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GR Letter

Adamantinasuchus navae: A new Gondwanan Crocodylomorpha (Mesoeucrocodylia) from the Late Cretaceous of Brazil

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Abstract

A new Late Cretaceous Mesoeucrocodylian from the Adamantina Formation (Bauru Basin), São Paulo State, Brazil is described. The main features of this new species are the short, high oreinirostral rostrum, the large laterally positioned orbital notches and external nares in the anteriormost portion of the rostrum. The mandible is robust and concave-shaped in relation to the skull. The dentition is highly specialized, with two prominent incisiform teeth, a hypertrophied caniniform, and seven molariform teeth. The molariform teeth are ornamented with denticles in their lingual surface and are smooth on their labial surface. The molariforms are elliptical in cross-section, presenting the largest axis in the labial-lingual direction. Such dental characteristics are unique among the terrestrial crocodylomorphs of the Gondwana.

Keywords: Crocodylomorpha; *Adamantinasuchus navae*; Mesoeucrocodylia; Cretaceous; Bauru Basin

1. Introduction

A high diversity of terrestrial crocodylomorph species has been found in the continental Cretaceous deposits in Brazil. Most of these species are found in sediments of the Bauru Basin, located in the southeastern region of Brazil. The Bauru Basin deposits include Crocodylomorpha specimens of Peirosauridae, Baurusuchidae and Ziphosuchia/Notosuchia groups.

The family Peirosauridae *sensu* Gasparini (1982), in the Bauru Basin, is represented by two species, *Peirosaurus tormini* Price, 1955 and *Uberabasuchus terrificus* Carvalho, Ribeiro and Avilla, 2004. Both species are found in the Marília Formation, located at the municipality of Uberaba (Minas Gerais State, Brazil).

The notosuchians are represented by *Mariliasuchus amarali* Carvalho and Bertini, 1999, described from deposits of the Adamantina Formation, a stratigraphic unit of Turonian–Santonian age (Carvalho and Bertini, 1998, 1999; Castro et al., 1999; Carvalho and Bertini, 2000) and *Sphagesaurus huenei* Price, 1950, described from rocks of the Adamantina Formation (Cenomanian–Campanian) and reviewed by Pol (2003).

The last group of terrestrial Crocodylomorpha are included in the family Baurusuchidae. Three species belonging to this family are found in the Adamantina Formation: *Baurusuchus pachecoi* Price, 1945; *Baurusuchus salgadoensis* Carvalho, Campos and Nobre, 2005 and *Stratiotosuchus maxhechti* Campos, Suarez, Riff and Kellner, 2001.

The present study analyses a new taxon of a terrestrial Crocodylomorpha related to Notosuchimorpha (*sensu* Carvalho et al., 2004), a clade of Mesoeucrocodylia. This clade is widespread on the Cretaceous of Gondwana, with many species in South America, Africa and Asia. The new species is represented by only one specimen from the Adamantina Formation, found at the municipality of Marília, São Paulo State, Brazil. The new species is characterized by a complex and specialized dentition, whose morphology is unique among the crocodylomorphs. It also displays clear-cut adaptations for a terrestrial life habit; i.e., the outer nostrils are placed in an anterior and vertical position and the large orbits in lateral position.

2. Geology

During the opening of the Atlantic Ocean, the continental division lead to the formation of a broad intracontinental

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depression, known as Bauru Basin (Fulfaro et al., 1994; Fernandes and Coimbra, 1996, 1999). With an area of roughly 370,000 km^2 it covers part of the current Brazilian states of Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso, Goiás and Minas Gerais (Fig. 1). The deposits found in the Bauru Basin are of continental origin and usually composed of siliciclastics, including conglomerates, sandstones, siltites and shales. Fulfaro et al. (1994), considered that these sediments were deposited during the Aptian and Maastrichtian (Upper Cretaceous). They are generally included in two groups of the Bauru Basin: the Caiuá and Bauru Groups (Soares et al., 1980; Fernandes and Coimbra, 1992, 1996).

Fernandes and Coimbra (1996) subdivided the Bauru Group in three formations, with different ages of deposition. The Adamantina Formation is the oldest one (Turonian–Santonian age, after Castro et al., 1999). It is formed by a sequence of sandstones, mudstones, siltites and clayish sandstones. Batezelli et al. (1999) redefined the lowest portion of the Adamantina Formation as the

