Cretaceous Research 117 (2021) 104626

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Dinosaur trampling from the Aptian of Araripe Basin, NE Brazil, as tools for paleoenvironmental interpretation

Ismar de Souza Carvalho [a,*], Giuseppe Leonardi [b], Aristóteles de Moraes Rios-Netto [a], Leonardo Borghi [a], Alexandre de Paula Freitas [a], José Artur Andrade [c], Francisco Idalécio de Freitas [d]

[a] Universidade Federal Do Rio de Janeiro, Instituto de Geociências, Departamento de Geologia, Avenida Athos da Silveira Ramos, 274, Bloco F, Ilha Do Fundão — Cidade Universitária, Rio de Janeiro, RJ, 21949-900, Brazil
[b] Istituto Cavanis, Dorsoduro 898, Venezia, 30123, Italy
[c] Agência Nacional de Mineração, Praça da Sé, 105 Centro, Crato, Ceará, 63.100-440, Brazil
[d] Geopark Araripe, Rua Carolino Sucupira s/n, Pimenta, Crato, Ceará, 63.100-490, Brazil

A R T I C L E I N F O

Article history:
Received 7 November 2019
Received in revised form
20 August 2020
Accepted in revised form 20 August 2020
Available online 28 August 2020

Keywords:
Dinoturbation
Load structures
Substrate consistency
Paleoenvironment
Araripe Basin

A B S T R A C T

Although fossil footprints are generally recognized by morphological data from autopodia, in some cases they can also be characterized by a sequential deformation of the substrate, since the footprint reaches many sedimentary levels beyond the surface. In such cases, these features are preserved as deformation structures which can be observed in cross-sections, making it difficult to identify their genesis. Thus, they are many times interpreted as load or liquefaction structures related to compaction, tectonism or fluidization, without a direct relationship with the trampling by terrestrial vertebrates and the pressure generated during the contact between a tetrapod autopodium and the substrate, leading to the origin of load structures with successive laminae deformation.

The research on the Araripe Basin, Brazil, allowed the discovery of many structures that are related to substrate deformation after dinosaur trampling. This offers a new tool for paleoenvironmental interpretations to this region, as well as it opens new perspectives for understanding ancient terrestrial ecosystems and the origin of deformational structures. Although dinoturbation observed in cross-section is still generally scarcely documented, it enables the understanding of environmental changes from terrigenous to carbonate lake scenarios that are so peculiar in this sedimentary succession. Their regional distribution opens new possibilities to the analysis of the spatial and temporal distribution of dinosaur-trampled structures.

1. Introduction

Araripe Basin is one of the interior basins of Northeastern Brazil, whose Cretaceous history spans from Berriasian to Cenomanian times (Fig. 1). Although dinosaur tracks are commonly found in the surrounding basins of Sousa, Uiraúna-Brejo das Freiras, Malhada Vermelha and Lima Campos, all of them occur in floodplain deposits of Berriasian-Hauterivian ages (Leonardi, 1994; Leonardi and Spezzamonte, 1994).

The footprints analyzed in this study are found in Aptian carbonate deposits, interpreted as produced on an alkaline lake margin, and show a distinct observational pattern compared with the other Northeastern interior basin tracks. They are three-dimensional casts in cross-section, as pillar-like morphologies, small- and large-sized concave-up and sub-cylindrical structures. This situation allows us to examine the deformation of the underlying layers and also the way in which the footprints were filled by the sediments deposited afterwards. The casts may also be presented as amorphous bulges or sedimentary layers deformed and downfolded, reaching one meter below the depositional surface. The interpretation of these tracks indicates the presence of quadrupedal (probably sauropod) and bipedal (theropod and

* Corresponding author.
E-mail addresses: ismar@geologia.ufrj.br (I.S. Carvalho), leonardigiuseppe879@gmail.com (G. Leonardi), rios.netto@geologia.ufrj.br (A.M. Rios-Netto), lborghi@geologia.ufrj.br (L. Borghi), alebpl@gmail.com (A.P. Freitas), jartur.andrade@yahoo.com.br (J.A. Andrade), idaleciocrato@gmail.com (F.I. Freitas).

https://doi.org/10.1016/j.cretres.2020.104626
0195-6671/

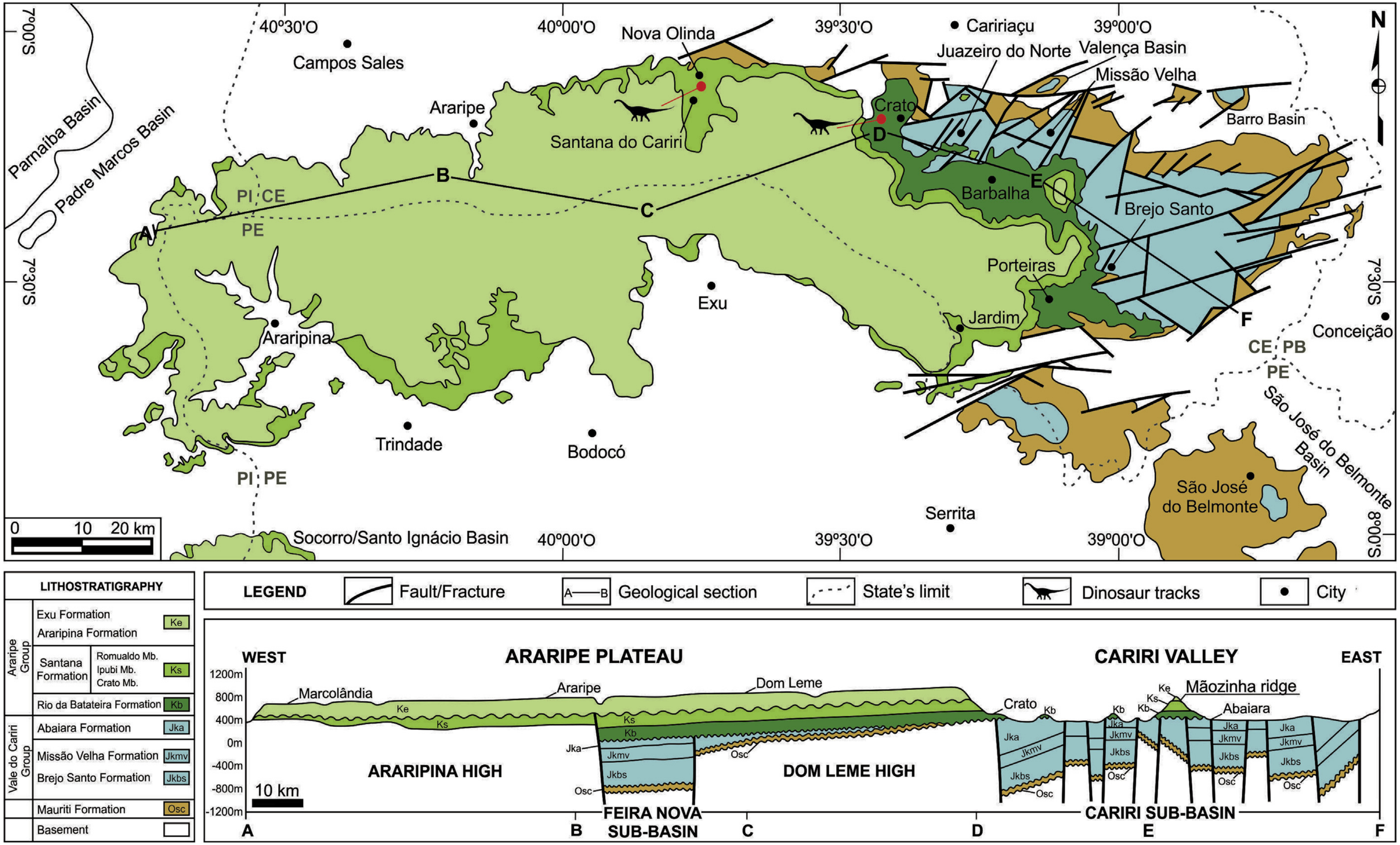

Fig. 1. Location of dinosaur tracks in the Araripe Basin, northeastern Brazil. The tracks occur in the Rio da Batateira and Santana formations (Aptian). Geological map modified from Assine (2007), Assine et al. (2014) and Rios-Netto et al. (2012a).

ornithopod) dinosaurs, providing new insights to the reconstruction of the terrestrial Cretaceous ecosystems in the Araripe Basin.

During the Cretaceous, tectonic events related to the Gondwana break-up caused major changes in the configuration of the South American continent. Then, many extinction and diversification events of the flora and fauna occurred as a response to the environmental changes (Bittencourt and Langer, 2011; Bronzati et al., 2015; Dunhill et al., 2016; Gorscak and O'Connor, 2016). Concerning the Southern hemisphere, the South Atlantic origin has driven deep modifications in climate, geographic configuration, distribution of land and seas (Arai, 2014a, b). Such context had a direct influence in the biotas, which were deeply modified by the South Atlantic tectonic scenarios. Nevertheless, in spite of the wide distribution in the Brazilian intracratonic and marginal sedimentary basins, the genesis of rocks originated in continental environments and the diversity of their fossils are poorly understood.

Besides an evaporitic interval, the local Alagoas Stage (approximately corresponding to the Aptian Stage) comprises the section known as “Pre-salt”, a sedimentary succession which, in the eastern Brazilian margin, presents a great exploratory importance. In the terrestrial interior basins, the Alagoas interval outcrops mainly in the Araripe Basin (Rio da Batateira and Santana formations), comprising relevant analogs to the paleoenvironmental interpretations of the Brazilian marginal basins, during the tectonic moment that led to the formation of all other intracratonic basins from northeastern Brazil (Carvalho and Leonardi, 1992; Carvalho et al., 1993, 1994, 1995). The study of this stratigraphic interval in the Araripe Basin contributes to the understanding of the paleogeographical evolution of South America during the Alagoas time interval, through an overview of the spatial and temporal changes in the paleoenvironments, in the context of the regional tectonostratigraphic evolution.

The Araripe Basin basement is composed of magmatic and metamorphic rocks and the basin is filled with clastic and chemical rocks. Proposals of lithostratigraphic subdivision of these rocks have been discussed and reviewed by many authors, although the most widely accepted terms for the lithostratigraphic units are the ones presented by Beurlen (1963, 1971), Ponte and Appi (1990), Ponte (1992), Neumann and Cabrera (1999), Assine (2007), Martill (2007) and Martill et al. (2007). The Aptian deposits comprise essentially fine-grained siliciclastic beds and laminated limestone with some inter-bedded levels of fine sandstones, marls and mudstones. These deposits occur in a rift-basin context, and are interpreted as floodplain areas and lacustrine environments (Neumann et al., 2002). One special aspect concerns the paleogeography of the last stages of crustal rupture of the Gondwana. The South Atlantic Ocean opening resulted in marine ingressions in the interior of the land mass, changing sharply the terrestrial environments, allowing a higher humidity in the interior of the continent (Carvalho and Pedrão, 1998; Carvalho, 2004; Medeiros et al., 2014) and the flourishing of many new ecological spaces.

