A sectorial toothed cynodont (Therapsida) from the Triassic Santa Cruz do Sul fauna, Santa Maria Formation, Southern Brazil

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ABSTRACT
A sectorial toothed cynodont from the Triassic Santa Cruz do Sul fauna, Santa Maria Formation, Parana Basin, southern Brazil, is described. The taxon is represented by a tiny portion of a right lower jaw which preserves partially the last postcanine. A comparative analysis of the postcanine morphology of the Santa Cruz do Sul specimen with South American Triassic cynodonts is made. The crown morphology of the Santa Cruz do Sul cynodont is closer to that of the juvenile single specimen of cf. *Probainognathus* from the Carnian Ischigualasto Formation and of juveniles of *Probainognathus jenseni* Romer, 1970 from the Ladinian Chañares Formation in Argentina. There are, however, some important differences between the tooth of the new specimen and those of *P. jenseni* juveniles, and therefore we provisionally assign the new Santa Cruz do Sul material to cf. *Probainognathus*. The fauna of Santa Cruz do Sul, dominated by traversodontid cynodonts, is now composed of a proterochampsid archosauriform, three traversodontids and two sectorial toothed cynodonts and we refer to it as *Santacruzodon* Assemblage Zone. We also propose the name of *Riograndia* Assemblage Zone for the faunas from the Upper Triassic Caturrita Formation, on the basis of the abundance yet restricted record of this taxon in these faunas. A brief summary of the Brazilian Middle and Upper Triassic biostratigraphy is presented within the framework of two different time scales.

KEY WORDS
Therapsida,
Cynodonts,
Probainognathus,
Triassic,
Santa Maria Formation,
biostratigraphy.

RÉSUMÉ
Un cynodonte à dentition sectorielle de la faune triassique de Santa Cruz do Sul, Formation Santa Maria, sud du Brésil.
Un cynodonte à dentition sectorielle de la faune de Santa Cruz do Sul, de la Formation Santa Maria, Bassin du Paraná, sud du Brésil, est décrit. Le taxon est représenté par une petite portion de la branche de la mandibule droite, avec la dernière post-canine partiellement préservée. Une analyse comparative de la morphologie de la post-canine du spécimen de Santa Cruz do Sul avec celle de cynodontes triassiques d'Amérique du Sud est réalisée. La morphologie de la couronne dentaire du cynodonte de Santa Cruz do Sul est semblable à celle présentée par l'individu jeune rattaché à cf. *Probainognathus* de la Formation Ischigualasto du Carnien d'Argentine et aussi à des spécimens jeunes de *Probainognathus jenseni* Romer, 1970 de la Formation Chañares du Ladinien d'Argentine. Toutefois, il existe d'importantes différences entre la dent du nouveau spécimen et celles de *P. jenseni* jeunes, de sorte que, provisoirement, l'on opte pour attribuer le matériel de Santa Cruz do Sul à cf. *Probainognathus*. La faune de Santa Cruz do Sul, dominée par des cynodontes traversodontides, est à présent composée d'un arcosauriforme proterochampside, trois traversodontides et deux cynodontes à dents sectorielles, et nous y faisons référence sous le nom de Zone-d'Assemblage de *Santacruzodon*. Il est également proposé le nom de Zone-d'Assemblage de *Riograndia* pour les faunes du Trias Supérieur de la Formation Caturrita, sur la base de l'abondance et de l'enregistrement restreint de ce taxon à cette faune. Un bref résumé de la biostratigraphie du Trias Moyen et Supérieur brésilien est présenté dans le cadre de deux différentes échelles temporelles.

MOTS CLÉS
Therapsida,
Cynodonte,
Probainognathus,
Trias,
Formation Santa Maria,
biostratigraphie.

INTRODUCTION

Triassic vertebrates are a landmark of the southern Brazilian fossil record, with the outcrops from the Santa Maria Formation recording a fauna interpreted as ranging from the Middle Triassic (?Anisian, Ladinian) to the Carnian (Schultz *et al.* 2000; Abdala & Teixeira 2004; Langer *et al.* 2007, but see discussion below), corresponding to the Sequence Santa Maria 2 of Zerfass *et al.* (2003). Several vertebrate groups including fish, parareptiles, archosaurs and therapsids are represented in beds of this unit (Perez & Malabarba 2002; Langer *et al.* 2007; Richter & Toledo 2008). The Santa Cruz do Sul fauna represents a recent addition to the knowledge of the Brazilian Triassic (Abdala *et al.* 2001; Bertoni-Machado & Holz 2006). This fauna is represented by a restricted outcrop know as "Schoenstatt Sanctuary" located on the SW outskirts of the city of Santa Cruz do Sul. A remarkable dominance of cynodonts is a highlight of this fauna where traversodontids are abundant and remains of carnivorous chiniquodontids and archosauromorph proterochampsids are also represented (Abdala *et al.* 2001; Abdala & Ribeiro 2002, 2003; Machado & Kischlat 2003). Four different traversodontids were originally recognized for this fauna (Abdala *et al.* 2001; Abdala & Ribeiro 2002): *Santacruzodon hopsoni* Abdala & Ribeiro, 2003; a second taxon, the largest form of this fauna, that was identified by Melo *et al.* (2009) as the Malagasy traversodontid *Menadon* (Flynn, Parrish, Rakotosamimanana, Ranivoharimanana, Simpson & Wyss, 2000) (Flynn *et al.* 2000; Kammerer *et al.* 2008); a third form represented by a tiny fragment of maxilla including four postcanines