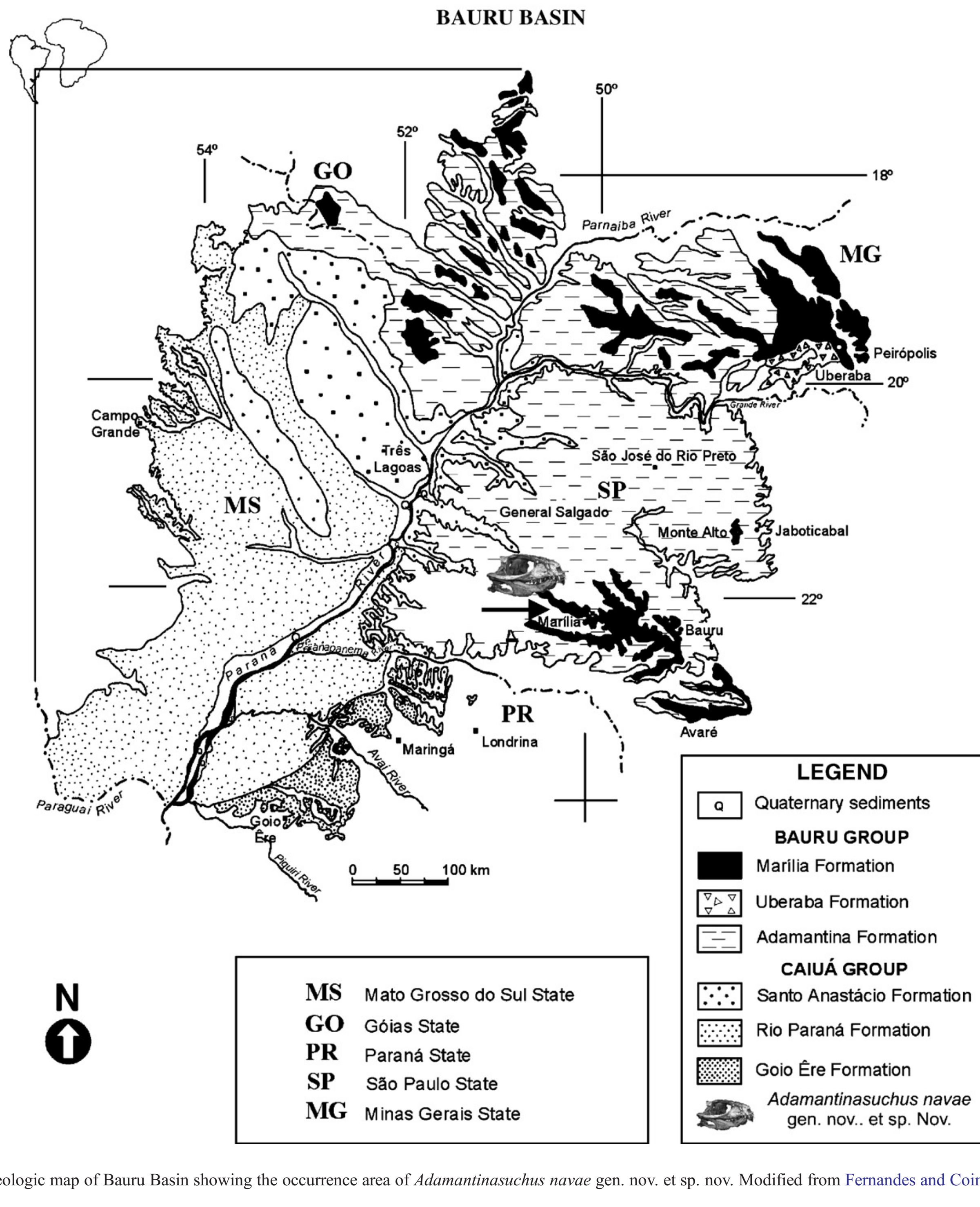

Fig. 1. Geologic map of Bauru Basin showing the occurrence area of *Adamantinasuchus navae* gen. nov. et sp. nov. Modified from Fernandes and Coimbra (1996).

Araçatuba Formation. The Uberaba Formation (Coniacian–Campanian age according to Goldberg and Garcia, 2000), which is restricted to the Triângulo Mineiro region (Minas Gerais State), is composed of thin sandstones interbedded with siltites, coarse sandstones, mudstones and volcanoclastic sediments. The last and most recent unit is the Marília Formation, composed of a sequence of conglomeratic sandstones, sandstones, mudstones and carbonatic levels (Soares et al., 1980; Garcia et al., 1999; Alves and Ribeiro, 1999; Andreis et al., 1999). Based on biostratigraphic data obtained from carophytes and ostracods, this last unit is considered as Maastrichtian (Dias-Brito et al., 2001).

The sedimentary rocks in which the new crocodylomorph was found belong to the Adamantina Formation. However, Batezelli et al. (1999) and Fernandes et al. (2003) considered that the outcrops where the fossils were found, located along the borders of the Peixe River at the Marília municipality, São Paulo State, Brazil, should be referred to as Araçatuba Formation.

3. Systematics

The classification of the new genus and species is based on comparative studies by Price (1945) and Gasparini (1982). The osteological names are based on Romer (1956), Hecht and Tarsitano (1983), Gasparini et al. (1991), Nobre and Carvalho (2002), Carvalho et al. (2005) and Richardson et al. (2002).

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
Mesoeucrocodylia Whetstone and Whybrow, 1983
Adamantinasuchus gen. nov.

Type species: *Adamantinasuchus navae* sp. nov.

3.1. Diagnosis

The jugal is triangular in transversal section and its lateral edge is extended laterally as a thin blade alongside the entire length. A large foramen on the anterolateral surface of the jugal is in-line with the nutrient foramina of the maxilla. The dentition displays a high degree of differentiation. There are three conical, prominent teeth in the premaxilla, the third one hypertrophied. All but the first of the maxillary teeth have a specialized morphology, with the labial surface smooth and the lingual surface bearing small denticles and longitudinal grooves. The teeth are spatula-shaped, with the larger width located at the labial-lingual axis. The first two teeth of the jaw are anteriorly projected.

3.2. Etymology

The generic name *Adamantinasuchus* is derived from the lithostratigraphic unit where the type material was collected–the Adamantina Formation from the Bauru Basin, Upper Cretaceous, Brazil–and the Greek word *souchos*, meaning crocodile. The species *A. navae* is named in honor of William Roberto Nava, who collected the type material in the municipality of Marília, São Paulo State, Brazil.

3.3. Holotype

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3.4. Stratigraphic context

Bauru Basin, Adamantina Formation. Upper Cretaceous: Turonian–Santonian age.

3.5. Locality

25 km SW from the municipality of Marília, São Paulo State, Brazil, near the reservoir dam that is used as water supply for that city (22°18′45.6″S; 50°01′48.8″W).

4. Description

The right lateral side of the skull, jaw, outer nostrils and part of the nasal and frontal bones are preserved. The posterior region of the skull is fragmented. Only the lateral-dorsal portion of the squamosal and part of the border of the upper temporal opening may be observed.

The dentition is preserved in the right premaxilla and maxilla. The right jaw displays only part of the posterior alveoli and three anterior teeth.

Among the remaining parts of the post-cranial skeleton, there are fragments of the right and left femora, some vertebrae, part of the radius and ulna and some metatarsal and phalanges. However, all those bones are very fragmentary.

4.1. Skull

The skull (Figs. 2 and 3A) is small, with its length reaching up to 60 mm and its height up to 30 mm. The snout is roughly triangular oreinirostral in cross-section, bearing a short rostrum with its middle posterior portion elevated. The only preserved indication of the position of the supratemporal opening is its outline against the postorbital. This outline indicates that the upper temporal opening was well-developed and placed at the lateral portion of the skull roof.

