



***Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid (Crocodyliformes) from the Bauru Basin, Brazil**

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Abstract

A remarkably diverse terrestrial mesoeucrocodylian fauna has been recovered from the continental Cretaceous of the Bauru Basin in fluvial and lacustrine deposits. Members of at least six distinct groups are now recognized, including notosuchids, sphagesaurids, candidodontids, peirosaurids, trematochampsids, and baurusuchids. These mostly terrestrial crocodyliforms potentially developed ecological strategies that allowed them to live in a hot and arid climate during the Cretaceous. A new genus and species of Baurusuchidae, *Campinasuchus dinizi* **gen. et sp. nov.**, is established on the basis of several partial skulls and skeletons from the Turonian-Santonian Adamantina Formation. This taxon is notable for its relatively short, anteriorly tapering snout, marked maxillary heterodonty with third maxillary and fourth dentary teeth extremely enlarged relative to other teeth, and the presence of a large anteroposterior depression on each palatine between the palatal fenestrae. The presence of yet another crocodyliform from the Adamantina Formation reinforces the idea that aridity, or maybe a seasonally warm and dry climate alternating with periods of higher rainfall, drove the diversification of terrestrial crocodyliforms throughout the Late Cretaceous.

Key words: *Campinasuchus dinizi*, Baurusuchidae, Crocodyliformes, Adamantina Formation, Bauru Basin, Brazil

Introduction

The inland continental basins of the Cretaceous of South America, Africa, Madagascar and Asia preserve a remarkable diversity of terrestrial crocodyliforms. Perhaps most notably, the Bauru Basin (southeastern Brazil) preserves species from at least six major groups including notosuchids, sphagesaurids, candidodontids, peirosaurids, trematochampsids and baurusuchids. This diversity was likely driven by ecological strategies that allowed survival in a hot and arid climate (Carvalho *et al.* 2010). Most were clearly terrestrial animals, living in semi-arid environments markedly distinct from the aquatic to semi-aquatic habitats of extant crocodylians. Late Cretaceous crocodyliform species currently described from the Bauru Basin include: *Baurusuchus pachecoi* Price, 1945, *Sphagesaurus huenei* Price, 1950a, *Itasuchus jesuinoi* Price, 1955, *Peirosaurus tormini* Price, 1955, *Mariliasuchus amarali* Carvalho and Bertini, 1999, *Stratiosuchus maxhechti* Campos, Suarez, Riff and Kellner, 2001, *Uberabasuchus terrificus* Carvalho, Ribeiro and Avilla, 2004, *Baurusuchus salgadoensis* Carvalho, Campos and Nobre, 2005, *Adamantinasuchus amarali* Nobre and Carvalho, 2006, *Mariliasuchus robustus* Nobre, Carvalho, Vasconcellos and Nava, 2007, *Montealtosuchus arrudacamposi* Carvalho, Vasconcellos and Tavares, 2007, *Sphagesaurus montealtensis* Andrade

and Bertini, 2008, *Armadillosuchus arrudai* Marinho and Carvalho, 2009, *Morrinhosuchus luziae* Iori and Carvalho, 2009, and *Baurusuchus albertoi* Nascimento and Zaher, 2010 (Andrade & Bertini 2008; Campos *et al.* 2001, 2005; Carvalho & Bertini 1999; Carvalho *et al.* 2004, 2005; Iori & Carvalho 2009; Marinho & Carvalho 2005, 2009; Nobre & Carvalho 2006; Nobre *et al.* 2005, 2007; Pol 2003; Price 1945, 1950a, b, 1955; Roxo 1936; Vasconcellos *et al.* 2004, 2008). The previously recognized taxon *Brasileosaurus pachecoi* Huene, 1931 is now considered a *nomem dubium*.

In comparison with other tetrapod clades known from Bauru Basin, mesoeucrocodylians are the most abundant (e.g. Carvalho *et al.* 2010). In this contribution, a new baurusuchid crocodyliform from the Late Cretaceous of the Triângulo Mineiro region (Minas Gerais State, Brazil) is named and described, thus expanding the known mesoeucrocodylian diversity of the Bauru Basin.

Geology and Paleoenvironmental setting

The origin of the Bauru Basin (Figure 1) is related to the opening of the Atlantic Ocean, when the continental rupture lead to intracratonic volcanic activity followed by a broad interior depression (estimated area of 370,000 km²) located between latitudes 18° S and 24° S (Fernandes & Coimbra 1996). The basin now covers part of the present southeastern Brazilian states of Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso, Goiás, and Minas Gerais (Fernandes & Coimbra 1996). Sediments deposited in the basin are divided into two main lithostratigraphic units: the Caiuá Group (Rio Paraná, Goio Erê and Santo Anastácio Formations) of Cenomanian-Turonian age, and the Bauru Group (Adamantina, Uberaba and Marília Formations) of Turonian-Maastrichtian age (Dias-Brito *et al.* 2001; Paula e Silva 2003; Paula e Silva *et al.* 2003).

The baurusuchid described here was found in outcrops of the Adamantina Formation, a unit that covers a large portion of the exposed area of the Bauru Basin. The Adamantina Formation is composed of fine-grained sandstones and siltstones with intercalations of red, oxidized mudstones of Turonian and Santonian age (Dias Brito *et al.* 2001). Deposition likely took place on an extensive alluvial plain reworked by fluvial systems alongside scattered shallow ephemeral lakes in an arid or semi-arid seasonal climate (Garcia *et al.* 1999; Goldberg & Garcia 2000; Fernandes & Basilici 2009). In addition to crocodyliforms, this stratigraphic unit yields a rich diversity of vertebrate and invertebrate ichnofossils, continental mollusks, arthropods, freshwater fishes, amphibians, squamates, theropod and sauropod dinosaurs, and birds (e.g., Bertini *et al.* 1993; Arruda *et al.* 2004; Carvalho *et al.* 2005).

The rich crocodyliform fauna of the Adamantina Formation is important for its potential correlation with other Upper Cretaceous basins in South America, Africa, Madagascar and India, and potentially Antarctica, and has significant paleoclimatic, paleoenvironmental, paleogeographical and paleobiogeographical implications (Carvalho *et al.* 2007; Krause 2003; Larsson & Gado 2000; Rogers *et al.* 2000; Sereno & Larsson 2009; Turner 2004; Wilson *et al.* 2001; Wu & Sues 1996). In comparison with the other tetrapod groups known from the Bauru Basin, crocodyliform fossils are relatively complete, better preserved and commonly associated with a diverse ichnological record including structures attributable to invertebrates, egg fragments, coprolites and tooth-marks (Carvalho *et al.* 2009; Fernandes & Carvalho 2006; Gracioso & Carvalho 2009; Vasconcellos & Carvalho 2007). This assemblage is particularly useful when dealing with paleoenvironmental and paleoecological reconstructions, normally unavailable with even complete body fossil specimens (Vasconcellos & Carvalho 2010).

The outcrop where the new specimens were found is located at Três Antas Farm, Campina Verde County, Minas Gerais State. The Adamantina Formation is exposed as a 15 meter succession of fine to coarse grained sandstones with calcrete surfaces (Figure 2). Notable are distinct levels of conglomeratic sandstones with alkali pebbles and sandstone intraclasts. The entire sequence shows convolute, fluidization and dish structures. At least six stratigraphic levels in the outcrop produce crocodyliform remains, primarily in fine-grained red sandstones.

The palaeoenvironmental setting of this fossil occurrence was interpreted as distal alluvial fans and alluvial plains subjected to sudden floods in a dry and hot climate. Local aridity was considered by Goldberg and Garcia (2000) to reflect global climatic conditions and the presence of topographic highs acting as geographic barriers to the movements of humid winds. There was probably a marked seasonality, with distinct rainy and dry seasons, as also interpreted for the deposits of other terrestrial Cretaceous crocodyliforms at this time globally. This likely led to stressed and unstable ecosystems (Campos *et al.* 2005; Carvalho & Bertini 1998, 2000; Carvalho *et al.* 2010). Freshwater ponds and rivers were scarce, generally drying out during long droughts thus restricting the fauna and flora of this region and likely driving adaptations to severe environmental conditions (e.g. Carvalho *et al.* 2010).

