Ismar de Souza Carvalho
Giuseppe Leonardi *Editors*

Dinosaur Tracks of Mesozoic Basins in Brazil

Impact of Paleoenvironmental and Paleoclimatic Changes

Springer

Chapter 9
Equatorial Dinosaurs During the Opening of Atlantic Ocean: The São Luís Basin Footprints

Ismar de Souza Carvalho and Rafael Matos Lindoso

9.1 Introduction

In the northeastern Brazil, the origin of South Atlantic Ocean led to the formation of vast subaerial environments suitable to generation of ichnological record. Such record includes mainly dinosaur trackways and isolated footprints commonly found also in the Sousa, Triunfo, Cedro, Malhada Vermelha, Lima Campos, Potiguar, Araripe basins, as well as in São Luís Basin, from Berriasian to Cenomanian (Leonardi 1980a, 1994; Leonardi and Spezzamonte 1994; Carvalho 2000, 2004; Carvalho et al. 2021; Leonardi and Carvalho 2021; Leonardi et al. 2021). Some of these ichnological records in Brazil shed light on most of our comprehension concerning the climate and paleoecological aspects during the break-up of Western Gondwana (Carvalho 2004; Carvalho et al. 2013, 2021; Leonardi and Carvalho 2021).

In the São Luís Basin (Fig. 9.1), northern Brazil, dinosaur isolated footprints and trackways have been attributed to small and large theropods, sauropods and ornithopods in six localities of São Luís and Alcântara counties (Carvalho and Gonçalves 1994; Carvalho 1994b, 1995, 2001; Carvalho and Araújo 1995; Carvalho and Pedrão 1998). The São Luís Basin ichnocenoses are considered to compose a megatracksite, and the most of these footprint-bearing strata are associated to Cenomanian tidal flat deposits in an estuarine environmental context (Rossetti 1997, 1998;

I. S. Carvalho (✉)
CCMN/IGEO, Departamento de Geologia, Universidade Federal do Rio de Janeiro, 21.910-200 Cidade Universitária, Ilha do Fundão, Rio de Janeiro, Estado do Rio de Janeiro, Brazil
e-mail: ismar@geologia.ufrj.br

Centro de Geociências, Universidade de Coimbra, Rua Sílvio Lima, 3030-790 Coimbra, Portugal

R. M. Lindoso
Departamento Acadêmico de Biologia. Av. Getúlio Vargas, Instituto Federal de Educação, Ciência e Tecnologia do Maranhão, Estado do Maranhão, 4 Monte Castelo, São Luís 65030-005, Brazil
e-mail: rafael.lindoso@ifma.edu.br

I. S. Carvalho and G. Leonardi (eds.), *Dinosaur Tracks of Mesozoic Basins in Brazil*,
https://doi.org/10.1007/978-3-031-56355-3_9

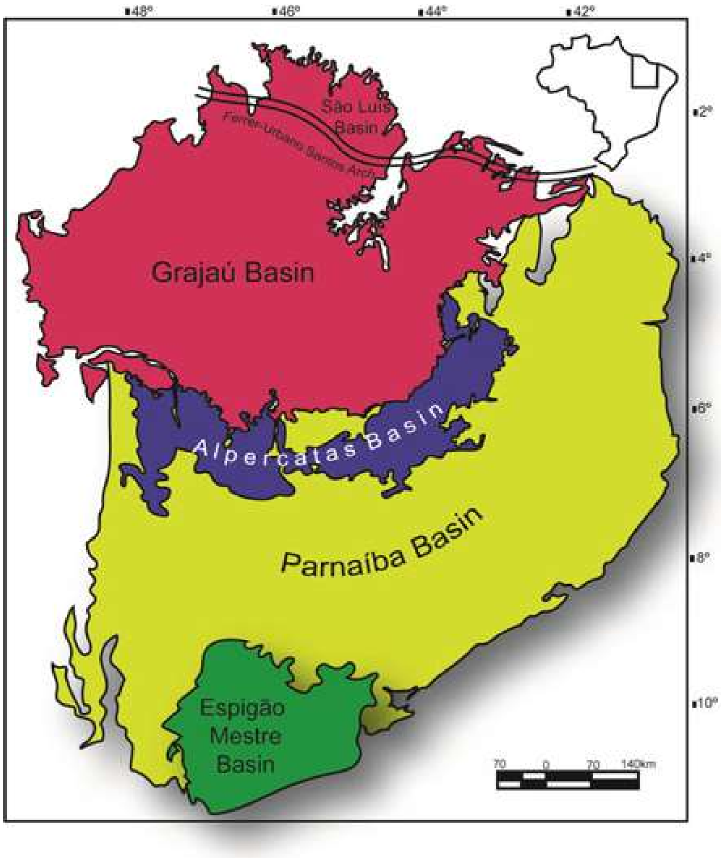

Fig. 9.1 Location map of São Luís Basin and its tectonic relationship with the Parnaíba Basin, Northeastern Brazil (modified from Pedreira da Silva et al. 2003)

Carvalho and Pedrão 1998; Carvalho 2001; Medeiros and Schultz 2001; Medeiros et al. 2014).

The São Luís Megatracksite, whose ichnosites are distributed in the borders of São Marcos Bay (23,600 km^2), occurs in the Alcântara Formation (Rossetti and Truckenbrodt 1997) and includes small and large theropods, sauropods and ornithischians (bipedal and quadrupedal) (Carvalho 2001). The potential trackmakers are physically represented by body fossils found in the region, in particular by isolated remains of *Spinosaurus* sp., *Carcharodontosaurus* sp., noasaurids and Unenlagiinae (Lindoso et al. 2012; Medeiros et al. 2014; Medeiros 2006; Letizio et al. 2022). Ornithischian remains are not yet represented in the São Luís Basin, however, those of sauropods include Titanosauridae and Rebbachisauridae (Medeiros et al. 2014; Medeiros and Schultz 2001, 2002; Lindoso et al. 2013, 2019). Other fossils found in the Alcântara Formation are palynomorphs, plants (angiosperms), invertebrate ichnofossils, mollusks (Mytilidae, Inoceramidae, Pectinidae, Plicatulidae, Limidae, Ostreidae, Trigonidae and Matricidae), fishes (Dipnoi, Elasmobranchii and Actinopterygii), reptiles (Crocodyliforms, Mosasauria, Chelonia and Pterosauria) (Oliveira 1958; Klein and Ferreira 1979; Carvalho and Pedrão 1998; Arai 2001; Castro et al. 2004; Elias et al. 2007; Lindoso et al. 2011; Medeiros et al. 2014; Moraes-Santos et al. 2001; Vilas Bôas and Carvalho 1999).

We present an update of the dinosaur ichnological record from the Alcântara Formation, São Luís Basin, northern Brazil, and we emphasize their paleoecological and paleoenvironmental significance on the Western Gondwana context.

9.2 Geological Context

The São Luís Basin (Maranhão State) is a rift marginal basin of 18,000 km^2, whose evolution is related to the origin of the Brazilian equatorial margin (Fig. 9.1). The initial rifting occurred during the Aptian, by the simple shear stress and lithospheric thinning. The depositional pre-Cretaceous history is related to the Parnaíba Basin (Carvalho and Pedrão 1998). The sedimentary thickness is 4,500 m (Aranha et al. 1990) and the Cretaceous outcrops where the dinosaur footprints occur are named as Alcântara Formation (Cenomanian). These rocks consist of reddish sandstones, siltstones, shales and mudstones, with some interbedded carbonates composed of marls and limestones. The main sedimentary structures are channel and planar cross-stratification, ripple-marks, liquefaction structures, mud-cracks, herring-bone cross-stratification and hummocky cross-stratification.

The footprints of Alcântara Formation are found in fine-grained quartzose sandstones distributed in the São Luís and Alcântara counties. This set of footprints, in the outcrops surrounding the São Marcos Bay, is temporally chronocorrelated and occur in the same paleoenvironmental setting. The footprints from these localities are in the context of the São Luís Megatracksite, a wide coastal plain where theropods, ornithischians and sauropods lived and were the main trackmakers.

The region where many dinosaur communities lived comprises an estuary in a low gradient coastal plain and nearshore environments submitted to tidal currents (Rossetti 1996a, b, c; Carvalho 2000). The environmental interpretation points out to estuarine, nearshore and shallow marine environments affected by both tide and storm processes (Klein and Ferreira 1979; Rossetti 1994, 1996a) under a hot and dry climate.

In the Cenomanian deposits that outcrops in the São Luís Basin there are two depositional intervals (Fig. 9.2). The lower succession consists of well sorted and fine-grained sandstones interpreted as a regressive interval—an upward transition from seaward to landward settings of upper shoreface, foreshore, tidal channel, and lagoon-washover environments. Such deposits revealed a prograding, barred coast probably formed on the seaward portion of a wave-dominated estuarine system (Rossetti 1996a). The footprint bearing-strata are found in the upper succession (Rossetti 1996b) that consists of tidal-dominated deposits attributed to channel, sand flat, delta, and bay fill depositional settings of an estuary. Rossetti (1996b) considered that the lower and upper successions are part of two incised valley fills. The lower succession was deposited at a time of slow rise in relative sea-level, meanwhile, the upper succession records the transition from the transgressive to the highstand systems tract of a younger incised valley.

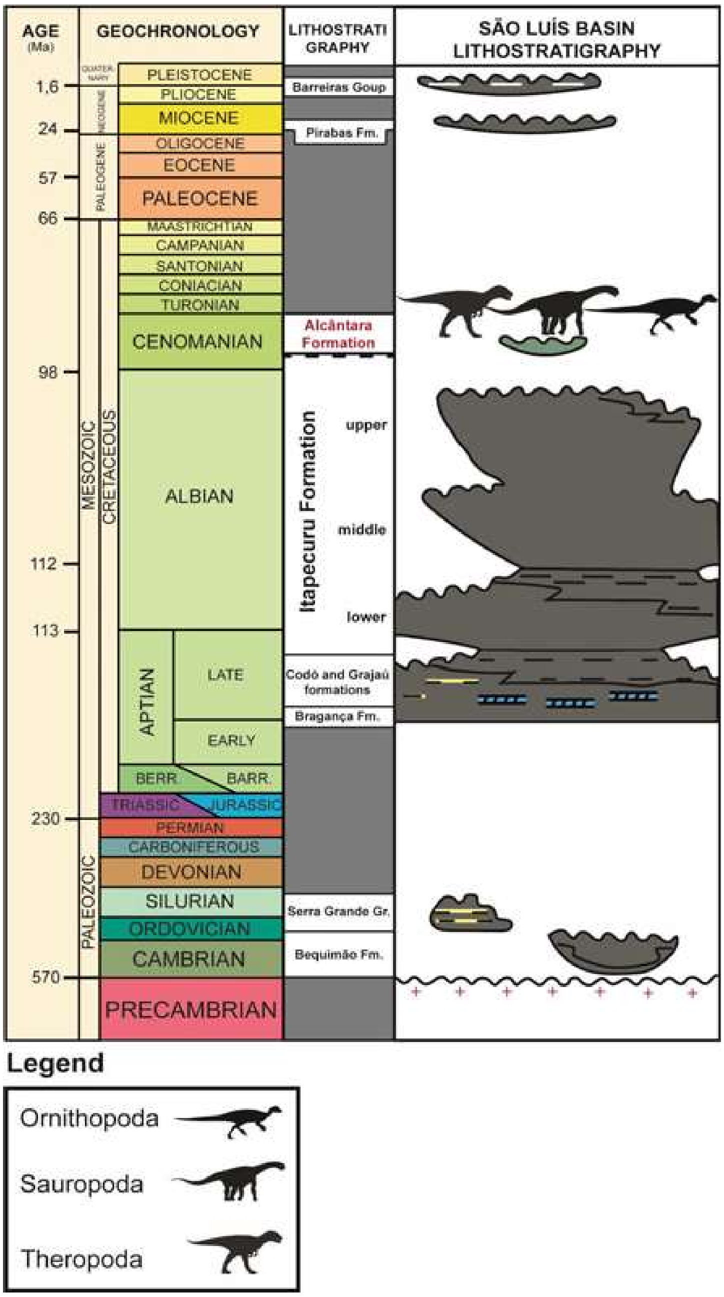

Fig. 9.2 Stratigraphic chart of São Luís Basin and the occurrence of dinosaur tracks (modified from Carvalho and Pedrão 1998)

9.3 Footprints: Diversity and Paleobiological Interpretation

Alongside the cliffs surrounding the São Luís Bay there are six ichnosites (Fig. 9.3) named as Ponta da Guia, Ponta do Farol, Praia do Boqueirão, Ilha do Medo, Praia da Baronesa and Praia Prefeitura de Alcântara (Carvalho and Gonçalves 1994; Carvalho 1995, 2001; Carvalho and Araújo 1995).

