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Multicusped crocodyliform teeth from the Upper Cretaceous (São José do Rio Preto Formation, Bauru Group) of São Paulo, Brazil

Felipe Chinaglia Montefeltro*, Carolina Rettondini Laurini, Max Cardoso Langer

Laboratório de Paleontologia, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto – Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901, Ribeirão Preto SP, Brazil

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ABSTRACT

The six peculiar multicusped teeth described here were collected from sediments of the Upper Cretaceous of São José do Rio Preto Formation, near Ibirá (northeastern São Paulo, Brazil). Their bulbous crowns are slightly labio-lingual compressed, and bear a main plus two accessory cusps, which conceal a well developed cingulum. Wear facets are seen on the main and distal accessory cusps. Comparison to the known Crocodyliformes with multicusped teeth show that the new material is not referable to "protosuchians" or eusuchians, nor related to two unnamed forms from Morocco and "notosuchians" such as *Uruguaysuchus, Chiamaerasuchus,* and *Simosuchus.* On the other hand, possible affinities with *Candidodon* and *Malawisuchus* were maintained based on shared traits. This includes teeth with the main cusp and some accessory cusps arranged in more than one axis, a previously defined unambiguous apomorphy of the putative clade composed of *Candidodon* plus *Malawisuchus.* The term Candidodontidae can be applied to this group, and defined as all taxa closer to *Candidodon itapecuruensis* than to *Notosuchus pachecoi,* and *Crocodylus niloticus.*

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1. Introduction

While extant Crocodyliformes have minimal teeth modifications, fossil members of the group show a considerable dental diversity, including multicusped teeth. This morphology was first recognized, and is better documented in "notosuchians" (Clark et al., 1989; Carvalho, 1994; Wu et al., 1995; Gomani, 1997; Buckley et al., 2000), but it was recently shown to be more widespread among Crocodyliformes, and also recognized in "protosuchians" (Sues et al., 1994; Pol et al., 2004) and Eusuchia (Ősi et al., 2007).

The "protosuchian" *Edentosuchus tienshanensis* (Young, 1973; Li, 1985; Pol et al., 2004) from the Early Cretaceous of Tugulu Group (Xinjiang, China), shows a peculiar multicusped dentition that is shared by two informally described "*Edentosuchus*-like" forms from Early Jurassic of Arizona (Sues et al., 1994). The "Kayenta form" has been discussed in literature, and included in phylogenetic analyses (Clark, 1994; Pol and Norell, 2004a,b; Pol and Apesteguia, 2005; Turner and Buckley, 2008) that confirmed its proximity to the Chinese *Edentosuchus*. *E. tienshanensis* and the North-American

* Corresponding author. *E-mail address:* feio_bio@yahoo.com.br (F.C. Montefeltro).

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forms show bulbous, crushing dentition with multiple small cusps along edges of the occlusal surface, which form the entire perimeter of a multicusped cingulum (Sues et al., 1994; Pol et al., 2004; Pol and Apesteguia, 2005; Turner and Buckley, 2008).

The eusuchian *lharkutosuchus makadii*, from the Upper Cretaceous Csehbánya Formation (western Hungary), shows a notable convergence with the "protosuchians" mentioned above. This taxon possesses two different morphologies of maxillary multicusped teeth. The more rostral elements have three aligned main cusps and a well developed lingual cingulum with multicusped ridges radiating from its apical region. More caudal teeth retain the three main cusps, but the multicusped ridges, as in the "protosuchian" taxa, form the whole perimeter of the cingulum; for more details see Ősi (2008).

Three different patterns of multicusped teeth are known among "Notosuchians." Teeth of *Uruguaysuchus aznarezi* and *U. terrai*, from Upper Cretaceous of Uruguay (Rusconi, 1933), and *Simosuchus clarki*, from Maevarano Formation (Upper Cretaceous) of Madagascar (Buckley et al., 2000), lack a cingulum, and have several cusps aligned in a single row. *Chimaerasuchus paradoxus*, from Wulong Formation (Early Cretaceous) of China (Wu et al., 1995), show teeth with several cusps forming three parallel rows, and a cingulum at the mesio-labial margin of the maxillary elements. *Candidodon*



Fig. 1. Map of the area of São José do Rio Preto, showing site where the teeth were collected.

itapecuruense, from the Itapecurú Group (Early Cretaceous) of Brazil (Carvalho and Campos, 1988), and *Malawisuchus mwakasyungutiensis*, from the "Dinosaur Beds" (Early Cretaceous) of Malawi (Gomani, 1997), show a main cusp and smaller accessory cusps arranged in more than one row. In addition, whereas *C. itapecuruense* has the cingulum restricted to the lingual side of the teeth (Carvalho, 1994), in *M. mwakasyungutiensis* the cingulum forms the entire perimeter of upper multicusped teeth, although it is lacking on the lingual side of lower ones (Clark et al., 1989; Gomani, 1997).

