



A new prozostroodontian cynodont (Therapsida) from the Late Triassic *Riograndia* Assemblage Zone (Santa Maria Supersequence) of Southern Brazil

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ABSTRACT

We report here on a new prozostroodontian cynodont, *Botucaraitherium belarminoi* gen. et sp. nov., from the Late Triassic *Riograndia* Assemblage Zone (AZ) of the Candelária Sequence (Santa Maria Supersequence), collected in the Botucaraí Hill Site, Candelária Municipality, state of Rio Grande do Sul, Brazil. The new taxon is based on a single specimen (holotype MMACR-PV-003-T) which includes the left lower jaw, without postdentary bones, bearing the root of the last incisor, canine and four postcanines plus one partial crown inside the dentary, not erupted, and two maxillary fragments, one with a broken canine and another with one postcanine. The features of the lower jaw and lower/upper postcanines resemble those of the prozostroodontians *Prozostrodon brasiliensis* from the older *Hyperodapedon* AZ and *Brasilodon quadrangularis* and *Brasilitherium riograndensis* from the same *Riograndia* AZ. The inclusion of *Botucaraitherium* within a broad phylogenetic analysis, positioned it as a more derived taxon than tritylodontids, being the sister-taxon of *Brasilodon*, *Brasilitherium* plus Mammaliaformes. Although the new taxon is based on few cranial elements, it represents a additional faunal component of the Triassic *Riograndia* AZ of southern Brazil, in which small-sized derived non-mammaliaform cynodonts, closely related to the origin of mammaliaforms, were ecologically well succeed and taxonomically diverse.

Key words: Cynodontia, Prozostroodontia, Santa Maria Supersequence, Triassic.

INTRODUCTION

The rich fossil tetrapod content from the Middle-Upper Triassic of southern Brazil is recorded in beds related to the Santa Maria Supersequence, in which four recognized faunal tetrapod associations succeed in time: *Dinodontosaurus*, *Santacruzodon*, *Hyperodapedon* and *Riograndia* Assemblage Zones (AZ) (Soares et al. 2011) (Fig. 1). In all of these biostratigraphic unities, whose proposed ages are

based on correlations with Argentinean and Malagasy faunas (Abdala and Ribeiro 2010), the non-mammaliaform cynodonts (Therapsida, Eucynodontia) account for a significant percentage of the recorded taxa, taxonomically comprising the most diverse group. In fact, the diversity of the derived non-mammaliaform probainognathian cynodonts, grouped into the Clade Prozostroodontia (*sensu* Liu and Olsen 2010), from the Upper Triassic Candelária Sequence (Santa Maria Supersequence) of southern Brazil is remarkable when compared to

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its global fossil record, based upon poorly preserved specimens. At least two prozostroodontians are known from the *Hyperodapedon* AZ (Bonaparte and Barberena 2001) and at least five from the younger *Riograndia* AZ (Bonaparte et al. 2001, 2003, 2005, 2010, 2012, Martinelli et al. 2005, Soares et al. 2011). Recent studies on these taxa have highlighted their essential contribution to the understanding of the mammaliaforms origin (Bonaparte et al. 2005, Luo 2007, Abdala 2007, Liu and Olsen 2010, Bonaparte 2012), illustrating the climbing mosaic of characters developed during the Middle-Late Triassic transition (Bonaparte et al. 2005, Martinelli and Rougier 2007, Martinelli and Bonaparte 2011, Bonaparte 2012, Rodrigues et al. 2012, 2013).

In the late Carnian *Hyperodapedon* AZ, the prozostroodontians *Therioherpeton cargini* Bonaparte and Barberena (1975) and *Prozostrodon brasiliensis* Bonaparte and Barberena (2001) are recognized, both displaying several derived features in the skull and dentition (e.g. lack of prefrontal and postorbital, constricted root in postcanines) that positioned them as basal prozostroodontians (Liu and Olsen 2010). From this AZ, *Charruodon tetracuspoidatus* Abdala and Ribeiro (2000) and *Trucidocynodon riograndensis* Oliveira et al. (2010) are also known. *Charruodon* was originally related to *Therioherpeton* due to the morphology of the lower postcanines; nonetheless, based on the deep and robust lower jaw (unexpected for *Therioherpeton* based on its skull), we consider that the phylogenetic position of *Charruodon* cannot be elucidated until new specimens come to light. On the other hand, *Trucidocynodon* represents a member of the Ecteniniidae (Oliveira et al. 2010, Martinez et al. 2013), which is positioned outside, as sister-group of Prozostrodonia (Martinez et al. 2013).

With regard to the prozostroodontian content, the early Norian *Riograndia* AZ includes *Riograndia guaibensis* Bonaparte et al. (2001) *Irajatherium hernandezii* Martinelli et al. (2005), *Brasilodon quadrangularis*, *Brasilitherium riograndensis*

Bonaparte et al. (2003), and *Minicynodon* Bonaparte et al. (2010). *Riograndia* is the most common cynodont of this AZ, represented by several exquisitely preserved specimens. *Riograndia* is considered as a basal member of the Tritheledontidae Clade (Bonaparte et al. 2001, Soares et al. 2011) or a basal Ictidosauria, sister-taxon of Tritheledontidae (*sensu* Martinelli et al. 2005, Martinelli and Rougier 2007). *Irajatherium* is still poorly represented in comparison to other cynodonts from this AZ. However, its dentition resembles that of *Chalimonia* from the Late Triassic of Argentina and *Pachygenelus* from the Early Jurassic of Africa (Martinelli and Rougier 2007). Hence, *Irajatherium* is positioned as a basal Tritheledontidae (Martinelli et al. 2005, Martinelli and Rougier 2007, Oliveira et al. 2011). *Brasilodon*, *Brasilitherium* (Bonaparte et al. 2003, 2005, 2012), and *Minicynodon* (Bonaparte et al. 2010, 2012) are relatively well-documented and they are crucial taxa in cynodont evolution because they constitute the sister-group of Mammaliaformes (e.g., Bonaparte et al. 2003, 2005, 2012, Abdala 2007, Martinelli and Rougier 2007, Luo 2007, Liu and Olsen 2010, Rodrigues et al. 2012, 2013, Ruff et al. 2014). Bonaparte et al. (2005) created the Family Brasilodontidae to include *Brasilodon* and *Brasilitherium*, and, subsequently, other taxa were included in it such as *Protheriodon estudianti* (Bonaparte et al. 2006, Bonaparte 2012). Some authors (e.g., Liu and Olsen 2010) pointed out that *Brasilodon* and *Brasilitherium* are synonym and also that a monophyletic Brasilodontidae has not been recovered (e.g., Abdala 2007). Notwithstanding these issues that are currently under revision, the impact that the discovery of the brasilodontids from the *Riograndia* AZ of southern Brazil has caused is unprecedented (Bonaparte et al. 2003, 2005, 2012, Rodrigues et al. 2012, 2013).

In this contribution, we present a new prozostroodontian cynodont from the *Riograndia* AZ of

the Candelária Municipality, state of Rio Grande do Sul, Brazil. The new taxon is described, compared and included in a broad phylogenetic analysis of cynodonts. Although based on a partial lower jaw and maxillary fragments, the specimen represents a new taxon of prozostroodontian

with several features shared with *Prozostrodon* from the *Hyperodapedon* AZ and especially with *Brasilodon* and *Brasilitherium* from the *Riograndia* AZ. The new specimen contributes to the understanding of the non-mammaliaform prozostroodontian diversity.

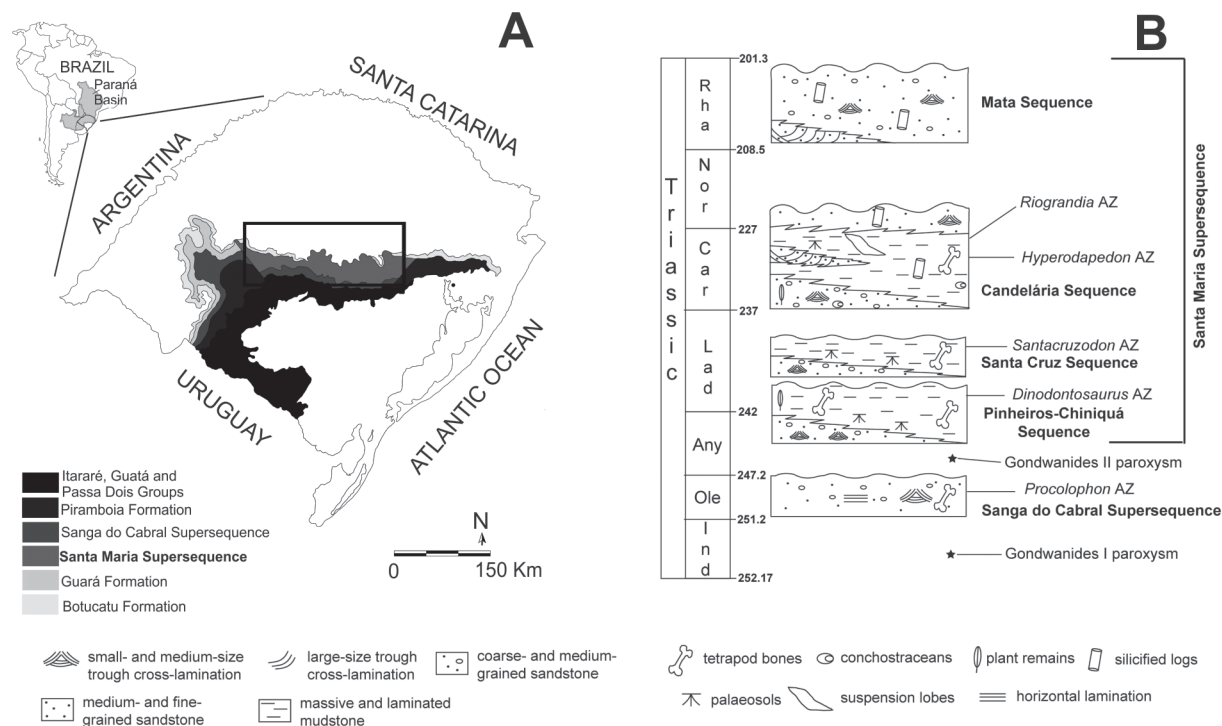


Fig. 1 - A: Geographical location of the Santa Maria Supersequence (Paraná Basin) in the state of Rio Grande do Sul, Brazil. **B:** Chronostratigraphy of the southern Brazilian Triassic, showing the four Assemblage Zones (AZ) based on tetrapods context. From Horn et al. 2004. Biostratigraphy after Soares et al. 2011. Abbreviations: **Any**, Anisian; **Car**, Carnian; **Ind**, Induan; **Lad**, Ladinian; **Nor**, Norian; **Ole**, Olenekian; **Rha**, Rhaetian.

