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A NEW CYNODONT FROM THE SANTA MARIA FORMATION, SOUTH BRAZIL, IMPROVES LATE TRIASSIC PROBAINOGNATHIAN DIVERSITY

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Abstract: The fossil record of non-mammaliaform probainognathian cynodonts is outstanding in the Late Triassic rocks of Brazil and Argentina. Approximately 15 genera are known, providing unique insights in the study of the major skeletal transformations prior to the mammalian condition. Globally, the diversity of probainognathians is possibly under-represented, as the discovery of small- to very small-sized taxa based on relatively well-preserved specimens is rare. Several species, for example much of the Laurasian record, are based on isolated teeth and jaw fragments. Here, we describe a new probainognathian from the Late Carnian *Hyperodapedon* Assemblage Zone of the Santa Maria Formation, south Brazil. *Alemoatherium huebneri* gen. et sp. nov. is based on a left lower jaw with almost complete dentition that exhibits a combination of features not seen in any other known probainognathian. Its slender lower jaw, anterodorsally bent process of the dentary, high number of lower incisors, reduced canine, triconodont-like postcanine teeth with mesiolingual and distolingual cingular cusps are all features that support the inclusion of *A. huebneri* as a member of the Prozostrodontia clade. This new find highlights the conspicuous probainognathian cynodont fossil record in southern Brazil, with a plethora of forms near the mammalian origin.

Key words: Cynodontia, Prozostrodontia, South America, Santa Maria Supersequence.

CYNODONT therapsids are abundant components of most Middle to Late Triassic tetrapod assemblages in southern Brazil and western Argentina (Abdala & Ribeiro 2010; Martinelli & Soares 2016). There are about 30 documented species of gomphodontids, cynognathids, traversodontids and probainognathians, within a time span ranging from the Anisian–Ladinian to the Norian (e.g. Abdala 1996; Bonaparte & Barberena 2001; Abdala & Giannini 2002; Bonaparte *et al.* 2005; Martinelli *et al.* 2005, 2009; Abdala & Ribeiro 2010; Oliveira *et al.* 2010; Soares *et al.* 2011, 2014; Martínez *et al.* 2013; Martinelli & Soares 2016; Martinelli *et al.* 2016). The most diverse and well-documented groups are the herbivorous/omnivorous traversodontid gomphodonts (e.g. Abdala & Giannini 2000; Abdala & Ribeiro 2003; Liu & Abdala 2014; Melo *et al.* 2015) and the faunivorous non-mammaliaform probainognathians (Bonaparte & Barberena 2001; Bonaparte *et al.* 2003, 2005, 2012; Martinelli *et al.* 2005, 2016; Oliveira *et al.* 2010). The fossil record of these groups comes from the San Rafael Block, Cuyana, Ischigualasto-Villa Unión, and Marayes-El Carrizal basins in Argentina (e.g. Romer 1973*a*; Martínez *et al.* 2013, 2015; Bonaparte & Migale 2015) and from the Santa Maria Supersequence (Paraná Basin) in southern Brazil (Langer *et al.* 2007; Oliveira *et al.* 2010; Soares *et al.* 2011; Martinelli & Soares 2016; Martinelli *et al.* 2016).

The Probainognathia clade (*sensu* Hopson & Kitching 2001; Liu & Olsen 2010) which includes the Mammalia crown-group (e.g. Rowe 1988; Kielan-Jaworowska *et al.* 2004) originated at least during the early Middle Triassic, exhibiting its greatest diversity during the late Middle–Late Triassic, and represents quite disparate groups regarding size and diet. Main non-mammaliaform representatives

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include ecteniniids, chiniquodontids, probainognathids, therioherpetids/dromatheriids, ‘brasilodontids’, ictidosaurs (Martínez & Forster 1996; Hopson & Kitching 2001; Bonaparte & Barberena 2001; Sues, 2001; Abdala & Giannini 2002; Martinelli & Rougier 2007; Oliveira *et al.* 2010) and possibly tritylodontids (this group has a dual position as Gomphodontia, e.g. Sues 1985; Hopson & Kitching 2001; or as Probainognathia, e.g. Kemp 1982, 1983; Abdala 2007; Liu & Olsen 2010; see also Luo 1994). Among probainognathians, decrease in size is evident especially in forms closely related to mammaliaforms (Rowe 1988; Ruta *et al.* 2013; see also Bonaparte 2012), but this seems not to be unidirectional in the clade. The diversity of cynodonts, especially probainognathians, is possibly under-represented, as the discovery of small- to very small-sized taxa based on relatively well-preserved specimens is rare. The description of several species, for example much of the Laurasian probainognathian record (e.g. Lucas & Oakes 1988; Hahn *et al.* 1984, 1987, 1994; Godefroit & Battail 1997; Sues 2001) are based on isolated specimens (mainly teeth and few fragmentary jaws). In this context, the fossil record of small-sized probainognathians is outstanding in the Late Triassic rocks of Brazil (e.g. Bonaparte & Barberena 2001; Bonaparte *et al.* 2003, 2005, 2012; Martinelli *et al.* 2005, 2016; Oliveira *et al.* 2011; Soares *et al.* 2011, 2014; Martinelli & Soares 2016) and Argentina (Romer 1970, 1973*b*; Bonaparte 1980; Bonaparte & Crompton 1994; Martínez & Forster 1996; Martínez *et al.* 1996; Martinelli & Rougier 2007) providing unique insights in the study of the major skeletal transformations prior to the mammalian condition (e.g. Luo 1994, 2007; Bonaparte *et al.* 2003, 2005, 2012; Kielan-Jaworowska *et al.* 2004; Martinelli & Rougier 2007; Rodrigues *et al.* 2013, 2014; Ruta *et al.* 2013; Ruf *et al.* 2014).

In this contribution, we describe a new probainognathian cynodont from the late Carnian *Hyperodapedon* Assemblage Zone (AZ) of southern Brazil based on a tiny isolated lower jaw with well-preserved dentition, which can be unambiguously differentiated from all other known cynodonts. The finding of such small specimen provides positive evidence on the hidden diversity of small-sized forms within Triassic faunal associations. Moreover, comments on two other cynodonts from the *Hyperodapedon* AZ (*Charruodon tetracuspidatus* and *Therioherpeton cargnini*) are drawn based on the re-study of the published specimens.

MATERIAL AND METHOD

The specimen studied here, UFSM 11579b, was found during the mechanical preparation of assorted dinosauromorph remains (UFSM 11579a) including silesaurids. They were unearthed during a 2014 joint fieldwork expedition by the Laboratório de Paleontologia, Universidade São Paulo (USP, Ribeirão Preto), and Laboratório de Estratigrafia e Paleobiologia, Universidade Federal de Santa Maria (UFSM, Santa Maria), in the outskirts of Santa Maria, Rio Grande do Sul, south Brazil (Fig. 1).

UFSM 11579b was included in the data matrix published by Liu & Olsen (2010) and modified by Martinelli *et al.* (2016). In addition, *Therioherpeton cargnini* was re-scored for some character-states (see Martinelli *et al.* 2017). Three extremely fragmentary taxa, which are comparable with *Alemoatherium*, were also included: *Santacruzgnathus abdalai* (based on UFRGS-PV-1121-T and Martinelli *et al.* 2016), *Microconodon tenuirostris* (based on Simpson 1926 and Sues 2001) and *Charruodon tetracuspidatus* (based on MCP-3934 PV and Abdala & Ribeiro 2000). Due to the incompleteness of the taxa, we performed three different analyses: the first only including *Alemoatherium huebneri*, the second also including *Santacruzgnathus abdalai* and *Microconodon tenuirostris*, and the third also including *Charruodon tetracuspidatus*. The modified data matrix was analysed under equally-weighted parsimony using TNT 1.5 (Goloboff & Catalano 2016). An heuristic search of 500 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 (= decay indices; Bremer 1994) and a bootstrap resampling analysis (Felsenstein 1985) were conducted. The character list, the modified data matrix, changes included for *T. cargnini*, and complete strict consensus trees are presented in Martinelli *et al.* (2017).

Several eucynodont specimens were examined first hand by AGM for comparison. The institutions in which these specimens are deposited are detailed in the text below. Otherwise, bibliographical sources were used and these are cited in the text.

GEOLOGICAL SETTING

The specimen UFSM 11579b comes from deposits of the Alemoa Member of the Santa Maria Formation at the site known as Cerro da Alemoa or Waldsanga (Fig. 1; Langer *et al.* 2007; Da Rosa 2004; Da-Rosa 2015) which have also yielded the type specimens of the dinosaur *Saturnalia tupiniquim* (Langer *et al.* 1999). Accordingly to recent sequence stratigraphy studies (Horn *et al.* 2014) these strata belong to the Candelária Sequence, Santa Maria Supersequence (Santa Maria 2 Sequence of Zerfass *et al.* 2003) which congregates the upper part of the Santa Maria Formation (Gordon 1947) and the lower part of the Caturrita Formation (Andreis *et al.* 1980). Two assemblage zones were recognized within the Candelária Sequence: the older *Hyperodapedon* AZ and the younger

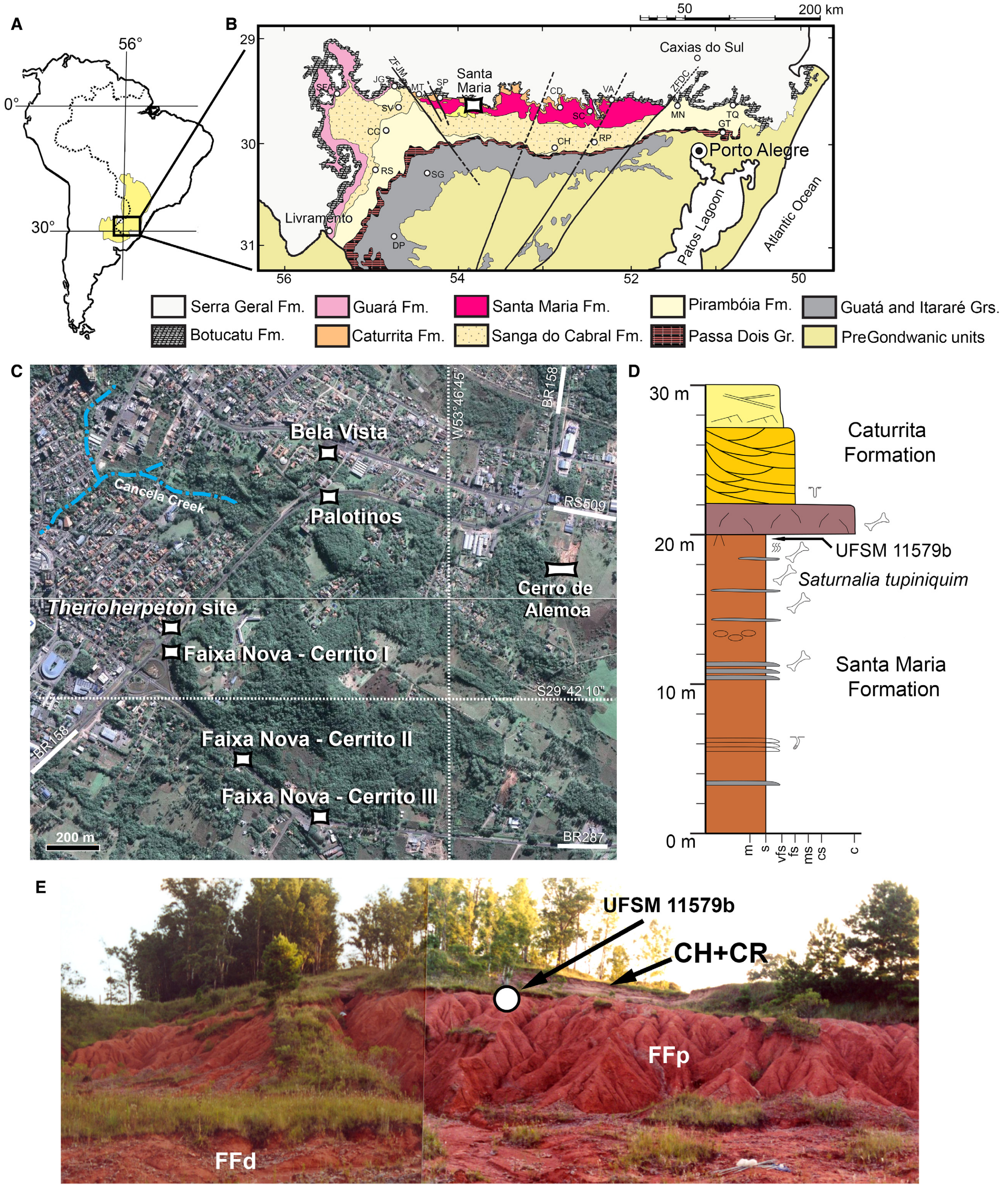


FIG. 1. Geographical and geological location of UFSM 11579b, holotype of *Alemoatherium huebneri*. A, Paraná Basin in South America. B, simplified geological map of the central portion of Rio Grande do Sul State (modified from Eltink *et al.* 2016), indicating Santa Maria city. C, selected outcrops in Santa Maria city (modified from Da-Rosa 2015) indicating the Cerro da Alemoa outcrop. D, sedimentary log from the Cerro da Alemoa outcrop, indicating the level of the studied specimen and other fossiliferous levels (modified from Da Rosa 2005). E, photograph of the outcrop, showing the channel and crevasse deposits (CH + CR) of the Caturrita Formation, and the distal (FFd) and proximal (FFp) floodplain deposits of the Santa Maria Formation, indicating the level of UFSM 11579b. Colour online.

