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A rich cynodont fauna of Santa Cruz do Sul, Santa Maria Formation (Middle-Late Triassic), southern Brazil

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With 10 figures

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Abstract: A new Triassic vertebrate fauna, known from over 100 specimens, is dominated by non-mammalian cynodonts.Three specimens represent sectorial-toothed chiniquodontids, while thirty-nine are traversodontids, of at least, four different types that are distinguished principally by postcanine morphology. The Santa Cruz do Sul is the only locality within the Santa Maria Formation characterized by the prevalence of cynodonts, and importantly documents a high traversodontid diversity for the South American Triassic.

Zusammenfassung: Eine neue Wirbeltier-Fauna, belegt durch über 100 Exemplare, besteht überwiegend aus Cynodontia. Drei Exemplare gehören zur Familie der lateral komprimiert-postcaninen Chiniquodontiden, während 39 andere der Familie der Traversodontiden angehören, von denen mindestens vier Typen sich hauptsächlich durch ihre postcanine Morphologie unterscheiden. Santa Cruz do Sul ist die einzige Fundstelle innerhalb der Santa-Maria-Formation, die durch die weite Verbreitung von Cynodontia charakterisiert ist; sie dokumentiert eindrucksvoll die große Diversität der Traversodontiden in der südamerikanischen Trias.

Key words: Cynodontia, Triassic, Brazil.

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Introduction

The State of Rio Grande do Sul in southern Brazil is distinguished by an abundant and diverse Triassic vertebrate fauna, shared, in part, with coeval sediments in western Argentina (BARBERENA et al. 1985a). Besides the numerous descriptive studies of their fossils, the red beds of the Santa Maria Formation have been the subject of faunal analysis. In an early work (BARBERENA 1977), the formation was divided into two units: (1) the Therapsid Assemblage Zone (= *Dinodontosaurus* Assemblage Zone of BARBERENA et al. 1985a, Fig. 1), embracing many isolated outcrops principally in the localities of Chiniquá and Pinheiros, and (2) the Rhynchocephalian Assemblage Zone (= *Scaphonyx* Assemblage Zone of BARBERENA et al. 1985a, Fig. 1) mostly concentrated in outcrops in the city of Santa Maria and its suburbs. BARBERENA et al. (1985b) later recognized four Local Faunas for the Santa Maria and Caturrita fortnations (Fig. 1), the latter, a newly recognized lithostratigraphic entity, representing the uppermost portion of the Santa Maria Formation (ANDREIS et al. 1980). Some of these local faunas, defined exclusively by vertebrate fossils, were the products of many isolated outcrops. The Therapsid Assemblage Zone of BARBERENA (1977) was divided by BARBERENA et al. (1985b) into the Pinheiros and the Chiniquá Local Faunas, and the Rhynchocephalian Assemblage Zone was renamed the Alemoa Local Fauna. In addition, BARBERENA et al. (1985b) defined the Botucaraí Local Fauna that included elements found in the Caturrita Formation. In recent years, a consensus has grown that the last mentioned formation should be subsumed as the uppermost part of the Santa Maria Formation (FACCINI et al. 1995, SCHULTZ 1995, SCHERER et al. 1995, but see HOLZ & SCHERER 2000). SCHULTZ (1995) recognized six vertebrate assemblages, five of them containing tetrapods, from the Santa Maria Formation (Fig. 1). The most basal (his Assemblage 2) includes a primitive rhynchosaur (SCHULTZ & AZEVEDO 1990) and an indeterminate dicynodont from the Porto Mariante locality. Assemblage 3 includes *Dinodontosaurus* and other dicynodonts, traversodontid and chiniquodontid cynodonts, rauisuchids and cerritosaurs archosaurs, and procolophonids, and corresponds to the Pinheiros and Chiniquá Local Faunas of BARBERENA et al. (1985b). Assemblage 4 has produced only fish scales and *Dicroidium* flora. Assemblage 5 consists of hyperodapedontinae rhynchosaurs, the traversodontid cynodont *Gomphodontosuchus*, the therioherpetid cynodont *Therioherpeton*, rauisuchids (?) fragments, aetosaurs, and the dinosaur *Staurikosaurus*. This assemblage corresponds to the Alemoa Local Fauna of BARBERENA et al. (1985b). Assemblage 6 comprises remains of the rhynchosaur *Scaphonyx sulcognathus* found at the locality of Linha Facão, and remains of the traversodontid cynodont *Exaeretodon*, and the basal archosauromorph *Proterochampsa* from an outcrop located approximately 12 km west of Candelaria city, on the BR 287 road. Finally, Assemblage 7 comprises the dicynodont *Jachaleria* as well as dinosaur teeth found at the Botucaraí Hill. These last two Assemblages were part of the Botucarai Local Fauna of BARBERENA et al. (1985b). SCHERER et al. (1995) and SCHULTZ et al. (1994, 1998), resurrected the biozonation scheme of BARBERENA (1977), by recognizing a Therapsid Biozone (= Pinheiros and Chiniquá Local Faunas of BARBERENA et al. 1985b) and a Rhynchosaurian Biozone (= Alemoa Local Fauna plus part of the Botucaraí Local Fauna of BARBERENA et al. 1985b, Fig. 1). In addition, SCHERER et al. (1995) proposed a *Jachaleria* Interval, an informal unit that encompassed the findings in the Botucaraí Hill locality.

