Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal

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LETHAIA

Mateus, O. & Milàn, J. 2010: A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. *Lethaia*, Vol. 43, pp. 245–257

A newly discovered dinosaur track-assemblage from the Upper Jurassic Lourinhã Formation (Lusitanian Basin, central-west Portugal), comprises medium- to large-sized sauropod tracks with well-preserved impressions of soft tissue anatomy, stegosaur tracks and tracks from medium- to large-sized theropods. The 400-m-thick Lourinhã Formation consists of mostly aluvial sediments, deposited during the early rifting of the Atlantic Ocean in the Kimmeridgian and Tithonian. The stratigraphic succession shows several shifts between flood-plain mud and fluvial sands that favour preservation and fossilization of tracks. The studied track-assemblage is found preserved as natural casts on the underside of a thin bivalve-rich carbonate bed near the Tithonian–Kimmeridgian boundary. The diversity of the tracks from the new track assemblage is compared with similar faunas from the Upper Jurassic of Asturias, Spain and the Middle Jurassic Yorkshire Coast of England. The Portuguese record of Upper Jurassic dinosaur body fossils show close similarity to the track fauna from the Lourinhã Formation. □ *Dinosaur tracks, Lusitanian Basin, Portugal, skin impressions, Upper Jurassic.*

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The Middle to Late Jurassic carbonate platforms of Portugal have yielded several of the largest and most important dinosaur tracksites in Europe (e.g. Dantas *et al.* 1994; Lockley *et al.* 1994a; Santos *et al.* 1994; Lockley & Meyer 2000), yet only recently the value of dinosaur tracks from Upper Jurassic siliciclastic deposits have been recognized. This paper discusses one such occurrence.

The Lourinhã Formation is exposed in central-west Portugal, mostly near to the town of Lourinhã (Fig. 1). The formation was deposited in the Lusitanian Basin and comprises more than 400 m of mostly terrestrial sediments, with some coastal intercalations (Kullberg *et al.* 2006) deposited during the early rifting stage of the Atlantic Ocean in latest Jurassic, Tithonian–Kimmeridgian times (Hill 1989). The sediments consist predominantly of thick beds of red and green clay, interbedded with massive fluvial sandstone bodies and heterolithic beds. The sandstone bodies are horizontally extensive, lenticular beds that in some instances are traceable for several kilometres in the exposed cliff sections along the coast. The sandstone lenses have been interpreted as distal alluvial fan facies originating from periods of extensive faulting (Hill 1989). The Lourinhã Formation contains a highly diverse vertebrate fauna comprising fish, amphibians, turtles, pterosaurs, crocodiles, dinosaurs and mammals (Antunes 1998; Antunes & Mateus 2003; Mateus 2006; Mateus *et al.* 2006), as well as dinosaur nests, eggs and embryos (Antunes *et al.* 1998; Mateus *et al.* 1998). The formation is also known for its fossil vegetation, namely plant fragments and large fossilized tree logs (Pais 1998). Yagüe *et al.* (2006) proposed a lithostratigrapic scheme for the continental Upper Jurassic of the Lusitanian basin, which includes the Bombarral, Sobral and Alcobaça Formations (including Consolação and Praia da Amoreira- Porto Novo Members) within the Lourinhã Group.

The succession shows abundant shifts between unconsolidated flood-plain mud and fluvial sandstone that favour recognition of fossil tracks. Within the last years, more than 30 well-preserved single tracks and small trackways of sauropods, theropods, thyreophorans and ornithopods have been discovered, both preserved *in-situ* on the original sedimentary surfaces and on loose blocks fallen to the beach caused by the extensive coastal erosion (Antunes & Mateus 2003; Milàn *et al.* 2005; Mateus & Milàn 2008).

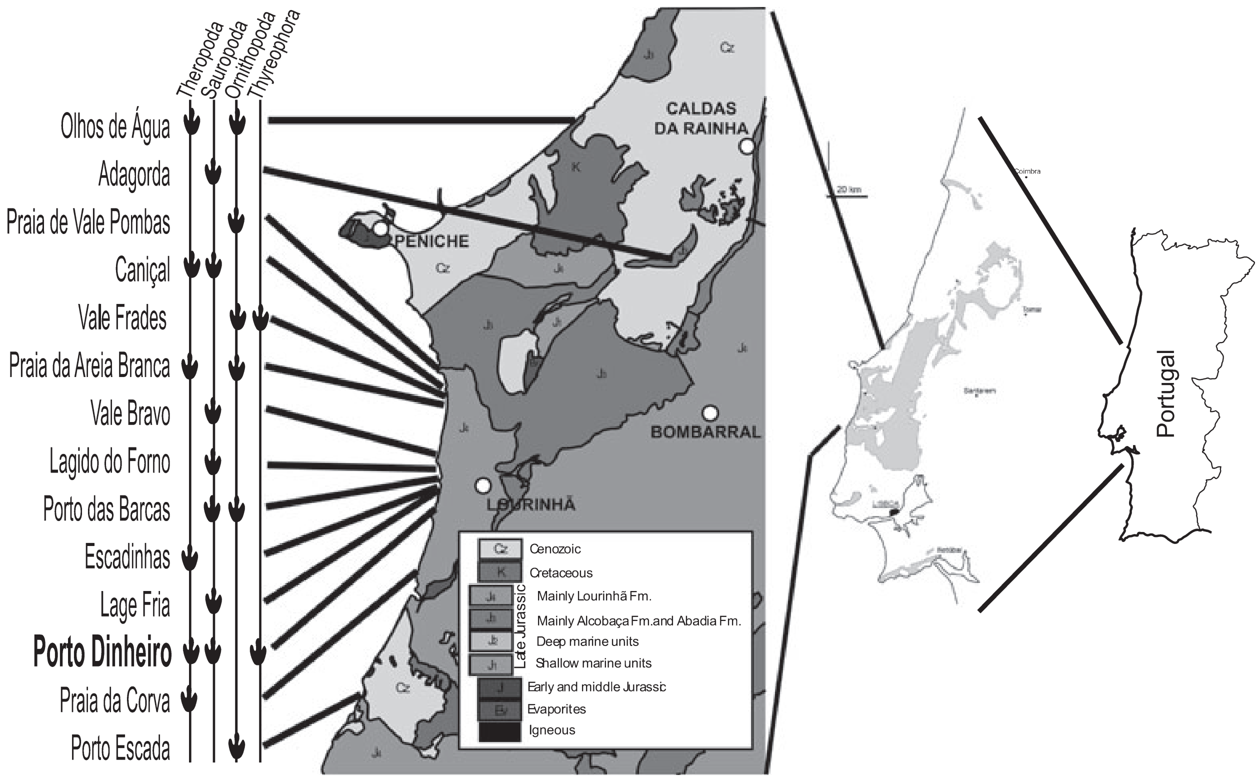

Fig. 1. Geological map of central-west Portugal (based on Alves *et al.* 2003) with main track localities depicted.

The aim of this study is to describe a new multi-taxon track assemblage found in the coast cliffs just south of the locality of Porto Dinheiro, to compare it with similar track faunas from the Middle Jurassic of England and the Upper Jurassic of Spain, and to compare it with the known dinosaur skeletal record from the Lourinhã Formation and the Upper Jurassic of Portugal.