The laterotemporal opening is slightly lengthened in its ventral portion and has a pointed apex that confers a triangular shape to the opening, with the three sides reaching almost the same length.

The orbits are large relative to the skull and are placed clearly in a lateral position. The outer nostrils are placed in an anterior and vertical position. The surface of the premaxilla, nasal, frontal and squamosal bear slight ornamentations.

Premaxilla—the contact between the premaxilla and mandible is not totally visible due to preservational aspects, but it is placed near the third hypertrophied teeth. Among all the preserved bones, the premaxilla displays the largest amount of ornamentations, represented by slight grooves or furrows. There is a small triangular projection, ventrally directed, at the anterodorsal region of the premaxilla bones, which forms the contact between the premaxillar bones of both sides of the skull. A small projection, dorsally directed and apparently grooved, is also present at the anteroventral region of the premaxilla. Such structure confers a clear anterior position to the external nares, which was probably separated from the bone by a cartilaginous or bony septum. In the premaxilla there are two incisiform teeth and on hypertrophied caniniform tooth.

Maxilla—the maxilla has a triangular shape, with its base well-developed in the anteroposterior axis. The outer surface of the maxilla is entirely smooth. At its base, there is a thin and long crest that covers up the entire alveolar border. Seven teeth with thecodont implantation are found in the maxilla, displaying differences in size and shape. At its posterior region, the maxilla is triangular and elongated towards its posterior end, forming a long suture with the jugal. Two large foramina are present posteriorly and three smaller foramina are present anteriorly, on the lateral surface of the maxilla. There is also a foramen at the contact with the premaxilla. Dorsally contacts the nasal and postero-dorsally the lacrimal.

Nasal—this is very incomplete. The only part of the nasal that can be observed is its most posterior portion, where it touches the frontal, which is formed by one thin, short and straight blade. Anteriorly the nasal is ventrally projected and slightly sculptured.

Prefrontal—the prefrontal has a triangular shape. The anterior portion of both prefrontals is fragmented. At its

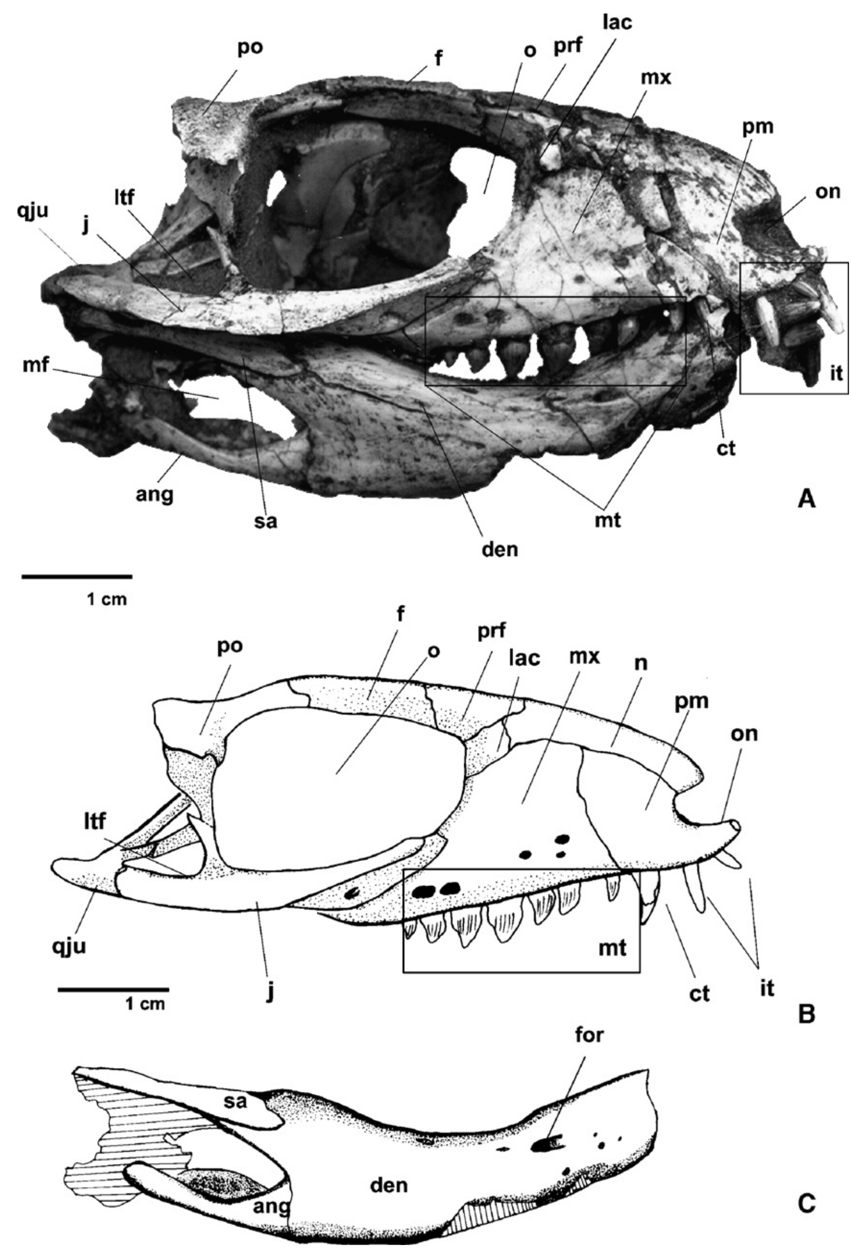

Fig. 2. *Adamantinasuchus navae* gen. nov. et sp. nov. (A) Skull and mandible in lateral right view; (B) schematic drawing of the skull in lateral right view; (C) schematic drawing of the mandible in lateral right view. ang—angular; ct—caniniform tooth; den—dentary; f—frontal; for—foramen; it—incisiform tooth; j—jugal; lac—lacrimal; ltf—laterotemporal fenestra; mf—mandibular fenestra; mt—molariform tooth; mx—maxilla; n—nasal; o—orbit; on—outer nostril; pm—premaxilla; po—postorbital; prf—prefrontal; qju—quadratojugal; sa—surangular.

ventral portion, the prefrontal forms a sinuous suture with the frontal. Its dorsal portion and its outer surface are completely smooth, without any trace of ornamentation. These surfaces probably represent the contact zone with the palpebral bone.

