

Jurassic dinosaurs from Brazil: the footprints from Parnaíba Province, Mosquito Formation

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ABSTRACT

Dinosaur footprints in the Parnaíba Province, Brazil are so far restricted to the Corda Formation (Upper Jurassic) and Itapecuru Formation (Lower Cretaceous). They are interpreted as predominantly belonging to theropods. In this study, fossil footprints are reported in sandstones from the Mosquito Formation (Lower Jurassic), municipality of Fortaleza dos Nogueiras, Maranhão State, Northeastern Brazil. The footprints occur in sedimentary succession interpreted as an aeolian-lacustrine environmental context (Macapá Member) representing the first deposits of the Mosquito Formation. The new ichnosite of Tangará Ecopark represents to date the most important occurrence of dinosaur tracks from the Brazilian Jurassic, with a large number of footprints allowing new insights into the dinosaur record from Brazil and new perspectives on their diversity and environmental distribution.

KEYWORDS: Footprints, Jurassic, Mosquito Formation, Parnaíba Basin, dinosaur tracks.

INTRODUCTION

The Jurassic dinosaur occurrences throughout the Brazilian Mesozoic basins are scarce, known only by some trackways, isolated footprints and few osteological elements (Leonardi, 1989; Francischini et al., 2015; Bandeira et al., 2021; Oliveira et al., 2022). The ichnological record is known from the Paraná Basin, southeast Brazil, in deposits of the Guará Formation. It is a fluvial-aeolian succession of sandstones with footprints referable to sauropod, theropod and ornithischian trackmakers (Scherer & Lavina, 2005; Dentzien-Dias et al., 2007; Francischini et al., 2015; Deiques et al., 2025). The bones are a few isolated samples: a vertebral centrum, a possible rib fragment and a tooth from the Araripe Basin (Melo & Carvalho, 2017; Ribeiro et al., 2024) and two caudal vertebrae from the Jatobá Basin (Bandeira et al., 2021; Oliveira et al., 2022).

In the present study, fossil footprints are reported in sandstones from the Mosquito Formation (Lower Jurassic), outcropping in the municipality of Fortaleza dos Nogueiras, Maranhão State, Parnaíba Province (Góes, 1995). The Parnaíba Province, formerly known as Parnaíba Basin, is a large polycyclic basin up to 3.5 km thick, 1,000 km long and 970 km wide in northeastern Brazil. It is located partially in Tocantins, Ceará, Piauí, Maranhão and Pará states, over a Precambrian crystalline basement with a complex lithostructural and tectonic framework (Cordani et al., 1984; Porto et al., 2022). As this area presents a polycyclic tectonic evolution and distinctive sedimentation, Góes (1995) proposed the term Parnaíba Province, an area with four depositional centres (Góes & Feijó, 1994): Parnaíba, Alpercatas, Grajaú and Espigão-Mestre basins (Fig. 1), filled with Ordovician to Neogene sediments, mostly of marine, but also fluvial, deltaic and desert environments.

The footprints and dinosaur tracks found in the Parnaíba Province (Fig. 2) are located in the Parnaíba, Espigão-Mestre and Grajaú basins (Carvalho, 2024). Currently, in the Parnaíba Basin, theropod tracks have been described, both as isolated and in short trackways (Ribeirão das Lajes



Fig. 1 - Geotectonic units of the Parnaíba Province, including distinct depositional areas (Pedreira da Silva et al., 2003). Red star indicates the area of Tangará Ecopark ichnosite.

- Fazenda Malhada Vermelha locality, Fortaleza dos Nogueiras county, Maranhão State); the footprints were identified by Assis et al. (2010) and reviewed by Lopes et al. (2024). They were assigned by the authors to the Triassic Sambaíba Formation, nonetheless, these tracks are in the sandstone intertraps of the overlying Mosquito Formation, dated to ~200 Ma (Merle et al., 2011; Marzoli et al., 2018), indicating that the ichnofauna is right above the Triassic upper boundary, within the Early Jurassic (Cohen et al., 2023). In the Espigão-Mestre Basin, seven sauropod trackways have been reported and described (Leonardi, 1980, 1994; De Valais et al., 2015; Lopes et al., 2021) assigned to the Corda Formation (Upper Jurassic–?Barremian), São Domingos township, Itaguatins locality, Tocantins State. In the Grajaú Basin an isolated footprint was found in the Itapecuru Formation (Aptian, Maranhão State), identified to as *Caririchnium* (Menezes et al., 2019).