Porto Dinheiro track assemblage

Identification of tracks

Theropod and ornithopod dinosaurs are both functionally tridactyl, and both leave tridactyl tracks, that at first glance can seem difficult to distinguish them. Theropod tracks are characterized by being longer than they are wide, with long narrow, often tapering, digits ending in long, sharp claw impressions (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991), and the divarication angle between digits II and IV is normally 50–60°, but can be as low as 35° and up to 75° (Thulborn 1990). Theropod trackways are set in a narrow gauge pattern, with high pace angulations, approaching 180° and a tendency for the feet to show slight inward rotation (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991). Ornithopod tracks are generally wider than they are long, the digits are short and rounded, and when present the imprints of the claws are blunt and rounded. The divarication angle between digits II and IV are normally in excess of 60°, their trackways are set in a broader pattern than theropods, and the feet often show an outward rotation (Moratalla *et al.* 1988; Thulborn 1990; Lockley 1991).

Stegosaur tracks are poorly known in the fossil record, and some confusion exists about the identification of stegosaur tracks. (Thulborn 1990; Whyte & Romano 1994, 2001; Lockley & Hunt 1998; Long 1998; Gierlinski & Sabath 2002; Lires *et al.* 2002; García-Ramos *et al.* 2006, 2008; Whyte *et al.* 2007; Lockley *et al.* 2008) The track named as *Deltapodus brodricki* (Whyte & Romano 1994, 2001), however, is a close fit for the flesh-out morphology of the stegosaur pedal skeleton. *Deltapodus* is characterized by entaxonic, crescent-shaped manus impression that is approximately twice as wide as long, and may have the impression of an inward-directed pollex claw. The pes of *Deltapodus* is generally triangular to subtriangular in outline, tridactyl and mesaxonic, with impressions of short, bluntly rounded digits and a maximum width across the base of the digit impressions (Whyte & Romano 1994).

Sauropods display an extreme degree of heteropody in their tracks, the sauropod manus track is crescent shaped, normally without indications of free digits, except for, in some genera, a prominent inward-directed pollex claw. The pes track is elongated, entaxonic, and can display from three to five short outward-rotated digit impressions (Thulborn 1990; Lockley 1991; Lockley *et al.* 1994b; Wright 2005). The manus-pes size ratio varies from 1:2 (Santos *et al.* 1994) to 1:5 (Lockley *et al.* 1994b), and sauropod trackways can be roughly divided into wide- and narrow-gauge trackways (Lockley *et al.* 1994b).

During field work in the summers of 2005 and 2006, several casts of dinosaur tracks were discovered on the beach and in the cliff section approximately 500 m north of the beach at Porto Dinheiro (Fig. 1). All the tracks were found as casts on the underside of large blocks fallen from a laterally extensive marine carbonate bed near the top of the cliff section (Fig. 2). This carbonate bed is the upper of two distinct 0.5-m-thick carbonate layers, rich in the bivalves *Isognomon* and *Eomiodon securiformis*, and represents short, marine transgressions. The *Isognomon/Eomiodon* layer with the tracks can be traced for several kilometres along the coastal cliffs, and the upper layer represent the interface between the Praia da Amoreira-Porto Novo Member and the Sobral Formation (= Praia Azul Member), recognized as Upper Kimmeridgian to Early Tithonian in age (Leinfelder 1987). The carbonate bed displays abundant tracks, and seven blocks with tracks were found within a distance of 20 m from each other, as well as several loose scattered down the cliff face. The preservation of the tracks is unusual in that the tracks are located on the underside of a marine limestone bed containing numerous large bivalves and large *Thalassinoides* burrows. The casts of the tracks contain several of the large bivalves, and bivalves are present between the digit impressions in some of the tracks, suggesting that the tracks were emplaced in shallow water or during a period of sub-aerial exposure.

The first track to be discovered from the locality was a large well-preserved cast of the right pes from a sauropod (Fig. 3), followed by several tridactyl theropod tracks, a stegosaur track and a giant-sized theropod track were found within a 20 m stretch of fallen blocks on the beach. Later, several tracks and fragments of tracks were recovered in loose blocks on the cliff face.

Sauropod tracks

Several natural casts of tracks was indentified as sauropod pes tracks as they range in size from 58 to 105 cm in length, are entaxonic, elongated piriform, with impressions of short, pointy, outward facing digits (Figs 3–5). Some specimens show evidence of short blunt claws and a division into digital pads (Figs 3, 4). The heel area of the foot consists of a large rounded pad, separated from the digit impressions by a more shallowly impressed area.

The casts of the individual digits, including the ungual insertion in digit II, are preserved exquisitely in the best-preserved cast (Fig. 3). Assuming that this

Fig. 2. Photography from the track-bearing locality, approximately 500 m north of Porto Dinheiro. A, the Upper Jurassic Lourinhã Formation is prominently exposed in steep cliff sections, and consists of thick beds of red and green clay, intercalated with horizontally extensive fluvial sandstone beds. Arrow indicates the location of the track fallen from the cliff section. B, the track assemblage originates from the underside of a prominent greyish, bivalve-rich marine carbonate bed located at the top of the cliff section.

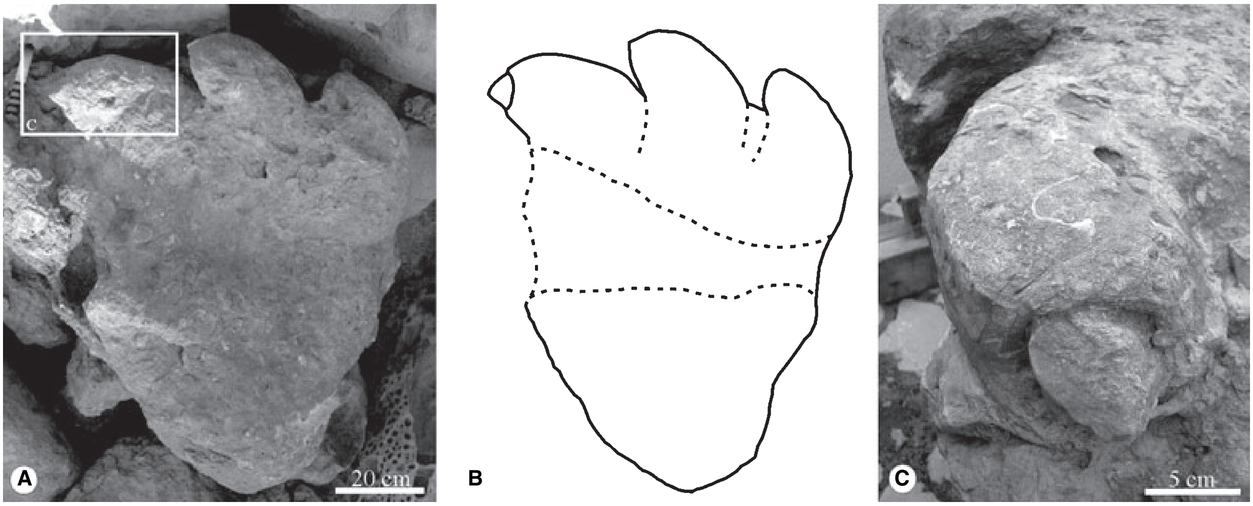

Fig. 3. A, natural cast of a large sauropod pes track from Porto Dinheiro. The track measures 105 cm in length and the casts of the digit impressions are sharp, well-defined and show the digits to be outwards directed. B, interpretative drawing of the track, showing the track to be divided into a triangular heel pad and, separated from the digital pads by a shallower area. C, close-up, head-on view of the cast of digit II on the large pes in A. This cast perfectly shows that the ungual is proximally enclosed by the fleshy digit.

