



An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil

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ABSTRACT

The Sphagesauridae is a family of Crocodyliformes exclusively known for the Brazilian Late Cretaceous Bauru Basin. This lineage reveals how diverse was the morphology and ecology of terrestrial Crocodyliformes during the Late Cretaceous of Gondwana. Here is described *Armadillosuchus arrudai* gen. et sp. nov., a sphagesaurid that presents some mammal-like morphological features, such as propalinal and alternate unilateral jaw occlusion pattern and heavy body armor, composed of a rigid shield and mobile-banded section as in extant armadillos (*Xenarthra*, *Dasypodidae*). These unusual morphological features contrast to the double row of osteoderms observed on the closest relatives of *A. arrudai*. As its mammal analogs, *A. arrudai* presents some evidence of fossoriality and an exclusive terrestrial life style in contrast to the extant alligatorids and crocodylids.

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1. Introduction

Mesoeucrocodylian remains are common finds in the Late Cretaceous Bauru Basin in Southeastern Brazil (Nobre and Carvalho, 2006), and the *Notosuchia* (*sensu* Ortega et al., 2000) are the most commonly found crocodylomorphs in this unit. Among the notosuchians from the Bauru Basin, there is an elusive group of crocodylians that in spite of the poor record, a family could be erected by Kuhn (1968) based on only two teeth of *Sphagesaurus huenei* (Price, 1950). More recently, a partial snout regarded as *S. huenei* was reported by Kellner et al. (1995), a nearly complete skull of *S. huenei* described by Pol (2003) and a new sphagesaurid, *Adamantinasuchus navae* Nobre and Carvalho, 2006 was described, shedding new light on the anatomy and systematics of the family.

The Sphagesauridae present some unusual dental features for crocodylians, such as the oblique disposition of the posterior teeth, keels bearing few and large tubercles positioned lingually on the upper teeth and labially on the lower ones on each of the posterior teeth, worn facets that suggest propalinal unilateral jaw movements and high heterodonty (Price, 1950; Kuhn, 1968; Pol, 2003).

New remains of sphagesaurids were found in General Salgado County, São Paulo State, Brazil. Among these findings, a nearly complete cranium articulated to part of the postcranial skeleton, left arm and a complex body armor composed of a rigid cervical shield and a mobile-banded section like those of extant armadillos (*Xenarthra*, *Dasypodidae*) described here as *Armadillosuchus arrudai* gen. et sp. nov., the most complete Sphagesauridae known to date.

The institutional abbreviations used in this article are as follows: UFRJ DG, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; and MPMA, Museu de Paleontologia de Monte Alto, Monte Alto, São Paulo, Brazil.

2. Geological setting

The Bauru Basin (Fulfaro et al., 1994; Fernandes and Coimbra, 1996, 1999), with an area of roughly 370,000 km², 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 throughout 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 composed of a sequence of sandstones, mudstones, siltites and clayish sandstones. Batezelli et al. (1999) redefined the lowest portion of the Adamantina Formation as the Araçatuba Formation. The Uberaba Formation (Coniacian–Campanian) (*sensu* Goldberg and Garcia, 2000), which is restricted to the Triângulo Mineiro region at 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

