



NEW RECORD OF *PROZOSTRODON BRASILIENSIS* (EUCYNODONTIA: PROZOSTRODONTIA) FROM ITS TYPE-LOCALITY (UPPER TRIASSIC, SOUTHERN BRAZIL): COMMENTS ON THE ENDOCRANIAL MORPHOLOGY

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ABSTRACT – Here we described a new specimen (UFRGS-PV-0543-T) of the non-mamaliaform cynodont *Prozostrodon brasiliensis*, collected in the Faixa Nova locality (Santa Maria City, State of Rio Grande do Sul, Brazil), which is referred to the Upper Triassic, *Hyperodapedon* Assemblage Zone. The new specimen includes a portion of the cranium (fragmented nasals, lacrimals, prefrontals, frontals, palatines, vomer, and fragments of the right premaxilla, left maxilla, and pterygoid), preserving the natural endocast of the nasal cavity, and a fragmented right dentary. The specimen is assigned to *P. brasiliensis* based on the absence of the postorbital bar, the shape and extension of the snout, the height of the horizontal ramus of the dentary, the position of the Meckelian groove, the morphology of the last postcanine (the only one with the crown partially preserved), and fitting size. The natural endocast is composed of sediment that filled in the nasal cavity. On the dorsal surface of the endocast, there is a longitudinal median sulcus formed by the median bony ridge. Laterally to this median sulcus, there is a longitudinal sulcus on each side formed by the lateral crests. The vomer is low and robust, tapering anteriorly and showing a dorsal groove along its entire length. Other aspects of the endocranial anatomy of UFRGS-PV-0543-T, including wide olfactory region and marked oval-shaped olfactory bulbs, are similar to those of other Late Triassic probainognathian cynodonts.

Keywords: Eucynodontia, μ CT-Scan, endocranial anatomy, nasal cavity, vomer.

RESUMO – Neste trabalho, descrevemos um novo espécime (UFRGS-PV-0543-T) do cinodonte não-mamaliaforme *Prozostrodon brasiliensis*, coletado na localidade Faixa Nova (Santa Maria, Rio Grande do Sul, Brasil), Triássico Superior, Zona de Associação de *Hyperodapedon*. O novo espécime é representado por uma porção do crânio (incluindo nasais fragmentados, lacrimais, pré-frontais, frontais, palatinos, vômer, e fragmentos da pré-maxila direita, maxila esquerda e pterigoide), que preserva o molde endocraniano natural da cavidade nasal, e um dentário direito fragmentado. O espécime é atribuído a *P. brasiliensis* baseado na ausência da barra pós-orbital, a forma e extensão do rostró, a altura do ramo horizontal do dentário, a posição do sulco Meckeliano, a morfologia do último pós-canino (o único com a coroa parcialmente preservada), e tamanho similar ao holótipo. O molde endocraniano natural é formado pelo sedimento que preencheu a cavidade nasal durante o processo de fossilização. Sobre a superfície dorsal desse molde, existem três sulcos longitudinais originados pela crista mediana e cristas laterais, presentes na superfície interna dos ossos que formam o teto da cavidade nasal. O vômer é baixo e robusto, afinado anteriormente e apresenta um sulco dorsal ao longo de todo o seu comprimento. Outros aspectos da anatomia endocraniana de UFRGS-PV-0543-T, incluindo ampla região olfatória e bulbos olfatórios ovais marcados, são semelhantes aos de outros cinodontes probainognátios do Triássico Superior.

Palavras-chave: Eucynodontia, μ CT-Scan, anatomia endocraniana, cavidade nasal, vômer.

INTRODUCTION

The South American fossil record provides important information on the origin and diversification of the major cynodont clade Probainognathia because several key taxa have been found in the Middle/Upper Triassic strata of Argentina and Brazil (Abdala & Ribeiro, 2010; Martinelli & Soares, 2016). In the rich Brazilian fossil-bearing sedimentary rocks of the Santa Maria Supersequence, Cynognathia, represented by Traversodontidae, declined in diversity from the Ladinian/Carnian to the Norian, whereas Probainognathia maintained a significant diversity through that time (Figure 1).

Prozostrodonia is a node-based group of probainognathian cynodonts defined as the least inclusive clade containing *Prozostrodon brasiliensis* (Barberena *et al.*, 1987), *Tritylodon longaevus* Owen, 1884 (Tritylodontidae), *Pachygenelus monus* Watson, 1913 (Tritheledontidae), and *Mus musculus* (Linnaeus, 1758) (Mammalia) (Liu & Olsen, 2010). Known Brazilian late Carnian prozostrodonts include *Prozostrodon brasiliensis*, *Therioherpeton cargini* Bonaparte & Barberena, 1975, *Alemoatherium huebneri* Martinelli *et al.*, 2017, and perhaps *Agudotherium gassenae* Stefanello *et al.*, 2020 (see Martinelli *et al.*, 2020 for a recent discussion). Coeval non-prozostrodontian Probainognathia are the ecteniniid *Trucidocynodon riograndensis* Oliveira *et al.*, 2010, and the enigmatic *Charruodon tetracuspidatus* Abdala & Ribeiro, 2000. The external cranial morphology of these probainognathian cynodonts has been studied (Barberena *et al.*, 1987; Bonaparte & Barberena, 2001; Oliveira, 2006; Pacheco *et al.*, 2018; Martinelli *et al.*, 2017b), but our knowledge of their internal anatomy remains poorly known. Endocranial anatomy has increasingly become a focus in synapsid research, and the internal nasal anatomy of several non-mammaliaform cynodonts has been described (*e.g.* Watson, 1913; Brink, 1955; Kühne, 1956; Bonaparte, 1966; Fourie, 1974; Kemp, 1979; Hillenius, 1994; Ruf *et al.*, 2014; Crompton *et al.*, 2015, 2017), but nearly nothing is known about this morphology in Brazilian Carnian probainognathians.

