

THE CONTINENTAL TETRAPOD-BEARING TRIASSIC OF SOUTH BRAZIL

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Abstract—The Rosário do Sul Group is one of the better-known tetrapod-bearing continental deposits of Triassic age. It crops out in central Rio Grande do Sul, south Brazil, and has yielded a fauna of more than 40 valid species, including temnospondyls, procolophonoideans, dicynodonts, cynodonts, sphenodontians, rhynchosaurs, and archosaurs. Its fossil record is herein briefly assessed, along with the stratigraphy of its bearing sequences. This includes the Early (perhaps earliest) Triassic Sanga do Cabral Formation, which correlates to the *Lystrosaurus*/“Impoverished” zones of the Karoo Basin, and a second major stratigraphic sequence of Mid-Late Triassic age that broadly corresponds to the Santa Maria and Caturrita formations. The lower, cynodont-dicynodont dominated fauna of that sequence is partially Chañarian (Ladinian) in age, and encompasses the *Dinodontosaurus* Assemblage-Zone. The Late Triassic fauna includes the *Hyperodapedon* and Ictidosaur assemblage-zones. The former, dominated by rhynchosaurs, includes some of the oldest known dinosaurs, and can be given an Ischigualastian (Carnian) age. The younger fauna contains advanced cynodonts and procolophonids, as well sphenodontians, most probably corresponding to the latest Triassic.

INTRODUCTION

The Rosário do Sul Group, and especially the Santa Maria Formation within it, are well known for their tetrapod record. These Triassic deposits crop out along a 500 km belt in the south-central portion of Rio Grande do Sul, south Brazil (Fig. 1). Fossil tetrapods are, however, not restricted to the Santa Maria Formation, but also abound in the Sanga do Cabral and Caturrita formations, which respectively lay below and above that stratigraphic unit (Andreis et al., 1980). Ages attributed to the Rosário do Sul Group are mainly based on biostratigraphic studies of its tetrapod assemblages, and extend for most of the Triassic, with evidence of Induan-Olenekian (Cisneros and Schultz, 2002), Anisian (Abdala and Sá-Teixeira, 2004), Ladinian (Abdala et al., 2001), Carnian (Langer, 2005a) and Norian (Rubert and Schultz, 2004) faunas.

This contribution includes a review of the fossil tetrapod record of the Rosário do Sul Group. Firstly, this is assessed according to the phylogenetic affinities of the valid taxa (Tables 1, 2), which are discussed based on most recent revisions of their taxonomic status. Thereafter, a second approach is taken, and current knowledge on the depositional sequences of the Rosário do Sul Group is used to order the fossil record of different sites in a stratigraphic framework. Finally, data on sequence stratigraphy of fossil-bearing deposits and phylogeny of fossil taxa are assembled to produce an as comprehensive as possible view of the faunal evolution of the South Brazilian Triassic.

Institutional abbreviations: MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul; UFRGS, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil. These are indicated only if there is no bibliographic reference to the specimen/taxon in question.

FOSSIL RECORD

The fossil biota of the Rosário do Sul Group includes a minimum of 45 formally proposed, and valid tetrapod species: one temnospondyl, four procolophonoideans, three dicynodonts, 15 cynodonts, one sphenodontian, five rhynchosaurs, and 16 archosaurs. The picture is, however, rather different in terms of abundance. Azevedo et al. (1990) quantified the fossil record of the Santa Maria Formation, where dicynodonts represent about 60% of the specimens collected in most Middle Triassic assemblages, while rhynchosaurs account for about 90% in those of Carnian age. Other faunas are, conversely, dominated by cynodonts (Abdala et al., 2001).

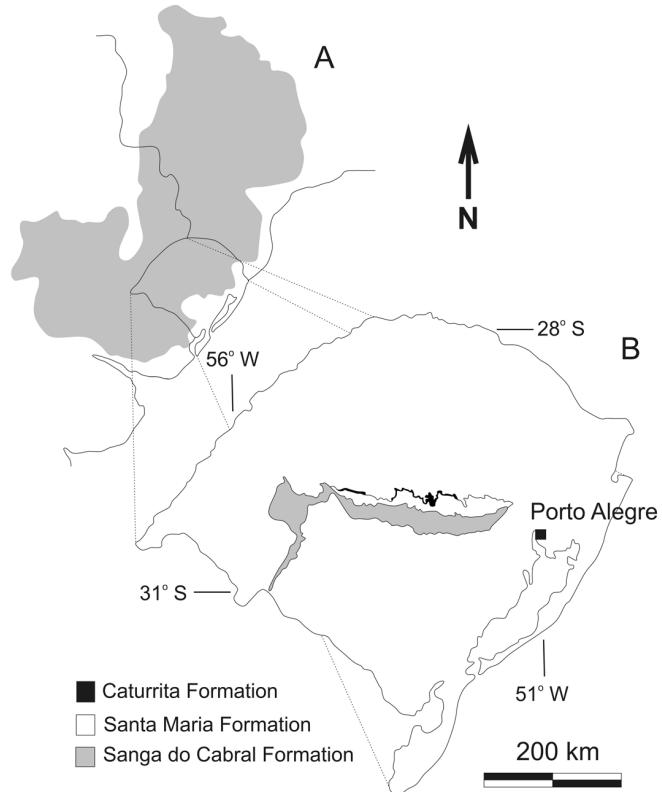


FIGURE 1. A, Map of the Paraná Basin (gray) in east-central South America, showing the location of Rio Grande do Sul, in south Brazil. B, Map of Rio Grande do Sul depicting the outcrop belt of the Rosario do Sul Group (based on DaRosa, 2005; DaRosa and Faccini, 2005).

Temnospondyli

Lavina and Barberena (1985) assigned fragmentary temnospondyl remains from the Sanga do Cabral Formation to the Lydekkerinidae and Rhytidosteidae, but these have been recently reviewed by Dias-da-Silva et al. (2005, see also Dias-da-Silva, 2003), and referred to either Rhytidosteidae or Temnospondyli *incertae sedis*. More complete mate-

TABLE 1. Fossil record presented by monophyletic hierarchy of Temnospondyli, Procolophonoidea, and Therapsida in the Rosário do Sul Group, Triassic of Rio Grande do Sul, Brazil.

Monophyletic hierarchy	Chronological/Stratigraphical range outside Brazil
Rhytidosteidae (Marsicano and Warren, 1998)	Late Permian-Olenekian (Marsicano and Warren, 1998; Warren et al. 2000)
<i>Sangaia lavinai</i> (Dias-da-Silva and Marsicano, 2006)	_____
Owenetidae (Cisneros et al., 2004)	Late Permian -Induan (Modesto et al., 2003)
<i>Candelaria barbouri</i> (Cisneros et al., 2004)	_____
Procolophonidae (Laurin and Reisz, 1995)	Late Permian -Rhaetian (Sues et al., 2000, Modesto et al., 2001)
Procolophoninae (DeBraga, 2003)	Induan-Olenekian (DeBraga, 2003; Spencer and Benton, 2004)
<i>Procolophon</i> (de Braga, 2003; Cisneros and Schultz, 2002; Dias da Silva et al., 2006)	<i>Lystrosaurus</i> Assemblage Zone and “Impoverished zone” (Neveling et al., 1999) and Fremouw Formation (Colbert and Kitching, 1975), Induan-Olenekian, Karoo Basin and Antarctica (Damiani et al., 2000)
<i>P. pricei</i> (Cisneros and Schultz, 2002)	Undefined stratum of the Karoo Basin (Cisneros and Schultz, 2002)
<i>P. brasiliensis</i> (Cisneros and Schultz, 2002)	_____
Leptoleurinae (DeBraga, 2003)	Olenekian-Rhaetian (Sues et al., 2000, DeBraga, 2003)
<i>Soturnia caliodon</i> (Cisneros and Schultz, 2003)	_____
Kannemeyeriformes (Maish, 2001)	Olenekian-Norian (Lucas, 1998; but see Thulborn and Turner, 2002)
<i>Dinodontosaurus pedroanum</i> (Lucas and Harris, 1996)	Chañares Formation, Ladinian, Argentina (Cox, 1965)
Stahleckeriidae (Vega-Dias et al., 2004)	Anisian-Norian (Lucas, 1998)
<i>Stahleckeria potens</i> (Vega-Dias et al., 2005)	_____
<i>Ischigualastia</i> sp. (Peruzzo and Araújo Barberena, 1995)	Ischigualasto Formation, Carnian, Argentina (Rogers et al., 1993)
<i>Jachaleria</i> (Vega-Dias and Shultz, 2004)	Los Colorados Formation, Carnian/Norian, Argentina (Bonaparte, 1982; Abdala et al., 2001)
<i>J. candelariensis</i> (Vega-Dias and Schultz, 2004)	_____
Cynodontia (Hopson & Kitching, 2001)	Late Permian-Recent
<i>Protheriodon estudianti</i> (Bonaparte et al. 2006a)	_____
Traversosontidae (Abdala et al., 2006)	Olenekian-Norian (Abdala et al., 2006)
<i>Luangwa</i> (Abdala and Sá-Teixeira, 2004)	Ntawere Formation, Anisian, Zambia (Abdala and Sá-Teixeira, 2004)
<i>L. sudamericana</i> (Abdala and Sá-Teixeira, 2004)	_____
<i>Traversodon stahleckeri</i> (Barberena, 1981a)	_____
<i>Santacruzodon hopsoni</i> (Abdala and Ribeiro, 2003)	_____
<i>Massetognathus</i> (Abdala and Giannini, 2000)	Chañares Formation, Ladinian, Argentina (Abdala and Giannini, 2000)
<i>M. ochagaviae</i> (Barberena, 1981b)	_____
<i>Gomphodontosuchus brasiliensis</i> (Hopson, 1985)	_____
<i>Exaeretodon</i> (Abdala et al., 2002a)	Ischigualasto Formation, Carnian, Argentina (Bonaparte, 1982)
<i>E. major</i> (Abdala et al., 2002a)	_____
<i>E. riograndensis</i> (Abdala et al., 2002a)	_____
Chiniquodontidae (Abdala and Giannini, 2002)	Ladinian-Carnian (Abdala and Giannini, 2002)
<i>Chiniquodon</i> (Abdala and Giannini, 2002)	Chañares and Ischigualasto formations, Ladinian-Carnian, Argentina (Abdala and Giannini, 2002)
<i>C. teotonicus</i> (Abdala and Giannini, 2002)	Chañares Formation, Ladinian, Argentina (Abdala and Giannini, 2002)
Clade 8 (Bonaparte et al., 2005)	Norian-Recent (Lucas and Hunt, 1994)
<i>Theroherpeton cargini</i> (Bonaparte and Barberena, 2001)	_____
<i>Charuodon tetracuspidatus</i> (Abdala and Ribeiro, 2000)	_____
<i>Prozostrodon brasiliensis</i> (Bonaparte and Barberena, 2001)	_____
Tritheledontidae (Sidor and Hancox, 2006)	Norian- Early Jurassic (Lucas and Hunt, 1994; Sidor and Hancox, 2006)
<i>Riograndia guaibensis</i> (Bonaparte et al., 1999)	_____
<i>Irajatherium hernandezi</i> (Martinelli et al., 2005)	_____
Brasildontidae (Bonaparte et al., 2005)	_____
<i>Brasildodon quadrangularis</i> (Bonaparte et al., 2005)	_____
<i>Brasilitherium riograndensis</i> (Bonaparte et al., 2005)	_____

rial includes a partial mandible (Dias-da-Silva, 1998) and skull. The latter was described by Dias-da-Silva et al. (2006a) as a new rhytidosteid, *Sangaia lavinai* (Dias-da-Silva and Marsicano, 2006). According to those authors, *Sangaia* is most closely related to the Indian form *Indobatrachops panchetensis*, from the Panchet Formation, Induan of the Damodar Valley (Chatterjee and Roy-Chowdhury, 1974; Lucas, 1998). In addition to these records from the Sanga do Cabral Formation, fragmentary temnospondyl remains were also reported from the Santa Maria Formation (Richter, 2001).

