



MORPHOLOGY OF THE DENTAL CARINAE IN *MARILIASUCHUS AMARALI* (CROCODYLOMORPHA, NOTOSUCHIA) AND THE PATTERN OF TOOTH SERRATION AMONG BASAL MESOEUCROCODYLIA¹

(With 7 figures)

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ABSTRACT. Carinated teeth are common in Mesoeucrocodylia, and the occurrence of denticles over the carinae is related to high predacious species, often referred as ziphodont. This characteristic is broadly recognized as homoplastic. Carinae morphology is cryptic, difficult to be studied under common techniques, and Scanning Electronic Microscopy (SEM) allows the access to detailed information, offering a higher degree of confidence. Previous SEM study allowed the recognition of true/false ziphodont patterns, according to the morphology of the denticles, but such studies on gondwanan mesoeucrocodyles are uncommon. *Mariliasuchus amarali* is an Upper Cretaceous notosuchian mesoeucrocodyle from South America (Bauru Group, Brazil), with carinated teeth and specialized dentition. Its geological and biochronological distribution are reappraised. SEM study of two teeth shows carinae composed of isolated tuberos anisomorphic true denticles, supporting previous study. Enamel ornamentation does not develop over the carinae, and fabric becomes anastomosed in middle and posterior teeth. Carinae only occur in posterior molariform teeth, related to food processing. Morphological variability of *Mariliasuchus* is commented, focusing on dentition. Overall characteristics, molariform morphology and wear planes support a non-predacious habit for *Mariliasuchus*. *Mariliasuchus* pattern could not be related to true/false ziphodont patterns, either by morphology or function, and is defined as ziphomorph. Ziphomorph pattern is evaluated within the range of mesoeucrocodyles. The detailed study of homoplastic characteristics, such as dental carinae, may provide useful apomorphic information for cladistic analysis.

Key words: Tooth morphology. Crocodylomorpha. Notosuchia. Cretaceous. Ziphomorphy.

RESUMO. Morfologia das carenas dentárias em *Mariliasuchus amarali* (Crocodylomorpha, Notosuchia) e a variação no padrão de carena em dentes de Mesoeucrocodylia basais.

Dentes carenados são comuns em Mesoeucrocodylia, e a ocorrência de denticulos sobre a carena está relacionada a espécies altamente predatórias, frequentemente referidas como zifodontes. Esta característica é amplamente reconhecida como homoplástica. A morfologia da carena é críptica, difícil de ser estudada através de técnicas comuns, e Microscopia Eletrônica de Varredura (MEV) permite acesso a informações detalhadas, oferecendo um grau maior de confiança. Estudos anteriores em MEV permitiram o reconhecimento de padrões zifodontes verdadeiro/falso, de acordo com a morfologia dos denticulos, porém este tipo de estudo em mesoeucrocodilos gondwânicos é incomum. *Mariliasuchus amarali* é um mesoeucrocodilo gondwânico do Cretáceo Superior da América do Sul (Grupo Bauru, Brasil), com dentes carenados e dentição especializada. Suas distribuições geológica e biocronológica são reavaliadas. Estudos em MEV de dois dentes mostraram que carenas são compostas por denticulos verdadeiros, tuberosos e anisomorfos, suportando estudo anterior. Ornamentação não se desenvolve sobre a carena, e o padrão se torna anastomosado em dentes médios e posteriores. Carenas ocorrem apenas em dentes molariformes, relacionados ao processamento do alimento. A variabilidade morfológica de *Mariliasuchus* é comentada, com foco em dentição. Características gerais, morfologia dos molariformes e a presença de planos de desgaste suportam um hábito não predatório para *Mariliasuchus*. O padrão de carenas de *Mariliasuchus*

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não pôde ser relacionado aos padrões zifodontes verdadeiro/falso, tanto por morfologia quanto por função, sendo aqui definido como zifomorfo. O padrão zifomorfo é avaliado dentro do espectro dos Mesoeucrocodylia. O estudo detalhado de características homoplásticas, como o carenamento de dentes, pode fornecer informações apomórficas úteis para análises cladísticas.

Palavras-chaves: Morfologia dentária. Crocodylomorpha. Notosuchia. Cretáceo. Zifomorfia.

INTRODUCTION

Features regarding dentition are widely used in evolutionary studies, including crocodylomorphs (*e.g.*, WOODWARD, 1896; RUSCONI, 1933; COLBERT, 1946; PRICE, 1950; BERG, 1966; KUHN, 1968; EDMUND, 1969; LANGSTON, 1956, 1975; GASPARINI, 1971, 1972; BUFFETAUT, 1976, 1979, 1982; BENTON & CLARK, 1988; CARVALHO & CAMPOS, 1988; CLARK *et al.*, 1989; BONAPARTE, 1991; BUFFETAUT & MARSHALL, 1991; ORTEGA *et al.*, 1993, 2000; CARVALHO, 1994; CLARK, 1994; WU & SUES, 1996; WU *et al.*, 1995; GOMANI, 1997; CARVALHO & BERTINI, 1999; BUCKLEY *et al.*, 2000; RIFF & KELLNER, 2001; PRASAD & BROIN, 2002; CLEMENS *et al.*, 2003; POL, 2003; SERENO *et al.*, 2003; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006). From general aspects (*e.g.*, arrangement between dental series) to very specific morphological features (*e.g.*, morphology of the carinae), information proved to be both useful and controversial to phylogenetic and paleoecologic aspects. Crocodylomorph teeth have a wide range of morphological variation, including number and arrangement of cusps, inclination and orientation of the apex, overall shape in lateral view, compression of the crown, compression of the root and presence of cingulus, base-to-apex ornamentation, among others (PRICE, 1950; CARVALHO, 1994; WU *et al.*, 1995; WU & SUES, 1996; GOMANI, 1997; BUCKLEY *et al.*, 2000; RIFF & KELLNER, 2001; NOBRE & CARVALHO, 2002; VASCONCELLOS & CARVALHO, 2005; ELIAS, 2006; TURNER, 2006; ZAHER *et al.*, 2006). The variations include convergences with mammalian dentition (CARVALHO & CAMPOS, 1988; CLARK *et al.*, 1989; BONAPARTE, 1991; CARVALHO, 1994; WU & SUES, 1996; WU *et al.*, 1995; GOMANI, 1997), with a similar nomenclature (incisiforms, caniniforms, and molariforms) referring to specialized teeth.

The term “ziphodont” have long been applied to Mesoeucrocodylia, including several genera from a broad range of families. Characters related to the ziphodont dentition are included (explicitly or not) as part of several works in phylogenetics (*e.g.*, BENTON & CLARK, 1988; CLARK *et al.*, 1989; CLARK, 1994; WU & SUES, 1996; WU *et al.*, 1995; GOMANI, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000;

CLEMENS *et al.*, 2003; POL, 2003; SERENO *et al.*, 2003; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006). The morphology of the carinae, present in several species, is of particular interest. ORTEGA *et al.* (2000) defined the Ziphosuchia as a group of Mesoeucrocodylia comprised by *Notosuchus*, *Libycosuchus*, and *Sebecosuchia*, which should have the ziphodont dentition, defined by the carinae morphology. Nevertheless, there is not much agreement on this characterization. As TURNER (2006) pointed out, for long time the use of ziphodont dentition is considered to be of limited value as phylogenetic information (LANGSTON, 1956; BERG, 1966; HECHT & ARCHER, 1977; TURNER & CALVO, 2005; ZAHER *et al.*, 2006).

Although used in previous studies (LANGSTON, 1956; BERG, 1966), the classical ziphodont dentition (LANGSTON, 1975) is defined as crocodylomorph teeth with morphology similar to equivalents observed in carnivorous dinosaurs. The concept is based on characteristics such as general tooth shape, apex morphology and presence of carinae. Ziphodont carinae are typically serrated and formed by isolated denticles. This idea was posteriorly modified by PRASAD & BROIN (2002), restricting the definition to the composition of the dental carinae, which allowed: a) some morphological variability in dental series and specimens; b) the recognition of other crocodylomorphs as ziphodont species (Fig.1). Examples of ziphodont crocodylomorphs, by this definition, include *Iberosuchus*, *Sebecus*, *Pristichampsus*, *Hamadasuchus*, and cf. *Araripesuchus wegeneri*.

PRASAD & BROIN (2002) also described another pattern, defined as false-ziphodont dentition, which is attributed to mesoeucrocodylians, such as *Asiatosuchus*, *Trematochampsia*, *Sarcosuchus*, and *Sphagesaurus*. False-ziphodont teeth are characterized by the presence of crenulations, composed by the extension of the enamel ridges over the carina. These ridges are often irregular, creating an anastomosing fabric over the labial and lingual teeth surface. When this fabric reaches out up to the mesial and distal borders, it modifies the morphology of the carinae, which usually have a continuous and uniform structure.

