



# A new *Pissarrachampsinae* specimen from the Bauru Basin, Brazil, adds data to the understanding of the *Baurusuchidae* (*Mesoeucrocodylia*, *Notosuchia*) distribution in the Late Cretaceous of South America

Gustavo Darlim<sup>a,\*</sup>, Ismar de Souza Carvalho<sup>b,c</sup>, Sandra Aparecida Simionato Tavares<sup>d</sup>, Max Cardoso Langer<sup>a</sup>

<sup>a</sup> Universidade de São Paulo, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Laboratório de Paleontologia, Av. Bandeirantes, 3900, Ribeirão Preto, SP, Brazil

<sup>b</sup> Universidade Federal do Rio de Janeiro, Instituto de Geociências, CCMN, 21.910-200 Av. Athos da Silveira Ramos 273, Rio de Janeiro, RJ, Brazil

<sup>c</sup> Centro de Geociências da Universidade de Coimbra, Portugal

<sup>d</sup> Museu de Paleontologia "Prof. Antônio Celso de Arruda Campos", Praça do Centenário, Centro, Monte Alto, SP, Brazil

## ARTICLE INFO

### Article history:

Received 7 January 2021

Received in revised form

18 July 2021

Accepted in revised form 18 July 2021

Available online 27 July 2021

### Keywords:

Notosuchia

Baurusuchidae

*Campinasuchus dinizi*

Distribution

Paleobiogeography

Adamantina Formation

## ABSTRACT

Baurusuchidae is one of the most diverse notosuchian groups, represented by ten formally described species from the Upper Cretaceous deposits of the Bauru and Neuquén basins, respectively in Brazil and Argentina. Among these, recent phylogenetic analyses placed *Wargosuchus australis*, *Campinasuchus dinizi*, and *Pissarrachampsina sera* within *Pissarrachampsinae*, whereas *Baurusuchinae* is composed by *Aphaurosuchus escharafacies*, *Aplestosuchus sordidus*, *Baurusuchus albertoi*, *Baurusuchus pachecoi*, *Baurusuchus salgadoensis*, and *Stratiosuchus maxhechti*. All baurusuchines, except for *Baurusuchus pachecoi* and *Stratiosuchus maxhechti*, were collected from the same locality of the Adamantina/Vale do Rio do Peixe Formation, i.e., Fazenda Buriti, near General Salgado, São Paulo. Recent works suggested that *Pissarrachampsinae* of that stratigraphic unit come only from outcrops in Minas Gerais, with a possibly older age equivalent to those of the Neuquén Basin members of the group. Here, we present a new *Pissarrachampsinae* specimen from Fazenda São José, a site near Fazenda Buriti, which challenges the proposed chronostratigraphic separation between the São Paulo and Minas Gerais baurusuchids, suggesting that both groups lived at about the same time.

© 2021 Elsevier Ltd. All rights reserved.

## 1. Introduction

Baurusuchidae is a well-known group of terrestrial and predatory notosuchians from the Late Cretaceous of Gondwana (Montefeltro et al., 2020). It was first described based on *Baurusuchus pachecoi* Price, 1945, which remained as the single species for the genus until the description of *Baurusuchus salgadoensis* by Carvalho et al., 2005. Since then, other baurusuchids were identified, such as *Cynodontosuchus rothi* (Gasparini 1972) and *Stratiosuchus maxhechti* (Campos et al., 2001). Yet, much of the morphological and phylogenetic information about Baurusuchidae is quite recent, as most

species were described in the last decade (Nascimento & Zaher, 2010; Montefeltro et al., 2011; Carvalho et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Cotts et al., 2017; Darlim et al., 2021). The group is restricted to the Bauru Basin, except for the Argentinean species *Cynodontosuchus rothi* and *Wargosuchus australis* from the Bajo de la Carpa Formation, and possibly the Pakistani *Pabweshi pakistanensis*, currently comprising eleven species (Woodward, 1896; Wilson et al., 2001; Martinelli and Pais, 2008; Darlim et al., 2021). Baurusuchidae is traditionally diagnosed by a reduced tooth formula and ziphodont dentition, a laterally compressed rostrum, and a verticalized quadrate (*sensu* Price, 1945). It corresponds to one of the most diverse notosuchian clades, with two subgroups recognized by Montefeltro et al. (2011), *Baurusuchinae* and *Pissarrachampsinae* (Darlim et al., 2021). The former group includes *Baurusuchus albertoi*, *Baurusuchus pachecoi*, *Baurusuchus salgadoensis*, *Stratiosuchus*

\* Corresponding author.

E-mail addresses: [gustavo.darlim@gmail.com](mailto:gustavo.darlim@gmail.com) (G. Darlim), [ismar@geologia.ufrj.br](mailto:ismar@geologia.ufrj.br) (I.S. Carvalho).

*maxhecti*, *Aplestosuchus sordidus*, and *Aphaurosuchus escharafacies*, and the latter *Pissarrachampsia sera*, *Campinasuchus dinizi*, and *Wargosuchus australis* (Campos et al., 2001; Nascimento and Zaher, 2010; Montefeltro et al., 2011; Carvalho et al., 2011; Godoy et al., 2014; Darlim et al., 2021). However, these subgroups have not been retrieved as monophyletic in some recent phylogenetic analyses (Fiorelli et al., 2016; Barrios et al., 2018; Leardi et al., 2018; Fernández-Dumont et al., 2020).

All Brazilian baurusuchids come from the Vale do Rio do Peixe Formation of Fernandes & Coimbra (2000), which is part of the Adamantina Formation described by Soares et al. (1980; see also Batezelli, 2015). Several of these were also collected in the same locality, known as Fazenda Buriti, near Prudêncio e Morais district, General Salgado, São Paulo, including *Aplestosuchus sordidus*, *Baurusuchus albertoi*, *Baurusuchus salgadoensis*, and *Gondwanasuchus scabrosus*, all of which, except for the latter, are baurusuchines (Marinho et al., 2013; Godoy et al., 2014). Pissarrachampsines, on the other hand, are restricted to the Adamantina/Vale do Rio do Peixe Formation of Minas Gerais and Bajo de la Carpa Formation, Neuquén Basin, in Argentina. Based on the age of the latter unit, Montefeltro et al. (2011) discussed a possible older age (i.e., Santonian) for the Pissarrachampsinae-bearing deposits of Minas Gerais, compared to those yielding baurusuchines in São Paulo.

Here, based on a first-hand comparative analysis of most relevant specimens, we describe a baurusuchid partial skull discovered in Fazenda São José (Fig. 1), near Fazenda Buriti, which has enough morphological evidence to be assigned to Pissarrachampsinae, specifically to *Campinasuchus dinizi*. *Campinasuchus dinizi* was described based first on cranial (Carvalho et al., 2011) and, posteriorly, on postcranial (Cotts et al., 2017). material from the Três Antas Farm, in Minas Gerais. This is the first record of pissarrachampsines in São Paulo, challenging previous assumptions that the taxon was restricted to the Bauru Group of Minas Gerais.

## 2. Geological settings

The specimen herein described was found at Fazenda São José (20° 36' 59,8" S 50° 29' 18,3" W), Prudêncio e Morais district, near General Salgado, São Paulo State, in a field work led by Prof. João Tadeu Arruda. The deposits exposed at Fazenda São José (see Castro et al., 2018) belong to the Vale do Rio do Peixe Formation described by Fernandes & Coimbra (2000), which corresponds to most of the Adamantina Formation as described by Soares et al. (1980). Such beds were radioisotopically dated in Fazenda Buriti by Castro et al. (2018), resulting in a late Coniacian to late Maastrichtian maximum depositional age, although the authors considered Campanian as the best age estimate. Previous studies based on biostratigraphic data from vertebrates, ostracods, and Charophyta broadly inferred a Turonian to Maastrichtian age for the Adamantina/Vale do Rio do Peixe Formation (Gobbo-Rodrigues et al., 1999; Dias-Brito et al., 2001; Santucci and Bertini, 2001; Marinelli et al., 2011).

Apart from the already mentioned baurusuchids *Baurusuchus salgadoensis*, *Baurusuchus albertoi*, *Gondwanasuchus scabrosus*, and *Aplestosuchus sordidus* (Carvalho et al., 2005; Nascimento & Zaher, 2010; Marinho et al., 2013; Godoy et al., 2014), Fazenda Buriti has also yielded other crocodyliform material, including eggs and the sphagesaurid *Caipirasuchus stenognathus*, as well as a mammal tooth, and snake vertebrae (Zaher et al., 2003; Pol et al., 2014; Castro et al., 2018), showing the fossiliferous richness of the outcrops around General Salgado.

## 3. Material and methods

UFRJ DG 402-R consists of a partially preserved skull containing both premaxillae, maxillae, nasals, and palatines, the anterior

portion of left jugal, the left ectopterygoid, and the anterior portion of both hemimandibles (anterior to the external mandibular fenestra), including dentary and splenial. Furthermore, the dentition of both upper and lower jaws is mostly preserved. Although incomplete, the recovered material is in good state of preservation (Fig. 2).

