



***Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil**

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Abstract

We describe a new species of Peirosauridae (Crocodyliformes, Mesoeucrocodylia), *Montealtosuchus arrudacamposi* **gen. nov. et sp. nov.**, from the Late Cretaceous (Turonian-Santonian) strata of the Bauru Basin, Brazil. *Montealtosuchus* was found at the outskirts of Monte Alto County in reddish sandstones of the Adamantina Formation. This specimen is exquisitely preserved with skull, mandible, postcranial and exoskeletal elements in articulation that provides critical information of the anatomy of this group. The occurrence of Peirosauridae in the Adamantina Formation (Turonian-Santonian) widens the chronostratigraphic range of this Mesoeucrocodylia taxon in Brazil. Recent analysis suggests that the Peirosauridae is restricted to the Late Cretaceous deposits of South America.

Key words: *Montealtosuchus arrudacamposi* **gen. nov. et sp. nov.**; Peirosauridae; Upper Cretaceous; Adamantina Formation; Bauru Basin

Introduction

The Bauru Basin comprises an area between latitudes 18° S and 24° S, and longitudes 47° W and 56° W, and covers an area over 370.000 km² in the southeast interior of Brazil, with outcrops in São Paulo, Minas Gerais, Mato Grosso do Sul and Goiás states. It is subdivided into two distinctive lithostratigraphic units: the Caiuá Group (Rio Paraná, Goio Erê and Santo Anastácio Formations; Cenomanian-Turonian) and the Bauru Group (Adamantina, Uberaba and Marília Formations; Turonian-Maastrichtian) (Fernandes 1998; Dias-Brito *et al.* 2001; Fernandes 2004) (Figure 1).

The rich fossil record of the Bauru Group has yielded a rich assemblage of vertebrate and invertebrate ichnofossils, continental mollusks, arthropods, freshwater fishes, amphibians, squamates, theropod and sauropod dinosaurs, birds and a diverse fauna of Crocodyliformes (Bertini *et al.* 1993; Dias-Brito *et al.* 2001; Arruda *et al.* 2005; Candeiro *et al.* 2006). The Crocodyliformes from Bauru Basin comprise at least five distinct groups of Mesoeucrocodylia: the notosuchids, sphagesaurids, baurusuchids, trematochampsids and peirosaurids (Carvalho *et al.* 2005).

The Peirosauridae are medium sized terrestrial predators and opportunistic scavengers with extensive exoskeleton such as dermal scutes (Vasconcellos 2006). *Peirosaurus tormini* Price 1955 was first described in the Marília Formation (Serra da Galga Member, Maastrichtian), near Peirópolis-Uberaba, Minas Gerais State, Brazil. It is represented by fragmentary cranial material but an extensive postcranial skeleton. Price (1955), based on dental features, suggested its relationship to other Upper Cretaceous Crocodyliformes, known at the

time as the *Sebecosuchia* Simpson, 1937.

This inference was revised by Gasparini (1982), based on a new specimen of *Peirosaurus tormini* from the Bajo de la Carpa Formation (Santonian), Neuquén Group, Argentina. The relationship between *Peirosaurus* and the *Sebecosuchia* was discarded, and the new monotypic family, the Peirosauridae, was erected to accommodate the *genus*. Later, Gasparini *et al.* (1991) described a new *genus* of Peirosauridae, *Lomasuchus palpebrosus* Gasparini, Chiappe & Fernandez 1991 from the same strata of as the Argentinian *Peirosaurus tormini* and, based on these new remains, redefined the familial diagnosis and systematic relations.

Carvalho *et al.* (2004) described another peirosaurid, *Uberabasuchus terrificus*, from the same locality of the Brazilian *Peirosaurus tormini*. The specimen is beautifully preserved, showing almost complete skull, mandible, axial and appendicular skeleton in partial articulation (Vasconcellos & Carvalho 2006).

