CIÊNCIAS DA TERRA
EARTH SCIENCES JOURNAL

Stegosaur tracks from the Upper Jurassic of Portugal: new occurrences and perspectives

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Journal webpage:
http://cienciasdaterra.novaidfct.pt/

ISSN: 0254 - 055X
eISSN: 2183 - 4431

Abstract

The record of Late Jurassic stegosaur tracks from the Lourinhã Formation (Kimmeridgian-Tithonian) is here revised. Thirty-eight dinosaur tracks, preserved as natural infill casts, are here reported, and thirty-two of them are attributed to the ichnogenus *Deltapodus*. Four of those present impressions of skin, with polygonal scales and random pattern. *Deltapodus* is the most common ichnogenus in the track record of the Lourinhã Formation. The sizes and shape suggest one single dacentrurine trackmaker, which could be *Miragaia longicollum*, also common in the same horizons.

Keywords: Stegosaur tracks, Lourinhã Formation, *Deltapodus*, skin impressions, Upper Jurassic

Resumo

O registo fossilífero de pegadas de estegossauros do Jurássico Superior da Formação da Lourinhã (Kimmeridgiano-Tithoniano) é aqui revisitado. Trinta e oito pegadas de dinossauros, preservadas como moldes naturais de preenchimento, são aqui apresentadas e trinta e dos delas são atribuídas ao icnogénero *Deltapodus*. Quatro delas apresentam impressões de pele, com escamas poligonais e um padrão aleatório. *Deltapodus* é o icnogénero mais comum no registo de pegadas da Formação da Lourinhã. As dimensões e morfologia sugerem um único taxon produtor de pegadas, que poderá ser *Miragaia longicollum*, também comum nos mesmos horizontes.

Palavras chave: pegadas de estegossauros, Formação da Lourinhã, *Deltapodus*, impressões de pele, Jurássico Superior

1. Introduction

1.1 Stegosaur Tracks

The research of the fossilized remains of stegosaur footprints is relatively recent, with the earliest publication from 1994 by Whyte & Romano, at the time misinterpreting the tracks as made by a sauropod. Since then, more stegosaur tracks. have been reported from Europe, North America, Asia, and Africa with two valid ichnogenera currently described (Tab. 1), *Deltapodus* Whyte & Romano, 1994 and *Stegopodus* Lockley & Hunt, 1998, even though it remains unsure if the differences observed between them represent a diversity in trackmaker foot morphology or if they are due to differential preservation (Lockley *et al.*, 2017).

Stegopodus czerkasi Lockley & Hunt, 1998 is known from the Morrison Formation in Utah (Lockley & Hunt, 1998; Gierliński & Sabath, 2008), is considered as the only valid *Stegopodus* ichnospecies. More tracks referred to *Stegopodus* isp. have been reported from the Bagå Formation, in Denmark (Milàn, 2011), the Tereñes Formation, in Spain (Piñuela *et al.,* 2002; Gierliński & Sabath, 2008); the Morrison Formation in Utah (Bakker, 1996; Gierliński & Sabath, 2008) and at Dinosaur Ridge, in Colorado (Mossbrucker *et al.,* 2008; Lockley *et al.*, 2015), and the Isli Formation, near Imilchi area in Morocco (Gierliński *et al.*, 2009). However, the attribution of the tracks from Spain remains uncertain: they were previously attributed to ornithopod trackmakers (Piñuela *et al.,* 2002), later reinterpreted as stegosaur-made (Gierliński & Sabath, 2008), before the original authors went back to the ornithopod hypothesis (Piñuela e*t al.,* 2016). An undetermined footprint from the Holly Cross Mountains, in Poland, might be referred as well to *Stegopodus* and would suggest a bipedal trackmaker as previously implied (Bakker, 1996; Gierliński & Sabath, 2002; Lockley *et al.*, 2017).

Ichnospecies	Location	Age	Reference
Indertermined ichnospecies (*Stegopodus*)	Holy Cross Mountains	Oxfordian	Gierliński & Sabath, 2002
Stegopodus czerkasi	Morrison Fm.	Tithonian	Lockley & Hunt, 1998 Gierliński & Sabath, 2008
Stegopodus isp.	Bagå Fm.	Bajocian-Bathonian	Milàn, 2011
	Morrison Fm.	Tithonian	Bakker, 1996 Gierliński & Sabath, 2008 Mossbrucker *et al.*, 2008 Lockley *et al.*, 2015
	Isli Fm.	Bathonian	Gierliński *et al.*, 2009
Deltapodus brodericki	Saltwick Fm.	Aalenian	Whyte & Romano, 1994, 2001
	Lourinhã Fm.	Kimmeridgian	Mateus & Milàn, 2010 Mateus *et al.*, 2011
	Morrison Fm.	Tithonian	Milán & Chiappe, 2009
	Villar del Arzobispo Fm.	Tithonian-Berriasian	Herrero Gascón & Pérez Lorente, 2016
	Camarillas Fm.	Barremian	Herrero Gascón & Pérez Lorente, 2016
	Artoles Fm.	Barremian	Herrero Gascón & Pérez Lorente, 2016
Deltapodus ibericus	Villar del Arzobispo Fm.	Tithonian-Berriasian	Cobos *et al.*, 2010
Deltapodus curriei	Qingshuihee – Hutubihe Fm. (Tugulu Group)	Early Cretaceous	Xing *et al.*, 2013
Deltapodus isp.	Lealt Shale Fm.	Bajocian-Bathonian	dePolo *et al.*, 2020
	Lajas Fm.	Bathonian-Callovian	Pazos *et al.*, 2019
	Iouaridène Fm.	Oxfordian-Kimmeridgian	Belvedere & Mietto, 2010
	Tereñes and Lastres Fm.	Kimmeridgian	Lockley *et al.*, 2008 Piñuela *et al.*, 2014
	Morrison Fm.	Tithonian	Lockley & Hunt, 1995 Lockley *et al.*, 2017
	Villar del Arzobispo Fm.	Tithonian-Berriasian	Mampel *et al.*, 2010 Alcalá *et al.*, 2012 Herrero Gascón & Pérez Lorente, 2013
	Magaña Fm.	Tithonian-Berriasian	Pascual-Arribas & Hernandez-Medrano, 2016
	Huérteles Fm.	Berriasian	Pascual *et al.*, 2012
	Tirgan Fm.	Aptian	Abbassi *et al.*, 2018
Deltapodus isp. (titanosauriform ?)	Kem Kem Beds	Cenomanian	Ibrahim *et al.*, 2014

Tab. 1. -Ichnospecies attributed to stegosaurian trackmakers.

Regarding *Deltapodus*, eight footprints from Saltwick Formation, in Yorkshire, were attributed to a sauropod trackmaker, despite noticing some peculiar features: (1) pes print more triangular in outline; (2) pes prints are mesaxonic; (3) presence of three blunt claws on the pes (whereas five were expected for sauropods); (4) pes digit impressions occur along the anterior margin; (5) pollex was inwardly directed (Whyte & Romano, 1994). The authors put forth that these may alternatively be stegosaur or prosauropod tracks, naming the new ichnogenus and ichnospecies *Deltapodus brodricki* Whyte & Romano, 1994.

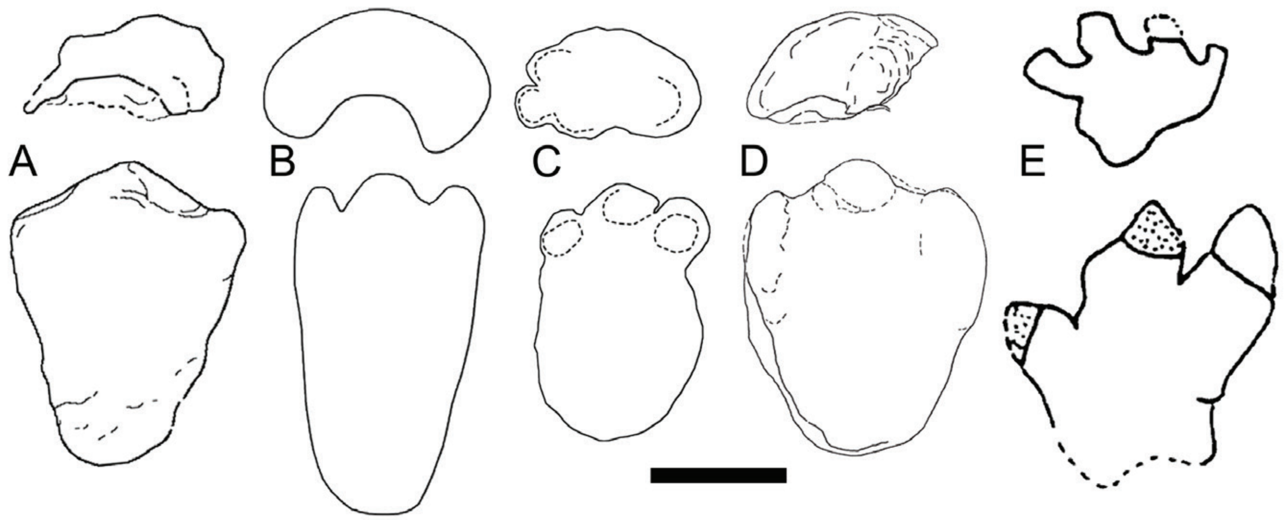

Fig. 1. -Holotype of stegosaur tracks. A - *Deltapodus brodricki* F00768 (from Whyte & Romano, 1994). B - *D. ibericus* 1CA23 (from Cobos *et al.*, 2010). C - *D. curriei* MGCM.SA2 (from Xing *et al.,* 2013). D - *Deltapodus* isp. MNS 2009/64 (from Pascual *et al.*, 2012). E - *Stegopodus czerkasi* (from Lockley & Hunt, 1998). Scale bar is 20cm for A-C and E, and 5cm for D.

However, during the description and reinterpretation of these unusual tracks, the authors reviewed their candidate for trackmakers using three approaches: skeletal/anatomical, ichnological and stratigraphical, finally determining that the *Deltapodus* trackmaker was probably a stegosaur (Whyte & Romano, 2001). While some authors propose this genus as a neosauropodian (Ibrahim *et al.*, 2014) or ankylosaurian (Gierliński & Sabath, 2008), the consensus nowadays is of a stegosaurian trackmaker for *Deltapodus*, because of the tridactyl configuration of the stegosaur pes (Pascual *et al.,* 2012; Pascual-Arribas & Hernández-Medrano, 2016, Lockley *et al.*, 2017). Tracks referred to *Deltapodus* isp. were recovered from the Iouaridène Formation, in Morocco (Belvedere & Mietto, 2010), the Morrison Formation, in Utah (Lockley & Hunt, 1995; Lockley *et al.*, 2017), and the Kem Kem beds, in Morocco (Ibrahim *et al.*, 2014). Spain has provided a vast Deltapodus track record, with reports from Tereñes and Lastres Formations (Lockley *et al.*, 2008; Piñuela *et al.,* 2014), the Villar del Arzobispo Formation (Mampel *et al.,* 2010; Herrero Gascón & Pérez Lorente, 2013), the Magaña Formation (Pascual-Arribas & Hernandez-Medrano, 2016), and the Huérteles Formation (Pascual *et al.*, 2012). There are also reports of the ichnogenus from the Middle Jurassic Lealt Shale Formation in Scotland (dePolo *et al.,* 2020), from the Middle Jurassic Lajas Formation in Argentina (Pazos *et al.,* 2019), and from the Aptian Tirgan Formation in Iran (Abbassi *et al.,* 2018).

Since its first report from the Saltwick Formation, *D. brodricki* has been referred to tracks from the Lourinhã Formation, in Portugal (Mateus & Milàn, 2010; Mateus *et al.*, 2011), the Morrison Formation, in Utah (Milàn & Chiappe, 2009), and the Villar del Arzobispo Formation, the Camarillas Formation, and the Artoles Formation, in Spain (Herrero Gascón & Pérez Lorente, 2017). There are two more *Deltapodus* ichnospecies currently described: *D. ibericus* Cobos *et al.*, 2010 from the Villar del Arzobispo Formation (Cobos *et al.*, 2010), and *D. curriei* Xing *et al.*, 2013 from the Qingshuihee – Hutubihe Formations (Tugulu Group), in China (Xing *et al.*, 2013).