Some isolated crocodyliform teeth collected in the "Kem Kem beds" (Albian-Cenomanian) of Morocco also possess a multicusped morphology (Larsson and Sidor, 1999). "Indet. Crocodyliform 1" is based on two teeth with laterally compressed crowns and three cusped parallel ridges. "Indet. Crocodyliform 2" is represented by a single tooth, which possesses an ovoid occlusal surface bearing a main cusped ridge, a larger putative distal cusp, and two sets of smaller cusps flanking the ridge. Larsson and Sidor (1999) do not assign those teeth to any particular crocodyliform group, but suggest that they may represent an independent acquisition for multicusped teeth within Crocodyliformes.

The present paper describes six isolated multicusped crocodyliform teeth collected from an outcrop of the São José do Rio Preto Formation (Upper Cretaceous), in northwest São Paulo (Brazil). These teeth are compared to other multicusped crocodyliform teeth, and the name Candidodontidae is redefined under the phylogenetic nomenclature system.



Fig. 2. LPRP/USP 0004, schematic outline of occlusal view showing the inferred orientation and wear facets in grey (A); photographs of same tooth in occlusal (B), mesial (C), distal (D), labial (E), and lingual (F) views. Abbreviations: dac, distal accessory cusp; dr, disto-labial ridge; lac, labial accessory cusp; mc, main cusp. Scale bar = 1 mm.



Fig. 3. LPRP/USP 0004 wear facet of main cusp on oclusal view. White arrowheads: example of unmistaken striae. Scale bare = 0.25 mm.

2. Geological setting

All material reported here was collected in a single outcrop (20°58'30.51"S; 49°14'17.48"W), previously referred to as "Vaca Morta," and located in the area of Ibirá, northwestern São Paulo, Brazil (Fig. 1). The site corresponds to a sub horizontal exposition of the São José do Rio Preto Formation (Bauru Group). This essentially sandy stratigraphic unit also includes conglomeratic deposits that concentrate the fossil record of the region. This includes bone fragments and other bioclasts (Ihering, 1911; Arid and Vizoto, 1970, 1971; Brandt-Neto et al., 2001), accumulated in fluvial bars of a braided river system (Fernandes and Coimbra, 2000).

Although the unique features of the Bauru Group deposits around São José do Rio Preto region were long recognized in the literature (Suguio et al., 1977), the proposition of a discrete stratigraphic unit (i.e.: São José do Rio Preto Formation) is relatively recent (Fernandes and Coimbra, 1996, 2000; Fernandes, 1998), and its age was not yet fully discussed. Based on ostracods and carophytes, Dias-Brito et al. (2001) found a Turonian-Santonian age for the Adamantina Formation that, in the classical litostratigraphic scheme of Soares et al. (1980), includes the deposits assigned to the São José do Rio Preto Formation by Fernandes and Coimbra (1996). Among the sites sampled by Dias-Brito et al. (2001) is that referred to as "Vila Ventura," which may correspond to the same outcrop prospected for the preset study. That dating was, however, questioned by various authors (Santucci and Bertini, 2001; Gobbo-Rodrigues et al., 2003), who propose a younger Campanian-Maastrichtian age for the Adamantina Formation. It is important to note that the São José do Rio Preto Formation corresponds to the upper part of the Bauru Group in the sampled area (Fernandes and Coimbra, 2000), which is congruent with a younger age for that unit.

3. Materials and methods

The specimens described here (LPRP/USP 0004-0009) are deposited at Laboratório de Paleontologia, FFCLRP-USP, Ribeirão Preto-SP, Brazil. They were collected along with other isolated vertebrate remains (Lepisosteiformes, Characiformes, Chelonii, and Sauropoda) and Crocodyliformes teeth (Baurusuchidae and "Goniopholididae"). One tooth (LPRP/USP 0004) was recognized *in situ* among unconsolidated sediments eroded from the bearing rock and accumulated over the exposed horizontal surfaces know as "lages." These sediments were also sieved in field using a 1 × 1 mm mesh, packed, and brought to the laboratory, where the other teeth were recognized after dry screening under a stereomicroscope.