Prozostrodon brasiliensis is a small probainognathian cynodont from the *Hyperodapedon* Assemblage Zone, Candelária Sequence, Santa Maria Supersequence, which has been dated as late Carnian (Langer *et al.*, 2018). Previous

knowledge of this taxon is based primarily on the holotype, which includes a partial cranium bearing the complete upper dentition, both dentaries with dentition, and postcranial bones (Barberena *et al.*, 1987; Bonaparte & Barberena, 2001; Guignard *et al.*, 2019). The specimen was found in the Faixa Nova locality (Da-Rosa, 2004), municipality of Santa Maria, State of Rio Grande do Sul. A second specimen was reported outside the type locality, in the Marchezan site, municipality of São João do Polêsine, based on a dentary with dentition (Pacheco *et al.*, 2018).

In this contribution we present a third specimen referable to *Prozostrodon brasiliensis* (UFRGS-PV-0543-T), which was discovered at the type locality of the species (Figure 1). Using microtomography, we studied this new specimen, with emphasis on the endocranial morphology of the nasal cavity.

MATERIAL AND METHODS

The specimen UFRGS-PV-0543-T was collected at the Faixa Nova locality, the same area where the holotype of *P. brasiliensis* was found in the 1980s (Figure 1). This area is located in Cerrito (or Cerriquito) Mount (Langer, 2005), Municipality of Santa Maria, State of Rio Grande do Sul. Several outcrops named Cerrito or Faixa Nova I, II, and III, plus the classic locality Cerro da Alemoa crop out around the hill (Da-Rosa, 2004) and the fossils collected there compose the ‘Cerro da Alemoa Local Fauna’ (Langer, 2005). In addition to the holotype of *Prozostrodon brasiliensis*, several fossils of Carnian tetrapods typical of the *Hyperodapedon* Assemblage Zone (AZ) (Figure 1) have been found in the outcrops that surround the hill (*e.g.* Bonaparte & Barberena, 1975; Da-Rosa, 2004; Langer, 2005; Brust *et al.*, 2018), such as the rhynchosaur *Hyperodapedon* Huxley, 1859, the aetosaur *Aetosauroides scagliai* Casamiquela, 1960, and the cynodont *Therioherpeton cargini*. The fossiliferous level of the *Hyperodapedon* AZ from the Cerro da Alemoa locality was dated in 233.23 ± 0.73 Ma (Langer *et al.*, 2018).

UFRGS-PV-0543-T was scanned with a μ CT scan Skyscan™ 1173 at the Laboratório de Sedimentologia e Petrologia of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre (Brazil), using 110 kV and 72 μ A. The scan resulted in 3,579 tomographic slices, with a voxel size of 15.16 μ m. Before segmenting the regions

