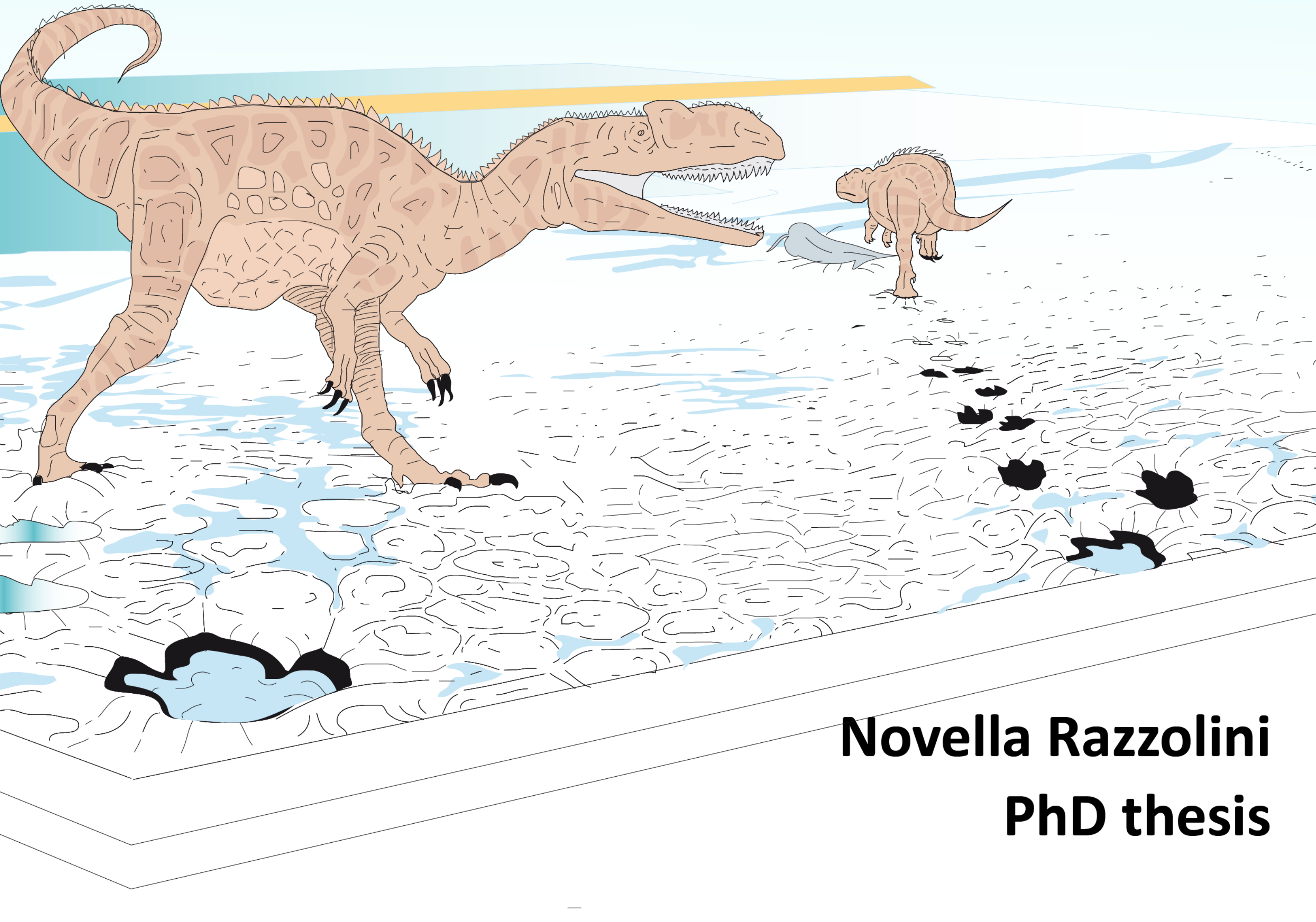
Morphological variation and ichnotaxonomy of dinosaur tracks

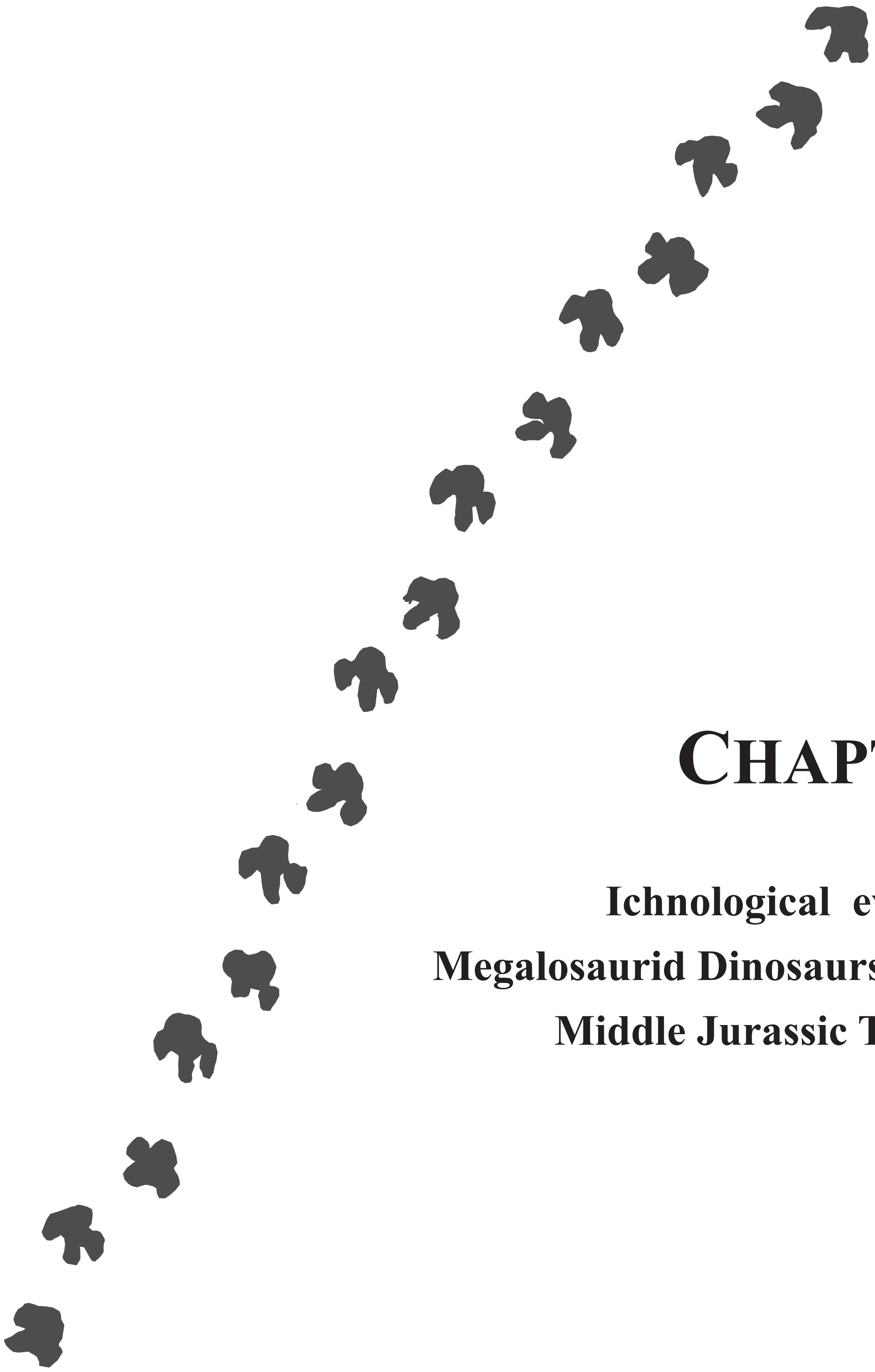
Linking footprint shapes to substrate and trackmaker's anatomy and locomotion



Novella Razzolini
PhD thesis

Part 4

Track morphological variation and Trackmaker's locomotion



CHAPTER 7

Ichnological evidence of Megalosaurid Dinosaurs Crossing Middle Jurassic Tidal Flats

AUTHOR'S CONTRIBUTION

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The author, N.L. Razzolini designed the project, undertook photogrammetry in the field, built the field 2-D map, performed sedimentary analyses, wrote the manuscript and prepared figures and tables.

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Ichnological evidence of Megalosaurid Dinosaurs Crossing Middle Jurassic Tidal Flats

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Novella L. Razzolini[1], Oriol Oms[2], Diego Castanera[3], Bernat Vila[1,4], Vanda Faria dos Santos[5] & Àngel Galobart[1,4]

A new dinosaur tracksite in the Vale de Meios quarry (Serra de Aire Formation, Bathonian, Portugal) preserves more than 700 theropod tracks. They are organized in at least 80 unidirectional trackways arranged in a bimodal orientation pattern (W/NW and E/SE). Quantitative and qualitative comparisons reveal that the large tridactyl, elongated and asymmetric tracks resemble the typical Late Jurassic-Early Cretaceous *Megalosauripus* ichnogenus in all morphometric parameters. Few of the numerous tracks are preserved as elite tracks while the rest are preserved as different gradients of modified true tracks according to water content, erosive factors, radial fractures and internal overtrack formations. Taphonomical determinations are consistent with paleoenvironmental observations that indicate an inter-tidal flat located at the margin of a coastal barrier. The *Megalosauripus* tracks represent the oldest occurrence of this ichnotaxon and are attributed to large megalosaurid dinosaurs. Their occurrence in Vale de Meios tidal flat represents the unique paleoethological evidence of megalosaurids moving towards the lagoon, most likley during the low tide periods with feeding purposes.

Megalosaurid dinosaurs were the dominant tetanuran theropods in the Middle Jurassic age[1], a time period generally featured by the scarcity of dinosaur fossils worldwide[2]. For this period of time, most of the theropod European record is assigned to the Megalosauridae family based on skeletal remains from France, England and Scotland[3–9]. In addition, the ichnological record, mostly concentrated in England, Scotland and Portugal[10–13] preserves various large track morphotypes that fit into the approximate size of *Megalosaurus*, a characteristic mid-to-large basal megalosaurid from the Bathonian of England[6,7]. The Lusitanian basin in West-Central Portugal bears two temporally significant theropod tracksites of Bathonian age: Algar dos Potes and Vale de Meios tracksites. Because of the poor dinosaur record in the Middle Jurassic, the description of new localities represents a very significant contribution to understand the composition of dinosaur faunas of that age. Particularly, the occurrence of new fossil evidence potentially related to megalosaurid theropods increases the knowledge of the clade in terms of diversity, taxonomy, behaviour and environmental distribution. New data from tracks and trackways is also of pivotal importance to ascertain trackmaker affinity and habitat. The aim of the present study is to formally describe the Vale de Meios tracksite (Figs 1–3), one of the largest theropod tracksites described worldwide from the Middle Jurassic. For this purpose we provide a detailed sedimentary analysis and an exhaustive description of the track morphology, preservation and ichnotaxonomy. Moreover, paleoenvironmental and paleoethological reconstructions are provided on the basis of the unique orientation and arrangement of the trackways on the tidal flat.

Materials and Methods

Two field campaigns in 2014 and 2015 produced a 2D cartography and photogrammetric models of the most interesting trackways and track morphologies (see Supplementary Information for three-dimensional models) at the Vale de Meios locality (Fig. 3). The whole outcrop was divided into 5 × 5 m squares and each square was provided with a letter and a number in order to locate tracks with x, y coordinates (Fig. 3A). Photogrammetric

[1]Mesozoic Research Group, Institut Català de Paleontologia 'Miquel Crusafont', C/ Escola Industrial 23, 08201 Sabadell, Catalonia, Spain. [2]Universitat Autonoma de Barcelona, Facultat de Ciències (Geologia), 08193, Bellaterra (Spain). [3]Bayerische Staatssammlung für Paläontologie und Geologie and GeoBioCenter, Ludwig-Maximilians-Universität, Richard-Wagner-Str. 10, 80333 Munich, Germany. [4]Museu de la Conca Dellà, carrer del Museu, 4, 25650, Catalonia, Spain. [5]Museu Nacional de História Natural e da Ciência – Universidade de Lisboa, Rua da Escola Politécnica, 58, 1250−102 Lisboa, Portugal. Correspondence and requests for materials should be addressed to N.L.R. (email: novella.razzolini@icp.cat)

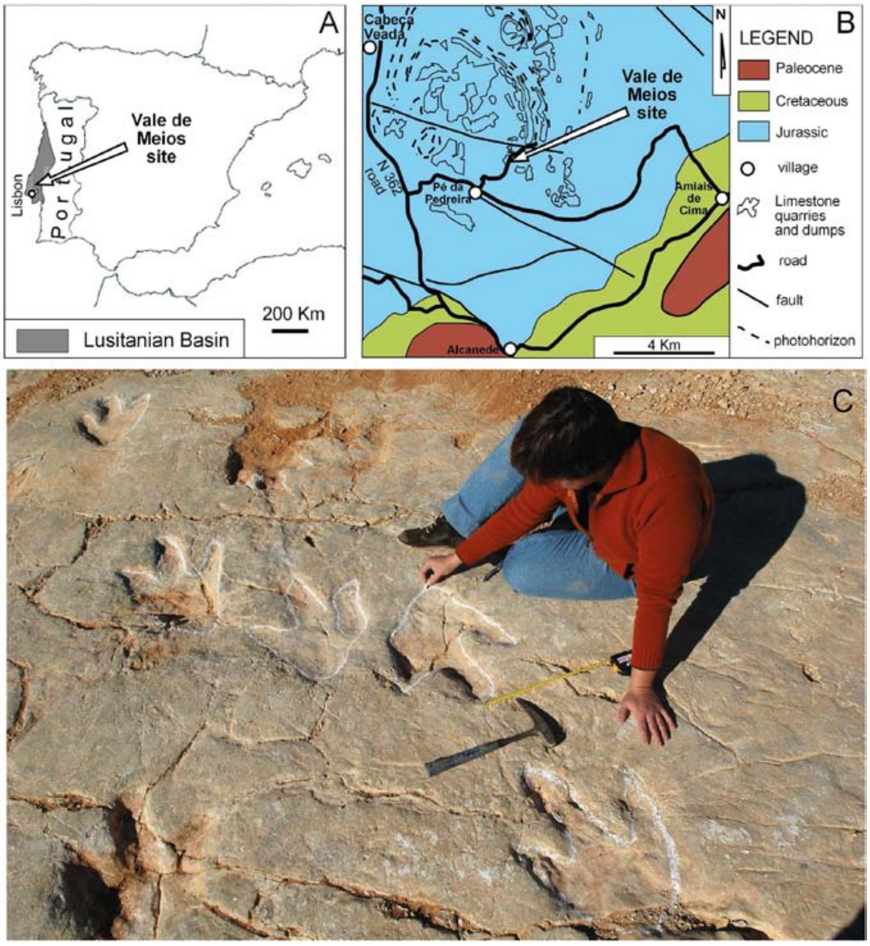

Figure 1. Geographical and geological setting of the Vale de Meios tracksite within the Lusitanian basin. (**A**) Outiline drawing of the Iberian Peninsula with location of Lusitanian Basin and the Vale de Meios site. Drawing originated through Adobe Illustrator CS5, version 15.1.0, www.adobe.com. (**B**) Compound of local geology and geography redrawn from Carvalho *et al.*[17] and originated through Adobe Illustrator CS5, version 15.1.0, www.adobe.com. (**C**) Part of the tracking surface of the Vale de Meios site. (Original drawings by O.O. and original photo by Luis Quinta).