GEOLOGICAL SETTING AND BIOSTRATIGRAPHY

The Upper Triassic Candelária Sequence corresponds to a third-order sequence placed in the Santa Maria Supersequence (*sensu* Zeffass et al. 2003, Horn et al. 2014) (Fig. 1). The basal portion of the Sequence consists of a coarsening-upward succession that begins with red mudstones interbedded with small-scale trough cross-bedded sandstone lenses. Rhythmites and sigmoidal massive to climbing cross-laminated sandstone bodies are also present (Soares et al. 2011). This facies association is interpreted as a lacustrine-deltaic depositional system in a humid climate (Holz

and Scherer 2000, Zeffass et al. 2003). The Candelária Sequence encompasses the *Hyperodapedon* AZ (*sensu* Abdala et al. 2001), in which the most abundant components are the rhynchosaur *Hyperodapedon* sp. and the traversodontid cynodont *Exaeretodon riograndensis* Abdala et al. (2002). Besides the aforementioned cynodonts (e.g., *Trucidocynodon*, *Therioherpeton*, *Charruodon* and *Prozostrodon*), its dinosaur content also deserves mention (Bittencourt and Kellner 2009, Langer et al. 1999, Cabreira et al. 2011). This faunal association enables us to correlate these levels with those of the Ischigualasto Formation from Argentina, whose basal layer was dated as

230.3-231.4 ± 0.3My (Rogers et al. 1993, Furin et al. 2006, Martinez et al. 2011). The top of the Candelária Sequence, where the younger *Riograndia* AZ is recognized, has an increased content of sandstone. The layers occur as narrow, massive or stratified (horizontal and trough cross bedding) lenses interpreted as amalgamated sandstone bodies related to high width/depth ratio channels. This succession is interpreted as the progressive replacement of a lacustrine-deltaic by a fluvial system (Rubert and Schultz 2004, Soares et al. 2011). The *Riograndia* AZ is characterized by a rich association of small tetrapods, such as the procolophonid *Soturnia caliodon* Cisneros and Schultz (2003), and the sphenodontid *Clevosaurus brasiliensis* Bonaparte and Sues (2006), among others, and the five taxa of advanced non-mammaliaform cynodonts aforementioned (*Riograndia*, *Brasilodon*, *Brasilitherium*, *Irajatherium* and *Minicynodon*). The dinosaurs are represented by the plateosaurid *Unaysaurus tolentinoi* Leal et al. (2003), the theropod (*sensu* Langer et al. 2009) *Guaibasaurus candelariensis* Bonaparte et al. (1999), and new specimens with sauropodomorph affinities (Bittencourt et al. 2013), plus the dinosauriform *Sacisaurus agudoensis* Ferigolo and Langer (2007). Also compose the *Riograndia* AZ the dicynodont *Jachalera candelariensis* Araújo and Gonzaga (1980), an indeterminate phytosaur (Kischlat and Lucas 2003), isolated teeth of archosaurs (Dornelles 1990), and a stereospondyl amphibian (Dias-da-Silva et al. 2009). This whole fauna occurs in a series of outcrops mainly located in Candelária and Faxinal do Soturno municipalities, and the record of *Riograndia guaibensis* in at least five of them, enables their correlation to the *Riograndia* AZ (Soares et al. 2011, Bittencourt et al. 2013). In turn, *Riograndia* AZ can be correlated to the fauna from the base of the Los Colorados Formation of Argentina (Early Norian) due to the presence of the same dicynodont genera, *Jachalera* (Bonaparte 1971, see also comments in Martinelli and Rougier 2007).

The Botucaraí Hill Site (*sensu* Bittencourt et al. 2013) crops out along the highway BR 287, Candelária Municipality, state of Rio Grande do Sul, Brazil (29° 40' 53" S; 52° 50' 28" W). This site is characterized by twelve meters of massive to laminar mudstones intercalated by centimeter massive sandstones lenses, followed by a layer of massive sandstones and another layer of trough cross bedded sandstone, one meter thick each. The holotype of the new cynodont was collected at the same level where several materials of *Jachalera* and some sauropodomorph dinosaur remains were found (Bittencourt et al. 2013) (Fig. 2).

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

CYNODONTIA Owen, 1861

EUCYNODONTIA Kemp, 1982

PROBAINOGNATHIA Hopson, 1990

PROZOSTRODONTIA Liu and Olsen, 2010

Botucaraitherium gen. nov.

DIAGNOSIS

Botucaraitherium is diagnosed by the following association of characters: upper postcanines with a prominent central cusp (A), with symmetric mesial and distal edges, two cusps mesio-lingually (cusp B) and disto-lingually (cusp C) arranged (being A>>B=C), and two accessory cuspules in the mesio-labial border and one cuspule in the disto-labial edge; the three main upper cusps form a subtle angle (opposite to the condition of the “reverse triangle pattern”); lingual surface of the crown of upper postcanines slightly concave, with a flexion; lower postcanines with a main large cusp a on the mesial half of the crown, followed by cusps c and d decreasing in size posteriorly, slightly curved backward; main cusp a totally asymmetrical, with a concave mesial edge and is about two times taller than the straight distal

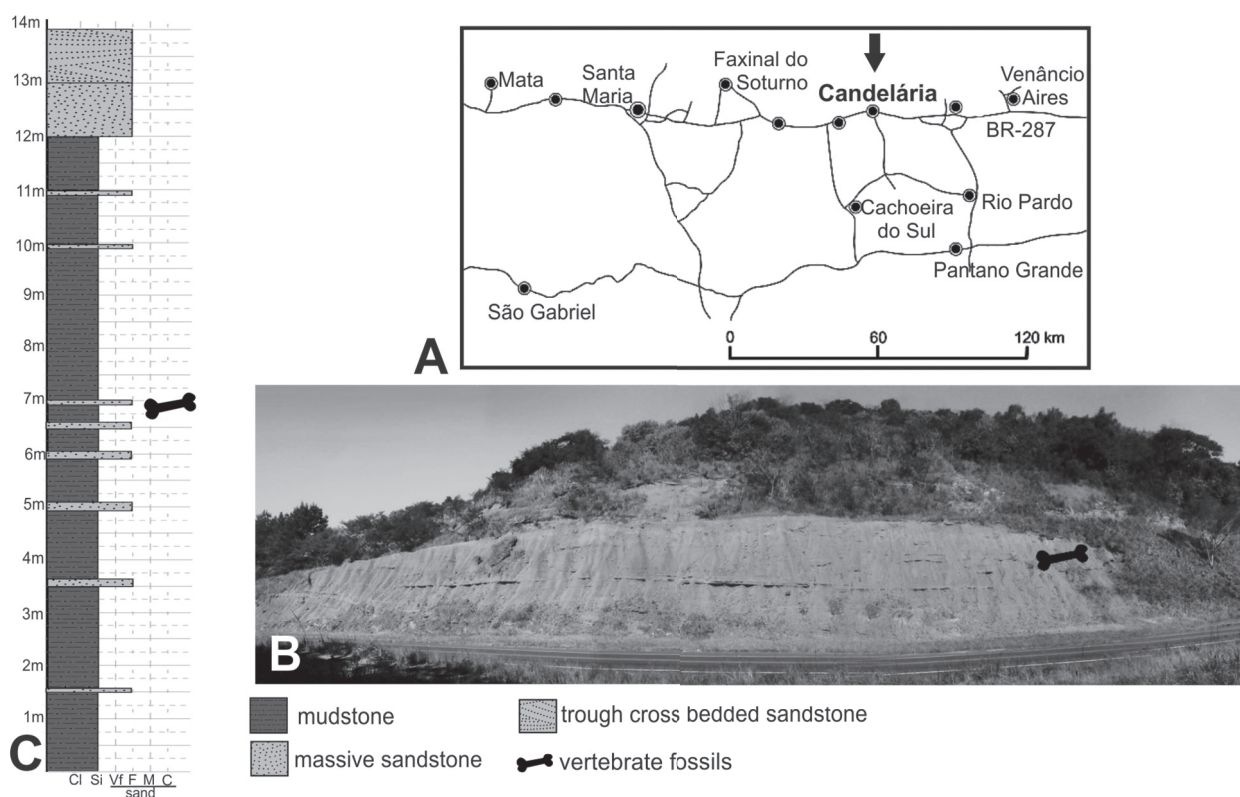


Fig. 2 - A: Road map with City of Candelária indicated. **B:** View of the Botucaraí Hill site, southern margin of BR 287 road, with the indication of the fossiliferous level. **C:** Log of the Botucaraí Hill Site.

edge; cusps c and d with symmetrical mesial and distal edges; reduced and basal positioned cusp b (cusp $a > c > d > b$); lower postcanines with multicuspitated lingual cingulum shelf, with small mesial cusp e; upper and lower postcanines with 8-shaped cross-section root; large diastema between canine and postcanines in adult stage; postcanine replacement including the loose of anterior postcanines, addition of new ones at the rear and substitution of other functional teeth.

TYPE AND ONLY KNOWN SPECIES

Botucaraitherium belarminoi sp. nov.

ETYMOLOGY

Botucaraí, in reference to the Botucaraí Hill, which dominates the landscape of the Candelary City (state of Rio Grande do Sul) and where there are

several outcrops with Triassic fauna. In one of these outcrops, Botucaraí Hill Site (*sensu* Bittencourt et al. 2013) the holotype was found. *Therium*, from the New Latin, that derives from the Greek *thērion*, which means “beast”, frequently used in mammals and close relative forms.