The localities of Ponta da Guia and Praia da Baronesa show the best-preserved footprints. In Ponta da Guia, the most striking footprints are the large-sized ones, distributed in seven short trackways, four of them parallel. Other footprints are found

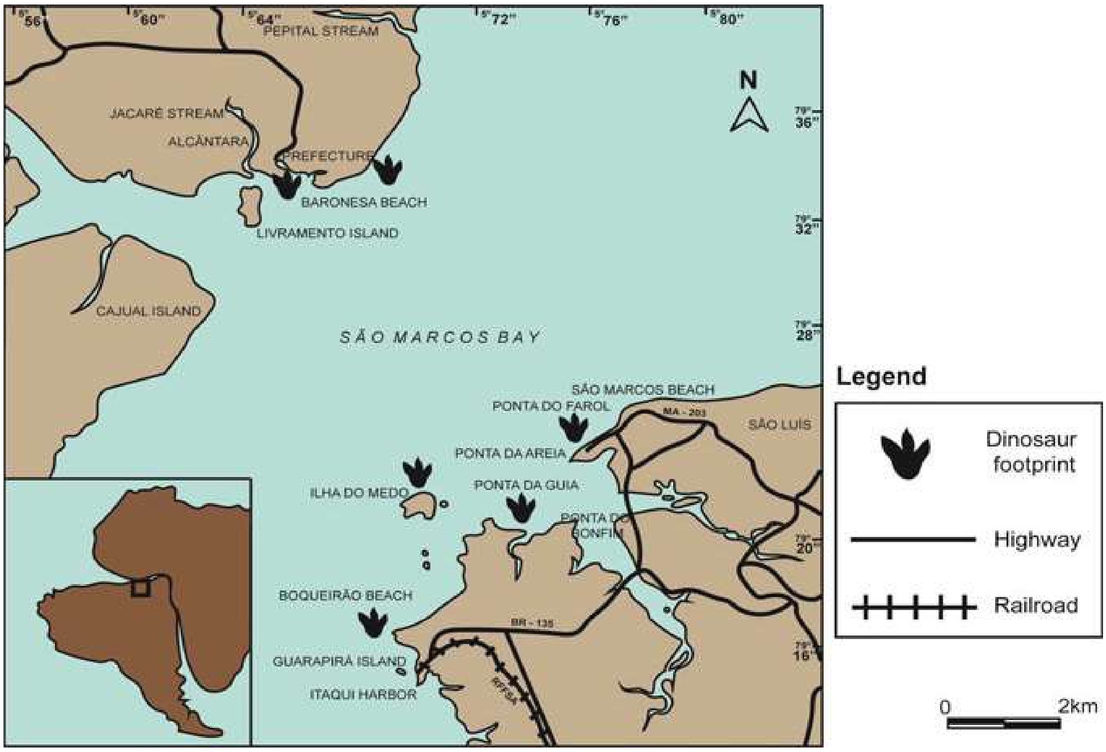

Fig. 9.3 The São Luís Megatracksite, Alcântara Formation, constituted of six ichnosites named as Ponta da Guia, Ponta do Farol, Praia do Boqueirão, Ilha do Medo, Praia da Baronesa and Praia Prefeitura de Alcântara (Baronesa Beach and Prefecture), and its paleogeographical position during the Cenomanian (lower left corner) (modified from Carvalho 2001)

in Praia da Baronesa, generally as isolated imprints, although there is a short trackway with three consecutive footprints.

9.3.1 Ponta da Guia Ichnosite

Seven short trackways (SLPG-A, SLPG-B, SLPG-C, SLPG-D, SLPG-E, SLPG-F and SLPG-G) four of them parallel, with tridactyl and mesaxonic footprints (Fig. 9.4). They are preserved as concave epirelief with 40–43 cm in width and 43–50 cm in length. The digits present the same size, and they are pointed or show claws. The trackways and footprints found in this ichnosite are described below; their codification SL means São Luís Basin and PG is the locality of Ponta da Guia.

SLPG-A is a trackway constituted of four consecutive tridactyl footprints (SLPG-A02, SLPG-A03, SLPG-A04 and SLPG-A05). The step angle is obtuse (165º) and the oblique pace presents an average value of 245 cm. The footprints are preserved as concave epirelief, with pointed digits (SLPG-A02 and SLPG-A05) or slightly rounded (SLPG-A03 and SLPG-A04), all almost the same size. The rear borders of the footprints are rounded and the preservation differences are related to the erosive surface where the footprints are found.

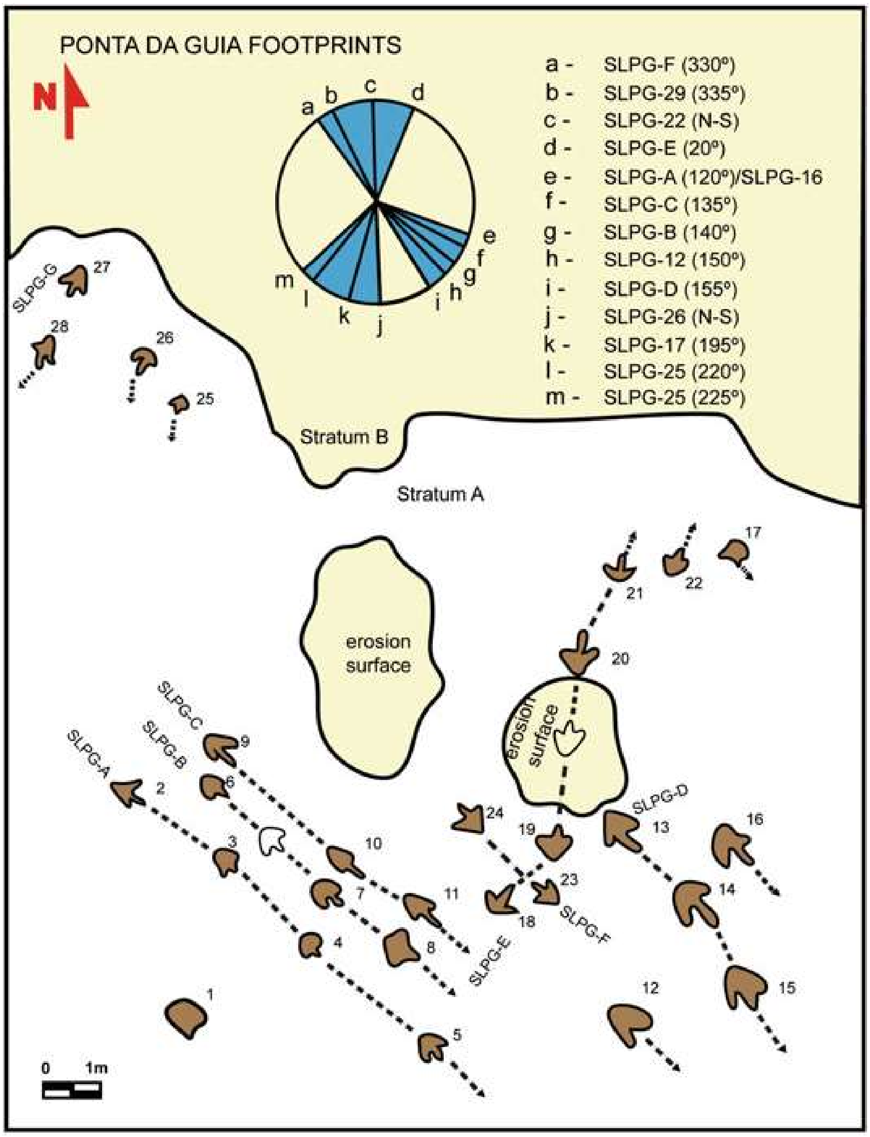

Fig. 9.4 Distribution map of the Ponta da Guia ichnosite with the theropod tracks (Carvalho 1994b)

SLPG-B trackway presents four consecutive footprints (SLPG-B06, SLPG-B s/nº, SLPG-B07 and SLPG-B08). The step angle is obtuse (170°) and the oblique pace presents an average value of 175 cm. The footprints are tridactyl, mesaxonic and show a rounded rear border (especially SLPG-B07 and SLPG-B08). They are preserved as concave epirelief in a recently eroded surface (Fig. 9.5).

The trackway SLPG-C (Fig. 9.5a) is constituted of three tridactyl consecutive footprints (SLPG-C09, SLPG-C10 and SLPG-C11). The step angle is obtuse (170°) and the oblique pace presents an average value of 257 cm, the longest one among the seven trackways of Ponta da Guia ichnosite. The digits are thin in their extremities and in the footprint SLPG-C09 there is a clear claw. The interdigital angles between digits II–III and III–IV are acute and the rear borders of the footprints are pointed.

Three consecutive footprints (SLPG-D13, SLPG-D14 and SLPG-D15) constitute the trackway SLPG-D (Fig. 9.5b). The step angle is 165° and the oblique pace

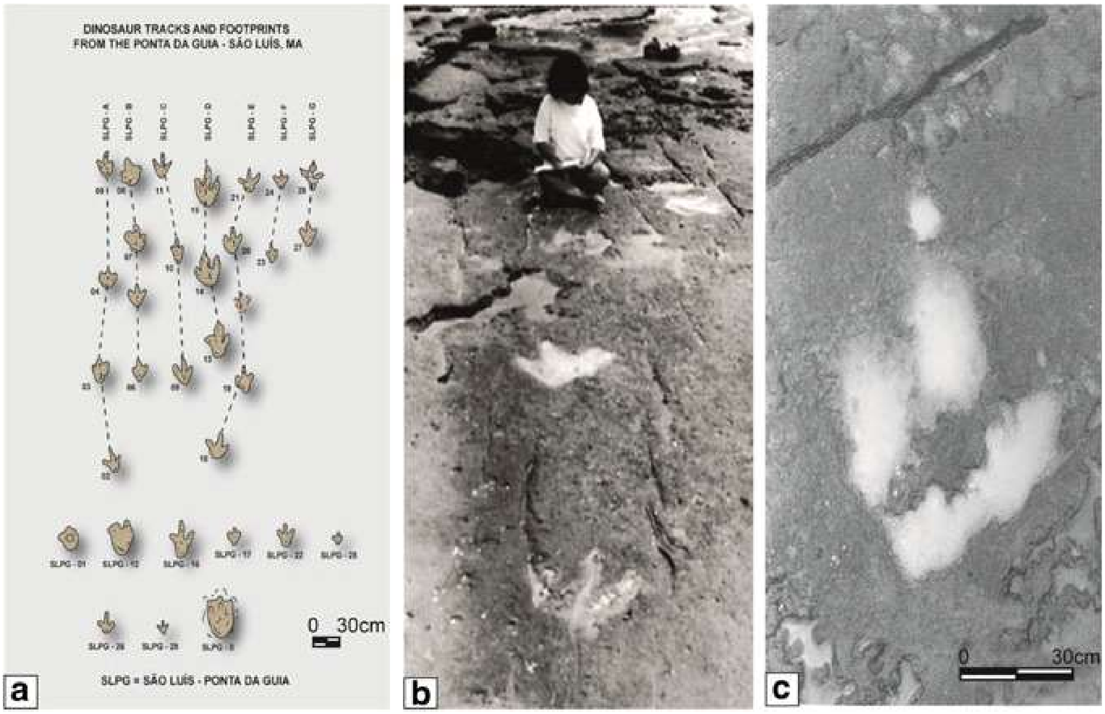

Fig. 9.5 Ponta da Guia ichnosite. **a** Trackways and isolated footprints from Alcântara Formation, Ponta da Guia; **b** The short theropod trackway (SLPG-D) with three footprints; **c** Detail of the large theropod footprint SLPG-D 15 (modified from Carvalho 1994b)

presents an average value of 238 cm. The footprints are tridactyl, mesaxonic with acute hypexes. There is a claw imprint in SLPG-D15 and the others (SLPG-D13 and SLPG-D14) present pointed digits. All they are preserved as concave epirelief (Fig. 9.5c).

The trackway SLPG-E is constituted of four non consecutive footprints (SLPG-E18, SLPG-E19, SLPG-E20 and SLPG-E21). Between the footprints SLPG-E19 and SLPG-E20 there is an erosion gap that interrupts the continuity of the bedding plane where the footprints are preserved. All of them are tridactyl, mesaxonic and with pointed digits. In the rear border of SLPG-E19 there is a prominent projection that suggests the presence of digit I. The step angle is 153° and the oblique pace presents an average value of 195 cm.

Two consecutive tridactyl and mesaxonic footprints (SLPG-F23 and SLPG-F24) are a portion of an incomplete trackway (SLPG-F). They are preserved as concave epirelief. The digits are pointed and the hypex between digits II–III and III–IV are acute. The oblique pace measures 190 cm.

The SLPG-G trackway is also constituted of two consecutive footprints (SLPG-G27 and SLPG-G28), tridactyl and mesaxonic. In SLPG-G28 there are claw imprints in all the three digits, with a very acute rear border. There are not claw imprints in the SLPG-G27, despite digit III being tapered. In both footprints the rear border is acute, indicating the probable presence of a digit I. The oblique pace measures 190 cm.

There are nine isolated footprints (SLPG-01, SLPG-12, SLPG-16, SLPG-17, SLPG-22, SLPG-25, SLPG-26, SLPG-29 and SLPG-0) in the same bedding surface of the trackways preserved as concave epireliefs (Fig. 9.5). In the SLPG-01 footprint does not preserve the digits. It has a rounded morphology and despite it being preserved as convex epirelief, the central area of the footprint is concave. SLPG-12 shows two digits with rounded extremities, without any evidence of claws. The hypex between these two digits is acute and the rear border of the footprint is rounded. SLPG-16 footprint is tridactyl, mesaxonic, with pointed digits, without claw impressions and presents a rounded rear border. Digit III is the larger and the hypexes between digits II–III and III–IV are rounded. The SLPG-17 footprint is tridactyl, mesaxonic and the extremities of the digits and hypexes are rounded. The rear border of the footprint is very acute suggesting the imprint of a digit I. The footprints SLPG-22 and SLPG-25 are tridactyl, mesaxonic and present digits of the same length with rounded anterior extremities and the rear border of the footprints are rounded. In SLPG-22 the hypexes between digits II–III and III–IV are rounded, while in SLPG-25 the hypex between digits II–III is rounded, while between digits III–IV is acute. The tridactyl and mesaxonic SLPG-29 footprint, despite showing digits with the same length, the anterior extremities are pointed, and the rear border of the footprint is acute. The hypexes between digits II–III and III–IV are acute. The footprint SLPG-26 is tridactyl, mesaxonic and the digit III is the largest. While digit III shows a pointed anterior extremity, in digits II and IV they are rounded. The hypex between digits II–III is rounded and between digits III–IV is acute. The rear border of the footprint is acute and slightly curved. The SLPG-0 is the biggest footprint in this ichnosite, with a length of 70 cm, penetrating 25 cm in the substrate. It is tridactyl, mesaxonic with short digits and rounded rear border. The hypexes between digits II–III and III–IV are wide and rounded. Digits II and IV are pointed and digit III presents a rounded anterior extremity. In the surrounding area of the footprint there is a deformation zone, probably corresponding to the displacement rim.

