



Dinosaur tracks from the Sítio Pereiros ichnosite, Triunfo Basin (Lower Cretaceous) and the dinosaur diversity in the Rio do Peixe basins, Northeastern Brazil

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ABSTRACT

The dinosaur tracks in the Rio do Peixe basins (Lower Cretaceous, Rio da Serra-Aratu stages) occur in at least 39 individual tracksites through approximately 98 stratigraphic levels in the western part of the State of Paraíba, Brazil. The Triunfo basin (one of the four Rio do Peixe basins) is a 480 km² asymmetric graben, located in the counties of São João do Rio do Peixe, Uiraúna, Poço, Brejo das Freiras, Triunfo, and Santa Helena, controlled by a NE transcurrent fault system. To date, only four isolated footprints and two incomplete trackways have been identified in the Antenor Navarro Formation. Among the isolated footprints, three probably belong to theropods. One incomplete trackway consists of just two digitigrade, rounded digits, suggesting they were made by a small ornithomimid. In this study we describe a new ichnosite, located at Sítio Pereiros, São João do Rio do Peixe county, Paraíba State. The one and a half meter thick succession of fine-grained sandstones, siltstones, mudstones and shales with ripple marks, climbing ripples and mud cracks of the Sousa Formation reveals a bedding plane with three trackways, with a total of 19 tridactyl, mesaxonid footprints. These trackways are interpreted as produced by theropods, two large and one smaller. In these beds there are also ostracods, spinicaudatans (conchostracans), and fragments of microvertebrates (fish scales, teeth and bones). The Sítio Pereiros ichnosite represents a deposition in a floodplain area, with temporary aerial exposure of the superficial sediments in which tracks were impressed. The ichnofauna from this locality increases knowledge of the theropod fauna from the Triunfo basin and the distribution of the dinosaur tracks throughout the interior basins of Northeastern Brazil.

Description of these new theropod tracks permits evaluation of the behavior of these three theropods, including inferences about trackmaker speed and the type of gait of the three animals, and also of their possible size. This is the 40th ichnosite in the Rio do Peixe basins, extending analysis of the types of trackmaker associations present at such ichnosites, as well as the dinosaur diversity represented at each of them. New interpretations are presented about the environments, and the relationship between the various groups represented in this region during the Early Cretaceous.

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1. Introduction

The Triunfo basin (also called the Uiraúna-Brejo das Freiras basin) is one of the four sedimentary sub-basins of the Rio do Peixe basins. The others are Sousa, Pombal, and Vertentes (Fig. 1), located in the western part of the Brazilian State of Paraíba. The Triunfo basin occurs in the counties of São João do Rio do Peixe, Uiraúna, Poço, Brejo das Freiras, Triunfo and Santa Helena, with 480 km² area. The Precambrian basement is composed of igneous (granites, gabbros, and diorites) and metamorphic (migmatites, gneisses, quartzites, and marbles) rocks. It is an intracratonic asymmetric graben, controlled by a NE transcurrent fault system, developed

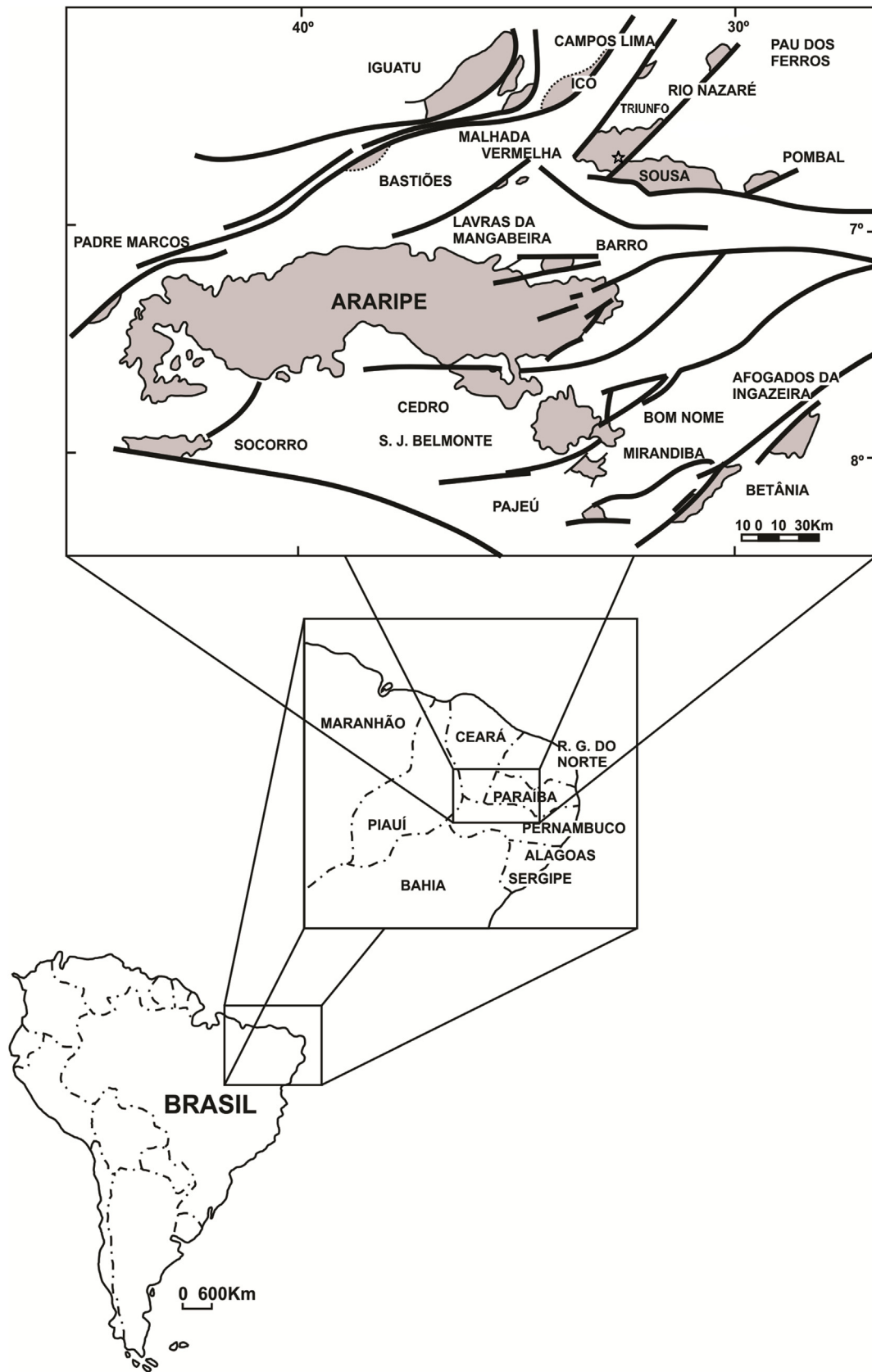


Fig. 1. Location map of the Triunfo basin in the context of the interior Northeastern Cretaceous basins of Brazil and location (marked with a star) of Sitio Pereiros ichnosite (Carvalho, 2004).

along preexisting structural trends of the basement during the opening of the South Atlantic Ocean (Carvalho et al., 2013a,b). The Mesozoic age of the sedimentary deposits in the Rio do Peixe basins, based on ostracods (Sousa et al., 2018, 2019) and palynological material, is characteristic of the Rio da Serra (Berriasian to Hauterivian) and Aratu (early Barremian) local stages (Lima and Coelho, 1987; Regali, 1990).

An important aspect of the Rio do Peixe basins is the abundant tetrapod ichnofauna consisting of footprints and trackways, mainly of theropods, sauropods, and ornithopods. There are also invertebrate ichnofossils, such as traces and burrows produced by arthropods and annelids (Fernandes and Carvalho, 2001). The abundance, distribution in the same stratigraphic levels and similar age allows us to interpret the numerous ichnosites from these basins as a megatracksite (Viana et al., 1993, sensu Lockley, 1991; Carvalho et al., 1993a,b, 1995a,b; Siqueira et al., 2011; Lockley and Meyer, 2022). Leonardi and Carvalho (2021) had recorded 37 ichnosites; two new ones were discovered by Leonardi (2021); another one is registered here, for a total of 40 ichnosites. Although the Triunfo basin presents few occurrences of tracksites in the context of the Rio do Peixe megatracksite (Leonardi and Carvalho, 2021; Lockley and Meyer, 2022) it is a good instance in which fossil footprints provide the main information about the dinosaur fauna of the region.

The analysis of a new tracksite, located at Sítio Pereiros, increases knowledge concerning the stratigraphic, spatial distribution and environments in which dinosaur tracks occur in the Triunfo basin, showing the diversity of preservation modes of a theropod track assemblage.

2. Geological context

The Triunfo basin is a depositional area located in the Borborema Tectonic Province, Northeastern Brazil. The succession is composed of Devonian marine deposits of the Santa Helena Group (Roesner et al., 2011; Silva et al., 2014), overlain by Cretaceous fluvio-lacustrine and Recent alluvial deposits (Sousa et al., 2019). A formal lithostratigraphic subdivision of the Cretaceous established the Rio do Peixe Group, and subdivided it into the Antenor Navarro, Sousa, and Rio Piranhas formations (Mabesoone, 1972; Mabesoone and Campanha, 1973/1974). The Cretaceous origin of this basin was a result of reactivation of basement transcurrent faults. The tilted blocks created a pronounced rupture in terrain topography, and in the southern part of the basin the decrease in gradient favored the establishment of meandering fluvial and lacustrine environments.

Roesner et al. (2011) identified Early Devonian rocks through palynological analysis from boreholes, showing a pre-Mesozoic history related to a Paleozoic deposition in a very distinct context of the Cretaceous sedimentation. Arai (2006) showed that the Mesozoic deposition (Rio do Peixe Group) resulted from crustal extension, at the inflection of NE–SW and E–W faults during Rio da Serra time (Berriasian–Hauterivian).

The Antenor Navarro and Rio Piranhas formations are composed of clastic rocks: breccias, conglomerates, sandstones, siltstones, shales, and mudstones, near the faulted margins of the basin. The main sedimentary structures are cross-channel and planar stratification. The deposits of the Sousa Formation comprise shales and mudstones interbedded with fine sandstones and siltstones.

