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Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil

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Abstract

Late Triassic deposits of the Paraná Basin, Rio Grande do Sul, Brazil, encompass a single third-order, tetrapod-bearing sedimentary sequence that includes parts of the Alemoa Member (Santa Maria Formation) and the Caturrita Formation. A rich, diverse succession of terrestrial tetrapod communities is recorded in these sediments, which can be divided into at least three faunal associations. The stem-sauropodomorph *Saturnalia tupiniquim* was collected in the locality known as 'Waldsanga' near the city of Santa Maria. In that area, the deposits of the Alemoa Member yield the 'Alemoa local fauna,' which typifies the first association; includes the rhynchosaur *Hyperodapedon*, aetosaurs, and basal dinosaurs; and is coeval with the lower fauna of the Ischigualasto Formation, Bermejo Basin, NW Argentina. The second association is recorded in deposits of both the Alemoa Member and the Caturrita Formation, characterized by the rhynchosaur '*Scaphonyx*' *sulcognathus* and the cynodont *Exaeretodon*, and correlated with the upper fauna of the Ischigualasto Formation. Various isolated outcrops of the Caturrita Formation yield tetrapod fossils that correspond to post-Ischigualastian faunas but might not belong to a single faunal association. The record of the dicynodont *Jachaleria* suggests correlations with the lower part of the Los Colorados Formation, NW Argentina, whereas remains of derived tritheledontid cynodonts indicate younger ages. The Late Triassic tetrapod-bearing sequences of northwest Argentina and south Brazil are essential to understanding the faunal succession during that time in south Pangea. The proposed scheme represents a comprehensive framework through which to correlate of these tetrapod faunas with those of other parts of the supercontinent, notably in India and southern Africa.

Keywords: Late Triassic; Santa Maria Formation; Paraná Basin; Rio Grande do Sul

1. Introduction

The stem-sauropodomorph *Saturnalia tupiniquim* (Langer et al., 1999; Langer, 2001, 2003) was collected in a rich historical fossil area, traditionally known as either 'Alemoa' (Bigarella et al., 1967; Colbert, 1970) or 'Km 3' (Beltrão, 1965). It is located at the northern slope of the Cerriquito Mount, in the eastern outskirts of the city of Santa Maria, Rio Grande do Sul state, Brazil. The fossil remains of Alemoa almost certainly were noticed by local inhabitants of Santa Maria, as well as by the first European scientific expeditions to explore the Rio Grande province during the 19th century. However, fossils collected from the area have been studied scientifically only since the beginning of the last century (Woodward, 1903; Langer et al., 2000).

During the early 20th century, various local amateur naturalists regularly explored the Alemoa area. Some collected material ended up in the possession of the German paleontologist Friedrich von Huene, who published a compendium describing the specimens, which mostly consisted of rhynchosaur remains (Huene, 1926). During the austral summer of 1928–1929, Huene collected in Rio Grande do Sul. Around Santa Maria, his crew explored the so-called 'sangas,' which represent large erosion areas that expose the typical red, fossiliferous mudstone of the region. In Alemoa, four main localities were prospected: the Grossesanga (or Sanga Grande) and localities 1–3 (Figs. 1 and 2). The most important of these were the Grossesanga and locality 1, also known as Waldsanga or Sanga do Mato

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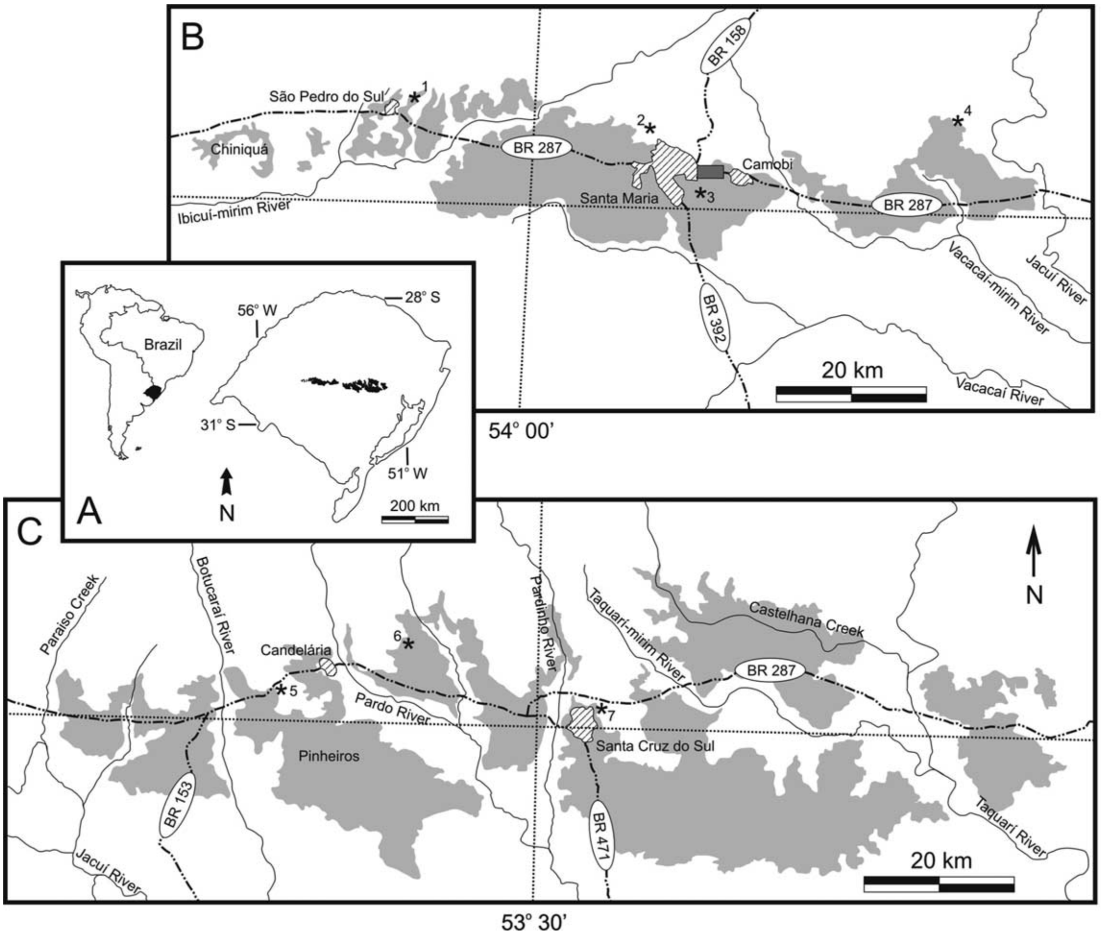

Fig. 1. Maps depicting the geographical distribution of the outcrop belt of the Alemoa Member, Santa Maria Formation (shaded), based on unpublished work by Ubiratan Faccini. (A) Location of Rio Grande do Sul in South America and the Alemoa belt within it. (B, C) Detail of the western (B) and eastern (C) parts of the Alemoa belt. Exposures extend from the classic localities of Chiniquá to the eastern banks of the Taquarí River. Main fossil sites discussed in the text: (1) Inhamandá, (2) Água Negra, (3) Faixa Nova, (4) Faxinal do Soturno, (5) Botucaraí Mount, (6) Linha Facão, and (7) Santa Cruz. Shaded rectangle in (B) indicates the approximate areas depicted in Figs. 2–4.

