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Gondwanasuchus scabrosus gen. et sp. nov., a new terrestrial predatory crocodyliform (Mesoeucrocodylia: Baurusuchidae) from the Late Cretaceous Bauru Basin of Brazil

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ABSTRACT

Baurusuchids are among the most common and diverse crocodyliform fossils from the Late Cretaceous Bauru Basin of Brazil. This inland continental basin was the habitat of a rich crocodyliform fauna containing five mesoeucrocodylian families, of which the Baurusuchidae represents highly specialized predatory crocodyliforms of terrestrial habits as indicated by their dental, cranial, and postcranial features. The large size they achieved, together with likely predatory adaptations, would suggest they competed and occupied theropod ecological niches in the Bauru Basin. Here we describe *Gondwanasuchus scabrosus* gen. et sp. nov., a medium-sized baurusuchid with a strongly laterally compressed skull, bearing unique dentition with deep apicobasal sulci and probably well-developed binocular vision. The cranial and dental features in *Gondwanasuchus* suggest that this active predator would have fed on small vertebrates and took the role of small theropods in terrestrial guild. *Gondwanasuchus* is the most distinctive baurusuchid known to date and enriches the knowledge on these important Gondwanan terrestrial predatory crocodyliforms.

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1. Introduction

The Late Cretaceous continental Bauru Basin of southeastern Brazil has yielded a rich crocodyliform fauna. Five mesoeucrocodylian families are recognized from the 300 m-thick sediments of the Adamantina and Marília formations: baurusuchids, sphagesaurids, notosuchids, peirosaurids, and trematochampsids (e.g., Price, 1945, 1950, 1955; Carvalho and Bertini, 1999; Carvalho et al., 2005, 2007, 2010a, 2011; Marinho and Carvalho, 2009; Iori and Carvalho, 2009, 2011). Among these, the Baurusuchidae is the most diverse and abundant crocodyliform family found in the Adamantina Formation (*sensu* Paula e Silva, 2003; Paula e Silva et al., 2005) that includes six species: (1) *Baurusuchus pachecoi* Price, 1945; (2) *B. salgadoensis* Carvalho, Campos & Nobre, 2005; (3) *B. albertoi* Nascimento and Zaher, 2010; (4) *Stratiotosuchus maxhechti* Campos, Suarez, Riff & Kellner, 2001; (5) *Campinasuchus dinizi* Carvalho, Teixeira, Ferraz, Ribeiro, Martinelli, Neto, Sertich,

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0195-6671/\$ — see front matter \odot 2013 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.cretres.2013.03.010 Cunha, Cunha & Ferraz, 2011; and (6) *Pissarrachampsa sera* Montefeltro, Larsson & Langer, 2011.

Baurusuchids are terrestrial crocodyliforms regarded as active cursorial predators, based on dental, cranial, and postcranial features (Price, 1945; Riff and Kellner, 2011; Vasconcellos and Carvalho, 2007). The distribution of these animals during the Late Cretaceous is exclusively Gondwanan, with *Cynodontosuchus rothi* and *Wargosuchus australis* from the Argentinean Bajo de La Carpa Formation (Neuquén Basin), *Pabwehshi pakistanensis* from the Pab Formation of Pakistan plus the Brazilian species (Woodward, 1896; Wilson et al., 2001; Martinelli and Pais, 2008; Carvalho et al., 2011; Montefeltro et al., 2011).

Here we describe a new baurusuchid based on a well-preserved partial skull and mandible from the Adamantina Formation (Turonian–Santonian). This material was found in close association with a large specimen of *Baurusuchus salgadoensis*, and at the same stratigraphic horizon of *Armadillosuchus arrudai* Marinho and Carvalho, 2009 (Marinho et al., 2011), showing the contemporaneous occurrence of these crocodyliform taxa (Fig. 1). The new taxon represents the most distinctive baurusuchid known to date in







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Fig. 1. Lithostratigraphic map of the eastern part of the Bauru Basin (modified from Fernandes and Coimbra, 2000), and stratigraphic profile of the Adamantina Formation at the Fazenda Buriti Paleontological Site, General Salgado County, Brazil.

that it displays a strongly laterally compressed skull, dentition bearing deep apicobasal sulci and probably binocular vision, thus adding a new bauplan to the diversity of these Gondwanan crocodyliforms.