Botucaraitherium belarminoi sp. nov.

HOLOTYPE

MMACR-PV-003-T, left lower jaw, without postdentary bones, bearing the root of last incisor, the canine, and four partially preserved postcanines plus one partial crown inside the dentary (not erupted), and two left maxillary fragments, one with a broken canine and the other with one postcanine and the root of the following two teeth.

DIAGNOSIS

Same as for genus.

ETYMOLOGY

belarminoi, named in honor of Mr. Belarmino Stefanello, a volunteer at the Museu Municipal Aristides Carlos Rodrigues, who found the fossil.

LOCALITY AND HORIZON

From the Botucaraí Hill Site (*sensu* Bittencourt et al. 2013) near the level where the dicynodont *Jachaleria* (Aráujo and Gonzaga 1980) and dinosaur remains with sauropodomorph affinities (Bittencourt et al. 2013) were recovered. It is located about 8 kilometers west of Candelária City, in a roadcut of the route BR-287, state of Rio Grande do Sul, Brazil (Fig. 2), Candelária Sequence, Santa Maria Supersequence (Zerfass et al. 2003, Horn et al. 2014), *Riograndia* AZ (Soares et al. 2011), possibly Early Norian (Fig. 1).

DESCRIPTION

The specimen MMACR-PV-003-T is mostly not well-preserved due to several breakages in the lower jaw and the maxillary fragments are isolated (Fig. 3). Only the lower canine, one upper and some lower postcanines preserve most of their crown. All the material included in the holotype specimen was found in association and corresponds to only one individual.

MAXILLA

The two available portions of maxilla are extremely fragmented, without much information. Based on the preserved teeth, they correspond to the left side of the skull. One of the fragments, which preserves the left canine, has the external surface anteroposteriorly concave, highlighting the prominent canine root (Fig. 3A). Just posterior to it there is a small foramen, facing anteriorly. The second fragment has a complete anterior postcanine and the two 8-shaped roots of the two following ones (described later) (Fig. 3B). Above the first broken postcanine (i.e. the first root) there is a concavity and subtle notch which possibly corresponds to a large exit of the infraorbital branch of the trigeminal nerve.

LOWER JAW

The dentary is only observed in medial view (Fig. 4). The jaw is anteroposteriorly larger than any of the known specimens of *Brasilodon*, *Brasilitherium* and *Minicynodon* from the same *Riograndia* AZ, and smaller than *Prozostrodon* from the *Hyperodapedon* AZ. The horizontal ramus is slender along the anterior half and becomes slightly deeper at the rear. Therefore, the alveolar level and the ventral margin of the horizontal ramus are slightly divergent posteriorly. The mandibular symphysis is unfused as in prozostroodontians (e.g., *Prozostrodon*, *Brasilodon*, *Brasilitherium*; Bonaparte and Barberena 2001, Bonaparte et al. 2003, 2005) and has some longitudinal ridges and a small foramen. The trough for the postdentary bones is relatively reduced and runs forward, becoming smaller, parallel to the ventral edge of the dentary. The dentary seems to be transversely wide at the angular process; this region is not well-preserved although its shape seems to be similar to that of *Prozostrodon* (UFRGS-PV-0248-T). Below the alveolar line, the dental lamina is observed, mainly at the level of the fourth postcanine. The dentary has a large diastema between canine and postcanines and the canine base and alveolar level of the incisor is positioned slightly dorsal to the alveolar level of the postcanine series (Fig. 4A). This condition is similar to that observed in *Prozostrodon*, *Brasilodon*, *Brasilitherium* (Bonaparte and Barberena 2001, Bonaparte et al. 2003, 2005) and other possibly related forms such as *Microconodon* and *Dromatherium* (Hahn et al. 1994, Sues 2001).

The coronoid process is broad anteroposteriorly and tall dorsoventrally (Fig. 4A). It rises behind the pc4 where its base is more transversely broad than the remaining edge. A clear scar for the coronoid bone is not observable at this region, possibly due to the bad preservation. The articular process of the dentary is broken at the rear, nonetheless it seems to be well-developed as in other prozostroodontians (e.g., *Prozostrodon*, *Brasilodon*).

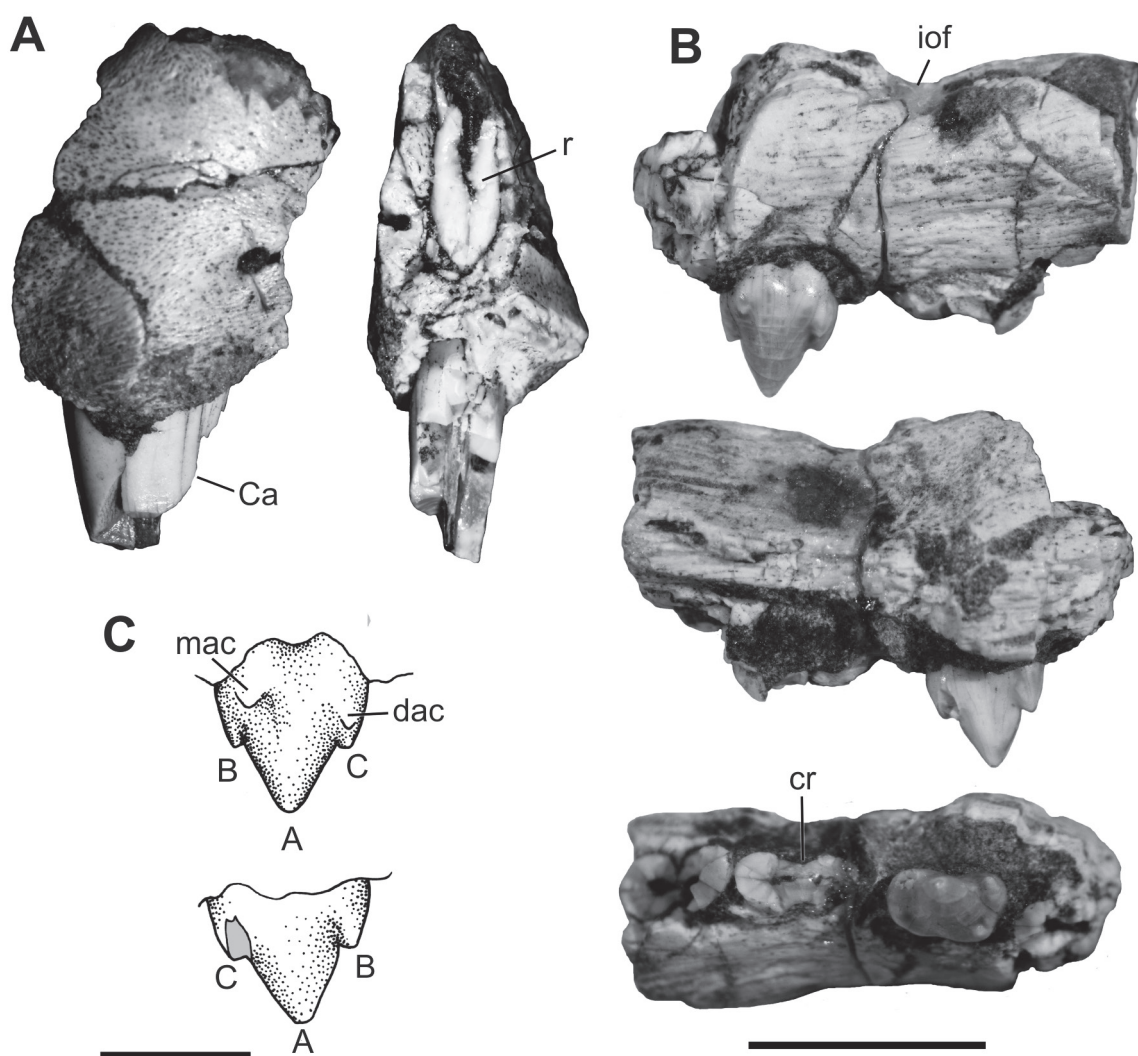


Fig. 3 - Holotype (MMACR-PV-003-T) of *Botucaratherium belarminoi* gen. nov. et sp. nov. **A:** Fragment of left maxilla with portion of canine in lateral and posterior views. **B:** Fragment of left maxilla with postcanine in lateral, medial and ventral views. **C:** Detail of upper postcanine in labial (lateral) and lingual (medial) views. Scale bars equals 5 mm in A and B and 2 mm in C. Gray areas indicate broken surfaces. Abbreviations: **A-C**, refers to name of cusps; **Ca**, upper canine; **cr**, constricted root; **dac**, distal accessory cusplule; **iof**, ventral edge of the infraorbital foramen; **mac**, mesial accessory cusplule; **r**, root.

Only the anterior 1/3 portion of the horizontal ramus of the dentary can be observed in lateral view. The surface is slightly convex dorso-ventrally and there are at least two small mental foramina below and anteriorly to the level of the canine.

UPPER DENTITION

The upper incisors are not preserved. One fragment of maxilla keeps the left canine which is partially broken. It is elliptical in cross section, at the base,

twice mesio-distally longer than transversely wide. The preserved mesial and distal edges are gently concave, without evidence of a ridge or crenulations (Fig. 3A). The mesial edge is subtle convex whereas the distal one is straight to slightly concave. The upper canine is larger than the lower one.

The other fragment of maxilla preserves one postcanine and the root of the following two (Fig. 3A). Unfortunately, there is no contact between both maxillary fragments, precluding any detail of the

first postcanine and the condition of the diastema. In addition, the upper postcanine count is unknown as is the exact position of the preserved postcanine.