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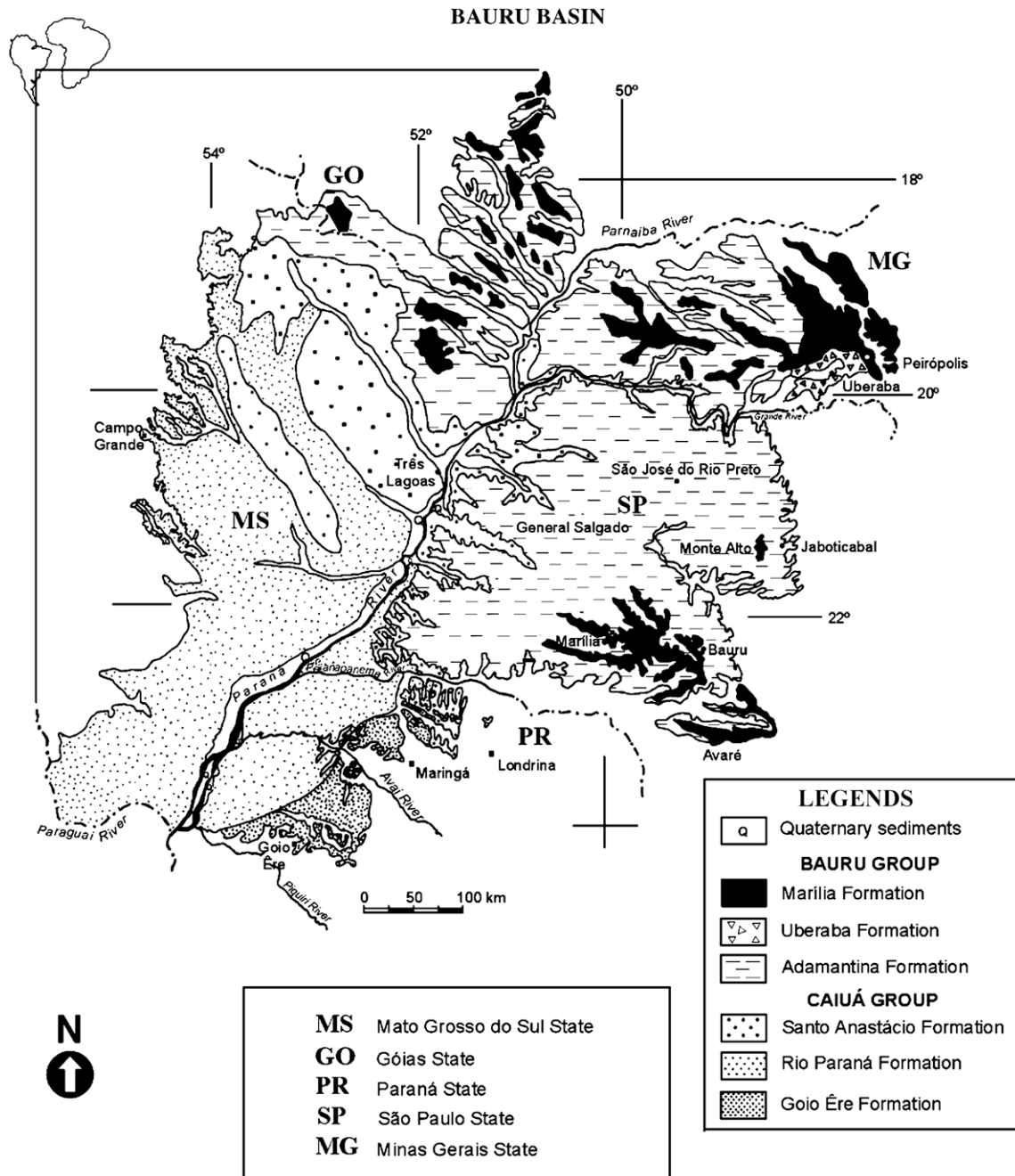


Fig. 1. Geological map of the Bauru Basin. Modified from Fernandes and Coimbra (1996).

(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). Fenandes (2004) proposed the division of the Adamantina Formation in four new formations: Araçatuba Formation, Vale do Rio do Peixe Formation, São José do Rio Preto Formation and Presidente Prudente Formation. The material here studied will be regarded as being from the Adamantina Formation, due to the fact that these outcrops are not yet studied in the view of this new proposition.

3. Systematic paleontology

Archosauria Cope, 1869
Crocodyliformes Hay, 1930

Notosuchia Gasparini, 1971
Sphagesauridae Kuhn, 1968
Armadillosuchus arrudai gen. et sp. nov.