The institutional abbreviations used in this article are as follows: UFRJ DG, Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; CPP, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Peirópolis, Uberaba, Minas Gerais, Brazil.

2. Geological setting

Gondwanasuchus was found in an outcrop of the Adamantina Formation (Turonian–Santonian of Bauru Basin; *sensu* Dias Brito et al., 2001) at Fazenda Buriti Paleontological Site, General Salgado County, Northwestern São Paulo State, Brazil (Carvalho et al., 2010b) (Fig. 1). This outcrop is composed of fine-grained sandstones and siltstones with intercalations of red oxidized mudstones, which were deposited on an extensive alluvial plain reworked by fluvial systems alongside scattered shallow ephemeral lakes in an arid or semi-arid seasonal climate (Fernandes and Coimbra, 1996; Garcia et al., 1999; Goldberg and Garcia, 2000; Fernandes and Basilici, 2009). The Bauru Basin was formed during the early breakup of Gondwana associated with the opening of the South Atlantic Ocean (Fernandes and Coimbra, 1996).

The fossil assemblage of Fazenda Buriti Paleontological Site is composed mostly by baurusuchid remains, represented by skulls, semi-articulated skeletons and complete specimens (Carvalho et al., 2010b). In addition, these outcrops have also yielded specimens of *Armadillosuchus arrudai*, anilioid snake vertebrae, invertebrate ichnofossils, and coprolites and egg remains attributed to crocodyliforms (Zaher et al., 2003; Arruda et al., 2004; Carvalho et al., 2010b; Marinho et al., 2011).

3. Systematic paleontology

Crocodyliformes Hay, 1930 (*sensu* Clark, in Benton and Clark, 1988) Mesoeucrocodylia Whetstone and Whybrow, 1983 (*sensu* Clark, in Benton and Clark, 1988) Notosuchia Gasparini, 1971 Baurusuchidae Price, 1945 Pissarrachampsinae Montefeltro, Larsson and Langer, 2011 *Gondwanasuchus* gen. nov.

Etymology: Generic name refers to the southern paleocontinent Gondwana as an allusion to the Gondwanan distribution of the Baurusuchidae, plus *souchus*, Greek for crocodile, leading to Latin, *suchus*.

Diagnosis: As for the type and only known species.

Type species: Gondwanasuchus scabrosus

Gondwanasuchus scabrosus sp. nov.

Holotype: UFRJ DG 408-R consists of well-preserved partial skull and mandible, lacking the skull roof, basicranial region and bones of the right side posterior to the anterior orbital margin (Figs. 2 and 3) and the remains of five cervical vertebrae and some associated cervical ribs.

Locality and horizon: The specimen was collected at Fazenda Buriti Paleontological Site, General Salgado County, Northwestern São Paulo State, Brazil, from the Adamantina Formation (Turonian– Santonian), Bauru Basin.

Etymology: Specific name from the Latin, *scabrosus* meaning rough due to the anteroventrally sloped palpebrals of the holotype that gives it a scabrous rough-look.

Diagnosis: Baurusuchidae with following combination of characters: an overhanging anterior portion of the rostrum containing four premaxillary teeth, which is separated from the maxilla by a deep notch for accommodating an enlarged lower tooth; heterodont dentition; five maxillary teeth; teeth with five or six wide and deep apicobasal sulci, making each tooth corrugated in crosssection; highly compressed maxillary teeth bearing finely serrated carinae; highly compressed skull and mandible; small antorbital fenestra; laterally projected slender jugal; laterally positioned postorbital; anteriorly facing orbits; rostrum sloped anteroventrally; nasal—frontal contact separating the prefrontals; dorsal margin of the jugal parallel to the palatal axis along all its length; laterally compressed mandible without lateral broadening at the symphysis at the level of the mandibular hypertrophied teeth.

4. Description

Skull

The snout represents almost half of the estimated total skull length. The skull is triangular in dorsal view, and the most peculiar feature is the extreme lateral compression observed along the sagittal axis.