Riograndia AZ. The cynodont record of all Santa Maria Supersequence assemblage zones is detailed in Figure 2.

The association with *Hyperodapedon* rhynchosaurs justifies the referral of the cynodont here described to the *Hyperodapedon* AZ. From the same outcrop, isolated teeth similar to those of *Gomphodontosuchus brasiliensis* have been recognized (Langer 2005*a*). In fact, the type specimen of that traversodontid may also have been collected from the same site (von Huene 1928; Langer 2005*a*; Langer *et al.* 2007). Correlations with dated strata from the Ischigualasto Formation (Ischigualasto – Villa Unión Basin) in western Argentina (e.g. Martínez *et al.* 2011, 2013) that share a similar faunal association (e.g. Langer 2005*b*; Langer *et al.* 2007) indicate that the *Hyperodapedon* AZ is late Carnian in age.

Institutional abbreviations. MCP-PV, Museu de Ciências e Tecnologia (Paleontological Collection), Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; MMACR-PV-T, Museu Municipal Aristides Carlos Rodrigues, Paleovertebrates – Triassic Collection, Candelária, Rio Grande do Sul, Brazil; MVP, Museu Vicente Pallotti, Santa Maria, Rio Grande do Sul, Brazil; NHMUK, Natural History Museum (PV, Vertebrate Palaeontology; R, Reptiles; M, Mammals), London, UK; PULR, Museo de Antropología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Instituto Miguel Lillo (Vertebrate Paleontology Collection), Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; PVSJ, Vertebrate Paleontology, Universidad Nacional de San Juan, San Juan, Argentina; SAM, Iziko South African Museum, Cape Town, South Africa (specimens observed at the Department of Organismal Biology, University of Chicago, Chicago, USA); UFRGS-PV-T, Universidade Federal Rio Grande do Sul (Vertebrate Paleontology, Triassic Collection), Porto Alegre, Brazil; UFSM, Coleção Paleontologia, Laboratório de Estratigrafia e Paleobiologia, Universidade Federal de Santa Maria, Santa Maria, Brazil.

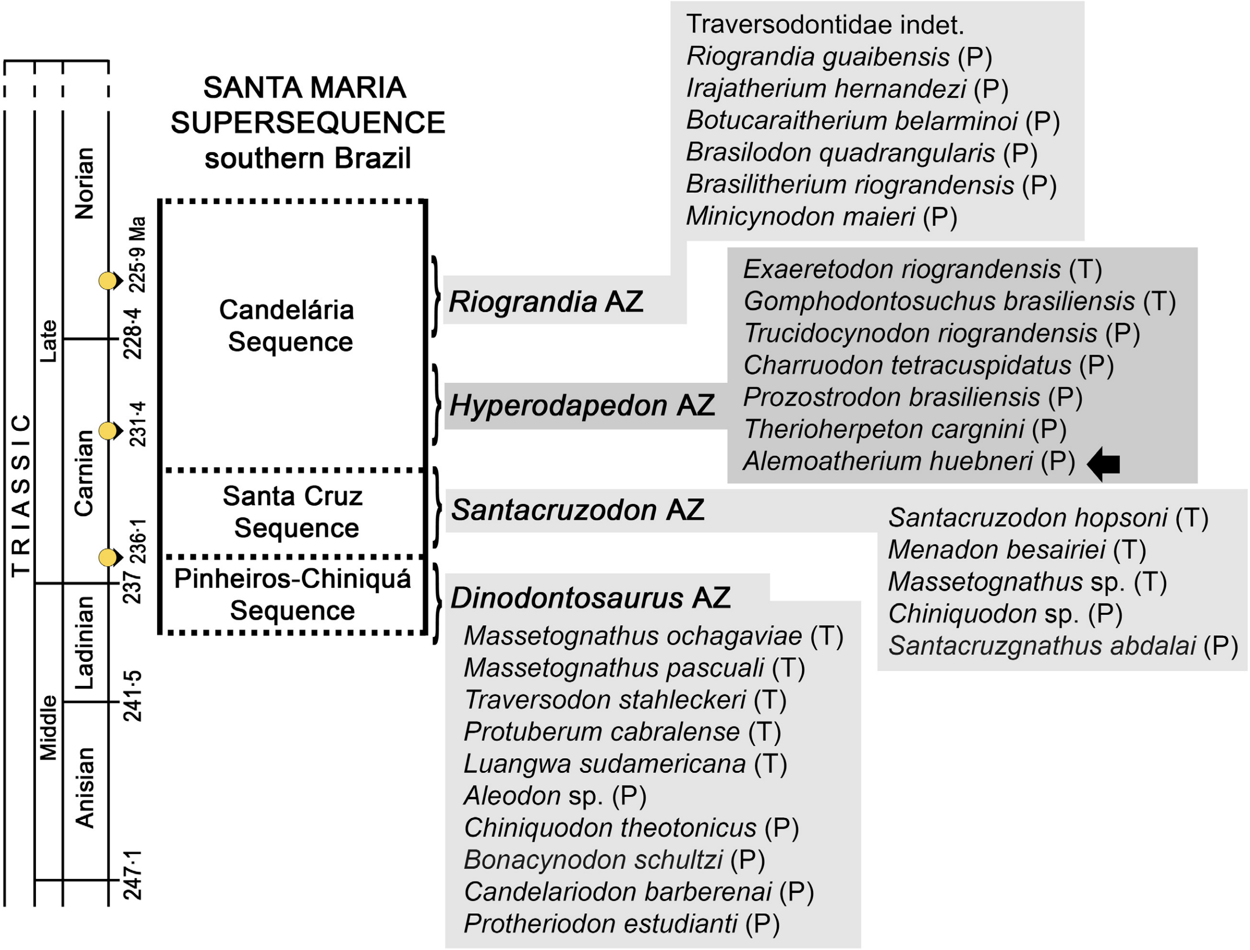


FIG. 2. Chrono- and biostratigraphy of the Triassic Santa Maria Supersequence with vertebrate assemblages zones (AZ) from southern Brazil, and the cynodont fossil content of *Hyperodapedon* AZ, where the holotype of *Alemoatherium huebneri* was found. The ages in the column follow Gradstein *et al.* (2012). The radiometric dating of 236.1, 231.4 and 225.9 Ma correspond to the first half of the Chañares Formation (Marsicano *et al.* 2016), the base of the Ischigualasto Formation, and the base of Los Colorados Formation (Martínez *et al.* 2013) respectively. *Abbreviations:* P, Probainognathia; T, Traversodontidae.

SYSTEMATIC PALAEONTOLOGY

THERAPSIDA Broom, 1905
CYNODONTIA Owen, 1861
EUCYNODONTIA Kemp, 1982
PROBAINOGNATHIA Hopson, 1990

Genus ALEMOATHERIUM nov.

LSID. urn:lsid:zoobank.org:act:F3C713FB-502F-461C-BC07-7CB7F0A87F83.

Type and only known species. *Alemoatherium huebneri* sp. nov.

Derivation of name. Alemoa, in reference to the region with a series of outcrops, where the type-locality (Cerro da Alemoa) is located. *Therium* from the New Latin that derives from Greek *thērion*, meaning beast, usually used for mammals and closely related forms.

Diagnosis. *Alemoatherium* is a small-sized probainognathian cynodont diagnosed by the following association of characters (autapomorphy marked with an asterisk*): slender dentary with the anterior portion of the horizontal ramus anterodorsally bent that holds a small symphysis; small, peg-like lower canine; five lower incisors, decreasing in size posteriorly, with i1 procumbent; pc1 with large cusp a and very reduced cusp c; pc1 of comparatively large size, similar to pc3 and slightly larger than the canine; asymmetrical sectorial postcanine teeth (pc3–pc6) with four mesiodistally aligned main cusps; height relation of main cusps in pc3–pc6: a > c ≫ b > d; pc4–pc6 with main cusp a with mesial edge about twice longer than the distal edge, and convex labial and straight lingual surfaces; one or two mesiolingual cingular cusps in a basal position; pc6 with a distolingual basal cingular cusp; posterior postcanine teeth with cusp b and mesiolingual cingular cusps forming a concave mesial margin for cusp d of the preceding tooth; and distally protruding cusp d, with a strongly concave distal edge at the crown/root boundary in pc4–pc6*.

Alemoatherium huebneri sp. nov.
Figures 3–6

LSID. urn:lsid:zoobank.org:act:E9043F80-8D99-4D24-B6FA-FD4AEB6B0F2E.

Holotype. UFSM 11579b, anterior half of left lower jaw with few *in situ* teeth and the last three postcanine teeth detached (Figs 3–6).

Derivation of name. *Huebneri*, in honour of Mrs Hilda Hübner (Latinized to Huebner), owner of the area where the holotype was unearthed.

Geographical provenance and age. Waldsanga or Cerro da Alemoa site; Alemoa Member, Santa Maria Formation; *Hyperodapedon* AZ, Candelária Sequence, Santa Maria Supersequence (Zerfass *et al.* 2003; Horn *et al.* 2014; Da-Rosa 2015); Carnian (Langer 2005*a*, *b*; Langer *et al.* 2007).

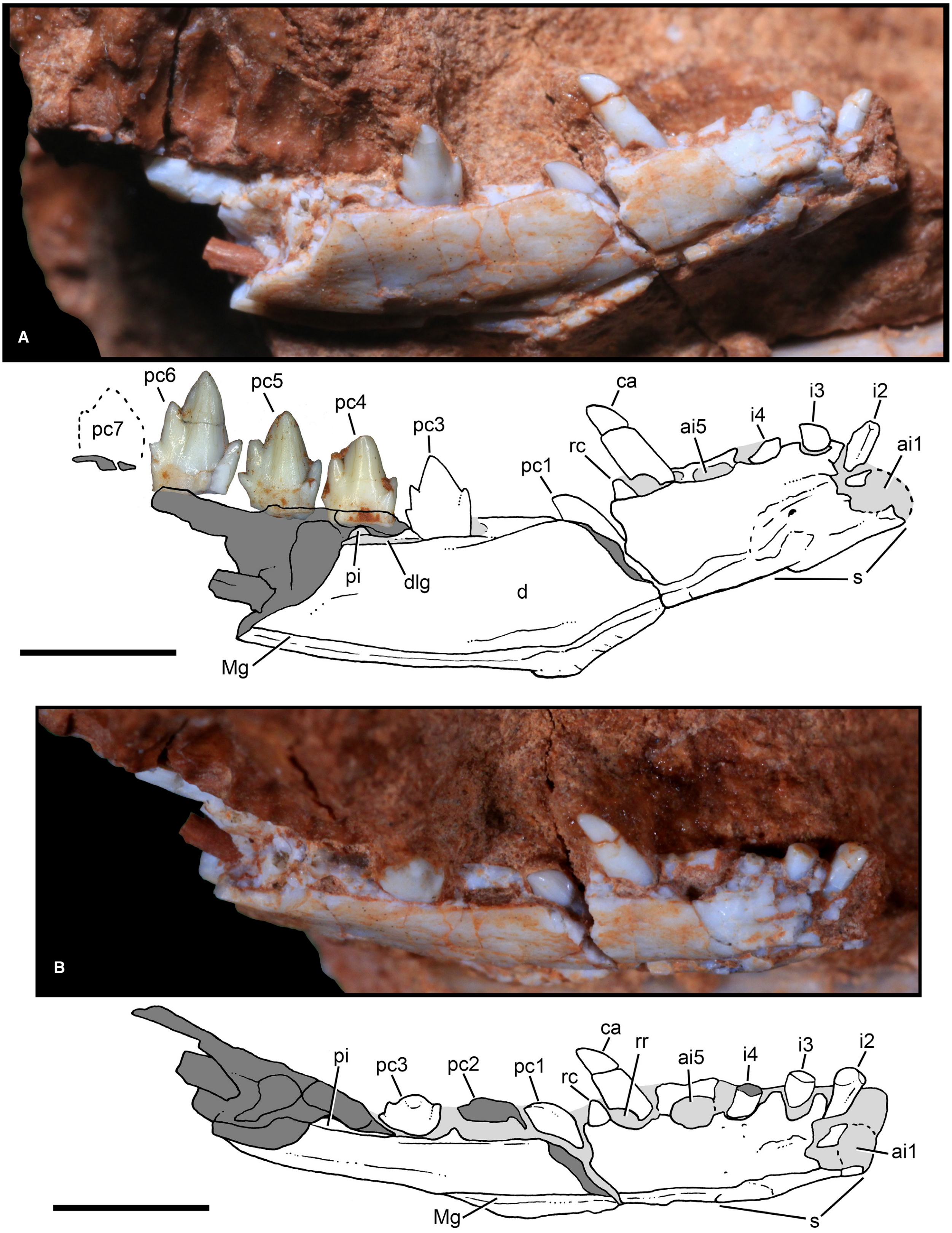
Diagnosis. As for genus.