The succession of the strata bearing the footprints is interpreted as a tidal plain, cut by freshwater channels and bordered by aeolian dunes, under a hot and dry climate (Carvalho 1995, 2004).

A gregarious behavior was interpreted to the Ponta da Guia ichnosite based on the parallel trackways SLPG-A, SLPG-B, SLPG-C, SLPG-D and two isolated footprints (SLPG-12 and SLPG-16) that point to the same southeastern direction. Other groups of footprints are grouped in a southwestern direction (SLPG-G, SLPG-25 and SLPG-26). These preferential directions probably are a sign of herding structure as observed by other authors (Currie 1983; Leonardi 1980b, 1989; Lockley 1986, 1991; Lockley et al. 1986, 1992; Thulborn 1990).

9.3.2 Ponta do Farol Ichnosite

It was identified just one isolated, tridactyl, digitigrade and mesaxonic footprint (SLPF-01) with pointed digits suggestive of claws. It is preserved as concave epirelief. It is 35 cm in width and 40 cm in length, with acute hypexes (38°) between digits II–III and III–IV (Fig. 9.6a). Nearby there are deformation structures associated with liquefaction that are similar to enlarged tridactyl footprints. Nevertheless, short sauropod tracks recently found at this locality (Fig. 9.7) enhance Ponta do Farol ichnosite for a promising paleobiological survey.

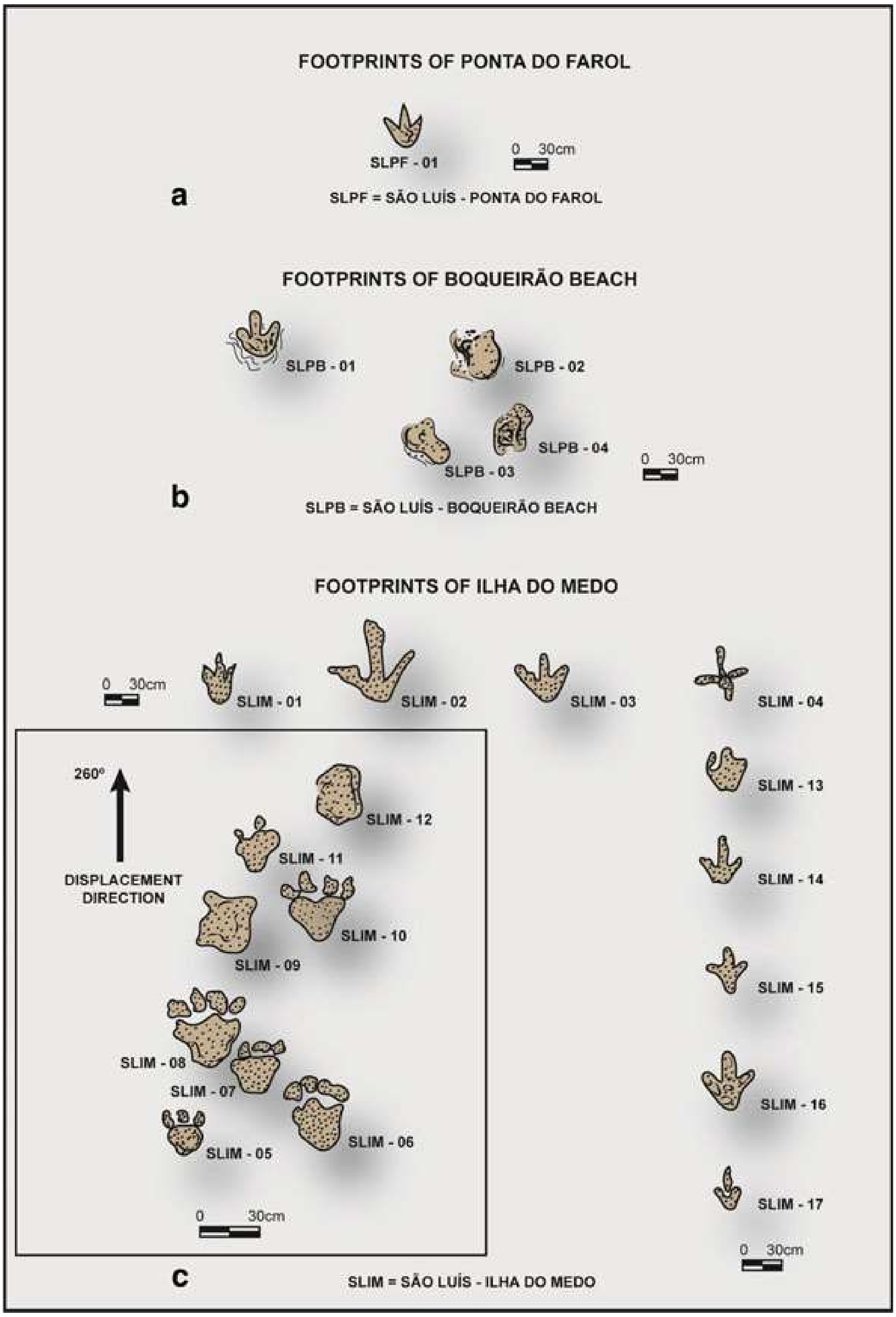

Fig. 9.6 Trackways and isolated footprints from Alcântara Formation. **a** Isolated footprint from Ponta do Farol ichnosite; **b** Theropod isolated footprint and short trackway with liquefaction footprints from Praia do Boqueirão ichnosite; **c** A short track and isolated footprints from Ilha do Medo ichnosite (modified from Carvalho 2001)

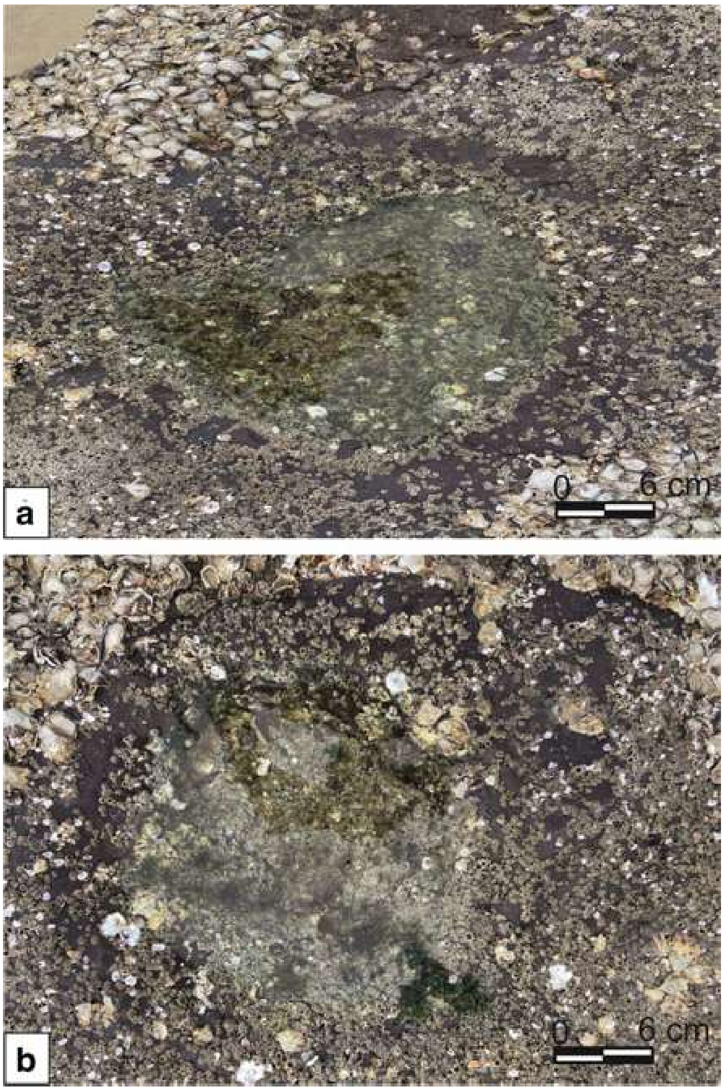

Fig. 9.7 Short sauropod tracks at Ponta do Farol ichnosite

9.3.3 Praia do Boqueirão Ichnosite

There are four isolated footprints in this ichnosite. They are preserved as concave epirelief in a fine-grained sandstone. Liquefaction structures may occur surrounding some footprints (SLPB-01), while the matrix on the posterior borders and digits show crenulations. SLPB-01 is 45 cm in width and 48 cm in length with rounded digits. In the other footprints (SLPB-02, SLPB-03, SLPB-04) it is not possible to identify the digits, as they are circular deformations with concentric rings ranging 30–40 cm in width and 40–45 in length. These features in waterlogged substrate are interpreted as the substrate deformation induced by the load of the trackmakers (Fig. 9.6b).

9.3.4 Ilha do Medo Ichnosite

This ichnosite shows sixteen isolated footprints and one short trackway (Fig. 9.6c). The isolated footprints are generally tridactyl, mesaxonic and preserved as concave epirelief. Their sizes range from 30 to 70 cm in width and 30 to 75 cm in length. There are no evident claws despite the digits of some footprints being pointed (SLIM-01, SLIM-02 SLIM-14, SLIM-15, SLIM-17) and with acute hypexes (interdigital angles of 35–45°), suggesting theropod trackmakers. The footprints SLIM-03, SLIM-13, SLIM-16 show more rounded digits, but present V-shaped rear borders, a dubious aspect to interpret as ornithopod trackmakers. They are 30–45 cm in width and 30–48 in length. The footprint SLIM-04 (55 cm in width and 55 cm in length) shows a cruciform pattern with two right-angle hypexes (90°), side by side. The opposite smaller digit is a possible digit I.

The short trackway SLIM is composed of eight footprints (SLIM-05, SLIM-06, SLIM-07, SLIM-08, SLIM-09, SLIM-10, SLIM-11, SLIM-12), with two distinct sizes and pattern. It is possible to observe three elongated digits, isolated from the plantar portion, in some of the smaller footprints (15–20 cm in width and 20–30 cm in length). They are alternated with tetradactyl footprints (SLIM-06, SLIM-08, SLIM-10) with rounded and elongated digits, in which the rear footprint borders are more acute (Fig. 9.6c). These show width and length (30–35 cm and 33–40 cm, respectively) bigger than SLIM-05, SLIM-07, SLIM-11, SLIM-12. The oblique pace between SLIM-06 and SLIM-08 (Fig. 9.8) is 45 cm, and between SLIM-05 and SLIM-07 is 30 cm. An ornithischian could be the trackmaker of this short trackway.

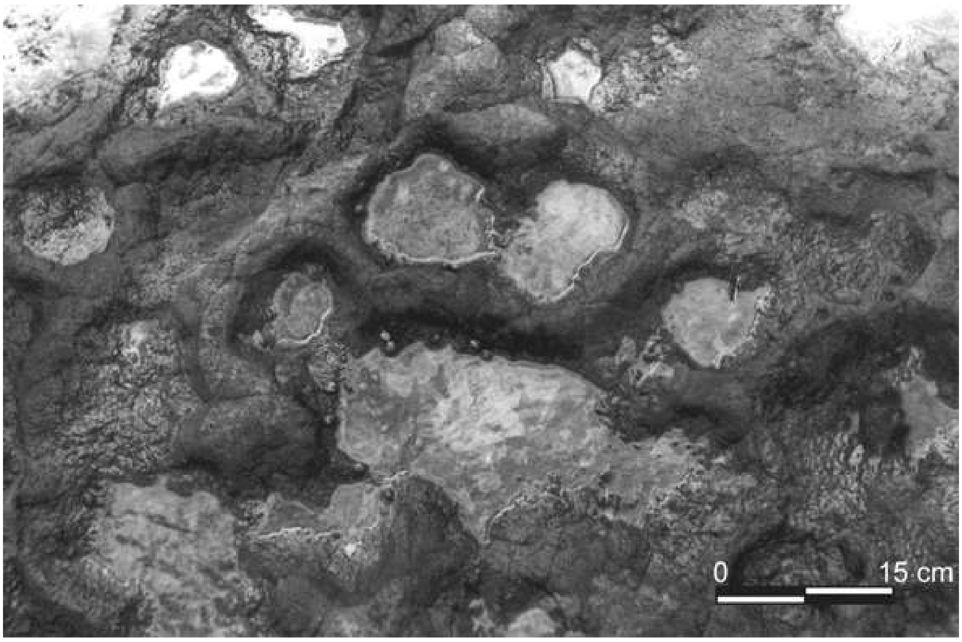

Fig. 9.8 A dubious tetradactyl footprint (SLIM-08) with rounded digits; it is interpreted as produced by an ornithischian trackmaker

9.3.5 Praia da Baronesa Ichnosite

The footprints from Praia da Baronesa ichnosite (Figs. 9.9 and 9.10) are tridactyl, mesaxonic, digitigrad, with evidence of claws and digital pads. They are smaller than the Ponta da Guia footprints, with 22–33 cm in length and the average value of 18 cm in width. There are twenty-two footprints preserved as convex epirelief in fine-grained sandstone, many of them showing a more reddish color (distinct from the greenish color of the surrounding matrix) and fluidization structures, surrounding the digits and rear borders (Carvalho and Gonçalves 1994). There are six isolated footprints (ALBA-11, ALBA-12, ALBA-13, ALBA-14, ALBA-15, ALBA-18) with pointed digits, some with claw impressions (ALBA-13, ALBA-14, ALBA-15, ALBA-18). The hypexes are acute and the interdigital angles between digits II–III and III–IV range from 30 to 45°. ALBA-15 is the smallest footprint of this set with 15 cm in width and 20 cm in length. The others (ALBA-13, ALBA-14 and ALBA-18) present a range of 30–45 cm in width and 30–48 cm in length.