preservation closely fits to only the basic morphology of a fleshed-out sauropod foot with toes, this track contributes to the understanding of an aspect of soft tissue morphology of sauropod feet, and shows the ungual is proximally enclosed by the soft tissue (Fig. 3). Perfect impressions of the skin are present on several patches on the underside and sides of the best-preserved casts (Figs 4, 6). Two different types of skin pattern are observed on the underside of the pes casts. In the palmar surface of the feet, the skin pattern is rough and tubercular with the scales arranged in a hexagonal pattern an each scale tubercle from 2 to 3 cm in diametre (Fig. 6). On the sides, the skin pattern becomes pointier with overlapping scales, with

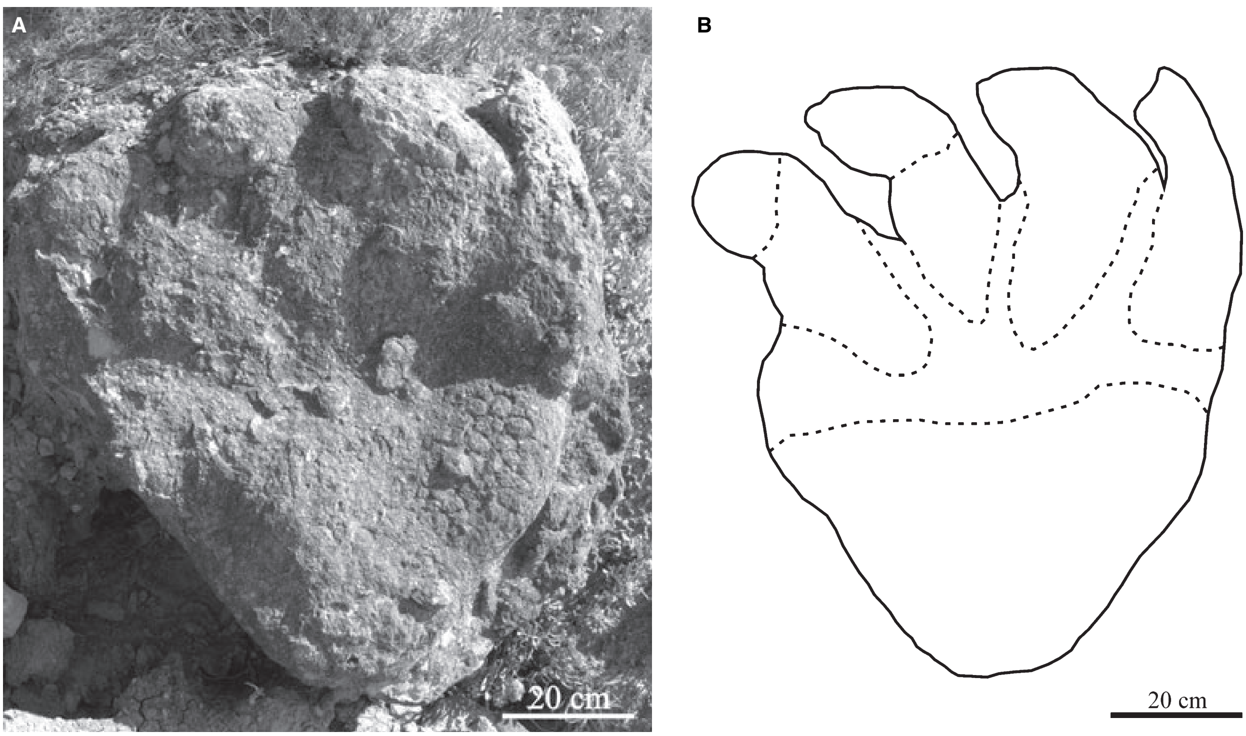

Fig. 4. A, large cast of a complete sauropod pes with impressions of four digits and well-preserved skin impressions in the the heel area. Notice the heel pad is separated from the digital pad impressions by a shallower area. B, interpretative drawing.

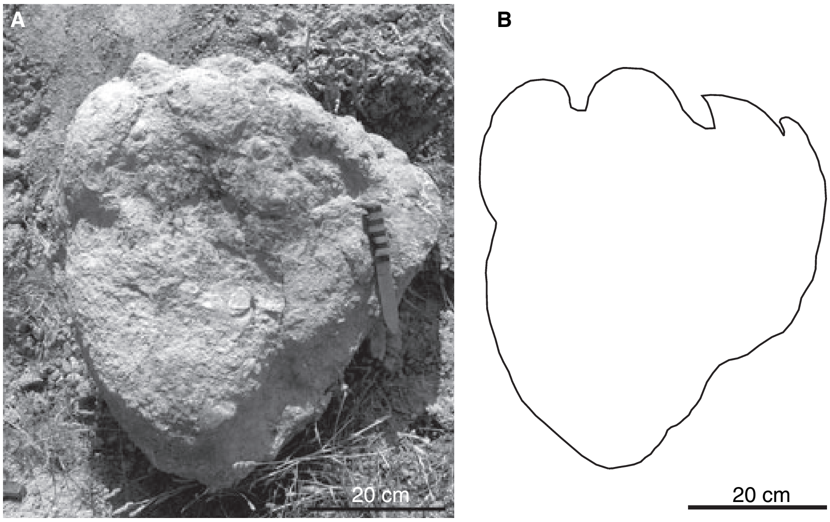

Fig. 5. A, cast of a smaller sauropod pes, measuring only 58 cm in length. B, interpretative drawing.

