ARTICLE IN PRESS

Journal of South American Earth Sciences xxx (xxxx) xxx

Contents lists available at ScienceDirect

Journal of South American Earth Sciences

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

Fossil footprints as biosedimentary structures for paleoenvironmental interpretation: Examples from Gondwana

Ismar de Souza Carvalho [a,*], Giuseppe Leonardi [b]

[a] Universidade Federal do Rio de Janeiro, 21.910-200 Av. Athos da Silveira Ramos 273, Instituto de Geociências. CCMN, Rio de Janeiro, RJ, Brazil
[b] Istituto Cavanis, Dorsoduro, 898, 30123, Venezia, Italy

ARTICLE INFO

Keywords:
Fossil footprints
Paleoenvironment
Gondwana

ABSTRACT

The origin and preservation of a track are related to many distinct environmental factors, concerning especially the substrate cohesiveness, plasticity, grain size, texture and water content. Then, the environment, through the sedimentation processes, plays a role that enhances the origin and quality of the tracks and their preservation. Three distinct contexts - tidal flats, aeolian, fluvial-lacustrine paleoenvironments, that encompass the majority of fossil footprints occurrences are analyzed. Footprints as biosedimentary structures, due to their close relationships with physical and chemical processes that control their formation, represent an important clue to paleoenvironmental interpretation. The present study is mainly based on the direct examination of ichnosites that allow us to evaluate the aspects of Mesozoic tracks from different regions of the paleocontinent Gondwana, currently correspondent to Argentina, Australia, Bolivia, Brazil, Congo, Iran, India, Madagascar and Morocco as sedimentary structures and their use in paleoenvironmental interpretations.

1. Introduction

A footprint can be considered at the same time to be both: a register of the impression of an autopodium, but also a biosedimentary induced feature, that produces a deformation in the substrate. There are no clear limits between these two interpretations of a footprint, as this many times do not present a faithful reproduction of the foot anatomy of the trackmaker. Besides, it is inadequate to isolate the structure produced by the direct contact of the foot on the substrate and the surrounding deformations. We can evaluate them through the perspective of a deformational process on the substrate, and then as a biosedimentary feature, that reflects environmental conditions.

These observations have already been exposed by Peabody (1948, 1955, 1959), who had introduced the concept of "extramorphologies" (Peabody, 1948, page 296), as a theoretical concept deriving from his observations on ichnological material. Then, the morphology of a footprint varies widely as the result of trackmaker anatomy, behavior (speed for example) and substrate consistency (Peabody, 1948, 1959). Extramorphology of a footprint includes non-anatomical features of the trackmaker, due to secondary locomotion effects, substrate conditions, and post-registration processes (Marchetti et al., 2020). These extra-morphological influences may origin new morphological patterns of the tracks as presented in a multivariate taxonomic analysis by Tucker and Smith (2004) in the study of a late Carboniferous vertebrate ichnofauna. Klein and Lucas (2010) evaluated this question of the footprints as the result of the interaction between animals and different substrates, in the analysis of the use of tetrapod footprints in biostratigraphy and biochronology. The extramorphological (substrate-controlled) phenomena can, in this way, influence in the ichnotaxonomic evaluation. There is also the possibility, as shown by Peabody (1947, 1948) in the study of crescentic impressions from the Lower Triassic Moenkopi Formation, of the formation of structures that can be similar to fossil tracks but are completely related to the sedimentary processes during deposition.

Marchetti et al. (2019 a) emphasized that the morphology of fossil tracks is a product of the anatomy of the producer, behavior of the producer, substrate conditions at the time of trace registration and post-registration processes. Only under ideal conditions for footprint registration, morphology is anatomy-consistent and suitable for ichnotaxonomy and trackmaker attribution (Peabody, 1955; Belvedere and Farlow, 2016; Marchetti, 2018; Marchetti et al., 2020).

A fossil footprint is a three-dimensional (3D) deformation structure that originated in loose ancient sediments by the foot of an animal, which is called the trackmaker and which acts as a paleopenetrometer

---

* Corresponding author.
E-mail addresses: ismar@geologia.ufrj.br (I.S. Carvalho), leonardigiuseppe879@gmail.com (G. Leonardi).

https://doi.org/10.1016/j.jsames.2020.102936
Received 21 March 2020; Received in revised form 25 September 2020; Accepted 30 September 2020

Please cite this article as: Ismar de Souza Carvalho, Giuseppe Leonardi, *Journal of South American Earth Sciences*, https://doi.org/10.1016/j.jsames.2020.102936

(Falkingham et al., 2010). During track registration, both the trampled surface and underlying sediments, whether they are laminated or not, are deformed under the trackmaker movement and load. During this complex process, all the particles, granules, pebbles and anything else forming or contained in the substrate are physically displaced. The consistency of the sediments exercises a strong control over the morphology of the track, and then the history of track formation and preservation can provide information about the properties of the sediments in which the track was created (Milàn, 2003; Dalman and Weems, 2013; Falkingham and Gatesy, 2014; Belvedere et al., 2017; Gatesy and Falkingham, 2017). A true track is produced on the surface that was in direct contact with the foot (Leonardi, 1987; Milàn et al., 2004; Milàn and Bromley, 2006). When only the general outline of the footprint is preserved, without indication of the fingers, fingerpads or footpads, the footprint represents a bioturbation structure, produced by the stirring of the substrate at the contact zone with the autopodium (Lockley, 1991; Gatesy, 2003; Lockley and Meyer, 2000; Platt et al., 2012; Lockley and Xing, 2015). After footprint registration, and before burial, exposed tracks can be quickly deteriorated and many destructive processes, including erosion, bioturbation (e.g. overprinting), weathering, deformation during burial events and reworking during successive depositional events lower dramatically their preservation potential (Laporte and Behrensmeyer, 1980; Nadon, 2001).

Footprints are biosedimentary structures that present a close relationship with the environment and the nature of the substrate. As biodeformation features, the understanding of their genesis can allow the paleoenvironmental interpretation (Avanzini, 1998; Gatesy et al., 1999; Falkingham et al., 2011; Platt et al., 2012; Díaz-Martínez et al., 2017; Menezes et al., 2019). Their use will be evaluated in some of the main Mesozoic tracksites from Argentina, Australia, Bolivia, Brazil, Congo, Iran, India, Madagascar and Morocco (Fig. 1).

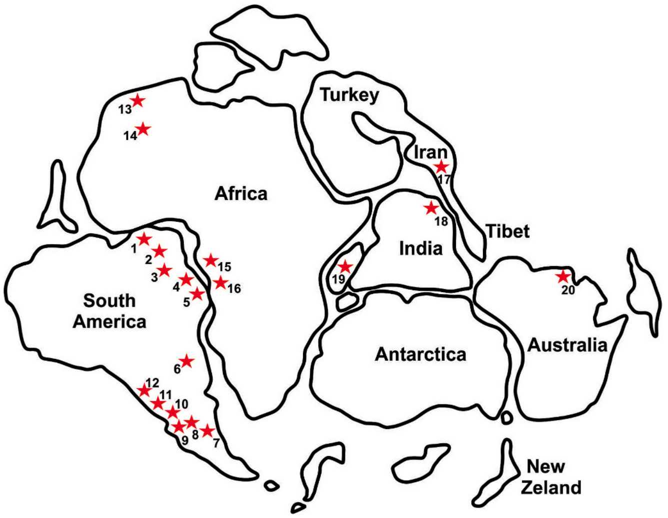

Fig. 1. Distribution of the main Mesozoic tracksites in the Gondwanic context evaluated to the paleoenvironmental interpretation after observational analysis and published data. 1. Carvalho (1994, 1995, 2001, 2004); Carvalho and Araújo (1995); Carvalho and Pedrão (1998). 2. Carvalho et al. (2018, 2019a, 2019b, 2020); 3. Carvalho (1996, 2000a,b); Carvalho et al. (2013); Leonardi (1979, 1989; 1991; 1994); Leonardi and Carvalho (2002a, 2020b); 4. Carvalho and Souza-Lima (2008); 5. Carvalho and Borghi (2008); 6. Leonardi (1977, 1980, 1981, 1994); Fernandes and Carvalho (2007, 2008); Leonardi and Carvalho, 2002a, 2002b; Leonardi et al. (2007); 7. De Valais (2011); 8. Leonardi (1994); Leonardi and Oliveira (1990); Citton et al. (2018); 9. Leonardi and Carvalho (2002a, 2020b); 10. Calvo and Rivera (2018); 11. Lockley et al. (2002); Meyer et al. (1999); 12. Leonardi (1984, 1994); Leonardi and Peredo (1985); Lockley et al. (2002). 13. Belvedere (2008); Belvedere et al. (2010); Boutakiout et al. (2019); 14. Ibrahim et al. (2014); 15. Leonardi and Carvalho (2020); 16. Mateus et al. (2016); 17. Abbassi and Madanipour (2014); 18. Pienkowski et al. (2015); 19. Wagensommer et al. (2012); 20. Romilio et al. (2017); Thulborn (2012); Thulborn et al. (1994).

2. Environments and track patterns

Preservation of animal footprints in the fossil record is strongly dependent on the history of track formation and preservation, although it is the grain size and the sedimentation regime that determines if preservation will take place and if a footprint will be incorporated and preserved into the sedimentary record. The possibility of preservation is minimal during long-lasting periods of exposure without any sedimentation, while it is favored by rapid and significant preservation events. The result is that in environments characterized by episodic sedimentation, footprints are most commonly preserved (Razzolini et al., 2014). Then, there are three distinct environmental contexts – tidal flats, aeolian, fluvial-lacustrine environments – that encompass the majority of fossil tracks occurrences.

The footprints are important to recognize an environment and its humidity - the substrate of sediments waterlogged, humid or dry can be a good indicator to the paleoenvironmental interpretation (Avanzini et al., 2000; Leonardi and Mietto, 2000; Dalla Vecchia, 2008; Getty et al., 2017; Melchor et al., 2019).

The preservation of a track demands specific requirements concerning especially the substrate cohesiveness, plasticity, grain size, texture and water content (Lockley et al., 1989). The environment, through the sedimentation processes, plays a role that enhances the footprints preservation as biosedimentary structures, related to the physical, chemical and microbiological processes that represent important clues to the paleoenvironmental interpretation (Lockley, 1986; Lockley and Conrad, 1991; Pérez-Lorent, 2015, 2017; Castanera et al., 2016; Noffke et al., 2019).

It is possible to identify footprints with well-defined morphologies or without a clear morphological identity with the trackmaker. Those with impressions of claws, nails, and of soft tissue such as the sole and phalangeal pads are considered to be produced in mud sediments with high plasticity and low water content. This context is easily recognized by the association of the footprints with raindrops and mud cracks that sometimes has their origin related to the outline of the track or as an extension of the digits (Carvalho, 2000 a; b). The dehydration of the muddy sediments produces structures similar to those ones described by Lockley and Conrad (1991). If the geological setting of the footprint is that of alluvial fan sediments, although it was also produced in a subaerial setting, its morphology is always restricted to the contour. In this case the track is related to a disruption of the depositional surface and can be considered as a bioturbation structure. There are some exceptions, as in the case of Antenor Navarro Formation tracks from Serrote do Letreiro (Sousa Basin, Lower Cretaceous, Brazil) that show well-defined contours due to the differential iron oxidation on the surface of the infilling material (Carvalho, 2000b). In subaqueous environments, there is a decrease in the morphological details of the footprints losing aspects such as nails, claws, pads and sole marks.

Many physical structures can result from the footprints, which represent an anisotropy in the substrate, produced in subaerial or subaqueous settings. Features such as fluidization, convolute, displacement rims, sandy slides, sandy crescents, radial and concentric cracks originated from the substrate properties and from the behavior of the track maker.

2.1. *Tidal flat*

The tidal flats are important environments for footprint preservation. In Gondwana, tidal flat paleoenvironments are recorded in Cretaceous of Argentina, Brazil, Morocco, Australia and India. The tracks are found both in the context of carbonatic platform and siliciclastic tidal flats.

In the Neuquén Basin (Agrio Formation, late Hauterivian-early Barremian, Argentina) theropod tracks are found in carbonates in a context of subaerial exposure of the subtidal deposits. Some tracks present a small displacement rim, allowing to infer the high cohesiveness of the substrate. They are documented in grainstones and packstones with early diagenetic dolomitization in a surface with wave ripples. Dolomitization and possible microbial stabilization of the substrate gave stability to the trampling surface thus enhancing the preservation of the tracks (Pazos et al., 2012).

