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Gondwana Research 13 (2008) 139 – 145
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GR Letter

Feeding behavior of the Gondwanic Crocodylomorpha *Mariliasuchus amarali* from the Upper Cretaceous Bauru Basin, Brazil

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Received 25 November 2005; accepted 1 August 2007
Available online 9 August 2007

Abstract

Mariliasuchus amarali Carvalho and Bertini, 1999 is a Cretaceous Crocodylomorpha (Notosuchia) from the Bauru Basin, Brazil. The feeding behavior of *M. amarali* is analysed and interpreted based on the articular–quadrate articulation, pattern of teeth occlusion and the chemical composition of coprolites. The articulation between the articular and quadrate bones and the teeth abrasion pattern allow to infer that this notosuchian probably moved the jaw antero-posteriorly, processing the food before swallowing it. *M. amarali* should have kept the food inside the oral cavity during the feeding process, increasing the effectiveness of mastication. The post-caniniform tooth row is medially displaced in relation to the skull, suggesting the presence of a large conjunctive tissue. The structure and shape of the anterior caniniform and incisiform teeth exclude the possibility of an entirely herbivorous diet. Based on the morphological data and on the physical and chemical analyses of coprolites, it is interpreted that it had omnivorous feeding habits. The shape and abrasion pattern of the incisiform teeth suggest that *Mariliasuchus* employed the prominent anterior incisiform teeth for an active digging behavior.

Keywords: Crocodylomorpha; Notosuchia; Cretaceous; Feeding behavior; *Mariliasuchus*

1. Introduction

During the opening of the Atlantic Ocean, the continental rupture lead to intracratonic volcanic activity and to the origin of a broad intracontinental depression in Brazil which is known as the Bauru Basin (Fernandes and Coimbra, 1996, Veevers, 2005) covering part of the present states of Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso, Goiás and Minas Gerais (almost 370,000 km^2). The basin is composed of three formations: Adamantina, Uberaba and Marília from base to top.

The Adamantina Formation covers a large portion of the exposed area of the Bauru Basin, across western São Paulo, Minas Gerais (Triângulo Mineiro), Mato Grosso do Sul (east and south) and southern Goiás States; and is composed of fine-grained sandstones and siltstones with intercalations of red mudstones of Turonian and Santonian age (Dias-Brito et al., 2001). Its deposition took place in a braided fluvial system on an extensive alluvial plain and alongside some ephemeral lagoons (Garcia et al., 1999).

So far a diverse and peculiar fauna terrestrial crocodylomorphs have been discovered from this lithostratigraphic unit such as notosuchids and baurusuchids and peirosaurids. Along with other tetrapods, this peculiar crocodylomorph fauna is important for their potential correlation with other Upper Cretaceous basins in South America, Africa, Madagascar and India, and potentially Antarctica for paleoclimatic, paleoenviromental, paleogeographical and paleobiogeographical studies. For example, the corroboration of an endemic Gondwanaland terrestrial fauna during the Cretaceous reinforced the hypothesis of an Early Cretaceous, or even a Late Cretaceous southernmost Gondwanic 'terrestrial route' linking South America and Indo-Pakistan via Antarctica (Carvalho and Bertini, 1999; Carvalho et al., 2004; Turner, 2004; Carvalho et al., 2005; Nobre and Carvalho, 2006; Yatheesh et al., 2006; Martinelli et al., 2007).