The specimen was originally found with the right lateral surface of the premaxilla and maxilla exposed on the rock-matrix. The material was prepared by SAST at the Paleontology Museum "Prof. Antonio Celso de Arruda Campos" in Monte Alto-SP. The rock matrix was removed using low impact hammers, and the fossil was stabilized using white glue *Cascarez* in different concentrations. At the end of the preparation, the skull and mandible were disarticulated.

### 3.1. Comparative material

*Aphaurosuchus escharafacies* LPRP 0697, *Aplestosuchus sordidus* LPRP 0229a, *Armadillosuchus arrudai* UFRJ DG 303R, MPMA 64-0001-04; *Baurusuchus pachecoi* DGM 299-R, *Baurusuchus salgadoensis* MPMA 62-001-02; UFRJ DJ 288-R, 308-R; *Campinasuchus dinizi* CPPLIP 1235, 1234, 1236, 1237, 1436; *Gondwanasuchus scabrosus* UFRJ DG 408-R; *Pissarrachampsia sera* LPRP 0019, 0018, 0020; *Stratiosuchus maxhecti* DGM 1477.

### 3.2. Institutional abbreviations

**CCPLIP**- Centro de Pesquisas Paleontológicas, L.I. Price, Uberaba; **DGM**- Museu de Ciências da Terra do Departamento Nacional de Produção Mineral, Rio de Janeiro; **LPRP**- Laboratório de Paleontologia de Ribeirão Preto; **MPMA**- Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos"; **UCR**- Universidade Estadual Paulista, Rio Claro; **UFRJ-DG**- Coleção de Macrofósseis da Universidade Federal do Rio de Janeiro, Departamento de Geologia.

## 4. Systematic paleontology

Mesoeucrocodylia Whetstone & Whybrow, 1983 *sensu* Benton & Clark, 1988

Notosuchia Gasparini 1971 *sensu* Sereno et al., 2001

Eunotosuchia Ruiz, Bronzati, Ferreira, Martins, Queiroz, Langer & Montefeltro, 2021

Xenodontosuchia Ruiz, Bronzati, Ferreira, Martins, Queiroz, Langer & Montefeltro, 2021

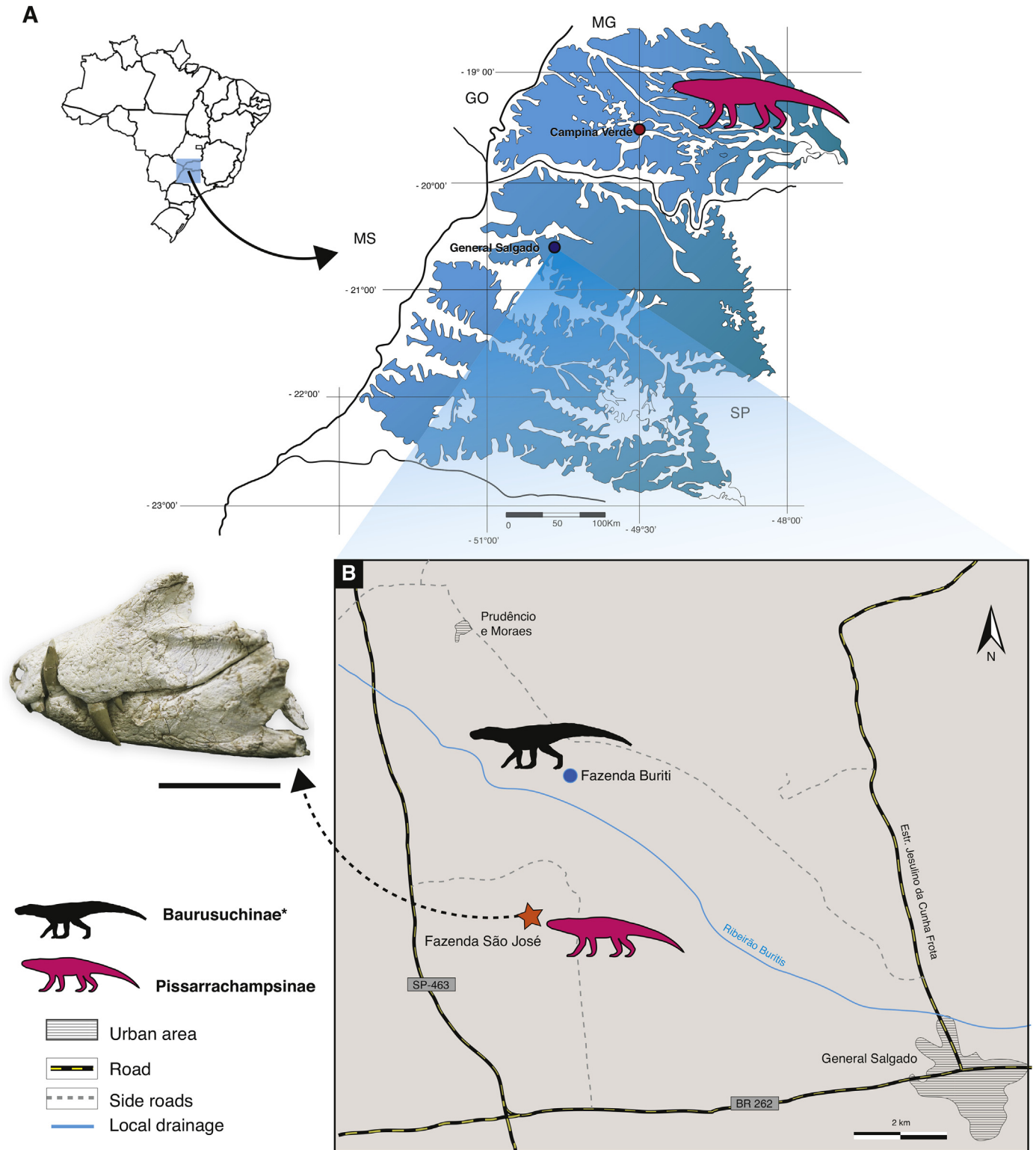
Baurusuchidae Price, 1945 [Darlim, Montefeltro & Langer, 2021]

Pissarrachampsinae Montefeltro, Larsson & Langer 2011 [Darlim, Montefeltro & Langer, 2021]

*Campinasuchus dinizi* Carvalho, Teixeira, Ferraz, Ribeiro, Martinelli, Neto, Sertich, Cunha, Cunha, Ferraz, 2011

*Locality and Horizon.* Adamantina/Vale do Rio do Peixe Formation, Bauru Group (Soares et al., 1980; Fernandes & Coimbra, 1996; Batezelli, 2005); Upper Cretaceous (ca. Coniacian–Campanian) of the Bauru Basin (Castro et al., 2018).

*Emended diagnosis.* Baurusuchid crocodyliform characterized by the following combination of features (autapomorphies marked with an asterisk): a short, low, laterally compressed rostrum; cranial table higher than dorsal border of rostrum; four premaxillary and five maxillary teeth; marked heterodonty, with third maxillary and fourth dentary teeth extremely enlarged relative to other teeth; last maxillary tooth placed almost at the level of anterior border of palatal (suborbital) fenestra; posteroventrally projecting quadrate; pit on the premaxilla for reception of first mandibular tooth placed lateral to first premaxillary tooth (or between first and second premaxillary

