The Triassic eucynodont *Candelariodon barberenai* revisited and the early diversity of stem prozostrodontians

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The dental anatomy of *Candelariodon barberenai* from the *Dinodontosaurus* Assemblage Zone (Pinheiros-Chiniquá Sequence, Santa Maria Supersequence, late Ladinian–early Carnian) of south Brazil, is redescribed. *Candelariodon* was originally classified as Eucynodontia incertae sedis and our analysis recovered this taxon deeply nested within Probainognathia, as the sister taxon of *Potheriodon* plus Prozostrodontia. The lower postcanine dentition of *Candelariodon* has several apomorphies shared with *Prozostrodon*, *Santacruzgnathus*, *Brasilodon*/*Brasilitherium*, and some basal mammaliaforms (*Morganucodon*, *Megazostrodon*), such as a lingual cingulum with discrete cusps e and g and two distinct morphologies in the tooth row. The reinterpretation of *Candelariodon* as a probainognatian cynodont more derived than *Probainognathus* and the rich Brazilian fossil record document an important adaptive radiation of non-mammaliaform prozostrodontians and closely related forms prior to the origin of the mammaliaform clade.

Key words: Cynodontia, Probainognathia, Prozostrodontia, *Dinodontosaurus* Assemblage Zone, South America, Brazil.

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Introduction

The Middle to Late Triassic continental tetrapod assemblages of southern Brazil and western Argentina have provided the most abundant and taxonomically diverse fossil record of non-mammaliaform probainognathian cynodonts worldwide (e.g., Abdala and Ribeiro 2010; Martinelli and Soares 2016). The plethora of forms described from these regions includes several species positioned near to the base of the mammaliaform clade (e.g., *Santacruzgnathus abdalai*, *Therioherpeton cargnini*, *Prozostrodon brasiliensis*, *Brasilodon quadrangularis*, *Riograndia guaibensis*, *Irajatherium hernandezi*, and *Chaliminia musteloides*) and illustrates the main evolutionary transformations in the skeleton towards the mammalian condition (e.g., Bonaparte and Barberena 2001; Bonaparte et al. 2005; Martinelli et al. 2005, 2016c; Martinelli and Rougier 2007; Ruta et al. 2013; Rodrigues et al. 2013, 2014; Ruf et al. 2014; Soares et al. 2014).

The *Dinodontosaurus* Assemblage Zone (AZ) of the Pinheiros-Chiniquá Sequence, Santa Maria Supersequence (Zerfass et al. 2003; Horn et al. 2014; Fig. 1), includes the oldest unambiguous cynodont records from the Triassic of Brazil (see Martinelli et al. 2016a for discussion on the taxonomy of cynodont remains from the Lower Triassic Sanga do Cabral Supersequence). The age of the *Dinodontosaurus* AZ is inferred on the basis of biostratigraphic correlations with the Chañares Formation of the Ischigualasto-Villa Unión Basin, western Argentina (Fiorelli et al. 2013; Marsicano et al. 2016) and radiometric dating of the overlying Santa Cruz Sequence (Philipp et al. 2013), both suggesting a late Ladinian–early Carnian age. Whereas the Chañares Formation yields two probainognathians, *Chiniquodon theotonicus* and *Probainognathus jenseni* (Abdala and Giannini 2002; Martinelli et al. 2016c), the *Dinodontosaurus* AZ includes five: *Chiniquodon theotonicus* (Abdala and Giannini 2002), *Aleodon cromptoni* (Martinelli et al. 2016b, 2017),

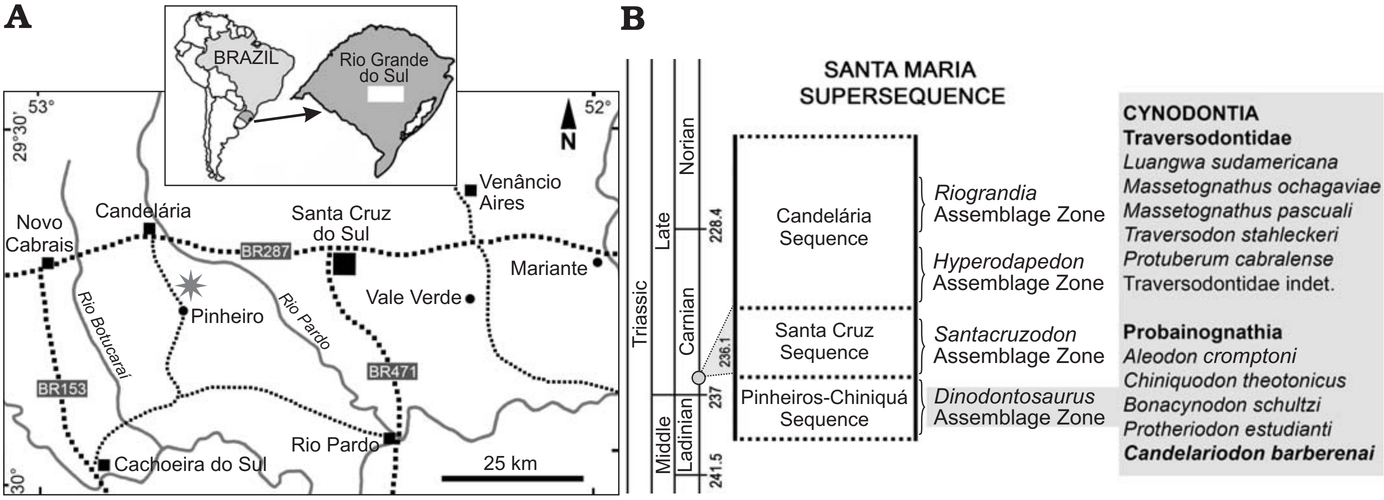


Fig. 1. Geographic (**A**, star indicates the type locality) and biostratigraphic (**B**) location of *Candelariodon barberenai*. The biostratigraphy follows Horn et al. (2014) and the dating (grey circle in B) corresponds to Philipp et al. (2013).

Bonacynodon schultzi (Martinelli et al. 2016c), *Protheriodon estudianti* (Bonaparte et al. 2006; Martinelli et al. 2016c), and *Candelariodon barberenai* (Oliveira et al. 2011). The same disproportion is seen in traversodontid gomphodonts, being represented by one species in the Chañares Formation (*Massetognathus pascuali*, according to Abdala and Giannini 2000) and six in the *Dinodontosaurus* AZ (*Luangwa sudamericana*, Abdala and Sá-Teixeira 2004; a *Scalenodon*-like form, Melo et al. 2014; *Massetognathus ochagaviae, M. pascuali*, Barberena 1981b; Liu et al. 2008; *Traversodon stahleckeri*, Barberena 1981a; Liu and Abdala 2014; and *Protuberum cabralense*, Reichel et al. 2009).

Of the above mentioned probainognathians from the *Dinodontosaurus* AZ, *Protheriodon estudianti* was included within brasilodontids (e.g., Bonaparte et al. 2006; Bonaparte 2013) or Prozostrodontia (Martinelli et al. 2016c), while the other species were classified as basal probainognathians (e.g., Hopson and Kitching 2001; Liu and Olsen 2010; Oliveira et al. 2010; Martinelli et al. 2016c). In particular, *Candelariodon barberenai* was classified as Eucynodontia incertae sedis (Oliveira et al. 2011). The authors also noted striking resemblances of one tooth with those of *Aleodon brachyramphus*, from the Manda Formation of Tanzania (Crompton 1955), and, to a lesser extent, with those seen in *Cromptodon mamiferoides* (Bonaparte 1972) from the Cerro de Las Cabras Formation of Argentina.

In this contribution we reinterpret the postcanine morphology of the holotype and only known specimen of *Candelariodon barberenai* and provide evidence that places this taxon phylogenetically close to the Prozostrodontia clade. Due to the age of the *Dinodontosaurus* AZ, the phylogenetic position of *C. barberenai* reinforces the hypothesis of a conspicuous diversification of non-mammaliaform prozostrodontians and closely related forms in older times, with at least two distinct morphotypes: one represented by *Candelariodon* and *Prozostrodon* and the other by tiny prozostrodontians such as *Therioherpeton*, *Brasilodon*, and possibly *Protheriodon* and dromatheriids, in addition to the disparate ictidosaur and tritylodontid (if this clade is considered within Probainognathia; see Luo 1994; Hopson and Kitching 2001; Abdala 2007; Liu and Olsen 2010) groups.

Institutional abbreviations.—MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MMACR-PV-T, Museu Municipal Aristides Carlos Rodrigues (Paleovertebrates-Triassic Collection), Candelária, Brazil; NHMUK, Natural History Museum (PV, Vertebrate Paleontology; R, Reptiles; M, Mammals), London, UK; PVL, Instituto Miguel Lillo (Vertebrate Paleontology Collection), Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; UFRGS-PV-T, Universidade Federal Rio Grande do Sul (Vertebrate Paleontology, Triassic Collection), Porto Alegre, Brazil; UMZC, University Museum of Zoology, Cambridge, UK.

Other abbreviations.—AZ, Assemblage Zone; a–g, cusps of postcanine crowns (following Crompton 1974); c, lower canine; i, lower incisors; pc, lower postcanine teeth.

