Max C. Langer, Ana M. Ribeiro, Cesare L. Schultz and Jorge Ferigolo

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 temnospondyl, procolophonoids, 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 procolophonoids, 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).

Temnospondyl

Lavina and Barberena (1985) assigned fragmentary temnospondyl remains from the Sanga do Cabral Formation to the Lydekkerinidae and Rhynchocephaliaeidae, but these have been recently reviewed by Dias-da-Silva et al. (2005, see also Dias-da-Silva, 2003), and referred to either Rhynchocephaliaeidae or Temnospondyl incertae sedis. More complete mate-
TABLE 1. Fossil record presented by monophyletic hierarchy of Temnospondyli, Procolophonoida, and Therapsida in the Rosário do Sul Group, Triassic of Rio Grande do Sul, Brazil.

<table>
<thead>
<tr>
<th>Monophyletic hierarchy</th>
<th>Chronological/Stratigraphical range outside Brazil</th>
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<tbody>
<tr>
<td><em>Sangaia lavinai</em> (Dias-da-Silva and Marsicano, 2006)</td>
<td>Late Permian -Induan (Modesto et al., 2003)</td>
</tr>
<tr>
<td>Owenetidae (Cisneros et al., 2004)</td>
<td>Late Permian -Rhaetian (Sues et al., 2000, Modesto et al., 2001)</td>
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<tr>
<td><em>Canodelaria barbouri</em> (Cisneros et al., 2004)</td>
<td>Induan-Olenekian (DeBraga, 2003; Spencer and Benton, 2004)</td>
</tr>
<tr>
<td>Procolophonidae (Laurin and Reisz, 1995)</td>
<td>Lystrosaurus 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)</td>
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<tr>
<td>Procolophoninae (DeBraga, 2003)</td>
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<tr>
<td><em>Procolophon</em> (de Braga, 2003; Cisneros and Schultz, 2002; Dias da Silva et al., 2006)</td>
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<tr>
<td><em>P. pricei</em> (Cisneros and Schultz, 2002)</td>
<td>Undefined stratum of the Karoo Basin (Cisneros and Schultz, 2002)</td>
</tr>
<tr>
<td><em>P. brasilensis</em> (Cisneros and Schultz, 2002)</td>
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<tr>
<td>Leptopleurinae (DeBraga, 2003)</td>
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<td>Kammeyeriiformes (Mai, 2001)</td>
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<tr>
<td><em>Dinodontosaurus pedroanum</em> (Lucas and Harris, 1996)</td>
<td>Chañares Formation, Ladinian, Argentina (Cox, 1965)</td>
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<tr>
<td>Stahleckeriidae (Vega-Dias et al., 2004)</td>
<td>Anisian-Norian (Lucas, 1998)</td>
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<tr>
<td><em>Stahleckeria potens</em> (Vega-Dias et al., 2005)</td>
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<tr>
<td><em>Ichigualastia</em> sp. (Peruzzo and Araújo Barberena, 1995)</td>
<td>Ischigualasto Formation, Carnian, Argentina (Rogers et al., 1993)</td>
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<tr>
<td><em>Juchaleria</em> (Vega-Dias and Shultz, 2004)</td>
<td>Ischigualasto Formation, Carnian/Norian, Argentina (Bonaparte, 1982; Abdala et al., 2001)</td>
</tr>
<tr>
<td><em>J. candelariensis</em> (Vega-Dias and Schultz, 2004)</td>
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<tr>
<td>Cynodontia (Hopson &amp; Kitching, 2001)</td>
<td>Late Permian-Recent</td>
</tr>
<tr>
<td><em>Protheriodon estuaneusii</em> (Bonaparte et al. 2006a)</td>
<td>Olenekian-Norian (Abdala et al., 2006)</td>
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<tr>
<td><em>L. sudamericana</em> (Abdala and Sá-Teixeira, 2004)</td>
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<tr>
<td><em>Traversodon stahlkekeri</em> (Barberena, 1981a)</td>
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<tr>
<td><em>Sanicruzodon hopsoni</em> (Abdala and Ribeiro, 2003)</td>
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<tr>
<td>M. ochagaviae (Barberena, 1981b)</td>
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<tr>
<td><em>Gomphodontosuchus brasiliensis</em> (Hopson, 1985)</td>
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<td><em>Exaeretodon</em> (Abdala et al., 2002a)</td>
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<td><em>E. major</em> (Abdala et al., 2002a)</td>
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<tr>
<td><em>E. riogravensis</em> (Abdala et al., 2002a)</td>
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<tr>
<td><em>Chiniquodontidae</em> (Abdala and Giannini, 2002)</td>
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<tr>
<td>Clade 8 (Bonaparte et al., 2005)</td>
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<tr>
<td><em>Therioherpeton cernini</em> (Bonaparte and Barberena, 2001)</td>
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<tr>
<td><em>Charvodon tetracispalidatus</em> (Abdala and Ribeiro, 2000)</td>
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<tr>
<td><em>Prozostrodon brasiliensis</em> (Bonaparte and Barberena, 2001)</td>
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<tr>
<td><em>Trithelodontidae</em> (Sidor and Hancox, 2006)</td>
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<tr>
<td><em>Roigandria gaubiensis</em> (Bonaparte et al., 1999)</td>
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<td><em>Irajatherium hernandez</em> (Martinelli et al., 2005)</td>
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<tr>
<td>Brasilidontidae (Bonaparte et al., 2005)</td>
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<tr>
<td><em>Brasilodon quadrangularis</em> (Bonaparte et al., 2005)</td>
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<tr>
<td><em>Brasilitherium riogravensis</em> (Bonaparte et al., 2005)</td>
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**Parareptilia**

