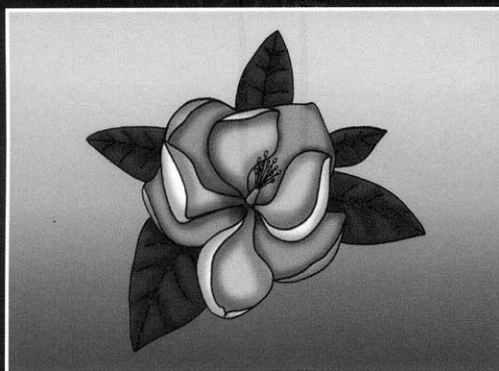


# Paleontologia: Cenários de Vida



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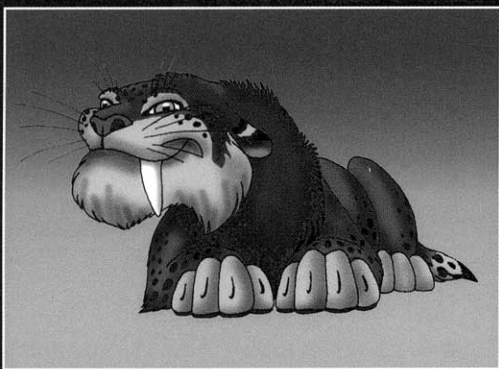
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# CRANIAL FEATURES OF *BAURUSUCHUS SALGADOENSIS* CARVALHO, CAMPOS & NOBRE 2005, A BAURUSUCHIDAE (MESOEUCROCODYLIA) FROM THE ADAMANTINA FORMATION, BAURU BASIN, BRAZIL: PALEOICHOLOGICAL, TAXONOMIC AND SYSTEMATIC IMPLICATIONS

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## ABSTRACT

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Some features of the skull of *Baurusuchus salgadoensis* Carvalho, Campos & Nobre 2005, a baurusuchid Mesoeucrocodylia from the Adamantina Formation of Bauru Basin, are described, discussed and reinterpreted. The punctures and perforations of the skull of *B. salgadoensis*, one of them previously described as the antorbital fenestrae, were interpreted as tooth-marks. The probable producer is a medium or large ziphodont terrestrial archosaur, possibly a baurusuchid or Abelisauridae. The choanae of *B. salgadoensis* bears some similarities with *Stratiotosuchus*. The choanae and the palatal surfaces seem to be similar among baurusuchids, notosuchids and sphagesaurids with minor differences. This similarity is congruent with recent phylogenetic hypotheses, supporting a closer relationship among these Cretaceous Mesoeucrocodylia taxa.

**Key-words:** *Baurusuchus salgadoensis*, Upper Cretaceous, Bauru Basin

## RESUMO

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Algumas características do crânio de *Baurusuchus salgadoensis* Carvalho, Campos & Nobre 2005, um baurussuquídeo Mesoeucrocodylia proveniente da Formação Adamantina da Bacia Bauru, são descritas, discutidas e reinterpretadas. As perfurações e depressões presentes no crânio de *B. salgadoensis*, uma delas descrita anteriormente como a fenestra antorbital, foram interpretadas como marcas de dentes. O provável produtor destas marcas é um arcossauro terrestre de médio à grande porte com dentes zifodontes, possivelmente um baurussuquídeo ou Abelisauridae. As coanas de *B. salgadoensis* e *Stratiotosuchus* apresentam semelhanças entre si. Em baurussuquídeos, notossuquios e esfagossaurídeos a coana e a superfície palatal apresentam algumas semelhanças. Estas similaridades são congruentes com recentes hipóteses filogenéticas, conferindo suporte à íntima relação sistemática entre estas taxa de Mesoeucrocodylia do Cretáceo.

**Palavras-chave:** *Baurusuchus salgadoensis*, Cretáceo Superior, Bacia Bauru

## 1. INTRODUCTION

The Bauru Basin comprises an area between latitudes 18° S and 24° S, and longitudes 47° W and 56° W, distributed over 370,000 km<sup>2</sup> in the southeast interior of Brazil, yielding outcrops in São Paulo, Minas Gerais, Mato Grosso do Sul and Goiás States. It is subdivided into two distinctive lithostratigraphic units: the Caiuá Group (Rio Paraná, Goio Erê and Santo Anastácio Formations; Cenomanian-Turonian age) and the Bauru Group (Adamantina, Uberaba and Marília Formations), Turonian-Maastrichtian age (Fernandes & Coimbra, 1996; Dias-Brito *et al.*, 2001; Candeiro *et al.*, 2006).