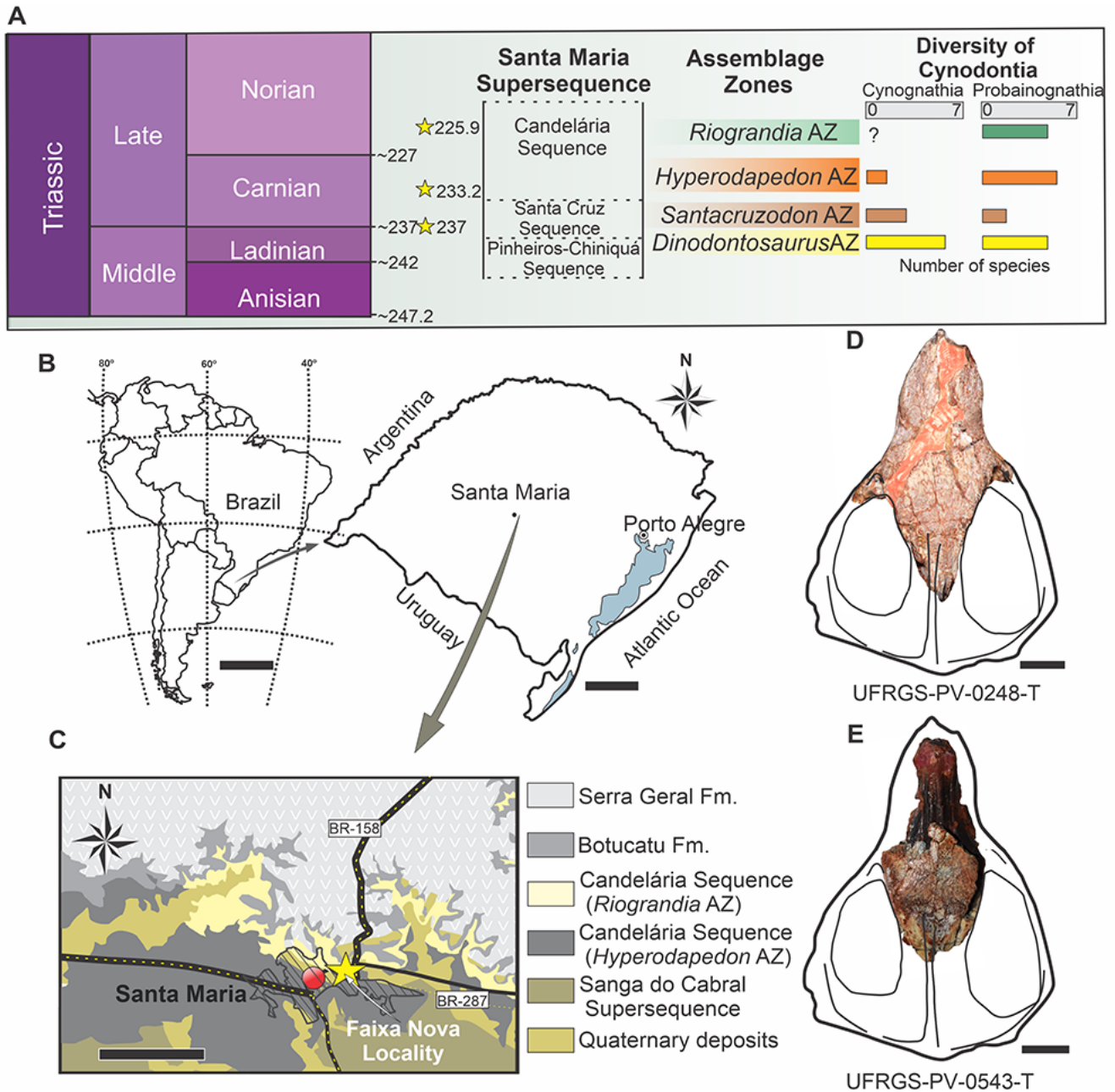


Figure 1. A, Chrono- and biostratigraphy of the Triassic of southern Brazil and diversity of non-mammaliaform cynodonts (chronostratigraphy based on Cohen *et al.*, 2013). Numerical ages from Triassic strata of Brazil are indicated by stars and are based on Langer *et al.* (2018) and Philipp *et al.* (2018). Sequence stratigraphy and biostratigraphy are based on Horn *et al.* (2014) and Schultz *et al.* (2020). B–C, Geological chart and location of Faixa Nova locality (Da-Rosa, 2004; Da-Rosa & Faccini, 2005; CPRM, 2006; Horn *et al.*, 2014). C–D, Holotype (C) and new specimen (D) of *Prozostrodon brasiliensis*. Scale bars = B, 1000 km; C, 10 km; D–E, 10 mm.

of interest, the slices without information were deleted, and the remaining files were cropped. The slices were manually segmented using Avizo® to generate 3D-models (.stl format). The cranial bones were virtually isolated from each other following the sutures between them. The frontonasal and vomeropalatine sutures are clearly visible, but the sutures between the bones of the lateral aspect of the cranium are more difficult to be completely identified (Figure 2). The resulting 3D-models were colored using Design Spark Mechanical 2.0®.

The anatomical nomenclature of the nasal cavity follows Crompton *et al.* (2015, 2017).

Institutional abbreviations: CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/ Universidade Federal de Santa Maria, São João do Polêsine, RS, Brazil; MVP, Museu Vicente Pallotti, Santa Maria, RS, Brazil; UFRGS-PV, Paleovertebrate Collection, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil.

SYSTEMATIC PALEONTOLOGY

CYNODONTIA Owen, 1861
 PROBAINOGNATHIA Hopson, 1990
 PROZOSTRODONTIA Liu & Olsen, 2010

Prozostrodon brasiliensis (Barberena, Bonaparte & Teixeira, 1987)
 (Figures 2–5)

Referred specimens. UFRGS-PV-0248-T (holotype), anterior half of the skull (Figure 1D), lower jaws, and several postcranial elements (see Bonaparte & Barberena, 2001 and Guignard *et al.*, 2019); CAPP/UFMS 0123, right lower jaw (Pacheco *et al.*, 2018).

New material. UFRGS-PV-0543-T, anterior portion of the cranium with fragmented right dentary (Figures 2–5).

Locality and horizon. Faixa Nova locality (Santa Maria, RS), *Hyperodapedon* AZ, late Carnian (Langer *et al.*, 2018).

Diagnosis. See Pacheco *et al.* (2018).

Comments. The specimen UFRGS-PV-0543-T is assigned to *P. brasiliensis* due to the absence of the postorbital bar, prefrontal shape and extension of the snout, the height of the horizontal ramus of the dentary, the position of the Meckelian groove, the morphology of the last postcanine (the only one with the crown partially preserved) and compatible size (Figure 1E) (Bonaparte & Barberena, 2001; Pacheco *et al.*, 2018).

Comparative description. Cranium: the specimen UFRGS-PV-0543-T preserves the middle (interorbital region) and part of the anterior portion of the cranium, which includes fragmented nasals, lacrimals, prefrontals, frontals, palatines, vomer, and fragments of the right premaxilla and pterygoid (Figures 2–3). Ventrally, the transverse lamina (see below) is exposed on the ventral region of the cranium because the secondary palate is not preserved (Figures 2A, 4). The cranium is similar in size to the holotype UFRGS-PV-0248-T of *Prozostrodon brasiliensis*, both substantially larger than the holotype MVP 22.05.04 of the coeval prozostrodont *Therioherpeton cargnini*. Histological analysis in long bones of the holotype of *P. brasiliensis* revealed that it was still growing at the time of death and likely had not reached sexual maturity (Botha-Brink *et al.*, 2018), which indicates that mature individuals can have even larger skulls.

Only the posterior portion of the nasals are preserved (Figures 2–3), missing the lateral part of the right bone due to the fragmentation. The nasal is thick and wide, with a flat dorsal surface, occupying most of the preserved portion of the cranial roof. In dorsal view, the frontonasal suture is anteriorly convex (Figure 3) with the frontals forming a triangular anterior projection at the anteromedial contact. In sagittal slices, the suture projects obliquely (anteroventral to posterodorsally), because the posterior portion of the nasal overlaps the anterior region of the frontal (Figure 2D). The nasal contacts the frontal posteriorly, and a portion of the frontal, the prefrontal, lacrimal, and maxilla, laterally.

