symphyseal region is long and narrow in LAPEISA-0001, reaching the level of the sixth dentary tooth (D6) (figure 4). The hemimandibles have a parallel orientation in the symphyseal region. From the posterior end of the symphysis the hemimandibles strongly diverge posterolaterally, giving the mandible the apomorphic “Y” shape of sphagesaurids and other “advanced notosuchians” (*Mariliasuchus* UFRJ DG 50-R, UFRJ DG 105-R, UFRJ DG 106-R, MZSP-PV 50; *Labidiosuchus*; *Notosuchus* MACN-1037, MACN-1041, MUCPv-35, MUCPv-147). In other notosuchians (baurusuchids, sebecids,

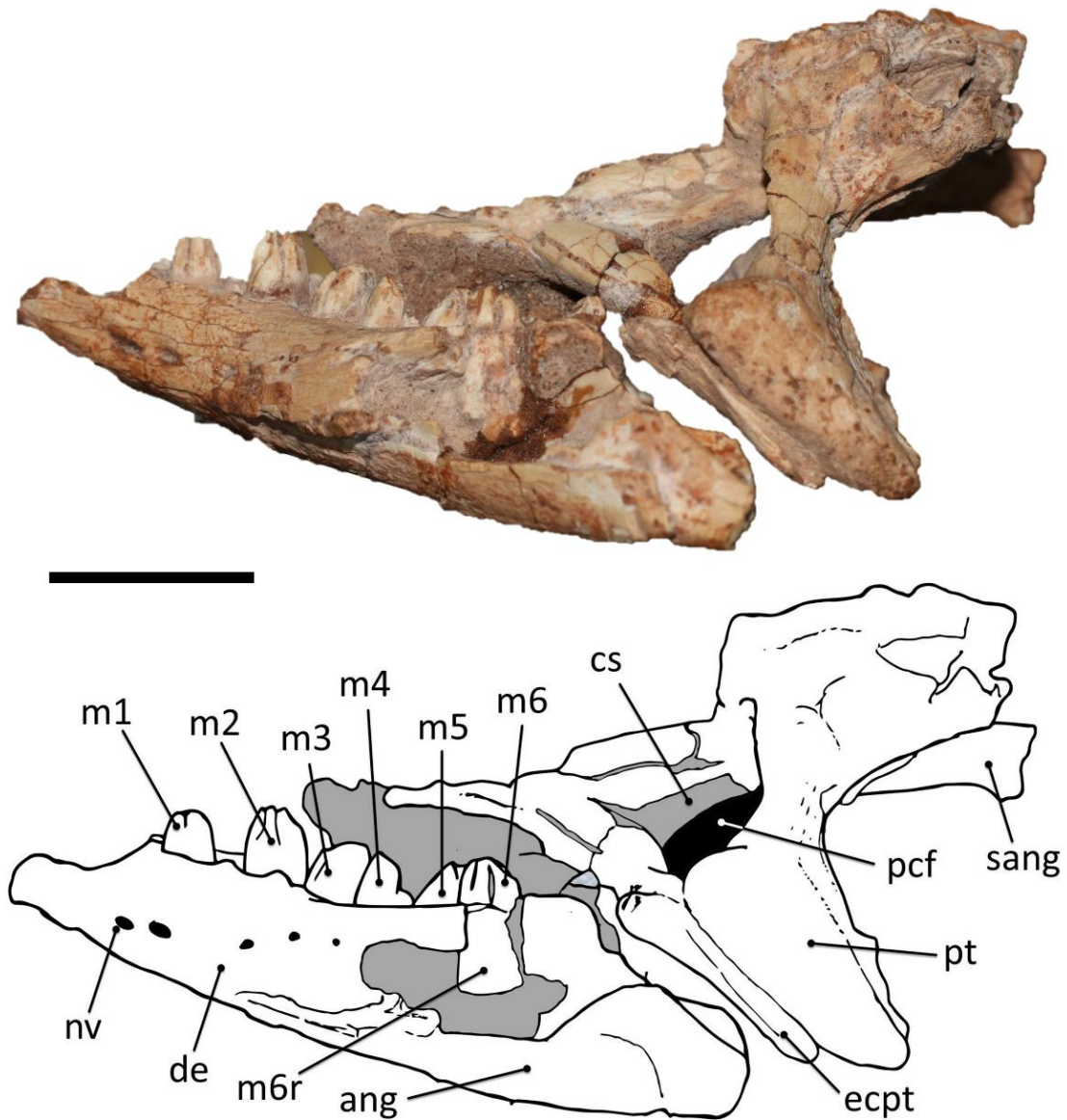
*Pakasuchus*, *Malawisuchus*, *Candidodon*, *Uruguaysuchus*, *Lybicosuchus*, *Araripesuchus*), the hemimandibles gradually diverge from one another. Pol *et al.* (2014) suggested that the *Morrinhosuchus* holotype has a “Y” shape mandible, but a newly described specimen with a more complete mandible (MPMA 12-0050/07) shows a distinct arrangement, with a long symphysis but no strong curvature posterior to that. In sphagesaurids in which the posterior half of the mandible is preserved, the hemimandibles become parallel posterior to the anterior edge of the mandibular fenestra. In LAPEISA-0001 they continue to diverge from one another at this point, resembling better the condition of non-sphagesaurid-Sphagesauria, such as *Mariliasuchus*, *Labidiosuchus* and *Notosuchus*.

Figure 7. Right lateral view of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001). The dark grey and light greys indicate presence of rock matrix and broken surfaces, respectively. **adf.**: adductor mandibular fossa; **amp.**: ascending medial process of the angular; **ang.**: angular; **cs.**: choanal septum; **de.**: dentary; **i3.**: incisiviform 3; **m1 to m5.**: molariforms; **mf.**: mandibular fenestra; **nv.**: neurovascular foramen; **pt.**: pterygoid; **saf.**: shallow anterior fossa of the surangular; **sang.**: surangular; **t.**: transitionary tooth. Scale bar = 2 cm.



(Source: the author)

Figure 8. Left lateral view of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001). The dark grey and light greys indicate presence of rock matrix and broken surfaces, respectively. **ang.:** angular; **cs.:** choanal septum; **de.:** dentary; **ecpt.:** ectopterygoid; **m1 to m6:** molariform teeth; **m6r:** root of molariform 6; **nv.:** neurovascular foramen; **pcf.:** parachoanal fenestra; **pt.:** pterygoid; **sang.:** surangular. Scale bar = 2 cm.



(Source: the author)

The mandibular symphysis is formed mostly by the dentaries, with a small participation of the dorsal portion of the splenial. The symphyseal region is anteroposteriorly long, tapering anteriorly in both lateral and dorsal views. The symphysis extends posteriorly to the level of D6, similar to the other species of *Caipirasuchus*. Although, the unique shape of the symphyseal region is present in all sphagesaurids and other Sphagesauria, *Caipirasuchus* presents a further

modified condition, in which the symphyseal region is three times longer than wide. The same region is only twice longer than wide in larger sphagesaurids (*Sphagesaurus*, *Armadillosuchus*, *Caryonosuchus*) and as long as broad in the other sphagesaurids and basal Sphagesauria (POL *et al.*, 2014).

**Dentary:** the dentary forms the greatest part of the symphysis and extends to the anterior margin of the mandibular fenestra (figure 7). Its lateral and ventral surfaces are weakly ornamented. In lateral view, the dorsal margin is slightly concave posteriorly to the region of the symphysis, and then upturns to the level of the last mandibular alveoli. The ventral profile of the dentary is anterodorsally directed at the symphysis and remain roughly straight posteriorly.

In ventral view, the contact between the dentaries is marked by a groove. The ventral surface of the dentaries is mostly well-preserved but the presence of breakages at the posterior region of the symphyseal region blurs the exact course of the dentary-splenic contact in this part.

The lateral surfaces of the dentaries are divided into two planes by a ridge. The dorsal plane corresponds to the alveolar shelf, a flat surface dorsolaterally oriented that extends beyond the labial margin of the alveoli. This shelf starts anteriorly between D5 and D6, extending posteriorly to the posteriormost mandibular alveolus. As a result, the tooth row is medially displaced compared to the lateral surface of the dentary, this is a common feature present in all Sphagesauria, *Morrinhosuchus*, *Malawisuchus* and *Pakasuchus* (POL *et al.*, 2014). The ventral plane is ventrally directed and comprises the major portion of lateral surface of dentary.

A row of enlarged foramina is present in the anterior portion of the lateral surface of the dentary above the ridge marking the limit of both mandibular planes. There are five preserved foramina in right ramus and four in the left. The anterior two foramina are enlarged, with almost twice the length of the posterior ones. The line of foramina present in LAPEISA-0001 is shared by all *Caipirasuchus*, as well as *Yacararani* and *Mariliasuchus*, although, in the latter, the foramina is not as enlarged as in sphagesaurids.

In dorsal view, the dorsal surface of the dentary is more restricted in the symphyseal region, gradually widening laterally after D6, at the level in which the alveolar shelf becomes more developed. An incomplete alveolar septum extends from the labial margin of the five posterior alveoli of the splenic, as in other species of *Caipirasuchus*, while the alveoli D5 and D6 are completely separated from each other by the septum. The presence of the complete septum of LAPEISA-0001 is also present in *Cai. montealtensis*, *Cai. paulistanus* and *Cai. stenognathus* but it is absent in *Cai. mineirus*.

Posterior to the toothrow, the dentaries are dorsoventrally expanded, contacting the angular just beneath the anterior margin of the mandibular fenestra, and the surangular at the dorsal margin of the external mandibular fenestra. In this region, the laterodorsal to medioventral inclination of the dentary is more pronounced in LAPEISA-0001 than in the other *Caipirasuchus*, and we considered it as an autapomorphy of the new taxon. In lateral view, the angular-dentary contact is anteroventrally inclined, so the dentary participates only in the anterior margin of the fenestra, being completely excluded from its anteroventral margin by the angular, as in most notosuchians.

The surangular-dentary contact is not preserved in the left hemimandible and it is hard to determine on the right side due to poor preservation. The posterodorsal branch of the dentary extends along the anterior portion of the dorsal margin of the mandibular fenestra. In the other *Caipirasuchus*, *Yacararani*, *Adamantinasuchus*, *Labidiosuchus* and *Mariliasuchus* (UFRJ DG 105-R, UFRJ DG 106-R, MZSP-PV 50), the dorsal ramus of the dentary is divided in two processes, one dorsal and one ventral, that overlies the anterior region of the surangular, forming a V-shaped contact between the bones in lateral view (POL *et al.*, 2014). In LAPEISA-0001 both processes are also present.

**Splénial:** the splenials in LAPEISA-0001 have a similar morphology to other “advanced notosuchians”. It covers most of the medial surface of mandibular ramus from the symphyseal region to the anterior margin of the adductor fossa. The surface of splénial is flat, smooth, and dorsoventrally high. The medial surface has an aperture at the level of the last dentary tooth, indicating the presence of a large and oval foramen *intermandibularis oralis*. This foramen is placed in the level of D9-10 in LAPEISA-0001, *Cai. paulistanus*, *Cai. montealtensis* and *Cai. stenognathus*, whereas it is more anteriorly positioned in *Cai. mineirus*, at the level of D8 (MARTINELLI *et al.*, 2018).

The posteriorly located foramen *intermandibularis oralis* present in LAPEISA-0001 is a feature shared by Sphagesauria, baurusuchids and sebecids (POL *et al.*, 2014). Although, a larger and slot-like foramen is only present in baurusuchids and sebecids (ORTEGA; BUSCALIONI; GASPARINI, 1996; SERENO; LARSSON, 2009; MONTEFELTRO; LARSSON; LANGER, 2011). There are minor variations in the location and size of the foramen *intermandibularis oralis* in the Sphagesauria. In *Morrinhosuchus*, *Notosuchus* and *Mariliasuchus*, the foramen is more dorsally positioned (POL *et al.*, 2014), while in sphagesaurids it has a more ventral disposition. Additionally, in LAPEISA-0001, *Cai. montealtensis* and *Cai. paulistanus*, the foramen length is approximately 50% of the height of the splénials, while in other Sphagesauria, the foramen is a smaller opening.



The anterior portion of the splenials is fragmentary, so there is no information about the contact with dentary and the participation of splenial in the symphysis. However, the posterior region of the dorsal surface of symphysis is preserved, and two protuberances medially displaced between D5 and D6 are interpreted as the anterior portion of both splenials, similar to other *Caipirasuchus* species. Due the preservational condition, it is not possible to confirm the presence of the peg in the posterior face of the symphyseal region nor the splenial depressions (*sensu* MONTEFELTRO; LARSSON; LANGER, 2011).