The preserved postcanine has the crown as long as tall, mesio-distally, and about two times long than wide. The crown is dominated by a central cusp (A), with symmetric mesial and distal edges, and two cusps mesio-lingually (cusp B) and disto-lingually (cusp C; the tip of this cusp is broken) arranged. Cusps B and C have quite similar sizes but cusp B is positioned slightly more dorsal than cusp C. In occlusal view, the three cusps form a subtle angle, opposite to the condition observed in mammaliaforms with the reverse triangle pattern (Crompton and Jenkins 1968). In addition, there are accessory cingular cuspules on the labial side. On the mesio-labial corner there are two tiny cuspules (the more mesial the smallest) which are the most dorsally positioned cusps of the crown. Hence, there is some considerable distance between these cuspules and cusp B. Also, these accessory cuspules make the mesial width of the crown slightly wider than the distal width. The disto-labial accessory cusp is near cusp C, at its dorsal base (Fig. 3C). In occlusal view the labial surface of the crown is fairly straight whereas the lingual one is concave, with a flexion. The root of this postcanine is entirely inside the alveolus, but in labial view, the beginning of a longitudinal groove can be observed, constricting the root. The size of the only known upper postcanine is considerably smaller than the lower ones, a condition observed in some other probainognathians (e.g., *Prozostrodon*, *Brasilodon*, *Irajatherium*, Bonaparte and Barberena 2001, Bonaparte et al. 2003, 2005, Martinelli et al. 2005).

The upper postcanine pattern of the *Botucaraitherium* is quite different from those of the tritheledontids (*Irajatherium*, *Chalimiania*), in which there are a mesiodistally compressed and transversely broad main cusp, with small mesial and distal cusps (with a labial cingulum in the postcanines of *Pachygenelus*; Gow 1980, Martinelli et al. 2005,

Martinelli and Rougier 2007). *Botucaraitherium* also differs from *Riograndia* because the latter taxon has up to nine cusps mesiodistally aligned without any cingulum (Bonaparte et al. 2001, Soares et al. 2011). The upper postcanines of *Prozostrodon* display four aligned cusps (A, B, C, D) (Bonaparte and Barberena 2001) without lingual cusps or any cingular cuspules. Thus, the upper postcanines of *Botucaraitherium* differ significantly from those of *Prozostrodon* in having three main cusps (instead of four) plus accessory labial cingular cuspules (Fig. 5A, B).

The upper postcanine pattern of *Botucaraitherium* is more closely related to that of *Brasilodon*, *Brasilitherium* and *Minicynodon* (Fig. 5A, C) (Bonaparte et al. 2003, 2005, 2010, 2012) than to any other prozostrodonian. Regarding the brasilodontids, its postcanines have a prominent central cusp (A), one mesial (B) and one distal (C), small accessory cusps aligned on the lingual side, and one mesial and one distal small cusp on the labial side, giving a symmetrical cusp arrangement. This pattern is consistent in all specimens of *Brasilodon* and *Minicynodon*, but in some specimens referred to *Brasilitherium* the distal labial accessory cusp is placed more posteriorly (Bonaparte et al. 2010, Martinelli and Bonaparte 2011).

Botucaraitherium is differentiated from brasilodontids by a notoriously more bulbous crown and two (not one) mesio-labial accessory cusps. These features have never been observed even in the largest specimens of the aforementioned brasilodontids. Therefore, we considered this feature as unique of *Botucaraitherium*, since in the large sample of brasilodontids from the *Riograndia* AZ, this condition was never observed.

In addition to the only preserved upper postcanine, the maxillary fragment preserves the root of the two following teeth. The roots increase in size posteriorly and are 8-shaped in cross-section, in which the longitudinal groove is present in both labial and lingual sides, with each lobe having its own root canal.

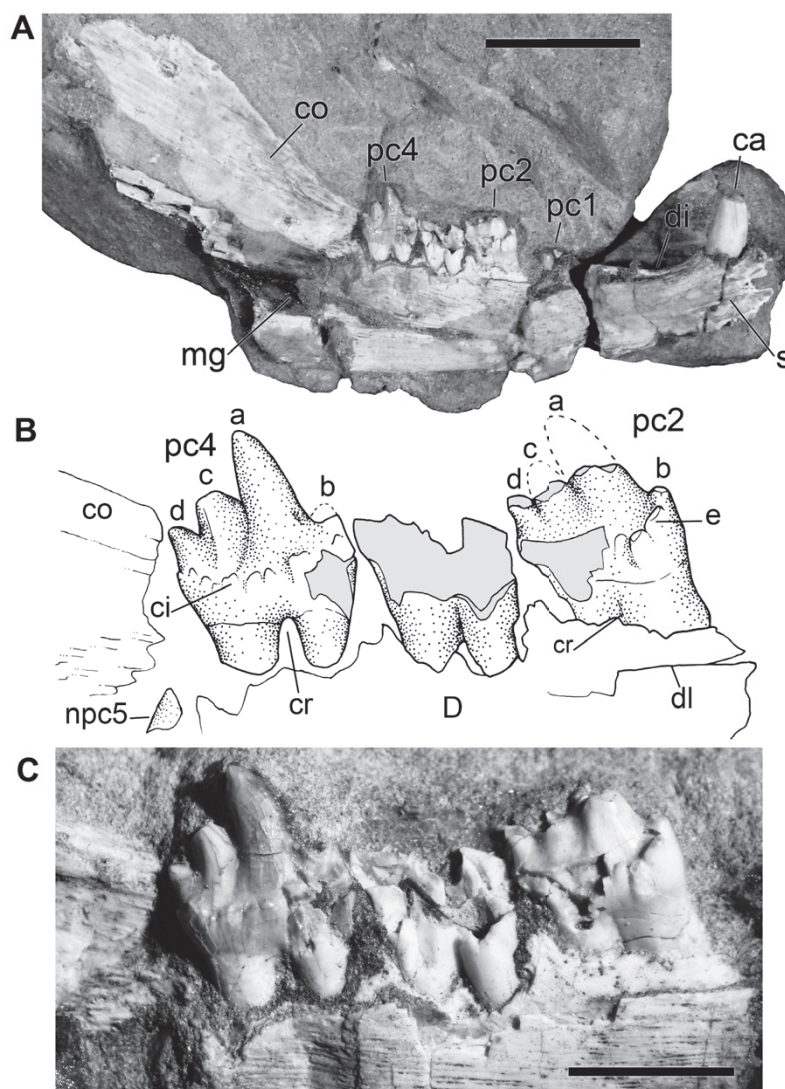


Fig. 4 - Holotype (MMACR-PV-003-T) of *Botucaraitherium belarminoi* gen. nov. et sp. nov. **A**: Left lower jaw in medial view. **B** and **C**: detail of the postcanines in medial view. Scale bar equals 10mm in **A** and 3mm in **B**. Gray areas indicate broken surfaces. Abbreviations: **a-e**, refers to name of cusps; **ca**, canine; **ci**, cuspidated cingulum; **co**, coronoid process of dentary; **cr**, constricted root; **D**, dentary; **dl**, dental lamina; **mg**, meckelian groove; **npc5**, non-erupted postcanine 5; **pc**, postcanine; **s**, symphysis.

LOWER DENTITION

The number of lower incisors is unknown. The root of the last incisor is preserved, which is circular in cross-section. It is next to the canine, indicating the lack of a diastema. Anteriorly to this root, the dentary is partially broken off and it is impossible to deduce the number and size of the other incisors (Fig. 4A). In *Brasilodon* there are three incisors and based on its dentary morphology the number of incisors for *Botucaraitherium* is likely to be the same.

The canine is broken at the tip (Fig. 4A). It is sub-circular in cross-section, with the mesial edge slightly convex and the distal one slightly concave. On the distal edge there is a thin longitudinal ridge, without serrations. The enamel covering the crown is very thin and a large portion of the root is observed outside the alveolus. There is a large diastema between the canine and the postcanines. Along the posteriormost portion of the diastema there is a mesio-distally oriented sulcus that could

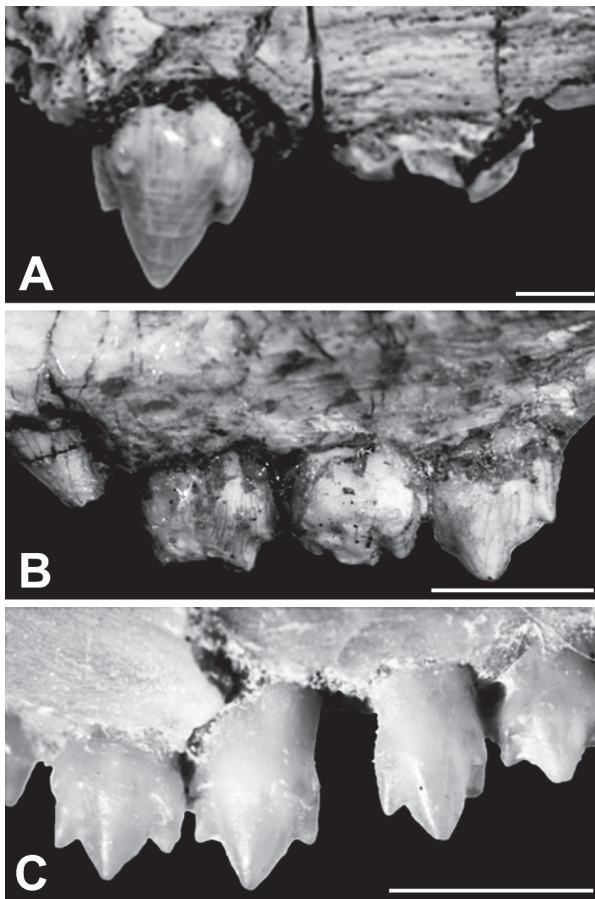


Fig. 5 - Comparisons of upper postcanines. **A:** *Botucaraitherium belarminoi* gen. nov. et sp. nov. (Holotype MMACR-PV-003-T) in left labial view. **B:** *Prozostrodon brasiliensis* (Holotype UFRGS-PV-0248-T) in left labial view. **C:** *Brasilodon quadrangularis* (Holotype UFRGS-PV-0611-T) in right labial view. Scale bar equals 1mm.

correspond to closed alveoli of the lost teeth. The loss of the anterior postcanines and concomitantly the enlargement of the diastema are a pattern observed in several taxa, such as some tritylodontids (e.g., *Oligokyphus*, *Tritylodon*; Kemp, 1982) *Brasilodon* and *Brasilitherium* (Martinelli and Bonaparte 2011), and some early mammaliaforms (e.g., *Sinoconodon*; Crompton and Luo 1993, Luo et al. 2004).