Parareptilia

In the Rosário do Sul Group, parareptiles are known based only on procolophonoideans (*sensu* Lee, 1995), whereas the possible occurrence of a pareiasaur (Schultz and Dias-da-Silva, 1999; Lucas, 2002) was dismissed by Cisneros et al. (2005). Four taxa were described: *Candelaria barbouri* Price, 1947 (see also DaRosa et al., 2004a); *Procolophon pricei* Lavina, 1983; *Procolophon brasiliensis* Cisneros and Schultz, 2002; and *Soturnia caliodon* Cisneros and Schultz, 2003. A further partial skull was

TABLE 2. Fossil record presented by monophyletic hierarchy of Sphenodontia, Rhynchosauria, Prolacertiformes, and Archosauria in the Rosário do Sul Group, Triassic of Rio Grande do Sul, Brazil.

Monophyletic hierarchy	Chronological/Stratigraphical range outside Brazil
Clevosauridae (Bonaparte and Sues, 2006)	Carnian-Early Jurassic (Fraser and Benton, 1989; Sues and Reisz, 1995)
<i>Clevosaurus</i> (Bonaparte and Sues, 2006)	Norian-Early Jurassic (Fraser, 1994; Sues and Reisz, 1995)
<i>C. riograndensis</i> (Bonaparte and Sues, 2006)	_____
Rhynchosauridae (Dilkes, 1998)	Anisian-Carnian (Langer and Schultz, 2000a)
"Mariante rhynchosaur" (Schultz and Azevedo, 1990)	_____
Hyperodapedontinae (Langer and Schultz, 2000b)	Ladinian?-Carnian (Flynn et al., 1999; Langer et al., 2000)
N. gen. <i>sulcognathus</i> (Langer and Schultz, 2000b)	_____
<i>Hyperodapedon</i> (Langer et al., 2000)	Ladinian?-Carnian (Flynn et al., 1999; Langer et al., 2000)
<i>H. huenei</i> (Langer and Schultz, 2000b)	_____
<i>H. mariensis</i> (Langer et al., 2000)	Ischigualasto Formation, Carnian, Argentina (Langer et al., 2000)
<i>H. sanjuanensis</i> (Langer et al., 2000)	Ischigualasto Formation, Carnian, Argentina (Langer et al., 2000)
Prolacertiformes (Benton and Allen, 1997)	Late Permian-Norian (Dilkes, 1998)
Archosauria (Gower and Sennikov, 2000)	Late Permian-Recent (Gower and Sennikov, 2000; Benton, 2004)
<i>Spondylosoma absconditum</i> (Galton, 2000, Langer, 2004)	_____
<i>Hoplitosuchus rauí</i> (Kischlat, 2000)	_____
" <i>Prestosuchus</i> " <i>loricatus</i> (Kischlat, 2000)	_____
cf. <i>Tarjardia</i> (Kischlat, 2000)	Chañares Formation, Ladinian, Argentina (Arcucci and Marsicano, 1998)
Proterochampsia (Kischlat, 2000)	Ladinian-Carnian (Hsiou et al., 2002)
<i>Cerritosaurus binsfeldi</i> (Price, 1946)	_____
<i>Proterochampsia</i> (Barberena, 1982)	Ischigualasto Formation, Carnian, Argentina (Bonaparte, 1982)
<i>P. nodosa</i> (Barberena, 1982)	_____
<i>Rhadinosuchus gracilis</i> (Kischlat, 2000)	_____
<i>Chanaresuchus</i> (Hsiou et al., 2002)	Chañares and Ischigualasto formations, Ladinian-Carnian, Argentina (Hsiou et al., 2002)
<i>C. bonapartei</i> (Hsiou et al., 2002)	Chañares Formation, Ladinian, Argentina (Bonaparte, 1982)
Phytosauria (Doyle and Sues, 1995)	Carnian-Rhaetian (Doyle and Sues, 1995; Lucas, 1998)
Aetosauria (Heckert and Lucas, 2000)	Carnian-Rhaetian (Heckert and Lucas, 2000)
<i>Aetosauroides</i> (Desojo and Kischlat, 2005)	Ischigualasto Formation, Carnian, Argentina (Bonaparte, 1982)
<i>Aetosauroides</i> sp. (Desojo and Kischlat, 2005)	_____
Rauisuchia (Gower, 2000)	Olenekian-Norian (Gower, 2000)
<i>Barberenasonchus brasiliensis</i> (Kischlat, 2000)	_____
Prestosuchidae (Parrish, 1993)	Anisian-Carnian (Gower, 2000)
<i>Prestosuchus chiniquensis</i> (Kischlat, 2000)	_____
<i>Procerosuchus celer</i> (Kischlat, 2000)	_____
" <i>Karamuru vorax</i> " (Kischlat, 2000)	_____
Rauisuchidae (Parrish, 1993)	Ladinian-Norian (Gower, 2000)
<i>Rauisuchus tiradentes</i> (Kischlat, 2000)	_____
Dinosauriformes (Sereno and Arcucci, 2004)	Ladinian-Recent (Benton, 2004)
<i>Sacisaurus agudoensis</i> (Ferigolo and Langer, 2006)	_____
Dinosauria (Padian and May, 1993)	Carnian-Recent (Benton, 2004)
<i>Teyuwasu barberenai</i> (Kischlat, 1999)	_____
Saurischia (Langer, 2004)	Carnian-Recent (Langer, 2004)
<i>Saturnalia tupiniquim</i> (Langer, 2003)	_____
<i>Guaibasaurus candelariensis</i> (Bonaparte et al., 2006b)	_____
Herrerasauria (Langer, 2004)	Carnian-Norian (Langer, 2004)
<i>Staurikosaurus pricei</i> (Novas, 1993)	_____
Sauropodomorpha (Langer, 2003)	Carnian/Norian-Late Cretaceous (Gauffre, 1993; Benton et al., 2000; Lucas and Hancox, 2001; Upchurch et al., 2004)
Plateosauridae (Yates, 2006)	Norian (Yates, 2003)
<i>Unaysaurus tolentinoi</i> (Leal et al., 2003)	_____

also referred to the genus *Procolophon* (Langer and Lavina, 2000; Dias-da-Silva et al., 2006b), but without further detail. According to Cisneros et al. (2004), *Candelaria barbouri* belongs to Owenettidae, and is the sister taxon of "*Owenetta*" *kitchingorum*, from the *Lystrosaurus* Assemblage Zone, Induan of the Karoo Basin, South Africa (Reisz and Scott, 2002), whereas the other three taxa belong to the Procolophonidae (Cisneros, 2006): *Procolophon* species (Cisneros and Schultz, 2002; Dias-da-Silva et al., 2006b) within Procolophoninae and *S. caliodon*

within Leptoleurinae (Cisneros, 2006). In addition, *S. caliodon* has been regarded by Cisneros (2006) as the sister taxon of *Hypsognathus fenneri*, from the Newark Supergroup, Norian-Rhaetian of the North American Atlantic Coast (Sues et al., 2000).

Dicynodontia

Dicynodonts have long been recognized in the Triassic of Rio Grande do Sul (Tupí-Caldas, 1936; Huene, 1942; Romer, 1943; Romer

and Price, 1944), and considered an important component of its biota (Barberena, 1977; Bonaparte, 1982). Despite this, current knowledge seems to indicate the presence of only three taxa: *Stahleckeria potens* Huene, 1938; *Dinodontosaurus pedroanum* (Tupí-Caldas, 1933; gen. Romer, 1943), and *Jachaleria candelariensis* (Araújo and Gonzaga, 1980; gen. Bonaparte, 1970). The genus *Chanaria* was also reported in south Brazil (Araújo, 1981), but it seems to represent a subjective synonym of *Dinodontosaurus* (King, 1988). In addition, Peruzzo and Araújo-Barberena (1995) assigned a partial skull to *Ischigualastia* sp., a genus otherwise known only in the Ischigualasto Formation, Carnian of Argentina (Cox, 1965; Rogers et al., 1993). This material has been referred to *Stahleckeria potens* by Lucas (2001), but for Vega-Dias (pers. com., January 2007) its current status is ambiguous (see also Vega-Dias and Schwanke, 2004a). Even so, Lucas (2001; Lucas and Heckert, 2002) proposed the occurrence of the genus *Ischigualastia* in Rio Grande do Sul, based on the material originally referred to *Jachaleria candelariensis*. Yet, a reassessment of the specimens by Vega-Dias and Schultz (2004; see also Vega-Dias and Schwanke, 2004b) found no evidence for such a taxonomic assignment. Lucas (2002) also proposed the occurrence of a second species of *Stahleckeria*, *S. impotens*, but this was also rejected by Vega-Dias et al. (2005). Beforehand, Lucas (1993a) had considered *Barysoma lenzii* (Romer and Price, 1944; gen. Cox, 1965) a junior synonym of *Stahleckeria potens*, an assignment never contested. Apart from these records (all belonging to the Santa Maria and Caturrita formations), the only other dicynodont reported for South Brazil are isolated stapes from the Sanga do Cabral Formation, one of which was tentatively assigned to *Lystrosaurus* (Schwanke and Kellner, 1999; Langer and Lavina, 2000).

Regarding nomenclatural aspects, following an application by Lucas (1992), the generic name *Diodontosaurus* Tupí-Caldas, 1936, was suppressed (ICZN 1995) in favor of *Dinodontosaurus* Romer, 1943. At the time (Lucas, 1992), *D. turpior* Huene, 1938, was considered the type species of *Dinodontosaurus*. Afterwards, however, Lucas and Harris (1996) regarded both, that species and *D. tener* Huene, 1938, as *nominum dubia*, with type material not even referable to *Dinodontosaurus* at the generic level. These two species were originally described by Huene (1938, 1942) as members of the genus *Dicynodon*, but transferred to *Dinodontosaurus* by Cox (1965). Yet, contra Lucas and Harris (1996) the decision of the ICZN (1995) did not suppress the species name *D. pedroanum* Tupí-Caldas, 1936. Therefore, as acknowledged by Lucas and Harris (1996), the first species name proposed in the literature, based on type material attributable to *Dinodontosaurus*, is *D. pedroanum* Tupí-Caldas, 1936, which is here used, following the synonymisation of *D. brevirostris* Cox, 1968, from the Chañares Formation, by Lucas and Harris (1996), as the only valid species of the genus.