The vertebrate tracks from Potiguar Basin (Brazil) come from the Jandaíra Formation, a carbonate succession of Turonian age. These sediments were deposited in a transgressive moment during the South American-Africa drifting. The fossils found in this succession show a Tethys Domain (the paleobiogeographical province influenced by the Tethys sea), in a wide carbonatic platform, subjected to subaerial exposition. In this context there is only an isolated footprint from Upanema county (Lajes Farm), Rio Grande do Norte State. It is a theropod footprint, probably impressed by a right foot, with narrow digits and low displacement rim. The third digit is short and partially collapsed in the proximal extremity. The hypexes are rounded and wide. The ratio footprint length to footprint width is about 1. One relevant aspect of the surface, in which this footprint is found is the occurrence of wrinkled structures. These are found in the context of algal mats dehydration. The occurrence of the biogenic structure represented by the footprint and the microbial interaction, shows a surface that was exposed temporarily and the probable action of the microbial mats in the preservation of the footprint. The importance of this occurrence, hitherto unpublished, is that it represents the first dinosaur track found in a Brazilian carbonate platform and the first tetrapod track from the Potiguar Basin. This unpublished track (see Fig. 9B) was found by the

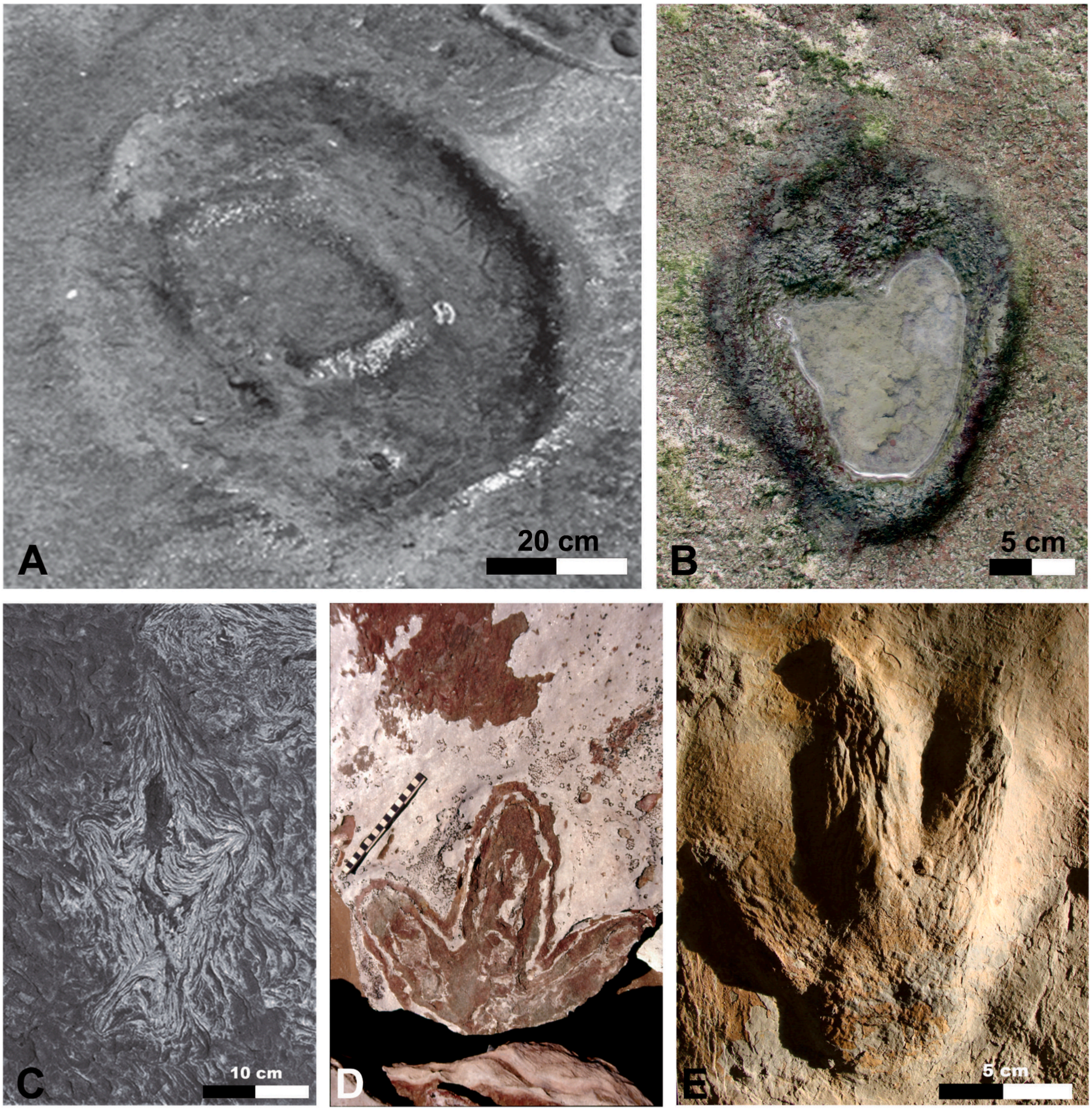

Fig. 2. A. Displacement rims of dinosaur tracks from Alcântara Formation (Cenomanian, São Luís Basin - Brazil), Prefeitura locality, Alcântara County, in a context of tidal flat A probable sauropod hind footprint; B. An elongated isolated track, with a partially preserved III toe; C. A theropod footprint from Alcântara Formation (Cenomanian, São Luís Basin – Brazil). The track presents a crenulation on all of its internal and external areas, that denotes a fluidization process in wet satured sandy sediments. D. At Riddell beach (Broome Sandstone, Berriasian – Hauterivian, Australia), an iguanodontid footprint with fluidization features in the sediments that fill the footprint, alternately by reddish and whitish sands. This slab, found in an area belonging to the local aborigines, is considered by them a sacred object. Scale bar in centimeters. E. Theropod footprint showing wrinkles arrangements interpreted as skin imprints. Shemshak Group (Jurassic, Iran), horizon 2 at the Bol-Yasel section, fluvial and deltaic deposits (Photo courtesy by Nasrollah Abbassi and Saeed Madanipour).

second author and Maria de Fátima C.F. dos Santos of Câmara Cascudo Museum of Natal on January 19th, 2008.

In the São Luís Basin (Alcântara Formation, Cenomanian, Brazil) the deposition occurred throughout wide siliciclastic tidal flats (Rossetti, 1997), in which dinosaur tracks are commonly found (Carvalho, 2001). The environmental context in this area comprises many sub-environments associated with an estuary that occupied a low-gradient coastal plain, in which Carvalho (1994, 1995), Carvalho and Araújo (1995), Gonçalves and Carvalho (1996) and Carvalho and Pedrão (1998), recognized distinct dinosaur communities with a probable ecologic "segregation" of large and small theropods. An estuary is characterized by a complex of fluvial and shallow marine environments such as tidal flats, salt marshes and lagoons (Reineck and Singh, 1986; Reading, 1996). These environments generally present fine-grained sediments such as clay and carbonate mud, that favored the formation of footprints, especially in the inter and supratidal sediments (Avanzini and Frisia, 1996; Dalla Vecchia et al., 2001). A good example is presented by Belvedere et al. (2017) in the description of the Aoufous Formation (Kem Kem beds, Late Cretaceous, Morocco) ichnofauna. There is a large number of theropods, turtles, crocodiles and possible pterosaurs tracks preserved in a siliciclastic succession interpreted as a coastal mudflat, close to the shoreline, with sabkhas and marginal ponds (Belvedere et al., 2013).

The footprints from Alcântara Formation show frequently two distinct preservational conditions. They can be rounded footprints with narrow high displacement rim, attributed to sauropods (Fig. 2A). The pad is flat and in the center there is a squared structure with also a displacement rim. The origin of such kind of track can be attributed to the superimposition of two successive footprints or to the mud suction during the lifting off of the pes from the substrate. There is no evidence of the digits and it probably belongs to a hind foot. Other kinds of footprints denote tridactyl pattern. There is here also a high displacement rim, surrounding the posterior border of the footprint. In the distal part of the footprint, the mud collapsed inside after the foot was lifted off the substrate, so the toe impressions, especially of digit III, are little visible. We suppose that this belongs to a theropod because of the ratio of length to width of the footprint (Fig. 2B). These tracks preserved in fine-grained carbonate sandstones, interbedded with argillaceous siltstones, were produced in a sand flat environment in the upper portion of a low-gradient tidal flat. The high dinoturbation was interpreted as due to the abundant dinosaurian fauna wandering in these subaerial exposure bedforms.

Another pattern of preservation is found in exposed bars in a tidal-channel environment. They are randomly oriented trackways or isolated footprints always associated with fluidization structures. Muddy and sandy bars are easily water-saturated sediments. Then, besides a plastic deformation of the substrate during the pression of the autopodia in the wet substrate, the fluidization of the substrate developing crenulated features surrounding the footprints is also possible. All the imprints denote a crenulation of sandy sediments showing a fluidization process during the track origin (Fig. 2C). The fluidization around the footprints is produced as the result of a "dinostatic pressure" (Carvalho, 1994, 2004) in water-saturated and low cohesive sediments. Such substrate aspect is corroborated by the impressions of digit I in many footprints. Kuban (1991) considered that this preservational character associated with the presence of metatarsal impressions in many footprints could be indicative of a response to a soft substrate. There are also other interpretations of elongated metatarsal impressions. As showed by Citton et al. (2015), in the study of Cretaceous elongated theropod tracks, these impressions could be a record of a complex locomotor behavior of a medium-sized theropod. The trackmaker adopted a crouched position as part of an activity as well as a resting phase suggested by sub-parallel, calcigrade tracks.

The fluidization structures are also observed in theropod tracks from other Gondwanic basins. In the upper section of Kem Kem beds (Cenomanian, Morocco) theropod footprints are found in thinly-bedded sandstones, siltstones, mudstones, and rare evaporites that are interpreted as overbank, lacustrine, and tidal-flat paleoenvironments (Ibrahim et al., 2014). Similarly to the Alcântara Formation footprints (Cenomanian, Brazil) it is possible to observe the crenulation of the sediments surrounding the digits, a clear evidence of water saturated sediments that fluidize after the foot impact. However, there is another process of fluidization, related to a post-origin of the footprint. In iguanodontid footprints from the Broome Sandstone (Berriasian – Hauterivian, Western Australia) there are the fluidization features in the sediments that fill the footprint. This is a secondary process not related to the original condition of the substrate that was deformed by the autopodium (Fig. 2D). It is important to stress that the fluidization processes are restricted to the interior area of the footprint, following its morphology. The liquefaction is not present in the whole strata where the tracks are found, but it is present only in the impacted area of a footprint.

However, some exquisite footprints, such as those ones preserved in the coal-bearing shale and siliciclastic deposits of the Shemshak Group (Toarcian-Bajocian, Jurassic, Iran), show V-shaped wrinkles arrangements over the digits imprint surface (Abbassi and Madanipour, 2014) that can be misinterpreted as fluidization structures (Fig. 2E). They are distinct from the fluidization processes due to striations from crosscutting wrinkles that give a reticulating aspect to the surface and correspond to the skin imprints as interpreted by Abbassi and Madanipour (2014).

There are also footprints that cause a large deformation of the substrate on tidal flat environments (Fig. 3A and B). The impact caused by sauropod feet and the subsequent patterns of deformation was analyzed by Thulborn et al. (1994) and Thulborn (2012) in the Broome Sandstone (Berriasian – Hauterivian, Australia). The Broome Sandstone is composed entirely of clastic sedimentary rocks, mainly fine-grained to coarse-grained red sandstones, with subordinate siltstones and also conglomerates deposited in a coastal plain with streams and channels, estuaries, deltas, swamps, ephemeral lakes and very shallow lagoons. The sauropod dinosaur tracks are common in thinly-bedded sandstones and siltstones of lagoonal origin, where they are often associated with ripple-marks, desiccation cracks and invertebrate trace fossils (Thulborn, 2012; Romilio et al., 2017). There are lateral and superficial disturbances of the substrate created by sauropods traversing thinly-stratified sediments, that deformed the substrate to such an extent that they remodeled the topography of the surface where they wandered (Fig. 3C). Besides the impressed sauropod pes on the surface, the boundary wall is steep and curves at the top. These features were designated as transmitted reliefs (underprints or ghost prints - Marty, 2008), zones of contorted bedding that underlie and surround the sauropod footprints, which eventually attain the size of minor tectonic features.

In India, dinosaur tracks are rarely described from the Gondwanic deposits (Ashok Sahni, Lucknow University, personal information, 2019). Nonetheless, there are theropod footprints from the Lower Jurassic of India (Lathi Formation, Jaisalmer Basin) that also occur in a tidal flat environment. They were interpreted as produced in a cohesive mud layer (Pienkowski et al., 2015) and this can be observed as they do not show any displacement rim or other deformational structure surrounding the footprints.

2.2. Aeolian environment

Although aeolian deposits are very restrictive to the preservation of tracks, there are some special conditions in which the footprints can be preserved. Generally related to a high stand phreatic level in dune areas or in the more humid region of the interdunes there is a great number of tracks found in aeolian sediments of the Botucatu Formation (Valanginian-Aptian, Brazil), La Matilde Formation (Middle Jurassic, Argentina), Candeleros Formation (Cenomanian, Argentina; De Valais, 2011; Candia Halupczok et al., 2018) and some tracks in the Loia

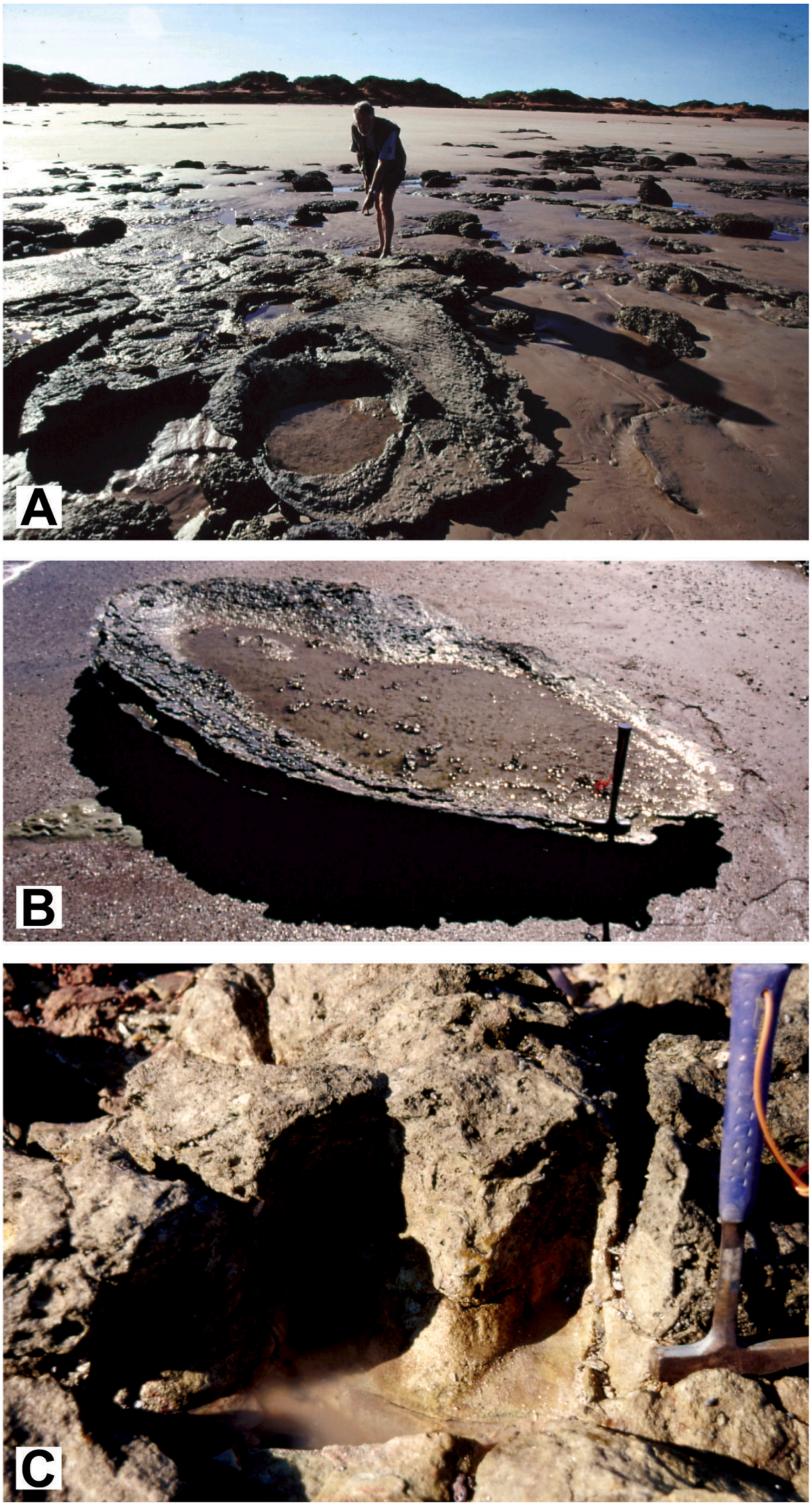

Fig. 3. A. The second author looks at the trampling surface by a herd of sauropods at Ganthaume beach, near Broome, Kimberley (Broome Sandstone, Berriasian – Hauterivian, Western Australia); B Two huge sauropod tracks at Riddell beach, Dampier Peninsula (Broome Sandstone, Berriasian – Hauterivian, Kimberley – Western Australia). The compacted sediment by the weight of the animal proved to be more consistent than the surrounding sediment, so that the tracks withstood erosion by the waves of the Indian ocean; C. Five kilometers north of Quandong Point ichnosite, along the beach, a cluster of some mounds, surmounted by the imprint of fossil cycadoideas, shows sauropod trackways running through the valleys between the mounds; and ornithopod footprints (like the one shown in the photo), buried in the deep mud of the mounds. Broome Sandstone, Berriasian – Hauterivian, Kimberley – Western Australia.