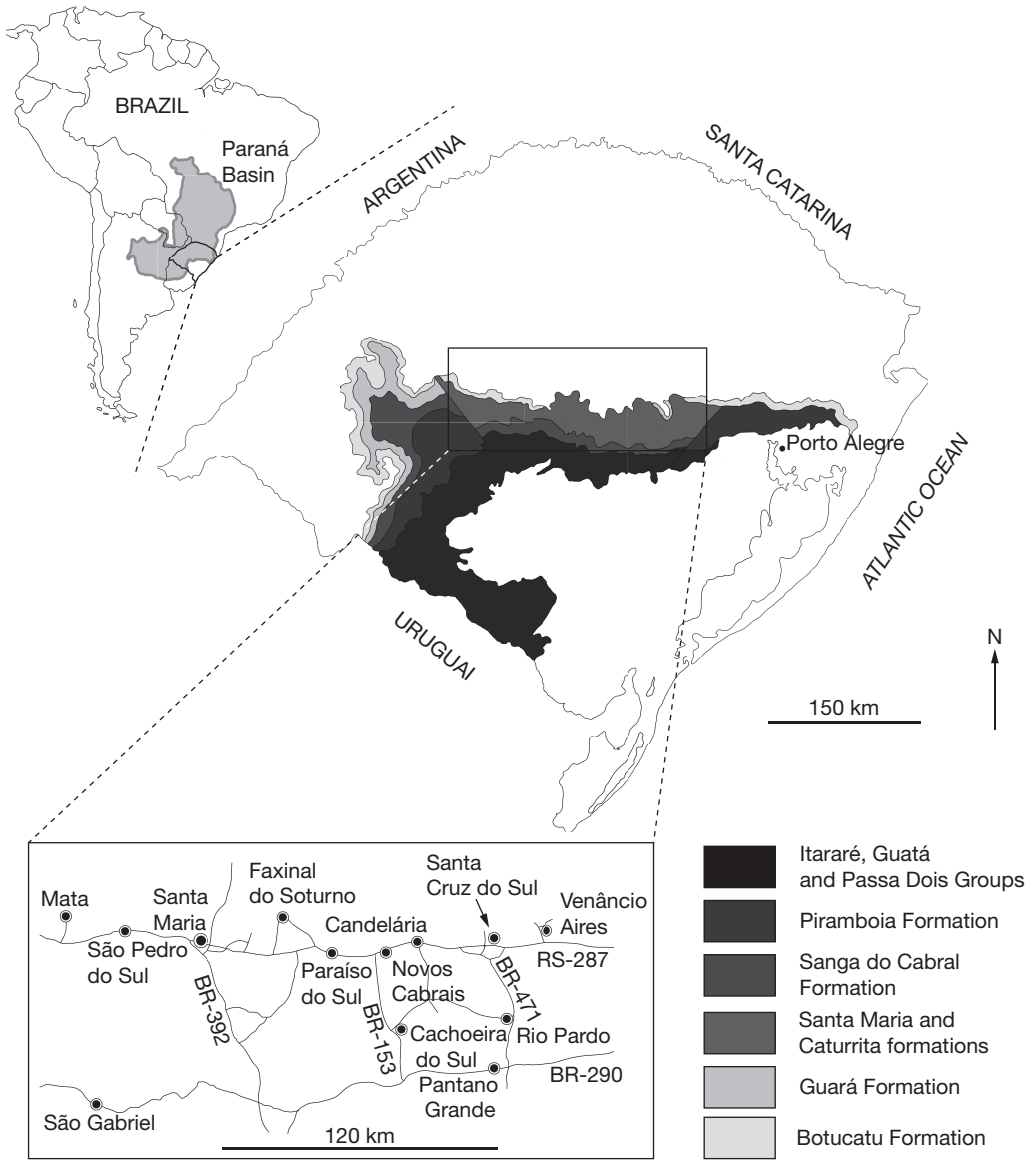

FIG. 1. — **A**, location of Triassic sediments in the State of Rio Grande do Sul. Extension of the Paraná Basin is indicated on the map of South America; **B**, location map of the Santa Cruz do Sul locality in the central region of Rio Grande do Sul state (modified from Bertoni-Machado & Holz 2006).

resembling the Laurasian traversodontid *Boreogomphodon* Sues & Olsen, 1990 (Abdala *et al*. 2001) and a form represented by a lower jaw presenting some features shared with basal traversodontids, including *Massetognathus* Romer, 1967 (Abdala *et al.* 2001).

Taxonomic and phylogenetic studies of the traversodontids from the Santa Cruz do Sul fauna suggested that this new fossil assemblage was transitional between the *Dinodontosaurus* and *Hyperodapedon* Assemblage Zones (AZ) typically

TABLE 1. — Number of individuals collected in the *Santacruzodon* Assemblage Zone.

	Number of individuals
Indeterminate cynodonts	72
Traversodontid cynodonts	40
Chiniquodontid cynodonts	3
cf. *Probainognathus*	1
Proterochampsid	1
Indeterminate remains	40
Total	157

TABLE 2. — Comparative measurements between UFRGS-PV1121T from the Santa Maria Formation and juveniles of *Probainognathus jenseni* Romer, 1970 (PVL 4445 and 4447) from the Chañares Formation in Argentina (in mm).

	UFRGS-PV 1121T	PVL 4445	PVL 4447
Length of the last postcanine crown	1.8	2.3	2.9
Length of the last four lower postcanines	5.7	9	10.7

recognized for the Santa Maria Formation (e.g., Scherer *et al.* 1995; Schultz *et al.* 2000), as traversodontid were represented by some taxa having features of Ladinian forms (e.g., Traversodontid type 3, see Abdala *et al.* 2001) whereas the record of *Menadon* suggests an upper Ladinian/lower Carnian age (Melo *et al.* 2009). Further preparation of material from this outcrop also indicates the presence of the traversodontid *Massetognathus* (Schultz & Langer 2007; Abdala pers. obs.), which is typical of the Ladinian faunas from Argentina and Brazil.

