

A new crocodylomorph (Sphagesauridae, Notosuchia) with horn-like tubercles from Brazil

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A new species of a bizarre notosuchian mesoeucrocodylian is reported here. *Caryonosuchus pricei* gen. et sp. nov. was found in the outcrops of the Adamantina Formation (Campanian–Masstrichtian) in São Paulo State, Brazil, and shows a typical sphagesaurid dentition: strong and short teeth, obliquely implanted with the crown of the upper teeth showing a rounded anteriolabial margin and a strong compressed posteriolingual edge developed into a carina, ornamented by developed ridges and denticles. Amongst the diagnostic features of the new taxon are the presence of horn-like tubercles on the premaxilla and maxilla, never reported in this group before. The occurrence of *C. pricei* increases the diversity of sphagesaurids and confirms that all members of this clade, only recorded in Late Cretaceous deposits from Brazil so far, share the same dentition.

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ADDITIONAL KEYWORDS: Bauru Group – *Caryonosuchus* – Crocodylomorpha – Sphagesauridae – *Sphagesaurus* – Upper Cretaceous.

INTRODUCTION

Several deposits in South America have provided fossil crocodylomorphs that have played an important role in the understanding of the evolutionary history of this group (e.g. Price, 1955; Kellner, 1987; Bonaparte, 1991; Gasparini, Chiappe & Fernandez, 1991; Brochu, 2003; Pol, 2005; Candeiro & Martinelli, 2006; Calvo *et al.*, 2007; Barbosa, Kellner & Viana, 2008; Campos *et al.*, 2011). Amongst the most interesting clades represented in the continent is the Notosuchia, whose known diversity has increased tremendously as a result of discoveries in recent decades

(e.g. Carvalho & Bertini, 1999; Pol & Apesteguía, 2005; Nobre & Carvalho, 2006; Andrade & Bertini, 2008a, b, c; Kellner *et al.*, 2009). Regarded as a typical Gondwanan group, those crocodylomorphs show remarkable variation in tooth morphology, suggesting diverse feeding habits (Kellner *et al.*, 2011, this volume).

Amongst the most bizarre notosuchians are the Sphagesauridae. The first species to be described was *Sphagesaurus huenei* by Price (1950), based on two isolated teeth. This species was later regarded as representing a distinctive family (Kuhn, 1968) characterized by an unusual dentition (see also Marinho & Carvalho, 2007; Andrade & Bertini, 2008a). Since then, several more specimens have been collected and classified as the genus *Sphagesaurus* (e.g. Kellner &

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Campos, 1999; Andrade & Bertini, 2008a) and as the species *S. huenei* (Pol, 2003).

Recently Marinho & Carvalho (2009) described *Armادillosuchus arrudai*, demonstrating that the Sphagesauridae is also diverse at the genus level. Another rostrum (DGM 1411-R), briefly reported in the literature (Kellner, Campos & Price, 1995; Kellner & Campos, 1999), also displays a distinctive cranial anatomy, further highlighting the diversity within sphagesaurids. In addition, it became clear with the newly described cranial remains that all the different species display basically the same dentition, which is undistinguishable from the type material of *S. huenei*.

In this paper we describe the specimen DGM 1411-R that represents a new taxon (*Caryonosuchus pricei* gen. et sp. nov.). Although a formal taxonomic revision of the Sphagesauridae is beyond the scope of this paper, the authors would like to note that one is needed because of the fact that *S. huenei* might be considered a *nomen dubium*.

ABBREVIATIONS

DES-UBris, Department of Earth Sciences, University of Bristol, Bristol, United Kingdom; DGM, DNPM, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil – presently the Earth Science Museum; IGCE-UNESP, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, Brazil; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MPMA, Museu de Paleontologia de Monte Alto, Monte Alto, São Paulo, Brazil; RCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Brazil; UFRJ DG, Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

SYSTEMATIC PALAEONTOLOGY

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
Mesoeucrocodylia Hay, 1930
Notosuchia Gasparini, 1971
Sphagesauridae Kuhn, 1968

CARYONOSUCHUS GEN. NOV.