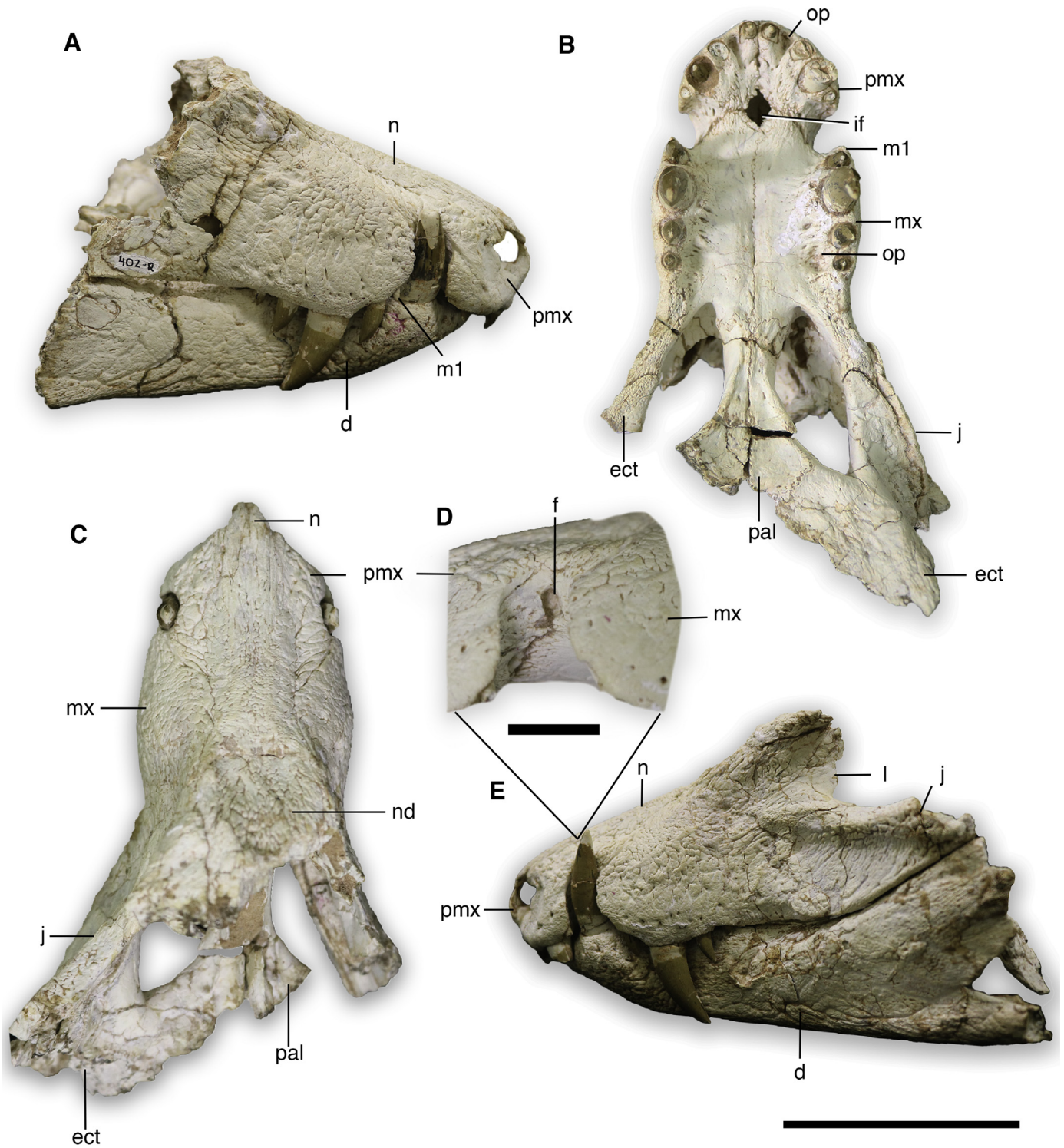


**Fig. 1.** Distribution of baurusuchids. **A**, Map of Brazil focusing on the Adamantina/Vale do Rio do Peixe Fm. in São Paulo and Minas Gerais states (modified from Fernandes, 2004); **B**, Schematic drawing showing the locality of the main outcrops near General Salgado-SP. Silhouettes indicate the baurusuchids subgroups: Baurusuchinae of Fazenda Buriti in black (*Baurusuchus albertoi*, *Baurusuchus salgadoensis*, and *Aplestosuchus sordidus* + the non baurusuchinae *Gondwanasuchus scabrosus*); Pissarrachampsine in pink occurring in Minas Gerais (*Pissarrachampsia sera*, and *Campinasuchus dinizi*) and in São Paulo (*Campinasuchus dinizi*). Star indicates the locality of UFRJ DG 402-R. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

teeth); marked constriction of the skull posterior to last maxillary tooth; ten dentary teeth; large anteroposterior depression on each palatine between palatal fenestrae;

ventrally flat ectopterygoid surface; anteriorly semi-circular maxilla-jugal suture; slender posterior process of jugal; dorsal nasal-maxillary suture strongly laterally concave; nasal-





**Fig. 2.** *Campinasuchus dinizi* specimen UFRJ DG 402-R. **A** right lateral view of cranium and mandible articulated; **B** ventral view of the cranium; **C** dorsal view of cranium; **D** close up of premaxilla-maxilla lateral suture within the notch for the reception of D4; **E**, left lateral view of cranium and mandible articulated. d, dentary; ect, ectopterygoid; f, foramen; if, foramen incisivum; j, jugal; l, lacrimal; m1, maxillary tooth 1; mx, maxilla; n, nasal; nd, nasal depression; op, occlusal pit; pal, palatine; pmx, premaxilla. Scale bar 10 cm (2 cm in D).

frontal contact reduced; ventral depression on splenial at mandibular symphysis; anteriorly convex dentary-splenial suture at mandibular symphysis in ventral view; conspicuously flattened ventral surface of palatine\*.

## 5. Description

**Premaxilla.** Both premaxillae are well preserved and articulated. The bone is subtriangular in lateral view. Anteriorly, its dorsal

projection forms an anteroposteriorly and lateromedially thin internarial bar, the dorsal tip of which is slightly curved posteriorly, forming an anteriorly convex surface. Dorsally, that tip contacts the pointed anteroventral tip of the nasal. Posterior to that, there is a relatively shallow perinarial fossa that is displaced laterally and extended along the entire premaxillary margin of the nasal cavity. Bordering the cavity, the fossa gradually becomes less marked anteriorly, towards the base of the internarial bar. In lateral view, the premaxillary body has a concave posterior margin that forms the anterior border of the premaxilla-maxilla notch for the reception of the dentary caniniform (D4). Within this notch, the premaxilla-maxilla is marked by an ovate foramen (Fig. 2D). From the anterior margin of the notch, there is an elongated depression extending anteroventrally at the lateral surface of the premaxilla. The premaxilla is well ornamented, the right bone bears one foramen right posterior to the perinarial fossa, whereas two foramina in the same portion are seen on the left side.

In ventral view, the premaxilla has a subtriangular shape. The medial margin of the alveoli is marked by thin and elongated grooves and few foramina scattered along the surface. Also, two anteroposteriorly elongated occlusal pits for the insertion of the first dentary teeth are present between the first and second premaxillary alveoli. The posteromedial corners of the ventral surface of the premaxillae forms the anterior margin of the foramen incisivum.

**Maxilla.** The maxilla is a heavily ornamented bone contacting the nasal dorsally, the premaxilla anteriorly, the lacrimal posterodorsally, and the jugal posteroventrally. The lateral alveolar margin of the bone is pierced by nine small foramina. Anteriorly, the maxilla has a convex lateral projection that forms the posterior portion of the premaxilla-maxilla notch for the insertion of the caniniform dentary tooth (D4). In lateral view, the ventral margin of the maxilla is convex where the bone bears teeth and becomes straight posterior to the last maxillary tooth (M5). This straight portion forms the posterior ramus of maxilla, which is lateromedially constricted. As mentioned above, the anterior suture with the premaxilla is marked by an ovate foramen, at the premaxilla-maxilla notch (Fig. 2D). Forming the posterior border of such foramen, the ventral portion of the anterior margin of the maxilla is anteriorly projected. As in the premaxilla, medial to the alveoli, the ventral surface of the maxilla is ornamented and bears scattered foramina. In that area, between the fourth and fifth maxillary teeth, there is a marked occlusal pit for the reception of the ninth dentary tooth (D9).

The maxilla articulates ventromedially with its antimere via a linear suture. Parasagittally to this suture, at its posteriormost portion that contacts palatines, the maxilla bears two inconspicuous elongated depressions. Posteriorly, the maxilla articulates with the palatine via a slightly anteriorly convex suture and forms the anteromedial border of the suborbital fenestra, the antero-lateral margin of which is formed by the posterior ramus of the maxilla. That ramus contacts the dorsal projection of the ectopterygoid medially and the anteriormost portion of jugal laterally.

**Nasal.** The nasals are partially fused to one another, but the suture is still recognizable anteriorly (Fig. 3C). It is an anteroposteriorly elongated bone, with an anteriorly project and ventrally curved portion of the internarial bar that contacts an equivalent process of the premaxilla. In dorsal view, this projection is conspicuous and gives this part of the skull a pointed shape. The dorsal surface of the nasal is flat and ornamented. More posteriorly the bone bears a rugose concavity, bordered by the anterior palpebral and supposedly by the anterior margin of the prefrontals, however this portion is damaged making it difficult to access such information. Laterally, the nasal contacts the dorsal surface of the premaxillae and maxillae via linear suture.

**Jugal.** The jugal is only partially preserved on the left side, including part of the infraorbital and antorbital portions. The bone

is also heavily ornamented at the ventral and anteroventral borders of the orbit and is marked dorsally by a conspicuous infraorbital ridge (*sensu* Montefeltro et al., 2011). Ventral to the ridge, elongated and dorsoventrally directed grooves are seen along the bone. Also, the ventral margin of the infraorbital region is conspicuously inclined anteroventrally towards the suture with the maxilla. The antorbital portion of the jugal contacts the maxilla and the lacrimal, but the sutures are not discernible due to the high ornamentation of that surface. The dorsal contact with the lacrimal is inferred by the dorsal end of the infraorbital ridge (Fig. 3D). Ventrally, the jugal articulates with the dorsal projection of the ectopterygoid.

**Lacrimal.** The lacrimal is only preserved in the left side, but lacks its posteriormost portion. Laterally, the lacrimal surface is less ornamented than that of the jugal and maxilla. Anteriorly, the lacrimal contacts the maxilla by an extended dorsoventrally linear suture. From its ventral contact with the jugal, the lacrimal extends dorsomedially, projecting laterally at its dorsal margin to form a platform for the anterior palpebral. Such contact between the lacrimal and the anterior palpebral precludes a dorsal exposure of the former bone. Furthermore, the dorsolateral projection provides to the lacrimal a laterally concave shape in posterior view. In that same view, a perforation is seen slightly below the lateral inflexion of the bone, which may represent the lacrimal duct.