Formation (Berriasian-Aptian, Democratic Republic of Congo), with very specific patterns of associated sedimentary structures.

In the Valanginian-Aptian tracks of the Botucatu Formation (Paraná Basin, Brazil) there is a large amount of mammalian and dinosaur tracks preserved on aeolian sediments (Leonardi, 1977, 1980, 1994). Almost all the footprints found in this unit are indicative of an up-hill progression of the track-makers on the dune foresets. Then, half-moon shaped small sandy slides were produced, indicating the foreset dip (Fig. 4A). In some cases, the footprints are deep and present more anatomical details. In these cases, the "crescent" structures are shorter. In other cases, the footprints are shallow, with no or poor anatomical details and the "crescent" is long (Fig. 4B). This is true to all the preserved tracks on these sandy surfaces of the Botucatu Formation, such as mammals, dinosaurs or invertebrate tracks. However, as discussed by Marchetti et al. (2019b, 2020) the trackway pattern and body position are largely influenced by the angle of inclination (dip) of the substrate being walked on. The environmental parameters of the substrate, such as consistency and inclination, and the trackmaker movements can change the original morphology of the footprints. This context is clearly possible for some trackways from the Botucatu Formation.

This phenomenon depends on the fact that if the dune sand was humid, the maker-foot details (digits, wrinkles etc.) were well recorded on the foreset surface, and the sand, behind the posterior margin of the footprint was compressed down-ward, but did not really slide down-hill; then the displacement rim was relatively high and its antero-posterior axis was short or very short (Fig. 4C and D). On the contrary, if the upper sand layer of the foreset was dry, then the details of the track would be not well imprinted and they would be in a short time or also immediately removed by the wind, blowing away the sand; and the impact of the feet on the foreset dry sand would produce long and shallow displacement rims. Some interpretations considered that Botucatu trackways can be undertracks because it is considered that no footprint can be clearly imprinted on dry sand. However, at least the tracks that do not present details and where the sand-crescents are long, ought to be interpreted as true tracks, not as undertracks, because no sand slides would evidently be produced underground, on a lower level, underneath the actual surface of the dune foreset, the day where the maker produced the trackway (Leonardi, 1980). However the aeolian environment, on wet and dry interdune and within draa slipface deposits, interpreted by Candia Halupczok et al. (2017) for the dinosaur tracks in Candeleros Formation (Cenomanian, Argentina) showed that they constitute biogenic deformation structures characterized by folded-up and/or brecciated sandstone levels formed under dry and/or wet substrate conditions with passive filling.

As can be observed in tracks from the Upper Triassic sandstones of Vera Formation (Los Menucos Group, Argentina), they are moderately well preserved and the shape of these tracks is mainly conditioned by the substrate consistency). The depositional environment of Vera Formation is fluvio-lacustrine (Fig. 5A), but the tracks are also found in volcaniclastic levels within this lithostratigraphic unit (Fig. 5B). As defined by Labudía and Berg (2001) the Vera Formation presents epiclastic sediments interbedded with volcanic ashes, volcanic tuff, dacitic pyroclastic fluxes and volcanic breccia. Although the main depositional

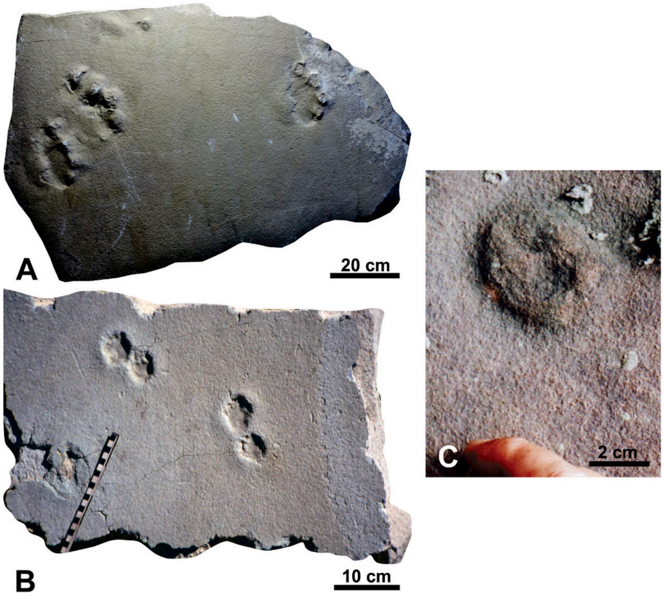

Fig. 5. A Dicynodont tracks from Los Menucos Basin (Rio Negro Province, Argentina) A. Slab MPCA 27029-3 (Museo Provincial Carlos Ameghino, Cipolletti) from Felipe Curuil ex quarry (Yancaqueo farm, east of the town of Los Menucos, Rio Negro) with a track-bearing surface interpreted as deposited in a proximal fluvial environment; B. Another hand-foot set of a small therapsid, on volcanic ash sandstone, of an upper level of the Vera Formation (Tscherig farm, Río Negro). Differences on preservation can be related to the moisture and sedimentological aspects of the substrate. The tracks are attributable to *Pentasauropus* isp. (A) and *Dicynodontipus* isp. (B); C. *Brasilichnium* footprint from the aeolian deposits of Kinshasa (Aptian –Cenomanian, Democratic Republic of Congo), in which the preservation shows no anatomical details. Photo courtesy (A) Paolo Citton.

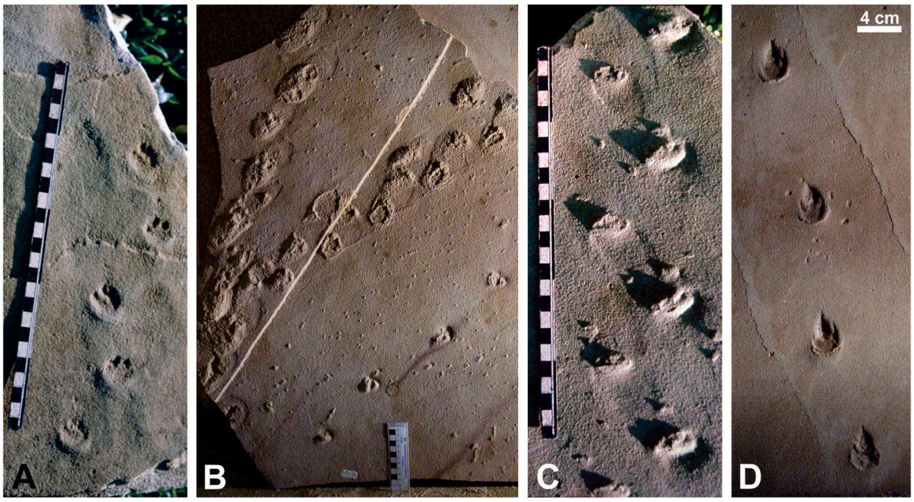

Fig. 4. A. Short crescent marks on de posterior border of fossil footprints from the aeolian deposits of Botucatu Formation (Valanginian-Aptian, Brazil). Scale bar in centimeters; B. Shallow footprints with no or poor anatomical details, produced on dry sandy surfaces of the Botucatu Formation, Valanginian-Aptian, Brazil. Sample LPP-IC-0054 (Universidade Federal de São Carlos, Photo courtesy Marcelo Adorna Fernandes). Scale bar in centimeters; C. A *Brasilichnium*-pattern trackway from the Botucatu Formation (Paraná Basin, Brazil). The track maker was a mammal progressing up hill. Observe the sand-slides behind the footprints borders. There are salt pseudomorphs associated with this trail. Scale bar in centimeters; D. A theropod trackway associated with aeolian ripple marks from the Valanginian-Aptian Botucatu Formation (Paraná Basin, Brazil). The track runs almost parallel to the ripples crest. The sand was probably very wet, so the footprints are deep and with anatomical detail. The sandy crescent is short and low. Photo courtesy Marcelo Adorna Fernandes.

environment occurs in a context of a fluvio-lacustrine basin, the volcaniclastic sediments (specially with volcanic ashes) are also controlled by wind deposition. Based on comparison with neoichnological experiments the trackmakers were interpreted to produce the tracks most likely on humid, not waterlogged nor dry, coarse sediments with a moderately plastic behavior, able to record the main anatomical features of the autopods (Citton et al., 2018).

In the Cretaceous deposits of Kinshasa (Democratic Republic of Congo; Berriasian-Aptian) there are mammaloid footprints discovered by the first author and attributable to the ichnogenus *Brasilichnium*, some of them pertaining to the species *Brasilichnium elusivum*. They are found in well lithified arkose, with coarse sand grains predominating over medium and fine ones. The footprints do not show clear morphological details, probably related to the coarse grain-size of the matrix (Fig. 5C). The footprints are preserved as concave epirelief, generally with an elliptical outline with the "lower" margin steep and accompanied, along all the preserved portion of it and lateral (or medial) side by a low and gentle but quite visible displacement rim. This is absolutely not a "sand-crescent", so no dune environment is supposed. However, there is also an elliptical footprint that presents a crescent-shaped displacement rim, typical of the dune environment that it is absolutely similar in all details and style to those found in the *Brasilichnium elusivum* tracks of the Botucatu Formation (Valanginian-Aptian, Brazil). These two distinct patterns of preservation are indicative that tracks from coarse grained sandstones (indicative of interdune deposits) present a low potential to the preservation of the track anatomy, and do not show prominent sand-crescent rim. Otherwise, the dune environment, in which the grain size is smaller and more homogeneous, allows the development of the sand-crescent structures (Leonardi and Carvalho, 2021). Concerning sandy deposits, it is important to observe the experimental evaluation of Falk et al. (2017) which concluded that wet and dry coarse sediments preserve tracks without fine details, but moisture coarse sediment might preserve the overall track shape and details as claw impressions.

2.3. Fluvial and lacustrine environments

In fluvial and lacustrine paleoenvironments, sub-environments like lakeshores and floodplains are the main favorable contexts allowing registration and preservation of tetrapod tracks, which undoubtedly strongly contribute to refining the paleoenvironmental interpretation.

As discussed by Lockley and Conrad (1991), distal fluvial floodplains and lakeshores preserve a quite high abundance, diversity and distribution of dinosaur footprints, allowing in many cases a detailed registration of footprint morphologies. In such paleoenvironments, the cyclic repetition of muddy, silty and fine-grained sandy sediments as the product of periodic flooding and shoreline variations, enhance in many successive surfaces the preservation potential of tracks, some of them clearly impressed in humid, compliant substrates during low standing water ponds. Some few exceptions show tracks in a high stand water level (Fig. 6A) Texture, composition, and moisture regulate the probability of initial track registration and final depth of penetration.

A striking example is represented by the plethora of dinosaur trackways from the Lower Cretaceous Sousa Formation (Rio da Serra - Aratu age) in the Rio do Peixe Basin, northeastern Brazil (Leonardi, 1979, 1989; 1991, 1994; Carvalho, 1996, 2000b; Leonardi and Carvalho, 2002a, 2002b). This lithostratigraphic unit records the deposition in a floodplain crossed by meandering rivers and with the development of perennial and temporary lakes (Carvalho, 2000a; Carvalho and Leonardi, 1992).