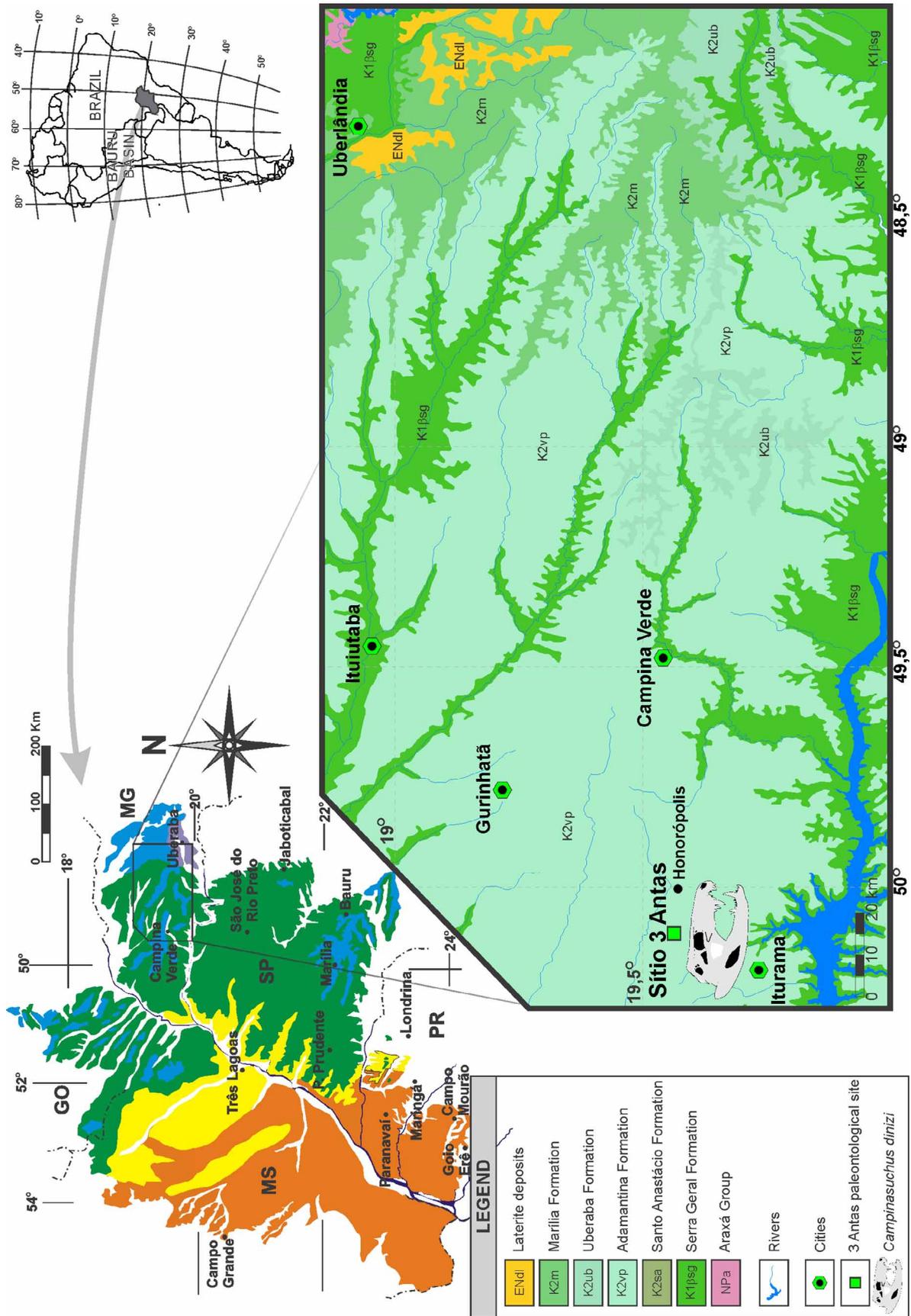


FIGURE 1. Bauru Basin geological map and the locality of *Campinasuchus dinizi* gen. nov. et sp. nov. (modified from Paula e Silva, 2003 and CPRM, 2010).

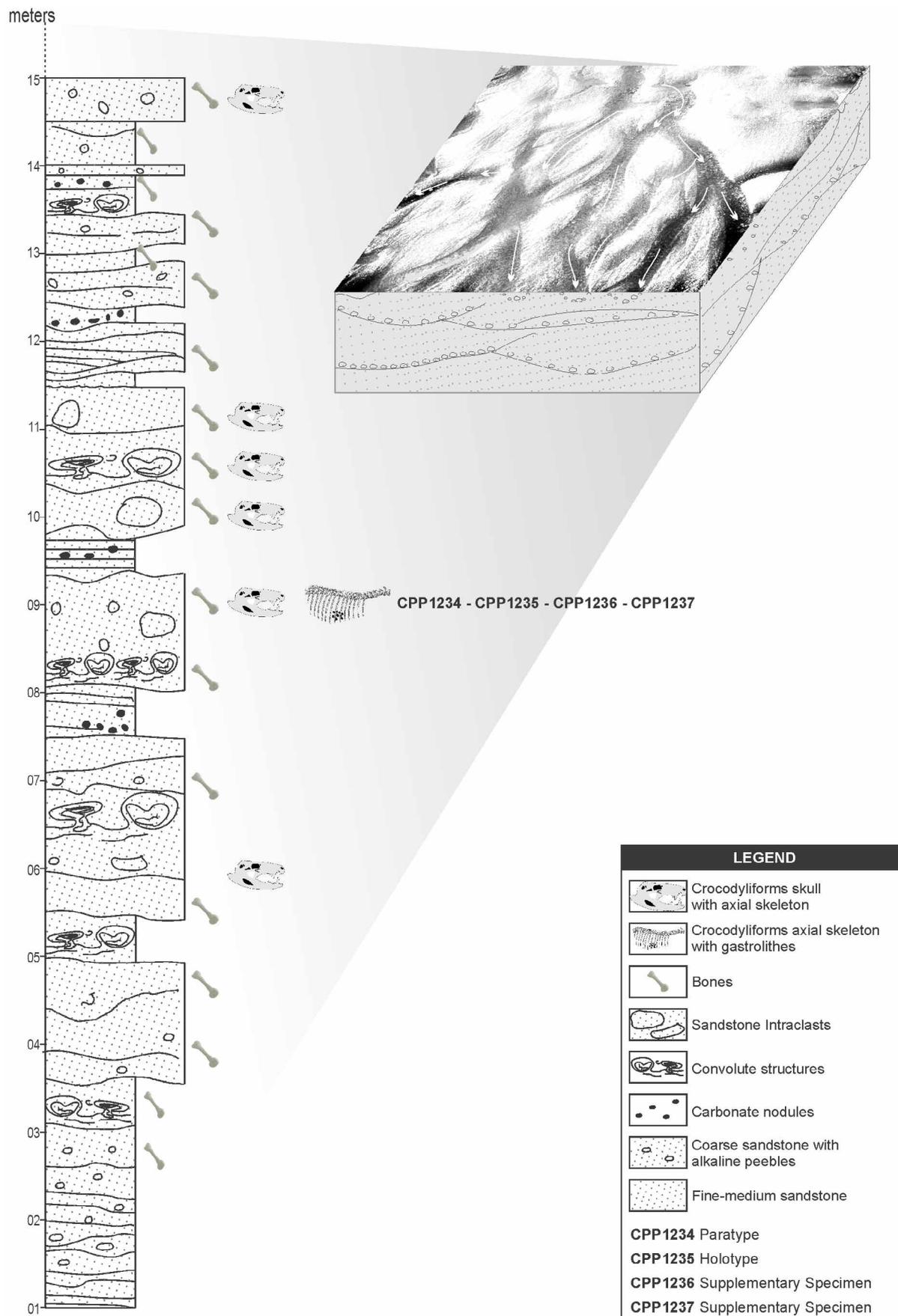


FIGURE 2. Stratigraphic profile of the Adamantina Formation (Bauru Basin) at Três Antas Farm, Campina Verde County, Brazil, in the locality which yielded the new Late Cretaceous baurusuchid species *Campinasuchus dinizi*.

South American Baurusuchid diversity

Baurusuchidae was first defined by Price (1945) to include crocodyliforms with elongate, laterally compressed skulls. Members are currently known from Brazil (Bauru Basin:Campos *et al.* 2001; Carvalho *et al.* 2005; Nascimento & Zaher 2010), Argentina (Neuquén Basin:Gasparini 1972; Martinelli & Pais 2008) and Pakistan (Pab Formation, Balochistan Province:Wilson *et al.* 2001), ranging in age from the Turonian to the Maastrichtian. All known members of Baurusuchidae can be considered medium- to large-sized terrestrial crocodyliforms often regarded as active cursorial predators based on dental, cranial and postcranial data (Arruda *et al.* 2005; Arruda Campos *et al.* 2005; Vasconcellos & Carvalho 2007, 2010).

A number of features distinguish baurusuchids from other basal mesoeucrocodylans. The quadrates are vertical to sub-vertical and the secondary palate is of “mesosuchian” type. The dentition is differentiated, with a tendency toward extreme reduction in number (especially in the maxilla) of ziphodont teeth. Ectopterygoids are anteroposteriorly large and contribute to the lateral borders of the internal narial openings.

Four baurusuchid species are currently recognized from the deposits of the Bauru Basin (Adamantina Formation, Turonian-Santonian, Brazil): *Baurusuchus pachecoi* Price, 1945; *Stratiotosuchus maxhechti* Campos, Suarez, Riff and Kellner, 2001; *Baurusuchus salgadoensis* Carvalho, Campos and Nobre, 2005, and *Baurusuchus albertoi* Nascimento and Zaher, 2010. In Argentina, two additional species are recognized from the Neuquén Basin (Río Neuquén Subgroup): *Cynodontosuchus rothi* Woodward, 1896 and *Wargosuchus australis* Martinelli and Pais, 2008 (Turner & Calvo 2005; Martinelli & Pais 2008).

Baurusuchus pachecoi (Price 1945) has a long and tall skull, with a laterally compressed rostrum. The external surface of many cranial elements are ornamented with irregular ridges. The external nares are undivided and positioned on the front of the snout. The orbits are laterally directed and there is no antorbital fenestra. The quadrates are directed ventrally and weakly posteriorly. All teeth are theropod-like, being laterally compressed with serrated carinae.

Baurusuchus salgadoensis (Carvalho *et al.* 2005) has a more straight posterior skull border than *B. pachecoi*. A narrow interfenestral bar on the parietals separates the supratemporal fenestrae. Additionally, the well preserved skull shows external nares divided by a bony septum, two well-fused supraorbitals (palpebral bones), and an elliptical orbit. Another distinctive feature with regard to *B. pachecoi* is the more rounded and less crenulated teeth.

Baurusuchus albertoi (Nascimento & Zaher 2010) was collected from the same outcrop as *B. salgadoensis*. This species is characterized by a jugal with a triangular and rugose ventrolateral anterior projection that is more ventrally developed than in other baurusuchids. The jugal infratemporal bar is dorsoventrally slender and anteroposteriorly as long as the inferior edge of the orbit. The lateral projection of the vertical portion of the squamosal is posteriorly concave. There is a well-developed ventromedial crest of the quadrate, dividing the descendent body of the quadrate into medial and anterior surfaces. The retroarticular process is lateromedially flattened and vertically oriented, with a posterodorsal expansion (Nascimento & Zaher 2010).