The frontal forms the roof of the interorbital region of the cranium and part of the lateral wall of the orbit (Figure 3). This bone shows a shallow depression at its anterior region, near the frontonasal suture. The frontal reduces in width posteriorly. On the posterolateral area of the frontal is located the articular surface for contacting the parietal, which is not preserved. The posteroventral region of the frontal delimits the anterodorsal limit of the interorbital vacuity (Figure 3C).

On the lateral side of the specimen, there are three ossifications that we interpreted from anterior to posterior as a fragment of the maxilla, lacrimal, and prefrontal bones (Figure 3). The lacrimal is visible in dorsal view and composes part of the lateral region of the preserved cranial portion (Figure 3). The prefrontal is seen in dorsal and lateral views and contacts medially the nasal, posteriorly the frontal, and anteriorly the lacrimal. The presence of the prefrontal was mentioned by Bonaparte & Barberena (2001) and subsequently codified as present in the phylogenetic analyses of Liu & Olsen (2010) and Martinelli & Rougier (2007). Later, it was considered as absent by Soares *et al.* (2014). More recently, it was considered present in the phylogenetic analysis of Wallace *et al.* (2019). Among prozostrodonts, the presence of a prefrontal bone is shared with *Pseudotherium argentinus* Wallace *et al.* (2019), disappearing in more derived forms, such as *Therioherpeton cargnini*, tritylodontids, ictidosaurs, ‘brasilodontids’, and mammaliaforms (Bonaparte & Barberena, 2001; Bonaparte *et al.*, 2005; Soares *et al.*, 2011; Wallace *et al.*, 2019). There is no postorbital bar in *Prozostrodon brasiliensis* as in other prozostrodonts (Liu & Olsen, 2010).

On the ventral surface of the frontal and nasal bones, there are three longitudinal crests (Figures 2H–J, 3E–F), which are also present in other non-mammaliaform cynodonts (*e.g.* Watson, 1913; Hillenius, 1994; Ruf *et al.*, 2014; Crompton *et al.*, 2015, 2017; Pusch *et al.*, 2019): the median bony ridge (that support the dorsal area of the cartilaginous nasal septum; Crompton *et al.*, 2017) (Figures 2H–J, 3E–F), which is the most developed, and two lateral crests (to support the cartilaginous nasoturbinals; Crompton *et al.*, 2017) (Figures 2H–J, 3E–F). The median ridge is formed by the medial meeting of both frontal bones (Figures 2I–J). This ridge forms a sharp ventral projection at its posteriormost portion (Figures 3E–F). In *Brasilodon quadrangularis* Bonaparte *et al.*, 2003 (UFRGS-PV-1043-T, formerly referred to *Brasilitherium riograndensis*, but see Liu & Olsen, 2010 and Martinelli *et al.*, 2017a), at the roof of the pars posterior of the nasal cavity, there is a well-developed median ridge formed by cancellous bone with a groove for the olfactory nerve on the lateral surface of this structure. This structure was interpreted by Ruf *et al.* (2014) as an ossified mesethmoid. However, Crompton *et al.* (2017) argued that the ridge of *B. quadrangularis* is similar to those of other non-mammaliaform cynodonts, and cannot represent a true mesethmoid, because a similar ridge is found in *Elliotherium kersteni* Sidor & Hancox, 2006, *Probainognathus jenseni* Romer, 1970, and *Massetognathus pascuali* Romer, 1967. However, in these taxa, the structure is divided by a midline suture, indicating that it is not an