The rich fossil record of the Bauru Group yields vertebrate and invertebrate ichnofossils, continental mollusks, arthropods, freshwater fishes, amphibians, squamata, theropod and sauropod dinosaurs, aves and a diverse fauna of crocodyliforms (Bertini *et al.*, 1993; Dias-Brito *et al.*, 2001; Arruda *et al.*, 2004; Carvalho *et al.*, 2005; Candeiro *et al.*, 2006; Nobre & Carvalho, 2006).

The crocodyliforms from the Adamantina formation of Bauru Basin comprise at least five distinct groups of Mesoeucrocodylia: notosuchids, sphagesaurids, peirosaurids, trematochampsids and baurusuchids (Carvalho *et al.*, 2005).

### 1.1 THE BAURUSUCHIDAE

The Baurusuchidae Price, 1945 are medium-sized, terrestrial crocodyliformes, regarded as active cursorial predators based on dental, cranial and postcranial data (Price, 1945; Riff & Kellner, 2001; Vasconcellos *et al.*, 2005a; Vasconcellos, 2006). They were first described by Price (1945), who considered the extreme similarity between Baurusuchidae and the eocene Sebecidae *Sebecus icaeorhinus* Simpson 1937. Later, Colbert (1946) expanded the description of *Sebecus* and evaluated their paleoecology. Both families, Baurusuchidae and Sebecidae, are included in Sebecosuchia.

Over the next 50 years many taxa related to the sebecosuchians, and some to Baurusuchidae have been described in South America, Africa, Pakistan and, possibly, Europe (Langston, 1956; Gasparini, 1972, 1981). From the Upper Cretaceous of Pakistan (Pab Formation) was described *Pabweshi pakistanensis* Wilson, Malkani & Gingerich, 2001. The specimen although is represented by only the most anterior part of the snout (premaxilla, maxilla, nasal and dentary, splenial and teeth), and is attributed to Baurusuchidae due to dental and general rostral features (Wilson *et al.*, 2001).

In the Upper Cretaceous of Argentina (Southern South America) numerous sebecosuchians were described, such as *Cynodontosuchus rothi* Woodward, 1896, *Penhuechesuchus enderi* Turner & Calvo, 2005, *Sebecus*, *Ilchunaia parca* Rusconi, 1946, *Ayllusuchus fernandezi* Gasparini, 1984, *Barinasuchus arveloi* Paolillo & Linares, 2007, *Langstonia huilensis* (Busbey III, 1986), *Zulmasuchus querejazus* (Buffetaut & Marshall, 1991) and *Bretesuchus bonapartei* Gasparini, Fernandez & Powell, 1993. These taxa were related to the sebecosuchian families Bretesuchidae, Sebecidae and Baurusuchidae.

Besides the type species of Baurusuchidae, *Baurusuchus pachecoi* Price 1945, two other species from the same family were described from São Paulo State, Brazil. Both come from the same stratigraphic strata as *Baurusuchus pachecoi*, but from distinct localities. The first is *Stratiotosuchus maxhechti* Campos Suarez, Riff & Kellner 2001, from Irapuru County (Riff, 2003). The second, *Baurusuchus salgadoensis* Carvalho, Campos & Nobre, 2005 came from General Salgado County, São Paulo State.

The later is represented by abundant specimens and an outstanding preservation state (Arruda *et al.*, 2004).

Some specimens related to *Sebecus* and/or to *Bretesuchus* are known, but are still undescribed. For example, the Brazilian early paleogene form (or forms) from Itaboraí Basin (Itaboraiense), Rio de Janeiro State (Gasparini, 1984; Gasparini *et al.*, 1993; Vasconcellos *et al.*, 2005b)

Herein, we adopt the last review of Baurusuchidae proposed by Paolillo & Linares (2007), with the following taxa: *Cynodontosuchus rothi*, *Baurusuchus pachecoi*, *Pabweshi pakistanensis*, *Stratiotosuchus maxhecti*, *Baurusuchus salgadoensis* and *Penhuechesuchus enderi*, and bearing the following characteristic features: premaxillo-maxillary suture in lateral view, basisphenoid widely exposed in ventral view, infratemporal fenestrae much longer than deep, post-caniniform dentary teeth with waves of size variation, sigmoidal outline of dentary tooth row in dorsal view, septate internal nares, less than ten maxillary teeth. (Carvalho *et al.*, 2005).

In consequence, the occurrence of the distribution of Baurusuchidae is restricted to Gondwanaland, specifically South America (Argentina and Brazil), and Pakistan, and their chronostratigraphical range to the Upper Cretaceous.

## 1.2 ON *BAURUSUCHUS SALGADOENSIS*

The description is based on a well preserved skull and mandible specimen from General Salgado County (São Paulo State, Brazil). *Baurusuchus salgadoensis* has some peculiar anatomical features.