The ventral surface of splenial is preserved only posteriorly to the symphysis, in which it is reduced to a thin lamina. The splenial forms the lingual alveolar wall from D6 to D10 as in other *Caipirasuchus*. The alveolar margins of the splenial expands labially in reduced triangular processes between each alveolus, these structures do not contact the correspondent processes of dentary, as a result forming an incomplete alveolar septum from D6 to D10, as in most notosuchians (ORTEGA; BUSCALIONI; GASPARINI, 1996; POL; APESTEGUÍA, 2005; POL *et al.*, 2014). Just behind and ventral the last dentary tooth, the splenial contacts the angular in a V-shaped suture. The contact splenial-surangular and its relationship with the mandibular fenestra is not assessible.

**Angular:** only the anterior portion of angular forming the ventral and anteroventral margins of the mandibular fenestra is present. The angular is U-shaped in cross section and is overlapped by the splenial medially and dentary laterally.

In LAPEISA-0001, a distinctive shallow fossa is present in the angular beneath and anteriorly to the external mandibular fenestra. This fossa is also present in other Sphagesauria, including *Cai. stenognathus*, *Cai. montealtensis*, *Adamantinasuchus*, *Yacarerani*, *Mariliasuchus* and *Notosuchus*, but it is absent in baurusuchids, sebecids, peirosaurids, mahajangasuchids and other notosuchians (e. g. *Simosuchus*, *Uruguaysuchus*, *Araripesuchus*, *Lybicosuchus*) (POL *et al.*, 2014). However, the condition in LAPEISA-0001 is unique, in which the anteroventral margin of the fossa at the external mandibular fenestra gradually merges with the floor of the Meckelian canal and does not form a prominent ridge as in the other *Caipirasuchus*.

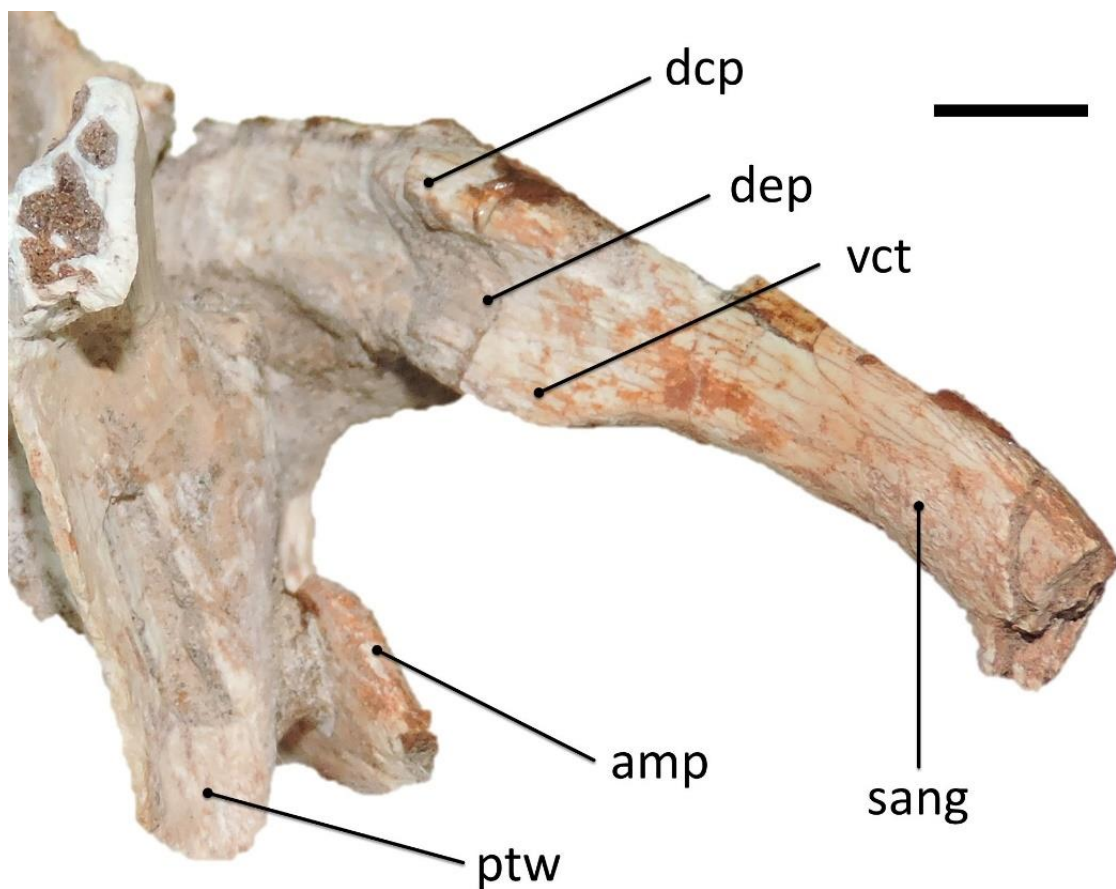
In the medial view, the angular has a large ascending medial process that forms the medial limit of the anterior edge of the internal mandibular fenestra (figure 9), similar to that in *Mariliasuchus* (UFRJ DG 105-R; UFRJ DG 106-R) and *Adamantinasuchus* (UFRJ DG 107-R). This process has a great discrepancy in size and shape among Sphagesauria. In *Cai. stenognathus*, the process is robust and bears a bulbous, rugose dorsal surface (POL *et al.*,



2014), while in other *Caipirasuchus*, *Yacarerani* and *Notosuchus*, it is less prominent, with almost the same height of the angular ramus posterior.

In ventral view, the angular tapers anteriorly. The suture with splenial has an anterior process that extends ventrally toward the anterior limit of the splenial, forming a “V-shaped” contact. In other *Caipirasuchus*, *Yacarerani*, *Marillasuchus* and *Notosuchus*, this contact is simpler, with little or no interdigitation between angular and splenial.

Figure 9. Medial view of the right mandibular ramus of *Caipirasuchus attenboroughi* sp. novae (LAPEISA-0001). **amp.:** ascending medial process of the angular; **dct.:** dorsal coronoid tuberosity; **dep.:** depression between coronoid tuberosities; **ptw.:** pterygoid wing; **sang.:** surangular; **vct.:** ventral coronoid tuberosity. Scale bar = 1 cm.



(Source: the author)

**Surangular:** the surangular forms the dorsal arch of the mandibular fenestra, preserved in LAPEISA-0001 from the contact with the dentary, anteriorly, to the posterodorsal margin of the external mandibular fenestra, posteriorly. The lateral contact of the surangular with the dentary is anteroventrally positioned compared with other *Caipirasuchus* species, with surangular occupying most of the dorsal margin of the mandibular fenestra, and limiting the

participation of the dentary. Although not complete, the surangular does not reach the last tooth alveoli differently from *Cai. mineirus* (MARTINELLI *et al.*, 2018).

In medial view, the anterior portion of the surangular bears two distinct rugose protuberances separated by a depression, the coronoid tuberosities (*sensu* POL *et al.*, 2014; figure 9). These tuberosities are a common feature in notosuchians, and the same morphology is present in sphagesaurids (*Caipirasuchus*, *Yacararani*, *Adamantinasuchus*), *Mariliasuchus*, and *Morrinhosuchus*. In baurusuchids, *Araripesuchus gomesii*, *A. tsangatsangana* and *Simosuchus*, the tuberosities are present, but they are smaller, with a less prominent depression between them (POL *et al.*, 2014). As in *Cai. paulistanus* and *Cai. montealtensis*, the dorsal coronoid tuberosity of LAPEISA-0001 is positioned posteriorly to the level of the posterior tip of the dorsal process of the dentaries, while in *Cai. stenognathus* and *Cai. mineirus*, the tuberosity is placed just below this process. The ventral coronoid tuberosity is well developed in LAPEISA-0001, facing the ascending medial process of the angular. In LAPEISA-0001, the longitudinal depression between the coronoid processes is shallower than in *Cai. stenognathus*, and similar to *Cai. paulistanus* and *Cai. montealtensis*. In the ventral surface of the surangular, just anterior to the ventral coronoid process, there is a shallow fossa, which was not possible to assess in *Cai. paulistanus*, *Cai. montealtensis* and *Cai. mineirus*, but it is present in *Cai. stenognathus* (POL *et al.*, 2014). In LAPEISA-0001 this fossa is rounded while in *Cai. stenognathus* it is more elongated and drop-shaped (POL *et al.*, 2014).

Posteriorly to the coronoid processes, the main orientation of the right surangular turns slightly medially, indicating that the jaw main axis becomes parallel to its counterpart from that point on. At the level of the mid-length of the mandibular fenestra, the surangular becomes a thin bone, consequently reducing the width of the mandibular ramus in dorsal view. A thin surangular is also a feature of other “advanced notosuchians”, but LAPEISA-0001 shows the most delicate condition of all taxa, being proportionally thinner than in smaller specimens as *Yacararani* and *Adamantinasuchus*.

**Dentition:** Only two isolated fragments of the teeth roots are preserved from the upper series, but most of its anatomy cannot be assessed. Additionally, there are two small fragments in the right ramus, labially positioned between D6-D7 and D7-D8, interpreted as remnants of maxillary teeth. This position indicates the characteristic occlusal pattern of the molariform teeth in sphagesaurids (POL *et al.*, 2014; IORI; CARVALHO, 2018).

The anteriormost symphyseal teeth are not preserved in LAPEISA-0001, and the first preserved teeth is estimated to be D3 in the right ramus (figure 4). However, the crowns in D3-D5 in the right ramus, and D4 in the left ramus are not preserved. The tooth crowns are better

preserved from D5-D10 on the left mandibular ramus and D6-D9 on the right ramus. Sphagesauria has a reduced dental formula and bear a degree of heterodonty (LECUONA; POL, 2008; MONTEFELTRO; LAURINI; LANGER, 2009; AUGUSTA; ZAHER, 2019). Based on the other species of *Caipirasuchus*, we were able to reconstruct the dental formula of LAPEISA-0001 as bearing a total of 10 teeth in each lower jaw, with D1-D3 considered as incisiviforms, D4 as a transitional/caniniform tooth, and D5-D10 as molariforms.

In LAPEISA-0001, as in most *Caipirasuchus*, the molariforms D6-D10 are set in a continuous alveolar groove, while the first molariform (D5) is placed in an alveolus isolated from D4 and D6. In *Cai. mineirus*, however, there is no diastema between D5 and D6, with all molariforms set in a continuous alveolar groove (MARTINELLI *et al.*, 2018). In *Cai. paulistanus* and *Cai. montealtensis*, the alveolar septum is formed only by the dentary, while in LAPEISA-0001 and *Cai. stenognathus*, it is formed both by the dentary labially and the splenial lingually (POL *et al.*, 2014).

The molariform teeth in sphagesaurids have a unique morphology with the crowns laterally compressed, teardrop shaped and deep, oval roots, and with the major axis displaced in an oblique orientation in relationship of the mandibular ramus. This particular configuration is called “sphagesauriform” (IORI; CARVALHO, 2018) and is also present in *Mariliasuchus*, *Labidiosuchus* and *Notosuchus*. In transverse section, the teeth of LAPEISA-0001 are more oval than the typical teardrop shape of other *Caipirasuchus* species, but this is possibly caused by taphonomic deformation rather than the real morphological condition. The other traits of the “sphagesauriform” condition, as the oblique orientation of the molariform teeth, are also present in LAPEISA-0001.