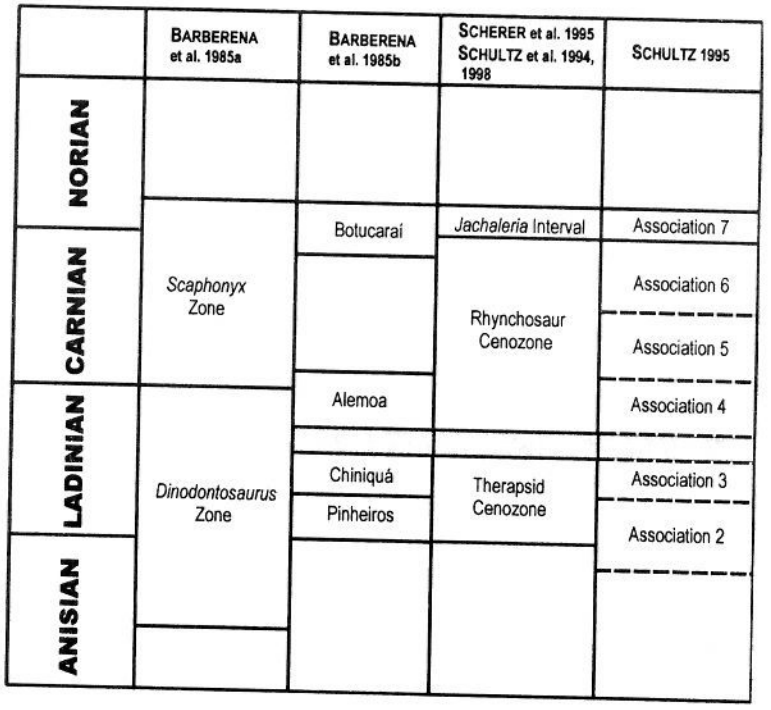

Fig. 1. Chart of the Faunal Assemblages proposed for the Santa Maria Formation. Dashed line indicate doubt in the temporal limit.

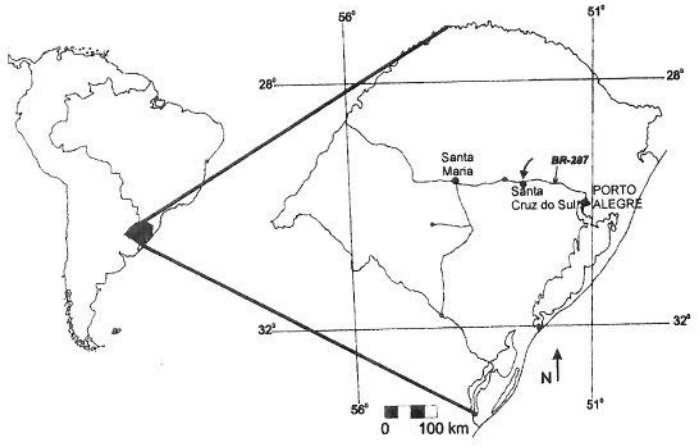

Fig. 2. Map of the Santa Cruz do Sul locality in the Rio Grande do Sul State, southern Brazil.

New discoveries at the Santa Maria Formation remarkably enlarged its faunal composition. Both a new therioherpetid cynodont (ABDALA & RIBEIRO 2000), found in the assemblage 6 of SCHULTZ (1995), and the prosauropod dinosaur *Saturnalia* (LANGER et al. 1999), from Assemblage 5 of SCHULTZ (1995), are new components of the Rhynchosaurian Biozone. Secondly, the dinosaur *Guaibasaurus* (BONAPARTE et al. 1999), tritheledontid cynodonts, and sphenodontids (FERIGOLO 1999, FERIGOLO et al. 1999) were collected in sandstones from outcrops close to Botucarai Hill, and seem to be part of the *Jachaleria* Interval fauna, or alternatively a new, younger one (FERIGOLO 1999).

Accordingly, dicynodonts appear to dominate the Therapsid Biozone and rhynchosaurs the late Rhynchosaurian Biozone (AZEVEDO et al. 1990). Cynodonts occur in all these faunas yet, while fairly numerous in Pinheiros and Chiniqua Local Faunas, they remain a subordinate group.