3.1. Teeth orientation

The difficulty of orienting amniotes isolated teeth is well recognized in literature (Larsson and Sidor, 1999; Clemens et al., 2003; Irmis and Parker, 2005). In the case of Crocodyliformes, this is further complex because of the mirror pattern of upper and lower multicusped teeth, and their oblique orientation in the jaw of some forms. All teeth dealt with in this contribution are very similar.



Fig. 4. LPRP/USP 0005, schematic outline of occlusal view showing the inferred orientation and wear facets in grey (A); photographs of same tooth in occlusal (B), mesial (C), distal (D), labial (E), and lingual (F) views. Abbreviations: dac, distal accessory cusp; dr, disto-labial ridge; lac, labial accessory cusp; mc, main cusp. Scale bar = 1 mm.



Fig. 5. LPRP/USP 0006, schematic outline of occlusal view showing the inferred orientation and wear facet in grey (A); photographs of same tooth in occlusal (B), mesial (C), distal (D), labial (E), and lingual (F) views. Abbreviations: dac, distal accessory cusp; dr, disto-labial ridge; lac, labial accessory cusp; mc, main cusp. Scale bar = 1 mm.

Accordingly, for descriptive purposes only, the morphology of the largest element (LPRP/USP 0004, Fig. 2A) is used as a template to orientate the other teeth, using the dental terminology proposed by Smith and Dodson (2003). The mesio-distal axis is inferred from the major axis of the tooth, where the wear facets of the main and one accessory cusp are located. This orientation was chosen based on the comparison with teeth of Candidodon itapecuruensis and Malawisuchus mwakasyungutiensis, the major axis of which is mesio-distal. This differs from the oblique orientation of the major axis of the teeth seeing in Notosuchus terrestris, Mariliasuchus amarali, and sphagesaurids (Nobre and Carvalho, 2006; Andrade and Bertini, 2008a,b,c; Lecuona and Pol, 2008; Marinho and Carvalho, 2009). The main cusp is accepted as mesial, so the accessory cusp lacking wear facet is placed on the labial side of the tooth. This orientation was arbitrarily chosen, because there is no unambiguous pattern of cuspid and cingulum positions among multicusped crocodyliforms that can be assumed in this case.

4. Systematic paleontology

Crocodyliformes Hay, 1930 Mesoeucrocodylia Whetstone & Whybrow, 1983 Candidodontidae Carvalho et al., 2004

4.1. Description

4.1.1. LPRP/USP 0004 (Figs. 2 and 3)

This tooth includes a complete crown and the uppermost part of the root. Between crown and root a weak constriction is

Table 1

Measurements (in mm) of LPRP/USP 0004-0007 and LPRP/USP 0009

Tooth	MDA	LLA
LPRP/USP 0004	3.4	3.0
LPRP/USP 0005	1.7	1.3
LPRP/USP 0006	1.0	0.9
LPRP/USP 0007	2.6	2.0
LPRP/USP 0009	1.3	1.0

Abbreviations: MDA, mesio-distal axis length; LLA, labio-lingual axis length.LPRP/ USP 0008 was not included because of its incompleteness. observed. The crown is bulbous and slightly labio-lingually compressed. Its surface is sculptured with regularly spaced apicobasal ridges that lack serration or tubercles, and are better seen mesially, mesio-buccally, and mesio-labially. The crown bears a main cusp and two accessory cusps, which are not aligned in a single row. One accessory cusp is located at the distalmost part of the mesio-distal axis, and the other in the labialmost part of labio-lingual axis. The accessory cusps mark the distal and labial boundaries of a well developed cingulum. The cingulum bears a disto-labially directed longitudinal ridge that extends from its external margin to the apex of the main cusp. Each side of the ridge is marked by depressions that set the limits of the accessory cusps. The main and distal accessory cusps bear wear facets that form a nearly continuous plane in lingual view. The wear facets show clear striations that are mostly disto-labialy to mesio-lingualy oriented (Fig. 3). The striae are not strictly parallel but indicate an unambiguous tooth-tooth occlusion and an active food processing.