Some tracks recovered from the Saltwick Formation suggest that stegosaurs were able to swim (Romano & Whyte, 2015). These were found near to *Deltapodus* tracks and had some features relatively compatible with *Deltapodus*. The authors did not find evidence of swimming manus prints, which is consistent with the distinctly shorter forelimbs of stegosaurs. These tracks have been assigned to *Characichnos* isp. Whyte & Romano, 2001b, ichnogenus for dinosaur swimming prints.

The morphology of the *Deltapodus*, manus is similar to titanosauriforms tracks from the Late Jurassic-Early Cretaceous, sharing a kidney-shaped morphology lacking claw marks (Cobos *et al.,* 2010; Castanera *et al.*, 2016; Pascual-Arribas & Hernández-Medrano, 2016): it is entaxonic, with the inner digits more developed than the outer ones) wider than long, has an irregular subcircular outline, but mostly shows a broadly crescentic and forwardly convex shape, its anterior margin can be more angular, and there is no clear digit impression (Whyte & Romano, 1994; Cobos *et al.*; 2010; Pascual *et al.*, 2012; Xing *et al.*, 2013; Pascual-Arribas & Hernández-Medrano, 2016). Although the record of stegosaur manus prints is scarce (Pascual *et al.*, 2012), it is possible to infer according to the fossil remains that these were functionally tetradactyl, with digits arranged in a semicircle (Senter, 2010). Regarding the morphology of *Deltapodus* pes (Fig. 1), they are tridactyl, elongated, mesaxonic with the middle digit being the more developed one, the outline varies from subtriangular to subcircular, with the outer lateral margins varying from nearly straight to convex, while the medial vary from nearly straight to concave (Whyte & Romano, 1994). The morphology of the digits suggests the existence of terminal hoofs or semi-claws (Whyte & Romano, 2001). A recent analysis reports more *Deltapodus* casts from the Galve sub-basin (Maestrazgo basin) in Spain, focusing on marks left by the “hooves”, skin scales and proposed models on autopodium characters and limb movements (Herrero Gascón & Pérez-Lorente, 2017). The authors observed a network of polygonal tuberculate scales not overlapping with no ordered variation of scale size and determined that the “hooves” leave three types of marks: (1) ellipsoidal; (2) rounded tubular projections, either straight or curved; (3) slightly tubular acuminate ones (Herrero Gascón & Pérez Lorente, 2017). The authors observed anterior and posterior depressions in foot marks and proposed it must be associated with two separate calluses, with metatarsal inclined and phalanges hardly able to move relative to each other’s. The limb movement model presented follows the motion sequence described in Thulborn & Wade (1989), and it is similar to the ones proposed by Romano & Whyte (2012) for sauropods.

In comparison, *Stegopodus* manus, is wider than long and entaxonic, as *Deltapodus*, but has well-defined four digits and a subcircular outline (Lockley & Hunt, 1998; Pascual *et al*., 2012, Lockley *et al*., 2017). The pes of *Stegopodus* is asymmetrical and only slightly longer than wide, tridactyl, and has more individualized blunt short digits which barely project beyond the hypex (Whyte & Romano, 2001; Gierliński & Sabath, 2008). The pes tracks referred to *Stegopodus* have been interpreted as evidence that stegosaurs could have been bipedal or semi-bipedal (Bakker, 1996; Gierliński & Sabath, 2008; Gierliński *et al*., 2009). However, the ichnogenus remains problematic (Lockley *et al.,* 2017), as since some tracks used as evidence for this bipedal hypothesis have been reattributed to ornithopod trackmakers (Piñuela *et al*., 2016).

When compared with the tracks and anatomy from different dinosaur trackmakers, it appears that *Deltapodus* cannot match tracks from ankylosaurid and ceratopsian trackmakers in morphology (Whyte & Romano, 2001). Gierliński & Sabath (2008) postulated that *Deltapodus* could be ankylosaurian, comparing it with *Tetrapodosaurus* Sternberg, 1932, an ichnogenus traditionally attributed to ankylosaurid trackmakers. However, Pascual *et al.* (2012) pointed differences between the two morphologies, and their remarks on the stegosaur and ankylosaur paleobiogeographic distributions are herein agreed with. Ibrahim et al. (2014) attributed manus prints to *Deltapodus* but attributed it to a neosauropod trackmaker (possibly titanosaur) referencing Wilson (2005), despite Wilson (2005) never mentioning *Deltapodus.* However, titanosauriform manus tracks are similar to *Deltapodus* (Cobos *et al*., 2010; Castanera *et al.,* 2016; Pascual-Arribas & Hernández-Medrano, 2016) and this case could a misinterpretation. As such, the occurrence of *Deltapodus* in the Late Cretaceous is here considered doubtful.

1.2 Stegosaur tracks and bones in Portugal

The first known occurrence of a stegosaur track in Portugal was reported by Mateus & Milàn (2008) of a single footprint classified as *D. brodricki*, and a second one in 2010 by the same authors. A later study focusing on stegosaur tracks described nine new tracks from the Lourinhã Formation, all attributed to *D. brodricki* (Mateus *et al*., 2011). The authors identified nine pes and two manus (included in this study) from different localities, some of them being the biggest *Deltapodus* footprints known. Tracks and trackway parameters are slightly different from *D. ibericus*, but general dimensions match appropriately. Three morphotypes, which could represent different ichnospecies, were identified: (1) straight sides converging to a rounded heel, with triangular shape; (2) relatively parallel sides, terminating in a drop-like shape; (3) and sub-parallel sides, with an angular heel outline (Mateus *et al.,* 2011)

The authors agreed in the attribution of *Deltapodus* trackmakers to stegosaurs, considering: (1) the articulated feet of *Kentrosaurus* and *Stegosaurus* match the digit characteristics of the footprints, following the pedal phalangeal formula 0-2-2-2-0 (Galton & Upchurch, 2004); (2) and the distribution of skeletal remains of stegosaurs is consistent with the widespread occurrence of *Deltapodus*. Furthermore, the attribution of the trackmaker to ankylosaurs is unlikely, since the only tridactyl known ankylosaur is from the Upper Cretaceous and remains from Middle and Upper Jurassic of Europe do not retain preserved anatomy of the feet.

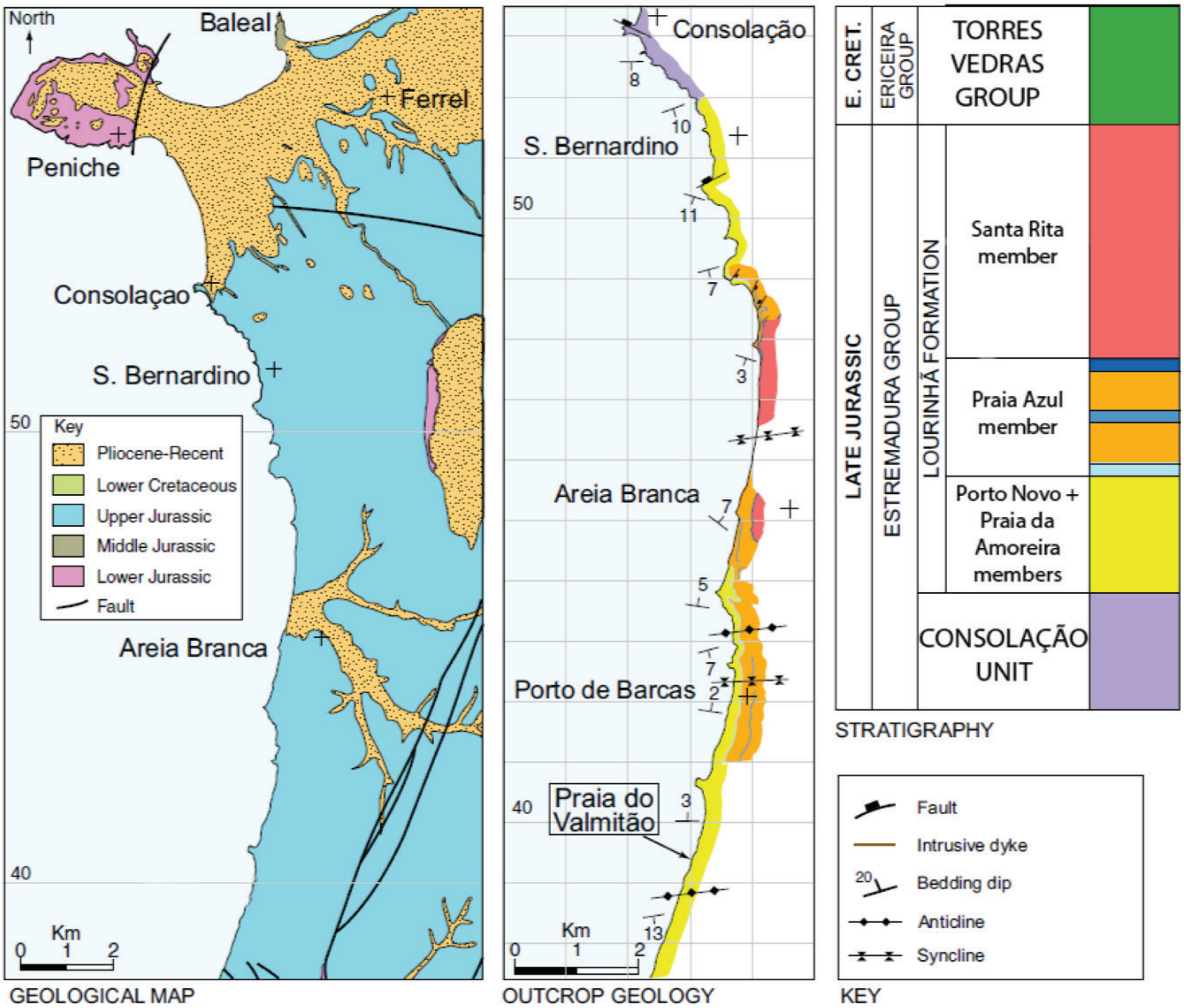

Fig. 2. -Geological map of the onshore part of the Consolação sub-basin south of Peniche, with the north-south section (modified from Gowland *et al.*, 2018) and the corresponding lithostratigraphic framework (based on Mateus *et al.*, 2017).

Fossilized skeletal remains of three stegosaur species have been found in Portugal, all from Upper Jurassic deposits of the Lusitanian Basin: possible *Dacentrurus (=Omosaurus) armatus* (Lapparent & Zbyszewski, 1957; Galton, 1991; Escaso *et al.*, 2007b), *Stegosaurus* cf. *ungulatus* (Escaso et al., 2007a) and *Miragaia longicollum* (Mateus *et al.,* 2009; Costa & Mateus, 2019).

Dacentrurus armatus (Owen, 1875) was the first representative stegosaur described and named. It was initially named *Omosaurus armatus* Owen, 1975, but was later renamed since the genus *Omosaurus* was preoccupied (Lucas, 1902). First found in the Kimmeridgian of England, several incomplete specimens have since been referred to the taxon in the Kimmeridgian-Tithonian of Portugal (Lapparent & Zbyszewski, 1957; Escaso *et al.*, 2007b; Galton, 1991; Maidment *et al.,* 2008).

