

Vertebrate dinoturbation from the Caturrita Formation (Late Triassic, Paraná Basin), Rio Grande do Sul State, Brazil

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Abstract

The Caturrita Formation is a lithostratigraphic unit that comprises the Ladinian–Eonorian sequence of the Paraná Basin. It has been interpreted as deposits of alluvial plains and meandering rivers. Purported fossil tracks found in this formation at Faxinal do Soturno County, Rio Grande do Sul State, Brazil, are concave circular-shaped structures, with a laminar deformation. Some show digitiform projections, and at least three are aligned. They are interpreted as a disruption of the substrate homogeneity caused by bioturbation of tetrapods. In some of these there is a distinct color pattern — more reddish than the surrounding substrate. This is interpreted as a result of differential diagenesis. The features remain enigmatic tracks but were probably made by prosauropod dinosaurs, the dominant terrestrial herbivore group from the end of the Triassic in Gondwana strata.

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1. Introduction

At the end of the Permian and the beginning of the Triassic, the Paraná Basin was an area undergoing a gradual terrestrialization process, due to the formation of the Pangean supercontinent. As a result, several terrestrial environments were established. The non-marine deposits, formed at that time, are represented by the Sanga do Cabral, Santa Maria and Caturrita formations in Rio Grande do Sul State, Brazil, and are characterized by a rich tetrapod fauna, that have long been used to correlate Triassic strata of Gondwana. In the rocks of the Caturrita Formation, circular and concave structures of various sizes have been found, ranging from a few to 50 cm. These enigmatic structures could represent tetrapod footprints, as suggested by Cargnin et al. (2001). They are analyzed below

and some are interpreted as tracks of large dinosaurs. The possibility of other interpretations, such as vegetation impressions and fish nests, are also considered but discounted.

2. Geological context

The Caturrita Formation is a lithostratigraphic unit of the Triassic Period in the Paraná Basin outcropping in Rio Grande do Sul State. It is composed of conglomeratic to fine sandstones, with channel, planar cross-stratifications and plane-parallel lamination. Pelites, siltites and sandy siltites are massive or show plane-parallel lamination (Andreis et al., 1980). The formation is interpreted as deposits of meandering rivers on an alluvial plain, showing several levels of paleosols, laterally associated with multi-episodic sandy facies, originating from fluvial channels. The paleoclimatic conditions during deposition were probably hot and humid (Andreis and Montardo, 1980). The formation is included in the Supersequence Gondwana II, which is considered Middle and Late Triassic (Milani, 2002). The Santa Maria Formation and the lower portion of the Caturrita Formation are a

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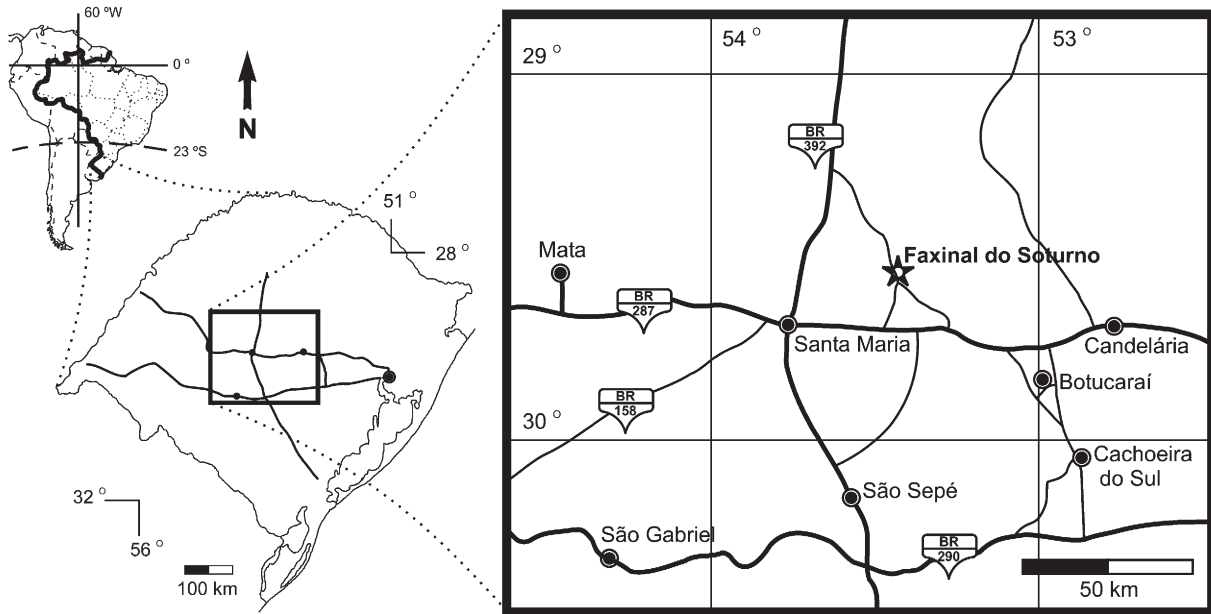