Maisch (2001) and Vega-Dias et al. (2004) performed phylogenetic analyses of Triassic dicynodonts, including the three Brazilian genera. The first author placed *Dinodontosaurus* as the basal most Dinodontosauridae, sister taxon of a clade composed of Chinese, Indian, African, Russian, and possibly Argentinean, Early-Mid Triassic forms (Sun, 1963; King, 1988; Cox, 1991; DeFauw, 1993; Battail and Surkov, 2000). In contrast, Vega-Dias et al. (2004) found that genus to represent the sister taxon to the Stahlekeriidae (sensu Maisch, 2001). This is composed of two clades, one composed of *Jachaleria* and *Ischigualastia*, and the other of *Stahleckeria* as the sister taxon to *Angonisaurus*, from the main strata of the Manda Formation (Abdala et al., 2005; "lower Manda" of Lucas, 1998), Anisian of Tanzania.

Cynodontia

Along with archosaurs, cynodonts represent the most diverse tetrapod clade in the Rosário do Sul Group. These include 15 formally proposed taxa, and three forms awaiting formal descriptions: a new chiniquodontid (UFRGS PV0146T; Oliveira, 2006), a basal traversodontid (Reichel, 2006; Reichel et al., 2007), and a probainognathian (UFRGS PV1051T; Oliveira et al., 2007) closely related to *Ecteninion* (Martinez

et al., 1996), from the Ischigualasto Formation, Argentina. The described taxa include six traversodontids, eight probainognathians, and a cynodont of ambiguous affinities, *Protheriodon estudianti* (Bonaparte et al. 2006a). All these forms were recorded in the Santa Maria and Caturrita formations, whereas only fragmentary postcranial remains of non-mammalian cynodonts have been collected in the Sanga do Cabral Formation (Abdala et al., 2002a).

The formally described traversodontids include: *Gomphodontosuchus brasiliensis* Huene, 1928 (see Hopson, 1985); *Traversodon stahleckeri* Huene, 1938 (see Barberena, 1981a); *Massetognathus ochagaviae* Barberena, 1981b; *Exaeretodon riograndensis* Abdala, Barberena and Dornelles, 2002; *Santacruzodon hopsoni* Abdala and Ribeiro, 2003; and *Luangwa sudamericana* Abdala and Sá-Teixeira, 2004. Additional records include the poorly known *Exaeretodon major* (Huene, 1938), originally described as a member of the genus *Traversodon* (see Huene, 1942; Barberena, 1974; Abdala et al., 2002b), and three unnamed forms described by Abdala et al. (2001) and Abdala and Ribeiro (2002). The genus *Megagomphodon* was also reported in south Brazil (Teixeira, 1995), but it was proposed to represent a subjective synonym of *Massetognathus* (Abdala and Giannini, 2000).

Recent hypotheses dealing with traversodontid phylogeny (Flynn et al., 2000; Hopson and Kitching, 2001; Abdala and Ribeiro, 2003; Abdala et al., 2006) place *Luangwa* as the basal most Brazilian member of the group, whereas *Traversodon* and *Santacruzodon* represent successively more derived forms. Abdala and Ribeiro (2003, but see Abdala et al., 2006) also proposed sister group relationships between *Luangwa* and "*Scalenodon*" *hirschsoni*, from possibly younger parts of the Manda Formation, Tanzania (Abdala and Ribeiro, 2003), and between *Santacruzodon* and *Dadodon isaloi*, from the Isalo Beds, Ladinian-Carnian of Madagascar (Flynn et al., 2000). *Massetognathus* is more derived than these (Godefroit and Battail, 1997; Flynn et al., 2000; Abdala and Ribeiro, 2003; Abdala et al., 2006), and sister taxon of a clade including *Gomphodontosuchus*, at the base, and a group composed of *Menadon besairiei*, from the Isalo Beds, Ladinian-Carnian of Madagascar (Flynn et al., 2000), *Scalenodontoides macrodontes*, from the Lower Elliot Formation, Carnian-Norian of South Africa (Anderson et al., 1998; Lucas and Hancox, 2001) and *Exaeretodon*. Regarding the three unnamed forms described by Abdala et al. (2001) and Abdala and Ribeiro (2002)—traversodontid type I belongs in the *Exaeretodon*-*Menadon*-*Scalenodontoides* clade, sharing more similarities with the former two taxa (Abdala and Ribeiro, 2002); type III of Abdala and Ribeiro (2002) shares features with *Boreogomphodon jeffersoni* Sues and Olsen, 1990, from the Turkey Branch Formation, Carnian of the Richmond Basin, Virginia (Sues and Olsen, 1990; Huber et al., 1993); while type III of Abdala et al. (2001) shares plesiomorphies with *Massetognathus*-grade traversodontids (Abdala and Ribeiro, 2002).

On the probainognathian (*sensu* Hopson and Kitching, 2001) part of the cynodont phylogenetic tree, a single formally proposed, and valid chiniquodontid is known for the Rosário do Sul Group (Abdala and Giannini, 2002): *Chiniquodon theotonicus* Huene, 1938, including forms previously assigned to *Belesodon magnificus* Huene, 1938, and *Probelesodon kitchingi* Teixeira, 1982. Further, various more "mammal-like" forms have recently been described or reviewed. These include the Trithledontidae *Riograndia guaiensis* Bonaparte, Ferigolo and Ribeiro, 2001, and *Irajatherium hernandezi* Martinelli, Bonaparte, Schultz and Rubert, 2005, which respectively represent (Martinelli et al., 2005) the basal most member of the group and a more derived sister taxon of the clade containing *Pachygenelus* and *Diarthrognathus*, from the Lower Jurassic of South Africa and Nova Scotia (Shubin et al., 1991; Lucas and Hunt, 1994; Lucas and Hancox, 2001). Two other taxa, *Theroherpeton carginini* Bonaparte and Barberena, 1975, and *Prozostrodon brasiliensis* (Barberena et al., 1987; gen. Bonaparte and Barberena, 2001), also seem to belong into the trithledontid-mammal lineage, but are placed either basal to that dichotomy or along either branch (Bonaparte et al., 2005; Martinelli et al., 2005; Sidor and Hancox, 2006; Oliveira, 2006), while

Charruodon tetricuspidatus Abdala and Ribeiro, 2000 (see also Oliveira, 2006), appears to be closely related to *Therioherpeton*. Finally, the brasiliodontid cynodonts *Brasilodon quadrangularis* Bonaparte, Martinelli, Schultz and Rubert, 2003, and *Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz and Rubert, 2003, belong in the mammalian branch (Bonaparte et al., 2005; but see Abdala, 2006; Oliveira, 2006).

Sphenodontia

Lepidosaurs of the Rosário do Sul Group are represented only by sphenodontians. Ferigolo (2000) described an unnamed form similar to *Clevosaurus*, while Bonaparte and Sues (2006) erected a new species of that genus, *C. riograndensis*, which may represent the same taxonomic entity described by Ferigolo (2000). According to Bonaparte and Sues (2006), *C. riograndensis* belongs to a clade of *Clevosaurus* species that also include *C. mcgilli* from the Lower Lufeng Formation, Lower Jurassic of China (Wu, 1994), *C. bairdi* from the McCoy Brook Formation, Hettangian of Nova Scotia (Sues et al., 1994), and a South African form from the Upper Elliot-Lower Clarens formations, Lower Jurassic of the Karoo Basin (Sues and Reisz, 1995).

Rhynchosauria

Rhynchososaurs are more diverse in the Rosário do Sul Group than in any other sedimentary deposit worldwide. According to recent reviews (Langer et al., 2000; Langer and Schultz, 2000a, b) five taxa are known. The “Mariante rhynchosaur” (Schultz and Azevedo, 1990), which lacks a formal designation, is closer to Middle Triassic rhynchososaurs, particularly *Stenaulorhynchus* from the Manda Formation, Anisian of Tanzania, than to other South American rhynchososaurs (Langer and Schultz, 2000a), all of which belong to the more derived Hyperodapedontinae (Langer and Schultz, 2000b). This “subfamily” most probably encompasses the material described by Huene (1929) as belonging to six different species: *Scaphonyx fischeri* Woodward, 1903, *S. australis* Huene, 1926, *S. eurichorus* Huene, 1926, *Cephalonia lotziana* Huene, 1926, *Cephalastronius augustispinus* Huene, 1926, *Cephalastron gondwanicum* Huene, 1926, and *C. brasiliense* Huene, 1926, all of which have been dismissed as *nomina dubia* (Huene, 1942; Sill, 1970; Langer, 1998; Langer and Schultz, 2000a, b). Langer et al. (2000) assigned all the more complete specimens previously referred to either *Cephalonia* (Huene, 1942) or *Scaphonyx* (Huene, 1942; Sill, 1970; Azevedo, 1984), along with that described by Tupí-Caldas (1933) as *Macrocephalosaurus mariensis*, into the widespread genus *Hyperodapedon* (Lucas and Heckert, 2002). They were allocated within two species: *H. mariensis* (Tupí-Caldas, 1933) and *H. sanjuanensis* (Sill, 1970), both of which also occur in the Ischigualasto Formation, Carnian of Argentina. In addition, a new species of *Hyperodapedon*, *H. huenei*, was erected by Langer and Schultz (2000b), while the form described as “*Scaphonyx*” *sulcognathus* (Azevedo and Schultz, 1987) was proposed to represent a new genus of Hyperodapedontinae, sister taxon to *Hyperodapedon* (Langer and Schultz, 2000b).

Prolacertiformes

No prolacertiform has been formally described for the Rosário do Sul Group, but Langer and Lavina (2000, see also Dias-da-Silva, 1998) attributed isolated elongated cervical vertebrae from the Sanga do Cabral Supersequence to that reptile group.

Archosauria

The diverse archosaur fauna of the Rosário do Sul Group includes taxa assigned to Phytosauria, Proterochampsia, “Rauisuchia,” Aetosauria, and Dinosauria. At least four proterochampsians are known: *Rhadinosuchus gracilis* Huene, 1938; *Cerritosaurus binsfeldi* Price, 1946; *Chanaresuchus bonapartei* Romer, 1971; and *Proterochamps nodosa* (Barberena, 1982). The latter has been referred to a new genus, *Barberenachampsia* Kischlat, 2000, but that name was not proposed

according to the rules of the ICBN (1999; article 16.1) - i.e., explicitly indicated as intentionally new. In addition, Kischlat and Schulz (1999) included *B. nodosa* along with *Proterochamps barrionuevoi*, from the Ischigualasto Formation, Carnian of Argentina (Sill, 1967), in a clade of two monospecific genera. Accordingly, we prefer to retain the original generic designation of Barberena (1982, see also Arcucci, 1989).