There are also short tracks with two (ALBA-01 and ALBA-02, ALBA-06A and ALBA-06B, ALBA-07 and ALBA-08, ALBA-09 and ALBA-10) three (ALBA-03, ALBA-04, ALBA-05) and five (ALBA-16, ALBA-17, ALBA-18, ALBA-19, ALBA-20) consecutive footprints. These present a wide range of sizes (ALBA-09 and ALBA-10—12 cm in width, 15 cm in length; ALBA-01 and ALBA-02—50 cm in width and 60 cm in length). Some footprints of distinct tracks (ALBA-03, ALBA-04 and ALBA-05; ALBA-06A and ALBA-06B; ALBA-07 and ALBA-08; ALBA-16) show crenulations of the matrix surrounding the footprints, that is an evidence of liquefaction. The trackway with the longest paces (ALBA-16, ALBA-17, ALBA-18, ALBA-19, and ALBA-20) shows an average oblique pace of one meter, and footprints with 15 cm in width and 25 cm in length. The footprints present pointed digits and acute hypexes with interdigital angles between digits II–III and III–IV ranging from 35 to 38º. ALBA-16 presents a liquefaction feature surrounding the footprint, with the crenulations of the matrix (Figs. 9.10a, 9.11).

A common feature in the Praia da Baronesa footprints is the contrasting colors from the surrounding substrate. There is a range from reddish to blue-gray colors, contrasting with the light greenish hue of the substrate (Fig. 9.11). Kuban (1991a) also observed this feature in dinosaur tracks of the Glen Rose Formation (Lower Cretaceous, Texas—USA) and explained this taphonomic aspect as the result of secondary sediment infilling on the original track depressions and oxidation of iron on the surface of infilling material. It is likely that the pressure from the foot on the substrate had the consequence of expelling water and perhaps salts or oxides in solution or suspension, thus locally changing the characteristics—and later the color—of the compressed soil. The deformation of the substrate with the liquefaction structures is the result of a "dinostatic pressure" in water-saturated and low cohesive sediments. Such substrate aspect is corroborated by the metatarsal impressions in many footprints (Carvalho 1994c). Kuban (1991b) considered that this preservation character could be indicative of a behavior response to a soft substrate, a low posture

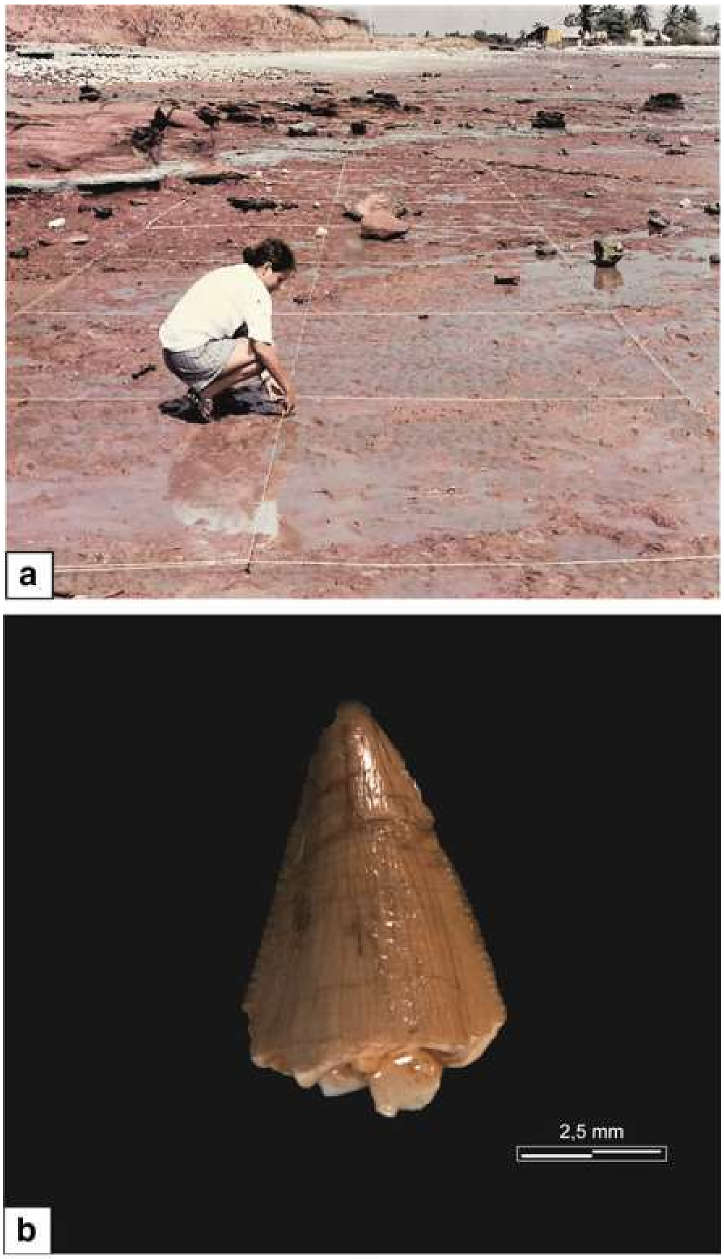

Fig. 9.9 **a** The outcrop of Praia da Baronesa ichnosite. **b** This is the locality where dinosaur remains and footprints are found in the same bedding plane; theropod tooth with probable dromeosaurid affinities found in the same surface of the dinosaur footprints

assumed whenever a dinosaur foraged in mud flats or shallow water for small food item, stalking large prey, or while approaching other dinosaurs.

9.3.6 Praia Prefeitura de Alcântara Ichnosite

In this ichnosite (Fig. 9.10b) there are two tridactyl footprints (ALPR-01, ALPR-02) and one with two digits (ALPR-03) preserved as concave epirelief. ALPR-01 shows more pointed digits than ALPR-02 and ALPR-03. They range from 20 to 30 cm in

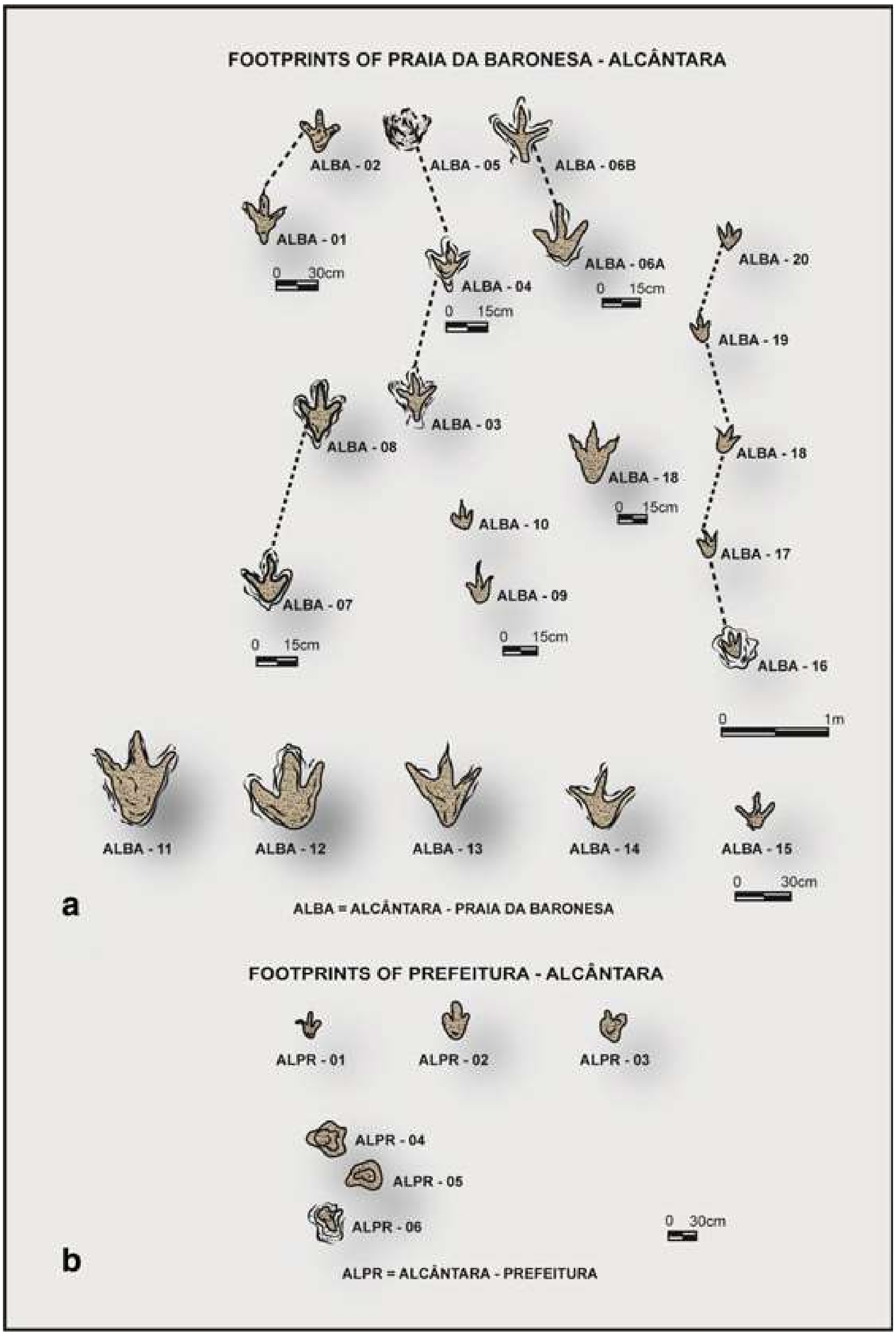

Fig. 9.10 Trackways and isolated footprints from **a** Praia da Baronesa and **b** Praia Prefeitura de Alcântara ichnosites (modified from Carvalho 2001)

width and 30–45 cm in length. Acute hypexes, with the angles between digits II–III ranging from 30 to 45° and digits III–IV 35 to 40°.

There are also four isolated rounded structures (Fig. 9.12), with concentric rings, that range from 30 to 40 cm in width and 40–45 in length. It is also possible to identify three consecutive similar structures (ALPR-04, ALPR-05, ALPR-06), with an average oblique pace of 60 cm, that are probably part of a short trackway. These

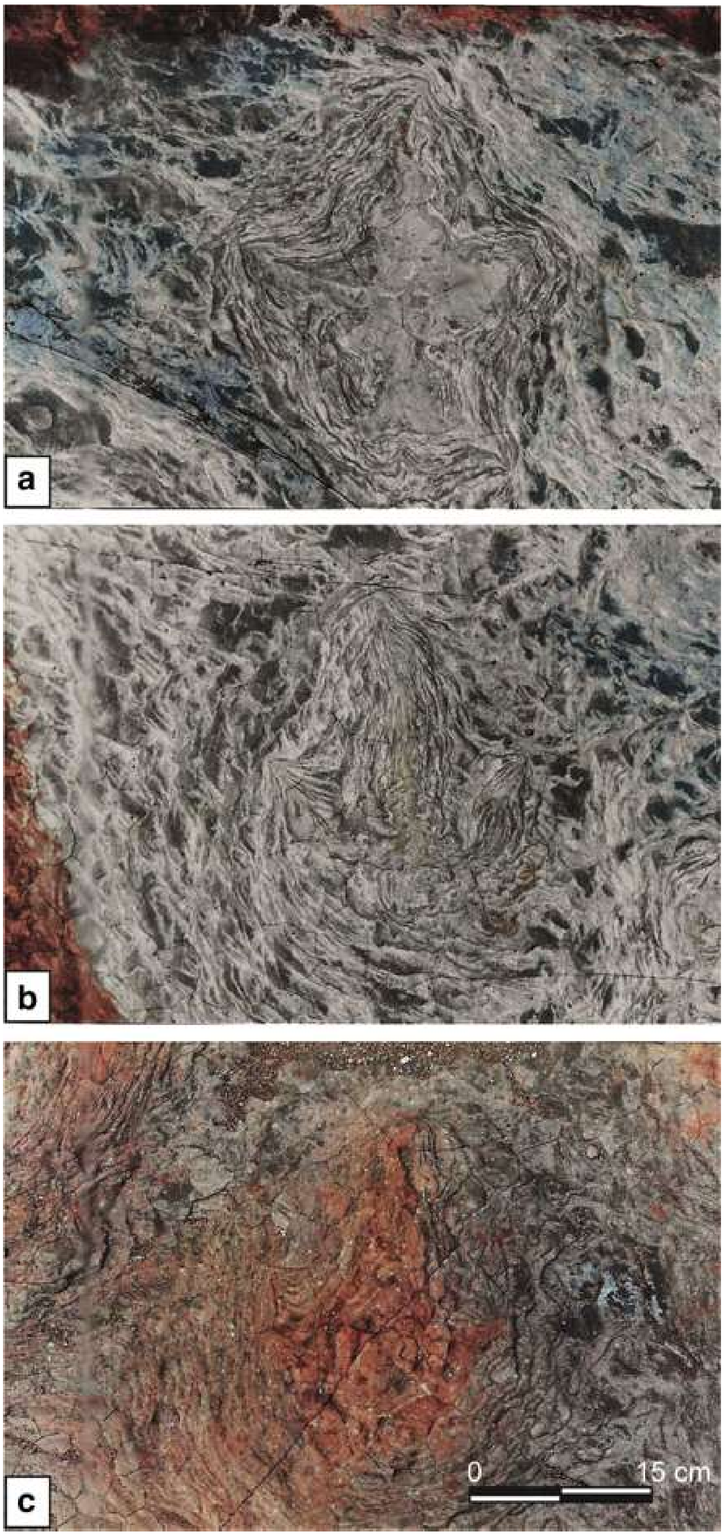

Fig. 9.11 Footprints from Praia da Baronesa ichnosite. The deformation of the substrate with the liquefaction structures is the result of a "dinostatic pressure" in water-saturated and low cohesive sediments. **a** A theropod footprint (ALBA 06B) surrounded by a liquefaction structure; **b** In some footprints, the crenulations also occur inside the imprint (ALBA 04); **c** A reddish color footprint surrounded by a greenish matrix with liquefaction structures

Fig. 9.12 Footprint from Praia Prefeitura de Alcântara ichnosite. Isolated rounded structure, with concentric rings, interpreted as liquefaction structures induced by a sauropod trackmaker

rounded structures are interpreted as liquefaction structures induced by sauropod trackmakers.