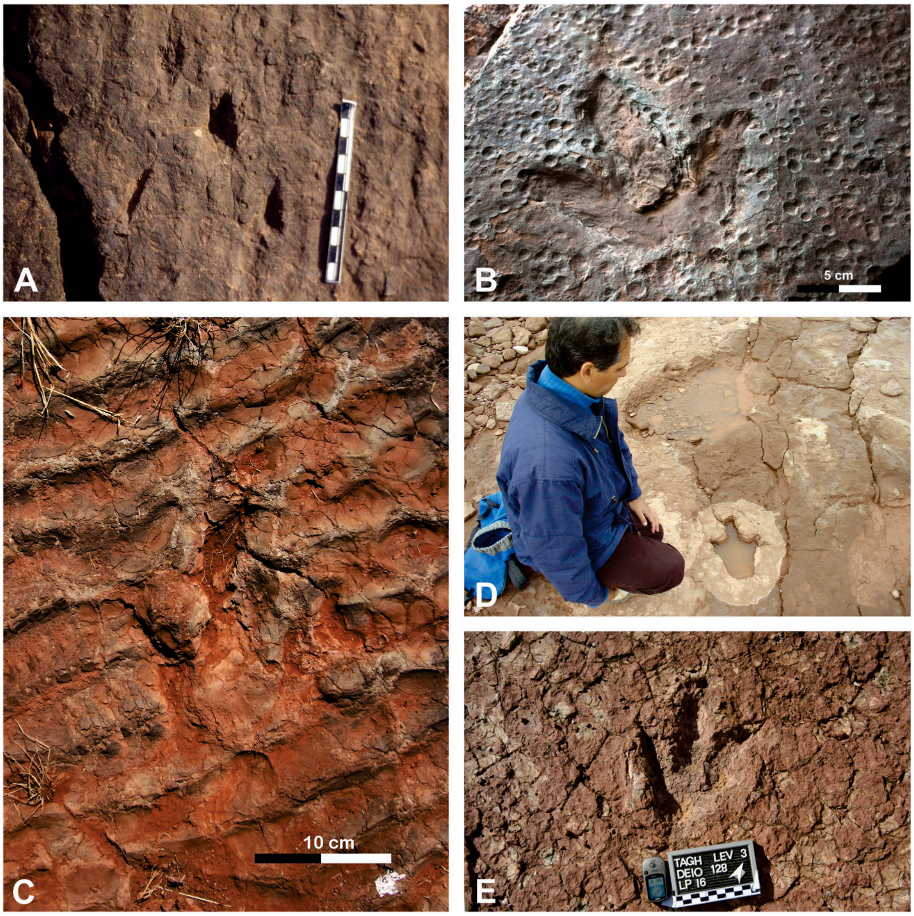

Fig. 6. A. A theropod footprint with the impressions of the extremities of three digits, indicating a swimming dinosaur, in a high stand water level. Observe the associated ripple marks and the quite common parallelism between the direction of the swimming animal and of the crests of the ripples. Level 16 of Caiçara-Piau Farm, Sousa Formation (Rio da Serra-Aratu age, Sousa Basin, Brazil). Scale bar in centimeters; B. An isolated small theropod footprint surrounded by raindrops prints, indicating a humid interval. Level 13/2, Caiçara-Piau Farm, Sousa Formation (Rio da Serra-Aratu age, Sousa Basin, Brazil); C. A theropod track from Araxá de Baixo, Sousa Formation (Rio do Peixe Basins, Brazil) associated with current ripple marks; D. In the photo, the first author observing a theropod track from the El Chocón (Rio Limay Subgroup, Upper Cretaceous, Argentina) showing a large rounded deformation surrounding the footprint; E. Floodplain deposits from the Iouaridène Formation (Late Jurassic, Morocco), in which there are microbial mat laminations, present theropod tracks originated in a firm substrate. In the photo a theropod footprint (*Megalosauripus* sp.) with well-defined borders and contour in a mudstone surface with mudcracks. Scale bar in centimeters. Photo courtesy of Matteo Belvedere.

The deposits are fine grained alluvial sediments, generally silt and mud, finely laminated, interrupted by some sandy intercalation. Mud cracks, convolute structures, ripple marks, climbing ripples, rain prints, and vertebrate and invertebrate bioturbation are widespread because of repeated exposure (Reineck and Singh, 1986).

The footprints and undertracks in the basins in northeastern Brazil were produced in subaerial and subaqueous settings. It is possible to identify footprints with well-defined morphologies or progressively losing their clarity due to their relationship with mud cracks, fluidization, convolute, and radial structures. Those ones with impressions of claws, nails, and soft tissue such as the sole and phalangeal pads, skin wrinkles and dermal scales impressions are considered to be produced in muddy sediments with high plasticity and low water content, probably in a subaerial setting of floodplains and marginal lake 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 (Fig. 6B). In subaqueous environments, there is a decrease in the morphological details of the footprints such as nails, claws, pads and sole marks (Fig. 6C). Therefore, the cohesiveness of a muddy sediment can allow the well-defined contour of a footprint (Calvo and Rivera, 2018), besides the complete deformation of the surrounding sediments (Fig. 6D) as observed in the floodplain tracks of El Chocón (Rio Limay Subgroup, Late Cretaceous, Argentina).

An example of a cohesive substrate based on the footprints morphology is presented by Belvedere (2008) and Belvedere et al. (2010) on the most diverse ichnocoenosis from Late Jurassic strata of Gondwana. Floodplain deposits from the Iouaridène Formation, Morocco, in which there are microbial mat laminations, show twenty-one trampled layers with dinosaur tracks (Fig. 6E). These are found in cyclic alternations of red mudstones (also carbonate-cemented mudstones) and very fine sandstones. The small theropods and huge sauropod tracks are relatively shallow, interpreted by Belvedere et al. (2010) as produced in a firm ground. The same interpretation was presented by Boutakiout et al. (2019) for the giant theropod footprints found at the Aït Mazigh site in the Iouaridène Formation. The presence of mud-cracks polygons that are bent in the extrusion rims, the brecciated bottom of footprints and the separation of mud polygons corroborate the interpretation that the dinosaurs stepped on a hardened soil.

The cohesiveness of a substrate also allows the preservation of detailed morphological aspects in a footprint, such as skin impressions. Mateus et al. (2016) in the study of Lower Cretaceous tracks from Angola (Catoca Mine) described the presence of sauropod skin impression preserved in mudstones. The presence of this feature in the tracks are a good evidence of the high cohesiveness and plasticity of the muddy sediment

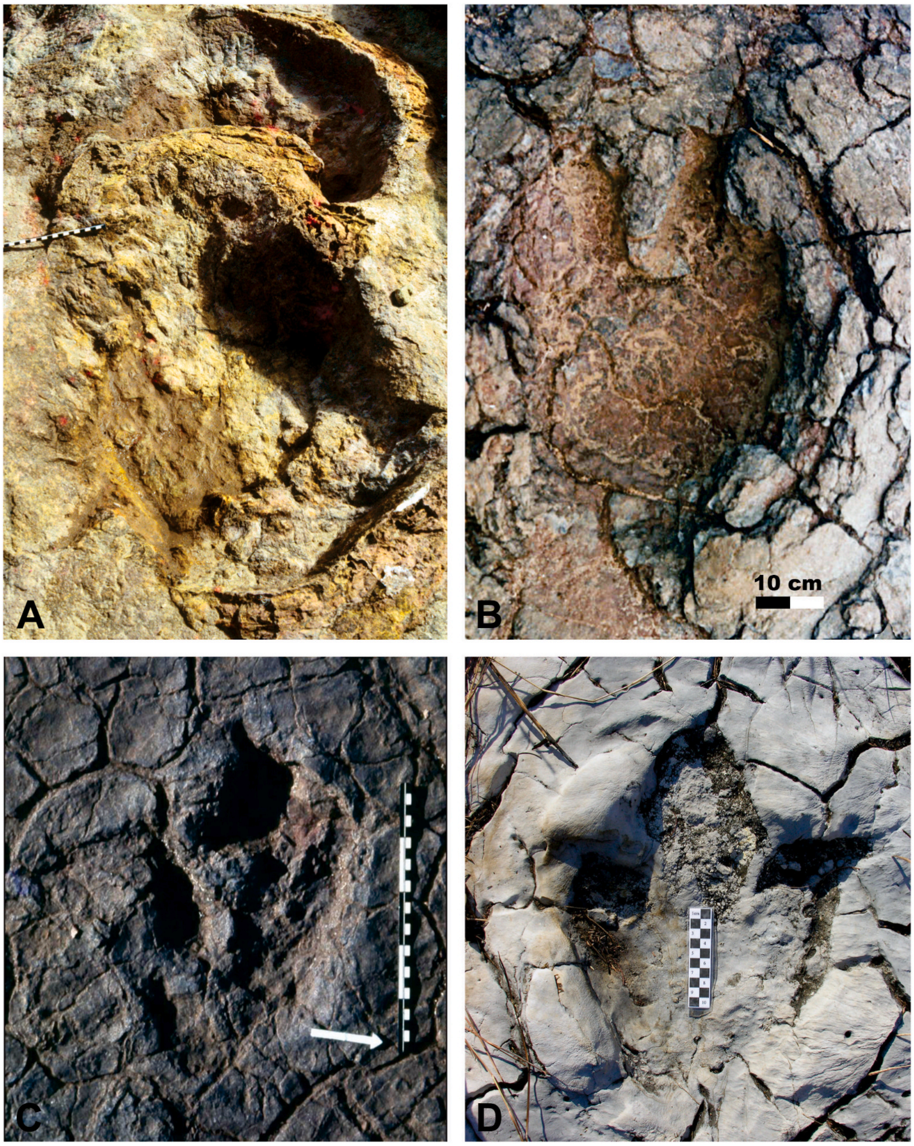

Fig. 7. A. A hand-foot set from one of the eight trackways of large sauropods (titanosaurids). Note the strong heteropody, because of the very wide hands; and the large and deep displacement rims. Toro Toro Formation (Campanian-Santonian, Toro Toro, Potosí - Bolivia). Scale bar in centimeters; B. *Sousaichnium pricei*, an Iguanodontidae track from Passagem das Pedras, Sousa Formation (Rio da Serra-Aratu age, Brazil). There is a displacement rim that favors and controls the radial and concentric cracks surrounding the footprint; C. A large theropod footprint surrounded by mudcracks, indicating that the track was originated before the dehydration process of the mud. Matadouro locality, Sousa Formation (Rio da Serra-Aratu age, Sousa Basin, Brazil). Scale bar in centimeters; D. Theropod footprint from Bemaraha Formation (Middle Jurassic, Madagascar) showing circular mud cracks along the displacement rim and others cutting through the rim at different angles as consequence of the drying sediment. Nonetheless, the footprint itself was not affected by the cracking (Photo courtesy by Alexander Wagensommer). Scale bar in centimeters.

when the impression was produced.

Another phenomenon tied to the substrate cohesiveness is the development of displacement rims of footprints, which are quite variable in size and form (Fig. 7A). Some of them 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 animal had impressed its feet into a surface of very plastic and/or waterlogged mud. Under these circumstances, the displacement rim of the hindfoot will frequently fill in and/or squash the horseshoe-shaped footprint of the forefoot from behind, so that it becomes very narrow or little more than a crescent-shaped slit. In other cases, and frequently, the displacement rim around a footprint is very low and narrow, indicating a 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.

Other kinds of displacement rims observed by us are:

- Elliptical displacement rims jointly around a pair or set of hand-foot prints in the trackway of a quadrupedal animal, mainly seen in sauropod track;
- Displacement rims which control the development of mud-cracks;

Aside from complete displacement rims, there are other analogous structures of expulsion:

- Compressed sediment between two toes, in the shape of a wedge, especially in footprints made by running theropods;
- Crescent displacement rims immediately in front of footprints in trackways made by running dinosaurs;
- Crescent-shaped convexities at the rear margins of each of the three incomplete digit impressions in footprints made by half-swimming trackmakers, as in many of the theropod footprints from Sousa Basin (Brazil).

To say that the positive (convex) volume of the displacement rim is almost the same as the negative (concave or void) volume of the corresponding footprint on the sediment surface, is probably a tautology. However, it is convenient here to stress this concept. Very deep footprints are indeed frequently associated with high and wide displacement rims. In contrast, the dinosaur footprints of the Rio do Peixe Basins (Brazil) are rarely very deep, and so their displacement rims generally have only modest dimensions, many times even with tracks of sauropods and large ornithopods. One has the impression that the superficial sediments were sufficiently plastic enough to receive the impression of the footprints, but that the sediment layers beneath the track-bearing stratum at the time tracks were impressed were often already hard, perhaps due to partial and early lithification, so that the feet of the trackmakers sank just through the thickness of the more recent and superficial layer. A good example of this phenomenon is the holotype of *Caririchnium magnificum* Leonardi (1984), in the Antenor Navarro Formation at Serrote do Letreiro (SOES 9, Sousa Basin, Brazil), produced by a very large, massive and heavy ornithopod, whose footprints are nonetheless very shallow, with very low and thin displacement rims.

Although the positive volume of the displacement rim is almost the same as the negative volume of the corresponding footprint, the key word here is almost, because one part of the volume of the sediment is not displaced, but rather compacted on the “sole” of the footprint. Consequently, there are at Sousa Basin not many very deep footprints. The deepest tracks are those of the main trackway of *Sousaichnium pricei* at Passagem das Pedras (SOPP 1, Fig. 7B) and especially some sauropod undertracks at Piau (SOCA level 13/3).

The mud cracks and their relationship with the footprints show distinct patterns of cracking. The processes of dehydration of the muddy sediments produce polygonal structures of distinct sizes. Therefore, the presence of a track in a muddy sediment previously to the dehydration processes allows a specific pattern of polygon. The area deformed by the footprint acts as a stress relief, inducing a preferential cracking in the surrounding margins of the footprint and from the extremities of the digits. This is a good indication that the track was produced during a high water content of the substrate (Fig. 7C).

The footprints found in the fine-grained and coarse limestones from Bemaraha Formation (Bajocian-lower Bathonian, Middle Jurassic, Madagascar) show a similar pattern in the mud cracks relationships with the footprints, although produced in a distinct substrate of that from the mudstones of Sousa Formation (Rio da Serra-Aratu age, Brazil). Wagensommer et al. (2012) observed that the mud cracks affected the mud displacement rims around dinosaur footprints from Bemaraha Formation (Middle Jurassic, Madagascar), but they rarely affect the footprint itself (Fig. 7D). When the sediment is soft, there is the possibility to develop prominent displacement rims around the footprints, besides deeply impressed tracks and often unclear outlines of the individual footprints. Then, after the dinosaur’s track in a subaerial exposure, there is the development of two distinct kinds of cracks – the circular cracks along the apex of the rim, formed as a direct consequence of sediment displacement; and those ones cutting through the rim at different angles as a consequence of the drying of the sediment.

In the central Bolivian Andes is found the Cal Orqo ichnosite and equivalent sites of Maastrichtian age that correspond to a megaichnosite which starts from the south of Peru (Vilquechico Formation), crosses the Bolivian Central Andes (El Molino Formation) and arrives to the south, in the province of Salta in Argentina (Yacoraite Formation), with a total extension of about 2,000 km. The Cal Orqo ichnosite (Sucre, Bolivia) contains a great number of trackways attributed to sauropods, ornithopods, theropods and ankylosaurs (McCrea et al., 2001; Meyer et al., 2001; Lockley et al., 2002). This unit represents a mosaic of lacustrine and marginal lacustrine facies. Sandstones represent the influence of fluvial and deltaic sedimentation encroaching on a perennial lake basin (Meyer et al., 1999; Lockley et al., 2002), informally named, in the text of didactic panels at the Geopark of Cal Orqo, as “Lake Branisa-Leonardi”. In this context the tracks are mainly preserved with the digits and in some cases anatomical details of footprint (Fig. 8A). Therefore, the sediment should present some plasticity as the development of displacement rims surrounding the tracks are very common (Fig. 8B). This same aspect is also observed in the Campanian Toro Toro ichnosite of Toro Toro Formation, Bolivia.