Another Brazilian baurusuchid, *Stratiotosuchus maxhechti* (Campos *et al.* 2001) has an elongate skull, the bones of which are heavily ornamented with irregular ridges. The anterior region of the skull is tall and the orbit is sub-rectangular in shape. The external nares are, anterodorsally located in a depressed area of the premaxilla and are separated from each other by a small bony septum (Campos *et al.* 2001). Further differing from *Baurusuchus*, *Stratiotosuchus* has only three premaxillary teeth.

There is also evidence of an additional species of *Baurusuchus* identified from an anterior portion of the skull and mandible (Brandt Neto *et al.* 1991, 2001) from the Adamantina Formation, which at present is not formally described.

Cynodontosuchus rothi is based on a partial rostrum, some caudal vertebrae, remains of the hind foot, and other fragmentary bones. The rostrum of *Cynodontosuchus* is not as tall as that of *Baurusuchus* and the maxilla contains five teeth (Woodward 1896; Buffetaut 1982) with a very large maxillary caniniform tooth (Steel 1973). The external nares were probably anteriorly directed. There is also a hypertrophied mandibular tooth (most likely the fourth) that fits into a notch between the premaxilla and the maxilla (Gasparini 1972). The anterior parts of the mandibular rami are slightly divergent and the symphysis is nearly twice as long as wide (Steel 1973).

Wargosuchus australis, from the Bajo de La Carpa Formation (Río Neuquén Subgroup, Santonian; Martinelli & Pais 2008), is based on a fragment of snout and a portion of the cranial roof. *Wargosuchus* possesses a deep median groove on the frontals, an extremely reduced contact between nasals and frontals, a large depression for the

olfactory bulbs, three large foramina surrounding the large, smooth perinarial depression, and a hypertrophied, conical last premaxillary tooth followed by a large paracanine fossa (Martinelli & Pais 2008).

Systematic paleontology

The classification of the new taxon was based on the comparative studies of Price (1945), Gasparini (1972), Gasparini *et al.* (1991), Campos *et al.* (2001), Carvalho *et al.* (2005), Vasconcellos and Carvalho (2007), Martinelli and Pais (2008) and Nascimento and Zaher (2010). The osteological terminology follows Iordanski (1975), Carvalho *et al.* (2005), Vasconcellos and Carvalho (2007), and Kley *et al.* (2010).

Crocodyliformes Hay, 1930 (sensu Clark, in Benton & Clark 1988)

Mesoeucrocodylia Whetstone & Whybrow, 1983

Baurusuchidae Price, 1945

***Campinasuchus* gen. nov.**

Derivatio nominis: *Campina* refers to the area where the fossil was found: Campina Verde County; *suchus* from the Greek *Suchos* that refers to the Egyptian crocodile-headed god Sebek.

Diagnosis: As for the type and only known species.

Type species: *Campinasuchus dinizi* gen. et sp. nov.

***Campinasuchus dinizi* sp. nov.**

Holotype: CPP 1235 (Centro de Pesquisas Paleontológicas L. I. Price, Peirópolis – Uberaba, Minas Gerais, Brazil), a well preserved posterior skull and partial rostrum (Plates 1, 2).

Horizon and locality: The specimen was collected at Três Antas Farm (19°30'47"S, 50°06'20"W), Honorópolis District, Campina Verde County, Minas Gerais State, Brazil from the Turonian-Santonian sediments of the Adamantina Formation, Bauru Basin.

Derivatio nominis: The specific name honors Izonel Queiroz Diniz Neto and the families Diniz and Martins Queiroz, owners of the Três Antas Farm, where the fossil was excavated.

Paratypes: CPP 1234, partial skull with occluded mandible missing posterior portion of the skull (Plates 3, 4). CPP 1236, nearly complete rostrum (Plates 5, 6). CPP 1237, partial skull and mandible and associated postcranial skeleton (Plates 7, 8).

Horizon and locality: The paratypes were collected at the same locality and stratigraphic level as the holotype.

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 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-frontal contact reduced; ventral depression on splenial at mandibular symphysis; anteriorly convex dentary-splenial suture at mandibular symphysis in ventral view.

Description

Skull. In comparison with other baurusuchids, *Campinasuchus dinizi* is notable for its much shorter and lower snout. The holotype (CPP 1235, Plates 1, 2) consists of an incomplete skull missing the anterior extremity of the

snout. Due to the weakly downturned rostrum the cranial table is higher in relation to the dorsal border of the snout (CPP 1234, Plates 3, 4). The skull lacks an antorbital fenestra (preorbital fenestra). The orbits are circular and laterally directed. The supratemporal fenestrae are medium-sized, elliptical, and smaller than the orbit. The infratemporal fenestrae are triangular and separated from the orbits by flattened, inset postorbital bars. In comparison with other baurusuchids, the dentition is markedly heterodont in size. The jaws contain with four premaxillary, five maxillary (although there is a possible sixth tooth in the specimen CPP 1236) and ten dentary teeth. The skull surface is ornamented with grooves and ridges.

The premaxillae are sub-rectangular elements in dorsal view, dorsally separated from each other by the nasals and vertically disposed. The external nares are located at the anterior-most extremity of the rostrum, medially divided by a thin bar (specimen CPP 1237, Plates 7, 8). In specimens CPP 1234 and CPP 1236, the area of the external nares are partially broken and presented as a single large opening. The external nares are bordered ventrally and laterally by the premaxillae and dorsally by the nasals. Each premaxilla has four conical teeth which are regularly spaced. The first premaxillary tooth is positioned in the anteriormost portion of the rostrum. It is followed by a second tooth of almost equal size. The third tooth is the largest and is rounded in cross section. Carinae and serrations on premaxillary teeth are absent. The fourth and last premaxillary tooth is the smallest of this series, and is labio-lingually elliptical in cross-section. An occlusal pit on the premaxilla for the first dentary tooth is located lateral to first premaxillary tooth (between the first and second premaxillary teeth), rather than posterior to the first tooth as in other baurusuchids. This is concordant with laterally divergent first premaxillary teeth.

The maxilla is sub-rectangular in shape in lateral view, contacting the premaxilla anteriorly within a partially enclosed notch for reception of the large fourth dentary tooth. The dorsal border contacts the nasal along its entire length, posteriorly contacting the lacrimal, jugal, and prefrontal (Plates 4, 5, 6). The maxilla-jugal suture is anteriorly convex. The surface of the maxilla is ornamented by small ridges and grooves. The maxillary dentition consists of five conical teeth (a possible alveolus for a sixth tooth is present in CPP 1236). All of the teeth are located in the anterior portion of the maxilla, separated by short diastemata. The first three teeth increase in size posteriorly. The first tooth is the smallest of this series, located along the margin of the notch at the premaxilla-maxilla contact. The second tooth is moderately compressed and possesses finely serrated carinae on the mesial and distal edges. The third maxillary tooth is the largest of the series, with serrated carinae. The last two teeth are also compressed mediolaterally with finely serrated carinae. The fourth tooth is the second largest of this series, and the fifth is almost the same size as the second maxillary tooth. The last maxillary tooth is located posteriorly at almost the level of the anterior margin of the palatal (suborbital) fenestrae. There is a marked constriction in the snout posterior to the last maxillary tooth. In CPP 1237, there is evidence of a rounded antorbital fenestra bordered anteriorly by the maxilla and posteriorly by the lacrimal. In the other specimens, this area is badly preserved.

The nasals are long and reach the narial border. They contact the premaxillae in the anteriormost portion of the rostrum, extending as a thin bar anteroventrally to separate the dorsal portion of the external nares. The preserved portion of the rostrum in CPP 1236 (Plates 5, 6) shows that the nasal contacts the premaxillae, maxillae, prefrontals, and frontals but there is no contact with the lacrimal. The nasals maintain a constant width along most of their length, abruptly narrowing at the anterior of the rostrum. Here, they participate in the internarial bar as a thin nasal lamina together with an upward projection of the premaxilla (Plates 7, 8). Posteriorly the nasals meet the prefrontal and frontal. The contact with the frontal is reduced. Dorsally, the nasal-maxillary suture is more laterally concave than in other baurusuchids.

The lacrimal is sub-rectangular in lateral view, contacting anteriorly the maxilla, ventrally the jugal, dorsally the prefrontal, and posteriorly forming the anterior border of the orbit. The lacrimals are oriented almost vertically. Although in CPP 1235 the lacrimals are badly preserved and sutures with other bones are difficult to recognize, on the left element there is a posteriorly opening foramen interpreted as the naso-lacrimal duct, located close to the suture with the prefrontal descending process.

The jugal contacts the maxilla anteriorly, the lacrimal dorsally, the quadratojugal posteriorly, and the postorbital along the postorbital bar. The lateral surface of the horizontal ramus of the jugal is ornamented with irregular furrows. The anterior suture with the maxilla is convex, and at this portion the jugal exhibits its highest point. The ventral margin of the orbit is delimited by a relatively straight border of the jugal. The ascending process, contributing to the postorbital bar, arises from the medial surface of the jugal. It is thin, straight, slightly posterodorsally inclined, and lacks sculpturing. The posterior process of the jugal forms a slender bar contacting the quadratojugal through an interdigitated suture. It forms the ventral border of the infratemporal fenestra.