Its main diagnostic characteristic is the presence of an antorbital fenestra. Such feature was not previously observed in any other Baurusuchidae or Sebecidae. Even though other features as the general shape of the skull roof, occipital slope and the bordering of the skull bones are regarded of diagnostic strength to support the species *Baurusuchus salgadoensis* as a valid taxa among Baurusuchidae (Carvalho *et al.*, 2005). A more detailed discussion on the nature of this antorbital fenestra (and other rostral unusual pits, holes and grooves) may shed new light on taxonomic and systematic status of this species.

Still, some structures on *Baurusuchus salgadoensis* skull were not described in detail, as the choanae, basicrania and occipital region. These structures are of particular interest in recent taxonomic and systematic analyses with special attention to its comparison with other Mesoeucrocodylia taxa as the sebecids, notosuchids, peirosaurids and sphagesaurids (Andrade *et al.*, 2006; Paolillo & Linares, 2007).

The present manuscript analyses the nature of this antorbital fenestrae and of other pits on the skull, as the more detailed description and comparison of the choanae, basicrania and occipital region.

## 2. SYSTEMATIC PALAEOLOGY

Crocodylomorpha Walker, 1970

Crocodyliformes Hay 1930 (*sensu* Clark, 1988)

Mesoeucrocodylia Whetstone & Whybrow 1983

Sebecosuchia Simpson 1937

Baurusuchidae Price 1945

Genus *Baurusuchus* Price 1945

*Baurusuchus salgadoensis* Carvalho, Campos & Nobre 2005

(Figures 1 and 2)

**Holotype:** MPMA-62-0001-02 (Museu de Paleontologia de Monte de Alto). Skull and mandible in good preservation although partially eroded and deformed.

**Locality:** Fazenda Buriti, Prudêncio e Morais District, General Salgado County, São Paulo State, Southeast of Brazil. Coordinates 20° 33' 57, 23" S and 50° 28' 03, 97" W.

**Stratigraphic context:** Bauru Basin, Adamantina Formation. Fine reddish cross-stratified sandstones. Upper Cretaceous (Turonian-Santonian, according to Dias-Brito *et al.*, 2001).

### 3. DESCRIPTION AND COMPARISON

The comparison of cranial features of the holotype specimen of *Baurusuchus salgadoensis* with other sebecosuchians are based on the descriptions of Price (1945), Wilson *et al.* (2001), Campos *et al.* (2001), Riff (2003), Carvalho *et al.* (2005), Turner & Calvo (2005) and Andrade *et al.* (2006). The osteological terminology follows Iordanski (1975) and Carvalho *et al.* (2005).

#### 3.1 SKULL

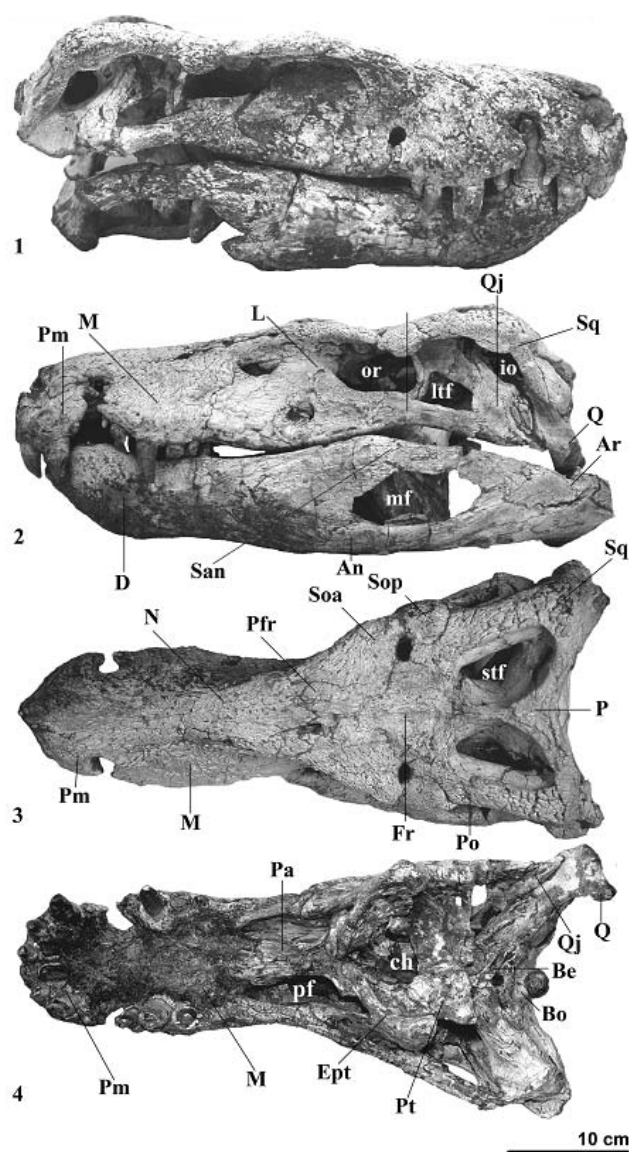
**Cranial openings:** The skull presents several unusual openings. Excluding those observed in symmetry in both lateral sides, the other ones are disposed randomly, differing in size, shape and texture. Some were attributed to anatomical structures (the antorbital fenestra) and others of smaller dimensions were left undiscussed by the original authors (Carvalho *et al.*, 2005).