models of tracks and three trackways (VM1, VM2 and VM3; Fig. 3B) were undertaken with Canon PowerShot G12 camara (focal length 6 mm, 3648 × 2432 resolution) following the general methodology of Mallison and Wings[14]. Point clouds were processed in AgisoftPhotoscan standard version 1.1.4. build 2021 software (http://www.agisoft.ru/). Photogrammetric models presented in this work count on 14 photos for track VMX.1 (0.6 mm of resolution), 15 photos for track VMX.2 (0.6 mm resolution), 209 photos for trackways VM1 and VM2 (2.25 mm of resolution) and 229 photos for trackway VM3 (2.25 mm of resolution). All these models are available as Supplementary Information files. Three-dimensional models were converted to colour maps in the open source CloudCompare software (v.2.6.1, http://www.danielgm.net/cc/). Contour lines (isolines) were obtained in free software Paraview 4.4.0 version (http://www. paraview.org/), importing scaled and oriented models with respect to the Z axis from CloudCompare (v.2.6.1) and they were set every 0.8 mm distance according to maximum and minimum heights of the plane where tracks are. Track length (TL) and width (TW), track ratio (TL/TW), inter-digital angles II^III and III^IV, pace length (PL), stride length (SL), pace angulation (ANG) were measured from trackway photogrammetries (Tables 1 and 2). Furthermore, in order to compare individual tracks, we calculated the anterior triangle ratio[15] as a way to explore the morphodynamic relationship between the mesaxonic index and the anterior shape of the studied tracks. The anterior triangle (AT) is an index measured from the distal point on the digital pads of digits II, III and IV and not from claw marks, which may be variably preserved[15]. The

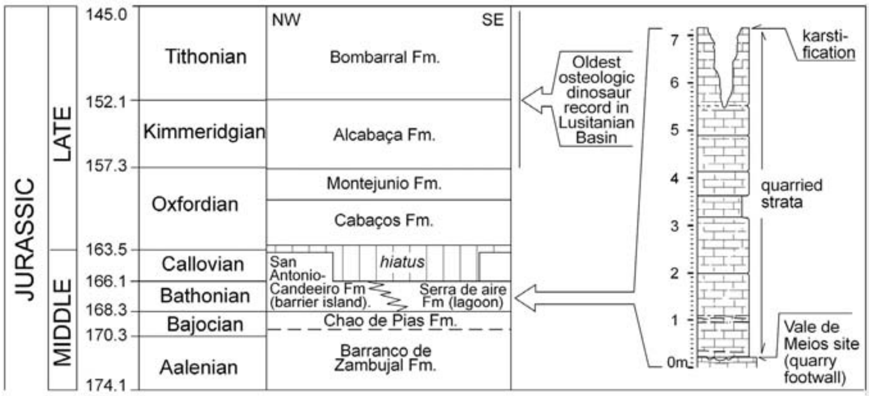

Figure 2. Local stratigraphy at Vale de Meios site and correlation with the stratigraphy of the Middle and Late Jurassic of the Maciço Calcareo Extremenho (Carvalho *et al.*[17], center). Left: chronology *sensu* Grandstein *et al.*[65].

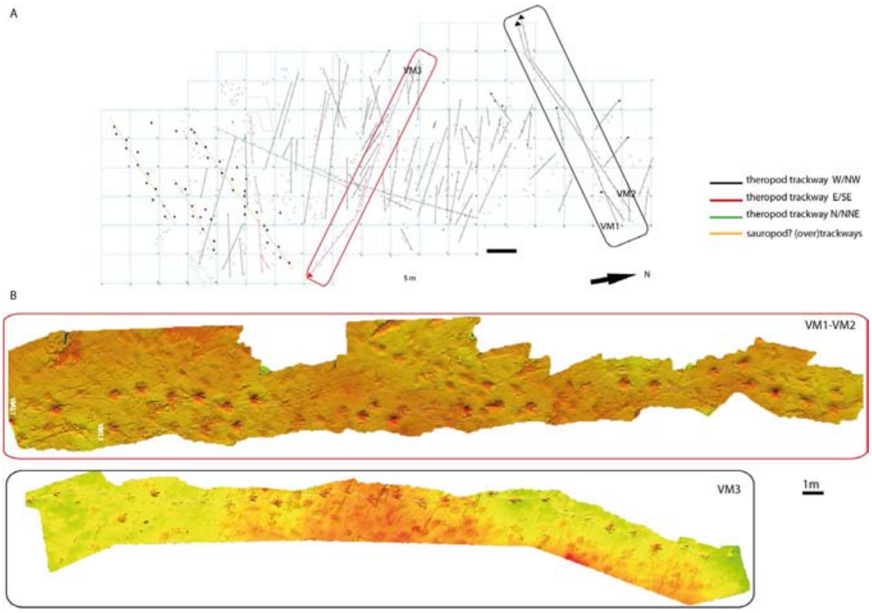

Figure 3. Cartography of the Vale de Meios site and photogrammetric models of three analysed trackways. (**A**) 2-D cartography of the Vale de Meios site, trackways directions indicated in the legend with different colours (black, red, green and orange). (**B**) 3-D photogrammetry models undertaken for three analysed trackways VM1, VM2 and VM3. See Supplementary Information for three-dimensional models visualization of trackways VM1, VM2 and VM3.

maximum height of the triangle is measured perpendicular to the transverse base of the triangle and expressed as the l/w ratio (AT l/w).

Sediment samples (IPS87258, IPS87264, IPS87259) were collected both on the track surface level and the infill inside the tracks (squares A10 and B5, Fig. 3A), and 10 thin sections were prepared for sedimentological (microfacies) and environmental determinations.

TRACKWAY	TL	TW	TL/TW	PL	SL	P.ANG
VM1.1	59,5	54,7	1,1		297,9	161
VM1.2	60,6	54,2	1,1	134,2	321,8	168
VM1.3	61,2	53,6	1,1	163,5	330,3	165
VM1.4	59,1	51,6	1,1	161,1	316,0	164
VM1.5	54,3	42,5	1,3	165,5	313,9	157
VM1.6	51,2	40,9	1,3	158,9	322,9	158
VM1.7	58,4	54,3	1,1	165,6	322,6	160
VM1.8	60,2	51,6	1,2	156,7	324,1	151
VM1.9	60,6	53,1	1,1	181,3	297,7	153
VM1.10	52,2	46,9	1,1	165,5	304,1	138
VM1.11	59,7	50,1	1,2	157,6	367,3	155
VM1.12	63,2	45,8	1,4	178,2	387,5	161
VM1.13	100,8	50,5	2,0	225,1	333,2	149
VM1.14	66,6	45,8	1,5	175,2		175
VM1.15	64,9	52,6	1,2	169,6	323,2	
VM1.16						
VM1.17	60,5	56,3	1,1			
VM1.18	57,7	50,5	1,1	153,0	311,3	
VM1.19	56,5	54,6	1,0	163,2	305,3	
VM1.20	68,8	52,4	1,3	151,7	342,2	
VM1.21	65,4	55,7	1,2	192,6	313,2	
VM1.22	61,1	54,4	1,1	138,1	293,2	
VM1.23	83,9	51,8	1,6	167,0	308,8	
VM1.24	69,1	50,5	1,4	141,0		
AVERAGE	**63,3**	**51,1**	**1,2**	**165,0**	**321,8**	**158**
SD	**10,6**	**4,1**	**0,2**	**19,6**	**23,0**	**9,01466073**
SPEED				**1,541 m/s**	**5,547 Km/h**	
VM2.1	60,1	47,1	1,3		233,3	128
VM2.2	58,2	54,5	1,1	135,4	255,4	139
VM2.3	61,7	44,7	1,4	120,8	306,8	142
VM2.4	74,6	50,6	1,5	155,7	300,3	171
VM2.5	83,4	52,7	1,6	159,3	295,6	150
VM2.6	73,7	63,9	1,2	145,5	296,4	169
VM2.7	63,2	62,1	1,0	167,5	287,0	160
VM2.8	68,0	52,2	1,3	141,1	278,2	144
VM2.9	60,6	47,3	1,3	158,9	285,2	149
VM2.10	54,1	49,8	1,1	155,4	305,8	154
VM2.11	72,5	59,8	1,2	147,0	307,0	150
VM2.12	76,2	65,3	1,2	165,3	309,2	154
VM2.13	79,9	61,3	1,3	156,0	306,0	155
VM2.14	72,3	58,9	1,2	161,3	303,5	156
VM2.15	80,6	46,3	1,7	148,7	317,0	126
VM2.16	75,3	60,6	1,2	157,8		135
VM2.17	65,3	59,8	1,1	169,9		165
VM2.18						166
VM2.19						
VM2.20	84,6	48,7	1,7			
VM2.21	65,1	48,6	1,3	177,2		
VM2.22	81,6	56,5	1,4	155,6	322,6	
VM2.23	72,8	56,7	1,3	170,1	306,8	
VM2.24	74,2	57,6	1,3	200,6	332,9	
VM2.25	76,5	63,8	1,2	169,3	365,7	
VM2.26	69,0	48,4	1,4	143,2	294,0	
VM2.27	82,1	61,5	1,3	210,8	323,5	
VM2.28	80,4	57,6	1,4	163,0	348,7	
AVERAGE	**71,8**	**55,2**	**1,3**	**159,8**	**303,7**	**151**
SD	**8,6**	**6,3**	**0,2**	**19,0**	**28,0**	**13,2465651**
Continued						

TRACKWAY	TL	TW	TL/TW	PL	SL	P.ANG
SPEED				**1,145 m/s**	**4,121 Km/h**	
VM3.1	37,8	25,3	1,5			
VM3.2				99,3	183,9	
VM3.3						
VM3.4	36,6	27,1	1,4			159
VM3.5	32,7	22,1	1,5	92,2		147
VM3.6	35,9	29,1	1,2	90,5	181,5	148
VM3.7	35,7	24,8	1,4	96,4	172,9	152
VM3.8	35,1	30,1	1,2	94,0	184,5	152
VM3.9	33,7	29,8	1,1	99,4	193,1	150
VM3.10	39,2	31,8	1,2	95,0	181,4	165
VM3.11	38,7	32,0	1,2	96,0	183,6	171
VM3.12	37,0	24,0	1,5	86,6	173,6	147
VM3.13	38,8	31,3	1,2	100,3	179,4	145
VM3.14	35,6	34,7	1,0	94,9	183,5	148
VM3.15	40,7	32,0	1,3	92,6	177,3	149
VM3.16	40,1	29,0	1,4	101,7	182,9	161
VM3.17	37,6	34,7	1,1	98,1	185,8	136
VM3.18	45,9	26,3	1,7	92,7	180,4	133
VM3.19	38,6	22,3	1,7	176,9	160,8	152
VM3.20	52,9	14,5	3,6	92,4	195,0	130
VM3.21	34,2	28,2	1,2	114,3	189,1	149
VM3.22	29,1	27,1	1,1	81,2	168,6	159
VM3.23	36,5	32,2	1,1	91,2	186,0	158
VM3.24	38,9	36,6	1,1	91,1	187,9	152
VM3.25	32,6	28,5	1,1	94,0	183,6	140
VM3.26	39,6	34,0	1,2	96,1	186,5	153
VM3.27	38,5	29,0	1,3	92,6	191,6	151
VM3.28	41,8	26,1	1,6	98,6	182,5	
VM3.29	49,5	34,4	1,4	97,4		
AVERAGE	**38,3**	**28,8**	**1,4**	**98,3**	**182,3**	**150**
SD	**5,0**	**4,8**	**0,5**	**17,1**	**7,7**	**9**
SPEED			**1,022 m/s**	**3,679 Km/h**		

Table 1. Complete measurements in centimeters (TL, SL, PL), angles (PANG) and ratio indexes (TL/TW and AT l/w) from trackways VM1, VM2 and VM3. Speed equation following Alexander[66] formula V = 0.25 g^0.5*SL^1.67*H^−1.17.

TRACKWAYS	TL	TL/TW	AT l/w	SL	PL	PANG
VM1	63.28	1.24	0.46–0.48	321.81	164.97	158°
VM2	71.77	1.31	0.40–0.48	303.66	159.79	151°
VM3	38.27	1.39	0.26–0.27	182.30	98.29	150°

Table 2. Average measurements in centimeters (TL, SL, PL), angles (PANG) and ratio indexes (TL/TW and AT l/w) from trackways VM1, VM2 and VM3.

Geological and Geographical setting. The Vale de Meios locality is found in the Middle Jurassic micritic limestones from the Maciço Calcário Estremenho (Limestone Massif of Estremadura, Lusitanian Basin), which encompasses the relief area of the central-west part of Portugal. The strata containing the analysed track were deposited in the eastern margin of the Protoatlantic Ocean, formed as a result of the rifting that started in the Midde Jurassic. At those times, the western part of the Iberian plate (present Portugal) contained the Lusitanian Basin, infilled by shallow marine carbonates (limestones and dolostones) and in the lower part by marly-limestones and marls[16,17].

Sedimentologically, the Middle Jurassic series from Portugal mainly include high-energy deposits originated in barrier-islands paleoenvironments and lagoonal and peritidal deposits formed within the protected areas of the internal back-barrier. Azerêdo *et al.*[18] suggested a depositional model for the Middle Jurassic of the Lusitanian Basin with an E/SE to W/NW carbonated-ramp system. During the Bajocian-Bathonian interval (Fig. 2), the eastern part of the basin was characterized by margino-marine and confined lagoon environments suggesting a system progradation from east to west[16]. The barrier island environment is represented by the Santo

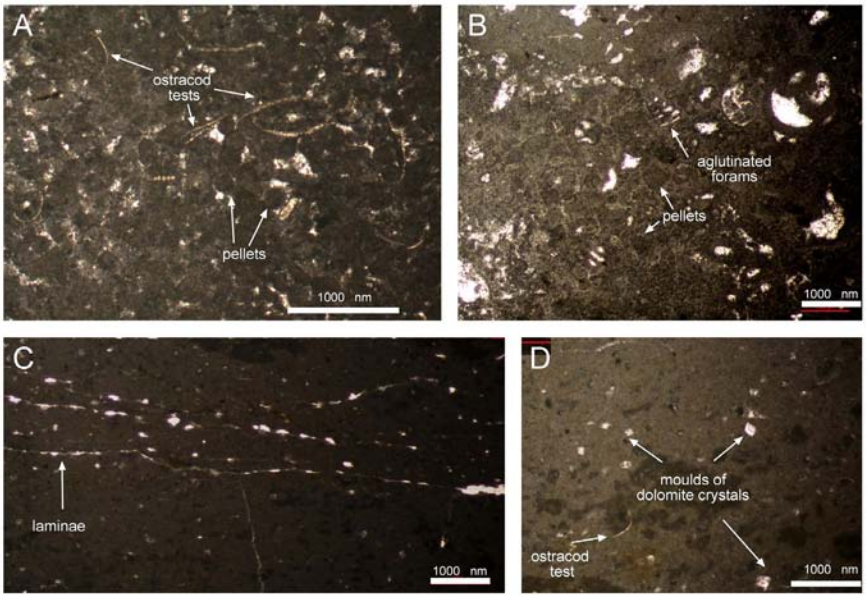

Figure 4. Thin sections of sediment samples IPS87258, IPS87264 and IPS87259 collected both on track surface level and tracks overfill. (**A,B**) massive limestone, (**B,C**) laminated limestone. Scale bar 1000 nm.

António-Candeeiros Formation, while the associated lagoonal and peritidal ones are represented by the Serra de Aire Formation. This last formation contains the Vale de Meios tracksite here reported, which is Bathonian in age after the occurrence of agglutinated foraminifera (i.e. *Alzonella cuvillieri*[19]).

Our sedimentological observations are in agreement with this scheme[16]. In the tracking surface two different kinds of limestones are present: a) massive limestone where footprints are produced; b) laminated limestone found as internal overtracks (*sensu* Marty[20]). Each of these two different types has distinct features when observed in thin sections (see examples in Fig. 4).

(a) *Massive limestone* (IPS87258, Fig. 4A; IPS87264, Fig. 4B). They correspond to grainstones[21] with pellets, ostracods tests and agglutinated foraminifera as main components. Although both fossils are found together, there is always a dominant one. When ostracodes are abundant (Fig. 4A), foraminifera are scarse and viceversa (Fig. 4B). This suggests small salinity variations within a similar environment, since ostracods are rather euryhaline (i.e, tolerant to such variations) if compared with foraminifera, which are more stenohaline (less tolerant), see pag. 618 of Flügel[22].
No lamination is observed. Sparitic and micritic matrix are found, therefore this microfacies can be classified both as pelbiosparite and pelbiomicrite, respectively[23]. In fact, both kinds of matrix are observed in a single thin section (Fig. 4A,B).