The main sedimentary structures are ripple marks, climbing ripples, mud cracks, convolute lamination, raindrops and features indicating liquefaction (Carvalho, 2000a,b; Carvalho and Leonardi, 1992; Fernandes and Carvalho, 2001; Nogueira et al., 2015; Leonardi and Carvalho, 2021).

These deposits reflect synrift sedimentation controlled by tectonic activity along preexisting structural trends of the basement

during the opening of the South Atlantic Ocean (Ponte, 1992; Mabesoone, 1994; Valença et al., 2003; Araújo et al., 2018; Rapozo et al., 2021; Oliveira et al., 2022). Deposition occurred along the faulted borders of the basins as alluvial fans (Mabesoone et al., 1979), changing to an anastomosing fluvial system more distally and also a meandering fluvial system with a wide floodplain with perennial and temporary lakes (Lima Filho et al., 1999; Carvalho, 2000a; Córdoba et al., 2008).

There are a few body fossil occurrences, including Ostracoda, Spinicaudata, Crocodyliformes and Dinosauria in the central-south region of the basin, and both invertebrate and vertebrate ichnofossils close to the northern margin (Carvalho, 1989; Leonardi, 1994; Carvalho, 1996, 2004, 2014; Carvalho and Nobre, 2001; Carvalho et al., 2002; Carvalho et al., 2017). The skeletal elements assigned to a dinosaur (Sauropoda), named *Triunfosaurus leonardii*, were found in the context of gravel bars of channelled flows (Rio Piranhas Formation). This is one of the oldest Cretaceous Titanosauriformes of South America, so common in the Late Cretaceous of Brazil and Argentina, which opens new perspectives on paleogeographical and temporal distribution of titanosaurian sauropods (Carvalho et al., 2014; Carvalho et al., 2017).

In the Cretaceous sediments of the Triunfo basin there are no microfossils to dating. By analogy with the sediments dated by microfossils and palynology in the Sousa basin (Lima and Coelho, 1987; Regali, 1990; Sousa et al., 2018, 2019), and considering the similarities among the vertebrate ichnofaunas, the main depositional phase in the Triunfo basin probably dates from between the Rio da Serra and Aratu stages (Berriasian–lower Barremian).

3. Methodology

The ichnological terminology and methods used in this study mainly follow Leonardi (1979a, 1987, 1994, 1997). The tracks are distributed on the surface of a stratum with a partial surface exposure. Then, to allow better observation of the distribution of the tracks they were partially excavated using chisels and hammers, removing the overlying strata that covered the surface with the footprints. After the excavation of the rock surface with footprints at Sítio Pereiros three trackways attributed to two large and one smaller theropod were observed, with a total of nineteen footprints.

This surface was gridded using nylon threads stretched at right angles forming squares with sides 1 m long, allowing the graphic representation of the parameters of footprints and trackways. The drawing of each 1 × 1 m square was then reproduced on a suitable smaller scale on graph paper, following the trackway meter by meter. The individual photographs of the footprints were made with a digital camera, and when contrast with the surrounding matrix was not clear they were delimited using chalk. The main procedures established by Falkingham et al. (2018) for documenting fossil ichnological data and for distinguishing tetrapod tracks from other structures (Lallensack et al., 2022) were also followed, despite the use of 3D imagery.

3.1. Sítio Pereiros tracks

The dinosaur track occurrences in the Rio do Peixe Group (Rio do Peixe basins), that crop out over an area of about 1730 km², are regarded as a megatracksite (megatracksite Type 3 sensu Lockley and Meyer, 2022) composed of the 39 tracksites (40 with this new one described here). Altogether, the 21 sites of the Sousa Formation in the Sousa Basin represent at least 98 stratigraphic levels dominated by isolated footprints and trackways of carnivorous dinosaurs (Leonardi and Carvalho, 2021; Leonardi, 2021). In total then, in the three formations that correspond to the Rio do

Peixe Group, there are 100 levels with ichnofaunas (including the description in this study). The locality of Sítio Pereiros ichnosite is a new one, located at Sítio Pereiros (6° 47' 20"S/38° 29'13"W), São João do Rio do Peixe county, Paraíba State, in the Triunfo basin. It is an instance of the importance of the footprints to provide information about the dinosaur fauna of a region.

The site a 1.5-m-thick succession of fine-grained sandstones, carbonate sandstones, mudstones and shales with ripple marks, climbing ripples and mud cracks of the Sousa Formation. In these strata, besides the dinosaur footprints, there are also ostracods, spinicaudatans (conchostracans), and microvertebrate fragments (fish scales, teeth and bones). The age of this deposit probably dates from Rio da Serra-Aratu stages (Berriasian–lower Barremian, Lower Cretaceous) by analogy with the sediments dated by ostracods and palynology in the Sousa Basin, and the similarities among the ichnofaunas.

The exposed superficial bedding plane (Fig. 2), of about 60 square meters, shows three trackways, with a total of 19 tridactyl, mesaxonic (i. e. roughly symmetrical about the axis of the 3rd digit) footprints preserved in a mudstone partially covered by a fine sandstone surface with ripple marks (Fig. 3A). Two trackways are subparallel (heading ~ SW) and one crosses in a ~E to W direction (Fig 3B). The two SW trackways (SJSP 1 and SJSP 3) present tridactyl footprints, with pointed digits. The other trackway (SJSP 2) shows 5 smaller tridactyl footprints with pointed digits. They are interpreted as produced by two large and one smaller theropods.

The trackway SJSP 1 (Fig. 4, Appendix A and B) has eight consecutive footprints regularly spaced. The footprints are tridactyl, mesaxonic and show pointed digits. In six of them it is possible to observe distinct impressions of claws. The trackway shows that its maker proceeded on a bearing of approximate SW (213°), had an average inner width of 0.10 m and a total length of at least 7.8 m. The length of steps (oblique pace) varies from 1.00 m to 1.40 m, with an average value of 1.14 m. The stride varies from 2.10 m to 2.70 m, with an average value of 2.37 m. The step angle varies from 150° to 164°, with an average value of 158°40' (Appendix B).

Trackway SJSP 2 (Fig. 5, Appendix A and B) shows five consecutive footprints (Fig. 5A). They are tridactyl, mesaxonic and show acuminate digits, with digit III the longest one. This trackway presents, as a whole, almost a W–E bearing (towards an azimuth of 86°). This trackway has an average inner width of 0.10 m and a total length of at least 5.50 m.

The trackway SJSP 3 (Fig. 6, Appendix A and B) has six consecutive regularly spaced footprints. They are tridactyl, mesaxonic and show pointed digits. The trackway presents an almost SW (206°) bearing, an average inner width of 0.18 m and a total length of at least 4.00 m. The length of steps (oblique paces) varies from 1.00 m to 1.20 m, with an average value of 1.13 m. The stride varies from 2.15 m to 2.65 m, with an average value of 2.36 m. The step angle varies from 162° to 178°, with an average value of 171°15' (Appendix B).

3.2. The behavior of the trackmakers

As already noted, the footprint/sediment relationship indicates that the three dinosaurs recorded in the locality Sítio Pereiros based on three fossil trackways of the Early Cretaceous did not act as an organized group, and that they were not inferred to have been registered at the same time. The same result is also shown by the behavior of these animals.

3.3. Posture

Theropods, large and small, were obviously nearly all bipedal (Molnar and Farlow, 1990, as for the large theropods), and produced very narrow trackways. Theropods, and especially the three from Sítio Pereiros ichnosite, kept the hind legs erect, with the left and

right feet placed directly beneath the body. In the pendulum on parasagittal planes that they performed walking or running, if they made a slight turn laterally with the legs, they did so, in the specific case, almost just to avoid crossing them.

In a few instances, in the basins of the Rio do Peixe, as in other basins, the mark of the tail is preserved, but not here. The rareness of tail impressions is usual for dinosaur trackways. Bipedals as well as quadrupeds, all of them almost always kept their tails clear of the ground. This theme is well played by Kim and Lockley (2013), who describe and comment on 38 records of dinosaur tails in the world. Then one can add the four cases of probable tail tracks of dinosaurs from the Rio do Peixe basins (Leonardi and Carvalho, 2021, pp. 376).

3.4. Bearings

The two trackways SJSP 1 and SJSP 3 are almost parallel, and only slightly divergent (by 7°), and are roughly directed towards an approximate bearing of SW, their makers advancing more or less parallel to the ripple mark crests. In contrast, SJSP 2 crosses these previous trackways, as well as the ripple mark crests, and its maker proceeded in an approximate E–W direction. Consequently, we can say that both rather large theropods that produced the trackways SJSP 1 and SJSP 3 were probably paralleling the water line or water's edge of a most likely alkaline lake. The trackmaker of the SJSP 2 trackway (a smaller theropod), instead, was probably exiting or entering the water.

It can also be observed that both theropods that produced the almost parallel trackways SJSP 1 and SJSP 3, walked more or less parallel to the direction of the transcurrent fault NE separating inter alia the Triunfo basin from the Sousa basin. As we have observed elsewhere (Leonardi, 1979b, 1991; Leonardi and Carvalho, 2021) the dinosaurs were often influenced in their direction of progression by features of the landscape, and particularly by the margins of the bodies of water; and in turn the landscape and bodies of water were controlled by the regional fault lines, transcurrent or not. It should also be noted that the margins of the bodies of water conditioned, anyway, apart from their direction, the impression and preservation of footprints of the local fauna. Without any doubt, in a semi-arid region such as the Triunfo basin, it was only on the edge of the bodies of water – as today – that the ground was sufficiently wet and plastic to be deformed, and then receive and maintain the footprints of the feet of the “passers-by”. In addition, again, it was only in environments of this type that the soil could gradually leave the tracks to consolidate and dry, so that they could possibly survive the next rainstorm or elevation of the level of the lakes. The presence of bacteria and microscopic algae also helped the preservation of the footprints, not only in general, but also specifically in these sediments – the microbialites – of the Rio do Peixe basins (Carvalho et al., 2013a,b).