The resulting surface becomes crenulated, giving the false impression, under observation by simple optical resources, that the carina is composed by several isolated denticles (PRASAD & BROIN, 2002). This pattern seems to be analogous to the true ziphodont morphology, but as PRASAD & BROIN (2002) point out, its structure is completely different (Fig.2). PRASAD & BROIN (2002) stress that the identification of patterns is especially difficult without sufficiently magnified views, and the use of Scanning Electronic Microscopy (SEM) can prove to be a valuable tool.

The morphological description of the carina as to two basic types, ziphodont and false-ziphodont, seems to be limited when the wide range of morphology types is taken into consideration. In fact, the nature of the denticles and their distribution over the crown, seems to be much wider. Also, several basal Mesoeucrocodylia were heterodont, and morphologic variation can be expected along the series. Thus, teeth morphological variation in crocodylomorphs should not be represented solely by “theropod-like” and “false-theropod-like” morphologies.

Furthermore, there seems to be a sample bias regarding information from Scanning Electronic Microscopy (SEM). Several scientific contributions

include detailed descriptions and images from dinosaur teeth, but most of them are almost totally dedicated to Laurasian theropods (FARLOW, 1987; CURRIE *et al.*, 1990; FARLOW *et al.*, 1991; FIORILLO & CURRIE, 1994; RAUHUT & WERNER, 1995; BUSCALIONI *et al.*, 1996; FRANCO-ROSAS, 2000). In the other hand, there are few publications dedicated to the dental morphology in crocodylomorphs, with the help of SEM (*e.g.*, CARVALHO, 1994; LEGASA *et al.*, 1994; PRASAD & BROIN, 2002; ANDRADE, 2005; ELIAS, 2006), and information about Gondwanan taxa is very limited. While this kind of information may be significant for evolutionary studies to crocodylomorphs, there is still a huge lack of knowledge regarding the descriptions of teeth from South-American taxa.

Among the South-American mesoeucrocodyles, the Brazilian *Mariliasuchus amarali* Carvalho & Bertini, 1999, from the Campanian of the Bauru Group (Araçatuba/Adamantina formations) is well known from several specimens (CARVALHO & BERTINI, 1999; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006). Tooth morphology was studied by ZAHER *et al.* (2006), under common optical techniques, describing the serrations as “composed of a series of round tubercles, instead of sharp denticles present in ziphodont crocodyliforms”.

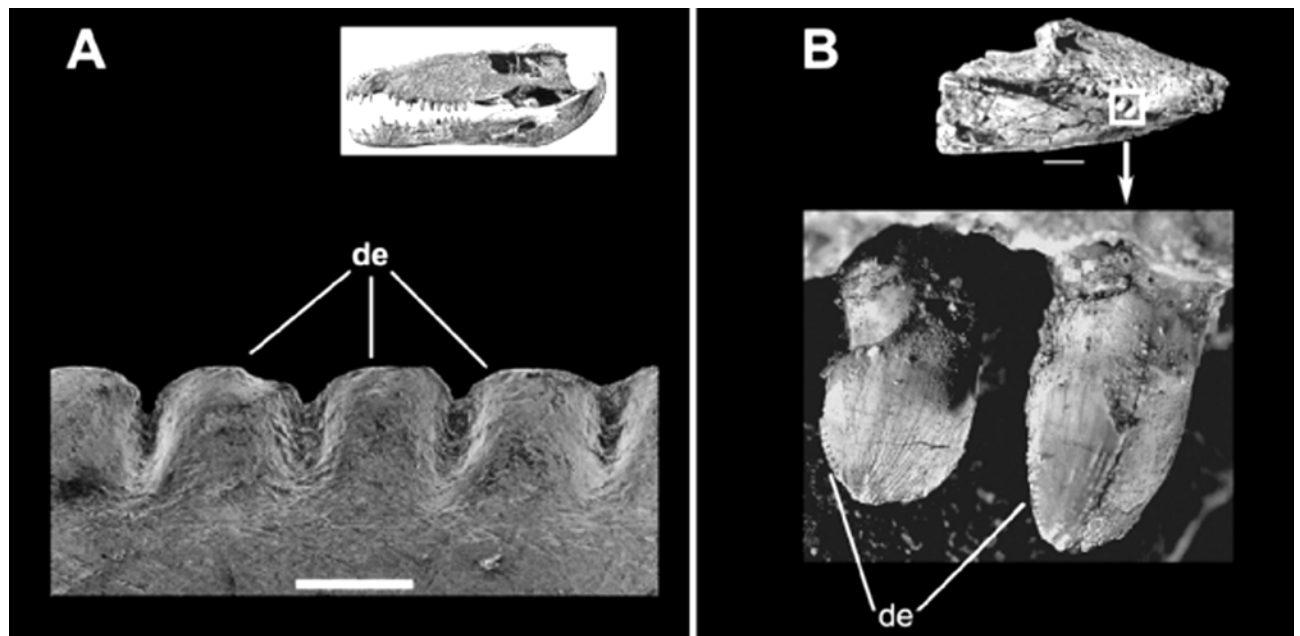


Fig. 1- Ziphodont crocodylomorphs, showing major features of the true ziphodont pattern: A) *Sebecus icaeorhinus* skull (above), with detail of the carina from MNHN (P) VIV-69, *Sebecus* sp. (below); B) cf. *Araripesuchus wegeneri*, GDF 700, holotype (above), with detail of its maxillary teeth bearing carinae, composed of true denticles (below). Scale bars = 0.1mm (A); 10mm (B). (A - adapted from COLBERT, 1946 and PRASAD & BROIN, 2002; B - adapted from ORTEGA *et al.*, 2000 and TURNER, 2006).

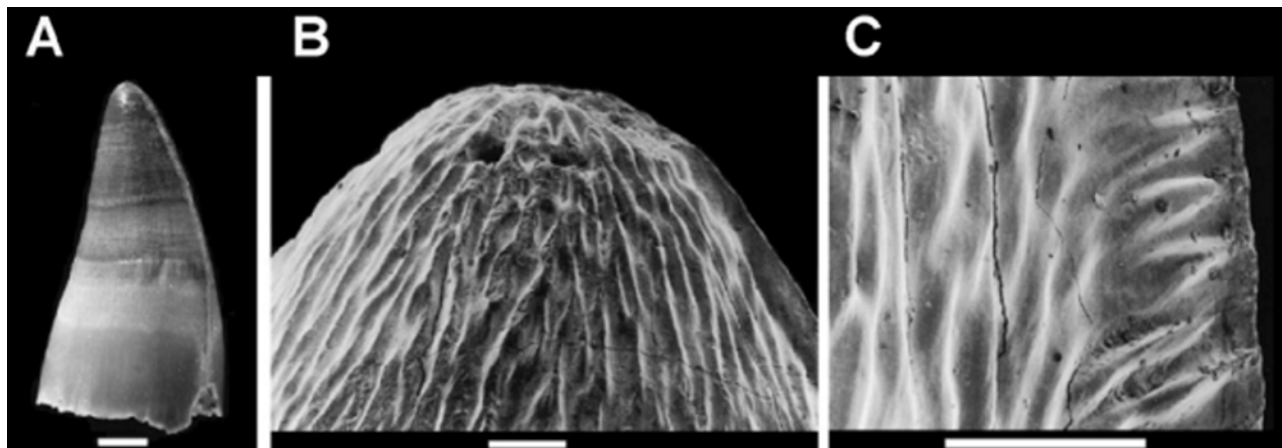


Fig.2- False-zipodonty in *Asiatosuchus*: A) general aspect of MNHN (P) AG-20, caniniform tooth; B) apex of the tooth MNHN (P) BR-15230, showing superficial ornamentation; C) detail of the carina of the tooth MNHN (P) BR-15230, showing ornamentation composed by enamel ridges that develop over the carina, resembling denticles of ziphosuchian Mesoeucrocodylia. Note that such condition is very difficult to identify without Scanning Electronic Microscopy. Scale bars = 10mm (A); 0.5mm (B-C). (Adapted from PRASAD & BROIN, 2002).

Here we study teeth from *Mariliasuchus amarali* under Scanning Electronic Microscopy, review the information provided by ZAHER *et al.* (2006) and compare this particular morphology to the typical ziphodont dentition. Functional aspects of *Mariliasuchus* are explored, to further demonstrate that this morphology is truly diverse from the ziphodont pattern.

MATERIAL AND METHODS

ABBREVIATIONS

Institutional. DES, Department of Earth Sciences, University of Bristol, Bristol, United Kingdom; GDF, MNHN (P) AG, MNHN (P) BR, MNHN (P) VIV, Muséum National d'Histoire Naturelle, Paris, France; IGCE-UNESP, Departamento de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, Brazil; MEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MN, Museu Nacional, UFRJ, Rio de Janeiro, Brazil; MUZUSP, MZSP-PV, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; URC, Museu de Paleontologia e Estratigrafia "Prof. Dr. Paulo Milton Barbosa Landim", Universidade Estadual Paulista, Rio Claro, Brazil.