Etymology: Generic name from the Spanish, *Armadillo* popular name for extant cingulates (Dasypodidae) from the Latin *armatus* for armed-one, and *souchus*, Greek for crocodile, leading to Latin, *suchus*. Specific name honors João Tadeu Arruda, who made many important fossil discoveries at General Salgado County in São Paulo State, Brazil.

Holotype: UFRJ DG 303-R (Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil) consists of an almost complete skull, complete cervical vertebrae and ribs, dorsal vertebrae and ribs, scapulae, a partial left coracoid, left humerus displaced anteriorly, left radius and ulna, most of the left

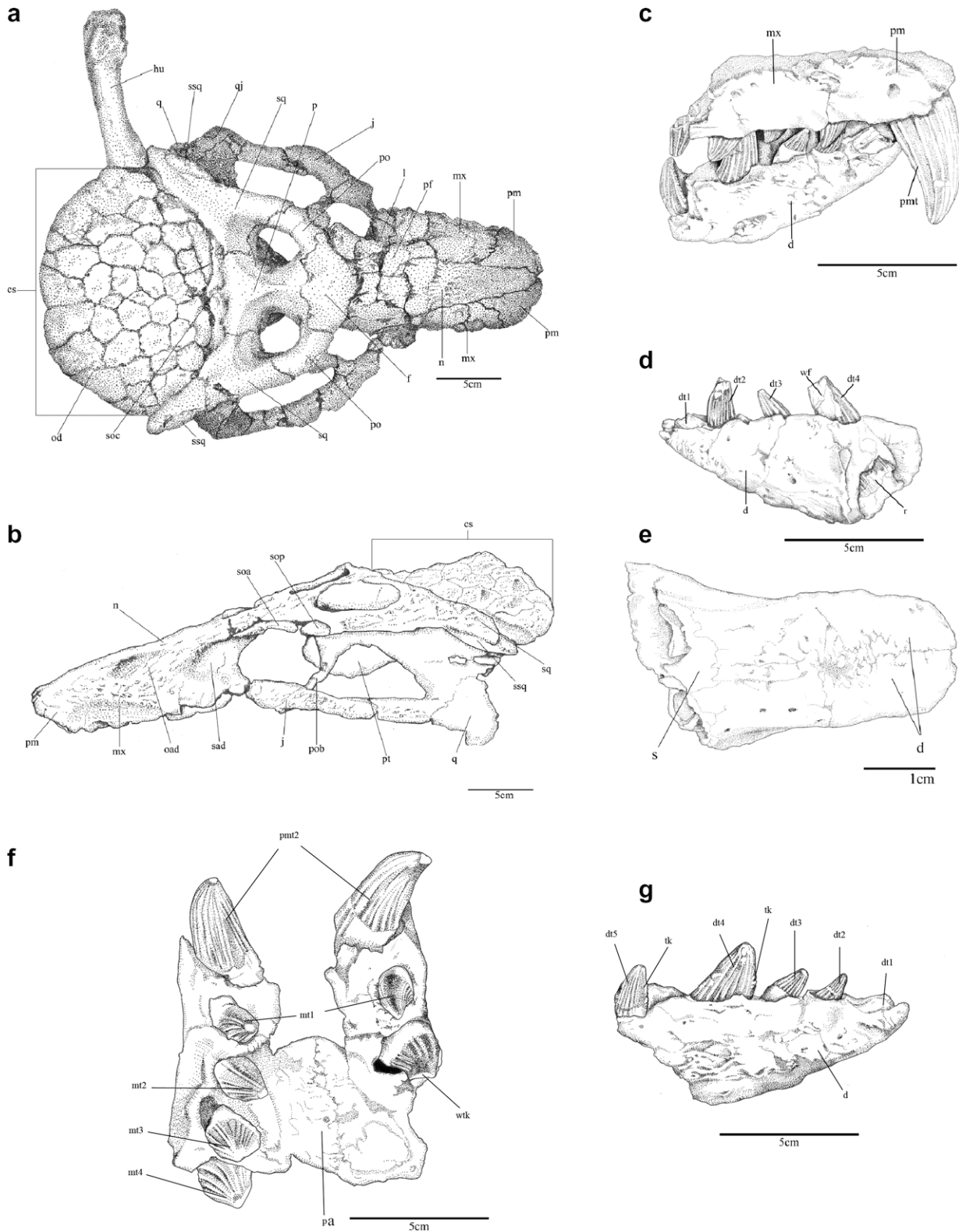


Fig. 2. *Armadillosuchus arrudai* gen. et sp. nov. (UFRJ DG 303-R), skull, cervical shield and humerus in (a) dorsal view, (b) lateral left view. *Armadillosuchus arrudai* gen. et sp. nov. (MPMA-64-0001-04), (c) fragmentary upper and lower jaws in occlusion, (d) left view of the lower jaw, (e) symphyseal region of the mandible in ventral view, (f) palatal view of the upper jaw remains, where the transverse orientation of the posterior maxillary teeth is observed and (g) right view of the mandible tuberculated keels of posterior teeth orientated labially. Abbreviations: cs, cervical shield; d, dentary; dt, dentary tooth; f, frontal; j, jugal; hu, humerus; l, lachrymal; mt, maxillary