Type species: Caryonosuchus pricei gen. et sp. nov.

Etymology: From the Greek *cáryon* meaning protuberances and *souchus*, meaning crocodile.

Diagnosis: The same as for the genus.

CARYONOSUCHUS PRICEI GEN. ET SP. NOV.

Holotype: Anterior portion of the skull and lower jaw housed at the Earth Science Museum of the Departamento Nacional da Produção Mineral under the number DGM 1411-R (cast at the Museu Nacional/UFRJ) (Figs 1–4).

Etymology: The specific name honours Llewellyn Ivor Price, a palaeontologist who described the genus *Sphagesaurus* and also had a partial (unpublished) manuscript on the specimen DGM 1411-R (Kellner *et al.*, 1995).

Type locality: Vicinity of Presidente Prudente City, south-west São Paulo State, Brazil.

Type horizon: Adamantina Formation, Bauru Group; Campanian to Maastrichtian (Gobbo-Rodrigues, Petri & Bertini, 1999, Batezelli *et al.*, 2003).

Diagnosis: Sphagesaurid that can be separated from all other members of this clade based on the following combination of characters (autapomorphies are indicated with an asterisk): rostrum with horn-like tubercles on the premaxilla* and on the maxilla*; rostrum showing rough ornamentation with grooves and bony ridges*; first tooth posterior to the premaxillary hypercaniniform is supported exclusively by the premaxilla; palatine ramus of maxilla covered by low crests and shallow wrinkles; shallow fossa present at symphysis, medial to the first three teeth.

Remarks: Kellner & Campos (1999) briefly mentioned the specimen DGM 1411-R and tentatively assigned it to *Sphagesaurus* sp., but in the light of new sphagesaurid material recently described in the literature, we regard this specimen as representing a new genus and species.

Description

The holotype of *Caryonosuchus pricei* (DGM 1411-R) consists of the anterior portion of the rostrum, whose bone surface is extremely well preserved (Fig. 1). The upper jaw shows both premaxillae and maxillae, with opposite elements unfused. The nasal is missing, exposing the internal region of the external naris. The tip of the dentary that was originally preserved in close contact with the upper jaw was separated during mechanical preparation. The upper teeth are in their natural position whereas several teeth of the lower jaw were displaced anteriorly during the fossilization process.

Premaxilla: The right premaxilla is more complete than the left and includes the palatine ramus (Fig. 1). This bone has an anterodorsal flange partially covering the external naris that forms a lateral notch. This flange is strongly ornamented, as is the dorsal part of the premaxilla. Two well-developed and ornamented horn-like tubercles are present. On the area of the tubercles, the ornamentation is composed of semicircular well-delimited deep pits and differs from the remaining part of the rostrum. Dorsally, near the suture with the nasal, the pits become shallower, less defined, and elongated, turning into an area covered by elongated sulci and crests that are orientated diagonally in respect to the sagittal plane.

Part of the internal surface of the right nasal cavity is preserved, more extensively than its left counterpart. Although the bone surface is smooth, there is a small area that is lightly ornamented.

The alveolar margins lack ornamentation. The left premaxilla shows one neurovascular foramen located laterally, in an area above the middle point between the first and the second premaxillary teeth. A second and smaller foramen is located posterodorsally, close to the suture with the maxilla.

The right palatine ramus of the premaxilla also shows light ornamentation, with a small foramen medial to the second tooth.

Premaxillary dentition: Two teeth are present in both premaxillae, all incomplete, showing oblique implantation as a result of paramesial rotation (Fig. 2). The first tooth on the left side shows a partial crown and the root, and most probably was a hypertrophied caniniform. The second tooth is entirely supported by the premaxilla.

Maxilla: Both maxillae are incomplete, with the right one better preserved than the left (Fig. 1). This bone partially overlies the premaxilla, a common feature in notosuchids (including other sphagesaurids). As in the premaxilla, the maxilla has the dorsal side heavily ornamented and the lateral side smooth, particularly close to the alveolar margin. At least two tubercles can be identified, which are smaller than the ones found in the premaxilla. The first is horizontally aligned with the two first ones whereas the second is located dorsally and medially in respect to those.