Kischlat and Schulz (1999) considered *Cerritosaurus* the basal most proterochampsian, whereas *Gualosuchus* and *Chanaresuchus* were proposed to form the clade Rhadinosuchidae (Machado and Kischlat, 2003) with *Rhadinosuchus*. This taxon was first classified as a rauisuchian by Huene (1942), but Kischlat (2000) suggested a proterochampsian affinity instead. Further proterochampsian material from Rio Grande do Sul was assigned to *Chanaresuchus* by Dornelles (1995), but the identity of the described specimen as *Chanaresuchus* instead of *Gualosuchus* or *Rhadinosuchus* can not be determined (Kischlat, 2000; Hsiou et al., 2002), as is also the case of a specimen recently studied by Machado and Kischlat (2003). Likewise, material referred to *Gualosuchus* (Barberena et al., 1985a) might represent either that genus or *Rhadinosuchus* (Kischlat, 2000). More recently, however, *Chanaresuchus bonapartei* was positively identified in South Brazil (Hsiou et al., 2002).

Within the crown-Archosauria (sensu Gauthier, 1986), phytosaurs have only been recorded based on a jaw fragment (Kischlat and Lucas, 2003) and possibly isolated teeth (Dornelles, 1990). Among suchians (sensu Parrish, 1993), aetosaurs are known based on material referred to the genus *Aetosauroides* (Zacharias, 1982; Kischlat, 2000; DaRosa and Leal, 2002). Two species names have entered the literature: *A. subsulcatus* (Zacharias, 1982) and *A. inhamandensis* (Barberena et al., 1985a, b), both of which are *nomina nuda*. Lucas and Heckert (2001) assigned the south Brazilian aetosaur material to *Stagonolepis robertsoni*, known from the Lossiemouth Sandstone Formation, Carnian of Scotland (Benton and Walker, 1995). That assignment was questioned by Desojo and Kischlat (2005), who proposed that the Brazilian specimens represent a new species of *Aetosauroides*. In fact, the whole synonymization of *Aetosauroides* and *Stagonolepis* (Heckert and Lucas, 2002) seems dubious (Desojo and Baez, 2005).

Most pseudosuchians (sensu Parrish, 1997) of the south Brazilian Triassic have been considered “rauisuchians,” a non-monophyletic group of ambiguous affinities (Parrish, 1993; Gower, 2000; Gower and Nesbitt, 2005). The Brazilian forms were reviewed by Kischlat (2000), and five species seem valid: *Prestosuchus chiniquensis* Huene, 1938; *Rauisuchus tiradentes* Huene, 1938; *Procerosuchus celer* Huene, 1938; *Barberenasuchus brasiliensis* Mattar, 1987; and “*Karamuru vorax*” Kischlat, 2000. Kischlat (2000) follows Parrish (1993), including *Rauisuchus* within a group of more gracile, possibly more derived “rauisuchians” - i.e., Rauisuchidae - that may also encompass (Parrish, 1993; Sulej, 2005): *Tikisuchus romeri* from the Tiki Formation, Carnian of India (Chatterjee and Majumbar, 1987); *Batrachotomus kupferzellensis* from the Lettenkeuper, Ladinian of Germany (Gower, 1999); *Teratosaurus silesiacus* from the Krasiejów fauna, Carnian of Poland (Sulej, 2005); *Postosuchus kirkpatricki* from various stratigraphic units (Long and Murry, 1995) within the Chinle Group (Lucas, 1993b), Carnian-Norian of southwestern USA (Lucas, 1998; see also Lehman and Chatterjee, 2005). On the contrary, *Prestosuchus chiniquensis*, and possibly *Procerosuchus celer*, seem to belong into a more basal group of robust “rauisuchians” - i.e., Prestosuchidae - that may also include (Parrish, 1993; Kischlat, 2000; Benton, 2004; Sen, 2005) Anisian forms such as *Ticinosuchus ferox* from the Grenzbitumenzone of Monte San Giorgio, Switzerland (Krebs, 1965), *Yarasuchus deccanensis* from the Yerrapalli Formation, India (Sen, 2005), and those from the Manda Formation of Tanzania (Charig, 1957), as well as the Argentinean forms *Luperosuchus fractus* from the Ladinian Chañares Formation (Romer, 1971), and *Saurosuchus galilei* from the Carnian Ischigualasto Formation (Alcober, 2000). In this context, Kischlat (2000) used various specimens previously attributed to *Prestosuchus chiniquensis*, including a nearly complete skull (Barberena, 1978), to establish a new taxon of Prestosuchidae:

"Karamuru vorax". This appears to represent a valid taxonomic entity, with a set of proposed diagnostic features. Yet, the nomenclatural problems raised above for *Barberenachampsia* also apply to "*Karamuru vorax*". Kischlat (2000) assigned the name to Kischlat and Barberena, without indication of a publication year, and none of the two publications referred to those authors in the reference list. Kischlat and Barberena (1999a, b), includes a nomenclatural proposition. It is beyond the scope of this paper to challenge the taxonomic status of "*Karamuru vorax*", but the name is better applied with caution until a formal description of the taxon is available. Finally, *Barberenasuchus brasiliensis*, first described as a sphenosuchid (Mattar, 1987; Mattar and Barberena, 1987), was considered by Kischlat et al. (1999; Kischlat, 2000) as a "rauisuchian" of unclear affinities. In addition, new material under study (Ferigolo et al., 2001; Mastrandionio et al., 2006) seems to represent new prestosuchids.

The dinosaur record of the Rosário do Sul Group is relatively rich for a Triassic deposit, with at least four different valid taxa. *Staurikosaurus pricei* Colbert, 1970, is an herrarasaurid (Novas, 1992; Galton, 2000; Langer, 2004), while *Guaiabasaurus candelariensis* Bonaparte, Ferigolo and Ribeiro, 1999, represents a saurischian possibly related to theropods (Bonaparte et al., 2006b; Langer, 2004; Langer and Benton, 2006). Two members of the sauropodomorph lineage are also known: *Saturnalia tupiniquim* Langer, Abdala, Richter and Benton, 1999, and *Unaysaurus tolentinoi* Leal, Azevedo, Kellner and Da Rosa, 2003. The former is the basal-most member of that lineage (Langer, 2003, 2004), while the latter is a member of the "prosaupod" clade Plateosauridae (Yates, 2006), which also includes *Plateosaurus*, known primarily from the Norian of Germany (Yates, 2003). Other putative South Brazilian dinosaurs are *Spondylösoma absconditum* Huene, 1926, *Teyuwasu barberenai* Kischlat, 1999, and *Sacisaurus agudoensis* Ferigolo and Langer, 2006. The latter belongs into the Dinosauriformes, and seems closely related to *Silesaurus opolensis* Dzik, 2003, from the Krasiejów Fauna, Carnian of Poland (Dzik, 2001). Yet, its position either basal to Dinosauria or in the ornithischian lineage is debated (Ferigolo and Langer, 2006). *Spondylösoma absconditum* might represent a "rauisuchian" (Galton, 2000, but see Langer, 2004), while *T. barberenai*, based on part of the material originally ascribed to *Hoplitosuchus rauí* Huene, 1938, is too fragmentary to have its affinities defined (Langer, 2004, but see Kischlat, 2000). Further material referred to the Dinosauria has been mentioned by Kischlat and Barberena (1999b).

Regarding archosaurs with uncertain affinities, Kischlat (2000) listed specimens originally described by Huene (1942) as "*Prestosuchus loricatus*" and *Hoplitosuchus rauí* (partim). In addition, material under study has been preliminarily identified as cf. *Tarjardia* (Kischlat, 2000), a basal crurotarsan according to Arcucci and Marsicano (1998).

STRATIGRAPHIC HIERARCHY AND FOSSIL SITES

The bio- and lithostratigraphy of the tetrapod-bearing Triassic beds of the Paraná Basin in south Brazil are relatively well known (Barberena, 1977; Barberena et al., 1985a, b; Schultz et al., 2000; Scherer et al., 2000; Lucas, 2001; Langer, 2005a). More recently, studies based on stratigraphic sequences (Faccini, 1989; Scherer, 1994; Fonseca, 1999; Zerfass et al., 2003; Rubert and Schultz, 2004) recognized two second-order sequences: Sanga do Cabral and Santa Maria Supersequences (*sensu* Zerfass et al., 2003), the latter of which may be further subdivided (Zerfass et al., 2003; Rubert and Schultz, 2004).

Sanga do Cabral Supersequence

The Sanga do Cabral Supersequence represents the lowest depositional sequence within the Rosário do Sul Group. This second-order sequence (Zerfass et al., 2003) corresponds to the Sanga do Cabral Formation of Andreis et al. (1980), which was deposited in a braided river system under an arid to semi-arid climate (Holz and Scherer, 2000). The poorly confined fluvial channels hosted ephemeral flash flood events

(Zerfass et al., 2003) that formed the intraformational conglomerates in which most of the fossil material is found (Holz and Souto-Ribeiro, 2000; Dias-da-Silva et al., 2006b). As a whole, the 50–100 m thick Sanga do Cabral Formation occurs in a nearly continuous 500 km long belt (Fig. 1) extending from the townships of Venâncio Aires to Santana do Livramento (Scherer et al., 2000), but fossils are better known from three areas/localities: Catuçaba, Rincão dos Weiss, and Cachoeira do Sul (Fig. 2).

The first and more thoroughly studied Catuçaba area, south of São Pedro do Sul (Barberena et al., 1981) has yielded indeterminate cynodonts (Abdala et al., 2002a), prolacertiforms (Dias-da-Silva, 1998; Langer and Lavina, 2000), and temnospondyls, including rhytidosteids (Dias-da-Silva, 2003; Dias-da-Silva et al., 2005), as well as the procolophonid *Procolophon pricei* (Lavina, 1983). From Rincão dos Weiss, south of Mata, *Procolophon brasiliensis* (Cisneros and Schultz, 2002) and an indeterminate species of the same genus (Langer and Lavina, 2000; Dias-da-Silva et al., 2006b) were recorded, while the holotype and only known specimen of *Sangaia lavinai* (Dias-da-Silva et al., 2006a) comes from the more eastern site of Cachoeira do Sul.