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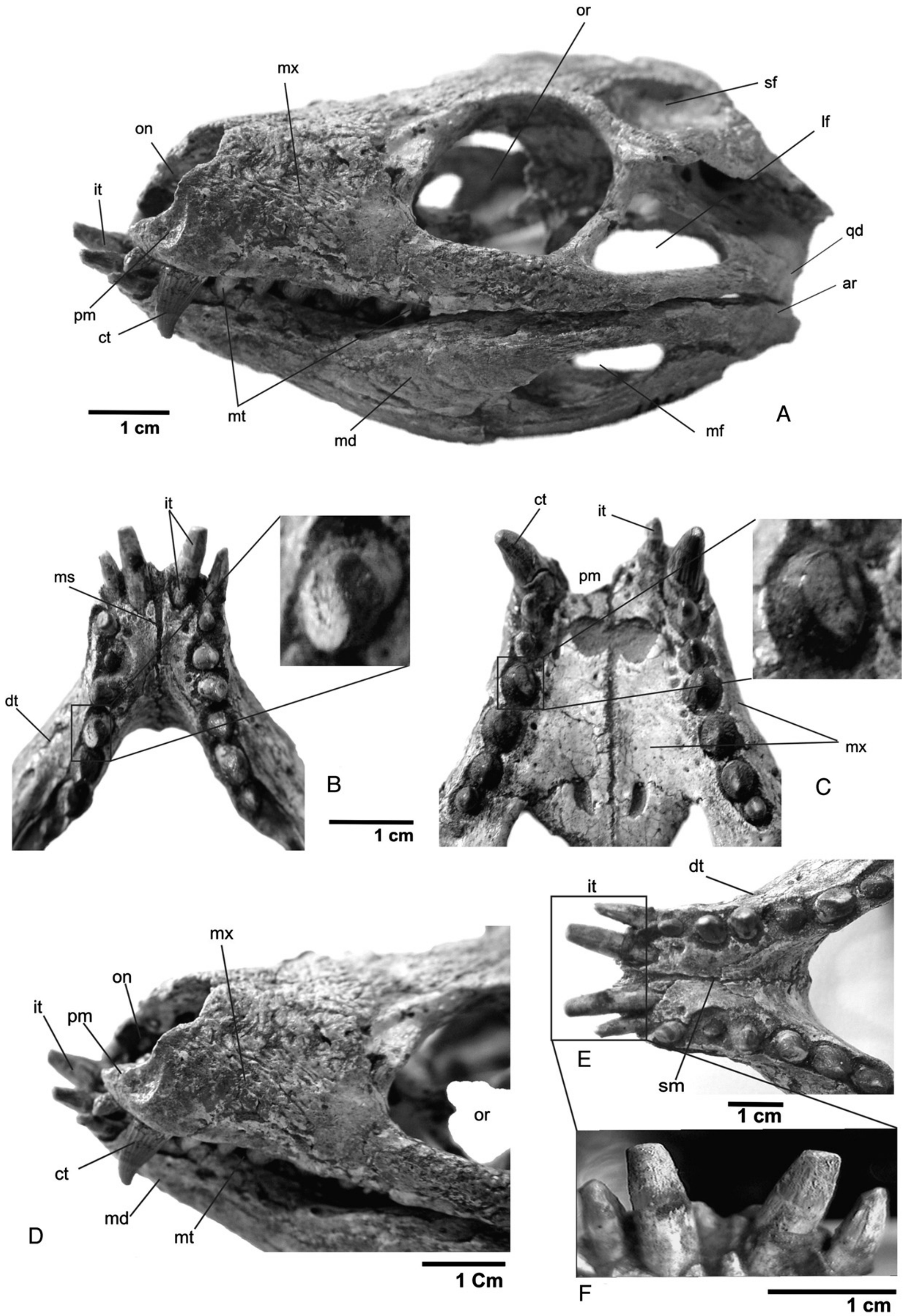
doi:10.1016/j.gr.2007.08.002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This study aims to analyse the feeding behavior of *Mariliasuchus amarali* Carvalho and Bertini, 1999, a notosuchid Mesoeucrocodylia crocodylomorph from the Adamantina Formation in the outskirts of the Municipality of Marília, São Paulo State, Brazil. The feeding habits of Cretaceous Mesoeucrocodylia have been a subject of discussion by many authors. Based on the morphology of skull and teeth, Bonaparte (1991) attributed an omnivorous diet to *Notosuchus terrestris* Woodward, 1896, and pointed out the possibility of antero-posterior jaw movements during food processing, because of the articulation structure between the articular and quadrate bones. Clark et al. (1989) and Gomani (1997) also agree that antero-posterior jaw movements are possible, if not probable, among the Notosuchia. Pol (2003) and Nobre and Carvalho (2006) suggested that the dental morphology of *Sphagesaurus huenei* Price, 1950, and *Adamantinasuchus navae* Nobre and Carvalho, 2006 including teeth occlusion, fore-aft jaw movements, and alternate unilateral jaw occlusion pattern presents characters indicating an unexpected feeding habit for a crocodylomorph.