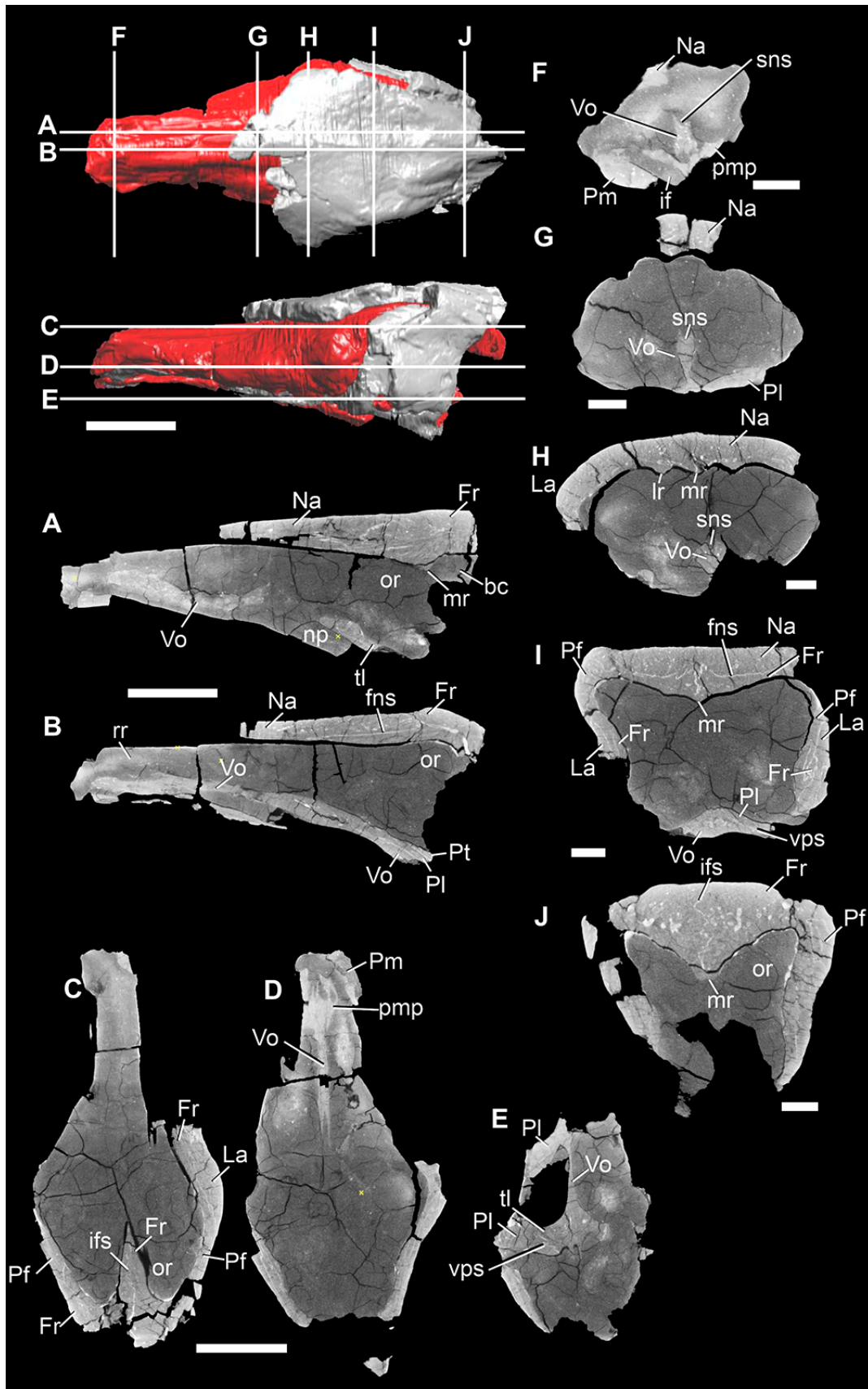


Figure 2. Tomographic slices (A–B, sagittal; C–E, axial; F–J, coronal) of the cranium of *Prozostrodon brasiliensis* (UFRGS-PV-0543-T), from the Upper Triassic of southern Brazil. **Abbreviations:** bc, brain cavity; fns, frontonasal suture; Fr, Frontal; if, incisive foramen; ifs, interfrontal suture; lr, lateral ridge; mr, median ridge; Na, Nasal; np, nasopharyngeal passage; Pf, Prefrontal; Pl, Palatine; Pm, Premaxilla; pmp, premaxillary process; Pt, Pterygoid; sns, sulcus for the nasal septum; tl, transverse lamina; or, olfactory region; Vo, Vomer; vps, vomeropalatine suture. Scale bar = A–E, 10 mm; F–J, 2.5 mm.