3.5. Manners of gait

In SJSP 1 trackway, the index SL/FL (stride length/footprint length) is 9.12, which indicates that the animal was walking in a certain speed, but did not run. As for the 2nd trackway, SJSP 2, the fact that the animal was running is also indicated by the very high SL/FL index (stride length/footprint length) = 16.87. We will later see at what speed this index can correspond. The trackmaker of the SJSP 3 trackway walked with a hasty gait, but did not run, as can be seen from the fact that the index SL/FL (stride length/footprint length) is 9.64. In this, its gait was very similar to that of the SJSP 1 trackway.

Trackways SJSP 1 and 3 are straight; SJSP 2 is instead slightly curved to the right (see Fig. 5A). Such fossil curved trackways are

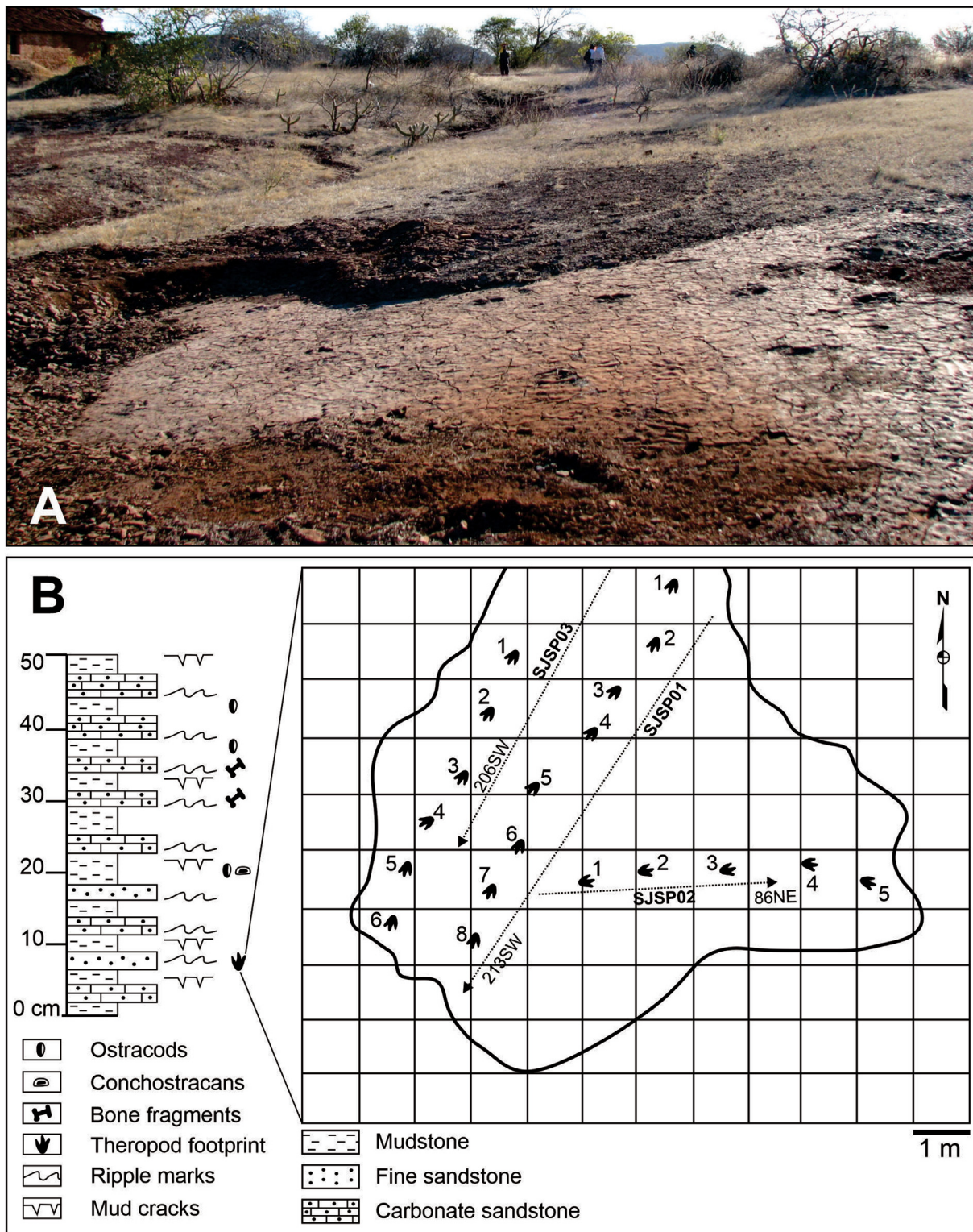


Fig. 2. Outcrop of Sousa Formation in the Triunfo basin at Sitio Pereiros ichnosite (A) and the footprints distribution in the surface strata (B) of Sousa Formation.

not very common. For example, in the Sousa basin, among 75 reasonably long trackways that can be examined for this purpose, only two are really curved rather than straight, those of Engenho Novo 1 (ANEN 1) and Piau-Caiçara 43 (SOCA 43). In contrast, the

dinosaur tracks in Brazilian basins (and in all the others) are usually indeed straight, because the trackmakers went from one place to another in a purposeful way (cf. Leonardi and Carvalho, 2021: fig. 4.66, Passagem das Pedras site).

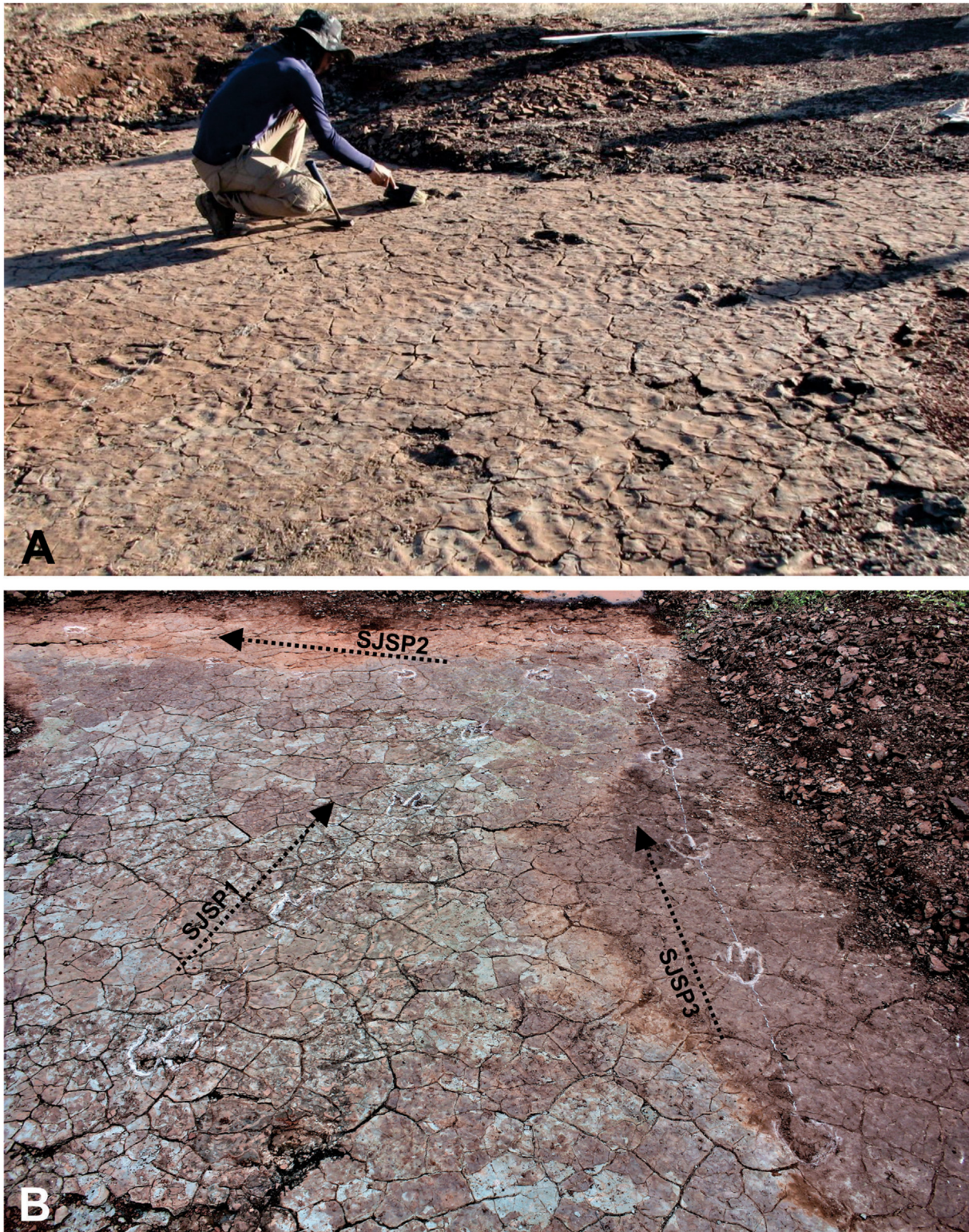


Fig. 3. Surface of the Sousa Formation strata (Triunfo basin) with the theropod trackways of the Sítio Pereiros ichnosite. Footprints preserved in a mudstone with mud cracks and superimposed ripple marks (A); two trackways (SJSP 1 and SJSP 3) are subparallel (SW) and one (SJSP 2) crosses them proceeding from W to E (Fig. 3B).