4.1.2. LPRP/USP 0005 (Fig. 4) and LPRP/USP 0006 (Fig. 5)

These teeth comprise almost complete crowns, except for the tip of the main cusp of LPRP/USP 0005, and the uppermost part of the roots. A weak constriction is also present between the crown and the root, and apicobasal ridges are seen, although not well developed as in LPRP/USP 0004. LPRP/USP 0005 is more laterally compressed, with a mesio-distal/bucco-labial ratio of 1.3. LPRP/USP 0006 is the smallest tooth described here (Table 1) with a main axis about 70% smaller than that of LPRP/USP 0004. Both teeth have the same cusp and cingulum pattern of LPRP/USP 0004. Yet, the accessory cusps are less developed relative to the main cusp, a feature more evident in LPRP/USP 0006. The placement of the labial accessory cusp is also slightly different. It is more distally located, so that the cingulum is less extensive compared to that of LPRP/USP 0004. On the opposite side, the ridge between the accessory cusps is more marked, and more apically projected than those cusps. The wear pattern in LPRP/USP 0005 is similar to that of LPRP/USP 0004, with wear facets present on the main and distal cusps. The distal accessory cusp is, however, almost wiped out by the extensive wearing. As in LPRP/USP 0004, the striations patterns of the wear facets also suggest a tooth-tooth occlusion. In LPRP/USP



Fig. 6. LPRP/USP 0007, schematic outline of occlusal view showing the inferred orientation and wear facets in grey (**A**); photographs of same tooth in occlusal (**B**), mesial (**C**), distal (**D**), labial (**E**), and lingual (**F**) views. **Abbreviations: dac**, distal accessory cusp; **dr**, disto-labial ridge; **lac**, labial accessory cusp; **mc**, main cusp. Scale bar = 1 mm.

0006 the wear facet is present only in the tip of main cusp, and wear striations are not clear. Yet, based on the wear facet angle of the main cusp, we accept the smaller accessory cusp as the distal one.

4.1.3. LPRP/USP 0007 (Fig. 6) and LPRP/USP 0008 (Fig. 7)

LPRP/USP 0007 represents an almost complete crown, lacking only the lingual part of the main cusp tip. LPRP/USP 0008 consists of a partial crown, with the entire labial face missing, exposing the internal structure of the tooth. Both teeth show a constriction at the



Fig. 7. LPRP/USP 0008, schematic outline of lingual view showing the inferred orientation and wear facets in grey (**A**); photograph of same tooth in lingual (**B**) view. **Abbreviations: dac**, distal accessory cusp; **mc**, main cusp. Scale bar = 1 mm.

crown base, and apicobasal ridges. Similarly to LPRP/USP 0005, LPRP/USP 0007 is more laterally compressed, but approached LPRP/ USP 0004 in having more marked apicobasal ridges on the mesial margin. The cusp arrangement and wear patterns of LPRP/USP 0007-0008 are nearly mirrored images of those seen in LPRP/USP 0004-0006. This suggests that they belong to rami of different sides (left/right), or different jaws (upper/lower) of similar animals. As in LPRP/USP 0005-0006, LPRP/USP 0007 has the labial accessory cusp displaced distally. In addition, it possesses a distinct ridge between the accessory cusps, which bears two weak expansions at the base of the main cusp.

4.1.4. LPRP/USP 0009 (Fig. 8)

This tooth is smaller (major axis representing about 62% of that of LPRP/USP 0004) and has less defined structures compared to the previously describes elements. It comprises a complete crown, with no apicobasal ridges on the surface and a more marked constriction at the base. Its labial surface is concave, instead of convex as in the other teeth. A main cusp is not clearly observed, but an equivalent blunt longitudinal ridge occupies the occlusal surface. Each end of this ridge bears an intumescence, the larger of which is inferred as homologous to the distal accessory cusp. In the labial side of the ridge there is a clear accessory cusp, and another possible cusp is seen at the mesio-labial region of tooth. The cingulum is less developed than that of the previously described teeth, but more marked in the area between the accessory cusps, which lacks the ridge observed in the other teeth. No wear facets have been recognized. Along with other traits (small size and no clear structure differentiation), this may suggest that the specimen either corresponds to a non-erupted tooth. Accordingly, we believe that it is not necessary to invoke taxonomy to explain the morphologic differences seen between LPRP/USP 0009 and the other teeth described here.