**Anterior palpebral.** The anterior palpebral is poorly preserved and only its anteriormost portion can be observed at the left side. In lateral view, the bone is ornamented and linear being slightly anterior to posteriorly inclined, and it can be seen in articulation with the dorsal surface of the lacrimal. In dorsal view, a clear suture is present possibly contacting anteriorly a posterolateral small portion of the nasal (Fig. 3), and medially the lateral surface of the highly damaged prefrontal.

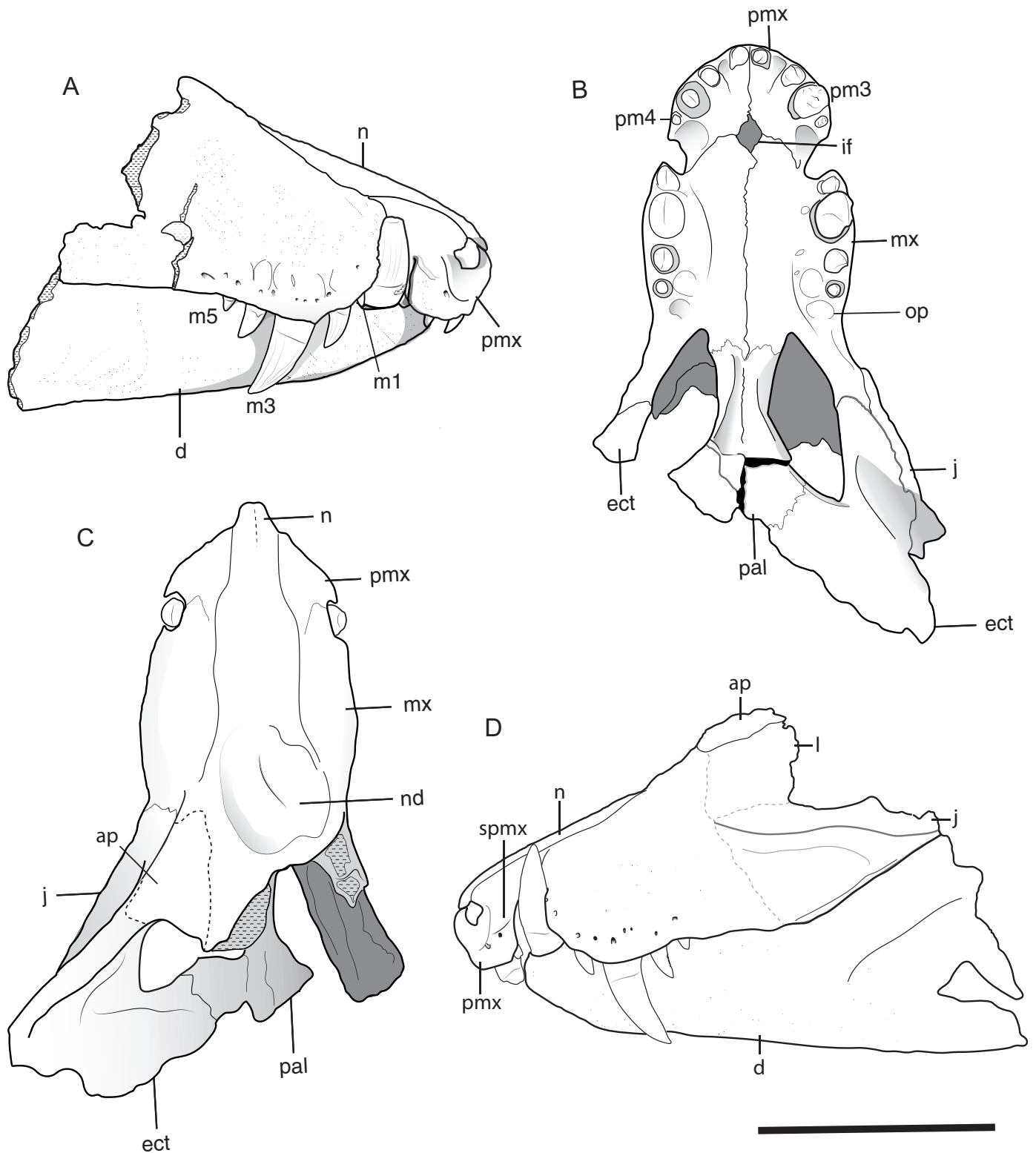
**Palatine.** The palatine pair forms a subtriangular element in ventral view (Fig. 2B). It contacts the maxilla anteriorly by a slightly anteriorly convex suture, which converges posteriorly near the sagittal line. The slightly concave lateral margin of the palatines forms the medial margin of the suborbital fenestrae. The anterior portion of the palatine is tubular, with a generally lateromedially convex ventral surface, but bearing a parasagittally elongated sulcus. More posteriorly, the bone gradually expands laterally, forming a flat ventral surface. It is possible to observe some foramina scattered on both the sulci and the flattened area. The posterolateral ramus of the palatine contacts the ectopterygoid.

In posterior view, even that the dorsal area is damaged, it is possible to observe at the anterior tubular portion the dorsal contact with the ventral area of the vomer, forming a continuous surface laterally. Medially it is possible to observe that the contact of both bones forms the nasopharyngeal duct (*sensu* Witmer, 1995) which is filled with rock matrix.

**Ectopterygoid.** The ectopterygoid is only preserved on the left side and presents two major portions: the ventral or ectopterygoid wings and the dorsolateral projection. The ventral portion of the ectopterygoid contacts the palatine medially and the pterygoid posteriorly (Fig. 2B). It is ventrally flattened and the ventralmost tip of the ectopterygoid wing is posteriorly oriented. The dorsolateral projection contacts the posterior ramus of the maxilla anteriorly and the medial portion of the jugal laterally. Its medial margin forms the posterior and posterolateral borders of the suborbital fenestra.

### 5.1. Mandible

**Dentary.** The dentaries are articulated to one another, but only the portion anterior to the external mandibular fenestra is preserved. It is a highly ornamented bone, including the symphyseal area and the diverging posterior portion. The conjoined mandibular



**Fig. 3.** Schematic drawings of *Campinasuchus dinizi* UFRJ DG 402-R. **A** right lateral view of the cranium and mandible articulated; **B** ventral view of cranium; **C** dorsal view of cranium; **D** left lateral view of cranium and mandible articulated. ap, anterior palpebral; d, dentary; ect, ectopterygoid; if, foramen incisivum; j, jugal; l, lacrimal; mx, maxilla; m1-3, maxillary teeth; n, nasal; nd, nasal depression; op, occlusal pit; pal, palatine; pmx, premaxilla; pm 3-4, premaxillary teeth. Scale bar: 10 cm.

symphyseal area is ovate in dorsal/ventral views, with its most mediolaterally wide portion at the level of D4 (Fig. 4A). The lower jaw is constricted posterior to that, until the seventh dentary tooth. This is the most mediolaterally narrow part of the mandible, which

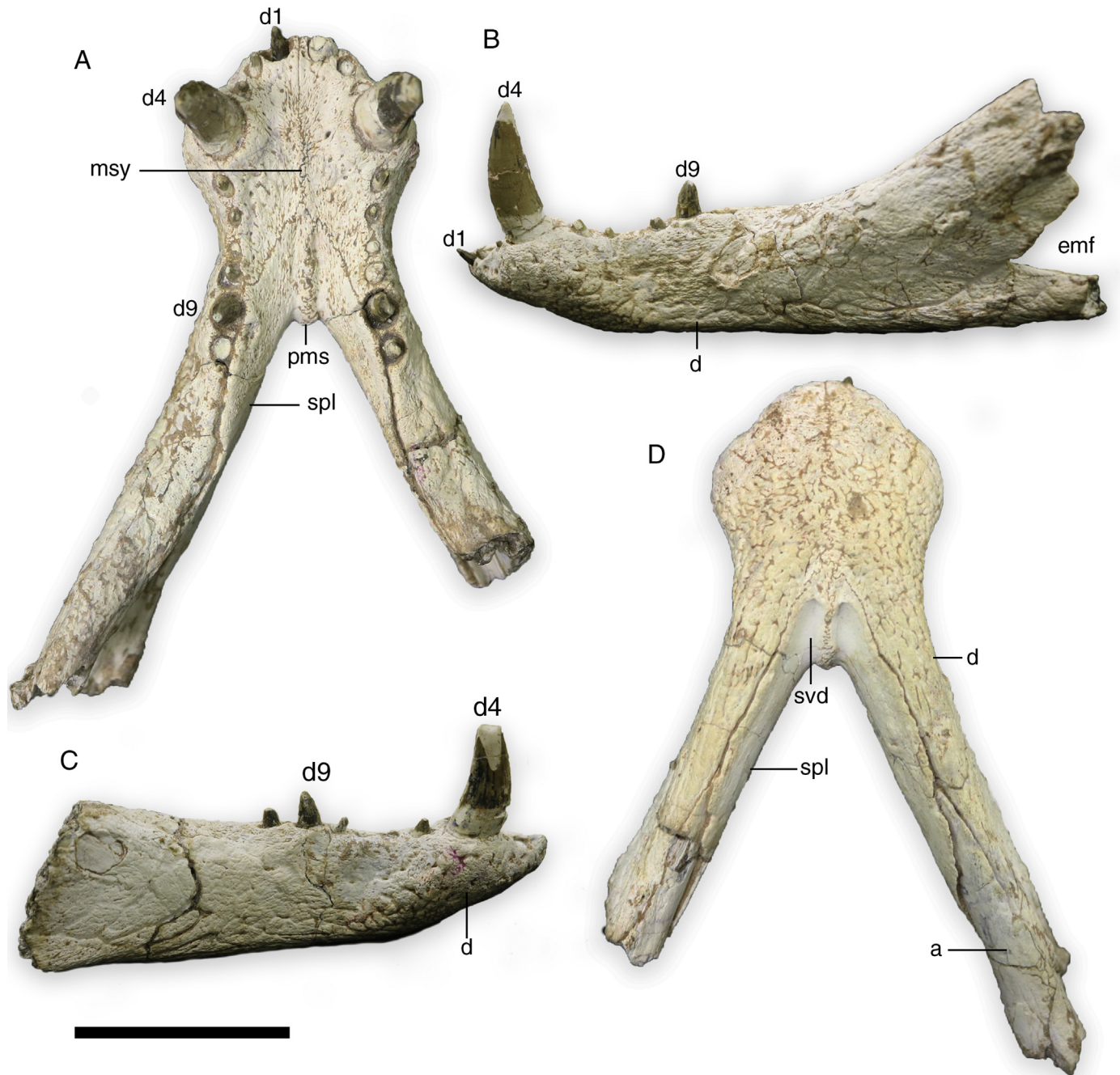
starts diverging posterior to that. In lateral view, the symphyseal area is dorsally projected, as typical of baurusuchids, whereas the dorsal margin of the mandibular rami gets conspicuously inclined dorsally as it approaches the external mandibular fenestra.