Material and methods

The holotype (MMACR PV-0001-T) of *Candelariodon barberenai* comes from the *Dinodontosaurus* AZ of the Pinheros-Chiniquá Sequence, Santa Maria Supersequence (Horn et al. 2014; Fig. 1). It corresponds to the lower portion of the traditional Santa Maria Formation (Gordon 1947) and the Santa Maria 1 Sequence of Zerfass et al. (2003). The outcrop that yielded MMACR PV-0001-T is located ~20 km south of Candelária city (state of Rio Grande do Sul, Brazil), in the Pinheiro (or Pinheiros) region (Fig. 1), an area in which several tetrapods characteristic of the *Dinodontosaurus* AZ have been discovered (e.g., Romer and Price 1944; Barberena 1977, 1981a, b; Barberena et al. 1985; Schultz et al. 2000; Bertoni-Machado et al. 2008; Martinelli et al. 2016b, c, 2017).

Candelariodon was compared to other probainognathians, based mainly on firsthand examination of specimens deposited in different institutions. Otherwise, bibliographic sources were used for comparisons. *Brasilodon quadrangularis* and *Brasilitherium riograndensis* were used along the text as two distinctive taxa, until the hypothesis of synonymy (Liu and Olsen 2010; Martinelli and Bonaparte 2011) is thoroughly tested (it is being done by the former author).

In order to test the phylogenetic affinities of MMACR PV-0001-T, this specimen was included in the data matrix of Liu and Olsen (2010), as modified by Martinelli et al. (2016c) with a few extra modifications on the scoring of *Protheriodon*, *Prozostrodon*, and *Brasilitherium* (Appendix 1). This modified data matrix was analyzed under equally-weighted parsimony using TNT 1.5 (Goloboff and Catalano 2016). A heuristic search of 100 replications of Wagner trees, followed by TBR branch-swapping algorithm (holding 10 trees per replication), was performed. All characters were treated as non-additive. Bremer support (Bremer 1994) and a bootstrap resampling analysis (Felsenstein 1985) were conducted. The modified data matrix is included in Appendix 2.

Systematic palaeontology

Therapsida Broom, 1905

Cynodontia Owen, 1861

Eucynodontia Kemp, 1982

Probainognathia Hopson, 1990

Genus *Candelariodon* Oliveira, Schultz, Soares, and Rodrigues, 2011

Type species: *Candelariodon barberenai* Oliveira, Schultz, Soares, and Rodrigues, 2011; monotypic, see below.

Candelariodon barberenai Oliveira, Schultz, Soares, and Rodrigues, 2011

Figs. 2, 3A, 4, 5A.

Holotype: MMACR PV-0001-T, almost complete left branch and anterior half of the right branch of the dentary, fused at the symphysis, bearing partial dentition, and an isolated posterior lower left postcanine tooth (Oliveira et al. 2011; Figs. 2, 3).

Type locality: ~20 km south of Candelária city, Pinheiro (or Pinheiros) region, Rio Grande do Sul, Brazil (Fig. 1).

Type horizon: *Dinodontosaurus* AZ of the Pinheros-Chiniquá Sequence, Santa Maria Supersequence, late Ladinian–early Carnian.

Emended diagnosis.—Probainognathian cynodont with the following combination of features (autapomorphies marked with an asterisk): tall horizontal ramus of the dentary and coronoid process; no angular process; fused mandibular symphysis; lower incisor alveolar level positioned above the level of the postcanine crowns; last lower incisor with strongly posteriorly curved crown; large lower canine without serrated edges; pc2–3 with large cusp a, tiny cusp b, small cusp c, accessory cusp g, faint lingual cingulum, and absence of cusp d*; pc2–4 transversely broader at distal half of the crown than mesially; posterior postcanines (pc5–8) mesiodistally longer than preceding ones; pc5 with continuous lingual cingulum, bearing accessory cusp g and at least cusps a, c, and d*; posterior postcanines with large, slightly posteriorly curved cusp a, small cusp b, cusp c larger than b, cusp d, accessory cusp e, and with non-continuous cingulum, absence of cusp g*.

Description.—*Dentary*: The dentary has a tall horizontal ramus and well-developed coronoid and articular processes (Fig. 2). The horizontal ramus has an almost straight ventral edge, parallel to the alveolar line. It is slightly convex dorsoventrally and about three times taller than the crown height of pc4 in lateral view. Hence, the horizontal ramus is relatively stout as usually found in probainognathians (e.g., *Probainognathus jenseni*, PVL 4445; *Bonacynodon schultzi*, MCT-1716-R; *Prozostrodon brasiliensis*, UFRGS-PV-248-T, Fig. 3B; *Botucaraitherium belarminoi*, MMACR-PV-003-T; *Riograndia guaibensis*, UFRGS-PV-0596-T). It differs from the low horizontal ramus of *Protheriodon estudianti* (UFRGS-PV-0962-T), *Santacruzgnathus abdalai* (UFRGS-PV-1121-T), and *Brasilitherium riograndensis* (UFRGS-PV-1043-T; Fig. 3C). A large mental foramen is observed at mid-height below pc2 and there are other small foramina nearby. The coronoid process is tall, with its dorsal edge broken off and the anterior margin wider at its base. It presents a large masseteric fossa on its lateral surface that extends anteriorly to about the level of the pc5 (Figs. 2A, 3A), as observed in most probainognathians (Hopson and Kitching 2001). The articular process of the dentary extends far posteriorly, but it is not completely preserved. Its ventral edge projects posterodorsally with the posteriormost tip positioned above the postcanine level, lacking an angular process, as in *Prozostrodon, Brasilitherium,* and some early mammaliaforms, such as *Haramiyavia* (Luo et al. 2015). Medially, the postdentary trough is reduced and at the inflection of the coronoid process there is no clear evidence of a facet or remnant of coronoid bone.

The straight ventral border of the dentary bends abruptly anteriorly at the level of pc1, forming an angle of ~140° and delimiting the posteroventral edge of symphysis (Fig. 2A). It is anterodorsally to posteroventrally inclined, being about twice as long as wide. There is no evidence of suture at the symphysis, indicating that both dentaries are fused, which is the condition in most non-prozostrodontian cynodonts (Hopson and Kitching 2001; Abdala 2007). The anterodorsal development of the dentary places the alveolar edge of incisors and canine above the level of the tip of postcanine crowns. This condition is also seen in *Prozostrodon* (Fig. 3B), *Brasilitherium* (Fig. 3C), and, to a lesser degree, in *Microconodon* and *Dromatherium* (Simpson 1926; Sues 2001). In *Botucaraitherium*, this portion is partially broken but the canine seems to be positioned in a higher position than the postcanine line.

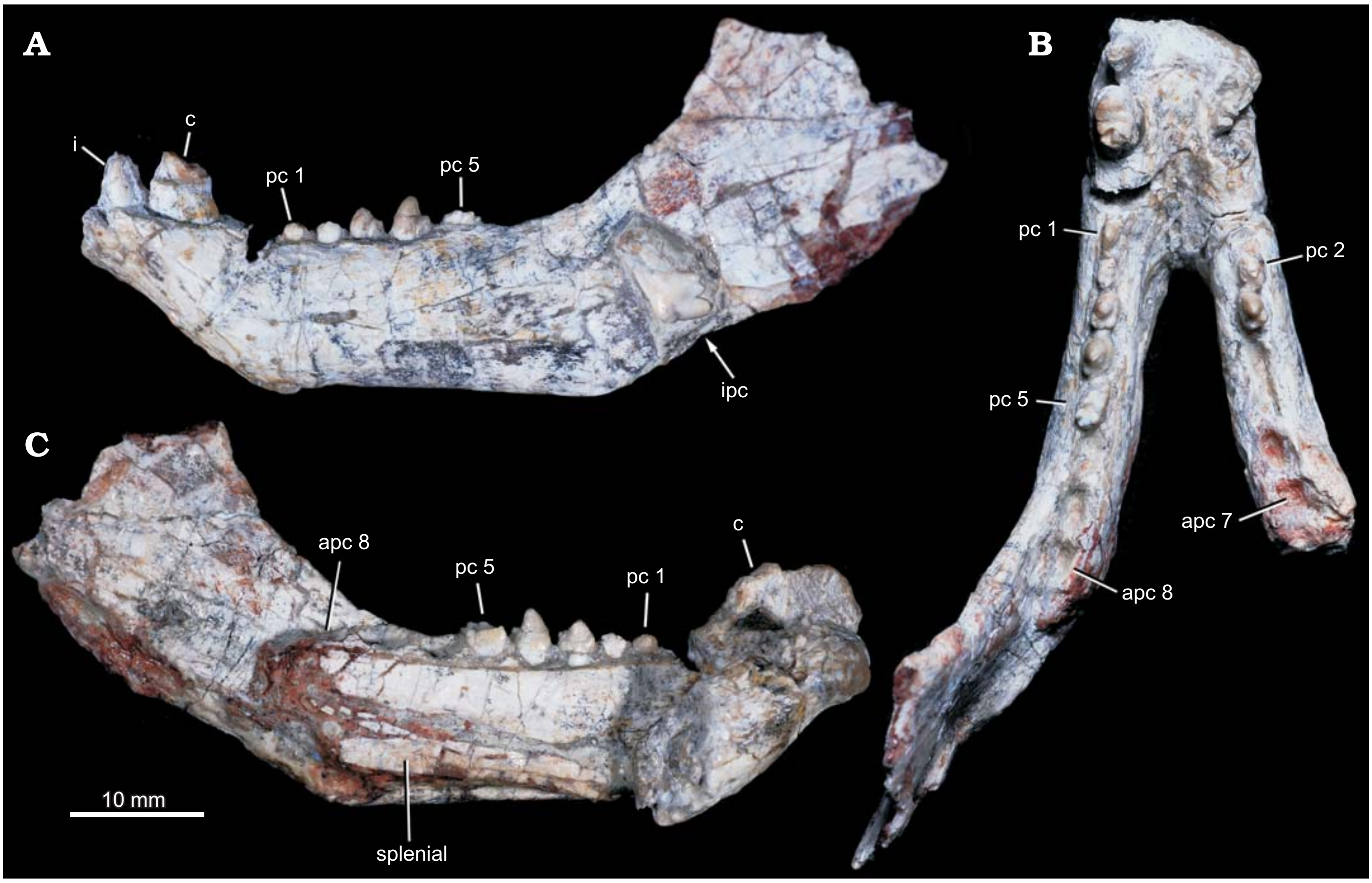


Fig. 2. Probainognathian eucynodont *Candelariodon barberenai* Oliveira, Schultz, Soares, and Rodrigues, 2011 (holotype, MMACR PV-0001-T) from the Middle–Late Triassic of Rio Grande do Sul state, Brazil. Lower jaw with partial dentition in left lateral (**A**), occlusal (**B**), and right medial (with part of right dentary detached) (**C**) views. Abbreviations: apc, postcanine alveolus; c, lower canine; i, lower incisor; ipc, isolated postcanine; pc, lower postcanine.