DESCRIPTION

UFSM 11579b includes the anterior half of the left lower jaw with empty alveoli of i1, i5, and pc2, incisors 2, 3, and 4 *in situ*, canine *in situ* with its replacement tooth at the mesiolingual base, pc1 not totally erupted, pc3 *in situ* (Fig. 3), pc4–pc6 with *in situ* roots and detached crowns (Fig. 6), and imprint of pc7 in the bearing rock. The dentary is broken off below the position for pc5–pc6, lacking the posterior part of the horizontal ramus, the postdentary trough, and the coronoid process. The preserved portion of the dentary and its dentition rest on the mudstone matrix; therefore, most of its lateral surface is not exposed.

Dentary. The dentary is slender and low, as in *Santacruzgnathus abdalai* (UFRGS-PV-1121-T; Martinelli *et al.* 2016), *Brasilitherium riograndensis* (e.g. UFRGS-PV-1043-T; Bonaparte *et al.* 2003, 2005, 2012), *Microconodon tenuirostris* (Simpson 1926; Sues 2001) and basal mammaliaforms such as *Morganucodon* spp. (NHMUK-PV-M 27221; Kermack *et al.* 1973) and *Megazostrodon rudnerae* (NHMUK-PV-M 26407; Crompton & Jenkins 1968; Crompton 1974). Its deepest preserved portion is just below the position of pc4, and is just slightly deeper than the crown height of that tooth (Fig. 3). The slender horizontal ramus of the dentary extends from the level of pc2 to the rear and bends anterodorsally just below pc1–pc2, forming an elongated process. The ventral margin of the horizontal ramus and the anterodorsal projection form an angle of about 150°. The alveolar border of the dentary is slightly convex (in lateral and medial views) at the horizontal ramus, but slightly concave anterior to the abrupt ventral angulation. The anterodorsal bent portion of the dentary places the alveolar level of the incisors above those of the postcanine teeth. The alveolar and ventral margins extend almost parallel along the horizontal ramus. Near the alveolar margin, a faint sulcus for the dental lamina is seen, more evident just medial to pc3. Medial to the root of pc4, there is an oval pit on the sulcus for the dental lamina, possibly related to its replacement tooth. The Meckelian groove is conspicuous and extends all along the preserved horizontal ramus of the dentary, parallel and close to the ventral border. The Meckelian groove wedges into the symphysis just below i4 (Figs 3–4).

The symphysis occupies the anterior half of the anterodorsal process of the dentary. It is identified by a rounded ridge that projects medially, positioned just below the alveolar margin and reaching posteriorly to the level of i4. This ridge forms the posterodorsal edge of the symphysis. The anterior portion of the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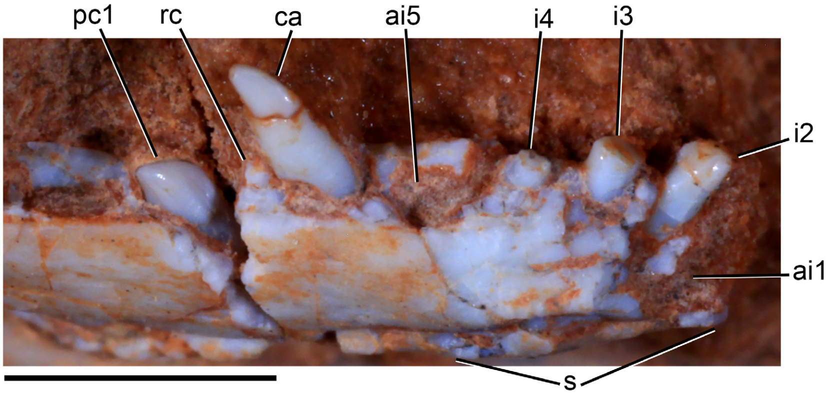


FIG. 4. Holotype UFSM 11579b of *Alemoatherium huebneri*. Detail of the anterior portion of left jaw in dorsomedial view. Scale bar represents 2 mm. *Abbreviations*: ai, alveolus incisor; ca, lower canine; i, lower incisor; pc, lower postcanine tooth; rc, replacement canine; s, symphysis. Colour online.

symphysis is broken up, exhibiting part of the alveolar cavity of i1. The medial surface of the symphysis is smooth with a tiny foramen at its posterodorsal edge (Figs 3–4). Such latter features indicate unfused lower jaws, as in several prozostrodontians (e.g. *Prozostrodon brasiliensis*, *Brasilodon quadrangularis*, *Riograndia guaibensis*, *Pachygenelus monus*).

Dentition. We infer the lower dental formula of *Alemoatherium huebneri* to be 5i/1c/7pc. The incisor count is based on the presence of the i1 alveolus, the *in situ* i2–i4, and an extra alveolus before the tooth interpreted as the canine (Fig. 4). The i1 alveolus is large, circular in cross-section, and faces anteriorly and slightly dorsally. The size of the alveolus indicates that i1 was procumbent and the largest of the series. i2 is small, but slightly larger than i3–i4, showing that the series decreases in size posteriorly (Fig. 4). The i2 crown is only partially preserved, slightly flattened mesiodistally with blunt labial and lingual edges. The lingual edge is more pronounced than the labial, possibly due to a stronger wear on the later side. Most of the tip of i2 is composed of a sub-horizontal, laterodorsally facing wear facet, indicating strong apical wear. The i2 root is partially exposed; it seems slightly oval in cross-section, with the narrower axis transversely oriented. The crown of i3 is almost entirely worn out, and there is no positive evidence that it is broken off. The worn out crown defines an oval surface in occlusal view, with the main axis mesiodistally oriented (Fig. 4). The root of i3 seems to be more circular than that of i2. The i4 has a partially broken crown, the morphology of which is not possible to clearly discern. This tooth seems not to be totally erupted, as its alveolus is slightly larger than the crown. Following i4, an empty alveolus indicates the presence of i5. It is close to the i4 alveolus and seems smaller than that of the canine (Figs 3–4).

The canine of *Alemoatherium huebneri* has the crown entirely preserved and it is almost out of the alveolus, exhibiting most of the root (Fig. 5). It is conspicuously smaller than the lower canines of other prozostrodontians (e.g. *Prozostrodon brasiliensis*, UFRGS-PV-248-T, Bonaparte & Barberena 2001; *Botucaraitherium belarminoi*, MMACR-PV-003-T, Soares *et al.* 2014). The crown is low, with slightly convex mesial and almost straight distal edges, lacking any kind of serrations. The lingual surface is less convex than the labial and its tip points posterodorsally. There is a small wear facet on the distal surface of the tip. The exposed root is circular in cross-section and has a conspicuous circular pit at the base of its distolingual surface. This represents a resorption pit, which is rarely observed in probainognathians, but more commonly documented in earlier cynodonts (e.g. *Thrinaxodon liorhinus*, NHMUK-PV-R 3731, NHMUK-PV-R 5480; Abdala *et al.* 2013). Leaning mesiolingually towards the root pit, there is a badly preserved element that seems to correspond to a partially-erupted canine tip. This seems to represent a relatively small canine, compared to the fully erupted one. *Protheriodon estudianti* also preserves a canine with its replacement (Bonaparte *et al.* 2006; Martinelli *et al.* 2016).

The postcanine dentition includes a first postcanine tooth in process of eruption, the alveolus of pc2, and functional pc3–pc6. The pc3 appears *in situ* and pc4 to pc6 are detached from the jaw with their respective moulds preserved in the mudstone matrix. In addition, there is a mould of another tooth, considerably smaller than the preceding pc5–pc6. This is considered to be pc7 (Fig. 3), but its crown has been lost. Due to the lack of the posterior portion of the horizontal ramus of the dentary, we are not sure that seven is the total number of lower postcanine teeth.

There is no diastema between the canine and the first postcanine tooth. pc1 was in the process of eruption and it is mostly inside the alveolus. However, due to a break in the dentary bone, it is possible to observe its crown (Fig. 5), which seems to be slightly larger than that of the canine. It is dominated by a large asymmetrical cusp, with convex mesial and almost straight distal edges. At the base of the distal margin of pc1 crown, a tiny cusp c is seen (Fig. 5). Pc1 has a thick enamel layer, which

FIG. 3. Holotype UFSM 11579b of *Alemoatherium huebneri*. Left partial jaw in medial (A) and dorsomedial (B) views, with accompanying line drawings. The isolated pc4, pc5, and pc6 are placed in position in A. Dark grey indicates broken surface and light grey indicates mudstone matrix. Scale bars represent 2 mm. *Abbreviations*: ai, incisor alveolus; ca, lower canine; d, dentary; dlg, dental lamina groove; i, lower incisor; Mg, Meckelian groove; pc, lower postcanine tooth; pi, replacement pit; rc, replacement canine; rr, reabsorbed root; s, symphysis. Colour online.

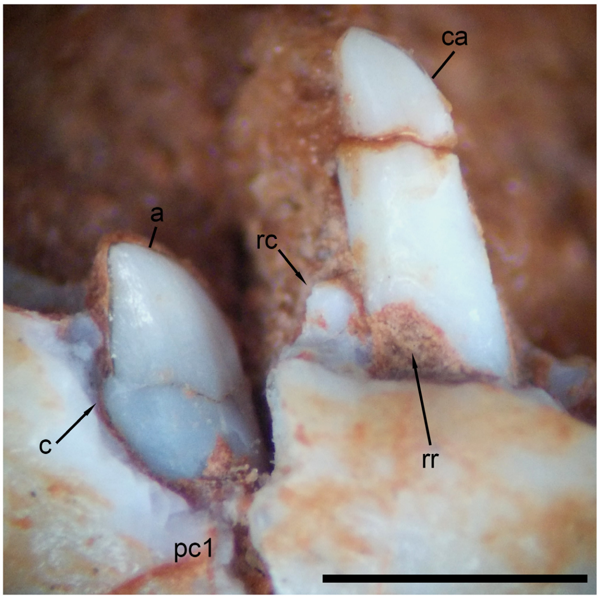


FIG. 5. Holotype UFSM 11579b of *Alemoatherium huebneri*. Detail of the canine and the first postcanine in medial view. Scale bar represents 1 mm. *Abbreviations*: a, c, lower crown cusps a and c; ca, lower canine; pc1, lower first postcanine; rc, replacement canine; rr, reabsorbed root. Colour online.

seems to be thicker in the labial than in the lingual surface of the crown. This is the surface that was directly in contact with the upper teeth during occlusion, and defines sharp mesial and distal cutting edges. The crown of the pc2 is missing. Its alveolus suggests it was intermediate in size between pc1 and pc3. pc 3 is well-preserved in its original place in the dentary. pc3 to pc6 have a similar cusp pattern, with slight differences, increasing considerably in size posteriorly (Figs 3–6). In that direction, the crowns also become apicobasally taller. This results partially from wear along the tooth row, as the anterior teeth bear extensively worn main cusps, whereas those of pc5 and pc6 remain unworn. pc3 to pc6 are transversely narrow, lacking both continuous lingual and labial cingula. However, one or more discrete cingular cusps are seen on the mesiolingual and distolingual corners of the crowns (Fig. 6).