When the skull is articulated, it is possible to notice that the inclination of the ventral margin of the jugal fits that of the mandible (Fig. 2E). This area also bears a longitudinal sulcus, positioned dorsal to the fenestra. In dorsal view, the medial portion of the symphyseal area is also ornamented and the suture with the antimere is slightly bulged. The ventral surface of the dentary is as ornamented as the lateral, with the medial suture with the splenial and angular clearly seen.

**Splenial.** Both splenials are completely preserved. The splenial comprises in a thin bone, located at the anteromedial portion of the mandible, contacting the dentary anterior and laterally, and the angular posteriorly. The posterior margin of the splenial forms

the anterior border of the internal mandibular fenestra and the medial wall of the Meckelian canal. The splenial is only ornamented in the dorsal portion of its medial surface, where a bulged suture with its antimere is present in the symphyseal area. This suture ends posteriorly in a peg-like protuberance (Fig. 4A). In ventral view, lateral to the symphysis, each splenial bears an anteroposteriorly directed shallow sulcus (Figs. 4D, 5D). The ventral extension of this sulcus, at the posterior face of the symphyseal area, is deeper than the inter-splenial suture. A large, anteroposteriorly elongated *intramandibularis oralis* foramen perforates the medial surface of the splenial, slightly posterior to the peg-like protuberance.



**Fig. 4.** Mandible of *Campinasuchus dinizi* UFRJ DG 402-R in **A**, dorsal; **B**, left lateral; **C**, right lateral; and **D**, ventral views. a, angular; d, dentary; d1-d9, dentary teeth; emf, external mandibular fenestra; msy, mandibular symphysis; pms, peg-like projection of mandibular symphysis; spl, splenial; svd, splenial ventral depression. Scale bar: 10 cm.

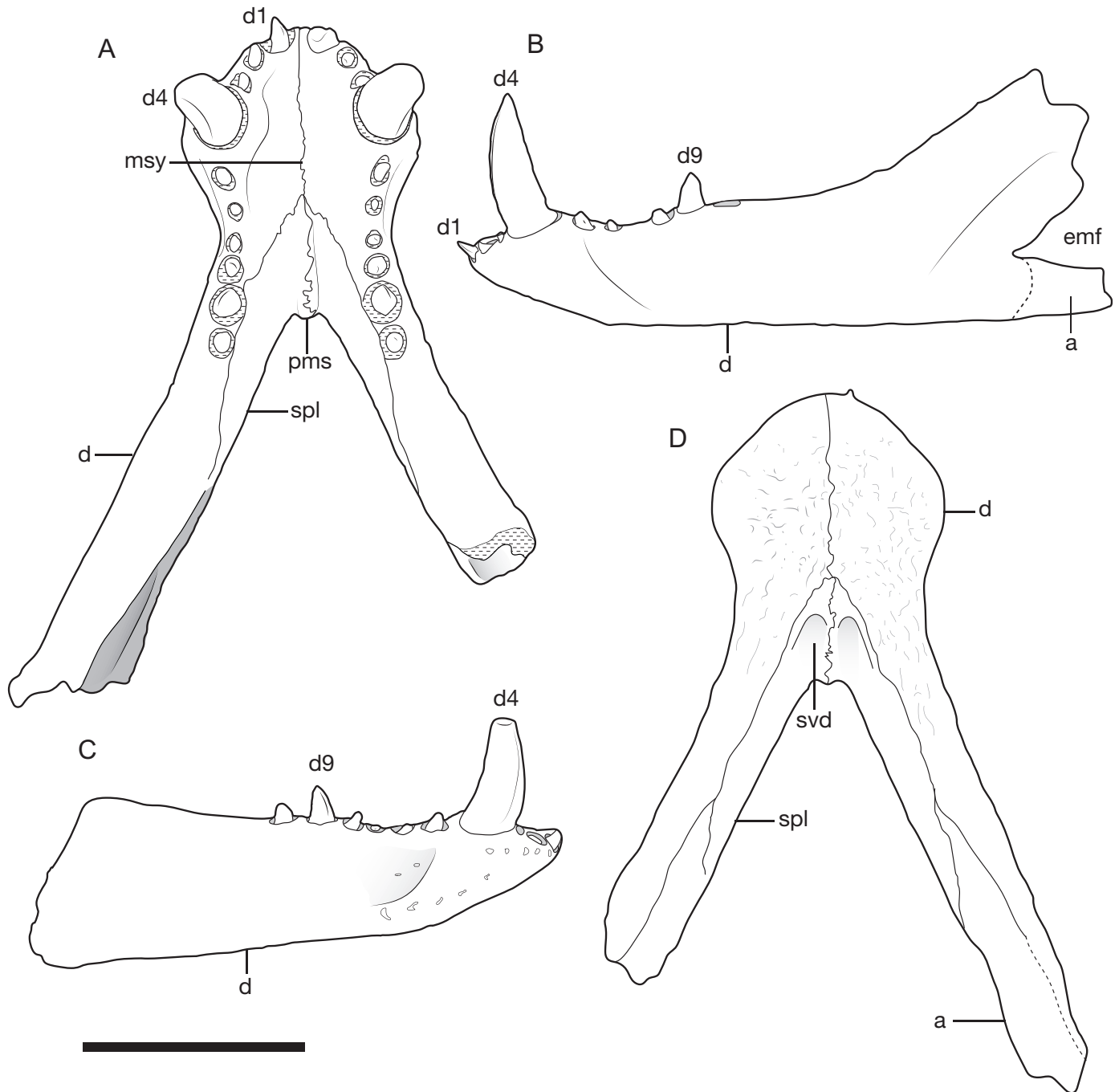
**Angular.** Only the anteriormost portion of both angulars are preserved. This part of the bone contacts the splenial medially and the dentary laterally (Fig. 5D). It has a tubular shape, forming the floor of the Meckelian canal, which extends anteriorly between the dentary and the splenials.

5.2. Dentition

The premaxilla possesses four teeth (pm1-4), the crowns of which are slightly curved posteriorly on their apicalmost portion, with serrated distal and mesial carinae. Both pm1 are preserved