These inferences on the feeding habits and diets of notosuchid crocodylomorphs may shed new light and broader view on the trophic web systems previously erected to Gondwanan vertebrate fauna.

2. General features of *Mariliasuchus* skull

The skull is robust and high, with a tubular shape, being thinner at the anterior region. The external nares are placed in a terminal and vertical position. The maxillary and dentary bones project to the outer side after the teeth insertion, causing a medial displacement of the dentition. Thus, the molariform teeth are just noticeable at the outer surface of the skull. The posterior half of the skull is much wider than the anterior one. The orbits are large and placed in a lateral to dorso-lateral position. The quadrate bone occupies a semi-vertical position in relation to the skull, and does not project posteriorly as in the recent crocodylomorphs. The articulation of the jaw with the skull is large at the posterior part, and its base is flat and formed by the surangular and articular bones (Nobre and Carvalho, 2001).

The robust mandible has a narrow and thinner part than that of the anterior portion of the skull and expanded posterior part, paralleling the shape of the skull. The mandible symphysis is well developed.

2.1. Dentition

The specimens UFRJ-DG 105-R and UFRJ-DG 106-R have preserved around 90% of the original dentition. The dention of the two specimens differs only in size and robustness of the teeth, due to ontogenetic factors. The present description is based on the specimen UFRJ-DG 106-R, whose preparation permitted disarticulation of the jaw from the skull, providing a better exposure of the dentition.

Fig. 2. Coprolite UFRJ-DG 129-IcV, referred to *Mariliasuchus amarali* Carvalho and Bertini (1999), from the Rio do Peixe outcrop, Adamantina Formation, Marília County. UFRJ-DG — Universidade Federal do Rio de Janeiro, Departamento de Geologia, IcV — Vertebrate Icnofossil.

The teeth structure of *Mariliasuchus* is robust, displaying an evident heterodonty, with incisiform, caniniform and molariform teeth. The complete dentition does not reach the edge of the first half of the orbit (Fig. 1A). The teeth implantation is thecodont, with deep and well developed roots. The dental sockets are not totally individualized, being formed only by a constriction at the borders of each tooth (Fig. 1B; C). The teeth are of variable size and the older ones are marked with strong wear facets.

There are three teeth in the premaxilla. The two first teeth are incisiform, rounded and prominent with an eroded apex (Fig. 1C). The third tooth is a hypertrophied caniniform, conical and with the pointed apex directed backwards (Fig. 1D). The tooth is robust, with both the crown base and the root rounded in cross section. The implantation of the root of the deep caniniform tooth causes a swelling of the external surface of the premaxilla.

The two first post-caniniform teeth are conical, with the pointed apex turned backwards. They are smaller than the posterior post-caniniform teeth. The four last posterior teeth are molariform, globular and slightly spatulated (Fig. 1B). Their crowns bear longitudinal striations. The carina and the apex of the newer teeth are slightly serrated. At the lingual surface of almost all the post-caniniform teeth, there is a deep wear facet extending from the apex to the crown base, producing a smooth surface and a chisel shape to each tooth (Fig. 1C).