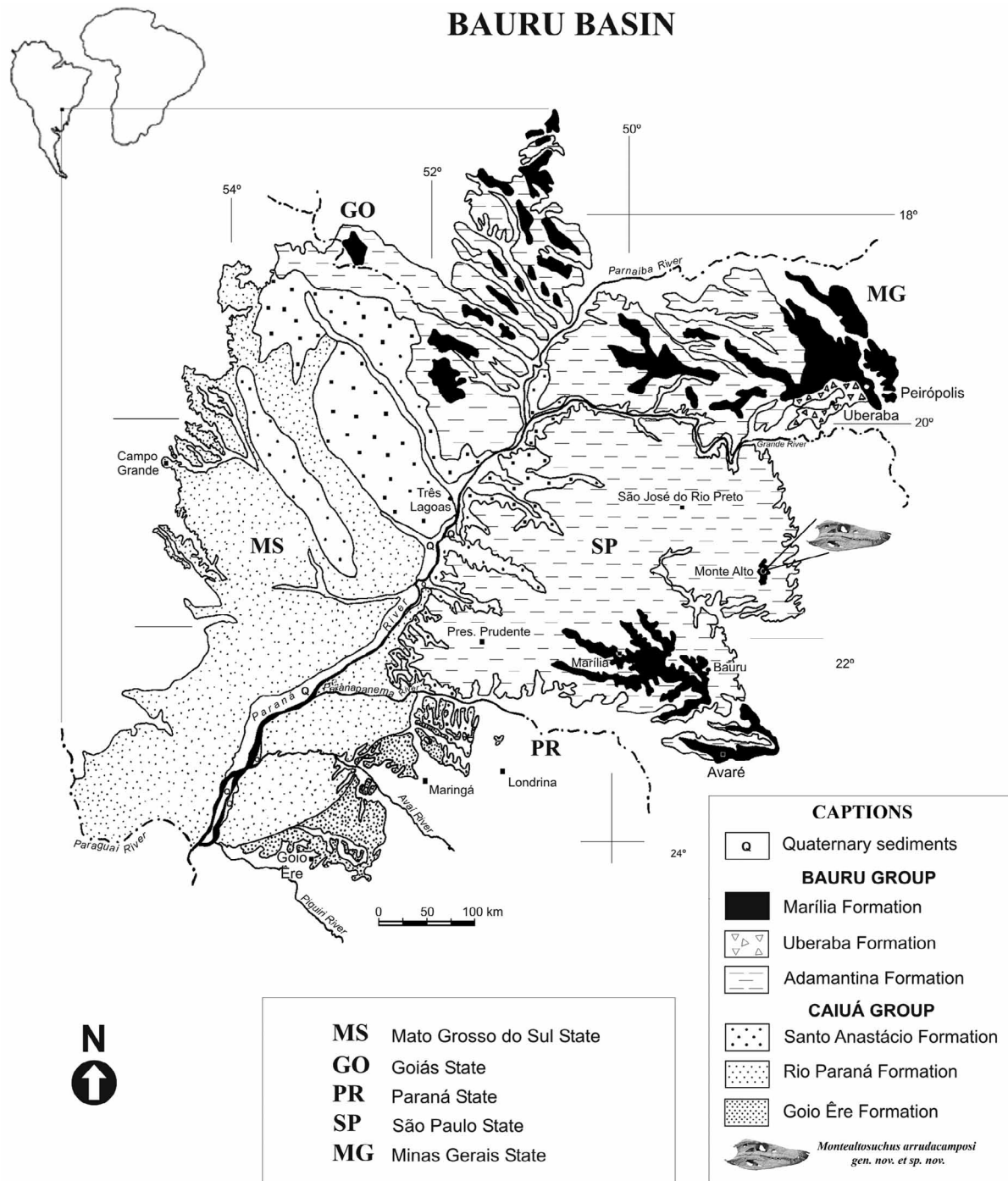


FIGURE 1. Bauru Basin (modified from Fernandes & Coimbra, 1996)

Outside South America, the occurrence of supposed peirosaurids is restricted to Africa and Madagascar. Buckley & Brochu (1999) described *Mahajangasuchus insignis* Buckley & Brochu, 1999 from the Upper Cretaceous Maevarano Formation (Campanian) of Mahajanga Basin, Madagascar. The mandibular and dental features of *Mahajangasuchus* indicate a close relationship with the Peirosauridae. Its type material lacked skull, only presented afterwards (Krause *et al.* 2006). In the following year, Larsson & Gado (2000) described *Stolokrosuchus lapparenti* from the Elrhaz formation of the Gadoufaoua (Lower Cretaceous, Aptian) in Republic of Niger. Based on phylogenetic analysis, Larsson & Gado (2000) allied *Stolokrosuchus* to the Peirosauridae. Most characters in their analysis were restricted to the premaxilla, although the general configuration of the skull suggests its relation to a longirostrine morphotype.

The distribution of Peirosauridae in time and space is so far restricted to the Cretaceous deposits of Gondwana continents, specifically to South America, North Africa and Madagascar, ranging in age from the Aptian of Niger (Elhaz Formation), the Santonian of Argentina (Bajo de la Carpa Formation), the Campanian of Madagascar (Maevarano Formation) to the Maastrichtian of Brazil (Marília Formation).

Systematic fieldwork in the Adamantina Formation by the Museu de Paleontologia de Monte Alto excavated a new species of Peirosauridae in the surroundings of the Monte Alto County, São Paulo State, southeast of Brazil. The outcrop is characterized by decimetric fine to very fine reddish sandstones with tabular geometries, with cross-stratifications; abundant clay intraclasts and rare, discontinuous, mudstone laminae. Invertebrate burrows are observed. The sediments were deposited in a braided river channel and peripheral ephemeral small ponds. The climate was hot with long arid periods punctuated by torrential rains and flash floods (Carvalho & Bertini 2000). The cross-stratified sandstone unit represents the successive floods of the rainy period and the taphocoenoses of the fossil assemblage contains a mixture of fluvial and pond deposits. The age of the Adamantina Formation is considered as Turonian-Santonian on the basis of microfloral and microfaunal remains (Dias-Brito *et al.* 2001).

The fossil assemblage in this outcrop is restricted to this new species of Peirosauridae, other fragmentary skull remains of Crocodyliformes and vertical invertebrate burrows (*Skolithos*).