Santa Maria Supersequence

According to Zerfass et al. (2003), the Santa Maria Supersequence, an up to 200 m thick second-order sequence, might be subdivided into three third-order sequences, Santa Maria sequences 1, 2, and 3. The former two approximately represents Sequence II of Faccini (1989), and is the only one with tetrapod fossils. The latter corresponds to Sequence III of Faccini (1989), also termed "Mata Sandstone," and is better known for its plant remains (Guerra-Sommer et al., 2000). In terms of lithostratigraphy (Andreis et al., 1980), the tetrapod-bearing rocks of these sequences include the Alemao Member of the Santa Maria Formation and the Caturrita Formation (Fig. 1). The former corresponds to the red mudstones that occur at the lower-mid levels of Sequence II of Faccini (1989), and at Santa Maria Sequence 1 and lower parts of Santa Maria Sequence 2 (Zerfass et al., 2003). Outcrops of the Alemao Member typically correspond to deep erosive gullies, the so called "sangas", that are relatively common in central Rio Grande do Sul. The sandier Caturrita Formation corresponds to the upper levels of Santa Maria Sequence 2 plus Santa Maria Sequence 3 (Zerfass et al., 2003), and to the upper levels of Sequence II (Rubert, 2003) plus Mata Sandstone in the scheme of Faccini (1989). As a whole, the Santa Maria Supersenquence crops out along a 250 km west-east belt extending from the townships of Mata to Taquari (Fig. 1).

Santa Maria Sequence 1

This 50 m thick third-order sequence includes a coarser lowstand systems tract, deposited by a high energy, low sinuosity river system, developed under a semi-arid climate, and a transgressive systems tract composed of massive or laminated mudstones, where the tetrapod fossil record is concentrated (Holz and Scherer, 2000; Zerfass et al., 2003). These correspond to deposits of either shallow lakes (Zerfass et al., 2003) or floodplains of an anastomosed fluvial system (Scherer et al., 2000).

Fossil tetrapods of the Santa Maria 1 Sequence occur in two main regions, Chiniquá and Pinheiros (Barberena et al., 1985a), as well as in various isolated localities (Fig. 2). The fossil record from the Chiniquá area, west of São Pedro do Sul, mainly reflects the efforts of Friedrich von Huene and his crew during the fieldwork of 1928–29, including: *Traversodon stahleckeri* (Huene, 1942; Barberena, 1981a), *Chiniquodon theotonicus* (Huene, 1942), *Dinodontosaurus pedroanum* (Tupi-Caldas, 1936), "*Karamuru vorax*" (Huene, 1942; Kischlat, 2000), "*Prestosuchus loricatus*" (Huene, 1942), and possibly *Spondylösoma absconditum* (Huene, 1942) from Cynodontier-Sanga (Huene, 1942), or Sanga Beles (Beltrão, 1965); *Stahleckeria potens* (Huene, 1942), *Exaeretodon major* (Huene, 1942), and *Spondylösoma absconditum* (Huene, 1942) from

Baum-Sanga; and *Prestosuchus chiniquensis* (Huene, 1942), *Procerosuchus celer* (Huene, 1942), and possibly *Chiniquodon theotonicus* (Huene, 1942), from Weg-Sanga. Additionally, all those localities have yielded the “*Dinodontosaurus*” material of Huene (1942), considered *nomina dubia* by Lucas and Harris (1996).

The Pinheiros region, south of Candelária (Barberena, 1977), was firstly explored during the thirties by a joint North American-Brazilian expedition (Romer, 1943; Romer and Price, 1944; Romer, 1969), and latter by Brazilian paleontologists (Price, 1947; Barberena, 1977; Araújo, 1981; Barberena et al., 1985b). A plethora of taxa was excavated from the “sangas” of two main areas: Bom Retiro, about 15 km southeast of Novo Cabrais, and Pinheiros itself, about 10 km south of the township of Candelária (Barberena, 1977). *Dinodontosaurus pedroanum* (Romer, 1943; Cox, 1965; Machado, 1992), *Chiniquodon theotonicus* (Romer, 1969; Fernando Abdala, pers. com. January, 2007), and *Massetognathus* (Teixeira, 1987, 1995) appear to occur in “sangas” of both areas, while a dubious record of *Stahleckeria potens* (Romer and Price, 1944; Lucas, 1993a) in the region of Candelária seems to come from Bom Retiro. “*Karamuru vorax*” (Barberena, 1978) and cf. *Ischigualastia* (Peruzzo and Araújo-Barberena, 1995) were also recovered in Bom Retiro, along with *Massetognathus ochagaviae* (Teixeira, 1987), from the site known as Sanga Pascual. In the area of Pinheiros, together with *Massetognathus* (Teixeira, 1995) and *D. pedroanum* (Machado, 1992), a rhadinosuchid proterochampsian (Dornelles, 1992; 1995; Kischlat, 2000) was recovered in the eponymous sanga. Besides, the sites referred to as “Sanga do Ribeiro” by Cox (1965) and Barberena (1977) appear to correspond to different places (see Machado, 1992). The latter is in Bom Retiro, whereas the former is located further south, and has yielded *D. pedroanum* (Machado, 1992). This dicynodont was also registered in other sites around Pinheiros, such as Sanga da Divisa and Sanga Hintz (Machado, 1992), while the holotype of *Candelaria barbouri* (Price, 1947) comes from an undetermined site in the region.

The other sites assigned by Barberena et al. (1985a) to the Pinheiros Local Fauna, Vila Melos and Rincão do Pinhal, are not located in that region (Fig. 2). The former is in the municipality of Vale Verde, and yielded *D. pedroanum* (Araújo, 1981; Machado, 1992), *M. ochagaviae* (Barberena, 1981b), and possibly “*K. vorax*” (UFRGS PV0152T). In the locality of Rincão do Pinhal, south of Agudo, was recorded *C. theotonicus* (Teixeira, 1982), *D. pedroanum* (Teixeira, 1979; Machado, 1992), *M. ochagaviae* (Teixeira 1987), and the new basal traversodontid of Reichel et al. (2007). More recently, various isolated sites (Fig. 2) have yielded a fossil fauna likely coeval to those of Pinheiros and Chiniquá. This is the case of the site of Dona Francisca (Ferigolo et al., 2001) where *Protheriodon* (Bonaparte et al., 2006a) and prestosuchid archosaurs (MCN PV 3585, 10004, 10005; UFRGS PV0629T) occur along with *D. pedroanum* (Machado, 1992) and *Massetognathus* (MCN PV 2293). In addition, the site known as Sítio Cortado, west of Novo Cabrais, has yielded *D. pedroanum*, *Candelaria barbouri*, (DaRosa et al., 2004a), the new traversodontid of Reichel et al. (2007), and most probably *Barberenasuchus brasiliensis* (Mattar, 1987). Nearby sites include Linha da Várzea (DaRosa et al., 2005) and Rincão da Porta (Machado, 1992), both of which yielded *D. pedroanum*.

The fossil fauna of other sites (Fig. 2), previously assigned to faunal associations within the Santa Maria 1 Sequence, are not straightforwardly correlated to those of Pinheiros and Chiniquá, and might correspond to older (Schultz, 1995; Abdala and Sá-Teixeira, 2004) or younger (Abdala et al., 2001) assemblages. The former group includes the type-locality of *Luangwa sudamericana*, between Vera Cruz and Candelária, the precise location of which is unknown (Abdala and Sá-Teixeira, 2004), and the site of Porto Mariante, in Bom Retiro do Sul, that yielded the “Mariante rhynchosaur” (Schultz and Azevedo, 1990) and *D. pedroanum* (Machado, 1992). On the contrary, the possibly younger assemblage of the site of Santuário Schoenstatt, in Santa Cruz do Sul (Abdala et al., 2001; Reichel et al., 2005; Bertoni & Holz, 2006), includes a chiniquodontid (Abdala et al., 2001), *Santacruzodon hopsoni* (Abdala

and Ribeiro, 2003), traversodontids with affinities to *Exaeretodon-Menadon*, *Massetognathus*, and *Boreogomphodon* (Abdala et al., 2001; Abdala and Ribeiro, 2002), and a rhadinosuchid archosaur (Machado and Kischlat, 2003).

Santa Maria Sequence 2

This up to 130 m thick third-order sequence includes tetrapod-bearing layers deposited in transgressive and highstand system tracts (Zerfass et al., 2003). In the scheme proposed by Zerfass et al. (2003), the former corresponds to the upper levels of the Alemao Member, Santa Maria Formation, whereas the latter represents the lower-mid portions of the Caturrita Formation of Andreis et al. (1980). In addition, Rubert and Schultz (2004) found sedimentological evidence to further segregate the upper levels of the Sequence II of Faccini (1989) - i.e., middle portion of the Caturrita Formation (Andreis et al., 1980), into strata bearing their “Ictidosaur Assemblage Zone”.

The transgressive systems tract of the Santa Maria 2 Sequence is mainly composed of mudstones, the higher concentration of early diagenetic carbonate in which suggests a drier climate in relation to that of the Santa Maria 1 Sequence (Zerfass et al., 2003). These were deposited in either shallow lakes (Zerfass et al., 2003) or in the floodplains of an ephemeral anastomosed river system (Fonseca and Scherer, 1998; Holz and Scherer, 2000). The latter scenario implies a seasonal climate, as also suggested by the color of the sediments (Holz, 1993). These red beds are typical from the outskirts of Santa Maria (Bortoluzzi, 1974), where Barberena et al. (1985a) defined the Alemao Local Fauna. This includes the fossil record of two main areas explored by Huene (1942) in the late twenties (Beltrão, 1965; Langer, 2005a), São José and Alemao, other more recently prospected sites around Santa Maria, as well as outcrops from different areas that seem to bear a coeval fauna (Fig. 2).

Fossil taxa from the Alemao area include *Staurikosaurus pricei* (Colbert, 1970) and *Teyuwasu barberenai* (Kischlat, 2000) from Sanga Grande, *Gomphodontosuchus brasiliensis* (Huene, 1928), *Saturnalia tupiniquim* (Langer, 2005a), and *Hyperodapedon* sp. from the Wald-Sanga, as well as *Hyperodapedon mariensis* (Tupí-Caldas, 1933), *H. sanjuanensis* (Huene, 1929), and *Cerritosaurus binsfeldi* (Price, 1946) from unspecified sites of the area. The sites of São José were mainly explored by Huene (1942), including *Rauisuchus tiradentes* and *Rhadinosuchus gracilis* from Zahnsanga, and *H. sanjuanensis* from Sanga Schramm. Among the other localities around Santa Maria (DaRosa, 2004, 2005), that known as Faixa-Nova has yielded *H. mariensis*, *H. sanjuanensis* (Schultz, 1991), and *Aetosauroides* (Desojo and Kischlat, 2005), while *Therioherpeton carnini* and *Prozostrodon brasiliensis* were collected in another site nearby Faixa-Nova (Bonaparte and Barberena, 1975; Barberena et al., 1987) that also yielded *H. mariensis* (Langer, 1996).