**Antorbital fenestrae:** It is large, with a longer axis oriented anteroposterioly, bearing rough borders. It faces slightly dorsally. It is not observed in both sides of the skull. Its interpretation is doubtful and will be discussed below

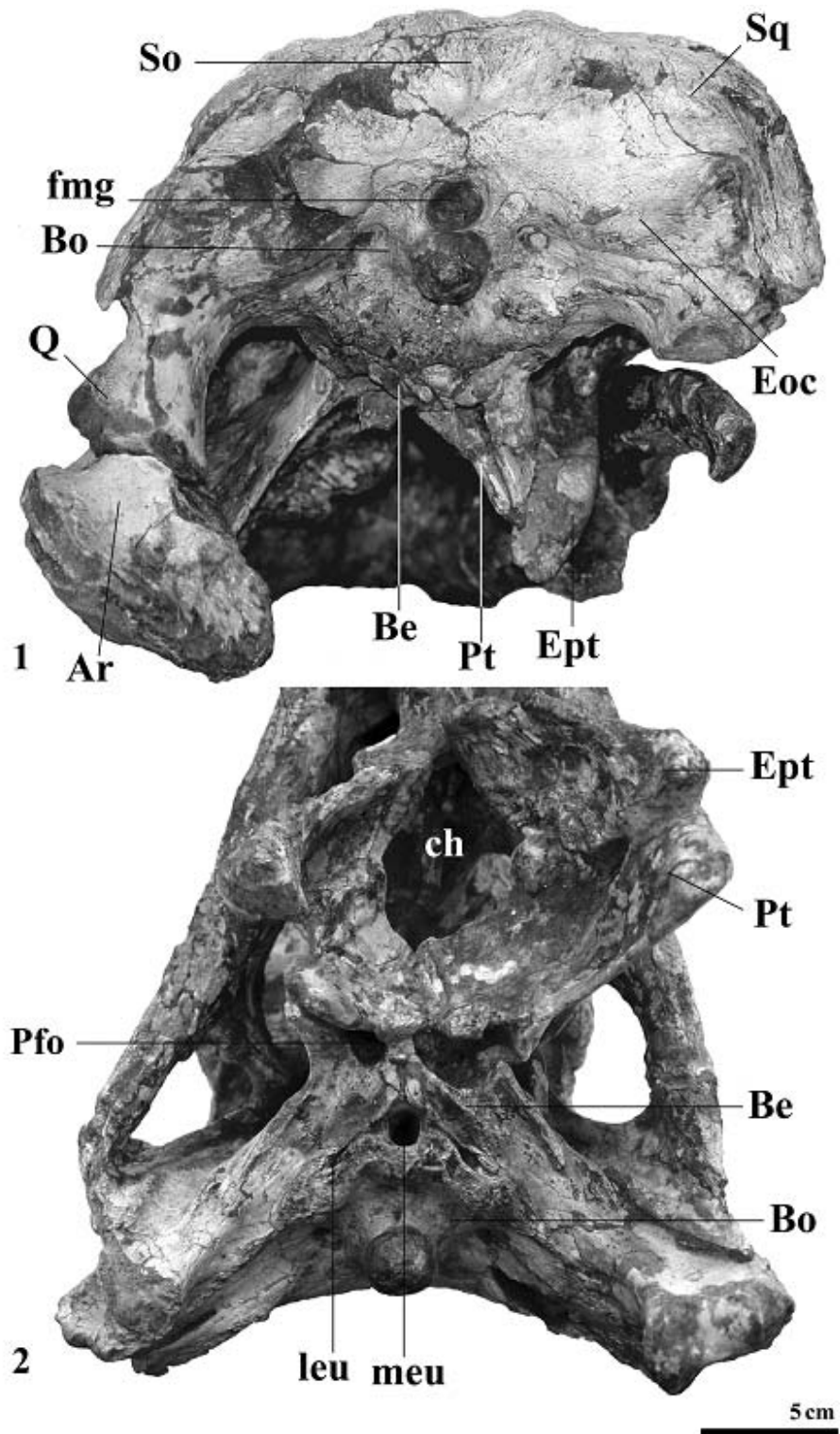
**Unusual marks:** The skull of *B. salgadoensis* presents several perforations on both sides. They are not symmetric, present rough texture, preferential axis and shallow grooves along this particular axis. Other, larger perforations, are elliptical or slightly round in shape, bearing no grooves (Figure 3).