Systematic palaeontology

The classification of the new specimen was based on the comparative studies of Price (1959), Price (1955), Gasparini (1982), Gasparini *et al.* (1991) and Carvalho *et al.* (2004). The osteological terminology follows Iordanski (1975) and Carvalho *et al.* (2004).

Crocodylomorpha Walker, 1970

Crocodyliformes Hay 1930

Mesoeucrocodylia Whetstone & Whybrow 1983

Peirosauridae Gasparini, 1982 (*sensu* Gasparini *et al.* 1991)

***Montealtosuchus* gen. nov.**

Etymology: The generic name *Montealtosuchus*, is derived from Monte Alto County

Diagnosis: The same as for species

Montealtosuchus arrudacamposi gen. nov. et sp. nov.

(Plate 1, 2)

Etymology: The species name, *arrudacamposi*, is in honor of Antonio Celso de Arruda Campos, eminent Brazilian paleontologist and professor.

Holotype: MPMA-16-0007-04 (Museu de Paleontologia de Monte de Alto). Skull, mandible and almost complete axial and appendicular skeleton, and articulated dorsal and ventral exoskeleton (osteoderms).

Locality: 14 km of Monte Alto, near the border between Monte Alto and Taiapu counties, São Paulo State, Southeast of Brazil.

Stratigraphic context: Bauru Basin, Adamantina Formation, Upper Cretaceous (Turonian-Santonian).



PLATE 1. Holotype of *Montealtosuchus arrudacamposi* gen. nov. et sp. nov. (MPMA-16-0007-04) in 1 dorsal view of skull and mandible; 2 lateral view of the skull; 3 lateral view of mandible; 4 palatal view; 5 dorsal view of mandible; 6 occipital view.

Diagnosis (skull): Snout moderately narrow, tubular in cross-section. Skull triangular in dorsal view. Anterior nasal process at the tip of snout, hanging over the external naris. Continuously sloping surface connecting the rostrum and skull table. A small slit-shaped notch for the 4th mandibular tooth at the contact

between maxilla and premaxilla. Five premaxillary conical teeth progressively increase in size posteriorly, all evenly spaced. Wedge-like maxillary process of the premaxilla present. *Foramen incisivum* with maxillary marginal contribution. Fourteen maxillary teeth in sinuous outline, with moderate heterodonty, displaying anterior sharp conical teeth and posterior low, laterally compressed globular teeth. Anterolateral external nares in vertical position. Nasals participating in a non-septate external nares. Orbits subsquare. Antorbital fenestrae present. Two triangular supraorbitals bordering dorsally the orbit. Postorbital bar ascending from the mesial border of the jugal. Supratemporal fenestrae elliptical, smaller than orbits, and set in a non-sculptured depression, bordered by the parietal, postorbital, squamosal and small contribution of the frontal. Supratemporal with minimal participation in skull table. Quadratojugal participates with the quadrate in skull-mandible articulation. Deep, square choanae, evenly composed by palatines and pterygoids. Palatine fenestrae elliptical, bordered by maxillae, palatines, ectopterygoids and pterygoids. Basioccipitals inclined toward the palatal surface. Exoccipitals wide and bend anteriorly and half of its height. Eustachian *foramina* closely disposed in “v” pattern, in the palatal view. Splenials participating in 1/3 of the symphysis. Symphysis extending to the 10th tooth. Mandible arched upward at anterior and posterior ends. Articular presents deep concave articular surface, with contribution from the surangular. Retroarticular process paddle-shaped and inclined dorsally and mesially. Mandibular fenestrae elliptical, aligned with the laterotemporal fenestrae. Eighteen dentary teeth show two morphotypes: anterior ones conical and sharp, with hypertrophied 4th tooth; posterior teeth globular, low, and laterally compressed. All premaxillary, except the first, maxillary and dentary teeth bear constricted basal crown and fine serrated carinae.

Description and comparison

Skull

General shape: The skull is triangular in dorsal view. The postorbital region is twice as wide as the rostrum. The skull table is slightly convex, and not much wide. The orbits are not visible from this region because of the interference of supraorbitals. In lateral view skull is moderately high and narrow, the postorbital part is twice as high as the rostrum. The lateral flanges of the cranial table are festooned and overhang the temporal region. The rostrum is tubular in cross-section (broad oreinrostral). A gentle and continuous slope connects the rostrum with the skull table. The posterior part of the skull is inclined ventrally and laterally, and the occipital region is vertical to the ventral limit of the basioccipital and then bends sharply anteriorly. The skull and mandible are uniformly sculptured with swallow grooves and pits, except in the temporal region. The total length of the skull is 265 mm, its height at orbit is 85 mm, its width at 3rd maxillary tooth is 55 mm, its width at orbit is 87 mm, and its width at quadrate is 124 mm. The general shape of the skull of *Montealtosuchus* is distinctive from that of *Peirosaurus*, *Lomasuchus* and *Uberabasuchus*. It has a relatively shorter rostrum than *Uberabasuchus* and narrower than *Lomasuchus* and the Argentinian *Peirosaurus*. In fact the Argentinian *Peirosaurus* dorsal rostrum outline is greater than the other three Peirosauridae, including the Brazilian *Peirosaurus* holotype. The parallel maxillary wall present in *Lomasuchus* and *Uberabasuchus* differs from the triangular aspect of *Montealtosuchus*. The rostrum-skull table slope is slightly different between *Uberabasuchus*, *Peirosaurus* and *Montealtosuchus*, as the former two display a clear discontinuous surface and the later lacks this feature. This is also seen in *Lomasuchus*.