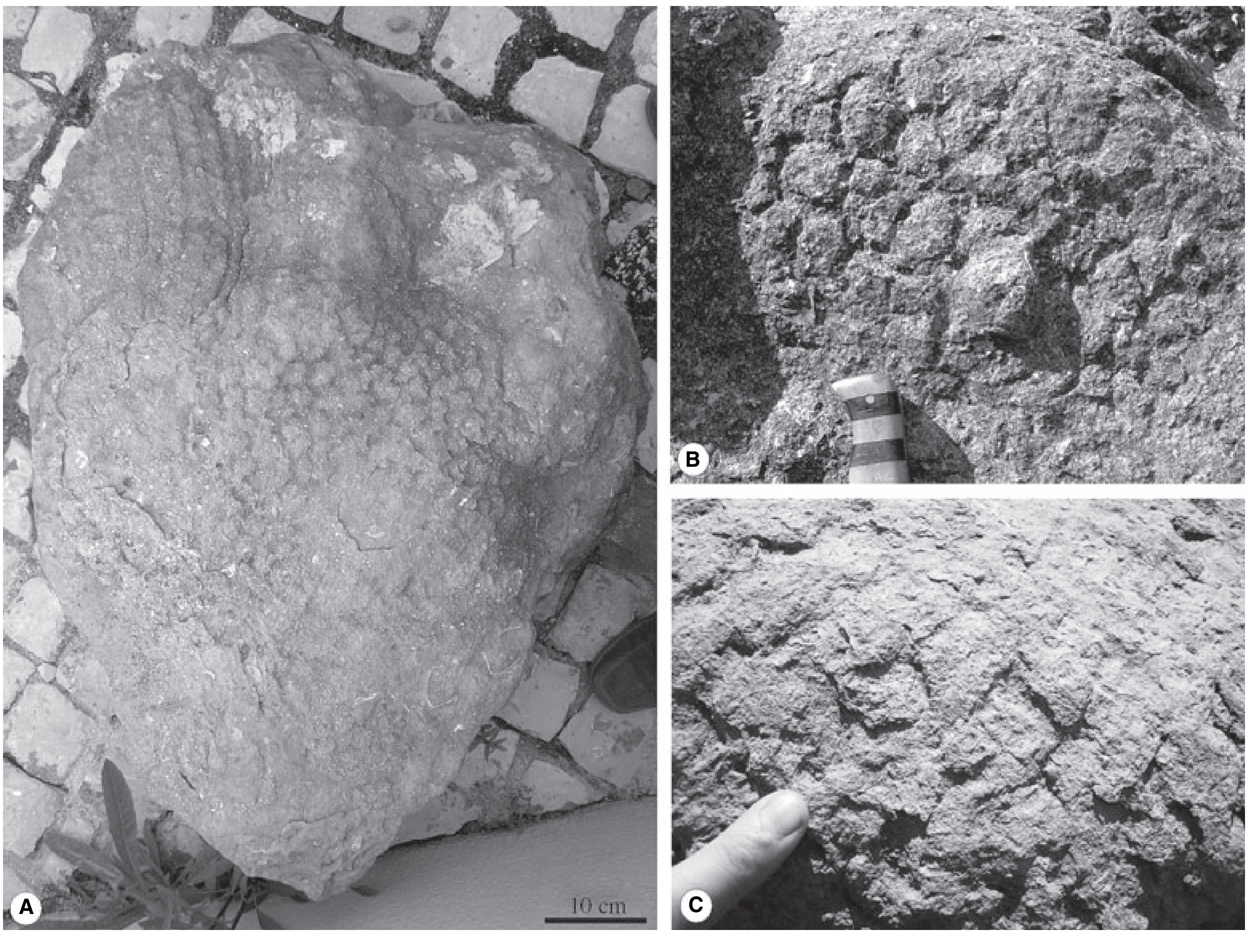

Fig. 6. Skin impressions from sauropod tracks. A, large track where the foot has slid through the mud, causing the formation of uni-directional elongated striations along one side of the track, while the palmar surface of the track is covered with the cast of a rough scaly skin. B, close up of the scaly skin impression. The skin scales covering the palmar surface of the foot are 2–3 cm in size and are arranged in a hexagonal pattern. C, on the side of the cast the skin tubercles appear as triangular overlapping scales.

the pointy end facing upward (Fig. 6C). On the walls of the cast, the scaled skin resembles a pattern of elongated parallel striations formed by the foot sliding sideways through the sediment (Fig. 6A).

Several additional casts of sauropod pes imprints and fragments of casts of various sizes were scattered down the cliff face. Yet, no casts of manus impressions have to date been identified with certainty.

Theropod tracks

Numerous natural casts of elongated, tridactyl mesaxonic tracks ranging in size from 30 to 79 cm in length are identified as theropod tracks (Figs 7–9). These tracks fall into three distinct size groups, the most abundant type is 30–35 cm long, with a low angle of divarication between the impressions of the outer digits. The tracks are slightly longer than wide and the impressions of the digits are long and cigar shaped, and in the best-preserved specimens, terminating in impressions of sharp claws (Fig. 7). The casts of the tracks are 5–12 cm deep, and some of them are deformed as if the foot slid sideways when it was brought down through the soft mud. The small tracks show only a very weak division of the digits into digital pads, which together with the cigar-shaped digit impressions refers them to the Jurassic ichnogenus *Therangospodus* (Lockley *et al.* 2000).

Two larger tracks, 52 and 54 cm long, respectively, represent a group of larger theropod trackmakers with long, narrow digit impressions that end with sharp claw impressions. The 52-cm track lacks the distal parts of the two outer digit impressions so the total width of the track is not measurable. The track is 54 cm long 46 cm wide (Fig. 8). One of the outer digit impressions is almost twice as wide as the others. This phenomena is previously described from the Lower Cretaceous track *Bueckeburgichnus maximus* Kuhn 1958, from the Wealden of Germany (Lockley 2007), and in the Maastrichtien track *Tyrannosauripus pillmorei* from New Mexico (Lockley & Hunt 1994) where in both cases digit II is significantly broader than digits III and IV (Lockley 2007). In the present case, however, we interpret the broadening of the digit impressions as double imprinting of the digit or partly overstepping of another track. A single giant-sized cast of a theropod track is 79 cm long, measured from the tip of digit III to the proximal end of the metatarsal pads (Fig. 9). The distal part of digit IV is broken off, and without the missing part of the digit, the track is 60 cm wide. A partial impression of the metatarsus is preserved, protruding 15 cm further back from the track, giving it a total length of 96 cm. The impressions of the digits are slender and the divarication angle between digits II and IV is estimated at 46°. Digit III has a lateral swelling in the middle of the digit (Fig. 9), similar to what is observed in *Tyrannosauripus pillmorei* (Lockley & Hunt 1994), but whether it represents pathology, or is a taphonomic artefact is at present uncertain.