The smaller ones are disposed mostly on the left side. They are generally round to elliptical shallow pits with closely 15 mm in length their longer axis, commonly associated with an anterior located shallow groove with an anteroposterior direction. Two of them can be seen on the left lateral surface (Figure 3.3) and another one on dorsal surface close to the contact between the nasal and frontal bones (Figure 3.4). The former two are set in a straight line, with their grooves aligned, and are located on the maxilla, close to the anterior margin of the anterior supraorbital. These grooves present unusual texture, rough and longitudinal scars.

The larger perforations (more than 15 mm), one on the right lateral surface and two others on the left lateral surface. The largest (25 mm length and 13 mm width) is located on the left side, initially considered as an antorbital fenestra, is deep and elliptic (Figure 3.1). It is located in the contact between maxilla and lacrymal, close to nasal. Although on lateral surface, the actual opening faces more dorsally than laterally. A small groove with longitudinal scars can be observed posterior to this perforation. The other one on the left surface is smaller (20 mm) and located on the maxilla. It is round and bears concentric scars and a small triangular lateroventral groove (Figure 3.2). The pit on the right side is round, located on the maxilla, close to the tooth row. It is tear-shaped and bears no groove or scar (Figure 3.5).

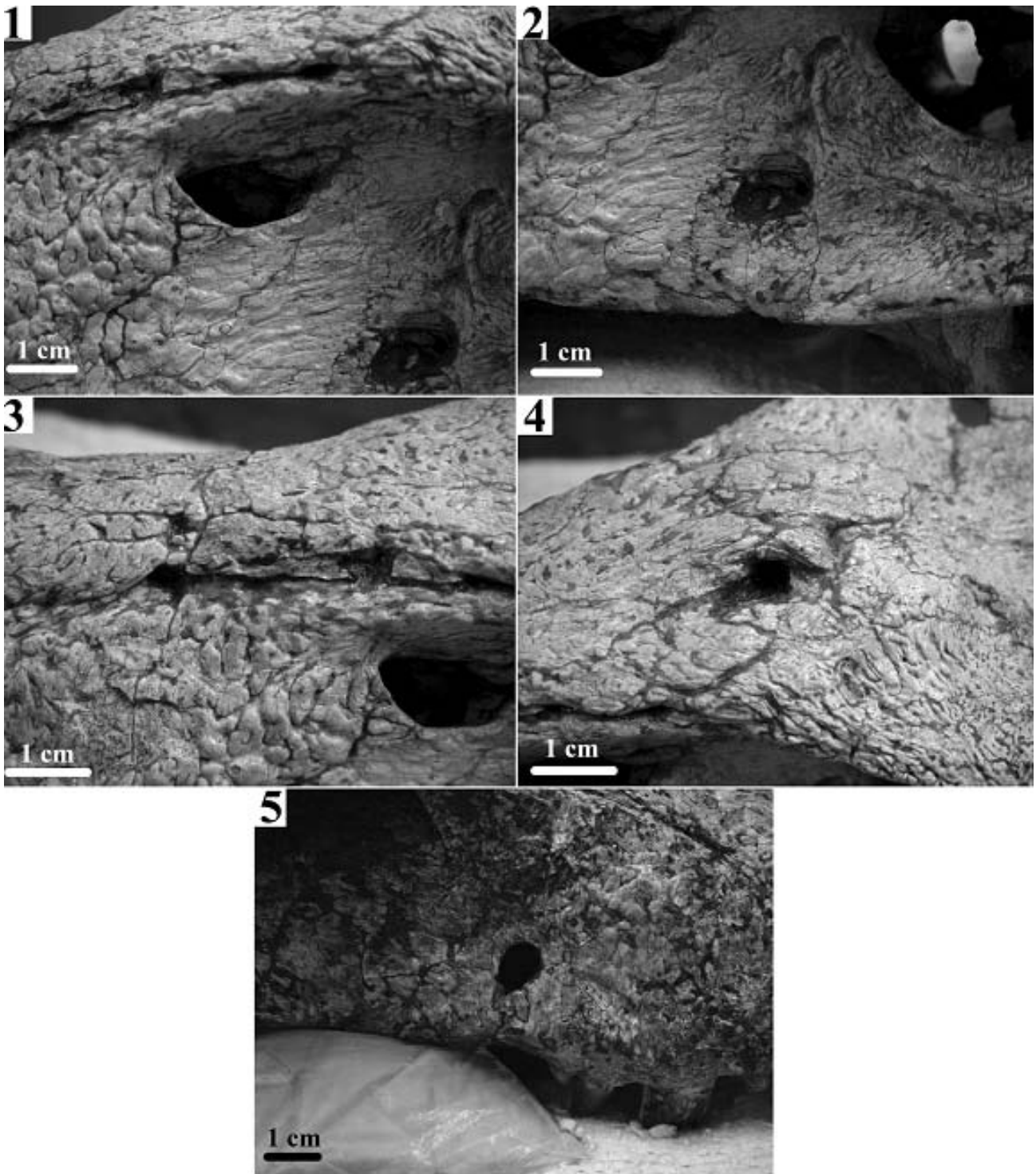


**Fig. 1:** Holotype of *Baurusuchus salgadoensis* (MPMA-62-0001-02) in (1) right lateral view of the skull; (2) left lateral view; (3) dorsal view and (4) palatal view.



**Fig. 2:** Holotype of *Baurusuchus salgadoensis* (MPMA-62-0001-02) in (1) right occipital view; (2) palatal view





**Fig. 3:** Holotype of *Baurusuchus salgadoensis* (MPMA-62-0001-02) in (1) right occipital view; (2) palatal view

**Choanae:** Composed by ectopterygoids and pterygoids. It is roughly subtriangular in shape, with a concave posterior margin, and is lateroposteriously surrounded by high, ventrally projected flanges of the pterygoid and ectopterygoid. Most of its internal and dorsal surfaces are eroded, preventing the recognition of septation, but the preserved surface seems to bear indications of a sept. The choana differs in shape from this of *Stratiotosuchus* (URC-R 75 specimen), which bears a wider and shorter choanae. It also resembles the choanae in *Barinasuchus*. In *Cynodontosuchus*, *Baurusuchus pachecoi*, *Pabweshi* and *Penhuechesuchus* this structure is unknown. In notosuchids *Mariliasuchus* Carvalho & Bertini, 1999 (UFRJ DG 106-R) and *Comahuesuchus* Bonaparte, 1991 and in the sphagesaurid *Sphagesaurus* Price, 1950, the choanae is composed anteriorly by the palatines and posteriorly by the pterygoids, although its general shape is similar to *Baurusuchus salgadoensis* (Andrade *et al.