Cranial openings: The supratemporal fenestra is wide and subelliptical bearing two distinct margins, one external and other internal; the surface between them is smooth, except for the temporal canal foramen. It is extensively surrounded by the parietals and postorbitals with smaller contributions from the squamosals and the frontals. The frontals hardly contribute to the inner outline of the fenestrae. The orbits are rectangular, being completely lateral and vertical, roofed by two supraorbital bones. The laterotemporal fenestra is triangular and smaller than the orbit, three times longer than high; it is formed by the quadratojugal and jugal and to a smaller extent by the postorbital. The *incisura otica* (superior lateral fenestra) is encircled by the quadrate

and squamosal. The temporal region also bears two other pneumatic *foramina*, lying anteroventrally to the *incisura otica*. The rostrum bears a semicircular antorbital fenestra, where a small and thin bone blade projects from the posterior and interior border of the fenestra. It is bordered by the lacrymal and maxilla in equal proportions. A small slit-shaped notch for the 4th mandibular tooth is present at the contact between maxilla and premaxilla. The *foramen incisivum* is elliptical reaching to the fourth premaxillary tooth, being bordered by maxilla and premaxilla. The palatine fenestra is elliptical, bordered by the maxilla anteriorly, by the palatines mesially, and by ectopterygoid and pterygoid posteriorly. The choana bears a small bony ridge in its dorsal surface (septum?), and is uniform in width and length; it is set in a smooth depression with featureless borders, composed equally by the palatines (anteriorly) and pterygoids (posteriorly). In frontal view the external nares are vertical and anterolateral in position and, although lacking septa, they exhibit a prenasal bony arch over its opening. The external nares are bordered by the premaxilla with a smaller contribution by the nasal and its arch. The medial eustachian and lateral eustachian *foramina* are visible in palatal view, due to the ventrally inclined position of the occipital surface. The lateral eustachian *foramina* are located posterodorsally in a “v” pattern, in relation to the medial eustachian foramen, being bordered by the basisphenoid, basioccipital and exoccipital. The *foramina* for the exit of cranial nerve XII and the *foramen magnum* are only visible from the occipital view.

The absence of an antorbital fenestra appears to be an autapomorphy for the Argentinian *Peirosaurus* among other Peirosauridae, although the preservation of this critical region is not perfect. The shape of orbits in the new species is rectangular, as in *Lomasuchus*, whereas in *Uberabasuchus* these are circular. The choanal shape of *Montealtosuchus* is similar to *Lomasuchus*, but this feature is not preserved in other Peirosauridae. The choanal outline is also very similar to that seen in the *Araripesuchus gomesii* Price, 1959.

Another similarities between Peirosauridae and *Araripesuchus* are the composition of the supratemporal fenestrae, general shape of the antorbital fenestrae (seen only in *Montealtosuchus*) and general outline of the skull in lateral and dorsal views.

Premaxilla: It is bordered by the maxilla and nasals. its contact with nasal is straight; its suture with maxilla shows a zig-zag pattern in dorsal view and in a wedge-like, delta-shaped, from palatal view. Although partially eroded, a smooth surface lateral to the external nares is recognizable, as in *Uberabasuchus* and *Peirosaurus*. a feature similar in all Peirosauridae.

Nasal: The bone is long with parallel mesial and lateral borders. It is slightly concave before the orbits, and gently slopes towards the frontals. It possesses two small projections between the prefrontals and frontals; it contacts the premaxilla, maxilla, prefrontal and frontal. With the exception of *Uberabasuchus*, in all Peirosauridae, including *Montealtosuchus*, the nasals do not contact the lacrimals.

Maxilla: Subvertical and moderately high. Its anterior border contacts the premaxilla, mesially contacts the nasal and its posterior border contacts the lacrymal, prefrontal and jugal.

Prefrontal: It is elliptical, longer than wider. The element is bounded by the nasal, maxilla, lacrymal, supraorbital and frontal. The internal portion of the prefrontal contributes to the anteromesial wall of the orbit.

Lacrymal: The bone is square and concave and forms the posterior part of antorbital fenestra and its internal laminae. It contacts the maxilla, jugal, supraorbital anterior and prefrontal, but not the nasals. It is very distinct from *Uberabasuchus* which is triangular and composed most of the anterior, dorsal and posterior borders of the antorbital fenestrae.

Supraorbital (anterior and posterior): It is also referred as palpebrals. The first one is larger than the second. Both are subtriangular in shape. The anterior one is longer than wide, and the posterior is as wide as long, both covering two-third of the dorsolateral border of the orbital region. They present a gentle convexity on the lateral margin of the skull that protects the orbits. In contrast, *Uberabasuchus* has a single supraorbital bone.