Outside of Santa Maria, *Hyperodapedon mariensis* and *H. sanjuanensis* were recorded in the municipality of Venâncio Aires (Langer, 1996), as well as from the area of Inhamandá, east of São Pedro do Sul. In the latter area, two sites are recognized, Inhamandá 1 has yielded *H. mariensis*, *H. huenei* (Langer and Schultz, 2000b), and *Aetosauroides* (Zacharias, 1982), whereas *H. sanjuanensis* is the only taxon recorded in Inhamandá 2 (Langer, 1996). Rhynchosaur and aetosaurs also occur in sites around São João do Polesine, *H. mariensis* (MCN PV 1875) from the locality of Predebon (Azevedo et al., 1999; DaRosa 2005) and *Aetosauroides* (MCN PV 2347) along with an indeterminate rhynchosaur (MCN PV 10101) from the site known as Piche (Outcrop 1 of Perez and Malabarba, 2002). The only temnospondyl remains known from the Santa Maria Supersequence (Richter, 2001) also comes from that area (Outerop 2 of Perez and Malabarba, 2002). Finally, *Hyperodapedon* (UFRGS PV1063T) also occurs in the site of Picada Escura, south of Candelária.

The highstand systems tract of the Santa Maria 2 Sequence represents a coarsening up succession that transitionally replaces the mudstones of the Alemao Member (Zerfass et al., 2003). This corresponds to

the progressive replacement of an ephemeral anastomosed fluvial-lacustrine system by a perennial braided fluvial system, which indicates an increase in the humid condition along that time (Holz and Scherer, 2000). At least one fossil-bearing site (Fig. 2) within the Caturrita Formation (Rubert and Schultz, 2004; DaRosa, 2005) seems to represent the lower levels of that section, beneath the middle portion of that stratigraphic unit, which yielded the “Ictidosaur Cenozoone” of Rubert and Schultz (2004). This is located about 9 km west from Candelária (3 km west of Botucarái Hill) and includes *Proterochampsia nodosa* (Barberena, 1982), *Exaeretodon riograndensis* (Abdala et al., 2002b), a rhynchosaur with affinities to *Hyperodapedon* (MCN PV3598), and perhaps *Charruodon tetracuspis* (Abdala and Ribeiro, 2000). In addition, the site of Linha Facão (Fig. 2), 6 km east of Candelária, has been often (Barberena et al. 1985b; Scherer, 1994; Schultz, 1995) correlated to the type-locality of *E. riograndensis*. It yielded the rhynchosaur N. gen. *sulcognathus* (Azevedo and Schultz, 1987) and *Hyperodapedon sanjuanensis* (Azevedo, 1984), but it is unclear if both come from the same stratigraphic levels. The former taxon also occurs in the upper levels of Faixa Nova and Wald-Sanga localities (Schultz, 1991), above the strata in which *Hyperodapedon* abound.

Exaeretodon has also been registered alongside rhynchosaur referable to *Hyperodapedon* in other sites of Santa Maria Sequence 2, such as Várzea do Agudo and Cidade dos Meninos, alluding to their possible correlation to the type-locality of *E. riograndensis*. Yet, although these sites correspond to the upper parts of the Alemao Member, there is no stratigraphic evidence their beds lay above those bearing the “Alemao Local Fauna” (DaRosa et al., 2004b; DaRosa, 2005). The site of Várzea do Agudo, also known as Janer or Cooperativa Agudo, yielded *Hyperodapedon* (MCN PV 3509), *Exaeretodon* (UFRGS PV0715T; Oliveira, 2006), a cynodont similar to *Ecteninion* (UFRGS PV 1051T), and possible dinosaur remains (Cabreira et al., 2006), whereas rhynchosaur possibly referable to *Hyperodapedon* (DaRosa, 2004), an aetosaur similar to *Aetosauroides*, and *Exaeretodon* (Weiss et al., 2003; Malabarba et al., 2005) were recorded in Cidade dos Meninos, north of Camobi. The latter taxon was also found in the lower part (MCN PV10001) of the type-locality of *Sacisaurus agudoensis*, in the outskirts of the town of Agudo.

In a detailed stratigraphic revision of the areas of Candelária and Faxinal do Soturno, Rubert and Schultz (2004) defined the sedimentological basis to distinguish the middle part of the Caturrita Formation of Andreis et al. (1980). This represents the full establishment of the braided fluvial system that deposited the coarser sediments of that stratigraphic unit. Tetrapods of this interval come basically from the surroundings of the Botucarái Hill, west of Candelária, and from the site of Linha São Luiz, about 2 km NW from Faxinal do Soturno (Fig. 2). The latter includes *Clevosaurus riograndensis* (Bonaparte and Sues 206), *Soturnia caliodon* (Cisneros and Schultz, 2003), *Riograndia guaiensis* (Soares, 2004), *Guaibasaurus candelariensis* (Bonaparte et al., 2006b), *Brasilodon quadrangularis* and *Brasilitherium riograndensis* (Bonaparte et al., 2003). Besides, fossils actually collected at Botucarái Hill, 6 km of Candelária, are solely *Jachaleria candelariensis* (Araújo and Gonzaga, 1980), an

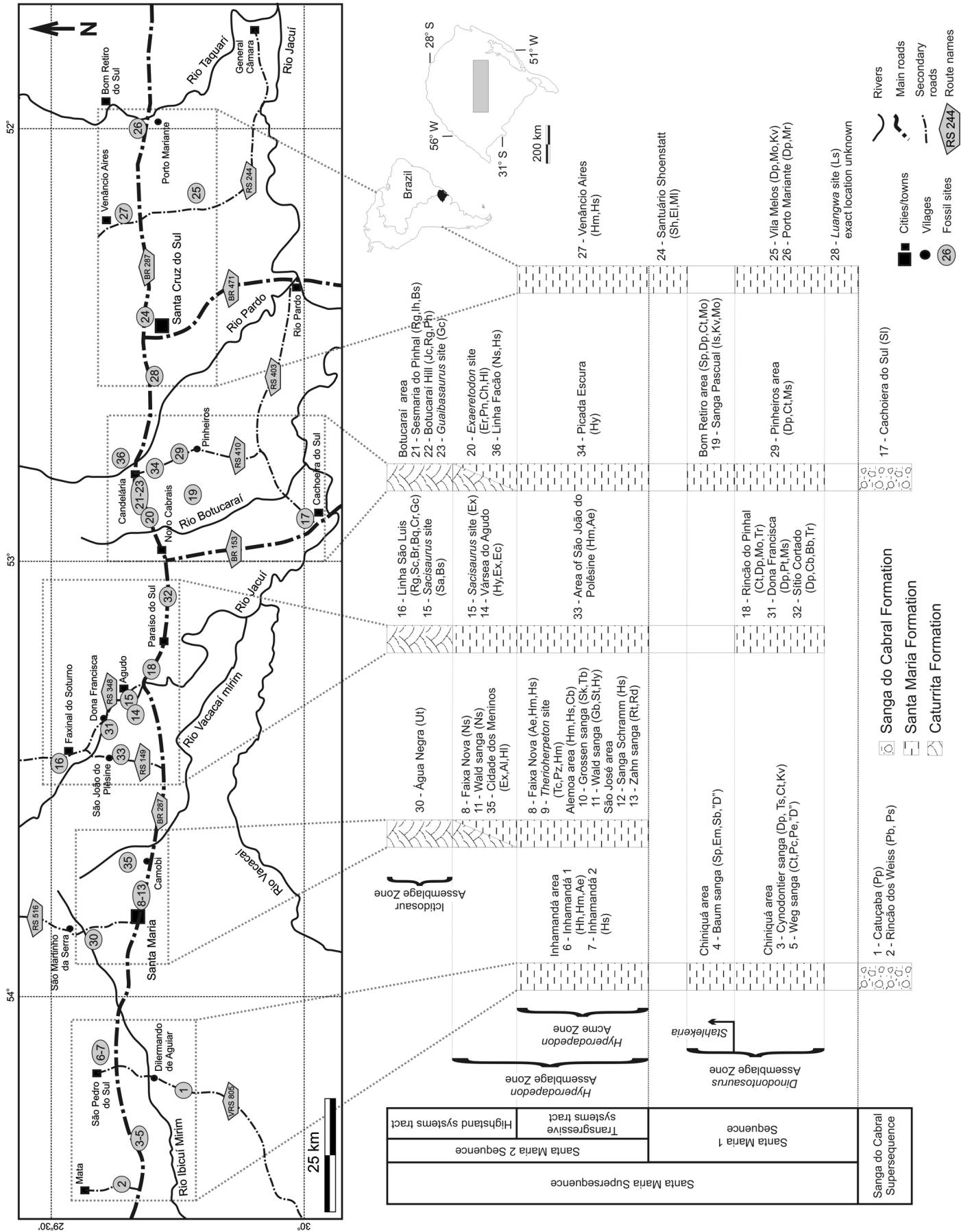
indeterminate phytosaur (Kischlat and Lucas, 2003), an isolated tooth of *Riograndia guaiensis* (UFRGS PV1062T), plus fragmentary archosaur remains (Dornelles, 1990; Kischlat & Barberena, 1999b; Kischlat, 2000). Other tetrapods of the area come from the type-locality of *Guaibasaurus candelariensis* (Bonaparte et al., 1999) and from the site of Sesmaria do Pinhal, respectively about 2.0 and 1.2 km west of the hill. The latter has yielded *Riograndia guaiensis* (Bonaparte et al., 2001), *Irajatherium hernandezi* (Martinelli et al., 2005), sphenodontians (MCN PV10104), and brasilotodontid cynodonts (MCN PV3001-3002). Isolated teeth (MCN PV10102) of the latter group were also recorded along with *Sacisaurus agudoensis* (Ferigolo and Langer, 2006), while the prosauropod *Unaysaurus tolentinoi* represents a further, but isolated record from the uppermost levels of the Caturrita Formation. According to Leal et al. (2003), it was recovered from a conglomerate in the site of Água Negra, 13 km north of Santa Maria, township of São Martinho da Serra.

FAUNAL TURNOVERS

Early studies of the Sanga do Cabral Biota (Barberena et al., 1981, 1985a; Lavina, 1983; Dias-da-Silva, 1998) suggested its correlation to the *Lystrosaurus* Assemblage-Zone of the Karoo Basin, South Africa (Groenewald and Kitching, 1995). More recently, the general scarcity of that fauna, together with preponderance of the genus *Procolophon*, prompted Cisneros and Schultz (2002; see also Dias-da-Silva et al., 2005) to propose its correlation to the *Procolophon* Zone (= lower part of the so-called “Impoverished zone”) of the Karoo Basin, as defined by Neveling et al. (1999). Yet, given that *Procolophon* occurs in both the *Lystrosaurus* Assemblage Zone and *Procolophon* Zone, Dias-da-Silva et al. (2006b) took a more conservative approach (Fig. 3) by correlating the Sanga do Cabral Formation to either of them (i.e., the entire Katberg Formation; see also Langer and Lavina, 2000; Abdala et al., 2002a), as also indicated by its “taphocorrelation” (Souto-Ribeiro and Holz, 1998). Indeed, the prevalence of *Procolophon* in the Brazilian sequence might represent a taphonomic bias (Dias-da-Silva et al., 2006b), and not a strong basis for its correlation to the “Impoverished zone”. The correlation with the Karoo Basin only allows the assignment of an undifferentiated Lower Triassic age (Shishkin et al., 1995; Damiani et al., 2000; Hancox and Rubidge, 2001) for the Sanga do Cabral Formation, but the occurrence of a basal rhytidosteid with affinities to *Indobatrachops* (Dias-da-Silva et al., 2006a), from the Panchet Formation (Cosgriff, 1984; Lucas, 1998; Yates and Sengupta, 2002), might prove to represent a complementary basis to define an Induan age for the Brazilian stratigraphic unit.