Lacrimal—the lacrimal contacts dorsally the prefrontal and nasal, and ventrally the maxilla.

Frontal—the middle region of the frontal becomes convex around the orbital opening. At the posterior portion of the frontal, a thin and interdigitated suture is still preserved, although the parietal is not preserved. At the medial portion it forms a slight crest alongside the bone. The outer surface of the frontal displays a slight convexity at its more anterior portion, contrasting with its flattened posterior area.

Orbits—the orbital opening is well developed, reaching almost the same length as the rostrum. The orbits have an elliptical shape and are placed laterally in the skull. Posteriorly the orbits are oriented in a more vertical position.

Postorbital—the postorbital is fragmentary. It has a square shape and is located in a posterolateral position relative to the frontal.

Jugal—the jugal is triangular in transversal section. It has a triradiate shape and is thin throughout almost all its length. Its outer surface is smooth. The anterior portion of the jugal has a foramen, which is well developed in relation to the bone size. At its lateral sides, the jugal has a marked crest that ends in a very thin edge, clearly seen at the middle portion of the bone. The jugal is arched medially, displaying a convex arch in lateral view. The jugal has its larger dorsoventral width at its anterior portion, next to the contact zone with the maxilla. From that area on, the jugal becomes gradually thinner, forming an elongated junction with the maxilla. At its posterior portion, the jugal is very thin and blade-like. The articulation with the quadrate is not clearly seen due to the preservation conditions. The postorbital bar is placed in an almost vertical position and has an oval shape in transversal section.

Quadratojugal—this is located in the posterior region of the laterotemporal fenestra. Posteriorly it presents a triangular shape, with its lateral border inflected ventrally.

4.2. Jaw

The jaw is strongly bent in the anteroposterior axis, resulting in a half-moon shape with a convex ventral surface. The mandibular fenestra is elliptical, with its lower edge a little more expanded dorsoventrally.

At the ventral and posterior sides, the dentary is limited only to the anterior portion of the mandibular fenestra. Thus, it is not excavated by that fenestra. At its most dorsal portion, the dentary extends towards the posterior end of the jaw, giving a triangular

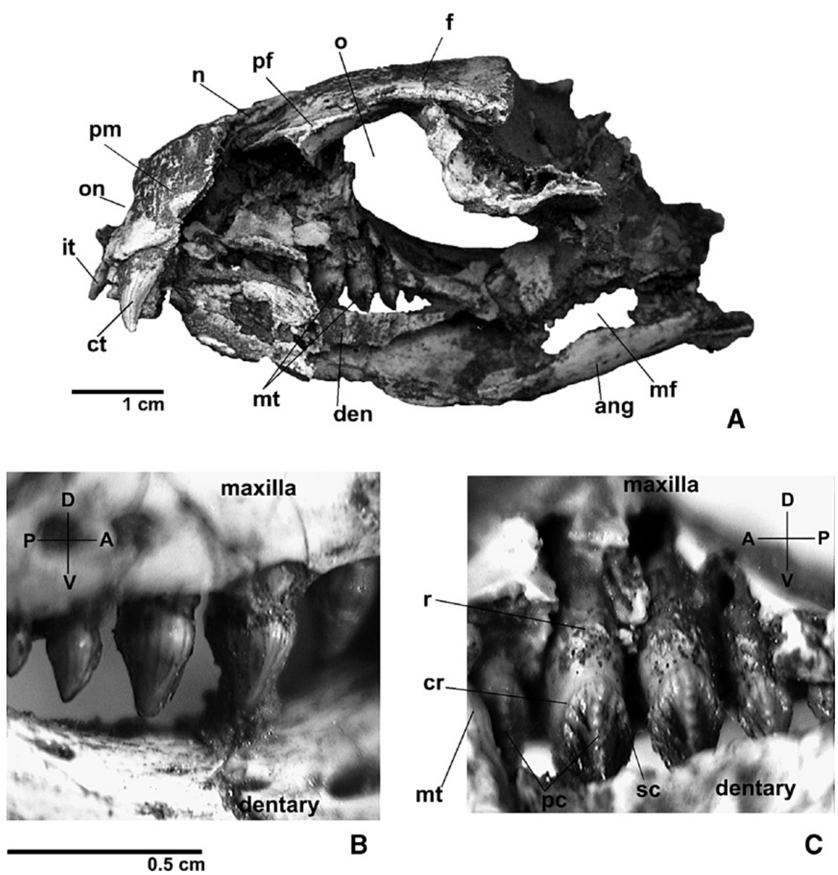

Fig. 3. *Adamantinasuchus navae* gen. nov. et sp. nov. (A) Skull in medial right view; (B) molariform tooth in labial view; (C) molariform tooth in lingual view. A—anterior; ang—angular; cr—crown; ct—caniniform tooth; D—dorsal; den—dentary; f—frontal; it—incisiform tooth; mf—mandibular fenestra; mt—molariform tooth; mx—maxilla; n—nasal; o—orbit; on—outer nostril; P—posterior; pc—principal crest; pm—premaxilla; pf—prefrontal; r—root; sc—secondary crest; V—ventral.

shape to that area. This area ends almost at the same position of the first half of the upper edge of the mandibular fenestra with the posterior portion more developed dorsoventrally than the anterior part. The dentary is smooth on its outer surface.

The surangular is triangular in cross-section, with its anterior portion more expanded dorsoventrally. At the contact zone with the mandibular fenestra, there is a slight, blade-like, lateral projection, which partially covers the upper portion of that opening. The anterior contact zone of the surangular with the dentary is elongated and overlapping. Posteriorly, the surangular is thinner and has a cylindrical shape.

The angular is excavated in its medial portion by the mandibular fenestra. At its anterior portion, the angular is expanded dorsally, forming a vertical contact zone with the dentary. The posterior portion of the angular is also slightly expanded upwards, forming a thin blade. The posterior portion of the jaw beyond the mandibular fenestra is entirely fragmented.