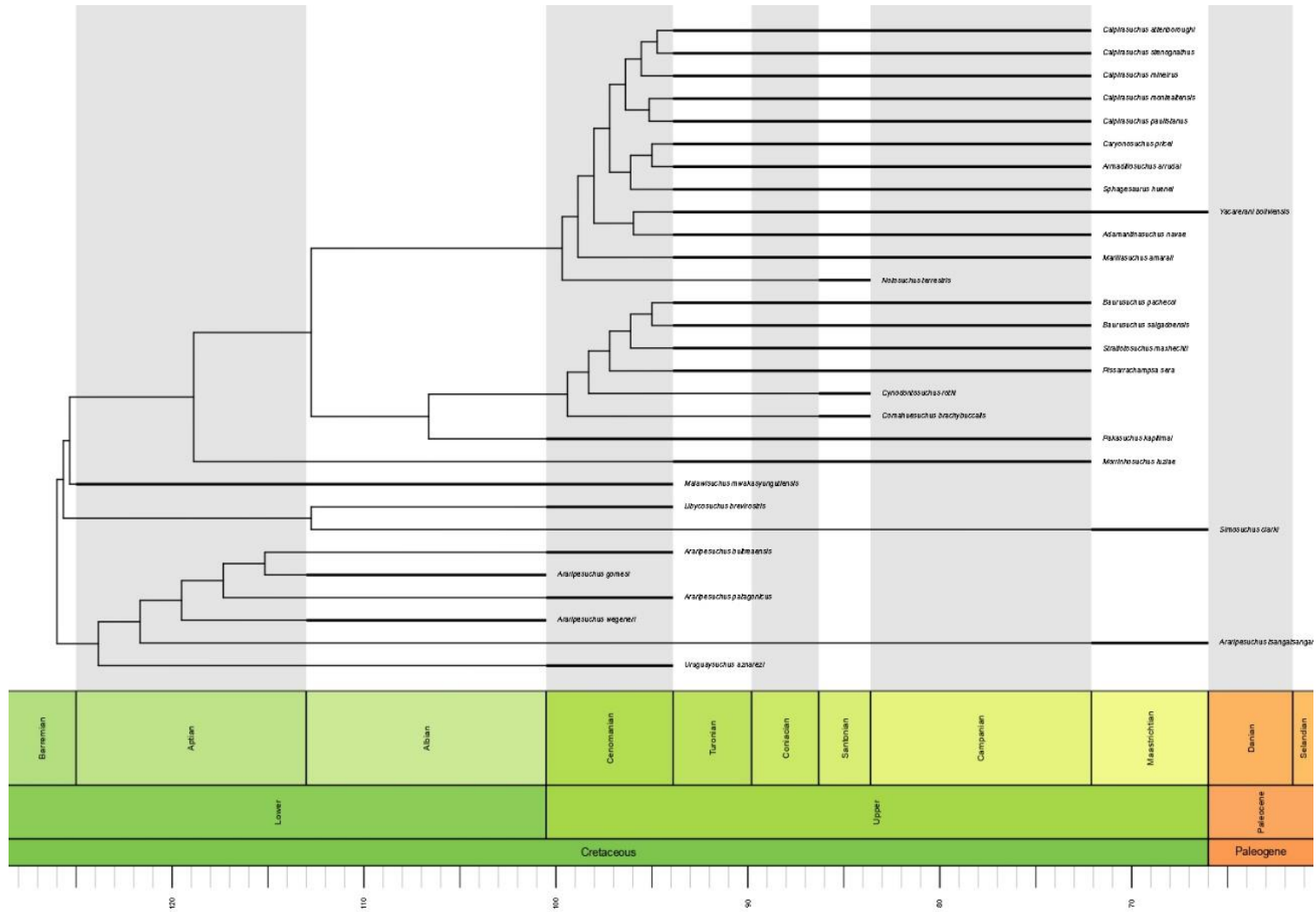
The molariform teeth of LAPEISA-0001 show a faint constriction between the bulbous crown and the root, a condition widely spread in Sphagesaurian, seen in other *Caipirasuchus* (MPMA 67-0001/00, MPMA 15-0001/90, MPMA 68-0003/12), *Armadillosuchus* (UFRJ DG 303-R), *Adamantinasuchus* and *Mariliasuchus* (UFRJ DG 105-R, UFRJ DG 106-R). The typical carinae present in the other *Caipirasuchus* species, *Armadillosuchus* and *Sphagesaurus* cannot be assessed in detail due the lack of most of the dentine in LAPEISA-0001. However, the few patches of preserved dentine seem to point to a less developed dentine coating in the new taxon. Even so, it is possible to recognize the apicobasal ridges in D5, D6, D7 and D9. Posteriorly in the lower tooth row, the teeth decrease in size while increasing the size of the alveolar septum. As such the D10 is much smaller than D6, in a condition that resembles *Cai. montealtensis*.

### 3.3. Phylogenetic relationships and definition

The updated data matrix provided a new perspective on the phylogenetic relationships among the Gondwanan notosuchians (figure 10). Three main aspects of our results are highlighted. The first one is the placement of LAPEISA-0001 within the genus *Caipirasuchus* (figure 10). The second is the presence of the clade encompassing what is previously called “advanced notosuchians” named Sphagesauria herein (figure 10) as a sister-group of the clade Baurusuchia. The third is the presence of the clade encompassing Gondwanan notosuchians, including uruguaysuchids, the usually called “basal notosuchians” (*Simosuchus*, *Libycosuchus* and *Malawisuchus*), and the group formed by Sphagesauria + Baurusuchia (ANDRADE; BERTINI, 2008a b; TURNER; SERTICH, 2010; POL *et al.*, 2012; POL *et al.*, 2014; DAL SASSO *et al.*, 2017).

In the next sections we summarize the synapomorphies of the major clades recovered in our analysis. As this study is focused in *Caipirasuchus*, we discuss both unambiguous and ambiguous synapomorphies for this clade.

Figure 10. Phylogenetic relationships of Notosuchia. The single most parsimonious tree after reduced strict consensus. The fragmentary taxa *Labidiosuchus* and *Lavocatchamps* was excluded of this analysis to avoid inconsistencies.



(Source: the author)

### 3.3.1. Phylogenetic definition

The term “advanced notosuchians” was first introduced by Pol *et al.* (2014) to encompass a clade deeply nested within Notosuchia that includes *Notosuchus*, *Mariliasuchus*, *Labidiosuchus* and Sphagesauridae. This informal name has been applied in several recent analyses with slight variable taxonomic content, including analyses based on independent data matrix (FIORELLI *et al.*, 2016; LEARDI; FIORELLI; GASPARINI, 2015; LEARDI *et al.*, 2015; MARTIN; DE BROIN, 2016; IORI *et al.*, 2018; LEARDI; POL; GASPARINI, 2018; PINHEIRO *et al.*, 2018; CORIA *et al.*, 2019). The presence of a clade with similar content in our analysis, which is also derived from independent data matrix, compelled us to apply the phylogenetic nomenclature to formally define this clade. We erected the name Sphagesauria for a branch-based clade for all Crocodyliformes that share a more recent common ancestor with *Sphagesaurus huenei*, *Caipirasuchus montealtensis*, *Mariliasuchus amarali* and *Notosuchus terrestris* than with *Baurusuchus pachecoi*, *Pissarrachampsa sera*, *Candidodon itapecuruensis*, *Araripesuchus gomesi*, *Sebecus icaeorhinus* and *Peirosaurus tormini*. The choice of the internal and external specifiers was based on the original content of “advanced notosuchians” and the variable content of the clade in previous analyses. As such, our internal specifiers allow that taxa that have been considered or excluded from “advanced notosuchians” in previous analysis, such as *Labidiosuchus*, *Simosuchus*, *Coringasuchus*, and *Morrinhosuchus* have their association to Sphagesauria confirmed or refuted in the future without requiring further redefinitions. In addition, the external specifiers were chosen to limit the use of the name to as close as possible to the original definition of the “advanced notosuchians” proposed by Pol *et al.* (2014) and avoiding redundancy with more traditional notosuchian suprageneric taxa in alternative phylogenetic topologies.

### 3.3.2. *Caipirasuchus attenboroughi* within the Genus *Caipirasuchus* (IORI; CARVALHO, 2011)

LAPEISA-0001 is included in *Caipirasuchus* Genus for which we erected the species *Caipirasuchus attenboroughi*. Since 2009, five species of *Caipirasuchus* were described, increasing the knowledge about the general morphology of the group. The new species could be assigned to the genus *Caipirasuchus* by the presence of a lateromedially narrow and anteroposterior long symphyseal region of the mandibula, three times longer than wider (char. 325, figure 4), posterior teeth with apicobasal crests and rugose enamel surface, the presence

of a diastema between the alveoli of D5 and D6, and a linear row of large neurovascular foramina in the lateral surface of the dentary, synapomorphies of the genus modified from Iori and Carvalho (2009) and Pol *et al.* (2014). We also recovered two new synapomorphies of the *Caipirasuchus* clade: an anteriorly pointed palatines and a broad nasopharyngeal duct.

Additionally, the specimen could be assigned to a new species due to six autapomorphies: 1. A well-developed crest in quadrate parallel to the exoccipital contact; 2. The relatively large angle between hemimandibles, with approximately 35° between them at the level between the symphysis and the mandibular fenestra; 3. mandibular rami that diverges to the level of the posterior half of mandibular fenestrae; 4. A fairly ventrolaterally inclined surface of the dentaries posterior to the toothrow; 5. the anteroventral margin of the external mandibular fenestra gently merges with the floor of the Meckelian canal; 6. The V-shape anterior process of angular in the contact with the splenial;

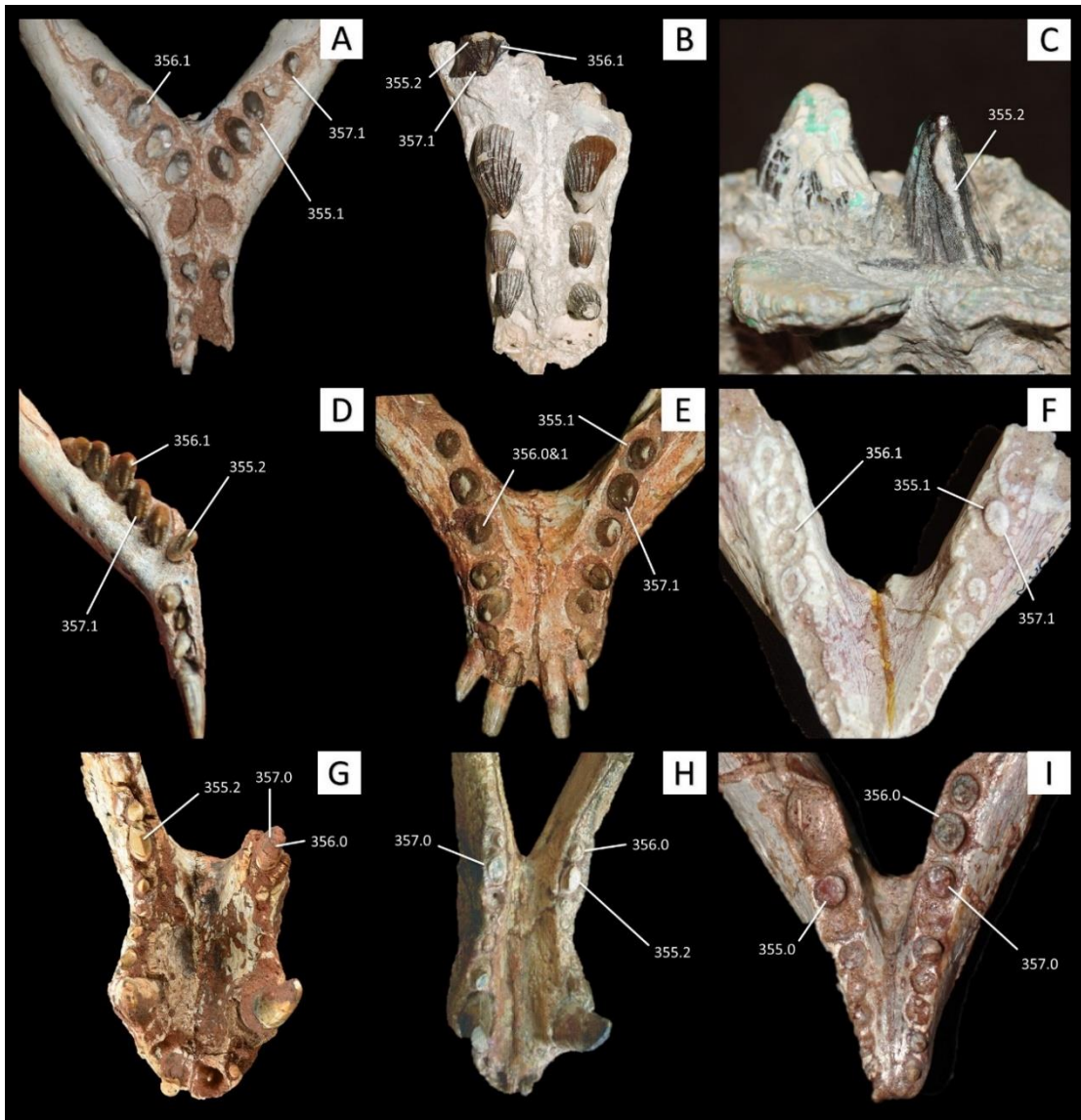
3.3.3. Baurusuchia, (MONTEFELTRO; LARSSON; LANGER, 2011), Sphagesauria (POL *et al.*, 2014) and *Morrinhosuchus* (IORI; CARVALHO, 2009)

*Morrinhosuchus* was previously placed in Sphagesauria (POL *et al.*, 2014; FIORELLI *et al.*, 2016; IORI *et al.*, 2018; MARTINELLI *et al.*, 2018). New remains of this taxa were described by Iori *et al.* (2018), including an almost complete skull, substantially increasing the character scoring for the taxon, including palatal and neurocranium characters not preserved in the holotype. In our analysis, *Morrinhosuchus* occupies the position of sister-group of the clade composed by Sphagesauria + Baurusuchia. This clade is supported by two unambiguous synapomorphies. In *Morrinhosuchus*, Sphagesauria and Baurusuchia, the pterygoid does not reach the suborbital fenestra due to the ectopterygoid-palatine contact (char. 237, st. 1). In more basal notosuchians, as *Mallawisuchus*, *Simosuchus*, *Libycosuchus*, *Araripesuchus*, *Uruguaysuchus*, sebecids, peirosaurids and mahajangasuchids, the pterygoid forms part of the posterior margin of the suborbital fenestra, a condition also presents in *Pakasuchus*, interpreted as a reversion to the plesiomorphic state. The long extension of the ectopterygoid over the pterygoid flange, covering at least half of the ventral surface of this projection (char. 254, st. 1) is also an unambiguous synapomorphy of clade 159. Among notosuchians, a similar condition is only present in *Anatosuchus* and *Mahajangasuchus*.