The fossil record of Santa Maria 1 Sequence (Zerfass et al., 2003) is usually assigned to a single biostratigraphic unit, the Therapsid (Barberena, 1977; Bonaparte, 1982; Schultz et al., 2000) or *Dinodontosaurus* (Barberena et al., 1985b; Lucas, 2001) “zones”, correlated to the Argentinean Chañares Formation (Bossi and Stipanicic, 2002). This scheme seems oversimplified, as suggested by the record of putatively older (Abdala and Sá-Teixeira, 2004) and younger (Abdala et al., 2001) fossil assemblages. Barberena et al. (1985a) attempted a geographically based chronologic refinement, proposing the Local Faunas of

FIGURE 2. Index map of part of central Rio Grande do Sul showing the location of main fossil sites, and composite stratigraphic sections of the major fossil-bearing areas. Ae = *Aetosauroides* sp, Al = *Aetosauroides*-like aetosaur, Bb = *Barberenasuchus brasiliensis*, Bq = *Brasilodon quadrangularis*, Br = *Brasilitherium riograndensis*, Bs = brasilotontid, Cb = *Candelaria barbouri*, Cr = *Clevosaurus riograndensis*, Ct = *Chiniquodon teotonicus*, Ch = *Charuodon tetracuspis*, “D” = *Dinodontosaurus* of Huene (1935-42), Dp = *Dinodontosaurus pedroanum*, Ec = *Ecteninion*-like cynodont, El = *Exaeretodon*-like traversodontid, Em = *Exaeretodon major*, Er = *Exaeretodon riograndensis*, Ex = *Exaeretodon* sp, Gb = *Gomphodontosuchus brasiliensis*, Gc = *Guaibasaurus candelariensis*, Hh = *Hyperodapedon huenei*, Hl = *Hyperodapedon*-like rhynchosaur, Hm = *Hyperodapedon mariensis*, Hs = *Hyperodapedon sanjuanensis*, Hy = *Hyperodapedon* sp, Ih = *Irajatherium hernandezi*, Is = cf. *Ischigualastia*, Jc = *Jachaleria candelariensis*, Kv = “*Karamuru vorax*”, Ls = *Luangwa sudamericana*, Ml = *Massetognathus*-like traversodontid, Mo = *Massetognathus ochagaviae*, Ms = *Massetognathus* sp, Mr = “*Mariante* rhynchosaur”, Ns = N. gen. *sulcognathus*, Pb = *Procolophon brasiliensis*, Pc = *Prestosuchus chiniquensis*, Pe = *Procerosuchus celer*, Ph = indeterminate phytosaur, Pn = *Proterochampsia nodosa*, Pp = *Procolophon pricei*, Ps = *Procolophon* sp, Pt = *Protheriodon estudianti*, Pz = *Prozostrodon brasiliensis*, Rg = *Riograndia guaiensis*, Rd = *Rhadinosuchus gracilis*, Rt = *Rauisuchus tiradentes*, Sb = *Spondylosoma absconditum*, Sc = *Soturnia caliodon*, Sa = *Sacisaurus agudoensis*, Sh = *Santacruzodon hopsoni*, Sk = *Staurikosaurus pricei*, Sl = *Sangaia lavinae*, Sp = *Stahleckeria potens*, St = *Saturnalia tupiniquim*, Tb = *Teyuwasu barberenai*, Tc = *Therioherpeton carginini*, Tr = traversodontid of Reichel et al. (2007), Ts = *Traversodon stahleckeri*, Ut = *Unaysaurus tolentinoi*.



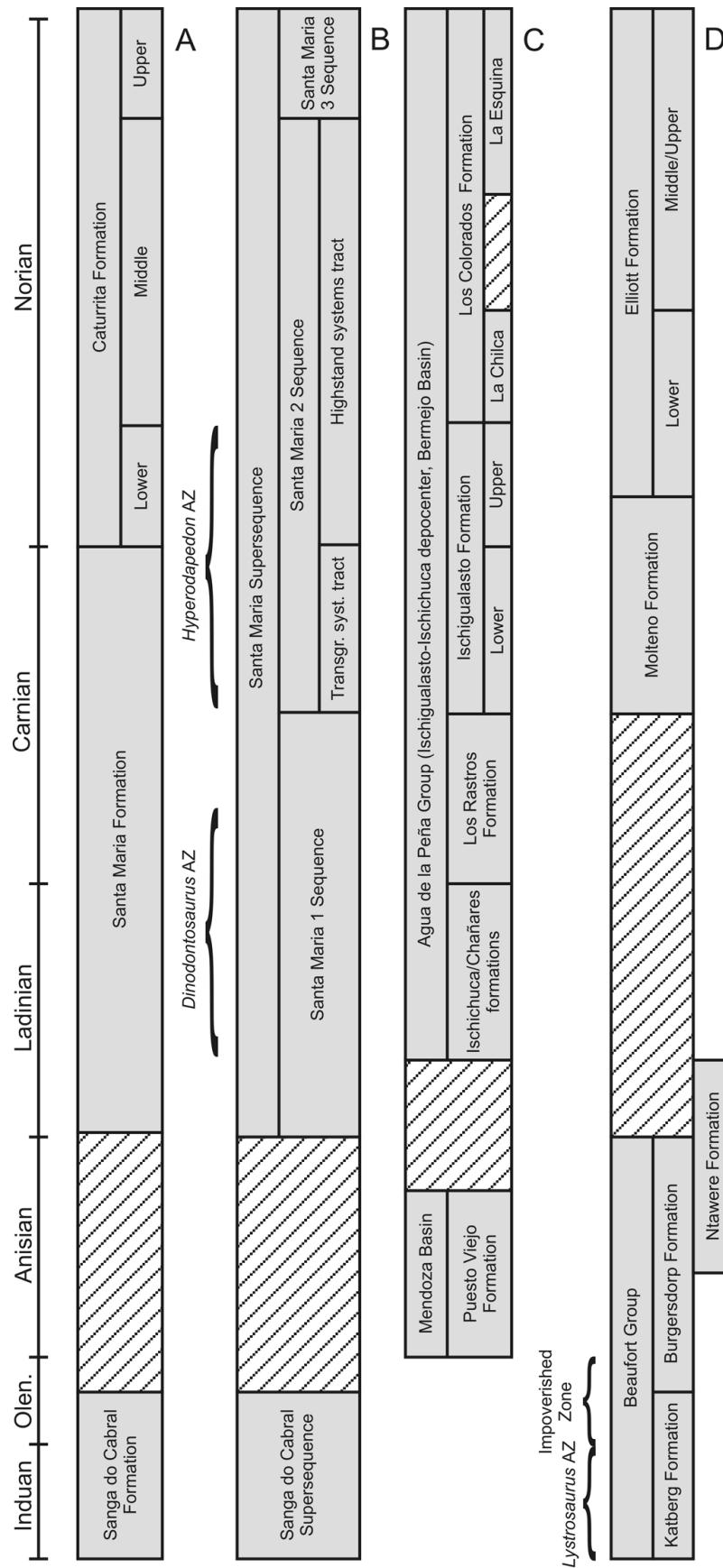


FIGURE 3. Comparison of the lithostratigraphy (A) and sequence stratigraphy (B) of the Rosário do Sul Group with general stratigraphic charts of the tetrapod-bearing Triassic of Argentina (C) and southern Africa (D). A, based on Andreis et al. (1980). B, based on Zerfass et al. (2004). C, based on Abdala et al. (2001) and Stipanicic (2002). D, based on Neveling et al. (1999), Lucas and Hancox (2001), Abdala and Sá-Teixeira (2004), and Abdala et al. (2005).

Chiniquá and Pinheiros, the latter of which assembles records from different localities from the eastern portion of the outcrop belt of the Alemoa Member, but no further studies followed that path. In the Chiniquá area, the record of *Chiniquodon theotonicus* and *Dinodontosaurus* in the Cynodontier-Sanga allows a rather straightforward correlation to the Chanás fauna, while more derived forms such as *Stahleckeria potens* and *Exaeretodon major*, from the Baum-Sanga, are suggestive of a younger age (see *Dinodontosaurus* vs. *Stahleckeria* zones of Cooper, 1982), even considering the doubt regarding the latter generic assignment. The situation is similar in the Pinheiros region. Records of *Dinodontosaurus*, *Massetognathus*, and *Chiniquodon theotonicus* support the correlation to that Argentinean stratigraphic unit, while the possible occurrence of *Ischigualastia/Stahleckeria* implies a younger faunal stage. The records of *Dinodontosaurus* and *Massetognathus* in Vila Melos, Rincão do Pinhal, and Dona Francisca, and of the former taxon in Sítio Cortado also indicate a correlation to the Chanás fauna, while those of *Luangwa* and perhaps the “Mariante rhynchosaur” suggest an older age for parts of the Santa Maria Formation (Schultz, 1995; Abdala and Sá-Teixeira, 2004). On the contrary, Abdala et al. (2001) proposed a younger age for their “Traversodontid biozone,” based on the comparison to a putative Late Ladinian-Early Carnian fauna from Madagascar (Flynn et al., 1999). That biozone includes an assemblage dominated by traversodontids, some of them showing features typical of Ladinian forms and others sharing characters of Carnian forms. This condition, in the absence of dicynodonts, suggests the placement of the Traversodontid Biozone above (Fig. 2) the “typical” faunas of the *Dinodontosaurus* biozone (Abdala et al., 2001; but see Lucas, 2001; Langer, 2005a).

The two antipodal hypotheses that could explain the tetrapod record of the Santa Maria 1 Sequence seem unlikely. It does not appear to correspond to a sole coexisting assemblage, given that the occurrence of *Luangwa* along with *Exaeretodon* or *Ischigualastia*, despite the uncertainty of these latter two records, goes against any current biochronological orthodoxy (Lucas, 1998; Abdala and Sá-Teixeira, 2004; but see Cooper, 1982; Ochev & Shishkin, 1989). It seems equally improbable that faunas of nearby sites, with no apparent stratigraphic separation between them, such as those within the Chiniquá and Pinheiros regions, have radically different ages. Accordingly, the isolated record of *Luangwa* seems to represent the current single evidence of an older, possibly Anisian poorly sampled fauna (Abdala and Sá-Teixeira, 2004, but see Cooper, 1982) within the Santa Maria 1 Sequence. The resemblance of the “Mariante rhynchosaur” to *Stenaulorhynchus* may support an older age also for the Porto Mariante locality. Yet, its poorly constrained phylogenetic position precludes more substantiated stratigraphic inferences. Indeed, given the occurrence of *Dinodontosaurus*, that assemblage (“Associação 3” of Schultz, 1995) is better correlated to the bulk of the Santa Maria 1 Sequence, which corresponds to a younger fauna (Fig. 3), the age of which is debatable. It shares index-fossils with the Chanás Formation, implying a Ladinian age (Lucas, 2001), but the record of *Exaeretodon/Menadon*-like cynodonts (Barberena, 1974; Abdala et al., 2001) and cf. *Ischigualastia* (Peruzzo and Araújo-Barberena, 1995) provides some evidence of a younger age for certain faunas. If the statuses of these records are confirmed (Abdala et al., 2002b; Lucas, 2001), two alternative scenarios are feasible: the fauna might be intermediate in age between those sampled from the Chanás and Ischigualasto formations of Argentina (see Bonaparte, 1982), but is probably more chronologically extensive (Fig. 3), congregating temporally separate assemblages (Fig. 2). Further taxonomic studies of the above mentioned key-taxa are, however, needed in order to segregate younger faunas from the otherwise typically Chanás fossil associations.