In 1995, a new Triassic vertebrate fauna was discovered by C. L. Schultz and M. C. Langer at the locality of Santa Cruz do Sul, approximately 150 km

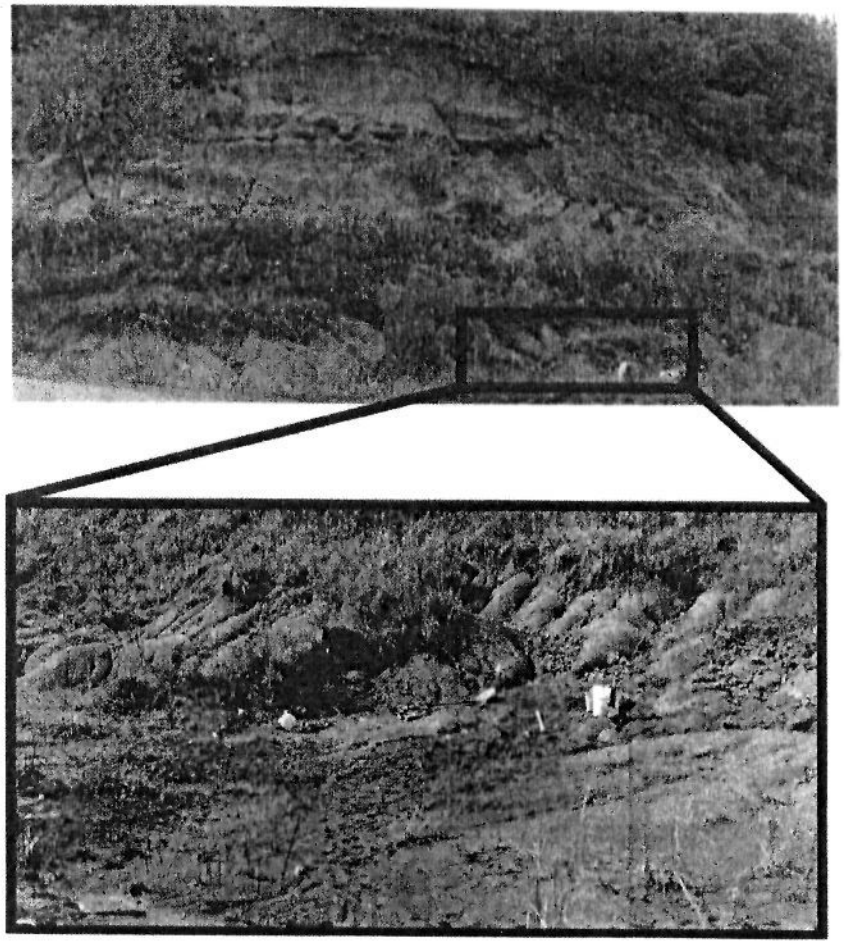

Fig. 3. View of the Santa Cruz do Sul outcrop and, below, its fossiliferous level.

west of Porto Alegre (Fig. 2). Additional collecting trips followed in 1997 and 1998, greatly increasing the number of specimens. Our attention was drawn to the predominance of cynodonts. In fact, only cynodonts are positively identifiable taxa among the total of specimens collected, encompassing both cranium and postcranium.

The outcrop (S 29° 44' 25".32, W 52° 27' 01".29) is located in the suburbs of the city of Santa Cruz do Sul (Fig. 2). Fossils occur in a 180-cm thick stratum of red mudstones with levels rich in calcium carbonate concretions. Overlying the fossiliferous level fine-grained sandstones are interbedded into the mudstones, which represent crevasse-splay deposits in a flood plain (Fig. 3). Most of the fossils consist of partial lower jaws, with skull fragments and isolated postcranial elements present in lesser numbers. A large fraction of the material is badly fragmented, hampering their confident anatomical and/or taxonomic identification.

The primary goal of this work is to provide a preliminary description of the components of the new fauna of Santa Cruz do Sul, indeed, one of the most diverse non-mammalian cynodont assemblages in the South American Triassic. Additionally, comparisons with other Triassic faunas containing cynodonts are made with the aim of establishing a temporal framework for this peculiar faunal assemblage.

Material

The material studied herein is reposited in the collections of the Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul (MCN PV), the Instituto de Geociências of the Universidade Federal do Rio Grande do Sul (UFRGS PV T) and the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul (MCP PV).

Most of the material ranges in size from tiny specimens, of 0.9 cm in length (four isolated postcanines), to lengths of 16 cm (skull) and 18 cm (a femur). There is a substantial representation of isolated lower jaws, most of them of 8 to 10 cm in length.

Results

Fig. 4 summarizes the identification of elements found at the Santa Cruz do Sul outcrop. Traversodontid cynodonts are, by far, the dominant group represented by, at least, four taxa, differentiated mainly on the basis of postcanine morphology. Three specimens of sectorial toothed chiniquodontid cynodonts were also recovered.