2. The vertebrate tracks of Araripe Basin

The tracks under study at the Araripe Basin are so far the unique register of dinosaur tracks in the Aptian context of the interior Cretaceous Brazilian basins. The Cretaceous history of Araripe Basin spans from Berriasian to Cenomanian times, and footprints have been identified in the counties of Crato and Nova Olinda, in Ceará State (Fig. 1).

The Aptian tracks are found in two distinct units: Rio da Batateira and Santana formations (Fig. 2). In these two contexts, the tracks are observed as cross-section casts. This kind of three-dimensional structure is an important tool for the reconstruction of the terrestrial Cretaceous ecosystems.

The Rio da Batateira Formation is composed of microconglomerates, coarse to fine sandstones, siltstones, mudstones and carbonate levels. These deposits are interpreted as related to fluvial and lacustrine environments (Rios-Netto and Regali, 2007; Paula Freitas, 2010; Paula Freitas and Borghi, 2011) of Aptian age (Alagoas local stage, Rios-Netto et al., 2012b). It is overlain concordantly by the Crato Member of the Santana Formation. The tracks at the first site, Crato County, are found in the third tectonosequence of Paula Freitas and Borghi (2011). This sequence outcrops in the Batateira River, and is interpreted by Paula Freitas (2010) and Rios-Netto et al. (2012a) as floodplain areas of meandering rivers and lacustrine environments (Fig. 2A). The load structures, herein interpreted as dinosaur footprints, are found in this succession. They are in sections measuring 15 cm–120 cm in length and 20 cm–100 cm in depth, and occur in fine-grained siliciclastic beds, such as shales, siltstones and fine sandstones.

The second site occurs in Nova Olinda County, in the Santana Formation (Crato Member). This lithostratigraphic unit is mainly composed of micritic limestone, with some levels of marls and fine-grained siliciclastic beds (Neumann and Cabrera, 2002 a, b). The carbonates are finely laminated and interpreted as microbial-induced in alkaline lakes. In the Santana Formation, the dinosaur tracks are found in fine-grained sandstones, intercalated with shales and laminated carbonates (Fig. 2B). They range from 35 cm to 100 cm in length and 30 cm–50 cm in depth. The pressure occurred during the contact of dinosaur autopodia and the substrate led to the deformation of the upper surface of the sediments, with the origin of load structures accompanying a concave aspect with successive laminae deformation. The substrate should be soft and moist, with a relatively high cohesiveness (Carvalho et al., 2018) allowing for the deformation of successive layers, and developing undertracks.

The dinoturbation index was defined as the degree of dinosaur trampling (Lockley and Conrad, 1989) and its intensity over a surface (light: 0–33%, moderate: 34–66%, and heavy: 67–100%). In the Rio da Batateira Formation, the dinoturbation index can be considered as heavy (Fig. 3A–F), while in the Santana Formation it is light (Figs. 4A–C and 5).

3. Tracks as load casts

Preservation of animal footprints in the fossil record is strongly dependent on taphonomic processes, although it is the grain size and the sedimentation regime that determines if preservation will take place and if a footprint will be incorporated into the sedimentary record. The possibility of preservation is minimal during long-lasting periods of exposure without any sedimentation, and preservation is favored by rapid and significant sedimentation events. Thus, footprints are most commonly preserved in environments of cyclic sedimentation. Pronounced intra-trackway variation in the El Frontal tracksite (Lower Cretaceous, Cameros Basin, Spain) informs how track geometry might be dominantly affected by substrate conditions during formation. The original substrate of the El Frontal tracksite was non-homogenous due to lateral changes in adjoining microfacies with a gradient of substrate consistencies across the site. This implies that, even when produced by a single trackmaker, a wide range of morphological patterns of the fossil tracks may occur (Razzolini et al., 2014). The final preservation of fossil vertebrate tracks in laminated sediments has been explained by the stabilization process of the sediment surface by microbial mats, which would cover the tracks and protect them from erosion (Carvalho et al., 2013). Generally, fine-grained sediments rendered them more suitable for footprint preservation. Microbially induced sedimentary structures are in fact observed in many of the fine-grained lithofacies where dinosaur tracks are also found, and the large number of these tracks may be related to the role of the mats in their preservation.

Deformation of the print-bearing surface, e.g. by a heavy animal, favors the preservation of underprints and transmitted prints on bedding planes beneath the primary footprint-bearing surface (subtraces or "under tracks", also called "ghost prints") (Sarjeant and Leonardi, 1987). Reworking of sedimentary substrates by terrestrial vertebrates was deemed important in disturbing the primary grain fabric and sedimentary structures by Laporte and Behrensmeyer (1980). Abundance of vertebrate bioturbation depends upon rates of trampling, texture and plasticity of the substrate, and also the subsequent permanent burial.

The pressure produced by the tetrapod autopodia on the substrate has been analyzed by several authors (García-Ramos and Valenzuela, 1977; Boyd and Loope, 1984; Valenzuela et al., 1988; Avanzini, 1998; Romano and Whyte, 2003, 2012; Falkingham et al., 2016) in relation to the mechanics of movement, the development of deformational structures, and the total substrate bioturbation. The grain size, consistency, plasticity and water content of the sediments are determinants of the preservation of anatomical details.

Tracks may occur as isolated or superimposed casts in cross-section, as pillar-like or concave-up morphologies, but casts are more commonly irregularly cylindrical to "U" shaped (with a larger basal diameter than at the top, usually undertracks), as can be observed in the Araripe Basin. Undulating forms that grade into load casts may be recognized as tracks when they occur along the same bedding plane adjacent to recognizable tracks, and when they have relief and dimensions similar to those of associated distinct tracks (Fig. 3A–D).

Milàn et al. (2006) analyzed the sediment deformation induced by theropod foot movements during a stride. They observed, based on the types of deformation, that different theropods adopted different walking strategies at different times. In layered sediments, this causes the formation of a stacked succession of undertracks that gradually becomes wider, shallower and less detailed downward. The deformation structures in a vertical section have proven successful in obtaining additional details about the walking kinematics, that rarely could be obtained from studying the true track at the surface (Milàn and Bromley, 2006). Then, there is the usefulness of vertebrate tracks for the correct interpretation of the trackmaker and the substrate consistency (Milàn et al., 2004, 2006). In Rio da Batateira Formation (Araripe Basin), it is also possible to observe the digit impressions in some of the casts, enabling their interpretation as belonging to bipedal or quadrupedal dinosaurs (Fig. 3E, F).

In the 3-D casts there is a section that shows evidence of digits, indicating the high plasticity of the substrate where the track was produced, similarly to the Villar del Arzobispo Formation, Kimmeridgian–Tithonian (Campos-Soto et al., 2019), Spain (Castanera et al., 2010). In this context, it is important to observe that the animal's behavior is also, to some extent, related to the palaeoenvironment: stable and unstable surfaces control aspects such as walking speed, acceleration and kind of gait.

Marty (2011) indicated that, after the foot impact, some structures are apparent on the surface (true track, overall track, underprint) and others hidden within the substrate (undertrack, deep track). Laboratory track simulations presented by Manning (2008) enabled the analysis of the magnitude and distribution of load acting on surface sediments, transmitting through and deforming subsequent layers (Fig. 4B, C). It was shown that many vertebrate tracks are transmitted features and do not represent 'true' surface tracks. Then, the substrate properties and the animal's behavior allow for a wide range of track morphologies. The main modes of footprint preservation can thus be evaluated as the relationship between the substrate and lower surface of the autopodia. This aspect is clear in the tracks at the Rio da Batateira and Santana formations, due to the deformation produced in the lower sedimentary levels after the footprint impact.

4. Interpretation of the Aptian Araripe tracks

The study of Avanzini (2001) showed that it is possible to identify dinosaur footprints in stratigraphic sections based on: spatial distribution of bird eyes and/or fenestrae, the presence and geometry of microfaults and thrusts on the base of the load casts, hardness and the shear of the laminites on the base of the structures, and the formation of circular, three-dimensional displacement rims.

Depending on the substrate, Falkingham et al. (2011) suggest using tracks (not only of dinosaurs, but vertebrate tracks in general) as if they were paleopenetrometers. In geotechnics and pedology, a penetrometer is a device used to gauge the resistance, the consistency and the structure of soil, mainly in house-building. The depth of a track could be seen and used in an analogous manner (with some due reservations) to study these characteristics of the paleosurface where the track was printed. Such a study would help analyze the paleoenvironment.

"Footprints are molds of the feet in the substrate over which the animal passed. A too hard and firm substrate will not allow the formation of footprints. If the upper surface of a layer is quite fine-grained and cohesive, neither too dry nor too wet, an exact impression of the undersurface of the feet may be produced. Not only the major morphological features, such as claws, nails or hoofs, but also less prominent ones, such as scales or even bristles, may be shown clearly in the mold. When the substrate is too coarse or dry, these details will not be shown. When too wet or too yielding, the impression may be deformed. If the substrate is submerged, the footprints may be severely marred or completely obliterated" (Sarjeant and Leonardi, 1987).

The physical properties of the substrate in which a footprint is found depend on the mineral composition, the organic content and how much the substrate is saturated by water. The penetration depth of a footprint in a substrate is related to the ground's resistance and the pressure exerted by the dinosaur foot (Fig. 6). Then, the morphology of tracks and the deformation of the substrate are directly linked to the physical state of the substrate, the vertical distance separating the tracking surface and the study surface, the shape of the dinosaur's foot, and the animal's behavior. The rate of plastic deformation depends, among many other factors, on the magnitude and duration of the applied stress (Pérez-Lorente, 2015). Another aspect concerns the weight distribution in the dinosaur foot. In bipedal dinosaurs, the third digit exerts a higher pressure on the substrate, conducting to greater deformation in the central area of the cast (Fig. 3E). On the other hand, a better distribution of weight occurs during the impact of a quadrupedal dinosaur's feet, allowing for a more uniformly rounded cast (Fig. 3D).