Fig. 1. Map indicating the locality of the outcrops of Novo Treviso, Faxinal do Soturno, Rio Grande do Sul State, Paraná Basin, Brazil.

sandstone-pelitic succession, named the Ladinian–Eonorian Sequence, according to Scherer et al. (2002).

3. Material and methods

The material analyzed occurs at an outcrop of the Caturrita Formation at the Novo Treviso locality, in Faxinal do Soturno County, Rio Grande do Sul State (Fig. 1). The structures are distributed over a surface of a massive fine quartz sandstone, exposed over an area of approximately 192 m², near the city church (Fig. 2). The structures were observed in situ in December 1998, and no samples were collected.

Surface mapping of the outcrop site was undertaken to record the distribution and orientation of the structures (Fig. 3). To

assist in the construction of the map, the site was divided into quadrangles of 1 m², marked with chalk directly on the rock. Afterwards, these quadrangles were photographed and used as the basis for the map. The photographs were taken with natural light at different angles of incidence. Further analyses were based on the map and photographs of the site. The sediment fillings of some of the structures were mechanically removed with the aid of cutters and blades.

4. Results

During the field study, the outcrop surface revealed many rounded structures of various sizes. In vertical section, most of the structures consist of semi-cylindrical tubes, with a flattened base



Fig. 2. Photograph of the surface preserving the ichnofossils, with several concave structures.