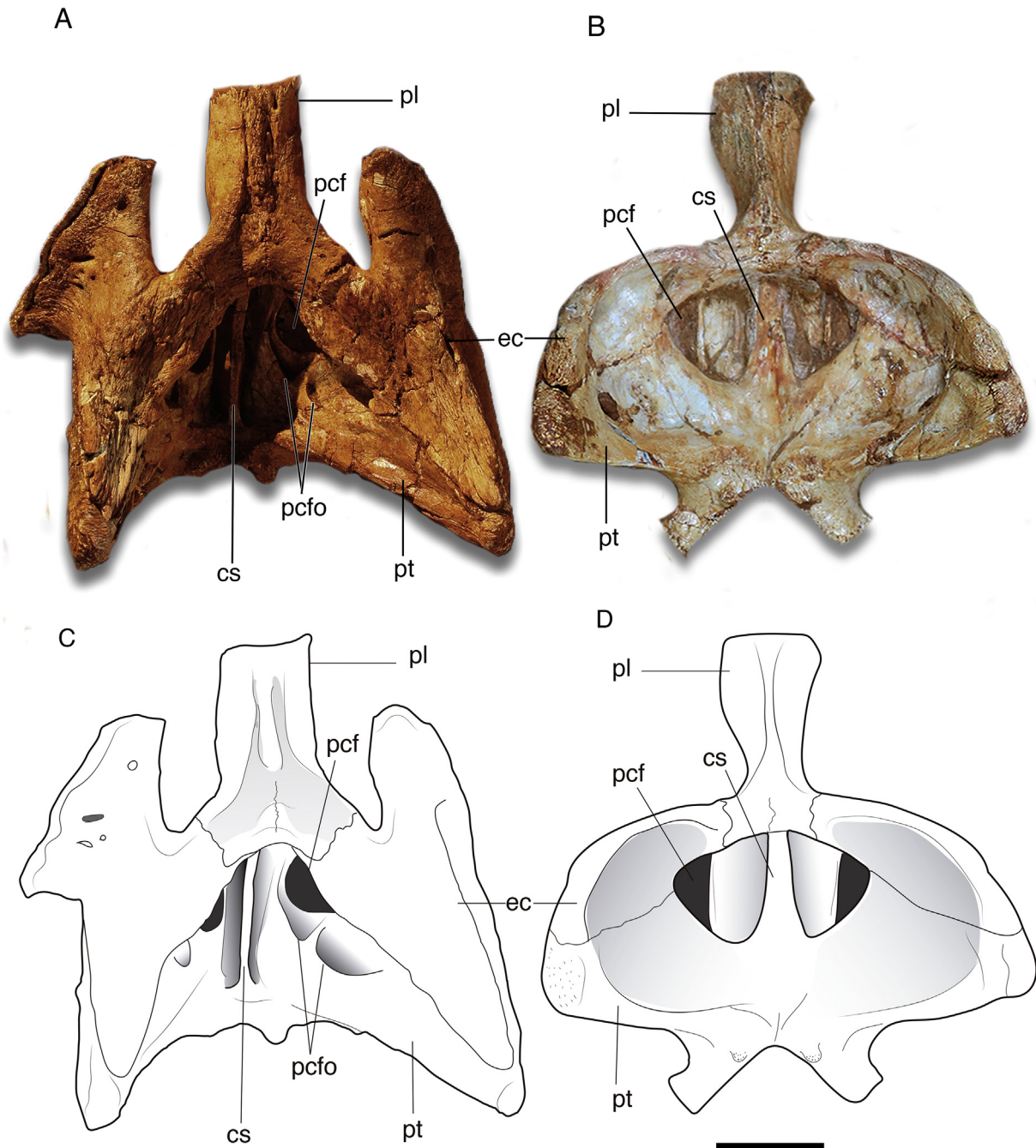
and positioned right below the base of nasal septum. The remaining premaxillary tooth crowns are broken, but it is possible to notice that the teeth gradually increase in size until they reach the hypertrophied pm3. On the other hand, pm4, located at the anterior margin of the premaxilla-maxilla notch, is the smallest premaxillary tooth (Fig. 2A).

The maxilla bears five teeth (m1-5), all also with crowns posteriorly curved on their apicalmost portion and with serrated distal and mesial carinae. M1 is the smallest of those teeth, positioned on the posterior border of the premaxilla-maxilla notch (Figs. 2A, 3A). In occlusion, its tip aligns to the posterior portion of the alveolus of



**Fig. 5.** Schematic drawings of the mandible of *Campinasuchus dinizi* UFRJ DG 402-R in **A**, dorsal; **B**, left lateral; **C**, right lateral; and **D**, ventral views. a, angular; d, dentary; d1-d9, dentary teeth; emf, external mandibular fenestra; msy, mandibular symphysis; pms, peg-like protuberance of mandibular symphysis; spl, splenial; svd, splenial ventral depression. Scale bar: 10 cm.





**Fig. 6.** Comparison between the choanal region of Baurusuchidae subgroups. **A**, Pissarrachampsinae (*Pissarrachampsia sera*, LPRP 0019); **B**, Baurusuchinae (*Aphaurosuchus escharafacies*, LPRP 0697). **C**, schematic drawing LPRP 0019 and **D**, LPRP 0697 respectively. cs, choanal septum; ec, ectopterygoid; pcf, parachoanal fenestra; pcfo, parachoanal fossae; pl, palatine; pt, pterygoid. Scale bar: 5 cm.

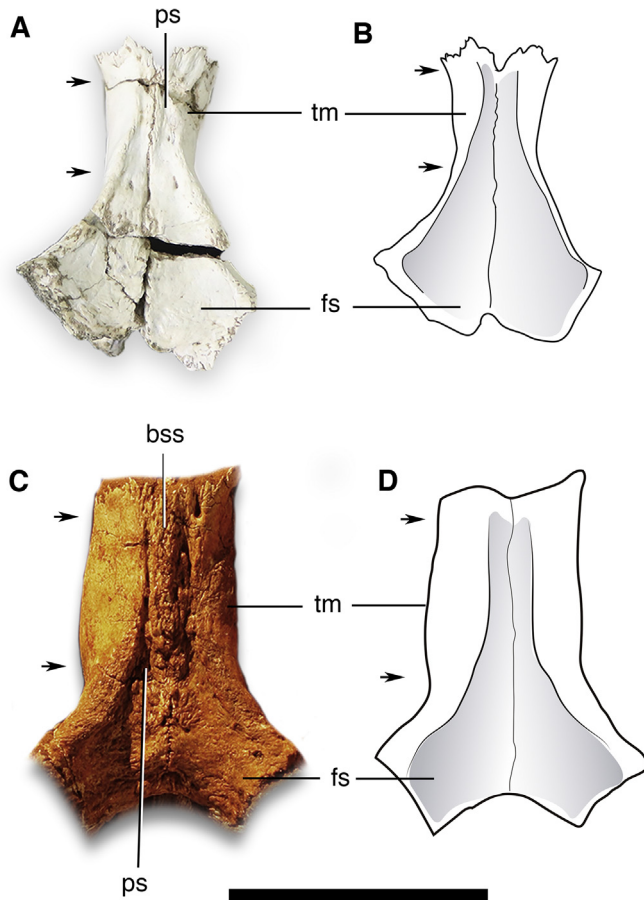
the fourth dentary tooth (d4). The maxillary dentition also increases in size posteriorly, with m2 almost three times longer than m1, and m3 representing a conspicuously hypertrophied tooth, extending in occlusion until the ventral border of the dentary. M4 is in almost of the same size as m2, as is m5 in relation to m1.

The dentary bears ten teeth (d1-d10), also with the ziphodont configuration, with three of them being the largest of the series. D1 is procumbent (*sensu* Godoy, 2011) forming an angle of ca. 45° to the general tooth line (Fig. 4B). In occlusion, it is inserted on an anteroposterioly elongated depression in the premaxilla, between pm1 and pm2. D4 is the hypertrophied caniniform tooth that in occlusion inserts in the premaxilla-maxilla notch, extending

dorsally until the dorsal surface of the nasal (Fig. 2E). D9 is located in a dorsally raised area of the dentary and inserts in a posteromedial occlusal pit of the maxilla. The remaining teeth are smaller and of almost the same size (Figs. 4A, 5A).

## 6. Discussion

In the original definition of Pissarrachampsinae, Montefeltro et al. (2011) listed key features for the identification of the group and its differentiation from Baurusuchinae (e.g., posterior portion of the nasal bearing a rugose broad depression, approximation of the prefrontals along their medial edges anteriorly, and presence of



**Fig. 7.** Comparison of the palatine morphology of pissarrachampsines in ventral view. **A**, palatine of *Campinasuchus dinizi* (UFRJ DG 402-R) and **B**, schematic drawing. **C**, palatine of *Pissarrachampsia sera* (LPRP 0019) and **D**, schematic drawing. Arrows indicate the extension of the tubular margin. bss, bulged sagittal suture; fs, flattened surface; ps, parasagittal sulcus; ts, tubular margin. Scale bar: 5 cm.

a midline longitudinal depression on anterior portion of the frontal). More recently, following Nascimento (2014), Darlim et al. (2021) provided a revised definition of the choanal pattern of the group, some of the main features of which include in a pair of conspicuous longitudinal row of foramina, two parasagittal sulci on the ventral surface of the palatine, ectopterygoid and pterygoid wings posteriorly directed, ectopterygoid mediolaterally flattened, pterygoid forming parachoanal fossae, and choanal septum lateromedially thin (Fig. 6). Although only partially preserved, several of those diagnostic traits are seen in UFRJ DG 402-R, including a rugose depression on the posterior portion of the nasals, conspicuous ventral palatine sulci, ectopterygoid mediolaterally flattened and posteriorly directed ectopterygoid, supporting its identification as a pissarrachampsine.

Among pissarrachampsines, the fragmentary nature of *Wargosuchus australis* and scarce overlapping of parts between UFRJ DG 402-R and the Argentinean taxon prevented their comparison. In relation to *Pissarrachampsia sera*, UFRJ DG 402-R does not have its ridged jugal-ectopterygoid suture exposed in lateral view, which is instead restricted the medial portion of the jugal. Also, the lateral surface of the latter bone is not pierced by small foramina as in *Pissarrachampsia sera*. Additionally, the number of maxillary teeth could also distinguish those taxa, given that *Pissarrachampsia sera* was described as having four maxillary teeth, the second of which being the largest. However, given that the anteriormost portion of

the maxilla (i.e., forming the posterior margin of the premaxilla-maxilla notch) is damaged in both the holotype (LPRP/USP 0019) and paratype (LPRP/USP 0018) of *Pissarrachampsia sera*, we do not consider this as reliable evidence to differentiate UFRJ DG 402-R from that taxon.