Anatomical. c, hypertrophied caniniform tooth; cr, tooth crown; de, carina denticle; Den, dentary; er,

enamel ridge; FMP, maxillo-palatinae fenestra; FSO, suborbital fenestra; laf, labial face; lif, lingual face; ma, maxillary tooth; Mx, maxilla; Pal, palatine; Pmx, premaxilla; ro, tooth root; Sp, splenial.

MATERIAL

Mariliasuchus amarali is a Notosuchia (*sensu* GASPARINI, 1971) and most probably a Notosuchidae (CARVALHO & BERTINI, 1999; ANDRADE, 2005; FIORELLI & CALVO, 2005; *contra* CARVALHO *et al.*, 2004; ZAHER *et al.*, 2006), as *Notosuchus terrestris* Woodward, 1896. Remains come from several outcrops, at the vicinities of the Marília City (NAVA, 2004), and are currently housed by several institutions, including MUZUSP, MN, UFRJ, and URC (ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006). It is agreed that *Mariliasuchus* comes from the Late Cretaceous of Bauru Group, in the vicinities of Marília City (CARVALHO & BERTINI, 1999, 2000; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006).

We studied two well-preserved isolated teeth from *Mariliasuchus amarali* under Scanning Electronic Microscopy. They were both found in close association to well-preserved and partially articulated *M. amarali* cranial and post-cranial remains (URC R•67, URC R•68, URC R•69). It is not certain if the teeth come from either one of those specimens or from a fourth individual. Furthermore, they could not have come from URC R•67, as this

specimen has a complete dental series preserved. The isolated teeth were respectively identified as URC R•74 (caniniform) and URC R•75 (molariform) by comparison with URC R•67 and URC R•68. All these specimens, including the teeth, came from the type-locality of the Rio do Peixe outcrop. The specimens of MN 6298-V and MN 6756-V were also studied for further comparison. MN 6298-V is composed of a partial skull, without the mandible, while MN 6756-V is composed of a well-preserved set of skull and mandible. This last specimen shows lateral compression (ZAHER *et al.*, 2006). In ZAHER *et al.* (2006; p.7, 2nd column, lines 8-15), the identification of these specimens is changed, as MN 6298-V is identified as MN 6756-V and vice versa.

GEOLOGICAL SETTINGS

A bibliographic review of *Mariliasuchus* shows some differences of interpretation on the origin of the specimens. CARVALHO & BERTINI (2000), VASCONCELLOS & CARVALHO (2005), CANDEIRO & MARTINELLI (2006), and ZAHER *et al.* (2006) considered that the remains came from the Adamantina Formation. ANDRADE (2005) and VASCONCELLOS & CARVALHO (2006) described them as originated from the Araçatuba/Adamantina formations. Divergences may be partially explained because of the different definitions of the Araçatuba sedimentary unit.

These sediments have been usually considered as the base of the Adamantina Formation (as in KELLNER & CAMPOS, 1999; DIAS BRITO *et al.*, 2001; CANDEIRO & MARTINELLI, 2006). BARCELOS (1984) referred this geological unit as Member Araçatuba. Its original definition as Araçatuba Formation (ZAINE *et al.*, 1980) was most recently modified (BATEZELLI, 1998, 2003; BATEZELLI *et al.*, 1999, 2003; FERNANDES *et al.*, 2003), extending the area of occurrence and lithologic column. Although CARVALHO & BERTINI (1999, 2000) and VASCONCELLOS & CARVALHO (2005) use the traditional definition (Araçatuba as a lithofacies of the Adamantina Formation), it should be noticed that specimens are always preserved in close association with pelitic sediments (CARVALHO & BERTINI, 1999, 2000). VASCONCELLOS & CARVALHO (2006) considered difficulties in the determination of the units and limits, assuming Araçatuba/Adamantina Formation for the UFRJ specimens. NOBRE & CARVALHO (2006) directly address the problem and state that Adamantina sediments on the margins of the Peixe River, at the base of the Rio do Peixe outcrop, are the same as the Araçatuba Formation, as defined by BATEZELLI *et al.* (1999) and FERNANDES *et al.* (2003).

ZAHER *et al.* (2006), describing the geologic settings of *Mariliasuchus*, refers to a single locality for all specimens, at the left margin of the "(...) *Agua Formosa creek (coordinates 22°20'28"S and 49°56'46"W), 10 km south from the urban area of Marília (...)*" (ZAHER *et al.*, 2006; p.2, 1st column, 2nd §). In the same paper, the authors provided locality and horizon as "(...) *a road cut at the left margin of the Peixe River, 18 km from the city of Marília, (...) from the upper part of the Adamantina Formation, Bauru Group*" (ZAHER *et al.*, 2006). Differences of distance are clearly due to the way they were obtained, as 10km is the distance in a straight line, taken from maps, and 18km can be understood as the distance taken using main roads necessary to access the outcrop. The locality itself is well known as Rio do Peixe outcrop from previous works (CARVALHO & BERTINI, 1999, 2000; ANDRADE, 2005) and there is no question as to which river is related the outcrop. The Peixe River spring is located northeastern to the GPS location provided by ZAHER *et al.* (2006), closer to Garça City. From its spring, the Peixe River flows to the western, passing through the *Mariliasuchus* locality and continuing West-Northwestern to the Parana River, without changing its name (*e.g.*, BATEZELLI, 1998). Further disagreement comes from the collection of *Mariliasuchus*. Most papers refer to the same Rio do Peixe outcrop, but referring to one or few specimens (CARVALHO & BERTINI, 1999, 2000; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006). ZAHER *et al.* (2006) declare that all specimens came from the same location, which is a broad definition, as 'location' could define 'outcrop', but also 'the vicinities of Marília City'. NAVA (2004), on the other hand, clearly states that *Mariliasuchus* remains have been found in at least four sites in the same region, and many specimens have been recovered from these outcrops. It is possible that *Mariliasuchus* specimens were collected in other outcrops, but unfortunately, localities and specimens were not individually identified by NAVA (2004), preventing further discussion. Nevertheless, holotype and URC specimens came from the type locality, vicinal road that gives access to Fazenda Doreto, Marília Municipality, 10km from the municipal headquarters, as described by CARVALHO & BERTINI (1999). No other locality has been officially identified. Some divergences regard the provenance of the materials in the lithologic column. The Rio do Peixe outcrop includes only the Araçatuba and the Adamantina formations. The limits of these sedimentary units are not clearly defined, as the Araçatuba Formation broadly interbeds with the Adamantina Formation (*e.g.*, BATEZELLI, 1998, 2003).

At least the holotype, the UFRJ specimens, and the URC specimens were recovered from a horizon close to the bottom of the lithological column (CARVALHO & BERTINI, 1999, 2000; VASCONCELLOS & CARVALHO, 2006; NOBRE & CARVALHO, 2006), where there is a significative contribution of silty matrix over sandstone (Araçatuba Formation *sensu* BATEZELLI, 1998; BATEZELLI *et al.*, 2003). As discussed previously, most studies agree that sediments at the base of the Rio do Peixe outcrop, where *Mariliasuchus* is originated, represents the contact between the Araçatuba and Adamantina formations, thus close to the bottom of the Adamantina Column (CARVALHO & BERTINI, 1999, 2000; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006). A different statement is provided by ZAHER *et al.* (2006), which consider the facies association as representative of the upper part of the Adamantina Formation, close to the contact of the Marília Formation (ZAHER *et al.*, 2006). The specimens are assigned in fact to four horizons (ZAHER *et al.*, 2006) in the columnar section of the referred outcrop, each one showing a different lithology. These are always rich in fine grained sediments, where brown/dark-brown shale interclasts are usually associated, and also a metric mudstone layer (ZAHER *et al.*, 2006). This description matches the upper section of the Araçatuba Formation (*sensu* BATEZELLI, 1998), and its intergrading contact with the Adamantina Formation.

Although disagreement is present in the bibliography, a conservative approach is here preferred. URC specimens came from the same locality and horizon provided for the holotype, and possibly for several other specimens, on the margins of the Peixe River, Rio do Peixe outcrop. The sediments associated with these specimens have been referred to as the Adamantina Formation (CARVALHO & BERTINI, 1999, 2000; VASCONCELLOS & CARVALHO, 2005), and several studies (BATEZELLI, 2003; BATEZELLI *et al.*, 1999, 2003; NOBRE & CARVALHO, 2006) recognized the same sediments as the gradational contact between the Araçatuba Formation *sensu* BATEZELLI, 1998. Type-horizon is therefore considered as the Araçatuba/Adamantina formations, rather than to the upper Adamantina column. As the Araçatuba and Adamantina formations are considered to be (at least) partially synchronic (BATEZELLI, 1998, 2003; BATEZELLI *et al.*, 1999, 2003; FERNANDES *et al.*, 2003), the occurrence of the same species in both sedimentary units is likely. In this context, we understand that there is no disagreement with most studies (CARVALHO & BERTINI,

1999, 2000; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006).