Traversodontid Type I (Fig. 5)

Material: a badly preserved skull associated with a series of vertebrae, scapulacoracoid and other postcraneal elements (MCN PV 2750); three lower jaws (UFRGS PV 432T, UFRGS PV 434T, UFRGS PV 463T).

Taxonomic group	Number of individuals
Indet. cynodonts	40
Traversodontid cynodonts	39
Chiniquodontid cynodonts	3
Indet. remains	29
Total	111

Fig. 4. Number of individuals present in the Santa Cruz do Sul Fauna.

Description: skull length 18 cm; conical incisors with a simple cusp, five or six upper postcanines. Mandibular ramus high and robust, between 11 cm and 16 cm in length; fused symphysis; portion of the jaw anterior of the canine dorsoventrally compressed; horizontal rami with a medially projected platform bearing the 6 postcanines; masseteric fossa extends anteriorly to the level of the third postcanine; angular process projected posteriorly; anterior portion of the coronoid process broad; last postcanine not covered labially by the coronoid process. Three forward directed incisor alveoli, the third being the smallest; canine separated by a short diastema from both incisisors and the postcanines; six postcanines showing extensive wear; first and last postcanines smallest; pc_2 larger than pc_1 but still significantly smaller than pc_{3-5}; third, fourth and fifth postcanines quadrangular with two anterior cusps united by a crest and two posterior low cusps, the labial one slightly overlapping the anterolabial cusp of the preceding postcanine; last postcanine ovoid in shape, with two tiny cuspules posteriorly.

There is no in situ association between the skull and lower jaws of the traversodontid type I. They are included in the same taxa by size correspondence, low postcanine number, and overall similarities with the cynodont *Menadon besairei* from the Isalo Group of Madagascar (Flynn et al. 2000). Traits such as the small size of the two first lower postcanine, and especially of the last one, and the dorsoventral flattening of the anterior portion of the lower jaw are also present in the Malagasy traversodontid (Abdala pers. obs.). In addition, traversodontid type I shows a mixture of features of Ladinian and Carnian cynodonts. The maxillary platform, the zygomatic arch, and the quadrate articulation site on the squamosal resemble those of the Ladinian cynodont *Massetognathus* (Romer 1967). The broad muzzle and

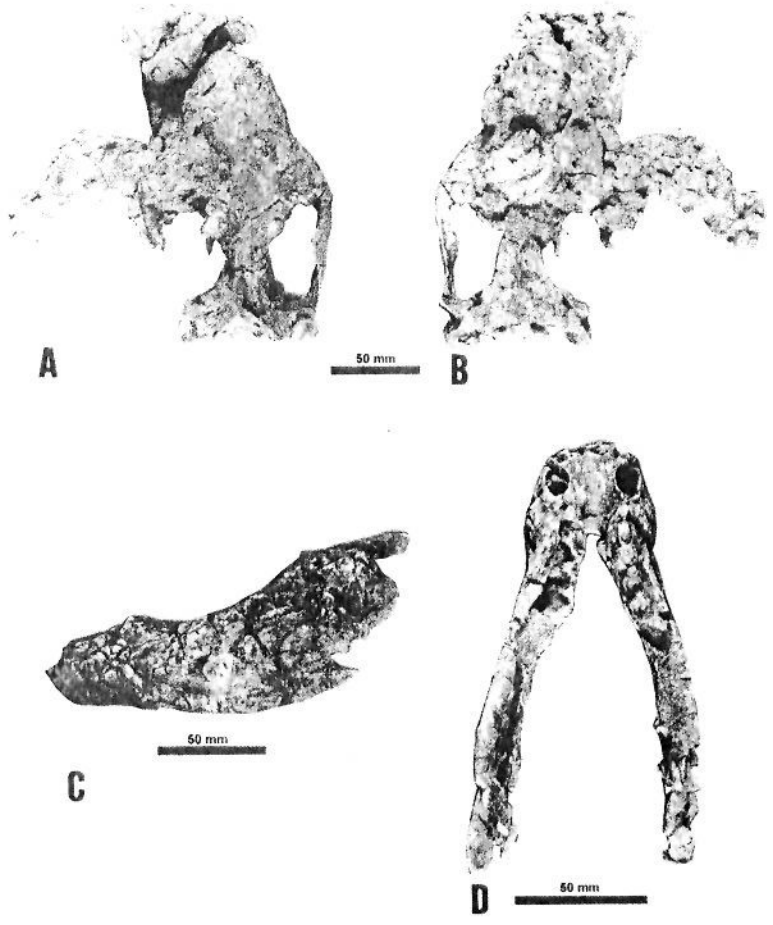

Fig. 5. Traversodontid Type I. A, B: MCN PV 2750, skull, associated with some postcranial elements, dorsal (A) and ventral (B) views. C, D: UFRGS PV 432T, lower jaw, lateral (C) and dorsal (D) views.

the zygomatic arch parallel to the cranial axis are recognized also in juveniles of *Massetognathus* (Abdala & Giannini 2000). The projection of the angular process, the small number of postcanines and the conical simple cusped incisors are features shared by *Exaeretodon*, a predominantly Carnian form.