GEOLOGICAL SETTING

The geological history of the Early Mesozoic in the Parnaíba Province, particularly in the central-southern region of Maranhão State, is complex with several questions arising from contemporary extrusive magmatic events related to the Gondwana fragmentation process, aeolian continental sedimentation and an increasing environmental humidification promoted by marine entry from the Equatorial Atlantic Ocean. Furthermore, the subsidence related to the basic magmatism of the Mosquito Formation (Vaz et al., 2007), favoured the continuous deposition of siliciclastic sediments, due to the accommodation space produced by tectonic activities linked to the opening of the Equatorial Atlantic (Góes & Feijó, 1994). In this environmental context, a dinosaur fauna inhabited the region, leaving traces of their locomotion

in the siliciclastic rocks exposed in outcrops along the Mosquito River in Tangará Ecopark (Medeiros et al., 2024), Fortaleza dos Nogueiras municipality. These ichnofossils are preserved in different sub-horizontal layers, constituting a sedimentary succession in the area with an estimated thickness of 40 meters.

The Early Jurassic dinosaur tracks analysed in this study come from the south area of the Parnaíba Province, the Parnaíba Basin, which Mesozoic sedimentation encompasses fluvial-lacustrine and aeolian deposits alternated between basaltic flows (Pedreira da Silva et al., 2003). The Jurassic deposits comprise the supersequence of the Mearim Group (Pastos Bons and Corda formations) limited by the basalts (Góes & Feijó, 1994) of Mosquito (Early Jurassic) and Sardinha (Lower Cretaceous) formations. These basic magmatic events correspond to the base and top, respectively, of the Jurassic–Early Cretaceous Sequence (Silva et al., 2020). In the studied area the Mosquito Formation is a sequence of basalt flows intercalated with fine and coarse sandstones. The Pastos Bons Formation is a succession of shales and sandstones interpreted as fluvial and aeolian deposits. The Corda Formation is represented by bimodal sandstones, with some mudstone levels, interpreted as a desert environment. The Sardinha Formation overlies the Corda Formation and is made up of volcanic rocks that are dominantly intrusive, with extrusive occurrences in the northeast of the basin.

Throughout the Jurassic and Cretaceous, magmatic flows and diabase dykes indicate the effects of the breakup of Pangea and Gondwana. The Mosquito Formation basalt flows are related to these events and reflect the first steps of the Atlantic opening linked to the Central Atlantic Magmatic Province (Araújo, 2017; Silva et al., 2020). The intercalations of sandstones with these basalts are indicative of a constant supply of sediments in aeolian and fluvial environments. The Tangará Ecopark ichnosite occurs in this context, alongside the outcrops of the Mosquito River.

The sedimentary succession of the area with dinosaur footprints belongs to the Mosquito Formation, Macapá Member (see Northfleet & Melo, 1967; Aguiar, 1971; Ballén et al., 2013). There are thick layers of diabases, as dikes and sills in the siliciclastic rocks, and fine-grained black to purplish tholeiitic basalts, massive to amygdaloidal, interspersed in sandstones and siltstones. Aguiar (1971) subdivided the Mosquito Formation into five members: Lower Basalt, Macapá Member, Middle Basalt, Tinguí Member and Upper Basalt. The Macapá and Tinguí members are, respectively, the lowermost and the uppermost portions of the unit, essentially siliciclastic. The Macapá Member is a succession of fine to medium sandstones with cross-stratifications, interpreted as deposited in an environmental context of aeolian dunes, sand sheets, fluvial and ephemeral lakes (Ballén et al., 2013). The facies analysis showed that the fine sandstones with adhesion ripples, sandstones with ripple marks, heterolithic sandstones and mudstones with wavy lamination indicate an interdunes context (Ballén et al., 2013). Sandstones with intraclasts, flat-parallel lamination, and thin layers of fine sandstones and algal mudstones were deposited in a playa lakes environmental context (Ballén et al., 2013). The Macapá Member was interpreted as an intertrap of a desert system with deposits of aeolian dune fields with humid interdunes, sand sheets with wadis and playa lakes (Ballén et al., 2013). Other siliciclastic rocks have been related to a playa lake margin sedimentary context (Tinguí Member, Ballén et al., 2013).

PARNAÍBA PROVINCE						
GEOCHRONOLOGY		DEPOSITIONAL ENVIRONMENT	LITHOSTRATIGRAPHY		DINOSAUR FOOTPRINTS	
ERA	PERIOD		GROUP	FORMATION		
MESOZOIC	CRETACEOUS	CST/LAGOON		ITAPECURU		
		FLUVIAL/LAKE MARINE		CODÓ		
				GRAJAÚ		
		MAGMATISM		SARDINHA		
	JURASSIC	AEOLIAN FLUVIAL/LAKE		CORDA		
				PASTOS BONS		
		ALN/FLV/MGMT		MOSQUITO		
	TRIASSIC	AEOLIAN	?-?-?	SAMBAÍBA		
	PALEOZOIC	PERMIAN	AEOLIAN/LAKE	BALSAS	MOTUCA	
			CST/MARINE SARKHA		PEDRA DE FOGO	
		AEOLIAN	PIAUI			
CARBONIFEROUS		FLUVIAL/DELTAIC MARINE	CANINDE	POTÍ		
		MARINE		LONGÁ		
DEVONIAN		FLUVIAL/DELTAIC MARINE		CABEÇAS		
		MARINE		PIMENTEIRAS		
		CST/LAGOON		ITAIM		
SILURIAN		FLUVIAL	SERRA GRANDE	JAICÓS		
MARINE		TIANGUÁ				
ORDOVICIAN	GLACIAL/FLUVIAL		IPU			