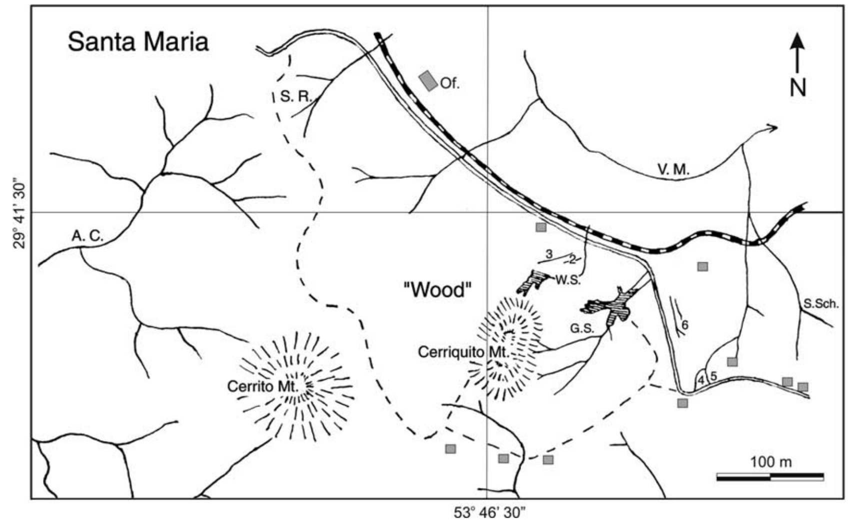

Fig. 2. Area between Santa Maria and São José during the late 1920s (redrawn from Huene and Stahlecker, 1931). Santa Maria was northeast of the map and São José just west of the Sanga Schramm. Abbreviations: 2, 3 = sangas 2 and 3 of the Alemoa complex, 4–6 = sangas of the São José complex, A.C. = Cancela Creek, G.S. = Grossesanga, Of. = railway station, S.R. = Sanga Ribas, S.Sch. = Sanga Schramm, V.M. = Vacacaí-Mirim River, and W.S. = Waldsanga. Symbols: gray squares = houses, full lines = water courses, stippled lines = tracks, double line = main road, and double stippled line = railway track.

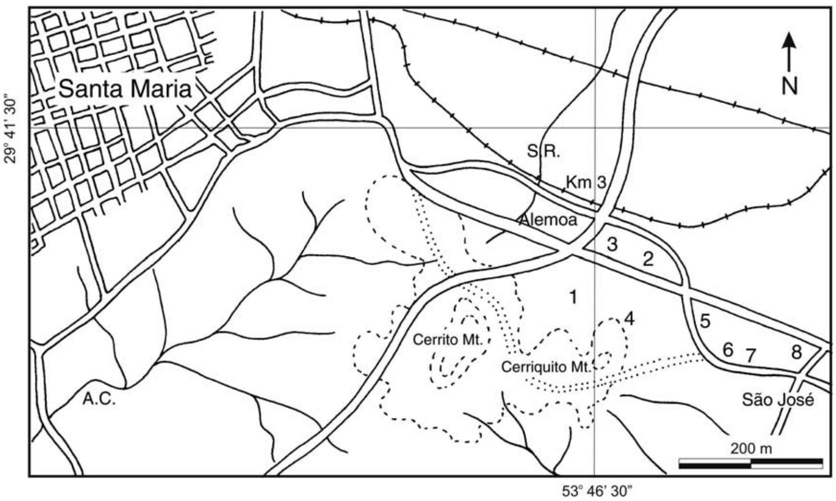

Fig. 3. Fossil localities west of Santa Maria during the mid-1960s (redrawn from Beltrão, 1965). Abbreviations are as in Fig. 1, except 1 = Sanga do Mato, 4 = Sanga Grande, 5–7 = sangas of the São José complex, and 8 = Sanga Schramm. Symbols are as in Fig. 1, except double dotted line = track, and full line with wider parts = railway track. Concentric lines around Cerrito and Cerriquito Mounts represent topographic curves. Localities 2, 3, 6, and part of 1 were destroyed at the time.

because it was located at the western edge of a small wood. According to Beltrão (1965), by the mid-1960s, sangas 2 and 3 were buried by the expansion of the urban area of Santa Maria, which also partially destroyed the Waldsanga. In contrast, the Grossesanga, which Beltrão (1965) called 'number 4' (Fig. 3), escaped destruction. As far as reconstructions of the geography of the Santa Maria outskirts in the 1920s and 1960s can show, the type locality of *Saturnalia tupiniquim* corresponds to what remains of the Waldsanga, probably its higher portion (stippled area in Fig. 2).

This article summarizes the current status of the south Brazilian Late Triassic sequence from a biostratigraphic viewpoint. Previously, information was fragmented in a series of papers that tackled specific geological or paleontological aspects. A reviewed ordination of faunal associations within the sequence also is presented. The south Brazilian Late Triassic is of particular interest because of the putative record of some of the oldest dinosaurs (Colbert, 1970; Langer et al., 1999) and sister groups of mammals (Bonaparte et al., 2003). Better knowledge about its biostratigraphy is essential for understanding the early radiation of the tetrapod groups that rose to dominate the terrestrial ecosystems during the Mesozoic and Cenozoic.

2. The Waldsanga

Among the sangas of Alemoa, the Waldsanga appears to be the most important in historical and paleontological terms. From that locality came the type and only specimen of the traversodontid *Gomphodontosuchus brasiliensis* Huene, 1928, and possibly the proterochampsid *Cerritosaurus binsfeldi* Price, 1946. In addition, most of the material described by Huene (1926) probably came from that locality, and he subsequently (Huene, 1935–1942) listed various specimens collected there. From the upper 'nonstratified' beds came an isolated archosaur calcaneum assigned to *Hoplitosuchus raui*, an indeterminate archosaur ulna and metatarsus, and several rhynchosaur remains attributed to *Scaphonyx fischeri*. The lower 'stratified' beds yielded remains of the rhynchosaur *Cephalonia lotziana*, as well as isolated material attributed to *Rauisuchus tiradentes*.

What remains of the Waldsanga is an area of approximately 300 m^2 in which a series of approximately 100 m long ravines exposes the mudstones of the Santa Maria area. The land belongs to descendants of G. Huebner, who was the owner of most of the Alemoa area at the time Huene collected there (Beltrão, 1965). It is located on RS 509 ('Faixa Velha de Camobi,' number 1945), exactly SE to the crossing of BR 392 (Fig. 4). Among the fossils described by Huene (1926, 1928, 1935–1942), those with current taxonomic/stratigraphic meaning are the type of *Gomphodontosuchus brasiliensis* and some materials assigned to *Scaphonyx fischeri* and/or *Cephalonia lotziana* that can be referred to *Hyperodapedon* (Langer et al., 2000).

The rocks presently exposed in the Waldsanga can be divided into six different facies (Fig. 5; see also Viana et al., 1998). Facies I is approximately 1.5 m thick, composed of a red laminated siltstone, and rich in calcium carbonate concretions. Accordingly, most fossils in this layer are strongly distorted by calcitic cementation, as discussed by Holz and Schultz (1998). Recently recovered specimens include nondiagnostic archosaur and rhynchosaur isolated remains, as well as coprolites.