3.6. Speeds

We calculated the three trackmakers speeds (km/h), following the method and formulas of Alexander (1989) as improved by Thulborn (1989, 1990). We calculated the value of h (the height at

the hip joint from the ground) using the formula: $h = yFL$, where y is an allometric coefficient, specific to each clade or form of dinosaur. The approximate speeds on the basis of the above data and the formulas are as follows: SJSP 1: $V_c \approx 8.7$ km/h; SJSP 2: $V_c \approx 12.9$ km/h; SJSP 3: $V_c \approx 9.09$ km/h. These data also correspond

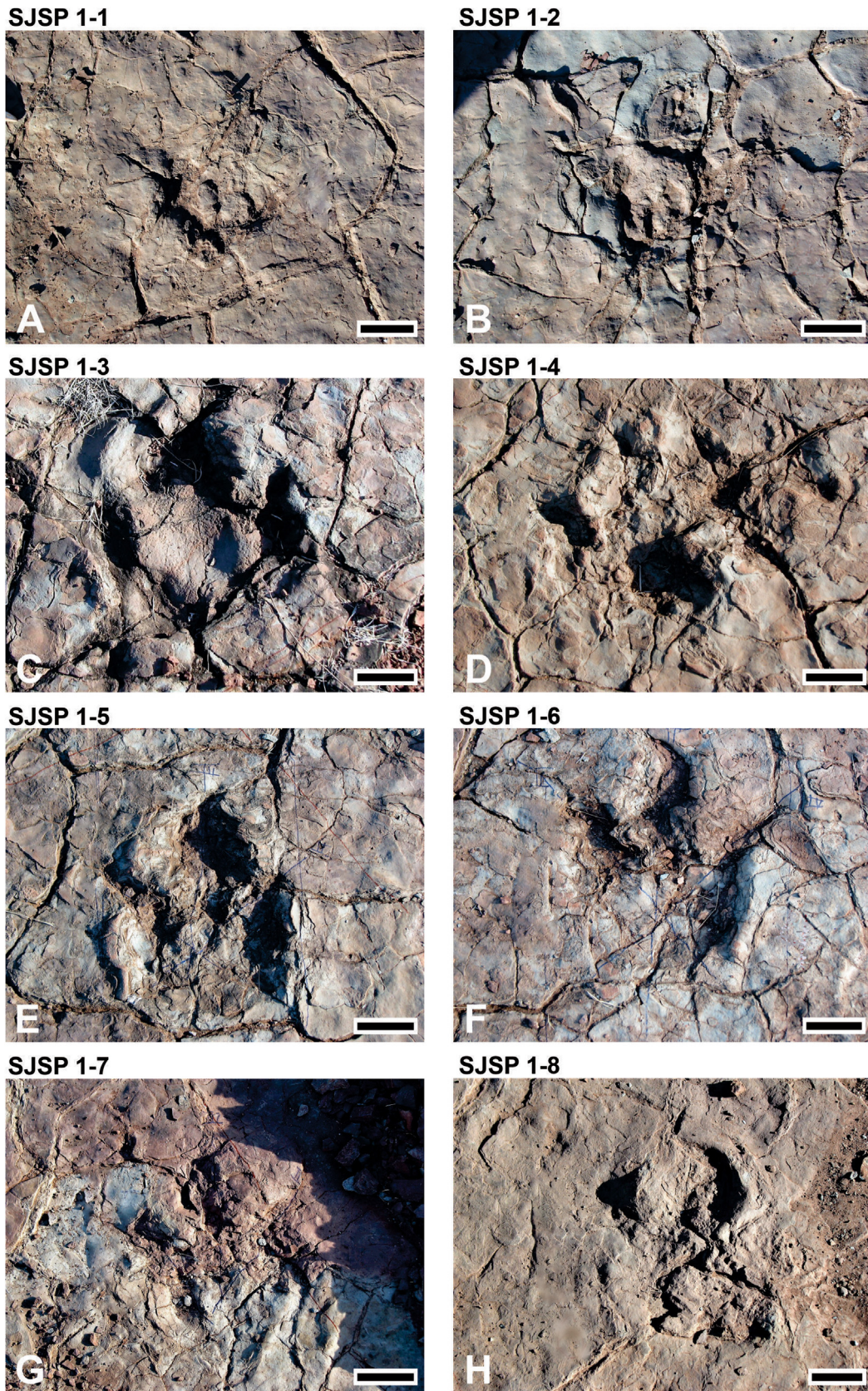


Fig. 4. Footprints from the SJSP 1 trackway, Sítio Pereiros ichnosite, Sousa Formation (Triunfo basin). Scale bar 5 cm.

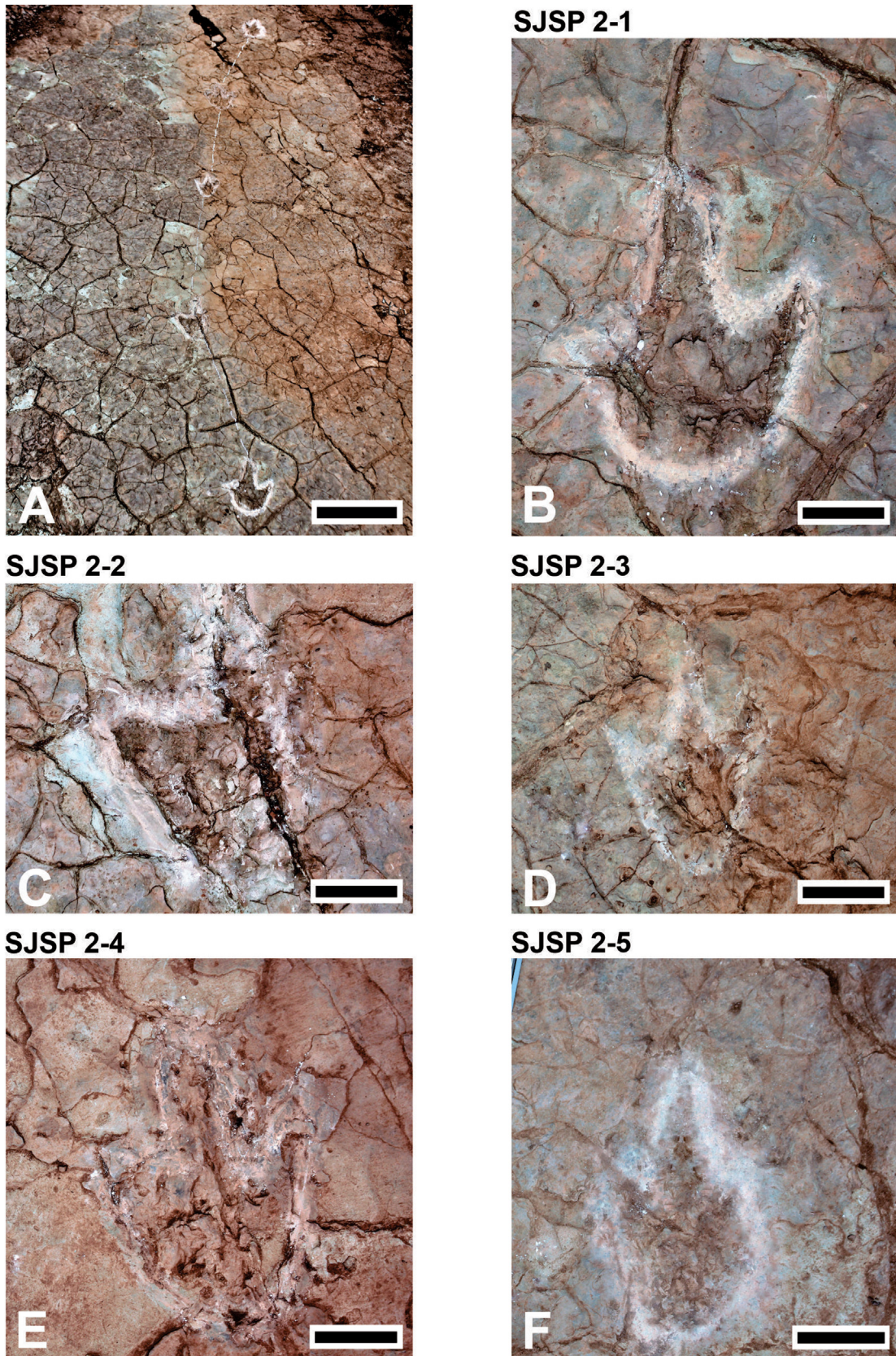
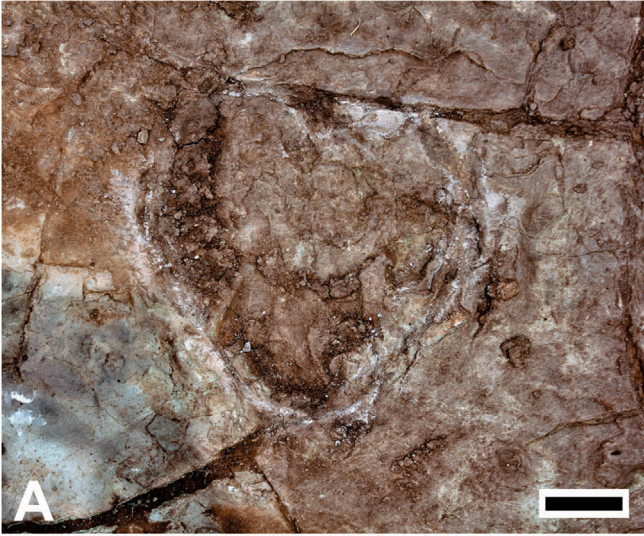
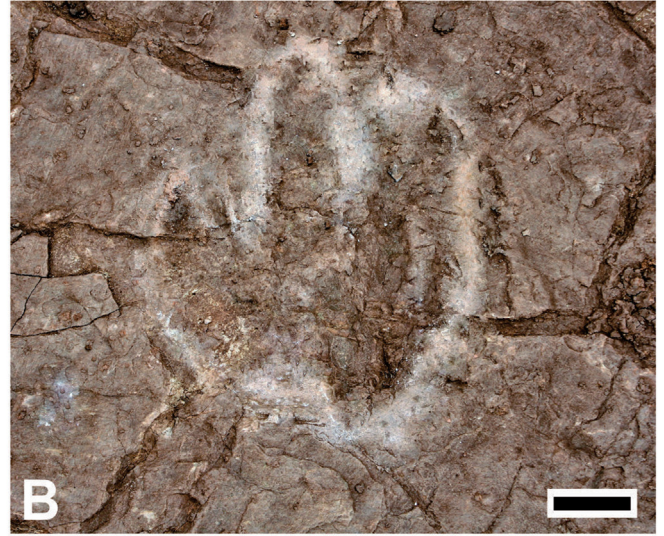


Fig. 5. Trackway SJSP 2 (A) and detail the its footprints (B, C, D, E and F), at Sítio Pereiros ichnosite, Sousa Formation (Triunfo basin). Scale bar 20 cm (A) and 5 cm (B, C, D, E, F).