There are nine teeth implanted in the dentary bone. The two first teeth are incisiform, cylindrical, large and projected anteriorly. The first tooth is larger and deeply abraded ventrally in an antero-posterior direction (Fig. 1E). The second tooth is smaller

Fig. 1. *Mariliasuchus amarali* Carvalho and Bertini (1999), UFRJ-DG 106-R. (A) Skull in left lateral view; (B) Dorsal view of the anterior part of the jaw showing the wear in the posterior teeth; (C) Ventral view of palate and upper dentition showing intense wear of the posterior molariform teeth. (D) Anterior and left lateral area of the skull with the prominent position of the incisiform, hypertrophied caniniform and molariform teeth with the well developed alveolar border; (E) Dorsal view of the lower jaws with the prominent incisiform teeth and the worn apex; (F) details of the ventral wear surface of the incisiform teeth. UFRJ-DG — Universidade Federal do Rio de Janeiro, Departamento de Geologia; ar — articular; ct — caniniform tooth; dt — dentary bone; exc — excrement; it — incisiform tooth; lf — laterotemporal fenestrae; mf — mandibular fenestrae; mt — molariform tooth; md — mandible; ms — mandibular symphysis; mx — maxillary bone; on — outer nostril; or — orbit; pm — pre—maxillar bone; qd — quadrate; and sf — supratemporal fenestrae.