Frontal: It is long, triangular and completely fused. The bone borders anteriorly the nasals and both prefrontals, and posteriorly the supraorbital and postorbital. It is flat in the skull roof area but becomes slightly convex in its bordering limits.

Jugal: The bone contacts the maxilla at the length of posterior border of the antorbital fenestrae, where it forms the lower, slightly sinuous margin. In anterior view, the jugal occupies the lowermost portion beneath the orbits and is laterally inclined and presents a small ventrolateral expansion. Posteriorly to the postorbital bar it has a gentle downward slope. The projection to the postorbital starts from its upper mesial surface.

Postorbital: In dorsal view it bends gently to meet the supraorbital and follows the curvature of the orbits, where it shows a concave shape. At its opposite border, it follows the curvature of the supratemporal fenestrae. The postorbital bone is concave externally.

Postorbital bar: Positioned mesially, the postorbital bar is stout, column-like, and smooth without any ornamentation. Its upper part, the postorbital component, is more steeply inclined than the lower part; its jugal component originates mesially as seen in *Uberabasuchus*.

Parietal: It is flattened in the center, convex at its posterior border and sharply inclined in the borders of the supratemporal fenestrae. The parietal has straight contacts, with the frontal, postorbital and squamosal and supraoccipitals.

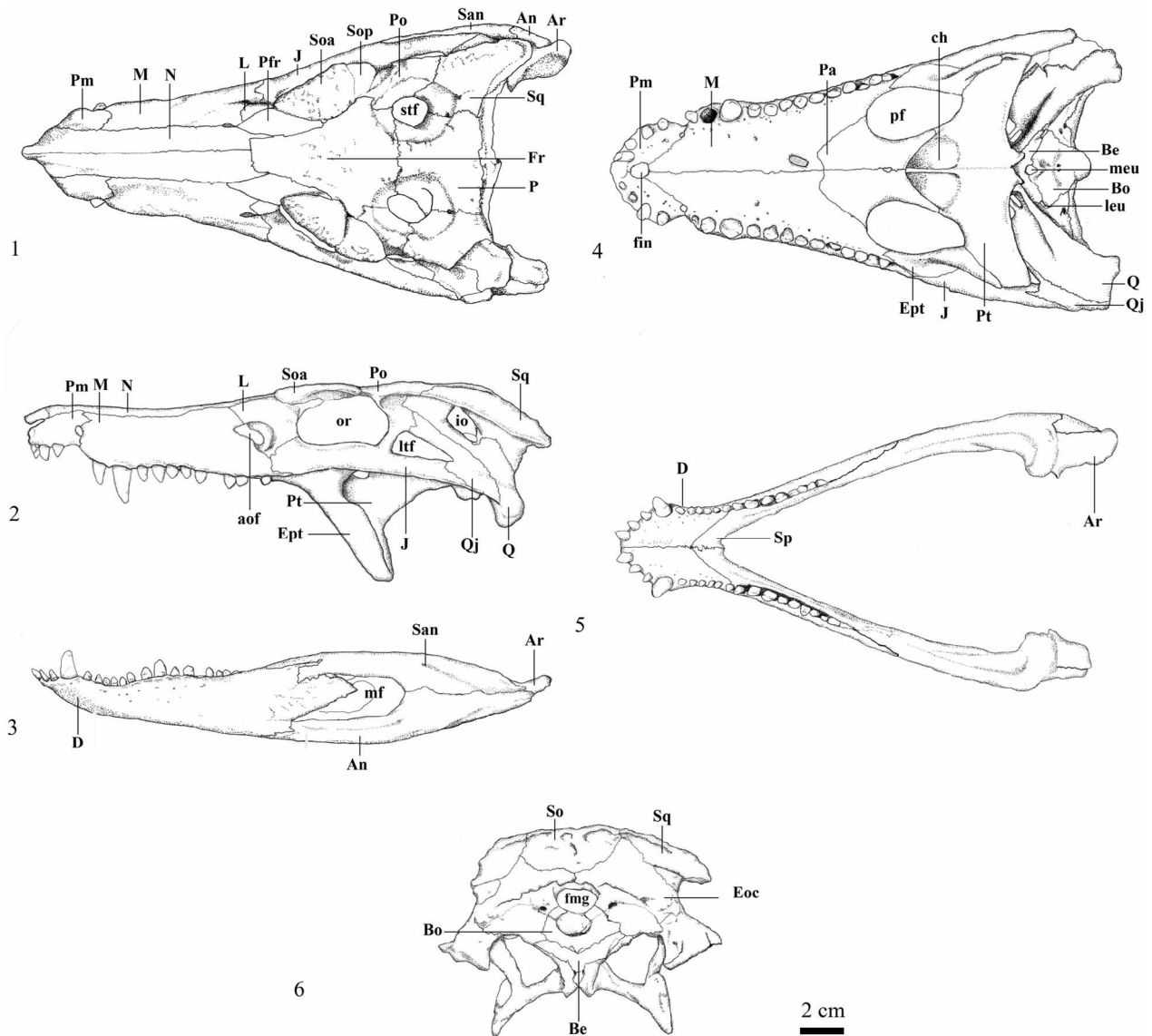


PLATE 2. Schematic drawing of the holotype of *Montealtosuchus arrudacamposi* **gen. nov. et sp. nov.** (MPMA-16-0007-04) in 1 dorsal view of skull and mandible; 2 lateral view of the skull; 3 lateral view of mandible; 4 palatal view; 5 dorsal view of mandible; 6 occipital view (Illustration by Deverson da Silva).