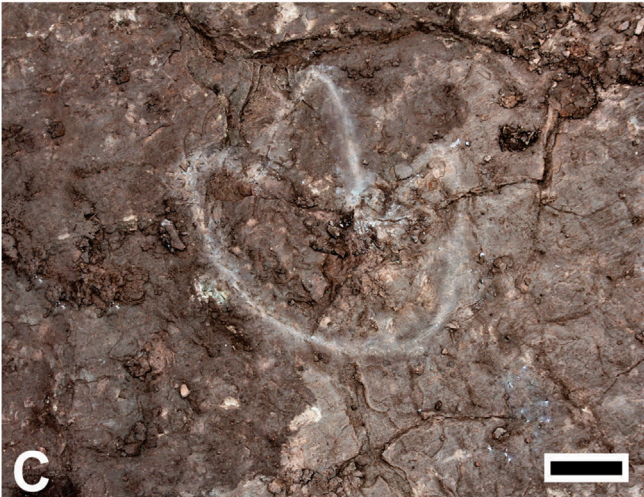
SJSP 3-1



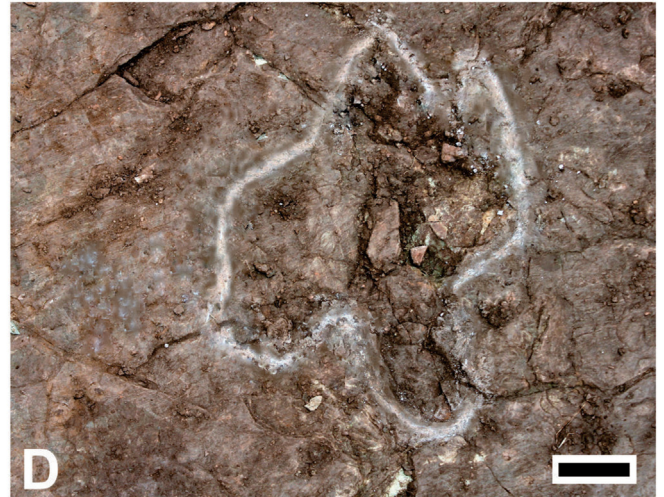
SJSP 3-2



SJSP 3-3



SJSP 3-4



SJSP 3-5



SJSP 3-6

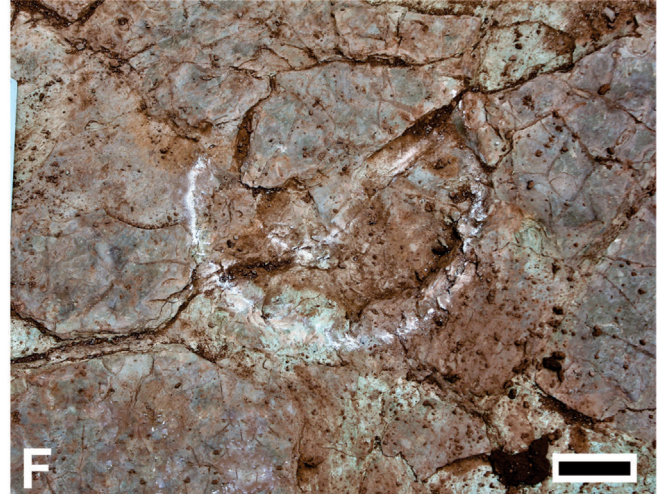


Fig. 6. Footprints from the SJSP 3 trackway, Sítio Pereiros ichnosite, Sousa Formation (Triunfo basin). Scale bar 5 cm.

rather well to the calculation of the relative length of stride, or kind of gait (Thulborn, 1989, 1990).

The three trackways on Sítio Pereiros ichnosite come to be in the middle band of the speeds of the tracks already calculated elsewhere for the basins of the Rio do Peixe, and also in that of the world ichnosites calculated elsewhere.

For comparison, the mean calculated speed (Vc) for the medium and large theropods of the Sousa Basin, (n = 62 individuals, including SOCA 493, 991, 150; 82.67% of all the trackways of this sample) is 5.57 km/h (Leonardi and Carvalho, 2021, p. 364). Again, the average calculated speed for all dinosaur tracks from the Sousa Formation alone (n = 55; 73.33% of all the trackways) is 5.23 km/h (Leonardi and Carvalho, 2021).

3.7. Social or individual behavior

We have already observed above that the three animals passed through the affected area at different times (though rather close), and that therefore there was no direct interaction between them, except that they lived, hunted, they fought for life in the same area and at the same time. All of them are interpreted as theropod trackways of large size (SJSP 1 and SJSP 3) and respectively of smaller size (SJSP 2). Thus, in this case, we cannot speak of social behavior among these theropods, but rather of individual behavior, as indeed is quite common for theropods. They seem to have been lone travelers, not only in these basins of the Rio do Peixe, but also in many other ichnosites in the world, unlike herbivores, especially sauropods, which in the Sousa Basin – and in many other places and times in the world – often traveled in large herds.

Another surprising fact, here and elsewhere, is that there is no trace of any interest of a track-maker with regard to trackways imprinted by individuals that passed before. No deviation, no deceleration, no sign of interest. The tracks continue (here on Sítio Pereiros ichnosite and elsewhere) without showing that their makers have moved away to take an interest in other dinosaur tracks.

4. Discussion

The way a footprint is preserved relates to its geological context. Its preservation for posterity requires specific substrate cohesiveness, plasticity, grain size, texture, water content and microbial processes (Leonardi, 1979a,b, 1984a,b, 2011; Lockley et al., 1989; Lockley and Meyer, 2000; Avanzini et al., 2000; Leonardi and Mietto, 2000; Dalla Vecchia, 2008; Marty et al., 2009; Li et al., 2011; Lockley and Xing, 2015; Getty et al., 2017; Pérez-Lorente, 2015, 2017; Citton et al., 2015; Castanera et al., 2016; Falkingham et al., 2016; Melchor et al., 2019; Noffke et al., 2001, 2019; Abrahams et al., 2020; Romano and Citton, 2020; Belvedere, 2008; Belvedere et al., 2022; Carvalho et al., 2022; Figueiredo et al., 2022). The presence of microbial mats in the sediments where the footprints are produced provide an early lithification favoring their preservation (Lockley, 1991; Avanzini et al., 1997; Paik et al., 2001; Marty, 2005; Conti et al., 2005; Phillips et al., 2007; Marty et al., 2009; Noffke, 2010; Carvalho et al., 2013a,b; Cariou et al., 2014; Noffke et al., 2019) as they can stabilize those surfaces by precipitation of calcium carbonate (Chafetz and Buczynski, 1992; Dupraz et al., 2004; Dupraz and Visscher, 2005; Noffke, 2010) and/or covering the tracks and protecting them from erosion with an organic felt (Avanzini, 1998; Conti et al., 2005; Marty, 2005). They also enhance the preservation potential of primary structures like ripple marks and mud cracks (Dai et al., 2015), as those observed in the Sítio Pereiros ichnosite. The occurrence of microbial structures in the Sousa basin was described by Silva Filho (2009). The large number of dinosaur tracks and associated sedimentary structures

in this basin (Sousa Formation) is certainly related to the role of biofilms in their consolidation. Petrographic slices show biofilms, disrupted carbonate microbial laminites, interbedded with very thin terrigenous microclastic beds, associated with footprints of Sousa Basin (Carvalho et al., 2013a,b).

There are few previously discovered tracks from the Triunfo basin. To date, only four isolated footprints and two incomplete trackways have been identified there in the Antenor Navarro Formation (Carvalho, 1989, 1996; Leonardi, 1994; Leonardi and Carvalho, 2021). The lithologies of these units are coarse, immature, poorly sorted, detrital sediments interbedded with siltstones, that were certainly a restrictive factor for fossil track preservation. The interpretation of these deposits is fan delta, alluvial fan, and braided/anastomosing fluvial environments. The footprints were probably produced during periodic interruption of sedimentation owing to discharge fluctuations toward the base of an alluvial fan deposit (Carvalho, 2000a,b). Despite the low preservation potential of alluvial fans and braided fluvial systems, dinosaur tracks and trackways are found in these contexts in the Sousa basin in fine sediments that were accumulated as subaerial sand bars (Carvalho, 1989, 1996; Carvalho and Leonardi, 1992). Among the previously described dinosaur tracks from Triunfo basin there are isolated footprints, three of them probably belonging to theropods. The others' poor preservation does not allow the identification of their makers. One incomplete trackway consists of just 2 digitigrade, tridactyl, and mesaxonic footprints. There is a protuberance at the proximal outline of the footprints that would correspond to digit I or to a more basal pad of digit IV. The rounded extremities of the digits, without clear claw marks, suggest they were made by a small ornithomimid (Carvalho and Leonardi, 2021).

The new tracks of Triunfo basin, the ones described herein, occur in a distinct geological context (Carvalho and Leonardi, 2022). They are found in mudstones intercalated with fine sandstones and siltstones of the Sousa Formation, in a surface with primary and secondary mud cracks. The sediments that formed the substrate over which the dinosaurs traveled allowed a better footprint preservation when compared with the coarse sediments of an alluvial fan. As the Sítio Pereiros ichnosite shows footprints preserved in fine clastic sediments (mudstones) they present a more detailed morphology.

The morphology of the tracks results from a set of factors such as the anatomy and behavior of the producer, syn-depositional and post-depositional processes (Peabody, 1955; Falkingham et al., 2010; Avanzini et al., 2012; Belvedere and Farlow, 2016; Marchetti, 2018; Marchetti et al., 2019, 2020). An important aspect concerning the morphology is the consistency of the sediments (Laporte and Behrensmeier, 1980; Lockley, 1991; Nadon, 2001; Gatesy, 2003; Milàn, 2003; Dalman and Weems, 2013; Falkingham and Gatesy, 2014; Belvedere et al., 2017; Gatesy and Falkingham, 2017), and this close relationship with the nature of the substrate allows the paleoenvironmental interpretations (Lockley, 1986; Avanzini, 1998; Gatesy et al., 1999; Milàn et al., 2004; Milàn and Bromley, 2006; Falkingham et al., 2010, 2011; Platt et al., 2012; Díaz-Martínez et al., 2018; Menezes et al., 2019). There are some requirements concerning the substrate cohesiveness, plasticity, grain size, texture and water content to allow the footprint to register (Lockley et al., 1989; Avanzini et al., 2000; Leonardi and Mietto, 2000; Dalla Vecchia, 2008; Getty et al., 2017; Melchor et al., 2019). Therefore, their preservation is controlled by the sedimentation events, which are minimal during long-lasting periods of exposure, but favored by rapid and episodic sedimentation (Razzolini et al., 2014).