On the left maxilla there are five neurovascular foramina positioned above the alveolar margin,

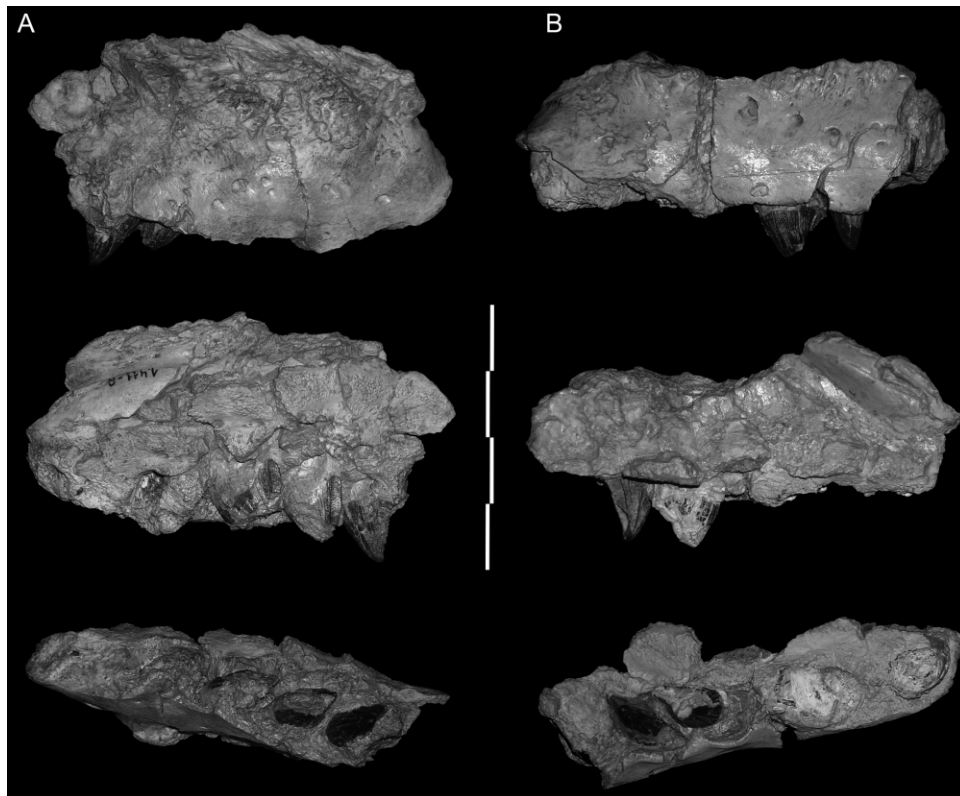


Figure 1. *Caryonosuchus pricei* gen. et sp. nov. (DGM 1411-R), rostrum in lateral (top), medial (middle), and ventral (bottom) views. Note that the right side of the specimen (A) is better preserved than the left side (B). Scale bar = 20 mm.