The crown of pc3 has four cusps: the main cusp a; a mesial, small cusp b; and two distal, small cusps c and d. Cusp b is positioned below the level of cusp c and is more transversely developed than either of the distal cusps. A continuous cutting edge is not formed between cusps a and b; instead, there is a shallow groove that descends to the lingual side of the crown. In occlusal view, cusp b is slightly more labially positioned than cusps c and d. Cusp c is in line with cusp a, forming a continuous cutting edge. Cusp d is the smallest cusp, and it is positioned near the crown-root boundary. It is slightly twisted lingually, with convex distolabial and flat lingual surfaces. There are no cingular cusps on the mesiolingual edge of the crown, which appear only in pc4–pc6. Instead, a very shallow vertical ridge is seen in the corresponding area. Some anterior postcanine teeth of juvenile specimens of *Probainognathus jenseni* have a similar ridge, but never develop discrete continuous lingual cingulum or cingular cusps (e.g. Martinelli *et al.* 2016).

The crown of pc4 has a dominant main cusp a, with a worn tip (Fig. 6). The wear facet is oval and is inclined dorsolabially, forming an angle of *c.* 45° with the apicobasal axis. Its lingual surface is subtly mesiodistally convex, whereas the labial one is almost flat, producing a D-shaped cross-section. In occlusal view, due to the wear facet, the enamel layer is not homogeneously distributed, with a thicker portion on the mesiolingual wall. Cusp a is asymmetrical, with the mesial margin about two times taller than the distal, as evident by the position of cusps b and c. The mesial portion of the crown bears two cusps. Cusp b is very small and placed in a basal position relative to cusp c (Fig. 6). It is positioned in the mesiolabial corner of the crown and is not connected to cusp a by a ridge, but instead a shallow notch is seen. The mesiolingual cingular cusp is slightly smaller than cusp b and placed in a lower position. In mesial view, both cusps form a concave longitudinal groove between them. Although it seems to indicate a quite rudimentary interlocking mechanism among postcanine teeth, we cannot confirm this because it is not clearly seen in the remaining elements. The distal portion of the crown bears cusps c and d. Cusp c is subcircular in cross-section, relatively larger than cusp b, and more apically positioned. Its mesial edge is ridged and short, and connects to the distal ridge of cusp a, forming a carnassial notch at its junction (Fig. 6). Cusp d is very small, similar in size to the mesiolingual cingular cusp. In addition, cusp d is more basally positioned than the remaining cusps. This cusp is in mesiodistal line with cusps a and c. Also, cusp d protrudes posterodorsally, forming a concave distal margin. According to their size and height in the crown, the cusp arrangement is as follows: $a \gg c \gg b >$ cingular cusp $\geq d$. In labial view, there is a shallow central groove at the base of the crown that is likely to indicate the presence of a longitudinal groove on the root (i.e. incipient root bifurcation).

As can be seen in Figure 6, pc5 is quite similar to pc4. The main differences are: (1) larger cusp b, with a transversely wide base that tapers abruptly apically; (2) the base of cusp b projects labially towards the base of cusp a forming a faint ridge; (3) two (instead of one) mesiolingual cingular cusps; and (4) cusp d more posteriorly curved, with a more strongly concave distal margin. In pc 5, main cusp a is unworn, resulting in a slightly taller tooth. The relatively large cusp b and the smaller mesiolingual cingular cusps produce a less concave mesial wall than in pc4 (Fig. 6).

The last postcanine, pc6, has subtle differences in crown shape relative to the previous teeth. Cusp b is similar to that of pc5. As in pc5, the base of cusp b projects labially towards the base of cusp a, however, in the pc6 a faint ridge is formed (Fig. 6). There is a single mesiolingual cingular cusp, as in pc4, showing that the number of cingular cusps is not constant along the series. Cusp d is partially broken, but it is evident that it protrudes posteriorly as in the preceding teeth. The main cusp a is totally unworn, with a sharp tip. Despite the aforementioned differences, both pc5 and pc6 have similar cusp arrangement to pc4. There are indications of constricted roots in pc4–pc6. In pc3, the base of the crown is positioned just at the alveolar level, so that the root morphology is not exposed.

Only an imprint of the pc7 crown is available. It is considerably smaller than those of pc4–pc6, similar in size to that of pc3. The exact morphology of this tooth is unknown, but it is apparently similar to the preceding ones.

The size variation in the tooth row is noteworthy: pc1 is almost equal to or slightly larger than the canine, pc1 and pc3 are nearly of the same size, there is an abrupt increase in size from pc4 to pc6, and then pc7 is small.

With the evidence at hand, we cannot properly determine the age of the holotype of *Alemoatherium huebneri*. The partially erupted i4, canine, and pc1 of UFSM 11579b indicate that tooth replacement was active when the animal died. At the same time, there are evident wear facets in i2, i3, and pc4. The presence of an apparently small-sized postcanine (pc7) at the rear of the tooth row is also not unambiguously indicative of a certain age. A small postcanine at the end of the maxillary tooth row is observed in individuals of different ages of *Thrinaxodon liorhinus* and, at least, in some juveniles of *Probainognathus jenseni* (Abdala *et al.* 2013). Based on these features, the holotype of *A. huebneri* could belong to a subadult individual, but only further specimens will help to confirm this.

DISCUSSION

Phylogenetic position of Alemoatherium huebneri

The first phylogenetic analysis, including only the holotype of *Alemoatherium huebneri*, resulted in 12 most parsimonious trees (L = 445; Ci = 0.47; Ri = 0.78). The strict consensus tree is shown in Figure 7A and Martinelli *et al.* (2017). *Alemoatherium huebneri* is depicted as a basal prozostrodontian, forming a politomy with *Prozostrodon brasiliensis*, *Therioherpeton cargnini* plus a more inclusive clade including ictidosaurs, tritylodontids, ‘brasilodontids’, *Adelobasileus cromptoni*, *Sinoconodon rigneyi*, and *Morganucodon* spp. (Mammaliaformes) (Fig. 7A). In fact, the inclusion of *A. huebneri* in this data matrix introduces conflicts and hampers the resolution of relationships among the basal prozostrodontians *P. brasiliensis* and *T. cargnini*, which have usually been resolved in other analyses (e.g. Liu & Olsen 2010; Martinelli *et al.* 2016). This problem is partly due to the incompleteness of *A. huebneri*, which was scored for only 14 characters (*c.* 10% of the total). In addition, the lack of lower jaws of *T. cargnini* and the incompleteness of the skull of both *T. cargnini* and *P. brasiliensis* generate problems for resolving this part of the tree. In this analysis, the characters that support the Prozostrodontia clade are: the anteroposterior extent of the secondary plates more than 45% of skull length (ambiguous, 36(1); unknown in *A. huebneri*); unfused dentary symphysis (ambiguous, 82(0); unknown in *T. cargnini*); upper postcanine root constricted (unambiguous, 106(1); unknown in *A. huebneri*); and lower postcanine root constricted (unambiguous, 107(1); unknown in *T. cargnini*).

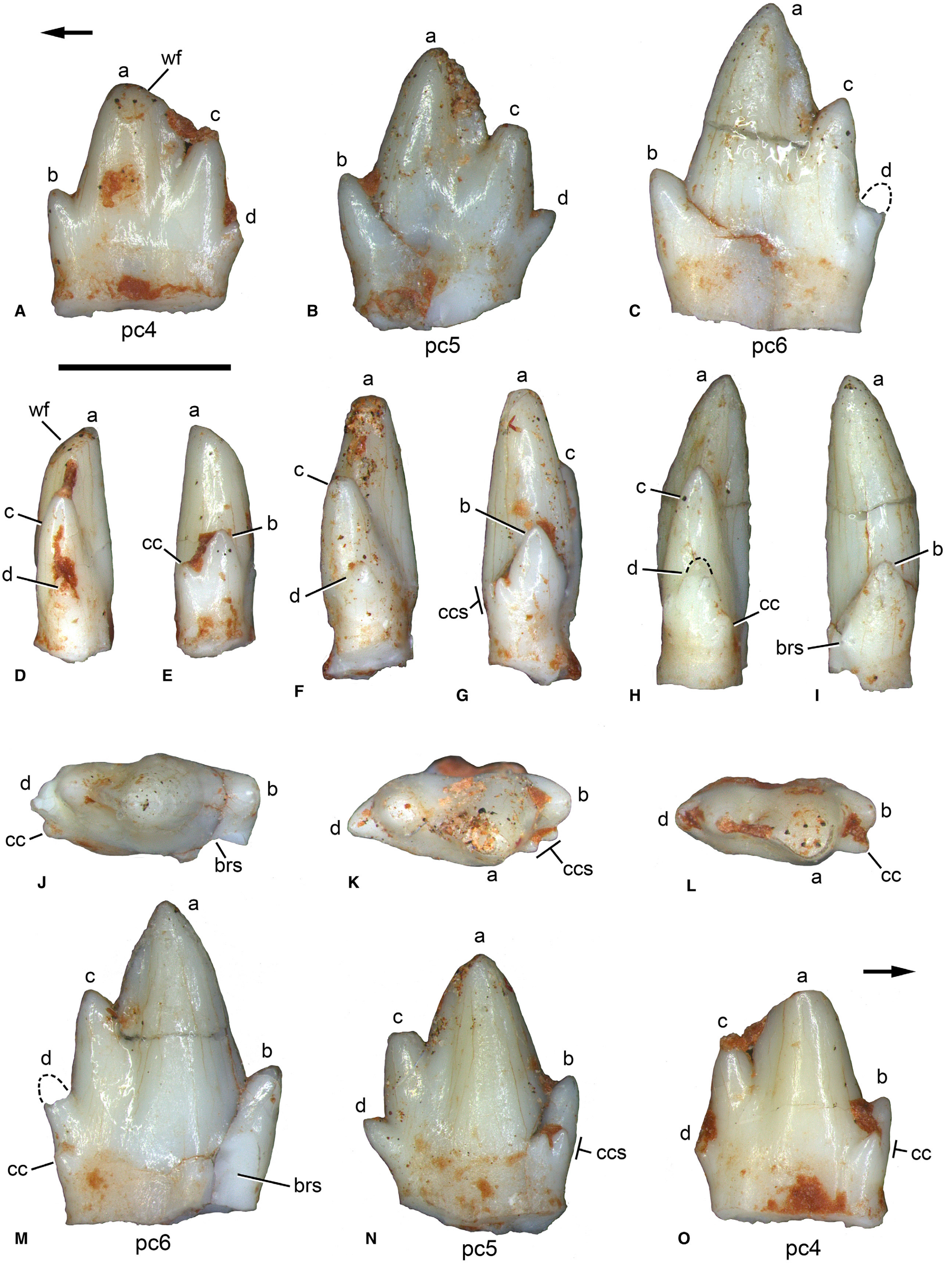
The second analysis, which added *Santacruzgnathus abdalai* and *Microconodon tenuirostris*, resulted in 308 most parsimonious trees (L = 446; Ci = 0.47; Ri = 0.78). As in the previous analysis, a large politomy is formed at the base of the Probainognathia clade, also collapsing *Pachygenelus monus* and *Riograndia guaibensis* (see Fig 7B). In this analysis one more character is added in support of the Prozostrodontia clade: three or fewer upper incisors (ambiguous, 94(2); unknown in both of the newly added taxa and in *Therioherpeton cargnini*).

The third analysis added *Charruodon tetracuspidatus* and produced 428 most parsimonious trees (L = 446; Ci = 0.47; Ri = 0.78). The inclusion of this taxon introduces a politomy formed by *Probainognathus jenseni*, *Bonacynodon schultzi* (collapsed probainognathids), *Protheriodon estudianti*, *C. tetracuspidatus* plus Prozostrodontia (also collapsed at the base as shown in the second analysis) (Fig 7C). The incompleteness of the newly added taxon is responsible for the ambiguity of the relationships amongst probainognathians. Further specimens and a more focused set of characters are needed to address these issues. As discussed below, these results show *Alemoatherium huebneri*, *S. abdalai* and *M. tenuirostris* nested within Prozostrodontia, and *C. tetracuspidatus* as an unstable taxon positioned among non-prozostrodontian probainognathians.