LEGEND	
	Sauropoda
	Theropoda
	Ornithopoda

Fig. 2 - Stratigraphic chart of Parnaíba Province (adapted from Vaz et al., 2007; Araújo, 2017; Pereira et al., 2021) and occurrences of dinosaur footprints and trackways (modified from Carvalho, 2024)

Tangará Ecopark ichnosite stratigraphic context

The succession with dinosaur footprints comprises sandstones interbedded with mudstones and silexites. The lowermost beds of the succession, outcropping close to Cachoeira Grande, show bimodal grain-size sandstones with medium to large tabular cross-stratifications, plane-parallel and low-angular cross-stratifications. At the uppermost beds of this succession, there are thin layers of very fine sandstone with wavy microbial laminations and levels of ferruginous silexites, interspersed with medium to fine sandstones, with dinosaur footprints. The middle portion of the succession, close to Cachoeira da Cascata, comprises layers of medium sandstones with wavy structures, gradually succeeded by a thick package (around 10 cm thick) of thin layers of very fine to fine sandstones with microbial laminations, ripples and levels (1-2 cm) of ferruginous silexites. At the uppermost part of the succession, nearby Cachoeira do Bebedouro, the lithotypes are characterised by very fine sandstones with microbial wavy laminations and levels of ferruginous silexites. These are interspersed with medium to fine sandstone layers with an abundant record of dinosaur footprints

and wavy microbial laminations. The uppermost beds present mudcracks and dinosaur footprints.

Two facies associations were identified for the studied interval: aggradational microbial strata and aeolian dunes (Fig. 3). Aggradational microbial strata facies association consists of fine to medium sandstones, well-sorted, arranged in horizontal strata and undulated layers, which can form centimetre to decimetre domes, sometimes draped by mud. Siliceous nodules are common. The horizontal strata are composed of irregular, corrugated millimetre laminations. In surface view, the laminations show wrinkled texture, small gas domes and sand cracks. The aeolian dunes facies association is composed of well-sorted sandstones, characterised by highly spherical and rounded grains, arranged in tabular packages of 0.5 to 2.5 m. These sandstones are composed of tangential cross-strata dipping from 22° to 28°, formed by grain flow and wind-rippled laminae, with a preferential direction of foresets dip to the southwest. Internally, the cross-strata are composed of grain flow and grain fall strata.

The dinosaur footprints from Tangará Ecopark ichnosite are found in the aggradational microbial strata facies. The corrugated horizontal strata, with wrinkled texture, small gas domes and sand cracks are interpreted as the product of growth of microbial mats (Noffke et al., 2002). The domal structures can be interpreted as siliciclastic stromatolites (Angonese et al., 2024; Noffke & Awramik, 2013). The siliciclastic nature of the sediments indicates that the trapping and binding processes of terrigenous grains by microbial mat are the main mechanism of stromatolite construction (Angonese et al., 2024). Sandstones with symmetrical ripples marks that occur intercalated with microbial strata indicate deposits generated by the action of fair-weather waves.

The succession (around 40 m thick) is interpreted as primarily related to dunes and aeolian sand sheets interlayered with continental playa lakes deposits, which favoured microbial activities that gave rise to the microbial wavy laminations. These laminations, parallel to each other, are in thick packages of very fine and fine sandstones, with microbially induced sedimentary structure (MISS), produced by bacterial organisms (Noffke, 2010). Flint is frequently present in these laminations, whose origin can be also attributed to the development of microbial mats. The microbialites occurring in the siliciclastic rocks along Mosquito Creek are enriched in iron (Fig. 4). The preservation of microbial wavy laminations may also be suggestive of a control related to rapid sediment deposition, followed by the deposition of fine sediments with a biofilm coverage (Noffke, 2010; Noffke et al., 2001, 2019).

MATERIALS AND METHODS

The herein described footprints come from seven outcrops of the Mosquito Formation, in the Fortaleza dos Nogueiras municipality, Maranhão State. The trampled surfaces outcrop in the Tangará Ecopark area, herein nominated as Tangará Ecopark ichnosite, with at least 78 footprints, isolated or as short trackways distributed throughout seven outcrops (Tab. 1).