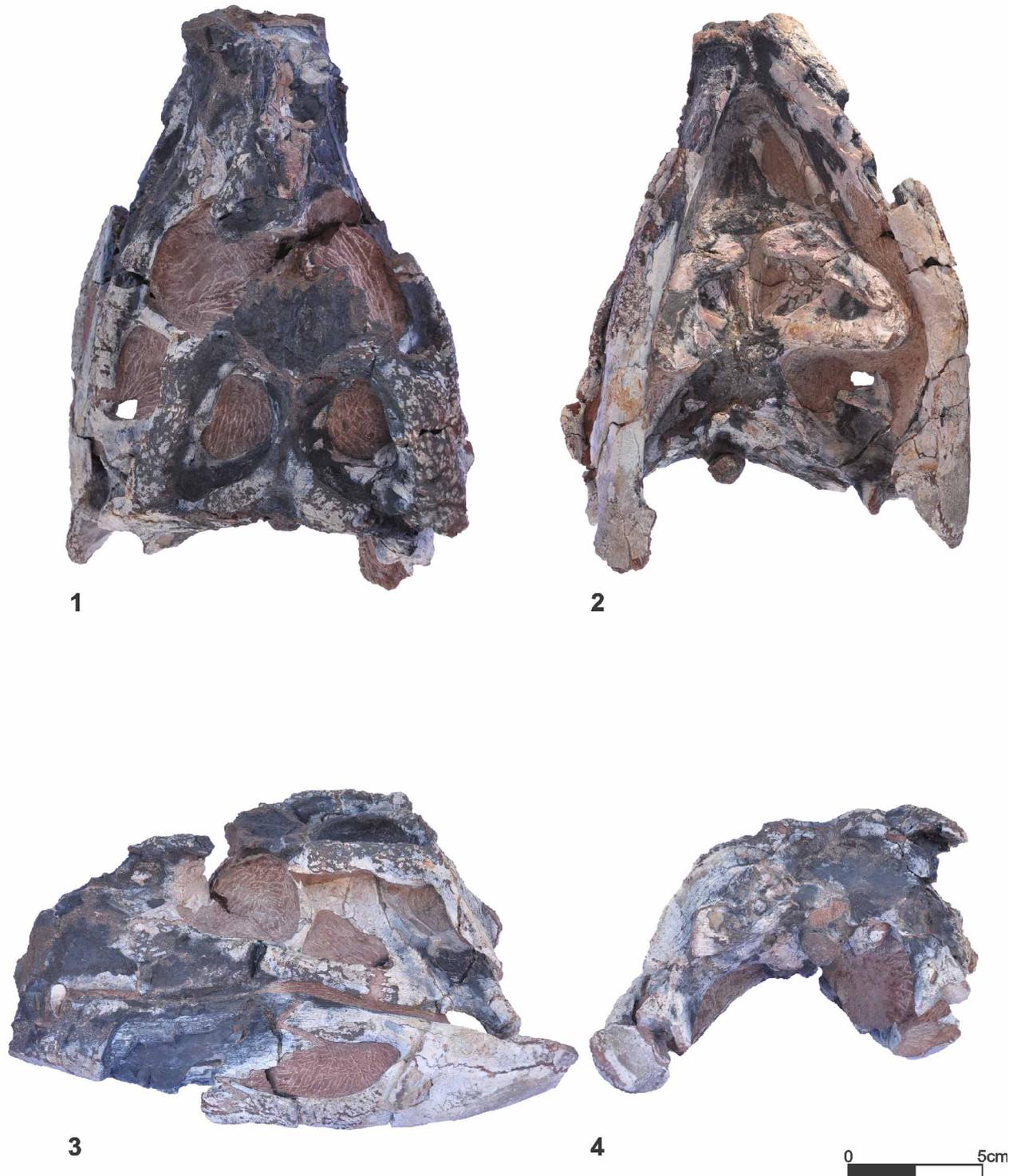


PLATE 1. Holotype skull and mandibles of *Campinasuchus dinizi* **gen. nov. et sp. nov.** (CPP 1235). 1, dorsal view; 2, palatal view; 3, left lateral view; and 4, occipital view.

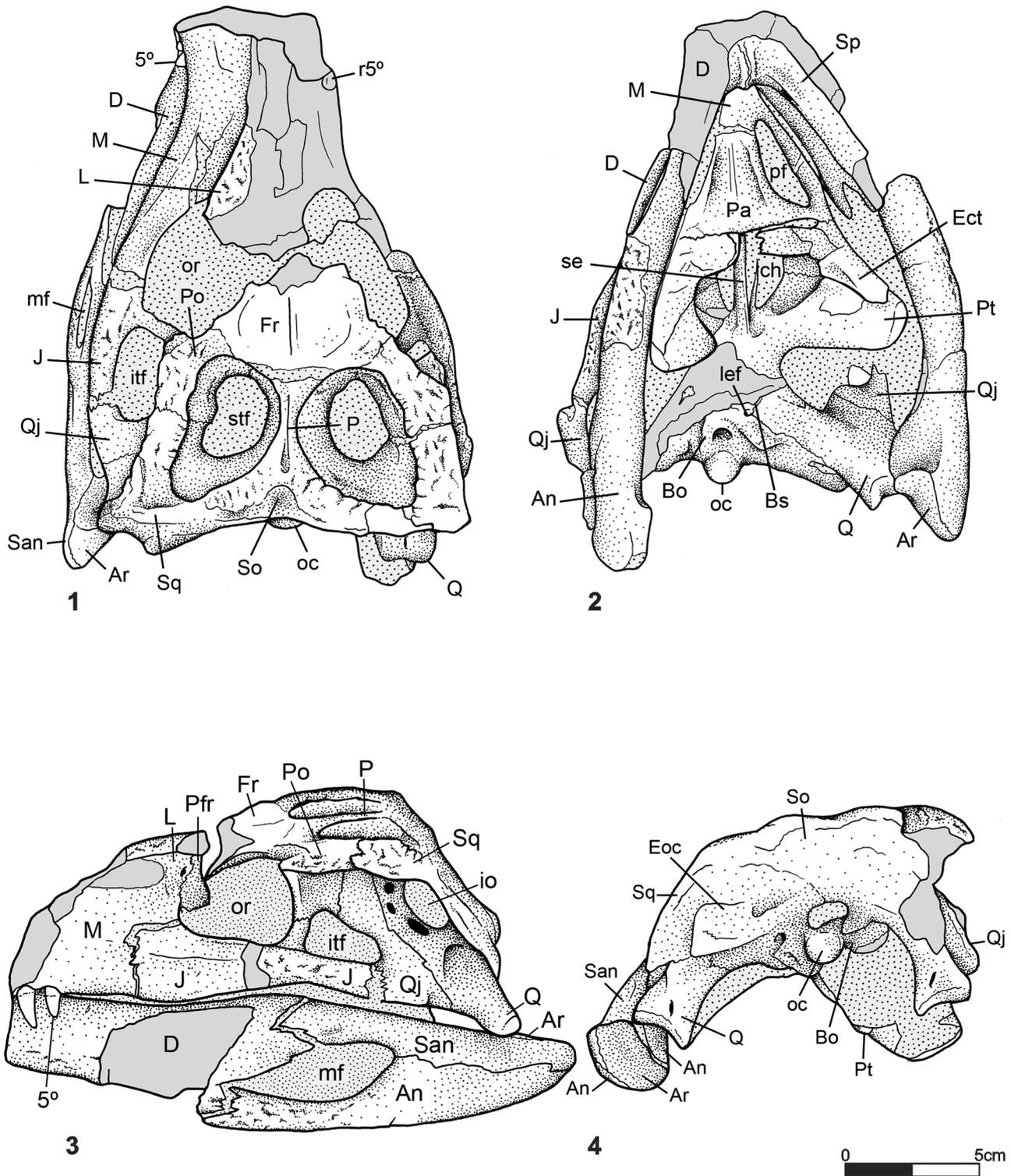


PLATE 2. Schematic drawings of the holotype skull and mandibles of *Campinasuchus dinizi* **gen. nov. et sp. nov.** (CPP 1235). 1, dorsal view; 2, palatal view; 3, left lateral view; and 4, occipital view. Grey indicates broken surfaces and regular dotted grey indicates matrix.

The prefrontal contacts the nasal, frontal and lacrimal. Each prefrontal is medially expanded, but they do not meet at the midline. The prefrontal is rectangular in shape, anteroposteriorly elongated, and elevated relative to the nasal and frontal. In CPP 1235, preserved on the left side is a portion of the descending process of the prefrontal, forming the anterior wall of the orbital cavity.