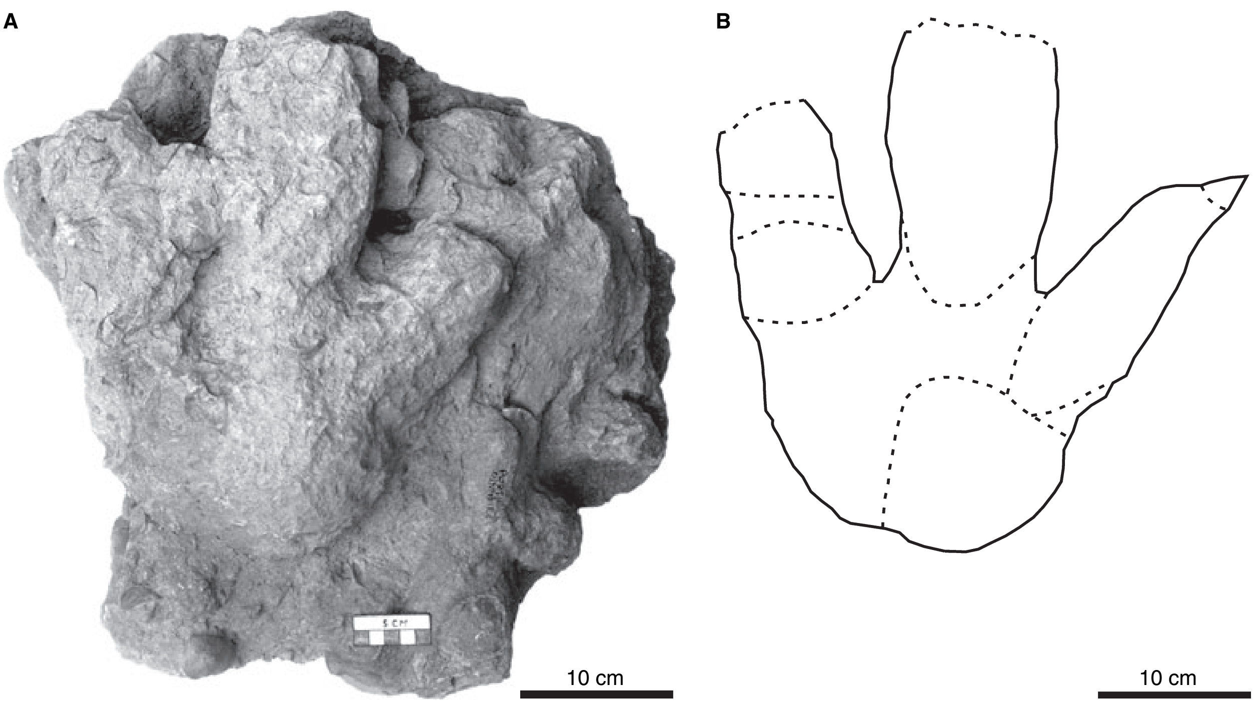

Fig. 7. A, the natural cast of the small tridactyl track is relatively well-preserved with impressions of long, slender, cigar-shaped digits. The track is 34 cm long and 32 cm wide. B, interpretative drawing.

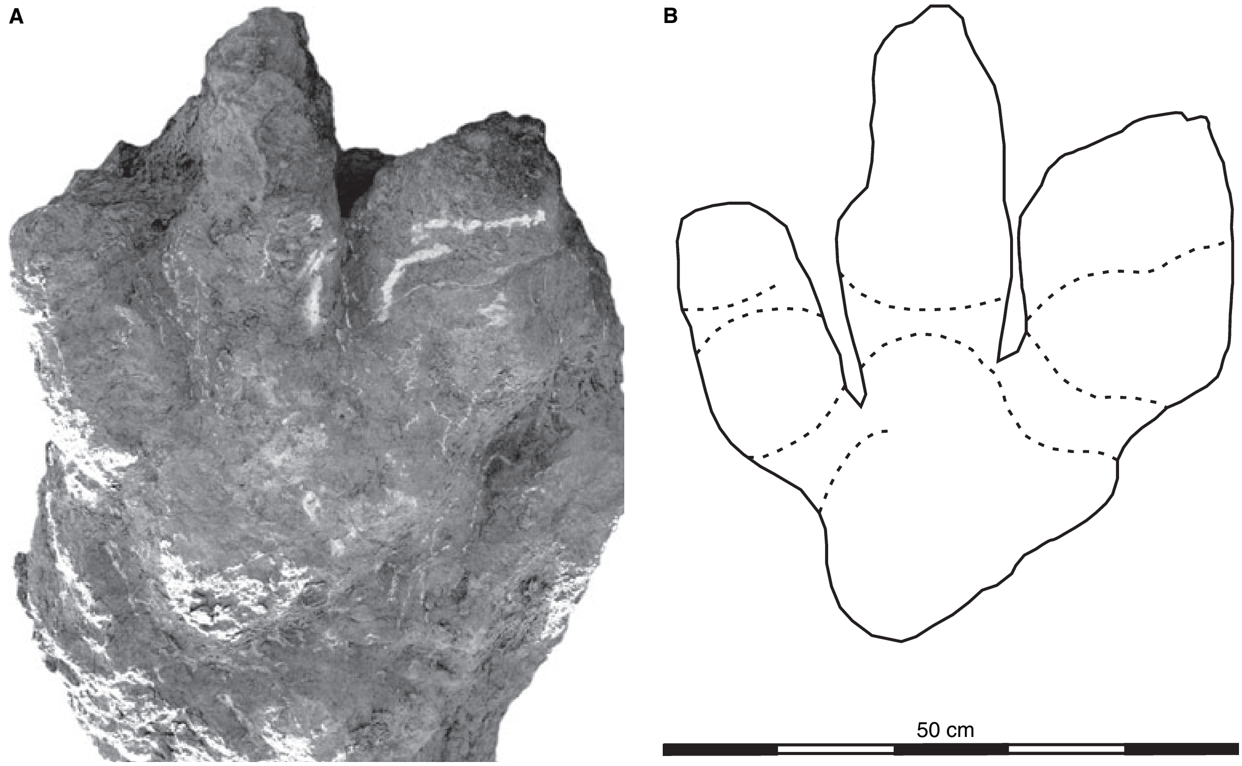

Fig. 8. A, medium-sized theropod track. This track is 54 cm long and 46 cm wide, with long slender digits divided into digital pads and terminating in sharp claws. B, interpretative drawing. The impression of the right digit is double as wide as the left digit and is interpreted as double imprinting of the digit.

In addition, a single cast of a deeply impressed theropod track was found on the sloping part of the cliff section in connection with the other tracks. The cast of the track is 40 cm long, 37 cm wide and 15 cm deep. The impressions of the digits are narrow and have preserved grooves formed by the claw being dragged down through the sediment. Fine striations from the scaly skin, 2–3 mm wide, are present on the outer side of the digit impressions. This track is preserved as a natural cast of fine-grained sandstone, and does not originate from the same stratigraphic level as the other tracks.

Stegosaur track

A single well-preserved natural cast of a tridactyl mesaxonic track, with very short, rounded, hooflike, forward facing digit impressions and a broad massive heel area is referred to *Deltapodus brodricki*, an ichnogenus made by a stegosaurian trackmaker (Whyte & Romano 1994, 2001). The cast of the track is 42 cm long, 32 cm wide, and on average 12 cm deep (Fig. 10). The cast is deepest in the area of the toes and the heel, with the middle part of the track less impressed into the substrate. A weak division into pads are present at the digits and faint striations from the skin being dragged through the sediment are sporadically preserved in the trackwalls. The track elongation and the digit count suggest that it is the pes print. This is the only stegosaur track found at the Porto Dinheiro locality, but a similar specimens have been found in connection with a large ornithopod track at the nearby beach of Vale Frades (Mateus & Milàn 2008), and additional hitherto undescribed specimens from the Lourinhã Formation are stored in the collection of Museu da Lourinhã. The dimensions of the track, 42 cm in long and 32 cm wide, fall well within the normal size of Middle Jurassic *Deltapodus* specimens from the Yorkshire coast of England (Whyte *et al.* 2007), and the Upper Jurassic of Asturias, Spain (García-Ramos *et al.* 2006; Lockley *et al.* 2008).

The record of stegosaur tracks is, by far, scarcer than what is observed in other dinosaur groups, and *Deltapodus* is so far restricted to the floodplain systems of the Middle Jurassic Yorkshire Coast of England (Whyte *et al.* 2007), the Upper Jurassic of Asturias, Spain (Lires *et al.* 2002; García-Ramos *et al.* 2006, 2008; Lockley *et al.* 2008), the Upper Jurassic of Portugal (Mateus & Milàn 2008) and Utah, North America (Milàn & Chiappe 2009).