The genus *Stegosaurus* Marsh, 1877 has been for a long time attributed only to specimens found in the Late Jurassic Morrison Formation of North America, until a specimen from the Kimmeridgian-Tithonian of Portugal, at the Casal Novo locality in Batalha, was described by Escaso *et al.* (2007a). The specimen presents several features which support its referral to the genus *Stegosaurus*, particularly relating it to *S. ungulatus*, notably a posterior edge of neural arch sloping posteriorly on the anterior cervical vertebrae and bifurcated apices of the anterior caudal neural arches (Escaso *et al.*, 2007a). This specimen supports the hypothesis of faunal exchange between North America and Iberia in the Late Jurassic (Escaso *et al.*, 2007a; Mateus, 2006)

Miragaia longicollum Mateus *et al.*, 2009 is one of the latest stegosaur species described, known from the Kimmeridgian-Tithonian of the Lourinhã Formation. The holotype consists of an anterior partial skeleton, with partial cranium, cervical and dorsal vertebrae, both anterior limbs, partial autopods and cervical dermal plates (Mateus *et al.*, 2009). It was classified with *D. armatus* in Dacenturinae (Mateus *et al.*, 2009), the sister-group to the clade Stegosaurinae. The most notable feature of *M. longicollum* is the number of cervical vertebrae (17), higher than any other known stegosaur, giving it a 'sauropod mimic' long-neck. This elongation could be the result of cervicalization of the dorsal vertebrae and the elongation of individual cervical vertebrae (Mateus *et al.*, 2009).

1.3 The Lourinhã Formation

The Lourinhã Fm. (Fig. 2) is named after the local town of Lourinhã, 70 km North of Lisbon. It is the most adopted term for the clastic continental succession sediments throughout the Lusitanian Basin, ranging in thickness from 200m to 1,100m (Leinfelder & Wilson, 1989; Wilson *et al.*, 1989, Taylor *et al.,* 2014). This variation according the paleogeographic position can be explained by the transitionnal/regressive boundaries between the members of the Lourinhã Fm. (Mateus *et al.*, 2017). Always considered as Late Jurassic in age, recent studies confirm its age range from Late Kimmeridgian to Late Tithonian, between the Consolação Unit and the Porto da Calada Formation (Taylor *et al.,* 2014; Mateus *et al.*, 2017). The base of the laterally extensive Lourinhã Fm. is traditionnaly taken as the first significant and sustained development of continental deposits, above either the shallow marine to estuarine sandstones of the Sobral Fm., the oolitic limestone of the Amaral Fm., the shelfal corbonates of the Consulação Unit/Alcobaça Fm., or the shelf to deepwater clastics of the Abadia Fm. (Taylor *et al.*, 2014). Its dominant continental deposits are sandy channel-fills and contemporaneous muddy floodplain deposits (Martinius & Gowland, 2011; Taylor *et al.*, 2014; Gowland *et al.,* 2018). The sedimentology of the Lourinhã Fm. suggests a semi-arid climate, in mean temperature range from 16°C to 19°C, with seasonal rainfall lower than 500 mm –wetter conditions than in the Morrison Fm. (Mateus *et al.*, 2017). With the Alcobaça Formation, it is the unit with more vertebrate remains in Portugal and even in Europe, and studies highlight shared fauna with the Morrison Formation, as an ephemeral land bridge allowed faunal exchange between North America and Iberia in the Late Jurassic (Mateus, 2006; Escaso *et al.*, 2007a; Mateus *et al.*, 2017).

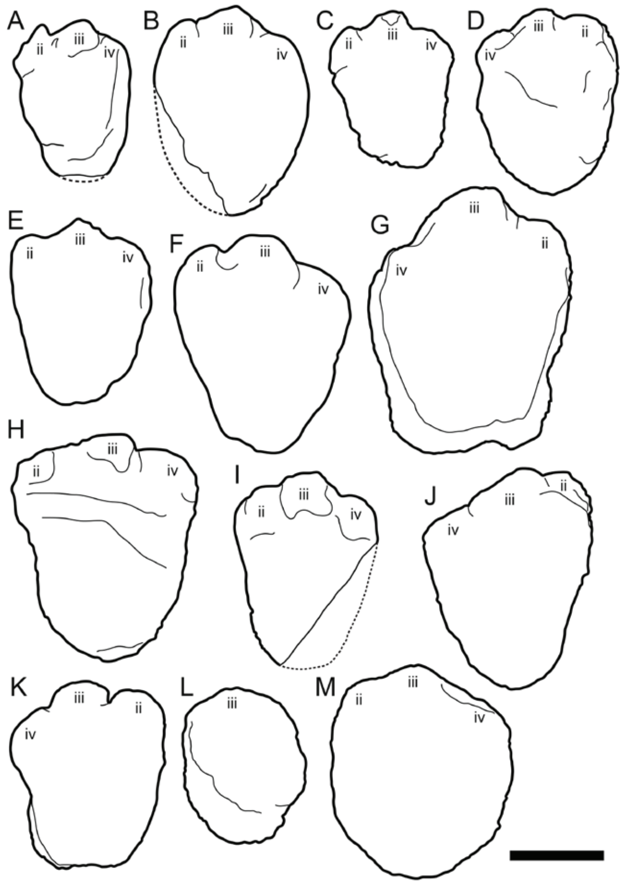

Fig. 3. -*Deltapodus* isp. pes track outlines. A - ML1334. B - ML1339. C - ML1342. D - ML1343. E - ML1344. F - ML1345.G - ML1346. H - ML1347. I - ML1348. J - ML1349. K - ML1350. L - ML2170. M - ML2171. The numbers correspond to the digits. Scale bar is 20cm.

2. Material & Methods

In this study, 27 new occurrences of stegosaur tracks from the Late Jurassic of the Lourinhã Formation are presented, as well as the aforementioned 11 tracks studied in previous papers (Mateus & Milàn, 2008; 2010; Mateus *et al.,* 2011), in a total of 38 tracks (30 pes and 8 manus). ML1344, ML1346 and ML1351, previously studied in Mateus *et al.,* 2011, were not located in the collections of Museu da Lourinhã at the time of writing, so confirmation of the observations and further description by the authors could not be done in this study. The tracks in this study are all preserved as natural casts (convex hyporeliefs) printed over mud, then filled by sand and silt, resulting in siltstone with fine and detailed mud-sand interface which allowed the preservation of skin scale impressions.

All the tracks were collected in rocks from the Lourinhã Formation, from different localities, never associated together in trackways (except for ML1342, associated with an ornithopod footprint

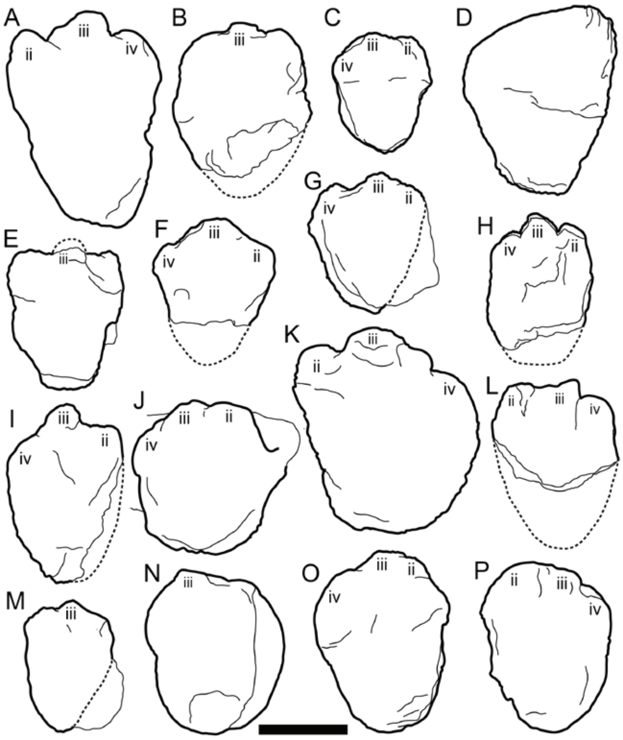

Fig. 4. -*Deltapodus* isp. pes track outlines. A - ML2172. B - ML2173. C - ML2174. D - ML2175. E - ML2176. F - ML2177. G - ML2181. H - ML2207. I - ML2231. J - ML2232. K - ML2234. L - ML2235. M - ML2237. N - ML2238. O - ML2239. P - ML2240. The numbers correspond to the digits. Scale bar is 20cm.

(Mateus & Milàn, 2008). The oldest occurrence is from Vale de Pombas, Amoreira-Porto Novo Member, Late Kimmeridgian, while the uppermost occurrence is from Porto das Barcas, top of Praia Azul Member, base of Tithonian.

Despite the different levels of preservation, comparison has been possible because general outline was mainly analyzed for each track, using broad categories to distinguish them (Castanera *et al.*, 2016). Three general outlines classifications are proposed for pes prints according to their medial and lateral margins and resulting shape: (1) the *circular* outline exhibits round margins; (2) the *rectangular* outline exhibits sides straight and parallel or subparallel (both margin lines seem to converge in one point far from the heel); (3) the *subtriangular* outline is defined by margin lines that seem to converge in one point near the heel area. For the manus, three general outlines in plantar view are distinguishable: (1) *horseshoe-shaped*, with a deep arch inward, towards the posterior side; (2) *arcuate* is wider than long, with a slight curve inwards, towards the posterior side, giving a reniform to crescentic shape; (3) *unarcuate* has the same characteristics as arcuate, without the posterior curve.

A virtual tridimensional model of each track was generated with the software Agisoft Photoscan 1.2.0.2152, all set with the plantar side facing upwards. The resulting models range in resolution between 45,166 and 205,920 faces. The tracks were photographed outside in the open, due to their size, with direct or dissipated sunlight. Photos of five cardinal faces of each track (anterior, posterior, lateral, medial and plantar faces) are presented as well. The 3D models and pictures are provided in the *Supplementary Information*.

For the paleobiodiversity analysis, the number of specimen occurrences of skeletal remains and number of tracks / trackways occurrences in both Portugal and the Morrison Formation were used. Only herbivorous groups of dinosaurs occurring in the Late Jurassic of these areas were considered, since these share the same ecological feeding niche to some extent. The groups considered were Stegosauria, Ankylosauria, Ornithopoda and Sauropoda. For analysis of skeletal occurrences, data from the Paleobiology Database (paleobiodb.org) was used. For analysis on tracks and trackways from Morrison Formation, data from literature (Lockley *et al.*, 1986, 1994, 2015, 2017; Lockley, 1987; Lockley & Hunt, 1999; Foster *et al.*, 2006; Gierliński & Sabath, 2008; Milàn & Chiappe, 2009) were used; for Portuguese tracks, data from the Lourinhã Museum collections was used.

All statistical analyses and plots ran using the software RStudio 0.99.879.

The distribution map of stegosaurs and stegosaur tracks was generated using the fossil collections data from fossilworks.org.

3. Description of the tracks

3.1 Ichnotaxonomy

In this study, 38 individual fossilized footprints are described, including 30 pes tracks and 8 manus tracks (ML1351, ML1352, ML2143, ML2179, ML2180, ML2229, ML2230 and ML2233). The attribution of each track has been remained as conservative as it can be, meaning only the higher taxonomic rank with good evidence has been proposed. For that purpose, only ichnogenera have been considered when it was possible. The general characters of the footprints are presented in Table 2. Length and width have been measured and reported only when each track was complete.