9.3.7 Paleobiological Interpretation

The footprints found at Ponta da Guia ichnosite were produced by two different dinosaur clades: Theropoda and Ornithopoda. The ones attributed to theropods are large-sized footprints. Four trackways present parallel orientation, a possible evidence of a gregarious behavior. The ornithopod footprints were assigned to hadrosaurians (Carvalho and Pedrão 1998). It would then be rather primitive hadrosaurs. Probably , during the Cenomanian, there was the dispersion of dinosaur faunas between the two American continents.

In Ponta do Farol ichnosite, the single isolated footprint is considered to be produced by a large-sized theropod trackmaker. At Praia do Boqueirão ichnosite the footprints are load deformations in the substrate and only one footprint denotes digits and the plantar impression, produced by a probable ornithopod trackmaker. The Ilha do Medo ichnosite presents isolated footprints of large-sized theropods, ornithopods and a probable short track of a quadrupedal ornithischian. A small-sized theropod and sauropod footprints are possible to be identified in the Praia Prefeitura de Alcântara.

The trackways at Ponta da Guia ichnosite show a set of four large-sized theropod trackways (SLPG-A, SLPG-B, SLPG-C and SLPG-D), that present high morphological similarity, moving in SE direction. The angular range of movement directions is only 20° (between 120 and 140°), and there is a quite standard intertrackway spacing between three of these trackways (SLPG-A, SLPG-B, SLPG-C). The regular space between adjacent trackways suggests animals walking in some kind of regular formation (Lockley 1991), that constitute good evidence to postulate the gregariousness among the producers (Fig. 9.13). Because there are tracks in different directions, it is possible to consider the absence of physical barriers in the configuration of the landscape that could have controlled this main movement direction of individuals. Despite gregarious behavior occurs more frequently among sauropods and ornithopods (Carvalho 1989; Leonardi 1980b, 1981; Lockley et al. 1986, 1992; Nadon 1993; Myers and Fiorillo 2009; Castanera et al. 2011, 2014; Lockley et al. 2012; Piñuela et al. 2016; Paik et al. 2020), there are many examples of parallel theropod trackways as an evidence of gregariousness among theropod dinosaurs (Leonardi 1984, 1989; Moreno et al. 2012; García-Ortiz and Pérez-Lorente 2014; McCrea et al. 2014; Lockley et al. 2015; Heredia et al. 2020; Hernández et al. 2023).

The other main theropod footprint assemblage is located at Praia da Baronesa ichnosite. It is composed of randomly oriented trackways and isolated small and medium-sized footprints. This is interpreted as the record of a "foraging area" for theropods, searching for food in small lagoons and channels of a tidal flat environment. During low-tide periods, subaerial exposure of the sediments allowed the dinoturbation (Carvalho and Pedrão 1998). The footprints are always associated with fluidization structures and present superficial color stains (blue-gray, green or red) which can be interpreted as produced in low cohesive sediments and a soft substrate (Carvalho and Leonardi 2021; Kuban 1991b). Such substrate aspect is corroborated by the metatarsal impressions (Carvalho 1994c; Carvalho and Pedrão 1998) in many footprints (e.g., ALBA-03, ALBA-04, ALBA-06B, ALBA-08). The elongate plantigrade footprints would be explained by a low posture assumed whenever a dinosaur foraged in mud flats or shallow water for small food items, stalking larger prey or while approaching other dinosaurs.

The fossils from the Alcântara Formation indicate a diverse vertebrate community that lived in the coastal forested areas surrounded by a dominantly dry environment. They indicate that during the mid-Cretaceous the northeastern South American and northern African continental fauna were more similar than to the austral South American one. This aspect allows us to interpret that faunal interchanges between these two continents may have persisted until the early Cenomanian through continental bridges (Calvo and Salgado 1996; Popoff 1988; Maisey 2000; Medeiros et al. 2014).

The main dinosaur fauna from the Alcântara Formation, as regards the body-fossils, comprises *Carcharodontosaurus* sp., Spinosauridae, noasaurids with *Masiakasaurus*-like teeth, Diplodocoidea and Titanosauridae (Medeiros and Schultz 2001, 2002, 2004; Medeiros et al. 2007, 2014; Lindoso et al. 2012, 2013) that can be related to the Cenomanian record of the Kem Kem beds, Morocco and to the Bahariya

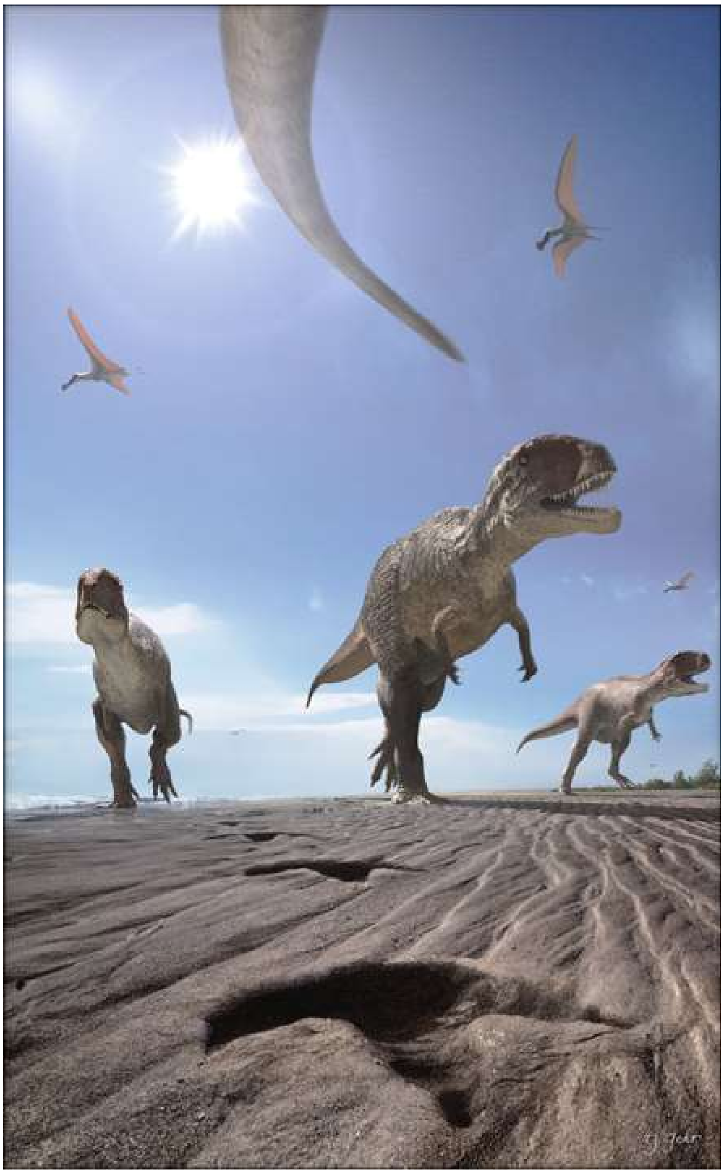

Fig. 9.13 The regular space between adjacent trackways suggests animals walking in some kind of regular formation, that is a good evidence to postulate the gregariousness among some of the large theropod trackmakers from Ponta da Guia ichnosite. Art by Guilherme Gehr

Formation, Egypt (Stromer 1915; Lapparent 1960; Benton et al. 2000; Richter et al. 2013; Medeiros et al. 2014; Ibrahim et al. 2020). The Theropoda were mainly identified through isolated teeth (Fig. 9.14) allowing the classification as *Charcarodontosaurus* sp., Spinosauridae, Dromeosauridae, Unenlagiinae and Noasauridae (Vilas Bôas 1999; Vilas Bôas and Medeiros 1997; Vilas Bôas et al. 1999; Medeiros 2006; Lindoso et al. 2012; Letizio et al. 2022). There is also a Spinosauridae named as *Oxalaia quilombensis* (Kellner et al. 2011).

The trackmakers from the Alcântara Formation can be related to the body-fossilsfound in this lithostratigraphic unit. Fossils of theropods are more diverse than sauropods, marked by the occurrence of Spinosauridae and Carcharodontosauridae (*Carcharodontosaurus* sp.) and the probable existence of more than one species of the former (Medeiros 2006; Richter et al. 2013; Medeiros et al. 2014). These two groups are good options as trackmakers to the large-sized footprints of the Ponta da Guia tracksite. Otherwise, small to medium-sized footprints from Praia da Baronesa and

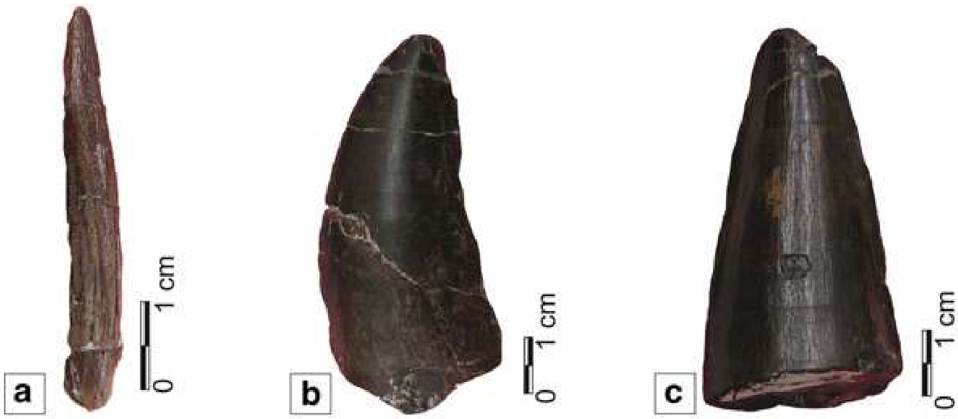

Fig. 9.14 Dinosaur remains from the bone bed Laje do Coringa, Cajual Island, Alcântara Formation, São Luís Basin. **a** Sauropoda tooth; **b** *Carcharodontosaurus* sp. tooth; **c** Spinosauridae tooth

Praia Prefeitura de Alcântara ichnosites, could be related to dromeosaurids, unenlagiinids or noasaurs. In both cases they are present as body-fossils in the Alcântara Formation, sometimes in the same stratigraphic surface as in the case of Praia da Baronesa ichnosite.

There is only one specimen of Rebbachisauridae sauropod formerly described to the Alcântara Formation, *Itapeuasaurus cajapioensis* (Lindoso et al. 2019). It is the northernmost record of Diplodocoidea in South America, and it seems that rebbachisaurids outnumbered titanosaurs in the early Late Cretaceous in northern South America, right before the steep decline of Rebbachisauridae (Barrett and Upchurch 2005; Lindoso et al. 2019). Nevertheless, there are also bone fragments and osteoderm assigned as Titanosauria (Lindoso et al. 2013; Medeiros et al. 2014); then it is very probable that the footprints interpreted as sauropods in the Praia Prefeitura de Alcântara ichnosite could be related to these two groups.

9.4 Paleogeographical Distribution of the Footprints

The ichnofossiliferous localities of São Luís Basin are in a paleoenvironmental and temporal context distinct from the other occurrences of Cretaceous footprints in Brazil. They record dinosaur ichnofaunas of a megatracksite (Lockley 1991) as they occur in stratigraphic correlated surfaces, with wide geographic distribution. The São Luís Megatracksite presents footprints preserved in a coastal environment, on a low gradient tidal flat, under hot and dry climate conditions (Pedrão et al. 1993; Carvalho 1994a, b, c; Carvalho and Pedrão 1998).

The low gradient coastal plain allowed the establishment of specific dinosaur groups, with a probable ecologic "segregation" of large-sized (Spinosauridae and Carcharodontosauridae) and medium to small-sized theropods (Dromeosauridae, Unenlagiinae and Noasauridae), throughout the exposed Cenomanian surfaces of the nearshore environments (Carvalho and Pedrão 1998).

The distribution of footprints along the outcrops of São Luís Bay is temporally related. The levels with teeth, bones and footprints of dinosaurs, besides other vertebrates, can be used to correlate the strata, as they are frequently identified in the outcrops of the basin. The outcrops with footprints record a same temporal event.

In coastal environments, footprints can be preserved in the intertidal zone when the tide begins its ebb. Thus, those originated early, in the ebb phase, will remain for a cycle of approximately 12 h, while those carried out in the tidal filling phase will not remain longer than 6 h until they are covered. A sandy beach with a steep slope is not the most appropriate environment for the preservation of tracks, as the rapid "washing" of the surface at each tidal cycle would be an agent of destruction of the footprints left by dinosaurs. On the other hand, in low gradient coastal plains, the ebb and flow of each tidal cycle occurs more slowly, favoring the preservation of trackways and footprints (Lockley 1991).