The footprints of Sítio Pereiros ichnosite are all preserved as concave epireliefs, sometimes with claws and digital pads (Fig. 4C). They are bordered by mud cracks and some of them show a

displacement rim (Fig. 4D) surrounding the rear outline and the digits (SJSP 1 trackway). The mud cracks have their origin related to the outline of the footprint (Fig. 4E) or as an extension of the digits. In this way, it is seen that the general shape and anatomical details of the foot, especially the digits, after being impressed in the mud, somehow, in the phase of mud dehydration and desiccation, control the opening and the direction of the mud cracks.

This was not a subaqueous environment, as in this context there is a decrease in the morphological clarity of the footprints, with poorly defined claws or pad marks (Lockley and Conrad, 1991; Prince and Lockley, 1991; Paik et al., 2001; Belvedere et al., 2010; Piñuela Suárez, 2015; Sciscio et al., 2016; Carvalho et al., 2021, 2022). The footprints of SJSP 1 trackway, with well-defined morphologies are interpreted to have been produced in sediments with high plasticity and low water content, probably in a subaerial setting of floodplains and lake margins. This setting is easily recognized in the Sousa basin where there are the association of footprints with raindrop impressions and mud cracks, the latter of which sometimes originated at the margins of the footprints or as distal extensions from the digits (Leonardi and Carvalho, 2021). The footprints of the other two trackways (SJSP 2 and SJSP 3) are shallow concave epireliefs associated with mud cracks that bordered them and frequently cut across the footprints (Fig. 5B). In this case they should be related to a later time of the substrate deformation, when the muddy sediment was drier.

The relationship of mud cracks and footprints shows distinct patterns of cracking related to the moment when the processes of dehydration of the sediments occurred. The impression of a foot in a sediment prior to the dehydration processes induces a preferential cracking in the surrounding margins of the footprint and from the extremities of the digits (Carvalho and Leonardi, 2021). In SJSP 1 footprints, there is the indication that the track originated when there was a high water content in the substrate. Other examples of this pattern are found in Bemaraha Formation (Middle Jurassic, Madagascar), but these rarely affect the footprint itself (Wagensommer et al., 2012, 2022). Therefore, the footprints of SJSP 2 and SJSP 3 trackways show a distinct pattern of mudcracks that frequently cross the footprints. We therefore conclude that the footprints of Sítio Pereiros ichnosite probably were produced in a subaerial setting in two distinct events. The footprints with well-defined morphologies with impressions of claws, and sole pads (trackway SJSP 1) and surrounded by displacement rims are considered to have been produced in sediments with high plasticity and low water content, probably in a subaerial setting of floodplains. The mud cracks mainly have their origin related to the contour of the track or as an extension of the digits. This pattern is also observed in other footprints from the Sousa basin (Carvalho, 2000a,b; Carvalho and Leonardi, 2021). When the footprints are produced in a more cohesive substrate, as with the ichnocoenosis from the Late Jurassic Iouaridène Formation, Morocco (Belvedere, 2008; Belvedere et al., 2010; Boutakiout et al., 2019), in which there are microbial mat laminations, there is a high potential to preserve footprints produced in a firm ground.

The brecciated bottom of footprints and the separation of mud polygons are common aspects within the footprints of SJSP 2 and SJSP 3 trackways from Triunfo basin, which indicate that the dinosaurs stepped on a harder, drier substrate than in the case of trackway SJSP 1. The absence of displacement rim around these footprints are also indicative of a compact and firm substrate.

The displacement rims of footprints are related to the substrate cohesiveness. The mud bulges developed when an animal impressed its feet into a surface of very plastic and/or waterlogged mud. In theropods, there is also compressed sediment between toes, in the shape of a wedge, especially in footprints made by running theropods (Carvalho and Leonardi, 2021). This aspect can

be observed in the footprints from trackway SJSP 1 (footprints SJSP 1–5, SJSP 1–6, SJSP 1–7 and SJSP 1–8).

The ostracods, spinicaudatans (conchostracans), skeletal remains and scales of fishes in the successive layers where the footprints occur are strong evidence of ponds in this environmental setting. The presence of spinicaudatans indicates that the ponds were mostly small and temporary, hot and shallow, and their water chemistry had an alkaline character (pH between 7 and 9) as observed in the Sousa basin (Carvalho and Carvalho, 1990; Carvalho, 1993). The sedimentary succession of fine sandstones, siltstones, mudstones and shales with mud cracks and ripple marks, in a cyclic deposition, interpreted as a deposition in a floodplain, with temporary aerial exposure of the superficial sediments, in which footprints could be impressed.

Floodplains of meandering fluvial rivers presents the finest grain size of all alluvial sediments where generally perennial and temporary lakes may develop in this area. Mud cracks, bioturbation, and other surface features are widespread because of repeated exposure (Reineck and Singh, 1986). This is a favorable environment for footprint preservation as floodplains cover a wide distribution area, with repetitive track-bearing strata. Thus, fluvial and lacustrine environments are favorable for recording and preserving dinosaur footprints, especially due to cyclic deposition of microclastic sediments in episodic flooding events and shoreline variations (Reineck and Singh, 1986; Lockley and Conrad, 1991) as also interpreted for the Sousa Formation in the Sousa basin (Leonardi, 1979b, 1991, 1994; Carvalho, 1996, 2000a,b, 2004; Carvalho and Leonardi, 1992; Santos et al., 2016; Calvo and Rivera, 2018).

The identification of the theropods responsible for the footprints from Sítio Pereiros ichnosite is difficult as there are few data on South American theropod skeletons, and especially skeletons of their feet, from Early Cretaceous. Abelisauroids, carcharodontosaurids and spinosaurids may have been theropod trackmakers of the Rio do Peixe basins. Some of the large theropod tracks are possibly attributed to large and very large (8–17 m long; Hendrickx et al., 2015) Spinosauridae, although they are only recognized from the fossil record in the Aptian deposits of the Araripe basin (Martill et al., 1996; Kellner and Campos, 2000; Sues et al., 2002) and Cenomanian of São Luís basin (Medeiros, 2006). The Carcharodontosauridae, medium-size to very large allosauroid theropods (6–14 m long; Hendrickx et al., 2015) are known from South America after the Valanginian (Novas et al., 2005; Coria et al., 2020). We remember here also the great *Meraxes*, which however is much later (Late Cretaceous; Canale et al., 2022). Nevertheless, it is more plausible that the large theropod tracks from the Rio do Peixe basins were produced by abelisauroids, as they are already present in the Berriasian–Valanginian of the Bajada Colorada Formation, Argentina (Canale et al., 2016). The smaller footprints (SJSP 2 trackway), with digit III substantially longer than digits II and IV should also be related to abelisauroids such as the Noasauridae from the Barremian–Aptian of La Amarga Formation, Argentina (Bonaparte, 1996). Other possible small trackmakers could be similar to *Santanaraptor* Kellner, 1999 and *Mirischia* Naish, Martill and Frey, 2004 (Aptian, Araripe basin), a velocisaurid and a basal coelurosaur respectively (Bonaparte, 2007).

It would be interesting to add some predictions or projections about the size of the theropod makers of these tracks from Pereiros site. It should be noted, first, that the estimation of the size of a dinosaur, even starting from the finding of bones, is usually much discussed and questionable, when the complete or almost complete skeleton is not found. Even more has been discussed the possibility of making projections relating to the weight of these animals.

Even more cautious one has to be when you want to attempt projections of this type starting from footprints and trackways. For



Fig. 7. Reconstruction of the environmental scenery with the theropod tracks of Sítio Pereiros, Sousa Formation, Triunfo basin (art by Deverson Silva). The three theropods recorded, based on the three trackways, are represented here together, although in reality they passed into the area at different times, with no evidence of social behavior.

an accurate study of such awkward problems see [Thulborn \(1990, pp. 234–256\)](#) and [Xing et al. \(2022\)](#).

For simplicity, given the small amount of ichnological material on this site, we will make a brief reference to this subject. The most likely hypothesis is the two SJSJ 1 and 3 trackways are abelisauroid, as mentioned above, and that they can be attributed to two specimens quite similar to each other in size (but not necessarily to the same form or kind). In this case, they may have been 4–4.5 m in length, and be high about 1.5–1.8 m on the back, just above the hip joint. The front part of the body and especially the head were normally held higher, but in different ways, according to the gaits and according to the occasions, as it happens to all bipedal animals. However, these last two measurements cannot be calculated from a bipedal trackway. The measures of length mentioned here are meant as approximate total length, from snout to the tip of the tail; although for the truth the dinosaur skeletons so completely preserved, for a comparison, are very scarce. The more, they are non-existent, as for abelisauroids. This suggested total length was then based on comparisons made on reconstructions, with the sole purpose of having an approximate idea of the linear size of the trackmakers.

It must be said, in favor of the total lengths suggested above, although they have not been calculated following the method proposed by [Ellemerger \(1972, p. 60\)](#), that they correspond rather well to the result that would give that method, that is 4.68 m for SJSJ 1 and, respectively, 4.41 m for SJSJ 3. The correspondence may be causal, but it is interesting. If one wanted to give a rough guess about the body mass of the two trackmakers mentioned, you could suggest a weight between 500 and 1000 kg, more likely for the first value. Following instead the formula ($\text{Hip height} \times 2.63$) suggested for theropods by [Xing et al. \(2021\)](#), total body lengths of the SJSJ 1 and 3 trackmakers, from snout to the tip of the tail, would be 342 cm and 329 cm respectively. The poor quality of the footprints of SJSJ 2 trackway and the fact that the animal was running in an irregular way, makes it more unlikely the possibility of giving data on its size and body mass. Without a doubt, however, it was a smaller and lighter animal than the other two.