Sectorial toothed cynodonts are, however, rare in the Schoenstatt assemblage, with chiniquodontid cynodonts being represented by at least three specimens. We describe in this contribution a new record of a sectorial toothed cynodont in the Santa Cruz do Sul fauna. The specimen is represented by a fragment of the lower jaw of a tiny animal, preserving the last postcanine. The morphology of the tooth resembles the postcanine pattern observed in juvenile specimens of *Probainognathus* Romer, 1970 from the Chañares fauna of Argentina (Abdala 1996) and to the labial margin of the posterior upper postcanines of cf. *Probainognathus* from the Ischigualasto Formation (Bonaparte & Crompton 1994), also in Argentina. Based on the exclusive record and abundance of these taxa in their respective faunas, we propose the naming of the faunas from Santa Cruz do Sul and the Caturrita Formation as, respectively, *Santacruzodon* and *Riograndia* Assemblage Zones. We also briefly discuss the biostratigraphy of the Middle-Upper Triassic Brazilian faunas in the context of two different time scales.

MATERIAL

INSTITUTIONAL ABBREVIATIONS

MCN — Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil;

MCP — Museu de Ciências e Tecnologia, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil;

MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;

PULR — Museo de Antropología, Universidad Nacional de La Rioja, Argentina; PVL, Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina;

PVL — Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina;

UFRGS — Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

MATERIAL

The studied material, UFRGS-PV1121T, is a fragment of a right lower jaw with the last postcanine and three alveoli preserved anteriorly some of them with remains of dental roots.

Comparative material consulted includes *Probainognathus jenseni* Romer, 1970, represented by juveniles: PVL 4445-4447, 4673, MCZ 4283, 4285, 4294 and adults: PULR 16*, 17* (holotype); PVL 4169, 4677, 4678, MCZ 4004, 4006, 4019, 4274, 4277-4280, 4293; *Charruodon tetracuspidatus* Abdala & Ribeiro, 2000: MCP 3934 PV; *Prozostrodon brasiliensis* Bonaparte & Barberena, 2001: UFRGS-PV 0248T; *Riograndia guaibensis*

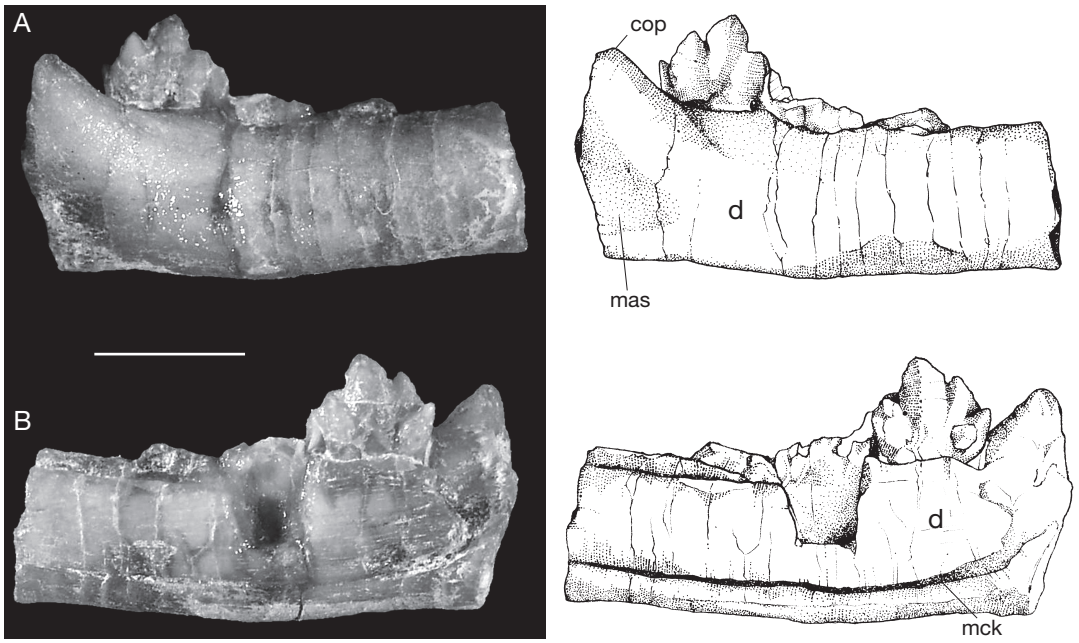

FIG. 2. — UFRGS-PV1121T fragment of the right lower jaw in buccal (**A**) and lingual (**B**) views. Abbreviations: **cop**, coronoid process; **d**, dentary; **mas**, masseteric fossa; **mkc**, meckelian canal. Scale bar: 2 mm.

Bonaparte, Ferigolo & Ribeiro, 2001: MCN-PV 2264, 2265, 2271; UFRGS-PV0596T, UFRGS-PV0624T; *Irajatherium hernandezi* Martinelli, Bonaparte, Schultz & Rubert, 2005: UFRGS-PV0599T; UFRGS-PV1068-T; *Protheriodon estudianti* Bonaparte, Soares & Schultz, 2006: UFRGS-PV0962T; *Brasilodon quadrangularis* Bonaparte, Martinelli, Schultz & Rubert, 2003: UFRGS-PV0611T, UFRGS-PV0628T, UFRGS-PV0765T; and *Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz & Rubert, 2003: UFRGS-PV0594T,UFRGS-PV0603T, UFRGS-PV0758T, UFRGS-PV0929T. PULR specimens marked with an asterisk were stolen from the collection.