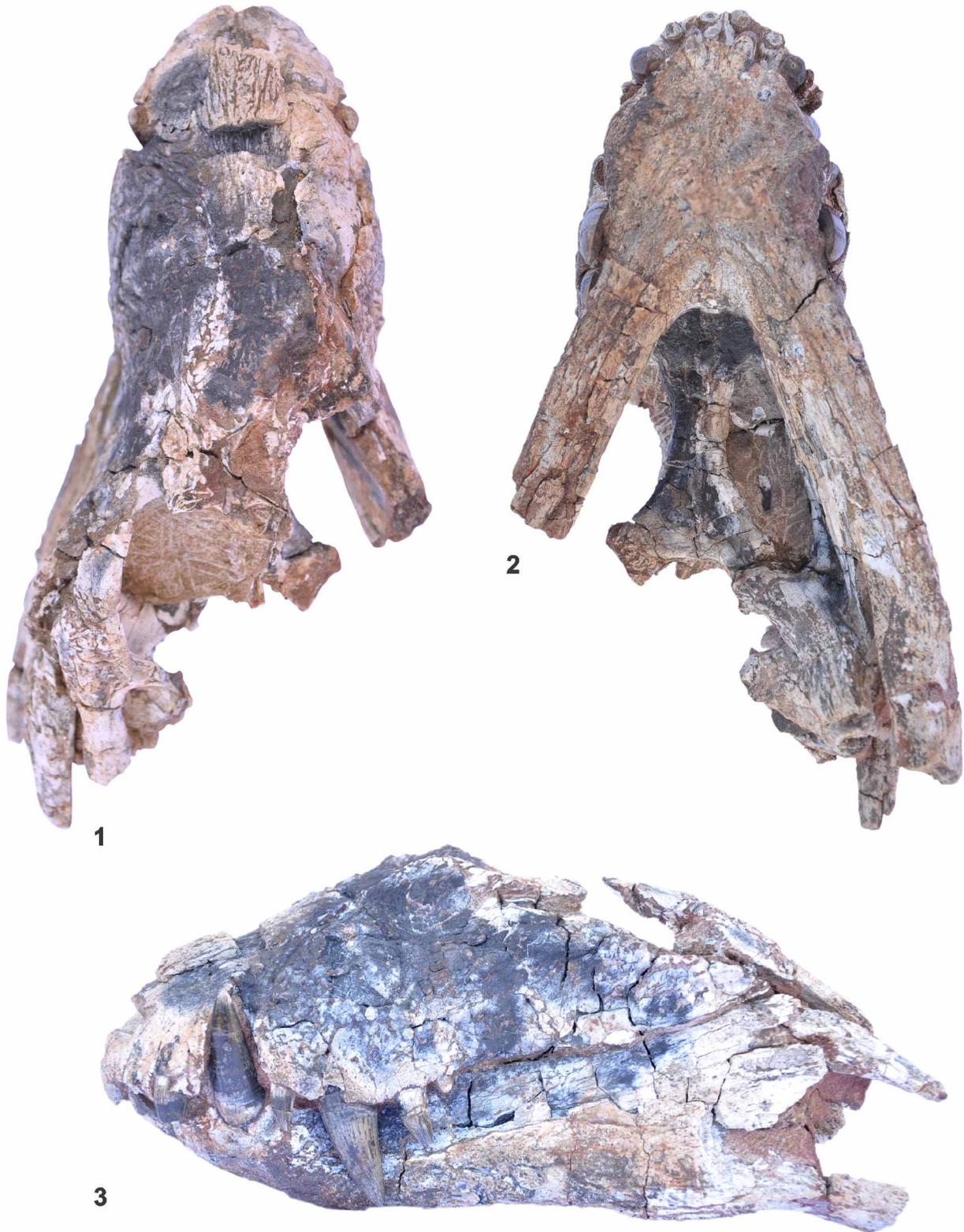


PLATE 3. Paratype of *Campinasuchus dinizi* **gen. nov. et sp. nov.** (CPP 1234). 1, dorsal view; 2, palatal view; and 3, left lateral view of the partial skull and mandible.

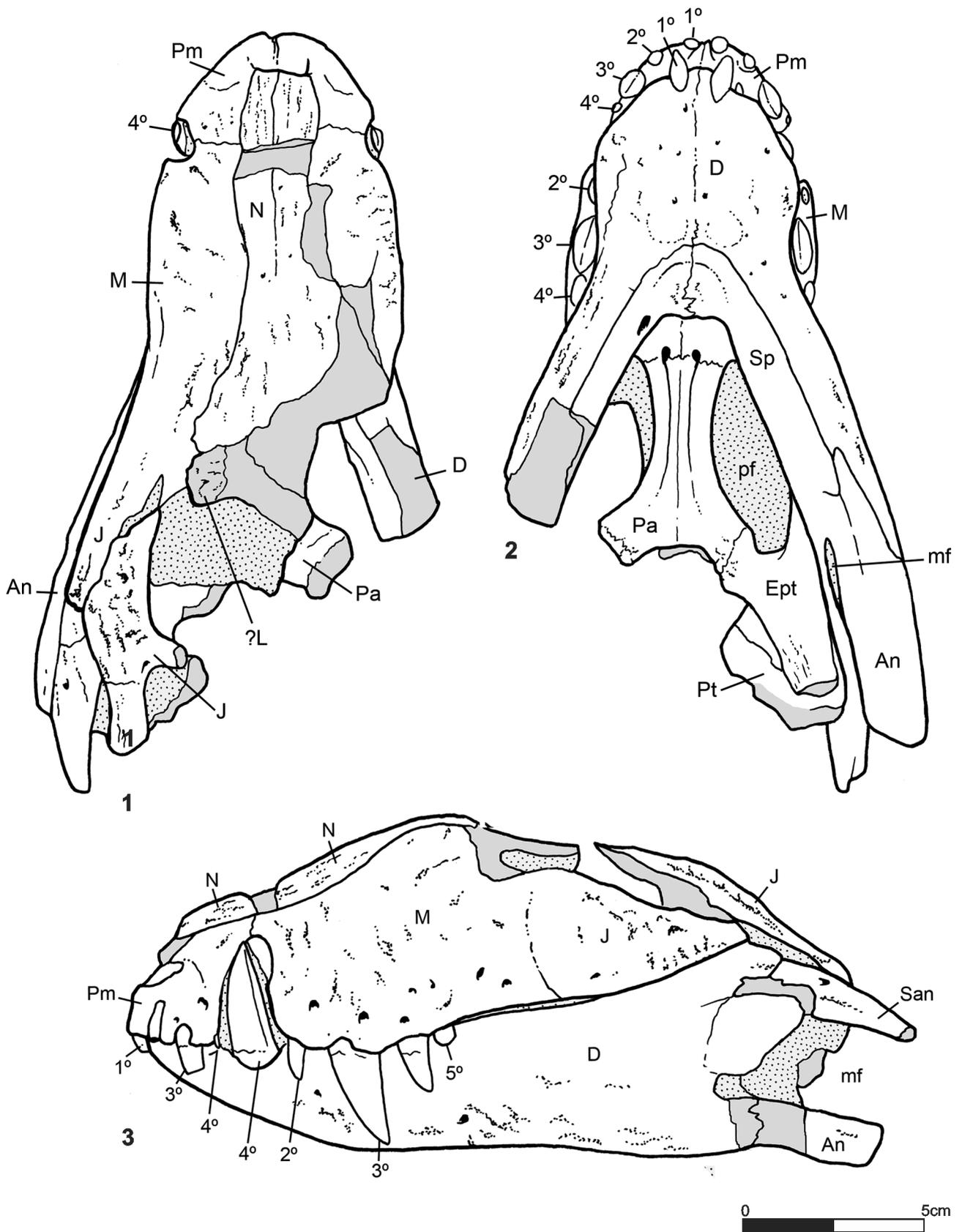


PLATE 4. Schematic drawings of the paratype of *Campinasuchus dinizi* **gen. nov. et sp. nov.** (CPP 1234). 1, dorsal view; 2, palatal view; and 3, left lateral view of the partial skull and mandible. Grey indicates broken surfaces and regular dotted grey indicates matrix.

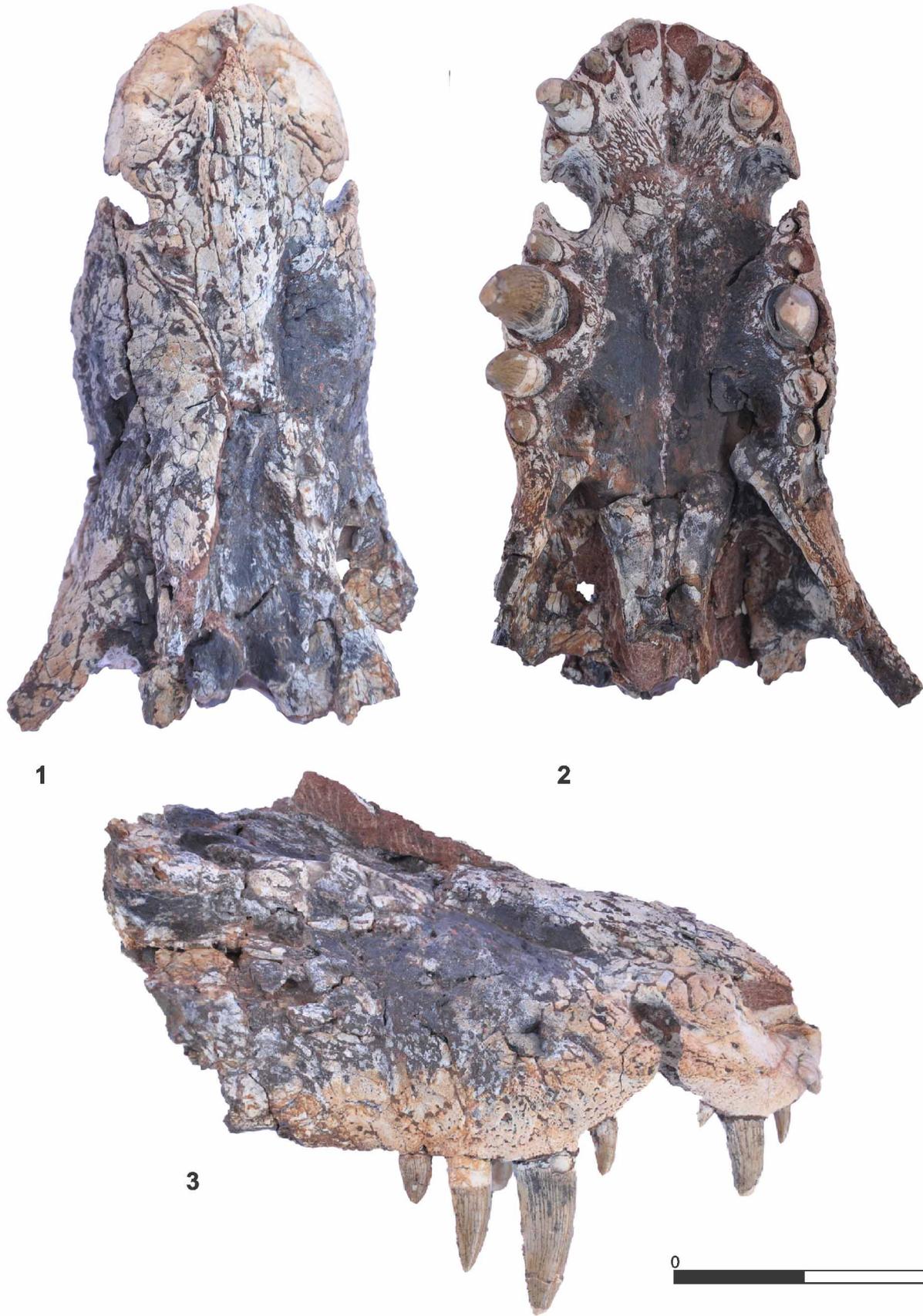


PLATE 5. Specimen CPP 1236 of *Campinasuchus dinizi* **gen. nov. et sp. nov.** 1, dorsal view; 2, palatal view; and 3, right lateral view of the partial skull.