Sphagesauria is nested with Baurusuchia and supported by one unambiguous synapomorphy. In our dataset, all members of this clade possess teeth strongly compressed laterally (char. 355, st. 1, figure 11), compared with *Morrinhosuchus* and *Mallawisuchus*. In

derived forms, such as baurusuchids and some sphagesaurids, the degree of compression is even higher (char. 355, st. 2, figure 11).

Figure 11. Mandibular and teeth characters of notosuchians. A. *Cai. montealtensis* (MPMA 68- 0003/12); B. *Armadillosuchus arrudai* (MPMA-64-0001-04); C. *Caryonosuchus pricei* (DGM 1411-R); D. *Yacararani boliviensis* (MNK-PAL 5063); E. *Mariliasuchus amaralis* (UFRJ DG 106-R); F. *Notosuchus terrestris* (MUCP-35); G. *Campinasuchus dinizi* (CPPLIP 1471) H. *Baurusuchus pachecoi* (DGM 299-R); I. *Morrinhosuchus luziae* (MPMA 12-0050/07).



(Source: the author)

### 3.3.4. Sphagesauria (POL *et al.*, 2014)

*Mariliasuchus* was recovered as the sister group of Sphagesauridae, and *Notosuchus* was recovered as sister group of the clade *Mariliasuchus* + Sphagesauridae. The relationship among



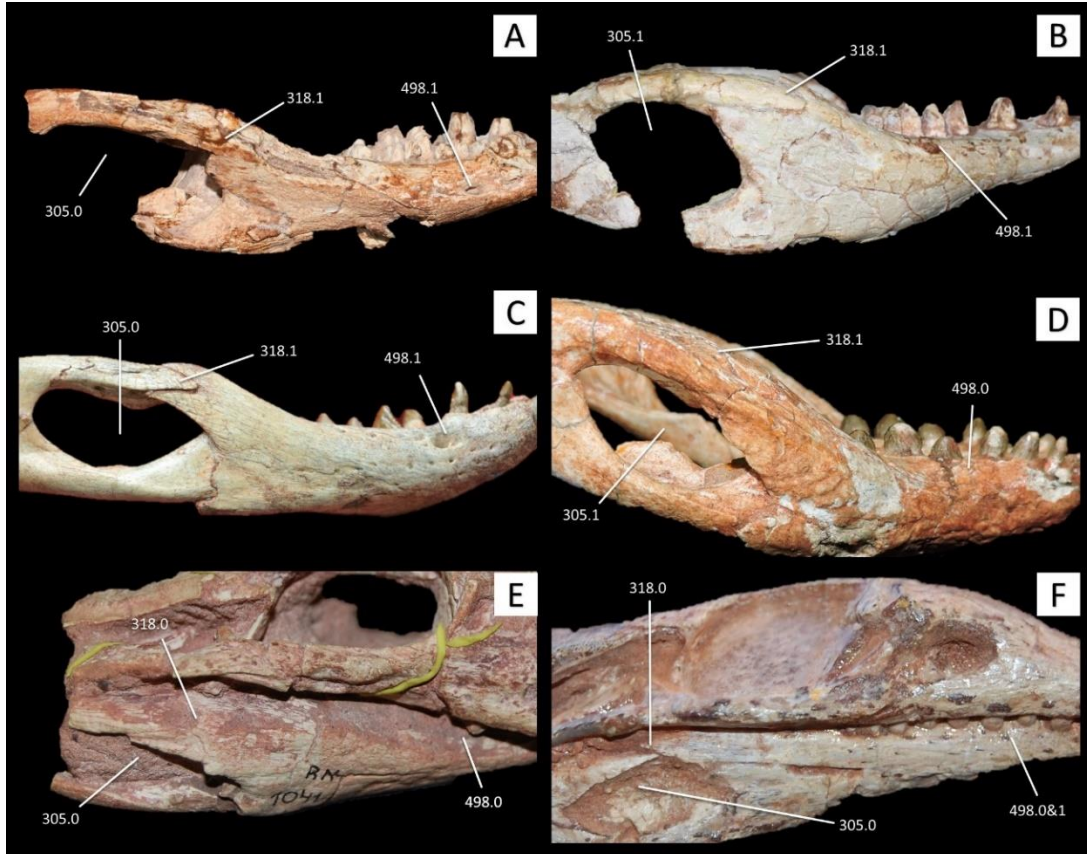
Sphagesauria is similar to that recovered by Pol *et al.* (2014) and subsequently works based in the same matrix.

The status of *Notosuchus* as a sister-group of the clade *Mariliasuchus* + Sphagesauridae is supported by six unambiguous synapomorphies, five of them related to the dentition and one observed in the lower jaw. The posterior teeth in *Notosuchus*, *Mariliasuchus* and all sphagesaurids are displaced obliquely to the longitudinal axis of the mandible (char. 356, st. 1, figure 11) and has a lateral asymmetric compression that gives a tear-drop shape to the crown (char. 357, st. 1 figure 11). This condition, called “sphagesauriform teeth” (IORI; CARVALHO, 2018), is unique among crocodyliforms and one of the most notable features of the clade. Two other synapomorphies regards the enamel surface of the mid to posterior teeth, which presents a ridged ornamentation (char. 361, st. 1), including apicobasal ridges (char. 362, st. 1). Among sphagesaurids, *Yacararani* and *Adamantinasuchus* show a reversion to the plesiomorphic condition in both characters. The presence of a transitional tooth in the premaxilla-maxilla contact (char. 376, st. 1) also supports Sphagesauria.

The mandible of Sphagesauria has a peculiar “Y” shape in dorsal/ventral view, due to the distal rami strongly curvature medially at mid-mandible (char. 307, st. 1). Among notosuchians, only *Lorosuchus* and *Bretesuchus* presents a similar configuration of the mandible, although not as marked as in Sphagesauria. In sphagesaurids, the condition of *Adamantinasuchus*, *Sphagesaurus* and *Armadillosuchus* is not known due to the incomplete preservation of the mandibular rami.

The clade *Mariliasuchus* + Sphagesauridae is supported by three unambiguous synapomorphies. In *Mariliasuchus* and sphagesaurids, the dentary-surangular contact is extremely modified, with the dentary divided into a ventral and a dorsal process, the dorsal process fits into the large notch between the medial and lateral rami of the bifurcated anterior end of the surangular (char. 318, st. 1, figure 12). *Notosuchus* and most notosuchians present a simple contact, with little interdigitation. The condition of large sphagesaurids is unknow. The other two unambiguous synapomorphies of this clade regards the modified teeth. Both *Mariliasuchus* and sphagesaurids have tubular heterogenic denticles (char. 318, st. 2). Among sphagesaurids, only *Cai. attenboroughi* and *Caryonosuchus* show a modified condition, with a smooth enamel surface and the presence of denticulated carinae, respectively. Also, *Mariliasuchus* and sphagesaurids have a rugose enamel surface (char. 497, st. 1), differentiating them from the smooth condition of the teeth of other notosuchians.

Figure 12. Mandibular characters of notosuchians, in right lateral view. A. *Cai. attenboroughi* (LAPEISA-0001); B. *Cai. paulistanus* (MPMA 67-0001/00); C. *Yacarerani boliviensis* (MNK-PAL 5063); D. *Mariliasuchus amaralis* (UFRJ DG 106-R); E. *Notosuchus terrestris* (MACN-1041); F. *Araripesuchus patagonicus* (MUCP-PV-269).



(Source: the author)

### 3.3.5. Sphagesauridae (KUHN, 1968)

The clade Sphagesauridae includes ten species arranged in three major groups: “basal sphagesaurids”, represented by *Adamantinasuchus* and *Yacarerani*; the *Caipirasuchus* lineage and its sister-group, the “large sphagesaurids”, that includes *Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus*. Sphagesauridae is supported by eight unambiguous cranial synapomorphies.

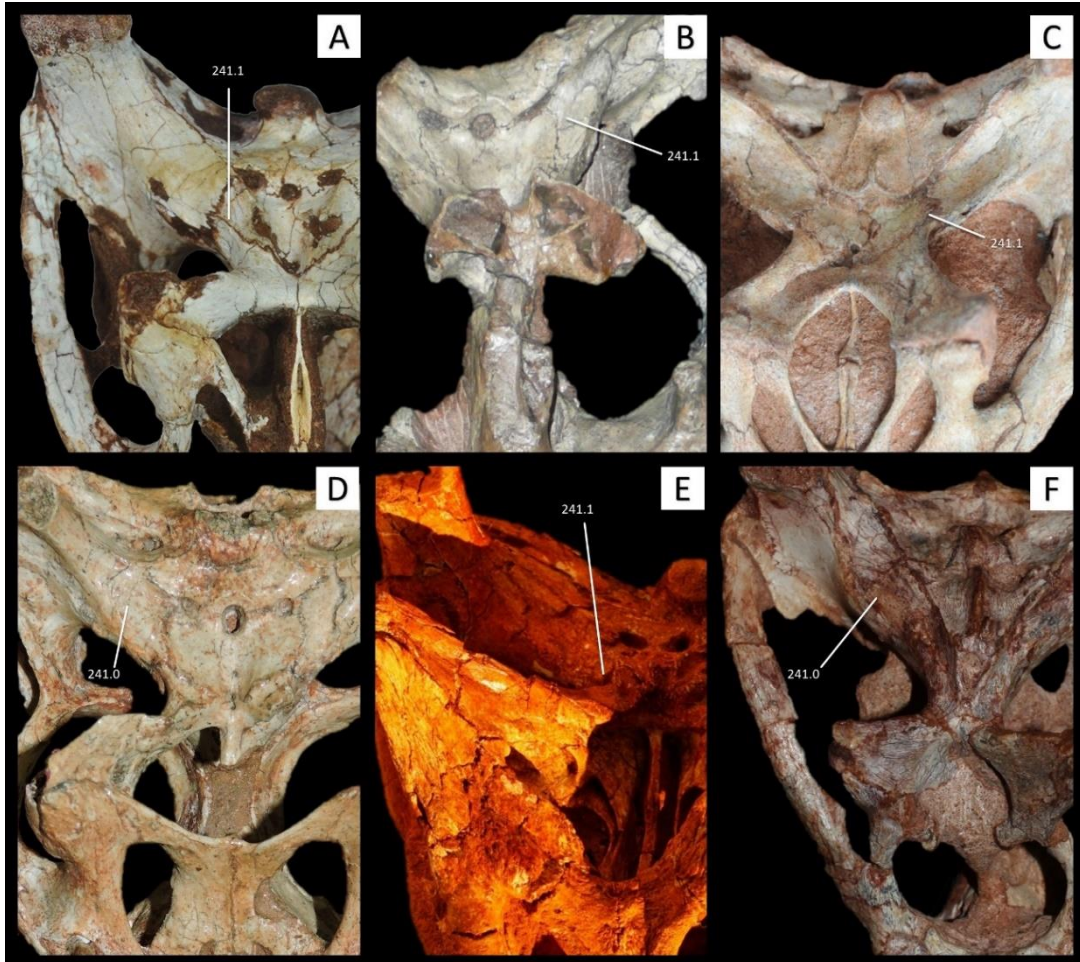
The first cranial synapomorphy is the absence of a foramen in the postnarial depression in the premaxilla (char. 41, st. 0), a condition widespread among crocodyliforms and found in most sphagesaurids. However, in *Mariliasuchus* and *Notosuchus*, as well in baurusuchids (*Baurusuchus pachecoi*, *Stratiotosuchus*, *Pissarrachampsia*), this foramen is also present, indicating that sphagesaurids have reversed to the plesiomorphic state. In the maxilla of sphagesaurids, the row of foramina is interrupted by a gap (char. 140, st. 1). The only exception

is the reversed condition of *Cai. mineirus*. Among other crocodyliforms, this gap is present only in *Pakasuchus*.