GEOLOGICAL SETTING

The Schoenstatt outcrop is located alongside road RS 287 near Santa Cruz do Sul city (UTM [22], 29°44'29"S; 51°27'01"W), about 150 km from Porto Alegre in the Rio Grande do Sul State (Fig. 1).

The stratigraphic section shows an approximately 20 meter thick mudstone succession of the Alemoa Member of the Santa Maria Formation topped by nearly 15 meters of fine to very fine sandstone of the Caturrita Formation (*sensu* Andreis *et al.* 1980).

The mudstone is massive or with millimetric, incipient lamination. The presence of rhyzolithes, some fibro-radial calcite and fractures filled by calcium carbonate are common. The basal 15 meters of the section are almost bare of fossils, whereas fossils and coprolites were found in association with melikarian nodules in the upper portion of the succession (level between 15 and 20 m, see Bertoni-Machado & Holz 2006: fig. 3). A huge concentration of the nodules, in association with calcite-filled fractures, also occurs above the fossiliferous level.

Facies of the Schoenstatt section are interpreted as floodplain deposits (lower mudstone levels including fossils remains) and fluvial channel (upper unfossiliferous sandstone levels).

Abdala *et al.* (2001) reported the presence of 82 cynodont specimens in the Santa Cruz fauna. New

findings and further preparation of materials from this locality allow for an update in the number of individuals of the fauna which is presented in Table 1. These values include specimens of the fauna deposited in the collections of the MCN, MCP and UFRGS. Considering the scattered fossilization mode and independent collection by the institutions involved, the number provided are approximate, especially in the values of indeterminate cynodonts and indeterminate remains. Taxonomical identification of individuals is based in cranial remains. Abdala *et al.* (2001) reported the presence of numerous isolated lower jaws, but subsequent field-work by MCN team collected a considerable proportion of postcranial material of cynodonts. Association of several of these postcranial materials with the skull is not possible. The estimation after our new analysis indicates the presence of 116 cynodonts from a total of 157 specimens. Traversodontid continue to be the most abundant taxa represented by 40 individuals, chiniquodontids is recognized by three non associated fragmentary remains and proterochampsid by one individual represented by six associated cranial fragments.

SYSTEMATIC PALEONTOLOGY

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

cf. ***Probainognathus*** sp.
(Figs 2; 3)

Description

UFRGS-PV-1121T is represented by a fragment of the right mandibular ramus of approximately 7 mm in length (Fig. 2). The horizontal portion is remarkably low and presents one ellipsoid empty alveolus, two alveoli preserving the base of the crowns and the fourth alveolus with a partial postcanine. The coronoid process is rising immediately behind the last postcanine, whereas the ventral margin of the horizontal ramus is straight (Fig. 5A). In medial view the meckelian canal is placed near the ventral margin of the dentary, at approximately one quarter of the height of the bone (Fig. 2B). Most of the meckelian canal is horizontal, except for the posterior portion, at the level of the preserved postcanine, which is directed postero-dorsally (Fig. 2B).

The preserved postcanine is 1.8 mm in anteroposterior length (Table 2) and shows a large main cusp, which is aligned with the anterior and posterior accessory cusps (Fig. 3). The top of the anterior accessory cusp is broken, yet, this cusp seems to be smaller than the posterior accessory one. An additional posterior accessory cusp is somewhat displaced towards the lingual side of the postcanine, but clearly visible in the labial margin (Fig. 3A). An also broken anterior lingual cusp is positioned at the base of the anterior accessory cusp, and probably is totally hidden from the labial view of the sectorial margin. There are two bulbous cingular cusps ventrally to the second posterior accessory cusp and the anterior lingual cusp respectively, and a posterior cingular crest (Fig. 3B). The root of the penultimate postcanine is single, as evidenced by the removal of bone in the lingual side of the mandibular ramus, with no evidence of a central furrow (Fig. 2).

Discussion

The tiny fragment of lower jaw with tooth described is more likely that of a juvenile individual. The tooth is composed of an aligned series of cusps oriented dorsally, with the most anterior and posterior cusps displaced lingually and with a lingual cingulum formed by bulbous cusps and a posterior crest. A comparison between the crown of UFRGS-PV 1121T and those of other South American sectorial toothed cynodonts follows. We restrict this comparison to the posterior lower postcanines, wherever possible (Fig. 4).

Chiniquodontid cynodonts are recorded in the Santa Cruz do Sul fauna (Abdala *et al.* 2001), in the Brazilian *Dinodontosaurus* Assemblage Zone (Huene 1936; Teixeira 1982) and also in the Chañares and Ischigualasto formations from Argentina (Abdala & Giannini 2002). The postcanines of this taxon show a strongly curved main cusp (Fig. 4A)