5. Discussion

Multicusped teeth evolved numerous times in tetrapod phylogeny. Yet, the occurrence of this feature along with apicobasal ridges is mainly known in Crocodyliformes (but see Stecher, 2008). In fact, based on the current phylogenetic orthodoxy, multicusped



Fig. 8. LPRP/USP 0009, schematic outline of occlusal view showing the inferred orientation and inconspicuous cusps in dashed lines (**A**); photographs of same tooth in occlusal (**B**), mesial (**C**), distal (**D**), labial (**E**), and lingual (**F**) views. Abbreviations: dac, distal accessory cusp; lac, labial accessory cusp; mac, mesio-labial accessory cusp; mc, main cusp. Scale bar = 1 mm.

post-caniniform teeth appeared independently several times within the group. Indeed, possible affinities of the material dealt with here include "notosuchians" (Clark et al., 1989; Carvalho, 1994; Wu et al., 1995; Gomani, 1997; Buckley et al., 2000), *Edentosuchus* and related forms (Sues et al., 1994; Pol et al., 2004), as well as *Iharkutosuchus* (Ősi et al., 2007) and the indeterminate forms from the Cretaceous of Morocco (Larsson and Sidor, 1999).

Because of the extreme discrepancy in cusp number and the absence in the described teeth of radiating cusped ridges, their possible "protosuchian" (Sues et al., 1994; Pol et al., 2004) and eusuchian (Ősi et al., 2007) affinities were discarded. Besides, "protosuchians" have the cingulum occupying the total perimeter of the teeth, a trait not observed in the new specimens. Equally, their affinity to the Moroccan indeterminate crocodyliforms (Larsson and Sidor, 1999) was rejected, because those teeth lack a clear cingulum, bearing a thickened occlusal surface formed of accessory ridges instead. Moreover, the spatulate crowns of "Indet. Crocodyliform 1" have cusps of similar size aligned in three longitudinal rows, a condition partially observed also in "Indet. Crocodyliform 2," but not in the specimens dealt with here.

Among "notosuchians," the affinity of the new material to *Simosuchus clarki* (Buckley et al., 2000) and the species of *Uru-guaysuchus* (Rusconi, 1933) was also rejected, because of their dissimilar morphology. These forms have strongly constricted at base and laterally compressed tooth crowns, which lack a cingulum and have cusps aligned in a single row. The restriction of the cingulum to a small area of the teeth could apparently approach the new teeth to those of *Chimaerasuchus paradoxus*. Yet, other traits of the Chinese form discourage this association. *C. paradoxus* has molariforms with a wide occlusal surface, bearing three longitudinal rows of cusps that decrease in size distally (Wu et al., 1995). In addition, the cusps have individual distal cutting edges.

In the absence of compelling alternatives, and based on some shared traits, the specimens described here are tentatively related to *Candidodon itapecuruense* (Carvalho and Campos, 1988) and *Malawisuchus mwakasyungutiensis* (Gomani, 1997). Shared traits include crowns constricted at base, with a bulbous shape, an unmistakable main cusp, and a small number of accessory cusps arranged in more than one axis. The latter feature is often used as an unambiguous synapomorphy of a clade composed of *Candidodon* + *Malawisuchus* (Pol and Norell, 2004a,b; Pol et al., 2004; Pol and Apesteguia, 2005; Zaher et al., 2006; Turner and Buckley, 2008). Yet, differently from these taxa, the new teeth show apicobasal ridges and have the number of accessory cusps reduced to two. Indeed, these teeth have a unique combination of features, and no other crocodyliform with multicusped dentition precisely matches its cusp and cingulum anatomy. Accordingly, we suggest that they belong to a single, possibly new taxon, but refrain from erecting a new name, as suggested for isolated teeth by Langston (1973) and Larsson and Sidor (1999).