In the Rosário do Sul Group, parareptiles are known based only on procolophonoidans (*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 calidon* 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.

<table>
<thead>
<tr>
<th>Monophyletic hierarchy</th>
<th>Chronological/Stratigraphical range outside Brazil</th>
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<tbody>
<tr>
<td>Clevosauroidae (Bonaparte and Sues, 2006)</td>
<td>Carnian-Early Jurassic (Fraser and Benton, 1989; Sues and Reisz, 1995)</td>
</tr>
<tr>
<td><em>Clevosaurus</em> (Bonaparte and Sues, 2006)</td>
<td>Norian-Early Jurassic (Fraser, 1994; Sues and Reisz, 1995)</td>
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<tr>
<td><em>C. riograndensis</em> (Bonaparte and Sues, 2006)</td>
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<tr>
<td>Rhynchosauridae (Dilkes, 1998)</td>
<td>Anisian-Carnian (Langer and Schultz, 2000a)</td>
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<td>“Mariante rhynchosaur” (Schultz and Azevedo, 1990)</td>
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<tr>
<td>Hyperodapodentinae (Langer and Schultz, 2000b)</td>
<td>Ladinian-Carnian (Flynn et al., 1999, Langer et al., 2000)</td>
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<tr>
<td>N. gen. <em>sulcognathus</em> (Langer and Schultz, 2000b)</td>
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<tr>
<td><em>H. huenei</em> (Langer and Schultz, 2000b)</td>
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<tr>
<td><em>H. marniensis</em> (Langer et al., 2000)</td>
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<td><em>H. sanjuanensis</em> (Langer et al., 2000)</td>
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<tr>
<td>Prolacertiformes (Benton and Allen, 1997)</td>
<td>Late Permian-Norian (Dilkes, 1998)</td>
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<tr>
<td>Archosauria (Gower and Sennikov, 2000)</td>
<td>Late Permian-Recent (Gower and Sennikov, 2000; Benton, 2004)</td>
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<tr>
<td><em>Spindylusoma absconditum</em> (Galton, 2000, Langer, 2004)</td>
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<tr>
<td><em>Hoplitosuchus rauti</em> (Kischlat, 2000)</td>
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<tr>
<td>“Prestosuchus” <em>loricatus</em> (Kischlat, 2000)</td>
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<tr>
<td>cf. <em>Tarjardia</em> (Kischlat, 2000)</td>
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<td>Proterochampsia (Kischlat, 2000)</td>
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<tr>
<td><em>Cerrotosaurus bisfieldi</em> (Price, 1946)</td>
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<td><em>Proterochampsia</em> (Barberena, 1982)</td>
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<td><em>P. nodosa</em> (Barberena, 1982)</td>
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<tr>
<td><em>Rhadinosuchus gracilis</em> (Kischlat, 2000)</td>
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<tr>
<td><em>Chanaresuchus</em> (Hsiou et al., 2002)</td>
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<td><em>C. bonopartei</em> (Hsiou et al., 2002)</td>
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<tr>
<td><em>Phytosaurus</em> (Doyle and Sues, 1995)</td>
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<td><em>Aetosaurus</em> (Heckert and Lucas, 2000)</td>
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<td><em>Aetosauroidea</em> (Desojo and Kischlat, 2005)</td>
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<tr>
<td><em>Aetosauroidea</em> sp. (Desojo and Kischlat, 2005)</td>
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<tr>
<td><em>Rauisuchia</em> (Gower, 2000)</td>
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<tr>
<td><em>Barberenasuchus brasiliensis</em> (Kischlat, 2000)</td>
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<td><em>Prestosuchidae</em> (Parrish, 1993)</td>
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<td><em>Prestosuchus chithiquensis</em> (Kischlat, 2000)</td>
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<td><em>Procerosuchus celor</em> (Kischlat, 2000)</td>
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<tr>
<td>“<em>Karamuru vorax</em>” (Kischlat, 2000)</td>
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<tr>
<td><em>Rauisuchidae</em> (Parrish, 1993)</td>
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<tr>
<td><em>Rauisuchus tiradentes</em> (Kischlat, 2000)</td>
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<tr>
<td><em>Dinosauriformes</em> (Sereno and Arcuri, 2004)</td>
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<tr>
<td><em>Sacisaurus agudoensis</em> (Ferigolo and Langer, 2006)</td>
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<tr>
<td><em>Dinosauria</em> (Padian and May, 1993)</td>
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<tr>
<td><em>Teyuwaus barrierai</em> (Kischlat, 1999)</td>
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<tr>
<td><em>Saurischia</em> (Langer, 2004)</td>
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<td><em>Saturnalia tugiuquim</em> (Langer, 2003)</td>
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<tr>
<td><em>Guatibasaurus candeiariensis</em> (Bonaparte et al., 2006b)</td>
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<tr>
<td><em>Herrerasaura</em> (Langer, 2004)</td>
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<tr>
<td><em>Staurikosaurus pricei</em> (Novas, 1993)</td>
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<tr>
<td><em>Saurorhombosaurus</em> (Langer, 2003)</td>
<td></td>
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<tr>
<td><em>Plateosauridae</em> (Yates, 2006)</td>
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<tr>
<td><em>Unaysaurus tomentinos</em> (Leal et al., 2003)</td>
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</table>