4.1. Why are theropods the only Sítio Pereiros ichnosite trackmakers?

As also found in the Sousa basin, the dominance of theropod footprints in the floodplain areas is attributed to an ecological zonation of the dinosaurian biota and/or a taphonomic artifact ([Carvalho, 2000a,b](#); [Leonardi and Carvalho, 2021](#)). The more common habitat of the theropods is the lowland areas, where the main environments are the low floodplain areas, with more humid and fine-grained sediments, that enhances the chances of their footprint preservation ([Fig. 7](#)).

It is not uncommon that theropod tracks are more abundant than those of herbivores. Without considering the three most recently discovered localities, including the one presented here, the percentage rate of theropod tracks in the basins of the Rio do Peixe in general is 79%. In particular, in the beds of the Sousa Formation, the percentage of theropods is even higher: up to 89.16%. These data differ from the theoretical model of a large prevalence of plant eaters and a small number of carnivores. The abundance of theropod footprints against herbivorous traces could be caused by a different level of activity of the respective trackmaker and/or the grouping of some taxa in particular environments. Furthermore, the prevalence of theropod tracks is typical of many ichnosites worldwide, and especially in South America ([Leonardi, 1991, 1994](#); [Leonardi and Carvalho, 2021](#)).

Indeed, a disproportion of plant-eaters and meat-eaters can sometimes develop in special environments (and facies), and

especially where sediments are most likely to be deposited, i. e. in low lands. If the dry season in the Early Cretaceous in the basins of the Rio do Peixe (especially where the sediments of the Sousa Formation were deposited) had been characterized by rare pools of water, these would have been places where animals tended to gather. This would have been especially true for the banks of temporary lakes during the lowering of the water level. Here the meat eater theropods would have probably waited for the big herbivores, or they would have frequented one after the other the rare points of water, in the necessity of hunting and feeding. In short, meat eaters were more active than herbivores, which almost stopped, grazing the vegetation. Carnivores walked much more, in search of prey, so they may have made many more footprints than large sauropods and ornithopods.

With 40 ichnosites in the basins of the Rio do Peixe, the situation is as follows. Against what one would expect in theory, with respect to values related to different groups of dinosaur tracks, ichnosites in which meat eaters outnumber plant eaters (32 sites out of 40; that is 80% of all sites) are more abundant than those in which the opposite occurs, (5 sites, 12.5%). There are also two sites with insufficient data or with tracks of dinosaurs that cannot be classified with safety (5%); and one site where the parity between theropods and herbivores is reached (2.5%). Besides, ichnosites in which there are only tracks of theropods are rather numerous in the basins of the Rio do Peixe. They are 19, out of 40 ichnosites, and correspond today to the 47.5% of all 40 ichnosites. One among them is the case of Sítio Pereiros ichnosite that we present herein. This high number of sites with apparent exclusive presence of theropods is well explained by [Pérez-Lorente \(2015, p. 325\)](#): “Because theropod footprints are the most abundant, so are outcrops with theropod footprints”.

In addition to these 19 ichnosites where only theropods are represented with tracks, there are: two ichnosites with tracks of theropods, sauropods, ornithopods and ankylosaurs (four clades, 5%); five ichnosites with tracks of theropods, sauropods, ornithopods (three clades, 12.5%); four ichnosites with tracks of theropods and sauropods (two clades, 10%); six ichnosites with tracks of theropods and ornithopods (two clades, 15%); one site with only sauropod tracks (2.5%); 1 site with only large unclassifiable herbivore tracks (2.5%); two ichnosites with uncertain or unclassifiable dinosaur tracks (no clades, 5%). There are also a few sites where rare tracks of animals (reptiles) of the mesofauna are also recorded, they are three (7.5% of all the 40 sites). These localities are Caçara-Piau, Serrote do Pimenta and Tapera. In addition to tetrapod tracks and traces, fish-trails ([Leonardi and Carvalho, 2021](#)) also occur.

5. Conclusions

The ichnofauna from Sítio Pereiros enhances the knowledge of the dinosaur fauna from Triunfo basin indicating the presence of large and small theropods, probably related to abelisauroids. This ichnosite registers a new geological context for the occurrence of dinosaur tracks in the Triunfo basin related to a temporary aerial exposition of the sediments in a floodplain area. There are mud cracks and ripple marks associated with the footprints. Some footprints show a displacement mud rim related to the substrate cohesiveness when the theropod dinosaurs impressed their feet into a surface of very plastic and humid sediment. The relationship of mud cracks and footprints show distinct patterns of cracking interpreted as related to the moment when the processes of dehydration of the muddy sediments occurred. Two patterns were here recognized. One pattern where the impression of a foot in a muddy humid sediment previously to the dehydration processes induces a preferential cracking in the surrounding contours of the footprints and starting from the extremities of the toes; the other

pattern generally crosses and brecciated the bottom of footprints and there is the separation of mud polygons. These new theropod tracks permits inferences about trackmaker speed and the type of gait of the three animals, and of their possible size.

The presence of only theropod tracks in this new locality Sítio Pereiros has suggested to us to control the phenomenon of the prevalence of theropods throughout the territory of the basins of the Rio do Peixe. This predominance has been confirmed. The result was also a review of the 40 ichnosites discovered so far in these basins, and an overview of the number and type of clades present in each of them.

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Author statement

Ismar de Souza Carvalho, conducted the fieldwork, conceived and designed the research; performed the analysis; interpreted obtained data; wrote the manuscript.

Giuseppe Leonardi, conceived and designed the research; performed the analysis; interpreted obtained data; wrote the manuscript.

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Appendix A. Description of the footprints and trackways

The description of the footprints and tracks follows the methodology of Leonardi (1979a,b, 1987) concerning the definitions and measurement of the footprints. The code SJSP is a reference to the county where the ichnosite was found (São João do Rio do Peixe – SJ) and to the locality of Sítio Pereiros (SP), in the Paraíba State, Brazil. All the footprints occur on a same bedding plane.

SJSP 1 (Fig. 4, Appendix B)

The footprints of SJSP 1 range from 24.0 to 28.0 cm in length and 16.6 to 28.5 cm in width. They are mesaxonic, tridactyl, with pointed digits. In some of them it is

possible to distinctly observe the impression of claws. The interdigital angles II–III range from 23° to 35° and angles III–IV from 27° to 40°. Footprints SJSP 1–1, SJSP 1–2, and SJSP 1–3 (Figs. 4A, 4B and 4C) present an angular rear outline, while SJSP 1–4, SJSP 1–5, SJSP 1–6 and SJSP 1–7 (Figs. 4D, 4E, 4F, 4G) show a rounded rear outline. Claw impressions are found in SJSP 1–1 (digits II and III), SJSP 1–2 (digit IV), SJSP 1–3 (digits II, III and IV), SJSP 1–4 (digits II, III and IV), SJSP 1–5 (digits II, III and IV), SJSP 1–6 (digits II, III and IV), SJSP 1–7 (digits II, III and IV), SJSP 1–8 (digits III and IV, Fig. 4H). There usually are not digital or “plantar” pads, although there are probably “plantar” pads in SJSP 1–3 and SJSP 1–4. The third toe consists practically of only one large rounded digital pad, and of a narrow peduncle that unites it to the other parts of the foot. In some cases, for example, in SJSP 1–3 and 6, this peduncle can be considered an additional digital pad. The index SL/FL (Stride length/footprint length) is 9.12.

The first two footprints (SJSP 1–1 and SJSP 1–2) are also preserved as concave epirelief, but they are filled in with the similar sediment of the overlying contiguous layer, so they seem to be convex in epirelief; but this is just a result of the infilling (it is a case of pseudoreverse relief). The others are concave epirelief with higher rims of displaced sediments.

These footprints, unlike those of the other two trackways, have a distinctive appearance that Li et al. (2011) call “tulip-shaped”, or even “lily-shaped”. We accept these truly expressive terms, but we could also characterize them with the name of “flame-shaped” tracks, because they recall the shape of a little campfire with three flames, of which the central (III) is much larger than the other two. This 3rd toe impression, in fact, is rather narrows to a pointed end, with the clear impression of the claws in some cases. The footprints that present this type of “flame” bulge, or lily petal, are the SJSP 1, and the following numbers 3, 5, 6 and 8. The other two toes, on the other hand, are much shorter than III, and very similar in length, and less expanded in the center. They arrive with the distal end where the bulge of toe III begins. Sometimes these outer toes are more or less straight; sometimes instead they bend, again in the form of lily petals or flames, respectively externally or medially. This happens especially in the footprints of serial number 4, 6 and 7.

The hypices seem to be generally rounded and not angular, probably because toe III, in its proximal free part, just above the junction line of the two corresponding hypices, it is very narrow. This situation probably depends on the fact that this toe had to be curved on the sagittal plane of the foot, and therefore almost entirely raised from the ground.

The impressions of the claws, when clearly visible in the III toe, as they are sometimes in the footprints (SJSP 1, 3–8), seem to be usually directed outwards (laterally). Especially noticeable, and separated from the toe, is the impression of the claw of toe III of the left footprint 8.

This type of footprint with a swollen toe III and the rounded hypices is not uncommon in the Basin of Sousa, the most generous of tracks. See for example the followings: in the Sousa Formation, the footprints or trackways Engenho Novo (ANEN) 16, Matadouro (SOMA) 2, Piau-Caigara (SOCA) 5bis, 54bis, 75, 91, 92, 97, 13498, 13499, 13693, 150, 151, 152, Poço do Motor (SOPM) 8, Sítio Saguim (SOSA) 4; in the Rio Piranhas Formation, Curral Velho (SOVC) 1 and 4. There are no examples of this style of footprints in the Antenor Navarro Formation (Leonardi and Carvalho, 2021). It is not easy to decide whether this morphotype with swollen digit III reflects the anatomy of their makers, or whether there is also an extra-morphological aspect, deformation of the footprint depending on the type of sediment and/or the behavior of the animal. This could reflect, for example, movements of the foot in the stages of initially placing the foot on the ground, any movement with the foot during the stance phase, or liftoff of the foot. One would have to evaluate this on the type of sediment and/or the behavior of the animal. This could be, for example, the way of moving the foot in the stages of placing the foot on the ground, any intermediate movement with the foot on the ground, and movement of lifting the foot. One has to see it case by case. In the case of the trackway SJSP 1, it seems that the shape of the footprint depends mainly on the anatomy of the foot and particularly of the III digit, given the constancy of the shape in the repetition of this pattern.