* 2006; Figures 1 and 2). The morphology of the choanae in *B. salgadoensis* is different from those of other Mesoeucrocodylia. The composition of the choanae border in Peirosauridae does not include the ectopterygoids but include an extensive participation of the palatines and a rectangular shape, as seen in *Lomasuchus* Gasparini, Chiappe & Fernandez, 1991 and *Hamadasuchus* Buffetut, 1994 (Gasparini *et al.*, 1991; Larsson & Sues, 2007). The same pattern is observed in *Araripesuchus* Price, 1949 (Andrade *et al.*, 2006, Figure 5).

**Occipital and palatal surfaces:** Supraoccipital: Laterally expanded, bearing two depressions separated by a short ridge. These depressions are possibly the insertion surfaces for the *Musculus splenius capitis*. The supraoccipital contacts shortly and laterally the squamosal, and ventrally the occipital in a sinuous line.

Exoccipital: Vertical and concave. Contacts the supraoccipital, squamosal, quadrate, and basioccipital. Two *foraminae* are visible, located lateroventrally, just below and aside the *foramen magnum*.

Basioccipital: Observed in occipital and palatal views, it is abruptly sloped between these two surfaces. It is concave in palatal view, forms the basis and neck of the occipital condyle. It bears two lateral projections and a medial one contacts the basisphenoid, granting it a “M” outline. The borders are swollen along the contact between the two bones. The contact between basioccipital lateral projections and basisphenoid harbors the long and elliptical lateral eustachian *foramina*. This pattern is observed in *Sphagesaurus* and *Mariliasuchus*.

Basisphenoid: Broad, anteriorly inclined. Compressed between the basioccipital and pterygoids, it bears stout mediolateral ridge, confluent to the contact of the quadrate and exoccipital. The contact with the basioccipital has a M-shaped outline. Close to the contact with the pterygoid two circular *foraminae* are observed. They are located below the posteroventral flanges of the pterygoid. A small ridge separates them, linking the basisphenoid and the pterygoid. These *foramina* are observed in *Stratiotosuchus* (DGM 1477-R and URC-R 75 specimens) although they are more elliptical and separated by a ridge. The M-shaped outline in the contact between basisphenoid and basioccipital, and the position of the lateral eustachian *foramina* bear similarity with analogous structures observed in *Sphagesaurus* and *Mariliasuchus*.