In the Toro Toro Basin, in the Upper Cretaceous (Campanian) of Toro Toro Formation, there is a large number of tracks attributable to sauropods, theropods and ankylosaurs (Leonardi, 1984, 1994; Lockley et al., 2002). There are two distinct main rocky pavements with tracks. In that one of yellowish sandstones, poorly sorted, with medium to coarse grained, and abundant in iron oxides (Leonardi and Peredo, 1985; Leonardi, 1994), the ankylosaur tracks – heavily armored animals – produce vertical shafts, without deformational surrounding rims (Fig. 8C). In another context the dinosaur track association found in some layers of medium to fine grained sandstone, with quartz grains and calcareous cement, presents eight exquisite trackways of very large sauropods (six adults and two juveniles titanosaurids) and thirty-two trackways of theropods, possibly abelisaurids. All of the forty trackways, sauropod and theropod together are subparallel, all of them heading for ~ N, and represented the first record of herding behavior among Late Cretaceous sauropods in South America (Leonardi, 1984, 1994; Lockley et al., 2002). Some of the theropods were sinking their feet into the large and deep displacement rims of the sauropods, which had apparently passed on that muddy plane before them. In the first locality, the ankylosaurian tracks are often deep; however, the displacement rims are here very low or absent; in the second locality, the footprints are also very deep, but the displacement rims are large and high, for the theropods and, a lot more, for the sauropods, whose displacement rims are true waves of lithified sandy mud. This is an excellent example of how the plasticity and cohesiveness of the sediments influence the track preservation and the production of the

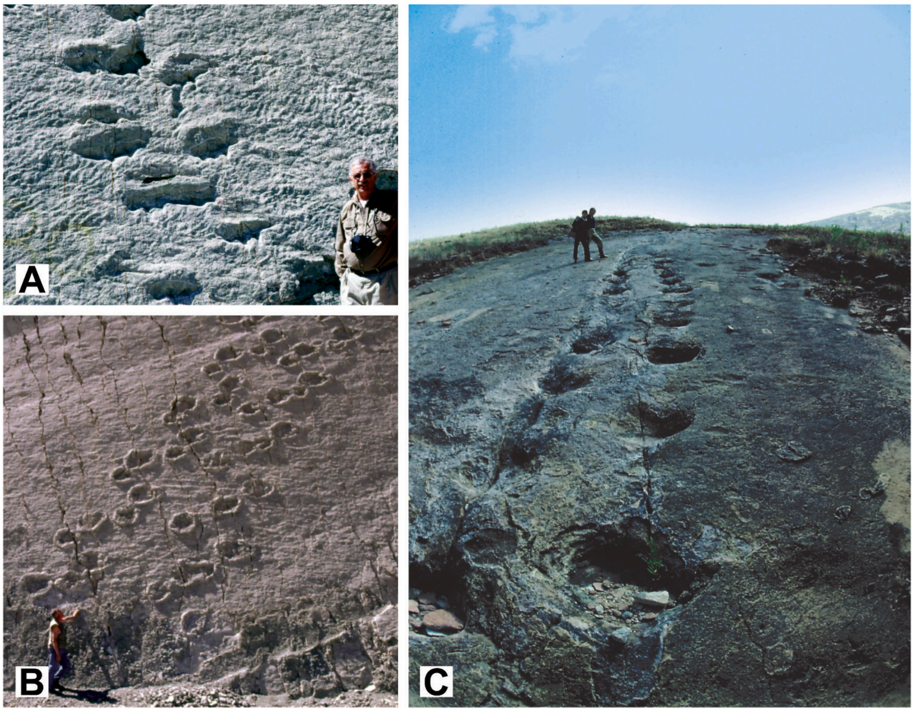

Fig. 8. A. One of the seven fine ankylosaur trackways discovered (1998) at Cal Orqo'o quarry (El Molino Formation, Maastrichtian, Bolivia). The trackmaker walked irregularly, with a low-stride gait. Note the high displacement rims and the ripple marks impressed by the waves of the ancient lake. In the photo, the Bolivian geologist Mario Suárez Riglos, one of the responsible by the discovery of the ichnosite; B. The Cal Orqo ichnosite (El Molino Formation, Maastrichtian, Bolivia) contains a great quantity of trackways with prominent displacement rims related to a wet substrate with high plasticity; C. In the Toro Toro Formation (Campanian-Santonian, Bolivia) the large (about 2000 m^2) track bearing surface of Mt. Huaillas with the twins ankylosaurian large trackways whose tracks are often deep; however, the displacement rims are very low or absent. Almost 60 bipedal dinosaur trackways cross obliquely these two deep trackways.

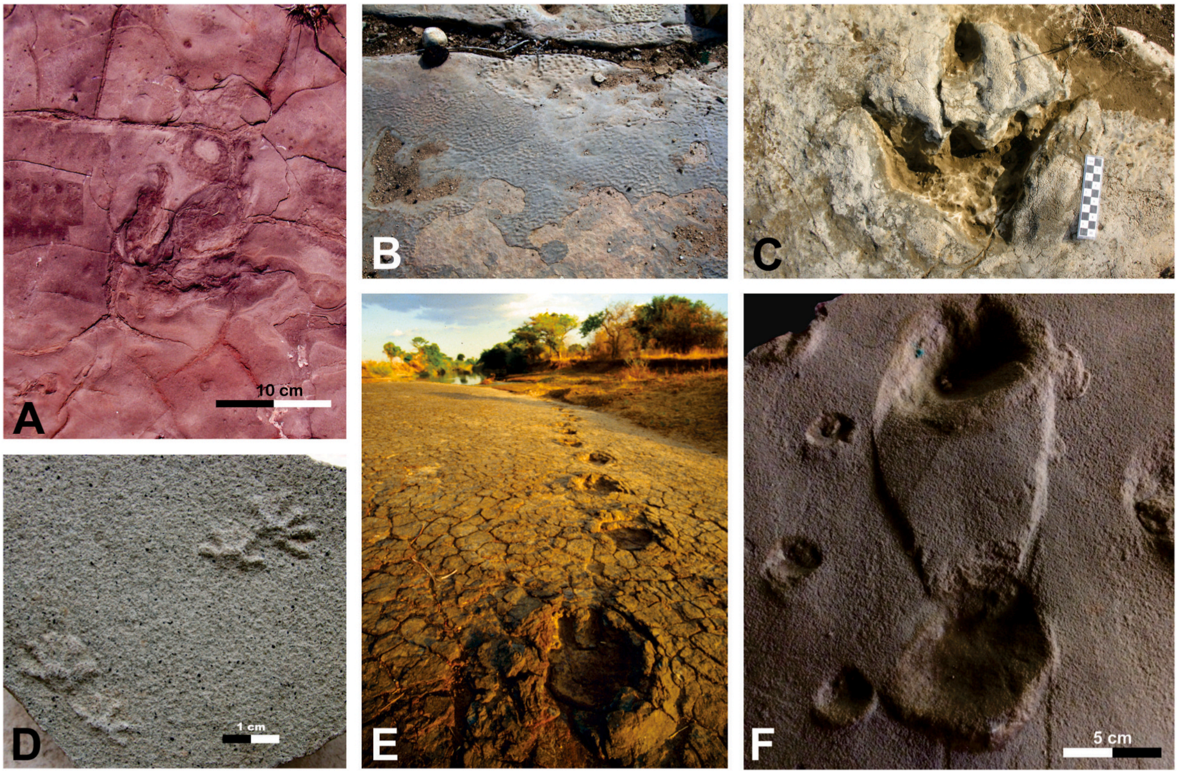

Fig. 9. A. The exquisite preservation of some tracks is related to the mediation of microbial mats in their preservation. Araçá, Rio Novo, Sousa Formation (Rio da Serra-Aratu age, Brazil); B. A theropod isolated footprint (bottom left) and wrinkled structures showing the interaction of microbial mats and the preservation of the track. Locality of As Lajes Farm, Jandaíra Formation, Potiguar Basin – Upanema, Rio Grande do Norte State, Brazil; C. A theropod footprint from Bemaraha Formation (Middle Jurassic, Madagascar). Surrounding the footprint delicate irregular cracks and a corrugate surface indicative of the algal mats shrinkage. Scale bar in centimeters; D. *Ameghinichnus patagonicus*, a track preserved in volcanic sediments of La Matilde Formation (Middle Jurassic, Argentina). The high quality of the preservation is indicative of very specific humidity condition in the substrate, allowing the cohesiveness of the clastic sediments; E. *Sousaichnium pricei* at Passagem das Pedras, Sousa Formation (Sousa Basin, Brazil). A large displacement rim surrounds each footprint, showing that the tracks were produced when the mud sediment was plastic and wet in a floodplain area; F. Two successive tracks showing a wide displacement rim, surrounding the footprints and mainly behind the footprints. The trackways are very deep and the displacement rim are long because the dry sand of the Botucatu Formation (Paraná Basin, Brazil). Sample UFRJ-DG s/n IcV. Photo C courtesy of Alexander Wagensommer.

displacement rims.

2.4. The role of microbial mats in the preservation of tracks

Based on actualistic approach on modern tidal-flats, Marty (2008) and Marty et al. (2009) showed that during and after footprint formation, microbial mats play an important role in preservation, as they covered and stabilized the tracks. They may be quickly lithified by the precipitation of calcium carbonate (Chafetz and Buczynski, 1992) and consequently enhance the potential preservation of footprints. Microbial mats are abundant in low latitudes where protected microtidal lagoons occur more frequently and provide varied ecospaces that allow the flourishment of benthic microbial communities (Marty, 2008).

The preservation of the dinosaur tracks from the Sousa Formation (Sousa Basin, Brazil) was interpreted as related to the footprint consolidation by early lithification due to the existence of algal biofilms (Fig. 9A) that prevented them from disintegration (Carvalho et al., 2013). The sediments would have been initially biostabilized leading to preservation by the biofilms (Noffke et al., 2001, 2019bib_Noffke_et_al_2001bib_Noffke_et_al_2019) followed by early cementation (calcification). However, the thick microbial mats that may form continuously, produce a strongly cohesive zone of low permeability, separating the underlying sediment from the atmosphere and protecting it against water loss, so that the sediment below a dry mat is not necessarily dry (Porada et al., 2007). Prints on such surfaces have a typical cracked surface, exhibit the gross outline of the foot, and are clearly deeper as some of the tracks observed at Passagem das Pedras, Sousa Basin (Brazil).

Fig. 9BAlso in the Jandaíra Formation (Maastrichtian, Potiguar Basin, Brazil) the microbial influence can be observed in the preservation of the fossil tracks (Fig. 9B). At Lajes farm, Upanema County, some levels of this unit present wrinkled surface resulted from microbial mats dehydration and mud-cracked surfaces. The wrinkles by microbial mats, show superimposed a shallow and medium-sized theropod track which was preserved by the intermediation of the algal mat. Similar features are observed in a track-bearing surface with mud cracks in the Foum Tataouine Formation (Middle Jurassic, Tataouine Basin – Tunisia). The dinosaur tracks are found in a succession of limestones and marls in a corrugate surface, interpreted as microbial mats, that avoided the weathering and erosion of the tracks (Contessi and Fanti, 2012).

In recent sediments, footprint morphology is generally related to the microbial mat thickness and water content of the mat and of the underlying sediments (Marty et al., 2009). In dry mats, generally poorly defined footprints or no footprints were produced, while in soaked ones the imprints are well-defined, sometimes with well-defined displacement rims (Marty, 2008). The formation of well-defined displacement rims around the prints of large dinosaurs occurs in thick, plastic, moist to water-unsaturated microbial mats on top of moist to water unsaturated sediment. These aspects are commonly observed in tracks from Sousa Basin (Rio da Serra-Aratu age, Brazil) by Carvalho et al. (2013) and from Bemaraha Formation (Middle Jurassic, Madagascar, Fig. 9C) by Wagensommer et al. (2012). Also in the Candeleros Formation (Upper Cretaceous, Argentina) the association of track preservation and microbial mats is present (Heredia et al., 2020). In this case the footprint consolidation and its early lithification probably occurred due to the existence of microbial mats that allowed a more cohesive substrate, preventing from erosion. The sediments were initially stabilized by early cementation and by the network of mat fabric over the tracks.

It is important to observe that not only microbials can allow exquisite preservation of tracks (a common sense nowadays in ichnology). The compositional nature of the substrate can play an important role in the track preservation. In the La Matilde Formation (Middle Jurassic, Argentina) there are some of the best preserved track fossils in floodplain deposits. The depositional conditions of La Matilde Formation are interpreted as a lowland setting associated with an active volcanic environment, with swamps and water bodies, probably derived from adjacent floodplains. The ichnofauna is dominated by small-bodied species, at least four dinosaurian ichnotaxa (Wildeichnus, Grallator, and the endemic Delatorrichnus and Sarmientichnus) and the mammalian Ameghinichnus. The tracks are natural molds and casts, in fine-grained sediments such as tuffaceous siltstones and sandstones (De Valais, 2011). In this case the nature of the substrate was certainly the main factor in the exquisite preservation of the tracks. The high plasticity and cohesiveness of volcanic ash allowed the fine detailed tracks preservation (Fig. 9D).

3. Discussion: footprints as biosedimentary structures

One of the most important factors in footprint preservation is the time of exposure. Fresh trampled surfaces can be in fact readily weathered up to destroyed due to erosional and sedimentary processes acting after track registration. If subaerial exposure is short (Tucker and Burchette, 1977), then the intrinsic preservation potential of tracks is enhanced. Another factor that influences preservation is that the deformation of the print-bearing surface, e.g. by a heavy animal, favors the preservation of underprints and transmitted prints. The reworking of sedimentary substrates by terrestrial vertebrates was considered as important in disturbing the primary grain fabric and sedimentary structures by Laporte and Behrensmeyer (1980) and there is a narrow range of sediment textures and moisture content, which will allow preservation of the tracks in the geological record (Table 1) Maybe restricted, vegetation-free areas marginal to lacustrine and fluvial paleoenvironments offer the best preservation potential, since footprints can be buried and preserved shortly after trampling (Fig. 9E). After footprint formation, which, as mentioned, strongly depends on the interactions between substrate properties and producers, preservation potential is enhanced in some paleoenvironments by the growth of microbial mats. Growing microbial mats provide early lithification to tetrapod tracks favoring their preservation in the geological record (Lockley, 1991; Avanzini et al., 1997; Paik et al., 2001; Phillips et al., 2007; Carvalho et al., 2013; Cariou et al., 2014).