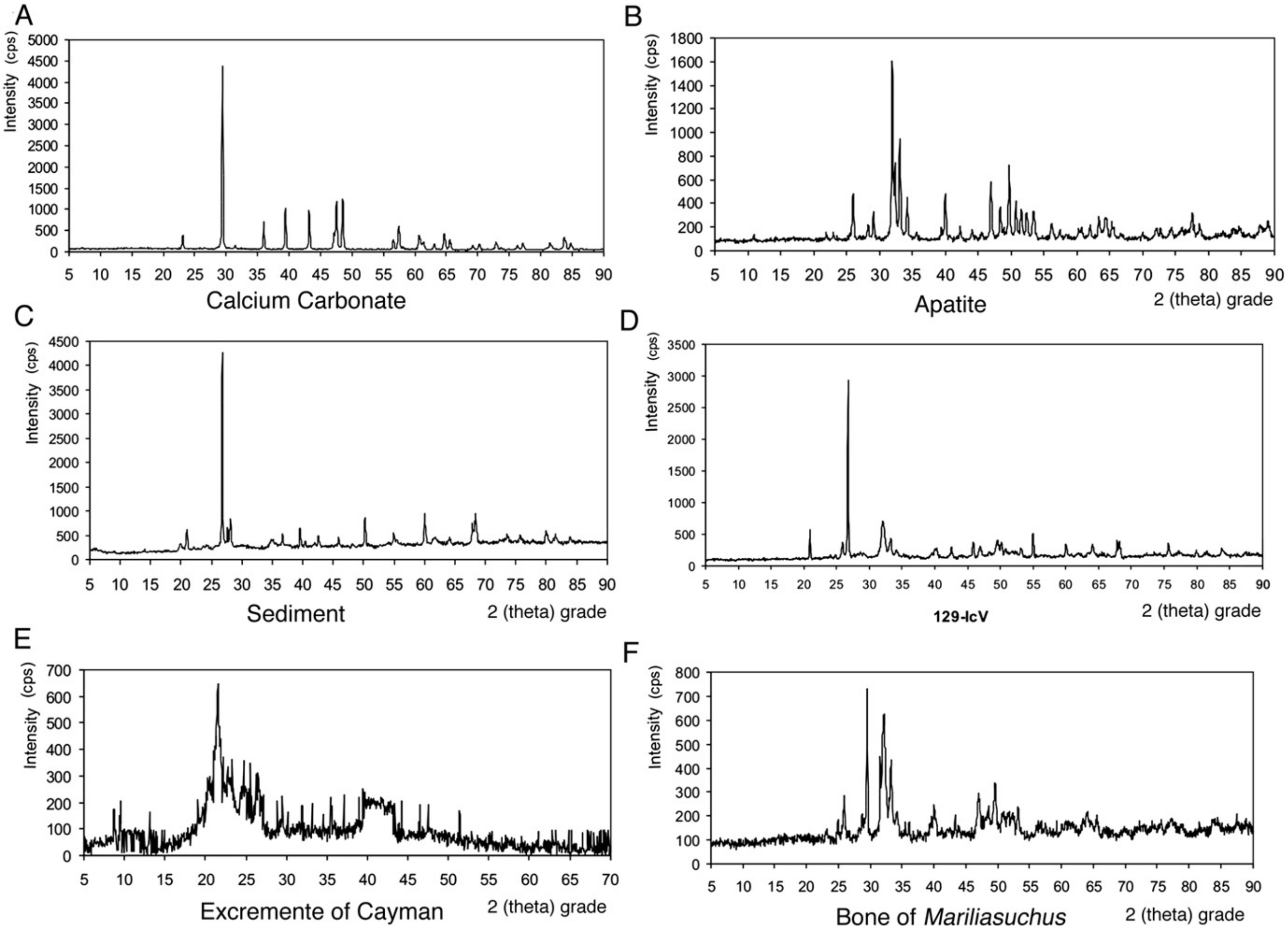

Fig. 3. X-ray diffractometer analysis of (A) calcium carbonate; (B) calcium phosphate; (C) sediment; (D) coprolite UFRJ-DG 129-IcV; (E) alligator excrement and (F) bone of *Mariliasuchus amarali* Carvalho and Bertini (1999).

with a pointed apex, and lacks signs of abrasion (Fig. 1F). The seven post-incisiform teeth present a different morphology, being globular to slightly spatulated, and antero-posteriorly longer than the preceding teeth. The crown is ornamented with longitudinal crests, deeper on the crown base than on the apex. In the newer teeth, the apex and the anterior and posterior carinaes have a slightly marked serration, which reaches the crown base. The larger, older teeth are deeply abraded on their labial surface (Fig. 1C).

3. Coprolites

Among the coprolites collected at the outcrop Rio do Peixe (Adamantina Formation), two samples are attributed to *M. amarali*, as their morphology is characteristic of crocodylomorphs and the fact that this particular outcrop only yielded *M. amarali* specimens so far. The sample UFRJ-DG 129-IcV (Fig. 2) presents an excellent preservational condition. It is cylindrical in shape, 6.04 cm long, 4.42 cm wide; white in colour, and posses isopolar extremities and a torsion along its own axis at the middle portion. The sample UFRJ-DG 202-IcV represents a fragment of the middle portion, with a maximum width of 4.23 cm, whitish internal colour and encloses a tooth internally.

The mineral composition of the coprolite was analysed qualitatively by X-ray diffractometry (Fig. 3) and qualitative X-ray fluorescence (Table 1) on removed powdered extracts from their coprolite matrix. According Souto (2003), the comparison between absorption bands of the infrared spectra (Fig. 4) of the

Table 1
Chemical composition of the sedimentary matrix (MS), coprolite UFRJ-DG 129-IcV and the extant *Caiman latirostris* excrement as determined from X-ray fluorescence, JPA (*na*) = no detected element

Samples	MS	*129-IcV*	JPA
Elements			
SiO_2	77.02	44.71	2.28
TiO_2	0.63	0.01	na
Al_2O_3	9.15	2.54	0.01
Fe_2O_3	3.87	0.64	1.73
MnO	0.01	3.34	0.01
MgO	1.84	0.01	0.01
CaO	0.73	21.91	47.89
K_2O	3.05	0.96	0.22
P_2O_5	0.01	16.65	28.64
SO_3	0.01	0.43	8.61
SrO	0.01	0.31	0.01
ZnO	na	na	1.45