Our comparative analysis also revealed that previously proposed autapomorphies of *Campinasuchus dinizi* (i.e., conspicuously large third maxillary and fourth dentary teeth and an anteroposteriorly elongated depression on the palatine) are actually shared with *Pissarrachampsia sera* (LPRP 0049, see Godoy et al., 2018, Fig. 1) and not diagnostic of the former species. However, we propose that a short anterior tubular area and a large flattened ventral surface of the palatine is unique to *Campinasuchus dinizi* (Fig. 7A,B), whereas a more tubular-shaped palatine, with a rounded ventrolateral surface that is more anteroposteriorly expanded, is typical of *Pissarrachampsia sera* (holotype LPRP/USP 0019; Fig. 7C,D). Yet, it is important to highlight that even having a longer tubular portion, the palatine of *Pissarrachampsia sera* still differs from those of Baurusuchinae (sensu Darlim et al., 2021) by having marked parasagittal sulci and not being medially convergent (e.g., not forming a lateromedially constricted palatine; Fig. 6).

Based on the above observations, we also suggest the reassignment of some previously published specimens of both pissarrachampsines species. LPRP/USP 0018 assigned to *Pissarrachampsia sera* by Montefeltro et al. (2011, Figure 11) has a conspicuously flattened ventral surface of the palatine similar to that of *Campinasuchus dinizi*, whereas CPPLIP 1236, one of the paratypes of *Campinasuchus dinizi* (Carvalho et al., 2011, Figure 5), preserves only part of the palatine, but clearly with more conspicuously rounded/bulged lateral margins, medially restricting the parasagittal sulci, as seen in the holotype of *Pissarrachampsia sera* (Fig. 7C). Hence, LPRP/USP 0018 and CPPLIP 1236 are here tentatively reassigned respectively to *Campinasuchus dinizi* and *Pissarrachampsia sera*, but it is clear that more comprehensive studies are needed to understand the morphological variation of the baurusuchids of the Adamantina/Vale do Rio do Peixe Formation in Minas Gerais.

Additionally, the specimen URC 73, consisting of a fragmentary cranium and mandible, referred as *Stratiotosuchus maxhechti* by Pinheiro et al. (2008) also has morphological similarities with pissarrachampsines. As previously noted by Montefeltro et al. (2011), the specimen presents some differences in relation to the holotype of *Stratiotosuchus maxhechti*, such as a foramen between the palpebrals, a small posttemporal fenestra and a non-ridged choanal septum, morphological features that can be related to taphonomic distortions and/or ontogenetic variation (Montefeltro et al., 2011, supplementary material). Although the specimen was not analyzed first-hand in the present work, we agree that URC 73 may not represent a *Stratiotosuchus maxhechti* specimen, and also highlight several features in common between URC 73 and pissarrachampsines (sensu Darlim et al., 2021): palatine presenting a flattened ventral surface with two conspicuous parasagittal sulci, posteriorly oriented and mediolaterally flattened ectopterygoid, conspicuously mediolaterally thin choanal septum, and post-choanal portion of the pterygoid anteroposteriorly short and dorsally recessed at the contact with the parabasisphenoid.

### 6.1. Paleogeographic distribution of Bauru Basin baurusuchids

Based on the Santonian age of the Argentinean pissarrachampsine *Wargosuchus australis*, Montefeltro et al. (2011) suggested that the Pissarrachampsinae-bearing deposits of the Adamantina/Vale do Rio do Peixe Formation in Minas Gerais could be older than those in São Paulo. Indeed, all Bauru Basin baurusuchines come from São Paulo, whereas pissarrachampsines were until now restricted to Minas Gerais. Yet, UFRJ DG 402-R shows that

the latter clade also occurs in Bauru Basin rocks of São Paulo, in a site (Fazenda São José) nearby the most diverse site for Baurusuchinae (Fazenda Buriti) and within the same geological context, revealing the sympatric occurrence of both major Baurusuchidae groups (Fig. 1).

The joint occurrence of pissarrachampsines and baurusuchines in São Paulo falsifies the hypothesis that those groups were chronologically separated, weakening the assumption that the deposits of the Adamantina/Vale do Rio do Peixe Formation in Minas Gerais are older than those in São Paulo. Radioisotopic ages for the Pissarrachampsinae-bearing deposits in Minas Gerais and Argentina, together with the discovery of better preserved Argentinean baurusuchid material will be important to further test these proposals and to better understand the past distribution of baurusuchids. For now, the tentative Campanian dating of the Adamantina/Vale do Rio do Peixe Formation by Castro et al. (2018), suggests that it is slightly younger than the Santonian Bajo de La Carpa Formation. This could suggest a more southern origin for Baurusuchidae and their later north-western dispersion. Such pattern agrees with the inferred tectonic dynamics of South America during the Cretaceous, where drainage connections between southern Argentina and central South America, from Aptian to the Late Cretaceous, probably allowed the interchange of the crocodyliform fauna (Carvalho et al., 2010). Yet, it is important to highlight that paleobiogeographic reconstructions, including the identification of ancestral areas and dispersal events, could be biased by several factors, such as the uncertain age of the Adamantina/Vale do Rio do Peixe Formation, the high endemism of Baurusuchinae, restricted to São Paulo state, and the high diversity of baurusuchids in the Adamantina/Vale do Rio do Peixe Formation (Celis et al., 2020) in comparison with the more fragmentary baurusuchid record in the Neuquén Basin, Argentina (Leardi et al., 2018).

## 7. Conclusions

The new specimen described here (UFRJ DG 402-R) is recognized as a Pissarrachampsinae, specifically as *Campinasuchus dinizi*, due to the presence of a ventrally flattened and posteriorly directed ectopterygoid, palatines ventrally flattened with two parasagittal sulci, short anterolateral tubular margins and a large flattened ventral surface of the palatine, and a depressed posterior portion of the nasal dorsal surface. This identification resulted from a short review of the baurusuchid palatine morphology, allowing the differentiation of *Campinasuchus dinizi* from *Pissarrachampsina sera* and a tentative reassignment of previously published specimens of both species. UFRJ DG 402-R represents the first record of Pissarrachampsinae in the Adamantina/Vale do Rio do Peixe Formation of São Paulo. This demonstrates that, during the Late Cretaceous, pissarrachampsines lived together with baurusuchines in the region, without any noticeable palaeobiogeographic barrier.

## Acknowledgments

We want to thank João Tadeu Arruda and Antonio Celso de Arruda Campos (in memoriam) for the efforts in the field work. Gustavo Darlim thanks Felipe Muniz, Julian Silva, and Thiago Facini, for helping during the visits to paleontological collections, and for Thiago Marinho (CCPLIP) and Rafael Costa (DGM) for allowing the study of baurusuchid fossils for comparison. Finally, we thank the reviewers Ane de Celis and Felipe C. Montefeltro for the time invested and for the constructive comments that definitely improved the manuscript. The research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) and by Conselho Nacional de Desenvolvimento

Científico e Tecnológico (CNPq). Gustavo Darlim is funded by FAPESP [2019/06311-4].