The premaxilla is subquadrangular in lateral view, and bounds the external nares except for a small anterodorsal portion. Anteriorly, the premaxillae project dorsally to form a delicate internarial bar that is in contact with the anteriormost projection of the nasals. The external nares are subcircular and laterally positioned, bounded anteriorly, ventrally and posteriorly by the premaxilla and anterodorsally by the nasal. Posteriorly, between the premaxilla and maxilla is the notch where a hypertrophied mandibular tooth (possibly the fourth) is housed during occlusion. The external premaxilla-maxilla suture is located dorsal to the notch, that is small and posterodorsally oriented. The ventral margin of the premaxilla is parallel to the palatal axis, while its dorsal margin is slightly sloped anteroventrally and contacts the nasal up to the external nares. The posterodorsal extremity of the premaxilla is slightly rugose as are the maxilla and nasal; the ventral border of the premaxilla is smooth and shows two neurovascular foramina in association with the third and fourth alveoli. On each premaxilla four alveoli, with teeth of circular cross-section and distally curved, are preserved.

The maxilla is deep, its anterior border is almost perpendicular to its ventral margin; the dorsal margin is sloped anteroventrally, and the posterior maxillary margin is oriented anterodorsally at an angle of almost 45°, making the maxilla subtriangular. The maxilla contacts the jugal along its anteroventral region, posterior to the lacrimal contact, and contacts the ectopterygoid ventrally of the jugal. The contact of the maxilla and lacrimal is dorsal of the maxilla-jugal contact and presents a small antorbital fenestra near the middle of its depth. The antorbital fenestra is oval with its major axis anterodorsally oriented. Posteriorly, near the antorbital fenestra, the maxillae show concave regions in its lateral surface that extend to the lacrimals (Figs. 1D and 2D). The maxilla is gently rugose on its anterodorsal portion and is smoother around the antorbital fenestra. The ventral maxillary region is smooth and bears small neurovascular foramina in association with its alveoli. Despite the mandible's occlusion, it is possible to observe that the



Fig. 2. Holotype of Gondwanasuchus scabrosus gen. nov. et sp. nov. (UFRJ DG 408-R) in lateral view (A), dorsal view (B), palatal view (C) and anterior view (D).

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Fig. 3. Schematic drawings of holotype of *Gondwanasuchus scabrosus* gen. nov. et sp. nov. (UFRJ DG 408-R) in lateral view (A), dorsal view (B), palatal view (C) and anterior view (D). Anatomical abbreviations: An: Angular; anf: antorbital fenestra; Ap: Anterior palpebral; D: Dentary; en: external nares; F: Frontal; itf: infratemporal fenestra; J: Jugal; L: Lacrimal; M: Maxilla; mf: mandibular fenestra; N: Nasal; or: orbit; Pa: Palatine; Pfr: Prefrontal; Pm: Premaxilla; Po: Postobital; Pp: Posterior palpebral; Pt Pterygoid; Qj: Quadratojugal; San: Surangular; sf: supraorbital fenestra; sof: suborbital fenestra; Sp: Splenial.

palatal region of the maxillae is narrow and convex anteriorly to the suborbital fenestrae, with a medial groove between them. Each maxilla bears five alveoli with all teeth preserved except the second left maxillary tooth.

The dorsal region of the lacrimal forms a laterally extended shelf (Fig. 2D) that contacts the nasal and prefrontal, and supports the anterior palpebral that overlaps it. The lacrimal contact with the anterior process of the jugal is not sutured. The lacrimal is not ornamented laterally, and the lacrimal foramen lies below the lacrimal shelf. In anterior view, the lacrimal is dorsoventrally curved because of the concavity of the anterior orbital wall (Fig. 2D).