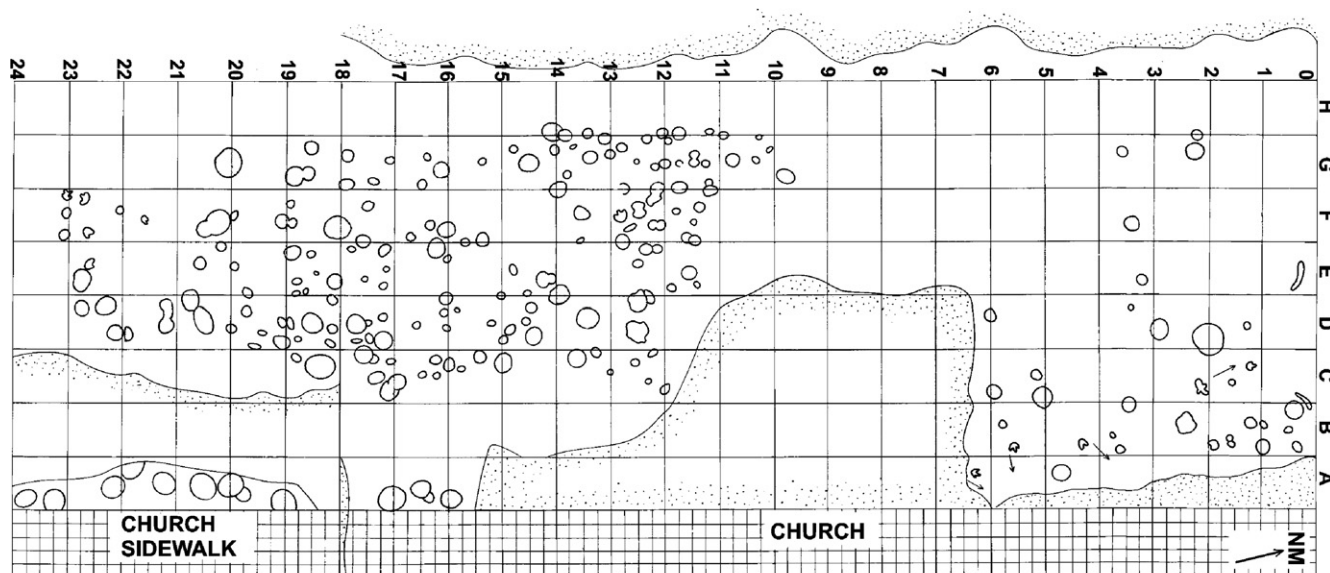


Fig. 3. Distribution map of the fossil footprints of Novo Treviso, Caturrita Formation.

(as in a dish) or gradually tapering to the base. These structures are filled by a grayish sand–clay sediment. Sometimes, the filling has a larger concentration of iron oxides, contrasting with the whitish sandstone. Usually, the smaller structures are shallower (about 1 cm deep) than the larger ones (about 5 cm deep). In relation to their morphology, the structures can be characterized as:

Finger-projection structures (Fig. 4a–d): They consist of concave impressions, with a rounded outline, with finger-like projections. These structures are characterized by the deformation of the subjacent layers, as observed during the field study. The number of projections varies from one to three and they may have acute or rounded extremities. At least three of these structures occur in sequence, with the projections pointing in the same direction. The size range is between 16 and 30 cm wide and between 12 and 27 cm long.

Circular deformation structures (Fig. 4e–f): These have a circular surface and resemble a dish when observed in transverse section. They are characterized by the deformation of the underlying sediment layers and have a diameter between 20 and 50 cm. Former attempts to remove the filling of these structures resulted in deep shafts.

Compound structures (Fig. 4g): They are characterized by the combination of a circular structure and a half-moon one, with the concavity oriented downwards. There is evidence of substrate deformation. The circular print has a diameter of 35 cm and the half-moon reaches 35 cm in maximum length.

5. Discussion

Footprints may have a low preservation potential, since surface impressions in soft sediments are readily eroded and destroyed as the succeeding bed is deposited. Under special circumstances they may be preserved from erosion, e.g. when periods of subaerial exposure are short (Tucker and Burchette, 1977). Another factor that influences preservation is that the

deformation of the print-bearing surface, e.g. by a heavy animal, favours the preservation of underprints and transmitted prints.

The reworking of sedimentary substrates by terrestrial vertebrates was considered as important in disturbing the primary grain fabric and sedimentary structures by Laporte and Behrensmeyer (1980). Abundance of vertebrate bioturbation depends upon rates of trampling, burial and varies from single, isolated tracks to thoroughly bioturbated sedimentary layers. The preservational aspect of the tracks depends on the texture and plasticity of the substrate and the opportunity for subsequent permanent burial. From observations of recent environments, Laporte and Behrensmeyer (1980) found that there is a narrow range of sediment textures and moisture content, which will allow preservation of the tracks in the geological record. Tracks and trackways are best preserved in a relatively narrow zone marginal to lake and fluvial environments where moist, vegetation-free, sands and silts are buried and protected after trampling.

Although some of the prints from the Caturrita Formation show similarity to tree trunk casts, preserved in upright position, such as the trunk casts from the late Paleozoic of Peru (Alleman and Pfefferkorn, 1991) and Argentina (Azcuy et al., 1987), there are striking differences. The tree trunk casts from Peru and Argentina are clearly delimited from the surrounding rock and wrapped by a carbonized film, whereas the structures under study have an indistinct outline. Besides, there is no evidence of roots or branches associated with these structures, nor any internal anatomic details.