Splenial: The right and left splenials are preserved on each ramus. It is a laminar bone that covers the entire Meckelian groove. It extends parallel to the ventral edge of the dentary and reaches the mandibular symphysis (Fig. 2C), where it contacts its counterpart. The splenials are as developed as in *Prozostrodon* and other non-prozostrodontian probainognathians, being slightly dorsoventrally taller than in *Brasilitherium* and *Riograndia*.

Incisors: The lower incisor number is unknown in *Candelariodon*. The last left incisor is the only preserved (Fig. 2A). It is small in comparison to the canine and positioned next to it, without diastema. The crown is sub-conical, strongly curved posteriorly, with a thick layer of enamel. The distal edge seems to form a distal ridge of enamel. There is a small wear facet on the labial surface of the tip. The curved crown, with a strongly convex labial surface and ridged distal edge, is a morphology also seen in *Prozostrodon*.

Canine: Both canines are poorly preserved. The right canine only preserves the root and the left one less than half of the crown (Fig. 2A, B). They are the largest teeth, oval in cross section, being about two times longer than width. There is no evidence of serrated edges. The preserved portion of the left canine has a concave distal edge, indicating a posteriorly curved crown, as is seen in *Prozostrodon* (Fig. 3B). There is a diastema between canine and postcanines, being slightly longer on the right side as evidenced by the loss of the right pc1 (but not the left pc1; see below).

Postcanine teeth: There are empty alveoli for the right pc1, pc4–7 and left pc6–8. Complete to fairly complete tooth crowns are represented in the right pc2–3 and left pc1–5, plus an isolated tooth laying on the lateral surface of the coronoid process of the dentary, here interpreted as a posterior left lower postcanine (see below) (Figs. 2A, B, 4, 5).

The postcanine tooth rows slightly diverge posteriorly and the last tooth is placed medial of the anterior base of the coronoid process (Fig. 2C). As indicated by alveolar dimensions, the postcanine teeth increase in size gradually to the rear. The right dentary is incomplete and only has seven tooth positions, with the position for pc8 only partially preserved. The right pc1 alveolus is small in comparison to the left one and is positioned very close to anterior wall of pc2 alveolus (Fig. 4). This condition together with the fact that the right canine-postcanine diastema is longer than the left one suggests that the anterior postcanines were lost during ontogeny, increasing the size of the diastema, as seen in some prozostrodontians (e.g., *Prozostrodon*, *Brasilodon*, *Sinoconodon*) and some gomphodonts (e.g., *Diademodon*, *Exaeretodon*) (Hopson 1971; Crompton and Luo 1993; Luo

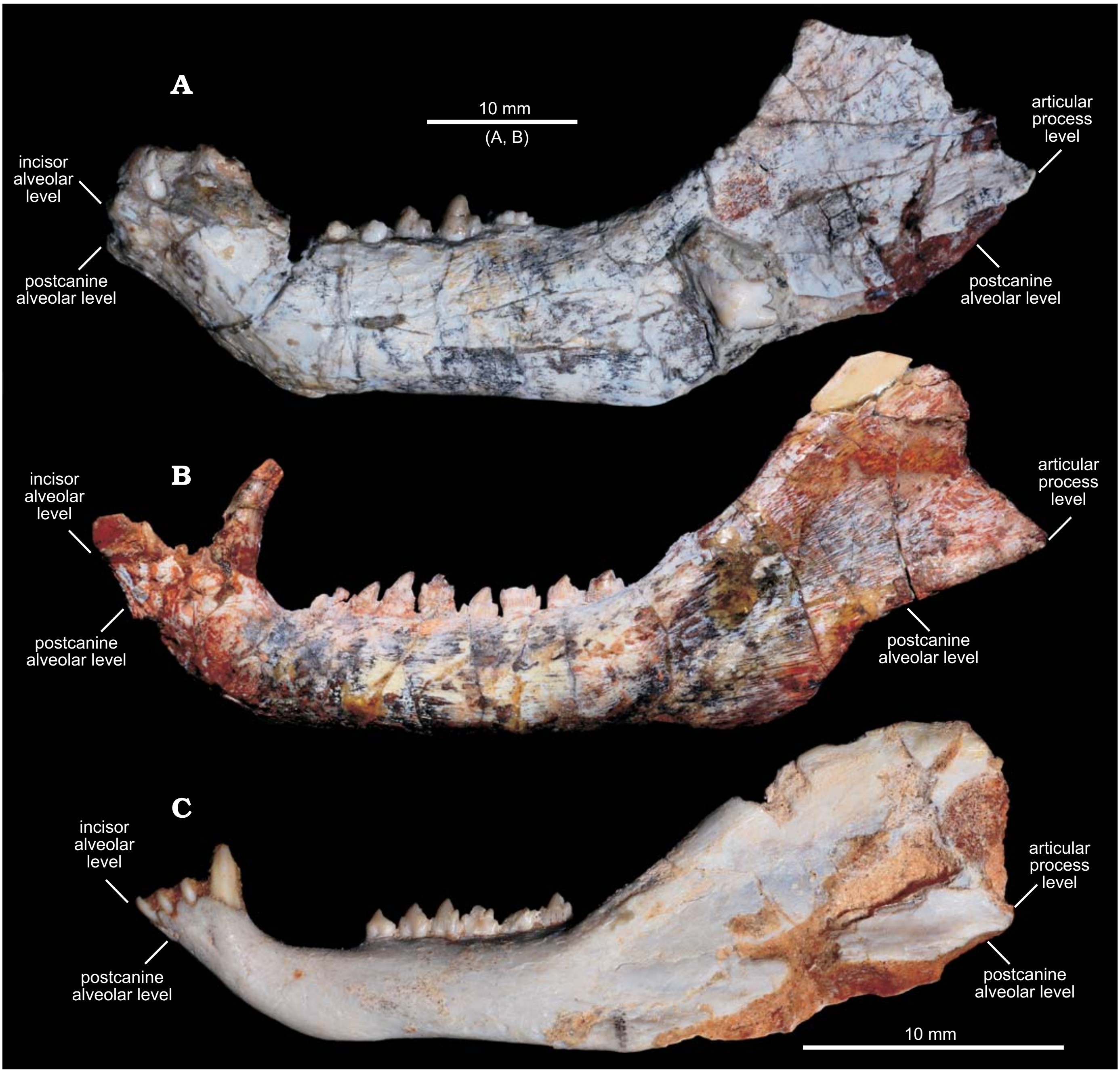


Fig. 3. Comparisons of dentaries of selected cynodonts in lateral view. **A**. Left dentary of *Candelariodon barberenai* Oliveira, Schultz, Soares, and Rodrigues, 2011 from the Middle–Late Triassic of Rio Grande do Sul state, Brazil (holotype, MMACR PV-0001-T). **B**. Right dentary (inverted) of *Prozostrodon brasiliensis* (Barberena, Bonaparte, and Teixeira, 1987) from the Late Triassic of Rio Grande do Sul state, Brazil (holotype, UFRGS-PV-248-T). **C**. Left dentary of *Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz, and Rubert, 2003 from the Late Triassic of Rio Grande do Sul state, Brazil (UFRGS-PV-1043-T). Abbreviations: aple, articular process level; ile, incisor alveolar level; pcle, postcanine alveolar level.

et al. 2004; Martinelli and Bonaparte 2011). Differences between the right and left postcanine tooth rows are common in eucynodonts. For example, in *Prozostrodon* (Fig. 6C) the left pc1 is absent and there is a substantial discrepancy in size between the large left and small right pc2.

The left pc1 is the smallest of the series. The crown is badly preserved, hampering the recognition of discrete cusps. However, it seems simpler and transversely narrower than pc2 (Fig. 4B–D).