Fragmented bones and teeth of fishes, crocodyliforms, chelonians and dinosaurs at Praia da Baronesa ichnosite allow us to consider them as the accumulation of debris in a tidal flat environment. The random footprints distribution in this ichnosite could indicate a "foraging area" for the theropods, where they wandered across searching for food (Carvalho 2001). The theropods would search for fishes, turtles and other organisms, foraging food in the exposed channels of the tidal plain. During low-tide periods, sub aerial exposure of the sediments allowed the preservation of their tracks (Carvalho and Pedrão 1998).

There is also a brief description of theropod tracks in the neighboring Parnaíba Basin, in the Triassic deposits of Sambaíba Formation (Fig. 9.15). However, the age of this unit is dubious and the morphology and large diversity of theropod tracks illustrated by Assis et al. (2010) is inconsistent with a Triassic age, being more probable a Cretaceous age. It is necessary a review of these outcrops and their tracks.

9.5 Paleoenvironmental and Paleoclimatic Contexts

The bedding surfaces with footprints are found in the context of the "upper succession" of the Alcântara Formation (Rossetti 1994, 1996a, b). This succession consists of tidal-dominated deposits assigned to channel, sand plain, delta, and bay-fill in an estuarine environment. Along the coast of a shallow sea an abundant dinosaur fauna roamed, recording their footprints on the seashore environments.

The strata at Ponta da Guia are interpreted as the result of tidal flat and aeolian sedimentation. The track-bearing strata are fine-grained sandstones, interbedded with argillaceous siltstones, that show small-sized channel and tabular cross-stratification, ripple-marks, mud-cracks and clay-balls, accumulated in a sand flat depositional environment. The theropod footprints were probably produced in the supra-tidal region of a low-gradient tidal flat, where the preservation potential is greater (Carvalho 1995; Carvalho and Gonçalves 1994).

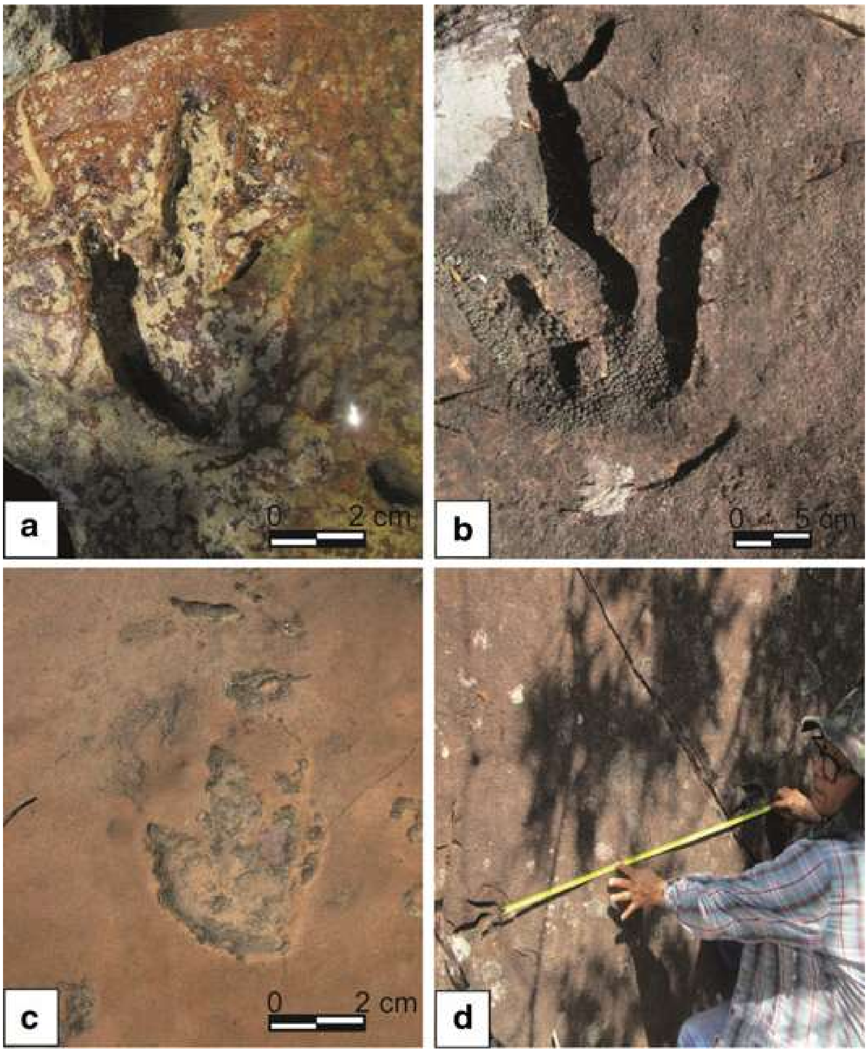

Fig. 9.15 Trackways and isolated theropod footprints from Fortaleza dos Nogueiras, south of Maranhão State, Parnaíba Basin

The fossil tracks and skeletal remains found in the fine-grained sandstones and siltstones of Praia da Baronesa ichnosite are related to a tidal channel setting (Fig. 9.16). During low-tide periods, subaerial exposure of the bedforms allowed them to be subject to dinoturbation. Ancient estuarine paleochannels also have high potential for burial and preservation of vertebrate skeletal remains (Eberth and Brinkman 1997). In the same track bearing surface of fine-grained sandstones occur many skeletal remains of a diversified fauna (Eugênio 1994) including fishes (Myliobatidae, Semionontidae, Enchodontidae and Sparidae families) and reptiles (Pelomedusidae testudines, Mosasauridae and Theropoda). The theropod remains (isolated teeth) are indicative of a clade with Dromeosauridae affinities (Vilas-Bôas and Medeiros 1997).

Through palynological analyses (Pedrão 1995) a better understanding was obtained of some environmental aspects under which the dinosaur fauna of São Luís Basin lived. The palynological content of outcrops in the east portion of the basin includes miospores, protozoans and polychaetas (Pedrão et al. 1993, 1995).

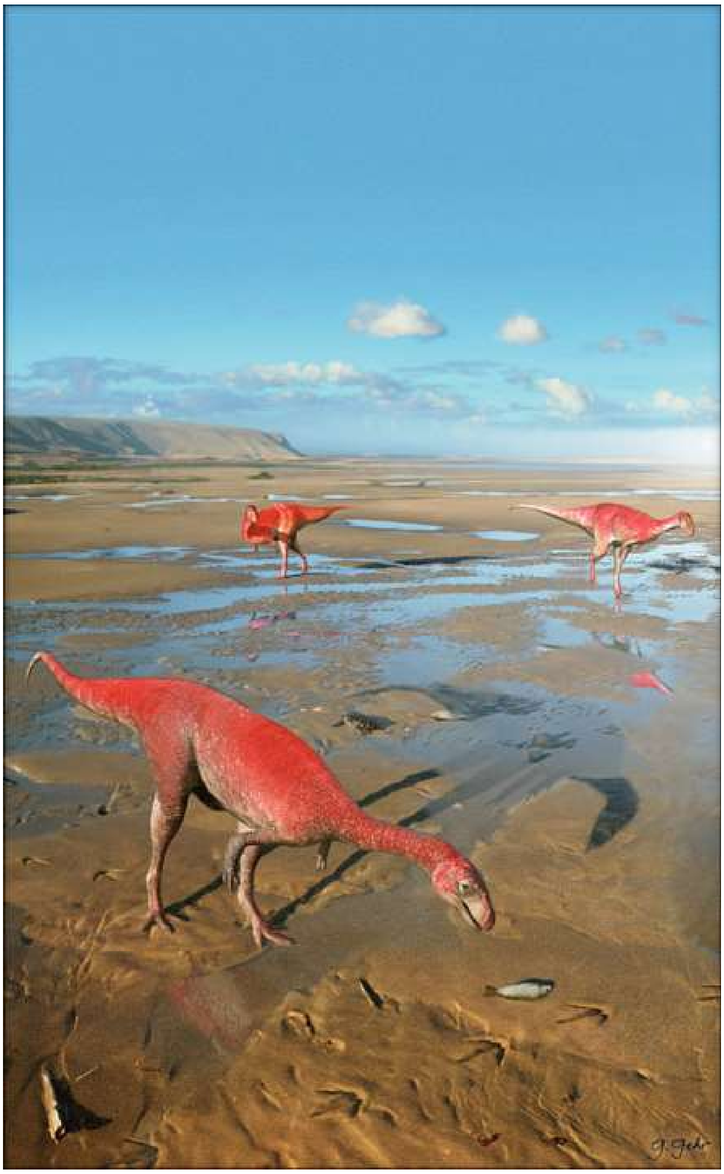

Fig. 9.16 Praia da Baronesa ichnosite shows small- and medium-sized theropod tracks living in a low-gradient coastal plain. The randomly-oriented trackways and isolated footprints are interpreted as the record of a "foraging area" for theropods. Art by Guilherme Gehr

Continental palynomorphs are pteridophyte spores (*Petrotriletes*), gymnosperm pollen grains (*Classopollis major*, *Equisetosporites ambiguus*, *Equisetosporites* spp., *Steevesipollenites* spp.), angiosperms (*Afropollis jardinus*, *Hexaporotricolpites emilianovi*, *Cretacaeiporites polygonalis, Cretacaeiporites mulleri*) and some taxa of doubtful botanical affinity (*Elateroplicites africaensis*, *Galeacornea causea* B, *Elaterocolpites castalaini*, *Elaterosporites* aff. *Klaszi* and *Sofrepites legouxae*). The main pollen group in this assemblage derives from gymnosperms (*Classopollis*) akin to plants of the Cheirolepideaceae family. Secondarily, there occur *Equisetosporites* and *Steevesipollenites* pollen grains. All of them are indicative of a hot and dry climate. The angiosperm pollen grains are rare, although the presence of *A. jardinus* indicates an equatorial climate. The occurrence of perisporate trilete spores in this assemblage also points to the same climate, and in addition, it is indicative of a fluvial influence in the depositional area (Carvalho and Pedrão 1998).

In this palynological assemblage is found marine plankton, including unicellular algae (Division Pyrrophyta, dinoflagellates) such as gonyaulacoids (*Spiniferites*), peridinioids (*Subtilisphaera cheit*) and condensates (*Florentinia* spp., *Oligosphaeridium* aff. *O. breviconispinum*). There are also chitinous remains of palynoforaminifera and scolecodonts (Fig. 9.17).

9.6 Conclusions

The fossil footprints from the São Luís Basin are a single record of the Cenomanian dinosaur fauna which inhabited the Brazilian equatorial margin during the first stages of the Equatorial Atlantic opening. The stratigraphic succession where the footprints are found consists of tidal-dominated deposits assigned to channel, sand plain, delta, and bay-fill in an estuarine environment. Along the coast of a shallow sea an abundant dinosaur fauna roamed, recording their footprints on the seashore environments. There are six ichnosites on the outcrops surrounding the São Luís bay distributed in the São Luís and Alcântara counties: Ponta da Guia, Ponta do Farol, Praia do Boqueirão, Ilha do Medo, Praia da Baronesa and Praia Prefeitura de Alcântara. These ichnosites record a same temporal event, in the context of a surface with wide geographic distribution, the São Luís Megatracksite.

Trackways and isolated footprints were interpreted as related to large and small theropods, sauropods and ornithischians (e.g., ornithopods) trackmakers. The dominance of large-sized theropod footprints is detected in the southern area of the basin, which includes the Ponta da Guia region. To the north, the ichnosites such as that one of Praia da Baronesa and Praia do Boqueirão show small- and medium-sized theropod tracks. The environmental context of a low-gradient coastal plain favored the establishment of specific dinosaur communities, with a probable ecologic "segregation" of large and other smaller dinosaurs. A gregarious behavior for some large-sized theropods is deduced from the analysis of the same oriented direction trackways from Ponta da Guia ichnosite. The randomly oriented trackways and isolated footprints from Praia da Baronesa ichnosite were interpreted as the record of a "foraging area" for theropods which, in this particular tidal plain environment, probably lived on a rather varied diet, composed of small tetrapods and invertebrates, fish, mollusks and so on. The palynological data of Cenomanian age is consistent with the inference of fluvial, lagoonal and shallow marine depositional environments under dry and hot climate. A tidal flat of a low-gradient coastal plain is the most likely environment inhabited by the trackmakers.