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 “*Owenetto* 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 Leptopleurinae (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 (Tupi-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 (Tupi-Calda, 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 Araujo-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 Schwанke, 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 Schwанke, 2004b) found no evidence for such a taxonomic assignment. Lucas (2002) also proposed the occurrence of a second species of Stahleckeria, S. inpotens, 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 Tupi-Calda, 1936, was suppressed (ICZN 1995) in favor of Dinodontosaurus Romer, 1943. At the time (Lucas, 1992), D. tarpior 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 nomina 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 Dicyonodon, 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 Tupi-Calda, 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 Tupi-Calda, 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 phyloge-netic 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 Stahleckeriidae (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 Angontaurus, 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 (Martínez 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 Si-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 Dadadon isolai, 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 theotonius 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 Triheledontidae Rigianella guaiabensops Bonaparte, Ferigolo and Ribeiro, 2001, and Irratherium hutchinsae 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, Therioherpeton cagninii Bonaparte and Barberena, 1975, and Protozoozodon brasiliensis (Barberena et al., 1987; gen. Bonaparte and Barberena, 2001), also seem to belong into the triheledontid-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
and Dinosauria. At least four proterochampsians are known: taxa assigned to Phytosauria, Proterochampsia, "Rauisuchia," Aetosauria, also include the entity described by Ferigolo (2000). According to Bonaparte and Sues (2006), the genus, Clevosaurus brasiliensis (Barberena, 1982). The latter has been referred to a new genus, Barberenachampsa Kischlat, 2000, but that name was not proposed according to the rules of the ICZN (1999; article 16.1) - i.e., explicitly indicated as intentionally new. In addition, Kischlat and Schulz (1999) included B. nodosa along with Proterochampsa 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 as the basal most proterochampian, whereas Gualosuchus and Chanarosuchus 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 proterochampian affinity instead. Further proterochampian material from Rio Grande do Sul was assigned to Chanarosuchus by Dornelles (1995), but the identity of the described specimen as Chanarosuchus 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, Chanarosuchus 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 Aetosaurus (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 Aetosaurus. In fact, the whole synonymization of Aetosaurus 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 “Karamurub voras” 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 hufelandi (from the Lettenkeuper, Ladinian of Germany (Gower, 1999); Ieratomosaurus 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) Asian forms such as Ticinosuchus jero from the Grenzbitemannzen of Monte San Giorgio, Switzerland (Krebs, 1965); Varosaurus tannenheimensis from the Yerrapalli Formation, India (Charig, 1957), as well as the Argentinean forms Luperosuchus francus from the Ladunian Chañares Formation (Romer, 1971), and Saurouschus galilei from the Carnian Ischigualasto Formation (Alcoker, 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 Barberenachampsa 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; Mastrantonio et al., 2006) seems to represent new preosuchids.

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 herrerasaurid (Novas, 1992; Galton, 2004; Langer, 2004), while Guaibasaurus candeliaiensis 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 basalmost member of that lineage (Langer, 2003, 2004), while the latter is a member of the “prosauropod” clade Plateosauridae (Yates, 2006), which also includes Plateosaurus, known primarily from the Norian of Germany (Yates, 2003). Other putative South Brazilian dinosaurs are Spondylodon absconditum Huene, 1926, Teyouswasa 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). Spondylodon absconditum might represent a “rauisuchian” (Galton, 2000, but see Langer, 2004), while T. barberenai, based on part of the material originally ascribed to Hoplitosuchus rau 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 rau (partim). In addition, material under study has been preliminarily identified as cf. Tarjardia (Kischlat, 2000), a basal crocodylomorph 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: Catucaí, Rincão dos Weiss, and Cachoeira do Sul (Fig. 2).