The left pc2 crown is also broken but the crown shape can be discerned on the right one. The right pc2 has a prominent cusp a, with its tip broken off, followed by a reduce cusp c, which is slightly labially displaced (Fig. 4A). There is an evidence of a sharp mesial edge that seems to indicate the presence of a reduced cusp b. In addition, there is an evidence of a small distolingual cusp, which is interpreted as cusp g (following Crompton 1974). Due to the position of cusps c and g, the distal half of the crown is transversely wider than

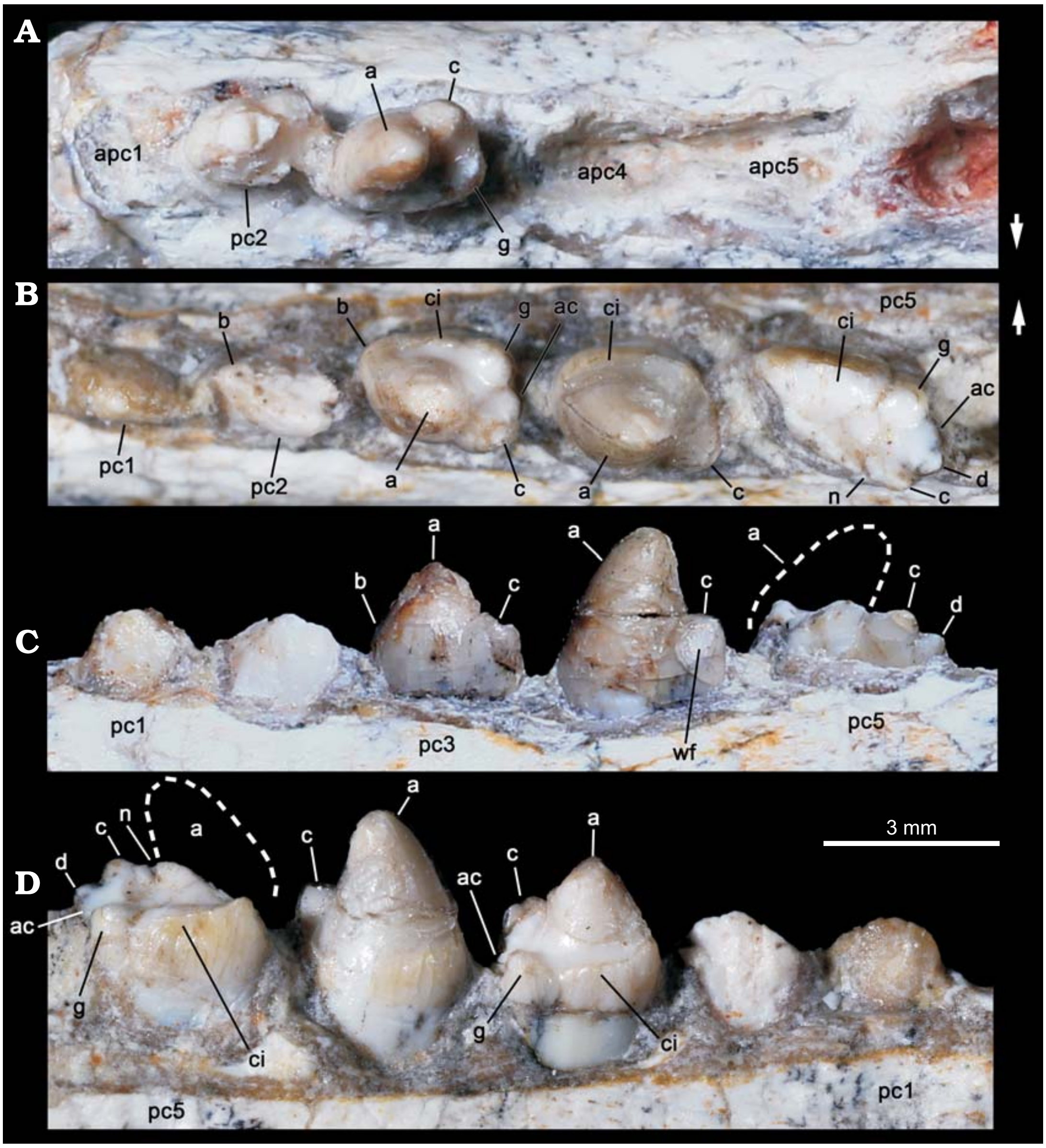


Fig. 4. Probainognathian eucynodont *Candelariodon barberenai* Oliveira, Schultz, Soares, and Rodrigues, 2011 (holotype, MMACR PV-0001-T) from the Middle–Late Triassic of Rio Grande do Sul state, Brazil. Detail of the lower postcanine dentition. Right tooth row in occlusal view (**A**) and left tooth row in occlusal (**B**), labial (**C**), and lingual (**D**) views. The dashed line represents the shape of cusp a. Arrows indicate lingual side. Abbreviations: a–g, cusps of the crown; ac, accessory cusp; apc, postcanine alveolus; ci, cingulum; n, notch between a/c cusps; wf, wear facet.

the mesial half. Such morphology is seen in middle postcanine teeth of sub-adult individuals of *Brasilitherium* (e.g., UFRGS-PV-603-T; Fig. 5C). In *Prozostrodon* there is also an accessory cusp on the distolingual corner of the crown of the anteriormost teeth, but due to the presence of other accessory cusps on the mesiolingual edge, the crown width is more homogeneous. Because the lingual cingular cusps are almost similar in size, the identification of a putative cusp g is not possible in *Prozostrodon* (Fig. 5B). Moreover, the anterior postcanine teeth of *Prozostrodon* have a cusp b, although very reduced, and the main cusp a is less bulbous and slightly posteriorly curved (Fig. 6C).

Both right and left pc3 of *Candelariodon* are well preserved. They have a pattern similar to pc2 but with accentuated features (Figs. 4, 5). The main cusp a is large, with a strongly convex mesial edge that descends to a very small cusp b, lingually located. The distal edge of cusp a is shorter than the mesial one and almost straight. It contacts the mesial edge of cusp c, without defining a conspicuous ("carnassial") notch. The cusp c is considerably larger than cusp b and labially displaced. The distolingual accessory cusp g is slightly smaller than cusp c, but considerably larger than cusp b. In the left pc3 there is a distal accessory cusp (Fig. 4B) that is not seen in the right pc3. This distal accessory cusp is not interpreted as the cusp d based on the morphology seen in pc5 (see below). Between the distal accessory cusp and cusp g there is a "v" shaped notch, deeper than the one between accessory cusp and cusp c. One of the most

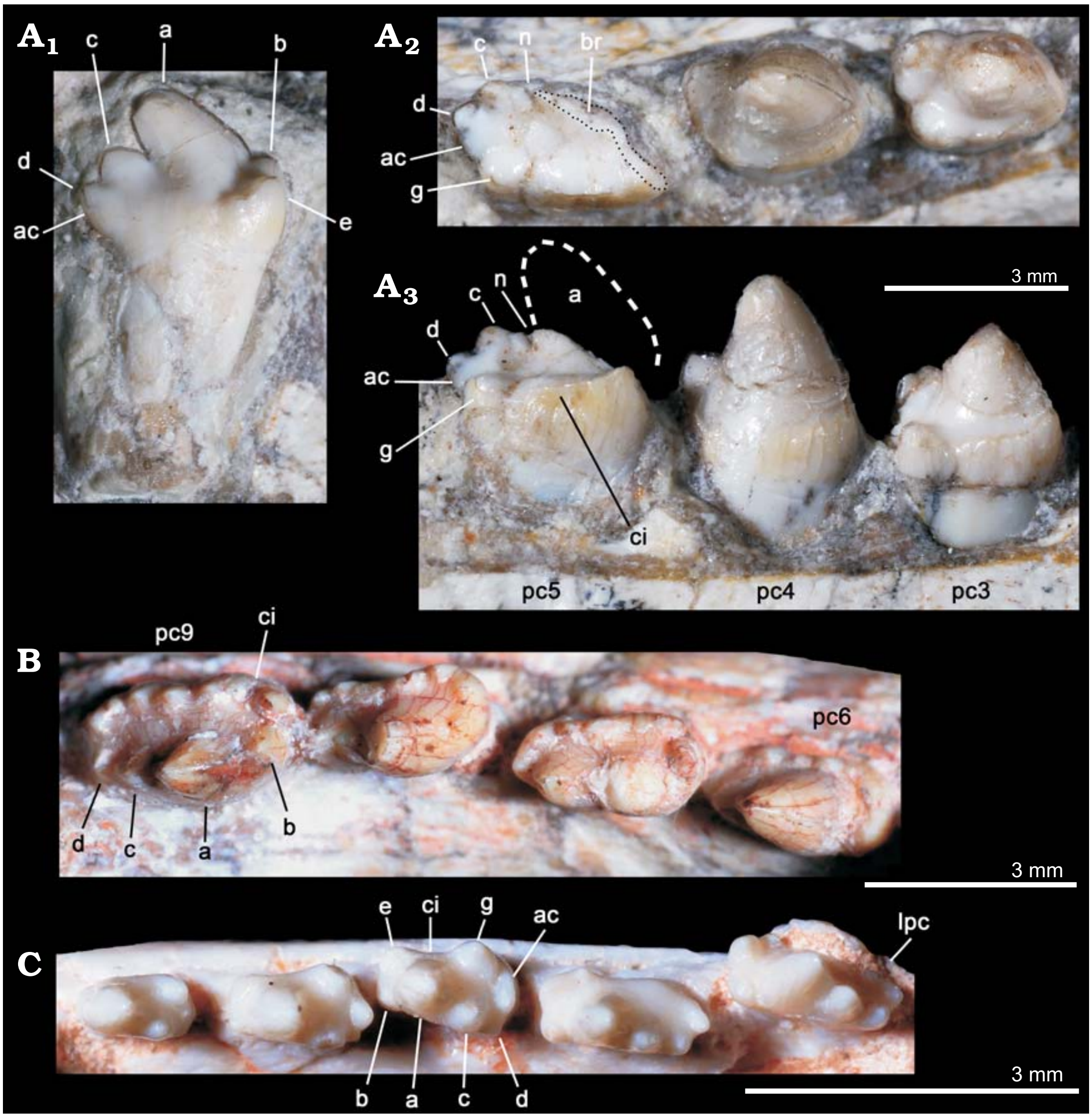
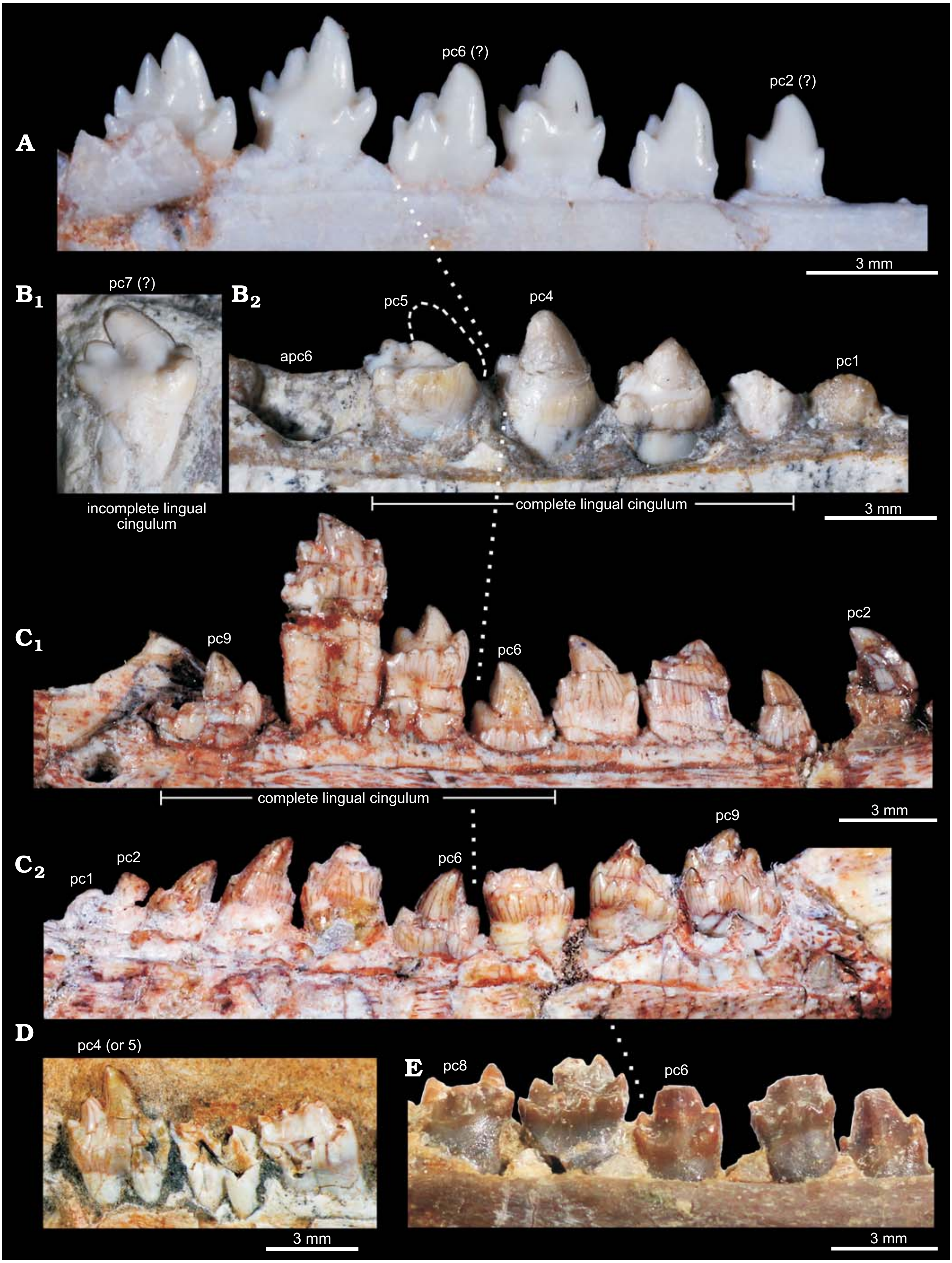