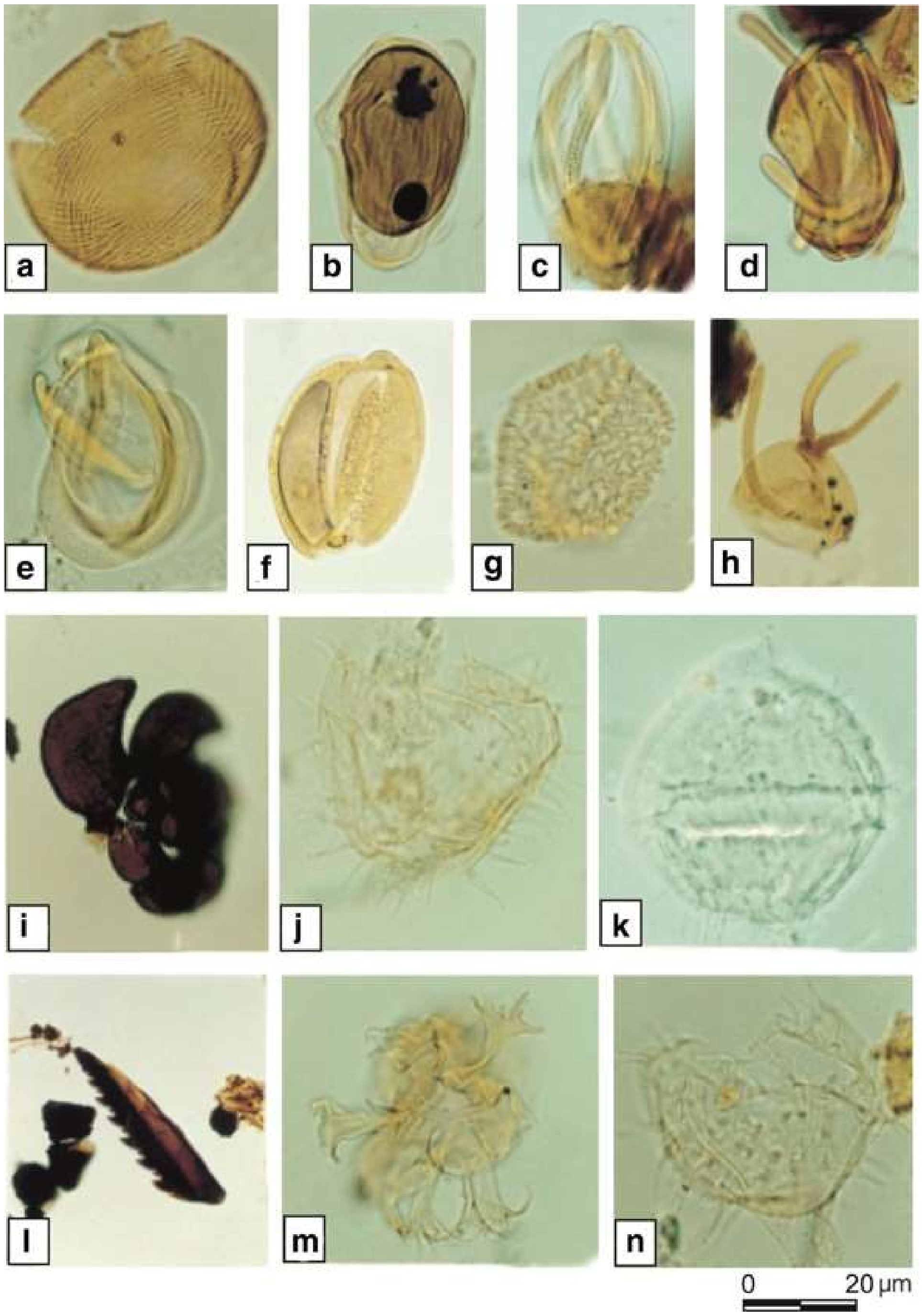

Fig. 9.17 The Cenomanian palynomorphs from the Alcântara Formation are consistent with the inference of a tidal flat of a low-gradient coastal plain under dry and hot climate inhabited by the dinosaur trackmakers. **a** *Classopollis major*, **b** *Equisetosporites ambiguous*, **c** *Galeacornea subtilis*, **d** *Elateroplicites africaensis*, **e** *Galeacornea causea*, **f** *Sofrepites legouxae*, **g** *Elaterosporites* aff. *klaszi*, **h** *Afropollis jardinus*, **i** palynoforaminifera, **j** dinoflagellate, **k** *Subtilisphaera cheit*, **l** scolecodonts, **m** *Oligosphaeridium* sp., **n** *Florentinia* sp. (modified from Carvalho and Pedrão 1998)

References

Arai M (2001) Palinologia de depósitos cretáceos no Norte e Meio-Norte do Brasil: histórico e estado-de-arte. In: Rossetti DF, Góes AM, Truckenbrodt W (eds) O Cretáceo na Bacia de São Luís e Grajaú. Coleção Friedrich Katzer, Museu Paraense Emílio Goeldi, Belém, pp 175–189

Aranha LGF, Lima HP, Souza JMP, Makmo RK, Figueiras JM (1990) Evolução tectônica e sedimentar das bacias de Bragança-Vizeu, São Luís e Ilha Nova. In: Raja Gabaglia GPR, Milani EJ (eds) Origem e evolução das bacias sedimentares. Petrobras, Rio de Janeiro, pp 221–234

Assis FP, Macambira JB, Leonardi G (2010) Dinossauros terópodes do Ribeirão das Lajes, primeiro registro fóssil da Formação Sambaíba (Neotriássico-Eojurássico), Bacia do Parnaíba: Fortaleza dos Nogueiras, Maranhão-Brasil. 2010. In: 45° Congresso Brasileiro de Geologia. Belém—PA. Sociedade Brasileira de Geologia, Boletim de resumos, p 1720

Barrett PM, Upchurch P (2005) Sauropodomorph diversity through time: paleoecological and macroevolutionary implications. In: Wilson JA, Curry Rogers KA (eds). Evolution and Paleobiology. University of California Press, The Sauropods, pp 125–156

Benton MJ, Bouaziz S, Buffetaut E, Martill D, Ouaja M, Soussi M, Trueman C (2000) Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. Palaeogeogr Palaeoclimatol Palaeoecol 157:227–246

Calvo JO, Salgado L (1996) A land bridge connection between South America and Africa during Albian-Cenomanian times based on sauropod dinosaur evidences. 39° Congresso Brasileiro de Geologia, Salvador. Sociedade Brasileira de Geologia, Anais, pp 392–393

Carvalho IS (1989) Icnocenoses continentais: bacias de Sousa, Uiraúna-Brejo da Freiras e Mangabeira. Rio de Janeiro, Dissertação de Mestrado, Universidade Federal do Rio de Janeiro 167 p

Carvalho IS (1994a) As ocorrências de icnofósseis de vertebrados na Bacia de São Luís, Cretáceo Superior, Estado do Maranhão. In: 3° Simpósio sobre o Cretáceo do Brasil, UNESP—Rio Claro, Boletim, pp 119–122

Carvalho IS (1994b) As pistas de dinossauros da Ponta da Guia (Bacia de São Luís, Cretáceo Superior—Maranhão, Brasil). An Acad Bras Ciênc 67(4):413–431

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

Carvalho IS (1995) As pistas de dinossauros da Ponta da Guia (Bacia de São Luís, Cretácio Superior—Maranhão, Brasil). An Acad Bras Ciênc 67(4):413–431

Carvalho IS (2000) Geological environments of dinosaur footprints in the intracratonic basins from Northeast Brazil during South Atlantic opening (Early Cretaceous). Cretac Res 21:255–267

Carvalho IS (2001) Pegadas de dinossauros em depósitos estuarinos (Cenomaniano) da Bacia de São Luís (MA), Brasil. In: Rossetti DF, Góes AM, Truckenbrodt W (eds) O Cretáceo na Bacia de São Luís-Grajaú. Museu Paraense Emílio Goeldi. Coleção Friedrich Katzer. MPEG Editoração, pp 245–264

Carvalho IS (2004) Dinosaur footprints from Northeastern Brazil: taphonomy and environmental setting. Ichnos 11:311–324

Carvalho IS, Araújo SAF (1995) A distribuição geográfica dos fósseis e icnofósseis de Dinosauria na Bacia de São Luís. In: 47ª Reunião Anual da Sociedade Brasileira para o Progresso da Ciência. São Luís, Resumos 2: 439

Carvalho IS, Gonçalves RA (1994) Pegadas de dinossauros neocretáceas da Formação Itapecuru, Bacia de São Luís (Maranhão, Brasil). An Acad Bras Ciênc 66(3):279–292

Carvalho IS, Leonardi G (2021) Fossil footprints as biosedimentary structures for paleoenvironmental interpretation: examples from Gondwana. J South Am Earth Sci 106: 102936. https://doi.org/10.1016/j.jsames.2020.102936

Carvalho IS, Pedrão E (1998) Brazilian theropods from the equatorial Atlantic margin: behavior and environmental setting. Gaia 15:369–378

Carvalho IS, 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 IS, Leonardi G, Rios-Netto AM, Borghi L, Paula Freitas A, Andrade JA, Freitas FI (2021) Dinosaur trampling from the Aptian of Araripe Basin, NE Brazil, as tools for paleoenvironmental interpretation. Cretaceous Res 117: 104626

Castanera D, Barco JL, Díaz-Martínez I, Gascón JH, Pérez-Lorente F, Canudo JI (2011) New evidence of a herd of titanosauriform sauropods from the lower Berriasian of the Iberian range (Spain). Palaeogeogr Palaeoclimatol Palaeoecol 310(3–4):227–237. https://doi.org/10.1016/j.palaeo.2011.07.015

Castanera D, Vila B, Razzolini N, Santos V, Pascual C, Canudo J (2014) Sauropod trackways of the Iberian Peninsula: palaeoetological and palaeoenvironmental implications. J Iber Geol 40(1):49–59. https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44087

Castro DF, Toledo CEV, Sousa EP, Medeiros MA (2004) Nova ocorrência de *Asiatoceratodus* (Osteichthyes, Dipnoiformes) na Formação Alcântara, Eocenomaniano da bacia de São Luís, MA, Brasil. Revista Brasileira de Paleontologia Revista Brasileira de Paleontologia 7(2):245–248

Currie PJ (1983) Hadrosaur trackways from the Lower Cretaceous of Canada. Acta Paleontologica Polonica 28(1–2):63–73

Eberth DA, Brinkman DB (1997) Paleoecology of an estuarine, incised-valley fill in the dinosaur park formation (Judith River Group, Upper Cretaceous) of Southern Alberta, Canada. Palaios 12:43–58

Elias FA, Bertini RJ, Medeiros MA (2007) Pterosaur teeth from the Laje do Coringa, middle Cretaceous, São Luís, Grajaú Basin, Maranhão State, Northern-Northeastern Brazil. Revista Brasileira De Geociências 37(4):1–9

Eugênio WS (1994) Aspectos Paleontológicos do Cretáceo da Baía de São Marcos, Maranhão, Brasil. Dissertação de Mestrado (Universidade Federal do Rio de Janeiro/Instituto de Geociências), 77 p (unpublished)

García-Ortiz E, Pérez-Lorente F (2014) Palaeoecological inferences about dinosaur gregarious behaviour based on the study of tracksites from La Rioja area in the Cameros Basin (Lower Cretaceous, Spain). J Iber Geol 40(1):113–127. https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44091

Heredia AM, Días-Martínez I, Pazos PJ, Comerio M (2020) Fernández DE (2020) Gregarious behaviour among non-avian theropods inferred from trackways: a case study from the Cretaceous (Cenomanian) Candeleros Formation of Patagonia, Argentina. Palaeogeogr Palaeoclimatol Palaeoecol 538:109480. https://doi.org/10.1016/j.palaeo.2019.109480

Hernández JPF, Hernández AT, Gascó-Lluna F, Valverde MC, Melón JMV, Miranda AR (2023) Analysis of gregarious behavior in theropod dinosaurs at the Peñaportillo tracksite (Munilla, La Rioja, Spain). In: Estraviz-López D et al. (eds) Palaeontological publications, Abstracts book of XXI EJIP/6th IMERP, 3: 40

Ibrahim N, Sereno PC, Varricchio DJ, Martill DM et al (2020) Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. ZooKeys 928:1–216. https://doi.org/10.3897/zookeys.928.47517

Kellner AWA, Azevedo SAK, Machado EB, Carvalho LB, Henriques DDR (2011) A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. An Acad Bras Ciênc 83:99–108. https://doi.org/10.1590/S0001-37652011000100006

Klein VC, Ferreira CS (1979) Paleontologia e estratigrafia de uma fácies estuarina da Formação Itapecuru, Estado do Maranhão. An Acad Bras Ciênc 51(3):523–533

Kuban GJ (1991a) Color distinctions and other curious features of dinosaur tracks near Glen Rose, Texas. In: Gillette DD, Lockley MG (eds) Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp 427–440

Kuban GJ (1991b) Elongate dinosaur tracks. In: Gillette DD, Lockley MG (eds) Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp 57–72

Lapparent AF (1960) Les dinosauriens du "continental intercalaire" du Sahara central. Mémoires la Société Géologique France 88(A): 3–56

Leonardi G (1980a) Dez novas pistas de dinossauros (Theropoda Marsh, 1881) na bacia do Rio do Peixe, Paraíba, Brasil. In: 2º Congreso Argentino de Paleontología y Bioestratigrafía, 1º Congreso Latino Americano de Paleontologia, Buenos Aires, 1978. Actas, Buenos Aires, 1980, Asociación Paleontologica Argentina, 1: 243–248

Leonardi G (1980b) Ornithischian trackways of the Corda Formation (Jurassic), Goiás, Brasil. In: 2° Congreso Argentino de Paleontología y Bioestratigrafía, 1º Congreso Latino Americano de Paleontología, Buenos Aires, 1978. Buenos Aires, 1980, Asociación Paleontologica Argentina, Actas 1: 215–222

Leonardi G (1981) Ichnological data on the rarity of young in North East Brazil dinosaurian populations. An Acad Bras Ciênc 53(2):345–346

Leonardi G (1984) Le impronte fossili di dinosauri. In: Ligabue G (ed). Sulle orme dei dinosauri. Venezia: Erizzo Editrice, pp 165–186

Leonardi G (1989) Inventory and statistics of the south American dinosaurian ichnofauna and its paleobiological interpretation. In: Gillette DD, Lockley MG (eds) Dinosaur Tracks and Traces. Cambridge University Press, New York, pp 165–178

Leonardi G (1994) Annotated Atlas of South America tetrapod footprints (Devonian to Holocene) with an appendix on Mexico and Central America. CPRM (Serviço Geológico do Brasil) Brasília