The distribution of weight on all four feet is also noticeable in quadruped dinosaurs; the weight can be loaded equally on the four feet, but more frequently most of it is leaned on the back side (=on the hind, on the "rear axle"). Based on these observations, we consider that, in graviportal ornithopods, most of the weight is usually loaded on the hind feet; so, in a not surprising way, quadrupedal trackways are not so frequent in this group (Haubold, 1971; Thulborn, 1990; Lockley, 1991; Pérez-Lorente, 2015). In northeastern Brazil, however, in the Lower Cretaceous Sousa Basin, there are good quadrupedal trackways like that of *Caririchnium* (Leonardi, 1984); and also *Sousaichnium* (Leonardi, 1979), that regularly leaned the right front-foot to the ground. They are clearly quadrupedal trackways and they have very large hind-feet and very

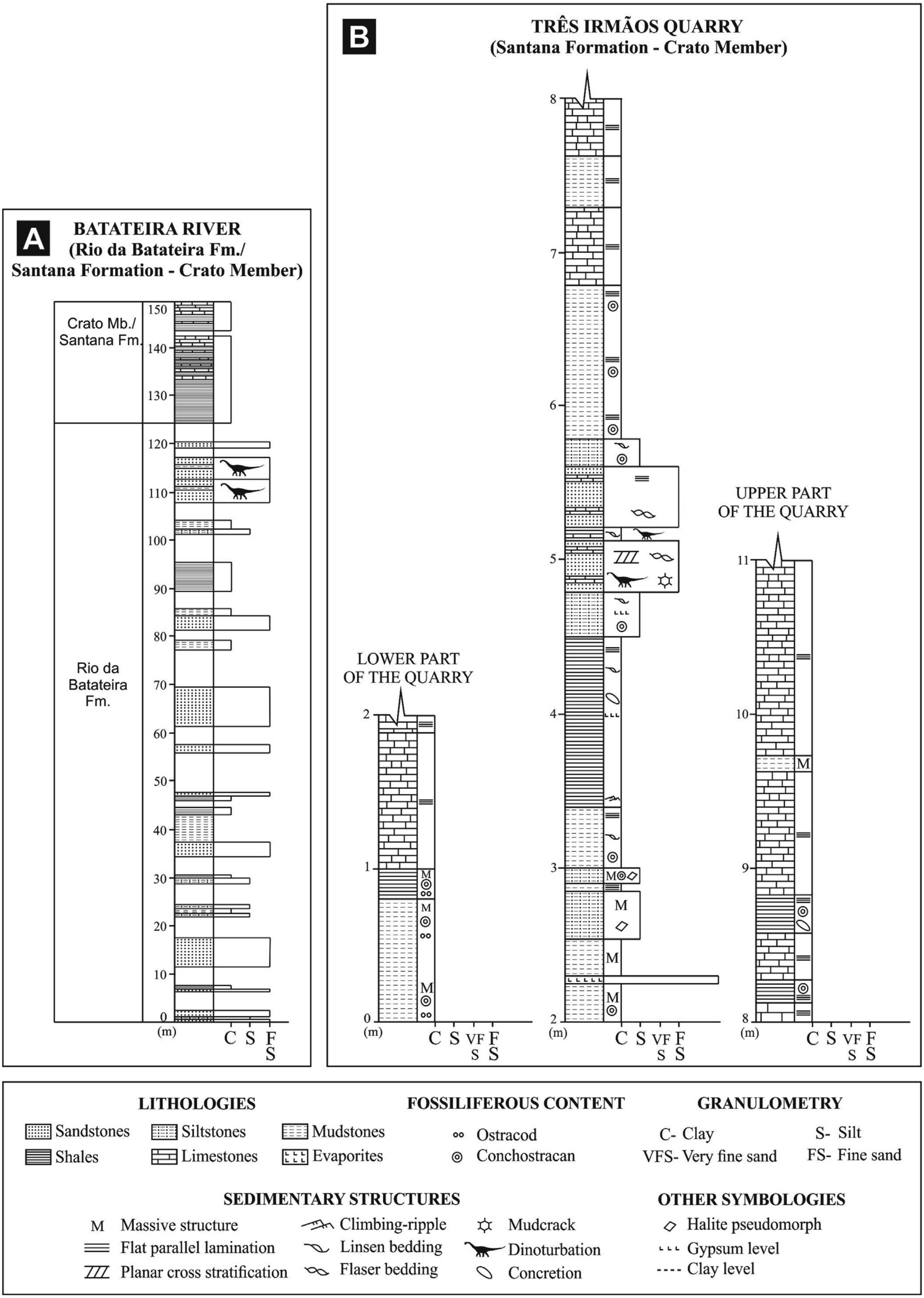

Fig. 2. A. Stratigraphic profile of Rio da Batateira Formation at the Batateira River site, Crato County. Dinosaur trampling is found in successive levels of fine-grained sandstones and shales; B. Finely laminated microbial carbonates of the Santana Formation (Crato Member), interpreted as having been deposited in carbonate lakes. The subaerial exposure of these lakes allowed them to suffer dinoturbation.

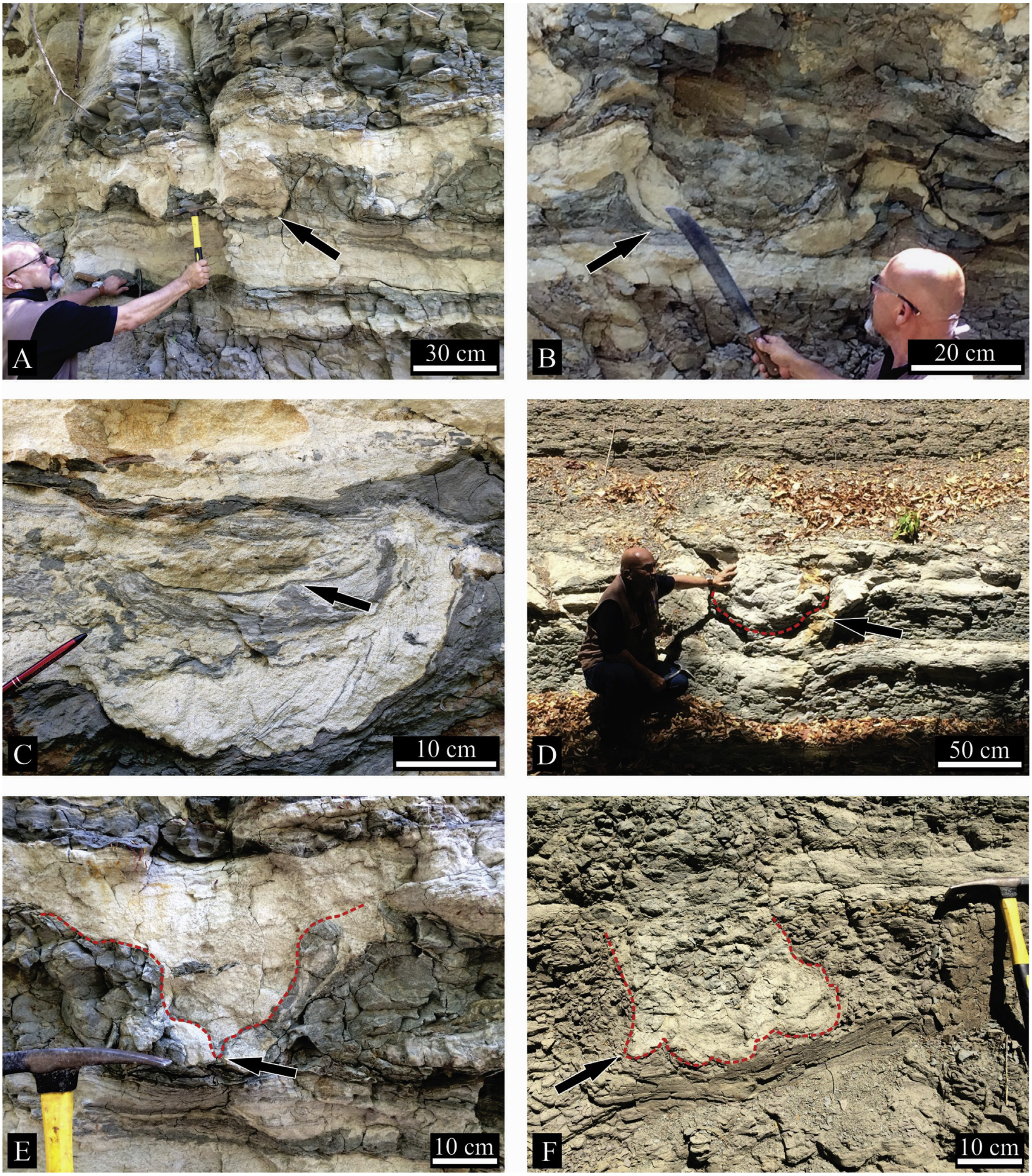

Fig. 3. Cross-section of tracks from the Rio da Batateira Formation, Araripe Basin. **A.** The cross-section through dinosaur tracks sometimes displays large structural variations, and the disturbed layers are the result of heavy vertebrate trampling; **B.** A quadrupedal dinosaur (probably sauropod) track. The deformation of sandstones and shales produced a large flattened depression, bordered by high declivity borders (displacement rims). Note that the lower layer was already lithified when the dinosaur foot reached it; **C.** Quadruped dinosaur track presenting a base larger than the upper part; **D.** The deformation produced by the foot impact can reach 100 cm below the surface, indicating an original muddy substrate due to high water content; **E.** In bipedal dinosaurs, the digit exerts a higher pressure on the substrate, conducting to a greater deformation in the central area of the cast; the arrow indicates the position of digit III; **F.** Section of a 3–D track cast. In the lower part of the cast, it is possible to observe the digit imprints, indicating a sauropod track. Arrows and dashed lines indicate the limits of the foot contact with the sediment, the original surface stepped on. Surrounding the footprints there are deformations induced by the foot load.