4.3. Dentition

The dentition (Fig. 3A and B) of the right premaxilla, right maxilla and right dentary are partially preserved. The tooth implantation is of the thecodont type, with heterodonty.

The first two premaxillary teeth are incisiform, small, pointed, cone-shaped and slightly grooved. The third premaxillary tooth is caniniform, hypertrophied in relation to the other two teeth, cone-shaped, pointed, with its apex inclined posteriorly and its crown bearing grooves. In the maxilla, there are seven teeth, with a morphology distinct from that present in the premaxillary teeth. The first three and the last two maxillary teeth are much smaller than the two middle teeth. The middle maxillary teeth may reach almost twice the size of the other maxillary teeth. All the maxillary teeth bear only one root, which is deep and oval in cross-section. Between the root and the crown, there is a small constriction. The crown base has also an oval shape in cross-section. The crown is compressed obliquely, which gives a spatula-shape to the tooth.

The labial surface of the maxillary teeth is smooth, bearing only very slight longitudinal grooves. The tooth apex is pointed and arched posteromedially (Fig. 3B). The lingual surface has a more complex morphology, which is entirely distinct from that of the labial surface. At the crown base, there is a series of denticles that become smaller towards to the apex of the teeth, forming a crested tooth. At each side of that crest, there is a slight depression forming a vertical furrow (Fig. 3C). The two larger middle molariform teeth also have a second series of denticles around the base of the crown at the lingual surface. From those denticles, small furrows are directed to the major crest. All the maxillary teeth are elliptical in transversal section and slightly inflected posteriorly. The teeth are longer along the labial-lingual axis then along the anteroposterior axis.

In the right mandibular ramus, only three teeth can be seen at the anterior portion of the dentary. One of the preserved jaw teeth contacts a maxillary tooth. The maxillary teeth have similar morphologies, but the dentary tooth has its labial surface with denticles. This forms a chisel contact zone with the lingual surface of the maxillary tooth. The denticles on the labial surface of the dentary teeth are similar to those on the lingual surface of the maxillary tooth.

4.4. Post-cranial skeleton (Fig. 4)

Femur—the right and left femora are partially preserved. The femur is moderately robust. It displays a slight torsion along the diaphysis. The femoral head is dorsally expanded, but the presence of an anteroposterior expansion gives a rounded shape proximally (Fig. 4A and B). Below the femoral head, there is a constriction, followed by another expansion, where a fourth trochanter is located, forming a rugose crest. From that point on, the diaphysis gets thinner, becoming cylindrical and gradually expanding towards the distal extremity of the bone.

Tibia—the distal and proximal extremities are not preserved and only the cylindrical and straight diaphysis is preserved.

Fibula—the diaphysis is cylindrical and is expanded gradually towards its distal extremity, which is flattened in an anteroposterior way. The diaphysis is oval in transversal section. The proximal extremity is not preserved.

Radius and ulna—these bones are not well preserved. Only the cylindrical and straight diaphysis of the radius can be seen, with its proximal extremity more expanded than the distal one (Fig. 4C). The ulna is slightly bowed, typical for crocodyliforms. The proximal extremity of the ulna is approximately three times wider than the diaphysis.

Forelimb autopodia—the right and left hands are partially preserved. The metacarpals have the distal extremities laterally expanded. The phalanges are short and apparently cylindrical, with the extremities slightly expanded.

5. Discussion

A. navae gen. nov. et sp. nov. differs from all other known Cretaceous crocodylomorphs by a series of unique characteristics. Its molariform teeth bear ornamentation composed by carinae and

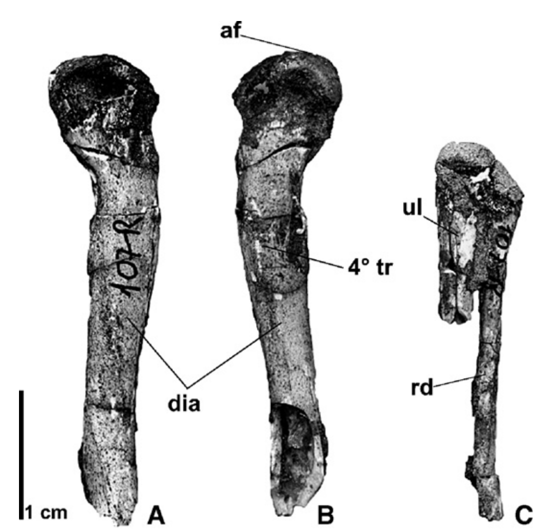

Fig. 4. *Adamantinasuchus navae* gen. nov. et sp. nov. Left femur in lateral (A) and medial (B) views; (C) left radius and ulna. af—articular facet; dia—diaphysis; rd—radius; ul—ulna; 4° tr—fourth trochanter.

denticles. The anterior carina is oriented in the lingual direction, while the posterior carina is oriented in the labial direction. The orbit is large and as long as the rostrum, whereas other Cretaceous crocodylomorphs have orbits that are generally shorter than the rostrum. The laterotemporal fenestra is triangular and placed in a vertical position on the skull. The jugal is laterally projected and its middle portion possesses a blade-like ridge.

A meaningful comparison may be made between *A. navae* gen. nov. et sp. nov. and *S. huenei* Price, 1950, a species also found at the Adamantina Formation (Price, 1950), Bauru Basin (Upper Cretaceous) and redescribed by Pol (2003). The two species show some similarities in relation to the teeth morphology. The anterior carina is oriented in the lingual direction, while the posterior carina is turned to the labial direction. In addition, *S. huenei* also bears seven maxillary and two premaxillary teeth, a condition similar to that found in *A. navae* gen. nov. et sp. nov. However, in contrast to *S. huenei*, the two premaxillary teeth of *A. navae* gen. nov. et sp. nov. are turned anteriorly and there is an additional hypertrophied caniniform teeth present between the maxilla and premaxilla. The orbit of *A. navae* gen. nov. et sp. nov. has an elliptical shape, with its larger axis represented by the anteroposterior axis. It is completely out of proportion when compared to the orbit of *S. huenei*. In the latter species, the orbit is relatively small and has a roundish to slightly oval shape (Pol, 2003). Moreover, in *S. huenei* the anterior portion of the orbit bears a triangular depression or pit (pre-orbital depression), placed at the outer surface of the maxilla that Pol (2003) referred to as the antorbital fossa. There is no comparable depression in *A. navae* gen. nov. et sp. nov. The frontal of *S. huenei* is slender, and separates the orbits by a short distance. They confer to the orbits a semilateral position in relation to the skull. The wider frontal of *A. navae* gen. nov. et sp. nov. places the orbits at a proportionally larger distance and in a more lateral position.