Tracks can occur as isolated or superimposed casts in cross-section, as pillar-like or barrel-like morphologies, but commonly the casts are irregularly cylindrical to ‘‘U’’ shaped (with a smaller basal diameter than at the top) as observed by Difley and Ekdale (2002). The depth of the depression depends both on the animal’s weight and the plasticity of the sediment. The vertical section deformation structures have proven successful in obtaining additional details about the walking kinematics that rarely could be obtained from studying the track at the surface (Milàn and Bromley, 2006). Then, there is a usefulness of vertebrate tracks to the correct interpretation of the trackmaker and the substrate consistency (Milàn et al., 2004).

Different types of tracks along the same trackway indicates that the substrate displayed heterogeneities in water content (Marty, 2008). In aeolian deposits the elongated displacement rim behind tracks indicates a rather dry substrate (Fig. 9F), while the presence of a short and thick displacement rim indicates a moist substrate.

Another aspect of deformation is observed in the fluvial and aeolian deposits of the Jurassic Guará Formation (Paraná Basin, Rio Grande do Sul, Brazil). The fossil tracks observed in the bedding plane are concave circular-shaped structures, with a laminar deformation (Silva et al., 2007). These were interpreted as a disruption of the substrate homogeneity caused by bioturbation of sauropod dinosaurs (Godoy et al., 2012; Silva et al., 2012).

In the Aptian of Araripe Basin (Santana and Rio da Batateira formations) tracks are vertical sections in a succession that intercalate marls and fine sandstones (Carvalho et al., 2020). According to Pérez-Lorente (2015) the penetration limit in which a footprint can sink in sediment occurs when the resistance to penetration of the foot is equal to the pressure applied. This will be directly related to the physical properties of the substrate, such as viscosity, consistency, and adherence. As the walls of some tracks in the Santana Formation (Crato

Table 1
Distinct biosedimentary patterns of the ichnological record as a response to substrate condition and paleoenvironments.

Track-related Structure	Substrate Condition	Paleoenvironmental Context
small displacement rim	humid, high cohesiveness, low water content	tidal flat, fluvial-lacustrine, aeolian
wrinkled structures	microbial mats, humid, high cohesiveness, subaerial exposition	tidal flat, fluvial-lacustrine, floodplain
mud collapse	waterlogged, low cohesiveness	supratidal, shoreline, estuary, marginal pond
narrow and high displacement rim, superimposed tracks	humid, high cohesiveness, low water content	tidal flat
fluidization structures	waterlogged, low cohesiveness, soft substrate, liquefaction	tidal flat, shoreline, fluvial-lacustrine, floodplain, marginal pond
impact structures, huge contorted bedding	humid, low cohesiveness, low water content	tidal flat, coastal plain, lagoon, fluvial-lacustrine, floodplain
long and shallow displacement rim	dry, low cohesiveness, low water content, low stand phreatic level	aeolian, dry interdune, dune
prominent "sand crescent"	dry, low cohesiveness, low water content, low stand phreatic level	aeolian, dry interdune, dune
short and deep displacement rim	humid, high cohesiveness, high stand phreatic level	aeolian, interdune, dune
folded-up levels	dry, low cohesiveness, low stand phreatic level	aeolian, dry interdune, dune
soft tissue, scale, wrinkle impressions	humid, high cohesiveness, high plasticity, low water content	fluvial, lake border, floodplain
track-cracks (cracks surrounding footprints limits and as digits extension)	waterlogged, high plasticity, high cohesiveness, high water stand level	fluvial, lake border, floodplain
displacement rim apex with circular cracks	humid, soft, high cohesiveness, low water content	fluvial-lacustrine, floodplain, temporary lake
random cracks crosscutting track	hard soil, low humidity, high cohesiveness, low stand phreatic level	fluvial-lacustrine, floodplain, temporary lake
extrusion rim with bent mud-cracks polygons	hard soil, low humidity, high cohesiveness, low water content	fluvial-lacustrine, floodplain
brecciated bottom of footprint	hard soil, low humidity, high cohesiveness, low water content	fluvial-lacustrine, floodplain
wide and thick displacement rim, mud bulges	waterlogged, high cohesiveness, high plasticity	fluvial-lacustrine, floodplain, lake border
horseshoe-shaped	waterlogged, high cohesiveness, high plasticity	fluvial-lacustrine, floodplain, lake border
low and narrow displacement rim	hard soil, low humidity, compact, high cohesiveness	fluvial-lacustrine, floodplain, lake border
crescent-shaped convexities on digits rear margins	waterlogged, aqueous, high stand phreatic level	fluvial-lacustrine, lake
positive volume of displacement rim smaller than the negative volume of the footprint	hard soil, low humidity, low water content, low stand phreatic level	fluvial-lacustrine, floodplain
well defined, regular displacement rim	microbial mats, humid, high cohesiveness, high plasticity	tidal flat, fluvial-lacustrine, floodplain

Member) are still vertical (even after the foot withdrawn), this is indicative that the original plasticity of the substrate was high (Fig. 10A). In the Rio da Batateira Formation, the tracking surface and layers below 40 cm thickness from the surface were deformed by dinosaur autopodia due to pressure over soft to moderately hard mud sediments, as there is no evidence of fractures or microfaults. The natural track casts penetrate into the underlying layers as large sub-cylindrical structures. The casts are amorphous bulges or sedimentary layers deformed and downfolded (Fig. 10B). The pressure produced by the autopodia on the substrate induces the development of these deformational structures, and the total substrate bioturbation. The association of the tracks from Rio da Batateira Formation can seem to be simple load casts, however, they are dinosaur overtrampling, and more in detail an association of theropod, small and large sauropod tracks (Carvalho et al., 2018).

Also in the Aliança Formation, as well as in the Sergi (Dom João age, Recôncavo Basin, Brazil) and Maceió formations (Aptian, Alagoas Basin, Brazil), there are shaft structures crossing the lamination (Carvalho and Borghi, 2008), that are interpreted as the result of load efforts by the autopodia of dinosaurs on the surface of interdune deposits and fluvial bars in alluvial plains. In the Aliança and Sergi formations, interpreted as a humid interdune environment, these shafts are up to 30 cm depth. In the Aliança Formation the shafts are shallower (15 cm depth) with a concave successive deformation of the sedimentary levels. In the Sergi Formation these shafts are associated with flame structures. The difference between these two patterns are probably related to the humidity of the substrate. Concave lamination should be related to drier sediments, while fluidization aspects with a more humid context (Carvalho and Borghi, 2008). In the Maceió Formation they are vertical shafts (Figs. 10C), 20 cm large and up to 46 cm deep, whose margins present the folding of the parallel lamination upwards (Carvalho and Souza-Lima, 2008).

Cross-section tracks such as those from the Araripe, Recôncavo, Alagoas basins (Lower Cretaceous, Brazil), Candeleros Formation (Cenomanian, Argentina) and from Bemaraha Formation (Middle Jurassic, Madagascar, Fig. 10D), that lack anatomical details, are difficult to assign to a particular trackmakers taxon. They are more useful in providing information concerning the distinct moments of the track formation and its relationship with the substrate (Díaz-Martínez et al., 2017). However, they point also to the presence of large animals (dinosaurs), otherwise unknown in those formations.

4. Conclusions

The analysis of tidal flats, aeolian and fluvio-lacustrine environments comprises some peculiar sedimentary features, which are originated during the footprint origin, that are related to the environment and the substrate properties.

Tracks from carbonatic platform and siliciclastic tidal flats present fine-grained sediments, such as clay and carbonate, that favored the preservation, especially in the inter and supratidal sediments. The footprints denote high displacement rim, fluidization structures or impact structures as the result of a "dinostatic pressure" in water-saturated and low cohesive sediments. The crenulation of the sediments surrounding the digits, is a clear evidence of water saturated sediments that fluidize after the foot impact. The foot pressure can also produce impact structures, large substrate deformation on tidal flat environments due the sauropod feet impact and the subsequent deformation below the sediment interface.

Aeolian deposits are generally restricted to the preservation of tracks, but high stand phreatic level in dune areas or in the more humid region of the interdunes, can allow preservation. The main sedimentary structures associated with footprints are half-moon shaped small sandy slides. The elongated displacement rim behind tracks indicates a rather dry substrate, while the presence of a short and thick displacement rim indicates a moist substrate.

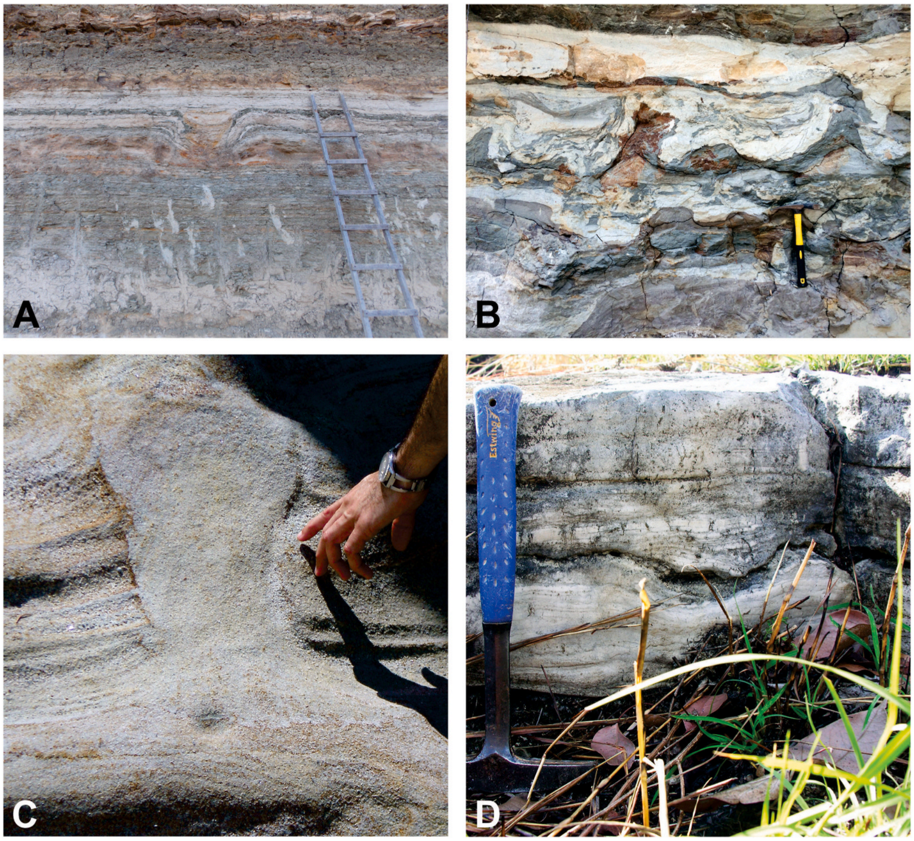

Fig. 10. A. Cross section of a dinosaur track in a quarry outcrop of the Santana Formation (Aptian, Araripe Basin, Brazil). The shaft walls are still vertical, an indicative of a high substrate plasticity; B. Riacho da Batateira Formation (Aptian, Araripe Basin, Brazil) dinosaur overtrampling resulting in a deformed convoluted stratum; C. Cross section of a footprint from the Maceió Formation (Aptian, Alagoas Basin, Brazil). The shaft structure crossing the lamination is interpreted as the result of load effort by a dinosaur autopodium on the surface of a fluvial bar in alluvial plains; D. A cross section of a dinosaur track below the Upper Track Level (UTL), Bemaraha Formation (Middle Jurassic, Madagascar), showing the deformation produced in the sedimentary laminae as the result of a dinoturbation process. Photo D courtesy by Alexander Wagensommer.

The lake borders and the floodplains are favorable contexts to exquisite tracks preservation. The cohesiveness of a muddy sediment can allow the well-defined contour of a footprint, besides the complete deformation of the surrounding sediments, as displacement rim, which is quite variable in size and form. Some of them are wide and thick, sometimes with the aspect of true bulges of mud, especially well developed in sauropod footprints. One important aspect is that the displacement rims can control the development patterns of mud cracks. Aside from complete displacement rims, there are other analogous structures of expulsion, including compressed sediment between two toes, in the shape of a wedge, especially in footprints made by running theropods; crescentic displacement rims immediately in front of footprints in trackways made by running dinosaurs; crescent-shaped convexities at the rear margins of each of the three incomplete digit impressions in footprints made by half-swimming trackmakers, as in many of the theropod footprints. In the floodplain area the processes of dehydration of the muddy sediments produce polygonal structures of distinct sizes. The area deformed by the footprint acts as stress relief, inducing a preferential cracking in the surrounding margins of the footprint and from the extremities of the digits. This is a good indication that the track was produced during a high water content of the substrate.

Tracks can also occur as isolated or superimposed casts in cross-section, as pillar-like or barrel-like morphologies, but commonly the casts are irregularly cylindrical to "U'' shaped. The natural track casts penetrate into the underlying layers as large sub-cylindrical structures. The casts are amorphous bulges or sedimentary layers deformed and downfolded. The pressure produced by the tetrapod autopodia on the substrate induces the development of these deformational structures, and the total substrate bioturbation.

The deformation in ancient sediments by the foot of an animal, provides insights into the nature of the substrate and paleoenvironment. The footprint impression physically moves the superficial surface and the underlying layers, particles, granules, pebbles and anything else that constitute the substrate. Footprints represent, in this way sedimentary deformations, whose preservation as a biosedimentary feature depends not only on chemical and physical factors but also on the activity of an organism.