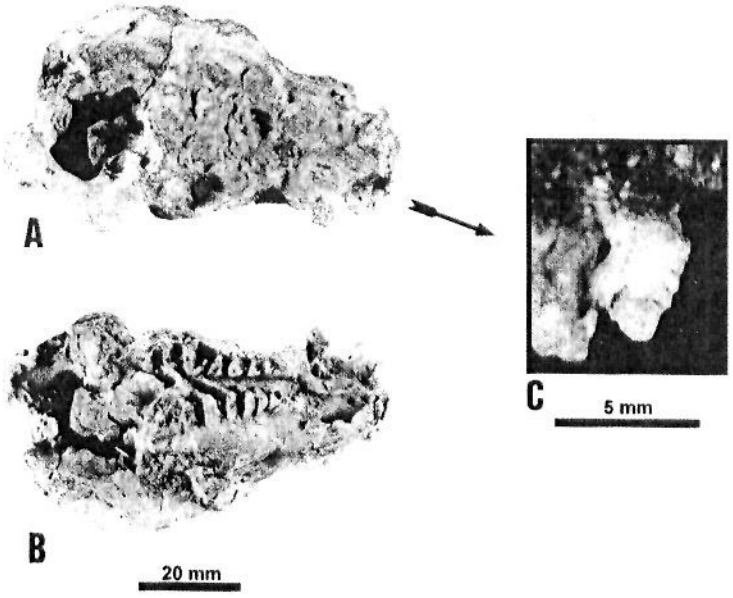

Fig. 6. Traversodontid Type II. A, B, C: MCN PV 2768, fragmentary skull, dorsal (A) and ventral (B) views and (C) upper incisor.

Traversodontid Type II (Fig. 6)

Material: three lower jaws (MCN PV2751, MCN PV 2752, MCP 4044 PV); fragmentary skull with lower jaws (MCN PV 2768); incomplete maxilla with postcanines (MCN-PV 2763); fragmentary skull and lowerjaw with postcanines (MCP 4034 PV).

Description: skull length approximately 8 cm (MCN PV 2768); descending flange of the jugal developed into a ball-shaped projection. Four incisors with five to seven mesial and distal marginal cuspules. Seven to 10 quadrangular upper postcanines, proportionally longer anteroposteriorly than in other traversodontids; deep occlusal basin; labial crest with three cusps, the posterior one strikingly large, representing more than half of the length of the labial crest; posterior transverse crest with three cusps; lingual and middle cusps in the transverse crest very close together, a basin separating them from the labial one; anterior transverse crest less developed

than the posterior one formed by a series of cingular cusps (at least 8 or 9). *Shallow mandibular ramus; symphysis fused; masseteric fossa extending* anteriorly to the level of postcanines seven to nine; small diastema between canine and postcanine; last two postcanines covered laterally by the ascending coronoid process. Three procumbent lower incisors, with five to seven mesial and distal marginal cuspules; nine to ten or eleven lower postcanines; anterior transverse crest with lingual and labial cusps of different sizes; deep occlusal basin; labial crest with two cusps and a posterior transverse crest as high as the anterior one.

This material most resembles the new Madagasean traversodontid *Dadadon isaloi* (FLYNN et al. 2000). Similarities such as the presence of a rounded suborbital process, and the number and overall structure of the upper postcanines are shared among these taxa. A matching incisor morphology is also known in *?Scalenodontoides plemmyridon* of Nova Scotia, Canada (HOPSON 1984; = *Arctotraversodon* of SUES et al. 1992).

Traversodontid Type III (Fig. 7)

Material: Incomplete right lower jaw, lacking coronoid process (MCN PV 2754).

Description: horizontal ramus deep, angular process not projected posteriorly. Three incisors and canine (all broken), separated by a small diastema from the 12 postcanines; anterior crest of postcanines bearing two cusps; labial facet on pc_{1-7} exceptionally worn; less wear displayed on pc_{8-9}.

This traversodontid lower jaw differs from the types above described in lacking a posteriorly directed angular process and in its proportionally deeper horizontal ramus. The lack of an angular process and the large number of postcanines are symplesiomorphies shared with basal traversodontids (including *Massetognathus*), differing from the most derived *Exaeretodon*.

Traversodontid Type IV (Fig. 8)

Material: four tiny upper postcanines (MCN PV 2748).