Facies II is 10.7 m thick and also composed of red laminated siltstones. However, the carbonatic concretions are less common, and the better preserved fossils, found in articulation or semi-articulated, indicate short transport

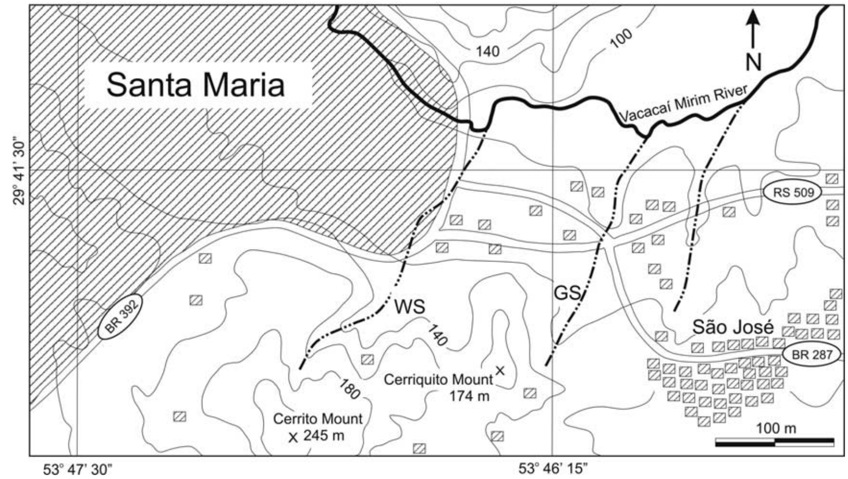

Fig. 4. Map depicting the eastern outskirts of Santa Maria, partially based on Bortoluzzi (1974). Abbreviations are as in Fig. 1. Symbols: shading = built-up areas, wide full lines = water courses, wide stippled lines = mislaid water courses, double line = main roads, and fine full lines = topographic curves.

(Holz and Barberena, 1994). One of the paratypes of *Saturnalia* (MCP 3846-PV) was found approximately 5 m from the base of the entire sequence, and the holotype (MCP 3844-PV) and the other paratype (MCP 3845-PV) were found, spaced 10–20 m from each other, 8.3 m away. Approximately 10.5 m from the base, *Gomphodontosuchus*-like traversodont teeth (F. Abdala, pers. comm.), as well as an unidentified rhynchosaur skeleton, were collected.

Facies III is 1.0 m thick and composed of a red conglomerate with carbonate concretions, silex pebbles, and siltstone fragments. Its upper part shows some signs of pedogenesis, along with thin discontinuous beds of carbonatic sandstone, bioturbations (including pedotubes), dissecation cracks, coprolites, and some bone fragments including a dentary of ‘*Scaphonyx*’ *sulcognathus*.

The top facies (IV–VI) are of fluvial origin and devoid of fossil remains. Facies IV occurs 12.7–14.5 and 15.0–16.7 m from the base of the sequence, and facies V occurs between these layers. Facies IV is composed of coarse to medium micaceous sandstones, with small (< 1 cm) siltic pebbles. It shows channel cross-stratification, and the paleocurrent is NNW directed. Facies V represents an intraformational

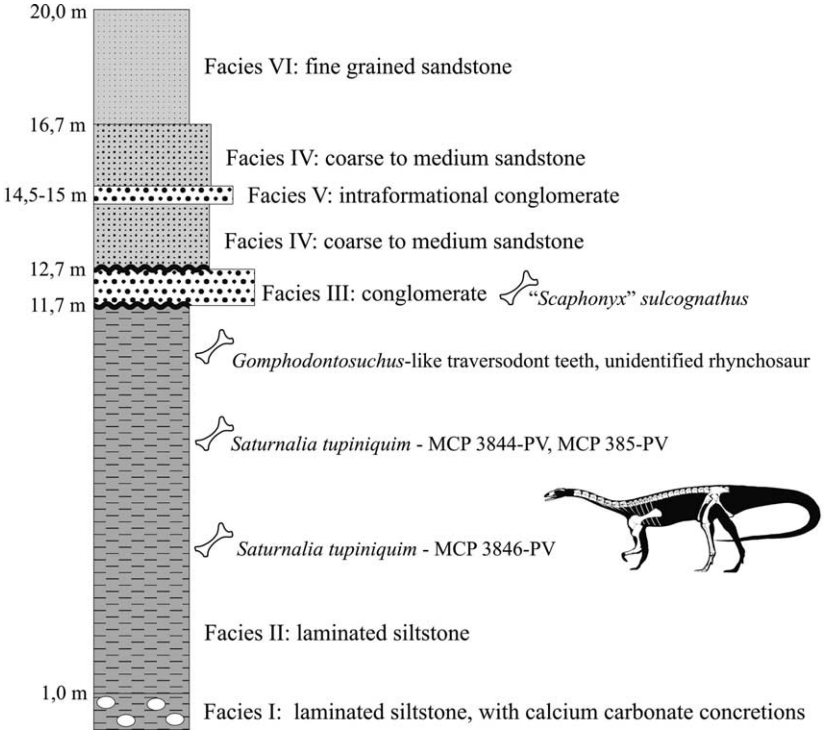

Fig. 5. Stratigraphic log of Alemoa Member and Caturrita Formation representing a NE–SW cross-section of the entire facies succession as presently exposed in the Waldsanga. Based on unpublished work by Somalia Viana. *Saturnalia tupiniquim* is depicted in silhouette.

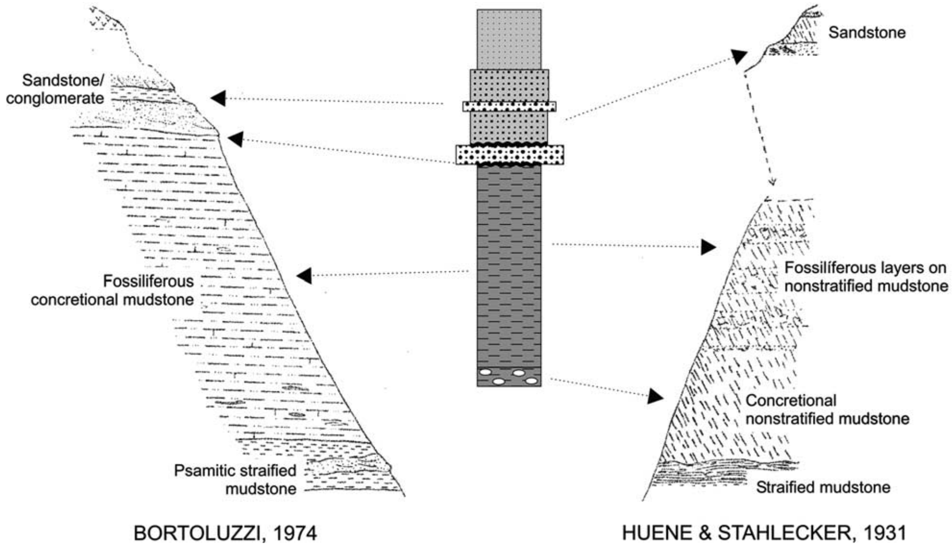

Fig. 6. Comparison of the stratigraphic log of Fig. 4 to those produced by Huene and Stahlecker (1931), for the Waldsanga and Bortoluzzi (1974) for the escarpments of the Cerriquito Mount.

conglomerate, including siltic plebes (0.5–1.0 cm) in a fine sandstone matrix. Facies VI occupies the top 3.3 m of the sequence. It is composed of orange, fine-grained micaceous sandstones, with fine laminations and channel cross-stratification (paleocurrents NNW).

The deposits of the Waldsanga can be compared to previous works on the geology of the Santa Maria area (Fig. 6). Huene and Stahlecker (1931) recognized the superposition of siltstones and coarser deposits (sandstones) in the outcrop, though the contact among the facies apparently was not exposed at the time. Partially based on the deposits of the Grossesanga, Bortoluzzi (1974) provides a better picture of the local stratigraphy in the escarpments of the Cerriquito Mount. As also appears in the Waldsanga, an abrupt contact was recognized between the mudstone facies and the overlying conglomerates and sandstones.