Specimen number	Member	General outline	Vertical striations	Skin impression	Digits	Dimensions (LxW (cm))	Ichnogennus
ML1334	Left pes	Rectangular	-	-	Slightly differentiated	?x24	*Deltapodus*
ML1339	Left pes	Possibly circular	-	-	Slightly differentiated	44x32	*Deltapodus*
ML1342	Left pes	Rectangular	-	-	Well differentiated	36x29	*Deltapodus*
ML1343	Right pes	Rectangular	Medial side in heel area	-	Slightly differentiated	35x29	*Deltapodus*
ML1344	Left pes	Rectangular	-	-	Slightly differentiated	42x32	*Deltapodu*s
ML1345	Left pes	Subtriangular	-	-	Well differentiated	41x33	*Deltapodus*
ML1346	Right pes	Rectangular	-	-	Well differen-tiated	56x44	*Deltapodus*
ML1347	Left pes	Rectangular	Subtle, heel area	On all plantar side	Slightly differentiated	50x41	*Deltapodus*
ML1348	Left pes	Possibly rectangular	Subtle, on medial side	On medial area of plantar area	Differentiated	43x34	*Deltapodus*
ML1349	Right pes	Subtriangular	On medial side	On medial -plantar mar-gin and heel	Slightly differentiated	43x36	*Deltapodus*
ML1350	Right pes	Rectangular	-	-	Well differentiated	39x32	*Deltapodus*
ML1351	Undet. manus	Arcuate	-	-	Not differentiated	28x45	*Deltapodus*
ML1352	Undet. manus	Horse-shoe shaped	Anterior face and sides	-	Not differentiated	22x34	Undetermined camarasauro-morph ichno-genus
ML2143	Left manus	Unarcuate	On the toes	-	Well differentiated	37x29	Undetermined non-neosauro-pod eusauropod ichnogenus
ML2170	Undet. pes	Circular	All around the margins	-	Not differentiated	33x24	*Deltapodus*
ML2171	Left pes	Circular	Medial side and lateral margin of heel	-	Slightly differentiated	39x33	*Deltapodus*
ML2172	Left pes	Subtriangular	-	-	Well differentiated	44x33	*Deltapodus*
ML2173	Undet. pes	Undet.	On one of the toes	-	Slightly differentiated	?x34	*Deltapodus*
ML2174	Right pes	Subtriangular	Subtle, on medial side	-	Slightly differentiated	25x21	*Deltapodus*
ML2175	Undet. pes	Subtriangular	On toes and plantar side	Possibly just before the hoof part	Not differentiated	42x34	*Deltapodus*
ML2176	Undet. pes	Rectangular	Subtle, on one of the sides and toe III	-	Slightly differentiated	34x27	*Deltapodus*

Tab. 2. -General footprint characters. “-“ represents lack of data: no striations / skin impression is preserved, or “heel” area / digit III is missing. “?” represents dimensions not taken because of the preservation of the tracks. The digits are described in plantar view.

Specimen number	Member	General outline	Vertical striations	Skin impression	Digits	Dimensions (LxW (cm))	Ichnogennus
ML2177	Right pes (?)	Subtriangular	-	-	Slightly differentiated	24x26	*Deltapodus*
ML2179	Undet. manus	Subtriangular	Subtle, on the side	-	Slightly differentiated	21x20	Undetermined basal thyreophoran ichnogenus
ML2180	Left (?) manus	Arcuate	-	-	Not differentiated	20x35	*Deltapodus*
ML2181	Right pes	Possibly subtriangular	-	-	Slightly differentiated	?x22	*Deltapodus*
ML2207	Right pes	Rectangular	Subtle, on the toes	-	Well differentiated	?x22	*Deltapodus*
ML2229	Undet. manus	Arcuate	All around the margins	-	Well differentiated	31x31	Undertermined ankylosaurian ichongenus
ML2230	Left manus	Unarcuate	-	-	Slightly differentiated	28x35	Undetermined non-neosauropod eusauropod ichnogenus
ML2231	Right pes	Undet.	Subtle, on lateral side	-	Differentiated	42x26	*Deltapodus*
ML2232	Right pes	Subtriangular	On the toes	-	Differentiated	30x29	*Deltapodus*
ML2233	Right manus	Arcuate	On the toes	-	Differentiated	26x33	*Deltapodus*
ML2234	Left pes	Subtriangular	On the toes and on the lateral side	-	Well differentiated	52x47	*Deltapodus*
ML2235	Left pes	Subtriangular	-	-	Slightly differentiated	?x27	*Deltapodus*
ML2236	Undet. pes	Undet.	On the lateral side	-	Undet.	?x27	Undetermined ichnogenus
ML2237	Undet. pes	Subtriangular	On the toes	-	Slightly differentiated	28x22	*Deltapodus*
ML2238	Undet. pes	Circular	All around the margins	-	Slightly differentiated	37x24	*Deltapodus*
ML2239	Right pes	Subtriangular	On medial side	-	Slightly differentiated	41x31	*Deltapodus*
ML2240	Left pes	Subtriangular	-	-	Slightly differentiated	?x29	*Deltapodus*

Tab. 2. - Cont. General footprint characters. "-" represents lack of data: no striations / skin impression is preserved, or "heel" area / digit III is missing. "?" represents dimensions not taken because of the preservation of the tracks. The digits are described in plantar view.

DINOSAURIA Owen, 1843
ORNITHISCHIA Seeley, 1888
THYREOPHORA Nopcsa, 1915
STEGOSAURIA Marsh, 1877

Ichnogenus: *Deltapodus* Whyte & Romano, 1994 (Fig. 3, Fig. 4, Fig. 5 A-C).

Etymology: From the Greek "δέλτα", delta, which refers to the basically triangular outline of the pes print, and "πούς", pods, meaning foot.

Distribution: From the Middle Jurassic of England to the Late Jurassic-Early Cretaceous of Portugal, Spain, North America, China, and Morocco.

Diagnosis (modified from Whyte & Romano, 1994) : Manus: 1) manus–entaxonic footprints; 2) broadly crescent-shaped in outline, and anteriorly convex; 3) occasional development of an inwardly (or medially) directed digit (pollex) impression; Pes: 4) generally oval, sub-triangular in outline; 5) internal side slightly concave; 6) pes prints mesaxonic, with three digit impressions as short projections or bluntly rounded points; Trackway: 7) medium gauge (internal trackway width moderately wide: approx. 0.10–0.30 m).

Description:ML1334 (see S1.1 and S2.1): Dimensions (LxW) – ?x24cm. Badly preserved, heel area is missing, as does the underside of digit IV, which seems to not have been filled. Some fracture lines are observable: one in the back cleaving the track in two distinctive blocks, and another from behind digit II to the hypex between digits III and IV. Digits III and IV are round while digit II is sharper. Digit III is broader and larger that the two other ones. The margins of the digits are visible and seem to lean outwardly. Despite missing the heel area, it is considered rectangular in general outline.

ML1339 (see S1.2 and S2.2): Dimensions – 44x32cm. Few characters preserved, extremely flat and slightly curved dorsally.

Part of the medial side is missing from behind digit II to the heel area, and two fracture lines are observable: one in the heel area and one from behind digit II to the hypex between digits II and III. Digits are round and their margins are observable and vertical. Despite the medial area missing, the general outline is considered circular.

ML1342 (see S1.3 and S2.3): Dimensions – 36x29cm. Well preserved outline but lacks most of the details. Two fracture lines present, one from behind digit II to digit III and another in the heel area. Digits are well differentiated, and their margins appear to be vertical. The collection number has been reattributed (previously ML 964; Mateus & Milàn, 2008) since this track was collected in a block with another footprint with which shared the same collection number. The general outline is rectangular, with a heel area slightly rounded.

ML1343 (see S1.4 and S2.4): Dimensions – 35x29cm. Well preserved. Some holes are present on the plantar side due to erosion. The digits are round, and their margins are vertical. The anterior area is deeper than the heel area. The track seems to lean inwards. The general outline is rectangular, with a round heel area.

ML1345 (see S1.5 and S2.5): Dimensions – 41x33cm. Well preserved. Plantar side exhibits a very smooth surface, with some grooves. The digits are round and well differentiated in plantar view, and their margins in anterior view seem to lean slightly outwardly. Anterior area is deeper than heel area, and digit III is deeper than the others. The general outline is subtriangular.

ML1347 (see S1.6 and S2.6): Dimensions – 50x41cm. Extremely well preserved, with scale impressions preserved on most of the plantar face. See 3.2 *Skin scales* for further description of the skin impression and preservation of the plantar side. Digits are round. There is no observable margin hypex between digits II and III. Digit margins lean slightly outwards. Digit area is deeper than heel area, and digit IV is deeper than the others. The general outline is rectangular.

ML1348 (see S1.7 and S2.7): Dimensions – 43x34cm. Well preserved, apart for missing area from behind digit IV to heel, with some skin impressions on medial face, and slightly curved ventrally. The plantar surface is mostly irregular, apart for next to medial face. Digits are round and differentiated in plantar view. Margins of digits III and IV are vertical whereas digit II leans outwards.

The shape of the medial margin seems to confer a rectangular general outline, but due to bad preservation of the lateral face, that designation is uncertain.

ML1349 (see S1.8 and S2.8): Dimensions – 43x36cm. Well preserved, exhibiting some round scale impressions. A large area in the middle of the plantar face has broken off. Digits are round. In anterior view, digit II is vertical, digit III leans slightly outwards and digit IV leans strongly outwards, giving the illusion that they are broken off in plantar view. The general outline is subtriangular.

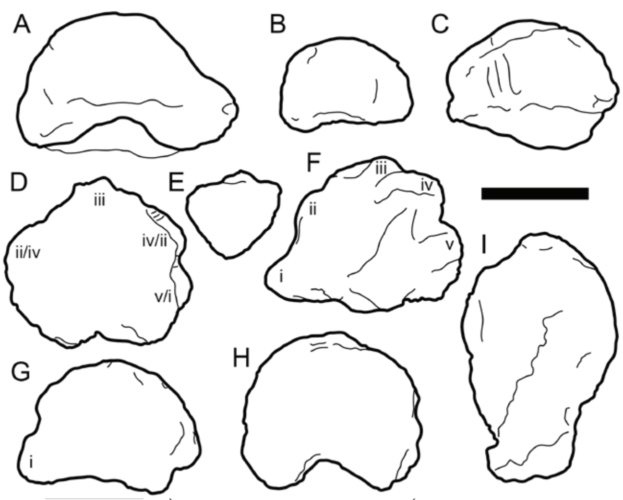

Fig. 5. -Manus track outlines. A-C - *Deltapodus* isp, ML1351, ML2180, ML2233. D - undetermined ankylosaurian ichnogenus, ML2229. E - undetermined basal thyreophoran ichnogenus, ML2179. F-G - undetermined non-neosauropod eusauropod ichnogenus, ML2143 and ML2230. H - undetermined camarasauromorph ichnogenus, ML1352. I - undetermined ichnogenus, ML2236. The numbers correspond to the digits. Scale bar is 20cm.

39x32cm. Well preserved, except for small part of heel area missing. Attached to rock block. plantar surface is smooth. Digits are round. Digit II seems to be vertical, but digit III and IV lean outwards. General outline is rectangular.

ML2170 (see S1.10 and S2.10): Dimensions – 39x33cm. Badly preserved pes, undetermined side, with barely visible digits. Margins seem to be vertical. Plantar surface is irregular, covered by small holes. Circular general outline.

ML2171 (see S1.11 and S2.11): Dimensions – 39x33cm. Digit IV is round and digits II and III are sharper. All digit margins are vertical. General outline is circular.

ML2172 (see S1.12 and S2.12): Dimensions – 44x33cm. Outline well preserved. Plantar surface is irregular, with some parts smooth and other covered by grooves. Prominent digits, digit II is sharp, and the others are rounder. Digits lean outwards. General outline is subtriangular.

ML2173 (see S1.13 and S2.13): Dimensions – ?x34cm. Mostly well preserved. Plantar surface is very irregular. Digits are round and their margins are vertical in anterior view. The toe area is deeper than heel area. Since most of the outline is badly preserved, the general outline is uncertain.

ML2174 (see S1.14 and S2.14): Dimensions – 25x21cm. Fairly preserved. Plantar surface is irregular. Digits are round but barely visible, even in anterior view. Digit IV margin following a sinuous route, leaning outward while digits II and III seem vertical. General outline is subtriangular.

ML2175 (see S1.15 and S2.15): Dimensions – 42x34cm. It presents a peculiar preservation. Deeper than most of the tracks found in the Formation. The toes area displays a very bulbar shape, as if the track was compressed. No digits distinguishable, but the anterior face and most of the sides are covered in vertical striations. Abnormally, striations on the plantar side of the heel area are observed. Small hillocks on anterior end of the plantar side could be interpreted as skin impression. General outline seems to be subtriangular.

ML2176 (see S1.16 and S2.16): Dimensions – 34x27cm. Poorly preserved: toe and heel areas are partially broken off. Digit margins leaning. Two digits are round, and one is sharp. General outline is rectangular.

ML2177 (see S1.17 and S2.17): Dimensions – 24x26cm. Poorly preserved, as most of the posterior area is missing. Three digits are slightly differentiated in plantar view. Digit IV deeper than the others. No vertical striations have been observed, and the plantar surface is regular and mainly rough. Because of the preservation, it is difficult to portray the general outline, but the partial ridges of digits II and IV seem to infer a subtriangular outline. It is a pes, as the track looks like to be mesaxonic, probably a right one.