Alemoatherim huebneri *as a new cynodont*

Other known probainognathian cynodonts from the *Hyperodapedon* AZ, which yielded *Alemoatherium huebneri* (Fig. 2) are the ecteniniid *Trucidocynodon riograndensis* (Oliveira *et al.* 2010), the enigmatic *Charruodon tetracuspidatus* (Abdala & Ribeiro 2000), and the prozostrodontians *Therioherpeton cargnini* (Bonaparte & Barberena 2001; Oliveira, 2006) and *Prozostrodon brasiliensis* (Bonaparte & Barberena 2001). Detailed comparisons with *T. cargnini* and *C. tetracuspidatus*, along with comments on these taxa, are provided below.

Trucidocynodon riograndensis is a large-sized basal probainognathian with a dentition typical of hypercarnivore habits (UFRGS-PV-1051-T; Oliveira *et al.* 2010). It has a deep and robust dentary with sectorial postcanine teeth. The cusps are mesiodistally aligned and recurved posteriorly, with conspicuous cusps a, c, and d that decrease in size posteriorly. Some postcanine teeth bear a tiny cusp b. Upper and lower postcanine teeth are also slightly imbricated, with the distal portion of the preceding tooth positioned labial to the mesial portion of the following. Conspicuously, the margins of all cusps are finely denticulated (UFRGS-PV-1051-T; Oliveira *et al.*


a
wf
c
b
d
A
pc4
a
c
b
d
B
pc5
a
c
b
d
C
pc6
wf
a
c
d
D
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cc
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2010). Such features, including the robustness of the jaw and the morphology of lower dentition, differ significantly from those of *Alemoatherium huebneri*.

The postcanine teeth of *Prozostrodon brasiliensis* clearly differ from those of *Alemoatherium huebneri* by the presence of a continuous lingual cingulum with up to six discrete cingular cusps in the most complex lower postcanines (UFRGS-PV-248-T; Bonaparte & Barberena 2001, Pacheco *et al.* 2017) (Fig. 8). Main cusp a of *P. brasiliensis* is also apicobasally shorter, and cusp b occupies a higher position on the crown (Fig. 8). In addition, some lower postcanines of *P. brasiliensis* have the main cusp a posteriorly inclined. The lower canine of *P. brasiliensis* is a large tooth and there are only four lower incisors (Fig. 8). Its symphyseal articular surface is considerably longer than that of *A. huebneri*, extending posteriorly to the level of the canine/postcanine diastema. Although, the holotype of *P. brasiliensis* (UFRGS-PV-248-T) is about four times larger than that of *A. huebneri*, the differences cannot be explained by ontogeny and the distinctive features listed above are of taxonomic value.

Regarding the other non-prozostrodontian probainognathians, *Alemoatherium huebneri* differs from *Chiniquodon theotonicus* (PVL 4444; Romer 1969*a*, *b*; Abdala & Giannini 2002), ecteniniids (e.g. *Ecteninion*, PVSJ 422; Martínez *et al.* 1996) and *Mitredon cromptoni* (Shapiro & Jenkins 2001) because these taxa have backwardly curved main cusps a, c, and d, larger canines, fewer lower incisors, and a robust lower jaw. These features also differentiate *Lumkuia fuzzi* (Hopson & Kitching 2001) from *A. huebneri*, the former being positioned in some phylogenies as the basal most probainognathian (Hopson & Kitching 2001; Ruta *et al.* 2013).

The postcanine tooth pattern of *A. huebneri* is more reminiscent of that seen in triconodont-like toothed probainognathids such as *Probainognathus jenseni* and *Bonacynodon schultzi*. Nonetheless, *A. huebneri* has a slenderer jaw, a higher number of lower incisors, cingular cusps on the mesiolingual and distolingual corners of the crown, and less developed cusps b and d in comparison to those two taxa (Martinelli *et al.* 2016).

Protheriodon estudianti is an eucynodont from the *Dinodontosaurus* AZ that was considered either as member of 'brasilodontids' (Bonaparte *et al.* 2006) or as the sister taxon of Prozostrodontia (Martinelli *et al.* 2016). Its anatomy is only partially known, but it closely resembles that of *Alemoatherium huebneri*. Both share a slender dentary and a high number of lower incisors (five in *A. huebneri* and four in *P. estudianti*; UFRGS-PV-0962-T, Martinelli *et al.* 2016). The available posterior lower postcanine teeth of *P. estudianti* have a large globular cusp a, small cusps b and c of apparently similar size, and crowns more constricted at the base. In contrast, *A. huebneri* has a flat and tall cusp a and a much reduced cusp b.

The lower postcanine teeth of *Candelariodon barberenai*, another taxon from the *Dinodontosaurus* AZ (Oliveira *et al.* 2011), are quite different from those of *Alemoatherium huebneri*, as a marked distinction is seen between its anterior and posterior postcanine teeth (MMACR-PV-0001-T; Martinelli *et al.* 2015). Also, its last sectorial postcanine teeth have a continuous lingual cingulum (Martinelli *et al.* 2015) and cusp c is not as prominent as in *A. huebneri*. In addition, *C. barberenai* has a large canine and an elongated mandibular symphysis.

Santacruzgnathus abdalai, from the *Santacruzodon* AZ, is based on a right lower jaw fragment with the last postcanine (Martinelli *et al.* 2016). It is similar in size to *A. huebneri* and they both have a slender jaw and a discrete Meckelian groove (Fig. 8). The postcanine tooth of *S. abdalai* differs from those of *A. huebneri* in having a mesiodistally longer and apicobasally shorter crown, with less prominent cusp a. Cusp d is much more developed and has a strongly convex distal edge, differing form the concave distal wall seen in *A. huebneri*. *S. abdalai* was related to prozostrodontians, due to its similarity with 'brasilodontids' (Martinelli *et al.* 2016). The similarity with *A. huebneri* is also conspicuous, indicating a close phylogenetic relationship.

Alemoatherium huebneri also clearly differs from ictidosaurs (*Riograndia guaibensis* plus Tritheledontidae *sensu* Martinelli & Rougier 2007). Indeed, the postcanine teeth of *R. guaibensis* are transversely narrow, lack a cingulum, and bear several small cusps (up to nine) in the cutting edges of the crown. Its lower jaw is robust and there is a hypertrophied lower incisor (i1) (Bonaparte *et al.* 2001; Soares *et al.* 2011). Differing from the pattern of *A. huebneri*, the postcanine teeth of tritheledontids, such as *Irajatherium hernandezi* (UFRGS-PV-0599-T; Martinelli *et al.* 2005), *Chaliminia musteloides* (PULR 081; Martinelli & Rougier 2007) and *Pachygenelus monus* (SAM 1315, SAM 1329, SAM 1394; Gow, 1980), bear three main cusps (a, c, d), which gradually decrease in size, with a continuous cingulum seen in some taxa. In addition,

FIG. 6. Isolated left postcanine teeth of holotype UFSM 11579b of *Alemoatherium huebneri*. Fourth postcanine tooth (pc4) in labial (A), distal (D), mesial (E), occlusal (L), and lingual (O) views. Fifth postcanine tooth (pc5) in labial (B), distal (F), mesial (G), occlusal (K), and lingual (N) views. Sixth postcanine tooth (pc6) in labial (C), distal (H), mesial (I), occlusal (J), and lingual (M) views. Scale bar represents 1 mm. *Abbreviations*: a–d, lower crown cusps a to d; cc(s), cingular cusp(s); brs, broken surface; pc, lower postcanine; wf, wear facet. Arrow indicates mesial direction. Colour online.

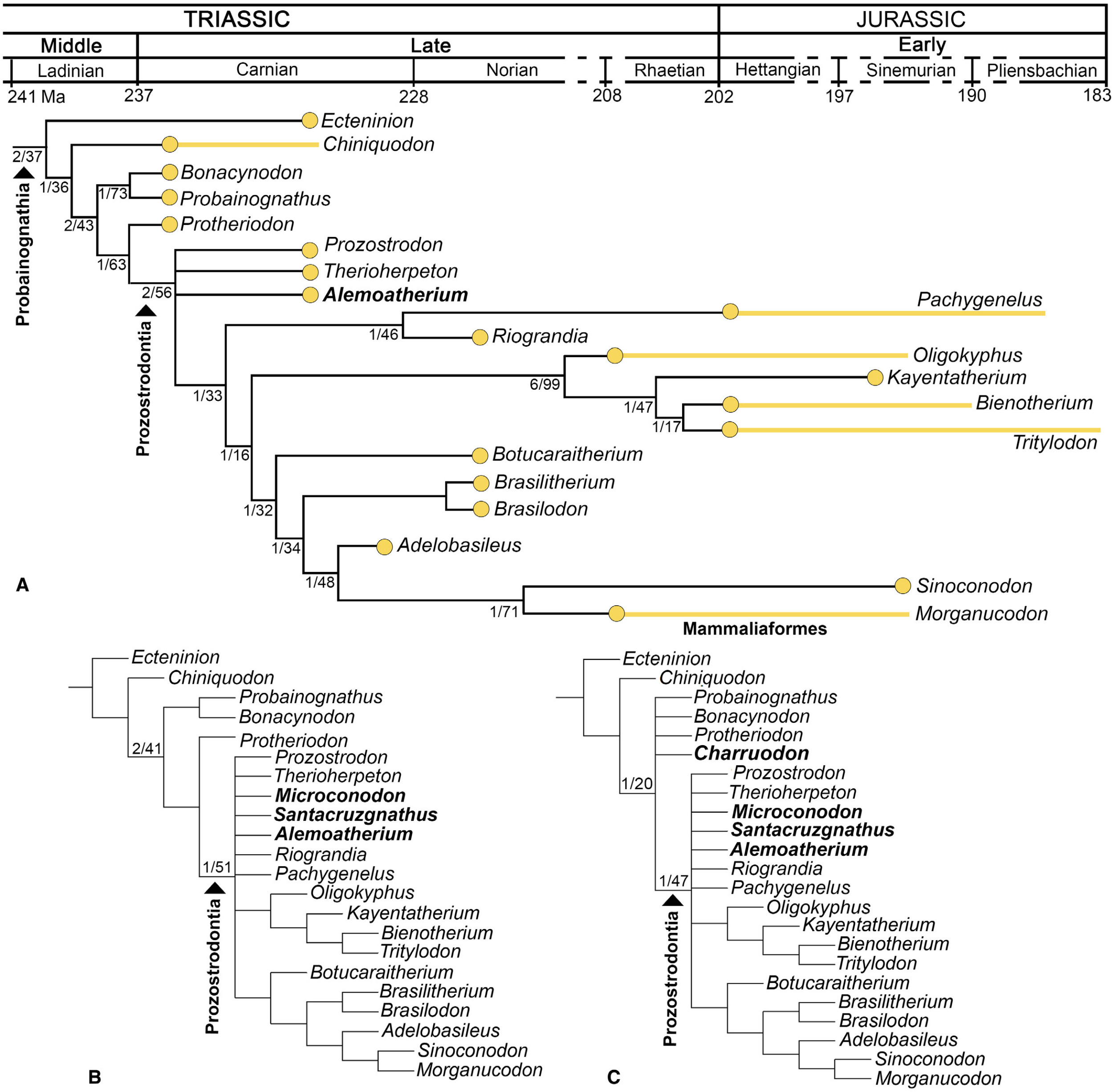


FIG. 7. Phylogenetic analyses. A, strict consensus tree of 12 most parsimonious trees of the first analysis, showing the Probainognathia clade with the phylogenetic position of *Alemoatherium huebneri*; shaded circles and lines indicate the span of the taxon. B, strict consensus tree of second analysis with the addition of *Santacruzgnathus abdalai* and *Microconodon tenuirostris*. C, strict consensus tree of third analysis with the further addition of *Charruodon tetracuspidatus*. The numbers at nodes indicate Bremer support and Bootstrap values, respectively. Colour online.

tritheledontids have tall and robust dentaries (e.g. Martinelli *et al.* 2005).