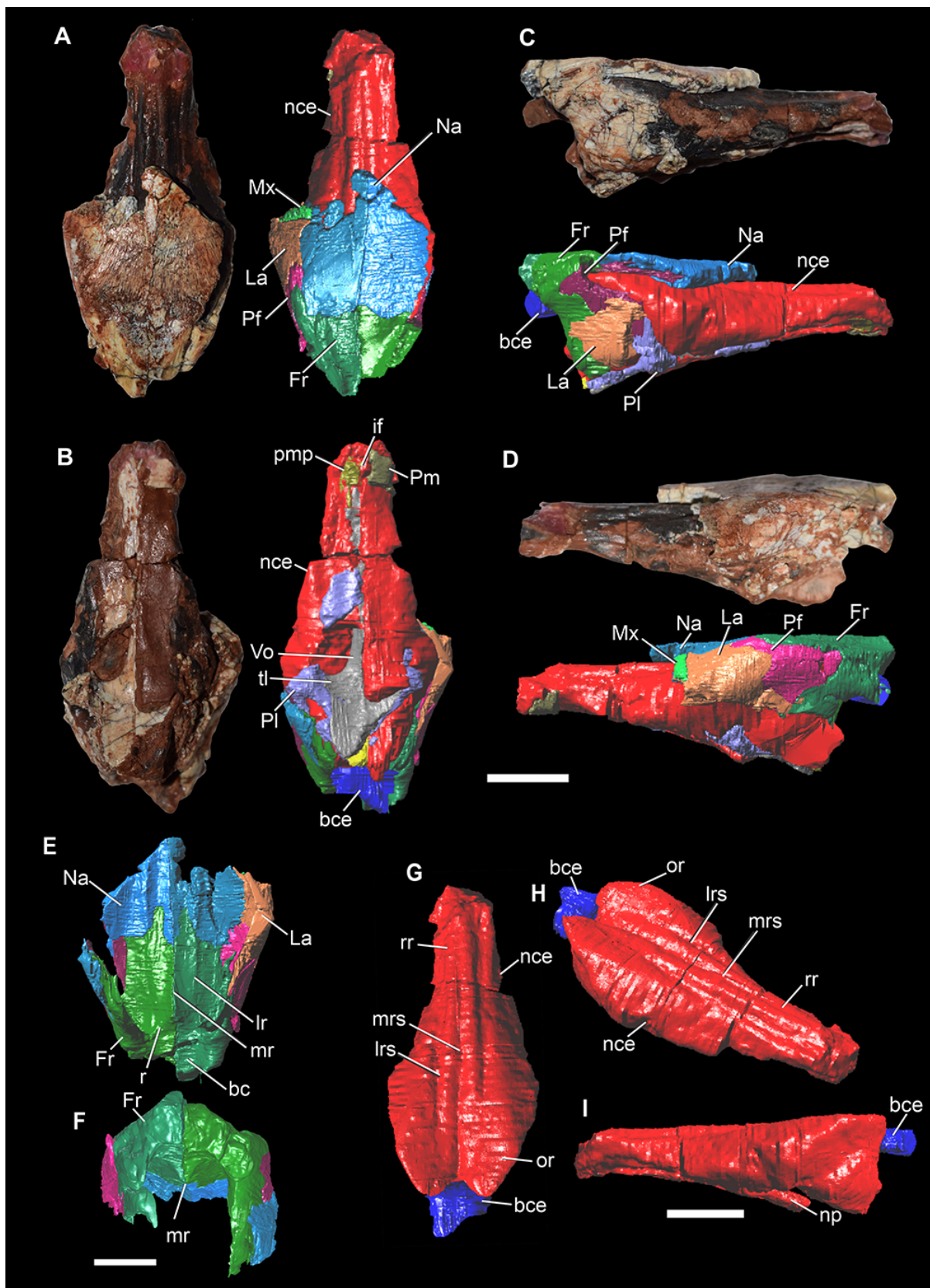


Figure 3. Cranium (A–F) and endocasts of the nasal cavity and brain (olfactory bulbs) (G–I) (photos and virtual 3D reconstructions) of *Prozostrodon brasiliensis* (UFRGS-PV-0543-T) from the Upper Triassic of southern Brazil, in dorsal (A, G), ventral (B, E), right lateral (C), left lateral (D, I), posterior (F), and lateral oblique (H) views. **Abbreviations:** bc, brain cavity; bce, brain cavity endocast; Fr, Frontal; if, incisive foramen; La, Lacrimal; lr, lateral ridge; lrs, lateral ridge sulcus; mr, median ridge; mrs, median ridge sulcus; Mx, Maxilla; Na, Nasal; nce, nasal cavity endocast; np, nasopharyngeal passage; or, olfactory region; Pf, Prefrontal; PI, Palatine; Pm, Premaxilla; pmp, premaxillary process; r, ridge delimiting the olfactory bulb from the pars posterior of the nasal cavity; rr, respiratory region; tl, transverse lamina; Vo, Vomer. Scale bars = A–D, F–I, 10 mm; E–F, 5 mm.

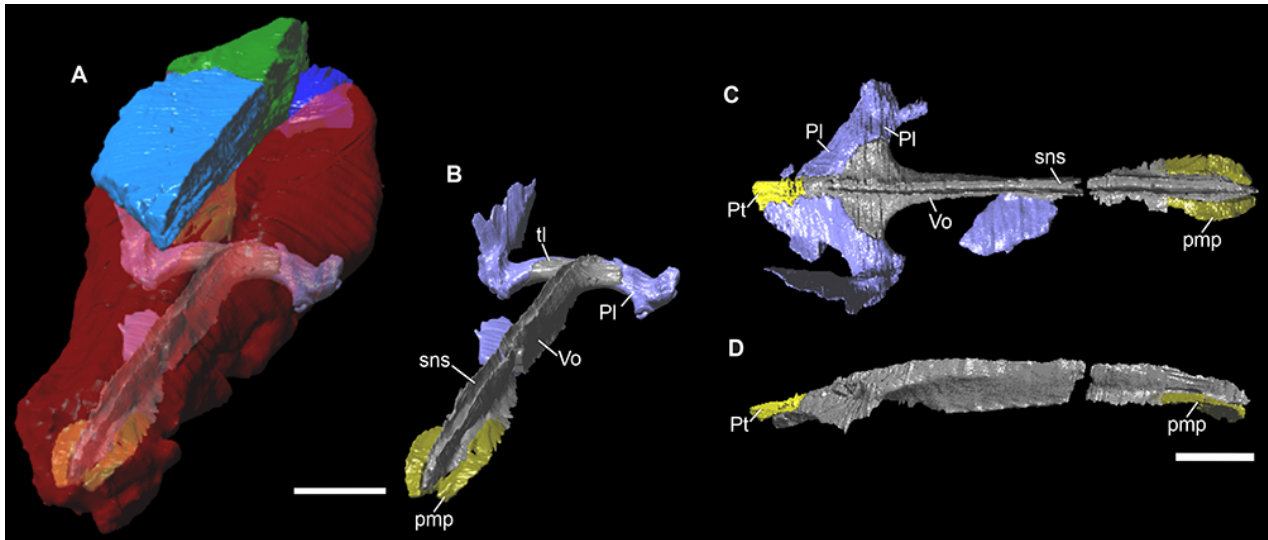


Figure 4. A, UFRGS-PV-0543-T with cranial bones (right side) and translucent nasal cavity endocast showing the vomer, in anterolateral view. **B–D**, virtual 3D reconstruction of the vomer in anterolateral (**B**), dorsal (**C**), and lateral (**D**) views. **Abbreviations:** Pl, Palatine; pmp, premaxillary process; Pt, Pterygoid; sns, sulcus for the nasal septum; tl, transverse lamina; Vo, Vomer. Scale bars = 5 mm.

independent ossification. The structure illustrated by Ruf *et al.* (2014; fig. 5A) is distinct from the pattern observed here in the coronal slices (Figure 2) and needs to be further addressed.

As in other non-mammaliaform eucynodonts and the basalmost mammaliaforms (Crompton, 1958; Kemp, 2009; Crompton *et al.*, 2017), UFRGS-PV-0543-T does not have an ossified cribriform plate, but it shows a clear limit between the pars posterior of the nasal cavity and the brain cavity formed by two oblique ridges connecting to the median ridge on the ventral surface of the frontals (Figure 3E).