The comparison with the general stratigraphic scheme of the Santa Maria Formation (Fig. 7), as defined by Andreis et al. (1980), shows that facies I and II of the Waldsanga are representative of the Alemoa Member of the Santa Maria Formation, which is a mainly pelitic sequence that seems to have been deposited in the floodplain of an anastomosed to meandering fluvial system (Holz and Scherer, 2000; Rubert and Schultz, 2004). Facies III–VI represent the Caturrita

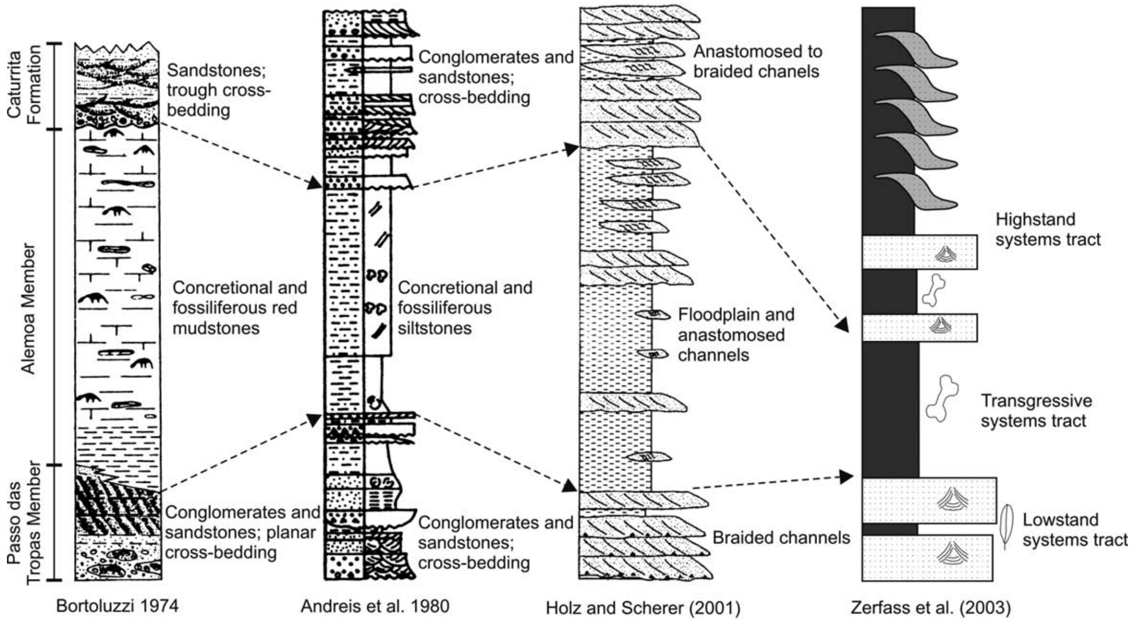

Fig. 7. Comparison of the regional stratigraphy of the Rosário do Sul Group, as reviewed by Bortoluzzi (1974), Andreis et al. (1980), Holz and Scherer (2000), and Zerfass et al. (2003).

Formation, a coarser sequence that was deposited in a braided fluvial system during a period of decreasing humidity (Rubert and Schultz, 2004). In addition, these two sets of facies (I–II and III–VI) seem to correspond, respectively, to part of the transgressive and highstand systems tracts within the 'Santa Maria 2 Sequence' of Zerfass et al. (2003). These authors provide an alternative interpretation of the deposits, in which mainly lacustrine environments (transgressive) are succeeded by fluviodeltaic systems (highstand).

3. Geological and paleontological settings: Alemoa Member and Caturrita Formation

The Triassic rocks of the Paraná Basin in Rio Grande do Sul state are represented by the Rosário do Sul Group, the lithostratigraphic subunits of which include the Sanga do Cabral, Santa Maria, and Caturrita Formations (Andreis et al., 1980), as well as the overlying Mata sandstone (Faccini, 1989; Holz and Scherer, 2000). The Santa Maria Formation is further subdivided into the Passo das Tropas and Alemoa Members (Andreis et al., 1980). As mentioned previously, the rocks exposed in the Waldsanga belong to the top of the Alemoa Member and the base of the Caturrita Formation (Fig. 7). In the scheme proposed by Zerfass et al. (2003), the bulk of the Santa Maria and Caturrita Formations fits in the 'Santa Maria 1' and 'Santa Maria 2' sequences, whereas the Mata sandstone corresponds to the 'Santa Maria 3 Sequence,' and the Sanga do Cabral Formation constitutes a separate sequence.

In biostratigraphic terms, the Alemoa Member traditionally is divided into a lower therapsid-rich fauna and an upper assemblage dominated by rhynchosaurs (Barberena, 1977; Bonaparte, 1982; Schultz et al., 2001). Most authors have dated these fossil associations as Ladinian and Carnian, respectively, but precise age assignments are lacking (Abdala et al., 2001; Lucas, 2002). As biostratigraphic units, they also have received different names in the literature (Barberena, 1977; Barberena et al., 1985a; Scherer et al., 1995; Schultz et al., 2001), but this article follows the nomenclature proposed by Lucas (2002) and employs the terms *Dinodontosaurus* and *Hyperodapedon* assemblage zones. Note, however, that these terms are used here to designate biostratigraphic units that are not identical to those defined by Lucas (2002).

It is worth noting that no clear-cut lithologic criteria have been devised to distinguish between the strata that yield the *Dinodontosaurus* and *Hyperodapedon* assemblage zones (Faccini, 1989; Scherer et al., 1995; cf. Zerfass et al., 2003). The exposition area of the Santa Maria sequence is patchy and occurs mainly in sangas or road cuts. Accordingly, the outcrops of the Alemoa Member (Fig. 1) have no lateral continuity and are stratigraphically ordered mainly on the basis of their fossil content. Increasing evidence suggests that a two-fold subdivision oversimplifies the biostratigraphy of the Alemoa Member. Equally oversimplified is the scheme proposed by Lucas (2002, 2003), in which the *Hyperodapedon* assemblage zone is considered to include the entire tetrapod fauna of the Caturrita Formation. Instead, clear evidence indicates that some assemblages within the latter lithostratigraphic unit are younger than that assemblage zone, and were the basis for proposing a new biostraigraphic unit within the Santa Maria sequence: the Ictidosaur assemblage zone (Rubert and Schultz, 2004).

The Alemoa Member in the Waldsanga corresponds to the transgressive systems tract of the Santa Maria 2 sequence (Zerfass et al., 2003). Its fauna typically represents, and by definition belongs to, the *Hyperodapedon* assemblage zone, which encompasses fossil assemblages of various isolated outcrops that may or may not be strictly coeval. Accordingly and following the approach of Barberena et al. (1985b), major fossil bearing areas are treated individually for correlation purposes (Fig. 8).

The type-area of the *Hyperodapedon* assemblage zone—namely, the 'Rhynchocephalia *sic*. association zone' of Barberena (1977)—is the outskirts of Santa Maria, where Barberena et al. (1985b) define the Alemoa local fauna. However, Barberena et al. (1985b) also assign fossil assemblages of other areas to that local fauna, which here is considered to encompass only fossil assemblages of the Alemoa Member around Santa Maria. Other than those of Alemoa, the most important of these assemblages is 'Faixa Nova' (see also Rosa, 2003). This relatively new outcrop, which was not exposed in Huene's times, is located on the southwestern slope of the Cerrito Mount (Fig. 1) and seems to represent a southern equivalent of the Waldsanga. Fossil taxa of the Alemoa local fauna occur on its pelitic lower beds, which are topped by coarser deposits that correspond to the Caturrita Formation.