The footprints were coded following the nomenclature proposed by Leonardi (1987) in which FN means the county of

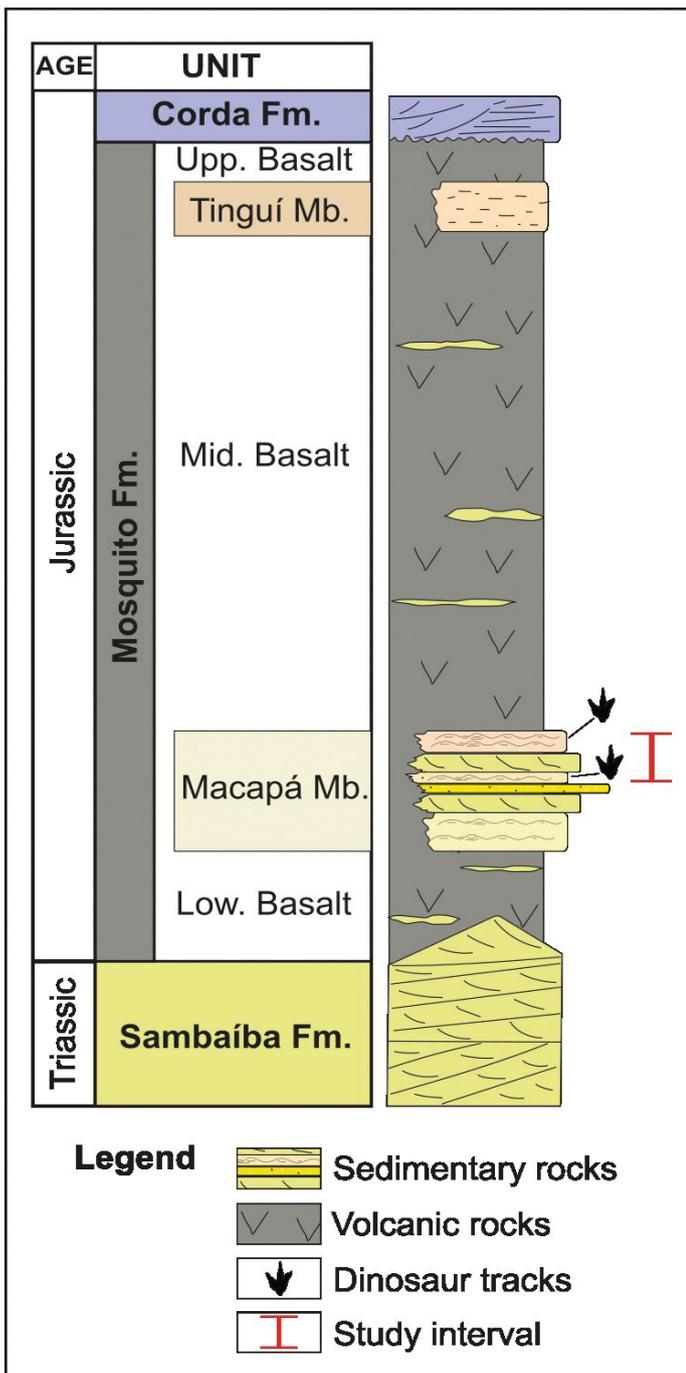


Fig. 3 - Stratigraphic succession of the Mosquito Formation (after Aguiar, 1971; Ballén et al., 2013; Michel et al., 2024) and the occurrence of fossil footprints in the Macapá Member.

Table 1 - Geographic location of the outcrops with dinosaur footprints at Tangará Ecopark ichnosite, Fortaleza dos Nogueiras county, Brazil.

Outcrops	Coordinates	Footprints codes
Outcrop 1	7° 1' 32.17" S/46° 6' 45" W	FNTA 01 to FNTA 13
Outcrop 2	7° 1' 32.68" S/46° 6' 1.33" W	FNTA 14 to FNTA 23
Outcrop 3	7° 1' 34" S/46° 5' 35" W	FNTA 24 to FNTA 34
Outcrop 4	7° 1' 32.60" S/46° 6' 1.79" W	FNTA 35 to FNTA 38
Outcrop 5	7° 1' 32.71" S/46° 6' 3.73" W	FNTA 39 to FNTA 55
Outcrop 6	7° 1' 33.19" S/46° 6' 0.89" W	FNTA 56 to FNTA 73
Outcrop 7	7° 1' 32.67" S/46° 6' 0.52" W	FNTA 74 to FNTA 78

Fortaleza dos Nogueiras, and TA the locality of Tangará Ecopark. Measurements and orientation were taken for each footprint. The specimens were photographed conventionally with a digital camera and according to the methodology for generating photogrammetric models. Associated footprints on the same surface were drawn on a plastic sheet (Fig. 5) and a drone was used for aerial photos of the study area following the methods by Romilio et al. (2017) and Petti et al. (2018). Some sketches of the rocky surfaces were mapped with a metric tape with the gridded quadrant system of 1 m² and then reproduced on a suitable smaller scale on graph paper (methodology by Leonardi, 1977, 1987).

The footprints from Tangará Ecopark ichnosite

The footprints are found in a succession of fine to medium sandstones with cross-bedding, ripple marks, and microbial surfaces. They were classified into five morphotypes (Fig. 6). Morphotype I is the largest, the footprint reference is FNTA 35 which is 24 cm wide and 39 cm long: it is tridactyl, mesaxonic, with an angular posterior edge, occasionally with the presence of digit I; angular hypexes and larger digit III, some with gentle bending from their middle portion.