The fauna of the transgressive systems tract of the Santa Maria 2 Sequence (Fig. 2) belongs entirely in the so-called *Hyperodapedon* Assemblage Zone (Lucas, 2001; Langer, 2005a), first envisaged by Barberena (1977) and assigned different names in the literature (Barberena et al., 1985a, b; Schultz et al., 2000; Abdala et al., 2001). This has been long recognized as partially (Bonaparte, 1982; Barberena et al., 1985a; Langer,

2005a) or totally (Barberena et al., 1985b; Schultz et al., 2000; Abdala et al., 2001; Lucas, 1998, 2002) coeval to the fauna of the Ischigualasto Formation, Argentina (Rogers et al., 1993). Indeed, the record of *Hyperodapedon*, *Aetosaurooides*, and herrerasaurid dinosaurs, plainly justifies that hypothesis, whereas the overwhelming dominance of the first genus might allow further scrutinizing. As discussed by Langer (2005a, b), a similar ecological scenario is found in the lower portions of the Ischigualasto Formation, as well as in deposits of other parts of the world, allowing the tentative correlation of a *Hyperodapedon* Acme Zone (Fig. 2) to both the lower portions of that Argentinean stratigraphic unit (Fig. 3) and other parts of Pangea. In chronological terms, a Carnian (= Ischigualastian) age is consensually admitted for that fossil assemblage (Abdala et al., 2001; Lucas, 2001; Schultz et al., 2000; Langer, 2005b; but see Furin et al., 2006).

As stated by Zerfass et al. (2003), the highstand systems tract of the Santa Maria 2 Sequence seems to encompass two distinct “biozones”, the lower of which belongs into the *Hyperodapedon* Assemblage Zone. This implies a subdivision of that biostratigraphic unit between transgressive and highstand systems tracts of the Sequence (Fig. 2), as already inferred by Schultz et al. (2000) for their “Rhynchosaur Cenozone”. The fauna of the *Hyperodapedon* Assemblage Zone, within the highstand systems tract of Santa Maria 2 Sequence, partly corresponds to “Associação 6” of Schultz (1995), which includes *Exaeretodon*, *Proterochampsia*, and possibly N. gen. *sulcognathus*. The former two taxa are useful for comparison to the Ischigualasto Formation fauna, while the latter allows a correlation (see below) to the lower portions of the highstand systems tract of the Santa Maria 2 Sequence in the area of Santa Maria (Zerfass et al., 2003, fig. 5), which lack records of *Hyperodapedon*. That genus is also missing from the upper part of the Ischigualasto Formation, where the only taxon represented is the abundant *Exaeretodon* (Rogers et al., 1993). This suggests the correlation (Fig. 3) of the upper Ischigualasto fauna to the south Brazilian *Exaeretodon*-bearing deposits (Langer, 2005a) from the type-locality of *E. riograndensis* and the sites of Várzea do Agudo and Cidade dos Meninos. This assumption is, however, jeopardized by both the new records of *Hyperodapedon*-like rhynchosauroids in these sites, and the putative stratigraphic correspondence of the latter two to those yielding the *Hyperodapedon* Acme Zone in the outskirts of Santa Maria (DaRosa 2005). On the contrary, *Exaeretodon* was still not recovered from typical *Hyperodapedon* Acme Zone faunas (Fig. 2). Therefore, although *Exaeretodon*-like forms occur in older assemblages within the Santa Maria Supersequence (Barberena, 1974; Abdala et al. 2001), it is possible to envisage a twofold subdivision (Fig. 4) for the *Hyperodapedon* Assemblage Zone. This includes an older *Hyperodapedon* Acme Zone, encompassing an *Exaeretodon* ghost-lineage, and a younger assemblage where that rhynchosaur is less abundant, occurring along with *Exaeretodon* (Fig. 4; note that these are not segregated in Figure 2).

In the Santa Maria 2 sequence, the record of N. gen. *sulcognathus* roughly matches that of *Exaeretodon*, providing further evidence of the above ordination. It may occur together with *Hyperodapedon* in Linha Fácão, a site often correlated to the type-locality of *E. riograndensis*, but also characterizes strata lying above those where *Hyperodapedon* abounds in the area of Santa Maria. It is, however, important to stress the conjectural nature of these correlations (Fig. 4). In fact, more collecting effort is needed in order to determine (1) if *Exaeretodon* is really missing from the sites where *Hyperodapedon* abounds, (2) if the latter is really less abundant, or even absent, in sites where *Exaeretodon* occurs, and (3) if *Hyperodapedon* occurs, or not, along with N. gen. *sulcognathus* in some sites. Before that, the task of ordinating these strata may prove unfeasible. In any case, even if slightly younger than the transgressive systems tract of the Santa Maria 2 Sequence (Langer, 2005a, b), there is no reason to assign the *Exaeretodon*-bearing faunas of its highstand systems tract an age other than Ischigualastian (Fig. 3; see also Lucas, 2001).

The upper “biozone” of the highstand systems tract of the Santa Maria 2 Sequence (Zerfass et al., 2003) was fully characterized by Rubert

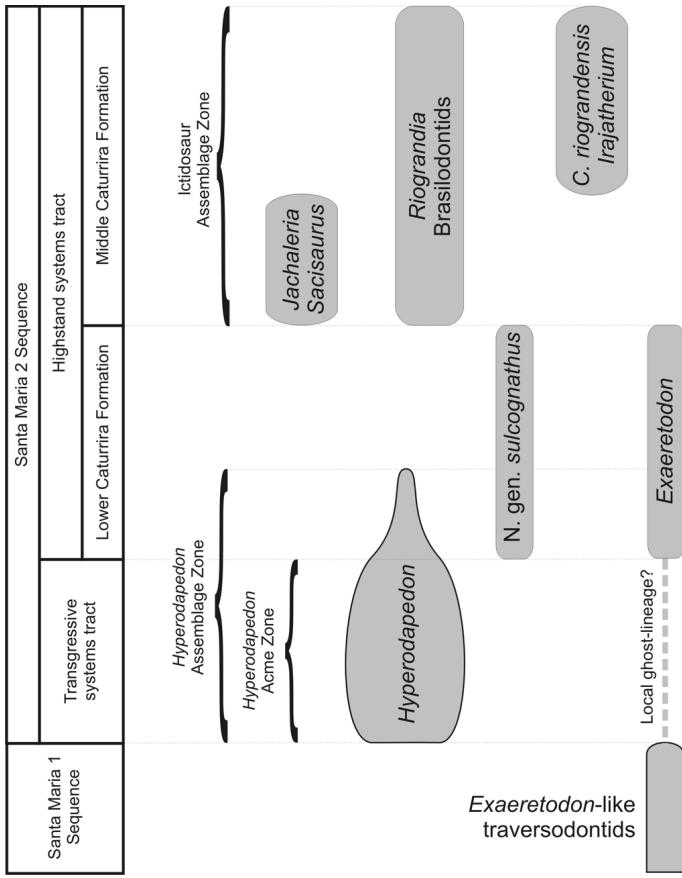


FIGURE 4. Stratigraphic distribution of certain tetrapod taxa in the Santa Maria 2 Sequence, based on the tentative ordination of their fossil assemblages.

and Schultz (2004) as to encompass the *Jachaleria*-level (Scherer et al., 1995; Schultz et al., 2000) and more recently discovered fossil assemblages into the “Ictidosaur Assemblage Zone”. This “biozone” is clearly post-Ischigualastian (Langer, 2005a, *contra* Lucas, 2001), and the record of *Jachaleria* allows a direct correlation to the La Chilca fauna of the Los Colorados Formation (Fig. 3). This has been considered of Late Carnian age (Abdala et al., 2001; see also Rogers et al., 1993), but new radiometric

data (Furin et al., 2006), supports its placement within the Norian. Although more indicative of the latter (Cisneros and Schultz, 2003), the record of most small tetrapods (e.g., *Riograndia guaiensis*, *Brasilodon quadrangularis*, and *Brasilitherium riograndensis*) does not contradict either age assignment (Langer, 2005a). On the contrary, the sister group relationship between the procolophonids *Soturnia* and *Hypsognathus* (Cisneros, 2006), and those of the cynodont *Irajatherium* (Martinelli et al., 2005) and the sphenodontian *Clevosaurus riograndensis* (Bonaparte and Sues, 2006) to Jurassic forms suggest younger ages. Regarding taxa of other possibly coeval sites, the sister group relation between *Unaysaurus* and *Plateosaurus* (Yates, 2006) suggests a Norian age, while that between *Sacisaurus* and *Silesaurus* (Ferigolo and Langer, 2004) indicates a Carnian age.

The above-mentioned set of ambiguous data prevents an accurate age assignment, and possible ordination of faunas within the “Ictidosaur Assemblage Zone” might help to explain this puzzle. Yet, contrary to the claims of Cisneros and Schulz (2003), there is no lithostratigraphic basis to ordinate any of the fossil bearing strata within that Assemblage Zone (Scherer, 1994; Rubert and Schultz, 2004). Indeed, it seems unlikely that faunas of nearby sites, with no apparent stratigraphic separation between them, such as those of Botucarai Hill and Sesmaria do Pinhal, have radically different ages. In this case, the whole fauna might be intermediate between those sampled at the localities of La Chilca and La Esquina, both from Los Colorados Formation (Bonaparte, 1982; Abdala et al., 2001), including the earliest records of certain clevosaurid, tritylodonid, and leptoleurine clades. Alternatively, it might congregate temporally separate assemblages. Given their separate occurrences and based on their phylogenetic affinities *Jachaleria candelariensis* and *Sacisaurus agudoensis* would be assigned to an older fauna, while *Irajatherium hernandezi* and *Clevosaurus riograndensis* would characterize a younger one (Fig. 4). In this case, forms that occur together with most of those taxa, such as *Riograndia* and brasiliodontid cynodonts would have longer temporal range, occurring along that entire time interval (Fig. 4).

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