(b) *Laminated limestone* (IPS87259, Fig. 4C,D). They correspond to mudstones[21] where ostracodes tests are abundant and foraminifera are absent. Micrite aggregates (peloids) are found and no strict pellets are observed. According to the components, this microfacies can be classified as pelbiomicrites[23]. Lamination is also visible in thin section (Fig. 4C) as clotted micrite layers with irregularly elongated, laminated fenestral pores (probably resulting from the deterioration of organic matter). This microfacies contains small isolated unimodal and euhedral relics of rhombohedrons, which are likley to have belonged to dolomite crystals[24] (see Fig. 4D).

Both microfacies would belong to the standard microfacies SMF 16: a) non-laminated peloid grainstone and packstone and b) laminated peloidal bindstone[22].

As a general observation, both microfacies display no mud-cracking evidence, meaning that the tracking surface did not undergo a strong dessication and therefore the tracking surface was a moisture-laden sediment. This does not exclude that some initial dessication cracks may be present at the Vale de Meios tracksite. In any case, cracking due to dinosaur activity seems to be the number one cause of non-tectonic cracking.

The Vale de Meios tracksite. The Vale de Meios tracksite (Figs 1–3) was first discovered in 1998 by the technicians of the natural park of the Serra de Aire e Candeeiros. Since its discovery, researchers of the National Museum of Natural History and Science (Lisbon, Portugal) presented preliminary evaluations on the site[13,16,25]. The locality, situated near Pé da Pedreira village (Alcanede, West-Central Portugal; 39°27'30.26“N, 8°49'11.07“W) has a total area of 7,500 m^2 (Fig. 3). The area shown in the map is of 4,275 m^2, with a total number of 711 recorded

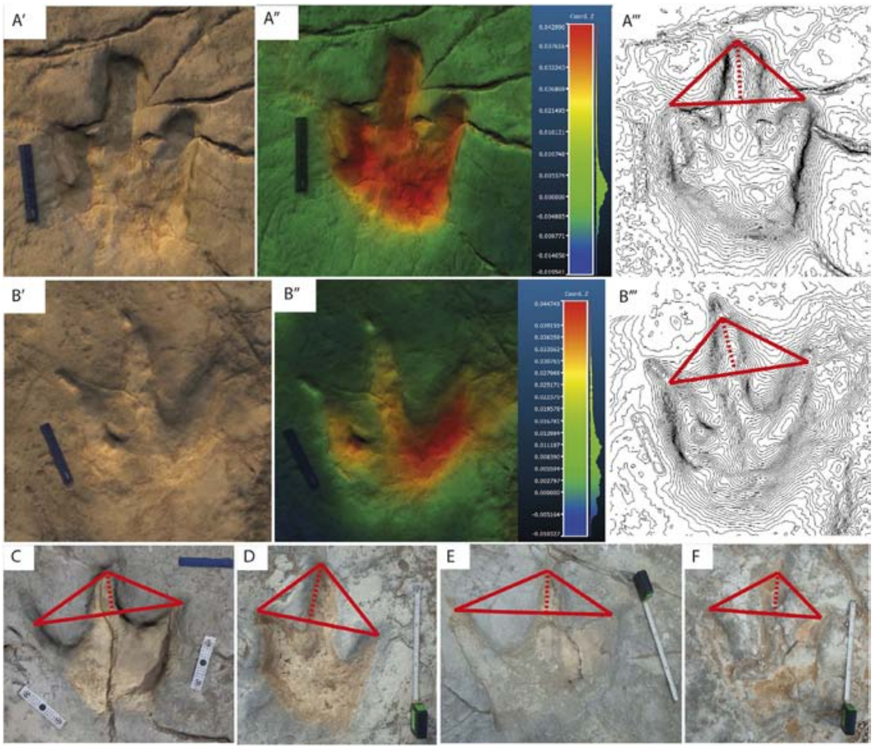

Figure 5. Morphometric comparison among track morphologies in the Vale de Meios tracksite. Triangles are drawn following Lockley[15], showing the index of mesaxony with the anterior triangle l/w relationship (AT l/w). A‴ track VMX.1, 0.462, B‴ track VMX.2, 0.351 (**C**) 0.278, (**D**) 0.486, (**E**) 0.267, (**F**) 0.368. Scale bar in (**A–C**), 15 cm; scale bar in (**D–F**) 30 cm. See supplementary Information for three-dimensional models visualization of tracks VMX.1 and VMX.2.

theropod tracks (but more than 3,000 estimated) organized in more than 80 trackways (Fig. 3A). The trackways are long (trackway lengths range from 30 to 40 meters) and show straight (unidirectional) paths with a bimodal orientation pattern. From the directional analyses we distinguished more than 10% of the trackways with an E/SE orientation while the majority of the trackways following the opposite W/NW orientation. There are some crossing areas between different trackways; most of them correspond to crossing trackways orientated in opposite directions. No evidence of trackways turning back or re-crossing themselves have been observed.

Systematic paleontology. *Megalosauripus isp*. Material. trackways VM1 (24 tracks), VM2 (28 tracks) and VM3 (29 tracks), two isolated tracks (VMX.1, VMX.2 illustrated in Fig. 5A′B′) and trackways VM4-VM80 from the 2-D cartography map in black, red and green colour (Figs 3A and 5C–F).

Locality. Vale de Meios tracksite, Pé da Pedreira (village nearby), Alcanede, West-Central Portugal.

Horizon. Serra de Aire Formation (Bathonian).

Description. Tracks are tridactyl, sometimes tetradactyl (hallux impression, Figs 6I,K and 7H), large (TL range from 22 cm to more than 80 cm), elongated (TL/TW ranges from 1.24 to 1.39) and asymmetric. The mesaxonic index ranges from weak mesaxony, implying a short developement of digit III or a longer distance between digit impressions II-IV to a stronger mesaxony, with a long development of digit III or shorter distance between digit impressions II-IV (anterior triangle l/w ranges from 0.26 to 0.48, Fig. 5A–F). They are featured by the general absence of clear pad impressions, although they do display them in tracks VMX.1 and VMX.2 (Fig. 5A′,B‴ and Supplementary Information for three-dimensional models), the presence of pointed claw marks, a slightly sigmoidal impression of digit III and a squared U-shaped metatarso-phalangeal impression. Interdigital angles are variable along a trackway, with general low values for both II^III and III^IV (minimum 22° maximum 40°) reflecting a minor parallelism of digits on the distal anterior half of the track. The difference between interdigital angles II^III and III^IV is usually less than 10°. Pace length and pace angulation are very irregular (e.g. in

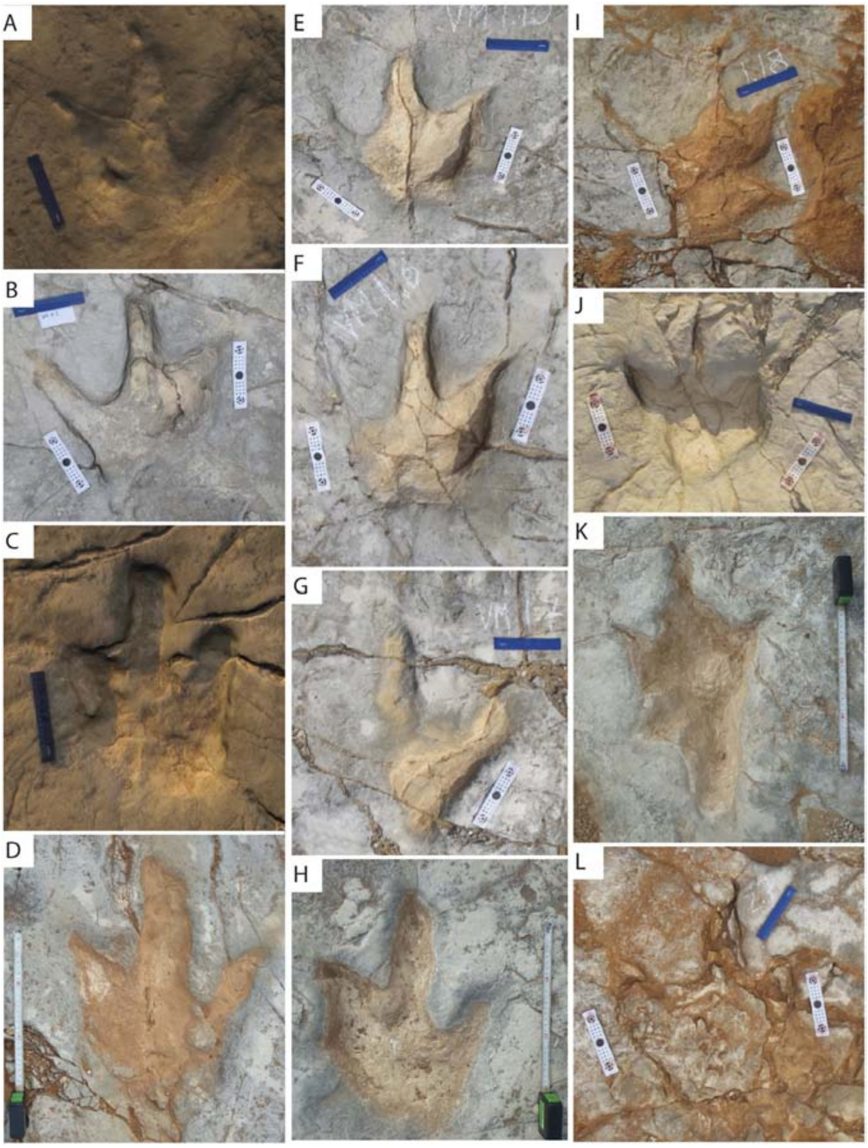

Figure 6. Different preservations observed in the Vale de Meios tracksite. (**A–D**) True tracks with degree of preservations between 2 and 3 (following Belvedere and Farlow[37]). (**H,I**) modified true tracks preservation. (**I,L**) true tracks with mud collapsing. This type of preservation of tracks accounts for the 5%, 75% and 20%, respectively in the whole tracksite.

trackway VM1, pace length SD ± 19.6, pace angulation SD ± 9.01, Table 1), with an inward rotation of the distal end of digit III impression with respect to the trackway middle line. Trackways VM1 (24 tracks) and VM2 (28 tracks) are directed toward W/NW and measure 35 and 40 meters respectively, while trackway VM3 (29 tracks) is directed toward E/SE and it measures 30 meters in total lengths. See Table 1 for full measurements, Table 2 for average measurements and Supplementary Information for three-dimensional models.

Remarks. Tracks from the Vale de Meios tracksite are here compared with the main valid large theropod ichnotaxa regardless of the geography and time-period (Fig. 8). *Kayentapus*[26] (Fig. 8A) do not fit into the studied

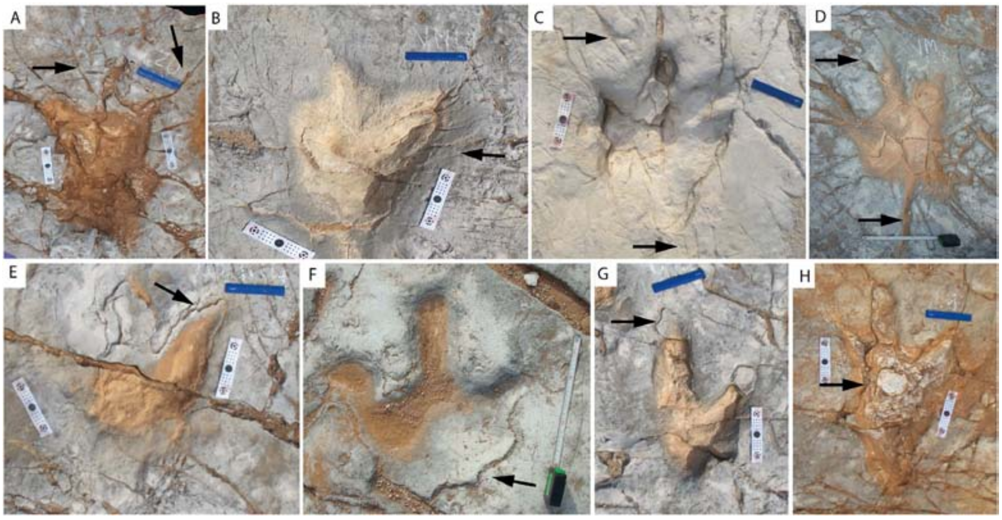

Figure 7. All types of preservations can display two associated features. (**A–D**) radial fractures; (**E–H**) internal overtrack (*sensu* Marty[20]).

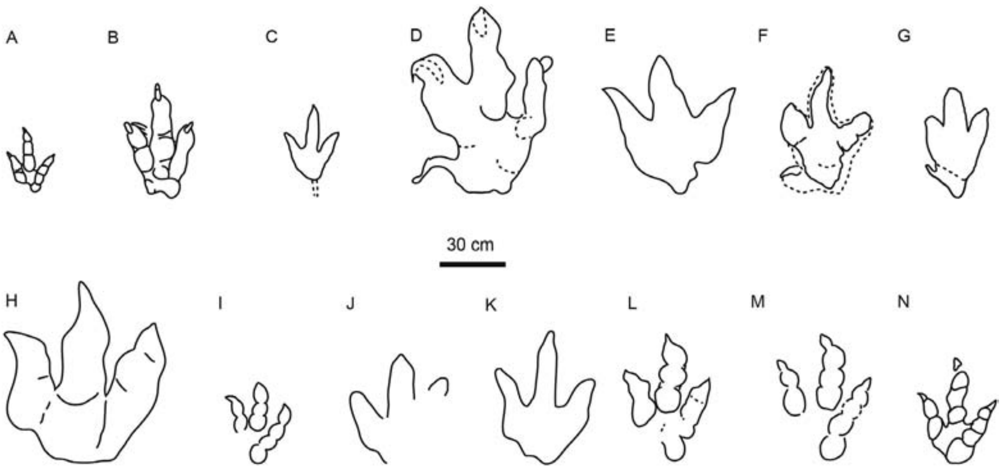

Figure 8. Redrawn outlines of the main large theropod ichnotaxa all to scale (30 cm). Left tracks are mirrored as right footprints. Drawing originated through Adobe Illustrator CS5, version 15.1.0, www.adobe.com. (**A**) *Kayentapus*[26]; (**B**) *Eubrontes*[27], (**C**) *Irenesauripus*[29], (**D**) *Tyrannosauripus pillmorei*[30], (**E**) *Bellatoripes fredlundi*[31], (**F**) *Bueckeburgichnus maximus*[32], (**G**) *Euthynichnium lusitanicum*[34], (**H**) *Iberosauripus grandis*[33], (**I**) *Megalosauripus uzbekistanicus*[35] (**J**) *Megalosauripus*-like[13], (**K**) *Megalosauripus*-like[12], (**L**) *Megalosauripus* from Arizona[34], (**M**) *Megalosauripus* from Utah (*sensu* Lockley *et al.*[34]), (**N**) *Megalosauripus*-like from Morocco[36] (All drawings redrawn by NLR).

tracks because of the smaller size, the higher TL/TW index, the wider width of the interdigital angles (considering variations) and the presence of diagnostic phalangeal pad formula, not consistently appreciable in Vale de Meios. Furthermore, TL/TW index in the studied tracks ranges from 1.24 to 1.40, differing greatly from that of *Grallator* (2.64 in Olsen *et al.*[27]) and *Eubrontes* (1.70 in Olsen *et al.*[27]; Fig. 8B). The AT l/w relationship for *Eubrontes* (0.58; Lockley[15]) and *Grallator* (1.22; Lockley[15]) display a much stronger mesaxony than the Vale de Meios tracks (from 0.26 to 0.48). Though, *Eubrontes* type tracks are of significantly varied morphologies in Jurassic and Lower Cretaceous formations in China, such as generally low TL/TW like 1.4 in Hanxi tracksite[28]. *Irenesauripus*[29] (Fig. 8C) from the Aptian–Albian of Canada strongly differs with the Vale de Meios tracks in the very narrow and slender digits and the larger interdigital angle. Besides some similarities in size and proportions of the 86-cm-long *Tyrannosauripus pilmorei* track[30] (Fig. 8D) and the recently erected new ichnogenus and ichnospecies *Bellatoripes fredlundi*[31] (Fig. 8E) from the Upper Cretaceous of North America, they differ from the Vale de Meios tracks especially on the robustness of the digit impressions, which are proximally wide and strongly taper distally, on the lack of a clear phalangeal pad formula and in wider metatarsal pad trace. The emended *Bueckeburgichnus maximus* track[32] (Fig. 8F) from the Lower Cretaceous of Germany is similar to the Vale de Meios tracks in size (TL: 56 cm) and in the medially-directed hallux impression, but they clearly differ in the presence of a more massive metatarsal area, in the lateral digits broadness and divergence of digit IV and in the longer digit III impression resulting in a stronger mesaxony (> 0.55)[33]. *Eutynichnium lusitanicum*[34] (Fig. 8G) is another large theropod described from the Late Jurassic of Portugal and diagnosed on the presence of an anteriorly oriented hallux, short metarsal and stocky and non taper digits impressions. Nontheless, in the few tetradactyl tracks preserved in the Vale de Meios tracksite, the hallux is medially oriented (Fig. 6I,K), the metatarsal is elongated (Fig. 7H) and digit impressions are slender and taper.