Prozostrodontians more closely related to Mammaliaformes include the *Riograndia* AZ 'brasilodontids': *Brasilodon quadrangularis*, *Brasilitherium riograndensis*, *Minicynodon maieri* and *Botucaraitherium belarminoi* (Bonaparte *et al.* 2003, 2005, 2010, 2012; Soares *et al.* 2014). The lower postcanine teeth of these forms bear a strong resemblance to those of *Alemoatherium huebneri*, mainly on the distribution and relative size of the cusps (Fig. 8). Nonetheless, 'brasilodontids' have: (1) anterior/middle postcanine teeth well-differentiated from the posterior ones; (2) more developed cingular cusps on the lingual side of the postcanine crown; (3) more developed cusps b and d; and (4) much constricted roots with a conspicuous eight-sided cross-section. In addition, the jaw of *A. huebneri* is slender as in 'brasilodontids', with the same anterodorsal projection of the dentary (Fig. 7)

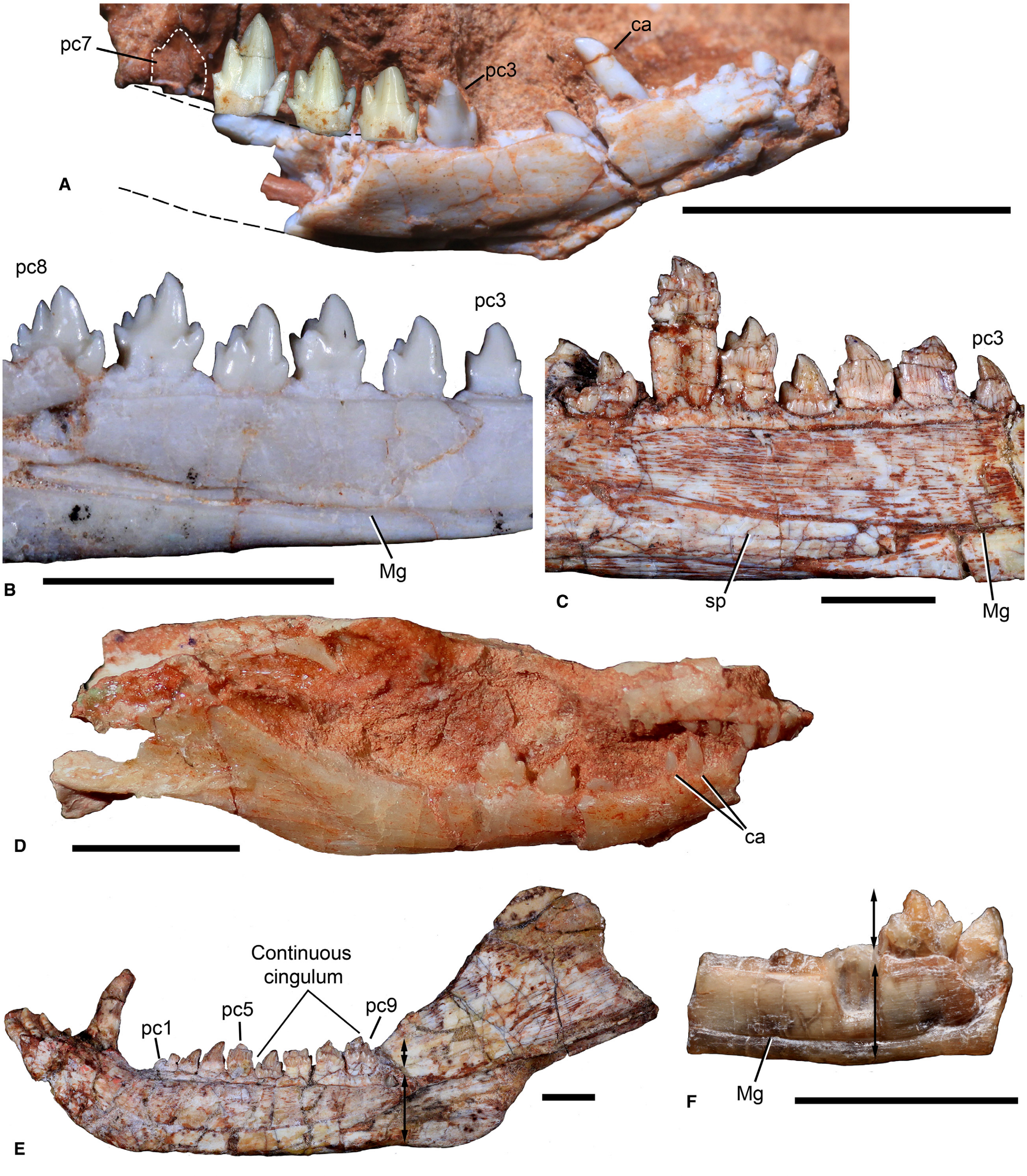


FIG. 8. Comparisons of *Alemoatherium huebneri* with selected prozostrodontians. A, left lower jaw of *Alemoatherium huebneri* (holotype UFSM 11579b) in medial view. B, detail of left postcanine teeth of *Brasilitherium riograndensis* (UFRGS-PV-0603-T) in lingual view. C, detail of left postcanine teeth of *Prozostrodon brasiliensis* (holotype UFRGS-PV-248-T) in lingual view. D, skull and jaw of *Brasilitherium riograndensis* (holotype UFRGS-PV-0594-T) in lateral view (inverted). E, right lower jaw of *Prozostrodon brasiliensis* (holotype UFRGS-PV-248-T) in medial view. Arrows on D and E represent crown height (upper) and dentary height (lower). F, right lower jaw of *Santacruzgnathus abdalai* (holotype UFRGS-PV-1121-T) in medial view. Scale bars represent 5 mm. *Abbreviations:* ca, lower canine; Mg, Meckelian groove; pc, lower postcanine; sp, splenial. Colour online.

and reduced/unfused mandibular symphysis. The similarities in the symphyseal region of *A. huebneri* and young individuals of *B. riograndensis* are noticeable (e.g. UFRGS-PV-598-T) supporting their close relationship (Fig. 7). Nonetheless, the incisor/canine homology in the latter taxon is still under study.

The North American Triassic dromatheriids *Microconodon tenuirostris* and *Dromatherium sylvestre* (Osborn 1886; Simpson 1926; Sues 2001) share with *Alemoatherium huebneri* a slender dentary with an anterodorsal projection (Fig. 9), but the latter is reduced in those taxa. Their postcanine dentition is unfortunately poorly known (Simpson 1926; Sues 2001) but they all differ from those of *A. huebneri* by the presence of a single main cusp in the anterior teeth and middle and posterior teeth with apicobasally shorter crowns, lacking a cingulum or cingular cusps on the lingual side (Fig. 9). Based on the preserved alveolus, the canine of *M. tenuirostris* is large, and there are only three incisors in both taxa (Simpson 1926; Sues 2001). Other dromatheriid cynodonts include *Rewaconodon tikiensis* from the Late Triassic of India, based on isolated upper and lower postcanine teeth (Datta *et al.* 2004). They are similar to those of *A. huebneri*, especially the holotype lower postcanine. This tooth has a transversely narrow crown with cusps a > c ≥ b ≫ d, and an incipient constriction in the root (Datta *et al.* 2004). However, *A. huebneri* differs from *R. tikiensis* by having cusp b much reduced and positioned in a much lower position on the crown, cingular mesiolingual cusps, and a less transversely narrow crown (Fig. 9).

Apart from *Microconodon tenuirostris*, *Dromatherium sylvestre* and *Mitredon cromptoni*, much of the Triassic record of non-mammaliaform probainognathians from Laurasia is based on isolated remains, mainly teeth, from Europe (e.g. France, Switzerland, Luxemburg, Belgium, Germany) and North America. Among them, numerous species of the genera *Pseudotriconodon* (Hahn *et al.* 1984, 1994), *Tricuspes* (Huene 1933; Godefroit & Battail 1997; Hahn *et al.* 1994), *Lepagia* (Hahn *et al.* 1987), *Gaumia*

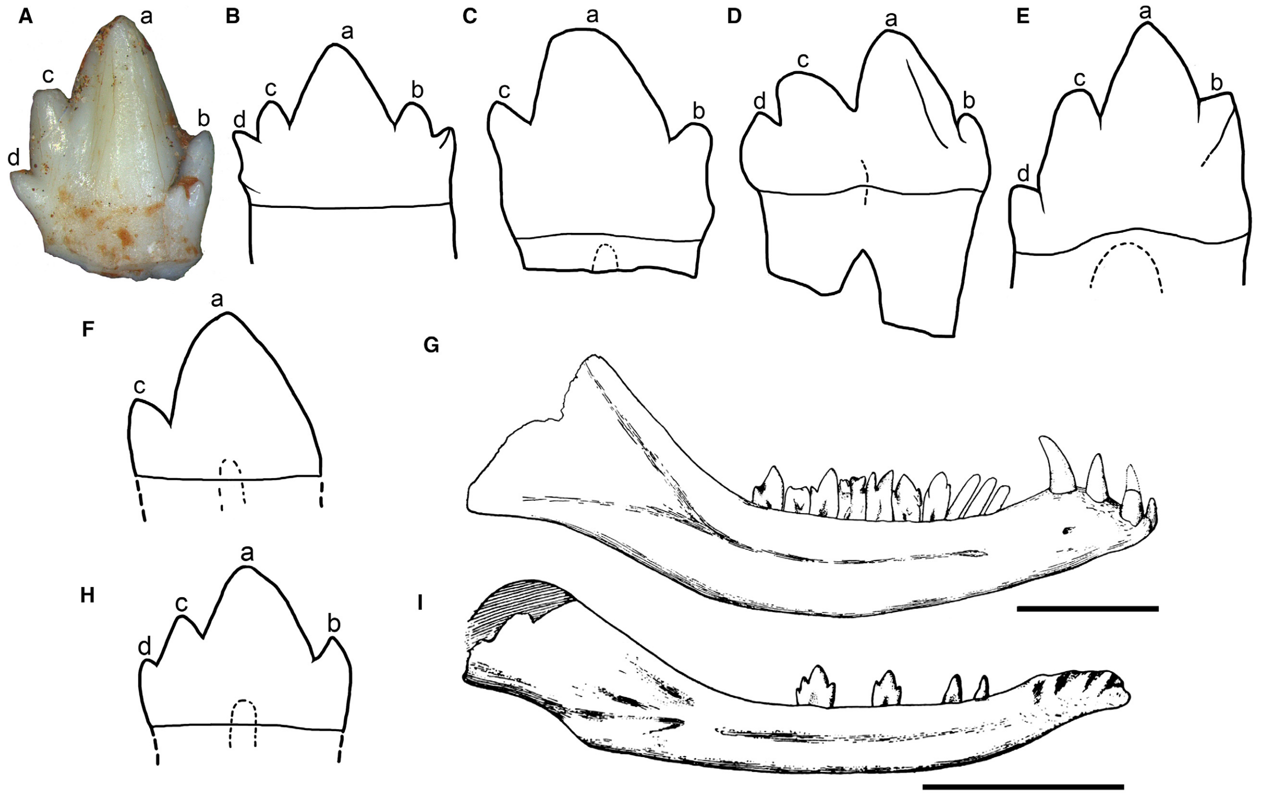


FIG. 9. Comparisons of *Alemoatherium huebneri* with selected non-South American probainognathians in lingual view. A, lower pc5 of *Alemoatherium huebneri* (holotype UFSM 11579b). B, lower postcanine of *Pseudotriconodon wildi* (inverted, modified from Hahn *et al.* 1994). C, lower postcanine of *Tricuspes sigogneauae* (inverted, modified from Hahn *et al.* 1994). D, lower postcanine of *Meurthodon gallicus* (inverted, modified from Russell *et al.* 1976). E, lower postcanine of *Rewaconodon tikiensis* (modified from Datta *et al.* 2004). F–G, lower postcanine (F) and right lower jaw (G) of *Dromatherium sylvestre* (modified from Simpson 1926). H–I, lower postcanine (H) and right lower jaw (I) of *Microconodon tenuirostris* (modified from Simpson 1926). Postcanine teeth are not to scale. Scale bars represent 5 mm (G, I). *Abbreviations:* a–d, lower crown cusps a to d. Colour online.

(Hahn *et al.* 1987) and *Meurthodon* (Russell *et al.* 1976; Sigogneau-Russell & Hahn 1994) have been recognized. The morphology of these taxa is reminiscent of that of *Alemoatherium huebneri* as they are all based on sectorial triconodont-like postcanine teeth (Fig. 9). Unlike *A. huebneri*, *Lepagia*, *Gaumia* and *Pseudotriconodon* have symmetrical postcanine teeth with a prominent main cusp a, reduced cusps b–e disposed in a line, and no cingulum (Fig. 9). The cusp arrangement of *Tricuspes* is more similar to that of *A. huebneri* than to that of *Pseudotriconodon*. However, cusp d is absent and cusps b and c seem to be larger than in *A. huebneri* (Fig. 9). The postcanine teeth of *Meurthodon* differ from those of *A. huebneri* by the absence of accessory lingual cusps, because cusps a and c are projected slightly posteriorly, and cusp d is larger than cusp b (Fig. 9), positioned in a much higher position on the crown (Russell *et al.* 1976; Sigogneau-Russell & Hahn 1994).