As in most notosuchians, *Yacararani* and *Caipirasuchus* have an elongated prefrontal anterior to the orbits, aligned with the longitudinal axis of the skull (char. 69, st. 0). *Mariliasuchus*, *Notosuchus*, *Comahuesuchus* and baurusuchids show a short and broad prefrontal, which is posteromedially-anterolaterally directed. Another cranial synapomorphy of Sphagesauridae is the dorsal exposition of the supraoccipital (char. 121, st. 1). *Yacararani*, *Cai. mineirus*, *Cai. montealtensis*, *Armadillosuchus*, as well *Morrinhosuchus*, *Comahuesuchus* and baurusuchids, show a more restrict exposition of the supraoccipital than mostly notosuchians, including *Mariliasuchus* and *Notosuchus*.

The fifth cranial synapomorphy is the convex postorbital-squamosal suture (char. 500, st. 1). This condition is present in *Yacararani*, *Cai. stenognathus*, *Cai. mineirus* and *Armadillosuchus*, reversed in *Cai. montealtensis* and unknown in the other sphagesaurids. Among notosuchians, only baurusuchids (*Baurusuchus*, *Stratiosuchus*, *Pissarrachampsia*) share this derived condition. In the sphagesaurids, the infraorbital region of the jugal is deeper than the infratemporal one (char. 148, st. 1). This is a variable condition among notosuchians, being acquired and lost in various lineages. It is present in *Baurusuchus*, *Pakasuchus*, *Stolokrosuchus* and mahajangasuchids but absent in *Mariliasuchus*, *Notosuchus*, *Stratiosuchus*, *Pissarrachampsia*, *Comahuesuchus*, and most peirosaurids (*Uberabasuchus*, *Montealtosuchus*, *Lomasuchus*, *Pepesuchus*, *Stratiosuchus*, *Barreirosuchus*). Another synapomorphy of sphagesaurids is the continuous contact between the jugal and the lacrimal (char. 143, st. 0, unknown in *Adamantinasuchus*, *Cai. attenboroughi*, *Armadillosuchus* and *Caryonosuchus*). In most notosuchians, including *Mariliasuchus*, *Notosuchus*, baurusuchids, peirosaurids, sebecids and *Araripesuchus*, the jugal presents a convex anterior edge along the contact which is filled by the maxilla. The poorly developed quadrate process of the pterygoid (char. 241, st. 1, figure 13) is present in all sphagesaurids in which the region is preserved. Among notosuchians, only baurusuchids and *Simosuchus* has a similar condition.

Figure 13. Neurocranium of notosuchians. A. *Cai. mineirus* (CPPLIP 1463, modified from Martinelli *et al.*, 2018); B. *Sphagesaurus huenei* (RCL-100); C. *Yacararani boliviensis* (MNK-PAL 5063); D. *Mariliasuchus amaralis* (UFRJ DG 106-R); E. *Pissarrachampsia sera* (LPRP/USP 0019, modified from Montefeltro; Larsson and Langer, 2011); F. *Morrinhosuchus luziae* (MPMA 12-0050/07).



(Source: the author)

### 3.3.6. Phylogenetic relationships within Sphagesauridae

*Adamantinasuchus* and *Yacararani* forms a clade supported by nine unambiguous synapomorphies, three related to cranial elements, one to the mandible and five to the bizarre dentition. The first cranial synapomorphy is the small nasal-maxilla contact (char. 50, st. 1), a condition unique among crocodyliforms. The second synapomorphy is the orientation of the external surface of the premaxilla and maxilla. In *Adamantinasuchus* and *Yacararani*, as well in *Pakasuchus* and some sebecids (*Sebecus icaeorhinus*, *S. querejazus*, *Bergisuchus*), these bones have a laterally orientation along its entire height (char. 136, st. 0). In other sphagesaurids, as well in most crocodyliforms, these bones are marked by two main orientations: its dorsal region faces dorsoventrally and its ventral region, laterally. The third

cranial synapomorphy is the height of the jugal beneath the orbit and the temporal region. In *Adamantinasuchus* and *Yacarerani*, this bone has the same depth toward its length (char. 149, st. 0), a condition shared by *Morrinhosuchus* and contrasting with other sphagesaurians, in which the suborbital portion has twice the depth of the infratemporal portion. In *Adamantinasuchus* and *Yacarerani*, the mandibular fenestra is horizontally positioned in relationship to the mandible longitudinal axis (char. 305, st. 0, figure 12). Only *Cai. attenboroughi* and *Notosuchus* share the same condition of the orientation among Sphagesauria.

Since the description of *Adamantinasuchus* and *Yacarerani*, its bizarre, modified dentition attracted attention (NOBRE; CARVALHO, 2006; NOVAS *et al.*, 2009; POL *et al.*, 2014), it is no surprise that most synapomorphies refer to their specialized teeth. These two taxa have a high degree of lateral compression in the crown of the posterior teeth (char. 355, st. 2, figure 11), as in *Armadillosuchus* and *Caryonosuchus* (see below). Two other synapomorphies are related to the enamel surface of the teeth. *Adamantinasuchus* and *Yacarerani* does not present the ridge ornamentation (char. 361, st. 0) and the apicobasal crests (char. 362, st. 0) common to other Sphagesauria, interpreted as a reversal to a condition found in more basal crocodyliforms (POL *et al.*, 2014). The absence of a great variation among the size of the premaxillary teeth (char. 369, st. 0) is also a synapomorphy of *Adamantinasuchus* + *Yacarerani*. This condition contrasts with other Sphagesauria in which the anterior premaxillary teeth are clearly smaller than the posterior ones. The last unambiguous synapomorphy of *Adamantinasuchus* and *Yacarerani* is the presence of a teeth wave of enlarged teeth in the maxillary (char. 371, st. 1), while no significantly variation of size in the maxillary teeth are found in other Sphagesauria.

The clade comprising the “large sphagesaurids” is supported as sister-group of *Caipirasuchus*, sharing nine synapomorphies, seven cranial and two dentition characters. In *Sphagesaurus* and most *Caipirasuchus* (unknown in *Cai. attenboroughi*), the suborbital fenestra is large, having a similar length to the orbits (char. 26, st. 1), far more prominent than the relatively small fenestrae of *Yacarerani*, *Mariliasuchus* and *Notosuchus*. The straight nasal-premaxillary suture (char. 54, st. 1) shared by this clade contrasts with the laterally concave suture of other sphagesaurians. However, that trait is possibly subject to ontogenetic variation, as indicated by *Mariliasuchus*, in which the contact is straight in juveniles (URC R67) and concave in adults (MZSP-PV 50) (ZAHER *et al.*, 2006; POL *et al.*, 2014). In *Cai. paulistanus*, *Cai. montealtensis*, *Cai. mineirus* and *Armadillosuchus*, the parietal is projected dorsally to the squamosal (char. 100, st. 1), while in *Yacarerani* and other Sphagesauria, it is placed at the same level. The presence of a characteristic ridge in the jugal-ectopterygoid contact (char. 152, st.1) is also a synapomorphy of clade of “large sphagesaurids”. The meatal chamber (*sensu*



MONTEFELTRO; ANDRADE; LARSSON, 2016) of *Cai. paulistanus*, *Cai. motealtensis* and *Armadillosuchus* is separated in two regions by a ridge on quadrate-quadratojugal (char. 190, st. 1). This region is not preserved in *Cai. attenboroughi*, *Cai. mineirus*, *Sphagesaurus* and *Caryonosuchus*. This derived feature is also present in baurusuchids (*Pissarrachampsa*, *Stratiotosuchus*, *Baurusuchus pachecoi*, *B. salgadoensis*).

In *Cai. paulistanus*, *Cai. montealtensis*, *Cai. mineirus* and *Sphagesaurus*, the maxilla comprises much of the anterior margin of the suborbital fenestra (char. 211, st. 0). As noted above, *Cai. stenognathus* and *Cai. attenboroughi* show a reversion to the condition of most sphagesaurians, including *Yacararani*, with the maxilla playing a minor role in the anterior margin of the fenestra. The absence of a crest in the basioccipital just below the occipital condyle in *Cai. attenboroughi*, *Cai. stenognathus*, *Cai. mineirus*, *Sphagesaurus* and *Armadillosuchus* (char. 271, st. 0) is considered a synapomorphy of the “large sphagesaurids”. The sagittal crest in basioccipital is a derived condition in crocodyliforms and is present in several notosuchian lineages (POL *et al.*, 2014), including *Mariliasuchus* and *Yacararani*, while *Notosuchus* shows interspecific variation (TURNER; SERTICH, 2010; POL *et al.*, 2014).

Accessory ridges on labial-lingual surfaces of mid to posterior teeth (char. 363, st. 1) are present in *Sphagesaurus*, *Armadillosuchus*, *Caryonosuchus* and *Caipirasuchus* (with the exception of the reversed condition of *Cai. attenboroughi*). The second synapomorphy of the dentition is the size of the maxillary teeth relative to the palatal portion of this bone. The specialized teeth of *Caipirasuchus* (except *Cai. attenboroughi*, which the condition is unknown) and large sphagesaurids are well developed, occupying a great area of the palate (char. 373, st. 1).

The clade comprising the larger species of sphagesaurids, *Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus* (POL *et al.*, 2014) is supported by two unambiguous synapomorphies regarding the dentition. To confirm data consistency, a second phylogenetic analysis was performed excluding *Caryonosuchus*, and the clade was still recovered with the same synapomorphies (see *Material and Methods*). In *Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus*, only two premaxillary teeth are present (char. 364, st. 4), contrasting with the four teeth of other “advanced notosuchians” (except *Adamantinasuchus*, which have three teeth). *Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus* lacks the transitional tooth found in the premaxilla-maxilla contact of other Sphagesauria, as in *Adamantinasuchus*.

*Armadillosuchus* and *Caryonosuchus* are nested together as a sister group of *Sphagesaurus* based in two unambiguous synapomorphies. The first is the absence of a small foramen in the premaxilla-maxilla contact (char. 134, st. 0), only observed in some individuals of

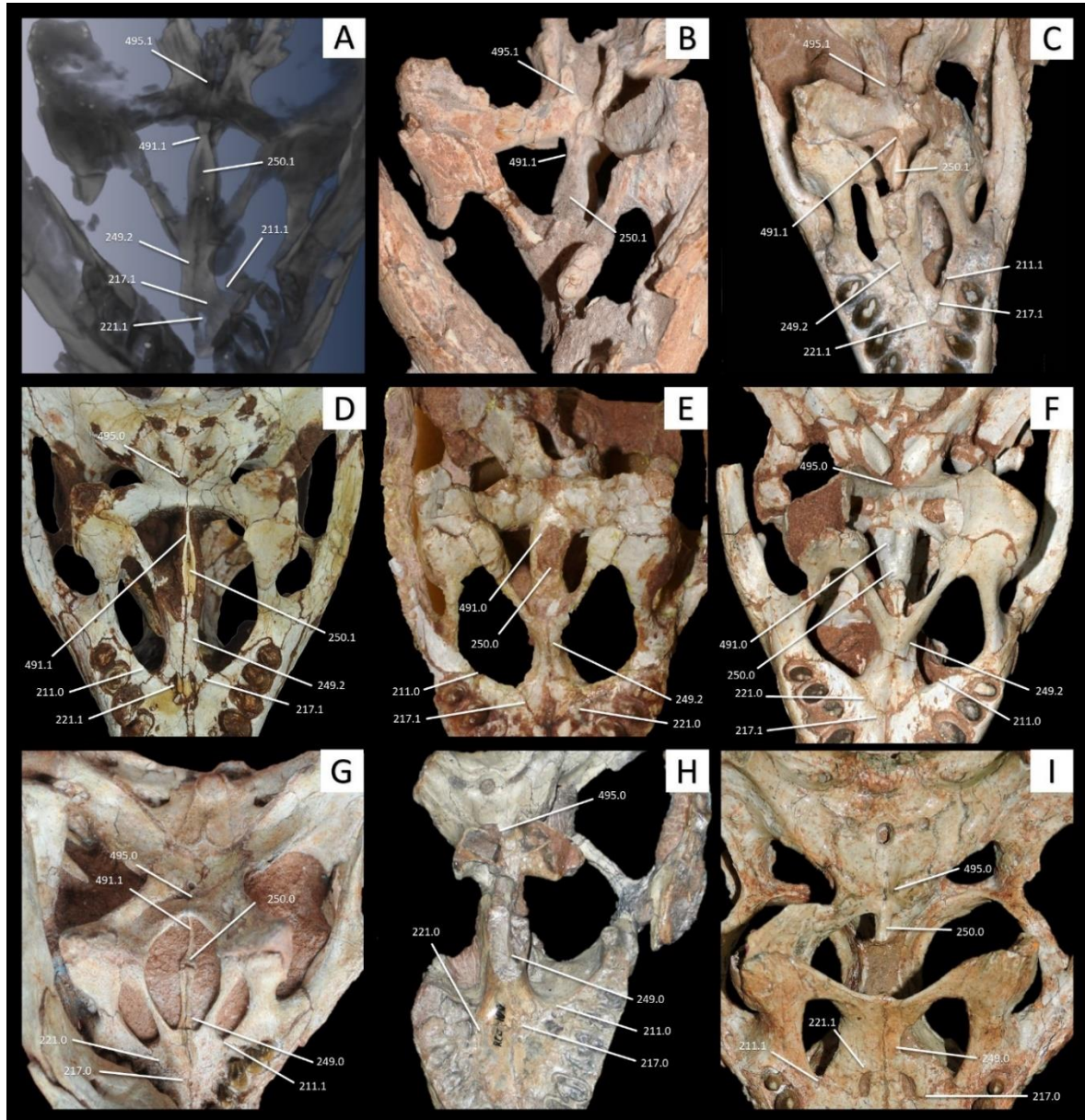
*Mariliasuchus* (UFRJ DG 106-R) among the Sphagesauria. The second is the highly laterally compression of the posterior teeth-crowns (char. 355, st. 2, figure 11) in contrast with the less compressed condition of *Sphagesaurus* and *Caipirasuchus*.