The rostrum of *S. huenei* is proportionally more elongated and lower in comparison to the rostrum of *A. navae* gen. nov. et sp. nov. The laterotemporal fenestra of *A. navae* gen. nov. et sp. nov. is three times smaller than the orbit, while in *S. huenei* they have almost the same size. In *A. navae* gen. nov. et sp. nov., the base of the laterotemporal fenestra is thin. In *S. huenei* the base of the laterotemporal fenestra is more expanded in the anteroposterior axis. The jugal in *A. navae* gen. nov. et sp. nov. is thin and triangular in transversal section, differing from *S. huenei* that has an L-shaped jugal anteriorly and is subcircular posteriorly (Pol, 2003).

Notosuchus terrestris Woodward, 1896 from the Río Colorado Formation, Upper Cretaceous—Argentina, differs from *A. navae* gen. nov. et sp. nov. mainly by the presence of an antorbital fenestra, general structure of the skull and in the morphology of the molariform tooth, that in *Notosuchus* is weakly groved. The skull of *Comahuesuchus brachybuccalis* Bonaparte, 1991 from the Río Colorado Formation, Upper Cretaceous—Argentina, is almost rectangular in shape in dorsal aspect, with an extremely short, wide, and rounded snout (Bonaparte, 1991; Martinelli, 2003). In *A. navae* gen. nov. et sp. nov., the skull is triangular in dorsal view and the external nares are narrowing. *Araripesuchus gomesii* Price, 1959 from the Santana Formation, Lower Cretaceous—Brazil (Price, 1959), has an antorbital fenestra, a hypertrophied caniniform in the maxilla and eleven to thirteen maxillary tooth, a very distinct pattern from *A. navae* gen. nov. et sp. nov. *Uruguaysuchus aznarezi* Rusconi, 1933 and *Uruguaysuchus terrai* Rusconi, 1933 from the Guichón Formation, Lower Cretaceous—Uruguay (Rusconi, 1933), also have an antorbital fenestra. Additionally, the presence of an orbital notch, the general shape of the skull, the position and total teeth number, all differ in *A. navae* gen. nov. et sp. nov. from *Uruguaysuchus*.

There are some similarities of *A. navae* gen. nov. et sp. nov. with another Cretaceous crocodylomorph species from the Adamantina Formation (Bauru Basin)—*M. amarali*, described by Carvalho and Bertini (1999). *M. amarali* has an orbit with a roundish to semi-elliptical shape, placed vertically at a 60° angle relative to the skull roof, and located in the same dorsoventral plane as the mandibular fenestra. In contrast, the orbit of *A. navae* gen. nov. et sp. nov. does not display any displacement to the ventral side and it is larger than in *M. amarali*, an aspect also observed when compared with younger specimens of this latter species. Moreover, *A. navae* gen. nov. et sp. nov. has an elliptical orbit, placed laterally in the skull, with a wider anteroposterior axis. The posterior region of the orbit is aligned dorsoventrally with the anterior-middle portion of the mandibular fenestra. This differs in adult and immature specimens of *M. amarali* as in this species the orbit begins at the anterior portion of the mandibular fenestra. The external nares of *A. navae* gen. nov. et sp. nov. are anteriorly placed and have a vertical to semi-vertical orientation, while in *M. amarali* they are placed clearly in a more vertical position. The jugal is roundish and stout in *M. amarali*, while in *A. navae* gen. nov. et sp. nov. it is slender, blade-like and triangular in transversal section. Additionally, the jugal of *A. navae* gen. nov. et sp. nov. is laterally projected, a condition similar to that in *Chimaerasuchus paradoxus* Wu, Sues and Sun, 1995 from the Wulong Formation (Lower Cretaceous), China (Wu et al., 1995; Wu and Sues, 1996). In *M. amarali*, the suture between the frontal and parietal is placed immediately above the posterior border of the orbit, while in *A. navae* gen. nov. et sp. nov. this suture is placed in the posterior border of the orbit. The bar formed by the jugal and post-orbital is inclined in *M. amarali*, contrasting with the vertical to slightly inclined position found in *A. navae* gen. nov. et sp. nov.

Six post-caniniform teeth are present in *M. amarali*, while seven teeth occur in *A. navae* gen. nov. et sp. nov. In both genera, the caniniform teeth are hypertrophied in relation to the other teeth and are implanted between the premaxilla and the maxilla. The anterior incisiform teeth are prominent in *M. amarali* and in *A. navae* gen. nov. et sp. nov. The adult specimens of *M. amarali* have a marked abrasion at the apex of the incisiform teeth, while *A. navae* gen. nov. et sp. nov. does not show this strong abrasion at the corresponding teeth. The posterior molariform teeth of *A. navae* gen. nov. et sp. nov. are entirely different from the corresponding teeth found in *M. amarali*. This latter taxon has molariform teeth with a globular shape, bearing marked longitudinal grooves and strongly abraded crowns. In transversal section, the teeth of *M. amarali* have an oval shape with its larger axis placed in an anterior-posterior position. There is no abrasion in the molariform teeth of *A. navae* gen. nov. et sp. nov.

Similar patterns of teeth ornamentation (especially the presence of denticulate molariform teeth) are found in *Candidodon* *itapecuruense* Carvalho and Campos, 1988, described from the Itapecuru Formation, Parnaíba Basin, Brazil (Lower Cretaceous), *Malawisuchus mwakasyungutiensis* Gomani, 1997, from Malawi, Africa (Lower Cretaceous), and *C. paradoxus* Wu, Sues and Sun, 1995, from the Wulong Formation, China (Lower Cretaceous). These taxa (Carvalho and Campos, 1988; Carvalho, 1994; Wu et al., 1995; Gomani, 1997) have teeth that also bear a major cuspid, which is abraded in *C. itapecuruense*. In contrast to these taxa, however, *A. navae* gen. nov. et sp. nov. has carinae and denticles only at the lingual surface of the molariform teeth.