Further debate also exists on the age of the Upper Cretaceous deposits from the Bauru Group. DIAS-BRITO *et al.* (2001) argues for a Turonian-Maastrichtian age for the Bauru Group, with a Campanian depositional hiatus, indicating an early age for the Araçatuba Formation, possibly Turonian. The proposal by DIAS-BRITO *et al.* (2001) is widely adopted (VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006; ZAHER *et al.*, 2006). Nevertheless, the existence of several gradational contacts between the Adamantina and Marília formations (BATEZELLI, 1998, 2003; BATEZELLI *et al.*, 1999, 2003), recognized by ZAHER *et al.* (2006), implies that a Campanian depositional hiatus is unlikely to occur. ZAHER *et al.* (2006) considers a Campanian to Maastrichtian age for *Mariliasuchus*, although accepting a modified version of the model proposed by DIAS-BRITO *et al.* (2001), and considering the lithologic column from the type-locality as representative of the upper Adamantina section.

Correlations based on charophytes, ostracods, and vertebrates (GOBBO-RODRIGUES *et al.*, 2000a, 2000b, 2000c; GOBBO-RODRIGUES, 2001; SANTUCCI & BERTINI, 2001) indicate that the Araçatuba Formation was most probably Campanian (Fig.3), rather than Turonian. Although the age attributed for *Mariliasuchus* is similar for ZAHER *et al.* (2006) (Campanian-Maastrichtian), both models represent different interpretations of the data available.

RESULTS AND DISCUSSION

DESCRIPTION OF THE MATERIAL

URC R•74 shows a caniniform morphology (Fig.4), slightly curved, the apex not acute. URC R•75 is a typical molariform (Fig.5) although not particularly well-developed. In both elements, there is no constriction between crown and root, though differences of color and surface allowed the recognition of the actual boundaries.

URC R•74 is small and could have been positioned as an anterior premaxillary tooth, but not the hipertrophied caniniform. It is comparable in size and general morphology to the regular premaxillary caniniforms of URC R•67. The crown is lightly curved, with a circular cross-section and no lateral compression. There was no evident difference between the lingual and labial surfaces. This tooth does not show any kind of serration, either in the

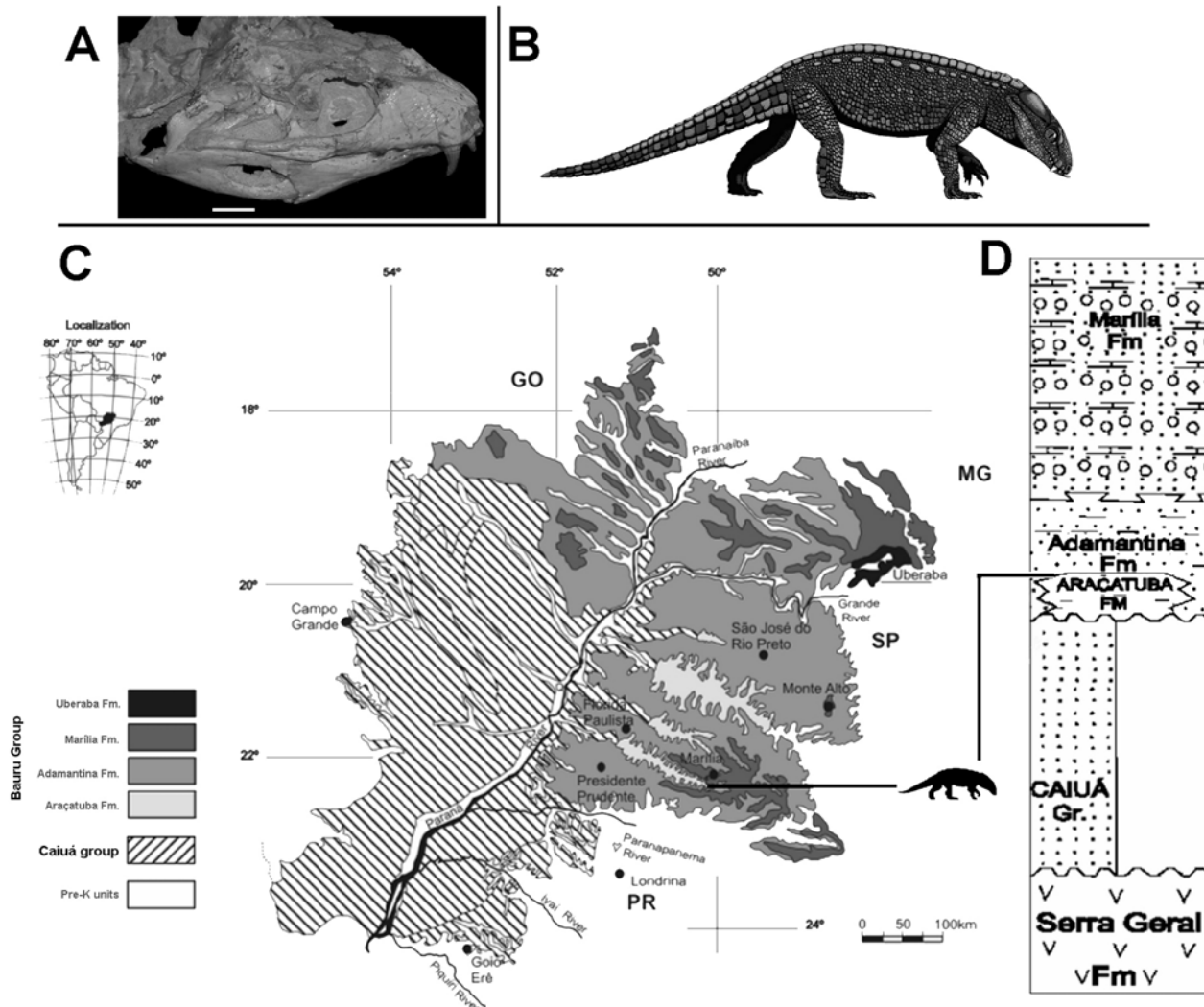


Fig.3- *Mariliasuchus amarali* and its geographical range: A) general aspect of the skull from URC R•67; B) artistic reconstruction of *Mariliasuchus*; C) map showing the geographical distribution of the sediments from the Bauru Group; D) lithologic column for the State of São Paulo, showing type-locality of holotype, UFRJ and URC specimens. Bar: 10mm (A). (B - illustration by Felipe A. Elias; C - modified from FERNANDES & COIMBRA, 1996; D - adapted from BATEZELLI *et al.*, 2003).

mesial or the distal surfaces. It rather had a smooth irregular surface, where base-to-apex ridges develop. The ridges are proportionally low and wide, are present through most of the crown length, and probably represent enamel ornamentation. The ridges do not progress to the apex, which seems to be a natural characteristic, as there is no indication that they were worn out or suffered physical erosion. The very apex is neither round, nor acute. It seems to have been worn out in a single, though irregular, plane.

URC R•75 is also small, and could have been either

a maxillary tooth, or one of the posterior mandibular teeth. Based on the morphology and comparison to URC R•68, it is more likely that the specimen represents the fifth left mandibular tooth. The crown is lanceolated in lateral view, but short and with a blunt apex. The lingual and labial surfaces are different, with a “D-shaped” cross-section. The lingual surface is not as convex as the the labial surface. Considered this interpretation, serrations developed preferentially on the mesial surface, while the distal surface shown a smoother area and denticles were not so easily characterized.