Description: length of the maxillary fragment 8.5 mm; triangular crown with a worn area forming a longitudinal furrow; two labial cusps, the posterior one huge; one or two lingual cusps, lacking a transverse crest, either anteriorly or posteriorly. The absence of the transverse crest could imply a less restricted anteroposterior movement of the lower jaws than in other traversodontids.

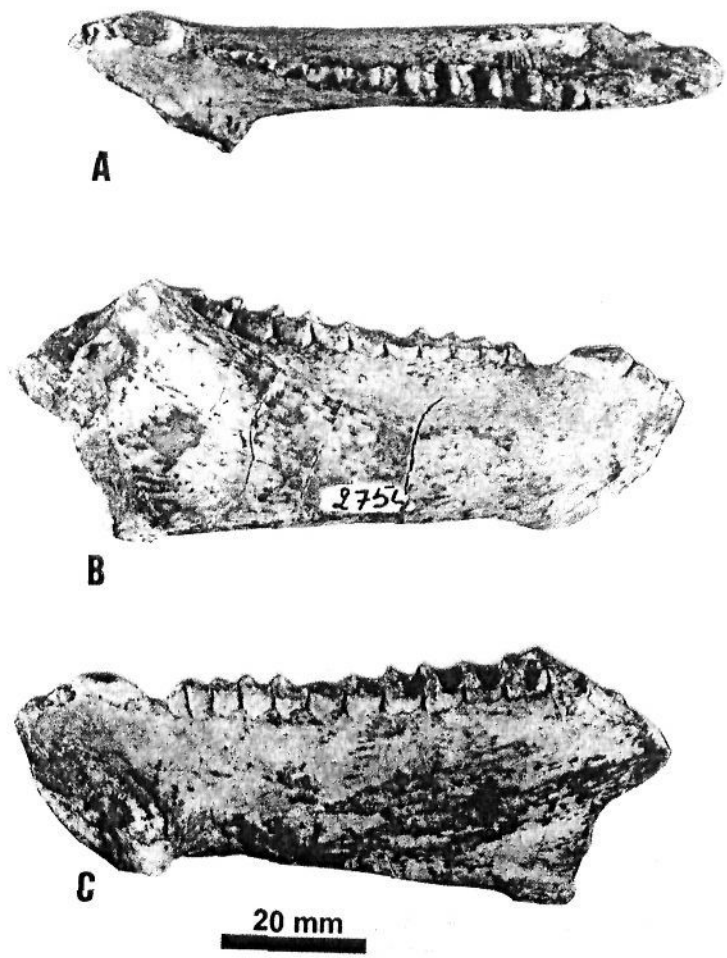

Fig. 7. *Traversodontid Type III.* A, B, C: MCN PV 2754, lower jaw, dorsal (A), lateral (B) and medial (C) views.

Features as the triangular outlined crown and the two labial cusps, resemble that of *Boreogomphodon* from the Turkey Branch Formation of Virginia (SUES & OLSON 1990), but this genus develops a posterior transverse crest.

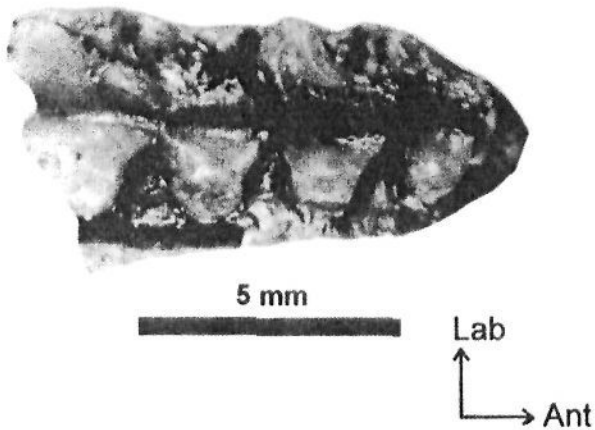

Fig. 8. Traversodontid Type IV. MCN PV 2748, fragmentary maxilla with four postcanines, ventral view.

Chiniquodontid (Fig. 9)

Material: skull fragment (MCN PV 2756), lower jaw (MCN-PV 2755) and an isolated humerus (MCN PV 2757).

Description: Four incisors, canine, and eight or nine postcanines in the skull fragment; elongated palate extended posteriorly to almost the level of the last postcanine; pc^3 with the main cusp slightly curved backwards, and a posterior accessory cusp. The more complex posterior postcanine present the main central cusp strongly curved backwards, a well developed posterior accessory cusp, relatively low on the crown, and a less developed anterior accessory cusp high on the crown. It is not possible to verify the presence of a cingulum on the upper postcanines. The lower jaw has seven or eight postcanines lacking a canine-postcanine diastema. The posterior postcanines are similar to those of the upper dentition but have an additional lingual cingulum, on pc_6 and probably pc_5, comprised of two cuspules, originated from the anterior accessory cusp. An isolated humerus is regarded to be chiniquodontid because of its greatly extended distal portion, which is remarkably similar to the condition observed in others representatives of this family (Romer & Lewis 1973, Abdala 1999).