Wu and Sues (1996) pointed out that the procumbent caniniform teeth of *C. paradoxus* could represent an adaptation for seizing food, while the molariform teeth would be used for crushing and processing it. They also suggested that the diet of *C. paradoxus* would include plants. Bonaparte (1991) indicated that *N. terrestris* would be able to accomplish anteroposterior movements with the jaw, due to the specialized articulation between the quadrate and articular bones that would facilitate a herbivore diet. The articulation area between the quadrate and the articular is incomplete in *A. navae* gen. nov. et sp. nov., preventing the analysis of the amplitude of jaw movements. Nevertheless, the quadrate of *A. navae* gen. nov. et sp. nov. is only slightly inclined in posterior direction, assuming an almost vertical position, as may also be observed in *M. amarali*, *N. terrestris*, *Malawisuchus mwakayasyungutiensis* and *Simosuchus clarki* Buckley, Brochu, Krause and Pol, 2000.

Some Cretaceous crocodylomorphs, such as *M. amarali*, may have included plants in their diet. The deep abrasion found on their molariform teeth, coupled with the particular abrasion pattern, point to an efficient processing of hard food items, allowed by a wider amplitude of jaw movements. Therefore, *A. navae* gen. nov. et sp. nov. presents probably a different mastication pattern, with only one kind of dorsoventral jaw movement, without indication of teeth abrasion. The anteroposterior movements of the jaw would not be possible in *A. navae* gen. nov. et sp. nov., due to the position of the molariform teeth (and its larger axis in the labial-lingual direction), and the occlusion pattern between the maxillary and jaw teeth. The diet of *A. navae* gen. nov. et sp. nov. may have been carnivorous (or necrophagous), including small animals and carcasses. There are other crocodylomorphs that lack anteroposterior (propalinal) jaw movement and that, therefore, were probably herbivorous or omnivorous. *S. clarki*, which has bizarre clove-shaped multicusped teeth, but lacked anteroposterior jaw movements was probably omnivorous for this reason (Buckley et al., 2000).

6. Conclusion

The outstanding teeth morphology of *A. navae* gen. nov. et sp. nov., the large orbit size, blade-like jugal and strong arching of the jaw, constitute a unique morphological combination among known crocodylomorphs.

In contrast to the other known Cretaceous species, *A. navae* gen. nov. et sp. nov. does not present any tooth abrasion due to mastication or related to anteroposterior jaw movements as observed in *S. huenei* and *M. amarali*. Its diet was probably carnivorous-necrophagous or omnivorous, based on the capture of small vertebrate prey and maybe also including the consumption of rotten carcasses. It is probable that the anterior teeth, both the incisiform and the hypertrophied caniniform teeth, were used for seizing the food, while the posterior molariform teeth would have served for crushing and cutting it.

Besides notosuchians, peirosaurids and baurusuchids, largely distributed in Gondwanaland, the new species reveals specialized Crocodyliformes, restricted to the Bauru Basin area, Brazil. *A. navae* gen. nov. et sp. nov. opens new perspectives of knowledge in the diversified fauna of Gondwana, and the ecological parameters that allowed their evolution.

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References

Alves, J.M.P., Ribeiro, D.T.P., 1999. Evolução diagenética das rochas da Formação Marília—Minas Gerais, Brasil. Simpósio sobre o Cretáceo do Brasil, vol. 5. UNESP, Boletim, Serra Negra, pp. 327–332.

Andreis, R.R., Capilla, R., Reis, C.C., 1999. Considerações estratigráficas e composição dos arenitos da Formação Marília (Cretáceo Superior) na região de Uberaba (MG). Simpósio sobre o Cretáceo do Brasil, vol. 5. UNESP, Boletim, Serra Negra, pp. 449–455.

Batezelli, A., Perinotto, J.A.J., Etchebehere, M.L.C., Fulfaro, V.J., Saad, A.R., 1999. Redefinição litoestratigráfica da unidade Araçatuba e da sua extensão regional na Bacia Bauru, Estado de São Paulo, Brasil. Simpósio sobre o Cretáceo do Brasil, vol. 5. UNESP, Boletim, Serra Negra, pp. 195–200.

Bonaparte, J.F., 1991. Los vertebrados fosiles de la Formacion Rio Colorado, de la, Ciudade de Neuquén y cercanias, Cretacico Superior, Argentina. Revista del Museo Argentino de Ciências Naturales Bernardino Rivadavia. Paleontologia 4, 17–123.

Buckley, G.A., Brochu, C.A., Krause, D.W., Pol, D., 2000. A pug-nosed crocodyliform from the Cretaceous of Madagascar. Nature 405, 941–944.

Carvalho, I.S., 1994. *Candidodon*: um crocodile com heterodontia (Notosuchia, Cretáceo Inferior—Brasil). Anais da Academia Brasileira de Ciências 66, 331–346.

Carvalho, I.S., Bertini, R.J., 1998. Paleoenvironments of the Brazilian Cretaceous notosuchians. Crocodilian Biology and Evolution Conference, 1998. Abstracts. Department of Zoology, The University of Queensland, Australia, p. 19.

Carvalho, I.S., Bertini, R.J., 1999. *Mariliasuchus*, um novo Crocodylomorpha (Notosuchia) do Cretáceo da Bacia Bauru, Brasil. Revista Geologia Colombiana 24, 83–105.

Carvalho, I.S., Bertini, R.J., 2000. Contexto geológico dos notossúquios (Crocodylomorpha) cretácicos do Brasil. Revista Geologia Colombiana 25, 163–184.

Carvalho, I.S., Campos, D.A., 1988. Um mamífero triconodonte do Cretáceo Inferior do Maranhão, Brasil. Anais da Academia Brasileira de Ciências 60, 437–446.