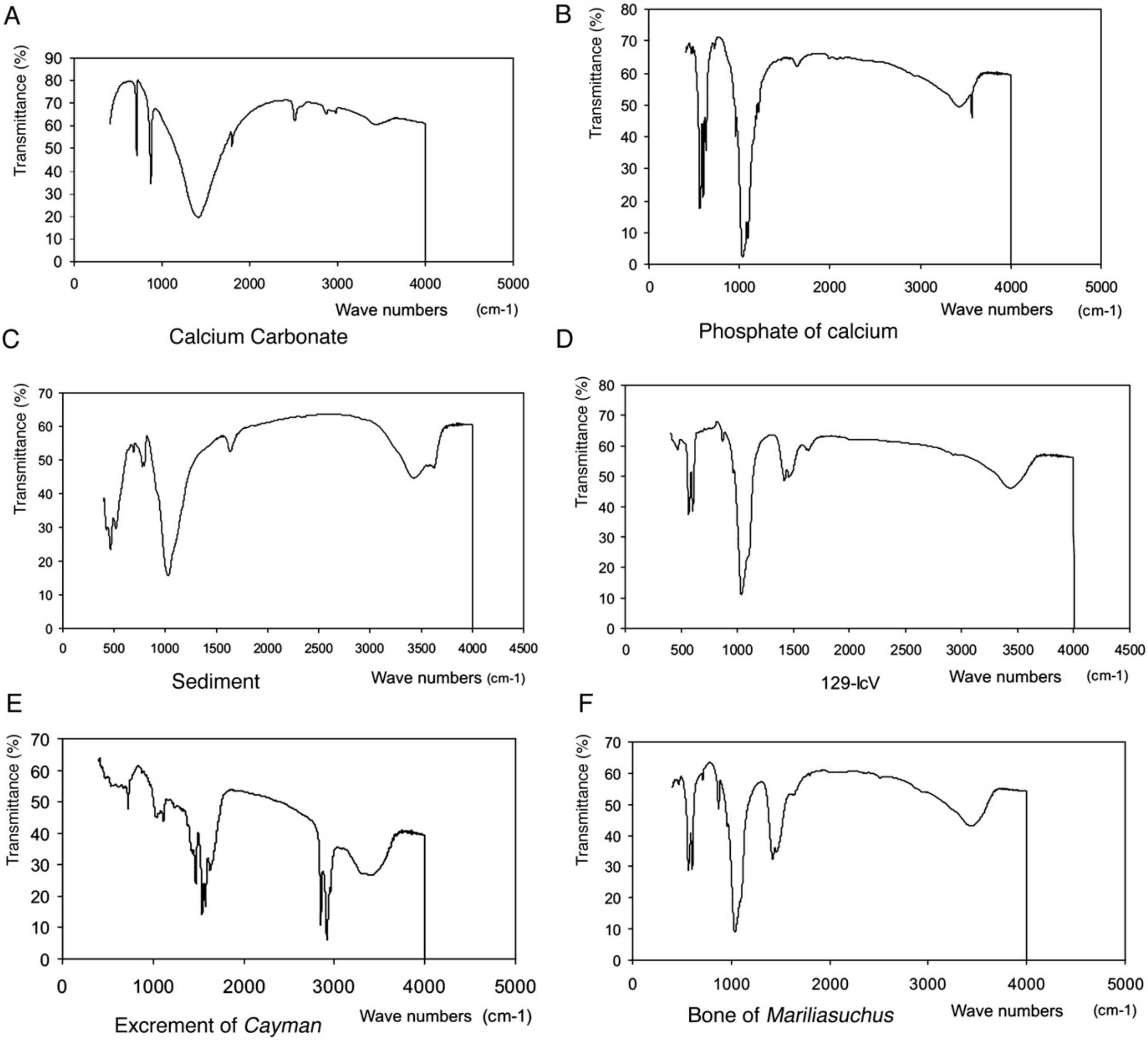

Fig. 4. Infrared spectra of (A) calcium carbonate; (B) calcium phosphate; (C) sediment; (D) coprolite UFRJ-DG 129-IcV; (E) alligator excrement and (F) bone of *Mariliasuchus amarali* Carvalho and Bertini (1999).

coprolites was made through the curves of apatite and calcium carbonate salts and those of the sedimentary matrix, *M. amarali* bones and droppings of an extant alligator (*Cayman latirostris* Daudin, 1802).