Fig. 5. Comparisons of postcanine teeth among selected eucynodonts. **A**. *Candelariodon barberenai* Oliveira, Schultz, Soares, and Rodrigues, 2011 (holotype, MMACR PV-0001-T) from the Middle–Late Triassic of Rio Grande do Sul state, Brazil; detail of the lower postcanine dentition, including isolated tooth interpreted as a left posterior postcanine, in lingual view (A_1) and left pc3–5 in occlusal (A_2) and lingual (A_3) views. **B**. *Prozostrodon brasiliensis* (Barberena, Bonaparte, and Teixeira, 1987) (holotype, UFRGS-PV-248-T) from from the Late Triassic of Rio Grande do Sul state, Brazil; last right lower postcanines in occlusal view. **C**. *Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz, and Rubert, 2003 (UFRGS-PV-0603-T) from from the Late Triassic of Rio Grande do Sul state, Brazil; left lower postcanines in occlusal view. The dashed line represents the shape of cusp a. Abbreviations: ac, accessory cusp; a–g, cusps of the crown; br, broken surface; ci, cingulum; lpc, last postcanine tooth; n, notch between a/c cusps; pc, lower postcanine.

conspicuous features of the pc3 is the presence of a faint, continuous cingulum connecting cusps b and g (Figs. 4B, 5A). There are two tiny notches at mid-length of the cingulum that do not define discrete crenulations or cusps. In occlusal view, pc3 has a width/length ratio of 0.7.

The pc4 has a large cusp a and small cusp c. The cusp b and accessory distolingual cusp g are not seen (Figs. 4B, 5A). However, this tooth has the same width/length ratio (= 0.69) as pc3. The lack of cusp g could be the result of breakage or perhaps due to wear (food processing and not tooth-to-tooth occlusion) on the crown. Based on the fact that the cusp g is smaller in the following teeth (i.e., pc5 and isolated posterior tooth, which have more sectorial shape), a less developed cusp g should be expected in pc4 than in pc3. A distal accessory cusp and cusp d is not discerned in pc4. In this postcanine, the lingual cingulum is better developed on the more mesial portion of the crown.

The pc5 is badly preserved with most of its mesiolabial portion broken off (Figs. 4B–D, $5A_2$, A_3). Based on the preserved portion and the size of the alveolus, it is considered a mesiodistally larger and transversely narrower tooth than pc4–3. Oliveira et al. (2011) considered the crown of pc5 as having two mesiodistal rows of four cusps each. They considered the labial row to be made up of cusps b', a', c', d', and the lingual row of cusps b", a", c", d", separated by a mesiodistally oriented groove. That morphology was found


A
pc6 (?)
pc2 (?)
3 mm
B1
pc7 (?)
incomplete lingual cingulum
B2
pc5
pc4
apc6
pc1
complete lingual cingulum
3 mm
C1
pc9
pc6
pc2
complete lingual cingulum
3 mm
C2
pc1
pc2
pc6
pc9
D
pc4 (or 5)
3 mm
E
pc8
pc6
3 mm

fairly similar to the condition seen in the probainognathian *Aleodon brachyramphus* (Oliveira et al. 2011), which is characterized by having a row of sectorial labial cusps (homologous to the sectorial cusps of other probainognathians) and a broad lingual cingulum (i.e., cingular platform, sometimes with evident crenulations or tiny cusps), much more developed than in other known probainognathians (UMZC T906; Crompton 1955; Abdala and Giannini 2002). As shown in Figs. 4, 5, it is evident that most of the mesiolabial region of the crown is broken off. This is evident by the lack of the enamel layer that is continuous in the other parts of the crown, as also seen in the remaining postcanine teeth, and the eroded surface. Therefore, the bulk of cusp a and the entire cusp b are not preserved. Nonetheless, the notch between the distal ridge of cusp a and the mesial ridge of cusp c is still present (Figs. 4B, 5A_3) and also adds supports to our interpretation. The cusp c is slightly labial, as in the remaining postcanine teeth, and smaller than the supposed size of cusp a. Distally, there is another cusp in line with cup c that is considered as cusp d. In addition, the pc5 has the accessory distolingual cusp g, which is present in previous teeth. Consequently, the morphology of pc5 is more complex than that of the preceding teeth, and it indicates that a discrete cusp d first appears in the pc5. Thus, the cusp interpreted as d in pc2–4 by Oliveira et al. (2011) is here considered as the accessory distolingual cusp g, which is kept all along the postcanine teeth (in pc1 and pc4 it is not observed due to preservation).

The pc5 also has a continuous cingulum, more transversely developed than that seen in pc3. It forms a shallow concavity between the main cusps a and c and its elevated lingual edge (Fig. 5A_2, A_3). Along the cingulum, at least two worn cusps are evidenced. This cingulum, however, is not comparable with the labial platform seen in the middle and posterior postcanine teeth of *Aleodon*, which form a large lingual platform (UMZC T906, NHMUK-PV-R-9390; Crompton 1955). A continuous lingual cingulum is observed in *Prozostrodon*, *Botucaraitherium*, *Brasilodon*, and some tritheledontids (*Pachygenelus*, *Diarthrognathus*; Gow 1980). In *Prozostrodon* the lingual cingulum bears up to nine tiny, discrete cusps (Bonaparte and Barberena 2001) (Figs. 5, 6). That number is smaller in *Botucaraitherium* (Soares et al. 2014) and *Brasilodon* (Bonaparte et al. 2005).

As consequence, the changes along the postcanine tooth row of *Candelariodon* are gradual, within a "triconodont-like" pattern, contrary to the original proposal of Oliveira et al. (2011) that recognized a drastic change of morphology only in pc5.