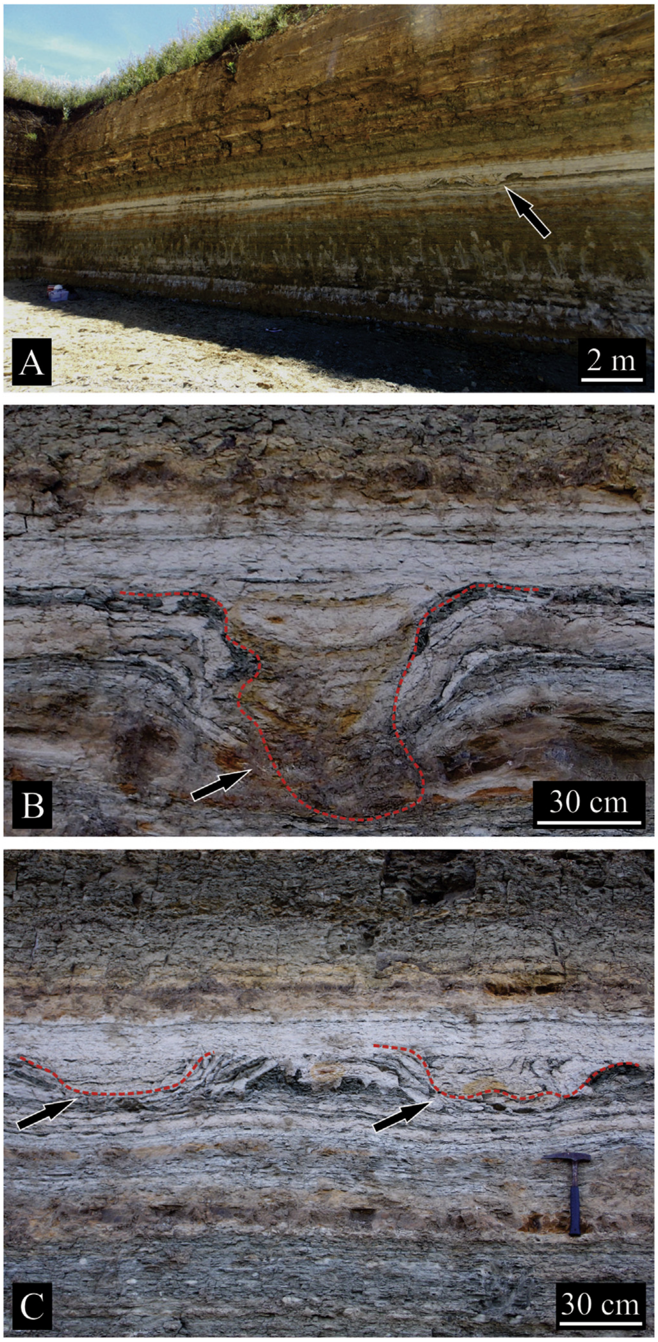

Fig. 4. A. An overview of the Pedreira Três Irmãos succession (Nova Olinda County), Santana Formation (Crato Member), with the trampling level (whitish color in the middle of the section). Track walls are sub-vertical (even after the foot was withdrawn), which is an indication that the original consistency (firmness) of the substrate was high; **B.** Close-up of a sauropod or large quadrupedal dinosaur track cast. The strongly bent and downfolded layers indicate a deformation due to a foot impact. It is a cast of the true track; **C.** These deformation tracks are found in a same stratigraphic interval eroded in its upper surface before the following deposition of fine sandstones. Arrows and dashed lines indicate the limits of the foot contact with the original surface stepped. Surrounding the footprints, there are deformations induced by the foot load. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

small forefeet. The same is true for *Caririchnium leonardii* (Lockley, 1987) Albian of Colorado (USA), and for some trackways attributed to hadrosaurs, like *Amblydactylus* (Sternberg, 1932). Ornithopods are considered, in general, bipeds, optionally quadrupeds, and this kind of gait could be true for some ornithopods occasionally found at the Araripe Basin.

The tracks observed in the Aptian stratigraphical units of Araripe Basin are vertical sections in a succession of intercalated marls and fine sandstones (Crato Member, Santana Formation, Figs. 4A and 5) and also fine sandstones and shales (Rio da Batateira Formation). The depth of the deformation from Crato Member is 50 cm under the depositional surface, while in Rio da Batateira Formation it can reach 100 cm, probably due to the higher plasticity of the substrate, similarly to some sauropod tracks from the Upper Jurassic of Spain (Valenzuela et al., 1988; García-Ramos et al., 2006). According to Pérez-Lorente (2015), the bearing capacity in which a foot can sink into sediment occurs when the resistance to penetration of the foot is equal to the pressure applied. This will be directly related to the substrate properties, such as plasticity and consistency. The analysis of Falkingham et al. (2011, 2014) discusses the aspects concerning this dynamic of the effects of different substrate models on track formation potential. As the walls of some of the Crato Member (Santana Formation) tracks are still vertical (even after the foot was withdrawn), it is an indication that the original substrate was soft, yet cohesive and competent (Fig. 4B), i.e., that the foot could enter deeply, but the sediment stayed together leaving sharp walls. The tracking surface and layers beyond the depth of 50 cm from the surface were deformed by dinosaur autopodia, due to the pressure over soft to moderately firm mud sediments, as there are no evidences of fractures or microfaults. This is distinct from the Rio da Batateira Formation tracks, where deformation can reach 100 cm depth of foot impact from the surface (Fig. 3D) as the result of a less firm substrate.

5. Paleoenvironmental interpretations based on dinoturbation

5.1. Tracks and carbonate lakes

The records of dinosaur tracks in the Araripe Basin occurred in a moment of environmental changes in alkaline carbonate lakes. They show the wide distribution of transitional siliciclastic to carbonate environments related to the deposition in an endorheic lake, during a hot and arid climate.

Carbonate environments are important for the preservation of fossil tracks (Leonardi and Mietto, 2000; Marty, 2008; Santos et al., 2013, 2015; Santos, 2016; Campos-Soto et al., 2017). An example of this is the deposition of Calcari Grigi di Noriglio Formation, in the Piattaforma di Trento (Lower Jurassic, Lavini di Marco, Italy). The carbonates were deposited in the margin of a tidal flat near a large continental area in tropical latitude. The tracks are found in the Lower Member − a carbonatic succession deposited in shallow waters, with episodical subaerial emersion and the presence of laminated stromatolites. Avanzini et al. (2000) analyzed this succession and demonstrated that, in the Lower Member, the laminated carbonates are due to the algae and microbial development. The depositional environment is interpreted as an inter-supratidal carbonate platform. These authors indicated the presence of iron oxides in small spherules (glaebulae), interpreted as having been produced by the bacterial activity during the soil formation. But the most striking features are the fine laminated microbial sediments in which the tracks are preserved. Although the interpretation of the preservation of the Calcari Grigi tracks is based on geochemical processes, especially dolomitization, Avanzini et al. (2000) illustrated many sedimentary structures typical of the subaerial dissection of algal mats, related to the track bearing surfaces.

Lacustrine carbonates also enable the preservation of a wide diversity of high-quality dinosaur footprints (Moratalla et al., 1995; Pérez-Lorente, 2017). In the analysis of the tracks in Cameros Basin

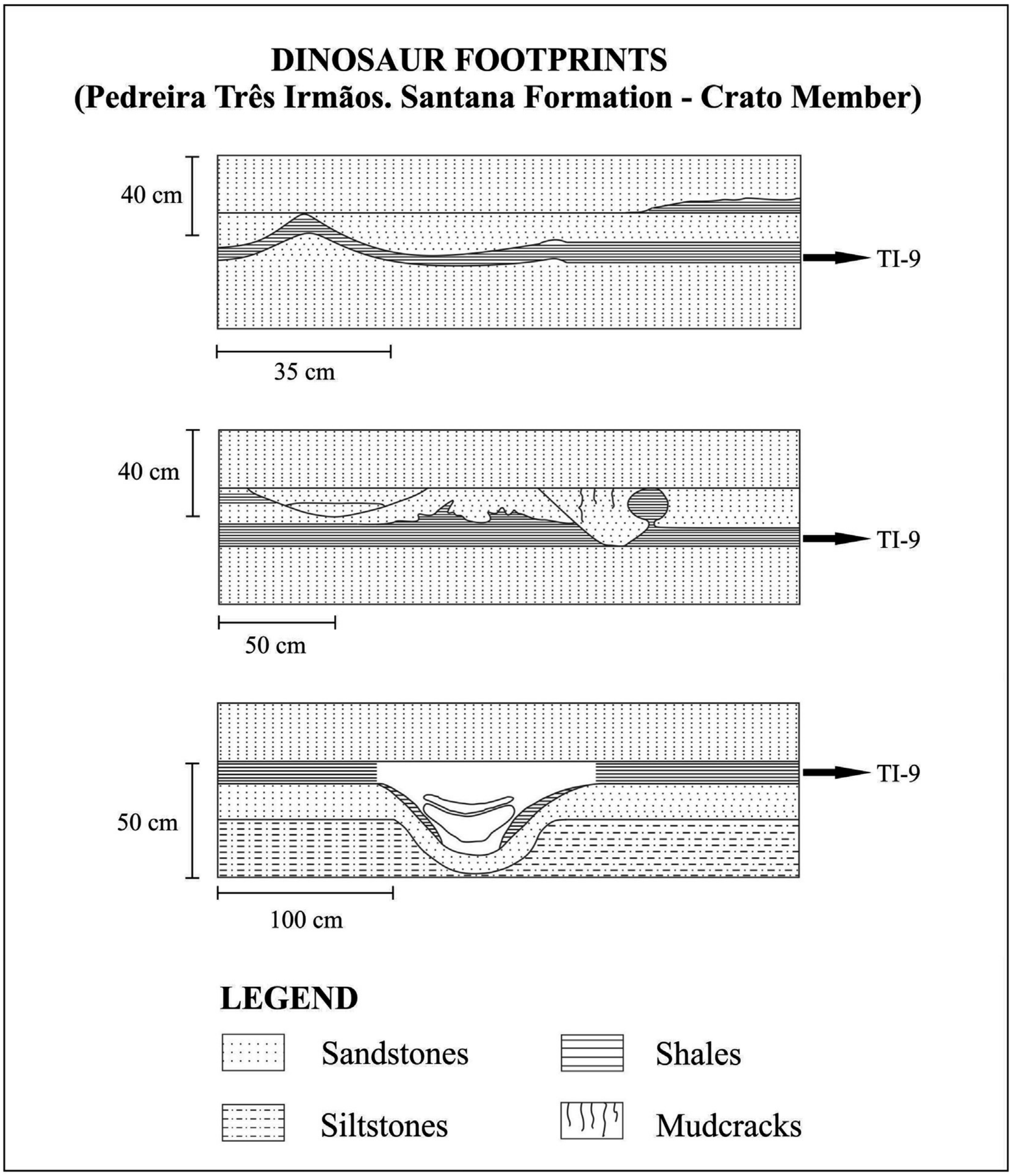

Fig. 5. Three morphology patterns of the dinoturbation at Santana Formation (Pedreira Três Irmãos) related to the cohesiveness of the substrate trampled by the dinosaurs. The dinoturbation index is considered light. The tracks are vertical cross-sections in a succession of intercalated marls and fine sandstones. Numbers and letters are references to biostratigraphical sampling.

(Lower Cretaceous, Spain), Pérez-Lorente (2015) showed a wide diversity of preservation modes of dinosaur tracks. The middle succession of the Enciso Group (Aptian) presents siliciclastic and limestone, interpreted as having been deposited in large lakes. The lakes were shallow, in the context of a continuous sheet of shallow water and some deeply flooded zones. In these fresh or brackish water lakes, mainly carbonate muds and gypsum were deposited. Fossil footprints are found in almost all environments, except in the open lake carbonate zones.

The relationship between carbonate and siliciclastic environments with microbial sedimentation has been described by many authors (Marty, 2008; Marty et al., 2006, 2010; Carvalho et al., 2013; Santos et al., 2013; Cariou et al., 2014). In the Reuchenette Formation (Switzerland, Upper Jurassic, Kimmeridgian), sauropod trackways occur in three track-bearing laminite intervals interbedded between shallow marine carbonate platform sediments, deposited in inter-to supratidal paleoenvironments in a subtropical climate. This is indicated by the macroscopic (stromatolitic lamination, desiccation cracks, wave ripples and invertebrate burrows) and microscopic features. Thin sections in the laminites of the tracksite shows wrinkled cryptomicrobial lamination, characterized by an alternation of clotted micrite and irregular seams enriched in organic matter (Marty et al., 2010). Another example is the Marnes de Besançon Formation, Jura Mountains (upper Oxfordian, France) where eight dinoturbation beds are found with true tracks, undertracks and overtracks (Cariou et al., 2014). The preservation of these dinosaur footprints in biolaminites allows for a detailed analysis of their mode of formation. The geological context where these tracks are recorded is a tidal-flat punctuated by frequent flooding and emersion phases followed by desiccation, microbial mat development, and new sediment inputs. Dinosaur tracks are found recorded in intertidal to supratidal settings.