The postcanine series includes five teeth (Fig 3). The pc1 consists of a main cusp that was in process of eruption. Unfortunately, at this region there is a large breakage that obscures the anatomy of the tooth.

The pc 2-4 are similar in size. Although the crown of pc2 and pc3 are extremely damaged, they show similar crown morphology. There is a main large cusp (a) on the mesial half of the crown, followed by two cusps (c and d) that decrease in size posteriorly. These three cusps are slightly posteriorly projected, but not to the degree of, for example, *Chiniquodon* (Abdala and Giannini 2002). The cusps are not bulbous and constitute the sectorial portion of the crown. Cusp a is totally asymmetrical with the mesial edge concave and about two times taller than the straight distal edge. Cusps c and d have symmetrical mesial and distal edges. On the mesio-labial edge of the crown, in a basal position, there is a small cusp b. In the pc2 and pc4 that better preserve the crown morphology, the cusp size is $a > c > d > b$. In the lingual side of the postcanines there is a well-developed cingulum with a small mesial cusp e (better observed in pc2), followed by a series of tiny cusps that reach the distal margin of the crown, forming a cingular shelf (Fig. 4B, C).

The posteriormost portion of the pc4 lies internally to the coronoid process. The postcanine roots are incipiently bifurcated, with a well-developed longitudinal groove. Just below the pc4, there is a main cusp (a) of a non-erupted last postcanine.

The tooth morphology of *Botucaraitherium* is reminiscent of *Prozostrodon* and brasilodontids. The multicuspitated lingual cingular shelf of *Botucaraitherium* is similar to that of *Prozostrodon*. In contrast, *Brasilodon* and *Brasilitherium* have less crenulated labial cingulum, and instead there are more discrete cusps (cusps e and g) (e.g., UFRGS-PV-0603-T). With regard to the main cusps, the crown is taller in *Botucaraitherium* than in *Prozostrodon*, and in the latter taxon, cusps a, b and c are more bulbous (less sectorials) with less contrast in height among them (Fig. 6).

TOOTH REPLACEMENT

The information on a single lower jaw is limited but a few comments on tooth replacement are possible. The large diastema posteriorly to the canine and

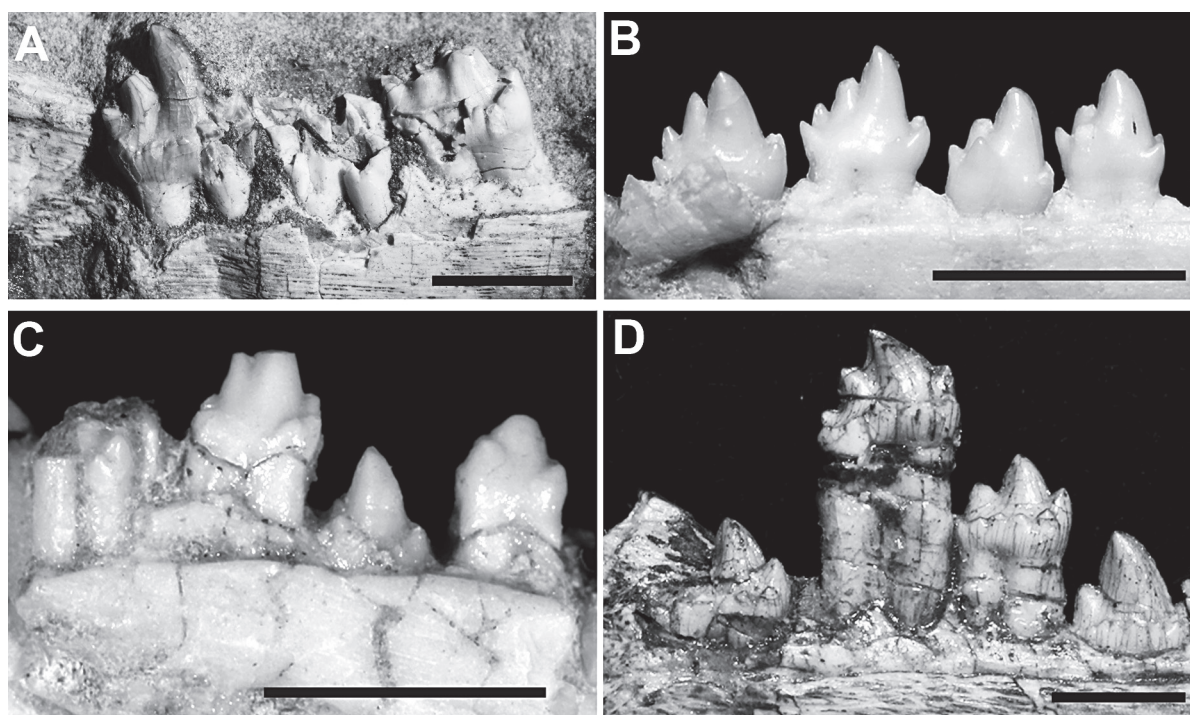


Fig. 6 - Comparisons of the right posterior lower postcanines in lingual view. **A:** *Botucaraitherium belarminoi* gen. nov. et sp. nov. (Holotype MMACR-PV-003-T). **B:** *Brasilitherium riograndensis* (UFRGS-PV-0603-T); **C:** *Brasilodon quadrangularis* (UFRGS-PV-0765-T). **D:** *Prozostrodon brasiliensis* (Holotype UFRGS-PV-0248-T). Scale bar equals 3 mm.

the closed mesial alveoli, indicate that the anterior most postcanines were lost and not replaced. The anteriormost postcanine (i.e., labeled along the text as pc1) partially inserted in the alveolus shows that some teeth of the series were replaced and the last postcanine (pc5), represented by a non-erupted tooth, indicates that new teeth were added at the rear. Among prozostroodontians, some mix of alternate and sequential replacement was observed in *Brasilodon* and *Brasilitherium*, being apparently polyphyodonty taxa (Bonaparte et al. 2003, 2005, Martinelli and Bonaparte 2011). It should be emphasized that the sequence of postcanine eruption and the number of replacement per locus at the non-mammaliaform prozostroodontians-mammaliaforms boundary is a matter still poorly understood.

DISCUSSION

Botucaraitherium belarminoi constitutes a new prozostroodontian cynodont from the *Riograndia* AZ

of southern Brazil. The holotype represents an adult individual, larger than any known brasilodontid from the same AZ. There are no recorded specimens of *Brasilodon* and *Brasilitherium* in the Botucaraí Hill Site. In turn, these taxa are relatively abundant in the Sesmaria do Pinhal 1 Site, located about 600 meters away (Bonaparte et al. 2003, 2005). In addition, within the Botucaraí region there is a record of *Brasilitherium*-like teeth in Sesmaria do Pinhal 3 Site, located about 1000 meters away from the Botucaraí Hill Site (Soares et al. 2011, Bittencourt et al. 2013).

The new species is clearly related to prozostroodontians, and especially to *Brasilodon* and *Brasilitherium* (Bonaparte et al. 2003, 2005), due to the morphology of the upper and lower postcanines (see Fig. 5, 6). They can be differentiated by the presence in *Botucaraitherium* of a well-developed multicuspitated lingual cingular shelf in lower postcanines and more bulbous upper postcanines, with more than one mesio-labial accessory cuspsules.

Its resemblance to *Prozostrodon*, from the older *Hyperodapedon* AZ, is also noteworthy. The lower dentition of both taxa is quite similar, especially because of the multicuspitated lingual cingular shelf. However, the sectorial portion of the postcanines of *Botucaraitherium* seems to be less bulbous with taller main cusps. The upper postcanines have stronger differences, due to the fact that the teeth of *Prozostrodon* are less quadrangular (with the exception of the last non-erupted postcanine of the holotype), and with three more developed accessory cusps in relation to the main cusp.

PHYLOGENETIC ANALYSIS

A parsimony analysis was performed based on 34 taxa and 145 morphological cranial, dental and postcranial characters (see Appendices 1 and 2), modified from the matrix presented by Liu and Olsen (2010). Some characters and codifications were modified (Appendix 1) and two new terminal taxa (i.e., *Brasilitherium riograndensis*

and *Botucaraitherium belarminoi*) were added. Liu and Olsen (2010) considered *Brasilodon* and *Brasilitherium* as synonyms; therefore, they used only *Brasilodon* as a terminal taxon. The proposal synonymy for these two species is a matter not clearly understood yet (see for example, Martinelli and Bonaparte 2011, Bonaparte et al. 2012) and will be further analyzed. We considered them as separate taxa in the current analysis.

The data matrix (Appendix 2) was analyzed using Maximum Parsimony with equally weighted characters with the computer program TNT 1.1 (Goloboff et al. 2008). All characters were treated as non-additive. The equally weighted parsimony analysis was conducted performing a heuristic search of Wagner trees with 500 random addition sequences, followed by TBR (Tree Bisection Reconnection), and saving 20 trees per round, which improve the searches and ensures to find all optimal trees.

Our analysis resulted in four most parsimonious trees of 441 steps, with a consistency index (CI)

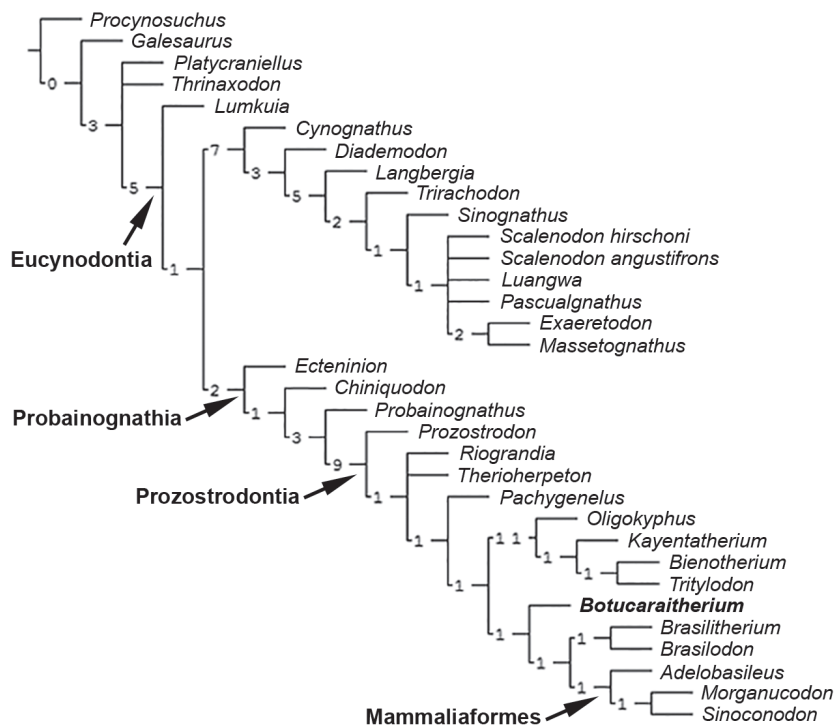


Fig. 7 - Strict consensus tree with Bremer index, positioning *Botucaraitherium belarminoi* gen. nov. et sp. nov. as a derived prozostrodonian.

of 0.481 and a retention index (RI) of 0.780. The strict consensus and Bremer index of each node are shown in Figure 7.