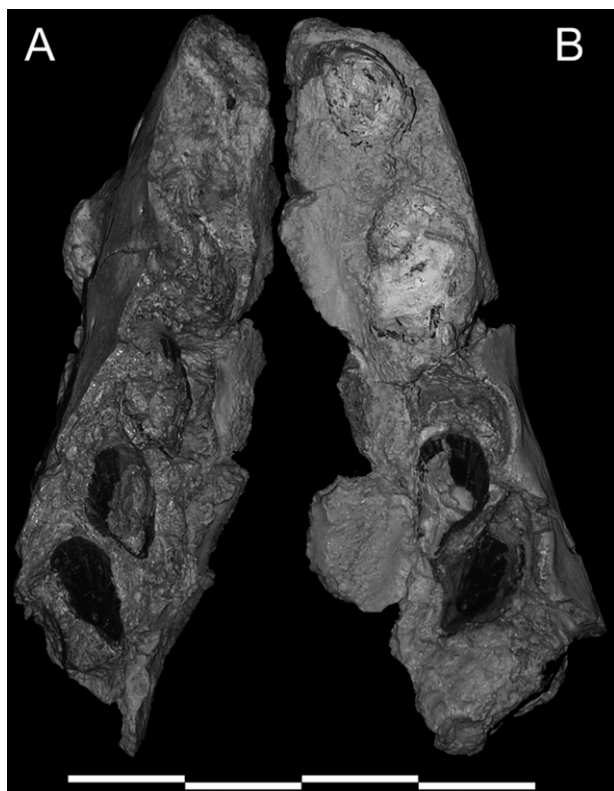


Figure 2. Ventral view of the right (A) and left (B) sections of the upper jaw of *Caryonosuchus pricei* gen. et sp. nov. (DGM 1411-R), showing the oblique disposition of posterior crowns. Scale bar = 20 mm.

forming an anterodorsally arched line. The two anterior-most foramina are located dorsal to the first maxillary tooth and the following are dorsal to the second maxillary tooth. On the right maxilla, the neurovascular foramina are arranged in a more irregular way. The palatine ramus is laterodorsally displaced, and has light but evident ornamentation composed of low crests and shallow wrinkles. Another series of six neurovascular foramina can be identified next to the teeth, on the right maxilla. These foramina are located medially to the teeth, in couples.

Maxillary dentition: There are three teeth preserved in each maxilla, but the third on the left side was damaged during the fossilization process (Fig. 2). All are obliquely implanted with each tooth having the posterolingual portion of the crown ending in a carina and the anteriolabial margin rounded, resulting in a teardrop cross-section. None of the roots are exposed.

The first maxillary tooth on the left side is better preserved than the one on the right side. The apex and part of the lingual portion are not complete. On the labial face, seven undivided ridges that reach the apex of the tooth are present. Smaller ridges,

restricted to the base of the crown can also be observed. On the lingual face there are remnants of only five ridges in the mesial-most section, whereas the remaining surface is destroyed. On both faces, the ridges are smooth, but the enamel is clearly ornamented in a pebbled pattern. Part of the root is dorsally exposed, showing an elliptic cross-section and oblique orientation, supporting the idea that this tooth has undergone paramesial rotation rather than a simple rearrangement of the crown.

Part of the enamel on the second maxillary tooth of the left side has been lost, exposing the dentine. The folded pattern shows that the ridges observed on the teeth express a structural characteristic of the crown, rather than a superficial ornamentation restricted to the enamel. As in the preceding tooth, seven main ridges are present in the labial face and five occur on the lingual side, again complemented by smaller ridges that do not reach the apex. The distance between ridges increases from the posterolingual to the anterolabial edges of the crown. The apex has a rounded shape. A wear surface is present, extending from the apex to the mid-length of the carina. No denticles or pebbled ornamentation can be identified on this surface. This worn down surface is neither a preservation artefact nor created during the collecting or preparation processes, but was produced *in vivo*, as the animal processed food. A similar wear surface is observed on the second maxillary tooth of the right side. This tooth has up to nine basiapical ridges on the labial surface of the crown.

On the third maxillary tooth of the right side, six labial and up to three lingual ridges can be identified. This crown shows a posterior carina, with an undulated basal section that lacks denticles, and an apical section that displays three denticles. No wear surface is observed.

Mandibular symphysis: Only the anterior end of the mandibular symphysis is preserved (Fig. 3). The ventral surface is eroded, suggesting that this portion of the specimen was exposed before collection. The anterior-most section is narrow and widens posterior to the third tooth. A concavity is present close to the anterior tip of the symphysis, positioned medial to the first three teeth. It is shallow, longer than wide, and unknown in other sphagesaurid specimens (including RCL 100).