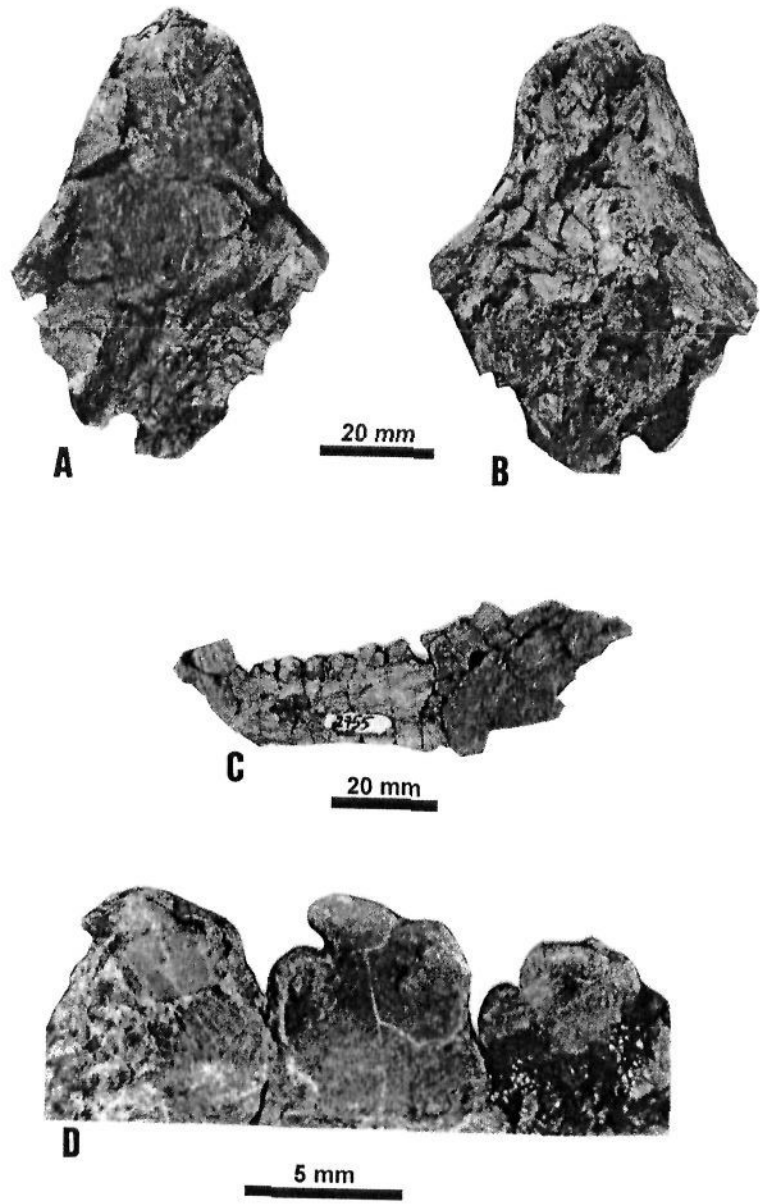

Fig. 9. Chiniquodontid. A, B: MCN PV 2756, fragmentary skull, dorsal (A) and ventral (B) views. C, D: MCN PV 2755, lower jaw, lateral (C) view and sixth postcanine in lingual view (D).

Discussion

According to FACCINI et al. (1995) the facies association present in the Santa Cruz do Sul outcrop characterizes the stratigraphic level called the "Santa Maria Sequence (or sequence 2)", which contains the faunal Assemblages 2 through 7 erected by SCHULTZ (1995). This sequence begins with a predominance of massive and laminated mudstones and gradually shows an upwards increase in the presence of the channel facies. The sandstone/mudstone ratio of our studied outcrop suggests that it represents a relatively high level within the sequence. This could explain the absence of dicynodonts, the most conspicuous group in the Therapsid Faunal Assemblage of the Santa Maria Formation. However, the absence of rhynchosaurs, the predominant taxa in the overlaying Rhynchosaur Faunal Assemblage, and the fact that the highly diversified traversodontids represented in Santa Cruz do Sul are unknown elsewhere in the Santa Maria faunal assemblages, suggest that this "cynodont-fauna" represents a temporal interval not previously recognized in the Santa Maria Formation. The Ischigualasto Formation, commonly correlated with the upper Santa Maria Formation that yields the Rhynchosaur assemblage (BARBERENA et al. 1985a, SCHULTZ et al. 1994), was dated 227.8 ± 0.3 millons years (ROGERS et al. 1993), matching to the base of the Carnian in ROSS et al. (1994) and GRADSTEIN & OGG (1996) timescales (but see BENTON, 1994; LUCAS, 1998; HECKERT & LUCAS, 2000 for Late Carnian proposals for this unit). In addition, a remarkable predominance of traversodontid cynodonts, was previously recorded in older units, such as the Ladinian Chañares Formation (ARCUCCI et al. 1994). Taking into account both arguments, we suggest a late Ladinian age for the Santa Cruz do Sul fauna.