4. Discussion

The adaptations presented by *M. amarali*, such as high and short rostrum, lateral orbits and anterior directed external nares, differ in several aspects to those found in recent crocodylomorph species. This suggests life and feeding habits different from those found in living crocodylomorph taxa. Bonaparte (1991) pointed out that the adaptations for intraoral food processing in *N. terrestris*, from the Upper Cretaceous of Neuquén Province, Argentina, were more similar to those of mammals than to extant crocodilians. The comparison of the morphological adaptations found in *Mariliasuchus* with different adaptative types in Mammalia gave us insights on this crocodylomorph life and feeding habits.

Bonaparte (1991) and Wu and Sues (1996) suggested that, in *N. terrestris* and *Chimaerasuchus paradoxus* Wu, Sues and Sun, 1995, the presence of hypertrophied caniniform teeth, with their apex directed backward, was an adaptation for seizing and holding the food. Clark et al. (1989) pointed out that the differentiation between caniniform and molariform teeth in *Malawisuchus mwakayungutiensis* Gomani, 1997, indicated diverse functions. Study of extant mammals reveal that the caniniform teeth may be involved in the capture and holding of the prey, whereas the molariform teeth are used for processing the food. In *M. amarali*, the hypertrophied caniniform teeth present the same build as the mammalian canines and are also noticeably robust.

This fact suggests that they were probably employed to exert force, needed to tear apart pieces of carcasses, as in recent carnivorous mammals. In support to this hypothesis, the dentary bone of *M. amarali*, more robust shape, is shorter than in recent crocodylomorphs, presenting an upward arching in its middle portion. These facts confer to the jaw a great mechanical resistance during the seizing act (Nobre, 2006).

The short rostrum of *M. amarali* contrasts with the long rostrum of the extant crocodylomorphs. Animals with a short rostrum exert a great biting force at the anterior portion of the snout. This is a common adaptation among the extinct and living vertebrates, especially in species with herbivorous and/or carrion-feeding habits (Busbey, 1995). Due to the morphological characteristics observed in the masticatory apparatus of *M. amarali*, it is difficult to postulate an exclusively herbivorous habit, however this does not preclude that it may have eventually included plant matter in its diet.

The incisiform teeth of the jaw of *M. amarali* presents a strongly abraded apex and anteriorly directed. To determine the function of these teeth, a comparison was made with the mammal superfamily Suoidea, composed by domestic and wild pigs (*Sus* sp.) and peccaries (*Tayassu* sp.). They have three incisiform rod-shaped teeth in the jaw, which are closely spaced and anteriorly projected. These animals employ their incisiform teeth to dig into the sediment or soil, when looking for food (Ewer, 1958; Sicuro and Oliveira, 2002). Their diet is composed of small invertebrates, remains of carcasses, and plants (small fruits, hard seeds and roots). This allowed us to establish a relationship between the shape and disposition of the incisiform teeth of *Mariliasuchus* and their function, which would be used for digging during the foraging process.

Fisher (1981) indicates that, the abrasion shown by the molariform teeth enamel is an indication of intraoral food processing. The strong abrasion *M. amarali* indicates this kind of intraoral food processing. In addition to this, the articular facet for the quadrate condyles, formed by the articular bone, is flat, wide and elongated, consequently allowing free movement for the articular process of the quadrate bone. This morphological arrangement permits an antero-posterior displacement of the jaw, which is independent in each side. Many authors pointed out that fore-aft jaw movements are probable among the Notosuchia, because of an anteroposteriorly extended articulation between the skull and the jaw that would allow these movements (Clark et al., 1989; Bonaparte, 1991; Gomani, 1997). The teeth abrasion in the molariform teeth of *Mariliasuchus* indicates that this antero-posterior movement was indeed performed. It would permit the grinding of the food by the labial surface of the maxillary teeth and the lingual surface of the mandibular teeth, which are both striated and granular.

In *M. amarali*, the posterior teeth are medially displaced in the maxillary and dentary bones. They do not extend beyond the rostrum outer edge being not visible externally, differing from the recent crocodylomorphs. Internal posterior teeth are also found in the maxillary and dentary bones of *N. terrestris*. Bonaparte (1991) considered this feature a suggestive evidence of a conjunctive tissue lip that would keep the food in the oral cavity during food processing.