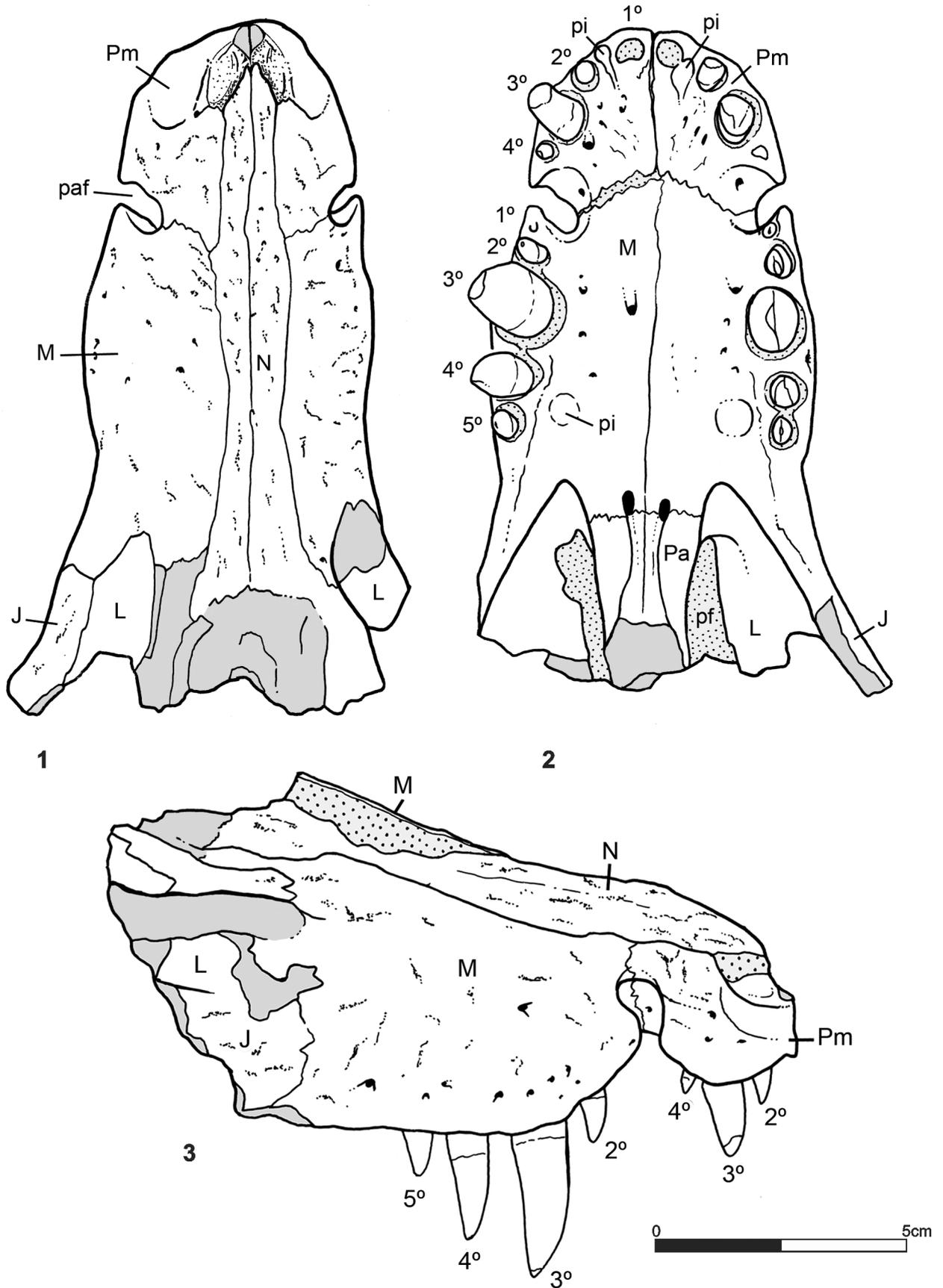


PLATE 6. Schematic drawings of specimen CPP 1236 of *Campinasuchus dinizi* **gen. nov. et sp. nov.** 1, dorsal view; 2, palatal view; and 3, right lateral view of the partial skull. Grey indicates broken surfaces and regular dotted grey indicates matrix.



PLATE 7. Specimen CPP 1237 of *Campinasuchus dinizi* **gen. nov. et sp. nov.** 1, left lateral view; 2, detail of the anterior portion of the rostrum, presenting the external nares; and 3, detail of bony septum that divides the external nares.

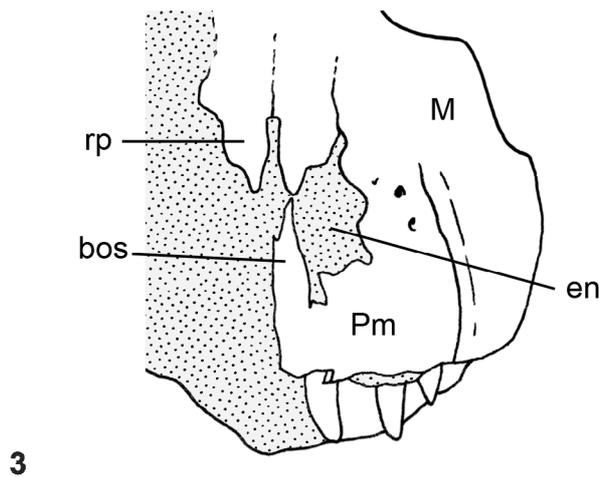
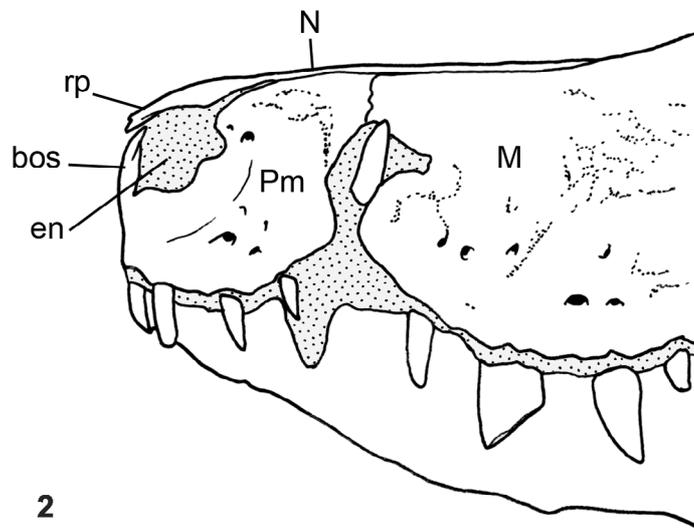
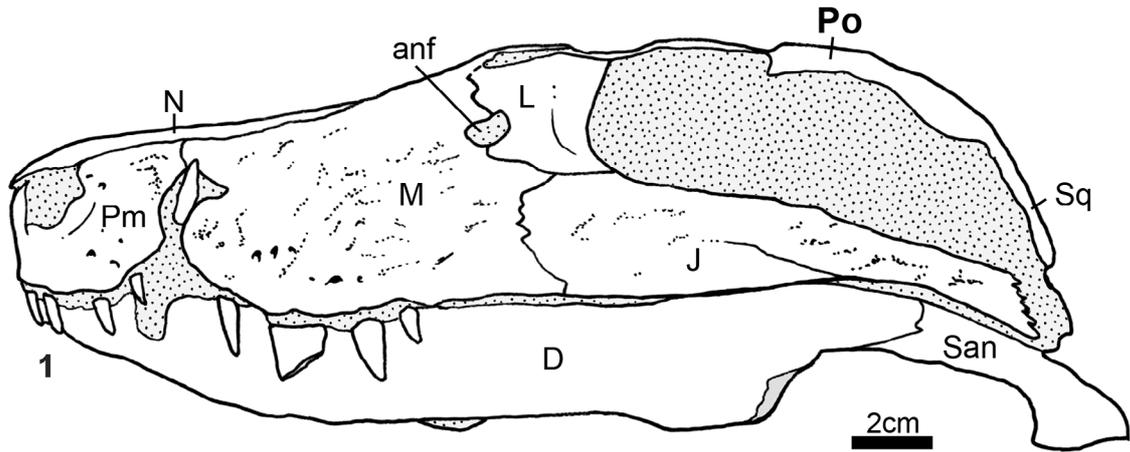


PLATE 8. Schematic drawings of specimen CPP 1237 of *Campinasuchus dinizi* **gen. nov. et sp. nov.** 1, left lateral view; 2, detail of the anterior portion of the rostrum, presenting the external nares; and 3, detail of bony septum that divides the external nares. Grey indicates broken surfaces and regular dotted grey indicates matrix.



PLATE 9. Reconstruction of the *Campinasuchus dinizi* skull in lateral view. 1, osteology and 2, life restoration in digital sculpture (art by Rodolfo Nogueira).

The frontals are fused forming a quadrangular bone bordered laterally by the prefrontal, anteriorly by the nasal, posteriorly by the parietal, and posterolaterally by the postorbital. The dorsal surface of the frontals is concave with a sharp and elevated medial crest running axially. Contact with the nasals is extremely reduced by the medial expansion of the prefrontal. The frontal contacts the prefrontals along a relatively straight suture. The frontal is higher in relation to the posterior border of the prefrontals. Based on CPP 1237, the frontal contributes slightly to the supratemporal fossa. In CPP 1235, it is difficult to observe this trait because sutures are not well preserved.