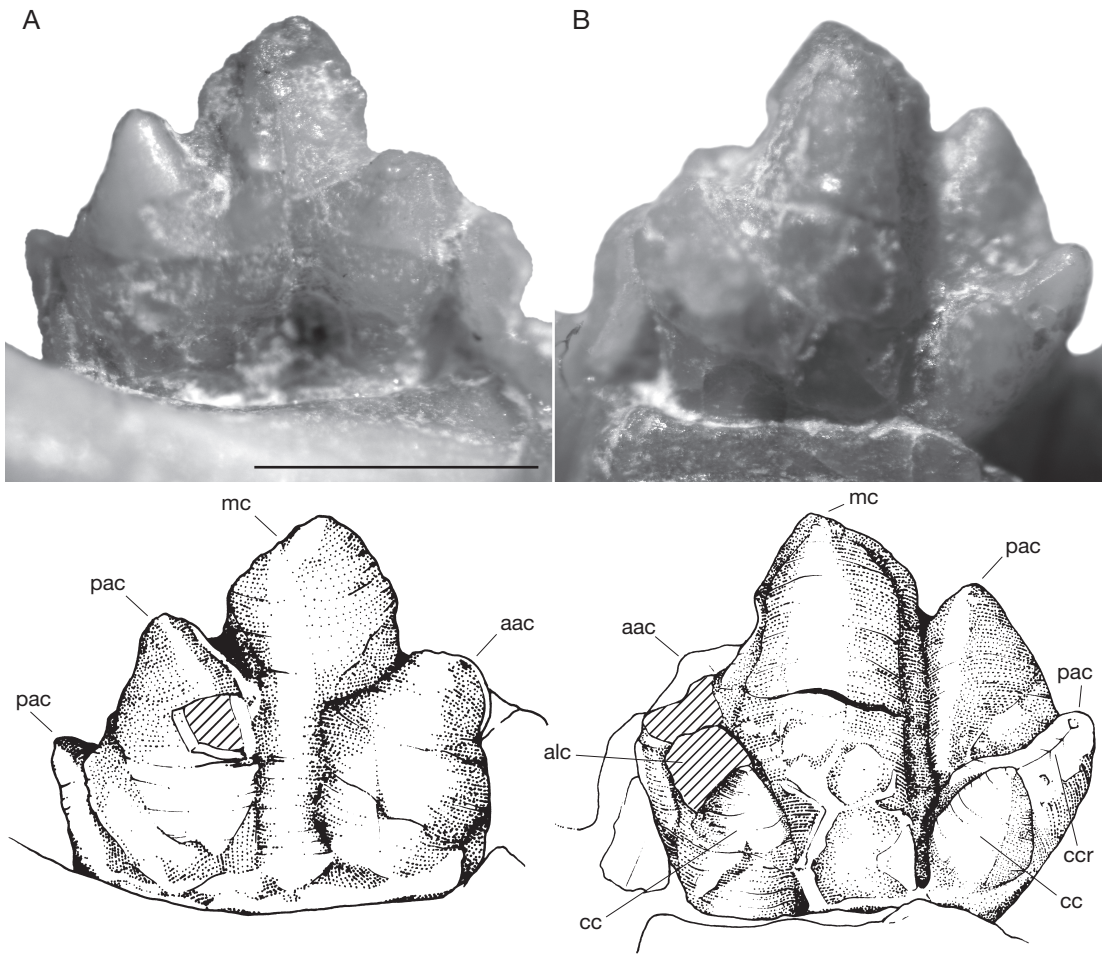

FIG. 3. — UFRGS-PV1121T detail of the last lower postcanine in buccal (**A**) and lingual (**B**) views. Abbreviations: **aac**, anterior accessory cusp; **alc**, anterior lingual cusp; **cc**, cingular cusp; **ccr**, cingular crest; **mc**, main cusp; **pac**, posterior accessory cusp. Scale bar: 1 mm.

and are therefore quite different from the new specimen from Santa Cruz do Sul.

Protheriodon estudianti, represented by a tiny, poorly preserved specimen, was recently described from the *Dinodontosaurus* AZ of the Santa Maria Formation (Bonaparte *et al.* 2006). Its posterior lower postcanines, visible only labially on the right side, show tiny accessory cusps in relation to the main one, being the overall morphology of the crown different from that of UFRGS-PV1121T. The small cynodonts *Charruodon tetracuspidatus* and *Therioherpeton cargnini*, from the Brazilian *Hyperodapedon* AZ are represented only by their holotypes. The posterior upper postcanine of *T. cargnini* (Fig. 4B) and the anterior lower one of *C. tetracuspidatus* (Fig. 4C), the only tooth crown known in each specimen, lack cingulum (Bonaparte & Barberena 1975, 2001; Abdala & Ribeiro 2000; Oliveira 2006).

Lower postcanines of the tritheledontids *Riograndia guaibensis* (Fig. 4D), *Chaliminia musteloides* (Fig. 4E) and *Irajatherium hernandezi* (Fig. 4F) show a decreasing height of the aligned cusps posteriorly (Bonaparte *et al.* 2001; Martinelli *et al.*

TABLE 3. — Taxonomic diversity of amniotes in the Santa Cruz do Sul fauna.

Therapsida
Cynodontia Owen, 1861
Santacruzodon hopsoni Abdala & Ribeiro, 2003
Massetognathus sp.
Menadon sp. traversodontid
cf. *Probainognathus* sp.
Chiniquodon sp.
Archosaurifomes Gauthier, 1986
Proterochampsidae Romer, 1966
Unnamed proterochampsid

2005; Martinelli & Rougier 2007) besides the lack of cingular cusps, being therefore different from the Santa Cruz do Sul specimen. Differences between UFRGS-PV1121T and the Late Triassic brasilodontids (Fig. 4H) are also clear because the lower postcanines in this group present a tiny anterior accessory cusp very low in the crown in relation to the main cusp (Bonaparte *et al.* 2003, 2005). The posterior accessory cusp is also more developed and high in the specimen from Santa Cruz do Sul.

Sectorial toothed cynodonts more similar to the new record of Santa Cruz do Sul are *Prozostrodon brasiliensis* from the Santa Maria Formation, Brazil, *Probainognathus jenseni* from the Middle Triassic Chañares Formation in Argentina and cf. *Probainognathus* sp. from the Carnian Ischigualasto Formation also in Argentina.