Author 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; conducted the field work; performed the analysis; interpreted obtained data; wrote the manuscript

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

Alexander Wagensommer, Simone D'Orazi Porchetti, Nasrollah Abbassi, Saeed Madanipour, Matteo Belvedere, Paolo Mietto, Paolo Citton, Christian A. Meyer and Marcelo Adorna Fernandes for kindly providing images from Madagascar, Iran, Morocco, Argentina, Bolivia and Brazil (Botucatu) footprints. To Heitor Francischini, Paolo Citton and Spencer Lucas for the detailed revision that improved the manuscript. Rafael Costa da Silva for the information concerning the geology of Guará Formation and Lorenzo Marchetti for the support about references on the extramorphologic concepts. To Ashok Sahni, for the information concerning fossil tracks from India. We also thank Fabiana Zandonai of the Center of Earth Sciences of the Civic Museum of Rovereto (Italy), Fabio Massimo Petti (Società Geologica Italiana), Marco Avanzini (Museo Tridentino di Scienze Naturali, Italy), Silvério Figueiredo (Instituto Politécnico de Tomar, Portugal), Pedro Proença Cunha (Universidade de Coimbra, Portugal), Félix Pérez-Lorente (Universidad de la Rioja, Spain), Laura Piñuela and José Carlos García-Ramos (Asturias, Museo del Jurasico de Asturias, Spain) for their support on field work and discussion on dinosaur tracks. Diogo Lins Batista, Ighor Dienes Mendes and Jaime Joaquim Dias helped with illustrations. We acknowledge the financial support provided by the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (Faperj E-26/202.910/2017/), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 303596/2016-3) and, by Cavanis Institute.

References

Abbassi, N., Madanipour, S., 2014. Dinosaur tracks from the Jurassic Shemshak Group in the central Alborz mountains (northern Iran). Geol. Carpathica 65 (2), 99–115.

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

Avanzini, M., Frisia, S., 1996. Sedimentologia e diagenesi degli orizzonti a impronte di dinosauro dei Lavini di Marco (Trentino Meridionale): implicazioni ambientali nel contesto paleogeografico del Giurassico Inferiore. Atti Ticinense di Scienze della Terra, Serie speciale 4, 33–46.

Avanzini, M., Frisia, S., Rinaldo, M., 2000. I Lavini di Marco nel Giurassico Inferiore: la ricostruzione di un antico ambiente di vita. In: Leonardi, G., Mietto, P. (Eds.), Dinosauri in Italia. Le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani. Accademia Editoriale, Pisa-Roma, pp. 247–272, 2000. 497 pp.

Avanzini, M., Frisia, S., Van den Driessche, K., Keppens, E., 1997. A dinosaur tracksite in an early liassic tidal flat in northern Italy: palaeonvironmental reconstruction from sedimentology and geochemistry. Palaios 12, 538–551.

Belvedere, M., 2008. Ichnological researches on the Upper Jurassic dinosaur tracks in the Iouaridène area (Demnat, Central High-Atlas, Morocco). PhD. Thesis. Dipartimento di Geoscienze. Università degli Studi di Padova, p. 121.

Belvedere, M., Farlow, J.O., 2016. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: the Next Steps. Indiana University Press, Bloomington, pp. 92–98.

Belvedere, M., Mietto, P., Ishigaki, S., 2010. A late Jurassic diverse ichnocoenosis from the siliciclastic Iouaridène Formation (central high Atlas, Morocco). Geological Quaterly 54 (3), 367–380.

Belvedere, M., Jalil, N.-E., Breda, A., Gattolin, G., Bourget, H., Khaldoune, F., Dyke, G.J., 2013. Vertebrate footprints from the Kem Kem beds (Morocco): a novel ichnological approach to faunal reconstruction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 383–384, 52–58. https://doi.org/10.1016/j.palaeo.2013.04.026, 2013.

Belvedere, M., Franceschi, M., Sauro, F., Mietto, P., 2017. Dinosaur footprints from the top of Mt. Pelmo: new data for Early Jurassic palaeogeography of the Dolomites (NE Italy). Boll. Soc. Paleontol. Ital. 56 (2), i–viii. https://doi.org/10.4435/BSPI.2017.10, 2017.

Boutakiout, M., Herrero, J., Ochoa, R., Pereda, J.C., Sáinz, J.L., Pérez-Lorente, F., 2019. Giant theropod footprints in the upper Jurassic of Morocco. Aït Mazigh site (central Atlas). Geogaceta 66, 83–86.

Calvo, J.O., Rivera, C., 2018. Huellas de dinosaurios en la costa oeste del embalse Ezequiel Ramos Mexía y alrededores (Cretácico Superior, Provincia de Neuquén, República Argentina). Bol. Soc. Geol. Mex. 70 (2) https://doi.org/10.18268/bsgm2018v70n2a11.

Candia Halupczok, D.J., Sanchez, M.L., Veiga, G.D., Apesteguía, S., 2018. Dinosaur tracks in the Kokorkom desert, Candeleros Formation (cenomanian, upper cretaceous), patagonia Argentina: implications for deformation structures in dune fields. Cretac. Res. 83 (2018), 194–2006. https://doi.org/10.1016/j.cretres.2017.10.017, 2017.

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., 1994. Contexto tafonômico das pegadas de terópodes da Praia da Baronesa (Cenomaniano, Bacia de São Luís). In: Boletim de Resumos Expandidos do 38° Congresso Brasileiro de Geologia, Camboriú, vol. 3. Sociedade Brasileira de Geologia, pp. 211–212.

Carvalho, I.S., 1995. As pistas de dinossauros da Ponta da Guia (Bacia de São Luís, Cretáceo Superior—maranhão, Brasil). An Acad. Bras Ciências 67, 413–431.

Carvalho, I.S., 1996. As pegadas de dinossauros da bacia de Uiraúna-Brejo das Freiras (Cretáceo Inferior, estado do Paraíba). Boletim do 4° Simpósio sobre o Cretáceo do Brasil. Águas de São Pedro, São Paulo, pp. 115–121.

Carvalho, I.S., 2000a. Geological environments of dinosaur footprints in the intracratonic basins of northeast Brazil during the Early Cretaceous opening of the South Atlantic. Cretac. Res. 21, 255–267.

Carvalho, I.S., 2000b. Huellas de saurópodos Eocretácicas de la cuenca de Sousa (Serrote do Letreiro, Estado da Paraíba, Brasil). Ameghiniana 37, 353–362.

Carvalho, I.S., 2001. Pegadas de dinossauros em depósitos estuarinos (Cenomaniano) da Bacia de São Luís (MA), Brasil. In: Rossetti, D.F., Góes, A.M., Truckenbrodt, W. (Eds.), O Cretáceo na Bacia de São Luís-Grajaú. Museu Paraense Emílio Goeldi, Coleção Friedrich Katzer, pp. 245–264.

Carvalho, I.S., 2004. Dinosaur footprints from northeastern Brazil: taphonomy and environmental setting. Ichnos 11, 311–321.

Carvalho, I.S., Araújo, S.A.F., 1995. A distribuição geográfica dos fósseis e icnofósseis de Dinosauria na Bacia de São Luís. In: Anais da 47ª Reunião Anual da Sociedade Brasileira para o Progresso da Ciência, vol. 2. São Luís, p. 439.

Carvalho, I.S., Leonardi, G., 1992. Geologia das bacias de Pombal, Sousa, Uiraúna-Brejo das Freiras e Vertentes (Nordeste do Brasil). An Acad. Bras Ciências 64, 231–252.

Carvalho, I.S., Borghi, L., 2008. Estruturas de dinoturbação na Bacia do Recôncavo: implicações Paleoambientais. In: Congresso Brasileiro de Geologia, vol. 5. Curitiba, p. 815.

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., Souza-Lima, W., 2008. Processos de dinoturbação na Formação Maceió (Cretáceo Inferior), Bacia de Sergipe-Alagoas. In: Simpósio Brasileiro de Paleontologia de Vertebrados, vol. 7. Boletim de Resumos, Paleontologia em Destaque, Edição Especial, pp. 61–62.

Carvalho, I.S., Borghi, L., Leonardi, G., 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. Cretac. Res. 44, 112–121.

Carvalho, I.S., Leonardi, G., Rios-Netto, A.M., Borghi, L., Paula Freitas, A., Andrade, J.A., Freitas, F.I., 2020. Dinosaur trampling from the Aptian of Araripe Basin, NE Brazil, as tools for paleoenvironmental interpretation. Cretac. Res. 117 (2021), 104626. In this issue.

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, p. 69. Resúmenes.

Carvalho, I.S., Rios-Netto, A.M., Borghi, L., Leonardi, G., 2019a. Dinoturbation Structures from the Aptian of Araripe Basin, Brazil, as Tools for Stratigraphic Correlation. STRATI 2019. Società Geologica Italiana, Roma, p. 262, 2019.

Carvalho, I.S., Rios-Netto, A.M., Borghi, L., Paula Freitas, A., Leonardi, G., Andrade, J.A., 2019b. Dinosaur trampling from the Rio da Batateira Formation – Lower Cretatecous of Araripe Basin, Brazil. Paleo Falls. Livro de Resumos, Évora, p. 21.

Castanera, D., Santos, V.F., Piñuela, L., Pascual, C., Vila, B., Canudo, J.C., Moratalla, J.J., 2016. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: the Next Steps. Indiana University Press, pp. 121–137, 2016.

Chafetz, H.S., Buczynski, C., 1992. Bacterially induced lithification of microbial mats. Palaios 7, 277–293.

Citton, P., Díaz-Martínez, I., de Valais, S., Cónsole-Gonella, C., 2018. Triassic pentadactyl tracks from the Los Menucos Group (Río Negro province, Patagonia Argentina): possible constraints on the autopodial posture of Gondwanan trackmakers. PeerJ 6, e5358. https://doi.org/10.7717/peerj.5358.

Citton, P., Nicosia, U., Nicolosi, I., Carluccio, R., Romano, M., 2015. Elongated theropod tracks from the cretaceous Apenninic carbonate platform of southern latium (central Italy). Palaeontol. Electron. 18, 1–12. https://doi.org/10.1016/content.2015.1340-elongated-theropod-tracks, 3.49A, palaeo-electronica.

Contessi, M., Fanti, F., 2012. Vertebrate tracksites in the Middle Jurassic-upper cretaceous of south Tunisia. Ichnos: An International Journal for Plant and Animal Traces 19 (4), 211–227.

Dalman, S.G., Weems, R.E., 2013. A new look at morphological variation in the ichnogenus Anomoepus, with special reference to material from the lower Jurassic Newark supergroup: implications for ichnotaxonomy and ichnodiversity. Bull. - Peabody Mus. Nat. Hist. 54 (1), 67–124.

Dalla Vecchia, F.M., 2008. The impact of dinosaur palaeoichnology in palaeoenvironmental and palaeogeographic reconstructions: the case of the Periadriatic carbonate platforms. ORYCTOS 8, 89–106.

Dalla Vecchia, F.M., Tunis, G., Venturini, S., Tarlao, A., 2001. Dinosaur track sites in the upper cenomanian (late cretaceous) of istrian Peninsula (Croatia). Boll. Soc. Paleontol. Ital. 40, 25–53.

De Valais, S., 2011. Revision of dinosaur ichnotaxa from the La Matilde Formation (Middle Jurassic), santa cruz province, Argentina. Ameghiniana 48 (1), 28–42.

Díaz-Martínez, I., Cónsole-Gonella, C., de Valais, S., Salgado, L., 2017. Vertebrate tracks from the paso córdoba fossiliferous site (Anacleto and allen formations, upper cretaceous), northern patagonia, Argentina: preservational, environmental and palaeobiological implications. Cretac. Res. https://doi.org/10.1016/j.cretres.2017.07.008, 2017.

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.

Falk, A.R., Hasiotis, S.T., Gong, E., Lim, J.-D., Brewer, E.D., 2017. A new experimental setup for studying avian neoichnology and the effects of grain size and moisture content on tracks: trials using the domestic chicken (*Gallus gallus*). Palaios 32 (11), 689–707. https://doi.org/10.2110/palo.2017.022.

Falkingham, P.L., Gatesy, S.M., 2014. The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. Proc. Natl. Acad. Sci. Unit. States Am. 111 (51), 18279–18284.

Falkingham, P.L., Margetts, L., Manning, P.L., 2010. Fossil vertebrate tracks as palaeopenetrometers: confounding effects of foot morphology. Palaios 25 (6), 356–360.

Falkingham, P.L., Bates, K.T., Margetts, L., Manning, P.L., 2011. The 'Goldilocks' effect: preservation bias in vertebrate track assemblages. J. R. Soc. Interface 8 (61), 1142–1154.

Fernandes, M.A., Carvalho, I.S., 2007. Pegadas fósseis da Formação Botucatu (Jurássico Superior - Cretáceo Inferior): o registro de um grande dinossauro Ornithopoda na Bacia do Paraná. In: Carvalho, I.S., Cassab, R.C.T., Schwanke, C., Carvalho, M.A., Fernandes, A.C.S., Rodrigues, M.A.C., Carvalho, M.S.S., Arai, M., Oliveira, M.E.Q., Org (Eds.), Paleontologia: Cenários de Vida. 1ed, 1. Editora Interciência, Rio de Janeiro, pp. 425–432, 2007.

Fernandes, M.A., Carvalho, I.S., 2008. Revisão diagnóstica para a icnoespécie de tetrápode Mesozóico *Brasilichnium elusivum* (Leonardi, 1981) (Mammalia) da Formação Botucatu, Bacia do Paraná, Brasil. Ameghiniana 45, 167–173.

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'. J. Vertebr. Paleontol., 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.

Getty, P.R., Aucoin, C., Fox, N., Judge, A., Hardy, L., Bush, A.M., 2017. Perennial lakes as an environmental control on theropod movement in the Jurassic of the hartford basin. Geosciences 7, 13. https://doi.org/10.3390/geosciences7010013.

Godoy, M.M., Binotto, R.B., Silva, R.C., Zerfass, H., 2012. Geoparques/propostas: quarta colônia (RS). In: Schobbenhaus, C., Silva, C.R., Org (Eds.), Geoparques Do Brasil: Propostas. CPRM, Rio de Janeiro, pp. 417–456.

Gonçalves, R.A., Carvalho, I.S., 1996. Contribuição o ao estudo da sedimentação da Formação Itapecuru – região de Itapecuru Mirim, Bacia do Parnaíba (Cretáceo Inferior), vol. 9. Revista de Geologia, Maranhão, Brasil, pp. 75–81.

Heredia, A.M., Díaz-Martínez, I., Pazos, P.J., Comerio, M., Fernández, D.E., 2020. Gregarious behavior among non-avian theropods inferred from trackways: a case study from the Cretaceous (Cenomanian) Candeleros Formation of Patagonia, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 538 https://doi.org/10.1016/j.palaeo.2019.109480, 2020.