tooth; mx, maxilla; n, nasal; oad, ornamented portion of the antorbital depression; od, osteoderms; p, parietal; pa, palate; pf, prefrontal; pmt, premaxillary tooth; pm, premaxilla; pmt, second premaxillary tooth; po, postorbital; pob, postorbital bar; pt, pterygoid; q, quadrate; qj, quadratojugal; r, root; s, splenial; sad, smooth portion of the antorbital depression; soa, anterior supraorbital; sop, posterior supraorbital; sq, squamosal; ssq, suprasquamosal; tk, tuberculated keel; wf, worn facet; wtk, worn tuberculated keel.

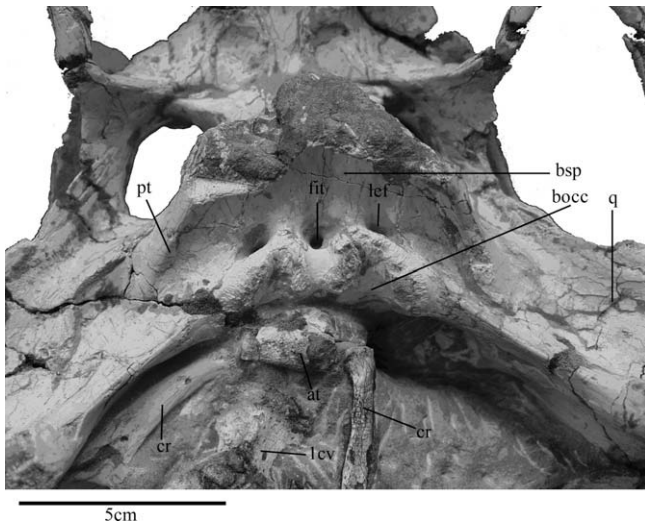


Fig. 3. *Armadillosuchus arrudai* gen. et sp. nov. (UFRJ DG 303-R) details of the occipital area in ventral view. Abbreviations: at, atlas; bocc, basioccipital, bsp, basisphenoid; cr, cervical rib; cv, cervical vertebra; fit, foramen intertympanicum; lef, lateral Eustachian foramen; q, quadrate; pt, pterygoid.

manus, complete cervical osteoderm shield and seven bands of imbricated osteoderms (Figs. 2 and 5).

Paratype: MPMA-64-0001-04 (Museu de Paleontologia de Monte Alto, Monte Alto, São Paulo, Brazil), premaxillae broken at the rostral end and dorsal portion, left maxilla broken after the second left tooth and dorsal portion, right maxilla broken after the fourth tooth and dorsal portion, lower jaw almost complete at the mandibular symphysis (Fig. 2c–d).