Morphotype II (footprint reference FNTA 76) has smaller dimensions, up to 8.8 cm wide and 16.6 cm long: tridactyl, mesaxonic with clear trace of digit I on the posterior edge; digit III is the largest. The presence of tapered claws is evident on all digits, narrower than those of Morphotype I; very acute hypexes.

Morphotype III (footprint reference FNTA 61) is 10.71 cm wide and 11.42 cm long: tridactyl, mesaxonic with gently curved and pointed digits; clear presence of claw traces. Digit III is larger than digits II and IV; acute angles of the hypexes; angular posterior margin.

Morphotype IV (footprint reference FNTA 07) is up to 13.6 cm wide and 19.9 cm long; pointed digits and digit III larger than the others; the hypexes between digits II-III and III-IV are narrow and elliptical; posterior edge of the footprint rounded, without digit I.

Morphotype V (footprint reference FNTA 52) is 11 cm wide and 19.5 cm long: tridactyl, mesaxonic with pointed digits; clear presence of claws. Digit III is larger than digits II and IV; wide elliptical hypexes; pointed rear border. Some footprints are preserved as concave epirelief, but some with partial sediment filling, masking the observation of digit impressions. In general, the digits are wider at their base and intermediate portion, except those observed in Morphotype II, whose digits are narrower and straighter. A detailed description of the footprints found at Fortaleza dos Nogueiras is ongoing and will be published in dedicated paper.

The Tangará Ecopark ichnosite area is geographically very far from other localities with Jurassic footprints, thus the comparison with records from other tracksites are just tentative. Foster et al. (2025) discussed the worldwide Jurassic footprints and trackways, as an updated report on the footprints from this time interval. The morphotype I is similar to *Anchisauripus sillimani* from the Lower Jurassic of Massachussets (Olsen et al., 1998; Foster et al., 2025) in the general shape and the indistinguishable pad traces, although the Brazilian specimen is much larger. This morphotype also exhibits similarity with *Irenesauripus* isp. from the Maastrichtian of Poland (Gierliński et al., 2008) in shape and size, and represents