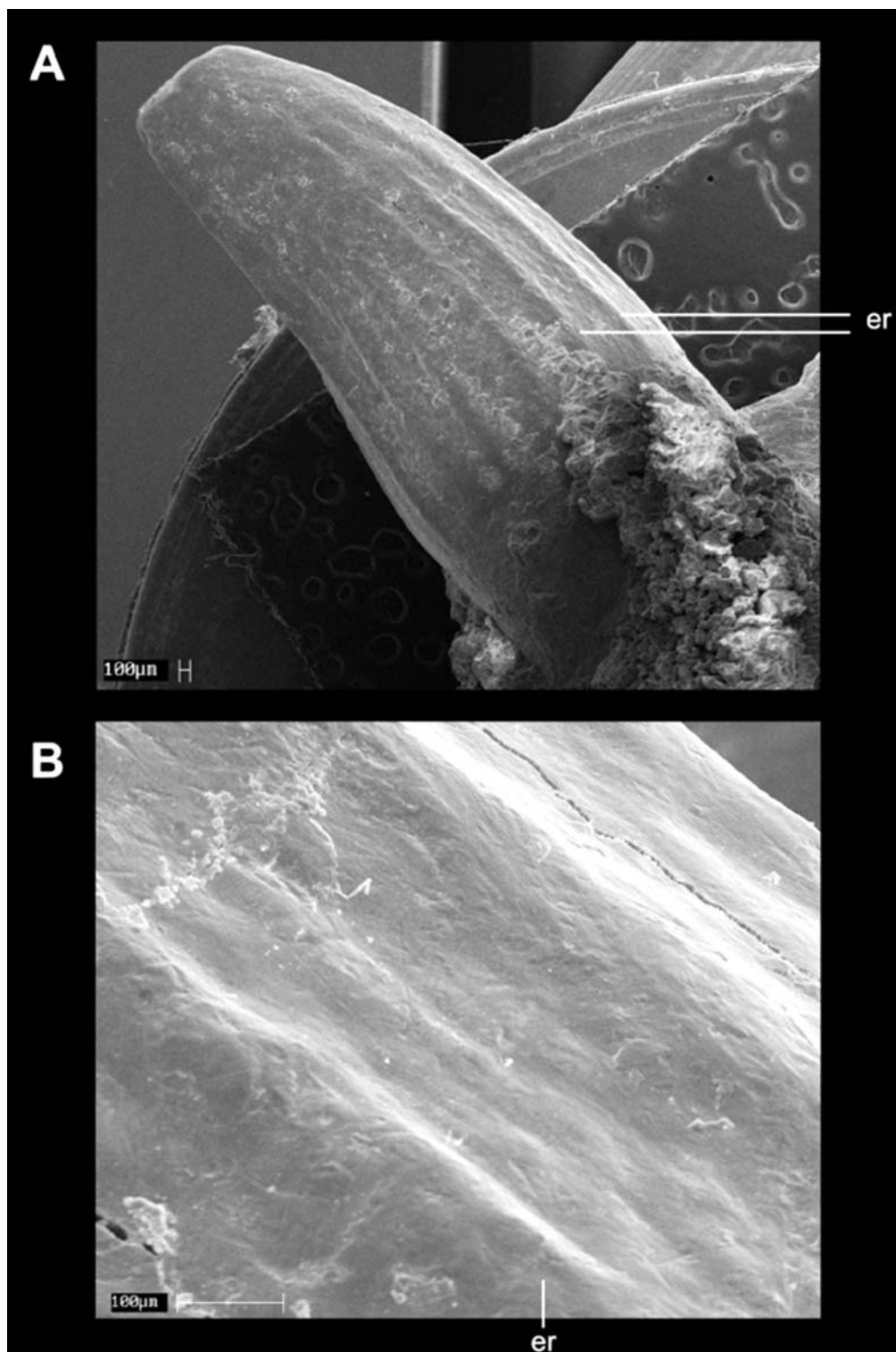


Fig.4- Labial view of the caniniform tooth URC R•74, from *Marilyasuchus amarali*, observed in scanning electronic microscopy: A) general aspect, showing the absence of carinae and the presence of ornamentation composed by base-to-apex enamel ridges; B) detail of the tooth surface, showing the ridges.

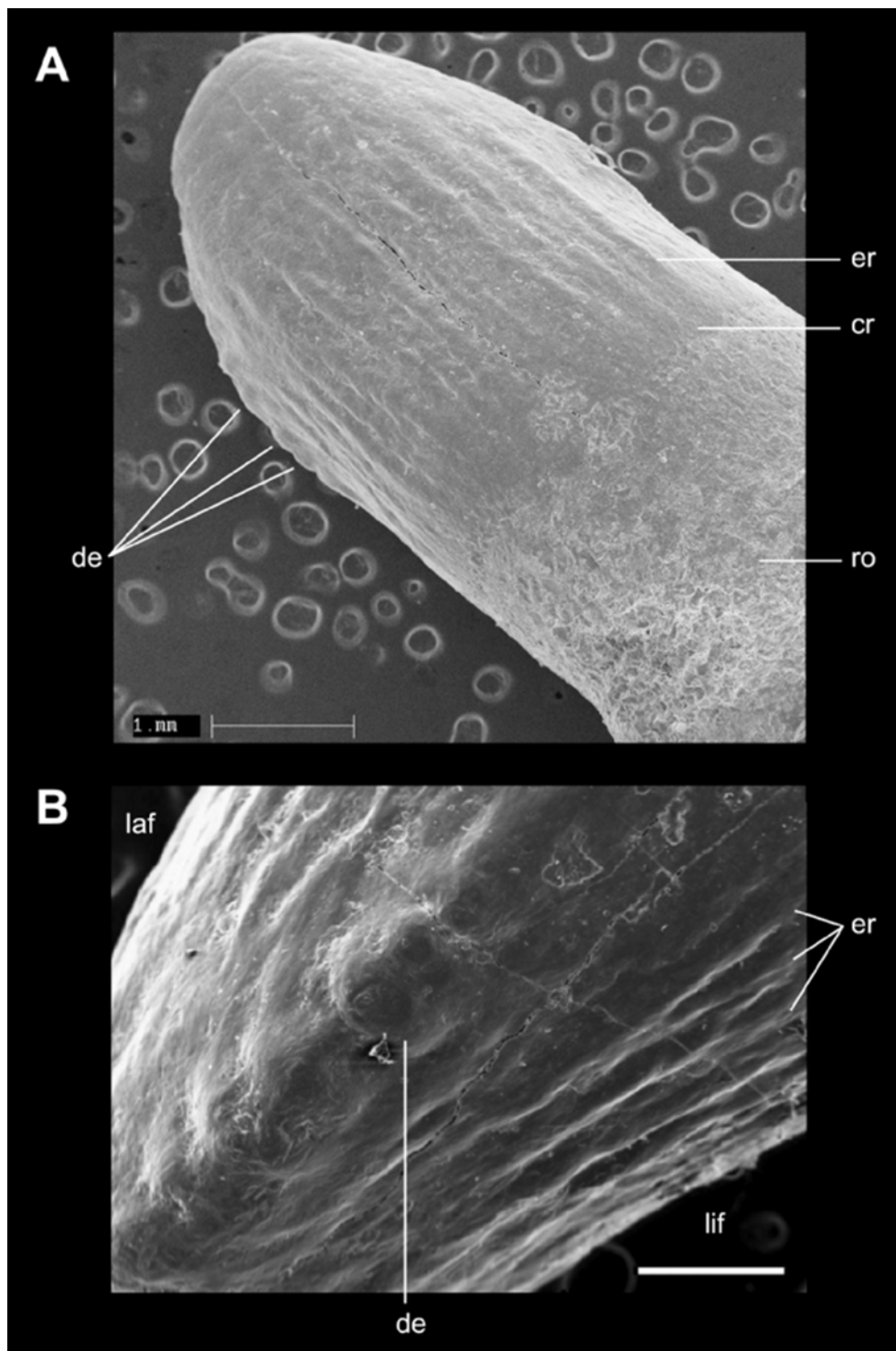


Fig.5- molariform tooth URC R•75, from *Mariliasuchus amarali*, observed in scanning electronic microscopy: A) general aspect from the molariform tooth in lingual view, showing the light ornamentation over the surface and the denticles at the border; B) detail of the denticles from the mesial border, with a very distinctive tuberosus profile. Note the anastomosed pattern composed by the enamel ridges present over the labial and lingual faces of the crown. Scale bar = 0.25mm (B).

Each carina is formed by a collection of rhomboidal denticles, undefined in shape (anisomorphic), with subcircular cross-section. They are tuberos, with an irregular aspect. Furthermore, no additional structures could be observed over the denticles, or between them (Fig.5), as in *Sebecus* denticles (Fig.1).

URC R•75 also has an ornamentation pattern quite evident on its surface, with ridges developing from base to apex, but in an anastomosed pattern. This ornamentation does not extend over the carinae denticles, as would be expected for a false-zipodont. These ridges are irregular and anastomosed. Observation of the dental series of URC R•67 and URC R•68 shows that this pattern progress from the anterior to the posterior teeth in a particular way. On the anteriormost teeth these crests or ridges are bigger and longer, occurring in smaller numbers, while in posterior teeth a greater number of ridges is present, and the anastomosis is more evident.

Although URC R•67 and URC R•68 could not be studied under SEM, observation under common optical resources can be included, especially regarding the carinae and wear surfaces. In URC R•68 the maxilla and the dentary are not bound together, and teeth can be examined in several positions, which is particularly important. The dental carinae are most likely situated on both mesial and distal surfaces, for most molariforms, but are present in all molariforms, without exception. Nevertheless, part of the dental series of URC R•68 had wear surfaces where the serrations should have developed, and it was impossible to positively identify the presence of denticles. Abrasion surfaces are plane, anteroposteriorly elongated and positioned over either the mesial or the distal border of the molariform teeth, but not on both surfaces of the same tooth. These planes can be especially seen on the sixth and seventh mandibular molariforms, and the opposing maxillary teeth. In mandibular molariforms, the worn planes are present only on the mesial surface, inclined anteriorly and labially. In the opposing maxillary teeth, these surfaces are present on the distal surface, facing posteriorly and lingually (Fig.6). The upper and lower wear surfaces match each other, and the complete set (maxilla, premaxilla and mandible) were found in occlusion, in close association (Fig.7).