The Vale de Meios tracks encompass *Iberosauripus grandis*[33] (Tithonian-Berriasian, Spain; Fig. 8H) in their minimum values for the TL/TW ratio (1.30; Vale de Meios: 1.24–1.40), AT l/w relationship (0.30; Vale de Meios: 0.26–0.48) and interdigital angles II^III and III^IV (<20°; Vale de Meios: >20°). The main morphological differences noticed are the broadness of the toes, the pad presence and the general symmetry of *Iberosauripus grandis*.

The Vale de Meios tracks display similar values with *Megalosauripus uzbekistanicus* (Fig. 8I) for the TL/TW ratio (1.21 in Fanti *et al.*[35]), the interdigital angles are 40° (II^III) and 30° (III^IV) and the AT l/w relationship (0.40 reported in Cobos *et al.*[33]). Furthermore, similar morphological features that *M. uzbekistanicus* shares with the Vale de Meios tracks are the sigmoidal impression of digit III, the presence of hallux (although it is not strictly an ungueal impression *sensu* Fanti *et al.*[35] in the Portuguese tracksite) and the shape of the phalangeal-metatarsal pad impression as observed in Fig. 7B of Fanti *et al.*[35]. The morphology of Middle Jurassic *Megalosauripus*-like tracks from the Cleveland basin[12] (Fig. 8H) and the Ardley Quarry[11] (Fig. 8I) is also very similar to the Vale de Meios tracks in the inward rotation of digit III, the moderate divergence of the weight-bearing toes (II-IV), the average TL/TW index (1.40). Furthermore, Late Jurassic *Megalosauripus*-like morphotypes recognized in Arizona and Utah (Fig. 8L,M; Lockley *et al.*[34]) and Morocco[36] (Fig. 8N) also recall the studied track morphologies.

For similarities with both qualitative and morphometric parameters of *Megalosauripus uzbekistanicus* together with the strong resemblance with the aforementioned *Megalosauripus*-like tracks, the Vale de Meios tracks are here assigned to *Megalosauripus* ichnogenus, representing the oldest occurrence of this ichnotaxon.

The assignment to *Megalosauripus* isp. is based on general morphology and morphometric ratios, irrespective of differences in the track lengths. Therefore, the intra-trackway track length variation discards the possibility that the site was crossed by a stock of taxonomically diverse theropods. This is the reason explaining that the track morphology remains the same among tracks with different sizes. As a result, isolated small-sized tracks could be the reflection of a high variety of preservational modes (due to different stages of substrate consistencies) or to different ontogenetic stages of the trackmakers. Finally, preservation of tracks could be strongly influenced by the tidal cycle, which produced preservations types such as modified true tracks and modified true tracks with mud collapsing through erosion and water saturation respectively.

Tracks preservation. Only few tracks are considered well-preserved while the rest are morphologycally affected by substrate consistency changes or taphonomical processes transforming true tracks with anatomical details and preservation grade between 2 and 3 (following Belvedere and Farlow[37]), into different gradients of modified true tracks according to water content, erosive factors (Fig. 6), primary features (i.e. radial fractures) and secondary features (i.e. internal overtrack formation, Fig. 7). Throughout the outcrop, no clear spatial distribution of these preservational types is observed. Tracks display three different types of taphonomic preservations:

(1) *True tracks with preservation grade between 2 and 3* (Fig. 6A–D). Following Belvedere and Farlow[37], this type of tracks is comprehended between grade 2, in which tracks preserve fairly clear and sharp toe marks, ungual marks and some digital pads recognizable and grade 3, in which all digit impressions are completely sharp and clear, digit walls well defined, ungual marks and distinct digital pads clearly preserved. As a result of the environmental setting, characterized by moist sediment, these types of tracks are not so common at the Vale de Meios tracksite (5%).

(2) *Modified true tracks* (Fig. 6E–H). This type of preservation, as described in Marty[21], is modified by physico-chemical (e.g.,weathering) and/or biological influences after they were made. It is the most abundant type of the site (75%), as it could be expected by the non-laminated nature of the tracking surface. Note that this preservation represents modified true tracks in the sense of Marty[20] and Marty *et al.*[38], that is to say, the track is not morphologically overestimated due to depth propagation.

(3) *Modified true tracks with mud collapsing* (Fig. 6I,L). These tracks result from water-saturated sediments and are evidenced by the collapse of the sediment inside the digits and ocasional metarsal and hallux impressions. It is remarkable that throughout VM1, VM2 and VM3 trackways, the degree of mud collapsing is variable, causing intra-trackway track length variability (*sensu* Razzolini *et al.*[39]).

Preservation of tracks could be strongly influenced by the tidal cycle, which produced preservation grades such as modified true tracks and modified true tracks with mud collapsing through erosion and water saturation respectively.

All three preservation types can display two associated features: radial fractures and internal overtracks (Fig. 7). Radial fractures have been described in literature of general and experimental ichnology[20,38,40,41]. In the Vale de Meios tracksite, radial fractures are found in most of the tracks (Fig. 6 and 7A–D), are always normal to the profile of the print and develop preferentially from the claws outwards. Typically, more than 10 fractures per

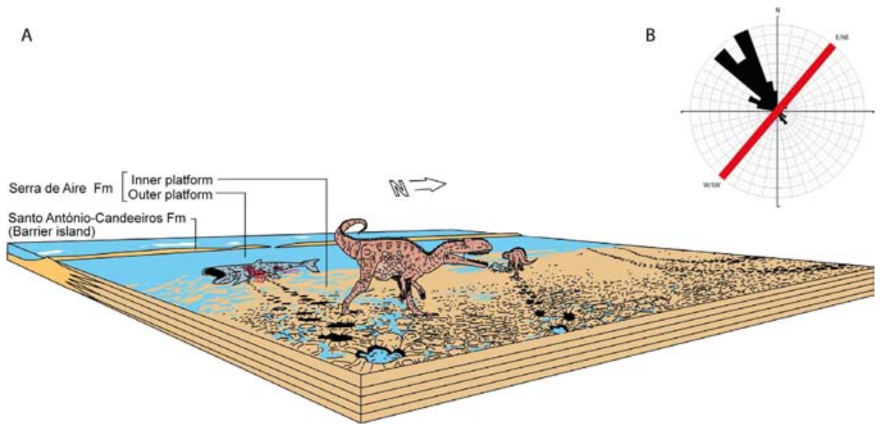

Figure 9. Paleoenvironmental and paleoethological reconstruction of the tidal flat crossed by megalosaurids feeding on exposed carcasses during low tides. Original drawing by Oriol Oms, originated through Adobe Illustrator CS5, version 15.1.0, www.adobe.com. (**A**) Orientation of the coastal barrier extrapolated from Azeredo *et al.*[18] (**B**) Rose diagram with directions of trackways resulted in a unidirectional bimodal orientation, normal to the coastal barrier one. Red line is the orientation of the barrier island.

track are observed and they may branch out. They reach a longitude of up to 50 cm and the width of the open space is variable, but generally less than 0.5 cm. These structures are not strictly linked to the ocurrence of the displacement rims as it happens in other cases (Fig. 5E in Marty *et al.*[38]). Other longer (centimeters to tens of meters) non-radial fractures are also observed (Fig. 7E).

Regarding internal overtracks (Fig. 7E–H, *sensu* Marty[20]) they are very common and can also be found in all the three preservation types. Probably, the lack of this feature in some tracks is the result of recent removal during quarry works. A remarkable feature is that overtrack sediment wedges towards the edges of the track. The samples collected (Fig. 4C,D) revealed that the thin lamination of the sediment inside the track is due to microbial mats. The track bottom (true track *sensu stricto*) was covered with water during tidal events and the resulting internal overtrack was induced by repeated growth of microbial mats in the wetter track interior, by the trapping of sediment, or by an alternation of both processes. After the track formation, microbial mats developed preferentially within the tracks, as observed by the internal overtracks (Fig. 7E–H). This kind of overtracks has been commonly reported in other tidal environments[21,38,42].

The relationship between tracks and associated features do not only provide a cross cutting sequence, but also clues to the origin of fractures. Non-radial fractures are tectonic joints, as supported by their length (up to tens of meters) and by the parallel disposition in joint families. Sometimes, non-radial fractures have calcite crystals infill. Additionally, non-radial fractures crosscut both the tracking surface and internal overtracks. In contrast, radial fractures never cut the internal overtrack, i.e. radial cracking is previous to the internal overtrack formation.

Trackmaker identification.

The Vale de Meios trackmakers are large theropods or megatheropods as their estimated hip heights overpass the threshold (250 cm) proposed by some authors[33,43] and the footprint length exceed 45 cm[20,43,44]. These theropod tracks are among the largest theropod tracks described worldwide[30,31,45,46]. Nevertheless, other very large tracks are known. In general, trackmaker identity should reflect the least inclusive group that bounds all taxa sharing similar morphological characteristcs and spatiotemporal distributions. Therefore, in order to ascertain which group of theropods might be the best trackmaker candidate for the studied tracks, we reviewed the bone record of large-sized theropods in the Middle Jurassic of Europe. In the Iberian Peninsula, the osteological remains for this clade at that age are absent; out of this region, theropod osteological remains are recovered mainly from England (*Duriavenator hesperis*[47]; *Megalosaurus bucklandii*[6], *Magnosaurus nethercombensis*[7]; *Cruixicheiros newmanorum*[8]), France (*Poekilopleuron bucklandii*[4,5]; *Dubreillosaurus valesdunensis*[3]). They are all Bajocian-Bathonian in age and have been attributed to the Megalosauridae family, which is the dominant clade for the Middle Jurassic in Europe.

The synapomorphy-based correlation of the trackmakers depends on appendicular and pedal elements, which are usually lost during fossilization[48]. Plus, the osteological convergence and substantial overlap in phalangeal proportions of the theropod foot would not allow a lower level distinction among different theropod taxa[48]. Buckley *et al.*[49] indicate that tracks are not consistently preserved so as to reproduce the proportions of the trackmaker's foot with perfect fidelity, especially during animal locomotion. However, considering additional data such as the size and the provenance (taking into account both temporal and spatial distributions)[48], there are no other possible candidates other than megalosaurids, as this is the unique group of large theropods capable to produce large tracks during the Bajocian-Bathonian times.

Megalosaurid behaviour inferred from tracks. The orientation patterns of the trackways can provide useful information about the behaviour and habitat propensity of the trackmakers, especially if there is some preferred orientation of the trackways[50,51]. For example, Day *et al.*[11] reported various trackways at the Ardley Quarry, a Middle Jurassic tracksite with similar theropod tracks and trackways. The Ardley Quarry trackways display a degree of parallelism, suggesting that the trackmakers movements were either constrained by a linear geographical feature, or that they were moving in a herd. Generally, unidirectional orientation patterns, together with other parameters (similar locomotion velocity, regular intertrackway spacing, identical pace rhythm) are the best evidence to suggest gregarious behaviour among the trackmakers[31,52]. It is noteworthy that this kind of behaviour is not usually reported in large theropods on the basis of the footprint record[53–56]. Moreover, the presence of a huge number of large theropod footprints (more than 700 hundred) is highly uncommon in the fossil record and the Vale de Meios tracksite is therefore a rare site of great paleobiological and paleoethological relevance.

The detailed picture of the Vale de Meios tracksite shows an inter-tidal flat crossed normally by large theropods showing a general bimodal orientation pattern. The tidal flat is located in an inner platform (i.e. landwards edge of a lagoon, Fig. 9A) with a coastal barrier arranged in a E/NE-W/SW orientation. The majority of trackways (black colour, Fig. 3A) follows a W/NW orientation, toward the barrier (Fig. 9B). In contrast, the E/SE direction of trackways (red colour, Fig. 3A) is directed opposite, towards the land edge of the inner platform.

Bimodal orientation patterns have often been associated with physical features of the paleoenvironment such as the shoreline[57,58] and also to the paleogeographic conditions[59]. For instance, the most common condition found in fossil and modern trackways is that of trackways running parallel to the shoreline, typically linked to migratory animals moving from one area to another within the lake[51]. Besides, these authors suggested "shoreline position exerts a stronger influence on the distribution of animal activity than any other environmental factor".

Nevertheless, the opposite trend is observed for the Vale de Meios trackways where the bimodal orientation pattern is represented by trackways (the majority of them) directed perpendicular to the shoreline. In fact, 90% of the trackways is subparallel and are heading to the barrier while 10% of the trackways is heading opposite to the barrier (E/SE direction). Cohen *et al.*[51] also reported perpendicular trackways to the shoreline suggesting that animals can approach the margin of the lake to "drink, forage, or pass by (or, in the case of carnivores, to hunt herbivores doing any of the above)". Following Getty *et al.*[56], if the subparallel orientation of the trackways is not caused by the gregarious behaviour, something else must have caused it. It should be noted that the parameters suggesting gregarious behaviour are not fully appreciable for the Vale de Meios trackways. Anyway, what seems clear is that the bimodal orientation pattern in the case of Vale de Meios is not related to the shoreline configuration as in the aforementioned papers. The sedimentological and taphonomic analyses together with data on the distribution and orientation of trackways permit us to infer theropod behavior throughout the tidal flat environment. Thus, the majority of trackways at Vale de Meios is likely to have been impressed during low tide periods, when the conditions to produce footprints are more suitable. The new surfaces exposed during the low tide periods favoured the preservation of footprints and the moisture-laden sediment counts for the variety of preservation modes (Fig. 6). A possible explanation for the direction of movement of the majority of trackways (black colour, Fig. 3A) is that of megalosaurids crossing the exposed area of the tidal flat when the water recides, that is to say during low tide periods. This hypothesis is based on the strong directionality (and bimodality) in theropod paths, normal to the barrier. The long linear trackways across the site represent a directional pattern (*sensu* Cohen *et al.*[51]) suggesting that the megalosaurids cross the tidal flat with a precise purpose (not milling).

The unusual behaviour of large theropods moving toward the coast had not been previously documented and entails the possibility that megalosaurids invaded the area to feed on fish, invertebrates and other vertebrates exposed on the tidal surface. Although there are examples in literature of gregarious behaviour in large theropods supported through both bonebeds[60] and trackways[31], it has been usually suggested that large theropods were solitary hunters[61,62] The numerous trackways might represent few individuals crossing the tidal flat recurrentely. In fact, some reports of theropods moving towards and away from the shoreline have been considered possible evidence of piscivory[58] or feeding on other vertebrate carcasses (*sensu* Roach and Brinnkman[63] and *contra* Ostrom[53]).