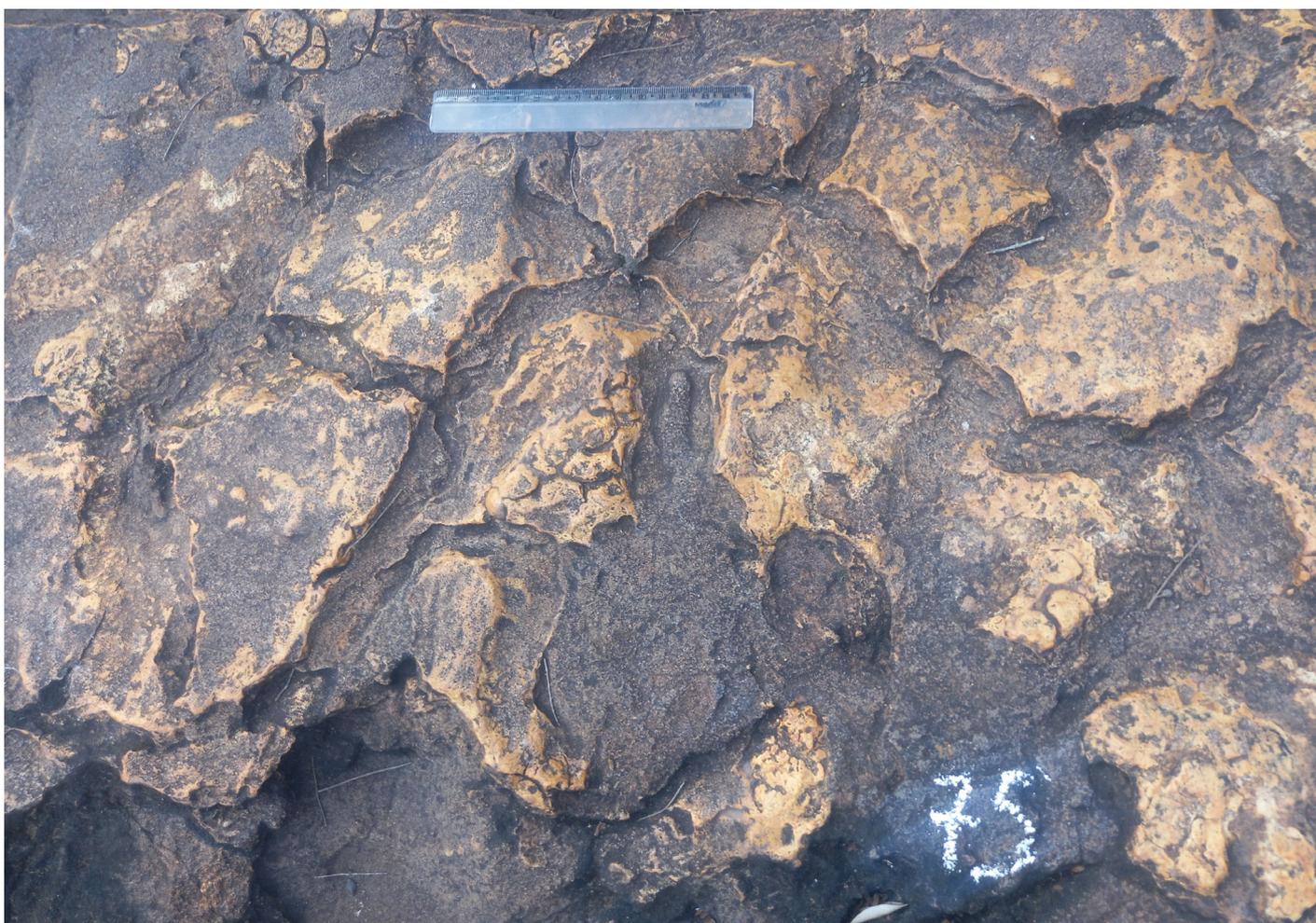


Fig. 4 - Ferruginous microbial surface with mudcracks and theropod footprints. The biofilms are a factor that improves the fossilisation record and in this context are probably related to marginal areas of playa lakes.

the largest theropod of the local biota, since no larger footprint was found among the specimens of the Tangará Ecopark ichnosite.

Morphotype II is similar to *Changpeipus carbonicus* from the Middle Jurassic of Morocco (Foster et al., 2025). This ichnospecies also occurs in Asia from Lower Jurassic to Lower Cretaceous (Young, 1960; Chen et al., 2006) and possibly in the Middle-Upper Jurassic of Australia. This morphotype has a very peculiar outline – it is triangular, less digitigrade with narrow digit imprints and a metatarsophalangeal pad in its rear border. Distinctly from the description presented by Young (1960), the Tangará Ecopark ichnosite specimens present digits II and IV with the same length.

Morphotype III is the most unusual as it is established based on only one footprint that occurs on a slab with several other traces. The third digit is mesially strongly curved and the fourth one is curved laterally; digit II is poorly preserved and thus its position is not clear. No simple correspondence is possible when comparing it with other Jurassic footprints. Anyway, it bears some similarities to *Anatopus palmatus* from Lower Jurassic of France (Lapparent & Montenat, 1967). The shared features are: curved digits and wide track span, so that the footprint is wider than longer. Nonetheless, *Anatopus* may represent an incomplete footprint related to *Grallator variabilis* (Lockley, 1998). These similarities may be just apparent and do not represent any real affinity.

Morphotype IV is comparable in shape to *Camptosauropus* isp., from the Middle Jurassic of Tajikistan, Asia, attributed to an ornithomimid dinosaur (Gabuniya & Kurmatov, 1988). It was considered *nomen dubium* by Díaz Martínez et al. (2015) due to inadequate diagnosis and poorly figured holotype (Foster et al., 2025). This morphotype could be compared to *Eubrontes* isp., mainly the general shape, digit angles, pad outlines and claw traces position. This ichnogenus has a broad distribution in Laurasia and Gondwana, ranging from Upper Triassic to Lower Cretaceous (Klein & Lucas, 2010). *Weiyuanpus* isp. from Lower Jurassic of China, a possible junior synonym of *Eubrontes* (Chen et al., 2006; Foster et al., 2025) is also similar in shape to morphotype IV. It also resembles *Saltopoides* (Lapparent & Montenat, 1967) from the Lower Jurassic of France, lately synonymised with *Grallator* (Lockley, 1998), a Triassic-Jurassic ichnogenus. Nonetheless, the track from Brazil does not exhibit distinct digital pads as many reports of *Grallator* (Olsen et al., 1998; Milàn, 2003). *Grallator*, along with *Eubrontes* and *Anchisauripus* are supposed to be an ontogenetic series instead of representing different trackmakers (Olsen et al., 1998). So, we can refer our morphotype IV to the *Eubrontes* – *Anchisauripus* – *Grallator* series and it can thus be tentatively attributed to Theropoda (Olsen et al., 1998). No similarities were recognised of morphotype V among any reported Jurassic footprint morphology.



Fig. 5 - A) Associated footprints in the same surface were drawn on a plastic sheet to facilitate morphological measurements; B) Isolated small theropod footprint FNTA 41 from outcrop 5. Scale bar = 20 cm.

JURASSIC DINOSAUR FOOTPRINTS FROM BRAZIL AND THE TANGARÁ ECOPARK TRACKMAKERS

Dinosaur footprints in Jurassic deposits of Brazilian basins are scarce (Christofolletti et al., 2021) and they are mostly present in the Guara Formation (Kimmeridgian–Tithonian, Parana Basin), a stratigraphic unit equivalent to the Tacuarembo Formation (Batovi Member), in Uruguay, that also present similar footprints (Francischini et al., 2015). The trackmakers from this unit are interpreted as sauropod, theropod and ornithischian dinosaurs, as probably Brazil and Uruguay shared similar Late Jurassic dinosaur fauna (Dentzien-Dias et al., 2007, 2008, 2012; Francischini et al., 2015, 2018; Mesa & Perea, 2010, 2015). The presence of

ceratosaurian and megalosauroid body fossils in the Tacuarembo Formation (Perea et al., 2003; Soto & Perea, 2008; Soto et al., 2020) suggests that this group could be the theropod producers of the Guara and Tacuarembo tracks.