ML2180 (see S1.18 and S2.18): Dimensions – 20x35cm. Entaxonic manus, with a crescentic general outline. Well preserved, with a fracture crossing it longitudinally on the lateral side. The plantar side is irregular, with a bulging shape. There are no digit impressions. However, the track is broader on the right side than the left side on plantar view, suggesting that the right part could be the impression of digit one, implying the track may be a left manus.

ML2181 (see S1.19 and S2.19): Dimensions – ?x22cm. Not well preserved in the toe area, and heel area is missing. The plantar surface is smooth, except for a wide groove in digit III. Digits II and IV seem to be round, while digit III is sharper, but this could be the result of the poor preservation. Digits margins leaning cannot be determined. Toe area is deeper than heel area, and digit IV deeper than the others. Margins of both sides suggest the general outline could be subtriangular.

ML2207 (see S1.20 and S2.20): Dimensions – ?x22cm. Poorly preserved, except anterior and lateral faces with detailed preservation. Substantial gap in the plantar surface and missing heel area. Digits are vertical and prominent with a round shape. General outline is rectangular.

ML2231 (see S1.21 and S2.21): Dimensions – 42x26cm. Well preserved, except for missing part of the medial side. Plantar surface is very irregular and covered by holes and grooves. Digits are round, but digits II and III become sharper in plantar side. Diminutive tip is observable on the top of digit III, antero-posteriorly curved, which could be a claw mark. Margins of the digits are vertical. Because of bad preservation of the medial side, the general outline cannot be determined.

ML2232 (see S1.22 and S2.22): Dimensions – 30x29cm. Well preserved, except for heel area and medial side. The track has been collected in its rock block, attached to the dorsal face. Digits are round. All the track is strongly leaning outwards, particularly visible in anterior view, while in plantar view the medial slope is entirely visible. Because of the strong angle of this leaning, it may be the result of geological movements and not the walking movement itself.

Despite the misleading leaning, the medial and lateral faces suggest a subtriangular general outline.

ML2233 (see S1.23 and S2.23): Dimensions – 26x33cm. Well preserved. Plantar surface is irregular, particularly with central part presenting a type of corrugated pattern. The slightly arcuate outline suggests it could be an entaxonic manus. However, it is wider than other manus tracks. Three main digits are visible in anterior view and plantar view, with vertical striations, although not well differentiated in plantar view. In dorsal view a fourth digit is distinguishable on the right, while the track is slimming toward the left. That would suggest it is a right manus.

ML2234 (see S1.24 and S2.24): Dimensions – 52x47cm. Well preserved. Plantar surface is very irregular, covered by irregular ridges. It is the biggest track described in this study. Digits are round and a small projection in the interdigital space between digits III and IV is observable, but its significance is unclear. As in ML1347, a bulge is observable posteriorly to digit III, which could be a skin fold behind the claw. Digit margins are vertical. General outline is subtriangular.

ML2235 (see S1.25 and S2.25): Dimensions – ?x27cm. Badly preserved: posterior half is missing and digits II and III are badly preserved. Plantar surface is smooth, with few grooves. The digit IV is round and its margin seems to be vertical. Although half of the track is missing, the margins of both sides suggest a subtriangular general outline.

ML2237 (see S1.26 and S2.26): Dimensions – 28x22cm. Well preserved. Deeper than wide. Plantar surface is irregular, covered by holes and invertebrate fossils. Digits are slightly sharp in plantar face, but rounder in anterior view. Digit margins are leaning slightly, but vertical near to plantar face. Toe area is deeper than the heel area. General outline is subtriangular.

ML2238 (see S1.27 and S2.27): Dimensions – 37x24cm. Track infill is well preserved, but the track itself has been subject to intense erosion, giving it very smooth rims and almost no digit impression. Digits are barely visible in anterior view and seem to be round. In plantar view, the entire track leans to the right. Plantar surface is irregular, covered by holes. General outline is circular, but it could be the result of erosion.

ML2239 (see S1.28 and S2.28): Dimensions – 41x31cm. Well preserved, except for digit II and part of digit III. Plantar surface is irregular, covered by holes and inclusions. Digit IV is round and what can be observed in digit III suggests the same. Margins of digits III and IV seem to be vertical. Toe area is deeper than heel area. General outline is subtriangular, with a round heel.

ML2240 (see S1.29 and S2.29): Dimensions – ?x29cm. Badly preserved, particularly in the anterior area where digits II and III are partially missing in plantar side. Plantar surface is irregular, covered by some grooves. Digits seem to be round and their margins are vertical. General outline is subtriangular.

Remarks: Most of the prints exhibit the usual morphology observed in *Deltapodus*: mesaxonic tridactyl pes, with a circular to subtriangular general outline; and entaxonic manus without clear digit impressions, with an arcuate general outline (Whyte & Romano, 1994, 2001). The general outline of ML2172, with a long and narrow print is similar to the one observed in the holotype of *D. ibericus* (Cobos *et al.,* 2010), and it is here attributed to *Deltapodus* as the descriptions are conservative for this paper. ML2180 has a slightly arcuate outline, slimming down toward its lateral side, broader than the one described in *D. brodricki* (Whyte & Romano, 2001), and is less curved that what is observed in kidney-shaped titanosauriforms tracks (Castanera *et al.,* 2016). However, it looks similar to tracks attributed to *Deltapodus* in Spain (Pascual *et al*., 2012; Piñuela *et al*., 2014; Pascual-Arribas & Hernández-Medrano, 2016), supporting this attribution for this track. The general outlines of ML2234 and ML2235 are closer to the one observed in a Chinese specimen attributed to *D. curriei* (Xing *et al*., 2013; MGCM. SA1p, Fig. 3 and 4) than the more circular-rectangular shape usually observed in other European specimens of *Deltapodus*. The digits are not as widely expanded as it can been observed in *Stegopodus* tracks. As tracks are here only attributed to the ichnogenus level, this track is attributed to *Deltapodus*. The subtriangular outline observed in ML2237 is similar to what can be observed in some specimens of *D. brodricki* (Whyte & Romano, 2001; Fig. 3.G.), and the track is so attributed to *Deltapodus*.

ANKYLOSAURIA Osborn, 1923

Undetermined ichnogenus (Fig. 5 D)

Description: ML2229 (see S1.30 and S2.30): Dimensions – 31x31cm. Mesaxonic manus with an arcuate outline, undetermined size. Well preserved, with an irregular plantar surface covered by small holes and grooves. Four digits are observed, arranged radially, but a fifth one could be unpreserved. The digits are round, and their margins are leaning.

Remarks: The track differs from the others in the sample, and to manus tracks usually attributed to stegosaur or sauropod trackmakers (Whyte & Romano, 2001; Cobos, 2010; Pascual *et al.,* 2012; Xing *et al.*, 2013; Piñuela *et al.*, 2014; Castanera *et al.*, 2016; Pascual-Arribas & Hernández-Medrano, 2016; Lockley *et al.*, 2017). However, it is tetradactyl (possibly pentadactyl), and the digits are arranged radially in the pattern of a star, which is one of the characteristics of ankylosaurian trackmaker (Carpenter, 1984; Thulborn, 1990; Pascual *et al.*, 2012).

The track is consequently attributed to an undetermined ankylosaurian ichnogenus, as no closer attribution could be given. It is here reported as the first ankylosaurian track from the Late Jurassic of Portugal.

Undetermined thyreophoran

Undetermined ichnogenus (Fig. 5E)

Description: ML2179 (see S1.31 and S2.31): Dimensions – 21x20cm. Deeper than long or wide. Well preserved, apart for a fracture crossing it horizontally near the plantar face. Seems to be mesaxonic and tridactyl, with no pollex apparent and a general outline subtriangular. Some vertical striations are visible in one of the sides. It could not be determined if it is a manus or a pes, nor from which side

Remarks: The track is difficult to interpret because of its unusual shape. However, when compared with previous works, the subtriangular general outline and the tridactyl mesaxonic manus without pollex print is similar to what can be observed in tracks from basal thyreophoran trackmakers (Whyte & Romano, 2001). However, their osteology is poorly known, and there is no skeletal remain described in the Late Jurassic of Portugal. As such this attribution remains tentative, as misinterpretation of this track remains a possibility.

SAUROPODA Marsh, 1878

EUSAUROPODA Upchurch, 1995

Undetermined ichnogenus (Fig. 5 F and G)

Description: ML2143 (see S1.32 and S2.32): Dimensions – 37x29cm. Entaxonic left manus, with five round digits and an evident pollex print. Digit margins are vertical. The plantar surface is irregular, with convolution in the palm area. The general outline is unarcuate, with a speech-bubble shape with a large digit I impression oriented in medial direction.

ML2230 (see S1.33 and S2.33): Dimensions – 28x35cm. Entaxonic left manus with unarcuate outline with a speech-bubble shape with a large digit I impression oriented in medial direction. It is flat and well preserved, with a smooth plantar surface covered in reliefs on the lateral side. At least four digits are observed, with maybe a fifth one missing, with an evident pollex track. The margins of the digits are poorly visible but seem to be vertical.

Remarks: ML2143 and ML2230 exhibits a speech-bubble shaped outline, with a large digit I impression oriented in a medial direction, which can be referred to Middle Jurassic non-neosauropod Euosauropoda (Castanera *et al.*, 2016). ML 2230 is thinner than ML2143, but both share a similar morphology. Consequently, both are attributed to the same undetermined ichnogenus, produced by non-neosauropod Eosauropoda trackmaker.

NEOSAUROPODA Bonaparte, 1986

CAMARASAUROMORPHA Salgado *et al.,* 1997

Undetermined ichnogenus (Fig. 5H)

Description: ML1352 (see S1.34 and S2.34): Dimensions – 22x34cm. Partial manus track. Well preserved. There is no digit impression. The general outline is crescentic to horseshoe-shaped.

Remarks: Originally considered as *Deltapodus* (Mateus *et al.*, 2011), the small size could have been the source of the former misinterpretation in the original description. The characteristic horseshoe-shaped observed for the general outline is usually observed in neosauropod manus (Whyte & Romano, 2001; Castanera *et al*, 2016). Crescentic shaped tracks are usually observed in diplodocids, while horse-shoe shaped tracks are observed in later neosauropod, it has been suggested that the transition could have occurred in camarasauromorph (Wright, 2005; Castanera *et al.,* 2016). As ML1352 appears to have a crescentic to horse-shoe shaped outline, it is here referred as an undetermined ichnogenus produced by camarasauromorph trackmaker.

Undetermined trackmaker

Description: ML2236 (see S1.35 and S2.35): Dimensions – ?x27cm. Badly preserved. The preservation makes its interpretation difficult and no clear general outline has been identified. Vertical striations in one ridge of the track, which could be the part where the digits are.

Remarks: Track remains undetermined, although it may be from a stegosaurian trackmaker.

3.2 Skin scales

Four footprints (ML1347, ML1348, ML1349 and ML2175) present small hillocks which are considered as impression of skin scales.

ML1347 is notably the one where the impression of skin scales is the clearest and best preserved, with almost all of its plantar side covered (Fig. 6). Only partially on digit II, digit IV, and the heel this type of texture does not occur, due to coarser sandy sediment on the surface (in the toes' case) or modification of the track (in the heel's case). Just behind digit III, there is a bulge that could be where the skin folds behind the claw. A tubular structure transversely through the middle of the footprint is observable, probably a branch over which the dinosaur walked.

While most of the track is covered by skin impression, the level of conservation differs from one spot to another. However, four main characters can be noticed: (1) the pattern of the scale seems to be random; (2) the scales in the center of the foot seem to be smaller than the ones on the ridge, but scales from the same area have the same size; (3) the scales are separated by small grooves in the center or running next to each other on the ridge; (4) the shape of the scales differs according the area where these are.

