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, Paraná 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 protorochampsid archosauromorph, 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.
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...
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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 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).

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).
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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.

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
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; *Brasilotodon 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.

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
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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)
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 carnini*, from the Brazilian *Hyperodapedon AZ* are represented only by their holotypes. The posterior upper postcanine of *T. carnini* (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. 2004).
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 cuspsules 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-

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 brasiliodontids (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

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**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. |          |          |          |
| Archosauromorpha Gauthier, 1986 |          |          |          |
| *Proterochampsidae* Romer, 1966 |          |          |          |
| Unnamed proterochampsid |          |          |          |
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-
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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