SJSP 2 (Fig. 5, Appendix B)

The length of steps (oblique paces) varies from 1.10 m to 1.50 m, with an average value of 1.30 m. The stride varies from 2.64 m to 3.25 m, with an average value of 2.91 m. The step angle varies from 162° to 179°, with an average value of 170°20’.

The trackmaker had to be a rather light and lean animal, and/or the soil had to be rather dry and not very plastic; with the result that the footprints are shallow and not very detailed.

The footprints of the SJSP 2 trail range from 16.5 to 18.0 cm in length with an average value of about 17.25 cm; and 12.0–13.0 cm in width, with an average value of about 12.2 cm. They are mesaxonic, tridactyl, with possible claw impression. There are no evident digital or plantar pads. Interdigital angles II–III range from 30° to 36° and angles III–IV from 30° to 40°. The footprints SJSP 2–1 (Fig. 5B), SJSP 2–4 (Fig. 5E) and SJSP 2–5 (Fig. 5F) show a rounded rear outline, while SJSP 2–2 (Fig. 5C) and SJSP 2–3 (Fig. 5D) present an angular rear outline. Claw impressions are found in SJSP 2–1 (in digits III and IV), SJSP 2–3 (in digits III and IV), SJSP 2–5 (in digits III and IV) and SJSP 2–4 (in digits II and III). No digital or plantar pads are seen. All footprints are preserved as concave epireliefs. As for the manner of measurement of the “free-digit”, the III toe is without doubt the longest; and between the outer toes, the IV is longer than the II. The index SL/FL (Stride length/footprint length) is approximately 16.87.

The five footprints of this trackway are absolutely distinct and well visible when the sunlight comes grazing, very low, in the early morning and at sunset. They are

very shallow, and then almost invisible in the hours when the sun is high. The displacement rim is also very low and not very distinct. For this reason, among other things, they were marked with chalk so that they could be better seen, both in their sequence and in order to better recognize the outline of each individual footprint.

The shape of the footprints of this trackway, although very difficult to interpret, is rather characteristic and uncommon, due to the length of the third toe compared to that of the two outer digits, and also because of the triangular shape. Digit III is much longer than the peripheral toes, and does not have the sinuous shape that is characteristic of the footprints of small theropods, of the group that are attributable to the plexus *Grallator/Eubrontes*. footprint, instead, is more like some footprints of the Sousa Formation of the Sousa basin: for example, the footprints and trackways Piau-Caiçara (SOCA) 153, 154, of the level 15 of this locality; and Passagem das Pedras (SOPP) 8 (Leonardi and Carvalho, 2021).

SJSP 3 (Fig. 6, Appendix B)

All in all, this is a bipedal and tridactyl trackway, clearly visible and recognizable as such for the periodicity of the sequence of its six footprints, and also because overall it is quite straight. However, the footprints are almost all shallow and of poor or modest quality; only the second and third are clearly tridactylous; perhaps even the first was. The fourth footprint looks incomplete, it shows something as a heel on the rear, but the three toes are indistinct. The last two (5 and 6), then, are only rounded cavities, and perhaps, after the impression of the foot in the mud, have been washed by a small wave, effacing the anatomical details. With such poor quality, it is not possible to compare these prints with other tracks of the basins of the Rio do Peixe, except for the broad identification of this as a theropod trackway. Although

claw marks are not evident, the relative narrowness of the interdigital angles and above all the extreme narrowness of the trackway do not suggest an ornithopodian identification. The trackway is straight and regular over the first three footprints, after which the animal made a small deviation towards the right, but then resumed movement in the initial direction. There is some irregularity in the lengths of the strides and in the step angle. This is always high, particularly in the last measurable step-angle, which is close to 180° (178°). The type of trackway, with very high step angles and poor footprints, makes it difficult to determine which tracks are right and which are left; this in turn makes it even more difficult to interpret the shape and style of the tracks.

The footprints of SJSP 3 trackway are 23.0–26.0 cm in length with an average value of about 24.5 cm and 15.5–26.0 cm in width, with an average value of about 21 cm. There are no digital or plantar pads. The interdigital angles II–III range from 30° to 38° and angles III–IV from 28° to 34°. The footprints SJSP 3–1 (Fig. 6A), SJSP 3–3 (Fig. 6C), and SJSP 3–5 (Fig. 6E) and SJSP 3–6 (Fig. 6F) present a rounded rear outline, while SJSP 3–2 (Fig. 6B) and SJSP 3–4 (Fig. 6D) show an irregular rear outline with a probable projection as a “heel”. However, this expansion of the back of the footprint may be, instead, the impression of toe 1st. The digits of all these footprints do not have claw impressions. There are no digital or plantar pads. All footprints are preserved as concave epireliefs. The index SL/FL (stride length/footprint length) is 9.64; it is an index quite similar to that of the SJSP 1 trackway.

Appendix B. Table with measurements of the trackways and footprints

Trackway-Footprints	Length of the trackway (m)	External width (m)	Inner width (m)	Stride (m)	Step Angle (°)	Velocity
SJSP 1	7.8	1.00	0.10	–	–	SL/h = 1.97 8.7 km/h
1–3	–	–	–	2.40	150	–
3–5	–	–	–	2.50	162	–
5–7	–	–	–	2.25	160	–
2–4	–	–	–	2.25	162	–
4–6	–	–	–	2.70	154	–
6–8	–	–	–	2.10	164	–
SJSP 2	5.50	0.45	0.10	–	–	SL/h = 2.5 12.9 km/h
1–3	–	–	–	2.85	170	–
3–5	–	–	–	2.64	162	–
2–4	–	–	–	3.25	179	–
SJSP 3	4.00	0.82	0.18	–	–	SL/h = 1.89 9.09 km/h
1–3	–	–	–	2.65	172	–
3–5	–	–	–	2.15	173	–
2–4	–	–	–	2.50	162	–
4–6	–	–	–	2.15	178	–
Trackway-Footprints	Morphology	Claw impression	Digital or Plantar pads	Digital angles II–III and III–IV	Preservation	-
SJSP 1	Mesaxonic, tridactyl, pointed digits, swollen toe III, rounded hypices.	–	-	Mean II–III – 28.28° Minimum II–III – 23° Maximum II–III – 35° Mean III–IV – 31.62° Minimum III–IV – 23° Maximum III–IV – 40°	Concave epirelief	-
SJSP 1 – 1	Mesaxonic, tridactyl, pointed digits, angular rear outline	Digits II and III	No digital or plantar pads	35° and 40°	Concave epirelief.	– Infilled.
SJSP 1 – 2	Mesaxonic, tridactyl, pointed digits, angled rear outline	Digit IV	No digital or plantar pads	30° and 27°	Concave epirelief.	– Infilled.
SJSP 1 – 3	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits II, III and IV	Probably plantar pads	23° and 29°	Concave epirelief	–
SJSP 1 – 4	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits II, III and IV	Probably plantar pads	23° and 27°	Concave epirelief	–

(continued)

Trackway-Footprints	Morphology	Claw impression	Digital or Plantar pads	Digital angles II–III and III–IV	Preservation	-
SJSP 1 – 5	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits II, III and IV	No digital or plantar pads	25° and 27°	Concave epirelief	–
SJSP 1 – 6	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits II, III and IV	No digital or plantar pads	30° and 40°	Concave epirelief	–
SJSP 1 – 7	Mesaxonic, tridactyl (two preserved digits), pointed digits, rounded rear outline	Digits II, III and IV	No digital or plantar pads	32° and 40°	Concave epirelief	–
SJSP 1 – 8	Mesaxonic, tridactyl, pointed digits, irregular rear outline	Digits III and IV	No digital or plantar pads	- and 23°	Concave epirelief	–
SJSP 2	–	–	–	Mean II–III – 32.75° Minimum II–III – 30° Maximum II–III – 36° Mean III–IV – 33.40° Minimum III–IV – 27° Maximum III–IV – 40°	–	–
SJSP 2 – 1	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits III and IV	No digital or plantar pads	36° and 40°	Concave epirelief	–
SJSP 2 – 2	Mesaxonic, tridactyl, pointed digits, angled rear outline	Without claw impressions	No digital or plantar pads	- and 27°	Concave epirelief	–
SJSP 2 – 3	Mesaxonic, tridactyl, pointed digits, angled rear outline	Digits III and IV	No digital or plantar pads	32° and 35°	Concave epirelief	–
SJSP 2 – 4	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits II and III	No digital or plantar pads	33° and 35°	Concave epirelief	–
SJSP 2 – 5	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Digits III and IV	No digital or plantar pads	30° and 30°	Concave epirelief	–
SJSP 3	–	–	–	Mean II–III – 34° Minimum II–III – 30° Maximum II–III – 38° Mean III–IV – 30.66° Minimum III–IV – 28° Maximum III–IV – 30°	–	–
SJSP 3 – 1	Mesaxonic, tridactyl, rounded rear outline	Without claw impression	No digital or plantar pads	Unclear digits	Concave epirelief	–
SJSP 3 – 2	Mesaxonic, tridactyl, pointed digits, angled rear outline with a probable heel (digit I)	Without claw impression	No digital or plantar pads	30° and 28°	Concave epirelief	–
SJSP 3 – 3	Mesaxonic, tridactyl, pointed digits, rounded rear outline	Without claw impression	No digital or plantar pads	38° and 34°	Concave epirelief	–
SJSP 3 – 4	Mesaxonic, probably tridactyl, pointed digits, irregular rear outline, with a possible heel (digit I)	Without claw impression	No digital or plantar pads	– and 30°	Concave epirelief	–
SJSP 3 – 5	Mesaxonic, tridactyl, pointed digits II and IV, rounded rear outline	Without claw impression	No digital or plantar pads	–	Concave epirelief	–
SJSP 3 – 6	Mesaxonic, unclear digits, rounded rear outline	Without claw impression	No digital or plantar pads	–	Concave epirelief	–