Squamosal: Most of this bone projects posteriorly from the rest of the skull roof. The bone is triangular, its squamosal surface is inclined lateroventrally along its lateral border, and posteroventrally in its posterior portion. This posteroventral part of the squamosal presents an extensive contact with the quadrate, running downward as it follows the quadrate morphology. Anteriorly it overhangs the temporal area along the postorbital. It displays a flange that bends ventrally and dorsally to enclose the temporal region. The sculpting is more evident than in any other skull bone.

Quadratojugal: The bone is elongated and strongly curved, projecting ventrally and posteriorly, from the posterior region of the skull. Although it extends extensively along the quadrate it has minimal lateral contribution to the jaw articulation.

Quadrate: It is moderately flexed ventrally to contact the quadratojugal. Here a small *foramina* is present, facing posteroventrally. Behind this foramen, the quadrate is strongly flexed ventrally, and expanded and differentiated into two condyles mesiolaterally. The innermost condyle is larger and more expanded mesially and posteriorly. The lateral condyle is composed by the quadrate with a small contribution from the quadratojugal.

Palatine: The bone has a shape of a blunt arrow in its contact with the maxilla, and encloses anteromedially the palatine foramen. It contacts the pterygoid at the mid-length of the choanae. Two lateral projections of the palatines embrace the anterior region of the choanae.

Pterygoid: The bone is large, laterally expanded and vertically flexed. It borders the palatine in the choanae. Its anterolateral part contacts the ectopterygoid, and after this contact, both bones are more ventrally flexed. The posteromesial region bears two small triangular expansions, diverging laterally from the mesial axis. This feature is seen in *Araripesuchus gomesii*.

Ectopterygoid: The bone is stout and complex. It joins the pterygoid in a long process lateroposteriorly, meets the jugal dorsally and anteriorly, and makes a brief contact to the maxilla.

Supraoccipital: It has a small contribution to the skull roof as it is visible in the occiput. It is laterally expanded and slightly concave. It contacts the squamosal laterally and the occipital ventrally. This feature may be an autapomorphy for *Montealtosuchus* among Peirosauridae.

Exoccipital: The bone is vertical and slightly concave, and slopes at its middle height to the palatal surface along with the bordering bones. It contacts the supraoccipital, squamosal, quadrate, and basioccipital. The exoccipital is pierced by two *foramina* for the XII cranial nerves, which are positioned more lateroventrally. The topographic position of these two foramina are similar in *Lomasuchus*, although less laterally developed.

Basioccipital: The bone is subhorizontal and visible only in palatal view, but less flattened than in *Lomasuchus*. It is saddle-shaped and bears two concave lateral surfaces bordering a small crest. This crest extends from the medial eustachian foramen to two-third of the length of the basioccipital. The borders are swollen with strong lateral knobs. The contact between basioccipital, quadrate and basisphenoid is penetrated by the lateral eustachian *foramina*.

Basisphenoid: It is broad and anteriorly inclined. The bone is compressed between the basioccipital and palatines, and bears a stout lateral ridge at the contact of the quadrate and exoccipital.

Mandible

General shape: The mandible is concave in lateral view, arched upward at the anterior and posterior ends. It is tubular to conform the shape of the rostrum, but becomes higher and wider posterior to the last tooth. Median symphysis is moderately long, reaching as far as the 10th mandibular tooth (52 mm) whereas in the Argentinian *Peirosaurus* it reaches the 8th tooth position. Sinuous grooves ornament the ventral and lateral surfaces. Mandibular fenestra is large and long, subtriangular in shape, with a bony lamina originating in the dentary mesially at the anterior margin. In contrast, the *Uberabasuchus* mandible in lateral view is flat at its mid-length, not concave as seen in *Montealtosuchus*.

Dentary: This is the longest element in the mandible and is stout and highly ornamented. The anteriormost part of the dentary is flattened; the dorsal surface is slightly concave behind the symphysis. Behind this flattened region, the dentary becomes vertical, inclined mesially, and becomes thin and compressed. It extends as

far back as the mandibular fenestra, where the anterior border becomes expanded into a mesial smooth bone lamina inside the mandibular fenestra. In *Uberabasuchus* this bony lamina is sculptured. The dentary articulates the angular and the surangular in intricate pattern. Its contact with the splenial is tight and sinuous. In *Montealtosuchus* the symphyseal part of the dentary is narrower than the condition in *Uberabasuchus*. The symphysis in *Montealtosuchus* is comparatively longer than that of *Uberabasuchus* and the Argentinian *Peirosaurus*, reaching considerably backward in the dentary tooth row.

Splenial: It forms one-third of the symphysis (1.5 mm) and articulated with the dentary in a sinuous, tight contact. The splenial symphysis accommodates 4 teeth along its length. It borders mesially the dentition from the 11th to the end of the tooth row in the form of a thin bony lamina. Its posterior end extends up to the position of the pterygoid.