The isolated tooth was originally considered as an upper postcanine tooth (Oliveira et al. 2011), by comparing with gomphodonts (*Diademodon* and *Andescynodon*) and based on the original interpretation of pc5 that made difficult the allocation of a more sectorial tooth at the rear of the tooth series. We interpreted here this tooth as a posterior left postcanine that should have occupied one of the three last empty alveoli. This tooth is more sectorial (i.e., it is mesiodistally longer and transversely narrower) than the remaining ones (Fig. 5A_1), as seen in some other prozostrodontians, such as *Prozostrodon* (Fig. 5B) and *Brasilitherium* (Fig. 5C). The crown of this isolated tooth of *Candelariodon* has a sectorial crest with main cusp a followed by cusps c and d, this latter being slightly lingually dislocated. Just lingual to the base of cusp d there is a small bulge that would be a remnant of the accessory distolingual cusp, present in more anterior teeth. The cusp a has a rounded tip and its main axis is posterodorsally inclined. The cusp b is small and low in position (Fig. 5A_1). Lingually to it, there are two accessory cingular cusps, being the more mesial cusp e, as large as cusp b, and the other one relatively smaller. Differing from the pc5, the cingulum is not lingually complete, being restricted to the mesiolingual corner of the crown. This postcanine tooth has a single root, differing from the constricted root pattern seen in most, but not all (e.g., *Pachygenelus*; Gow 1980), prozostrodontians (Hopson and Kitching 2001; Liu and Olsen 2010).

There is no positive evidence to consider this isolated tooth as an upper postcanine. The changes in tooth crown morphology along the row are similar to that observed in *Brasilitherium* (e.g., UFRGS-PV-603-T; Bonaparte et al. 2003). Importantly, in *Prozostrodon* and *Botucaraitherium* the cuspidated cingulum is maintained in the last teeth, a condition not seen in *Candelariodon*.

The distribution of enamel on the postcanine teeth of *Candelariodon* is noteworthy. The external walls of the crown exhibit a thick layer of enamel with a yellowish coloration, but the inner walls of the cusps and cingulum have a whitish coloration, suggesting the lack of enamel or the presence of a very thin layer. This enamel pattern is clearly seen in both right and left pc3, left pc4–5, and the isolated tooth. Particularly the enamel, if present, is extremely thin in the lingual portion of the crown-root boundary of the isolated tooth, where the cingulum is absent.

Clear evidence of wear is seen in the left pc3, having apical wear on the main cusp a, and the left pc4, with an oval wear facet on the labial surface of cusp c (Figs. 4C, 5A_2, A_3).

← Fig. 6. Comparisons of postcanine teeth among selected eucynodonts. **A**. *Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz, and Rubert, 2003 (UFRGS-PV-603-T) from the Late Triassic of Rio Grande do Sul, Brazil; left postcanines. **B**. *Candelariodon barberenai* Oliveira, Schultz, Soares, and Rodrigues, 2011 (holotype, MMACR PV-0001-T) from the Middle–Late Triassic of Rio Grande do Sul, Brazil; isolated left posterior postcanine (B_1) and left pc1–5. **C**. *Prozostrodon brasiliensis* (Barberena, Bonaparte, and Teixeira, 1987) (holotype, UFRGS-PV-248-T) from the Late Triassic of Rio Grande do Sul, Brazil; left (C_1) and right (C_2) postcanine rows. **D**. *Botucaraitherium belarminoi* Soares, Martinelli, and Oliveira, 2014 (holotype, MMACR-PV-003-T) from the Late Triassic of Rio Grande do Sul, Brazil; last left postcanines. **E**. *Thrinaxodon liorhinus* Seeley, 1894 (NHMUK-PV-R3731) from the Early Triassic of South Africa; left postcanine row. All teeth are in lingual view. The dashed line in pc5 represents the shape of cusp a. The dotted line indicates the point where postcanine teeth change their morphology radically. Abbreviations: apc, alveolus of postcanine tooth; pc, postcanine tooth.

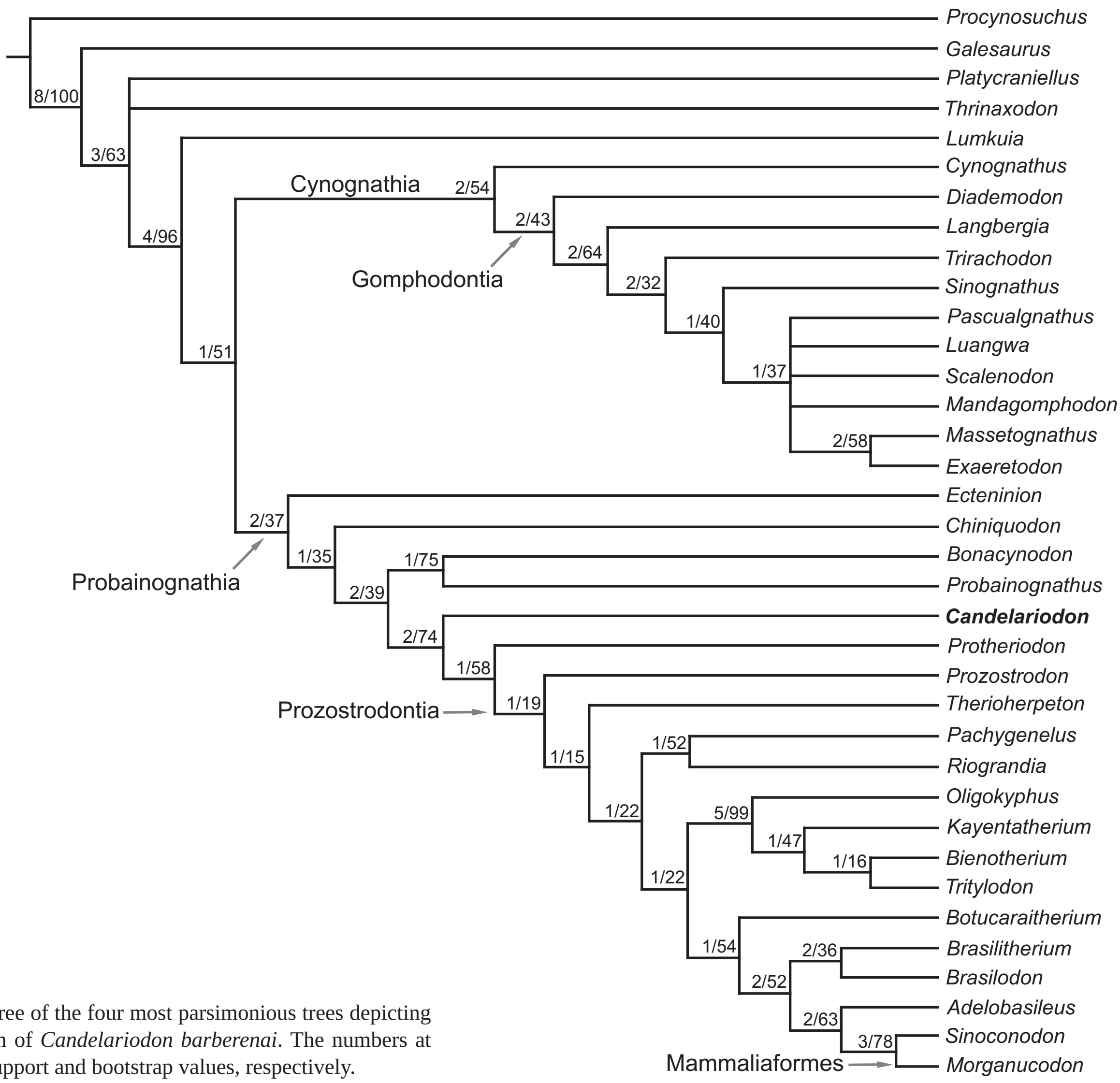


Fig. 7. Strict consensus tree of the four most parsimonious trees depicting the phylogenetic position of *Candelariodon barberenai*. The numbers at nodes indicate Bremer support and bootstrap values, respectively.

Stratigraphic and geographic range.—*Dinodontosaurus* AZ of the Pinheros-Chiniquá Sequence, Santa Maria Supersequence, late Ladinian–early Carnian, Middle–Late Triassic. Pinheiro region, Rio Grande do Sul, Brazil.

Discussion

Phylogenetic position of *Candelariodon barberenai*.—The present phylogenetic analysis resulted in four most parsimonious trees (tree length = 443 steps; consistency index = 0.47; retention index = 0.78), and the consensus tree is presented in Fig. 7. The resolution of the monophyletic groups is complete in Probainognathia (Fig. 7), recovering *Candelariodon* as the sister taxon of *Protheriodon* plus Prozostrodontia. *Candelariodon* plus the less inclusive clades is supported by the presence of a mediolaterally thick anterior margin of the coronoid process (character 86[1], unambiguous) and presence of lingual cingulum (character 115[0], ambiguous). This latter feature is unknown in *Protheriodon* and is also present in the basal cynodont *Thrinaxodon* (Crompton 1963; Abdala et al. 2013). Although the phylogenetic resolution of taxa crownward *Probainognathus* is still conflictive due to incompleteness of several taxa (e.g., *Protheriodon*, *Prozostrodon*, *Therioherpeton*), *Candelariodon* is deeply nested within Probainognathia, closely related to *Protheriodon* and prozostrodontians (Fig. 7). The inclusion of several putative dental features (relationships of main cusps, morphologic changes along postcanine tooth row, features on the cingulum) will be necessary to elucidate the inter-relationships of prozostrodontians and closely related forms. Up to now most analyses (including the one presented here) deal with a broad spectrum of disparate cynodonts (e.g., Hopson and Kitching 2001; Abdala 2007; Oliveira et al. 2010; Ruta et al. 2013; Martinelli et al. 2016c) and are focused on major relationships among main clades.