## References

- Barrios, F., Bona, P., Carabajal, A.P., Gasparini, Z., 2018. Re-description of the cranio-mandibular anatomy of *Notosuchus terrestris* (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Patagonia. *Cretaceous Research* 83, 3–39.
- Batezelli, A., 2015. Continental systems tracts of the Brazilian Cretaceous Bauru Basin and their relationship with the tectonic and climatic evolution of South America. *Basin Research* 29, 1–25.
- Batezelli, A., Gomes, N.S., Perinotto, J.A.D.J., 2005. Petrografia e evolução diagenética dos arenitos da porção norte e nordeste da Bacia Bauru (Cretáceo Superior). *Revista Brasileira de Geociências* 35, 311–322.
- Benton, M.J., Clark, J.M., 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton, M.J. (Ed.), *The phylogeny and classification of the tetrapods*, 1. Clarendon Press, Oxford, pp. 295–338.
- Campos, D.A., Suarez, J.M., Riff, D., Kellner, A.W.A., 2001. Short note on a new Baurusuchidae (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil. *Boletim do Museu Nacional, Nova Série, Geologia* 57, 1–7.
- Carvalho, I.S., Campos, A.C.A., Nobre, P.H., 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research* 8, 11–30.
- Carvalho, I.S., Gasparini, Z.B., Salgado, L., Vasconcellos, F.M., da Silva Marinho, T., 2010. Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 297, 252–262.
- Carvalho, I.S., Teixeira, V.P., Ferraz, M.L., Ribeiro, L.C.B., Martinelli, A.G., Neto, F.M., 2011. *Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid (Crocodyliformes) from the Bauru Basin, Brazil. *Zootaxa* 287, 19–42.
- Castro, M.C., Goin, F.J., Ortiz-Jaureguizar, E., Vieytes, E.C., Tsukui, K., Ramezani, J., Batezelli, A., Marsola, J.C.A., Langer, M.C., 2018. A Late Cretaceous mammal from Brazil and the first radioisotopic age for the Bauru Group. *Royal Society of Open Science* 5, 180482.
- Celis, A., Narváez, I., Arcucci, A., Ortega, F., 2020. Lagerstätte effect drives notosuchian palaeodiversity (Crocodyliformes, Notosuchia). *Historical Biology* 1–10.
- Cotts, L., Pinheiro, A.E.P., Marinho, T.S., Carvalho, I.S., Di Dario, F., 2017. Postcranial skeleton of *Campinasuchus dinizi* (Crocodyliformes, Baurusuchidae) from the Upper Cretaceous of Brazil, with comments on the ontogeny and ecomorphology of the species. *Cretaceous Research* 70, 163–188.
- Darlim, G., Montefeltro, F.C., Langer, M.C., 2021. 3D skull modelling and description of a new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the Late Cretaceous (Bauru Basin) of Brazil. *Journal of Anatomy* 1–41.
- Dias-Brito, D., Musacchio, E.A., de Castro, J.C., Maranhão, M.S.A.S., Suárez, J.M., Rodrigues, R., 2001. Grupo Bauru: uma unidade continental do Cretáceo no Brasil - concepções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. *Revue de Paléobiologie* 20, 245–304.
- Fernandes, L.A., 2004. Mapa litoestratigráfico da parte oriental da Bacia Bauru (PR, SP, MG), escala 1: 1.000. 000. *Boletim Paranaense de Geociências* 55.
- Fernandes, L.A., Coimbra, A.M., 1996. Bacia Bauru (Cretáceo superior, Brasil). *Anais da Academia Brasileira de Ciências* 68, 195–205.
- Fernandes, L.A., Coimbra, A.M., 2000. Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). *Revista Brasileira de Geociências* 30, 717–728.
- Fernández-Dumort, M.L., Bona, P., Pol, D., Apesteguía, S., 2020. New anatomical information on *Araripesuchus buittreraensis* with implications for the systematics of Uruguasuchidae (Crocodyliformes, Notosuchia). *Cretaceous Research* 113, 104494.
- Fiorelli, L.E., Leardi, J.M., Martín, E., Pol, D., Basile, G., Grellet-Tinner, G., 2016. A new Late Cretaceous crocodyliform from the western margin of Gondwana (La Rioja Province, Argentina). *Cretaceous Research* 60, 194–209.
- Gasparini, Z.B., 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo Infraorden de los Mesosuchia (Crocodylia). *Ameghiniana* 8, 83–103.
- Gasparini, Z., 1972. Los Sebecosuchia (Crocodylia) del territorio argentino. Consideraciones sobre su "status" taxonómico. *Ameghiniana* 9, 23–34.
- Gobbo-Rodrigues, S.R., Petri, S., Bertini, R.J., 1999. Ocorrências de ostrácodes na Formação Araçatuba do Grupo Bauru, Cretáceo Superior da Bacia do Paraná e possibilidades de correlação com depósitos isócronos argentinos - parte I: Família Hylocypridae. *Acta Geologica Leopoldensia* 23, 3–13.
- Godoy, P.L., 2011. Evolução dos dentes procumbentes em Mesoeucrocodylia, com a descrição da mandíbula de um possível Baurusuchidae juvenil (Crocodyliformes, Mesoeucrocodylia). Universidade de São Paulo, Monografia.
- Godoy, P.L., Montefeltro, F.C., Norell, M.A., Langer, M.C., 2014. An additional Baurusuchid from the Cretaceous of Brazil with evidence of interspecific predation among crocodyliformes. *PLoS One* 9, e97138.
- Godoy, P.L., Ferreira, G.S., Montefeltro, F.C., Vila-Nova, B.C., Butler, R.J., Langer, M.C., 2018. Evidence for heterochrony in the cranial evolution of fossil crocodyliforms. *Palaeontology* 61, 543–558.
- Leardi, J.M., Pol, D., Gasparini, Z., 2018. New Patagonian baurusuchids (Crocodylomorpha; Notosuchia) from the Bajo de la Carpa Formation (Upper Cretaceous; Neuquén, Argentina): New evidences of the early sebecosuchian diversification in Gondwana. *Comptes Rendus Palevol* 17 (8), 504–521.
- Marinho, T.S., Iori, F.V., Carvalho, I.S., Vasconcellos, F.M., 2013. *Gondwanasuchus scabrosus* gen. et sp. nov., a new terrestrial predatory crocodyliform



- (Mesoeucrocodylia: Baurusuchidae) from the Late Cretaceous Bauru Basin of Brazil. *Cretaceous Research* 44, 104–111.
- Martinelli, A.G., Pais, D.F., 2008. A new baurusuchid crocodyliform (Archosauria) from the Late Cretaceous of Patagonia (Argentina). *Comptes Rendus Palevol* 7, 371–381. <https://doi.org/10.1016/j.crpv.2008.05.002>.
- Martinelli, A.G., Riff, D., Lopes, R.P., 2011. Discussion about the occurrence of the genus *Aelosaurus* Powell 1987 (Dinosauria, Titanosauria) in the Upper Cretaceous of Brazil. *Gaea* 7, 34–40.
- Montefeltro, F.C., Larsson, H.C.E., Langer, M.C., 2011. A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the late cretaceous of Brazil and the phylogeny of Baurusuchidae. *PloS One* 6, e21916. <https://doi.org/10.1371/journal.pone.0021916>.
- Montefeltro, F.C., Lautenschlager, S., Godoy, P.L., Ferreira, G.S., Butler, R.J., 2020. A unique predator in a unique ecosystem: modelling the apex predator from the Late Cretaceous crocodyliform-dominated fauna in Brazil. *Journal of Anatomy* 237, 323–333.
- Nascimento, P.M., 2014. Revisão da família Baurusuchidae e seu posicionamento filogenético dentro do clado Mesoeucrocodylia. Universidade de São Paulo.
- Nascimento, P.M., Zaher, H., 2010. A new species of *Baurusuchus* (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Brazil, with the first complete postcranial skeleton described for the family Baurusuchidae. *Papéis Avulsos de Zoologia* 50, 323–361.
- Pinheiro, A.E.P., Bertini, R.J., Andrade, M.D., Neto, R.M., 2008. A new specimen of *Stratiotosuchus maxhechti* (Baurusuchidae, Crocodyliformes) from the Adamantina Formation (Upper Cretaceous), Southeastern Brazil. *Revista Brasileira de Paleontologia* 1, 37–50.
- Pol, D., Nascimento, P.M., Carvalho, A.B., Riccomini, C., Pires-Domingues, R.A., Zaher, H., 2014. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PloS One* 9, e93105.
- Price, L.I., 1945. A new reptile from the Cretaceous of Brazil. *Notas Preliminares e Estudos. Divisão de Geologia e Mineralogia. Ministério da Agricultura. Rio de Janeiro, Brasil* 25, 1–8.
- Ruiz, J.V., Bronzati, M., Ferreira, G.S., Martins, K.C., Queiroz, M.V., Langer, M.C., Montefeltro, F.C., 2021. A new species of *Caipirasuchus* (Notosuchia, Sphagesauridae) from the Late Cretaceous of Brazil and the evolutionary history of Sphagesauria. *Journal of Systematic Palaeontology* 1–23.
- Santucci, R.M., Bertini, R.J., 2001. Paleogeographical and biochronological distributions of the Bauru Group titanosaurids (Saurischia, Sauropoda) Upper Cretaceous of southeastern Brazil. *Revista Brasileira de Geociências* 31, 307–314.
- Sereno, P.C., Larsson, H.C.E., Sidor, C.A., Gado, B., 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294, 1516–1519.
- Soares, P.C., Landim, P.M., Fulfaro, V.J., Sobreiro Neto, A.F., 1980. *Ensaio De Caracterização Estratigráfica Do Cretáceo No Estado De São Paulo: Grupo Bauru*. *Revista Brasileira de Geociências* 10, 177–185.
- Wilson, J.A., Malkani, M.S., Gingerich, P.D., 2001. New crocodyliform (Reptilia, Mesoeucrocodylia) from the Upper Cretaceous Pab Formation of Vitakri, Balochistan (Pakistan), vol. 30. Contributions from the Museum of Paleontology of the University of Michigan, pp. 321–336.
- Whetstone, K.N., Whybrow, P.J., 1983. A “cursorial” crocodylian from the Triassic of Lesotho (Basutoland), southern Africa, vol. 106. University of Kansas, pp. 1–37. Occasional papers of the museum of natural history.
- Witmer, L.M., 1995. Homology of facial structures in extant archosaurs (birds and crocodylians), with special reference to paranasal pneumaticity and nasal conchae. *Journal of Morphology* 225, 269–327.
- Woodward, A.S., 1896. On two mesozoic crocodylians, *Notosuchus* (genus novum) and *Cynodontosuchus* (gen. nov.) from the red sandstones of Territory of Neuquén (Argentina). *Anales del Museo de La Plata*, pp. 1–20.
- Zaher, H.D., Langer, M.C., Fara, E., Carvalho, I.S., Arruda, J.T., 2003. A mais antiga serpente (Anilioidea) brasileira: Cretáceo Superior do Grupo Bauru, General Salgado, SP. *Paleontologia em Destaque* 44, 50–51.