Leonardi G, Spezzamonte M (1994) New tracksites (Dinosauria: Theropoda and Ornithopoda) from the Lower Cretaceous of the Ceará, Brasil. Studi Trentini di Scienze Naturali. Acta Geologica 69: 61–70

Leonardi G, Carvalho IS (2021) Dinosaur Tracks of Brazil: A Lost World of Gondwana. Indiana University Press, Bloomington, U.S.A.. p 462

Leonardi G, Santos MFCF, Barbosa FHS (2021) First dinosaur tracks from the Açu Formation, Potiguar Basin (mid-Cretaceous of Brazil). An Acad Bras Ciênc 93(Suppl. 2):e20210635. https://doi.org/10.1590/0001-3765202120210635

Lindoso RM, Elias, FA, Medeiros MA, Santos RAB, Pereira AA (2011) Pterosaur teeth from the Alcântara Formation, Cretaceous of Brazil. In: Calvo J, Porfiri J, Riga BG, Santos D (eds) Editorial de La Universidad de Cuyo, pp 171–177

Lindoso RM, Medeiros MA, Carvalho IS, Marinho TS (2012) *Masiakasaurus*-like theropod teeth from the Alcântara Formation, São Luís Basin (Cenomanian), northeastern Brazil. Cretac Res 36:119–124

Lindoso RM, Marinho TS, Santucci RM, Medeiros MA, Carvalho IS (2013) A titanosaur (Dinosauria: Sauropoda) osteoderm from the Alcântara Formation (Cenomanian), São Luís Basin, Northeastern Brazil. Cretac Res 45:43–48

Lindoso RM, Medeiros MAA, Carvalho IS, Pereira AA, Mendes ID, Iori FV, Sousa EP, Arcanjo SH, Silva TCM (2019) A new rebbachisaurid (Sauropoda: Diplodocoidea) from the middle Cretaceous of northern Brazil. Cretaceous Res 104:10419. https://doi.org/10.1016/j.cretres.2019.104191

Lockley MG (1986) The paleobiological and paleoenvironmental importance of dinosaur footprints. Palaios 1:37–47

Lockley MG (1991) Tracking dinosaurs: a new look at an ancient world. Cambridge University Press, Cambridge, MA, 238pp

Lockley MG, Houck KJ, Prince NK (1986) North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. Geological Soc Am Bull 97(10): 1163–1176

Lockley MG, Hunt A, Holbrook J, Matsukawa M, Meyer C (1992) The dinosaur freeway: a preliminary report on the Cretaceous megatracksite, Dakota Group, Rocky Mountain front range, and high plains, Colorado, Oklahoma and New Mexico. In: Flores RM (ed) Field Guidebook—Mesozoic of the Western Interior. SEPM 1992 Theme Meeting. Rocky Mountain Section, Colorado State University, Publications and Creative Services. Fort Collins, Colorado, pp 39–54

Lockley MG, Huh M, Gwak SG, Hwang KG, Paik IS (2012) Multiple tracksites with parallel trackways from the Cretaceous of the Yeosu City Area Korea: implications for gregarious behavior in ornithopod and sauropod dinosaurs. Ichnos 19(1–2):105–114. https://doi.org/10.1080/10420940.2011.625793

Lockley MG, McCrea R, Alcala L, Cart K, Martin J, Hadden G (2015) A preliminary report on an assemblage of large theropod tracks from the Cretaceous Dakota Group, Western Colorado: evidence for gregarious behavior. In: Sullivan RM, Lucas SG (eds) New Mexico museum of natural history and science. Bulletin 67, Fossil Record 4: 179–183

Letizio LA, Bertini RJ, Medeiros MA (2022) New evidence of putative Unenlagiinae (Deinonychosauria, Theropoda) in the São Luís-Grajaú Basin, Albian– Cenomanian, State of Maranhão, Brazil. Revista Brasileira de Paleontologia 25(2):157–164

Maisey JG (2000) Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretac Res 21:281–314

McCrea RT, Buckley LG, Farlow JO, Lockley MG, Currie PJ, Matthews NA, Pemberton SG (2014) A 'terror of Tyrannosaurs': the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. PLoS ONE 9(7):e103613. https://doi.org/10.1371/journal.pone.0103613

Medeiros MA (2006) Large theropod teeth from the Eocenomanian of northeastern Brazil and the occurrence of Spinosauridae. Revista Brasileira de Paleontologia 9(3):333–338

Medeiros MA, Schultz CL (2001) Uma paleocomunidade de vertebrados do Cretáceo médio, Bacia de São Luís. In: Rossetti DF, Góes AM, Truckenbrodt W (eds) O Cretáceo na Bacia de São Luís e Grajaú. Coleção Friedrich Katzer, Museu Paraense Emílio Goeldi, Belém, pp 209–221

Medeiros MA, Schultz CL (2002) A fauna dinossauriana da Laje do Coringa, Cretáceo médio do Nordeste do Brasil. Arquivos do Museu Nacional 60(3):155–162

Medeiros MA, Schultz CL (2004) *Rayososaurus* (Sauropoda, Diplocoidea) no meso-Cretáceo do Norte-Nordeste Brasileiro. Revista Brasileira de Paleontologia 7(2):255–279

Medeiros MA, Freire PC, Pereira AA, Santos RAB, Lindoso RM, Coêlho AFA, Passos EB, Júnior ES (2007) Another African dinosaur recorded in the Eocenomanian of Brazil and a revision of the Laje do Coringa site. In: Carvalho IS, Cassab RCT, Schwanke C, Carvalho MA, Fernandes ACS, Rodrigues MAC, Carvalho MSS, Arai M, Oliveira MEQ (eds) Paleontologia: Cenários de Vida, Rio de Janeiro: Interciência 1: 413–423

Medeiros MA, Lindoso RM, Mendes ID, Carvalho IS (2014) The Cretaceous (Cenomanian) continental record of the Laje do Coringa flagstone (Alcântara Formation), northeastern South America. J S Am Earth Sci 53(2014):50–58. https://doi.org/10.1016/j.jsames.2014.04.002

Moraes-Santos HM, Melo CCS, Toledo PM, Rossetti DF (2001) Ocorrência de Pleurodira na Formação Alcântara (Albiano-Cenomaniano), Bacia de São Luís, MA. In: Rossetti DF, Góes AM, Truckenbrodt W (eds) O Cretáceo na Bacia de São Luís e Grajaú. Coleção Friedrich Katzer, Museu Paraense Emílio Goeldi, Belém, pp 235–244

Moreno K, Valais SD, Blanco N, Tomlinson AJ, Jacay J, Calvo JO (2012) Large theropod dinosaur footprint associations in western Gondwana: behavioural and palaeogeographic implications. Acta Palaeontologica Polonica 57(1): 73–83. https://doi.org/10.4202/app.2010.0119

Myers TS, Fiorillo AR (2009) Evidence for gregarious behavior and age segregation in sauropod dinosaurs. Palaeogeogr Palaeoclimatol Palaeoecol 274(1–2):96–104. https://doi.org/10.1016/j.palaeo.2009.01.002

Nadon GC (1993) The association of anastomosed fluvial deposits and dinosaur tracks, eggs, and nests: implications for the interpretation of floodplain environments and a possible survival strategy for ornithopods. Palaios 8:31–44

Oliveira PE (1958) Notas preliminares e estudos sobre a idade do calcário de Ponta Grossa, Estado do Maranhão. Departamento Nacional da Produção Mineral/Divisão de Geologia e Mineralogia, 1–7 (Boletim 107)

Paik IS, Kim HJ, Baek SG, Seo YK (2020) New evidence for truly gregarious behavior of ornithopods and solitary hunting by a theropod. Episodes 43(4): 1045–1052. https://doi.org/10.18814/epiiugs/2020/020069

Pedrão E (1995) Palinoestratigrafia e evolução paleoambiental de rochas sedimentares aptianas-cenomanianas das bacias de Bragança-Viseu e São Luís (Margem Equatorial Brasileira). Dissertação de Mestrado (Universidade Federal do Rio de Janeiro/Instituto de Geociências), 215 pp (unpublished)

Pedrão E, Arai M, Carvalho IS, Santos MHB (1993) Palinomorfos cenomanianos da Formação Itapecuru - análise palinológica do afloramento da ponta do Farol, município de São Luís (MA). In: 13º Congresso Brasileiro de Paleontologia, 1º Simpósio de Paleontologia do Cone Sul, São Leopoldo, 1993, Companhia de Pesquisa de Recursos Minerais, Boletim de Resumos, p 61

Pedrão E, Carvalho IS, Martins FJC, Santos MHB (1995) Palinoestratigrafia e análise quantitativa de amostras de superfície da Formação Itapecuru, Bacia de São Luís. PETROBRAS-CENPES, Rio de Janeiro, 5 p., 2 figs., 2 plates

Pedreira da Silva AJ, Lopes RC, Vasconcelos AM, Bahia RBC (2003) Bacias Sedimentares Paleozóicas e Meso-Cenozóicas Interiores. In: Bizzi LA, Schobbenhaus C, Vidotti RM, Gonçalves JH (eds) Geologia, Tectônica e Recursos Minerais do Brasil. Brasília: CPRM, pp 55–85

Piñuela L, García-Ramos JC, Romano M, Ruiz-Omeñaca JI (2016) First record of gregarious behavior in robust medium-sized Jurassic Ornithopods: evidence from the Kimmeridgian trackways of Asturias (N. Spain) and some general considerations on other medium-large ornithopod tracks in the Mesozoic record. Ichnos 23(3–4): 298–311. https://doi.org/10.1080/10420940.2016.1178640

Popoff M (1988) Du Gondwana à l'Atlantique Sud: les connexions du fossé de la Bénoué avec les bassins du Nord-Est brésilien jusqu'à l'ouverture du golfe de Guinée au Crétacé Inférieur. Journal of African Earth Sciences (and the Middle East) 7(2):409–431. https://doi.org/10.1016/0899-5362(88)90086-3

Richter U, Mudroch A, Buckley LG (2013) Isolated theropod teeth from the Kem Kem beds (early Cenomanian) near Taouz. Morocco. Paläontologische z. 87(2):291–434

Rossetti DF (1994) Morphology and internal structures of mixed tide and storm—generated bedforms: Upper Cretaceous Itapecuru Formation, Northern Brazil. In: 14th International Sedimentological Congress, Recife, 1994, Abstracts pp A21–A22

Rossetti DF (1996a) Genesis of large-scale cross beddings from the Cenomanian Upper Itapecuru Formation. Northern Brazil. In: 4° Simpósio sobre o Cretáceo do Brasil, Águas de São Pedro, 1996, Sociedade Brasileira de Geologia, Boletim pp 147–149

Rossetti DF (1996b) Depositional evolution of two estuarine successions: the Upper Itapecuru Formation, São Luís Basin, Northern Brazil. In: 39º Congresso Brasileiro de Geologia, Salvador, 1996, Sociedade Brasileira de Geologia, Anais 1: 187–188

Rossetti DF (1996c) Sequence stratigraphy and depositional evolution of the Itapecuru Formation (Late Cretaceous) in the São Luís Basin, Northern Brazil. Acta Geologica Leopoldensia 19:111–126

Rossetti DF (1997) Facies analysis of the lower succession of the Upper Itapecuru Formation, São Luís Basin, northern Brazil. In: Costa ML, Angelica R (eds) Contribuições à Geologia da Amazônia, Belém, Falângola, pp 241–284

Rossetti DF (1998) Facies architecture and sequential evolution of incised valley estuarine fills: the Cujupe Formation (Upper Cretaceous to lower Tertiary), São Luís Basin, northern Brazil. J Sediment Res 68(2):299–310

Rossetti DF, Truckenbrodt W (1997) Revisão estratigráfica para os depósitos do Albiano-Terciário Inferior(?) na Bacia de São Luís, Maranhão. Boletim do Museu Paraense Emílio Goeldi, Série Ciências da Terra 9:29–41

Stromer E (1915) Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten -Ägyptens. II- Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 3-Das original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften 28(3):1–32

Thulborn T (1990) Dinosaur tracks. Chapman and Hall, St Edmundsbury Press Ltd., Great Britain, 410pp

Vilas Bôas I (1999) Dentes de terópodes e associação fossilífera da Praia da Baronesa, Alcântara, MA (Formação Itapecuru, Bacia de São Luís). In: 16º Congresso Brasileiro de Paleontologia, URCA, Crato, Boletim de Resumos, p 125

Vilas Bôas I, Carvalho IS (1999) Mosasaurios de la Formación Itapecuru (Cretácico Superior), playa de la Baronesa, Alcântara (Estado de Maranhão), Brasil. In: XV Jornadas Argentinas de Paleontología de Vertebrados, 1999. Ameghiana, La Plata, Argentina, 36(4):24 R

Vilas Bôas I, Carvalho IS (2001) Répteis marinhos (Mosasauria e Plesiosauria) do Cretáceo Superior da Bacia de São Luís (Maranhão, Brasil). In: Rossetti DF, Góes AM, Truckenbrodt W (eds) O Cretáceo na Bacia de São Luís-Grajaú. Coleção Friedrich Katzer, Ed. Museu Paraense Emílio Goeldi, pp 223–233

Vilas Bôas I, Medeiros MA (1997) Theropod teeth (dromeosaurids?) from the Itapecuru Formation, Maranhão—Brasil. In: Jornadas Argentinas de Paleontologia de Vertebrados, 1997, La Rioja. Programa y Resumenes, Ameghiniana 13: 35

Vilas Bôas I, Carvalho IS, Medeiros MA, Pontes H (1999) Dentes de *Carcharodontosaurus* (Dinosauria, Tyrannosauridae [sic]) do Cenomaniano, Bacia de São Luís (Norte do Brasil). An Acad Bras Ciênc 71(4):846–847