The scale impressions, although closely similar and mostly random, can be separated in four texture patterns observable over the track (Fig. 6): (a) *circular scales 2 to 3 mm wide*: in the center of the track, covering most of the track. Spaced by grooves of 1 to 2 mm. Mostly eroded in the very center. Also, behind digit III; (b) *ovoid scales 5 to 7 mm wide*: on the medial part of the heel, with a groove of 1 to 2 mm, almost crescentic shape, alluding to fish scales; (c) *circular scales 3 to 4 mm wide*: closer to the sides, slightly bigger close to the lateral face. Spaced by 2 mm grooves; (d) *hexagonal or rectangular scales 5 to 7 mm wide:* limited to the lateral ridge of the track, from the posterior end to digit IV. Without grooves between them.

ML1348 only preserved skin scale impressions on the medial margin, from behind digit II to the sandy agglomerate that covers most of the palmar surface. ML1349 only preserved skin scale impressions on its medial margin of the heel. On both tracks, the skin scale impressions share the same characters observed in ML1347 and exhibit a pattern similar to the pattern (d), with hexagonal to rectangular scales. In ML1349,

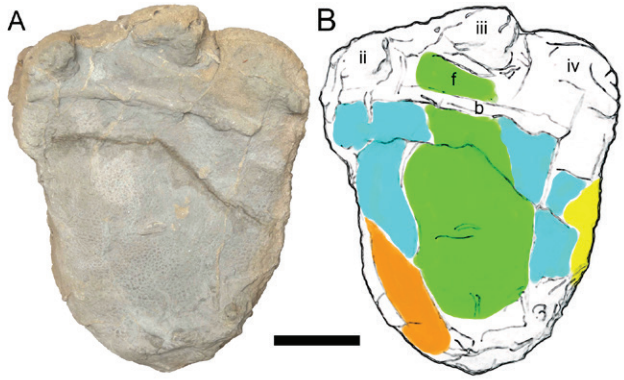

Fig. 6. -Detail of skin impression on ML1347. A - picture in plantar view exhibiting the skin impressions, B - sketch with rough location of the different patterns observed: circular scales 2 to 3 mm wide (green); ovoid scales 5 to 7 mm wide (orange); circular scales 3 to 4 mm wide (cyan); hexagonal or rectangular scales 5 to 7 mm wide (yellow). b, tubular structure from branch, f, fold of skin, ii, second digit, iii, third digit, iv, fourth digit. Scale bar equals 10 cm.

vertical striations along the medial surface, which are interpreted as traces of the entrance of the foot into the substrate (see discussion).

3.3 Mechanics and movement

Of the 38 footprints in this study, 23 present vertical striations, in the wall of the infill of both pes and manus. The striations are similar in size and shape, regardless of side or autopodium. These marks can occur anywhere in the rim of the track, but mostly on the front, where the digits are.

ML2175 is the only track presenting striations in parts other than the ridges, namely in the plantar side of its heel area, and also one with the most peculiar shape. It is possibly a composed track, with drag movement or combination of two tracks. Indeed, the front part of the track presents a bulbar shape, as if the track had been compressed afterwards. However, nor the striations in the front neither the plantar surface in the groove seems to have been subject to this kind of constrain. Furthermore, some striations on the right side of the track (with the plantar view upside) are continuous and do not seem to have been altered, and these striations are not vertical but almost horizontal.

3.4 Size

As stated in previous studies (Cobos *et al.,* 2010; Mateus *et al*., 2011), *Deltapodus* footprints are longer than wide. The linear trend curve in Fig. 7, drawn from complete pes tracks measurements used in this study, show that all the tracks (small, medium, and large) have the same L/A index and were made by

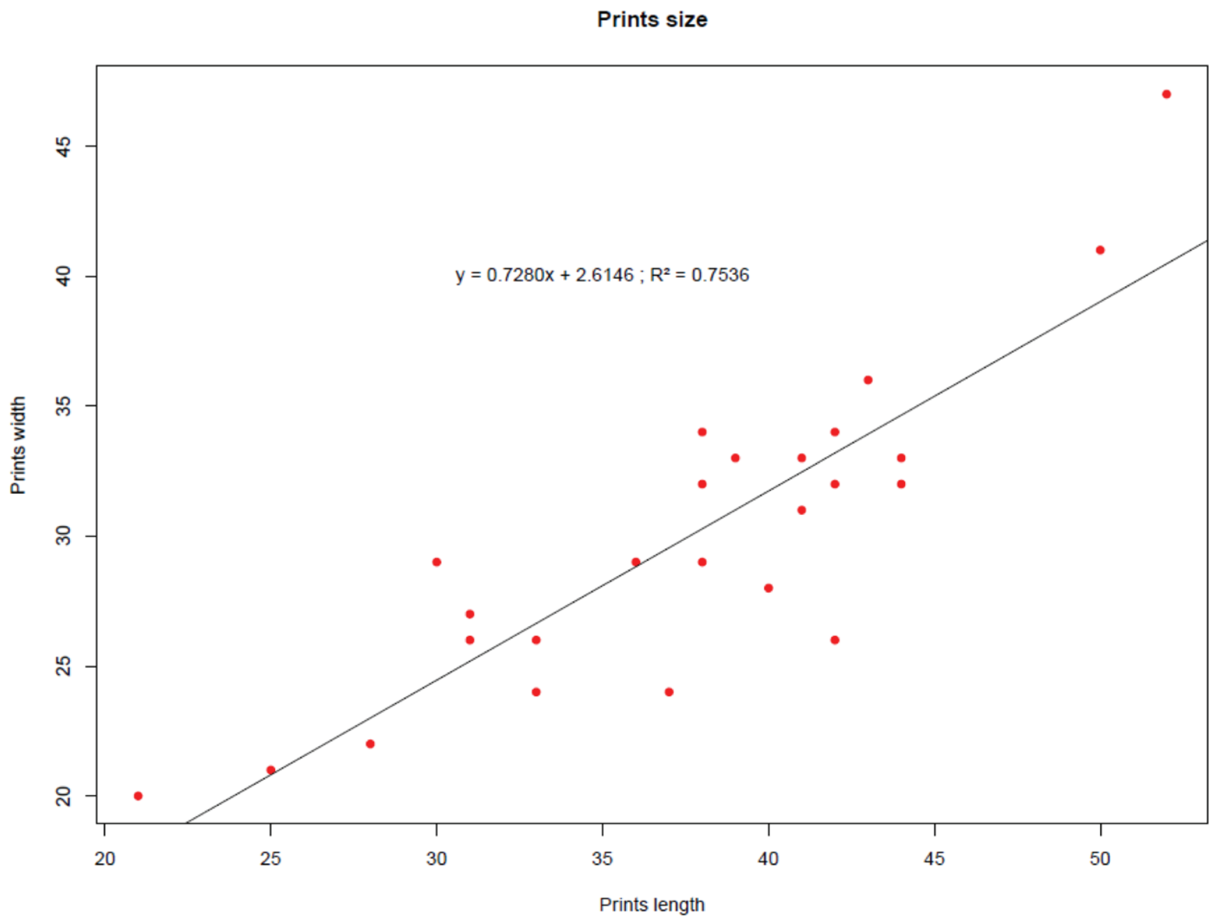

Fig. 7. -Relationship proportions between pes footprint length and width (in cm) of *Deltadopus* from Lourinhã Formation. Black line is linear trend curve ($y = 0.7280x + 2.6146$; $R^2 = 0.7536$).

only one type of trackmaker. The measurements both have isometric link, stating:

$$width=(0.7280\times length)+2.6146$$

The distribution of the footprints according to length and width (see Fig. 8) was also studied. Both show a mostly homogenous distribution expected for a random population. However, the density curve shows a slight bump, giving it a shape not entirely Gaussian. The main parameters of the distribution are indicated in Table 3.

3.5 Track record and paleobiodiversity comparisons

All stegosaur tracks from Portugal are from Lourinhã Formation layers, where the most common fossilized herbivore trackmaker footprints were found. It appears that the ichnoassociation and the bone record are different (Fig. 9): 32 tracks are attributed to stegosaur trackmakers, representing 68,63% of the known record of dinosaur tracks from the Lourinhã Formation, but only 13 stegosaur skeletal occurrences have been reported, representing only 25% of the herbivore skeletal record. In the coeval layer of the Morrison Formation, the scenario appears different: sauropods and ornithopods are more abundant both in skeletal and track records than stegosaurs and ankylosaurs, which are poorly represented.

Each record has also been compared between the two formations (Fig. 9). Skeletal occurrences have a similar pattern of distribution: sauropods are in majority in both the Lourinhã and the Morrison Formations (53.85% and 66.35% respectively), while ankylosaurs are in minority (1.92% and 1.72% respectively). Ornithopod and stegosaur records have

	min	1st Q	mean	median	3rd Q	max
Length	21	36	39.24	41	43	56
Width	20	26	31.19	32	33	47

Tab. 3. -Main parameters of tracks distribution according to length and width

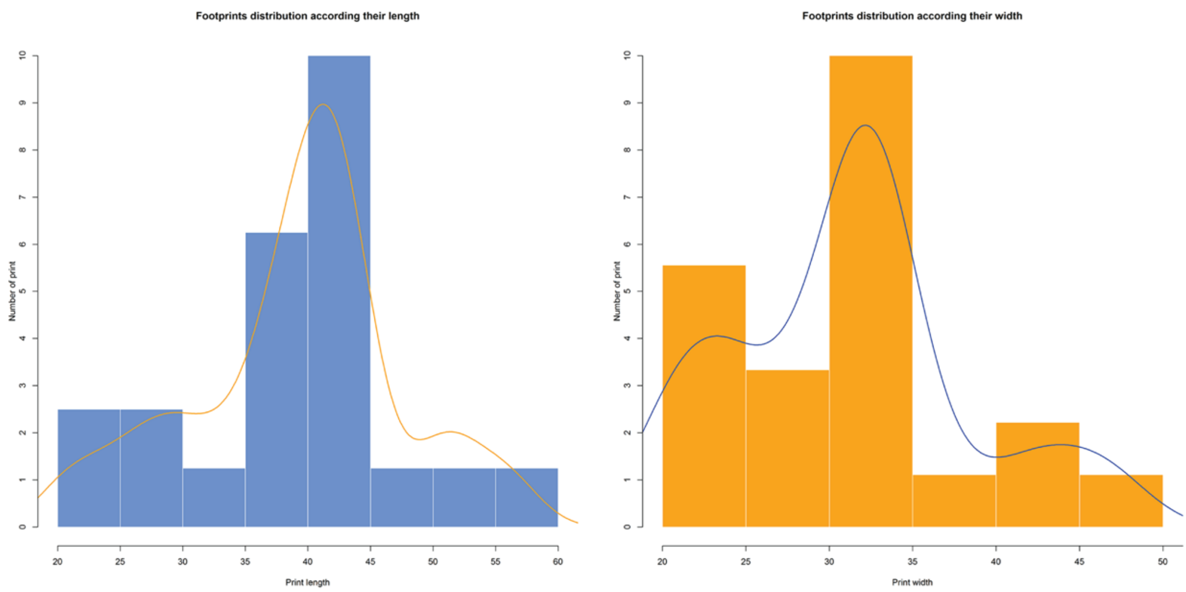

Fig. 8. -Histogram of footprints distribution according to length (left) and width (right). Curve lines show density.

similar distribution, however the former are less abundant than the later in Portugal, while it is the other way around in US. However, the proportions of each group in the track and trackway record are completely different between both formations. Stegosaur tracks are scarce in the Morrison Formation (6.02%), while they are extremely common in the Lourinhã Formation (62.75%). Sauropods are dominant in the track and trackway record of the Morrison Formation, and are fairly represented in the Lourinhã Formation (29.41%). Ornithopod tracks seem to be fairly represented in the Morrison Formation (24.06%), while there is only one recorded from the Lourinhã Formation. Ankylosaur tracks are poorly represented in both formations, with one record each.

4. Discussion

Among all the tracks, 32 have been attributed to *Deltapodus*, one to a basal thyreophoran trackmaker, one to an ankylosaur trackmaker, three have been reattributed to a sauropod trackmaker, and one remains undetermined.