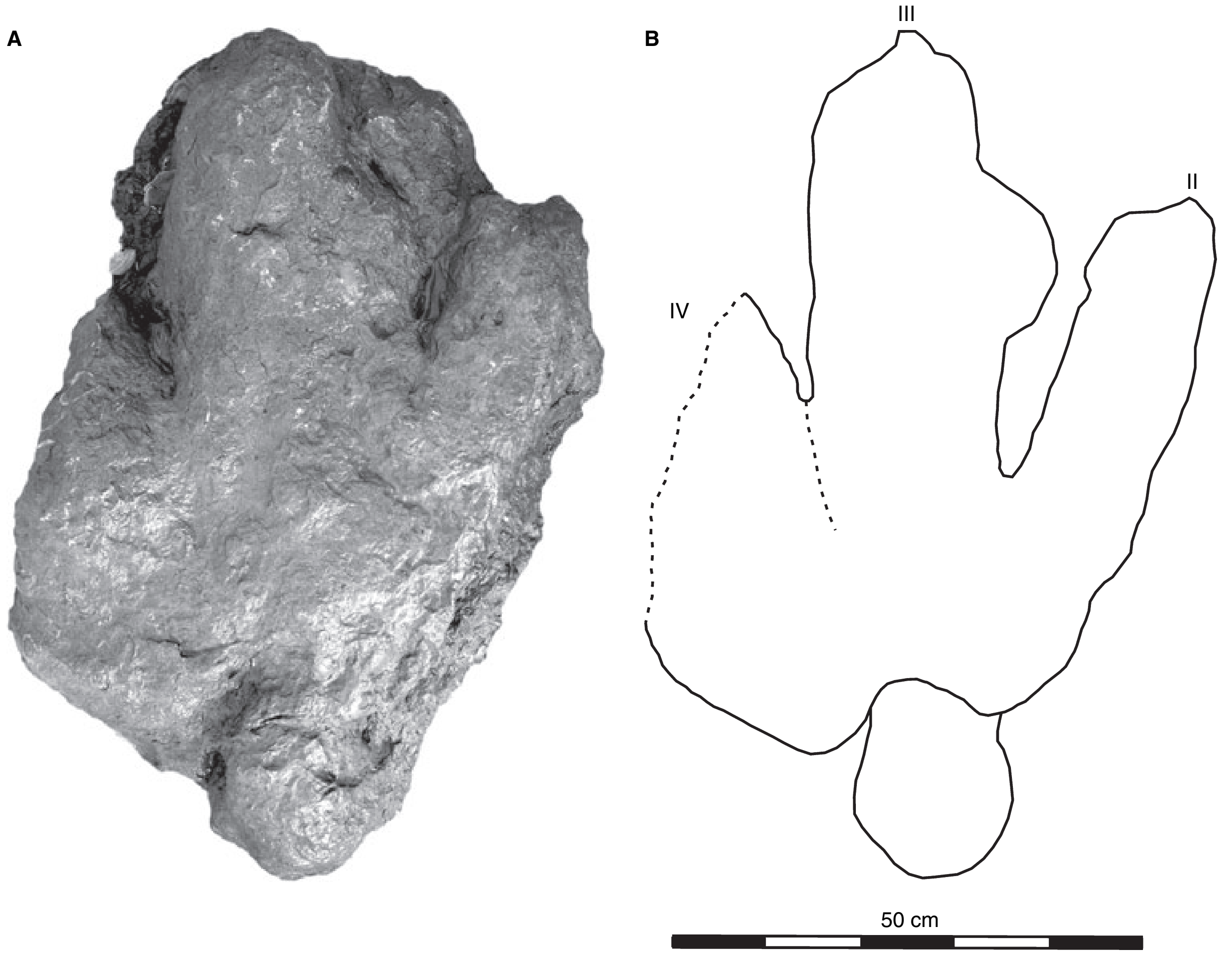

Fig. 9. A, track from a large-sized theropod. The track measures 79 cm in length and 60 cm in width without the missing distal part of digit IV. When the length of rearward protruding metatarsus impression is added the total length of the track is 96 cm. This track is among the largest theropod tracks ever found in the Jurassic. B, interpretative drawing.

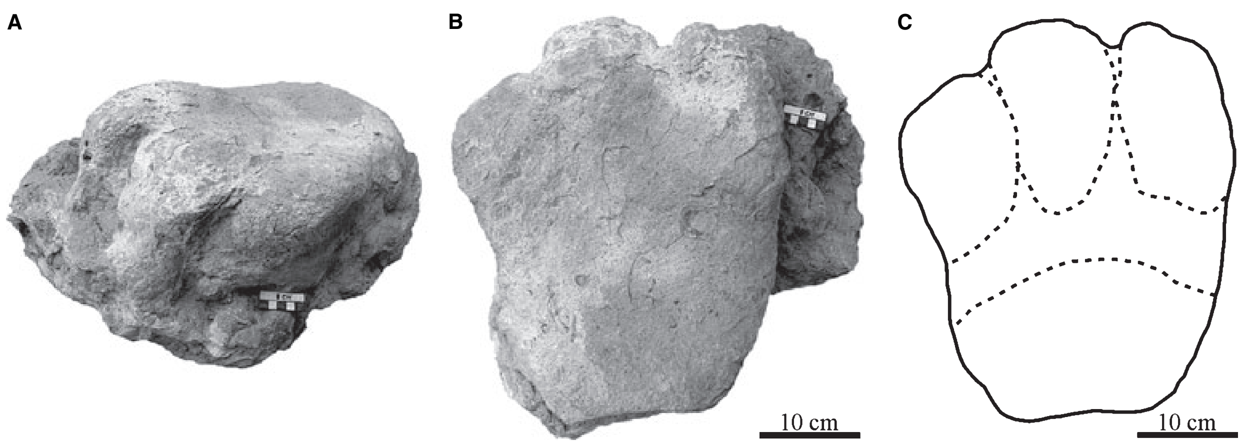

Fig. 10. A, natural cast of a stegosaur pes print. The foot had sunk to a considerable depth in the sediments forming steep trackwalls with preserved striations from the skin. B, the track is tridactyl, 42 cm long and 32 cm wide, and close to symmetrical along the midline. The casts of the digits are short, blunt and forward facing. The sole of the foot shows a weak division into a rounded heel pad and three elongated pads at the digits. C, interpretative drawing of the track with pedal pads indicated by broken lines.

Dinosaurs from the Lourinhã formation

Since 1863, the Lourinhã Formation has provided abundant well-preserved skeletal remains of a diverse dinosaur fauna. Table 1 summarizes the Upper Jurassic dinosaurs described from Portugal and additional information about the type specimen and locality is provided when it concerns a type specimen described from Portugal. The exposures around Porto Dinheiro (Lourinhã Municipality) have provided the majority of the dinosaur finds from the Upper Jurassic of Portugal, and the locality is the stratotype for *Dinheirosaurus lourinhanensis* and *Trimucrodon cuneatus*, and the mammal *Pinheirodon*. The surrounding areas have in addition provided remains of thyreophorans, *Dacentrurus*, aff. ornithopods, *Dryosaurus* and *Phyllodon*, several genera of large and small theropods including *Lourinhanosaurus*, and at least four different sauropods (Table 1).