### 3.3.7. *Caipirasuchus* (IORI; CARVALHO, 2009)

The clade *Caipirasuchus* includes five species of small to medium size sphagesaurids, *Cai. paulistanus*, *Cai. montealtensis*, *Cai. stenognathus*, *Cai. mineirus* and *Cai. attenboroughi*. Of that, *Cai. paulistanus*, *Cai. montealtensis* form a clade, outgroup to the remaining species. The clade composed by *Cai. paulistanus* and *Cai. montealtensis* is also present in the analysis of Pol *et al.* (2014) and Martinelli *et al.* (2018).

The monophyly of *Caipirasuchus* is supported by two unambiguous synapomorphies related to the secondary palate, and three ambiguous synapomorphies based on cranial characters. The first unambiguous synapomorphy is the shape of the maxillo-palatine suture (char. 217, st. 1, figure 14). In all *Caipirasuchus*, the palatine is pointed anteriorly, giving an acute shape to the contact. However, in the holotype of *Cai. montealtensis* (MPMA 15-0001/90), the contact between these bones is lateromedially straight. In *Yacararani* and *Sphagesaurus*, the anterior portion of the palatines is rounded, while the condition of other sphagesaurids is unknown. The second unambiguous synapomorphy is the massive nasopharyngeal duct (char. 249, st. 2, figure 14), which contrasts with the gracile condition of *Yacararani*.

Figure 14. Palatal and neurocranium characters of Sphagesauria. A. CT-scan image of *Caipirasuchus attenboroughi* (LAPEISA-0001); B. *Cai. attenboroughi* (LAPEISA-0001); C. *Cai. stenognathus* (MZSP-PV 139, modified from Pol *et al.* 2014); D. *Cai. mineirus* (CPPLIP 1463, modified from Martinelli *et al.*, 2018); E. *Cai. paulistanus* (MPMA 67-0001/00); F. *Cai. montealtensis* (MPMA 68-0003/12); G. *Yacarerani boliviensis* (MNK PAL 5063) H. *Sphagesaurus huenei* (RCL-100); I. *Mariliasuchus amaralis* (UFRJ DG 106-R).



(Source: the author)

Three other unambiguous synapomorphies are restricted to cranial elements but are not accessible in LAPEISA-0001, but they are all presents in the other species of the genus. That includes the presence of an antorbital fenestra (char. 12, st. 1), a variable condition among notosuchians that is absent in other sphagesaurids, *Mariliasuchus* and *Baurusuchia*, but present in *Notosuchus*, *Morrinhosuchus* and *Lavocatchampsa*. Another ambiguous synapomorphy is



the relative length of the lacrimal in relationship with the frontal, which is subequal in *Caipirasuchus* (char. 63, st. 1) contrasting with the shorter lacrimal of *Adamantinasuchus*, *Yacararani* and *Armadillosuchus*. Finally, the third ambiguous synapomorphy is the triangular process of the jugal between the maxillo-ectopterygoid contact (char. 502, st. 1), a trait not found in any other crocodyliform known.

The matrix of Pol *et al.* (2014), and subsequently of Martinelli *et al.* (2018), compares the relative length of the symphyseal region of the mandibula between “advanced notosuchians”. In this case, one of the unambiguous synapomorphies of *Caipirasuchus* is the long symphyseal region, three times longer than wider, being shorter in other Sphagesauria. Due to the restriction of the scoring of this character only to Sphagesauria, in previous analyses, we chose not to include it in our matrix, avoiding the conflict with the taxonomically more inclusive character 325 of our data matrix.

The *Cai. paulistanus* + *Cai. montealtensis* clade shares four unambiguous synapomorphies, three of them refers to cranial characters. First, the absence of a shallow fossa on the supratemporal fenestra, present in *Cai. stenognathus*, *Cai. mineirus*, *Armadillosuchus*, and *Yacararani* (char. 99, st. 1). The second cranial synapomorphy is the oblique orientation of the anterior margin of the frontal (char. 503, st. 0), as in *Notosuchus* and *Morrinhosuchus*. In *Cai. stenognathus*, *Cai. mineirus*, *Armadillosuchus*, *Yacararani* and *Mariliasuchus*, the margins are parallel to each other. These two synapomorphies cannot be scored for *Cai. attenboroughi*. The third cranial synapomorphy is the flat ventral surface of the internal nares that tapers anteriorly (char. 492, st. 1), in contrast with the posteriorly tapered septum of the other *Caipirasuchus*, *Yacararani*, *Mariliasuchus* and *Notosuchus*. The fourth unambiguous synapomorphy is related to the size and position of the anterior foramen intramandibularis oralis. In *Cai. paulistanus* and *Cai. montealtensis*, this foramen is larger than the foramen of *Cai. stenognathus* and *Cai. mineirus* (char. 310, st. 1). *Cai. attenboroughi* also presents a well-developed foramen, which is interpreted as being acquired homoplastically.

The clade comprising *Cai. stenognathus* + *Cai. mineirus* + *Cai. attenboroughi* shares six unambiguous synapomorphies, three of the secondary palate, two cranial and one mandibular. The presence of maxilla-palatine fenestrae (char. 221, st. 1, figure 14), a trait also presents in *Mariliasuchus* and *Notosuchus*, but absent in other sphagesaurids (*Sphagesaurus*, *Yacararani*). The other two synapomorphies are observed in the choanal septum. The ventral surface of this structure has a markedly groove on its ventral surface (char. 250, st. 1, figure 14), a trait absent in other Sphagesauria. In addition, the septum tapers in its posterior third in members of this clade (char. 491, st. 1, figure 14), whereas in the other *Caipirasuchus*, the width remains the

same thorough. The lacrimal shape, as long as broad in *Cai. stenognathus* and *Cai. mineirus* (char. 64, st. 1), as well in *Adamantinasuchus* and *Morrinhosuchus*, but the lacrimal is longer than broad in *Cai. paulistanus*, *Cai. montealtensis* and the other Sphagesauria. The presence of paired ridges located medially on the ventral surface of the basisphenoid (char. 267, st. 1), a condition present in only few notosuchians, including *Notosuchus*, baurusuchids and *Araripesuchus tsangatsangana*. The last synapomorphy is the placement of the distalmost tip of the retroarticular process in relationship with the glenoid fossa. In *Cai. stenognathus* and *Cai. mineirus*, this feature is placed more dorsally than the glenoid fossa (char. 353, st. 1), a unique condition among notosuchians.

*Cai. stenognathus* and *Cai. attenboroughi* are nested together within *Caipirasuchus* based on two unambiguous synapomorphies. In these taxa, the maxilla has a small participation in the anterior margin of the suborbital fenestra (char. 211, st. 1, figure 14), a similar condition present in *Mariliasuchus*, *Notosuchus* and *Morrinhosuchus*. In other sphagesaurids, the maxilla occupies a relatively larger portion of the margin of the fenestra, a condition widespread among notosuchians. The second synapomorphy is related to the relationship of the pharyngeal tube and the choanal region. These two taxa are the only known crocodyliforms that has an opened connection between the pharyngeal tubes opening and the choanal region (char. 495, st. 1, figure 14) instead of having a wall on the pterygoid that encloses this passage anteriorly.

### 3.4. Biogeographical analysis

The LRTs showed that the M0 model was the best fit between the two models. AICc also supports DEC rather than DIVALIKE (table 1). The results from the “harsh” and “relaxed” analyses didn’t differ from the “starting” analyses, thus we focus our discussion on the DEC M0 “starting” results.

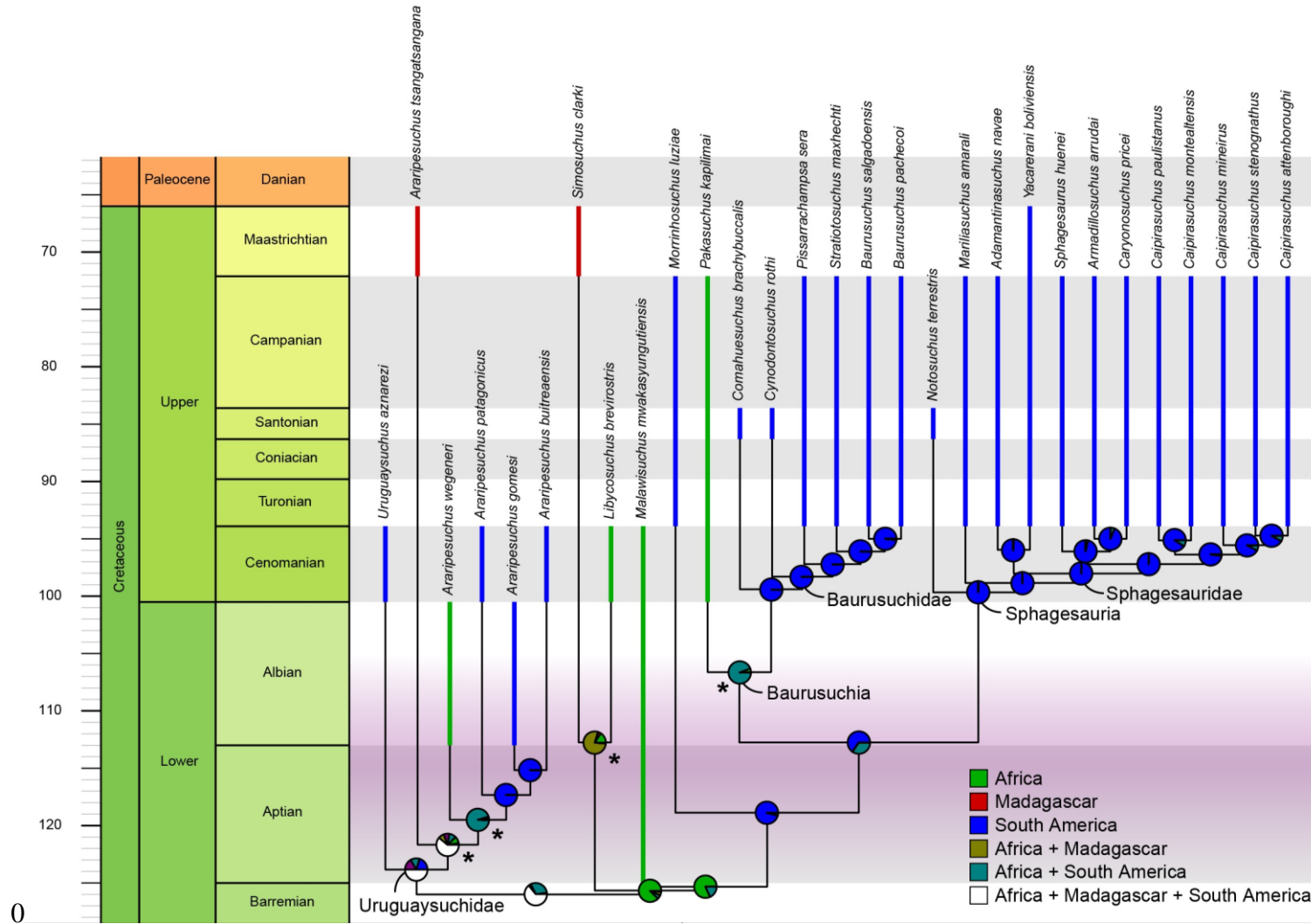
Table 1. Summary of results and statistical comparisons between the models (i.e., DEC, and DIVALIKE, M0, and M1 models) used for the analyses. **AIC**: Akaike information criterion; **AICwt**: weight Akaike information criterion; **LnL**: likelihood; **p**: number of free parameters in each model; **d**, **e** and **w** are the estimated parameter values for each model.

model	LnL	numparams	d	e	w	AICc	AICwt
DEC M0	-23,86	2	0,0077	0,0027	1	52,18	0,54
DEC M1	-24,53	3	0,0053	0,0031	0,13	56,01	0,08
DIVA M0	-24,35	2	0,016	0,0053	1	53,17	0,33
DIVA M1	-25,16	3	0,013	0,0053	0,29	57,28	0,043

(Source: the author)

The best fitted model estimates a broad range including Africa, South America and Madagascar as the most probable ancestral area of the “derived notosuchians” (figure 15). This clade splits from other notosuchians by the end of the Barremian. The irradiation of uruguaysuchids occurred also in this joint area, but a bit later, during the beginning of the Aptian. Africa was estimated as the ancestral area for the clade comprising the “basal notosuchians” + (Sphagesauria + Baurusuchia), which also splits from other notosuchians during the Barremian. Sphagesauria + Baurusuchia diverged during the Albian, most probably in South America, although a South-American-African range is less probable (~40%). Another joint distribution was estimated for Baurusuchia, in Africa and South America. The origin and irradiation of Sphagesauridae and Baurusuchidae represent the last great diversification wave of notosuchians, and both occurred solely South America during the beginning of the Late Cretaceous.