Dental and lower jaw features.—The complexity seen in the postcanine tooth row of *Candelariodon*, from the late Ladinian–early Carnian *Dinodontosaurus* AZ, is noteworthy when compared with coeval probainognathians, such as

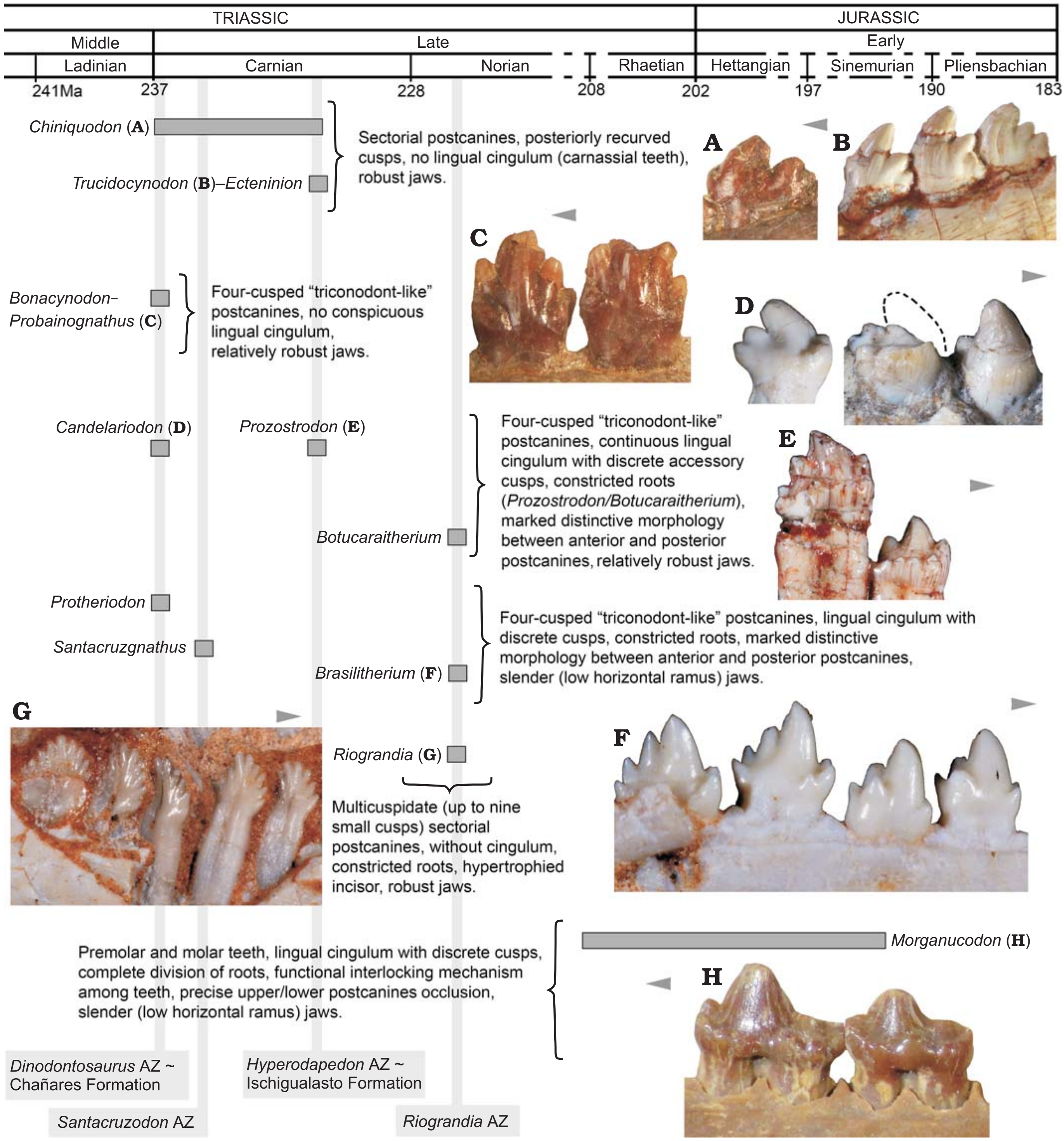


Fig. 8. Main dental features of selected non-mammaliaform probainognathians and one mammaliaform (*Morganucodon*) disposed in a time scale. **A**. *Chiniquodon theotonicus*, PVL 4444, left lower postcanine in labial view. **B**. *Trucidocynodon riograndensis*, UFRGS-PV-1051-T, left lower postcanines in labial view. **C**. *Probainognathus jenseni*, PVL 4445, right lower pc5–6 in lingual view. **D**. *Candelariodon barberenai*, MMACR PV-0001-T, left lower postcanines in lingual view. **E**. *Prozostrodon brasiliensis*, UFRGS-PV-0248-T, left lower postcanines in labial view. **F**. *Brasilitherium quadrangularis*, UFRGS-PV-0603-T, left lower postcanines in labial view. **G**. *Riograndia guaibensis*, UFRGS-PV-0833-T, left lower postcanines in lingual view. **H**. *Morganucodon watsoni*, NHMUK-PV-M-U273, right postcanines in lingual view. Arrows indicate mesial side of the dentition.

Chiniquodon, *Bonacynodon*, and *Probainognathus* (Fig. 8). With the exception of the chiniquodontid *Aleodon*, which has postcanine teeth with a well-developed lingual platform (Crompton 1955; Abdala and Giannini 2002), other basal probainognathians were more notably adapted to carnivory (e.g., *Chiniquodon*, *Trucidocynodon*, *Ecteninion*; Abdala and Giannini 2002; Martínez et al. 1996; Oliveira et al. 2010) or developed simple "triconodont-like" postcanines, without conspicuous lingual cingulum and constricted roots (e.g., *Probainognathus*, *Bonacynodon*; Romer 1970; Martinelli et al. 2016c) (Fig. 8). Nonetheless, the dentition of *Candelariodon* can be easily divided in two morphotypic patterns: (i) anterior teeth with a sub-square occlusal shape dominated by large cusp a and cusp c, plus an accessory well developed lingual cusp g, and a continuous, faint lingual cingulum; (ii) posterior teeth with an elongated crown, with a sectorial margin with cusps a to d, accessory lingual cusps (e and g), and continuous or truncated lingual cingulum.

In *Candelariodon*, the lingual cingulum in lower postcanines, including putative accessory cusps, is considered a derived feature among probainognathians, being present in *Prozostrodon*, *Santacruzgnathus*, *Botucaraitherium*, *Brasilodon*, *Brasilitherium*, *Pachygenelus*, *Diarthrognathus* (e.g., Gow 1980; Bonaparte and Barberena 2001; Bonaparte et al. 2003, 2005, 2012; Soares et al. 2014; Martinelli et al. 2016c), and early mammaliaforms (e.g., *Megazostrodon*, *Morganucodon*; Crompton 1974; Mills 1971; Parrington 1973; Gow 1986) (Figs. 5, 6, 8).

In the Early Triassic basal cynodont *Thrinaxodon*, posterior postcanine teeth of young individuals also develop a lingual cingulum similar to that present in probainognathians (Crompton and Jenkins 1968). The occurrence of such structures in *Thrinaxodon* and more derived forms highlights the plasticity of some dental features in cynodont evolution and the diversity of processes in tooth replacement mechanisms producing different kind of morphologies along ontogeny. However, the complexity along the tooth row of *Candelariodon* is not seen in *Thrinaxodon*, which in addition has less developed articular process of the dentary, reduced coronoid process, less developed masseteric fossa on the dentary, and more active tooth replacement, among several other plesiomorphies in the skull (e.g., Fourie 1974; Abdala et al. 2013; Jasinoski et al. 2015).

Candelariodon has well developed dentary as in other eucynodonts, with a tall coronoid process, large masseteric fossa, elongated articular process, thin and laminar splenial, and reduced postdentary trough (Figs. 2, 3). Its horizontal ramus is relatively tall, as commonly occurs in most eucynodonts. Among prozostrodontians, a relatively tall dentary is seen in ictidosaurs, tritylodontids, *Prozostrodon* (Sues 1986; Bonaparte and Barberena 2001; Martinelli et al. 2005; Martinelli and Rougier 2007; Soares et al. 2011), and, to a lesser extent, in *Botucaraitherium* (Soares et al. 2014), *Sinoconodon* (Crompton and Luo 1993; Luo 1994), and a few some early mammaliaforms (e.g., *Haramiyavia*; Luo et al. 2015). In contrast, *Protheriodon*, *Santacruzgnathus*, dromatheriids, *Brasilitherium* (Fig. 3), and some early mammaliaforms (Simpson 1926; Luo et al. 2001; Sues 2001; Bonaparte et al. 2003, 2005; Gill et al. 2014; Martinelli et al. 2016c) have slender and dorsoventrally low dentaries, with a very discrete Meckelian groove. The dentaries are fused in *Candelariodon*, as in most non-prozostrodontian eucynodonts (Hopson and Kitching 2001). In contrast, unfused mandibular symphysis is considered a synapomorphy of prozostrodontians (Liu and Olsen 2010). This condition is also reported in basal cynodonts, such as *Procynosuchus*, *Thrinaxodon*, and *Galesaurus.*

Consequently, the postcanine morphology of *Candelariodon*, together with other jaw features, supports the placement of this taxon close to the prozostrodontian clade (Fig. 7), and highlights the diversity of taxa crownward *Probainognathus* with conspicuous mammal-like features in the Middle–Late Triassic of Brazil (Fig. 8). Such unexpected diversity of disparate species (*Candelariodon*, *Protheriodon*, *Prozostrodon*, *Therioherpeton*, *Riograndia*, *Irajatherium*, *Brasilitherium*; Fig. 8) indicates for an adaptive radiation of a group of mammaliaform-like probainognathians, prior to the origin of the mammaliaform clade, that was only recently recognized as an important component of Late Triassic ecosystems.