The jugal is slender and long, extending from the anterior orbital edge to the posterior corner of the infratemporal fenestra. The contact of the jugal with the maxilla is smooth whereas the contact of the jugal and quadratojugal is heavily sutured. Transversally, the jugal is narrow with its dorsal region projected laterally, forming a longitudinal ridge. The anterior process of the jugal is the deepest portion, decreasing posteriorly. The longitudinal ridge is lower, becoming accentuated and more laterally projected at the rear. Ventral to the infratemporal fenestra, the jugal ridge is horizontal, thus parallel to the palatal axis; it is dorsoventrally compressed forming a slight dorsal curvature in the skull's posterior ventral margin. Due to the lateral projection of the ridge, the postorbital bar is located medially to the jugal's dorsolateral margin. The postorbital bar is rod-like, circular in cross-section, medioposteriorly curved and constitutes the lower half of the posterior orbital margin. The jugal is ornamented with subdued rugosities at its lateroventral region, by small pits at the ridge's mid-region, and by slightly larger pits at its lateroventral region. The quadratojugal is posteriorly broken, but it projects anteriorly and contacts the postorbital at the infratemporal fenestra's apex. The orbit is large, anteriorly placed, longer than deep, with its rim composed by the lacrimal anteriorly, by the jugal ventrally, by the jugal's postorbital process posteroventrally, and by the postorbital posterodorsally. Due to the missing skull roof bones, only the palpebrals seem to limit the orbit dorsolaterally in the location of the frontal. In anterior view, the postorbital bar is more laterally positioned than the anterior orbital wall (due to the medial flexure of the lacrimal) and snout, exposing the orbit anteriorly (Figs. 1D and 2D). The anterior position of the large orbits suggests the presence of a highly advanced binocular vision in *Gondwanasuchus*, while the low and narrow snout cleared its sight lines, as seen in theropod dinosaurs, indicating its visual acuity for predation (Stevens, 2006).

The postorbital is broken posterodorsally. The anterior region of the infratemporal fenestra is limited by the jugal's postorbital process, ventrally by the jugal, posteriorly by the quadratojugal and by the postorbital at its dorsal apex. Its descending process corresponds to half of the orbit's depth and is a very thin structure. The posterior surface of the postorbital is transverse to the sagittal axis and forms a 90° angle with its preserved posterolateral portion. Dorsally, a small surface is preserved, fused to the posterior palpebral. The infratemporal fenestra is subtriangular, with the dorsal apex positioned at its anterior half. The antero-posterior length of the fenestra is $\sim 2/3$ of the orbit's length and $\sim 1/2$ of its depth. The fenestra faces slightly dorsally due to the position of the postorbital bar and quadratojugal.

The nasal is long, narrow, with its lateral and medial margins parallel along its anterior half, and is ornamented by wrinkles and small pits. The nasal broadens abruptly at its middle region and is almost twice as wide at its posterior half, but retains parallel lateral and medial margins (Fig. 2B). Posteriorly, the nasal contacts the prefrontal and anterior palpebral, and projects posteriorly to contact the frontal (Fig. 2D). The posterior half of the nasal is concave medially. The nasal projects anteriorly to form the dorsal portion of the internarial bar in conjunction with the premaxilla.

The palatine is narrow and slightly shorter than the suborbital fenestra. The palatine is slightly broader posteriorly than anteriorly

in palatal view. The medial contact between the palatines is straight and the palatal surface is flat. The contact of the maxilla and palatine is sutured and transversely straight at the anterior suborbital border. The palatine contacts the ectopterygoid with a small posterolateral surface in palatal view. Transversally the palatine is triangular, with a 90° ventromedial angle.

In palatal view, the ectopterygoid of *Gondwanasuchus scabrosus* is slender, in contrast to those of other baurusuchids, and partially caps the ventral pterygoid border, composing the posterolateral portion of the palate. The posterolateral ectopterygoid ramus extends to the pterygoid's ventral extremity, near the ventral margin of the angular. The angle between the anterolateral ramus of the ectopterygoid and its anteromedial ramus is ~75°, corresponding to the posterior margin of the suborbital fenestra. The ectopterygoid contacts the maxilla ventrally to the jugal below the middle of the ventral orbital border. Only a small portion of the pterygoid is preserved, and in part, it is supported by sediment. The pterygoid wings diverge ~60° to the sagittal axis and ~45° to the palatal axis. The contact with the palatine is vertical, and dorsally the pterygoid has a small anterior projection.

The anterior palpebral is large, and bears a few marginal rugosities; it is not sutured to the adjacent bones. The bone is subtriangular with anterior, medial, and posterior expansion, and is longer than the major axis of the orbit. In lateral view, it gently slopes anteroventrally. The anteromedial border displays discrete serration-like tubercles, while the posteromedial border is slightly concave and smooth. The anteromedial border is projected medially forming a sharp crest above the prefrontal. In dorsal view, the anteromedial border is parallel to the sagittal axis, while the lateral border is curved like the jugal ridge. The posterior palpebral is very small and subtriangular, and is ornamented by rugosities and small pits. Its anteromedial border shows discreet serration-like tubercles as in the anterior palpebral. The contact of palpebrals is not preserved, but its extremities could possibly touch, forming an oval supraorbital fenestra with an antero-posterior major axis.