Discussion – tracks and trackmakers

Tracks and trackways are biogenic sediment structures, dependent on different taphonomical processes than bodyfossils in order to be preserved, and are commonly found in sedimentary settings where few or no body fossils are preserved. The Lourinhã Formation is a rare example where both tracks and skeletal remains are found well preserved and can supplement each other in the faunal descriptions. The possible track makers can be tentatively identified considering the well-preserved morphology and dimensions of the tracks, and the estimated body sizes in the list of Upper Jurassic dinosaurs from Portugal (Table 1). The suggested trackmaker for the small theropod tracks 30–40 cm long is *Lourinhanosaurus antunesi*, which is a small- to medium-sized tetanuran theropod with an estimated total body length of 4–6 m (Table 1). Two possible trackmakers exist for the medium-sized theropod tracks with lengths of 52–54 cm. A *Ceratosaurus* sp. with an estimated body length of 5–7 m and the allosaur *Allosaurus europaeus* is estimated to be 6–8 m long (Table 1). The giant-sized theropod track with a total length of 79 cm is tentatively referred to *Torvosaurus* which, with a body length of 8–12 m, was the largest theropod in the world during the Upper Jurassic. An almost complete *Torvosaurus* maxilla, 63 cm long, from an animal with an estimated skull length of 158 cm was found in the Lourinhã Formation in 2003 (Mateus *et al.* 2006), and limb bones from a similar sized animal has previously been found in the area (Mateus *et al.* 2006). Following the formula suggested by Alexander (1976), that the hip height of a dinosaur can be estimated as four times the length of the foot, the animal responsible for the large track stood 3.5 m tall at the hips. A theropod track with an estimated total length of 82 cm found in the Upper Jurassic of Asturias, Northern Spain (García-Ramos *et al.* 2006) is morphologically different, in that the digit impressions is longer and more slender than in the Portuguese specimen. This suggests that more than one type of giant theropod existed in Europe during the latest Jurassic. The Upper Jurassic theropod tracks from Portugal and Spain are the largest Jurassic theropod tracks in the world, and only the tyrannosaur track *Tyrannosauripus pilmorei* from the Maastrichtian of New Mexico is larger, being 86 cm long and 64 cm wide (Lockley & Hunt 1994). However, if the additional length of the metatarsus impression is included in the specimen from Porto Dinheiro, then the total length of the track is 96 cm. When including the length of the metatarsus, the large theropod track from Asturias is 103 cm long (García-Ramos pers comm. 2009).

The sauropod track lengths range from 58–105 cm, and are dominated by tracks of almost 1 m in length. Several sauropod trackmakers are known from the Lourinhã Formation (Table 1), and the diplodocid *Dinheirosaurus lourinhanensis* with an estimated total body length in excess of 20 m was excavated within 500 m from the track locality, making it a possible trackmaker.

Two stegosaurs are known in the Upper Jurassic of Portugal: *Dacentrurus armatus* and *Stegosaurus* cf. *ungulatus* (Escaso *et al.* 2007). The knowledge about *Dacentrurus* autopodium morphology is not sufficient to be able to infer differences between *Dacentrurus* and *Stegosaurus* tracks. As far as the trackmaker is concerned, the stegosaur tracks of Porto Dinheiro are attributed to Stegosauridae indet.

No tracks from ornithopod dinosaurs have so far been found at the Porto Dinheiro locality, but tracks and trackways from ornithopods are known from the nearby cliff sections of Porto das Barcas (Antunes & Mateus 2003) and Vale Frades (Mateus & Milàn 2008), and it is likely that ornithopod tracks will turn up during future research and excavations in the area around Porto Dinheiro.

The polygonal texture of the skin impressions is similar to that described in sauropod tracks from the Morison Formation in Utah and Wyoming (Lockley & Hunt 1995; Platt & Hasiotis 2006), the Upper Jurassic of Asturias, Spain (García-Ramos *et al.* 2002, 2006) and the Cretaceous Haman Formation, Korea (Yang *et al.* 2003; Lockley 2007), where the skin impressions initially were misidentified as the marine trace fossil *Paleodictyon* (Yang *et al.* 2003).

Table 1. The Upper Jurassic dinosaur fauna of Portugal, with a tentative estimation of the body length range.

Species	Taxonomy	Type specimen (code, horizon, age and locality)	Size range estimation (m)	Main references
Ceratosaurus sp. Madsen & Welles 2000	Theropoda: Ceratosauria		5–7	Mateus *et al.* 2006
Torvosaurus cf. *tanneri* Galton & Jensen 1979	Theropoda: Tetanurae		8–12	Mateus *et al.* 2006
Lourinhanosaurus antunesi Mateus 1998	Theropoda: Tetanurae: Megalosauridae	ML317, Lourinhã Fm. Kimmerigdian, Peralta (Lourinhã)	4–6	Mateus 1998
Allosaurus europaeus Mateus *et al.* 2006	Theropoda: Tetanurae: Allosauridae	ML415, Lourinhã Fm. Kimmerigdian, Vale Frades	6–8	Mateus *et al.* 2006
Aff. *Paronychodon* sp.	Theropoda: Tetanurae: Coelurosauria		1–2	Rauhut 2000
cf. *Archaeopteryx* sp.	Theropoda: Tetanurae: Coelurosauria		<1	Rauhut 2000
cf. *Compsognathus* sp.	Theropoda: Tetanurae: Coelurosauria		<1	Zinke 1998
Aviatyrannis jurassica Rauhut 2003	Theropoda: Tetanurae: Coelurosauria	MG (ex-IPFUB Gui Th 1), Camadas de Alcobaça, Kimmeridgian, Guimarota	<l2	Rauhut 2003
Apatosaurus sp.	Sauropoda: Diplodocidae		>20	Mateus 2005
Dinheirosaurus lourinhanensis Bonaparte & Mateus 1999	Sauropoda: Diplodocidae	ML414, Lourinhã Fm., Kimmeridgian, Porto Dinheiro	>20	Bonaparte & Mateus 1999
Lourinhasaurus alenquerensis Lapparent & Zbyszewski 1957	Sauropoda: Macronaria	MG-4956 and others, Arranhó Unit, Late Kimmeridgian/Lower Tithonian, Moinho do Carmo	>15	Lapparent & Zbyszewski 1957; Dantas *et al.* 1998
Lusotitan atalaiensis Lapparent & Zbyszewski 1957	Sauropoda: Macronaria: Brachiosauridae	MG4798 and others, Lourinhã Fm. Kimmerigdian, Peralta (Lourinhã)	>15	Lapparent & Zbyszewski 1957; Antunes & Mateus 2003
Dracopelta zbyszewskii Galton 1980	Thyreophora: Ankylosauria	MG5787, Freixial Fm., Tithonian, Praia do Sul	4–6	Galton 1980; Pereda-Suberbiola *et al.* 2005
Dacentrurus armatus Owen, 1875	Thyreophora: Stegosauridae		5–7	Lapparent & Zbyszewski 1957
Stegosaurus cf. *ungulatus* Marsh, 1879	Thyreophora: Stegosauridae		5–7	Escaso *et al.* 2007
Alocodon kuehnei Thulborn 1973	Ornithopoda: 'Fabrosauridae'	MG (ex-IPFUB P X 1), Cabaços Fm., Oxfordian, Pedrógão	<2	Thulborn 1973; Age by Azerêdo *et al.* 2002
Trimucrodon cuneatus Thulborn 1973	Ornithopoda: 'Fabrosauridae'	MG (ex-IPFUB), Lourinhã Fm., Kimmeridgian, Porto Dinheiro	<2	Thulborn 1973
Aff. *Dryosaurus* sp.	Ornithopoda: Dryosauridae		<2	Mateus 2007
Hypsilophodon sp.	Ornithopoda: Hypsilophodontidae		1–2	Thulborn 1973
Phyllodon henkeli Thulborn 1973	Ornithopoda: Hypsilophodontidae	MG (ex-IPFUB), Alcobaça Beds, Kimmeridgian, Guimarota	<1	Rauhut 2001; Thulborn 1973
Draconyx loureiroi Mateus & Antunes 2001	Ornithopoda: Camptosauridae	ML434, Lourinhã Fm. Kimmerigdian, Vale Frades	5–7	Mateus & Antunes 2001