Ibrahim, N., Varricchio, D.J., Sereno, P.C., Wilson, J.A., Dutheil, D.B., Martill, D.M., Baidder, L., Zouhri, S., 2014. Dinosaur footprints and other ichnofauna from the cretaceous Kem Kem beds of Morocco. PloS One 9 (3), e90751. https://doi.org/10.1371/journal.pone.0090751.

Klein, H., Lucas, S.G., 2010. Tetrapod footprints - their use in biostratigraphy and biochronology of the Triassic Tetrapod. Geological Society, London, Special Publications 334, 419–446.

Kuban, G.J., 1991. Elongate dinosaur tracks. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 57–72.

Laporte, L.F., Behrensmeyer, A.K., 1980. Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. J. Sediment. Petrol. 50, 337–346.

Leonardi, G., 1977. On a new occurrence of tetrapod trackways in the Botucatu Formation in the state of São paulo, Brazil. Dusenia 10 (3), 181–183.

Leonardi, G., 1979. Nota Preliminar Sobre Seis Pistas de Dinossauros Ornithischia da Bacia do Rio do Peixe (Cretáceo Inferior) em Sousa, Paraíba, Brasil. Anais Academia brasileira de Ciências 51 (3), 501–516.

Leonardi, G., 1980. On the discovery of an ichno-fauna (vertebrates and invertebrates) in the Botucatu Formation s.s. in Araraquara, São Paulo, Brazil. Anais da Academia brasileira de Ciências 52 (3), 559–567.

Leonardi, G., 1981. Novo Ichnogênero de Tetrápode Mesozóico da Formação Botucatu, Araraquara, SP. An Acad. Bras Ciências 53, 793–805.

Leonardi, G., 1984. Le impronte fossili di dinosauri: pp. 161-186, 27 plates. In: Bonaparte, J.F., et al. (Eds.), Sulle orme dei dinosauri. Venezia-Mestre, Erizzo, 1984, p. 335. Esplorazioni e ricerche, IX).

Leonardi, G., 1987. Glossary and Manual of Tetrapod Footprint Palaeoichnology. Departamento Nacional da Produção Mineral Brasil, Brasília, p. 117.

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., 1991. 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 American Tetrapod Footprints (Devonian to Holocene), vol. 35. Departamento Nacional da Produção Mineral/Companhia de Pesquisa e Recursos Minerais), p. 247.

Leonardi, G., Mietto, P., 2000. Le piste liassiche dei Lavini di Marco. In: Leonardi, G., Mietto, P. (Eds.), Dinosauri in Italia. Le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani. Accademia Editoriale, Pisa-Roma, pp. 169–246, 2000. 497.

Leonardi, G., Oliveira, F.H., 1990. A revision of the Triassic and Jurassic tetrapod footprints of Argentina and a new approach on the age and meaning of Botucatu Formation footprints (Brazil). Rev. Bras. Geociencias 20, 216–229.

Leonardi, G., Peredo, H.D., 1985. Manadas de Dinosaurios Maastrichtienses en Toro Toro, Potosí, Bolivia. In: Congresso Brasileiro de Paleontologia, vol. 9. Resumos, Sociedade Brasileira de Paleontologia. Fortaleza, Ceará, Brazil. Fortaleza, 1985.

Leonardi, G., Carvalho, I.S., 2002. Jazigo icnofossilífero do Ouro, Araraquara, SP. In: Schobbenhaus, C., Campos, D.A., Queiroz, E.T., Winge, M., Berbert-Born, M., Org (Eds.), Sítios Geológicos e Paleontológicos do Brasil. 1ed. Brasília, vol. 1. Companhia de Pesquisa e Recursos Minerais, pp. 39–48.

Leonardi, G., Carvalho, I.S., 2002. The Dinosaur Footprints from Rio do Peixe Basins. Departamento Nacional da Produção Mineral. Sítios Geológicos e Paleontológicos do Brasil. SIGEP. http://www.unb.br/ig/sigep/sitio026/sitio026english.htm.

Leonardi, G., Carvalho, I.S., 2020. Vertebrate Trace Fossils: the Congo's *Brasilichnium* mammaloid fossil footprints. Ital. J. Geosci. 140 (1) https://doi.org/10.3301/IJG.2020.24. In this issue.

Leonardi, G., Carvalho, I.S., Fernandes, M.A., 2007. The desert ichnofauna from Botucatu Formation (upper Jurassic - lower cretaceous), Brazil. In: Carvalho, I.S., Cassab, R.C.T., Schwanke, C., Carvalho, M.A., Fernandes, A.C.S., Rodrigues, M.A.C., Carvalho, M.S.S., Arai, M., Oliveira, M.E.Q., Org (Eds.), Paleontologia: Cenários de Vida. 1ed, vol. 1. Editora Interciência, Rio de Janeiro, pp. 379–392, 2007.

Lockley, M.G., 1986. The paleobiological and paleoenvironmental importance of dinosaur footprints. Palaios 1, 37–47.

Lockley, M.G., 1991. Tracking Dinosaurs: A New Look at an Ancient World. Cambridge University Press, Cambridge, p. 238.

Lockley, M., Conrad, K., 1991. 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., Meyer, C., 2000. Dinosaur Tracks and Other Fossil Footprints of Europe. Columbia University Press, New York, p. 323.

Lockley, M.G., Xing, L., 2015. Flattened fossil footprints: implications for paleobiology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 426, 85–94.

Lockley, M.G., Matsukawa, M., Obata, I., 1989. Dinosaur tracks and radial cracks: unusual footprint features. Bulletin of the National Science Museum, Tokyo, Series C 15, 151–160.

Lockley, M., Schulp, A.S., Meyer, C.A., Leonardi, G., Mamani, D.K., 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behavior. Cretac. Res. 23 (3), 383–400.

Marchetti, L., 2018. Can undertracks show higher morphologic quality than surface tracks? Remarks on large amphibian tracks from the early Permian of France. J. Iber. Geol. 1–11.

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, F., Melchor, R.N., Farlow, J.O., 2019 a. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. Earth Sci. Rev. 193, 109–145, 2019.

Marchetti, L., Voigt, S., Lucas, S.G., Francischini, H., Dentzien-Dias, P., Sacchi, R., Mangiacotti, M., Scali, S., Gazzola, A., Ronchi, A., Millhouse, A., 2019 b. Tetrapod ichnotaxonomy in eolian paleoenvironments (Coconino and De Chelly formations, Arizona) and late Cisuralian (Permian) sauropsid radiation. Earth Sci. Rev. 190, 148–170.

Marchetti, L., Francischini, H., Lucas, S.G., Voigt, S., Hunt, A.P., Santucci, V.L., 2020. Paleozoic vertebrate ichnology of grand canyon national park. Chapter 9. In: Santucci, V.L., Tweet, J.S. (Eds.), Grand Canyon National Park: Centennial Paleontological Resource Inventory (Non-sensitive Version). Natural Resource Report NPS/GRCA/NRR—2020/2103. National Park Service, Fort Collins, Colorado, pp. 333–379.

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., Strasser, A., Meyer, C.A., 2009. formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. Ichnos 16 (1), 127–142.

Mateus, O., Marzola, M., Schulp, A.S., Jacobs, L.L., Polcyn, M.J., Pervov, V., Gonçalves, A.O., Morais, M.L., 2016. Angolan ichnosite in a diamond mine shows the presence of a large terrestrial mammaliamorph, a crocodylomorph, and sauropod dinosaurs in the Early Cretaceous of Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. https://doi.org/10.1016/j.palaeo.2016.12.049, 2017.

McCrea, R., Lockley, M.G., Meyer, C.A., 2001. Global distribution of purported ankylosaur track occurrences. In: Carpenter, K. (Ed.), The Armored Dinosaurs. Indiana University Press, pp. 413–454.

Meyer, Ch A., Lockley, M.G., Leonardi, G., Anaya, F., 1999. Late cretaceous vertebrate ichnofacies of Bolivia-facts and implications. J. Vertebr. Paleontol. 19, 63A suppl. to #3.

Meyer, C.A., Hippler, D., Lockley, M.G., 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia – facts and implications. In: 7th International Syposium on Mesozoic Terrestrial Ecosystems. Associación Paleontológica, vol. 7. Publicación Especial, Argentina, pp. 133–138.

Melchor, R.N., Rivarola, D.L., Umazano, A.M., Moyano, M.N., Mendoza Belmontes, F.R., 2019. Elusive Cretaceous Gondwanan theropods: the footprint evidence from central Argentina. Cretac. Res. 97 (2019), 125–142. https://doi.org/10.1016/j.cretres.2019.01.004.

Menezes, M.N., Araújo-Júnior, H.I., Dal' Bó, P.F., Medeiros, M.A.A., 2019. Integrating ichnology and paleopedology in the analysis of Albian alluvial plains of the Parnaíba Basin, Brazil. Cretac. Res. 96, 210–226, 2019.

Milàn, J., 2003. Experimental Ichnology -experiments with track and undertrack formation using emu tracks in sediment of different consistencies, with comparisons to fossil dinosaur tracks. Cand. Scient. Thesis. Geological Institute, University of Copenhagen 91.

Milàn, J., Bromley, R.G., 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. Palaeogeogr. Palaeoclimatol. Palaeoecol. 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.

Nadon, G.C., 2001. The impact of sedimentology on vertebrate track studies. In: Currie, P.J., Tanke, D.H., Carpenter, K., Skrepnick, M.W. (Eds.), Mesozoic Vertebrate Life. Indiana University Press, pp. 395–407.

Noffke, N., Gerdes, G., Klenke, T., Krumbein, W.E., 2001. Microbially induced sedimentary structuresda new category within the classification of primary sedimentary structures. J. Sediment. Res. 71, 649–656.

Noffke, N., Hagadorn, J., Bartlett, S., 2019. Microbial structures and dinosaur trackways from a Cretaceous coastal environment (Dakota Group, Colorado, U.S.A.). J. Sediment. Res. 89, 1096–1108.

Paik, I.S., Kim, H.J., Lee, Y.I., 2001. Dinosaur track-bearing deposits in the Cretaceous Jindong Formation, Korea: occurrence, palaeoenvironments and preservation. Cretac. Res. 22, 79–92.

Pazos, P.J., Lazo, D.G., Tunik, M.A., Marsicano, C.A., Fernández, D.E., Aguirre-Urreta, M. B., 2012. Paleoenvironmental framework of dinosaur tracksites and other ichnofossils in Early Cretaceous mixed siliciclastic-carbonate deposits in the Neuqu'en Basin, northern Patagonia (Argentina). Gondwana Res. https://doi.org/10.1016/j.gr.2012.02.003, 2012.

Peabody, F.E., 1947. Current crescents in the Triassic Moenkopi Formation. J. Sediment. Petrol. 17, 73–76.

Peabody, F.E., 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. Bulletin of the Department of Geological Sciences, University of California 27, 295–468.

Peabody, F.E., 1955. Taxonomy and the footprints of tetrapods. J. Paleontol. 29, 915–918.

Peabody, F.E., 1959. Trackways of living and fossil salamanders. Publications in Zoology. University of California 63 (1), 1–72.

Pérez-Lorente, F., 2015. Dinosaur Footprints & Trackways of La Rioja. Indiana University Press, p. 363.

Pérez-Lorente, F., 2017. Developments and contributions in the study of La Rioja dinosaur footprints (Spain). Spanish Journal of Palaeontology 32 (1), 171–184.

Phillips, P.L.J., Ludvingson, G.A., Joeckel, R.M., Gonzalez, L.A., Brenner, R.L., Witzke, B. J., 2007. Sequence stratigraphic controls on synsedimentary cementation and preservation of dinosaur tracks: example from the lower Cretaceous, (Upper Albian) Dakota Formation, Southeastern Nebraska. U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology 246, 367–389.

Pienkowski, G., Branski, P., Pandey, D.K., Schlögl, J., Alberti, M., Fürsich, F.T., 2015. Dinosaur footprints from the Thaiat ridge and their palaeoenvironmental background. Jaisalmer Basin, Rajastan, India, Volumina Jurassica 13 (1), 17–26.

Platt, B.F., Hasiotis, S.T., Hirmas, D.R., 2012. Empirical determination of physical controls on megafaunal footprint formation through neoichnological experiments with elephants. Palaios 27, 725–737.

Porada, H., Bouougri, E., Ghergut, J., 2007. Hydraulic conditions and matrelated structures in tidal flats and coastal sabkhas. In: Schieber, J., Bose, B.K., Eriksson, P. G., Banerjee, S., Altermann, W., Catuneau, O. (Eds.), Atlas of Microbial Mat Features Preserved within the Clastic Rock Record. Elsevier, Amsterdam, pp. 258–265.

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.

Reading, H.G. (Ed.), 1996. Sedimentary Environments: Processes, Facies and Stratigraphy. 3.Ed. Blackwell, Oxford, p. 688.

Reineck, H.E., Singh, I.B., 1986. Depositional Sedimentary Environments, second ed. Springer-Verlag, Berlin, p. 551.

Romilio, A., Hacker, J.M., Zlot, R., Poropat, G., Bosse, M., Salisbury, S.W., 2017. A Multidisciplinary Approach to Digital Mapping of Dinosaurian Tracksites in the Lower Cretaceous (Valanginian– Barremian) Broome Sandstone of the Dampier Peninsula. Western Australia, PeerJ, p. 26. https://doi.org/10.7717/peerj.3013.

Rossetti, D.F., 1997. Internal architecture of mixed tide- and storm-influenced deposits: an example from the Alcântara Formation, northern Brazil. Sediment. Geol. 114, 163–188.

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 Res. 11, 303–310, 2007.

Silva, R.C., Barboni, R., Dutra, T., Godoy, M.M., Binotto, R.B., 2012. Footprints of large theropod dinosaurs and implications on the age of Triassic biotas from Southern Brazil. J. S. Am. Earth Sci. 39, 16–23.

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 Autralia. Gaia 10, 85–94.

Tucker, M.E., Burchette, T.P., 1977. Triassic dinosaur footprints from South Wales: their context and preservation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 22 (3), 195–208.

Tucker, l., Smith, M.P., 2004. A multivariate taxonomic analysis of the Late Carboniferous vertebrate ichnofauna of Alveley, Southern Shropshire, England. Palaeontology 47 (3), 679–710.

Wagensommer, A., Latiano, M., Leroux, G., Cassano, G., Porchetti, S.d'O., 2012. New Dinosaur Tracksites from the Middle Jurassic of Madagascar: Ichnotaxonomical, Behavioural and Palaeoenvironmental Implications. Palaeontology 55 (1), 109–126.