Mandibular dentition: The right side of the symphysis holds three conical teeth and part of one crown (Figs 3, 4). The first three pairs are mostly procumbent, as in other sphagesaurids and notosuchids. They are very inclined, which is attributed to the taphonomic compression suffered by the specimen

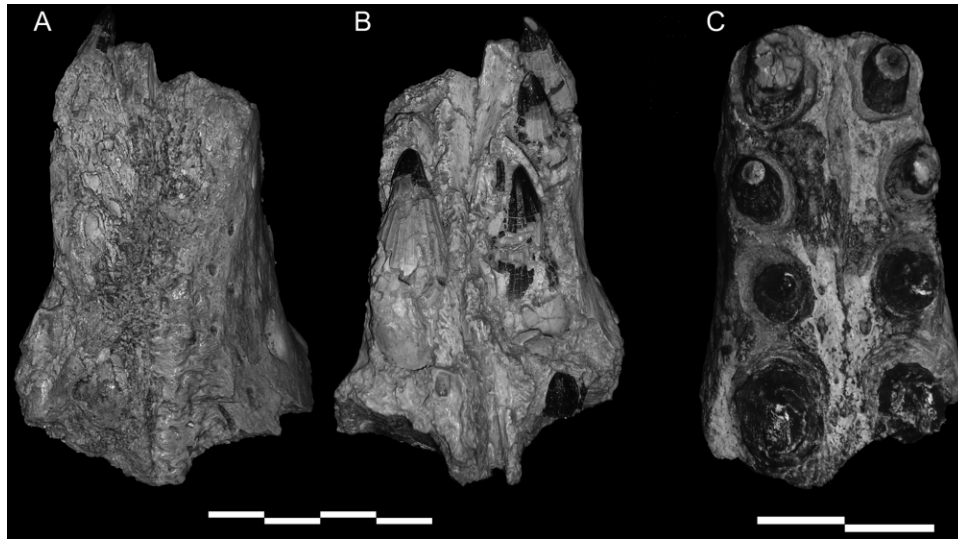


Figure 3. Symphysis of *Caryonosuchus pricei* gen. et sp. nov. (DGM 1411-R), in ventral (A) and dorsal (B) views, in comparative view with the symphysis of *Sphagesaurus huenei* (RCL-100) (C). Note the concave area on the anterior section of the symphysis of *C. pricei* and its wedge-like profile in ventral view. Scale bars = 10 mm.

during the fossilization process. All teeth bear isomorphic, smooth, and nonserrated basiapical ridges and an apical wear facet, which is small and inclined.

Only the apical section of the fourth tooth of the right side is preserved, displaced from its original anatomical position (Fig. 4C). The apex is clearly compressed, consistent with the reversed teardrop morphology typical of sphagesaurids. Additionally, this tooth bears at least three lateral ridges and a carina. Although the medial and basal portions of the carina are not preserved, it is possible to identify three conspicuous denticles in the preserved section. These are proportionally large when compared with the denticles of other ziphosuchian crocodylians, and correspond to what Prasad & Broin (2002) classify as true denticles. However, these denticles are tuberos and do not correspond to the typical cuneiform morphology found in theropodomorph dentitions of highly predacious crocodylomorphs (e.g. *Baurusuchus*, *Stratiotosuchus*, *Sebecus*). They are rather similar to the denticles of *Mariliassuchus*, corresponding to the ziphomorph pattern *sensu* Andrade & Bertini (2008c).

DISCUSSION

The most striking characteristic of *Caryonosuchus pricei* is the autapomorphic presence of horn-like tubercles on the dorsal surface of the premaxilla and the maxilla. Rostral tuberosities such as the ones displayed by the new species are autapomorphic and have never been reported in any other crocodylomorph.

These contrast with the more common horn-like laterodorsal projections present in a few fossil and living Eusuchia (e.g. *Ceratosuchus*, Voay, *Crocodylus siamensis*), which also do not constitute true horns (Brochu, 2007). Apart from the presence of false horns, *C. pricei* also has a very specific pattern of distribution of these structures: the first three are aligned in tandem, with the fourth tubercle medial and posterior to the third. Furthermore, the new species is the only sphagesaurid showing very conspicuous ornamentation over the rostrum, composed of a series of wrinkles, furrows, and sulci that changes to a pattern of deep pits and grooves (as defined by Buffrénil, 1982), similar to the one found in neosuchians.

In extant crocodyliforms, the areas of the skull with such intense ornamentation are covered by only a small amount of soft tissue, mostly dermic/epidermic. It is not likely that these tuberos structures acted as support for true keratinous horns in *C. pricei*.