Figure 15. Ancestral area reconstructed basing on the DEC M0 on the *Notosuchia* consensus tree (excluding *Anatosuchus minor* and *Sebecia*). Asterisks marks vicariance events.



(Source: the author)

## 4. DISCUSSION

### 4.1. Sphagesauria in a biostratigraphic context

Sphagesaurids are endemic to deposits of South America. Apart from *Yacarerani*, recorded from the Cajones Formation, Bolivia (NOVAS *et al.*, 2009), all the other species were found in the Adamantina Formation of the Bauru Group, Brazil (POL, 2003; NOBRE; CARVALHO, 2006; IORI; CARVALHO, 2009; MARINHO; CARVALHO, 2009; KELLNER *et al.*, 2011a; IORI; CARVALHO, 2013; POL *et al.*, 2014; MARTINELLI *et al.*, 2018). *Caipirasuchus attenboroughi* represents the first evidence not only of a sphagesaurid, but of a crocodyliform, in the Santo Anastácio Formation, expanding the fauna known for the Bauru Basin.

The Bauru Basin is a Cretaceous stratigraphic unit of approximately 370.000 km<sup>2</sup> in extension (FERNANDES; RIBEIRO, 2014), in the south-central portion of the South American platform, which is outcropping in part of southern Brazil (BATEZELLI, 2015). In lithostratigraphic terms, the Bauru basin is composed by two distinct groups: the Bauru and Caiuá groups (FERNANDES; COIMBRA, 1996; FERNANDES, 1998). The Caiuá Group is composed by Goio-Erê, Rio Paraná and Santo Anastácio Formations (BATEZELLI, 2015), and outcrops especially in the western por portion of the basin. The suggested paleoenvironment to the deposit is called Caiuá paleodesert, a tangle of dunes and plains of arid climate (FERNANDES; RIBEIRO, 2014).

The chronostratigraphy of the Bauru basin is debatable, especially regarding the age of Caiuá Group and the stratigraphy of Santo Anastácio Formation. Evidences converges to form a “classical interpretation” that the formations of the Caiuá Group are older than that of the Bauru Group (LANGER *et al.*, 2019). According to this interpretation, an Aptian-Albian age was assumed to the Caiuá Group, based on lithostratigraphic analysis, paleoclimatic data and the stratigraphic comparison with the Bauru group (FULFARO *et al.*, 1999; DIAS-BRITO *et al.*, 2001). This age is corroborated by the register of tapejarid pterosaurs in the Goio-Erê formation (MANZIG *et al.*, 2014), similar to Chinese forms of Aptian (WANG; ZHOU, 2003; BATEZELLI, 2015). Additionally, Batezelli (2010; 2015) defined the same age to the possible limits of the deposits of the Caiuá group based on biostratigraphy correlation and tectonic events that occurred in correlate areas, a condition also supported in other studies (SOARES *et al.*, 1980; MENEGAZZO; CATUNEANU; CHANG, 2016). A second possibility, however, is that the deposits of the Santo Anastácio formation does not belong to the Caiuá Group, representing the oldest deposits of the Bauru group, marked by a putative local discontinuity between the

Santo Anastácio Formation and other rocks traditionally associated with the Caiuá Group (SILVA; KIANG; CHANG, 2009, 2016). Finally, some authors argue a Late Cretaceous age to the Caiuá Group basing in inferred depositional synchronicity with rocks of the younger Adamantina Formation (FERNANDES; RIBEIRO, 2014; LANGER *et al.*, 2019).

Due to the absence of more precise studies about the age of the Caiuá Group, any inference of age to this groups (and consequently, to *Cai. attenboroughi*) must contain caveats. According to the hypothesis of an Aptian-Albian age to the deposits of the Santo Anastácio, *Caipirasuchus attenboroughi* represents not only the first record of a sphagesaurid from the Lower Cretaceous but the oldest Sphagesauria, expanding the temporal range of this clade to the Lower Cretaceous. However, if Santo Anastácio formation belongs to the Bauru Group as its earlier deposits, the range of Sphagesauridae is shortened, but *Cai. attenboroughi* remains older than the other sphagesaurids. In the last scenario, Santo Anastácio is chronorelated to the Adamantina Formation, making *Cai. attenboroughi* contemporary to the other sphagesaurids, and restricting the temporal range of Sphagesauria to the Late Cretaceous. In this study, we assume this last hypothesis, as in Langer *et al.* (2019), due to the statement that a biostratigraphy based on pterosaurs, the major vertebrate reference in the Caiuá Group studies on biostatigraphy, is weakened by the scarce general record of this group.

For the Adamantina Formation, where all the other Brazilian sphagesaurids are from, three main interpretations based on biostratigraphic correlation were presented. The first established a Turonian-Santonian age for the formation based on ostracods and carophytes (DIAS-BRITO *et al.*, 2001; MARTINELLI; RIFF; LOPES, 2011). The second, a Campanian-Maastrichtian age, also based in ostracods and carophytes, as well sauropods (GOBBO-RODRIGUES; PETRI; BERTINI. 1999; FERNANDES; COIMBRA, 2000; SANTUCCI; BERTINI, 2017; BATEZELLI *et al.*, 2003; SILVA; KIANG; CHANG, 2003). A third hypothesis expands the range to a Cenomanian-Campanian age, based on a comparison between the fossil assemblages of the Adamantina Formation and correlated formations (MENEGAZZO; CATUNEANU; CHANG, 2016). Recently, the first radioisotopic dating in Adamantina formation and the Bauru group indicates a post-Turonian maximal age ( $\leq 87.8$  Ma) (CASTRO *et al.*, 2018). The Cajones formation, in which several specimens of *Yacarerani* are from, is placed in the Maastrichtian, by the presence of fish remains (LÓPEZ, 1975; AGUILLERA; SALAS; PEÑA, 1989; POL *et al.*, 2014) and posteriorly considered as Turonian-Santonian due to the similarities with *Adamantinasuchus* (NOVAS *et al.*, 2009; POL *et al.*, 2014).

Two other fragmentary taxa were proposed by Pol *et al.* (2014) to be included in Sphagesauridae and, as a consequence, in Sphagesauria (“advanced notosuchians”),

*Labidiosuchus*, from the Marilia Formation, Bauru Group, and *Coringasuchus*, from Alcântara Formation, Itapecuru Group, NE Brazil. The Marilia Formation was regarded as Campanian-Maastrichtian, based on faunal correlation, overlaying the Adamantina Formation (POL *et al.*, 2014; CASTRO *et al.*, 2018). The Alcântara Formation is estimated to be early Cenomanian, based on its paleovertebrate assembly (KELLNER *et al.*, 2009). If that is the case, *Coringasuchus* is one of the oldest sphagesaurids known. However, the fragmentary nature of the specimens of both taxa precludes its scoring in our phylogenetic data-matrix.

The chronological range of the other two Sphagesauria, *Mariliasuchus* and *Notosuchus*, are also within the Late Cretaceous. As in sphagesaurids, *Mariliasuchus amarali* and *M. robustus* are found in Adamantina Formation deposits (CARVALHO; BERTINI, 1999; ZAHER *et al.*, 2006; NOBRE *et al.*, 2007). The remains of *Notosuchus* were found in deposits of the Bajo de La Carpa Formation (Neuquén Group) (POL *et al.*, 2014). Based on its paleovertebrate fauna, a Santonian age was proposed to this formation (GARRIDO, 2010; POL *et al.*, 2014), corroborated by the overlapping of the Anacleto Formation, dated to the Lower Campanian by paleomagnetic data (DINGUS *et al.*, 2000; POL *et al.*, 2014). The recently described *Llanosuchus tamaensis* (FIORELLI *et al.*, 2016), from the Los Llanos Formation (western Argentina), was recovered as the sister-group of *Notosuchus* (FIORELLI *et al.*, 2016; MARTINELLI *et al.*, 2018). Ostracods and charophytes suggests a possibly Campanian age to this formation (CARIGNANO; HECHENLEITNER; FIORELLI, 2013; HECHENLEITNER *et al.*, 2014).

#### **4.2. The radiation of notosuchians in Gondwana**

The phylogenetic relationship among notosuchians is in state of flux and, in general, only derived clades are confirmed to be monophyletic by multiple data-matrix. However, the relative position of the monophyletic clades varies substantially (MONTEFELTRO *et al.*, 2013; POL *et al.*, 2014; FIORELLI *et al.*, 2016; MARTIN; DE BROIN, 2016; GEROTO; BERTINI, 2018; PINHEIRO *et al.*, 2018). One of the explanations for such proliferation of alternative phylogenetic relationships rely on the fact that most records of notosuchians are restricted to the Late Cretaceous of Gondwana landmasses (especially South America, Africa and Madagascar). At this time, many of the derived groups are supposedly established, while the record of notosuchians in early deposits is patchy, resulting in several ghost lineages and obscuring the phylogenetic relationship (TURNER; SERTICH, 2010; POL; LEARDI, 2015; BRONZATI; MONTEFELTRO; LANGER, 2015).

An Aptian-Albian irradiation of the major groups of notosuchians was suggested (TURNER; SERTICH, 2010; POL *et al.*, 2014; BRONZATI; MONTEFELTRO; LANGER, 2015). According to Pol and Leardi (2015), this irradiation was followed by two high diversity peaks: the first occurring during the late Early Cretaceous in Africa, encompassing peirosaurids, uruguaysuchids and “basal forms”, and the second, in the middle Late Cretaceous of South America, represented mainly by Sphagesauria and baurusuchids from Adamantina and Bajo de La Carpa formations. Our biogeographical analysis reflects partially this scenario (figure 15), indicating that the origin of the basalmost node possibly occurred in the end of the Barremian (figure 15), in a stage in which the flux of notosuchians between South America, Africa and Madagascar was possible. Following, we present an overview of the chronostratigraphic relationship, the possible age and landmasses to the initial irradiation of the clades of derived notosuchians and the role of the fragmentation of Gondwana in the biogeography of the major lineages of notosuchians.

Uruguaysuchids are taken as the prime example of vicariance among notosuchians due to the records of *Araripesuchus*, the only notosuchian genera found in more than one Gondwanan landmass (PRICE, 1959; BUFFETAUT; TAQUET, 1979; SERENO; LARSSON, 2009; KRAUSE *et al.*, 2019). Remains of *Araripesuchus* were found in Albian (*A. gomesii*) and Cenomanian (*A. patagonicus*, *A. buitreaensis*) deposits of South America; Albian (*A. wegneri*) and Cenomanian (*A. rattoides*) of Africa; and Maastrichtian (*A. tsangatsangana*) in Madagascar. All known remains of *Uruguaysuchus* come from Guinchón Formation (SOTO; POL; PEREA, 2011), which age is still debated. Correlation based on the record of other “basal” notosuchians, such as *Candidodon* and *Araripesuchus*, indicates an early Late Cretaceous age to these deposits, possibly Cenomanian (SOTO; POL; PEREA, 2011; SOTO; PEREA; CAMBIASO, 2012). Uruguaysuchids split from the other notosuchians by the Barremian, also in a stage that allowed the flux between South America, Africa and Madagascar (figure 15). This reflects the occurrence of distinct taxa in these landmasses, even when they were completely isolated from each other.