Locality and horizon: Late Cretaceous (Turonian-Santonian), Adamantina Formation, Bauru Basin, at General Salgado County, São Paulo State, Brazil.

Diagnosis: A Sphagesauridae bearing two premaxillary teeth, the second ones are hypertrophied caniniforms; posterior maxil-

lary teeth present the major crown axis obliquely oriented with few large tubercles disposed in one lingual keel (Fig. 4); lower jaw is narrow and elongated at the symphyseal region; the first dentary teeth facing anteriorly; fourth dentary teeth slightly flattened laterally and have anterior keels; the fifth dentary teeth has the major crown axis obliquely oriented with the tuberculated keel facing the labial margin, and occluded behind the third maxillary teeth; basioccipital-basisphenoid suture marginate the foramen intertympanicum posteriorly; foramen intertympanicum in the basisphenoid; basioccipital-basisphenoid suture marginate the lateral Eustachian foramina posteriorly and laterally; lateral Eustachian foramina aligned to the foramen intertympanicum (Fig. 3); antorbital depression divided into two parts: a smooth and deeper and an ornamented and shallower one; body armor with two distinct parts: a cervical shield and a banded dorsocervical section; hexagonal osteoderms compose most of the cervical shield.

4. Comparative description

The remains of the holotype cranium are well preserved, and only the ventral portion of the maxilla, premaxilla and palatal region are missing. There are some teeth embedded in the sediments at the palatal region. These teeth make it possible to correlate the paratype to the holotype. The postcranial remains are represented by the complete cervical series and two dorsals with the respective ribs, the medial portion of the left coracoid, left and right scapula, left humerus, left radius and ulna, complete left manus, cervical dermal shield and seven rows of osteoderms of the mobile-banded section of the body armor. The paratype was found in close association to the holotype. The teeth preserved on its maxilla are identical to those preserved within the skull of the holotype. Also, the maxilla and premaxilla, postcranial remains like osteoderms and appendicular elements are similar to UFRJ DG 303-R, providing proper evidence that both specimens were of the same species.

The teeth morphology and disposition of *Armadillosuchus arrudai* provided a powerful shearing scissors-like mechanism, where

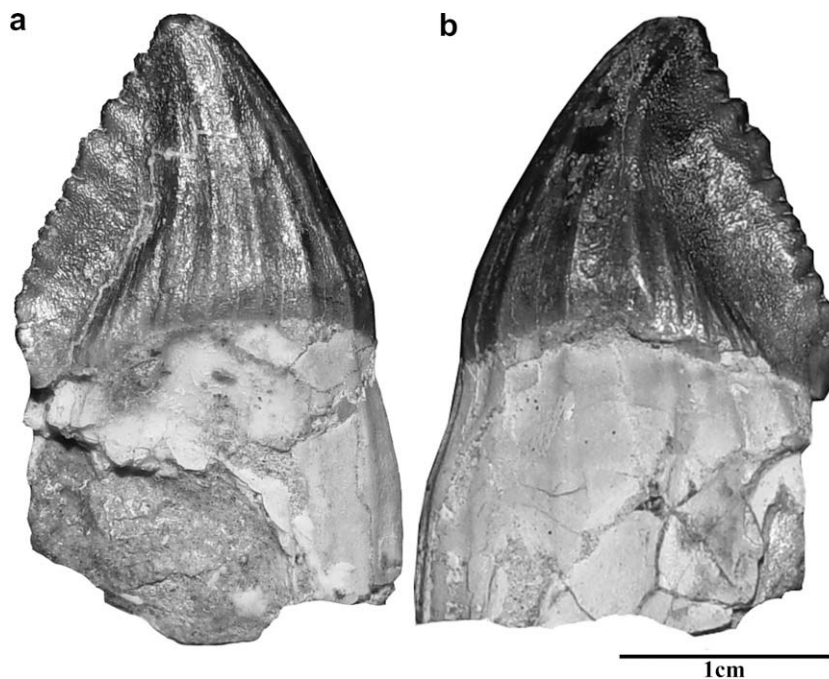


Fig. 4. *Armadillosuchus arrudai* gen. et sp. nov. UFRJ DG 303-R tooth in anterior (a) and posterior view (b).