Worn areas have also been found in hypertrophied caniniforms of both URC R•67 and URC R•68. In URC R•67 there is an eroded plane on the left caniniform mesial crown surface. The worn plane is positioned on the tip of the crown, developing over the mesial surfaces of the teeth. In URC R•68 this worn plane is

also preserved in the right hypertrophied caniniform, but it is more labial than mesial. This feature is not exclusive from URC specimens and is figured for MZSP-PV-50 (ZAHER *et al.*, 2006). In fact, VASCONCELLOS & CARVALHO (2005) also report wear surfaces in UFRJ DG-105-R e UFRJ DG-106-R. Furthermore, ZAHER *et al.* (2006) describe extensive wear facets on the lingual surfaces of some second to fourth maxillary and sixth to eighth mandibular teeth of MZSP-PV-50 and MZSP-PV-51. Extensive lingual worn surfaces can also be seen in three MN 6756-V maxillary molariforms, and at least in one of MN 6298-V. In MN 6756-V mandible, the sixth pair of molariforms show apical-labial wear surfaces.

Another aspect of *Mariliasuchus* deserving attention is that molariform teeth can show a certain degree of paramesial rotation, resulting into a slightly oblique implantation, as observed by several authors (ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006). The distal carina is positioned coincident with the sagittal plane of the skull. This can be observed both in the maxilla and mandible. In URC R•68 this is more evident in three of the most developed right maxillary molariforms, and also from the sixth to the eighth right mandibular molariforms. As previously reported, this particular disposition can also be seen in MZSP PV-50 (ZAHER *et al.*, 2006), on two maxillary pairs, and MN 6298-V and MZSP PV-51 (ZAHER *et al.*, 2006), for three maxillary pairs. At least in the mandible from MZSP PV-50 (ZAHER *et al.*, 2006), MZSP PV-51 (ZAHER *et al.*, 2006) and MN 6298-V, there is a slight degree of rotation in the fifth to the eighth teeth. The pattern is more evident in URC R•68, and also in a variable degree and not in all the same mandibular teeth for the other specimens, but it is present.

CARINAE AND TEETH FROM *MARILIASUCHUS AMARALI* AND THE CONCEPT OF ZIPHOMORPH DENTITION

The morphology observed in these isolated teeth of *Mariliasuchus amarali* shows clearly the presence of true denticles constituting a serrated border, on the molariform tooth observed. These structures are coherent with the description provided by ZAHER *et al.* (2006) for teeth of other specimens, although in their descriptions they preferred to consider these structures as tubercles. Observations using SEM allowed to clearly state that the ornamentation does not participate in the composition of the carina and the denticles are real and individualized structures. This excludes completely the possibility of these teeth as to be characterized as false-zipodont teeth.

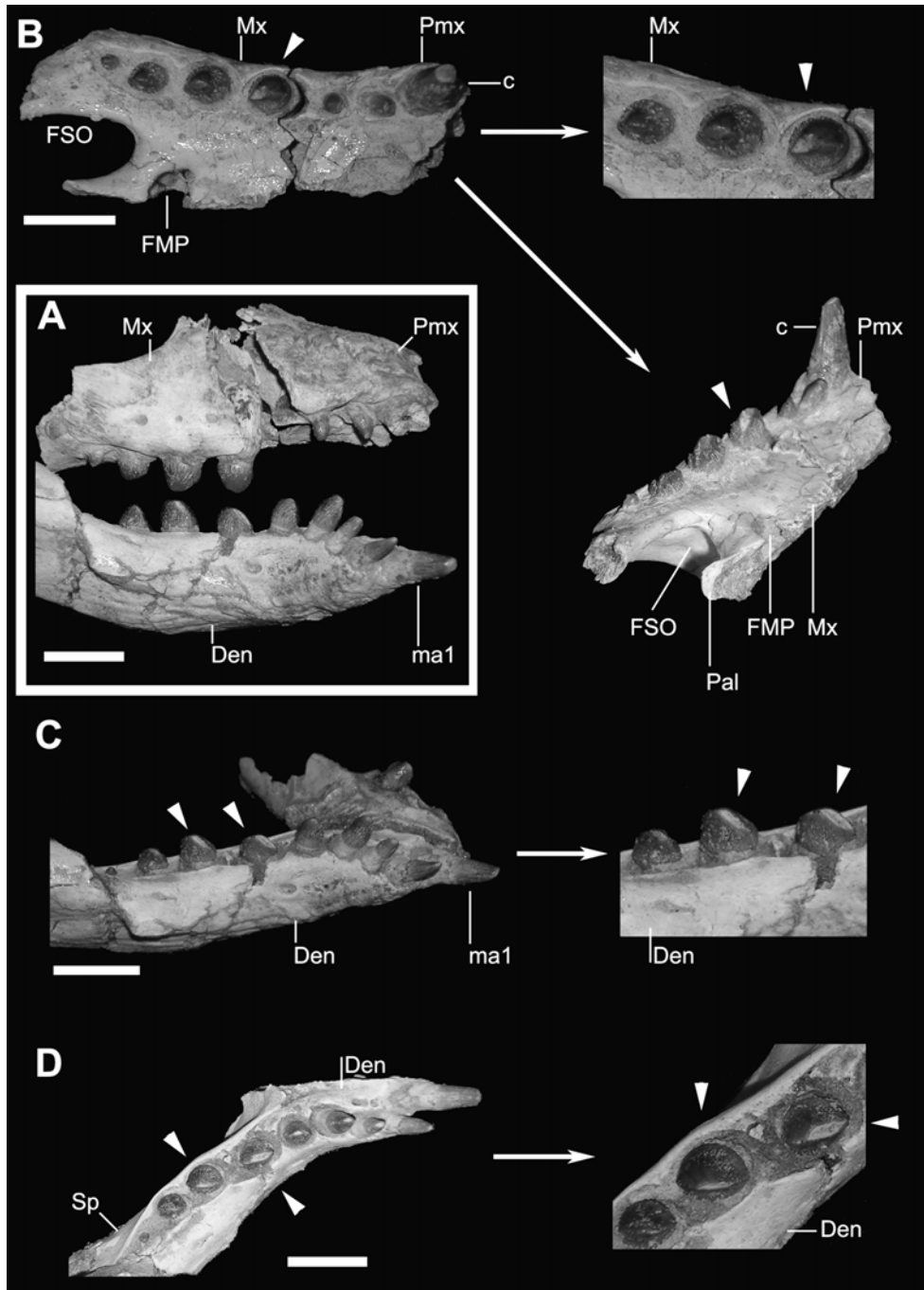


Fig.6- *Mariliasuchus amarali* URC R•68, observed in several views, showing the occurrence of elongated wear surfaces in maxillary and mandibular teeth: A) general aspect in lateral view; B) the right premaxilla-maxilla, and detail of where abrasions can be observed in the distal border of a molariform, in palatal (above) and posteromedial (below) views; C) mandible set in latero-dorsal view, and detail showing abrasions on the mesial border of the sixth and seventh teeth; D) right mandible in dorsal view, and detail showing abrasions on the mesial border of the sixth and seventh teeth. Main wear surfaces indicated by white pointers. Note the inclination of the wear surfaces in maxillary (lingual) and mandibular (labial) teeth; the complementary arrange of the mandibular and maxillary teeth; the presence of obliquely implanted teeth on the maxilla and the mandible, and a certain degree of variation on this condition along the dental series. Bar = 10mm.