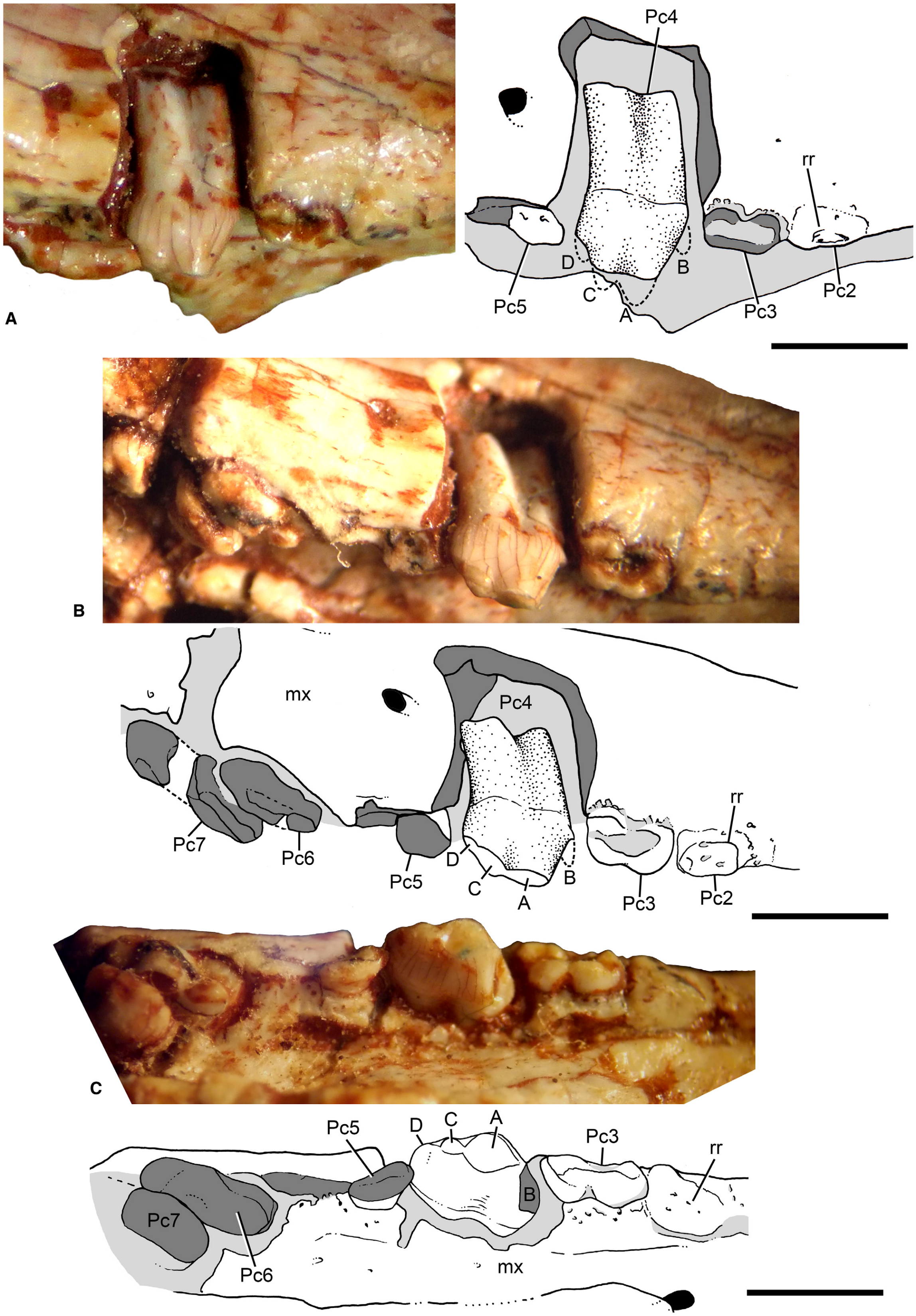
The slender dentary, its anteroventral projection, and reduced symphysis are features that *Alemoatherium huebneri* shares with *Brasilodon quadrangularis*, *Brasilitherium riograndensis*, *Minicynodon maieri*, *Microconodon tenuirostris* and early mammaliaforms (e.g. *Morganucodon* spp., Kermack *et al.* 1973; *Megazostrodon rudnerae*, Crompton & Jenkins 1968; Crompton 1974). The lower jaw of *Therioherpeton cargnini* is mostly unknown, but it is expected to have a similar morphology to that of *A. huebneri* (see below). Unfortunately, most cynodonts included within Dromatheriidae (or Therioherpetidae according to Hahn *et al.* 1994) are based on isolated teeth only, hampering more detailed comparisons. Nonetheless, the dentition of *A. huebneri* exhibits a more complex triconodont-type pattern by having discrete cingular cusps on the lingual side of the crown. Regarding the South American fossil record, the postcanine dentition of *A. huebneri* is more similar to that of *Santacruzgnathus abdalai,* from the *Dinodontosaurus* AZ, and of the complex *Brasilodon quadrangularis*, *Brasilitherium riograndensis*, *Minicynodon maieri* (Bonaparte *et al.* 2003, 2005, 2012) from the younger *Riograndia* AZ, as suggested in the comparisons above and its phylogenetic placement (Fig. 7). More complete specimens of some taxa are needed to better resolve their phylogenetic relationships, and to understand dental morphological variation along tooth rows and in ontogenetic series, which may have deep implications for their taxonomy and palaeobiology.

Alemoatherium, Therioherpeton *and* Charruodon

Among the probainognathians known so far from the *Hyperodapedon* AZ, *Therioherpeton cargnini* (Bonaparte & Barberena 1975, 2001) is the one that most closely resembles *Alemoatherium huebneri* regarding size and postcanine morphology. Yet, several inconsistencies in the published data on *T. cargnini* (e.g. Bonaparte & Barberena 1975, 2001; Oliveira 2006) hamper such comparisons, and a revaluation based on the re-examination of its holotype was necessary. That specimen (MVP 05.22.04), which was found about 1.5 km southwest of the site of *A. huebneri*, includes a partial skull lacking the primary palate and the basicranium, partial upper dentition on the right maxilla, an isolated partial lower postcanine crown, a posterior fragment of the right dentary attached to the skull, and several partially articulated postcranial elements**.** The material was studied by Bonaparte & Barberena (1975, 2001) and Oliveira (2006), in addition to studies of its cranial cavities conducted by Quiroga (1984). Re-examination has led us to reinterpret certain features, especially regarding the dental and humeral morphology.

The upper postcanine teeth of *Therioherpeton cargnini* are badly preserved with the exception of one tooth that was considered to be Pc5 by Bonaparte & Barberena (1975, 2001) and Pc4 by Oliveira (2006). The former authors identified eight upper postcanine teeth, whereas the latter possibly only seven, as corroborated here. Pc1 and Pc2 include the remains of only the roots in the process of resorption, as indicated by the presence of irregular tissue and very small pits (Fig. 10). The crowns of these postcanine teeth were drawn in occlusal view in Oliveira (2006), but they are not preserved (Fig. 10). Pc3, Pc5, Pc6 and Pc7 have most of their crowns broken off, with no evidence of their original morphology (Fig. 10). They are transversely narrow and increase posteriorly in mesiodistal length. Pc4 is the best preserved tooth. It is transversely narrow, with four mesiodistally aligned cusps (A–D) and no evidence of a cingulum or cingular lingual cusps. The main cusp A is large and occupies most of middle and mesial portions of the crown. Its tip is partially broken. Cusp C is larger than cusps B and D and positioned next to cusp A. Only the base of cusp B is preserved, so that its development is unknown; although it is positioned closer to the alveolar level than cusp D. Cusp D is also broken, with the base preserved, and seems to be smaller than cusp B. The root has a well-defined constriction, with a deep groove developed all along (Fig. 10). It is impossible to perform a direct comparison with *Alemoatherium huebneri*, as no upper dentition is available for the new taxon.

The only available lower postcanine tooth of *Therioherpeton cargnini* is broken in two pieces: the lower half of the crown and most of main cusp a. Both portions are glued to a hard piece of matrix that does not correspond to the original bearing rock of the specimen (Fig. 11A). The isolated cusp a is large, with a conspicuous distal cutting edge that contacts the mesial edge of cusp c, as in other probainognathians (e.g. *Probainognathus jenseni*,


A
Pc4
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D
B
C
A
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C
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Prozostrodon brasiliensis, *Brasilitherium riograndensis*, *Alemoatherium huebneri*). Both cusps b and d seem to be separated by deep V-shaped notches from the adjacent cusp, and all cusps seem to be in an upright position. In Figure 11, we include the reconstruction of this tooth by Bonaparte & Barberena (1975, 2001) (Fig. 11E) and Abdala & Ribeiro (2000) (Fig. 11F). However, the available specimen indicates that the apices of cusps a and c are not as smooth as shown in these reconstructions. Consequently, we propose a new interpretation (Fig. 11D) that is quite similar to that already presented by Hahn *et al.* (1994, fig. 2a). This tooth differs from those of *A. huebneri* in being mesiodistally longer and apicobasally shorter. Also, cusp d is more developed and positioned further away from cusp c than in any postcanine teeth of *A. huebneri*. Due to its incompleteness, including a broken lingual surface at the base of the crown, it is not possible to see if *T. cargnini* has accessory lingual cusps. There are none in the upper postcanine teeth, but we are not sure if this feature is conservative between the upper and lower dentition.

Based on the slender snout and zygomatic arches, and the small lower jaw portion attached to the right side of the skull, it is likely that *Therioherpeton cargnini* possessed a slender lower jaw, possibly similar to that of *Protheriodon estudianti*, *Santacruzgnathus abdalai*, *Brasilodon quadrangularis*, *Brasilitherium riograndensis* and the taxon here described, unlike the robust lower jaw of *Charruodon tetracuspidatus* (see below).

Oliveira (2006) described a distal end of a humerus of *Therioherpeton cargnini* not published by Bonaparte & Barberena (1975, 2001). He mentioned that only the entepicondylar foramen was present, as commonly found in mammaliforms (Jenkins & Parrington 1976). Nonetheless, our re-examination of the material indicates that the ectepicondylar foramen, partially covered by sediment, is also present, as seen in most other cynodonts (e.g. Jenkins 1971; Bonaparte & Barberena 2001; Martinelli *et al.* 2005; Oliveira *et al.* 2010). This new information was included in the phylogenetic data matrix (see also figure in Martinelli *et al.* 2017).

Most phylogenetic analyses place *Therioherpeton cargnini* in a near-Mammaliaformes position among probainognathians (e.g. Hopson & Kitching 2001; Bonaparte *et al.* 2005; Martinelli & Rougier 2007; Ruta *et al.* 2013) within the clade Prozostrodontia (Liu & Olsen 2010; Soares *et al.* 2014; Martinelli *et al.* 2016) as supported by several apomorphic traits such as a slender zygomatic

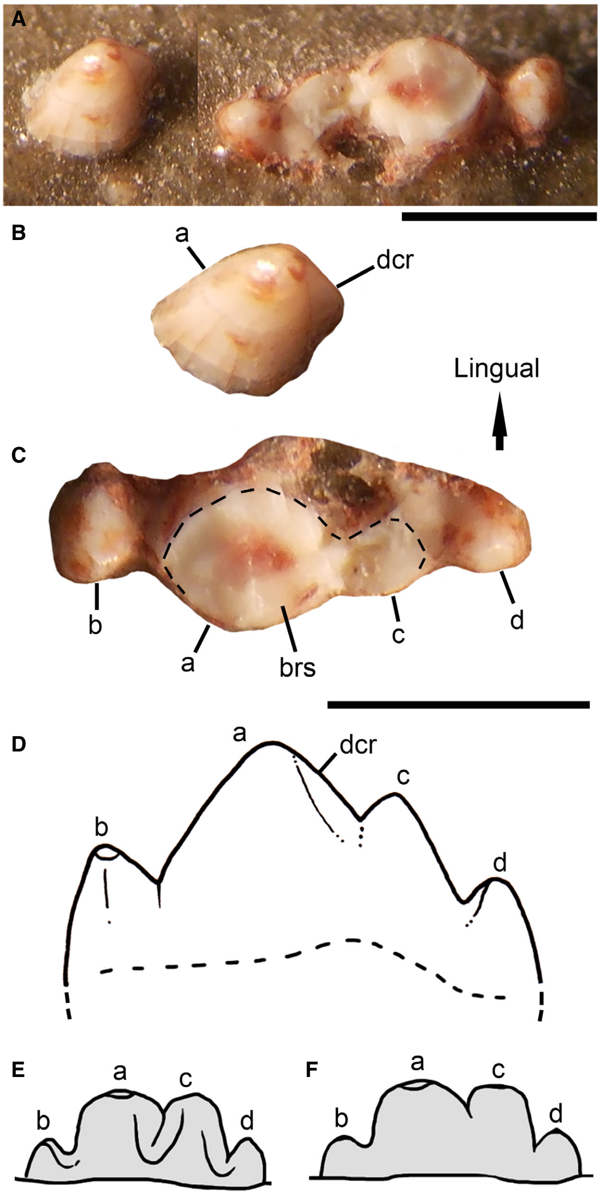

FIG. 11. Isolated lower postcanine tooth of holotype MVP 05.22.04 of *Therioherpeton cargnini*. A, lower postcanine tooth glued in two parts (main cusp a on the left and part of the crown on the right) on a piece of rock. B–C, details of the apical portion of cusp a (B) and base of the crown (C). D–F, reconstruction based on the available lower postcanine tooth (D) in comparison with the reconstructions presented by Bonaparte & Barberena (1975, 2001) (E), and Abdala & Ribeiro (2000) (F). Scale bars represent 1 mm (A–D); E and F are not to scale. *Abbreviations*: a–d, lower crown cusps a to d; brs, broken surface; dcr, distal crest. Colour online.