5.2. Substrate consistency

Another characteristic phenomenon tied to the substrate is the development of displacement rims around the footprints, which are quite variable in size and form, and are often also present if the footprint can be seen only in section. Some of these rims are wide and thick, sometimes with the aspect of true bulges of mud, now evidently lithified. Such conspicuous mud bulges are especially well developed in sauropod footprints, of both the fore- and hind limbs. In these cases, the very heavy animals had impressed their feet into a surface of very plastic and/or waterlogged muds (Leonardi, 1987, 1989; Thulborn, 1990; García-Ramos et al., 2002, 2009; Piñuela, 2018). Under these circumstances the front prints were partially overprinted by the subsequent hind tracks, so that it becomes very narrow or little more than a crescent-shaped slit. In other cases, and frequently at our sites, the displacement rim around a footprint is very low and narrow, indicating a more compact and firm mud. In other instances, it seems as though the weight of successive overlying layers deposited over the tracks compressed and squashed the footprints and their displacement rims (Lockley and Xing, 2015; Piñuela Suárez, 2015).

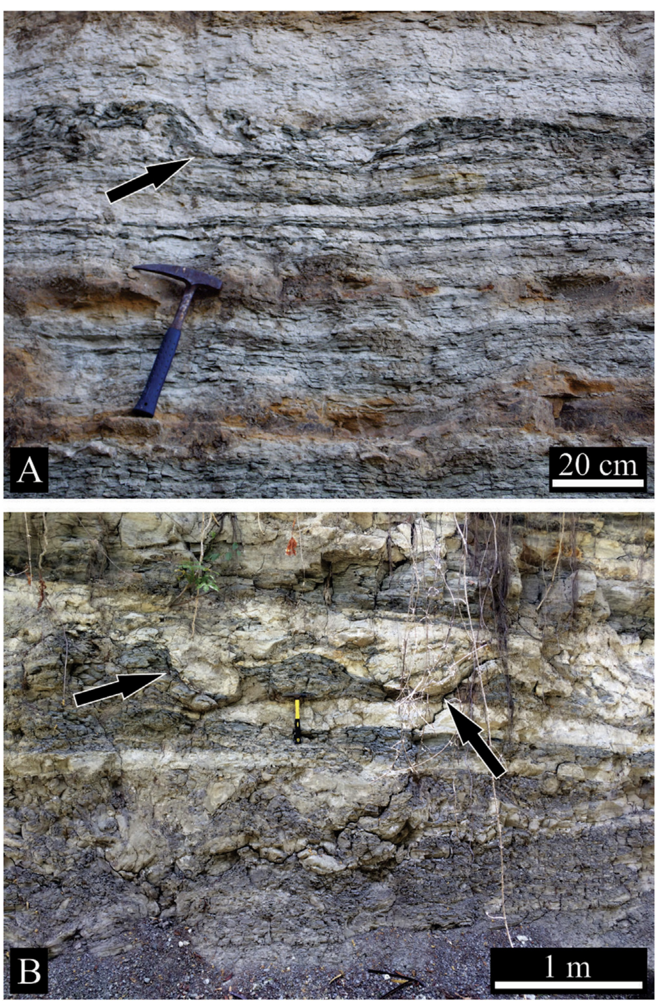

Fig. 6. The foot impact on the surface can also represent 'true' surface tracks. This is clearly observed in the Santana Formation (A) and Rio da Batateira Formation (B), where the superficial track is not followed by successive deformation of the underlying sediments. Arrows indicate the limits of the foot contact with the sediment, the original surface stepped on.

In the Anacleto (lower Campanian) and Allen (upper Campanian-lower Maastrichtian) formations (Río Negro Province, Argentina), Díaz-Martínez et al. (2018) identified tracks preserved in a cross-section, i.e., a track preserved in a view perpendicular to the bedding plane. These are concave structures caused by deformation, with their bases flat or slightly curved downward in relation to the bedding. They are distributed in two distinct environments: meandering fluvial and shallow lacustrine systems, that are associated upward to an aeolian setting. Another important aspect is that the bedding surface shows wrinkle structures, indicative of microbial mats. In the Elliot Formation (Lower Jurassic, South Africa), interpreted as a temporary fluvial deposit, Sciscio et al. (2016) also observed soft sediment deformation structures, especially close to the upper bedding plane, and vertical sections showing soft sediment deformation directly beneath depressions on the upper bedding plane of the horizontally laminated sandstones. They were interpreted as deformation related to the loading effect by a dinosaur foot. Then, it was demonstrated that morphological differences are mainly due to variations in the substrate rheology. In the alluvial plains and meandering river deposits of the Triassic Caturrita Formation (Paraná Basin, Brazil) the fossil tracks observed in the bedding plane are concave, circular-shaped structures, with a laminar deformation. Silva et al. (2007) interpreted these features as a disruption of the substrate homogeneity caused by bioturbation of prosauropod dinosaurs. The distinct color pattern, more reddish than the surrounding substrate, was interpreted as a result of differential diagenesis.

The amount of collapse of the sedimentary levels below the superficial track is a function of the cohesiveness of the sediment and the depth of the footprint. The lower the cohesiveness and the deeper the tracks, the easier the mud collapses. The study of La Senoba footprints in siliciclastic rocks (Enciso Group, upper Barremian-Aptian, Spain) showed that, even in a single trackway, the same features are not always present: physical properties of the mud – including consistency, viscosity, and thixotropic behavior, water content, and also the extent to which algal mats covered the surface – affected their preservation potential (Pérez-Lorente, 2015). The dinoturbation features from the Araripe Basin show cohesiveness that is different than that of the substrate in the Aptian deposits. In Santana Formation, they occur in a context of more cohesive sediments, as the walls of the structures are verticalized and they are still well defined (Fig. 4B) when compared with those from Rio da Batateira Formation. In this last unit, the mud collapse and the deeper deformation in the substrate indicate a more waterlogged substrate, that enables a greater deformation of the plastic substrate.

The true tracks, undertracks and overtracks in the Cretaceous basins of Northeastern Brazil were generally produced in subaerial and subaqueous settings. It is possible to identify footprints with well-defined morphologies or progressively losing their evidence and their typical aspect due to their association with mud cracks, fluidization, convolute and radial structures (Carvalho, 2000a, b). Those with impressions of claws, nails, and soft tissue, such as the sole and phalangeal pads, are considered to be produced in mud sediments with high plasticity and low water content, probably in a subaerial setting of floodplains and marginal lakes areas. This context is easily recognized by the association of the footprints with raindrops and mud cracks that sometimes has its origin related to the contour of the track or as extension of the digits. The dehydration of the muddy sediments produces structures similar to those described by Lockley and Conrad (1989). If the geological setting where the footprints were produced was an alluvial fan, despite having also been produced in a subaerial setting, their morphology is almost always restricted to the contour. If the bottom is a firm ground or semiconsolidate sediment, the preservation of the tracks can be good or excellent, which is very frequent in the tracksites of the Kimmeridgian of Asturias (Piñuela Suárez, 2015).

Since the substrate is the major control in determining the final track morphology, the tracks are excellent structures to analyze the substrate consistency where the animal has walked (Gatesy et al., 1999; Falkingham et al., 2011; Piñuela Suárez, 2015; Díaz-Martínez et al., 2018). Cross-sections of tracks such as those from the Araripe Basin, which lack anatomical details, are difficult to assign within a particular trackmaker's ichnotaxon and/or taxon. They are more useful to provide information concerning the distinct moments of the track formation and its relationship with the substrate (Moratalla, 2009, 2011; Avanzini et al., 2012; Falkingham and Gatesy, 2014; Piñuela Suárez, 2015; Razzolini, 2016; Gatesy and Falkingham, 2017; Herrero Gascón and Pérez-Lorente, 2017; Díaz-Martínez et al., 2018). It was also demonstrated by Piñuela (2012), Piñuela Suárez (2015), and García-Ramos et al. (2009) that some morphological changes, in the same track from surface to the lower levels, lead to deep theropod undertracks looking like ornithopod tracks.

The natural track casts of Rio da Batateira and Santana formations (Aptian, Araripe Basin) penetrates into the underlying layers as small and large sized concave-up and sub-cylindrical structures. The casts are generally presented as amorphous bulges or sedimentary layers deformed and downfolded. They are typical for dinosaur track casts, and can be explained by dinoturbation processes. In this context, the preservation aspect of the tracks depends on the texture and plasticity of the substrate and the opportunity for permanent burial. The pressure produced by the tetrapod autopodia on the substrate induces, besides the mechanics of movement, the development of these deformational structures, and the total bioturbation that, together with the grain size, consistency, plasticity and water content of the sediments, are determinants to the preservation of anatomical details (Boyd and Loope, 1984; Avanzini, 1998), which is not observed in these natural casts found in Rio da Batateira and Santana formations.

The size of the tracks of the Santana Formation indicates larger dinosaurs, although a specific identification of the trackmakers is not possible. They can be considered deep tracks that are defined by Gatesy (2003) as true tracks, made by a trackmaker sinking deeply into soft mud. The foot penetrates through the sediment, and the true track is located within the sediment and may reveal information about the conditions of the foot. In a track cross-section, track penetration depth is the maximum depth (measured from the tracked surface) where undertracks or deformation of the sediment are still discernible (Marty, 2008). Deep footprints are found in soft mud of floodplain depressions or near rivers, where the water table was close to, or slightly above, the surface. According to Lockley (1986), deeper tracks are sometimes made in water as deep as about 50 cm. Although the Santana Formation tracks were produced in soft sediments, it is considered that these showed high cohesiveness, allowing the penetration of the feet to develop a shaft structure without sediment collapse. Otherwise, in the case of Rio da Batateira Formation, although the feet also sunk deeply in the substrate, high deformation of the sedimentary laminae occurred, an indicative of the low cohesiveness of the deposits.

Similar track casts are found in North Horn Formation (Maastrichtian, Utah – USA). They are commonly less than about 40 cm across and about 40 cm deep. Therefore, individual tracks with pillar-like, cylindrical morphologies may measure from about 25 to about 53 cm in apparent diameter, and about 47 cm deep. Irregular bulges and rounded surfaces on the basal portions of tracks are possibly amorphous impressions of the short toes of herbivores (Difley and Ekdale, 2002). In ichnosites of the Lower Cretaceous of the Hekou Group (China), La Rioja (Spain) and the Lower Jurassic Calcari Grigi di Noriglio (Italy), similar features were interpreted as sauropod track casts (Avanzini, 2001; Pérez-Lorente, 2015; Xing et al., 2015). This probably reflects the fact that large-sized sauropod tracks resist weathering and are more easily found. Xing et al. (2015) assumed that this apparent low diversity in the Hekou Group (China) is an artifact resulting from the small sample area and the fact that all the outcrops are cross-sections where bedding planes are scarce and limited to small surfaces.