The description of these different footprints highlights the diversity in shape and size in *Deltapodus* footprints in Portugal, even if some present missing parts due to bad preservation. *Deltapodus* pes tracks are mesaxonic tridactyl, with a circular to subtriangular general outline, and manus tracks are entaxonic without clear digit impressions, with an arcuate general outline (Whyte & Romano, 1994, 2001). Even in the tracks with bad preservation, these characteristics could be observed.

4.1 Skin impression

ML1347, ML1348, ML1349 and ML2175 preserve the skin pattern of the scales on the arch of the foot. In the best-preserved specimen - ML1347 - four patterns have been observed: (a) circular scales 2 to 3mm wide; (b) ovoid scales 5 to 7mm wide; (c) circular scales 3 to 4mm wide: and (d) hexagonal or rectangular scales 5 to 7mm wide. The difference in size may be due to the walking biomechanics during the step cycle: the scales on the margins let bigger marks because they follow the movement of the foot during walking, while the ones in the center just spot the surface (Guillaume *et al.*, 2017). ML1349 supports this hypothesis, with the margin-closest scale impressions extending into vertical striations along the medial surface, which are interpreted as traces of the entrance (or exit) of the foot into the substrate (Mateus *et al.*, 2011; Herrero Gascón & Pérez Lorente, 2017). Differences in the shape probably result from conservation issues: the center of the arch was more exposed to erosion and more sandy sediment occurs in this area in ML1347, which may have resulted in less detailed preservation (Guillaume *et al.*, 2017). Despite the differences observed in shape, size, and space between the scales, the general pattern appears to be a uniform distribution with faint random variations. The stegosaur foot scale pattern, especially the one observed on the lateral ridge, looks similar to the one observed on the rib cage of the stegosaur *Hesperosaurus mjosi* Carpenter *et al.*, 2001 (SMA 0018) with small, non-imbricating and polygonal scales separated by shallow and narrow grooves (Christiansen

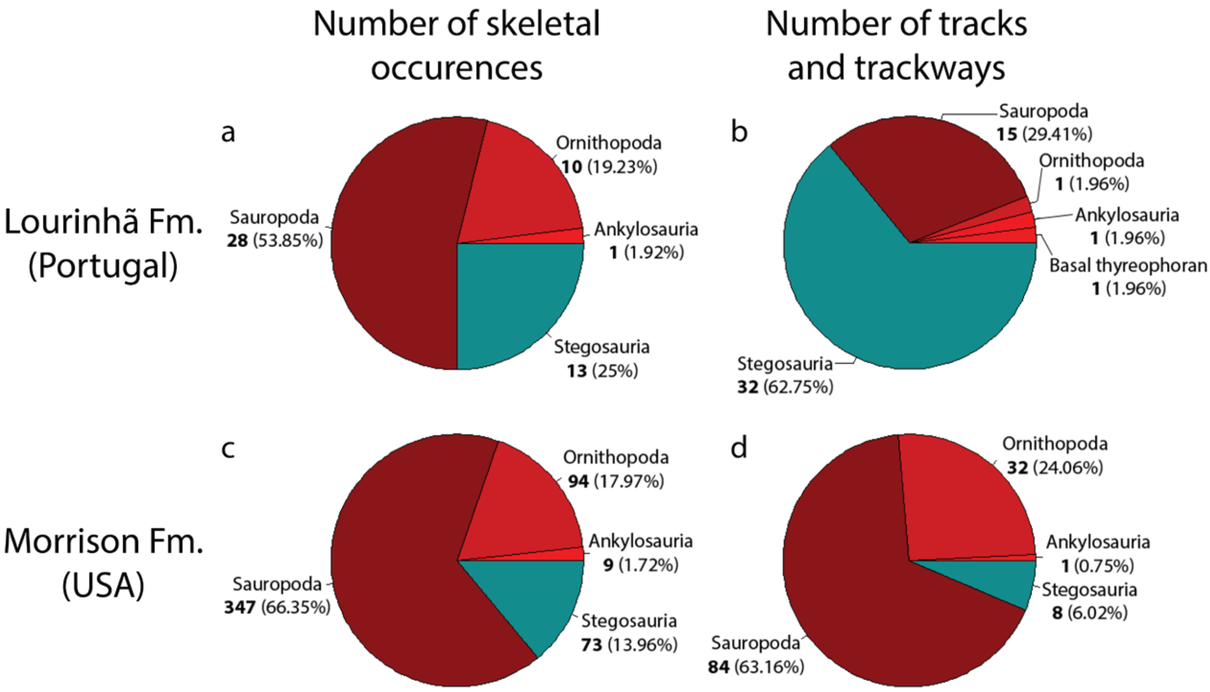

Fig. 9. -Specimen of skeletal occurrences and tracks/trackways in the Lourinhã Formation and Morrison Formation. A - number of skeletal occurrences in Lourinhã Formation (n=52). B - number of tracks/trackways in Lourinhã Formation (n=50). C - number of skeletal occurrences in Morrison Formation (n=523). D - number of tracks/trackways in Morrison Formation (n=125).

& Tschopp, 2010). The pattern observed in the center and medial area of ML 1347 shares similarities with the one observed in the foot of *Concavenator corcovatus* Ortega *et al.*, 2010 (MCCM-LH 6666), which evidences a random pattern and scales approximately circular (although slightly bigger than those in ML 1347), which is also similar to what is observed in birds (Cuesta *et al.*, 2015). The skin pattern from the tracks herein is also similar to the pattern in sauropod footprints, but distinguishable since sauropods exhibit interlocked polygonal scales, arranged in rosettes (Platt & Hasiotis, 2006; Kim *et al.*, 2010), while stegosaurs exhibit round to hexagonal scales, arranged uniformly without interlocking and separated by grooves.

4.2 Biomechanics and limb movement

The presence of a bulge before the digits on some tracks, interpreted as where the skin folds behind the claw, and very short digit impressions may suggest that stegosaurs had a digitigrade foot structure but a plantiportal foot use. This means that the animal walked on its digits, but the heel bones rested on fat tissues, as in elephants (Michilsen *et al.*, 2009). Consequently, the model proposed by Herrero Gascón & Pérez Lorente (2017) is here approved. A large number of specimens presenting vertical striations on their lateral margin have already been reported in other European specimens of *Deltapodus* (Lockley *et al.*, 2008: Mateus *et al.*, 2011; Herrero Gascón & Pérez Lorente, 2017). These are here interpreted as marks of the skin irregularity in the mud walls produced during entry and exit of the pes in the substrate (Mateus *et al.*, 2011; Herrero Gascón & Pérez Lorente, 2017). These enable more detailed study on the footprints to try to figure out the mechanics composition of stegosaurs walking. The apparent homogeneity between the different track sizes and sides suggests that these parameters do not interfere with the locomotion.

One of the tracks, ML2175, presents different remarkable characters distinguishing it from the others: a bulbar shape toe area and striations on plantar view in the heel area. It is considered that this track could be the cast of a complete step cycle of the stegosaurian trackmaker (Avanzini *et al.,* 2011), the only one from the sample to preserve traces of the exit of the pes during this process. To explain the features of this tracks according to what was observed in others, this is the scheme proposed : (1) the stegosaur puts its pes flat on the ground; (2) the pes moves forward, explaining horizontal striations on the sides and plantar view and the bulbar shape in toes area; (3) finally, the pes, leaning forward, raises following the direction of inclination, explaining the vertical striations in toes area without the mark of them (Herrero Gascón & Pérez Lorente proposal, 2016).

4.3 Paleobiodiversity

When comparing the track and trackway record with the distribution of specimen skeletal remains, from both Lourinhã and Morrison Formations, it appears skeletal occurrences shared similar distributions, stegosaur being slightly more represented at the loss of sauropods in the Lourinhã Formation, while the tracks and trackways have two different distribution patterns. In Lourinhã Formation, the stegosaurs seem to dominate the track record, while they are shadowed by both sauropods and ornithopods in the Morrison Formation. However, this could be explained by a sampling bias. Indeed, only one ornithopod track has been reported in the Lourinhã Formation, while they are fairly represented in the Morrison Formation (Foster *et al.*, 2006; Lockley *et al.*, 2015, 2017), and seem as common as stegosaurs in the skeletal record. However, small footprints could have been misattributed to theropods, as both groups have close morphologies (Moratalla *et al.*, 1998; Mateus *et al.,* 2008). Sauropods seem also underrepresented in the track record of the Lourinhã Formation when comparing with the Morrison Formation (Foster *et al.,* 2006; Lockley *et al.*, 2015, 2017). This underrepresentation could be due to a collecting bias, as sauropod tracks in the Lourinhã Formation can be big-sized and not easy to collect (Mateus & Milàn, 2010). On the other hand, the ankylosaur track record in both formations reflect the scarcity of their respective skeletal remain (Lockley *et al.*, 2017), and it has been suggested that the underrepresentation of stegosaur tracks toward their skeletal fossil record could be due to a dichotomy between paleoenvironmental preference and preservational modes in the Morrison Formation (Lockley *et al.,* 2017). This suggests that the Lourinhã Formation stegosaurian track sample presented here may fairly represent their actual abundance.

Data from the skeletal and track records suggest stegosaurs were very common in the Late Jurassic of Portugal, which could reflect a sympatric ecological partitioning within the same habitat. Indeed, the Late Jurassic Portuguese fauna is known for its large-bodied sauropods (Mateus *et al.*, 2009, 2014; Mocho *et al.*, 2016), with the gigantic *Lusotitan atalaiensis* de Lapparent & Zbyszewski, 1957, *Lourinhasaurus alenquerensis* de Lapparent & Zbyszewski, 1957, *Zby atlanticus* Mateus *et al.*, 2014, and *Supersaurus lourinhanensis* (Bonaparte & Mateus, 1999); while small and medium-sized sauropods can be observed in contemporaneous fauna in the Morrison Formation (Whitlock, 2011; Mateus *et al.*, 2014). Until now, only small and medium-sized ornithopods have been reported from the Lourinhã Formation, namely the described *Draconyx loureiroi* Mateus & Antunes, 2001 and *Eousdryosaurus nanohallucis* Escaso *et al.*, 2014, However, isolated material would indicate that bigger members of this group were also present in this formation, although not as big as suggested by the sole ornithopod track reported so far (Mateus & Milàn, 2008; Rotatori *et al.*, 2020). Consequently, it seems there was an "empty" ecological niche for intermediate herbivorous in the Lourinhã Formation, which may have been filled by stegosaurs (Mateus *et al.*, 2009), explaining why their tracks were so abundant, while their skeletal record may be somewhat underrepresentative.

4.4 Identity of the different trackmakers

The mani tracks ML2143 and ML2230 are both attributed to an undetermined non-neosauropod Eusauropoda ichnogenus, because of the characteristic unarcuate speech-bubble shaped general outline (Castanera *et al.*, 2016). This morphology suggests that this group of dinosaurs had metacarpals arranged in a semi-tubular structure (Milàn *et al.*, 2005; Santos *et al.*, 2009; Mateus *et al.*, 2014; Castanera *et al.*, 2016 and references therein), which has been proposed for the reconstruction of the manus in *Z. atlanticus*, a turiasaurian dinosaur from the Lourinhã Formation (Mateus *et al.*, 2014). *Z. atlanticus* has been found in the Amoreira and Porto Novo members, reflecting a similar distribution and time range attributed to the footprints. Consequently, *Z. atlanticus*, or a similar dinosaur, is considered as the trackmaker of ML2143 and ML2230, even though they would be a late occurrence of that morphology (Castanera *et al.*, 2016).

