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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

Juan Vitor Ruiz

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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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Comissão Examinadora

Prof. Dr. Felipe Chinaglia Montefeltro
UNESP – Câmpus de São José do Rio Preto
Orientador

Dr. Mario Bronzati Filho
USP – Ribeirão Preto

Dr. Júlio Cesar de Almeida Marsola
UNESP – Câmpus de São José do Rio Preto

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).

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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).

LIST OF FIGURES

Figure 1 – Bauru Basin map.	19
Figure 2 – <i>Caipirasuchus paulistanus</i> and <i>Cai. attenboroughi</i> holotypes.	22
Figure 3 – <i>Cai. attenboroughi</i> , ventral view.	24
Figure 4 – <i>Cai. attenboroughi</i> , dorsal view.	25
Figure 5 – <i>Cai. attenboroughi</i> , maxilla and palatines.	27
Figure 6 – <i>Cai. attenboroughi</i> , occipital fragment.	32
Figure 7 – <i>Cai. attenboroughi</i> , right lateral view.	34
Figure 8 – <i>Cai. attenboroughi</i> , left lateral view.	35
Figure 9 – <i>Cai. attenboroughi</i> , medial view of the right mandibular ramus.	39
Figure 10 – Cladogram with the results' phylogenetic relationships.	43
Figure 11 – Mandibular and teeth characters of notosuchians.	46
Figure 12 – Mandibular characters of notosuchians.	48
Figure 13 – Neurocranium characters of notosuchians.	50
Figure 14 – Palatal and neurocranium characters of notosuchians.	54
Figure 15 – Cladogram with the biogeographical analysis results	58

LIST OF TABLES

Table 1 – Summary of results and statistical comparisons of the BioGeoBEARS analysis	57
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LIST OF ABBREVIATIONS AND ACRONYMS

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

km	Kilometer
cm	Centimeter
Ma	Million years ago

SUMMARY

1	INTRODUCTION	16
2	MATERIALS AND METHODS	19
2.1	Field work and preparation	19
2.2	Tomography	20
2.3	Phylogeny	20
2.4.	Biogeographical analysis	20
3	RESULTS	21
3.1	Systematic paleontology	21
3.2	Comparative description	23
3.3	Phylogenetic relationships and definition	42
3.3.1	Phylogenetic definition	44
3.3.2	<i>Caipirasuchus attenboroughi</i> within the Genus <i>Caipirasuchus</i>	44
3.3.3	Baurusuchia, Sphagesauria and <i>Morrinhosuchus</i>	45
3.3.4	Sphagesauria	46
3.3.5	Sphagesauridae	48
3.3.6	Phylogenetic relationships within Sphagesauridae	50
3.3.7	<i>Caipirasuchus</i>	53
3.4	Biogeographical analysis	56
4	DISCUSSION	59
4.1	Sphagesaurids in a biostratigraphic context	59
4.2	The radiation of notosuchians in Gondwana	61
5	CONCLUSION	67
	REFERENCES	68

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; BUCKLEY *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 *Caipirausuchus*, closely related to *Cai. stenognathus* and *Cai. mineirus*

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 represents 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 elucidates with more details the origins of the derived clades of notosuchians.

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