Other similar structures are the fossil fish nests described by Feibel (1987) and biogenic sedimentary structures formed by rays (Howard et al., 1997; Martinell et al., 2001). Excavations made by the feeding activity of elasmobranchs are broad, shallow, surface depressions that are roughly circular holes up to 30 cm deep (Howard et al., 1997). Although the superficial shape of these excavations is similar to the vertebrate tracks from the Caturrita Formation, they differ in their lower portions. The ray excavations have a lower steep-walled bioturbated portion with an inclined angle to the upper dish-shaped laminated part. Besides, the

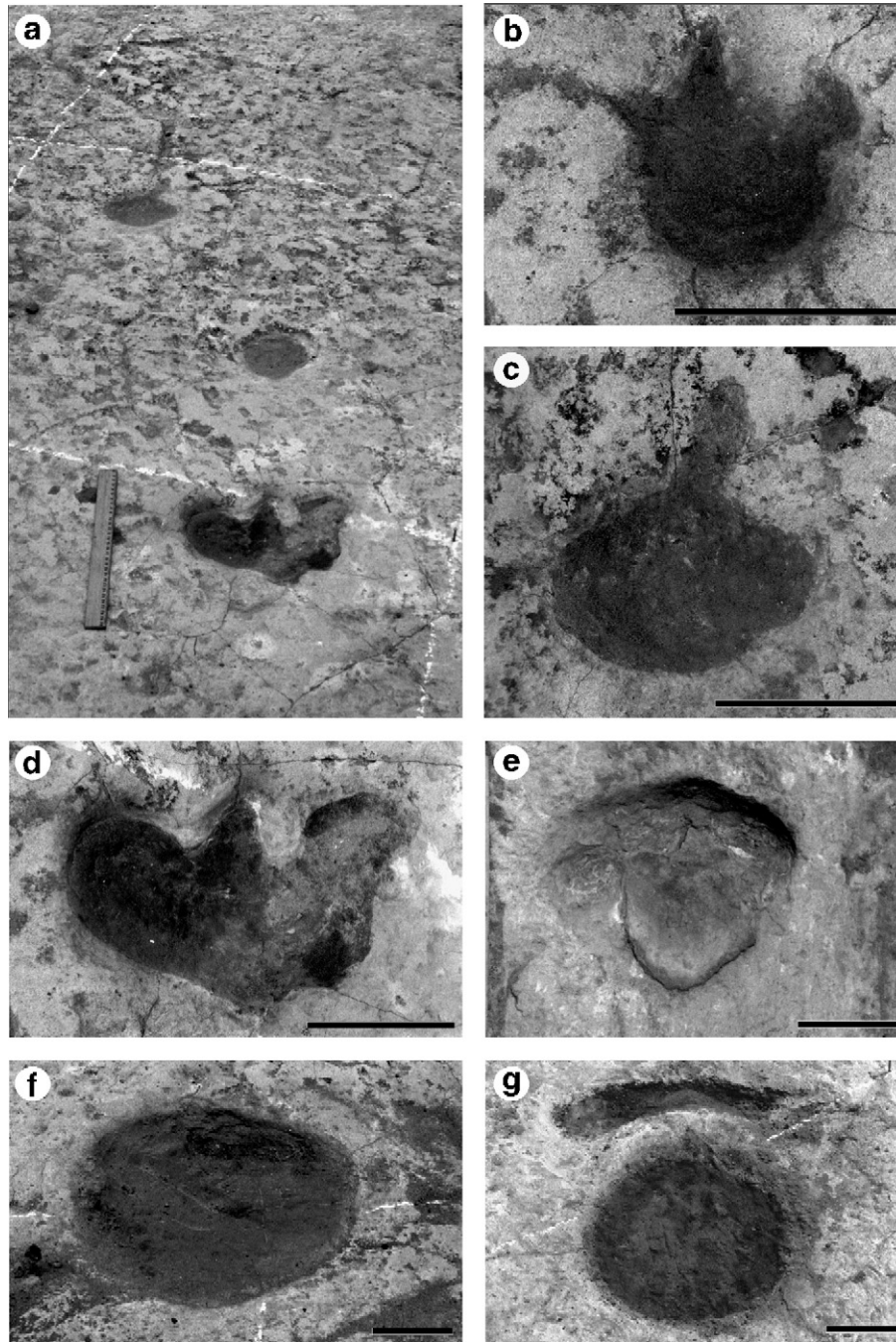


Fig. 4. Morphological categories of deformation structures: (a) sequence of three finger-like structures; (b–d) finger-like structures; (e–f) circular deformation structures; (g) composite structure. Scales: (a) = 30 cm; (b–g) = 10 cm.