A new Triassic fauna has been discovered in Madagascar. This fauna, which has so far yielded procolophonids, rhynchosaurs, dinosaurs, sphenodontians, dicynodonts and cynodonts, is regarded provisionally to be late Ladinian-early Carnian age (FLYNN et al. 1999, 2000). The cynodonts of this fauna are chiniquodontids and traversodontids (FLYNN et al. 2000; ABDALA pers. obs.). The latter, also highly diversified, are represented by a *Massetognathus*-like form, a new taxon, similar to but distinct from *Gomphodontosuchus* and *Exaeretodon*, and a third unpublished taxon (FLYNN et al. 1999, 2000). The described Malagasy traversodontids show notable similarities to traversodontid types I and II from Santa Cruz do Sul (ABDALA pers. obs.). Similarities on faunal composition among the Santa Cruz do Sul and the Madagascar faunas, even when restricted just to cynodonts, let us infer by another line of evidence, a late Ladinian (but no necessarily early Carnian) age for this new South American fauna.

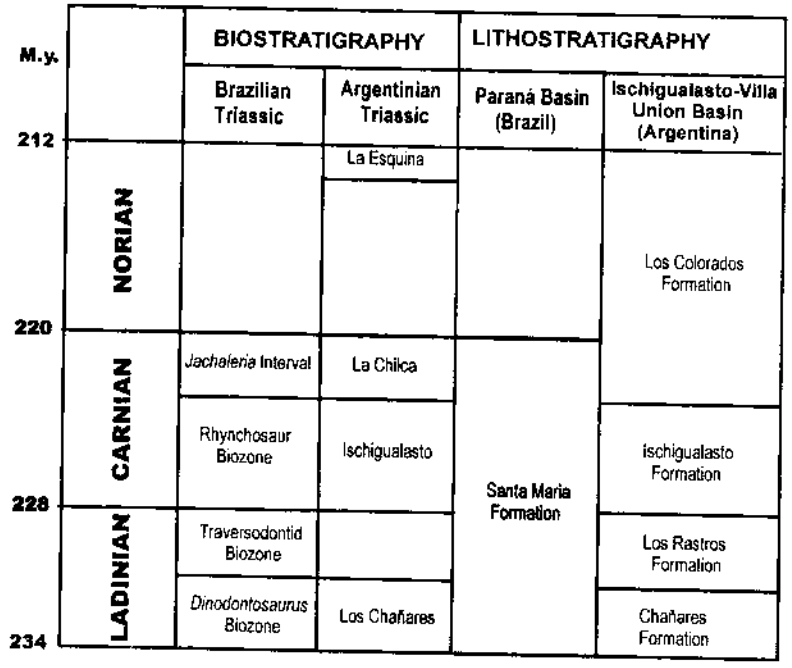

Fig. 10. Biostratigraphic chart of the Santa Maria Formation. Time scale based on Ross et al. (1994).

As result of our study, a biostratigraphic chart is proposed (Fig. 10) with a new late Ladinian traversodontid biozone (represented by the Santa Cruz do Sul fauna) between the *Dinodontosaurus* and Rhynchosaur Biozones. Regarding the radioisotopic dating of the Ischigualasto Formation and its suggested sedimentation rates - probably in 1 to 4 millions years – (ROGERS et al. 1993) an early to middle Carnian age is here considered for the Ischigualasto Formation and, by faunal correlation, for the Rhynchosaur Biozone of the Santa Maria Formation. Besides, the isolated record of the dicynodont *Jachaleria colorata* in transitional beds between the Ischigualasto and Los Colorados formations in La Chilca locality of Argentina (BONAPARTE 1982) is probably of a late Carnian age (also suggested by COX 1991 and BATTAIL 1993). In this way, the *Jachaleria* Interval of the Santa Maria Formation, previously considered as early Norian (SCHULTZ et al. 1994, 1998) is here regarded as late Carnian.

The temporal hiatus between the Therapsid and the Rhynchosaur faunal Assemblages of the Santa Maria Formation (SCHULTZ et al. 1998) appears to be bridged by the fauna of Santa Cruz do Sul. More interestingly, this new fauna is suggestive of the existence of a more extensive fauna throughout the temperate paleolatitudes of Gondwanaland (PARRISH et al. 1986), one that is characterized by highly similar traversodontid and chiniquodontid cynodonts.

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