In the four most parsimonious trees obtained, the affinities of *Botucaraitherium* with the brasilodontids are supported. Indeed, *Botucaraitherium* is positioned as a more derived taxon than tritylodontids, as the sister group to the clade composed by *Brasilodon* and *Brasilitherium* plus Mammaliaformes. Despite the fragmentary aspect of the new taxon, especially the characters of the dentary and dentition give support to this relationship.

The presence of *Botucaraitherium* in the *Rio-grandia* AZ (Fig. 8), adding to the already known brasilodontids, reinforces the idea that the non-mammaliaform prozostrodonians enjoyed their greater representativeness during the Late Triassic in South America, which outlined the evolutionary scenery where the most profound anatomical steps related to the origin of mammaliaforms have taken place.



Fig. 8 - Artistic reconstruction of *Botucaraitherium belarminoi* gen. et sp. nov., by Jorge Blanco.

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INSTITUTIONAL ABBREVIATIONS

MMACR-PV-T, Museu Municipal Aristides Carlos Rodrigues, (Paleovertebrates, Triassic collection), Candelária, Rio Grande do Sul, Brazil; **UFRGS-PV-T**, Universidade Federal do Rio Grande do Sul (Paleovertebrates, Triassic collection), Porto Alegre, Rio Grande do Sul, Brazil.

RESUMO

Nós reportamos aqui um novo cinodonte prozostrodonite, *Botucaraitherium belarminoi* gen. et sp. nov., do Triássico Tardio da Zona de Assembleia (ZA) de *Rio-grandia* da Sequência Candelária (Supersequência Santa Maria), coletado no afloramento Sítio Botucaraí, no município de Candelária, Rio Grande do Sul, Brasil. O novo táxon está baseado em um único espécime (holótipo MMACR-PV-003-T) o qual inclui a mandíbula esquerda, sem os ossos pós-dentários, com a raiz do último incisivo preservada, o canino e quatro dentes pós-caninos, além de uma coroa parcial, não erupcionada, do quinto pós-canino, e dois fragmentos maxilares, um com um canino quebrado, e outro portando apenas um dente pós-canino. As feições mandibulares e dentárias assemelham-se àquelas dos cinodontes prozostrodonites *Prozostrodon brasiliensis* da ZA de *Hyperodapedon*, mais antiga, e de *Brasilodon*

quadrangularis e *Brasilitherium riograndensis* da mesma ZA de *Riograndia*. A inclusão de *Botucaraitherium* em uma ampla análise filogenética posicionou-o como um táxon mais derivado do que os tritilodontídeos, sendo o táxon-irmão de *Brasilodon*, *Brasilitherium* e mais Mammaliaformes. Apesar de o novo táxon ser baseado em poucos elementos cranianos, ele representa um componente faunístico adicional na ZA de *Riograndia* do Triássico sul-brasileiro, na qual os cinodontes não-mamaliaformes de pequeno tamanho, intimamente relacionados à origem dos mamíferos, foram ecologicamente bem sucedidos e taxonomicamente diversos.

Palavras-chave: Cynodontia, Prozostrodontia, Superseqüência Santa Maria, Triássico.

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Appendix 1. Phylogenetic Analysis

Botucaratherium was included into the phylogenetic framework of Liu and Olsen (2010), which constitutes the largest matrix of non-mammaliaform cynodonts to date. This matrix is based upon several previous contributions, including that of Hopson and Barghusen (1986), Rowe (1988), Wible and Hopson (1993), Lucas and Luo (1993), Luo (1994), Luo and Crompton (1994), Martínez et al. (1996), Hopson and Kitching (2001), Luo et al. (2002), Bonaparte et al. (2003, 2005), Sidor and Smith (2004), Martinelli et al. (2005), Abdala (2007), Martinelli and Rougier (2007), and Oliveira et al. (2010).

The data matrix of Liu and Olsen (2010) was modified for the current analysis:

1) CHANGES IN SCORINGS OF TAXA:

Character 01: *Prozostrodon* changes from 1 to 2 (based on Bonaparte and Barberena 2001). *Riograndia* changes from 0 to 1 (based on Bonaparte et al. 2001, Soares et al. 2011)

Character 07: *Therioherpeton* changes from ? to 1 (based on Bonaparte and Barberana 2001, Oliveira 2006).

Character 11: *Brasilodon* changes from 1 to 2.

Character 13: *Prozostrodon* changes from 0 to 1 (based on UFRGS-PV-0248-T; Martinelli et al. 2005, Martinelli and Rougier 2007).

Character 14: *Prozostrodon* changes from 1 to 2 (based on UFRGS-PV-0248-T; Martinelli et al. 2005, Martinelli and Rougier 2007).

Character 19: *Riograndia* changes from ? to 0 (based on Bonaparte et al. 2001, Soares et al. 2011).

Character 26: *Riograndia* changes from ? to 0 (based on Soares et al. 2011).

Character 27: *Riograndia* changes from ? to 1 (based on Bonaparte et al. 2001).

Character 30: *Prozostrodon* changes from ? to 2.

Character 35: *Riograndia* changes from 2 to 1. *Brasilodon* changes from 2 to 1 (based on Bonaparte et al. 2005).

Character 37: *Brasilodon* changes from ? to 1 (based on Bonaparte et al. 2005).

Character 93: *Prozostrodon* changes from 0 to 1 (based on UFRGS-PV-0248-T).

Character 96: *Exaeretodon* and *Scalenodon angustifrons* change from 1 to 0 (due to change in character definition).

Character 98: *Brasilodon* changes from ? to 0.

Character 103: *Prozostrodon* changes from 0 to 1.

Character 119: *Brasilodon* changes from 0 to 0+1.

2) CHANGES IN CHARACTER DEFINITION:

Character 37 (modified according to Hopson and Kitching 2001, Martinelli and Rougier 2007: ch. 47): Length of palatine relative to maxilla in secondary palate: shorter (0); about equal (1); longer (2).

Character 96 (redefined): Incisors: all of similar size (0); some incisor large (1).

Character 106 (new state and re-ordered): Upper postcanine roots: single (0); constricted root, with incipient longitudinal groove (1); divided into two longitudinal aligned roots (2); multiple roots (more than two) (3).

Character 107 (new state and re-ordered): Lower postcanine roots: single (0); constricted root, with incipient longitudinal groove (1); divided (2).

3) ADDITION OF NEW TAXA:

Brasilitherium riograndensis (Bonaparte et al. 2003, 2005, 2012).

Botucaratherium belarminoi (this paper).

Luangwa drysdalli

??00?1000?0000010121001111????1110?00001??00101000000?2??00000??0??????????1011201011
??113110100012[12][12]000-202100-12010??110110000??1100000000

Massetognathus pascuali

0111110010000000110101111101121110200001000001010000001211000000000011011102011011[12]
01011??11311021110211000-222100-120100000101101000??1100000000

Exaeretodon argentinus

00111110100000111121012111011211101[01]00010?00010100010002110000000000?101????01101121
1011??113210010102[12][12]000-120100-122100000001101001111100000000

Scalenodon angustifrons

??10?1?0000000??1101012111????1101?0?1??00010100?0000211000000?000??0????0?[01]0?12??0
11??113110100012[12][12]000-202100-1201????????????????????????

Scalenodon hirschoni

??0010????001?11????111011211101?0?0?0?00????????????1?000?0?????1??1?0?0?[01]??1??011
??113220001002[12][12]000-222100-1201????????????????????????

Chiniquodon theotonicus

11101010100000101011000001011[12]11112100011000010100000001000000000000?1?01???11101120
1011120001100000000010000--00-100000??000011010001110000?0000

Lumkuia fuzzi

??1000101000000?00000000010?1201101001010100010010?000000100000000000001000011011201
000120001100000000010000--00-10000????001????????????0????

Ecteninion lunensis

001??0021000002000000000000?1[01]11100002011100010100?10001010000000000110011021110110
01011??00011000001[01]0010000--00-?00000??1??110??0????0??????

Probainognathus jenseni

0110100210000010010110000101121111100001110001000000001100000000000011001102111021001
011120001100000010000000--00-00110000?000110??0??11000?0000

Therioherpeton cargini

?????0121?11122?2100??0??????1111??00
0????????0?0?1100--00-?00000??1?00?????????1111110011

Riograndia guaibensis

0113101211111221?10??0000111201111120110001020000?0000102000010001121102?13????0030111
1??001211001100[12]001100--00-10100????????????????????????

Pachygenelus monus

20131012111112212100100000011201112120110001020000100001020000101??121102213132020301
111120012210010001000010--00-002001??0001111101??1111111111

Prozostrodon brasiliensis

21?010?2????1221?1?????????112?1111?1??0301111?00
10000000111001100--00-001000??000?????0???1111110000

Botucaraitherium belarminoi

?????0??0???11????01
??????001?001110--01-00????????????????????????????????????

Brasilodon quardangularis

[01]000?0121121122120001000?00?1201111102110001021001?0?112220?00111011211022131320?03
01111?0011100001011001110--01-001[01]1??????0111?11????????????