The Guara Formation is a lithostratigraphic unit deposited in a fluvial-aeolian setting in an arid to semi-arid paleoenvironment (Scherer & Lavina, 2005, 2006). The footprints occur mainly in the sand sheets, and one theropod trackway in the aeolian dunes (Dentzien-Dias et al., 2007; Francischini et al., 2015). The occurrence of dinosaur footprints in arid, and even more arid settings (e.g., the earliest Cretaceous Botucatu Formation: Leonardi & Carvalho, 1999; Leonardi et al., 2007; Fernandes et al., 2011; Carvalho & Leonardi, 2024; Peixoto et al., 2025), shows that dinosaurs were capable to inhabiting extensive arid dune fields. The paleoenvironment recorded in the intertraps of Mosquito Formation would be less arid than the cited examples. There were dunes, but the water availability was sufficient for the development of wet interdunes and playa lakes colonised by microbial communities. The footprints of Mosquito Formation were preserved in the sediment stabilised by these microbial communities.

Although the morphologies are important to evaluate the diversity of ichnofaunas (Castanera et al., 2015, 2018; Farlow, 2018) and also to analyse the trackmaker behavioural patterns (Citton et al., 2017), the landmarks that allow the geometric morphometrics on footprints show a great subjectivity. Leonardi & Carvalho (2021) indicate that this is a consequence of the fact that footprints are in part the foot-substrate interplay, that results in many morphological possibilities.

Tridactyl footprints are very difficult elements of identification and classification. They can present a great variability in their aspects, forms, outlines and relationship with the substrate (Foster et al., 2025). This is the result of the relationships between the sedimentological properties of the substrate, the foot morphology and the behaviour of the trackmaker (Farlow et al., 2015; Sciscio et al., 2016; Perez-Lorente, 2015; Xing et al., 2018; Razzolini et al., 2014; Marchetti et al., 2019; Carvalho & Leonardi, 2020; Krapovickas, 2024). Besides, the relationships between theropod groups are so diverse (Hendrickx et al., 2015) that it is difficult to establish the real diversity of dinosaurs based on the footprints morphologies. In Northeastern Brazil, some osteological remains of Jurassic dinosaurs are found in the Araripe (Melo & Carvalho, 2017) and Jatoba basins (Bandeira et al., 2021). This indicates that basal Carcharodontosauria (Bandeira et al., 2021), a basal lineage of neotheropods represented by *Dilophosaurus* and close relatives, could have occurred during the Middle–Late Jurassic (Oliveira et al., 2022), as well as Abelisauridae (Ribeiro et al., 2024).

These groups are better represented later, throughout the Cretaceous, but it is not possible to exclude neotheropods, such coelophysoids, as the producers of some of the Tangara Ecopark ichnosite footprints (Fig. 7). Meanwhile, there are also large footprints similar to those produced by Cretaceous groups exclusively found in arid environments, as the ichnospecies *Farlowichnus rapidus* (Botucatu Formation: Leonardi et al., 2024), and abelisaurid footprints from fluvial-lacustrine environments (Leonardi & Carvalho, 2021; Carvalho & Leonardi, 2024). Therefore, the morphology of the footprints at Tangara Ecopark ichnosite