Carvalho, I.S., Ribeiro, L.C.B., Avilla, L.S., 2004. *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. Gondwana Research 7, 975–1002.

Carvalho, I.S., Campos, A.C.A., Nobre, P.H., 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. Gondwana Research 8, 11–30.

Castro, J.C., Dias-Brito, D., Musacchio, E.A., Suarez, J., Maranhão, M.S.A.S., Rodrigues, R., 1999. Arcabouço estratigráfico do Grupo Bauru no oeste Paulista. Simpósio sobre o Cretáceo do Brasil, vol. 5. UNESP, Boletim, Serra Negra, pp. 509–515.

Dias-Brito, D., Musacchio, E.A., Castro, J.C., Maranhão, M.S.A.S., Suárez, J.M., Rodrigues, R., 2001. Grupo Bauru: uma unidade continental do Cretáceo do Brasil—concepções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. Revue de Paléobiologie 20, 245–304.

Fernandes, L.A., Coimbra, A.M., 1992. A cobertura cretácea suprabasáltica no Estado do Paraná e Pontal do Paranapanema. In: Congresso Brasileiro de Geologia, 37, 1992. Resumos Expandidos, 2, 506–508.

Fernandes, L.A., Coimbra, A.M., 1996. A Bacia Bauru (Cretáceo Superior, Brasil). Anais da Academia Brasileira de Ciências 68, 195–205.

Fernandes, L.A., Coimbra, A.M., 1999. Paleocorrentes da parte oriental da Bacia Bauru (KS, Brasil). Simpósio sobre o Cretáceo do Brasil, vol. 5. UNESP, Serra Negra, pp. 51–57.

Fernandes, L.A., Giannini, P.C.F., Góes, A.M., 2003. Araçatuba Formation: palustrine deposits from the initial sedimentation phase of the Bauru Basin. Anais da Academia Brasileira de Ciências 75, 173–187.

Fulfaro, V.J., Perinotto, J.A.J., Barcelos, J.H., 1994. A margem goiana do Grupo Bauru: implicações na litoestratigrafia e paleogeografia. Simpósio sobre o Cretáceo do Brasil, vol. 3. UNESP, Boletim, Rio Claro, pp. 81–84.

Garcia, A.J.V., da Rosa, A.A.S., Goldberg, K., 1999. Paleoenvironmental and paleoclimatic controls on early diagenetic processes and fossil records in continental Cretaceous sandstones in Brazil: a petrologic approach. Simpósio. sobre o Cretáceo do Brasil, vol. 5. UNESP, Boletim, Serra Negra, pp. 491–495.

Gasparini, Z., 1982. Una nueva familia de cocodrilos zifodontes cretácicos de América del Sur. In: Congreso Latinoamericano de Geología, 5, 1981. Actas, v. 4, Buenos Aires, 317–329.

Gasparini, Z.B., Chiappe, L.M., Fernandez, M., 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodilians. Journal of Vertebrate Paleontology 11, 316–333.

Goldberg, K., Garcia, A.J.V., 2000. Palaeobiogeography of the Bauru Group, a dinosaur-bearing Cretaceous unit, northeastern Paraná Basin, Brazil. Cretaceous Research 21, 241–254.

Gomani, E.M., 1997. A crocodyliform from the Early Cretaceous Dinosaur Beds, Northern Malawi. Journal of Vertebrate Paleontology 17, 280–294.

Hecht, M.K., Tarsitano, S.F., 1983. On the cranial morphology of the Protosuchia, Notosuchia and Eusuchia. Neues Jahrbuch Für Geologie Und Paläontologie. Monatshefte 11, 657–668.

Martinelli, A.G., 2003. New cranial remains of the bizarre notosuchid *Comahuesuchus brachybuccalis* (Archosauria, Crocodyliformes) from the Late Cretaceous of Río Negro Province (Argentina). Ameghiniana 40, 559–572.

Nobre, P.H., Carvalho, I.S., 2002. Osteologia do crânio de *Candidodon itapecuruense* (Crocodylomorpha, Mesoeucrocodylia) do Cretáceo do Brasil. In: Simpósio Sobre o Cretáceo Do Brasil 6, Simposio Sobre El Cretacico De América Del Sur, 2, 2002. Boletim, 77–82.

Pol, D., 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. Journal of Vertebrate Paleontology 23, 817–831.

Price, L.I., 1945. A new reptile from the Cretaceous of Brazil. Rio de Janeiro, Departamento Nacional da Produção Mineral, Notas preliminares e estudos. Boletim 25 (8 pp.).

Price, L.I., 1950. On a new Crocodilia, *Sphagesaurus* from the Cretaceous of the State of São Paulo, Brazil. Anais da Academia Brasileira de Ciências 22, 77–83.

Price, L.I., 1959. Sobre um crocodilídeo notossúquio do Cretácico brasileiro, vol. 188. DNPM, Divisão de Geologia e Mineralogia, Boletim, Rio de Janeiro. 55 pp.

Richardson, K.C., Webb, G.J.W., Manolis, S.C., 2002. Crocodiles: inside out. A guide to the Crocodilians and their Functional Morphology. Surrey Beatty and Sons, Australia. 172 pp.

Romer, A.S., 1956. The Osteology of the Reptiles. University of Chicago Press, Chicago. 772 pp.

Rusconi, C., 1933. Sobre reptiles cretáceos del Uruguay (*Uruguaysuchus asnarezi* n.g. n.sp.) y su relaciones com los notossúquidos de Patagonia. Boletin del Instituto de Geologia y Perforaciones 19, 1–64.

Soares, P.C., Landim, P.M.B., Fulfaro, V.J., Sobreiro Neto, A.F., 1980. Ensaio de caracterização estratigráfica do Cretáceo no Estado de São Paulo: Grupo Bauru. Revista Brasileira de Geociências 10, 177–185.

Wu, X.C., Sues, H.D., 1996. Anatomy and phylogenetic relationships of *Chimaerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. Journal of Vertebrate Paleontology 16, 688–702.

Wu, X.-C., Sues, H.-D., Sun, A., 1995. A plant-eating crocodyliform reptile from the Cretaceous of China. Nature 376, 678–680.