the tuberculated keels of the upper teeth join the tuberculated keels of the lower teeth in a tooth–tooth occlusion as in *Sphagesaurus huenei* and *Adamantinasuchus navae*. *Armadillosuchus arrudai* teeth exhibit some anteroposterior wear similar to that seen in *Sphagesaurus huenei*, where parallel striae suggest a propalinal fore–aft jaw movement and an alternate unilateral jaw occlusion pattern (Pol, 2003). These worn surfaces present on *Armadillosuchus arrudai* teeth suggest that the occluding movement included a large anteroposterior component and probable omnivory (Pol, 2003; Nobre and Carvalho, 2006). The symphyseal region of the mandible of *Armadillosuchus arrudai* is long and narrow as in *S. huenei*, *A. navae* and most of the notosuchians (Gasparini, 1971; Bonaparte, 1991; Carvalho and Bertini, 1999). The first dentary teeth are oriented forward like those of *A. navae* and *Mariliasuchus amarali* (Carvalho and Bertini, 1999), and differently in *S. huenei* that possessed these teeth dorsally orientated. Also, the fifth dentary teeth occlude anterior to the third maxillary ones in *Armadillosuchus arrudai*, while it occludes anteriorly to the first maxillary teeth in *S. huenei* (Pol, 2003). The function of these teeth might be related to an underground foraging habit. Considering this habit for *Armadillosuchus arrudai* and the tooth wear observed, it is plausible to think that these animals might have fed on mollusks, arthropods or even roots, pines and other plant material.

The skull of *Armadillosuchus arrudai* is robust and flattened dorsoventrally, but still oreinostral as most of the Notosuchia, with a few exceptions like *Comahuesuchus brachybuccalis* (Bonaparte, 1991). The skull roof is wide, with the squamosals projected lateroventroposteriorly. There is a suprasquamosal, an accessory bone attached to both squamosals. The snout is strongly ornamented and proportionally wider and longer than in *S. huenei* and *A. navae*.

There is a cervical shield composed of many hexagonal osteoderms that are firmly attached by lateral sutures articulated to the skull. The whole perimeter of the shield is convex, so it could articulate independently to the skull and the posterior portion of the dermal armor. This shield is rigid, and the posterior border is ornamented with parallel horizontal ridges. Posteriorly to the cervical rigid osteoderm shield, there is a mobile-banded body armor section composed by imbricated osteoderms. The mobile section of the body armor was dislocated posteriorly due to the taphonomic process. The imbricated osteoderms of the banded dorsal armor are like most of the crocodyliform osteoderms: rectangular and ornamented by circular pits. The first to the fifth mobile bands are composed by four paralleled osteoderms, while the sixth and seventh are reduced to two. The morphology of the osteoderms of the last band resembles the posterior dorsal ones of extant Crocodylia, wide anteriorly and narrow posteriorly. This might indicate that



Fig. 6. Life reconstruction of *Armadillosuchus arrudai* gen. et sp. nov.

posteriorly to the seventh band of trunk osteoderms, *Armadillosuchus arrudai* had a single–double row of dorsal bony plates from this point to the caudal series. Despite the unique features, the overall morphology of the body armor of *Armadillosuchus arrudai* resembles those of the extant armadillos (Xenarthra, Dasypodidae).

Armadillosuchus arrudai was found in close association with many complete and articulated *Baurusuchus salgadoensis* (Carvalho, Campos and Nobre, 2005 (Crocodyliformes, Baurusuchidae) skeletons (Arruda et al., 2004). These remains are often found in these conditions, which might be related to burrowing habits, as seen in extant alligatorids and crocodylids, and at least one dinosaur, *Oryctodromeus cubicularis* (Varricchio et al., 2007). *Armadillosuchus arrudai* has some morphological characteristics that point to a burrowing habit, such as a long and wide scapula, robust manus claws, robust neck and skull and anteriorly facing teeth worn at its anteriormost part of the apices.