Only the anteriormost portion of the prefrontals and frontal were preserved. The preserved portion of the prefrontal is anteriorly rounded and posteriorly narrower, granting it a "teardrop" shape. The frontal projects anteriorly, medially to the prefrontals making a small contact to the nasals. The frontal broadens posteriorly.

Mandible

Like the skull, the mandible is strongly compressed laterally. The dentary is transversely narrow and shallow. Its depth remains almost constant throughout its length. Posterior to the mandibular symphysis, the dentary is weakly concave at the third maxillary tooth. The symphyseal region is extremely narrow in contrast to the other baurusuchids that shows expansion at the fourth dentary alveolus. The anteroventral edge of the dentary is oriented anterodorsally in a 45° angle in relation to the palatal axis. The mandible is heavily ornamented with several small rounded and slit-like pits, especially at the symphyseal region, extending to the position of the fifth maxillary tooth. Small foramina are sparsely distributed posteriorly to the level of the mid orbital length.

The splenial is almost flat and smooth. In palatal view, it is possible to observe the contact of the splenials with the dentaries at the posterior portion of the mandibular symphysis. The splenials are sutured together, whereas the splenial-dentary contact is overlapping. The *intermandibularis oralis* foramen is large and oval, with its major axis positioned anteroposteiorly. Posteriorly, the splenial composes the anterior wall of the inner mandibular fenestra, and contacting posteroventrally the angular. The external mandibular fenestra has a "teardrop" shape with the anterior extremity anteroventrally oriented and its posterior extremity posterodorsally oriented. The dentary limits the anterodorsal portion up to almost half of the fenestra's length and a small anteroventral region. The surangular borders the dorsal half of the fenestra up to its posterior end where the mandible is broken. The angular is represented only by a small portion and bounds the external mandibular fenestra ventrally.

Dentition

The dentition has the most distinctive traits of Gondwanasuchus scabrosus with the development of vertical grooves on the outer surface. The teeth bear five or six deep and wide apicobasal sulci that converge apically and are interspersed with ridges (Fig. 4). There are four premaxillary and five maxillary teeth. The premaxillary teeth curve over their distal half, have circular cross-sections and lack carinae. Of note, the teeth's surfaces have five or six apicobasal sulci (Fig. 4A). The first premaxillary tooth displays the strongest curvature which grant it a hooked aspect. The second and third teeth are similar in morphology, with virtually identical crown heights. The fourth premaxillary and the first maxillary tooth are very small and positioned adjacent to the premaxillamaxilla notch. The second maxillary tooth is slightly laterally compressed, its crown is lower than those of the third and fourth maxillary teeth, and bears a distal serrated carina at their apical region. The third and fourth maxillary teeth are laterally compressed, with mesial and distal serrated carinae (Fig. 4B). The third maxillary tooth is the largest of the upper jaw. The fifth maxillary tooth is similar in morphology to the third and fourth maxillaries, except that its crown is much lower. Because the mandible is occluded, only one mandibular tooth (probably the fourth) is observed at the premaxilla-maxilla notch. This mandibular tooth is highly enlarged, but similar in morphology to the third and fourth maxillary teeth and bears a distal serrated carina. The mandibular and maxillary teeth show three apicobasal sulci on their labial surfaces, and there are likely three additional sulci on the lingual surfaces. The serrated carinae observed in the teeth of Gondwanasuchus are composed of chisel-like, subquadrangular denticles, distributed with a density of five denticles per millimeter along the mesial carinae, and four denticles per millimeter along the distal carinae. The serrations are morphologically homogeneous, but they are deeper at the mid-region of the carinae and were likely used like a 'steak knife' for cutting flesh (Fig. 4B).