Surangular: The bone extends anteriorly to the posterior end of the antorbital fenestra. The surangular encloses the upper border of the mandibular fenestra. It has the same length as the angular and it extensively contacts this bone in a butt joint. It participates lateroventrally in the jaw articulation and postarticular process. This feature is absent in *Uberabasuchus*.

Angular: Its length is at least two-third of the mandibular ramus. It borders ventrally the mandibular fenestrae.

Articular: The bone is square in dorsal aspect and concave. Its anteriormost lateral border joins the surangular and the angular; the posteriormost component participates in the formation of the jaw articulation. The glenoid is concave, barrel-shaped, bordered anteriorly and posteriorly by a thin ridge and its mesial surface is inclined ventrally. The posterior portion of the articular (retroarticular process) is anteroposteriorly expanded, which rises vertically after a concave surface. Its mesial border gently slopes ventrally. In *Uberabasuchus* the articular is less developed laterally and the retroarticular process is not as long as in *Montealtosuchus*. Moreover, the surangular and the quadratojugal do not take role in the formation of the jaw joint in *Uberabasuchus*, unlike the condition in *Montealtosuchus*. In fact, this feature is unknown in other Peirosauridae.

Dentition

General shape: The dental formula is 5 premaxillary, 14 maxillary and 18 mandibular teeth. The dentary and maxillary dental formula matches with that of *Lomasuchus*, with 14 maxillary teeth, but differs from that of *Uberabasuchus*, which bears only 12 maxillary and 12 mandibular teeth. The anteriormost teeth of the mandible, maxilla and those of premaxilla are sharp and conical, but the posterior ones became more bulbous and lateromesially compressed. All teeth bear serrated carinae, but in some teeth, the feature is eroded and damaged. The posterior ones bear more pronounced carinae and serration. The serration and carinae are composed only of enamel, not dentine. The crown of each teeth is separated from the base by a well defined constriction, which is deeper in the posterior ones. The teeth are set on undulating mandibular and maxillary alveolar margins. Even considering the discordance of dental formula, the general pattern of tooth size, form and characteristics are similar. *Montealtosuchus* possesses comparatively more low bulbous teeth.

Premaxilla: These teeth become progressively bigger from the anterior to posterior region; the first three are small, and the last two are larger and more evenly spaced. The first tooth is the smallest in the series, followed by the slightly bigger second tooth; the third and fifth are bigger than the first and second ones. The fourth tooth is the largest in the series. The second to fifth premaxillary teeth have finely serrated keels. The size pattern of these teeth is similar to that of *Peirosaurus*, *Lomasuchus* and *Uberabasuchus*.

Maxilla: These teeth show some degree of heterodonty. The three most anterior teeth are conical but slightly compressed, and are progressively bigger, with the lingual side slightly flattened and the labial side convex. All teeth possess anterior and posterior keels, finely serrated. The largest tooth in this series is the third, followed by the second one. The remaining eleven teeth are smaller, bulbous, laterally compressed, and finely serrated. The tips of the maxillary dentition have a sinuous outline, displaying two waves of teeth in lateral view. The second and third teeth are dislocated more laterally, while the rest lies in a straight line in dorsal

perspective. Three teeth pass the anterior margin of the palatine fenestra, unlike the condition in *Lomasuchus*, where only two teeth surpass this margin.

Dentary: The first three teeth are of the same size, displaying a slightly flat lingual surface. The fourth is the largest, conical in shape, slightly inclined posteriorly and mesially. The fourth dentary tooth projects upward and fits into a notch between the premaxilla and maxilla. In lateral view, the mandibular dentition shows a sinuous margin, marked by two sets of waves. The summit of first one is represented by the large 4th tooth, whereas the second summit is formed by the 12th tooth, also large. In either side of the waves the smaller teeth occur. In dorsal view, the posterior mandibular teeth are aligned in a straight line by the 11th; and became more lingual in position compared with the maxillary ones.

Discussion

Non South-American Peirosauridae

Prior to the description of *Mahajangasuchus* from the Upper Cretaceous of Madagascar, the Peirosauridae were considered an endemic member of South American Mesoeucrocodylia (Gasparini *et al.* 1991). Buckley & Brochu (1999), in their phylogenetic analysis, regard *Mahajangasuchus* as a sister-group of Peirosauridae that form a monophyletic group with Trematochampsidae and *Araripesuchus*. Later, Carvalho *et al.* (2004) revised Peirosauridae, and show a closer relation between *Uberabasuchus* and *Mahajangasuchus* than any other South American Peirosauridae, based on skull characters. Since the type material of *Mahajangasuchus* lacked skull, the hypothesis of its close affinity with *Uberabasuchus* was tenuous. Further, the mandible in *Mahajangasuchus* bears none of the traits observed in Peirosauridae, such as seen in *Uberabasuchus* and *Montealtosuchus*. Recently Krause *et al.* (2006) presented an illustration of the skull material of *Mahajangasuchus*, which is significantly different from any known Peirosauridae (Krause *et al.* 2006, figure 2). Analysis based on postcranial material suggests that *Uberabasuchus* was more closely related to *Peirosaurus* than to *Mahajangasuchus*, which shown to possess an intermediate set of features between Peirosauridae and Trematochampsidae (Vasconcellos 2006). Several recent phylogenetic analyses (Ortega *et al.* 2000; Tykoski *et al.* 2002; Turner & Calvo 2005; Turner 2006) support the hypothesis that *Mahajangasuchus* is a sister group of Peirosauridae, as originally proposed by Buckley & Brochu (1999), as well the endemism of Peirosauridae in South America, as indicated by Gasparini *et al.* (1991).