Further morphological features separate *C. pricei* from the other sphagesaurids. *Armadillosuchus* differs from the new species by the presence of procumbent premaxillary and dentary teeth and an antorbital depression. *Sphagesaurus huenei* (RCL-100) has a comparatively higher skull (in lateral view) and the maxillar portion of the palate smooth, differing in those features from *Caryonosuchus*. The symphysis of the former widens more gradually whereas in *Caryonosuchus* the anterior tip is comparatively thinner (Fig. 2).

Sphagesaurus montealtensis also has a comparatively higher skull and the premaxillary dentition reduced to one tooth (Andrade & Bertini, 2008a),

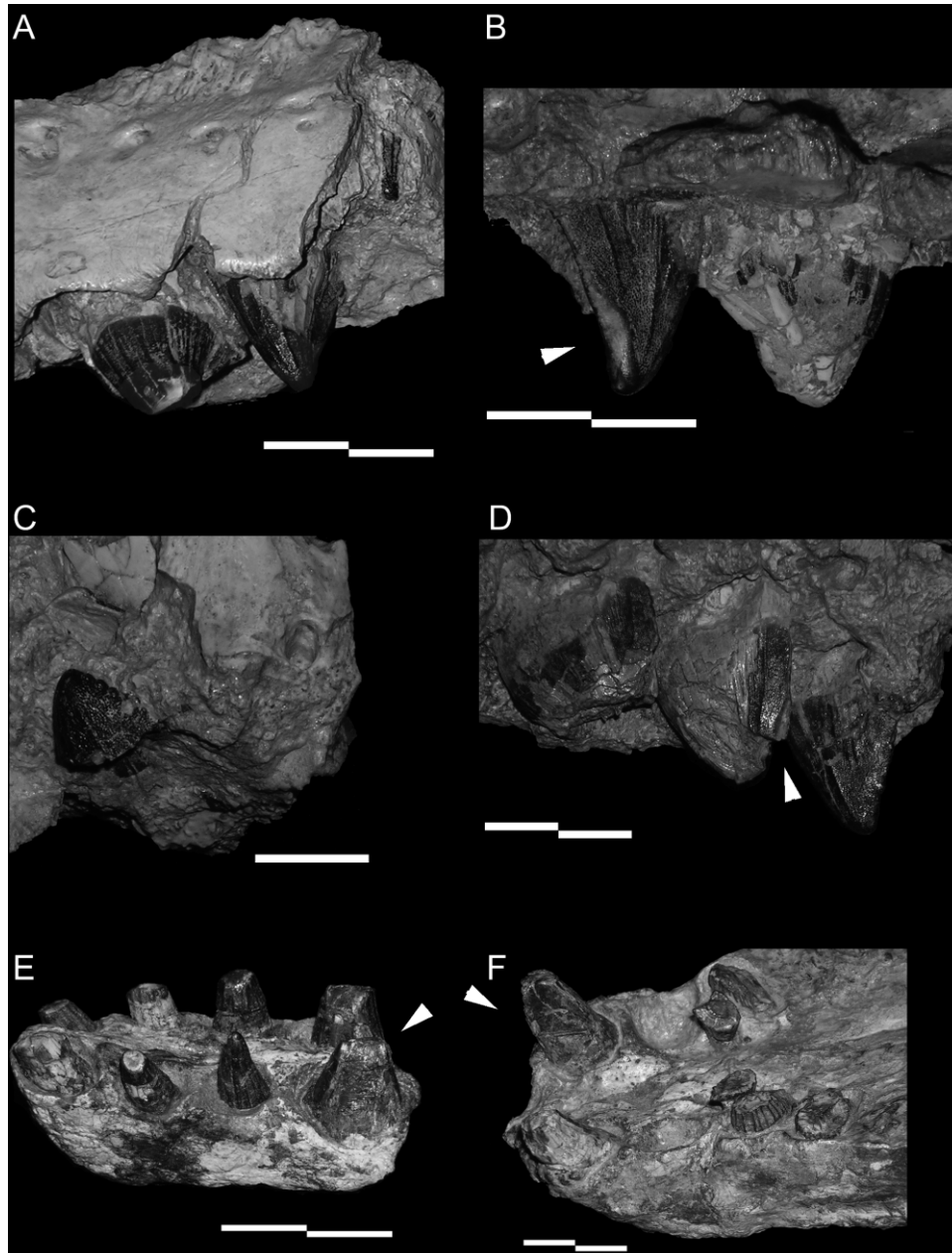


Figure 4. Dentition of *Caryonosuchus pricei* gen. et sp. nov. (DGM 1411-R), in detail. A, ventrolateral view of teeth of the left side, showing the labial face of the crowns with basiapical ridges; B, lingual face of the same teeth, where the pebbled ornamentation and a wear facet are evident. C, apex of symphyseal crown showing tuberos denticles. D, maxillary tooth of the right side, showing the denticulated carina and wear facet. E, symphysis of *Sphagesaurus huenei* (RCL-100) with the first four mandibular pairs of teeth, the last showing extensive wear. F, palate of *S. huenei* (RCL-100) showing the premaxillary hypertrophied caniniforms and the first maxillary teeth. In comparison, RCL-100 shows the same general features, but its ridges seem to be more numerous when compared with the dentition of *C. pricei*. Note that in (A) that the basiapical ridges are evident even in areas where the enamel was not preserved and the dentine is exposed; in (F) the crowns of the fifth dentary teeth are preserved, attached to the palate. White pointers indicate wear facets. Scale bars = 10 mm.

whereas *Caryonosuchus* has a comparatively more anteroposteriorly elongated skull and two premaxillary teeth. *Sphagesaurus montealtensis* also shows a slight constriction of the anterior portion of the maxilla (at the third tooth) with the lateral surface slightly concave, whereas in *Caryonosuchus* the lateral margin is straighter. Lastly, the palatal ramus of the maxilla in *S. montealtensis* has stronger ornamentation than in *Caryonosuchus*.

FINAL REMARKS