Prozostrodon brasiliensis posterior lower postcanine sectorial margin is also tetracuspidated in labial view but, different from UFRGS-PV1121T, the posteriormost marginal cusp is not displaced lingually and there is a well-developed lingual cingulum formed by a series of clearly differentiated isolated cusps (Barberena *et al.* 1987: fig. 4G). In addition, the postcanine roots have a furrow, especially well developed in the most posterior postcanines (Bonaparte & Barberena 2001).

Several adult specimens of *Probainognathus jenseni* show a worn out postcanine series with the teeth showing chisel-like edges (Romer 1970). Postcanines of juveniles of this species present a main cusp with an aligned anterior and two posterior accessory cusps, whereas an additional anterior accessory cusp is displaced lingually (Fig. 4I). The lingual cingulum in the lower postcanines of juveniles is mostly formed by cingular crests originating from the anterior and posterior cusps (Abdala 1996). In some cases it is possible to recognize the presence of a few tiny isolated cuspules contributing to the cingulum. There is no evidence of a furrow in the postcanine roots. Several characters observed in the only preserved postcanine crown of UFRGS-PV1121T, including the lingual location on the crown of the anterior lingual cusp and the second posterior accessory cusp, and the presence of cingular cusps and a lingual cingular crest, are similar to those of *P. jenseni* juveniles. UFRGS-PV 1121T is remarkably smaller than the juvenile specimens of *P. jenseni* currently known (see Table 2 for comparative measurements) and presents some important differences that should be mentioned. The posterior lower postcanines of *P. jenseni* show a comparatively taller and anteroposteriorly shorter crown, and the horizontal ramus of the lower jaw is comparatively taller than that of the specimen of Santa Cruz do Sul.

A tiny (approximately 40 mm of skull length) juvenile specimen from the Ischigualasto Formation was also described as cf. *Probainognathus* sp. (Bonaparte & Crompton 1994). The lower postcanines are not visible due to jaw occlusion, whereas the posterior uppers show four aligned cusps in labial view, the second being the largest. The morphology of these upper postcanines is similar to the labial morphology of the lower postcanine of UFRGS-PV1121T, both in the number and degree of development of the marginal cusps as well as in the general proportion between the height and anteroposterior length of the crown. Unfortunately it is not possible to observe the lingual side of the postcanines from the Ischigualasto Formation specimen, hampering a complete knowledge of its tooth morphology.

The postcanine preserved in the new specimen from Santa Cruz do Sul is therefore very similar, in labial view, to the posterior upper postcanines of cf. *Probainognathus* sp. from the Ischigualasto Formation. There is also a general similarity between the lower postcanine of UFRGS-