The inferred piscivory diet of megalosaurids is not unexpected and has been documented by stomach contents in *Poekilopleuron*[64]. Allain[3] stated that the inclusion of fishes as part of the megalosaurid diet is consistent with both taphonomic and phylogenetic data. Moreover, the deposits yielding the described megalosaurid taxa indicate paralic and shallow marine environments, including marine-influenced lagoon[9] and coastal mangrooves grounds[3]. These data combined with the trackway evidence from Vale de Meios may suggest that megalosaurids frequented this palaeonvironment, and similar to spinosaurids, would have been opportunistic carnivores, feeding on terrestrial vertebrates but also on fishes. In this regard, the long trackways documented at Vale de Meios tracksite reveal a stock of large megalosaurids moving to the shoreline and back from the land to the coastal barrier and invading new exposed areas of the tidal flat. The reason of such striking behaviour could be the occasional piscivory diet of megalosaurids, as these large theropods would take advantage of new exposed areas to feed on fishes and other vertebrates.

Conclusion

The Vale de Meios limestone quarry from the Serra de Aire Formation, Bathonian in age (Santarém, West-Central Portugal) is a key and unique reference for understanding the composition and distribution of the Middle Jurassic theropod fauna, especially due to both the ichnological and osteological record for this age being extremely scattered. In this study, tracks and trackways from the whole tracksite are assigned to *Megalosauripus* isp. according to quantitative and qualitative analyses and comparisons undertaken. This ichnogenus occurrence, traditionally reported for the Late Jurassic-Early Cretaceous, should therefore be expanded also to the Middle Jurassic. The Vale de Meios tracks are among the largest theropod tracks ever reported, and they were produced by large individuals of the Megalosauridae family, the dominant tetanuran clade during this age in Europe. Furthermore, this is the first tracksite in which *Megalosauripus* is in a probable coincident correlation with megalosaurids. The directional analyses of trackways, which are preserved in an inter-tidal flat located at the edge of a lagoon, reveals that various individuals crossed a tidal flat in accordance to tide cycles, directing toward the barrier during low tide periods, probably for feeding purposes on exposed vertebrate. Such clear bimodal orientation arrangement (forth and back) interpreted as single or small aggregates of large theropods individually moving toward a carcass on the shoreline is highly uncommon as it is the presence of such a large number of large theropod footprints.

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Author Contributions

N.L.R., B.V., V.F.S. and À.G. designed the project. N.L.R. undertook photogrammetry in the field. N.L.R., À.G. and V.F.S. built the field 2-D cartography. N.L.R. and O.O. performed sedimentary analyses and thin sections. N.L.R., D.C. and B.V. performed the research. N.L.R., O.O., D.C., B.V., V.F.S. and À.G. wrote the manuscript. N.L.R and O.O. prepared figures.

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Ichnological evidence of Megalosaurid Dinosaurs Crossing Middle Jurassic Tidal Flats

Novella L. Razzolini[1*], Oriol Oms[2], Diego Castanera[3], Bernat Vila[1,4], Vanda Faria dos Santos[5], Àngel Galobart[1,4]

[1:] Mesozoic Research Group, Institut Català de Paleontologia 'Miquel Crusafont', C/ Escola Industrial 23, 08201 Sabadell, Catalonia, Spain

[*] Correspondence to novella.razzolini@icp.cat

[2]:Universitat Autonoma de Barcelona, Facultat de Ciències (Geologia), 08193, Bellaterra (Spain)

[3]: Bayerische Staatssammlung für Paläontologie und Geologie and GeoBioCenter, Ludwig-Maximilians-Universität, Richard-Wagner-Str. 10, 80333 Munich, Germany.

[4]: Museu de la Conca Dellà, carrer del Museu, 4, 25650, Catalonia, Spain.

[5]: Museu Nacional de História Natural e da Ciência – Universidade de Lisboa, Rua da Escola Politécnica, 58, 1250−102 Lisboa, Portugal

Supplementary Data 1. Digital reconstruction of trackways VM1 (24 tracks) and VM2 (28 tracks) directed toward W/NW and measure 35 and 40 meters respectively. Downloadable, interactive 3D PDF file and 3D model in .ply format generated through Agisoft Photoscan software available here: https://figshare.com/s/4a0cc7cd871e17b0c3d2,

10.6084/m9.figshare.3198673.

(Note: all 3D PDF files and 3D models, Supplementary Data 1-4, may be downloaded here: https://figshare.com/s/2224473dc15a8c17a3d4)

Supplementary Data 2. Digital reconstruction of trackways VM3 (29 tracks) directed toward E/SE and it measures 30 meters in total length. Downloadable, interactive 3D PDF file and 3D model in .ply format generated through Agisoft Photoscan software available here:

https://figshare.com/s/412e5c47d578b363fb48

10.6084/m9.figshare.3405763

Supplementary Data 3. Digital reconstruction of tridactyl track VMX.1 described as *Megalosauripus* isp. from the Middle Jurassic of the Vale de Meios tracksite (Portugal) Downloadable, interactive 3D PDF file and 3D model in .ply format generated through Agisoft Photoscan software available here:

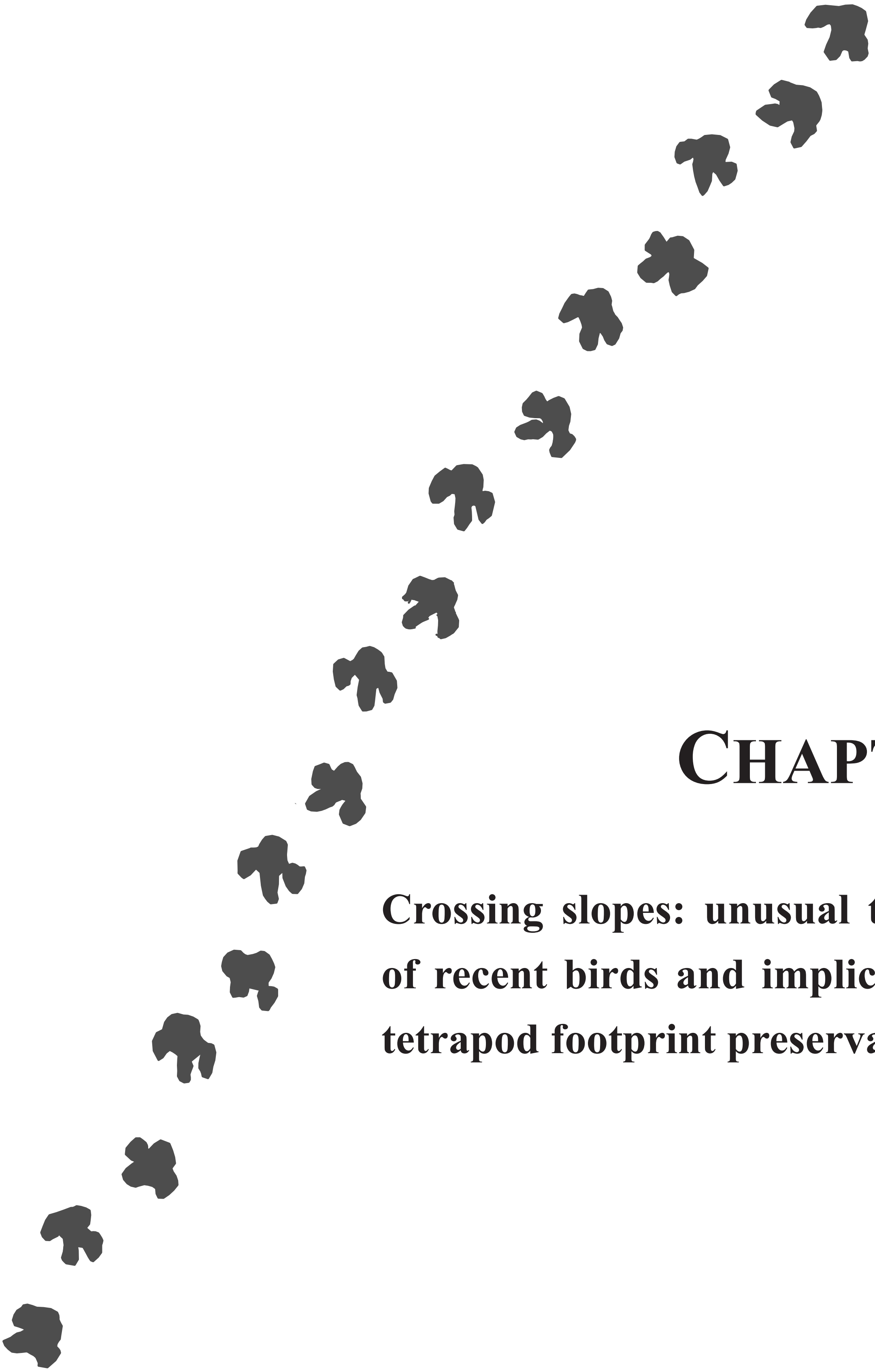
https://figshare.com/s/37ceeda03719449a900b

10.6084/m9.figshare.3398530

Supplementary Data 4. Digital reconstruction of tridactyl track VMX.2 described as *Megalosauripus* isp. from the Middle Jurassic of the Vale de Meios tracksite (Portugal) Downloadable, interactive 3D PDF file and 3D model in .ply format generated through Agisoft Photoscan software available here:

https://figshare.com/s/33012aa15335884c3313

10.6084/m9.figshare.3398533



CHAPTER 8

Crossing slopes: unusual trackways of recent birds and implications for tetrapod footprint preservation

AUTHOR'S CONTRIBUTION

Razzolini, N.L. and Klein., H. Crossing slopes: unusual trackways of recent birds and implications for tetrapod footprint preservation.

(Under- review Ichnos Special Issue).

The author, N.L. Razzolini, designed the hypothesis, analysed the trackway in the field (trackway interpretation), undertook photogrammetric models and constructed the three-dimensional models of the analysed tracks, conducted all the measurements of tracks and trackway in the computer models, wrote the manuscript and prepared the figures and tables.

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Crossing slopes: unusual trackways of recent birds and implications for tetrapod footprint preservation

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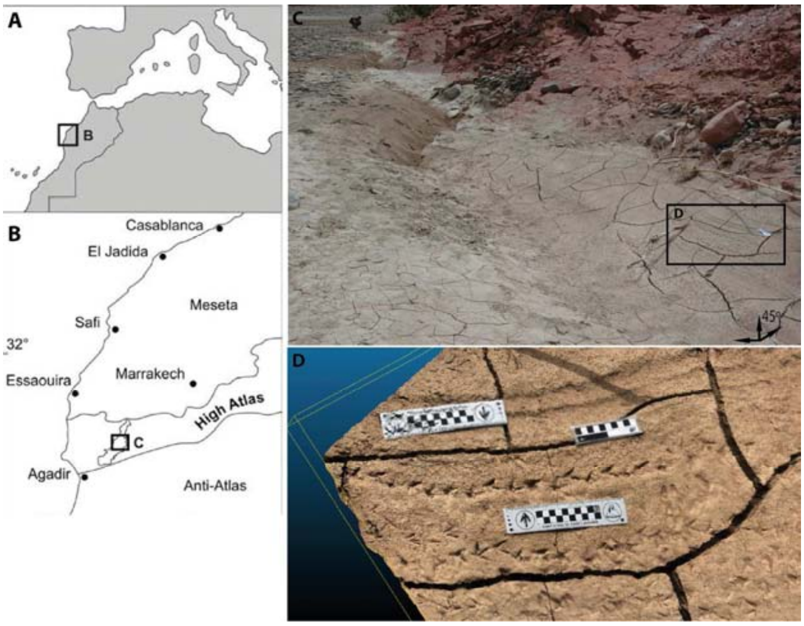

Figure 1. Geographical setting of the studied birdtrackway. A–B.Position of the Argana Basin and study area in the western High Atlas of Morocco. C. Field aspect of the studied trackway, crossing a 45º sloping surface on a mud crack portion. D) Photogrammetric 3-D model of the studied bird trackway 1.
267x205mm (300 x 300 DPI)

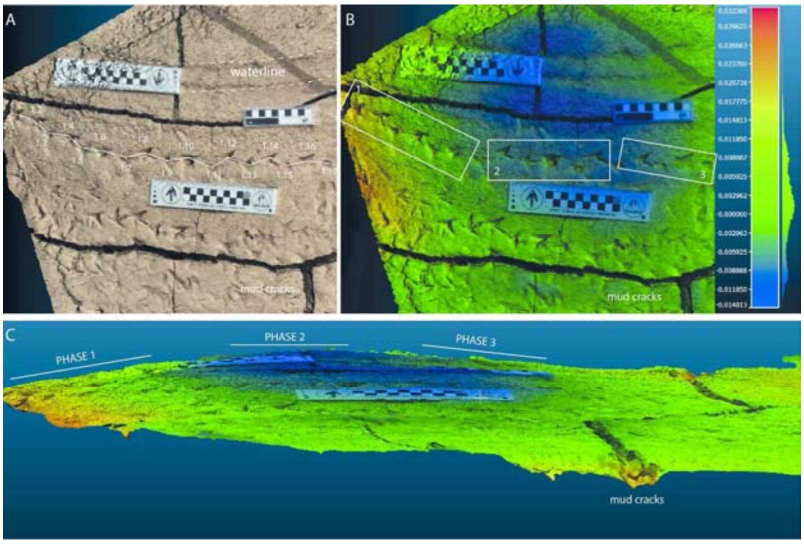

Figure 2. Three-dimensional models of bird trackway 1. A) Photogrammetric model from field photos undertaken on the mud-crack portion of the sloping surface: tracks numbered as 1.1 (right track), 1.2 (left track). Notice water level marks indicated on the 3-D model displaying a subparallel arrangement with respect to the studied trackway. B. Depth analyses on the 3-D photogrammetric model. Trackway is divided into three portions 1,2 and 3, corresponding to different phases in C. C. Model tilted by 90° showing PHASE 1, 2 and 3 of trackmaker movement reflected in the trackway and according to the mud crack wavy nature and to the change in trackmaker kinematics. Scale bars 10 cm and 20 cm.
294x197mm (300 x 300 DPI)

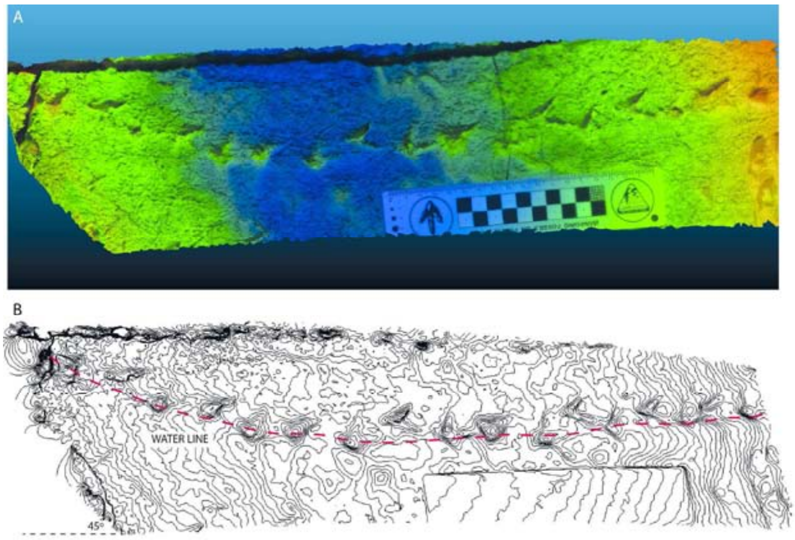

Figure 3. Detail and zoom selection of the bird trackway: A) Depth analyses of the 3-D model displaying two main areas of depth on the trackway segment (green to blue and blue to green); B) contour lines 3-D model showing sediment ridges in correspondence of digit IV impressions of right tracks.
291x198mm (300 x 300 DPI)