excavation of sediment by stingrays does not produce plastic deformation features in the substrate, as made by vertebrate footprints in a saturated medium (Martinell et al., 2001).

As noted during the field study of the structures, they are characterized in vertical sections by the deformation of the lower layers. The depth of the deformation (up to 40 cm) is a common feature in footprints of large tetrapods, produced by the foot pressure, that ruptures the substrate homogeneity and sometimes creates a raised rim around the track. Tracks that are weathered and eroded before burial would lose all or part of the raised periphery, according to Laporte and Behrensmeyer (1980). Therefore, the

tracks do not correspond necessarily to the original interface between the animal autopodia and the substrate. Some of them, as there are no morphological details, could be undertracks produced at different times. In any case, the depth of the depression depends both on the animal's weight and the plasticity of the sediment, as observed by Laporte and Behrensmeyer (1980), and with the transmitted effect the deformation can reach 50 centimeters (Romano and Whyte, 2003). The color patterns result from different rates of fluid percolation producing a halo of yellow-reddish oxidation around the deformed region of the footprints. Similar features were observed by Kuban (1989) in his analysis of

the Glen Rose Formation footprints (Early Cretaceous, USA) and by Carvalho (1994) in the dinosaur footprints of the Alcântara Formation (Late Cretaceous, São Luís Basin, Brazil). As pointed out by these authors, the color contrast between the footprints and the substrate is the result of secondary filling of original footprints and by the oxidation of the iron in the filling material.

The pressure produced by the tetrapod autopodia on the substrate has been analyzed by several authors (Avanzini, 1998; Boyd and Loope, 1984) in relation to the mechanics of movement, the development of deformational structures, and the total substrate bioturbation. The grain size, consistency, plasticity and water content of the sediments are determinants of the preservation of anatomical details. Generally, only the outline of the footprint is preserved, without indication of the fingers, fingerpads or footpads. In these cases, the footprints represent bioturbation structures, produced by the stirring of the substrate at the contact zone with the autopodium (Lockley and Meyer, 2000; Lockley, 1991).

The finger-projection structures (Fig. 4b–d) could correspond to plantigrade undertracks created by large-size animals and still showing vestiges of digit impressions. Another possibility is that the depth of the depression, inducing the preservation of the digits, depends on the animal's weight and the plasticity of the sediment. The three sequential footprints (Fig. 4a) may represent a trackway made by a bipedal or semi-bipedal animal. The other footprints do not form sequences that may be confidently characterized as trackways, due the intense bioturbation of the sediment. The size of the circular deformation structures is similar to those of the finger-projections, possibly representing distinct preservational patterns attributed to the activity of the same animal.

Although footprints have not yet been found in the continental sediments of Camian–Eonorian of the Paraná Basin, some Middle and Late Triassic footprints have been described from Pangea, including diversified tracks registered from south-western Gondwana, especially in the Argentinean localities. The tetrapod track assemblage from the Cuyana Basin (Upper Triassic–Carnian), Portezuelo Formation, has a faunal assemblage of non-mammalian therapsids (small cynodonts and large dicynodonts) and a quite diverse archosaur fauna, which includes crurotarsal archosaurs and dinosaurs (sauropodomorphs and theropods). It is the most important one described for the lower Mesozoic of South America, although other Triassic track records have been recorded from west-central Argentina and northern Patagonia (Marsicano and Barredo, 2004; Melchor and De Valais, 2006).