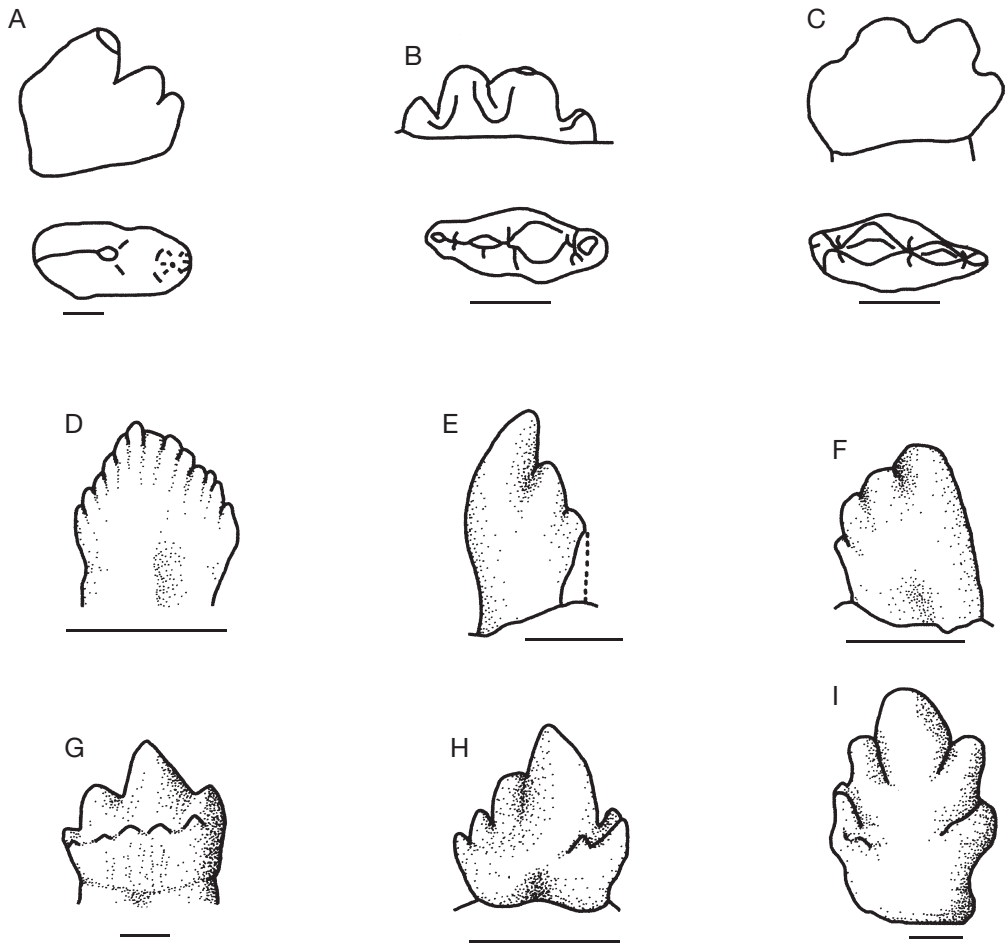

FIG. 4. — Lower postcanines of sectorial toothed cynodonts: **A**-**C**, in lateral (above) and occlusal (below) views; **D**-**I**, in lingual view; **A**, *Chiniquodon*; **B**, *Therioherpeton*; **C**, *Charruodon*; **D**, *Riograndia*; **E**, *Chaliminia*; **F**, *Irajatherium*; **G**, *Prozostrodon*; **H**, *Brasilitherium*; **I**, *Probainognathus* (juvenile); **A**, **B**, **C**, from Abdala & Ribeiro (2000); **D**, from Soares (2004); **E**, from Martinelli & Rougier (2007); **F**, from Martinelli *et al*. (2005); **G**, from Bonaparte & Barberena (2001); **H**, from Bonaparte *et al.* (2003); **I**, from Abdala (1996). Scale bars: **A**-**C**, 10 mm; **D**-**I**, 1 mm.

PV1121T with those of juvenile *P. jenseni* from the Chañares Formation. Taking into account the fragmentary nature of UFRGS-PV1121T, the differences mentioned above to juveniles of *P. jenseni* and the overall similarity to the specimen from the Ischigualasto Formation, we provisionally identify this specimen from Santa Cruz do Sul as cf. *Probainognathus*. Additional material is necessary to provide a more precise taxonomic identification of this taxon in Santa Cruz do Sul as well as in Ischigualasto.

THE FAUNA OF SANTA CRUZ DO SUL AND THE BRAZILIAN TRIASSIC BIOSTRATIGRAPHY

Two groups, cynodonts and archosauriforms, and six different taxa are now recognized in Santa Cruz do Sul (Table 3). Traversodontid cynodonts is the most abundant group recorded in the fauna, a similarity shared with the Ladinian Chañares fauna from Argentina (Rogers *et al.* 2001). The traversodontid *Santacruzodon* is the most abundant

taxon in the Brazilian fauna, whereas *Massetognathus*, which is also recorded in Santa Cruz do Sul (Schultz & Langer 2007), is the most common representative from the Chañares Formation. In Santa Cruz do Sul there is also the traversodontid *Menadon* (Melo *et al.* 2009), that occurs in Madagascar (Flynn *et al.* 1999). Among the carnivorous cynodonts represented in Santa Cruz do Sul (Table 3), chiniquodontids are also known from the Ladinian of Argentina and Brazil and the Carnian of Argentina, whereas *Probainognathus* is represented in the Ladinian and cf. *Probainognathus* in the Carnian, both from Argentina. Considering that the traversodontid *Santacruzodon* only known from the Santa Cruz do Sul fauna is the most abundant taxon, we propose the name *Santacruzodon* Assemblage Zone to refer to the fauna from this locality, instead of the previously used Traversodontid Biozone (Abdala *et al*. 2001; Rubert & Schultz 2004).

The more remarkable similarities of the *Santacruzodon* AZ are with the upper Ladinian/lower Carnian "Isalo II" fauna from Madagascar, which yielded chiniquodontids, *Menadon* and another traversodontid that resemble forms from the Santa Cruz do Sul fauna (Flynn *et al.* 1999, 2000; Flynn & Wyss 2002; Abdala & Ribeiro 2003; Langer *et al.* 2007). Dicynodonts, a fairly common group in Middle and Late Triassic faunas from Gondwana, are absent from the *Santacruzodon* AZ and poorly recorded in the Malagasy fauna (Flynn *et al.* 1999). Archosauriforms are represented by proterochampsids, an endemic South American group, in Santa Cruz do Sul, and by basal archosaurs in Madagascar (Goswami *et al.* 2005). An important difference between these faunas is the abundant record of rhynchosaurs in the Isalo II fauna (Langer *et al.* 2000; Flynn & Wyss 2002), whereas this group is unknown in the *Santacruzodon* AZ. The mixture of Ladinian traversodontids with taxa related to Carnian forms in the Santa Cruz do Sul fauna, is interpreted as supporting an intermediate temporal placement between the Brazilian Ladinian *Dinodontosaurus* AZ and the Carnian *Hyperodapedon* AZ dominated by rhynchosaurs, and thus coincident with the age proposed for the Malagasy assemblage (Abdala & Ribeiro 2003). The record of cf. *Probainognathus* in Santa Cruz do Sul is another strand of evidence correlating with Ladinian and Carnian faunas. *Massetognathus* is thus by far only known from the Argentinean Chañares and the Brazilian *Dinodontosaurus* AZ. *Chiniquodon* cf. *Probainognathus* Huene, 1936 and proterochampsids are known in both Ladinian and Carnian faunas from Brazil and Argentina.

Besides the *Santacruzodon* AZ, at least three other faunal associations can be recognized in the Triassic Santa Maria and Caturrita formations (Fig. 5). The oldest one, dominated by dicynodonts, is the *Dinodontosaurus* AZ that, considering the stratigraphic scale of Gradstein & Ogg (2004: fig. 5A), would span from probably the Upper Anisian to the Lower Ladinian. The Anisian age for the lower bound of this AZ is based on the record in outcrops from the Santa Maria Formation of *Luangwa*, a traversodontid cynodont known from African Anisian beds (Abdala & Teixeira 2004). In addition, recent phylogenetic analyses support a monophyletic clade including the Mariante rhynchosaur, recorded in association with *Dinodontosaurus*, and Anisian rhynchosaurs (Montefeltro 2008). Above the *Santacruzodon* AZ is recognized the rhynchosaur-dominated *Hyperodapedon* AZ representing a Carnian fauna. Finally, in levels of the Caturrita Formation, there are faunas mostly represented by small animals and referred to as Ictidosauria Cenozone (Rubert & Schultz 2004) or Ictidosaur Assemblage Zone (Langer *et al.* 2007). Considering that the tritheledontid (= ictidosaur) *Riograndia guaibensis* is one of the most common representatives and unique to this fauna, we propose the name *Riograndia* Assemblage Zone to refer to this fauna (Fig. 5). This younger Triassic fauna, representing a very important new addition to the knowledge of the Brazilian Triassic, is part of the Middle Norian in Gradstein & Ogg (2004) time scale (Fig. 5A).