Conclusions

The holotype specimen of *Candelariodon barberenai*, a cynodont from the Middle–Late Triassic of south Brazil, was revisited and new conclusions about its dental anatomy and phylogeny were exposed. Its crown morphology has a suite of apormorphies, such as lingual cingulum with discrete cusps (e and g) and distinctive morphologies between anterior and posterior postcanine teeth, that are reminiscent of the pattern represented in non-mammaliaform prozostrodontians and basal mammaliaforms. This is also supported by a phylogenetic analysis that placed *Candelariodon* as the sister taxon of a clade formed by *Protheriodon* plus Prozostrodontia.

The radiation of probainognathians is clearly evident in the fossil record (e.g., Hopson and Kitching 2001; Bonaparte et al. 2005; Liu and Olsen 2010; Oliveira et al. 2010; Soares et al. 2011; Ruta et al. 2013; Martinelli and Soares 2016), with disparate morphotypes (e.g., ecteniniids, chiniquodontids, probainognathids, ictidosaurs, tritylodontids, dromatheriids, and “brasilodontids”) during the Middle–Late Triassic. For many years, tritheledontids and tritylodontids were the “most mammal-like” cynodont groups, diversified mostly during the Jurassic (see Luo 1994). Nonetheless, the new discoveries in Brazil and reinterpretations of already known fossils have demonstrated that non-mammaliaform prozostrodontians (e.g., *Prozostrodon*, *Santacruzgnathus*, *Therioherpeton*, *Brasilodon*) and very closely related forms (e.g., *Candelariodon*, *Protheriodon*) with triconodont-like dentition, and a morphological plan similar to some early mammaliaforms (e.g., *Morganucodon*, *Megazostrodon*) were extremely diverse during the Middle–Late Triassic. Consequently, the fossil record of non-mammaliaform probainognathians in the Triassic of Brazil is noteworthy and an unexpected amount of forms is being recovered showing a hidden and broad diversity by the late Middle and early Late Triassic.

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Appendix 1

Changes in character-states for *Protheriodon estudianti*:

Character 11. Changes from (?) to (1). The braincase has a moderate lateral expansion.

Character 22. Changes from (?) to (0). Low posteroventral process of the jugal, as seen in the right side of the skull.

Character 36. Changes from (0) to (1). Length of secondary palate represents more than 45% of skull length.

Character 107. Changes from (0) to (1). Constricted lower postcanine roots, as seen in posterior preserved teeth.

Change in character-states for *Prozostrodon brasiliensis*:

Character 17. Changes from (?) to (2). Low zygomatic arch based on the preserved anterior base of the arch.

Changes in character-states for *Brasilitherium riograndensis*:

Character 94. Changes from (0) to (0+1). The sample of specimens of this species shows changes in incisor number along ontogeny.

Character 95. Changes from (1) to (0+1). The sample of specimens of this species shows changes in incisor number along ontogeny.

Appendix 2

Data matrix used in the phylogenetic analysis, based on Liu and Olsen (2010), plus the modifications of Martinelli et al. (2016c) and those from Appendix 1.

Procynosuchus delaharpeae	000000010000000000000000000000000000000000000000000000000000001[01]00000000000000000 000001000000000100010000000--00-0000000000000-00000000000000002
Galesaurus planiceps	010000000000000000100000100001100000000000000000000000000000000000000000000010000100 00000000110010000001000 0--00-1000000001100????00??0??0000000
Thrinaxodon liorhinus	01[01]000000000000000000000000001110000000000000000000000000000000000000001001010000 10000011000110000001000000 0--00-1000000001100-00000000000?0000?
Platycraniellus elegans	0110000000000000000110000000001011000000 0??00000000?0000000000000000000101??101000?101 0?0??0001?0?100000000000--0?-0?000??????????????????????????
Cynognathus crateronotus	00000000000000000102100211000001110000101110001010 0?0000000000000100000111001011011201 0111200011010001000100 00--00-10010000001110000000110000000000
Diademodon tetragonus	[01]0000000000000000102201211100011110000000111000101000000000[01]00000000000000000100101111 12010111211311010001200100010 0100?00010000111100000001100000000000
Trirachodon berryi	11100100[01]00000001121011111010011101002011100010100000002100000000000001101110201101 11 0101112113110100012111000201101 00101???01111000000????00000000
Sinognathus gracilis	1020?100100000??11010011110?1?1?1010?0011000010100???????00000?000?011011102011011 10101 1??113120000002?0?00?201100?0201??????????????????????????
Langbergia modisei	0010000000000000001210111110100111010000110000101?0?000?21??0000000001?0?11????10111010 11121131101000120010002011010 0101?????1????????????????????
Pascualgnathus polanskii	1020?1001000000001122012111011?1110100001??000101?0???0?2?00000???0?0??????????[01]0?1201 011??113210000002[12][12]000-110100-12010???1101??0000??1000000000
Luangwa drysdalli	??00?1000?000001012100111 1????1110?00001???00101000000?2??00000???0?????? ?????1011201011 ??113110100012[12][12]000-202100-12010???110110000???1100000000
Massetognathus pascuali	011111001000000011010111110112111020000100000101000000121100000000000110111020110 11[12] 01011??11311021110211000-222100-12010000 0101101000??1100000000
Exaeretodon argentinus	001111101000001111210121110112111 01[01]00010?00010100010002110000000000?101????01101121 1011??113210010102[12][12]000-120100-12210000000110100111110000000 0
Scalenodon angustifrons	??10?1?0000000??1101012111?????1101?0??1??00010100?0000211000000?000??0?????0?[01]0?12??0 11??113110100012[12][12]000-2 02100-1201?????????? ????????????????
Mandagomphodon hirschoni	???0010?????001?11?????1110112111 01?0?0?0??00????????????1?000?0?????1??1?0?0?[01]??1???011 ??11 3220001002[12][12]000-222100-1201??????????????????????????

Lumkuia fuzzi	??1000101000000?00000000010?120110100101010001001 0?00000010000000000000010000110112010 00120001100000000010000--00-10000?????001????????????0?????
Chiniquodon theotonicus	1110101010000010101100000101 1[12]11112100011000010100000001000000000000?1?01???11101120 10111200011000000000010000--00-100000??000011010001110000?0000
Ectenion lunensis	001??002100000200000000000 0?1[01]1110000201110001010 0?1000101000000000001100110211101100 1011??00011000001[01]0010000--00-?00000???1??110??0?????0???????
Probainognathus jenseni	01101002100000100101100001011211111000011100010000000 00110000 000000001100110211102100 10 1112000110000000000000--00-10110000?000110???0??11000?0000
Bonacynodon schultzi	??1??0?21??000??01011000?10??211111000?????0?????0????????????0??000???????????0?0001?1112? 001?0000?100000000--00-?0110??????????????????????????
Therioherpeton cargnini	?????0121?11122?2100??0????????1111??000 ????????0?0?1100--00-?00000??1?00?????????1111110011
Riograndia guaibensis	201310121111122121001000001112011121201100010200 00?0000102000010001121102?13???0003011 11??0012110011001001100--00-10100??????????????????????????
Pachygenelus monus	2013101211111221210010000001120111212011000102000010000102000010 1??121102213132020301 11112001221001000100001 0--00-002001???0001111101??1111111111
Prozostrodon brasiliensis	21?010?2????122121?????????112?1111?1????????????????????????? ???????????????????0301111??00 10000000111001100--00-001000???000?????0???1111110000
Botucaraitherium belarminoi	?????0?? ????????????????0???11????01? ?????001?001110--01-00??0??????????????????????????
Protheriodon estudianti	??0??0????1?????2000100???????011111??0?1?0??11????? 100001?00?000100--00-?010????????????? ??????????????
Brasilodon quadrangularis	[01]000?0121121122120001000?00?12011111121100010210 01?0?112220?00111011211022131320?030 1111??00111000010110011 10--01-001[01][01]??????0111??11????????????
Brasilitherium riograndensis	0000?0121121122120001000000?1201111102110001021011?01112220???11?011211022131320103011 1 1??001[01][01]0000 1011001110--01-001[01]1????????????11????????1111
Tritylodon longaevus	102-1111110112211102001111011211102122110000110110110102 12111101101031102203120200311 11 1??1132210-22-222-32-2-1100-03221??????210??????1?????1111
Oligokyphus major	[12]??-1111?10112???102010110?1?2?1??21????????110?10110102?21111011000310022031202003111 11??1132110-22-222-32-2-1100-0322111100?2101111??1121111111
Bienotherium yunnanense	102-11111101122111?201?111011211102122110000110110110?02?01111?110?031??22131?0200311111 ??1132110-22-222-32-2-1100-03221??????210??11??????111111
Kayentatherium wellesi	102-11111?0112211102011111111201102122110000110110110102121111?110?0311022131202003111 1 1121132110-22-222-32-2-1100-0322?11100021011?1111121??1111
Adelobasileus cromptoni	???????01121?2?????????????????0??????21100010210 11?21112210000101110??????????????????????? ???
Sinoconodon rigneyi	0002?0101121122120001000?01?121111210211001103101 1?21112221011101010????????0?302030111 2??20010000010010022 10--00-10101???????????? ??????????????
Morganucodon spp.	0?02?010112112212000 2?000011111111210211001103201112111222011211111121102213243020301 11 2122221000001011002210--01-0010111111001111111??1121111111
Candelariodon barberenai	??13??111??????? 00??00??00?0??--?0-00??????????????????????????????