Rhynchosaurs represent approximately 90% of the fossil content (in number of specimens) of the Alemoa local fauna (*sensu* Barberena et al., 1985b; Azevedo et al., 1990). These reptiles occur in all the prospected fossil localities of the Alemoa Member in the area of Santa Maria, where two different species of the genus *Hyperodapedon*—*H. mariensis* and *H. sanjuanensis*—are known (Langer and Schultz, 2000a,b). Tetrapods of the Alemoa local fauna (as defined herein), other than those already discussed and collected in the Waldsanga, include (1) the basal dinosaur *Staurikosaurus pricei* (Colbert, 1970) from the Sanga Grande, (2) an aetosaur, possibly related to *Aetosauroides/Stagonolepis*, from Faixa Nova (Kischlat, 2000; Lucas and Heckert, 2001; Rosa and Leal, 2003), and (3) the 'ictidosaurid' cynodonts *Therioherpeton cargnini* and *Prozostrodon brasiliensis* (Bonaparte and Barberena, 1975, 2001; Barberena et al., 1987; Abdala and Giannini, 2002), collected in a single spot in Faixa Nova approximately 50 m south of the aetosaur occurrence (C. Schultz, pers. comm.). In addition, Kischlat (1999, 2000) recently reviewed the archosaurs collected in the Alemoa area,

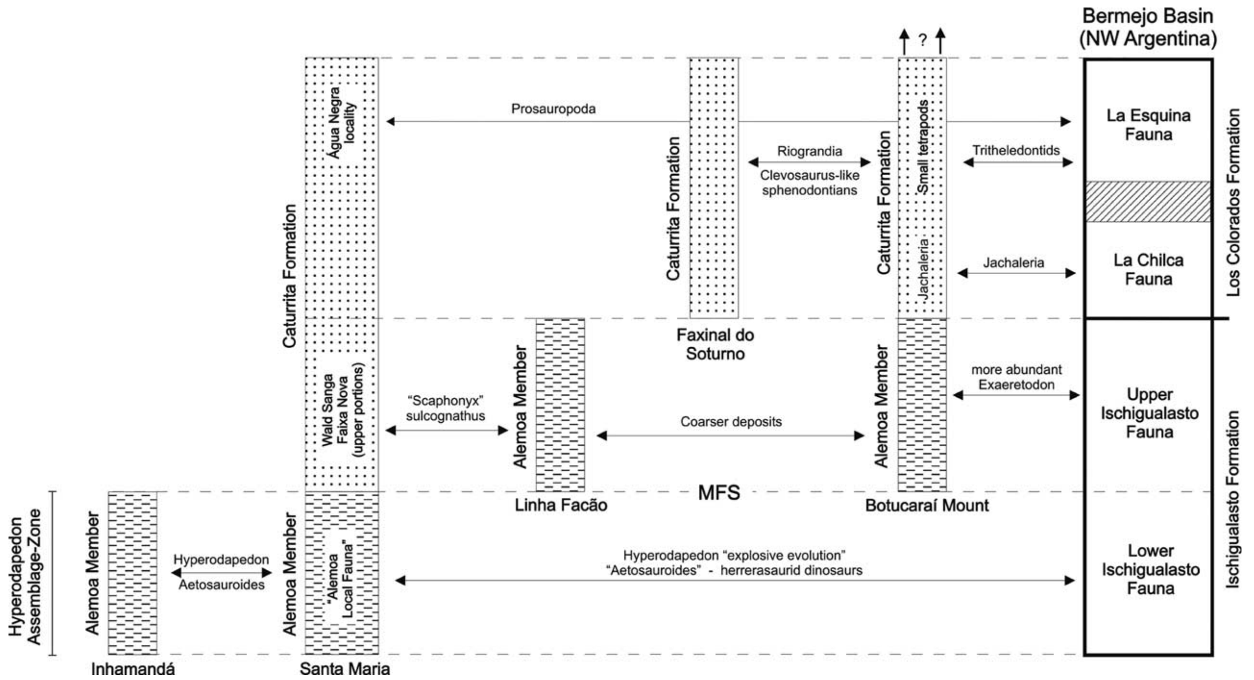

Fig. 8. Correlation of selected Late Triassic tetrapod assemblages of the Alemoa Member and Caturrita Formation in Rio Grande do Sul, Brazil, with the faunal succession of the Ischigualasto sequence (Bermejo Basin, NW Argentina). MFS = maximum flooding surface of Zerfass et al. (2003).

primarily described by Huene (1935–1942), which include (1) *Rhadinosuchus gracilis*, a possible proterochampsid, (2) the poorly known *Hoplitosuchus raui*, whose related specimens might be partially dinosaur, and (3) the gracile ‘rauisuchian’ *Rauisuchus tiradentes*.

Fossil assemblages of two areas not in the outskirts of Santa Maria also have been assigned to the *Hyperodapedon* assemblage zone (Barberena et al., 1985b; Schultz et al., 2001): the Inhamandá and Botucaraí Mount localities (for other incompletely studied fossil localities possibly related to the assemblage zone, see Azevedo et al., 1999a; Ferigolo and Ribeiro, 2000). The Inhamandá locality, in the area of São Pedro do Sul (Fig. 1), yielded an aetosaur very similar to *Aetosauroides scagliai* (Zacarias, 1982; Kischlat, 2000; Lucas and Heckert, 2001), as well as two species of *Hyperodapedon*: *H. mariensis* and the more basal *H. huenei* (Langer and Schultz, 2000a). *Hyperodapedon sanjuanensis* is not known in Inhamandá, but an isolated skeleton was recorded in a locality a few kilometers south of it (Langer, 1996). Because of the presence of *Hyperodapedon* and the aetosaur, the Inhamandá fossil fauna is considered coeval to the Alemoa local fauna (Fig. 8). In geological terms, the Alemoa Member at Inhamandá also corresponds to the transgressive systems tract of the Santa Maria 2 sequence (Zerfass et al., 2003).

Close to the Botucaraí Mount, near the town of Candelária (Fig. 1), the upper levels of the Alemoa Member yield the proterochampsid *Proterochampsa nodosa* (Barberena, 1982), the traversodontid *Exaeretodon riograndensis* (Abdala et al., 2002), a still unstudied rhynchosaur (A.M. Ribeiro, pers. comm.), and possibly the therioherpetid *Charruodon tetracuspidatus* (Abdala and Ribeiro, 2000). A similar association between *Exaeretodon* and an undetermined rhynchosaur is known from a new and still undescribed fossil assemblage of the Alemoa Member in the area of Agudo (A.M. Ribeiro, pers. comm.). *Proterochampsa* and *Exaeretodon* formerly were included with the dicynodont *Jachaleria* in the Botucaraí local fauna of Barberena et al. (1985b), but revisions of the local stratigraphy of the area (Scherer et al., 1995; Rubert and Schultz, 2004) reveal that *Jachaleria* comes from a different sedimentary sequence that overlies the Alemoa Member and may represent the Caturrita Formation (Schultz et al., 2001). These two distinct faunal associations were included by Zerfass et al. (2003) in the higstand systems tract of the Santa Maria 2 sequence, which is stratigraphically higher than the transgressive systems tract that encompasses the deposits of the Alemoa Member in the area of Santa Maria.

The exact provenance of the type and only specimen of *Charruodon* is uncertain. It was found in the collection of MCT-PUCRS with only ‘Butucaraí area’ as the provenance account. Accordingly, it might have come from either the lower beds (Alemoa Member) or the coarser upper sequence (Caturrita Formation), though information gathered by the collectors of the material and its fossilization pattern suggests the former (A.M. Ribeiro, pers. comm.). Therefore, the fauna of the Alemoa Member in Botucaraí Mount includes definitively only *Proterochampsa* and *Exaeretodon*, both of which are unknown in the Alemoa beds around Santa Maria.