Several differences with the Geologic Time Scale 2004 (Gradstein & Ogg 2004), concerning the Triassic time scale have been raised recently (see among others, Muttoni *et al.* 2004; Furin *et al.* 2006; Lehrman *et al.* 2006). The modified time scale (Fig. 5B) is based mainly on magnetostratigra-

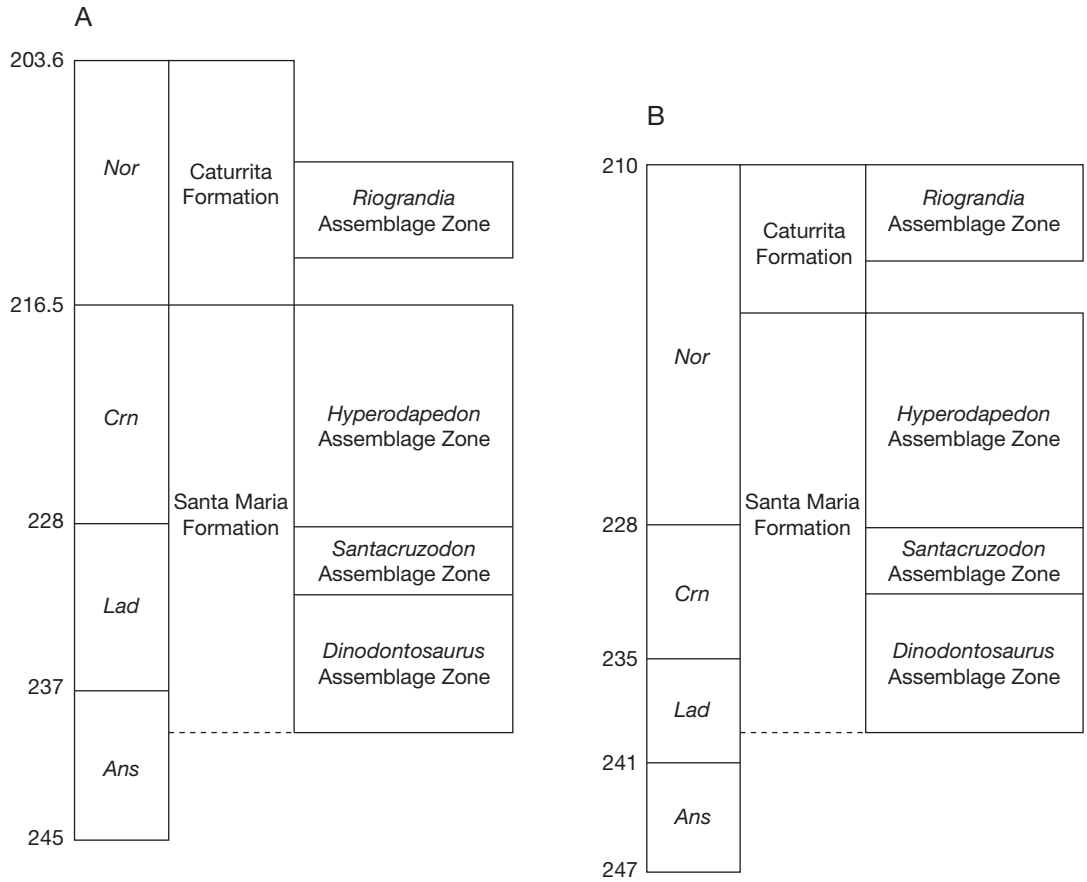

Fig. 5. — Chrono- and biostratigraphy of southern Brazilian Triassic units: **A**, Geologic Time Scale 2004 (from Gradstein & Ogg 2004); **B**, time scale after Muttoni *et al.* (2004 and reference cited therein), except for the Anisian lower age, after Lehrmann *et al.* (2006). Dashed line is inferred extension of the base of the *Dinodontosaurus* Assemblage Zone suggested by the record of the traversodontid *Luangwa* and the Mariante rhynchosaur (see text).

phy, conodont biostratigraphy and high precision dates of marine sediments and their correlation with the continental Newark astrochronological polarity time scale (Kent & Olsen 1999). The main differences between this proposal and the Geologic Time Scale 2004 are the temporal extension of the Norian to 228 Ma and of the Carnian to 235 Ma (Fig. 5B), implying a temporal range of the Upper Triassic that is approximately two-thirds of the complete Triassic (Gallet *et al.* 2003). In the context of the Muttoni *et al.* (2004) time scale, almost all the southern Brazilian Triassic record, historically regarded as Middle-Late Triassic, would be restricted to the Upper Triassic (Fig. 5B). The *Dinodontosaurus* AZ, as well as the Chañares Formation, would extend from the upper Ladinian to the lower Carnian, the *Santacruzodon* AZ would be upper Carnian, the *Hyperodapedon* AZ and also the Ischigualasto Formation would be lower to middle Norian, and the *Riograndia* AZ would be upper Norian.

The use of different time scales will indeed influence our understanding of the timing of the origin and first diversification pulse of important Mesozoic clades, including dinosauriforms, dinosaurs, mammaliamorphs and mammaliaforms.

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