The manus track ML1352 is attributed to an undetermined camarasauromorph ichnogenus, because of its characteristic crescentic to horse-shoe shaped outline (Castanera *et al.*, 2016). It has been proposed that all neosauropods would have metacarpals arranged in tubular structures producing horse-shoe shaped tracks (Milàn & Mateus, 2005, Castanera *et al.*, 2016 and references therein). However, more crescentic-shaped tracks would have occurred in diplodocids, with a wider metacarpal arch, while other neosauropods would produce complete horse-shoe shaped tracks; and this transition may have occurred in camarasauromorphs (Wright, 2005). ML1352 may represent one of these "transitional" tracks, although its small size suggests it has been produced by a juve-

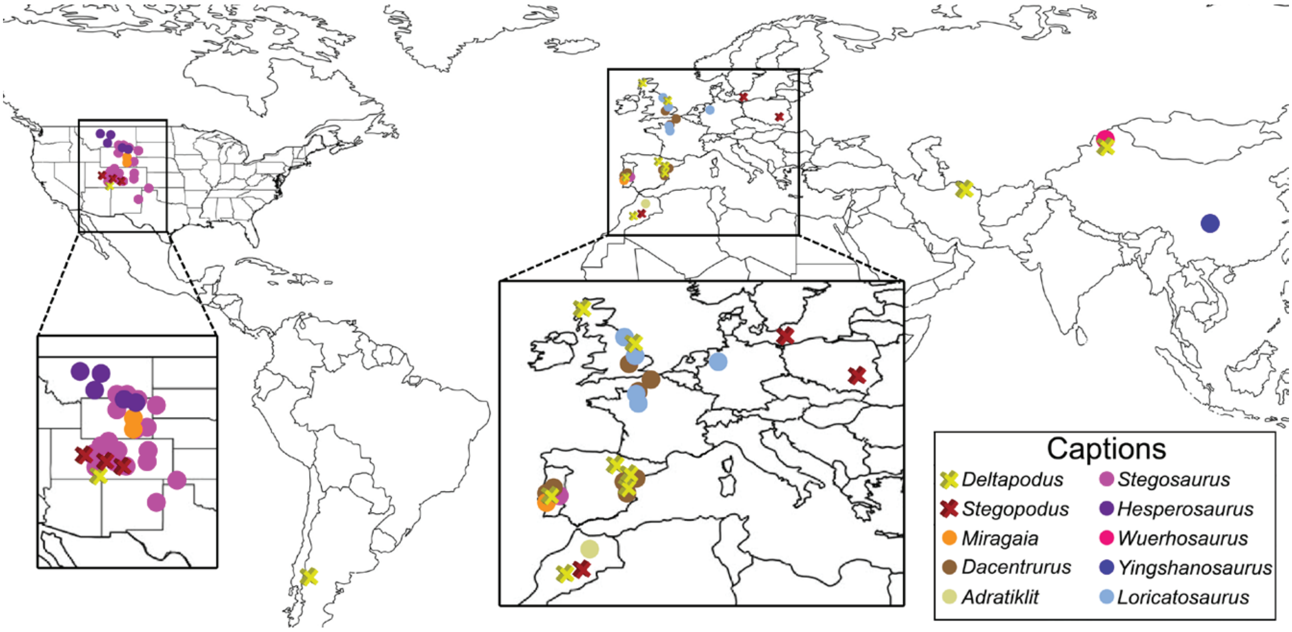

Fig. 10. -Map of world distribution of *Deltapodus*, *Stegopodus*, Dacentrurines, and Stegosaurines (data from *fossilworks.org* and literature used in Table 1). Map from Scotese, 2014.

nile individual. *L. alenquerensis* is the only camarasauromorph reported in the Late Jurassic of Portugal (Mocho *et al.*, 2014), reflecting a similar distribution and time range attributed to the footprint, so it is considered as the probable trackmaker of ML1352.

ML2179 exhibits a mesaxonic tridactyl track with subtriangular general outline, but it remains difficult to interpret. However, these features can be observed in basal thyreophoran tracks although their anatomy remain poorly known for the manus (Whyte & Romano, 2001). Only the partial jaw of a putative basal thyreophoran has been reported in the Early Jurassic of Portugal (*Lusitanosaurus liasicus* de Lapparent & Zbyszewski, 1957) so this attribution remains to be supported by skeletal remains found that confirm the occurrence of these animals. Paleobiogeography and systematics of thyreophorans from the Late Jurassic of Portugal is currently in progress and may clarify this part of dinosaur history.

ML2229 is a tetradactyl (possibly pentadactyl) manus track, with digits arranged radially in the pattern of a star, which is characteristic of ankylosaurian tracks (Carpenter, 1984; Thulborn, 1990; Pascual *et al.*, 2012). It is so referred to an undetermined ankylosaurian ichnogenus and is the first track of this kind reported from the Late Jurassic of Portugal. The Lourinhã Formation produced only one nodosaurid species, *Dracopelta zbyszewskii* Galton, 1980 (Mateus, 2006) found in the Assenta member (Galton, 1980; Suberbiola *et al.,* 2005). A preserved autopodium, referred as a manus, shared similarities with the manus of *Sauropelta* (Suberbiola *et al.*, 2005), which is pentadactyl with the toes spreading out radially, distributing the weight over a large area (Carpenter, 1984). Therefore, *Dracopelta* is here referred as the probable trackmaker of ML2229.

All the stegosaur tracks are here attributed to the ichnogenus *Deltapodus*. *Deltapodus* and *Stegopodus* had probably stegosaurians trackmakers according to: (1) their morphology; (2) the pes and manus anatomy in stegosaurs; (3) and the overlying occurrences of footprints and skeletal remains in time and space (Pascual *et al.*, 2012; Lockley *et al.*, 2017). However, differences observed between both ichnogenera have been questioned if they represented a true diversity in the morphology of stegosaur trackmaker feet or are due to variable preservation, as it has been highlightened (Li *et al.*, 2012; Lockley *et al.*, 2017). Those differences led to propose that *Stegopodus* tracks were evidences of a bipedal locomotion in its trackmakers (Bakker, 1996, Gierliński & Sabath, 2002, Lockley *et al.*, 2017), but other tracks debunked this assessment (Mossbrucker *et al.*, 2008; Piñuela *et al.*, 2016) and the bipedal stegosaur hypothesis remains controversial (Lockley *et al.*, 2017).

In the Morrison Formation, the occurrence of both ichnogenera (Fig. 10) reflects the stratigraphic distribution of *Stegosaurus* (Milàn & Chiappe, 2009; Pascual-Arribas & Hernández-Medrano, 2016; Lockley *et al.*, 2017), but *Stegopodus* seems to be much more common than *Deltapodus*. Abundant skeletal remains of stegosaurines are known from the Morrison Formation (*Stegosaurus* and *Hesperosaurus*; Lockley *et al.*, 2017), but dacentrurines are also known from this formation, as *Alcovasaurus longispinus* Galton & Carpenter, 2016 was recently reinterpreted as the first confirmed dacentrurine in North America, congeneric with *Miragaia longicollum* (Costa & Mateus, 2019).

In Europe, *D. brodricki* was suggested to have been produced by the stegosaurs *Loricatosaurus* Maidment *et al.*, 2008 and *Dacentrurus*, which respectively occur in the Middle Jurassic of France and England, and the Late Jurassic of England, France, and the Iberian Peninsula, while *Dacentrurus* was also proposed as the trackmaker of *D. ibericus* (Cobos *et al.*, 2010; Pascual-Arribas & Hernández-Medrano, 2016). Other *Deltapodus* isp. tracks are usually referred to *Dacentrurus* (Pascual *et al.*, 2012; Pascual-Arribas & Hernández-Medrano, 2016).

The *Deltapodus* tracks found in the Lourinhã Formation could have been impressed by one of the three stegosaur species known in the Formation (*Miragaia longicollum*, *Dacentrurus armatus*, or the apparently less common *Stegosaurus* cf. *ungulatus*), if not by the three of them. The similar shapes with different sizes observed in the tracks suggest these footprints were made by only one kind of trackmaker and the variations observed in size are only result of ontogeny. Fig. 8 shows curves not fully Gaussian, suggesting too that the sample is not absolutely consistent with only one population, but with two different populations with very similar foot proportions but probably in different stages of growth.

The tracks herein described and previous publications show that in western Europe *Deltapodus* is relatively abundant while *Stegopodus* is rare, in opposition to what is observed in North America (Fig. 10). As such, just considering the geographic distribution, abundance and diversity of stegosaurian skeletal and track records in the Late Jurassic of Europe and North America, it is here found more suggestive that *Stegopodus* was produced by stegosaurines and *Deltapodus* by dacentrurines. This hypothesis is found here to be more supported than the reverse, but at this point can only be suggested and not be confirmed with the available data. Indeed, stegosaurines and dacentrurines do not offer osteological differences that could be used to conclusively assign each to these ichnogenera, as the autopodium skeleton is a case of the most homologous among stegosaurs (Galton, 1985; Maidment *et al.*, 2008), and the complete dacentrurine pes remains unknown so far (Galton, 1985; Mateus *et al.*, 2009). This hypothesis may be representative and correlate with the origin of these clades – that dacentrurines originated in Europe and stegosaurines in North America sometime in the Middle Jurassic –, and, as a landbridge connected the two continents in the Callovian-Oxfordian (Mateus, 2016), some members of each groups transitioned to the other continent, resulting, from the Late Jurassic, in the occasional stegosaurine occurrences in Europe and dacentrurine occurrences in North America. However, these origins can only be suggested too, as no strong evidence of ancestors to these respective stegosaur clades has been found from before the Late Jurassic. The current evidence for this hypothesis does not rule out the alternative hypothesis that both stegosaurines, dacentrurines, and maybe other stegosaurs could leave both *Deltapodus* and *Stegopodus* tracks, being the differences in these ichnogenra due to other factors than taxonomy.

In Asia, *Wuerhosaurus* is the only stegosaur known from the Tugulu Group, and stegosaur remains (potentially *Wuerhosaurus* isp.) has been recovered from the same strata that preserved the track site of *D. curriei*, but *Wuerhosaurus* was not proposed as possible trackmaker of *D. curriei* since no evidence support that hypothesis (Xing *et al.*, 2013). In this case, this track could have been made by a currently unknown dacentrurine, or *Wuerhosaurus* left tracks closer in morphology to those from dacentrurines than other stegosaurines, or, alternatively, that stegosaurines could leave *Deltapodus* tracks too. The only stegosaurian tracks reported from Gondwana, found in Morocco (Gierliński *et al.*, 2009; Belvedere & Mietto, 2010), have not been referred so far to a specific trackmaker, as there was no stegosaurian known skeletal material from the country, nor Africa, until *Adratiklit boulahfa* Maidment *et al.*, 2020 was recently reported. In their phylogeny, the authors found this new species more closely related to dacentrurine stegosaurs than other stegosaur taxa (Maidment *et al.*, 2020).

5. Conclusions

During this study, 38 footprints were described from the Late Jurassic of Portugal, including 32 stegosaur tracks, one undetermined track, three sauropod tracks, the first record of an ankylosaurian track, and a basal thyreophoran track. All tracks have been photographed and modelled in digital 3D through photogrammetry. Some of these present impressions of skin scales, alike but distinguishable from sauropods, while similar to birds. Most of the tracks present vertical striations, resulting of the movement during the step, which allow a glimpse into the mechanics of walking. One case presents marks of the complete walking process, including entry and take off the pes. Considering the shape, size, skin scales, and limb movement, the conclusions herein are consistent with previous studies on *Deltapodus* tracks. Finally, the stegosaur track record suggests that these dinosaurs were probably common in the Upper Jurassic of Portugal, and their geographic distribution compared with the skeletal record suggests that most likely *Deltapodus* tracks were made by dacentrurine trackmakers, such as *Miragaia*, while *Stegopodus* were made by stegosaurine trackmakers.

6. Supplementary Information

Pdfs containing the 3D models (Supplementary Information 1), and the anterior, lateral, plantar, medial and, posterior (Supplementary Information 2) views of the tracks are available in the Ciências da Terra Web Page (https://cienciasdaterra.novaidfct.pt).

Acknowledgments

We are grateful to Jesper Milàn in his participation on the discovery and collection of most of the tracks in this study; to Alexandra Tomás (Museu da Lourinhã) for the access to the specimens from the museum collection; and to Museu da Lourinhã, for providing us with the equipment and location for this study. Alexandre R. D. Guillaume (SFRH/BD/144665/2019) and Francisco Costa (SFRH/BD/148035/2019) hold each a doctoral grant funded by the Fundação para a Ciência e Tecnologia (FCT-MCTES) of Portugal.

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