Accordingly, this fauna cannot be directly correlated with the Alemoa local fauna.

In the Waldsanga, the highstand systems tract of the Santa Maria 2 sequence (Zerfass et al., 2003) is represented by the Caturrita Formation (facies III–VI). This stratigraphic unit was proposed by Andreis et al. 1980 (see also Holz and Scherer, 2000) to represent the coarser and upper levels of the Rosario do Sul Group, which are dominated by fluvial sandstones. The facies have been recognized not only around Santa Maria (Rubert and Schultz, 2004) but also in the fossiliferous areas of Candelária (Scherer et al., 1995) and Faxinal do Soturno (Faccini in Ferigolo, 2000). The single vertebrate fossil recovered from the Caturrita Formation in the Waldsanga is a dentary belonging to the rhynchosaur ‘*Scaphonyx*’ *sulcognathus*, which came from the basal conglomerate (facies III). ‘*S.*’ *sulcognathus* is a distinctive hyperodapedontine rhynchosaur that, according to its peculiar set of derived cranial features and plesiomorphic tooth morphology, belongs to a genus of its own (Langer and Schultz, 2000a,b). It also was registered in the upper and coarser facies of the Faixa Nova locality, which seems to represent the lateral continuation of the Caturrita Formation, as exposed in the Waldsanga.

The type material of ‘*S.*’ *sulcognathus* comes from the lamitic upper levels of the Alemoa Member in the fossil locality known as Linha-Facão (Azevedo and Schultz, 1987; Schultz et al., 2001), located east of Candelária (Fig. 1). Because ‘*S.*’ *sulcognathus* can be considered a local biochron that correlates the lower beds of the Caturrita Formation around Santa Maria and the upper beds of the Alemoa Member in Linha Facão, the faciological distinction between the Alemoa Member and the Caturrita Formation may not represent a reliable basis for time correlation, at least between distant areas such as Santa Maria and Linha Facão. The rhynchosaur *Hyperodapedon sanjuanensis* also was reported in the area of Linha Facão (Azevedo, 1984), but its precise provenance is unknown (C. Schultz, pers. comm.), so this record will not be considered further for biostratigrafic purposes.

Linha Facão is relatively close the Botucaraí Mount (Fig. 1), and Barberena et al. (1985b) suggest correlations between the fossil assemblages of these two localities. More specifically, Schultz (1995) relates the fauna of Linha Facão to that of the Alemoa Member in Botucaraí. These fossil-bearing strata share faciological resemblance and had been assigned to the Caturrita Formation (Barberena et al., 1985b; Azevedo and Schultz, 1987) before their reinterpretation as representatives of the Alemoa Member. Barberena (1982) mentions that the strata in which the holotype of *Proterochampsa nodosa* was found is composed of mudstones that are sandier than typical Alemoa beds of Santa Maria. The increase in arid conditions through the Triassic sequences in southern Brazil (Rubert and Schultz, 2004) predicts an upward coarsening of the lithology along the Alemoa Member and may provide the basis to correlate such strata.

As proposed by Schultz (1995), the fossil assemblage of the Alemoa Member in the Botucaraí area may represent a younger faunal stage compared with that of the Alemoa local fauna (Fig. 8). Evidence for this proposal includes the following: (1) the two faunas do not correspond in terms of taxonomic content, (2) the sediments of the Alemoa Member are coarser in the Botucaraí area, and (3) the Alemoa Member in Botucaraí might be cross-correlated with the Caturrita Formation in Santa Maria through the Linha Facão deposits. Zerfass et al. (2003) assign the Alemoa local fauna-bearing deposits in Santa Maria to the transgressive systems tract of the Santa Maria 2 sequence but relate the tetrapod-bearing beds of Botucaraí to the higher highstand systems tract.

Also in the Botucaraí Mount and above the Alemoa Member, deposits of the Caturrita Formation occur. According to Scherer et al. (1995), these deposits represent a different stratigraphic sequence that yields fossils of *Jachaleria candelariensis* (Araújo and Gonzaga, 1980; cf. Lucas, 1998, 2003). The occurrence of this dicynodont seems to mark a faunal stage distinct from, and younger than, any of those previously discussed herein (Scherer et al., 1995; Abdala et al., 2001; Rubert and Schultz, 2004). Additional material from the same outcrop includes vertebrae and partial pelvic elements of a possible herrerasaurid dinosaur (Kischlat and Barberena, 1999), as well as isolated archosaur teeth (Dornelles, 1990) that conform to a fragmentary mandible simphysis with phytosaur affinities (Kischlat and Lucas, 2003). According to Kischlat (2000), the isolated teeth are similar to those of *Parasuchus* (Chatterjee, 1978), though the symphisis itself more resembles *Mystriosuchus* (Hungerbühler, 2002). More recent accounts, however, dismiss any taxonomic assignment of this material further than Phytosauria indet. (Kischlat and Lucas, 2003; A. Hungerbühler, pers. comm.).

Recently, new localities assigned to the Caturrita Formation, near the Botucaraí Mount, have yielded important tetrapod remains, including the basal saurischian *Guaibasaurus candelariensis* (Bonaparte et al., 1999); small cynodonts with tritheledontid affinities such as *Riograndia guaibensis* (Bonaparte et al., 2001) and *Irajatherium hernandezi* (Martinelli et al., 2002, 2005); and fragmentary sphenodontian remains (Ferigolo, 1999, 2000), preliminarily identified as a new species of *Clevosaurus* (J. Bonaparte, pers. comm.). In the locality in which the small-sized forms (cynodonts and sphenodontians) occur together, no large tetrapods have been recovered. Schultz et al. (2001) attempt to correlate some occurrences to that of *Jachaleria* in a single biostratigraphic unit, but more detailed stratigraphic studies (e.g. Rubert and Schultz, 2004) are needed to determine whether the fossil assemblages of the different localities of the Caturrita Formation belong to the same local fauna. Ferigolo et al. (1999) suggest a possible Early Jurassic age for the deposits bearing the cynodonts and sphenodontians, which is not consistent with the record of *Jachaleria*.

Ferigolo (1999, 2000) provides accounts of a new small-tetrapod fossil assemblage that shares similarities with that discussed for the Botucaraí area. It was registered in the area of Faxinal do Soturno (Fig. 1) in deposits assigned to the Caturrita Formation. Its fauna includes (1) a sphenodontid similar to *Clevosaurus* (Ferigolo, 2000), (2) the leptopleuronine procolophonid *Soturnia caliodon* (Ferigolo, 2000; Cisneros and Schultz, 2003), (3) jaw fragments with morganucodont affinities (Ferigolo, 1999; Ribeiro et al., 2001), and (4) *Brasilodon quadrangularis* and *Brasilitherium riograndensis*, two mammal-like small cynodonts (Bonaparte et al., 2003). According to its stratigraphic position and fossil content, this fauna might be coeval with other assemblages of the Caturrita Formation in Rio Grande do Sul. Recent fieldwork reveals the presence of *Riograndia* and *Guaibasaurus* in this fossil site (C. Schultz, pers. comm.), which reinforces its correlation with the Botucaraí Mount fauna.

Another important fossil locality in the Caturrita Formation is Água Negra (Beltrão, 1965; Rosa et al., 1998; Leal et al., 2002), northwest of Santa Maria (Fig. 1). Its beds seem to represent a younger stratigraphic sequence compared with those of other tetrapod-bearing localities in the area, such as the typical Alemoa beds that encompass the Alemoa local fauna and the base of the Caturrita Formation, which yielded ‘*Scaphonyx*’ *sulcognathus*. The only recorded body-fossil in the area corresponds to a prosauropod dinosaur with uncertain affinities (Azevedo et al., 1999b; Kellner et al., 1999; Leal and Azevedo, 2003).