The coprolite morphology of the two samples is very similar, indicating that both samples were probably produced by animals belonging to the same group. They are in the same stratigraphical level of *Mariliasuchus* and show similar morphology of crocodylomorph coprolites in comparison with excrements produced by modern crocodiles (Gans, 1976; Fisher, 1981). The whitish colour displayed by both samples is a consequence of the presence of apatite and calcite. These minerals are commonly found in fossil droppings associated to carnivourous animals (Edwards, 1973). The torsion of the middle portion of the coprolite sample UFRJ-DG 129-IcV is a characteristic feature observed frequently in fossil droppings and attributed to the plastic consistency of fresh dung (Sawyer, 1981).

The coprolite structure shown by the diffractometry revealed high amounts of hydroxyl-apatite ($Ca_5(PO_4)_3$) and smaller amounts of quartz crystals (SiO_2). The analyses by fluorescence indicated the presence of higher chemical concentrations of phosphorous (16.65%) and silica (44.71%), calcium (21.91%) and; the lower concentrations of aluminum (2.54%), manganese (3.34%) and potassium (0.96%). The presence of potassium allows us to interpret that the coprolite producers did not have an exclusively carnivorous diet, as this element is mostly found in droppings of herbivorous and omnivorous animals (Rodriguez de La Rosa et al., 1998).

The infrared spectrum of the coprolites showed higher amounts of apatite mineral (560 and 600 Cm^{-1}) and lower amounts of carbonate (1.400 and 1.440 Cm^{-1}), both found mostly in fresh and fossilized bones. The presence of apatite in coprolites suggests that the samples were produced by animals with a basically carnivorous diet (Hallgren, 1987). However, the higher silica content (1.000 and 1.050 Cm^{-1}) found in these coprolites (and also in extant alligators) indicates that part of the silica excretion probably resulted from the incorporation of vegetables in the diet (Sawyer, 1981; Souto, 2001) along with the sediment, although it could also be interpretated as a incorporation through the fossil diagenetic process.

5. Conclusion

Based on the kind of articulation between the quadrate and articular bones and the teeth abrasion pattern, it is inferred that *M. amarali* executed antero-posterior jaw movements, processing the food before swallowing it. This interpretation is reinforced by the analysis of other crocodylomorphs from the Cretaceous of Gondwana (Clark et al., 1989; Bonaparte, 1991; Pol, 2003), suggesting that the presence of this unusual feeding strategy was widespread in the notosuchian crocodyliforms.

The medial displacement of the post-caniniform teeth in relation to the lateral snout surface suggests the existence of a lip made of conjunctive tissue, indicating that *M. amarali* may have kept the food inside the oral cavity during food processing, thus increasing the effectiveness of mastication. The structure and shape of the caniniform and incisiform teeth excludes the possibility that *Mariliasuchus* had an exclusively herbivorous diet. Based on the cranial morphological features, the physical and chemical analysis of the coprolites, it is possible to infer that *Mariliasuchus* had omnivorous feeding habits. The shape of the incisiform teeth, coupled with their abrasion pattern, shows that *Mariliasuchus* had employed the procumbent anterior incisiform teeth for active digging of sediment during forage.

The feeding habits and diet of these peculiar crocodylomorphs widen and add complexity to the trophic web systems across the Gondwanland, erecting new possibilities for paleoecoclogical niche distribution among vertebrates in South America, Africa, Madagascar and India.

Acknowledgments

To Willian Roberto Nava (Museu de Paleontologia de Marília) for collecting the fossils and support during the field activities. To Carlos André de Castro Bezerra (UFRJ), Katia Maria Nunes de Gabon (UFRJ), Cleonice Silveira Martins (UFRJ) for X-ray diffractometry and fluorescence analyses. To Leonice Bezerra Coelho for infrared analyses (UFRJ). To Diego Pol (Trelew Museum) for the revision of this manuscript. This study was supported by Instituto Virtual de Paleontologia/Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Grant n° 305780/2006-9).

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