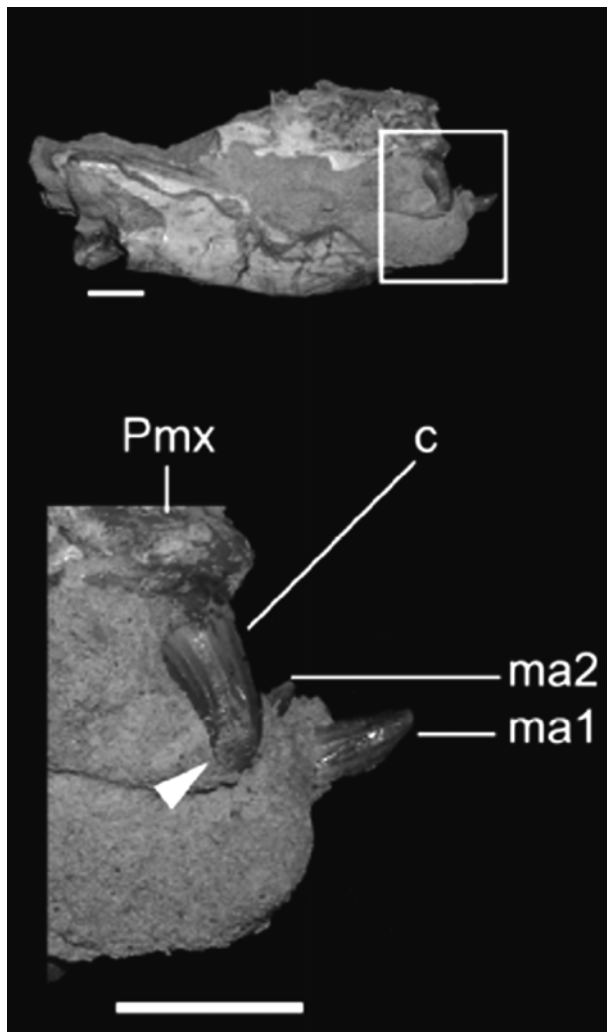


Fig.7- *Marliasuchus amarali* URC R•68 in lateral view, during cleaning procedures. The set was found in close association (above). Detail (below) shows the right hypertrophied caniniform tooth, and the eroded surface exposed labially, indicated by the white marker. Scale bar = 10mm.

Study using SEM provide definitive identification that, in *Marliasuchus*, denticles are far different in relation to typical ziphodont crocodylomorphs. *Marliasuchus* shows clearly isolated and anisomorphic denticles, with tuberous shape. In ziphodont teeth, the carina is also formed by isolated denticles, but each denticle is more elongated, with a subrectangular to elliptical base. Ziphodont denticles are usually very close to each other and constitute a long series of repetitive isomorphic denticles. Each denticle may be keeled itself, as in *Sebecus*, although this is not the case for other ziphodont forms (e.g., cf. *Araripesuchus wegneri*).

Furthermore, overall morphology of the teeth is very different from the carnivorous blade-like teeth, found either in *Sebecus* or in other ziphodont mesoeucrocodyles. Ziphodont crocodylomorphs develop carinae over highly compressed teeth, usually blade-like caniniforms. According either to the definitions figured in LANGSTON (1975) and PRASAD & BROIN (2002), *Marliasuchus* cannot be characterized as a ziphodont form, as suggested by ZAHER *et al.* (2006), which was confirmed by observation under different techniques, as SEM and optical microscopy.

Since the definitions of true ziphodonty and false-ziphodonty do not apply to *Marliasuchus amarali*, a more adequate terminology should be used. We define this pattern as the ziphomorph pattern, here characterized by teeth with anisomorphic, tuberous, and well-spaced true denticles composing a carina, with ornamented enamel surface (fabric) that does not developed onto the carina. This definition is important and especially useful as recognition of an independent evolutionary condition or an apomorphic character state.

As previously pointed out by many authors (LANGSTON, 1956; BERG, 1966; HECHT & ARCHER, 1977; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006), ziphodont dentition is of little phylogenetic value. The original definition certainly constituted a homoplastic condition and this explains the limited value of this information. On the other hand, detailed studies on particular morphologies about carinae morphological variability can be potentially useful, providing apomorphic information. At the moment, the ziphomorph dentition constitutes a unique condition, therefore useful as diagnostic character for *Marliasuchus* (as in ZAHER *et al.*, 2006). Similar tuberous denticles may be found in other genera, such as *Sphagesaurus*, *Notosuchus* and *Adamantinasuchus*. Detailed observation on the morphology of teeth and carinae, with additional comparison between specimens, is important and may provide reliable phylogenetic information regarding these taxa.

The use of modern techniques, such as SEM, should allow more precise definitions of the carinae in crocodyliforms and, eventually, the recognition of at least a few additional apomorphic patterns from the known ziphodont types. Such studies are important, as homoplastic generalizations may be converted in useful phylogenetic information, reducing “noise” in phylogenetic analysis.

MORPHOLOGICAL VARIATION OF TEETH AND DENTITION IN *MARILIASUCHUS AMARALI*

Previous works (CARVALHO & BERTINI, 1999; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006) provided a series of contributions on the knowledge of *Mariliasuchus*. Some morphological variation can be accounted for the material. The differences reported by VASCONCELLOS & CARVALHO (2006) for UFRJ specimens are mainly assumed as ontogenetic, though for UFRJ DG 56-R a taphonomic aspect should be considered, as this skull is not well-preserved. ZAHER *et al.* (2006), on the other hand, considered that MZSP-PV-51 could represent another species. Variation included the presence of: *foramen incisivum*, denser ornamentation, wider parietal width between the supratemporal fenestrae, and the presence of a frontal longitudinal ridge. At the moment, these variations were only identified for MZSP-PV-51 (ZAHER *et al.*, 2006) and URC specimens seem not to have such characters. Parietal width between the supratemporal fenestra is small for URC R•67, as in MN 6298-V, UFRJ DG-50, and MZSP-PV-50, but larger for MZSP-PV-51, UFRJ DG-106-R, and MN 6756-V. The description of ZAHER *et al.* (2006) presents the opposite condition to MN specimens, result of the mistaken reference of the identification codes. Variation on the skull table and parietal morphology is also known from *Notosuchus* (ANDRADE, 2005; FIORELLI, 2005), and might be related to sexual dimorphism, but proper data from a wider range specimens should be added before this hypothesis endure further consideration.

Although most of the carinae features described by ZAHER *et al.* (2006) could be verified, the additional tubercles on the base of the molariform crown labial surface are not present in any of the URC specimens. This is possibly due to the position of this molariform along the series, as URC R•75 was probably the fifth mandibular tooth. Ontogenetic differences constitute an alternative hypothesis, as the URC specimens are most likely subadults, thus younger than MZSP-PV-50.

The posteromedial orientation of the distal crest is common throughout the URC and MZSP specimens, especially related to molariform teeth that occlude with each other and are particularly developed, both on the maxilla and mandible (Fig.6). Nevertheless, this feature occurs in a clearly irregular manner along the range of individuals, and some of the teeth are not rotated, while others are clearly oblique. Differences could not be assigned to ontogenetic

stages, and though the particular condition of UFRJ-DG material is unknown, VASCONCELLOS & CARVALHO (2005, 2006) report that a dietary ontogenetic variation is unlikely for *Mariliasuchus*. If *Mariliasuchus* maintained the same feeding pattern through its development, there is no basis for assuming that ontogenetic changes might be related to variations of tooth rotation. Variation could be due to preservation bias, but then the same variation would be expected to be present in the anterior dentition. To the moment, it can only be considered that *Mariliasuchus* by far does not show the regular arrangement of teeth for Mesoeucrocodylia, where the carinae are coincident to the dental series.

FUNCTIONAL INTERPRETATION OF THE ZIPHOMORPH PATTERN IN *MARILIASUCHUS AMARALI*

The differences observed between the three morphological patterns (ziphodont, false-ziphodont, and ziphomorph) are probably related to functional aspects of food processing and/or diet composition. The first two patterns are usually related to top-predator mesoeucrocodylians. Most typical ziphodont teeth has well developed carinae present in anterior, if not all teeth, as in *Baurusuchus*, *Pehuenchesuchus*, and *Sebecus* (RIFF & KELLNER, 2001; PRASAD & BROIN, 2002; TURNER & CALVO, 2005). These teeth are often compressed and strongly curved, exhibiting a typical morphology of a predator tooth. *Baurusuchus* seems to fit into this pattern for most characteristics, although teeth are more convex in the labial than in the lingual surface (RIFF & KELLNER, 2001), not as compressed as in the typical ziphodont forms. In cf. *Araripesuchus wegneri* the morphology diverge broadly from the original definition (LANGSTON, 1975), as teeth do not show the same caniniform profile, although laterally compressed (PRASAD & BROIN, 2002; TURNER & CALVO, 2005; TURNER, 2006). While *Baurusuchus* is considered to present a ziphodont (theropodomorph) dentition (RIFF & KELLNER, 2001), the same can only be accepted for *Araripesuchus* by the broad ziphodont definition of PRASAD & BROIN (2002).

While the ziphodont theropod-like dentition is broadly used as a parameter to infer diet in crocodylomorphs, the same cannot be said for their contrapart, the ornitopods, sauropods, and prosauropods. It is true, though, that several herbivore dinosaurs had carinated teeth (GALTON, 1973, 1985, 1986; BARRETT, 2000). GALTON (1973, 1985, 1986) considers that differences on the carinae morphology (coarser denticles, less numerous, projecting at 45 degrees

from the crown surface) should be indication of herbivore habit in prosauropods. At least partially, the ziphomorph pattern fits into *Mariliasuchus* description, except for the angle of denticle implantation. The projecting angle may not be relevant in this case, as denticles are round and tuberos, and it would be difficult to consider that a specific attack-angle could be of particular relevance. Furthermore, teeth specialization is not a prime requirement of herbivore diet, as other adaptations may allow food processing without leaving an evident fossil signal. This is exemplified by *Protorosaurus* (Late Permian, Germany), as mentioned by BARRETT (2000). At least two specimens of this archosauromorph showed a gut content of *in situ* gastric mill and plant material from conifers and pteridosperms, even though possessing recurved and conical teeth (MUNK & SUES, 1993).