The dicynodont trackways found in the Moenkopi Formation (Middle Triassic, USA) named as *Therapsipus cumminsi* Hunt, Santucci, Lockley and Olson, 1993, present a pentadactyl pes and a pentadactyl manus of large size with concave posterior margins and blunt digits (Hunt et al., 1993a,b), that are quite distinct from the Caturrita Formation footprints.

The ichnogenera *Tetrasauropus*, *Brachychirotherium*, *Grallator* and *Barrancapus* were described by Hunt et al. (1993a,b) from the Tucumcari Basin (east-central New Mexico, USA). These authors suggested *Brachychirotherium* footprints were made by aetosaurs. Also from this basin, Lockley et al. (1992) recognized *Pseudotetrasauropus*, as the probable tracks of a prosauropod. This last ichnogenus is also common in other Late

Triassic units such as the Sheep Pen Sandstone (Late Triassic, USA), where the tracks show the partial impressions of the four digits recognized in this ichnogenus (Lockley et al., 1993). However, this ichnogenus is very similar to *Evazoum siriguii* recently described by Nicosia and Loi (2003) and probably made by sub-cursorial prosauropods. Marsicano and Barredo (2004) described a set of tracks from the Portezuelo Formation (Carnian, Argentina), named as type FB, in which pes impressions are anteroposteriorly elongated and their anterior border is slightly convex; the pedes are broader anteriorly with a rounded apex posteriorly. The manus impressions are generally slightly less impressed than those of the pes; they are transversally oval and imprinted in front of, or external to the pes impressions. The trackways show a relatively high pace angulation and narrow pace width, evidences that the track-maker is related to Dinosauria, that was interpreted as a facultatively bipedal prosauropod dinosaur. Such footprints are similar to the Compound Structures (Fig. 4g) described above from the Caturrita Formation, with a combination of circular and a half-moon structures, with the concavity downwards.

Other localities from the Late Triassic in Gondwana from which prosauropod dinosaurs were reported in the Karroo Basin, South Africa. The Elliot Formation presents prosauropod tracks ascribed to *Tetrasauropus* and *Pseudotetrasauropus* (Ellenberger, 1970, 1972, 1974; Ellenberger et al., 1970).

Despite the absence of footprints in the Middle and Late Triassic beds of the Paraná Basin, a rich and diversified tetrapod fauna has been reported, showing the rapid diversification of the archosaurs and non-mammalian cynodonts during the middle and upper half of the Triassic in Pangea, especially in the Gondwana localities. These occurrences are found in the higher levels of the Rhynchosauria Cenozoone of the Alemoa Member of the Santa Maria and Caturrita Formation and in the beds of the *Jachaleria* level of the Caturrita Formation. Although these occurrences have been represented as distinct biozones (Barberena et al., 1985; Schultz et al., 2000), they are considered as biochronological equivalents by some authors (Lucas, 2001). They are attributed to the same depositional sequence — Santa Maria 2 Sequence of the Santa Maria Supersequence (Zerfass et al., 2003). The fauna is represented mainly by rhynchosaur, dinosaurs, rauisuchians, aetosaurian archosaurs and non-mammalian cynodonts of the typical Rhynchosauria Cenozoone (Schultz et al., 2000). In different outcrops of the Caturrita Formation dicynodonts, traversodontid, tritheledontid and brasilodontid cynodonts, rhynchosaur, basal archosauromorphs, a phytosaur, saurischians, prosauropods, procolophonids, and sphenodontids are found.

The analysis and interpretation of the described footprints indicate that they were made by animals with a large body size. Therefore, they were probably not made by procolophonids, sphenodontids, cynodonts, rhynchosaur, aetosaurs or archosaurs such as *Proterochampsia nodosa* Barberena, 1982, since these were all animals of small to medium size.

Considering possible body size, the dicynodont *Jachaleria candelariensis* Araújo and Gonzaga, 1980 could reach lengths up to 3 m, a size large enough to produce the footprints. However, trackways of the ichnospecies *T. cumminsi* Hunt, Santucci,



Fig. 5. Reconstruction of a prosauropod dinosaur, probable producers of the dinoturbation of Novo Treviso, by Ariel Milani Martine.