Stolokrosuchus, another problematic taxon, does not exhibit some of the diagnostic features of Peirosauridae listed by Gasparini *et al.* (1991): vertical external nares, parallel lateral borders of the nasals, 14-15 maxillary teeth, hypertrophied teeth in the maxilla and mandible, oreinrostral snout, blunt-arrow contact between palatines and maxillae in the palate. The absence of these features clearly exclude *Stolokrosuchus* from the Peirosauridae. Jouve *et al.* (2006) on the basis of longirostrine forms, grouped *Stolokrosuchus* with the Pholidosauridae and Thallatosuchia in a new phylogenetic analysis.

Once *Mahajangasuchus* and *Stolokrosuchus* are excluded from Peirosauridae, the geochronological and paleobiogeographical implications become clear: the Peirosauridae appear to be restricted to South America, more specifically to the Upper Cretaceous deposits, to the Turonian – Maastrichtian strata from Argentina and Brazil.

Chronostratigraphic significance of *Montealtosuchus*

The geochronological range displayed by the Peirosauridae was bracketed by lower and upper ranges: the earliest occurrence represented by *Lomasuchus* and the Argentinian *Peirosaurus* in the Santonian of Argentina (Bajo de la Carpa Formation) and the latest record by *Peirosaurus* holotype and *Uberabasuchus* from the Maastrichtian (Marília Formation), Brazil. The new species, *Montealtosuchus arrudacamposi* from the Turonian-Santonian of Bauru Basin extends the lowest stratigraphic range of this group in South America.

The Argentinian mesoeucrocodylian fauna from Santonian strata (Neuquén Basin, Bajo de la Carpa For-

mation) includes notosuchids, baurusuchids and peirosaurids, while in Brazil, the chronocorrelated strata (Adamantina Formation, Turonian-Santonian) yields notosuchids, baurusuchids and sphagesaurids.

The new Peirosauridae enhances the richness of the mesoeucrocodylian fauna of Adamantina Formation, adding more complexity to the paleoecological relationships. This is a new terrestrial predator and scavenger, and offers a new tool of correlation between Brazilian and Argentinian Late Cretaceous strata.

Conclusions

The general shape and diagnostic features of the Peirosauridae proposed by Gasparini *et al.* (1991) are present in *Montealtosuchus arrudacamposi* gen. nov. et sp. nov., supplemented by new features in the choanae and the occipital region.

A close relationship is proposed between the genus *Uberabasuchus* and *Montealtosuchus* because of similarities in the structure of mandible.

The main differences between *Montealtosuchus* and *Peirosaurus*, *Lomasuchus* and *Uberabasuchus* are encountered in the margins of the antorbital fenestrae, skull-mandible articulation, number of teeth in the maxilla and supraoccipital position.

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Appendix.

Referred Material

Araripesuchus gomesii (DGM 423-R); *Peirosaurus tormini* (DGM 433-R; MOZ 1750 PV); *Lomasuchus palpebrosus* (MOZ 4084 PV); *Mahajangasuchus insignis* (AU 8654); *Stolokrosuchus lapparenti* (MNN GDF 601); *Uberabasuchus terrificus* (CPPLIP 630).

Institutional abbreviations

AMNH— American Museum of Natural History, USA; CPPLIP — Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Brazil; AU - Antananarivo University, Madagascar, MNN GDF — Musée National de Niger, Niger; DGM — Divisão de Geologia e Mineralogia do Departamento Nacional de Produção Mineral, Brazil; MPMA — Museu de Paleontologia de Monte Alto, Brazil; MOZ — Museo Professor-Dr. Juan A. Olsacher, Argentina

Anatomical abbreviation

An — Angular; aof — antorbital fenestra; Ar — articular; Be — Basisphenoid; Bo — Basioccipital; D — Dentary; Eoc — Exoccipital; Ept — Ectopterygoid; fin — *foramen incisivum*; fmg — *foramen magnum*; Fr — Frontal; io — *incisura otica*; J — Jugal; L — Lacrymal; leu — lateral eustachian foramen; ltf — laterotemporal fenestra; M — Maxilla; meu — medial eustachian foramen; mf — mandibular fenestra; N — Nasal; or — orbit; P — Parietal; Pa — Palatine; pf — palatine fenestra; Pfr — Prefrontal; Pm — Premaxilla; Po — Postobital; Pt — Pterygoid; Q — Quadrate; Qj — Quadratojugal; San — Surangular; So — Supraoccipital; Soa — Anterior supraorbital; Sop — Posterior supraorbital; Sp — Splenial; Sq — Squamosal; stf — supratemporal fenestra.