The parietals are fused and contact the frontals anteriorly, the supraoccipital posteriorly, and the squamosal posterolaterally. It is a very narrow triradiate bone that borders the medial and posterior margins of the supratemporal fenestrae. The dorsal surface of the parietal is higher than the frontal. Between the supratemporal fenestrae, the parietal forms a narrow, raised ridge. The supratemporal fenestra is smaller than the orbit; the medial margin formed by the parietal is convex, while it is straight along the lateral border. They extend beyond the limits of the infratemporal fenestra, nearly reaching the posterior border of the skull.

The postorbital is a robust bone that dorsally contacts the frontal, squamosal and parietal, and ventrally contacts the jugal and quadratojugal. Posteromedially, the postorbital forms the curved border of the supratemporal fenestra, meeting the squamosal along a broad straight suture. Dorsally, the postorbital is heavily ornamented. The anterior descending process of the postorbital forms a prominent crest decreasing ventrally that forms the posterodorsal edge of the orbits. At its contact with the jugal, it is circular in cross-section. The posterior descending process is smaller and laminar, and contacts the quadratojugal through a dorsoventrally oriented suture located immediately posterior to the dorsal corner of the infraorbital fenestra. In CPP 1235, the postorbital has an anteriorly oriented depression on its anterolateral border, above the anterior descending process, that possibly corresponds to the facet for a palpebral bone.

In dorsal view, the squamosal is V-shaped, with its point forming the posterolateral corner of the cranial table. Anteriorly, it contacts the postorbital, medially the parietal and supraoccipital, but these latter sutures are not clearly observed in the holotype CPP 1236. In dorsal view, the squamosal forms the posterior and lateral borders of the supratemporal fenestra and, in lateral view, it limits dorsally and posteriorly the otic recess. The ventrolateral-process of the squamosal descends posteroventrally to contacts the quadrate through an almost vertical suture, located immediately posterior to the *incisura otica*. In posterior view, the suture between squamosal and exoccipital is partially observed in the left paraoccipital process of CPP 1235. In this specimen, the process of the squamosal descends to reach the level of the occipital condyle. The angle between the plane of the skull roof (squamosal) and the quadrate is 60°.

The quadratojugal is a dorsoventrally elongate element. It contacts anteriorly the jugal, anterodorsally the postorbital, posteriorly the quadrate, and probably posterodorsally the squamosal. The suture with the jugal is interdigitated, almost vertical and positioned close to the posteroventral corner of the infratemporal fenestra. The suture with the quadrate is almost straight running in posteroventral-to-antrodorsal direction. Near the ventral border of the skull, this suture is strongly interdigitate process delimiting the post. The ascending process delimiting the posterior border of the triangular-shaped infratemporal fenestra is constricted in its middle region, at the level of lower edge of the *incisura otica*.

The quadrate is posteroventrally inclined 45° relative to the skull roof. It contacts anteriorly the quadratojugal, dorsally the squamosal, and posteriorly the exoccipital. The pterygoid process of the quadrate is robust and well developed; however, at present the contacts with basisphenoid and pterygoid could not be observed clearly. The contact with the exoccipital is partially visible in ventral view. The lateral surface of the quadrate has a shallow depression for muscle attachment located posterior to the suture with the quadratojugal and below the otic recess. Dorsally, the otic recess of the quadrate is highly fenestrated. The condylar surface is rounded and faces posteroventrally, the medial condyle more ventrally projected than the lateral one. In the posterior view, the quadrate has an oval, laterally opened foramen.

The supraoccipital is a triangular-shaped bone that contacts the parietal, squamosals and exoccipitals; however the sutures among these elements are not clear. It is exposed on the cranial roof, separating the parietal from the posterior margin of the skull. The contribution of the supraoccipital to the occipital wall is unknown because of the poorly preserved sutures among elements in the available specimens.

The exoccipitals meet medially, dorsal to the foramen magnum. They extend laterally into the paroccipital processes, which contact the quadrates and squamosals. Unfortunately, sutures in this region are unclear.

The basioccipital comprises the small, rounded occipital condyle and forms a narrow tuberosity that extends laterally. It forms the ventral border of the foramen magnum and is inclined, facing posteroventrally.

The basisphenoid is partially preserved in CPP 1235. On the left side of this specimen, there is a small, circular foramen, interpreted as the lateral Eustachian foramen, located on the suture between the basisphenoid and basioccipital.

The pterygoids are partially preserved. They meet to form a large plate behind the internal nares and expand laterally to form flattened laminar lateral pterygoid flanges. Here they meet the ectopterygoid along their lateral border. The posterior projection of the pterygoids is badly preserved in CPP 1235 (not available in CPP 1237 at present) precluding any information about its contact with the basicranial portion.

The ectopterygoids contact the medial surface of the jugals along a broad suture. They extend ventrally to contact the pterygoid flanges and anteromedially to contact the palatines, forming the lateral borders of the secondary choanae. The palatal surface of the ectopterygoids is flat and laminar, in contrast to the ventrally concave ectopterygoids of other baurusuchids.

The palatines are triangular and contact the maxilla anteriorly. They border two elongated suborbital fenestrae positioned anteriorly. A large anteroposteriorly directed depression is present on each palatine between the mid line and the suborbital fenestra. In CPP 1234 and CPP 1236, these depressions end in a oval foramen, located immediately anterior to the transverse palatine-maxillar suture.

Mandible. The mandible is partially preserved and still in articulation with the skull in the holotype (CPP 1235), CPP 1234, and CPP 1237. In general morphology, it is sub-triangular in lateral view, becoming shallower anteriorly. The splenials participate in the mandibular symphysis. A transverse depression on the ventral surface of the splenials is present at the symphysis, posterior to the dentary-splenial suture. In ventral view, the dentary-splenial suture is anteriorly convex within the symphysis. In lateral view, the mandibular outline varies in its height along its length. There is a slight elevation of the dorsal margin dorsal to the mandibular fenestra. The external surface of the mandible is sculptured the same manner as the skull.

The dentary forms the majority of the mandibular length and contains ten teeth. Anteriorly, the dentary is overhung by the premaxilla, the first tooth creating an occlusal pit between the first and second premaxillary teeth. The fourth dentary tooth is extremely enlarged in comparison with the other teeth and fits into a partially enclosed notch in the rostrum at the premaxilla-maxilla contact. This tooth has a rounded transverse section and possesses serrated carinae on the mesial and distal edges. Posteriorly, the dentary extends as far as the mandibular fenestra, forming the anterodorsal edge of the fenestra. The dentary does not extend beneath the fenestra. The fused dentary symphysis is long and extends posteriorly as far as the level of the sixth dentary tooth. The splenials contribute extensively to the symphysis, meeting the dentary along an anteriorly convex suture. The posterior margin of the mandibular symphysis is at the level of the ninth dentary tooth. Posteriorly the splenials border the anterior margins of the mandibular fenestrae.

The angular contacts the dentary anteriorly and posteriorly meets the surangular and articular. It delimits the ventral margin of the mandibular fenestra. This fenestra is large, with its main portion located posterior to the orbit, roughly at the level as the infratemporal fenestra. The angular is elongated with the dorsal and ventral borders nearly parallel to the jaw margins.

The surangular is relatively straight. It borders the mandibular fenestra dorsally, contacting the dentary anteriorly and the angular posteroventrally. The suture with the angular is straight. The left articular of the holotype (specimen CPP 1235) is complete. The glenoid consists of two distinct fossae for articulation with the quadrate condyles. The lateral fossa is anteroposteriorly larger than the medial one, faces dorsally, and has a posterior sharp crest. The medial fossa is smaller and inclined to face dorsomedially. The retroarticular process is sub-triangular in dorsal view, and is directed posterolaterally.

Comparisons and discussion

This new taxon—*Campinasuchus dinizi*—differs morphologically from other baurusuchids most notably by its relatively shorter, anteriorly tapering, and downwardly directed snout (Plate 9). *Baurusuchus salgadoensis* has a

straight posterior skull border continuous with the dorsal margin of the rostrum, two fused palpebral bones, an elliptical orbit, and a convex frontal, features not found in *C. dinizi*. Additionally, the supratemporal fenestrae are smaller than the orbit, differing from the relatively large fenestrae of *Baurusuchus salgadoensis*. Due to the fragmentary nature of *Baurusuchus albertoi* these features cannot be assessed in this species. Another notable feature of *C. dinizi* is the position of the mandibular fenestra, located posterior to the orbit, nearly at the level of the infratemporal fenestra.

The skull of *Stratiotosuchus maxhechti* is heavily ornamented with irregular ridges, in contrast with *Campinasuchus dinizi*, in which the surface of the skull is ornamented with irregular grooves and ridges. The orbit is sub-rectangular in *Stratiotosuchus*, differing from the circular orbit of *Campinasuchus*. In *Stratiotosuchus* the supratemporal fenestra is larger than in *Campinasuchus* and pear-shaped, the infratemporal fenestra is subtriangular and is smaller than the supratemporal fenestra, and the external nares are anterodorsally located in a depressed area of the premaxillae, and are separated from each other by a small bony septum. The premaxilla is short and contains three ziphodont teeth, while the premaxilla of *Campinasuchus* contains four teeth, similar to *Baurusuchus*. The maxilla of *Stratiotosuchus* is sub-rectangular in shape, with the lateral surface nearly vertical and forming most of the lateral part of the rostrum. The dorsolateral portion of the maxilla is also very thick, making the skull of *Stratiotosuchus* larger and longer than those of *Baurusuchus* and *Campinasuchus*. The nasal of *Stratiotosuchus* is long and forms the posterior border of the external nares; the suture between the nasals and the frontal is V-shaped. The prefrontal forms the anterodorsal border of the orbit and is trapezoidal in shape. Posterior to this bone, the postorbital forms the anterolateral margin of the supratemporal fenestra. The jugal is robust, with a well-marked lateral flange, extending anteriorly well before the orbit (Campos *et al.* 2001). These features all differ from *Campinasuchus*. Interestingly, both *Campinasuchus* and the holotype of *Stratiotosuchus* differ from a specimen recently assigned to *Stratiotosuchus* by Pinheiro *et al.* (2008), in which the quadrate is nearly vertically oriented. However, in both *Campinasuchus* and the referred specimen of Pinheiro *et al.* (2008), the last maxillary tooth is close to the level of the anterior edge of the suborbital fenestra, a condition markedly different from that observed in the holotype of *Stratiotosuchus*. Further analyses will be necessary to clarify the taxonomy of this referred specimen.