Lockley and Olson, 1993, attributed to dicynodonts, display a smaller breadth and stride (Hunt et al., 1993a,b), incompatible with the footprints under analysis (Fig. 4a). Besides, dicynodonts have footprints with a straighter posterior margin and a width much greater than the length.

The aetosaurs found in the Rhynchosauria Cenozoone indicate similarities with *Stagonolepis* Agassiz, 1844 (Heckert and Lucas, 2002), armored tetrapods with body size ranging between 2.5 to 4.5 meters long (Casamiquela, 1961), although the fossils from Brazil redescribed by Lucas and Heckert (2001) are much smaller than this, being around 1 m long. They are quadrupedal animals, and the footprints called *Brachychirotherium*, assigned to aetosaurs by Hunt et al. (1993a,b) and Haubold (1986), are quite different from the structures analyzed here.

The body size attributed to the dinosaurs *Staurikosaurus pricei* Colbert, 1970 and *Saturnalia tupiniquim* Langer, Abdala, Richter and Benton, 1999 (from the Rhynchosauria Cenozoone) and *Guaibasaurus candelarai* Bonaparte, Ferigolo and Ribeiro, 1999 (*Jachaleria* Level) also indicates that they were animals not sufficiently large to have produced the Caturrita Formation footprints. *Staurikosaurus*, a small theropod dinosaur, and *Saturnalia*, a primitive sauropodomorph, have a relative small size (length of approximately 150 cm, accordingly to Langer et al., 1999; Kellner, 2000), whereas *Guaibasaurus* has a posterior foot with a length around 20 cm (Bonaparte et al., 1999), incompatible with the footprint size under consideration. An analysis of the legs of primitive sauropods, in particular *Guaibasaurus*, indicates that digit I is very reduced. Thus, despite the tetradactyl autopodium morphology, it would display a

functional behavior similar to a tridactyl animal. Besides, digit III is much more prominent than digits II and IV. These features were not observed in the analyzed footprints.

The prosauropod *Unaysaurus tolentinoi* Leal, Azevedo, Kellner and Da Rosa, 2004 was a large animal (Leal, 2001; Leal et al., 2004), judged by the dimensions of the skull (near 30 cm). Although some prosauropod footprints show a tridactyl pattern, generally they are entaxonic. In movement the Prosauropoda create a large track, with the footprints revealing an oval outline, forming angles between 16° and 22° in relation to the middle line of the track (Thulborn, 1990). Proportionally, the width of the footprints amounts to 75% to 85% of their total length. The impressions of the hands have an oval or elliptic outline, are laterally elongated and comparatively smaller than the impressions of the posterior autopodia (Thulborn, 1990). These characteristics are compatible with some footprints from the Caturrita Formation that could therefore be attributed to Prosauropoda (Fig. 5).

According to Sereno (1999) and Carrano and Wilson (2001) the initial radiation of sauropodomorph dinosaurs might have occurred during the Middle Triassic. The widespread record of prosauropod footprints, as that present in the Argentinean Cuyana Basin (Carnian), the Brazilian Paraná Basin (Ladinian–Eonorian) and the Karroo Basin (Carnian–Norian) reinforces the assumption (Marsicano and Barredo, 2004) of an earlier distribution of these dinosaurians in Western Gondwana than previously recorded by body fossils.

6. Conclusions

The enigmatic ichnofossils of Novo Treviso, Rio Grande do Sul State, Brazil are interpreted as prints made by large-sized animals. These footprints present a reddish color caused by the differential diagenesis between the track and the surrounding matrix. Despite the limitations in ichnotaxonomic studies, due to the difficulty of defining the characters of the footprints, based on the morphology of one track and several isolated footprints, some of them may be attributed to Prosauropoda. This is potentially important data about the presence of this group in the Late Triassic of Brazil, enlarging the geographic distribution of Prosauropoda footprints in South America and in this way showing a wide distribution of this herbivore dinosaurian fauna in Western Gondwana.

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