Brasilitherium riograndensis

0000?0121121122120001000000?1201111102110001021011?01112220???11?011211022131320103011
11????010100001011001110--01-001[01]1?????????????11?????????1111

Tritylodon longaevus

102-1111110112211102001111011211102122110000110110110102121111011010311022031202003
11111??1132210-22-222-32-2-1100-03221??????210??????1?????1111

Oligokyphus major

[12]??-1111?10112???102010110?1?2?1??21????????110?10110102?211110110003100220312020
0311111??1132110-22-222-32-2-1100-0322111100?2101111??1121111111

Bienotherium yunnanense

102-11111101122111?201?111011211102122110000110110110?02?01111?110?031??22131?02003
11111??1132110-22-222-32-2-1100-03221??????210??11??????111111

Kayentatherium wellsi

102-11111?011221110201111111201102122110000110110110102121111?110?0311022131202003111
11121132110-22-222-32-2-1100-0322?11100021011?1111121??1111

Adelobasileus cromptoni

??????01121?2????????????????????0??????2110001021011?21112210000101110????????????????????
????????????????0?????0??1????????????????????????????????

Sinoconodon rigneyi

0002?0101121122120001000?01?1211112102110011031011?21112221011101010?????????0?302030111
2??2001000001001002210--00-10101????????????????????????

Morganucodon oehleri

0?02?0101121122120002?00001111111210211001103201112111222011211111211022132430203011
12122221000001011002210--01-0010111111001111111?1121111111



ERRATUM

A new prozostrodonian cynodont (Therapsida) from the Late Triassic *Riograndia* Assemblage Zone (Santa Maria Supersequence) of Southern Brazil

MARINA B. SOARES, AGUSTÍN G. MARTINELLI and TÉO V. DE OLIVEIRA

ABSTRACT

- Linha 1 – leia-se ‘**We report here on...**’
- Linha 2 – leia-se ‘from the **Late Triassic Riograndia...**’
- Linha 4 – leia-se ‘includes **the** left...’
- Linha 10 – leia-se ‘positioned it as a **more derived** taxon...’
- Linha 11 – leia-se ‘tritylodontids, **being** the sister-taxon...’
- Linha 11 – leia-se ‘*Brasilitherium* **plus** Mammaliaformes’
- Linha 13 – leia-se ‘...cynodonts, **closely** related...’

INTRODUCTION

- Coluna 2, linha 2 – adicionar ‘(Abdala and Ribeiro 2010)’ após ‘Malagasy faunas
- Coluna 2, última linha – leia-se ‘based upon **poorly** preserved’

PÁGINA 2

- Coluna 1, parágrafo 2, linha 7 – leia-se ‘...and **postorbital, constricted** root...’
- Coluna 1, parágrafo 2, linha 15 – leia-se ‘...lower jaw (unexpected for *Therioherpeton* based on its skull), we consider...’ [[**adicionar o trecho entre parênteses e remover o trecho que começa com ‘that differs’ até ‘Therioherpeton’s one’**]
- Coluna 2, linha 7 – leia-se ‘(*sensu* Martinelli et al...’
- Coluna 2, linha 10 – leia-se ‘cynodonts from this...’
- Coluna 2, linha 22 – colocar uma vírgula após ‘e.g.’
- Coluna 2, linha 25 – leia-se ‘et al. 2012, 2013, **Ruff et al. 2014**’
- Coluna 2, linha 30 – colocar uma vírgula após ‘e.g.’
- Coluna 2, linha 33 – colocar uma vírgula após ‘e.g.’

PÁGINA 3

- Coluna 1, linha 1 – leia-se ‘...do Sul, Brazil. The new...’
- Coluna 2, linha 2 – leia-se ‘...*Riograndia* AZ. **The new specimen contributes to the understanding of the non-mammaliaform prozostrodonian diversity.**’ (termina aqui o parágrafo)
- Coluna 2, parágrafo 2, linha 8 – colocar vírgula após ‘e.g.’

PÁGINA 4

Coluna 1, linha 21 – substituir ‘prosauropod’ por plateosaurid

Coluna 1, linha 24 – leia-se ‘...(1999), **and new specimens with sauropodomorph affinities (Bittencourt et al. 2013)**, plus the dinosauriform...’

Coluna 1, linha 30 – leia-se ‘1990), **and** a stereospondyl...’

Coluna 1, linha 32 – remover ‘and new materials...’ até ‘...(Bittencourt et al. 2013).’

Coluna 1, última linha – leia-se ‘Bonaparte 1971, see also comments in **Martinelli and Rougier 2007**’

Coluna 2, linha 2 – leia-se ‘**crops out** along the...’

Coluna 2, linha 4 – leia-se ‘(29° 40’ 53” S; 52° 50’ 28” W). **This site** is characterized...’

Coluna 2, linha 10 – leia-se ‘The **holotype of the** new cynodont...’

Coluna 2, parágrafo 2, linha 11 – leia-se ‘of the crown of **upper postcanines** slightly...’

Coluna 2, parágrafo 2, linha 13 – remover os parênteses em (a)

PÁGINA 6

Coluna 1, parágrafo 3, linha 4 – leia-se ‘(Fig. 3). **Only the** lower canine, **one** upper and...’

Coluna 1, parágrafo 4, linha 4 – substituir size por side

Coluna 1, parágrafo 4, linha 4 – leia-se ‘...skull. **One of the fragments, which preserves the left canine,** has the external surface **anteroposteriorly** concave...’

Coluna 1, parágrafo 4, linha 6 – após root adicionar ‘(Fig. 3A)’

Coluna 1, parágrafo 4, linha 10 – leia-se ‘the **two** following ones (described later) **(Fig. 3B)**’

Coluna 1, última linha – leia-se ‘...large exit of the **infraorbital branch** of the trigeminal...’

Coluna 2, linha 1 – leia-se ‘The dentary...’

Coluna 2, linha 2 – leia-se ‘The jaw is **anteroposteriorly** larger than...’

Coluna 2, linha 11 – colocar vírgula após ‘e.g.’

Coluna 2, linha 18 – leia-se ‘be **transversely wide** at the...’

Coluna 2, linha 19 – leia-se ‘although **its shape** seems to be...’

Coluna 2, linha 26 – colocar ‘(Fig. 4A)’ após postcanine series

Coluna 2, parágrafo 2, linha 2 – adicionar ‘(Fig. 4A)’ após dorsoventrally

Coluna 2, última linha – colocar vírgula após e.g.

PÁGINA 8

Coluna 1, linha 2 – adicionar (Fig. 3A) após crenulations

Coluna 1, parágrafo 2, linha 2 – substituir Fig. 4 por Fig. 3A

Coluna 1, parágrafo 3, linha 22 – colocar ‘(Fig. 3C)’ após dorsal base

Coluna 1, última linha – colocar vírgula após e.g.

Coluna 2, parágrafo 2 – este parágrafo deve ficar como abaixo:

The upper postcanine pattern of the *Botucaraitherium* is quite different from those of the tritheledontids (*Irajatherium*, *Chalimiania*), in which there are a mesiodistally compressed and transversely broad main cusp, with small mesial and distal cusps (with a labial cingulum in the postcanines of *Pachygenelus*; Gow 1980, Martinelli et al. 2005, Martinelli and Rougier 2007). *Botucaraitherium* also differs from *Riograndia* because the latter taxon has up to nine cusps mesiodistally aligned without any cingulum

(Bonaparte et al. 2001, Soares et al. 2011). The upper postcanines of *Prozostrodon* display four aligned cusps (A, B, C, D) (Bonaparte and Barberena 2001) without lingual cusps or any cingular cuspules. Thus, the upper postcanines of *Botucaratherium* differ significantly from those of *Prozostrodon* in having three main cusps (instead of four) plus accessory labial cingular cuspules (Fig. 5A, B).

Coluna 2, parágrafo 3, linha 3 – leia-se ‘(Fig. 5A, C)’

Coluna 2, parágrafo 3, linha 5 –adicionar ‘non-mammaliaform’ antes de ‘prozostrodonian.’

Coluna 2, parágrafo 3, penúltima linha – substituir ‘cuspule’ por ‘cusp’

Coluna 2, parágrafo 4 – este parágrafo deve ficar como abaixo:

‘*Botucaratherium* is differentiated from brasilodontids by a notoriously more bulbous crown and two (not one) mesio-labial accessory cusps. These features have never been observed even in the largest specimens of the aforementioned brasilodontids. Therefore, we considered this feature as unique of *Botucaratherium*, since in the large sample of brasilodontids from the *Riograndia* AZ, this condition was never observed.’

Coluna 2, parágrafo 5 – leia-se ‘**In addition to the only preserved upper postcanine, the maxillary fragment preserves the root of the two following teeth. The roots increase in size posteriorly and are 8-shaped in cross-section...**

PÁGINA 9

Coluna 1, linha 2 – leia-se ‘...lingual sides, with each lobe having its own root canal.’

Coluna 1, parágrafo 2, linha 5 – leia-se ‘...it is impossible to **deduce** the number **and size** of the other incisors (**Fig. 4A**). In *Brasilodon*...’

Coluna 1, parágrafo 2, última linha – ‘...*Botucaratherium* **is likely to be** the same.’

Coluna 1, parágrafo 3, linha 1 – substituir (Fig. 3) por (Fig. 4A)

Coluna 2, linha 9 – colocar vírgula após e.g.

Coluna 2, linha 12 – colocar vírgula após e.g.

Coluna 2, parágrafo 2, linha 2 - substituir (Fig. 3) por (Fig. 4A)

Coluna 2, parágrafo 2, linha 4 – leia-se ‘...obscures **the anatomy of the tooth.**’

Coluna 2, parágrafo 2, linha 6 – substituir ‘possess’ por ‘show’

PÁGINA 10

Coluna 1, penúltima linha – substituir ‘which better preserved’ por ‘that better preserve’

Coluna 2, linha 5 – após ‘shelf’ adicionar ‘(Fig. 4B, C)’

Coluna 2, parágrafo 3, linha 1 – substituir ‘pattern’ por ‘morphology’

Coluna 2, parágrafo 3, linha 7 – colocar vírgula após e.g.