4. Correlations of the Late Triassic faunas of south Brazil

The correlation with the fossil tetrapod assemblages of NW Argentina (Ischigualasto–Ischichuca depocenter, Bermejo Basin; Stipanicic and Marsicano, 2002) has always been of prime importance for understanding the Triassic biostratigraphy in south Brazil. The deposits of the Santa Maria and Ischigualasto sequences are exposed in geographically close regions, and their fossil records share important similarities. The nearly continuous sedimentation of the Ischigualasto sequence (Milana and Alcober, 1995; Milana, 2002) occurred over a time span that seems equivalent to most, if not all, of that involved in the deposition of the Late Triassic rocks of Rio Grande do Sul (i.e. the Upper Santa Maria and Caturrita Formations). In addition, unlike the situation in south Brazil, the exposition areas of the Ischigualasto sequence are laterally continuous, and the fossil assemblages of different localities can be ordered in a precise lithostratigrafic framework. In this section, the previously mentioned south Brazilian faunal associations are correlated with those of the Ischigualasto sequence.

The Santa Maria Formation as a whole traditionally has been considered older than the Ischigualasto Formation. In most cases (Bonaparte, 1966, 1973; Colbert, 1970; Anderson and Cruickshank, 1978; Benton, 1983), this designation has been the result of considering it as a single biostratigraphic unit and not taking into account the separation between the *Dinodontosaurus* and *Hyperodapedon* assemblage zones. Yet, even authors that adopted such a division (Bonaparte, 1982) still consider the *Hyperodapedon* assemblage zone slightly older than the Ischigualasto Formation, without giving sufficient reasons for this assumption. More appropriately, recent accounts have considered the *Hyperodapedon* assemblage zone coeval to the Ischigualasto Formation (Ochev and Shishkin, 1989; Lucas, 1998; Abdala et al., 2001).

With regard to the ‘Traversodontid biozone’ of Abdala et al. 2001 (see also Lucas, 2002), the presence of chiniquodontids suggests a maximal age equivalent to that of the *Hyperodapedon* assemblage zone; the latest record of these cynodonts seems to be the Ischigualasto Formation (Abdala and Giannini, 2002). In addition, the presence of a basal traversodontid such as *Santacruzodon* (Abdala and Ribeiro, 2003), together with the absence of *Hyperodapedon*, supports a pre-*Hyperodapedon* assemblage zone age for the Santa Cruz fauna. However, the occurrence of traversodontids (‘Type I’ of Abdala and Ribeiro, 2002) related to forms nested within the *Gomphodontosuchus*-*Exaeretodon* clade (Flynn et al., 2000; Abdala and Ribeiro, 2003) suggests a faunal stage equivalent to those in which *Exaeretodon*-like traversodontids are present in the absence of hyperodapedontine rhynchosaurs (*sensu* Langer and Schultz, 2000a,b), such as is possibly the case of the Chiniquá local fauna (Barberena et al., 1985b; Abdala et al., 2002). It seems premature, however, to define a distinct biostratigraphic unit for the fauna of Santa Cruz before additional, especially noncynodont, material is recovered (cf. Machado and Kischlat, 2003). Because mainly cynodonts were identified in the fauna of Santa Cruz, it is likely that its peculiar composition reflects locality-specific ecologic and/or geographic conditions rather than a different age. The fauna might represent merely a local variation of *Dinodontosaurus* or *Hyperodapedon* assemblage zone assemblages.

The Alemoa local fauna typically represents the *Hyperodapedon* assemblage zone and is characterized by an overwhelming dominance of the rhynchosaur *Hyperodapedon* in a remarkable ecological scenario defined by Romer (1962) as the ‘explosive evolution of rhynchosaurs.’ In the Bermejo Basin, a similar dominance of *Hyperodapedon* occurs in the lower portions of the Ischigualasto Formation (Rogers et al., 1993; Bonaparte, 1997). Other members of the Alemoa local fauna, such as the aetosaur *Aetosauroides* and herrerasaurid dinosaurs, are more abundant in the lower beds of that lithostratigraphic unit. Accordingly, the Alemoa local fauna is regarded as coeval with the lower portions of the Ischigualasto Formation (Fig. 8).

Forms such as *Exaeretodon* and *Proterochampsa*, which are unknown in the Alemoa local fauna but occur together in the Alemoa Member of the Botucaraí Mount area, are present in the Ischigualasto Formation. However, though *Proterochampsa* remains inconspicuous throughout most of the sequence, the abundance of *Exaeretodon* seems to increase along with the decline in rhynchosaurs (Rogers et al., 1993). This trend suggests a correlation between the Alemoa beds of Botucaraí and the upper portions of the Ischigualasto Formation (Fig. 8), in line with the possible upper stratigraphic position of the former in relation to the deposits bearing the Alemoa local fauna around Santa Maria. Accordingly, Schultz's (1995) 'faunal association 6,' characterized by '*Scaphonyx*' *sulcognathus*, *Proterochampsa*, and *Exaeretodon*, might prove coeval with the fauna of the upper Ischigualasto Formation.

In the Bermejo Basin, the dicynodont *Jachaleria* occurs in the La Chilca locality, in the lower portion of the Los Colorados Formation (Bonaparte, 1997; Stipanicic and Marsicano, 2002), which suggests a correlation of the *Jachaleria*-bearing deposits of the Caturrita Formation in Botucaraí with the fauna of La Chilca. *Guaibasaurus*, in contrast, is known only from south Brazil, and its phylogenetic position is too poorly constrained (Langer, 2004) to provide correlations with the Argentinean sequence. However, basal saurischians, such as *Guaibasaurus*, are more typical of the Ischigualasto Formation than of the upper portions of the Los Colorados Formation, such as the La Esquina fauna (Bonaparte, 1972, 1982; Arcucci and Coria, 2003).

The correlation of the small-tetrapod assemblages of Botucaraí is more controversial (Fig. 8). Bonaparte et al. (2001) (see also Martinelli et al., 2004) suggest that *Riograndia* represents a tritheledontid, a group of cynodonts that include *Chaliminia*, from the La Esquina fauna (Bonaparte, 1980), as well as Lower Jurassic forms (Gow, 1980; Shubin et al., 1991). This claim could indicate a younger age for the small-tetrapod fauna of Botucaraí in relation to the *Jachaleria*-bearing beds. Yet, Bonaparte et al. (2001) state that *Riograndia* presents the expected dental morphology to give rise to forms such as *Chaliminia*. This suggestion is corroborated by the work of Martinelli et al. (2004), which defines *Riograndia* as the basal-most tritheledontid. In addition, the sister taxa to Tritheledontidae plus Mammaliaformes (*sensu* Martinelli et al., 2004) appears to be *Therioherpeton* (see also Kemp, 1982; Sues, 2001) and *Prozostrodon*, both from the Faixa Nova locality. Thus, the phylogenetic position of *Riograndia* supports an intermediate age for its assemblage between the Alemoa local fauna and the La Esquina fauna. This age is consistent with the putative correlation of the small-tetrapod assemblage of Botucaraí with the *Jachaleria*-bearing beds of Argentina and Brazil. In contrast, the more derived phylogenetic position of *Irajatherium hernadezi* (Martinelli et al., 2005) suggests a younger (perhaps Jurassic) age for that assemblage and challenges the association of small-tetrapod-bearing deposits and *Jachaleria* in Botucaraí to the same local fauna.