Both the upper jaws bear teeth in all stages of eruption and show size gradation on alternate tooth rows from which the tooth



Fig. 4. The dentition of *Gondwanasuchus scabrosus* **gen. nov. et sp. nov.** (UFRJ DG 408-R); Second right premaxillary tooth (A) and fourth right maxillary tooth (B). **Abbreviations: m 1–5**: maxillary tooth and corresponding position 1–5; **pm 1–4**: premaxillary tooth and corresponding position 1–4.

replacement pattern can be inferred. Alternations of younger and older teeth are evident in the upper jaw. The teeth, irrespective of size, are firmly held in the alveoli in thecodont fashion. In the odd-numbered series of the upper jaw, teeth one (pm1) and three (pm3), five (m1) and seven (m3) form two separate series of increasing size toward the rear; in the even-numbered teeth, six (m2) and eight (m4) show a similar trend of increasing size (Fig. 4). Teeth four (pm1) and five (m1) are erupted at the level of the alveolus, whereas tooth nine (m5) is slightly above the alveolar border (Fig. 4). Thus, the upper jaw exhibits waves of tooth replacement proceeding from back to front as in other reptiles (Edmund, 1960).

5. Discussions and conclusions

Gondwanasuchus scabrosus exhibits the following baurusuchid synapomorphies: a laterally compressed rostrum, a prominent premaxilla-maxilla notch for the reception of the hypertrophied mandibular tooth, medial contact of the prefrontals with abbreviated frontal-nasal contact, reduced dentition, caniniform maxillary teeth, and ziphodont dentition (Price, 1945; Gasparini, 1972; Carvalho et al., 2005; Martinelli and Pais, 2008). Montefeltro et al. (2011) proposed the Subfamily Pissarrachampsinae to include Pissarrachampsa sera and Wargosuchus australis. Both taxa display a posterior portion of the nasal dorsal surface with a broad, rugose depression, prefrontals approximating along their medial edges anteriorly allowing a reduced frontal-nasal contact, and the presence of a midline longitudinal depression on the anterior portion of the frontal. Campinasuchus dinizi also has a contact between the frontal and nasals through the medial approach of the prefrontals (Carvalho et al., 2011), as in W. australis and P. sera characterizing it as a Pissarrachampsinae. In addition, G. scabrosus presents all the diagnostic features proposed by Montefeltro et al. (2011) for the Pissarrachampsinae, indicating that this new species represents a baurusuchid more closely related to W. australis, C. dinizi and P. sera than to other baurusuchids, such as Baurusuchus and Stratiotosuchus. In these latter genera, the two prefrontals touch medially precluding a nasal-frontal contact. Despite the shared feature at the skull roof, G. scabrosus is characterized by the following autapomorphies: teeth with wide and deep apicobasal sulci, an enlarged, caniniform fourth dentary tooth, highly compressed skull and mandible, laterally projected slender jugal, and anteriorly facing orbits with a large component of stereoscopic vision (Fig. 5).

The skull of *Gondwanasuchus scabrosus* is oreinirostral, with vertical lateral snout walls, short and very narrow snout (*sensu* Busbey, 1995). Oreinirostral snouts are stronger than platyrostrals in anterior biting (Rayfield and Milner, 2008), but would be more susceptible to the stresses caused by medially directed forces and increases of axial torque generated by the rolling behavior of extant platyrostral crocodilians (Bolt, 1974). These resistance characteristics of oreinirostric skulls suggest that terrestrial crocodyliforms would not invoke rolling as a mechanism for the destabilization and dismemberment of prey, but would possibly adopt methods to acquire and subjugate prey similar to *Varanus komodoensis*, as suggested by Busbey (1995).

In lateral view, the nasals of *Gondwanasuchus scabrosus* are more anteroventrally sloped than other baurusuchids, particularly when compared to *Baurusuchus* and *Stratiotosuchus* where the nasals are almost parallel to the palatal axis (Carvalho et al., 2005; Campos et al., 2001). In anterior view, *G. scabrosus* has the most strongly laterally compressed skull of all baurusuchids, with a palatal width of 18 mm and snout depth of 28 mm between the third maxillary teeth. The lateral maxillary wall is straight and more vertical in anterior view than in *Baurusuchus pachecoi, B. salgadoensis, Stratiotosuchus maxhechti, Wargosuchus australis, Campinasuchus dinizi* and *Pissarrachampsa sera*; these species have dorsomedially curved maxillae, with a broader dorsal exposure (see Carvalho et al., 2005; Campos et al., 2001; Martinelli and Pais, 2008; Carvalho et al., 2011; Montefeltro et al., 2011).