In certain phylogenetic contexts (Pol and Norell, 2004a,b; Pol et al., 2004; Pol and Apesteguia, 2005; Zaher et al., 2006; Turner and Buckley, 2008), Candidodon itapecuruense and Malawisuchus mwakasyungutiensis form a clade into which the material described here could also be assigned. This clade has no proposed name as such, but Candidodontidae (Carvalho et al., 2004), typified by C. itapecuruense, is available. The term was first used by Nobre and Carvalho (2002) to congregate Candidodon, Malawisuchus, and Araripesuchus (Price, 1959), following the results of an unpublished phylogenetic analysis (Avilla, 2002). Later, Carvalho et al. (2004) formally proposed Candidodontidae, using the precepts of phylogenetic nomenclature, as a node-based taxon. This includes Candidodon itapecuruense and Mariliasuchus amarali, as internal specifiers, following the outcome of their phylogenetic study. Yet, this definition is problematic if applied to alternative phylogenetic hypotheses that also include these taxa (e.g.: Zaher et al., 2006; Andrade and Bertini, 2008a; Turner and Buckley, 2008; Pol and Gasparini, 2009). Using those topologies as a template, Candidodontidae sensu Carvalho et al. (2004) would encompass forms traditionally associated to "notosuchian" and "sebecosuchian" suprageneric taxa that have priority over Candidodontidae, e.g.: Notosuchidae (Dollo, 1914), Baurusuchidae (Price, 1945), Sphagesauridae (Kuhn, 1968), Sebecidae (Simpson, 1937), Uruguaysuchidae (Gasparini, 1971) and Comahuesuchidae (Bonaparte, 1991). Likewise, the affinity of Araripesuchus to other "notosuchians" is uncertain (Clark, 1994; Ortega et al., 2000; Turner, 2006; Jouve et al., 2006; Larsson and Sues, 2007), restricting the use of Candidodontidae sensu Avilla (2002).

Accordingly, we suggest a new stem-based phylogenetic definition for Candidodontidae as all taxa closer to *Candidodon itapecuruensis* than to *Notosuchus terrestris*, *Uruguaysuchus aznarezi*, *Comahuesuchus brachybuccalis*, *Sphagesaurus huenei*, *Baurusuchus pachecoi*, and *Crocodylus niloticus*. The fossil external specifiers were chosen in order to avoid redundancy with the more traditional "notosuchian" suprageneric taxa they typify, whereas *C. niloticus* is included to avoid a highly inclusive and redundant Candidodontidae in the unlikely possibility that *C. itapecuruensis* is found to be more closely related to eusuchians than to other "notosuchians." This definition also allows the inclusion of *Malawisuchus mwakasyungutiensis* and/or *Mariliasuchus amarali* within Candidodontidae, if future work more firmly establishes their phylogenetic affinity.

Additionally, the presence of striae and pits on the wear facets of crocodyliform teeth are clear evidence of complex jaws movements (Pol, 2003; Andrade and Bertini, 2008a,b,c; Lecuona and Pol, 2008; Ősi and Weishampel, 2009). Among "notosuchians," striated wear facets have been described for Spahagesaurus huenei, Mariliasuchus amarali, and Notosuchus terrestris. Macrowear structures, patterns of wear facets, and cranial features indicate a main anteroposterior lower jaw movement in these taxa. This is particularly suggested based on the fine parallel striae on the teeth of Sphagesaurus huenei, which also indicate a tooth-tooth occlusion (Pol. 2003). For Malawisuchus mwakasyungutiensis the same anteroposterior lower jaw movement was inferred (Clark et al., 1989; Gomani, 1997), but the wear facets do not indicate tooth-tooth occlusion (Clark et al., 1989). The new teeth described here, which is presumably closer to M. mwakasyungutiensis than to the other taxa, bear clear macrowear striae related to tooth-tooth occlusion. Given the recently proposed phylogenetic branching of these taxa (Zaher et al., 2006; Andrade and Bertini, 2008a; Turner and Buckley, 2008; Pol and Gasparini, 2009), tooth-tooth occlusion may represent a more deeply rooted synapomorphy of notosuchians. In addition, the striae on the described teeth are not strictly parallel, suggesting a more complex jaw movement not restricted to the anteroposterior plane, as also seen in *Iharkutosuchus* (Ösi and Weishampel, 2009). Yet, more complete material, including jaw elements, is necessary to confirm this inference.

6. Conclusions

The new isolated teeth described here represent a taxon of Crocodyliformes registered for the first time in the Upper Cretaceous Bauru Group. They possess a complex crown morphology, with multiple cusps and a cingulum. Some of the possible affinities of the new teeth were discarded, but an association with *Candidodon itapecuruense* and *Malawisuchus mwakasyungutiensis* is possible, given the sharing of unique traits and absence of more plausible hypotheses. The relative position of these two "notosuchians" remains controversial, but some phylogenetic hypotheses suggest that they form a clade. This may be termed Candidodontidae and include the specimens described here. In this context, the newly described teeth would represent the most recent record of the *Candidodon/Malawisuchus* clade, which was previously recognized only in pre-Turonian deposits (Gomani, 1997; Rossetti, 2001; Santos and Carvalho, 2004).

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