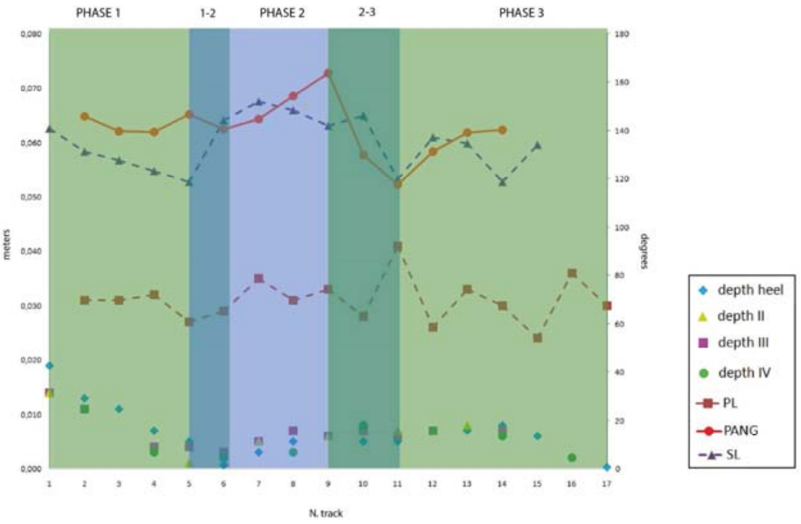

Figure 4. Double Y graphic showing in the X axis the number of the track, in the left Y axis values for PL, SL and depth of "heel" and digit impressions, in the right Y axis values for PANG in degree. The graphic was divided into the corresponding phases identified by the change in values of measurements. Transitional phases 1–2 and 2–3 are highlighted as the moment in which the trackmaker changes its gait in accordance to the variation in the slope of the surface.
239x153mm (300 x 300 DPI)

Crossing slopes: unusual trackways of recent birds and implications for tetrapod footprint preservation

Novella L. Razzolini[1] and Hendrik Klein[2]

[1] *Institut Catala de Paleontologia Miquel Crusafont, C/ Escola Industrial, 23, E-08201, Sabadell (Barcelona) Catalonia, Spain*

[2] *Saurierwelt Paläontologisches Museum, Neumarkt, Germany*

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Address correspondence to Novella L. Razzolini, Institut Català de Paleontologia Miquel Crusafont, Carrer de l'Escola Industrial, 23, Sabadell, Barcelona, Spain,. E-mail: novella.razzolini@icp.cat

Abstract

In a neoichnological study, the trackway of a small recent bird crossing the slope of a river bank is documented and analyzed in detail. It was preserved along the Issene River in the western High Atlas of Morocco. Photogrammetry and 3D techniques were used revealing three different phases in the trackmaker's movement that were essentially controlled by adaptation to the slope inclination and the wavy mud-cracked surface. This is reflected in the variation of different parameters such as stride length, pace length, pace angulation and imprint depth of different digits. An alternating "didactyl" preservational pattern is observed with the left (uphill) tracks showing only digits III and IV, the right (downhill) tracks only digits II and III being present. This is interpreted to be partly due to water activity and erosion of digits along the midline of

the very narrow trackway, as it is indicated by preserved water level marks at the same height. Furthermore, when passing the slope, different weight distribution on outer and inner digits, respectively, may have contributed to this phenomenon. The study might be helpful for understanding fossil counterparts formed in similar uneven terrain.

INTRODUCTION

Neoichnological observations are important for the understanding of fossil tetrapod footprints and their preservation. There is an increasing number of studies, especially those of extant birds but also other tetrapods (McKee, 1947; Brand, 1996; Farlow and Pianka, 2000; Bromley, 2001; Milàn and Bromley, 2006, 2008; Roberts, 2008; Farlow and Elsey, 2010). In recent years, three-dimensional modelling through technologies such as laser scanner (Bates et al., 2008), X-ROMM (Falkingham and Gatesy, 2014) and photogrammetric methods (sensu Mallison and Wings, 2014) have been progressively used for trackway documentation and reconstruction of the whole ontogeny of the track, based also on data from extant animals. During a field trip in occasion of the First International Congress of Continental Ichnology (ICCI) 2015 in Argana Basin, Morocco, we observed numerous trackways of small living birds, preserved in fine-grained sand-silt substrate along the inner part of a river bank bordering the dried out portion of the Issene river, about 1,5 km south of Irerhi village and close to a Permian tracksite (N30°49'26.8"W009°04' 55.2"). The footprints are associated with large mud cracks of posterior formation (Fig. 1A–C) and can possibly be attributed to Limicola-like charadriiforms that are common in this region and environment (Oriol Oms, pers. comm.). A longer trackway segment with seventeen successive pes imprints was the most interesting one, showing an alternate track morphology due to the absence of digit II and IV impressions in left and right tracks, respectively. This trackway segment is recorded perpendicular to the 45º slope of the bank and describes an arch of a circumference with its central angle being 163º (Fig. 1C–D). Two parallel lines, interpreted as water level marks during flooding season, are observed 15 cm above and subparallel to the trackway (Fig. 2A). In the following study, we describe these footprints from the Issene river based on a larger data set from our documentation (Table 1). A 3-D model was created in order to add qualitative and quantitative data showing track morphological and morphometrical variability recorded along the trackway. Finally, we discuss and interpret the influence of underlying topography and substrate conditions on the gait of the trackmakers and track morphology.

MATERIALS AND METHODS

The trackway, which is here numbered as trackway 1 (T1), consists of 17 tracks (1.1–1.17; Fig. 2A) placed with a very narrow pattern. Field photos were taken with iPhone5s camera (focal length of 35 mm with a resolution of 3264 x 2448) and with Nikon D70 (focal length 93 with a resolution of 3008 x 2000). Photogrammetry was undertaken following the general methodology explained in Mallison and Wings (2014) and terminology was used following Lockley et al. (2015). Point clouds were processed in Agisoft Photoscan standard version 1.1.4. build 2021software (http://www.agisoft.ru/) with a total number of 63 photos. The 3-D model was converted to colour map in the open source CloudCompare software (v.2.6.1, http://www.danielgm.net/cc/). Contour lines (isolines profile) were obtained in free software Paraview 4.4.0 version (http://www.paraview.org/), importing scaled and oriented model with respect to the Z axis from CloudCompare (v.2.6.1) and they were set at a 1 mm distance according to maximum and minimum heights of the plane where tracks are. Measurements of track length (TL), track width (TW), pace length (PL), stride length (SL), pace angulation (PANG), depth of the heel (dH) and digits II, III and IV (dII, dIII, dIV) were undertaken in CloudCompare (v.2.6.1) software. Average and Standard deviation (SD) are also calculated for all the presented parameters. All measurements shown in Table 1 are in meters.

RESULTS: DESCRIPTION OF TRACKWAYS AND TRACKS

The trackway segment is 0.5 m long and consists of 17 successive tracks (Fig. 2A) numbered as 1.1 (right), 1.2 (left) and so on. The average pace length (PL) is 0.031 m, with a standard deviation of ±0.004, and the stride length (SL) is 0.060 m with a standard deviation of ±0.005. The average pace angulation (PANG) is 142º. It is observed that the trackmaker is affected by two overlapping substrate-related scenarios: a) the bird is moving perpendicular to a 45º sloping surface (Fig. 1C); b) the mud-crack where the bird trackway is impressed is wavy (Fig. 2B-C). The effect of the interplay between the sloping surface and the mud-crack dynamics causing the wavy topography along the trackway portion is controlling changes in gait-related parameters (Fig. 2B-C). These changes are here divided into three main phases in the trackmaker's kinematics (Fig. 4).

Phase 1 (from track 1.1 to track 1.5): all parameters show a tendency in decreasing their values gradually and consistently. In detail, PL shows a gradual and regular decrease in length with a total shortening of 0.005 m (from 0.031 m to 0.027 m); SL decrease is also very regular, displaying a total shortening of 0.010 m (from 0.062 m to 0.052 m); depths recorded for heel and digit impressions also display a decrease in their values with respect to the tracking surface set at "0" of the colour scale bar (Fig. 2-3). In detail, dh decreases from 0.019 m to 0.005 m, dII (recorded only for two right tracks) decreases from 0.014 m to 0.001 m, dIII decreases from 0.014 m to 0.004 m and dIV (recorded only for two left tracks) decreases from 0.011 m to 0.003 m. Note that PANG registers small changes in correspondence to the general decreasing tendency for PL and SL.

Phase 2 (from track 1.6 to track 1.9): between two peaks representing phases transition (1-2 and 2-3 respectively, Fig. 4), parameters generally display a tendency in stabilizing their values. In detail, two changes reflected in parameters PL, SL and depths are concentrated between tracks transitioning from phases 1-2 (tracks 1.5-1.6) and from phases 2-3 (tracks 1.9-1.11). During the actual phase 2 (from track 1.6 to track 1.9) SL and PL increase their lengths with respect to phase 1 and they maintain these values with very small variations (see Table 1 for measurements). The PANG also increases greatly with respect to phase 1 until it registers a peak (track 1.9) in correspondence to the stabilization of the PL and SL parameters.

Phase 3 (from track 1.11 to track 1.17): during phase transition 2-3, PANG and SL strongly decrease with respect to phase 2, recording values that are similar to phase 1, PL increases with respect to previous phases 1 and 2 and depth values appear to display almost no variations. While PANG gradually increases, an alternate pattern with irregular lengths for SL and PL characterizes the actual phase 3 (tracks 1.11-1.17). Furthermore, during this phase, depth values recorded for "heel" and digit impressions show a general decreasing tendency.

Footprints in the trackway show a strong tendency toward didactyly: tracks were observed to display a complementary pattern of lack of the impressions of external digit

IV and internal digit II in right and left tracks, respectively. Left tracks always lack the internal digit II, with the exception of track 1.16 in which also a digit III impression is missing. Complementary, right tracks usually lack the external digit IV impressions with the exception of tracks 1.3, 1.11, 1.15 and 1.17 in which all three toes are lacking or indistinct, leaving only a faint metatarso-phalangeal and/or hallux impression, that makes the measurement of track parameters impossible. Digit III is always visible and impressed in all left tracks (with the exception of track 1.16) but absent (or unappreciable) in five right tracks 1.3, 1.11, 1.13, 1.15 and 1.17. Track length (TL, average 27 mm, SD ± 0.003) could only be measured for all left tracks and right tracks 1.1, 1.5, 1.7, 1.9. Track width could not be quantified due to the alternating lack of the internal digit II impression in left tracks and external digit IV impression in right tracks.

Contrarily to the field observations, depth analyses undertaken (contour lines model, Fig. 3B) show that tracks are strictly speaking tetradactyl or anisodactyl with the hallux faintly impressed and positioned mostly in line with the axis of digit III, showing a general asymmetry in the geometry of the tracks. In detail, left tracks, characterized by the consistent absence of digit II impression, display steeper walls in digits III and IV impressions and a slight inward rotation of digit III with respect to the midline. In right tracks, digit IV impression is completely worn off or only deducible from the contour lines and colour ramp map as a very shallow and weak substrate deformation (Fig. 3A-B). In these tracks, digits II and III impressions are quite consistently appreciable with the exception of tracks 1.3, 1.15 and 1.17 in which all three toes are missing, showing a faint "heel" impression only.

DISCUSSION

The importance of systematic experimental study of trackways of living animals for the understanding of some fossil counterparts have always been underscored (Padian and Olsen, 1984) and various researchers (McKee, 1947; Brand, 1996; Roberts, 2008) have widely contributed to this statement with laboratory controlled trackways on sloped surfaces. The advantage of studying the extant *Limicola*-like trackway is that the trackmaker foot anatomy and the substrate conditions are known parameters (*sensu* Falkingham, 2014) that allow the reconstruction of the trackmaker's kinematics in accordance to the surface.

With this example, it is possible to interpret separately the factors biasing track morphology in order to use them when studying fossil tracks.

We here discuss the role of known factors (sloped surface, water activity and foot anatomy) on determining the changes reflected by the three phases described in Fig. 4, and causing the apparent non-correspondence between track morphology and foot anatomy.

During the three different phases, SL, PL, PANG and depths of "heel" and digit impressions, respectively, are decreasing, increasing-stabling and alternating their values. In Phases 1 and 3 values decrease and/or show an alternating pattern in values suggesting an irregular foot adjustment on an uneven surface. Phase 2 shows an increase in values with respect to phase 1 and then a stabilization of values. Moreover, the green-to-blue and blue-to-green areas observed in the colour map of the 3-D model (Figs. 2– 3), correspond to phases 1, 2 and 3 (Fig. 4), differentiated on the basis of both kinematic and surface variation recorded while the trackmaker crossed the sloped surface (Fig. 2). Increase/decrease for these values (Fig. 4, Table 1) with respect to a previous phase correspond to transitional phases 1–2 and 2–3, when the trackmaker's gait changes in accordance to the variation in the slope degree (Fig. 2 and 3). Brand (1996) indicated that differences in gait are significantly reflected in PANG rather than in the SL. While this is definitely true for quadrupedal trackmakers, in our study, it is important to add SL, PL and depths recorded for "heel" and digit impressions as indicative of a gait-transition of bipeds related to a change in the surface slope (Fig. 4). The three phases are, therefore, interpreted as general adjustments to the wavy portion of the mud crack by increasing/decreasing SL, PL and PANG as moving across uncertain and uneven surfaces would suggest (*sensu* Wilson et al., 2009).

It is observed that the trackway midline geometry draws a circumference arch perpendicular to the 45º slope of the inner river bank, very similar and subparallel to the arrangement of the two water line marks recorded above the studied trackway (Fig.2 and 3B). Contour lines show ridges indicating an earlier (lower) water level (red dotted line in Fig. 3B). The trackway dynamic shows a high alignment in positioning digit II of left tracks in the same line as digit IV of right tracks. Furthermore, the ridges correspond to the absence of external digit IV (right tracks) and internal digit II (left tracks) impressions, which were washed off by the water.

As regarding track morphologies, they display an alternating digit-preservation pattern in which right tracks do not show digit IV impressions and left tracks do not show digit II impressions. Water erases digit II of left tracks and digit IV of right tracks, leaving the trackway with the observed complementary alternating pattern. This selective washing off of digit impressions is possible because of the very narrow trackway gauge, one foot in front of the other, an effect of the ethology of charadriiform birds observed to generally walk on the water-line. The unusual "didactyl " track morphology observed in the field is the result of the interaction among three components: 1) substrate (slope, wavy mud-crack), 2) water activity and 3) trackmaker kinematics adjusting to the irregular crossed area. This adjustment is particularly noticed in the different weight distribution when walking along the slope, with emphasis to digits III and IV (left side) and digits II and III (right side). Brand (1996) stated that trackways made on sloped, submerged mud or sand, sloped dry sand and sloped damp sand rarely included the full complement of toes.

In paleoichnology, substrate conditions and trackmaker kinematics are usually two variables that are reconstructed from a biased track morphology. In the studied trackway, if the substrate and surface slope were unknown variables (i.e. post-tectonic fossil surface with no indication of a slope), the increasing/decreasing pattern registered in SL, PL and PANG throughout the three phases together with the lack of digit impressions II-IV in right and left tracks respectively, could be misleading to an abnormal gait inference for the trackmaker. Moreover, trackways made on sloped surfaces differ from trackways made on level surfaces, and this could hinder attempts to identify the trackmaking animals responsible for modern or fossil trackways (Brand, 1996).

CONCLUSIONS

The studied trackway documents real time responses to the interaction of (1) substrate quality, (2) inclination (slope of surface and wavy nature of mud crack portion), (3) environmental factors (water activity indicated by water level marks, washing off lateral digits II and IV for left and right tracks, respectively) and (4) trackmaker kinematics adjusting to the complex terrain.

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Figure 1. Geographical setting of the studied bird trackway. A–B.Position of the Argana Basin and study area in the western High Atlas of Morocco. C. Field aspect of the studied trackway, crossing a 45º sloping surface on a mud crack portion. D) Photogrammetric 3-D model of the studied bird trackway 1.