The bizarre Chinese crocodyliform *Chimaerasuchus paradoxus* is often positioned as sister group of *Sphagesaurus huenei* (Pol, 2003; Zaher et al., 2006), and therefore the closest relative of the Sphagesauridae or a basal taxon of the family. Unlike *Armadillosuchus arrudai* and the other Sphagesauridae, *C. paradoxus* has tritylodontid-like maxillary teeth with three longitudinal rows of recurved cusps, and short and broad mandibular symphysis region (Wu et al., 1995). The right mandible ramus preserved of *C. paradoxus* in dorsal view is almost longitudinal, with the symphyseal region slightly projected medially, while sphagesaurids mandibles are long, narrow and project laterally at the posterior portion of the symphysis. These differences observed in *C. paradoxus* would exclude it from the Notosuchia clade (see Fig. 6).

5. Conclusions

Evidence from the *Armadillosuchus arrudai* specimens suggest that these animals would have been omnivores with some degree of herbivory and also have fed on hard materials like roots, pines, mollusks and dried carcasses. Even though mollusk remains were not found associated to *Armadillosuchus arrudai*, the sediments that compose the sandstone from this deposit were deposited in a fluvial lacustrine environment, and might have been the habitat of bivalve mollusks, commonly found in other sites of the Adamantina Formation. The hot semi-arid climate would rapidly dry carcasses that would have been eaten by *Armadillosuchus arrudai*. This kind of hard and abrasive material may have produced the worn surfaces and striations seen in *Armadillosuchus arrudai* and *Sphagesaurus huenei*. Further analysis on the dentition morphology, wear and jaw movements will be discussed in another study.

The morphological data collected from the Sphagesauridae suggest that these crocodylians and the notosuchids should be separated from *C. paradoxus*, which should be grouped in another clade. *C. paradoxus* does not resemble in any way the Notosuchia, as that species possessed tritylodontid-like maxillary teeth with

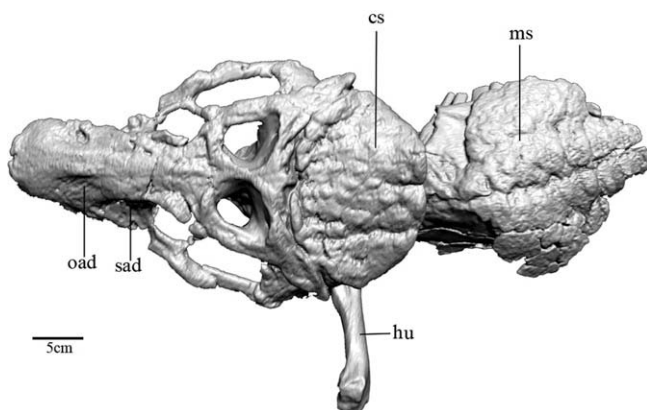


Fig. 5. 3D reconstruction in dorsal view of *Armadillosuchus arrudai* gen. et sp. nov. from CT scan images. Abbreviations: cs, cervical shield; hu, humerus; ms, mobile-banded shield; oad, ornamented portion of the antorbital depression; sad, smooth portion of the antorbital depression.

three mesial–distal oriented rows of cusps (Wu et al., 1995). The morphology of the Sphagesauridae is different from any other Notosuchia, as those are the only Mesoeucrocodylia to bear the posterior teeth with major axis transverse to the maxilla and dentary. Therefore, Sphagesauridae is an endemical family of Mesoeucrocodylia of the Upper Cretaceous of Gondwana. The evidence of endemism of sphagesaurids to the Bauru Basin may support that some tetrapod forms were exclusive to Gondwanan landmasses during the Cretaceous, as proposed by Bonaparte (1991).

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