The first and more thoroughly studied Catucaí 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 Supersequence 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 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 pedroavum (Tupi-Caldas, 1936), “Karamuru vorax” (Huene, 1942; Kischlat, 2000), “Prestosuchus” loricatus (Huene, 1942), and possibly Spondylodon absconditum (Huene, 1942) from Cynodontier-Sanga (Huene, 1942), or Sanga Beles (Beltrão, 1965); Stahleckeria potens (Huene, 1942), Exaeretodon major (Huene, 1942), and Spondylodon absconditum (Huene, 1942) from
Baum-Sanga; and Prestosuchus chiniquensis (Huene, 1942), Procerosuchus eceler (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 protorochampsian (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 Aguado, 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 Candelária barbouri “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 Alleoa 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 Alleoa, 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 Alleoa area include Staurokosaurus 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 (Tupi-Caldas, 1923), H. sanjuanensis (Huene, 1929), and Cerritosaurus bensfeldi (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 Zahnsga, 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 Aetosauroidea (Desojo and Kischlat, 2005), while Therioherpeton carymonti and Prozoodrothosaurus 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. hueunei (Langer and Schultz, 2000b), and Aetosauroidea (Zacharias, 1982), whereas H. sanjuanensis is the only taxon recorded in Inhamandá 2 (Langer, 1996). Rhynchosauras 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 Aetosauroidea (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 (Outcrop 2 of Perez and Malabarba, 2002). Finally, Hyperodapedon (UFRGS PV01653T) 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 Alleoa Member (Zerfass et al., 2003). This corresponds to
the progressive replacement of an ephemeral anastomosed fluvial-lacus-
trine system by a perennial braided fluvial system, which indicates an in-
crease 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 Cenozone” of Rubert and Schultz
(2004). This is located about 9 km west from Candelária (3 km west of
Botucari Hill) and includes Protocochampsia nodosa (Barberena, 1982),
Exaeretodon riograndensis (Abdala et al., 2002b), a rhynchosaur with
affinities to Hyperodapedon (MCN PV3598), and possibly Charuodon
tetracuspidatus (Abdala and Ribeiro, 2000). In addition, the site of Linha
Fação (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 rhynchosaurus 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
abund.

Exaeretodon has also been registered alongside rhynchosours re-
ferrable 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
seem to correspond to the upper parts of the Alemoa Member, there is no
stratigraphic evidence their beds lay above those bearing the “Alemoa
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 1051V,
and possible dinosaur remains (Cabeira et al., 2006), whereas
rhynchosours possibly referable to Hyperodapedon (DaRosa, 2004), an
aetosaur similar to Aerassoauroidea, 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 aguadoensis, in the outskirts of the
town of Agudo.