This kind of phenomenon is easier to be observed and understood, and is more convincing, as produced by dinoturbation in the Asturian Upper Jurassic successions (Northern Spain), where the infilling of very deep dinosaur (often sauropod) tracks is white sandstone, and the substrate where the large animals walked was soft mud, later diagenized in marls or mudstones. The Lastres Formation (Kimmeridgian) presents in this context a large amount of true tracks and undertracks of a fluvial-dominated deltaic system flowing into a shelf lagoon (García-Ramos et al., 2006; Piñuela Suárez, 2015; Piñuela et al., 2011a, b, 2016).

5.3. Dinoturbation structures

The dinosaur tracks in the Rio da Batateira Formation may look like simple load casts; however, they are herein interpreted as a level with dinosaur overtrampling, and, more in detail, an association of bipedal and small and large quadrupedal dinosaur tracks. By the time these footprints were produced, there was a hyperpycnal stream in an intermittent lake, and the climate was hot and humid. Thus, the assumed interpretation is that the dinosaur tracks were produced in the lake's margins (Fig. 7). Successive flooding, and subsequent sediment influx, with the stabilization by early cementation and by the microbial mat fabric over the tracks, enabled their preservation.

In the Santana Formation, only large sauropod tracks have been found so far. They were preserved as shaft molds and more superficial deformations, probably related to a taphonomic process. One possibility to explain this kind of preservation was analyzed by Sanz et al. (2016) in the Huérteles Formation (Cameros Basin, Berriasian, Spain). These authors, based on a conceptual model of very well-defined sauropod tracks in three dimensions (due to natural outcrops of sections in the field), showed that soft sediments that become progressively more rigid and resistant at depth are not appropriate for tracks. In this case, a more rigid, but not very resistant, superficial layer (caused by desiccation), overlying a softer layer that is extruded to form a displacement rim, shows better preservation of sauropod trackways. The form of the displacement rim depends partly on the geometry of the footprint. These tracks could be filled up with water due to the phreatic level, if the latter was close to the ground surface. The simulations also demonstrate that track depth alone is insufficient to differentiate true tracks from undertracks.

The impact caused by sauropod feet and the patterns of deformation were analyzed by Thulborn (2012) and Thulborn et al. (1994) in the Broome Sandstone (Lower Cretaceous – Australia). It was possible to observe lateral and superficial disturbances of the substrate created by sauropods traversing thinly-stratified sediments, deforming the substrate to such an extent that they remodeled the topography of the landscape they inhabited. In addition to the sauropod autopodia impressed on the surface, the boundary walls are steep and curved at the top. These features were designated as transmitted reliefs (underprints or ghost prints), zones of contorted bedding that underlie and surround the sauropod footprints, which occasionally attain the size of minor tectonic features. The sauropod dinoturbation in the Santana

Fig. 7. A scene during Rio da Batateira times, with supposed theropod and sauropod trackmakers. Life reconstruction of the paleoenvironmental setting of these tracks (Art by Deverson Silva, Pepi).

Fig. 8. A scene of the track formation and preservation during Crato times, Araripe Basin. A shallow carbonate lake, with some fine siliciclastic sediments and colonized by microbial mats (Art by Deverson Silva, Pepi).

Formation also occurred in soft sediments, but in a distinct environmental context. They are found in fine-grained sediments, such as purely terrigenous, intercalated with carbonate muds. There are erosional features in the upper part of some tracks, showing that they were readily eroded and destroyed as the succeeding sediments were deposited. The possibility of preservation is minimal during long-lasting periods of exposure, without any sedimentation, and favored by rapid and significant preservation events. The Santana dinoturbation structures are interpreted as having been produced in an alkaline lake margin, with intermittent freshwater influx (Fig. 8).

An important aspect of these dinosaur track occurrences is the evidence of some groups scarcely represented by osteological remains in the Araripe Basin, such as the sauropods. Their tracks are the first evidence in the Aptian deposits of the pre-salt context, enhancing a new overview in the terrestrial ecosystems during the Early Cretaceous in the Northeastern Brazilian basins.

6. Conclusions

The dinoturbation found in Rio da Batateira and Santana formations, contextualized stratigraphically, enabled a proper analysis of paleoenvironmental aspects and the biota diversity of Aptian terrestrial environments in the Araripe Basin. The new data contributed to an overview of the spatial and temporal changes in the paleoenvironments of the time interval related to the pre-salt deposits.

These biodeformation structures are temporal markers of subaerial exposition surfaces throughout the basin, recording cyclical changes in the environmental conditions during the deposition in the carbonate lakes.

These tracks were produced in an exposed waterlogged substrate or in a flooded area, where the liquefaction of the sediments and local deformation, in the case of more cohesive sediments, were possible. The evaluation of these tracks and their relationship with the substrate allow for the understanding of the deformation due to a foot impact, and the construction of a model for the cross-section track formation. They also show behavioral insights into the trackmaker biology, substrate properties, and environmental factors. They are an important tool for the reconstruction of the terrestrial Cretaceous ecosystem in the context of the Araripe Basin. It is noteworthy that no sauropod body fossils were so far found either in this formation or in the whole Araripe Basin.

CRediT authorship contribution statement

Ismar de Souza Carvalho: Conceived and designed the research; Conducted the field work; Performed the analysis; Interpreted obtained data; Wrote the manuscript. **Giuseppe Leonardi:** Conceived and designed the research; Performed the analysis; Wrote the manuscript. **Aristóteles de Moraes Rios-Netto:** Interpreted obtained data; Wrote the manuscript; Project administration. **Leonardo Borghi:** Interpreted obtained data; Wrote the manuscript. **Alexandre de Paula Freitas:** Conducted the field work; Interpreted obtained data; Wrote the manuscript. **José Artur Andrade, Francisco Idalécio de Freitas:** Conducted the field work; Interpreted obtained data.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to Eduardo Koutsoukos, Laura Piñuela and Peter L. Falkingham for the detailed and careful revision that improved this manuscript. We are also indebted to Marco Avanzini (Lavini di Marco, Museo Tridentino di Scienze Naturali), Fabio Massimo Petti (Società Geologica Italiana) Félix Pérez-Lorente (Universidad de la Rioja), James O. Farlow, Laura Piñuela and José Carlos García-Ramos (Asturias, Museo del Jurásico de Asturias) for their support on field work and discussion on dinosaur tracks and dinoturbation, which enabled the interpretation of the dinoturbation structures in the Araripe Basin; Jaime Joaquim Dias (Rio de Janeiro Federal University) and Deverson Silva for the images and drawings. We acknowledge the support from Shell Brasil Petróleo Ltda. and the strategic importance of the support given by ANP (Brazil's National Oil, Natural Gas and Biofuels Agency) through its R&D levy regulation. Financial support was also received from Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil, grant 303596/2016-3 and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro, grant E-26/202.910/2017.

References

Arai, M., 2014a. Aptian/Albian (Early Cretaceous) paleogeography of the South Atlantic: a paleontological perspective. Brazilian Journal of Geology 44 (2), 339–350.

Arai, M., 2014b. Reconstituições paleo-oceanográfica e paleoclimática do Oceano Atlântico no Cretáceo, baseadas em dinoflagelados. In: Carvalho, I.S., Garcia, M.J., Lana, C.C., Strohschoen Jr., O. (Eds.), Paleontologia: Cenários de Vida - Paleoclimas, first edition, vol. 5. Editora Interciência, Rio de Janeiro, pp. 45–62.

Assine, M., 2007. Bacia do Araripe. Boletim de Geociências da Petrobras 15, 371–390.

Assine, M., Perinotto, J.A.J., Andriolli, C., Neumann, V.H., Varejão, F.G., Mescolotti, P.C., 2014. Sequências deposicionais do Andar Alagoas da Bacia do Araripe, Nordeste do Brasil. Boletim de Geociências da Petrobras, Rio de Janeiro 22 (1), 3–28.

Avanzini, M., 1998. Anatomy of a footprint: Bioturbation as a key to understanding dinosaur walk dynamics. Ichnos 6, 129–139.

Avanzini, M., 2001. Possibili impronte di dinosauro nel Giurassico inferiore del Monte Pasubio e dei Monti Lessini settentrionali (Italia nord-orientale). Studi Trentini di Scienze Naturali. Acta Geologica 76 (1999), 183–191.

Avanzini, M., Frisia, S., Rinaldo, M., 2000. I Lavini di Marco nel Giurassico inferiore: la riconstruzione di um antico ambiente di vita. In: Leonardi, G., Mietto, P. (Eds.), Dinosauri in Italia. Accademia Editoriale, Pisa-Roma, pp. 245–272.

Avanzini, M., Piñuela, L., García-Ramos, J.C., 2012. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. Lethaia 45, 238–252.

Beurlen, K., 1963. Geologia e estratigrafia da Chapada do Araripe. In: 17 Congresso Nacional de Geologia, Recife, Boletim Recife, Sociedade Brasileira de Geologia. Núcleo Pernambuco, p. 47.

Beurlen, K., 1971. As condições ecológicas e faciológicas da Formação Santana na Chapada do Araripe (Nordeste do Brasil). Anais da Academia Brasileira de Ciências 43 (suplemento), 411–415.

Bittencourt, J.S., Langer, M.C., 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. Anais da Academia Brasileira de Ciências 83, 23–60.

Boyd, D.W., Loope, D.B., 1984. Probable vertebrate origin for certain sole marks in Triassic redbeds of Wyoming. Journal of Paleontology 58, 467–476.

Bronzati, M., Montefeltro, F.C., Langer, M.C., 2015. Diversification events and the effects of mass extinctions on Crocodyliformes evolutionary history. Royal Society Open Science 2, 140385.

Campos-Soto, S., Cobos, A., Caus, E., Benito, M.I., Fernández-Labrador, L., Suarez-Gonzalez, P., Quijada, I.E., Mas, R., Royo-Torres, R., Alcalá, L., 2017. Jurassic Coastal Park: A great diversity of palaeoenvironments for the dinosaurs of the Villar del Arzobispo Formation (Teruel, eastern Spain). Palaeogeography, Palaeoclimatology, Palaeoecology. https://doi.org/10.1016/j.palaeo.2017.06.010.

Campos-Soto, S., Benito, M.I., Cobos, A., Caus, E., Quijada, I.E., Suárez-González, P., Mas, R., Royo-Torres, R., Alcalá, L., 2019. Revisiting the age and palaeoenvironments of the Upper Jurassic–Lower Cretaceous? Dinosaur-bearing sedimentary record of eastern Spain: Implications for Iberian Palaeogeography. Journal of Iberian Geology 45 (3), 471–510.