Sphenodontians are unknown in the Ischigualasto sequence, but those recorded in Botucaraí and Faxinal do Soturno have been regarded as closely related to *Clevosaurus* (Ferigolo, 2000). This taxon is mainly known from Jurassic strata (Evans and Kermack, 1994; Wu, 1994; Sues et al., 1994; Sues and Reisz, 1995), but its type species, *C. hudsoni*, comes from the Cromhall Quarry, a 'Fissure Fill' deposit in west England (Fraser, 1994), which is usually dated as Late Triassic (Walkden and Fraser, 1993; Benton and Spencer, 1995). In addition, according to Wu (1994), the outgroup to *Clevosaurus* seems to be *Brachyrhinodon taylori*, which comes from the Lossiemouth Sandstone Formation in Scotland (Benton and Walker, 1985; Fraser and Benton, 1989). This formation is considered coeval to the *Hyperodapedon* assemblage zone of the Santa Maria Formation (Ochev and Shishkin, 1989; Lucas, 1998) and older than the Triassic 'Fissure Fill' deposits of west England. As discussed by Ferigolo (2000), the presence of *Clevosaurus*-like sphenodontians in Botucaraí and Faxinal do Soturno implies a younger faunal stage in relation to that of the typical Alemoa beds, but the Latest Triassic or Early Jurassic age of those faunas cannot be accessed on the basis of the sphenodontian record.

The deposits of Faxinal do Soturno also yield *Riograndia*, fragmentary remains with morganucodont affinities (Ferigolo, 1999; Ribeiro et al., 2001), as well as closely related taxa (Bonaparte et al., 2003). Early mammals, morganucodonts included, range from Late Triassic to Early Jurassic (Luo et al., 2002) and have been known from strata considered coeval to the *Hyperodapedon* assemblage zone, as is the case of *Adelobasileus* (Lucas and Hunt, 1990, 1994) from the Tecovas Formation in west Texas (Lucas, 1998) and *Gondwanadon* (Datta and Das, 1996) from the Tiki Formation in the Son-Mahanadi Valley, India (Chatterjee and Roy-Chowdhury, 1974; Satsangi, 1987). These records do not allow more precise age assignments than that given by *Riograndia* and the sphenodontids. However, the record of the leptopleuronine procolophonid *Soturnia caliodon* suggests a Triassic age for the deposits of Faxinal do Soturno (Cisneros and Schultz, 2003). Leptopleuronines occur exclusively in Late Triassic deposits (Small, 1997; Sues and Baird, 1998; Spencer, 2000; Sues et al., 2000), whereas procolophonids as a whole are not known in Jurassic faunas (Olsen et al., 1998).

In conclusion, sedimentological and biostratigraphic data indicate that the fossil assemblages of the Caturrita Formation in both Botucaraí and Faxinal do Soturno represent a younger faunal stage than those of the Alemoa Member in both Santa Maria and Botucaraí. The *Jachaleria*-bearing deposits are probably equivalent to the La Chilca fauna in the Ischigualasto sequence. The fauna of Faxinal do Soturno is pre-Jurassic and might prove to be coeval with the *Jachaleria*-bearing beds. The small-tetrapod assemblage of

Botucaraí resembles that of Faxinal do Soturno, but the record of *Irajatherium* hints at a younger age. A recent review of the Caturrita Formation biostratigraphy in Botucaraí and Faxinal do Soturno was presented by Rubert and Schultz (2004), who indicate that the deposits belong into a single stratigraphic interval within the latest Triassic that overlies the typical fossil-bearing rocks of the Alemoa Member. Their study was carried out independently of the work presented here, but they converge in various details.

The Água Negra locality has yielded only the isolated record of a prosauropod dinosaur. Previous taxonomic accounts suggest that it is a typical member of the group (Kellner et al., 1999; Leal and Azevedo, 2003), and more derived than *Saturnalia* from the Alemoa local fauna. In the Bermejo Basin, typical prosauropods occur only in the fauna of La Esquina in the upper portions of the Los Colorados Formation, though they might be present in assemblages considered older than that. Such is the case of *Azendohsaurus* from the Argana Formation in Morocco (Gauffre, 1993a; cf. Jalil and Knoll, 2002), '*Euskelosaurus*' and *Antetonitrus* from the Lower Elliot Formation in South Africa (Gauffre, 1993b; Lucas and Hancox, 2001; Yates and Kitching, 2003), and *Thecodontosaurus* from some 'Fissure Fill' deposits in west England and Wales (Fraser, 1994; Benton and Spencer, 1995; Benton et al., 2000; Yates, 2003). Based solely in the prosauropod record, little can be said about the stratigraphic position of the Água Negra locality beyond what was suggested by the local litostratigraphy. It is younger than the Alemoa local fauna and probably younger than the beds yielding '*Scaphonyx*' *sulcognathus* (Fig. 8).

5. Conclusions

The Late Triassic deposits of the Paraná Basin in Rio Grande do Sul encompass a single tetrapod-bearing sedimentary sequence: the third-order Santa Maria 2 sequence (Zerfass et al., 2003), which includes a lower transgressive systems tract that is better known in the area of Santa Maria, including deposits of the Alemoa Member, Santa Maria Formation (Bortoluzzi, 1974). Its fossil record is typified by the Alemoa local fauna that includes the rhynchosaur *Hyperodapedon*, an aetosaur referred to *Aetosauroides*, and basal dinosaurs. The fauna is considered coeval with that of the lower part of the Ischigualasto Formation, Bermejo Basin, NW Argentina.

The upper highstand systems tract of the Santa Maria 2 sequence (Zerfass et al., 2003) encompasses sediments previously assigned to the upper part of the Alemoa Member, Santa Maria Formation, and to the Caturrita Formation and seems to include at least two different faunal associations. The first occurs in deposits previously assigned to the Alemoa Member in the localities of Linha Facão and Botucaraí Mount (Scherer et al., 1995) and the base of the Caturrita Formation in the area of Santa Maria. Typical fossils include the rhynchosaur '*Scaphonyx*' *sulcognathus* and the cynodont *Exaeretodon*. The fauna is tentatively correlated with that of the upper part of the Ischigualasto Formation in NW Argentina.

Various other localities of the Caturrita Formation in Botucaraí Mount, Faxinal do Soturno, and Santa Maria yield tetrapod remains (Rubert and Schultz, 2004). It is unclear if they belong to the same faunal association, but all appear to correspond to post-Ischigualastian faunas in the Bermejo Basin. The record of the dicynodont *Jachaleria* in Botucaraí suggests correlations with the lower part of the Los Colorados Formation in NW Argentina, whereas remains of derived tritheledontid cynodonts indicate a younger age.

The correlation between the Late Triassic tetrapod-bearing sequences of northwest Argentina and south Brazil is essential to understanding the faunal succession during that time interval in south Pangea. The proposed scheme is believed to represent an adequate framework for the relative dating of these tetrapod occurrences in relation to those of other parts of the supercontinent, notably in India and southern Africa.

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Note added in proof

The prosauropod of Água Negra locally has been recently described [Leal, L.A., Azevedo, S.A.K., Kellner, A.W.A., Da Rosa, A.A.S., 2003. A new early dinosaur (Sauropodomorpha) from the caturrita Formation (Late Triassic), Paraná Basin, Brazil. Zootaxa 690, 1–24] as *Unaysaurus tolentinoi*, and considered closely related to the genus *Plateosaurus*, from the Norian of Central Europe. A recent phylogenetic study of basal sauropodomorphs (Yates & Kitching, 2003) includes *Plateosaurus* within a group also composed of *Riojasaurus and Coloradisaurus* (from the Los Colorados Formation of northwester Argentina), as well as Jurassic forms from South Africa and China. *Unaysaursus* possesses some diagnostic traits of this group, and this suggests a Norian to Early Jurassic age for its bearing strata.

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