BARRETT (2000) points out that, regarding crocodylomorphs, dinosaurs, and lepidosauromorphs, the existence of certain features could indicate an herbivore diet, as extensive tooth wear associated with jaw antero-posterior motion, development of molariform teeth, loss/modification of premaxillary teeth, and the presence of a dental battery. Most of these features also apply for *Mariliasuchus*. Nevertheless, Barrett's concept of herbivory does not exclude the carnivory, only indicating that the taxon is closer to the herbivorous end of the dietary spectrum (BARRETT, 2000). The same author also points out that dental correlates to omnivory have never been properly identified, meaning that it is only possible, to a certain extent, indicate the presence of vegetal or animal material in the diet, but not a definitive statement about feeding.

Nevertheless, *Mariliasuchus* certainly cannot be characterized as possessing a generalized dentition. In fact, as other notosuchians, there are clearly caniniform, incisiform and molariform teeth, which were functionally fitted for specific, and maybe complementary tasks. Its dentition showed carinae with denticles only in molariform teeth, as pointed out by ZAHER *et al.* (2006), and this does not fit into a predator dentition for two main reasons: (1) serrations are not developing over anterior teeth, but over more posterior ones; (2) serrations are not developing over caniniforms, but over molariforms. Serrations are thus missing from all teeth that, for excellence, could be related to prey capture, especially the anterior

hypertrophied caniniforms (Fig.6). Carinae are only present over the surface of teeth that could not participate of prey capture, particularly the sixth and seventh mandibulatory teeth and the corresponding maxillary molariforms. This suggests that the carinae were important elements in food processing, not in capturing and killing prey. General aspects of the dentition and the distribution of the carinae on the dental series constitute evidence that *Mariliasuchus* was not a typical predator, such as *Sebecus* or *Baurusuchus*. Furthermore, the morphology of the denticles also support a non-predatorial habit for *Mariliasuchus*. As denticles are tuberos, they resemble a miniature molar tooth. Its value as a slashing tool should be no better than poor. Other general features support this hypothesis, as the long symphysis, high coronoid process and short rostrum (Figs.3,6). Dental features include proportionally short molariforms, mesiodistally and labiolingually expanded.

Three mandibulatory pairs of teeth (sixth to eighth) and corresponding maxillary pairs are especially enlarged in all specimens (ZAHER *et al.*, 2006, p.10, Fig.6), suggesting that they were able to cope with higher mechanical stress. Apart from this, VASCONCELLOS & CARVALHO (2006) previously concluded that the ontogenetic development of some skull elements (*e.g.*, mandibular fenestra, laterotemporal fenestra) might indicate a gain of strength and resistance in the skull of *Mariliasuchus*, during its lifetime. Although there are other species clearly more adapted for a durophagic diet, such as *Sphagesaurus* (POL, 2003; ANDRADE, 2005), the skull and teeth of *Mariliasuchus* (Fig.6) seems to be more fitted to foraging on harder and more abrasive items than to a diet of soft meat. The procumbent anterior dentition is clearly not what can be expected for a predator, although it may fit the idea of an insectivore species.

The occurrence of antero-posterior jaw movements in *Mariliasuchus* is possible, as the glenoid fossae are elongated (ANDRADE, 2005; ZAHER *et al.*, 2006). This has been considered evidence of high-fiber ingestion in crocodylomorphs and other tetrapods (MAYNARD SMITH & SAVAGE, 1959; WU *et al.*, 1995; WU & SUES, 1996; SUES, 2000), but in a similar way the character could fit some very specific highly predatory forms (CLARK *et al.*, 1989; BARRETT, 2000). Herbivory was already proposed for *Notosuchus terrestris*, and related to the specialized

dental morphology and jaw articulation (BONAPARTE, 1987, 1991; CARVALHO, 1994). These would allow a masticatory process resembling the ones observed in mammals, and inferred for therapsids and ornithischian dinosaurs (BONAPARTE, 1991). The elongated mandibular articulation is concordant with worn surfaces of teeth in several *Mariliasuchus* specimens (VASCONCELLOS & CARVALHO, 2005; ZAHER *et al.*, 2006). The disposition of URC R•68 wear facets clearly supports this idea (Fig.6). The oblique implantation would allow apex to apex action. This contact becomes more extensive and lateral between the sixth to eighth mandibular teeth and corresponding maxillary molariforms. The oblique disposition of these elements allowed at least some contact between the lingual surfaces of maxillary teeth and labial surfaces of mandibular molariforms, resulting in inclined worn facets. Upon the existence of such an organized apparatus, food intake probably demanded elaborated processing of items, most likely undertaken by median maxillary and posterior mandibular molariforms.

The presence of abrasion in the labial face of the hypertrophied caniniform is a special case, as it could not be produced by occlusion. These wear planes may constitute the effect of a preservation bias, as these teeth are highly exposed and could have been eroded. These facets could also develop as the result of a particular action over substrate (*e.g.*, bark, soil), and would fit in the specialized dentition of *Mariliasuchus*.

The rounded denticles of the carinae, the general skull structure, and the robust teeth from *Mariliasuchus amarali*, were not well suited for a typical predator. Molariform teeth are rather better tools for crushing or crumble fibrous, hard and/or abrasive food items (BONAPARTE, 1991; WU *et al.*, 1995; WU & SUES, 1996; SUES, 2000). Abrasion is supported, in this case, by the occurrence of wear facets of *Mariliasuchus* molariform teeth. The existence of anterior-posterior abrasion planes is probably the result of fore-after movements of the mandible of *Mariliasuchus* (ZAHER *et al.*, 2006).

While ziphodont crocodylomorphs are usually identified as carnivorous predators, *Mariliasuchus* had a ziphodont dentition that was probably best suited for dealing with a variety of hard or fibrous items (*e.g.*, coarse leaves, seeds, pinecones, but also arthropods), and inclusion of

these in the diet is most likely, according to the information presented here and elsewhere (VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006). Evidence is composed by the morphology of the carinae and its denticles (ziphodont pattern), in association with several other indicators, such as: absence of carinae and specialization of the anterior dentition; morphology of the jaw-joint articulation; elongation and inclination of wear planes; preferential occurrence of wear planes in posterior teeth; posterior dentition composed of non-shearing molariforms. All those features are indicative of ingestion of plants, while does not exclude the intake of animal material (*e.g.*, arthropods, worms, small vertebrates). The teeth morphology and interpretation are very different for *Mariliasuchus* and ziphodont crocodylomorphs, such as *Baurusuchus* and *Sebecus*. The inclusion of items other than meat is likely and, by morphological and functional aspects, its characterization as a ziphodont species seems highly inaccurate, or at least an unnecessary simplification.

CONCLUSIONS

The dentition of *Mariliasuchus* shows what we characterize as ziphodont carinae. This pattern is defined as carinae composed by tuberos anisomorphic true denticles, without the development of enamel ornamentation over the denticles composing the carinae. In *Mariliasuchus*, the ziphodont pattern is associated with molariform teeth, and its function is related to food processing rather than prey capturing and killing. At least in *Mariliasuchus*, the typical ziphodont and the new ziphodont patterns are functionally different, the first one related to prey capture and killing (LANGSTON, 1956, 1975), and the second one to food processing. Elaborated food intake and preference for hard and abrasive food items is supported by general skull features, elongated glenoid fossae and the dentition, development of molariforms, and the occurrence of wear facets (MAYNARD SMITH & SAVAGE, 1959; WU *et al.*, 1995; WU & SUES, 1996; SUES, 2000; ZAHER *et al.*, 2006). *Adamantinasuchus*, *Sphagesaurus* and *Notosuchus* show similar dental features that suggest that the ziphodont pattern is present in these taxa.

The ziphodont pattern does not provide reliable phylogenetic information because it represents a

homoplastic feature, the result of overlooking cryptic information. The study of carinae morphology under SEM will provide further information for several taxa, as foreseen by PRASAD & BROIN (2002), and shall provide useful apomorphic characters for phylogenetic studies. Information on tooth morphology of several species of Mesoeucrocodylia is especially poor, but should contribute to the resolution of several systematic and taxonomic problems on the evolution of this particular group. The description here of the ziphosph pattern also brings the idea of a wider range of diverse, unique morphologies and specializations, which were present during the Cretaceous.

Additionally, comparative investigations among dental material from Crocodylomorpha, Dinosauria, and other groups of the Archosauromorpha, may help the characterization of species and morphotypes, allowing the distinction of isolated teeth.

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