Cariou, E., Olivier, N., Pittet, B., Mazin, J.-M., Hantzpergue, P., 2014. Dinosaur track record on a shallow carbonate-dominated ramp (Loulle section, Late Jurassic, French Jura). Facies 60, 229–253.

Carvalho, I.S., 2000a. Geological environments of dinosaur footprints in the intracratonic basins from Northeast Brazil during the South Atlantic opening (Early Cretaceous). Cretaceous Research 21, 255–267.

Carvalho, I.S., 2000b. Huellas de saurópodos de la Formación Antenor Navarro (Cretácico temprano de la Cuenca de Sousa), Serrote do Letreiro, Paraíba, Brasil. Ameghiniana 37, 353–362.
Carvalho, I.S., 2004. Dinosaur Footprints from Northeastern Brazil: Taphonomy and Environmental Setting. Ichnos 11, 311–321.
Carvalho, I.S., Leonardi, G., 1992. Geologia das bacias de Pombal, Sousa, Uiraúna-Brejo das Freiras e Vertentes (Nordeste do Brasil). Anais da Academia Brasileira de Ciências 64, 231–252.
Carvalho, I.S., Pedrão, E., 1998. Brazilian theropods from the Equatorial Atlantic margin: behavior and environmental setting, vol. 15. Gaia, Lisboa, pp. 369–378.
Carvalho, I.S., Viana, M.S.S., Lima Filho, M.F., 1993. Os icnofósseis de vertebrados da bacia do Araripe (Cretáceo Inferior, Ceará - Brasil). Anais da Academia Brasileira de Ciências 65, 459.
Carvalho, I.S., Viana, M.S.S., Lima Filho, M.F., 1994. Dinossauros do Siluriano: um anacronismo crono-geológico nas bacias interiores do Nordeste?. In: 38° Congresso Brasileiro de Geologia, Boletim de Resumos Expandidos, vol. 3. Sociedade Brasileira de Geologia, Camboriú), pp. 213–214.
Carvalho, I.S., Viana, M.S.S., Lima Filho, M.F., 1995. Bacia de Cedro: a icnofauna cretácica de vertebrados. Anais da Academia Brasileira de Ciências 67, 25–31.
Carvalho, I.S., Borghi, L., Leonardi, G., 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. Cretaceous Research 44, 112–121.
Carvalho, I.S., Melo, B.G.V., Borghi, L., Rios-Netto, A.M., Andrade, J.A.F.G., Freitas, F.I., 2018. Dinosaur tracks from the Aptian (Early Cretaceous) of Araripe Basin, Brazil. In: Simpósio Latino-Americano de Icnología, vol. 4. Santa Marta, Colombia, Resúmenes, p. 69.
Castanera, D., Canudo, J.I., Díaz-Martínez, I., Herrero Gascón, J., Pérez-Lorente, F., 2010. Grandes contramoldes de icnitas de saurópodos en el Thitónico-Berriasiense de la Formación Villar del Arzobispo em Galve (Teruel). In: 5° Congreso del Jurásico de España. Colunga, Comunicaciones, pp. 178–183.
Díaz-Martínez, I., Cónsole-Gonella, C., de Valais, S., Salgado, L., 2018. Vertebrate tracks from the Paso Córdoba fossiliferous site (Anacleto and Allen formations, Upper Cretaceous), Northern Patagonia, Argentina: Preservational, environmental and palaeobiological implications. Cretaceous Research 83, 207–220. https://doi.org/10.1016/j.cretres.2017.07.008.
Difley, R.L., Ekdale, A.A., 2002. Footprints of Utah's last dinosaurs: track beds in the Upper Cretaceous (Maastrichtian) North Horn Formation of the Wasatch Plateau, Central Utah. Palaios 17, 327–346.
Dunhill, A.M., Bestwick, J., Narey, H., Sciberras, J., 2016. Dinosaur biogeographical structure and Mesozoic continental fragmentation: a network-based approach. Journal of Biogeography 2016, 1–14.
Falkingham, P.L., Gatesy, S.M., 2014. The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. Proceedings of the National Academy of Sciences 111 (51), 18279–18284.
Falkingham, P.L., Bates, K.T., Margetts, L., Manning, P.L., 2011. The 'Goldilocks' effect: preservation bias in vertebrate track assemblages. Journal of the Royal Society Interface 8 (61), 1142–1154.
Falkingham, P.L., Hage, J., Bäker, M., 2014. Mitigating the Goldilocks effect: the effects of different substrate models on track formation potential. Royal Society Open Science 1, 140225.
Falkingham, P.L., Marty, D., Richter, A., 2016. Introduction. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: The Next Steps. Indiana University Press, pp. 3–11.
García-Ramos, J.C., Valenzuela, M., 1977. Hallazgo de huellas de pisada de vertebrados en el Jurasico de la costa asturiana entre Gijón y Ribadesella. Breviora Geológica Astúrica 2, 17–21.
García-Ramos, J.C., Piñuela, L., Lires, J.L., 2002. Icnitas de dinosaurios, tipos de sedimento y consistencia del substrato. In: Congreso Internacional sobre Dinosaurios y otros Reptiles Mesozóicos de España, Resúmenes, Logroño, pp. 25–26.
García-Ramos, J.C., Piñuela, L., Lires, J.L., 2006. Atlas del Jurásico de Asturias. Ediciones Nobel, Oviedo.
García-Ramos, J.C., Piñuela, L., Avanzini, M., Ruiz-Omeñaca, J.I., 2009. Deep theropod undertracks look like ornithopod tracks. A conclusion from a three-dimensional study of dinosaur-footprints. In: 10th International Symposium on Mesozoic Terrestrial Ecosystems and Biota. Universidad Autónoma de Madrid, Teruel, pp. 279–281.
Gatesy, S.M., 2003. Direct and Indirect tracks features: what sediment did a dinosaur touch? Ichnos 10, 91–98.
Gatesy, S.M., Falkingham, P.L., 2017. Neither bones nor feet: track morphological variation and "preservation quality". Journal of Vertebrate Paleontology, e1314298. https://doi.org/10.1080/02724634.2017.1314298.
Gatesy, S.M., Middleton, K.M., Jenkins Jr., F.A., Shubin, N.H., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399 (6732), 141–144.
Gorscak, E., O'Connor, P.M., 2016. Time-calibrated models support congruency between Cretaceous continental rifting and titanosaurian evolutionary history. Biology Letters 12, 20151047. https://doi.org/10.1098/rsbl.2015.1047.
Haubold, H., 1971. Ichnia Amphibiorum et Reptliorum Fossilium. Handbuch der Paläoherpetologie, pt. 18. Gustav Fischer, Stuttgart, Germany and Portland, USA vii + 124 pp.
Herrero Gascón, J., Pérez-Lorente, F., 2017. Hoof-Like unguals, skin, and foot movements deduced from *Deltapodus* casts of the Galve Basin (Upper Jurassic-Lower Cretaceous, Teruel, Spain). Ichnos 24 (2), 146–161. https://doi.org/10.1080/10420940.2016.1223655.
Laporte, L.F., Behrensmeyer, A.K., 1980. Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. Journal of Sedimentary Petrology 50, 337–346.
Leonardi, G., 1979. Nota Preliminar Sobre Seis Pistas de Dinossauros Ornithischia da Bacia do Rio do Peixe (Cretáceo Inferior) em Sousa, Paraíba, Brasil. Anais da Academia Brasileira de Ciências 51 (3), 501–516.
Leonardi, G., 1984. Le impronte fossili di Dinosauri [The fossil footprints of dinosaurs]. Sulle Orme dei Dinosauri, La Casa Editrice Erizzo, pp. 164–186.
Leonardi, G., 1987. Glossary and manual of tetrapod footprint palaeoichnology. Departamento Nacional da Produção Mineral, Brasil, Brasília.
Leonardi, G., 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 165–178.
Leonardi, G., 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene) with an appendix on Mexico and Central America. CPRM (Serviço Geológico do Brasil, Brasília.
Leonardi, G., Mietto, P., 2000. Le piste liassiche di dinosauri dei Lavini di Marco. In: Leonardi, G., Mietto, P. (Eds.), Dinosauri in Italia. Accademia Editoriale, Pisa-Roma, pp. 169–246.
Leonardi, G., Spezzamonte, M., 1994. New tracksites (Dinosauria: Theropoda and Ornithopoda) from the Lower Cretaceous of the Ceará, Brasil. Studi Trentini di Scienze Naturali. Acta Geologica 69 (1992), 61–70.
Lockley, M.G., 1986. The paleobiological and paleoenvironmental importance of dinosaur footprints. Palaios 1, 37–47.
Lockley, M.G., 1987. Dinosaur footprints from the Dakota Group of Eastern Colorado. Mountain Geologist 24, 107–122.
Lockley, M.G., 1991. Tracking Dinosaurs: A New Look at an Ancient World. Cambridge University Press, U.S.A., Cambridge, p. 238.
Lockley, M., Conrad, K., 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the Western USA. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 121–134.
Lockley, M.G., Xing, L., 2015. Flattened fossil footprints: implications for paleobiology. Palaeogeography, Palaeoclimatology, Palaeoecology 426, 85–94.
Manning, P.L., 2008. *T. rex* speed trap. In: Carpenter, K., Larson, P.L. (Eds.), *Tyrannosaurus rex*; The Tyrant King. Indiana University Press, Bloomington, pp. 204–231.
Martill, D.M., 2007. The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of north-east Brazil: a historical review and an appraisal of the biochronostratigraphic utility of its palaeobiota. Cretaceous Research 28 (6), 895–920.
Martill, D.M., Bechly, G., Loveridge, R., 2007. The Crato Fossil Beds of Brazil: Window into an Ancient World. Cambridge University Press.
Marty, D., 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chenevez—Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat paleoenvironment and dinosaur diversity, locomotion and palaeoecology. GeoFocus 21, 1–278.
Marty, D., 2011. Formation, taphonomy, and preservation of vertebrate tracks. Dinosaur Tracks – Obernkirchen 37. April 14-17, Abstracts.
Marty, D., Meyer, C.A., Billon-Bruyat, J.-P., 2006. Sauropod trackway patterns expression of special behaviour related to substrate consistency? An example from the Late Jurassic of northwestern Switzerland. Hantekeniana 5, 38–41.
Marty, D., Belvedere, M., Meyer, C.A., Mietto, P., Paratte, G., Lovis, C., Thüring, B., 2010. Comparative analysis of Late Jurassic sauropod trackways from the Jura Mountains (NW Switzerland) and the central High Atlas Mountains (Morocco): implications for sauropod ichnotaxonomy. Historical Biology 22 (1), 109–133.
Medeiros, M.A., Lindoso, R.M., Mendes, I.D., Carvalho, I.S., 2014. The Cretaceous (Cenomanian) continental record of the Laje do Coringa flagstone (Alcântara Formation), northeastern South America. Journal of South American Earth Sciences 53, 50–58.
Milàn, J., Bromley, R.G., 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. Palaeogeography, Palaeoclimatology, Palaeoecology 231, 253–264.
Milàn, J., Clemmensen, L.B., Bonde, N., 2004. Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) – undertracks and other subsurface deformation structures revealed. Lethaia 37, 285–296.
Milàn, J., Avanzini, M., Clemmensen, L.B., García-Ramos, J.C., Piñuela, L., 2006. Theropod foot movement recorded by Late Triassic, Early Jurassic and Late Jurassic fossil footprints. New Mexico Museum of Natural History and Science Bulletin 37, 352–364.
Moratalla, J.J., 2009. Sauropod tracks of the Cameros Basin (Spain): Identification, trackway patterns and changes over the Jurassic-Cretaceous. Geobios 42, 797–811.
Moratalla, J.J., 2011. The Lower Cretaceous dinosaur movements through the lacustrine system of the Cameros Basin (Spain) written in their tracks. Dinosaur Tracks – Obernkirchen 45. April 14-17, Abstracts.
Moratalla, J.J., Lockley, M.G., Buscalioni, A.D., Fregenal-Martínez, M.A., Meléndez, N., Ortega, F., Pérez-Moreno, B.P., Pérez-Asensio, E., Sanz, J.L., Schultz, R.J., 1995. A preliminary note on the first tetrapod trackways from the lithographic limestones of Las Hoyas (Lower Cretaceous, Cuenca, Spain). Geobios 28 (6), 777–782.
Neumann, V.H., Cabrera, L., 1999. Uma nueva propuesta estratigráfica para la tectonosecuencia post-rifte de la cuenca de Araripe, Nordeste de Brasil. In: 5° Simpósio sobre o Cretáceos do Brasil. UNESP, Rio Claro, Boletim, pp. 279–285.