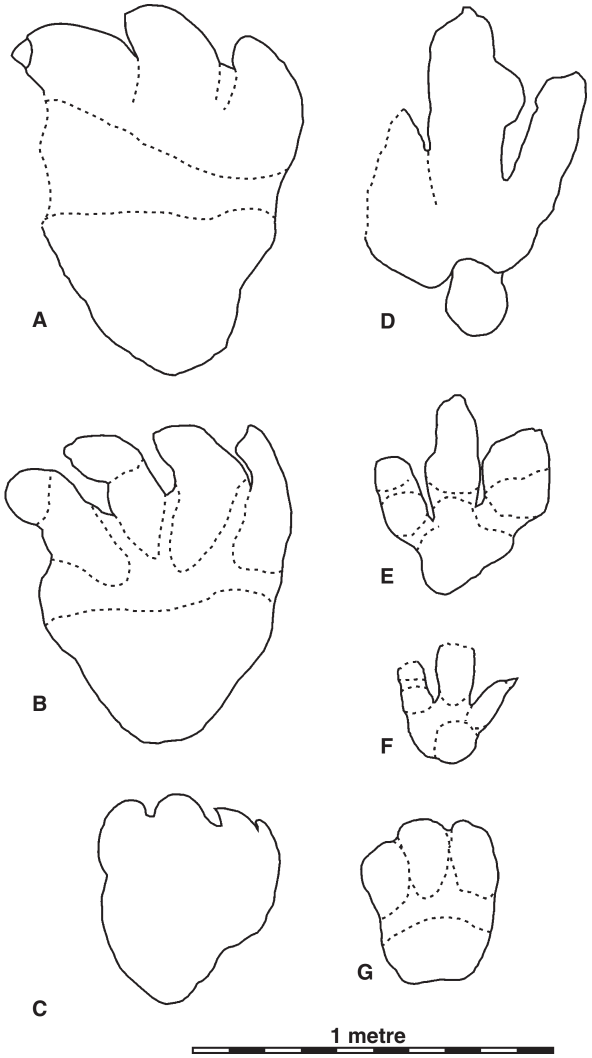

Fig. 11. Comparative silhouettes of the sizes and types of tracks from Porto Dinheiro, attributed to sauropods A–C theropods D–F, and stegosaur G. All tracks drawn to same scale.

The dinosaur ichnofauna described from Porto Dinheiro comprises sauropod tracks ranging in length from 58 to 105 cm, a stegosaur track 42 cm long and theropod tracks from 30 to 79 cm in length (Fig. 11). When the ichnofauna from Porto Dinheiro are combined with the trackfauna previously described from the Lourinhã Formation (Antunes & Mateus 2003; Milàn *et al.* 2005; Mateus & Milàn 2008), the total known dinosaur ichnofauna comprises sauropods, ornithopods, theropods and thyreophorans. All the tracks except for the stegosaur tracks occur in sizes from medium to gigantic. Contemporaneous coastal and deltaic deposits of Asturias, northern Spain, likewise contains diverse dinosaur ichnofaunas (García-Ramos *et al.* 2006), but in addition to the dinosaur tracks, they also contain tracks from turtles, crocodiles and pterosaus (Avanzini *et al.* 2005, 2007; García-Ramos *et al.* 2006; Lockley *et al.* 2008). The Middle Jurassic Cleveland Basin of the Yorkshire Coast of England contains a similar diverse trackfauna including tracks from dinosaurs, turtles and crocodiles (Whyte *et al.* 2007). Abundant swimming traces attributed to dinosaurs, crocodilians, turtles and fish has in addition been described from the Yorkshire Coast. In contrast to the Upper Jurassic track record of Lourinhã, Portugal and Asturias in Spain, the only skeletal remains found associated with the rich trackfauna from the Middle Jurassic Yorkshire Coast of England, is a single partial vertebra (Romano & Whyte 2003). No swimming traces or tracks from either crocodiles or turtles have so far been found in the Lourinhã Formation, but teeth and skeletal remains of both are commonly encountered (Mateus 2006), and it is expected that crocodile, pterosaur and turtle tracks will turn up during future ichnological research in the area.

This diversity of tracks in the Lourinhã Formation reflects a diverse dinosaur fauna, which is also represented by abundant well-preserved skeletal remains of dinosaurs and other vertebrates (Antunes & Mateus 2003; Mateus 2006). This makes the Lourinhã Formation an important taphonomic window into the Upper Jurassic continental ecosystem.

Conclusion

In summary, we conclude that:

1. The Lourinhã Formation (Kimmeridgian/Tithonian) contains a rich and diverse dinosaur ichno- and somatofossil fauna, and is important for understanding of the Upper Jurassic continental ecosystem and faunal assemblages.
2. The Porto Dinheiro locality (Lourinhã Formation, Upper Kimmeridgian/Lower Tithonian) shows a diverse dinosaurian ichnofauna comprising tracks from stegosaurs, medium- and large-sized theropods, and medium- to large-sized sauropods.
3. New sauropod tracks provide new information about soft tissue anatomy of the sauropod feet in that one track has preserved the perfect cast of the ungual insertion into the soft tissue of the digit. Other tracks have preserved evidence of the palmar surface of the foot being divided into distinct pads, and impressions of hexagonal skin pattern, with skin scales of 2–3 cm, adding to the scarce reports of sauropod autopodia skin impressions, and in great detail showing the distribution and arrangement of the skin tubercles.

4. A new large theropod track, tentatively attributed to *Torvosaurus*, is among the largest theropod track known from the Upper Jurassic. For this theropod track 79 cm (possibly 96 cm) in length, the trackmaker would have had a hip height around 3.5 m.
5. Despite the scarce global record, new stegosaur pes tracks are reported here.

Acknowledgements. – The research of JM was supported by the Danish Natural Science Research Council, and OM by fellowship SFRH/BPD/25291/2005 of the Portuguese 'Fundação para a Ciência e Tecnologia'. Finn Surlyk, Department of Geography and Geology, University of Copenhagen kindly read and made useful suggestions to an early draught of the manuscript. Dennis Ry Hansen, Department of Geography and Geology, University of Copenhagen was of great assistance during the hunt for tracks. We thank the Municipality of Lourinhã and Horácio Mateus for the collecting efforts. Two anonymous reviewers provided helpful comments and suggestions to the manuscript.

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