In a detailed stratigraphic revision of the areas of Candelária and
Faxinal do Soutorno, Rubert and Schultz (2004) defined the sedimento-
logical 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 Botucari Hill, west of Candelária, and from the site of Linha São
Luiz, about 2 km NW from Faxinal do Soutorno (Fig. 2). The latter in-
cludes Cleurosaurus riograniensis (Bonaparte and Sues 206), Soturnia
calidodon (Cisneros and Schultz, 2003), Riogranaia gracilis (Soares,
2004), Guaibasaurus candelariensis (Bonaparte et al., 2006b), Brasiliodon
quadrangularis and Brasilitherium riograndeis (Bonaparte et al., 2003).
Besides, fossils actually collected at Botucari Hill, 6 km of Candelária,
are solely Jachaleria candelariensis (Araújo and Gonzaga, 1980), an
indeterminate phytosaur (Kischlat and Lucas, 2003), an isolated tooth of
Riogranaia gracilis (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 Suenaria do
Pinhal, respectively about 2.0 and 1.2 km west of the hill. The latter has
yielded Riogranaia gracilis (Bonaparte et al., 2001), Irajatherium
hernandez (Martineili et al., 2005), sphenodontians (MCN PV10104),
and brasilodontid cynodonts (MCN PV3001-3002). Isolated teeth (MCN
PV10102) of the latter group were also recorded along with Sacisaurus
aguadoensis (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 correla-
tion with the Karoo Basin only allows the assignment of an undifferen-
tiated 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 rhynchosaur 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 strati-
graphic 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”, corre-
related to the Argentinean Chañares Formation (Bosio and Sipanic, 2002).
This scheme seems oversimplified, as suggested by the record of puta-
tively older (Abdala and Sá-Teixeira, 2004) and younger (Abdala et al.,
2001) fossil assemblages. Barberena et al. (1985a) attempted a geographi-
cally 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 = Aetosauros sp, Al = Aetosauros-like aetosaur, Bb = Barberanerachus brasiliensis, Bq = Brasiliodon quadrangularis, Br = Brasilitherium riograndensis, Bs = brasilodontid, Cb = Candelaria barbouri, Cr = Cleurosaurus riograniensis, Ch = Charuodon tetracuspidatus, “D” = Dinocestusaurus of Huene (1935-42), Dp = Dinodontosaurus pedroamor, Ec = Ecteninion-like cynodont, El = Exaeretodon-like traversodontid, Em = Exaeretodon major, Er = Exaeretodon riograndensis, Ex = Exaeretodon sp, Gb = Gomphodontosaurus brasiliensis, Gc = Guaibasaurus candelariensis, Hb = Hyperodapedon huenei, Hl = Hyperodapedon-like rhynchosaur, Hm = Hyperodapedon mariaensis, Hs = Hyperodapedon sanjuanensis, Hy = Hyperodapedon sp, Ih = Irajatherium hernandez, Is = cf. Ichigualastia, Jc = Jachaleria candelariensis, Kv = “Karapuru vorax”, Ls = Luangwa sudaamericana, M1 = Massetognathus ochagaviae, Ms = Massetognathus sp, Mr = “Mariante rhynchosaur”, Ns = N. gen. sulcognathus, Pb = Procolophon brasiliensis, Pd = Prestosuchus chiniquensis, Pc = Procerosuchus celer, Pb = indeterminate phytosaur, Pm = Proterochampsia nodosa, Pr = Procolophon pricei, Ps = Procolophon sp, Pt = Proteriodon estudi, Px = Prozostrodon brasiliensis, Rg = Riogranaia gracilis, Rd = Rhdniosaurus gracilis, Rl = Raisuchus tiradentes, Sb = Spondylomas abscindum, Sc = Soturnia calidodon, Sa = Sacisaurus aguadoensis, Sh = Santacruzodon hopsoni, Sk = Saurikosaurus pricei, Sl = Sangaiia lavinai, Sp = Stahleckeria potens, St = Saturnalia tupiniquim, Tb = Teyuwasu barberenai, Tc = Therioherpeton cargnini, Tr = traversodontid of Reichel et al. (2007), Ts = Traversodon stahleckeri, Ut = Unaysaurus tolentinoi.
Chiniquá and Pinheiros, the latter of which assembles records from different localities from the eastern portion of the outcrop belt of the Alemão Member, but no further studies followed that path. In the Chiniquá area, the record of *Chiniquodon theotonicus* and *Dinodontosaurus* in the Cygodontier-Sanga allows a rather straightforward correlation to the Chañares fauna, while more derived forms such as *Stableckeria potens* and *Exaeretodon major*, from the Baum-Sanga, are suggestive of a younger age (see *Dinodontosaurus* vs. *Stableckeria* 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 *Ichigualastia/Stableckeria* 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 Chañares 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 traversodontoids, 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 *Ichigualastia*, 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 suggest an older age also for the Porto Marante 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 Santa Maria 1 Sequence (Zerfass et al., 2003), which lack records of *Hyperodapedon*. That genus is also missing from the upper part of the Ichigualastia Formation, where the only taxon represented is the abundant *Exaeretodon* (Lucas, 2005a). This suggests the correlation (Fig. 3) of the upper Ichigualastia 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 rhynchosaurs 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 Facão, 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 or 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 Ichigualastian (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-Ishigualastian (Lango, 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 guaibensis*, *Braziliodon quadrangularis*, and *Brazililitherium 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 *Cleveosaurus riograndensis* (Bonaparte and Sues, 2006) to Jurassic forms suggest younger ages. Regarding taxa of otherwise possible 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 Schultz (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 clevisaurid, trielodontid, and leptopleurine 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 hermandei* and *Cleveosaurus 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 ranger, occurring along that entire time interval (Fig. 4).

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