Since the discovery of two isolated teeth from different localities that became the holotype and paratype of *S. huenei* (Price, 1950), several more specimens of this bizarre group named Sphagesauridae have been described. Despite the fact that those teeth are quite distinct from any other group of crocodylomorphs, and at that time fulfilled the requirements to establish a new taxon (see Kellner, 2010 for a discussion about the problematic nature of identifying species in the fossil record), it is now clear that they are not sufficient to distinguish the members of this clade from each other and a review of the whole group is needed.

Besides *S. huenei*, to which a complete skull and partial lower jaw (RCL-100) has been assigned (Pol, 2003), two other taxa are classified in this clade: *Sphagesaurus montealtensis* and *Armadillosuchus arrudai*. *Caryonosuchus pricei* adds to the multiplicity of this weird group of crocodylomorphs. Besides the conspicuous features of their dentition that unite them, based on the cranial material known so far the Sphagesauridae are clearly a diversified group, comprising taxa that show several morphological variations including the presence of protuberances on the rostral end of the skull (*Caryonosuchus*), extreme reduction of premaxillary teeth and a small antorbital fenestra (*S. montealtensis*), and a particular shape of the maxilla (*S. huenei* – RCL-100) and the basioccipital–basisphenoid region (*Armadillosuchus*). Unfortunately, almost nothing is known regarding the postcranial elements, except for a few described features of *Armadillosuchus*, which include an unusual body armour (Marinho & Carvalho, 2009).

There is agreement that the particular disposition of the posterior teeth in sphagesaurids provided a powerful shearing mechanism, but disagreement remains about their feeding habits. Price (1950) regarded these crocodylomorphs as predators, whereas Kellner *et al.* (1995) raised the possibility that they might have also been scavengers. Pol (2003) observed extensive wear facets on the postcanine teeth suggesting both lateral and fore-aft movement of the jaw. Marinho & Carvalho (2007) suggested that they might have been omnivorous and Andrade & Bertini (2008a) illustrated *S.*

montealtensis feeding on plant material. At this point it is difficult to establish the diet of this unusual clade of crocodylomorphs that has so far only been found in Late Cretaceous deposits of Brazil.

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