The nasal cavity of UFRGS-PV-0543-T does not show any evidence of ossified turbinals. Thin ossifications are present inside the nasal cavity of *Brasilodon quadrangularis* (UFRGS-PV-1043-T), which Ruf *et al.* (2014) interpreted as ossified naso- and ethmoturbinals. Turbinal-like bones are also present in the nasal cavity of *Pseudotherium argentinus* (Wallace *et al.*, 2019). Crompton *et al.* (2017) suggested that the evidence presented by Ruf *et al.* (2014) is not strong enough to confirm if *B. quadrangularis* already displayed ossified turbinals. Hence, the study of more specimens of these Late Triassic prozostroodontians is necessary to better understand when these structures emerged in cynodonts. The vomer (Figure 4) (maximum height of 4.5 mm and 27 mm length) is a perpendicular lamina at the sagittal plane of the nasal cavity, diminishing in height anteriorly, similar to *B. quadrangularis* and *P. argentinus* (Ruf *et al.*, 2014; Wallace *et al.*, 2019). It shows a long dorsal sulcus for the cartilaginous nasal septum extending from the level of the incisive foramen up to the posteriormost region of this bone, almost reaching the pterygoid, such as *Diademodon tetragonus* Seeley, 1894, *Thrinaxodon liorhinus* Seeley, 1894, and *B. quadrangularis* (Brink, 1955; Fourier, 1974; Ruf *et al.*, 2014). According to Crompton *et al.* (2017) in *Probainognathus jenseni* and *Elliotherium kersteni*, the sulcus does not extend on its

anterior region and is present only on the posterior two thirds in the former and on the posterior half in the latter. The vomer of *Prozostrodon brasiliensis* is proportionally lower and the premaxillary process is laterally more expanded and rounded than in *B. quadrangularis* (Ruf *et al.*, 2014). In *B. quadrangularis* there is at least a portion of the nasal septum that is ossified (Ruf *et al.*, 2014), which is not present in UFRGS-PV-0543-T.

At the posterior end of the vomer, the lateral wings contact laterally the transverse process of the palatine. In this contact, the palatine overlaps the vomer, forming the transverse lamina (= *lamina terminalis* in Ruf *et al.*, 2014) (Crompton *et al.*, 2017). This structure consists of two obliquely and anteriorly oriented laminae that converge medially. The lamina forms the floor of the olfactory chamber and the roof of the nasopharyngeal passage at the posterior region of the nasal cavity (Figures 5B–D). At the posteriormost region of the vomer, a small portion of the pterygoid is preserved, overlapping this bone.

Endocranial casts: there is a natural endocast formed by sediment that filled in the nasal cavity (Figures 2–3) and brain cavity. The nasal cavity endocast shows a long respiratory region and wide olfactory region (maximum width: 20 mm) (Figures 3G–H). On the dorsal surface of the endocast of the nasal cavity, there is a longitudinal median sulcus, formed by the median bony ridge (Figures 3G–H), and lateral sulcus at both sides of the central one formed by the lateral crests (Figures 3G–H). It was possible to reconstruct the anterior portion of the olfactory bulbs, which are oval-shaped and separated by a narrow longitudinal sulcus (Figures 4H–K) like in *Probainognathus jenseni*, *Chiniquodon theotonicus* von Huene, 1935, *Therioherpeton cargini*, *Riograndia guaibensis* Bonaparte *et al.*, 2001, and *B. quadrangularis* (Quiroga, 1979, 1980, 1984; Rodrigues *et al.*, 2014, 2019; Hoffmann *et al.*, 2019; Kerber *et al.*, in press).