Neumann, V.H., Cabrera, L., 2002a. A Tendência Expansiva do Sistema Lacustre Aptiano-Albiano do Araripe Durante sua Evolução: Dimensões e Morfologia. IG. Série B, Estudos e Pesquisas. Recife - PE 11, 176–188.
Neumann, V.H., Cabrera, L., 2002b. Características hidrogeológicas gerais, mudanças de salinidade e caráter endorréico do sistema lacustre Cretáceo do Araripe, NE Brasil. Revista de Geologia (UFC), Fortaleza, CE 15, 43–54.
Neumann, V.H., Cabrera, L., Mabesoone, J.M., Valença, L.M.M., Silva, A.L., 2002. Ambiente sedimentar e fácies da seqüência lacustre Aptiana-Albiana da bacia do Araripe, NE do Brasil. In: 6° Simpósio sobre o Cretáceos do Brasil. UNESP, Boletim, São Pedro, pp. 37–41.
Paula Freitas, A.B.L., 2010. Análise estratigráfica do intervalo siliciclástico aptiano da bacia do Araripe (Formação Rio da Batateira). Dissertação (Mestrado em Geologia). Instituto de Geociências, Universidade Federal do Rio de Janeiro, Rio de Janeiro, p. 9.
Paula Freitas, A.B.L., Borghi, L., 2011. Fácies sedimentares e sistemas deposicionais siliciclásticos aptianos da bacia do Araripe. Geociências 30 (4), 529–543.
Pérez-Lorente, F., 2015. Dinosaur footprints and trackways of La Rioja. Indiana University Press.
Pérez-Lorente, F., 2017. Developments and contributions in the study of La Rioja dinosaur footprints (Spain). Spanish Journal of Palaeontology 32 (1), 171–184.
Piñuela, L., 2012. Dinosaur true tracks and undertracks. Recognition criteria and nomenclature problems. The Asturian case (Spain). In: Qijiang International Dinosaur Tracks Symposium, pp. 91–95. Abstract Book, Chongqing.
Piñuela, L., 2018. Tipo y grado de consistencia del sustrato: papel determinante en la clasificación de las huellas de dinosaurios. In: 4° Simposio Latinoamericano de Icnologia, (SLIC 2018, Santa Marta, Colombia). Resúmenes, p. 11.
Piñuela, L., García-Ramos, J.C., Ruiz-Omeñaca, J.I., 2011a. Dinosaur tracks in an ancient lower deltaic plain-interdistributary bay, p. 29. Dinosaur Track Symposium, 2011, Obernkirchen.
Piñuela, L., García-Ramos, J.C., Ruiz-Omeñaca, J.I., 2011b. Dinoturbation: a common ichnofabric in the fluvial and deltaic facies of the Upper Jurassic of Asturias (N Spain). In: Rodríguez-Tovar, F.J., García-Ramos, J.C. (Eds.), Abstract Book of the XI International Ichnofabric Workshop. Museo del Jurásico de Asturias (MUJA), Colunga, pp. 157–161.
Piñuela, L., Delvene, G., García-Ramos, J.C., 2016. Dinosaur footprints and bivalve trace fossils in a point-bar deposit. Lastres Formation (Kimmeridgian) of Asturias, North Spain. Abstract Book, UNESCO Geopark Naturtejo/International Ichnological Association, Castelo Branco, pp. 126–127. Ichnia 2016.
Piñuela Suárez, L., 2015. Huellas de dinosaurios y de otros reptiles del Jurásico Superior de Asturias. Tesis Doctoral. Universidad de Oviedo.
Ponte, F.C., 1992. Origem e evolução das pequenas bacias cretácicas do interior do Nordeste do Brasil. In: 2° Simpósio sobre as Bacias Cretácicas Brasileiras, Rio Claro (SP), Resumos expandidos. UNESP, pp. 55–58.
Ponte, F.C., Appi, C.J., 1990. Proposta de revisão da coluna litoestratigráfica da Bacia do Araripe. In: 36° Congresso Brasileiro de Geologia. Anais 1, 211–226.
Razzolini, N., 2016. Morphological variation and ichnotaxonomy of dinosaur tracks: linking footprint shapes to substrate and trackmaker's anatomy and locomotion. PhD Thesis. Universitat Autonoma de Barcelona, p. 188.
Razzolini, N.L., Vila, B., Castanera, D., Falkingham, P.L., Barco, J.L., Canudo, J.I., Manning, P.L., Galobart, A., 2014. Intra-trackway morphological variations due to substrate consistency: the El Frontal dinosaur tracksite (Lower Cretaceous, Spain). PloS One 9 (4), e93708. https://doi.org/10.1371/journal.pone.0093708.
Rios-Netto, A.M., Regali, M.S.P., 2007. Estudo bioestratigráfico, paleoclimático e paleoambiental do intervalo Alagoas (Cretáceo Inferior) da bacia do Araripe, nordeste do Brasil (Poço 1-PS-11-CE). In: Carvalho, I.S., et al. (Eds.), Paleontologia: Cenários de Vida, first edition., vol. 2. Editora Interciência, Rio de Janeiro, pp. 479–488.
Rios-Netto, A.M., Paula-Freitas, A.B.L., Carvalho, I.S., Regali, M.S.P., Borghi, L., Freitas, F.I., 2012a. Formalização estratigráfica do Membro Fundão, Formação Rio da Batateira, Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. Revista Brasileira de Geociências 42 (2), 281–292.
Rios-Netto, A.M., Regali, M.S.P., Carvalho, I.S., Freitas, F.I., 2012b. Palinoestratigrafia do Intervalo Alagoas da Bacia do Araripe. Revista Brasileira de Geociências 42 (2), 331–342.
Romano, M., Whyte, M.A., 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. Proceedings of the Yorkshire Geological Society 54, 185–215.
Romano, M., Whyte, M.A., 2012. Information on the foot morphology, pedal skin texture and limb dynamics of sauropods: evidence from the ichnological record of the Middle Jurassic of the Cleveland Basin, Yorkshire, UK. Zubia 30, 45–92.
Santos, V.F., 2016. Dinosaur tracksites in the Middle Jurassic of Maciço Calcário Estremenho (west-central Portugal): a geoheritage to be enhanced. Comunicações Geológicas 103 (Especial I), 55–58.
Santos, V.F., Callapez, P.M., Rodrigues, N.P.C., 2013. Dinosaur footprints from the Lower Cretaceous of the Algarve Basin (Portugal): New data on the ornithopod palaeoecology and palaeobiogeography of the Iberian Peninsula. Cretaceous Research 40, 158–169.
Santos, V.F., Callapez, P.M., Castanera, D., Barroso-Barcenilla, F., Rodrigues, N.P.C., Cupeto, C.A., 2015. Dinosaur tracks from the Early Cretaceous (Albian) of Parede (Cascais, Portugal): new contributions for the sauropod palaeobiology of the Iberian Peninsula. Journal of Iberian Geology 41 (1), 155–166.
Sanz, E., Arcos, A., Pascual, C., Pidal, I.M., 2016. Three-dimensional elasto-plastic soil modelling and analysis of sauropod tracks. Acta Palaeontologica Polonica 61 (2), 387–402.
Sarjeant, W.A.S., Leonardi, G., 1987. Substrate and Footprints. In: Leonardi, G. (Ed.), Glossary and Manual of Tetrapod Footprint Palaeoichnology. Brasília, DNPM (Geological Survey of Brazil, Brasília).
Sciscio, L., Bordy, E.M., Reid, M., Abrahams, M., 2016. Sedimentology and ichnology of the Mafube dinosaur tracksite (Lower Jurassic, eastern Free State, South Africa): a report on footprint preservation and palaeoenvironment. PeerJ 4, e2285. https://doi.org/10.7717/peerj.2285.
Silva, R.C., Carvalho, I.S., Schwanke, C., 2007. Vertebrate dinoturbation from the Caturrita Formation (Late Triassic, Paraná Basin), Rio Grande do Sul State, Brazil. Gondwana Research 11, 303–310.
Sternberg, C.M., 1932. Dinosaur tracks from Peace River, British Columbia. National Museum of Canada Bulletin 68, 59–85.
Thulborn, T., 1990. Dinosaur Tracks. Chapman and Hall, London.
Thulborn, T., 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. PloS One 7 (5), e36208. https://doi.org/10.1371/journal.pone.0036208.
Thulborn, T., Hamley, T., Foulkes, P., 1994. Preliminary report on sauropod dinosaur tracks in the Broome Sandstone (Lower Cretaceous) of Western Australia. Gaia 10, 85–94.
Valenzuela, M., García-Ramos, J.C., de Centi, C.S., 1988. Las huellas de dinosaurios del entorno de Ribadesella. Central Lechera Asturiana.
Xing, L., Li, D., Lockley, M.G., Marty, D., Zhang, J., Persons IV, W.S., You, H., Peng, C., Kümmell, S.B., 2015. Dinosaur natural track casts from the Lower Cretaceous Hekou Group in the Lanzhou-Minhe Basin, Gansu, Northwest China: Ichnology, track formation, and distribution. Cretaceous Research 52, 194–205.