Figure 2. Three-dimensional models of bird trackway 1. A) Photogrammetric model from field photos undertaken on the mud-crack portion of the sloping surface: tracks numbered as 1.1 (right track), 1.2 (left track). Notice water level marks indicated on the 3-D model displaying a subparallel arrangement with respect to the studied trackway. B. Depth analyses on the 3-D photogrammetric model. Trackway is divided into three portions 1,2 and 3, corresponding to different phases in C. C. Model tilted by 90° showing PHASE 1, 2 and 3 of trackmaker movement reflected in the trackway and according to the mud crack wavy nature and to the change in trackmaker kinematics. Scale bars 10 cm and 20 cm.

Figure 3. Detail and zoom selection of the bird trackway: A) Depth analyses of the 3-D model displaying two main areas of depth on the trackway segment (green to blue and blue to green); B) contour lines 3-D model showing sediment ridges in correspondence of digit IV impressions of right tracks.

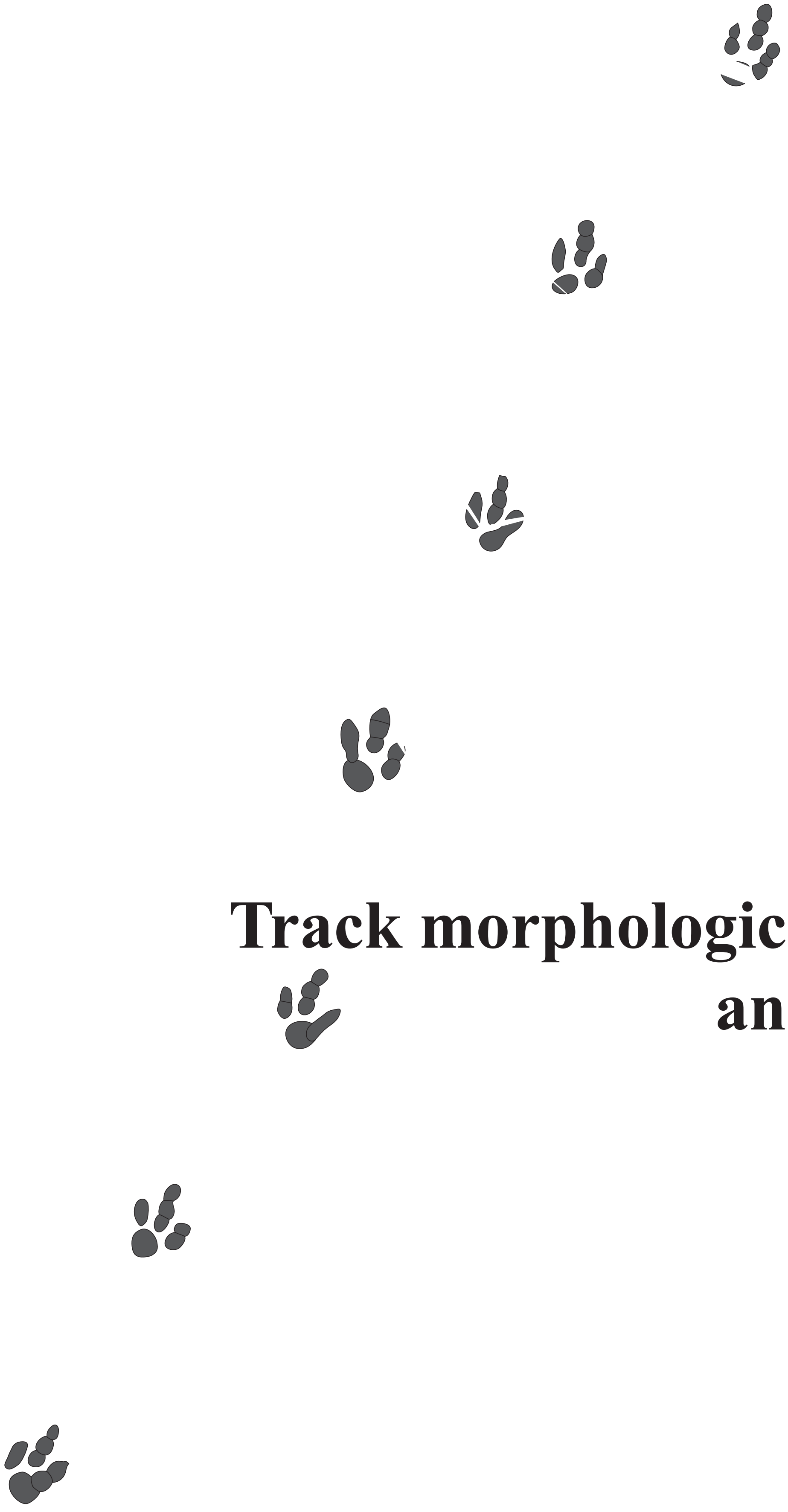
Figure 4. Double Y graphic showing in the X axis the number of the track, in the left Y axis values for PL, SL and depth of "heel" and digit impressions, in the right Y axis values for PANG in degree. The graphic was divided into the corresponding phases identified by the change in values of measurements. Transitional phases 1–2 and 2–3 are highlighted as the

moment in which the trackmaker changes its gait in accordance to the variation in the slope of the surface.

Table 1. Quantitative measurements for trackway 1. TL, track length, dH, dII, dIII and dIV depth of "heel", digit II, III and IV impressions, PANG, pace angulation, PL pace length and SL stride length. All measurements in meters, PANG in degrees. L, R, left and right respectively referred to track number.

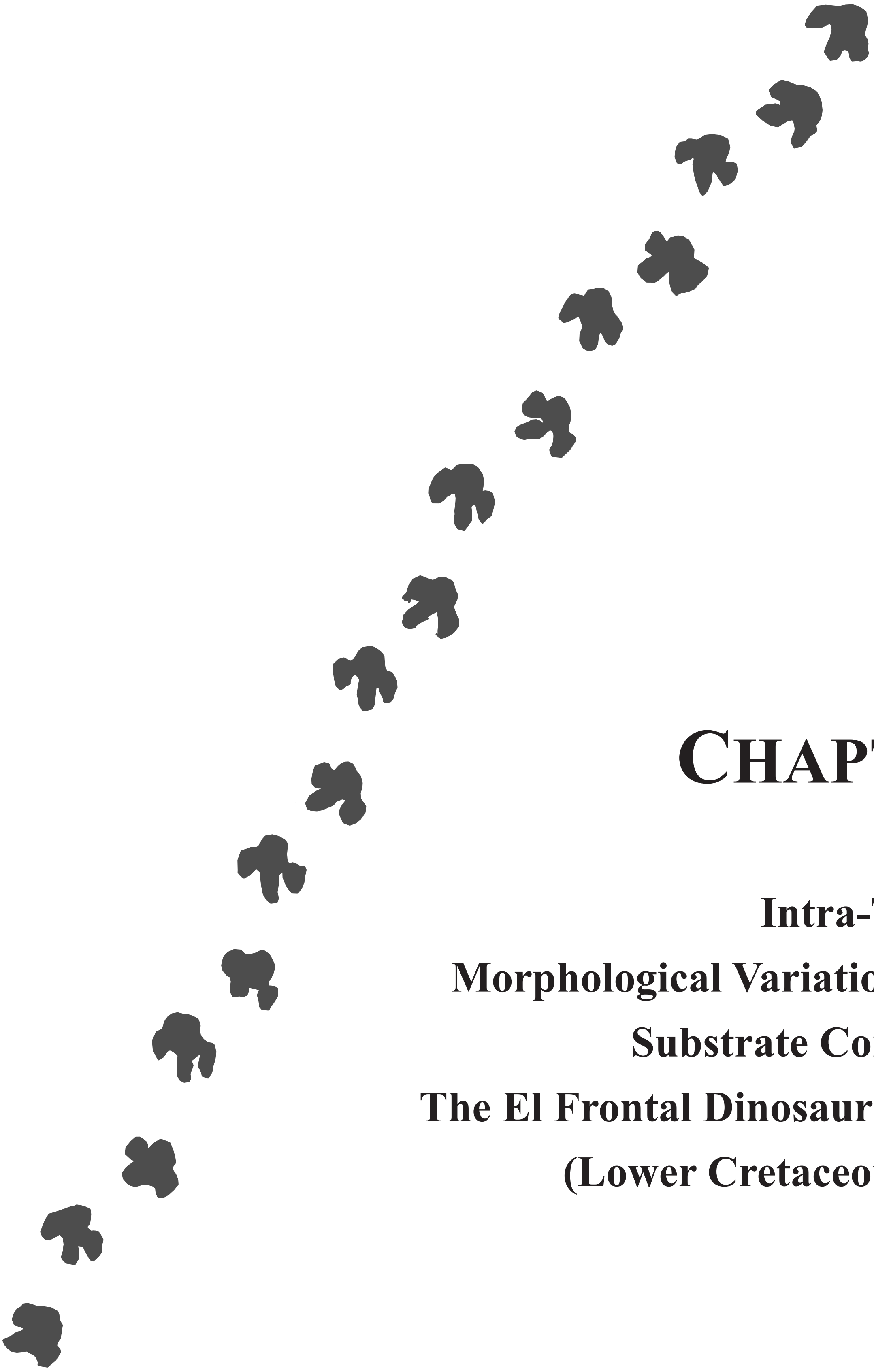
TRACK N.	TL	dH	dII	dIII	dIV	DIGIT MISSING	PANG	PL	SL
1.1 R	0,026	0,019	0,014	0,014		IV		0,0310	0,0626
1.2 L	0,026	0,013		0,011	0,011	II	146	0,0310	0,0584
1.3 R		0,011				II-III-IV	140	0,0320	0,0568
1.4 L	0,024	0,007		0,004	0,003	II	139	0,0270	0,0547
1.5 R	0,021	0,005	0,001	0,004		IV	147	0,0290	0,0528
1.6 L	0,023	0,001		0,003	0,002	II	141	0,0350	0,0641
1.7 R	0,028	0,003	0,005	0,005		IV	145	0,0310	0,0676
1.8 L	0,029	0,005		0,007	0,003	II	154	0,0330	0,066
1.9 R	0,028	0,006	0,006	0,006		IV	164	0,0280	0,0631
1.10 L	0,024	0,005		0,007	0,008	II	130	0,0410	0,065
1.11 R		0,005	0,007	0,006		IV	118	0,0260	0,0533
1.12 L	0,030	0,007		0,007	0,007	II	131	0,0330	0,061
1.13 R		0,007	0,008			III-IV	139	0,0300	0,0598
1.14 L	0,031	0,008		0,007	0,006	II	140	0,0240	0,0528
1.15 R		0,006				II-III-IV	155	0,0360	0,0596
1.16 L	0,034	0,002			0,002	II-III		0,0300	
1.17 R		0,000				II-III-IV			
AVERAGE	**0,027**	**0,006**	**0,007**	**0,007**	**0,005**		**142**	**0,0311**	**0,060**
SD	**0,004**	**0,005**	**0,004**	**0,003**	**0,003**		11,45	**0,004**	**0,004**

Table 1. Quantitative measurements for trackway 1. TL, track length, dH, dII, dIII and dIV depth of "heel", digit II, III and IV impressions, PANG, pace angulation, PL pace length and SL stride length. All measurements in meters, PANG in degree.



PART 5

Track morphological variation and Substrate



CHAPTER 9

Intra-Trackway Morphological Variations Due to Substrate Consistency: The El Frontal Dinosaur Tracksite (Lower Cretaceous, Spain)

AUTHOR’S CONTRIBUTION

Razzolini, N.L., Vila, B., Castanera, D., Falkingham, P.L., Barco, J.L., Canudo, J.I., Manning, P.L., Galobart, À. 2014. Intra-Trackway Morphological Variations Due to Substrate Consistency: The El Frontal Dinosaur Tracksite (Lower Cretaceous, Spain).

PLoS ONE 9(4): e93708.

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The author, N.L. Razzolini, designed the hypothesis, analysed the trackway in the field (trackway interpretation, parameter measurements), undertook photogrammetric models and constructed the three-dimensional models of the analysed tracks, prepared the post-processing of the LiDAR scans and constructed the digital outcrop model of the trackway, conducted all the measurements of tracks and trackway in the field and through the computer models, conducted the statistical analyses and their interpretation, performed sedimentary analyses, wrote the manuscript and prepared the figures and tables.

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Intra-Trackway Morphological Variations Due to Substrate Consistency: The El Frontal Dinosaur Tracksite (Lower Cretaceous, Spain)

Novella L. Razzolini[1]*, Bernat Vila[1,2], Diego Castanera[2], Peter L. Falkingham[3,4], José Luis Barco[5], José Ignacio Canudo[2], Phillip L. Manning[6,7], Àngel Galobart[1]

1 Institut Català de Paleontologia Miquel Crusafont, Carrer de l'Escola Industrial, 23, Sabadell, Barcelona, Catalonia, **2** Grupo Aragosaurus-IUCA, Departamento de Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Zaragoza, Spain, **3** Department of Comparative Biomedical Sciences, Structure and Motion Laboratory, Royal Veterinary College, London, United Kingdom, **4** Department of Ecology and Evolutionary Biology, Division of Biology and Medicine, Brown University, Providence, Rhode Island, United States of America, **5** Paleoymás S.L. Pol. Empresarium, Zaragoza, Spain, **6** Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania, United States of America, **7** School of Earth, Atmospheric and Environmental Sciences, University of Manchester, Manchester, United Kingdom

Abstract

An ichnological and sedimentological study of the El Frontal dinosaur tracksite (Early Cretaceous, Cameros basin, Soria, Spain) highlights the pronounced intra-trackway variation found in track morphologies of four theropod trackways. Photogrammetric 3D digital models revealed various and distinct intra-trackway morphotypes, which reflect changes in footprint parameters such as the pace length, the track length, depth, and height of displacement rims. Sedimentological analyses suggest that the original substrate was non-homogenous due to lateral changes in adjoining microfacies. Multidata analyses indicate that morphological differences in these deep and shallow tracks represent a part of a continuum of track morphologies and geometries produced by a gradient of substrate consistencies across the site. This implies that the large range of track morphologies at this site resulted from similar trackmakers crossing variable facies. The trackways at the El Frontal site present an exemplary case of how track morphology, and consequently potential ichnotaxa, can vary, even when produced by a single trackmaker.

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Competing Interests: José Luis Barco declares the affiliation to the company Paleoymás. There are no patents, products in development or marketed products to declare. This does not alter the authors' adherence to PLOS ONE policies on sharing data and materials.

* E-mail: novella.razzolini@icp.cat

Introduction

Track morphology is determined by both the trackmaker and the substrate characteristics [1–4]. Although it is widely accepted that the substrate is a major control in determining the final track morphology [1,2,5–7], studying this dynamic formation process is challenging given the fact that most foot-sediment and sediment-sediment interactions are highly complex, rapid and hidden from view [8–10]. Baird [11] stated that a trackway is not a simple record of anatomy; instead, it is a record of how a foot behaves under a distinct locomotory pattern as it makes contact with a particular substrate. The way in which sediments behave before, during, and after a track is formed and the subsequent processes that may further modify, enhance, or disguise a track has been much neglected [1,12]. Hence, to understand the formation and preservation of tracks, it is essential to understand the mechanics of soils and rheology [13–15].

Traditionally, ichnology has primarily studied tracks and trackways as two-dimensional traces (e.g., [16,17]), rarely considering the substrates mechanics and prevailing condition at the time a track-maker's foot made contact with a sediment. For ichnological analyses to be well founded, footprints must be documented by methods that avoid inaccurate representations of track morphology, which can distort or obscure potentially important data [18]. Recent advances agree that the foot's contact with a substrate can only be understood by taking a three-dimensional approach to explain track formation [1,5,19–21]. The variation in track morphology due to sediment consistency can be observed and quantified through the use of three-dimensional (3-D) technologies (i.e. using laser scanning or photogrammetry to show depth analyses and vertical cross sections) [22–25] with the intention to integrate quantitative analytical techniques with the traditional ichnotaxonomic definition. Light Detection And Range (LiDAR) techniques [22,23,26] together with photogrammetry methods [27] complement the classic ichnological data acquisition by providing accurate data on 3-D specimens.