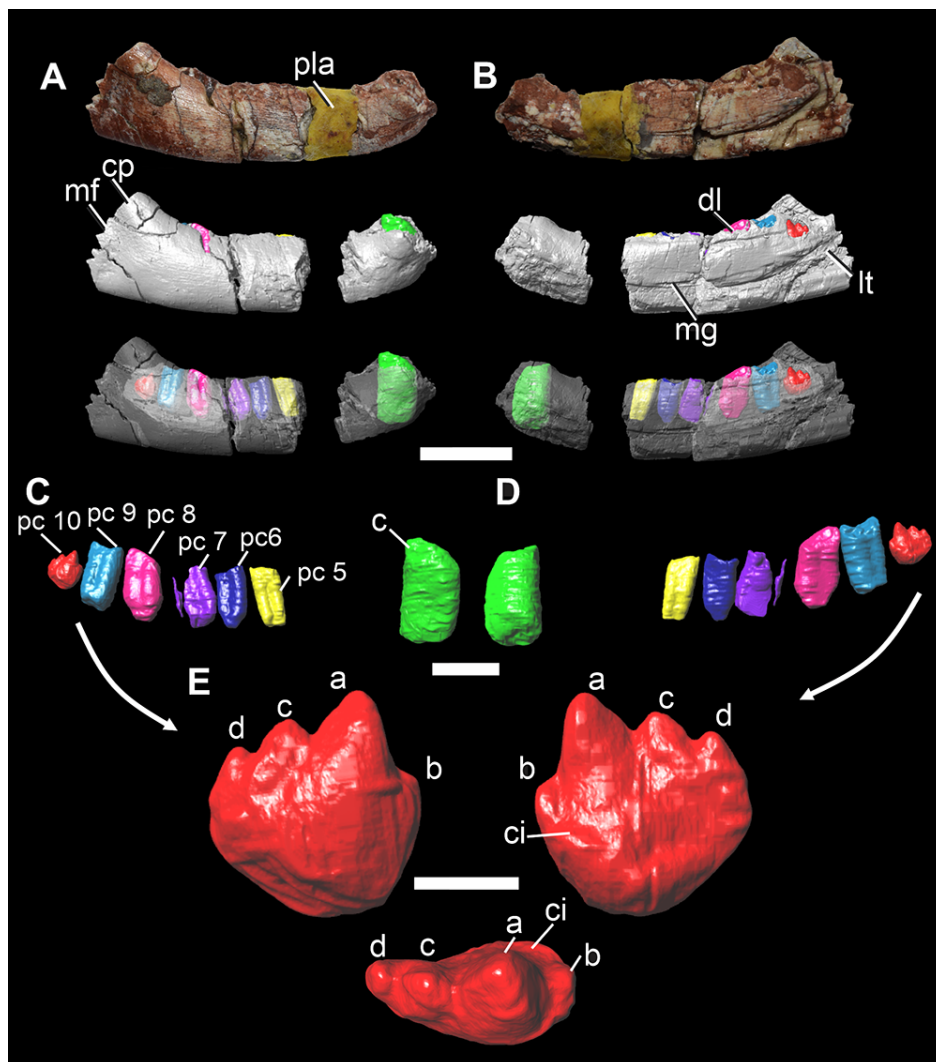


Figure 5. Photos and three-dimensional reconstructions of the right dentary (A–B) and teeth (C–E) of *Prozostrodon brasiliensis* (UFRGS-PV-0543-T), from the Upper Triassic of southern Brazil. A–B, right dentary in lateral (A), and medial (B) views; C–D, canine and postcanines in labial (C) and lingual (D) views; E, last postcanine in labial, occlusal, and lingual views. **Abbreviations:** a–d, cusp names; ci, cingulum; cp, coronoid process; dl, groove for dental lamina; lt, lateral trough for postdentary bones; mf, masseteric fossa; mg, Meckelian groove; pc, postcanine; pla, plaster. Scale bars: A–B, 10 mm; C–D, 5 mm; E, 1.5 mm.

Lower jaw and teeth: UFRGS-PV-0543-T preserves a partial horizontal ramus of the right dentary, symphysis (very damaged), and the anteriormost region of the coronoid process (Figure 5). Two fragments of the horizontal ramus are united by a portion reconstructed in plaster. The dentary is robust, similar to that of the holotype of *Prozostrodon brasiliensis* (but not to the degree of *Charruodon tetracuspoidatus*; Martinelli *et al.*, 2017b). It differs from the slender and low dentaries observed in *Santacruzgnathus abdalai* Martinelli *et al.*, 2016, *Brasilodon quadrangularis*, *Alemoatherium huebneri*, *Microconodon tenuirostris* Osborn, 1886, and basal mammaliaforms (see Bonaparte *et al.*, 2003, 2005; Sues, 2001; Martinelli *et al.*, 2016, 2017a). Below the base of the coronoid process, it is located the anteriormost portion of the masseteric fossa (Figure 5A). On the medial surface, the Meckelian groove is exposed at the middle portion of the dentary, which is posteriorly connected to the trough for the postdentary bones and runs the dentary parallel to its ventral margin (Figure 5B). The location of the groove is similar to

that of other specimens of *P. brasiliensis* (UFRGS-PV-0248-T; CAPP/UFMS 0123), whereas in *A. huebneri* the Meckelian groove is closer to the ventral margin of the dentary (Martinelli *et al.*, 2017b). UFRGS-PV-0543-T also exhibits pits on the groove for the dental lamina.

UFRGS-PV-0543-T preserves the intra-alveolar portions of the canine and the last five postcanines, all of them missing the crown (Figure 5). Analyzing the space between the canine and the first preserved postcanine (pc) of UFRGS-PV-0543-T in comparison to other specimens of *Prozostrodon brasiliensis* (see Pacheco *et al.*, 2018), we interpret these teeth as the pc 5 to pc 9. At the distal end of the tooth row, there is a postcanine (pc 10?) inside the crypt (3 mm length), which is the best-preserved tooth (Figure 5C). This unerupted and partially formed tooth is “triconodont-like”, bearing four cusps, as in the other specimens of *P. brasiliensis*, *Botucaratherium belarminoi* Soares *et al.*, 2014, and *Therioherpeton cargini* (Martinelli *et al.* 2017b). The cusp a is the largest (Figure 5C). It is vertically oriented, followed

distally by the cusps c and d. Cusp a is not distally curved as in ecteniniids (Oliveira *et al.*, 2010), and *Agudotherium gassenae* Stefanello *et al.* 2020, or the pc 6 and pc 9 of the holotype of *P. brasiliensis*, but resemble the homolog cusp of the pc 8. The mesial cusp b is less sharp than cusp c and d and very low in the crown. All the cusps are slightly lingually oriented (Figure 5C). An incipient lingual cingulum is present (Figure 5C), more evident on the region lingual to the cusp b, but not as developed as in the pc 8 and pc 9 of the holotype of *P. brasiliensis*. The crown morphology also resembles the only known lower postcanine of *T. cargini* (see Martinelli *et al.*, 2017b). However, the cusp a of UFRGS-PV-0543-T is more developed, and there is no evidence of a cingulum in *T. cargini*, although preservation of the lower crowns is incomplete. The roots of the postcanines show an incipient bifurcation marked by a longitudinal groove (Figure 5).

FINAL REMARKS

A new specimen (UFRGS-PV-0543-T) of *Prozostrodon brasiliensis* is reported, furnishing novel information on this taxon. UFRGS-PV-0543-T has a prefrontal, confirming the presence of this bone as interpreted by Bonaparte & Barberena (2001). The use of μ CT data provided information on the endocranial morphology of this prozostrodon, permitting to reconstruct its vomer and other internal structures. The median crest of *P. brasiliensis* is formed by the medial meeting of the frontal bones, such as most non-mammaliaform cynodonts, and it is less developed than in *Brasilodon quadrangularis*, which can show an ossified mesethmoid. Other endocranial morphological traits of this new specimen (*i.e.* wide olfactory region, nasal cavity endocast showing grooves originated by median and lateral crests, marked oval-shaped olfactory bulbs) are similar to other Late Triassic probainognathian cynodonts such as *Therioherpeton cargini*, *Riograndia guaibensis*, and *B. quadrangularis*.

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