Three taxa of “basal” notosuchians and *Morrinhosuchus* forms consecutive sister-groups of the major dichotomy comprising Sphagesauria and Baurusuchia in our analysis (figure 10). This group emerged in the end of Barremian in Africa (figure 15). *Libycosuchus* and *Simosuchus* are nested together, as in Turner and Sertich (2010) and Montefeltro *et al.* (2013). *Simosuchus* represents one of the youngest notosuchian lineages in the Maastrichtian of the Maeravarno Formation, in Madagascar (BUCLKEY *et al.*, 2000). The remains of *Libycosuchus* were found in Bahariya Formation, Libya, dating to Cenomanian (BUFFETAUT, 1976). A



quadrate fragment recovered from In Beceten Formation, a Conician-Santonian formation of Niger, was mistakenly identify as a remain of *Libycosuchus* by Buffetaut (1976), but it was associated to *Hamadasuchus* (LARSSON; SUES, 2007; MEUNIER; LARSSON, 2017). According to our analysis, Madagascar plays an important role in the origin of the clade comprising *Simosuchus* and *Libycosuchus*. The last common ancestor of both taxa probably has an African/Malagasy distribution.

*Malawisuchus* is possibly older than most notosuchians, since the Dinosaurs Beds of Malawi, is commonly regarded as Aptian (PENTEL'KOV; VORONOVSKY, 1979; COLIN; JACOBS, 1990; EBY *et al.*, 1995; GOMANI, 1997; ANDRZEJEWSKI *et al.*, 2019). However, a Late Cretaceous age was recently proposed to the Dinosaur Beds due to correlation with vertebrate assemblages of other African deposits, appearing to be related to the Mtuka Member of the Galula Formation (LE LOEUFF *et al.*, 2012; WIDLANSKY *et al.*, 2018).

The lineage of *Morrinhosuchus* + (Sphagesauria + Baurusuchia), split from *Mallawisuchus* by the Barremian-Aptian, becoming the oldest South-American clade in our analysis (figure 15). *Morrinhosuchus* was recovered from Adamantina Formation deposits (IORI; CARVALHO, 2009; IORI *et al.*, 2018), being contemporaneous to most sphagesaurids, apparently splitting from its sister group by the middle of the Aptian.

*Pakasuchus* was considered a “basal” ziphosuchian, with close affinities with *Malawisuchus* (POL *et al.*, 2014; MARTIN; DE BROIN, 2016; DAL SASSO *et al.*, 2017; MARTINELLI *et al.*, 2018). In our analysis, *Pakasuchus* was recovered as a member of Baurusuchia. A closer affinity to South-American derived notosuchians than to African taxa was already suggested by Sertich and O'Connor (2014) and Meunier and Larsson (2017). The remains of *Pakasuchus* was found in the Namba Member of the Galula Formation deposits, Tanzania (O'CONNOR *et al.*, 2010; WIDLANSKY *et al.*, 2018). Historically, this formation is associated to the mid-Cretaceous (O'CONNOR *et al.*, 2010; POL *et al.*, 2014). However, a new magnetostratigraphic study indicates a Cenomanian-Campanian age to the Namba Member (WIDLANSKY *et al.*, 2018). Our analysis indicates an Albian origin of the baurusuchians in South America and Africa, much probably due to the phylogenetic position of *Pakasuchus*, older than most baurusuchians, and as it basalmost member (figure 15). Younger baurusuchians, however, come from Late Cretaceous deposits of South America, including most baurusuchids and the enigmatic *Comahuesuchus*, reflecting the South-American origin of this clade recuperated in our analysis. The split between the *Pakasuchus* and derived baurusuchians lineages occurred in the middle of the Albian.

Baurusuchidae is one of the most geographically and temporally restrict clade of crocodyliforms (MONTEFELTRO; LARSSON; LANGER, 2011), with most of its taxa found in only two formations, Adamantina (PRICE, 1945; CAMPOS, 2001; CARVALHO; CAMPOS; NOBRE, 2005; NASCIMENTO; ZAHER, 2010; MONTEFELTRO; LARSSON; LANGER, 2011; CARVALHO *et al.*, 2011; MARINHO *et al.*, 2013; GODOY *et al.*, 2014) and Bajo de La Carpa (WOODWARD, 1896; MARTINELLI; PAIS, 2008; LEARDI; POL; GASPARINI, 2018). The only probable exception is *Pabwehshi*, a fragmentary specimen from Pab Formation, Maastrichtian of Pakistan (WILSON; MALKANI; GINGERICH, 2001). *Comahuesuchus* was recovered as the sister-group of Baurusuchidae, as in the phylogeny in Montefeltro *et al.* (2013), and similar to that presented by Pol *et al.* (2014), Martin and De Broin (2016) and Martinelli *et al.* (2018). The remains of *Comahuesuchus* are also found in Bajo de La Carpa Formation (MARTINELLI, 2003).

The irradiation of Sphagesauria was proposed to occurred in the Late Cretaceous (POL *et al.*, 2014). This hypothesis is supported by the lack of records of Sphagesauria in other landmasses than South America. Our analysis, however, indicates that the split between Sphagesauria and Baurusuchia occurred in the boundaries between Aptian-Albian (figure 15), with Sphagesauria remaining restrict to South America, diversifying in the middle Late Cretaceous. The endemism of Sphagesauria can be challenged by a reanalysis of three isolated teeth, referred to an indeterminate crocodyliform, described by Larsson and Sidor (1999) from Kem Kem Beds, Cenomanian of Morocco. These teeth are very modified, with an overall structure that resembles the specialized molariforms of *Yacararani* and *Adamantinasuchus*. If these teeth indeed represent sphagesaurid records, it is be the first record of a Sphagesauria outside South America, and the oldest confirmed occurrence for this clade, possibly implying an older irradiation of this clade.

A Barremian radiation of the derived forms of notosuchians can partially explain the erratic distribution of the Late Cretaceous taxa in Gondwana by the Pan-Gondwanan hypothesis (SERENO; WILSON; CONRAD, 2004). According to this, the basal members of the main lineages of notosuchians could be scattered across the major Gondwanan landmasses, becoming isolated as the fragmentation of the continents continues along the Cretaceous. Although, Gondwana fragmentation into a western and an eastern portions began in Early Jurassic (EAGLES; KÖNIG, 2008; KLIMKE *et al.*, 2018; KRAUSE *et al.*, 2019), it took a long time to each of the major landmasses to become completely isolated from each other. It was in this unstable period that we suggest that the radiation of the notosuchians lineages happened. Tectonic evidences indicates that the South Atlantic begins to separates the Western Gondwana

into South America and Africa by the Hauterivian (CHANNELL *et al.*, 1995; GRANOT; DYMENT 2015; KRAUSE *et al.*, 2019), but land bridges remained connecting both continents at least until the Albian (LAWVER; GAHAGAN; COFFIN, 1992; MÜLLER; ROYER; LAWVER, 1993; PLETSCHE *et al.*, 2001; TURNER; SERTICH, 2010). Indo-Madagascar was disconnected to Antarctica and Australia at the Aptian (KRAUSE *et al.*, 2019), and by the Cenomanian, Madagascar split from the Indian Subcontinent (KRAUSE *et al.*, 2019). Finally, land bridges connecting South America to Antarctica probably existed during until the Late Cretaceous (HAY *et al.*, 1999), giving the presence of ankylosaurids in the Campanian of Antarctica (OLIVERO *et al.*, 1991) and the flow of marsupials between South America and Australia (WOODBURNE; ZINSMEISTER, 1984).

Although Sphagesauria are restricted to South America, Late Cretaceous notosuchians are found in other Gondwanan landmasses in a time in which they are isolated by oceanic barriers. Mahajangasuchids are found in Madagascar (BUCKLEY; BROCHU, 1999) and Africa (SERENO; LARSSON, 2009), and peirosaurids were recovered from deposits of South America (PRICE, 1955; KELLNER, 1987; GASPARINI; CHIAPPE; FERNANDEZ, 1991; CARVALHO; RIBEIRO; ÁVILLA, 2004; CARVALHO; VASCONCELLOS; TAVARES, 2007; LEARDI; POL, 2009; MARTINELLI *et al.*, 2012; BARRIOS; PAULINA-CARABAJAL; BONA, 2016; LIO *et al.*, 2016; FILIPPI; BARRIOS; GARRIDO, 2018; CORIA *et al.*, 2019; LAMANNA *et al.*, 2019), Africa (BUFFETAUT, 1994; SERTICH; O'CONNOR, 2014) and Madagascar (RASMUSSEN; SIMONS; BUCKLEY, 2009). The presence of *Araripesuchus* and peirosaurids in both Africa and South America has been suggested as an indication of bidirectional flow of these notosuchians across the landmasses (TURNER; SERTICH, 2010). A specialized tooth of *Simosuchus*, once known as endemic to Madagascar, was recently recovered from the Late Maastrichtian deposit of Kallamedu Formation, India (PRASAD *et al.*, 2013). The inclusion of *Pakasuchus* among Baurusuchia expands the geographical range of Baurusuchia to Africa and to an early Late Cretaceous time. This supports the hypothesis that baurusuchids could be present in other continents apart South America before the Aptian, explaining the occurrence of *Pabwehshi* in the Maastrichtian of Pakistan, a time in which the Indian Subcontinent was already isolated from other landmasses.

One of the greatest puzzles in the biogeography of notosuchians is the enigmatic *Chimaerasuchus paradoxus* (WU; SUES, 1996) from the Aptian-Albian Wulong Formation, China. To date, it is the only known putative Mesozoic notosuchian from Asia. In several analyses, it was recovered among derived notosuchians, including as sister group of *Sebecia* (POL *et al.*, 2014; FIORELLI *et al.*, 2016; MARTINELLI *et al.*, 2018), and more commonly

related to Sphagesauria, being nested with *Notosuchus* (WU; SUES, 1996) and *Sphagesaurus* (POL, 2003; POL; APESTEGUÍA, 2005; TURNER; BUCKLEY, 2008; NOVAS *et al.*, 2009; TURNER; SERTICH, 2010; BRONZATI; MONTEFELTRO; LANGER, 2015). The record of a Lower Cretaceous notosuchian from Central Asia could be explained by the Pan-Gondwanan Hypothesis, considering an even early irradiation of derived notosuchians and a possibly global distribution of notosuchians. Assuming the distribution of *Chimaerasuchus* as relictual, however, is weakened by the absence of Mesozoic notosuchians in North America (TURNER; SERTICH, 2010).

Another evidence of the role of Pan-Gondwanan Hypothesis in the biogeography of notosuchians is the record of *Razanandrongo*, the putative oldest known notosuchian, in Sakahara formation, Bathesian of Madagascar (MAGANUCO; DAL SASSO; PASINI, 2006; DAL SASSO *et al.*, 2017). A recent reanalysis of this taxa indicates that it is deeply nested within ziphosuchians, with a close relationship with sebecosuchians (DAL SASSO *et al.*, 2017). Similar to the case of *Chimaerasuchus*, the presence of a highly derived notosuchian in the Mid-Jurassic reinforces the hypothesis that the irradiation of notosuchians must have happened in a less fragmented Gondwana, before the Late Cretaceous. A Jurassic age to the emergence of notosuchians was already parallelly proposed by Bronzati, Montefeltro and Langer (2015) and Pol and Leardi (2015).

## 5. CONCLUSION

*Caipirasuchus attenboroughi* represents the first crocodyliform from Santo Anastácio Formation. It expands the presence of notosuchians in Bauru Basin as well as the geological range of Sphagesauridae, which is known for only two other formations. *Cai. attenboroughi* represents the fifth species of the genera, making *Caipirasuchus* the second more species-rich genera of notosuchians to date, surpassed only by *Araripesuchus*, with six species. Unlike this, however, *Caipirasuchus* remains restricted to South America, reinforcing the endemism of Sphagesauria. Our phylogenetic analysis recovered a clade of “derived” notosuchians that includes uruguaysuchids, *Simosuchus*, *Libycosuchus*, *Malawisuchus*, *Morrinhosuchus* and a clade formed by Sphagesauria (named herein) + Baurusuchia. This implies that the initial radiation of these forms must have occurred in a pre-Aptian time, supporting a Pan-Gondwanan Hypothesis to explain the distribution of many derived forms across different landmasses in Late Cretaceous, such as *Araripesuchus*, *Simosuchus* and baurusuchids. This hypothesis is supported by our BioGeoBEARS analysis, which allowed a new perspective of the evolutive history of the notosuchians in Gondwana. The results reinforce that notosuchians are spread thorough Gondwana during the Early Cretaceous, with Late Cretaceous taxa, as *Simosuchus* and *Araripesuchus tsangatsangana*, representing relictual forms of clades once much more widespread. Sphagesauria could potentially represent a latter case of endemism, as this clade evolved to a diverse range of forms restrict to South America, during the Late Cretaceous. As in many topics in notosuchian evolution, the discovery of new materials, especially from Early Cretaceous of South America and other less prospected Gondwanan landmasses, as Antarctica, could elucidate with more details the origins of the derived clades of notosuchians.

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