Coluna 2, parágrafo 3, linha 9 – substituir ‘cups’ por ‘cusps’

Coluna 2, parágrafo 4, linha 2- substituir noteworthy por ‘possible’

Coluna 2, parágrafo 4, linha 5 – leia-se ‘The anterior most **postcanine (i.e., labeled along the text as pc1)** partially inserted...’

Coluna 2, parágrafo 4, linha 11 – após ‘*Brasilitherium*’ até o fim do parágrafo, deve ser lido da seguinte maneira

‘being apparently polyphyodonty taxa (Bonaparte et al. 2003, 2005, Martinelli and Bonaparte 2011). It should be emphasized that **the sequence of postcanine eruption and the number of replacement per locus** at the non-mammaliaform prozostroodontians-mammaliaforms boundary is a matter still poorly understood. **(remover Deep analyses... até o final)**

PÁGINA 11

Coluna 1, parágrafo 1 – após ‘the same AZ.’ Até o fim do parágrafo, deve ser lido da seguinte maneira

There are no recorded specimens of *Brasilodon* and *Brasilitherium* in the Botucaraí Hill Site. In turn, these taxa are relatively abundant in the Sesmária do Pinhal 1 Site, located about 600 meters away (Bonaparte et al. 2003, 2005). In addition, within the Botucaraí region there is a record a *Brasilitherium*-like teeth in Sesmária do Pinhal 3 Site, located about 1000 meters away from the Botucaraí Hill Site (Soares et al. 2011, Bittencourt et al. 2013).

Coluna 1, parágrafo 2, linha 3 – leia-se ‘...2003, 2005), **due to the morphology of the upper and lower postcanines (see Fig. 5, 6).** They can be...

Coluna 2, linha 1 – leia-se ...to *Prozostrodon*, **from the older *Hyperodapedon* AZ, is also noteworthy.**’ (finalizar a frase aqui, removendo ‘since this taxon...’ até ‘Hyperodapedon AZ’)

Coluna 2, linha 9 – substituir more notorious por ‘stronger’

Coluna 2, linha 9 – leia-se ‘due to the fact that the teeth’

Coluna 2, linha 10 – substituir being por ‘are’

PÁGINA 12

Coluna 1, linha 6 – substituir taxa por ‘taxon’

Coluna 1, parágrafo 1, última linha – substituir ‘units’ por ‘taxa’

Coluna 2, parágrafo 2, linha 4 – substituir ‘a less inclusive’ por ‘more derived’

Coluna 2, parágrafo 2, linha 4 – substituir ‘but outside’ por ‘as the sister group to’

Coluna 2, parágrafo 3, linha 2 – após ‘AZ’ adicionar ‘(Fig. 8)’

Coluna 2, parágrafo 3, linha 3 – substituir ‘Prozostrodonia’ por ‘non-mammaliaform prozostroodontians’

Coluna 2, parágrafo 3, linha 4 – substituir its por ‘their’

Coluna 2, parágrafo 3, linha 7 – leia-se ‘...steps **related to the origin of mammaliaforms** have taken place.

PÁGINA 13

Acknowledgments, linha 3 – após ‘Rodrigues’ colocar (Candelária, RS)

Acknowledgments, linha 7 – Antes de ‘Funds were...’ adicionar a seguinte frase: ‘We also thank to Jorge Blanco for the skillful drawing of Botucaraitherium (Fig. 8).’

Acknowledgments, última linha – adicionar a frase seguinte no final do parágrafo: ‘We are grateful for the comments of Dr. Guillermo Rougier, Dr. Ricardo Martinez, the anonymous reviewer and the Editor of AABC, Dr. Alexander Kellner, which greatly improved the Ms.’

RESUMO

Coluna 1, Linha 1 – substituir ‘Aqui é reportado’ por ‘Nós reportamos aqui’

Coluna 1, Linha 2 – adicionar ‘do Triássico Tardio’ antes de ‘da Zona de Assembleia’

Coluna 1, Linha 6 – substituir ‘uma’ por ‘a’

Coluna 1, penúltima linha – substituir ‘menos inclusivo’ por ‘mais derivado’

Coluna 1, última linha – substituir ‘e como táxon-irmão’ por ‘sendo o táxon-irmão’

Coluna 2, linha 1 – leia-se ‘...**mais** Mammaliaformes.’

REFERÊNCIAS

Adicionar a referência abaixo antes de Araújo and Gonzaga 1980:

ABDALAF AND RIBEIRO AM. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida, Cynodontia) in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 286: 202-217.

Adicionar a referência abaixo antes de Sidor and Smith 2004:

RUFF I, MAIER W, RODRIGUES PG AND SCHULTZ CL. 2014. Nasal anatomy of the non-mammaliaform cynodont *Brasilitherium riograndensis* (Eucynodontia, Therapsida) reveals new insights into mammalian evolution. *The Anatomical Record* 297(11): 2018-2030.

FIGURA 3 – substituir pela figura 3 enviada pela autora

FIGURA 4 – é a figura 3 anterior

FIGURA 8 – adicionar a nova figura

PÁGINA 132 – Coluna 1, parágrafo 2, linha 16 – adicionar espaço entre consider e that

PÁGINA 133 – Coluna 2, linha 2 – substituir

‘In our view, the new specimen contributes to the clarification of the characters transformation within non-mammaliaform prozostroodontians and on the understanding of its diversity.’

Por

‘The new specimen contributes to the understanding of the non-mammaliaform prozostroodontian diversity.’

PÁGINA 134 – Coluna 2, linha 4 – adicionar um ponto antes de ‘This’

PÁGINA 136 – Coluna 1, penúltima linha – colocar um ‘the’ após ‘exit of’

PÁGINA 138 – Coluna 2, parágrafo 3 – o parágrafo 3 deve ser exatamente como abaixo:

Botucaraitherium is differentiated from brasilodontids by a notoriously more bulbous crown and two (not one) mesio-labial accessory cusps. These features have never been observed even in the largest specimens of the aforementioned brasilodontids. Therefore, we considered this feature as unique of Botucaraitherium, since in the large sample of brasilodontids from the Riograndia AZ, this condition was never observed.

Coluna 2, parágrafo 4 – o parágrafo 4 deve ser exatamente como abaixo:

In addition to the only preserved upper postcanine, the maxillary fragment preserves the root of the two following teeth. The roots increase in size posteriorly and are 8-shaped in cross-section, in which the longitudinal groove is present in both labial and lingual sides, with each lobe having its own root canal.

PÁGINA 140 – Coluna 1, linha 5 - colocar vírgula após e.g. / Coluna 2, linha 13 – leia-se ‘preserve’ (remover o d)

PÁGINA 141 – Coluna 1, linha 1 – leia-se ‘most postcanines were lost and not replaced. The anterior most postcanine (i.e., labeled along the text as pc1) partially inserted in the alveolus...’

PÁGINA 142 – Coluna 1, linha 2 – remover a parte que era observação desta assessoria: **‘finalizar a frase aqui, removendo ‘since this taxon was found in the older Hyperodapedon AZ.’**

TÍTULO DO TRABALHO – Colocar itálico em Riograndia

PÁGINA 2 – Coluna 1, parágrafo 3, linha 3 – remover ‘Ferigolo and Ribeiro, 2001’

PÁGINA 134 – Coluna 1, linha 21 – remover ‘and’ antes do ‘the’

PÁGINA 138 – Coluna 2, linha 5 – colocar itálico em ‘Prozostrodon’

PÁGINA 141

Coluna 2, linha 7 – leia-se ‘is a record of *Brasilitherium*-like...’

Coluna 2, parágrafo 2, linha 3 – remover espaço entre ‘...2003, 2005)’ e a vírgula

PÁGINA 143

Coluna 1, parágrafo 2, linha 2 – colocar itálico em Botucaraitherium

Coluna 1, parágrafo 2, linha 3 – colocar itálico em Botucaraitherium

Coluna 1, parágrafo 2, linha 5 – colocar itálico em Brasilodon

Coluna 1, parágrafo 2, linha 6 – colocar itálico em Botucaraitherium

Acknowledgments, linha 9 - colocar itálico em Botucaraitherium

PÁGINA 1674 – segunda coluna: excluir *maieri*

PÁGINA 1675 – A legenda da Fig. 1 está incompleta: Substituir por:

Fig. 1 - A: Geographical location of the Santa Maria Supersequence (Paraná Basin) in the state of Rio Grande do Sul, Brazil. **B:** Chronostratigraphy of the southern Brazilian Triassic, showing the four Assemblage Zones (AZ) based on tetrapods context. From Horn et al. 2004. Biostratigraphy after Soares et al. 2011. Abbreviations: **Any**, Anisian; **Car**, Carnian; **Ind**, Induan; **Lad**, Ladinian; **Nor**, Norian; **Ole**, Olenekian; **Rha**, Rhaetian.

PÁGINA 1674 – primeira coluna: ,amongothers, – SEPARAR!

PÁGINA 1677 – Legenda da Fig. 2 errada. Substituir por:

Fig. 2 - A: Road map with City of Candelária indicated. **B:** View of the Botucaraí Hill site, southern margin of BR 287 road, with the indication of the fossiliferous level. **C:** Log of the Botucaraí Hill Site.

PÁGINA 1678 – Segunda coluna: O correto é Fig. 4 e não Fig. 3

PÁGINA 1679 – Legenda da Fig. 3: excluir Gray areas (está repetido)

PÁGINA 1680 – segunda coluna: colocar *Riograndia* em itálico

PÁGINA 1683 – primeira coluna: juntar anterior most = anteriormost

PÁGINA 1684 – primeira coluna: retirar ‘

PÁGINA 1685 – primeira coluna: Acrescentar: dentition na frase

... dentary and dentition give support ...

PÁGINA 1685 – segunda coluna: substituir Vertebrate collection por Paleovertebrates

PÁGINA 1688 – as referências não estão em duas colunas ...

PÁGINA 1689 – *Riograndia* em itálico

PÁGINA 1691 – escrever *guaibensis* ao invés de *guaibaensis*