#### 4. DISCUSSION

Carvalho *et al.* (2005) interpreted the large aperture present at the right side of the skull as an antorbital fenestra. But such structure presents no symmetrical double on the left side. In fact, all other baurusuchids bear no antorbital fenestrae.

None of these unusual marks appear to be anatomical or structural in nature, but seem to be bitmarks. This interpretation is supported by numerous studies based on the shape, texture and associated features in various taxa (Buffetaut, 1983; Evans, 1983; Fiorillo 1991; Erickson & Olson, 1996; Jacobsen, 1997, 1998; Tanke & Currie, 1995, 1998). The preservation of these marks is favored by the highly resilient nature of the crocodylian skull, especially those taxa with laterally compressed skulls as the baurusuchids (Busbey III, 1995).

Most authors agree that comparing the distribution pattern, morphology and size of the tooth-marks with the known predatory taxa could shed light on the tooth-mark producer identity and the nature of ecological interaction, if they originated from an interspecific or intraspecific fighting behavior, predator-prey relationship or scavenging.

The size and shape of larger tooth-marks seem to exclude baurusuchids as probable producers. They does not match the teeth of baurusuchids that even tough zipodont (Price, 1945; Riff & Kellner, 2001; Carvalho *et al.*, 2005), they are not as elliptical as tooth-marks. These large elliptical and deep tooth-marks could be associated to larger archosaurs with more elliptical and zipodont teeth in cross-section, as Abelisauridae theropod. These dinosaurs are known in the Adamantina Formation, but only as isolated teeth (Bertini *et al.*, 1993; Candeiro *et al.*, 2006).

The smaller tooth-marks, more circular and shallow, match similar marks observed in the holotype of *Baurusuchus pachecoi* (Stephane Jouve, pers. com.) and in the tail osteoderms of a baurusuchid (UFRJ-DG 262-R) found at Jales County, São Paulo State, described by Avilla *et al.* (2004). The same shape is observed in *B. salgadoensis*, circular to elliptical shallow punctures with delicate grooves following the major axis of the more elliptical marks. These could be associated to baurusuchids intraspecific fighting behaviour, as was suggested by Avilla *et al.* (2004), due to teeth size and morphology (Riff & Kellner, 2001). Although other predators, as theropod dinosaurs, could produce this tooth-marks as these animals present tooth variation along their jaws. The hypothesis of a crocodylian producer seems to be highly probable, as a head-biting behavior has been observed in extant species (Cott, 1961), and the pattern of tooth-marks and associated damage are similar to those observed in extant species attacks (Njau & Blumenschine, 2006)

The grooves present in some tooth marks are interpreted as scar or drag marks, due to the action of “strike and-pull back” done by the predator. This is the particular tactical behavior of attack of many animals bearing zipodont teeth, including theropod dinosaurs, crocodyliforms, and monitor lizards (Colbert, 1946; Busbey III, 1995; Snively & Russell, 2007).

The two types of tooth-marks and their probable producers are not mutually excluding. Both producers could carve independent tooth-marks on different occasions. Whether these tooth-marks were produced on a combat, predator-prey or scavenging interactions is difficult to determine.

On the other hand, this could indicate three scenarios: one with the intraspecific competition among baurusuchids; the second, where the baurusuchid was prey of an abelisaurid; and the third, and less

probable, that the holotype of *Baurusuchus salgadoensis* received the marks from a scavenger. Since the dual pattern of tooth-marks, two independent scenarios could have occurred.

In conclusion, the presence of an antorbital fenestra is rejected, and the diagnosis of *Baurusuchus salgadoensis* should be revised to consider this new interpretation. The new data should be taken into consideration in future taxonomic and systematic approaches of the group as well provide new insights on the probable producer of the tooth-marks.