FIG. 10. Upper postcanine teeth of holotype MVP 05.22.04 of *Therioherpeton cargnini*. A, detail of right Pc4 and surrounding teeth in lateral view with accompanying line drawing. B–C, detail of part of the right upper postcanine tooth row in lateroventral (B) and ventromedial (C) view. Dark grey indicates broken surface and light grey indicates mudstone matrix. Scale bars represent 2 mm. *Abbreviations*: A–D, upper crown cusps A to D; mx, maxilla; Pc, upper postcanine tooth; rr, reabsorbed root. Colour online.

arch, no prefrontal and postorbital bones, a posteriorly extensive secondary palate, and constricted root on postcanine teeth (Bonaparte & Barberena 2001). *Therioherpeton cargnini* and *Alemoatherium huebneri*, both from the same *Hyperodapedon* AZ of the Santa Maria region, are the smallest cynodonts from this AZ and further specimens of both taxa will be necessary to better understand their taxonomic and phylogenetic relationships.

Charruodon tetracuspidatus is another enigmatic probainognathian from the *Hyperodapedon* AZ, found in the municipality of Candelária (Abdala & Ribeiro 2000). The only known specimen is its holotype, composed of a left dentary fragment with three incisor alveoli, the canine root, three postcanine teeth *in situ*, and an isolated lower postcanine tooth, interpreted as pc5 (MCP-3934 PV; Abdala & Ribeiro 2000). Abdala & Ribeiro (2000) tentatively referred *C. tetracuspidatus* to Therioherpetidae due

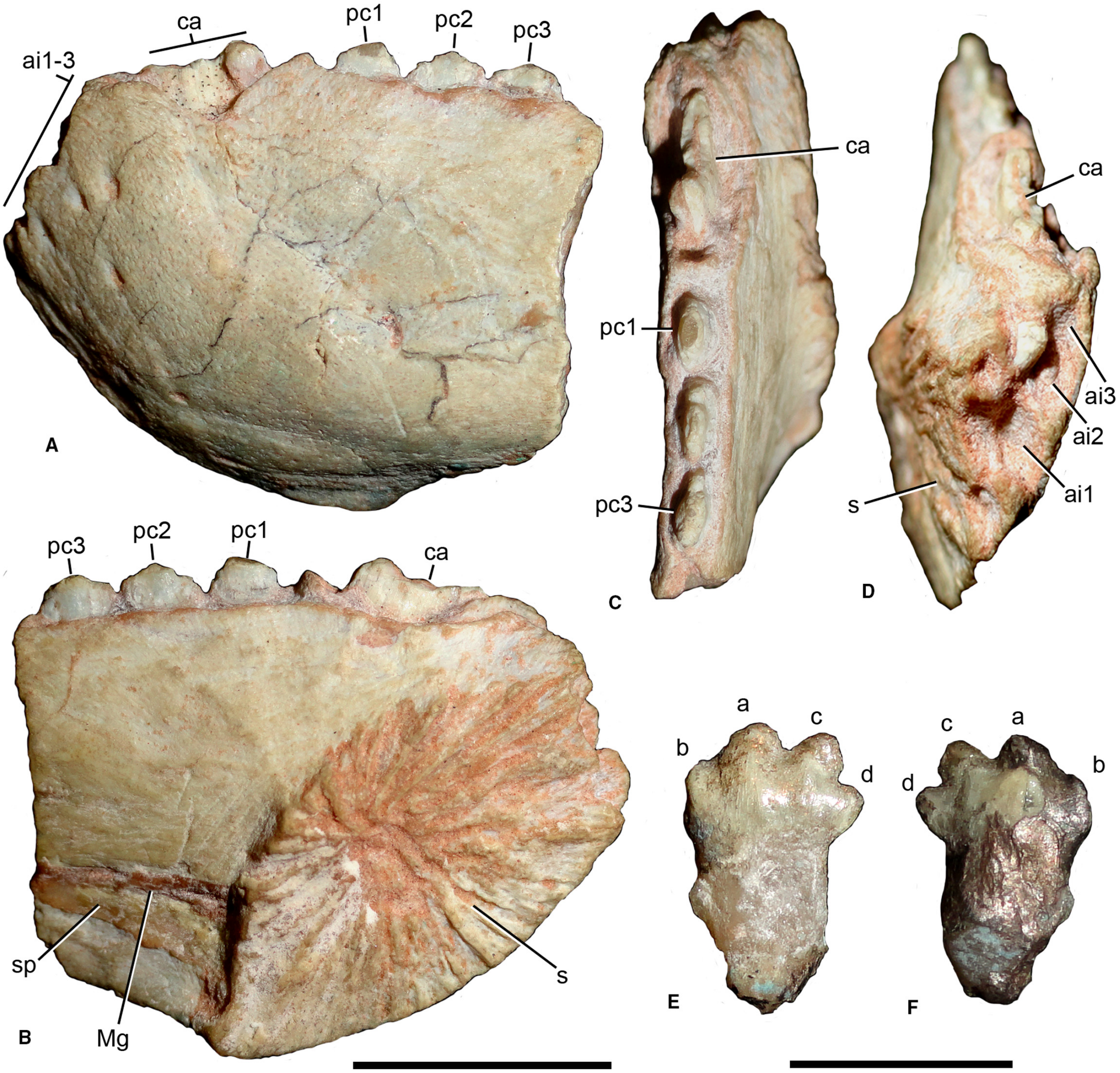

FIG. 12. Partial jaw and postcanine tooth of holotype MCP-3934 PV of *Charruodon tetracuspidatus*. A–D, anterior portion of left lower jaw in lateral (A), medial (B), dorsal (C) and anterodorsal (D) view. E–F, detail of isolated lower left postcanine tooth, interpreted as pc5, in labial (E) and lingual (F) views. Scale bars represent 10 mm (A–D); 5 mm (E, F). *Abbreviations*: a–d, lower crown cusps a to d; ai, alveolus incisor; ca, lower canine; Mg, Meckelian groove; pc, lower postcanine tooth; s, symphysis; sp, splenial. Colour online.

to the resemblances in postcanine morphology with *Therioherpeton cargnini* (see above; Fig. 11). Later, Oliveira (2006) stated that *C. tetracuspidatus* might be a junior synonym of *T. cargnini* due to the 'great similarity' in crown morphology between both taxa. In addition, Oliveira (2006) included the ictidosaur *Riograndia guaibensis* within Therioherpetidae based on one character state: imbrication angle of the posterior postcanine teeth increasing posteriorly. In addition, the author also mentioned that *R. guaibensis* and *C. tetracuspidatus* share a similar symphyseal morphology.

Inferences of similarity between the lower postcanines of *Charruodon tetracuspidatus* and *Therioherpeton cargnini* have been based on the tooth reconstruction of the latter taxon provided by Bonaparte & Barberena (1975, 2001; see also Abdala & Ribeiro 2000), and on *Meurthodon gallicus* (Russell *et al.* 1976; Sigogneau-Russell & Hahn 1994). However, it is evident, based on our new reconstruction of the lower postcanine tooth of *T. cargnini* (Fig. 11) that the lower postcanine teeth of *C. tetracuspidatus* differ significantly from those of *T. cargnini* and other South American probainognathians. In *C. tetracuspidatus* the four cusps are lined up, opened like a fan, without a main prominent one (Fig. 12). Cusps a and c are almost equal in size and slightly larger than cusps b and d. Cusps a, c and d are separated by a U- or open V-shaped notch (Fig. 12), with the cusp d strongly directed posteriorly. The crown is considerably low and mesiodistally elongated, and the mesial edge is transversely wider than the distal, which is sharp in occlusal view. In addition, there is no evidence of constriction on the postcanine tooth roots. The preserved portion of the lower jaw of *C. tetracuspidatus* is stout and tall, with a massive symphysial region. This type of jaw does not match the slender skull of *T. cargnini*. Consequently, based on the aforementioned features, we regard *C. tetracuspidatus* as considerably different to *T. cargnini*.

Furthermore, *Charruodon tetracuspidatus* was thought to be similar to the European *Meurthodon gallicus* (Russell *et al.* 1976; Sigogneau-Russell & Hahn 1994) (Fig. 9). Indeed, the postcanine teeth of both genera have some resemblances, especially in the posterior inclination of the cusps. In *M. gallicus*, cusp a is the main cusp, larger than cusp c, and the cusps have conspicuous crested mesial and distal edges (Fig. 9), differing from the globous cusps of *C. tetracuspidatus* (Fig. 12). In addition, tooth roots are completely separated in *M. gallicus*, whereas *C. tetracuspidatus* has a single root, even lacking a constriction. The former condition is indeed unusual among non-mammaliaform cynodonts with sectorial postcanine teeth; only occurring in *Sinoconodon* and mammaliaforms (Crompton 1974; Crompton & Luo 1993; Luo 1994).

Alemoatherium huebneri differs significantly from *Charruodon tetracuspidatus*. Its lower jaw is low, slender, with a small and smooth symphysis and a discrete Meckelian groove, whereas that of *C. tetracuspidatus* is tall with a conspicuous symphysis. The latter taxon has only three lower incisors and the four-cusped lower postcanine teeth lack a main prominent cusp and the cusps are opened like a fan, differing significantly from the pattern of *A. huebneri* (Fig. 6).

Based on the discussion provided above, we consider *Charruodon tetracuspidatus* to be a bizarre probainognathian, possibly representing a still poorly known group of stout-jawed faunivorous cynodonts. It is clearly distinct from *Therioherpeton cargnini*, *Alemoatherium huebneri*, *Meurthodon gallicus* and other known probainognathians, with a valid taxonomic status as proposed by Abdala & Ribeiro (2000).

CONCLUSION

A new, tiny prozostrodontian cynodont is described on the basis of a partial jaw with almost complete dentition, from the Carnian *Hyperodapedon* AZ of southern Brazil. The new taxon, *Alemoatherium huebneri*, exhibits mandibular and dental features that are also shared by other non-mammaliaform prozostrodontians and early mammaliaforms, including: a slender jaw, anterodorsally bent process of the dentary, five lower incisors, reduced canine, and triconodont-like postcanine teeth with lingual cingular cusps. In addition, *A. huebneri* shares features with some Late Triassic taxa traditionally included within dromatheriids, such as *Rewaconodon tikiensis* from India and *Dromatherium sylvestre* and *Microconodon tenuirostris* from North America, indicating a still poorly documented and understood world-wide distribution of advanced probainognathian cynodonts. The presence of another cynodont phylogenetically close to early mammaliaforms in the Carnian of Brazil may indicate a still under-represented diversity of small- to very small-sized prozostrodontian taxa. Some features of *Therioherpeton cargnini* are revaluated here, and indicate that its postcanine dentition is noticeably different to that of *Charruodon tetracuspidatus*; both from the *Hyperodapedon* AZ.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/42E5B1D6-1312-44C0-8642-F78E55CA6C32

Data for this study (including character list and data matrix) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.q2m2v

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