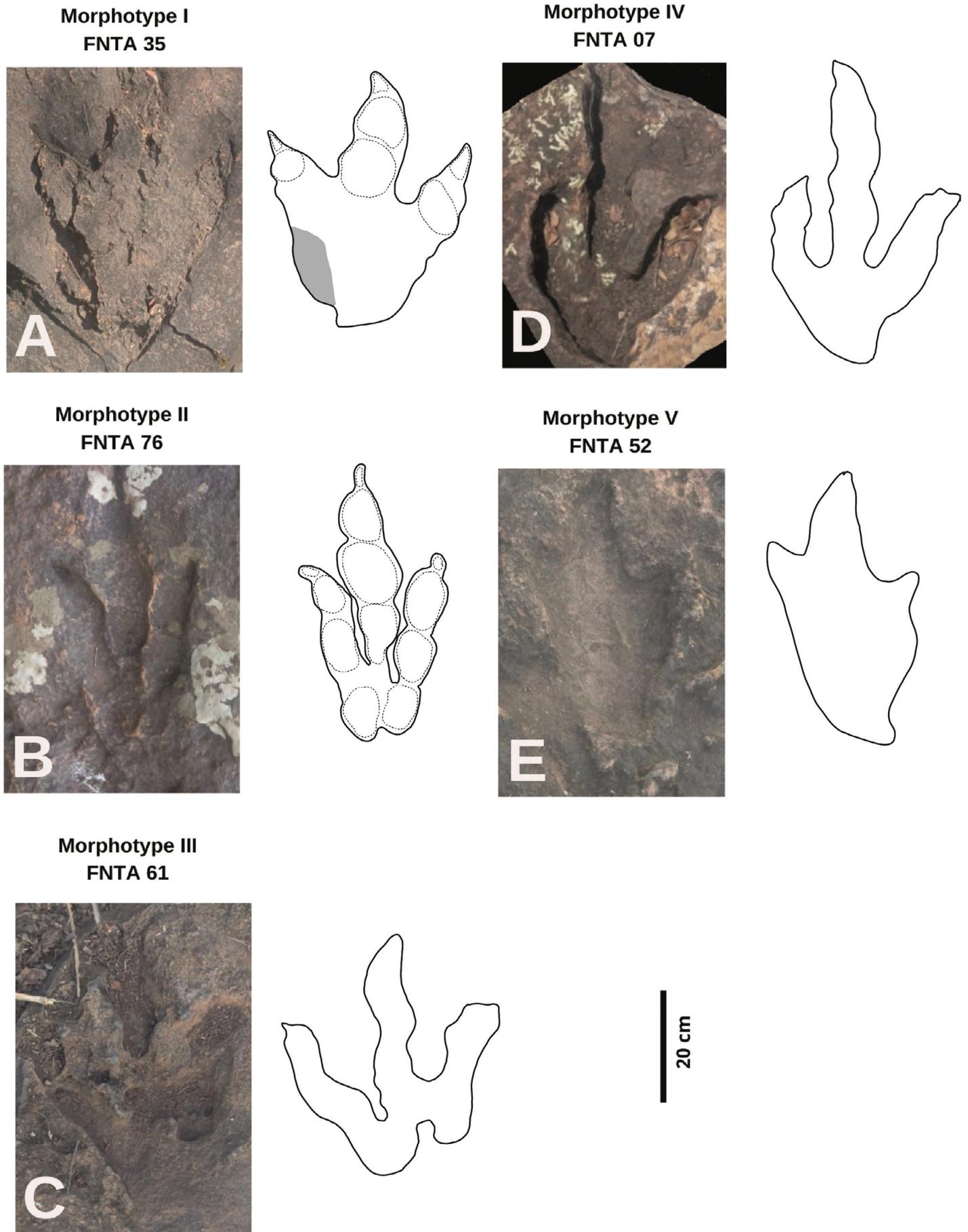


Fig. 6 - Five distinct morphotypes identified in the Tangará Ecopark ichnosite. These are the main patterns, nonetheless there is a wide range of sizes and morphology among the analysed 78 footprints.

probably records a pattern that will become more common later in the geological record. Scisio et al. (2017) indicated that the megatheropod footprints from the Elliot Formation (Lesotho), and other Lower Jurassic units, could be related to new palaeoecological strategies resulting from changes in both climate and predator-prey dynamics at the outset of the Jurassic. The appearance of megacarnivores in the Early Jurassic is an evolutionary phenomenon that was repeated on multiple occasions throughout the Mesozoic.

CONCLUSIONS

The ichnofossiliferous assemblage of the Mosquito Formation (Macapá Member) indicates an abundance of fossil footprints distributed across seven outcrops and distinct stratigraphic levels, representing a new Early Jurassic ichnosite. These dinosaur footprints occur in sandstones trapped between basalt layers. An aspect associated with the abundance of dinosaur footprints is related to the frequent intervals with biofilms in the sedimentary succession. The microbial activities are linked with stressing temporary aquatic environments in arid regions allowing the stabilisation of the bedding surfaces, improving in this way the preservation of the dinosaur tracks. The study of the Tangará Ecopark ichnosite is highly relevant to enhance the knowledge about the Jurassic continental fauna of Gondwana, and better

evaluate the effects of the Central Atlantic Magmatic Province (CAMP) eruptions in the changes of the structure of the early Mesozoic continental faunal community.

At least five groups of medium to large theropods trackmakers can be distinguished at the Tangará Ecopark ichnosite based on the occurrence of respectively five track morphotypes. In some of these footprints, digit III, sometimes twice the length of the other digits, resembles that of footprints from other Cretaceous basins in Northeastern Brazil. Based on the age of the Mosquito Formation and the size of some ichnites, an Early Jurassic age is assumed for the footprints described in this study. It is difficult to establish based on footprint morphologies the real diversity of dinosaurs. Basal lineage of neotheropods represented by *Dilophosaurus* and close relatives could have occurred during the Middle–Late Jurassic of Northeastern Brazil, as well as Abelisauridae and coelophysoids, the probable trackmakers of the Tangará Ecopark ichnosite footprints.

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Fig. 7 - Environmental reconstruction of the Tangará Ecopark ichnosite with a large diversity of theropods during the Early Jurassic of Parnaíba Basin (art by Guilherme Gehr).

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