The external nares of *Gondwanasuchus scabrosus* is similar to that of the other baurusuchids with anterolateral openings except for *Stratiotosuchus maxhechti*, in which the external nares are located more anterodorsally (Montefeltro et al., 2011). The premaxilla of *G. scabrosus* is subrectangular in lateral view, proportionally longer and shallower than in other baurusuchids. The only exception is *S. maxhechti* in which the premaxilla projects posterodorsally to the rostral notch.



Fig. 5. Life reconstruction of Gondwanasuchus scabrosus gen. nov. et sp. nov. right lateral (A), anterior (B), dorsal (C) and oblique (D) views. Art by Rodolfo Nogueira.

Gondwanasuchus scabrosus' dentition is similar in tooth number to Baurusuchus pachecoi, B. salgadoensis and Campinasuchus dinizi with four premaxillary and five maxillary teeth, but differs from *Stratiotosuchus maxhechti* which contains three premaxillary and five maxillary teeth, and *Pissarrachampsa sera* with three premaxillary and four maxillary teeth (Campos et al., 2001; Riff and Kellner, 2011; Montefeltro et al., 2011). *Campinasuchus dinizi* (specimen CPP 1236) bears five teeth at the left maxilla and only four at the right maxilla. This difference in the number of teeth at the left and right maxilla of CPP 1236 seems to be related to the size of the rostral notch, where the right notch is broader posteriorly and obliterates the first maxillary alveolus. The enlargement of the rostral notch of *S. maxhechti* and *P. sera* might be related to the reduced dentition of these taxa, that diverge from most baurusuchids.

Baurusuchid teeth are usually smooth with discreet longitudinal and transverse lines (Riff and Kellner, 2001). In contrast, the teeth of Gondwanasuchus are laterally compressed with serrated anterior and posterior edges; the labial and lateral surfaces are marked by apicobasal sulci associated with coarse flutings, making these teeth formidable weapons. The slender and recurved premaxillary teeth of Gondwanasuchus scabrosus were probably used for catching prey, whereas the strong maxillary teeth with corrugated surface and serrated edges were deployed for puncturing and killing struggling prey, aided by the enlarged lower caniniform tooth, which could slide in the premaxilla-maxilla notch to provide a strong grip. The posterior maxillary teeth are more laterally compressed than other baurusuchid teeth and do not show wear facets. The longitudinal sulci on the teeth of Gondwanasuchus could have provided additional structural strength to prevent any break during capturing and killing prey.

Gondwanasuchus is one of the smallest known baurusuchids, with a preserved skull length of 128 mm and estimated total length of about 150 mm. The holotype presents a mosaic of juvenile and adult features. Some juvenile characteristics include: loosely sutured cranial and mandibular elements as well as proportionally large orbits, while the well-developed ornamentation features in the cranial and mandibular bones suggest adult or subadult features (Mook, 1921). Most likely, the holotype of *Gondwanasuchus scabrosus* represents a subadult of a small to medium-sized species of Baurusuchidae.

Baurusuchids are considered by many authors as crocodyliforms that occupied the role of medium to large-sized predators in the terrestrial realms of the Bauru Basin, due to the inferred terrestrial habits of the family based on dental, cranial and postcranial features and to the large size that they could reach (Gasparini et al., 1993; Vasconcellos and Carvalho, 2007; Martinelli and Pais, 2008; Riff and Kellner, 2011). Gondwanasuchus scabrosus clearly displays some baurusuchid characteristics that resemble those of theropods, such as strongly laterally compressed maxillary teeth and skull. The snout overhangs anteroventrally, and the orbits are more anteriorly placed (Figs. 2D and 3D) suggesting a highly advanced binocular vision as inferred for Tyrannosaurus rex and other theropods used to accurately judge position of prey (Stevens, 2006). Due to the oreinirostral skull, which would not support medially directed force or high axial torque as well as premaxillary teeth adapted to subjugation, Gondwanasuchus most likely fed on small vertebrates and carcasses, possibly occupying the ecological niches of small theropods. If Gondwanasuchus could consistently engage prey with its formidable teeth, it could have exploited a predatory niche in the absence of theropods.

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