The Argentinean baurusuchid *Cynodontosuchus rothi* is based on a partial rostrum. The rostrum of *Cynodontosuchus* is not as tall as that of *Baurusuchus* and *Campinasuchus* and contains five maxillary teeth (Woodward 1896; Buffetaut 1982 b), including a very large maxillary caniniform (Steel 1973). There are probably three small conical teeth in the premaxilla. In *Campinasuchus* there are four premaxillary and five maxillary teeth, with an interalveolar diastema between the first and the second premaxillary teeth for reception of the first mandibular tooth. As in other baurusuchids, *Cynodontosuchus* has a hypertrophied mandibular tooth (probably the fourth) that fits into a notch between the premaxilla and maxilla (Gasparini 1972). The anterior part of the mandibular rami are slightly divergent and the symphysis is nearly twice as long as wide (Steel 1973), differing from the wider symphysis of *Campinasuchus*.

Wargosuchus australis, also from Argentina, is based on a fragment of a snout and a portion of the cranial roof (Martinelli & Pais 2008). *Wargosuchus* possesses a deep median groove on the frontals, an extremely reduced contact between nasals and frontals due to the presence of medially expanded prefrontals, a large depression for the olfactory bulbs, three large foramina surrounding the large, smooth perinarial depression, and a hypertrophied, conical last premaxillary tooth followed by a large paracanine fossa. All of these features were considered diagnostic of this species (Martinelli & Pais 2008). Differing from *Baurusuchus* and *Stratiotosuchus*, *Wargosuchus* and *Campinasuchus* are now known to share the presence of prefrontals without a median contact, a plesiomorphy typical of most crocodyliforms. Nonetheless, as previously suggested, the medial extension of the prefrontals (making contact in *Baurusuchus* and *Stratiotosuchus* and, thus, precluding a nasal-frontal contact) could be a potential synapomorphy of Baurusuchidae (Martinelli & Pais, 2008). As such, the condition shared between *Wargosuchus* and *Campinasuchus* seems to be plesiomorphic with regard to other baurusuchids.

Pabwehshi pakistanensis Wilson, Malkane and Gingerich, 2001, from the Pab Formation (Maastrichtian, Balochistan Province) of Pakistan, is known from a snout and an anterior portion of the left and right mandibular rami fused at the symphysis (Wilson *et al.* 2001). This taxon represents a medium-sized baurusuchid, with a reduced anterior portion of the rostrum retaining three premaxillary teeth. It is characterized by autapomorphies such as: a dorsally inset first premaxillary alveolus; a prominent premaxillary lip overhanging the external nares; a diverticulum in the posterodorsal corner of the external naris; an enlarged, caniniform sixth dentary tooth; reduced fourth

and fifth dentary teeth; and a fossa positioned just posterior to the second maxillary tooth (Wilson *et al.* 2001). These features all distinguish *Pabwehshi* from *Campinasuchus*.

Phylogeny. Despite a multitude of well preserved and nearly complete specimens and strong support for monophyly of Baurusuchidae, the phylogenetic position of the clade among basal mesoeucrocodylians remains poorly resolved. Potentially convergent similarities between baurusuchids and sebecids, including a laterally compressed rostrum and serrated, laterally compressed teeth, is the primary source of conflict between different phylogenetic hypotheses (e.g. Benton & Clark 1988; Buckley & Brochu 1999; Buckley *et al.* 2000; Clark 1994; Ortega *et al.* 1996; Pol 2003; Sereno *et al.* 2003; Tykoski *et al.* 2002; Turner & Calvo 2005; Turner Sertich 2010). Historically, these similarities have influenced workers to unite *Sebecus* and *Baurusuchus* in Sebecosuchia (e.g. Colbert 1946; Buffetaut 1982). Among the earliest phylogenetic analyses of crocodyliform interrelationships, Benton and Clark (1988) proposed two hypotheses of relationships for basal metasuchians, the first supporting the inclusion of *Baurusuchus* and *Sebecus* in Sebecosuchia, the other placing *Baurusuchus* basally among notosuchian taxa and *Sebecus* closer to the root of Neosuchia. Further analyses by Clark (1994) reinforced the latter hypothesis of a more basal position for *Baurusuchus*. Conversely, Gasparini *et al.* (1991), recovered a monophyletic Sebecosuchia (*Sebecus icaeorhinus* Simpson, 1937 + *Baurusuchus pachecoi* Price, 1945), supported by the following synapomorphies: laterally compressed rostrum, absence of antorbital fenestra, internal nares very large, a strongly concave palate, and vertical pterygoids. The addition of other Tertiary sebecids such as *Bretesuchus bonapartei* Gasparini, Fernandez and Powell, 1993 and *Sebecus huilensis* Langston, 1965 did not alter this hypothesis (Gasparini *et al.* 1993). More recently, a monophyletic Sebecosuchia, including various baurusuchid and sebecid taxa, has been recovered by many other authors (e.g. Buckley & Brochu 1999; Buckley *et al.* 2000; Ortega *et al.* 1996; Pol 2003; Sereno *et al.* 2003; Tykoski *et al.* 2002; Turner & Calvo 2005; Turner & Sertich 2010). The close relationships of Sebecosuchia with other notosuchian taxa led Ortega *et al.* (2000) to unite them in a common clade, Ziphosuchia (*Notosuchus* + *Libycosuchus* + Sebecosuchia). Sebecosuchian interrelationships were explored extensively by Turner and Calvo (2005) whose analyses included up to seven sebecid and baurusuchid taxa including *Baurusuchus* and *Pabwehshi*. Topologies produced in this analysis recovered baurusuchids nested as derived members of Sebecosuchia, with weak support for Sebecidae and Baurusuchidae. Alternatively, the analysis of Larsson and Sues (2007) placed *Baurusuchus* basally among metasuchians and recovered a close relationship between sebecids and peirosaurids (+ *Pabwehshi*) in a monophyletic Sebecia. A slightly modified version of this hypothesis was presented by Sereno and Larsson (2009), nesting *Baurusuchus* among derived notosuchians. Regardless of proposed relationships between baurusuchids and sebecids, nearly all recent analyses recover Baurusuchidae deeply nested among derived notosuchians (e.g. Carvalho *et al.* 2004; Sereno & Larsson 2009; Turner & Sertich 2010).

Carvalho *et al.* (2004) redefined Sebecosuchia (establishing the monophyletic taxon Baurusuchoidea; (however, Sebecosuchia has priority), as the most recent common ancestor of *Sebecus* and Baurusuchidae. This clade was supported by the combination of the following synapomorphies: distance from the anterior orbital edge to the anterior contour of rostrum at least twice than the distance from anterior orbital edge to posterior parietal limit; presence of a premaxillo-maxillary notch; the last premaxillary alveolus is not the largest of premaxillary tooth row; teeth are set in isolated alveoli; caudal branch of quadrate being at least as long as broad; enlarged second or third alveolus of maxilla; skull roof square-shaped or rectangular and with a longitudinal dominant axis; lateral surface of the straight jugal not visible in ventral view. Furthermore, Baurusuchidae Price, 1945 was redefined as the most recent common ancestor of *Baurusuchus* and *Stratiotosuchus* and all of their descendants. This clade is supported by the combination of the following synapomorphies: presence of a foramen at 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; septated internal nares; and fewer than ten maxillary teeth. The new taxon *Campinasuchus dinizi* is here considered a member of this clade, sharing these features.

Conclusion

Campinasuchus dinizi constitutes a new genus and species of Baurusuchidae that increases the diversity of terrestrial crocodyliforms from the continental Cretaceous deposits of Brazil. This new taxon is notable for its short

snout and marked tooth size heterodonty relative to other known baurusuchid taxa. The geology of its locality indicates an environment marked by long dry intervals interrupted by periods of heavy rains that created relatively deep lakes and temporary ponds during flood periods. Climatic seasonality, with a relatively warm and arid climate alternating with wet periods, was potentially an important driver of crocodyliform diversity and abundance in the continental environments of the Brazilian Late Cretaceous.

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Anatomical abbreviations:

An: Angular; Ar: articular; anf: antorbital fenestra; Bs: Basisphenoid; Bo: Basioccipital; bos: bony septum; ch: secondary choana; D: Dentary; en: external nares; Eoc: Exoccipital; Ept: Ectopterygoid; Fr: Frontal; io: *incisura otica*; itf: infratemporal fenestra; J: Jugal; L: Lacrymal; leu: lateral eustachian foramen; M: Maxilla; mf: mandibular fenestra; N: Nasal; oc: occipital condyle; or: orbit; P: Parietal; Pa: Palatine; paf: paracaniniform fossa; pf: palatine fenestra; Pfr: Prefrontal; pi: pit on premaxilla; Pm: Premaxilla; Po: Postobital; Pt: Pterygoid; Q: Quadrate; Qj: Quadratojugal; rp: rostral process; r: tooth root; San: Surangular; se: septum; So: Supraoccipital; Sp: Splenial; Sq: Squamosal; stf: supratemporal fenestra. Numbers refer to tooth positions.

Institutional abbreviation:

CPP—Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Brazil