The choanae structure is peculiar and very specific among the observed baurusuchids. The similarity between *Baurusuchus salgadoensis*, *Stratiotosuchus* and *Barinasuchus* is evident although each bear their own particularities, especially their shape and biometry. A similarity in the general shape of choanae is observed among baurusuchids, notosuchids and sphagesaurids alike, but major differences as the organization and participation in the borders of the choanae still sets them apart from baurusuchids. But, in other hand, clusters them together, baurusuchids, notosuchids and sphagesaurids, when compared to neosuchian-related taxa as the araripesuchids, peirosaurids and trematochampsids is congruent with phylogenetic hypotheses of the group (Ortega *et al.*, 2000; Turner & Calvo, 2005; Larsson & Sues, 2007)

The detailed description of osteological features of occipital and palatal surfaces of *Baurusuchus salgadoensis* displayed similarities between the former and other Mesoeucrocodylia as *Sphagesaurus* and *Mariliasuchus*. As most baurusuchids are fragmentary or poorly described, especially their occipital and palatal regions, it is difficult to compare and establish their differences and similarities.

## 5. CONCLUSIONS

The unusual puncture marks and grooves on the skull of *Baurusuchus salgadoensis* are interpreted as tooth-marks probably produced by a medium to large archosaur with ziphodont teeth, as a baurusuchid or Abelisauridae theropod dinosaur. Although the actual tooth-mark producer or the paleoecological context in which they were carved cannot be diagnosed precisely, both baurusuchids and abelisaurids are strong candidates. Both are terrestrial cursorial predators and scavengers, bear ziphodont teeth, probably used the same kind of slashing bite and occur in the same stratigraphical unit, the Adamantina Formation, being the largest predators of that period in terrestrial areas continental Brazil.

*Baurusuchus salgadoensis* does not present an antorbital fenestrae. This does not invalidate nor does change its systematic relationships, but should be taken into account in future systematic hypotheses.

The choanae in *Baurusuchus salgadoensis* features small but consistent differences when compare to *Stratiotosuchus*, thus adding further taxonomic distinction of the former taxa. The difference between the choanae of the baurusuchids and notosuchids and sphagesaurids are relatively smaller than this observed with other taxa, such as *Araripesuchus*, Peirosauridae and Trematochampsidae. These differences are restricted to minor bone border participation.

The choanae shape and bone borders, and palatal surfaces are concordant with recent phylogenetic hypotheses that display a closer relationship between baurusuchids with notosuchids and sphagesaurids.

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## 8. APPENDIX

### 8.1 REFERRED MATERIAL

*Barinasuchus arveloi* (MAAT-0260); *Baurusuchus pachecoi* (DGM299-R); *Baurusuchus salgadoensis* (MPMA-62-0001-02); *Baurusuchus* indet. (UFRJ-DG 262-R); *Cynodontosuchus rothi*, (MLP 66-IV-16-25); *Stratiotosuchus maxhechti* (DGM 1477-R and URC 75); *Pabweshi pakistanensis* (GSP-UM 2001); *Araripesuchus gomesii* (DGM 423-R); *Comahuesuchus brachybuccalis* (MOZ-P-6131); *Hamadasuchus rebouli* (ROM 52620), *Lomasuchus palpebrosus* (MOZ 4084 PV); *Mariliasuchus amarali* (UFRJ DG 106-R) and *Sphagesaurus sp.* (MPMA-15-1/90).

### 8.2 Institutional abbreviations

DGM - Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Brazil; GSP-UM - Geological Survey of Pakistan-University of Michigan collection, USA; MAAT - Museo Alberto Arvelo Torrealba, Barinas, Venezuela; MPMA - Museu de Paleontologia de Monte Alto, Brazil; MLP - Museo de La Plata, Argentina; MOZ - Museo Professor-Dr. Juan A. Olsacher, Argentina; ROM - Royal Ontario Museum, Canada; UFRJ-DG - Universidade Federal do Rio de Janeiro, Departamento de Geologia, Brazil; URC - Museu de Paleontologia e Estratigrafia Prof. Dr. Paulo Milton Barbosa Landim, Universidade Estadual Paulista, Campos Rio Claro, Brazil

### 8.3 Anatomical abbreviations

An - Angular; Ar - articular; Be - Basisphenoid; Bo - Basioccipital; D - Dentary; Eoc - Exoccipital; Ept - Ectopterygoid; fin - *foramen incisivum*; fmg - *foramen magnum*; Fr - Frontal; io - *incisura otica*; J - Jugal; L - Lacrymal; leu - lateral eustachian foramen; ltf - laterotemporal fenestra; M - Maxilla; meu - medial eustachian foramen; mf - mandibular fenestra; N - Nasal; or - orbit; P - Parietal; Pa - Palatine; pf - palatine fenestra; Pfo - Pterygoid foramen; Pfr - Prefrontal; Pm - Premaxilla; Po - Postobital; Pt - Pterygoid; Q - Quadrate; Qj - Quadratojugal; San - Surangular; So - Supraoccipital; Soa - Anterior supraorbital; Sop - Posterior supraorbital; Sp - Splenial; Sq - Squamosal; stf - supratemporal fenestra.