The present study concentrates on the quantification of morphological variability of tridactyl dinosaur tracks documented at the El Frontal tracksite (Lower Cretaceous, NW Iberian Peninsula), which were briefly mentioned in previous works [28–

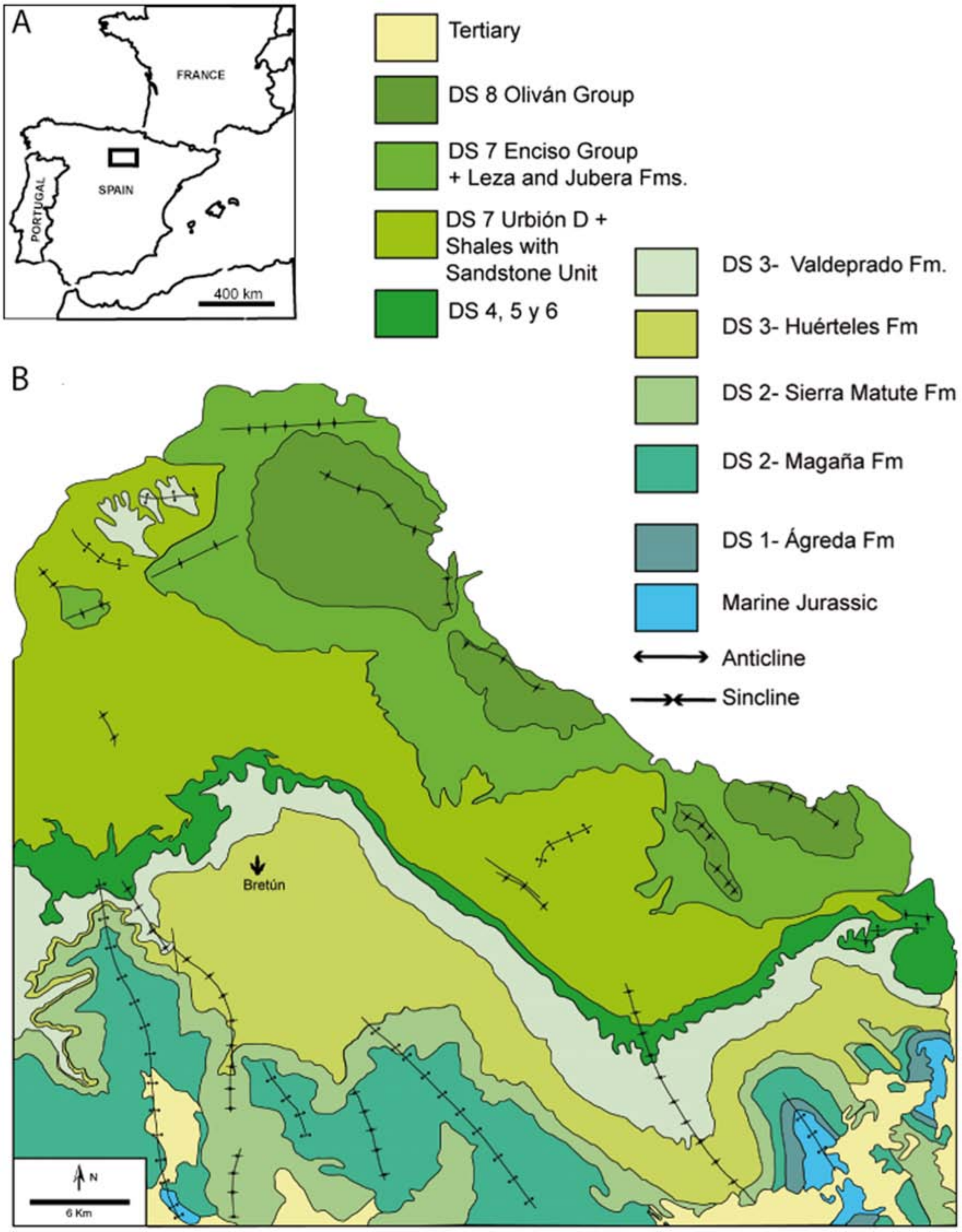

Figure 1. Geographical and geological setting of the El Frontal tracksite (Bretun, Soria). The location of Bretun locality within the Iberian Peninsula is inside the black square. The tracksite locates in DS-3 of the Huerteles Fm [32]. Geological map modified from Castanera et al. [33].
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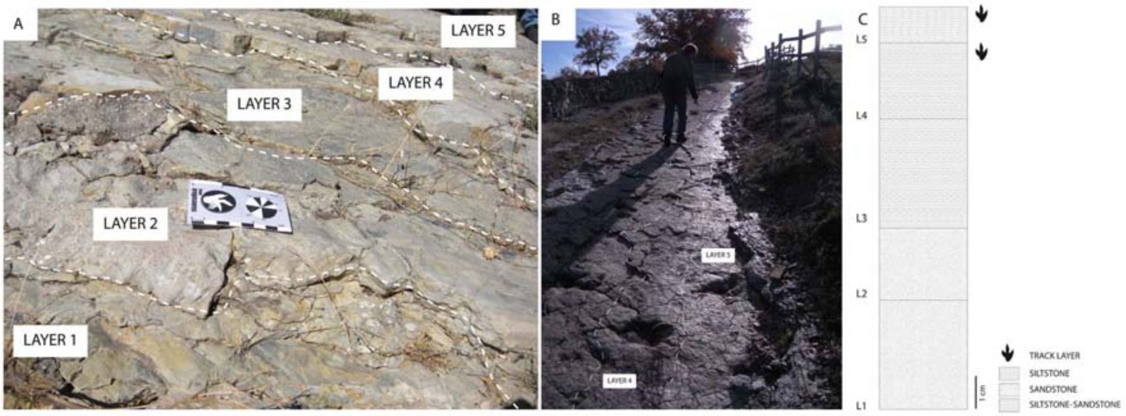

Figure 2. Tracksite microlayers organization. A) The El Frontal tracksite is composed of 5 different centimeter-thick layers that intercalate gray siltstones, limestone and sandy-siltstones. Scale bar equals 8 cm. B) El Frontal track layers 4 (penetrative tracks) and 5 (tracking surface), where all the studied tracks originated. When thin layer 5 is not preserved, tracks are found in level 4. C) Stratigraphical log of the five layers found in the El Frontal tracksite. Theropod tracks are found in layers 5 and 4. Scale bar equals 1 cm.
doi:10.1371/journal.pone.0093708.g002

31] but never studied in detail. The aim of this work is to quantify the inter- and intra-trackway morphological variation *sensu* [10] recorded in different track shapes to underpin the variability in track morphology when track-maker is kept constant. This study will focus on four long trackways that are characterized by a range of track morphologies that are considered as indicators of rheological conditions.

Geological Setting

The El Frontal site is found in the Cameros Basin (Soria, Spain), which is located northwest of the Iberian range. The sedimentary infill of the Cameros basin was divided in eight depositional sequences, with deposits predominantly from continental environments [32] (Fig. 1). The sedimentation was dominantly continental as demonstrated by alluvial and lacustrine deposits [34], but includes some sporadic marine incursions [35–38]. The tracksite

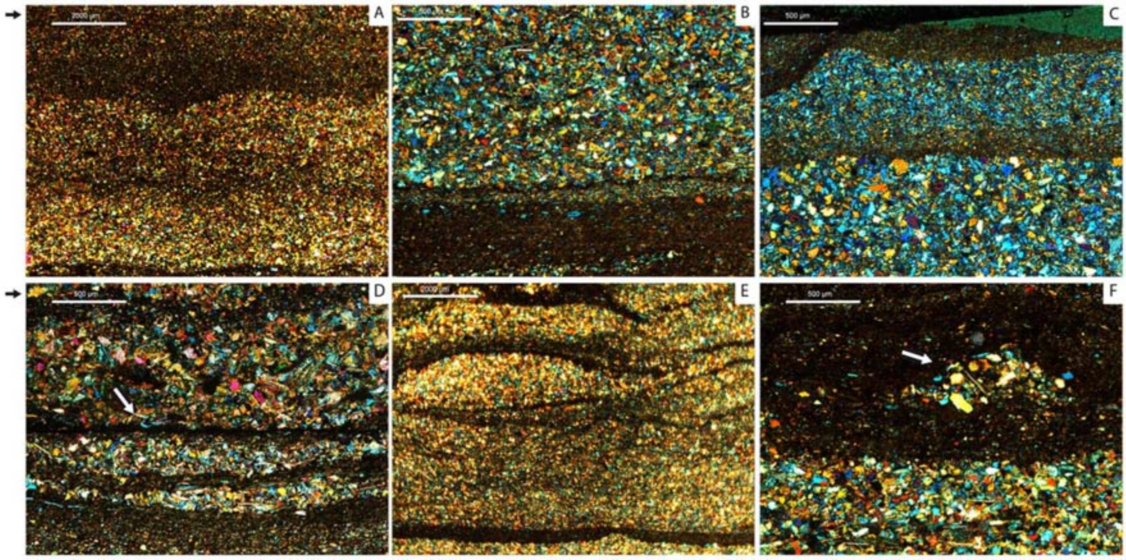

Figure 3. Thin sections IPS-82477a-d of layers 4 and 5 of the El Frontal tracksite. A) Sandstone intercalated by siltstone-mudstone bands in which chlorite minerals are scarce (<5%); B) High quartz concentration (>60%) and scarce presence of clay minerals in mud bands; C)Sandstone-siltstone in which the grain size decreases from the bottom to the top; D) Sandstone intercalated by siltstone, mineral clays are abundant (>60%); E) Deformation structures (mud drapes); F) Deformation structure (symmetrical ripple). Black arrows indicate the top of the laminae, white arrows indicate deformation structures. Scale bars are 2000 µ for A, 500 µ for B, C, D, F and 2000 µ for E.
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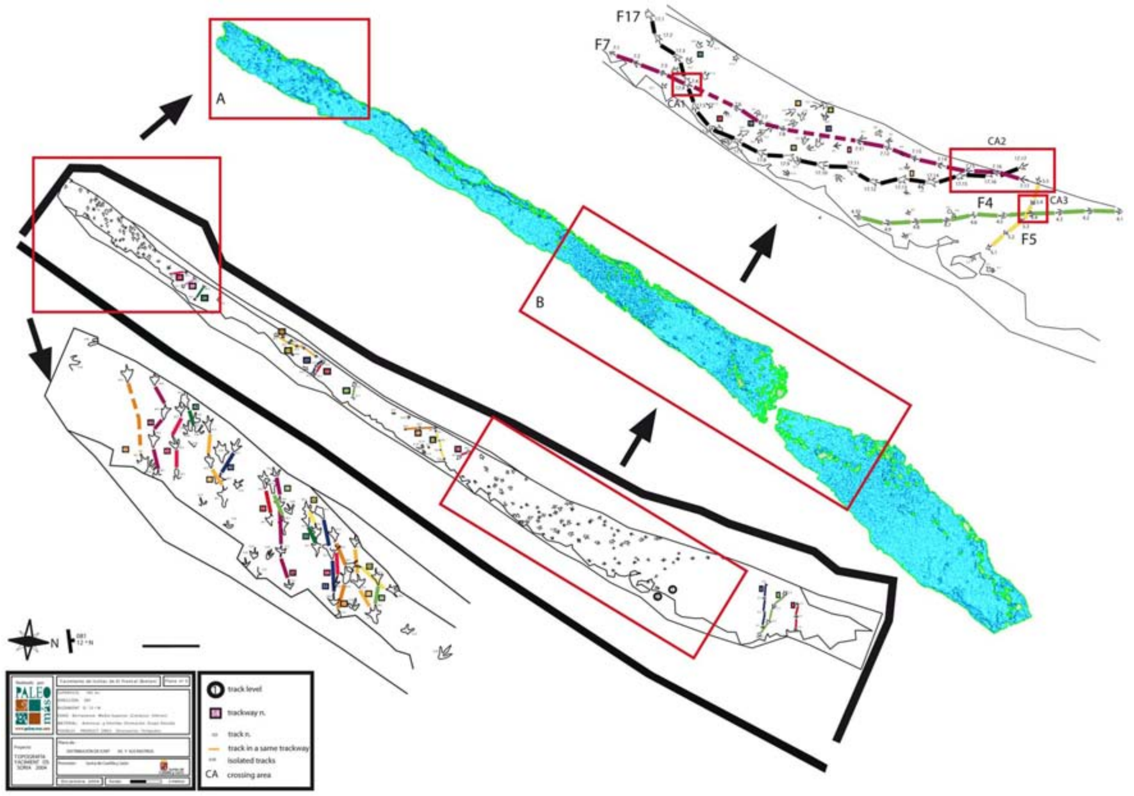

Figure 4. Cartography and 3-D model of the El Frontal tracksite resulting from the LiDAR scanning (grey colour), modified from Barco et al. [44] and designed by Paleoymas SL. In the red rectangles (A and B) are the details of the areas with the highest density of tracks. The studied area is detailed in the rectangle B. Studied trackways F17, F7, F5 and F4 are coloured respectively with black, pink, yellow and green. doi:10.1371/journal.pone.0093708.g004

falls in the DS-3 (depositional sequence, Fig. 1) and belongs to the Oncala Group. It is subdivided into the Huérteles (which includes the El Frontal tracksite) and Valdelprado formations and dates to the Berriasian [32,35,39,40]. The depositional sequence DS-3 follows a pattern of alluvial fans and lacustrine sediments that thin laterally (northwesterly) to fluvial and fluvio-lacustrine deposits [32]).

Recent interpretation describes the Huérteles Formation as characterized by terrigenous sediments (fluvial system) in the western sector of the eastern Cameros Basin and by an increase in shallow, coastal, carbonate-sulphate water bodies to the east, implying that the connection of the Cameros basin with marine areas was much stronger [38] than previously considered [34]. A series of sedimentary structures that crop out near the El Frontal tracksite, (i.e. inclined heterolithic stratification, flaser, rhythmic alternations of sandstones and lutites, symmetrical ripples, mud-drapes) are indicative of a tidally-influenced fluvial-deltaic environment [37,38].

The El Frontal tracksite is 150 meters apart from the outcrops of the Fuente Lacorte tracksite reported by Aguirrezabala and Viera [28] and Sanz et al. [29]. The latter is stratigraphically lower with respect to the studied locality. The lithology of the El Frontal tracksite is composed of 5 different layers that include intercalated organic rich gray siltstones mudstones and sandy-siltstones (Fig. 2A–C). In detail, trackways and isolated tracks are produced and impressed in layer 5 (tracking surface). Layer 5 is a 1 cm-thick siltstone with occasional mud cracks (Fig. 2C) which sometimes is not preserved, and tracks and trackways are found as undertracks in the underlying layer, layer 4. This is characterized by a 2–3 cm thick sandstone-siltstone (Fig. 2B–C). The first set of laminas (Fig. 3A–C) observed at different areas of the tracksite reveals that layer 4 and 5 are composed of quartz (>60%), and minor abundance of phyllosilicates, and chlorite minerals (Fig. 3A–C). It has a grain-supported fabric with quartz ranging from fine to medium size, yielding a moderately sorted composition. The chlorite minerals (<5%) and other planar minerals are very scarce in the mudstone band in the clay matrix. The second set of laminas including layer 4 and 5 was collected not far from the first (Fig. 3D–F) and is composed of sandstone intercalated with mudstone. In these laminas, sedimentary structures, such as mud drapes (Fig. 3D, 3E) and symmetric ripples (Fig. 3F) are observed. These are characterized by a higher percentage of chlorite minerals (>60%) that concentrate in the mudstone band in the clay matrix. Mud drape structures form when a sediment undergoes intermittent flows, leading to alternating sand and mud layers [37]. Symmetrical ripples are formed when a horizontal oscillation generates wave ripples formed by rolling grains in shallow water [41], and they are commonly found associated with mud drapes [37].

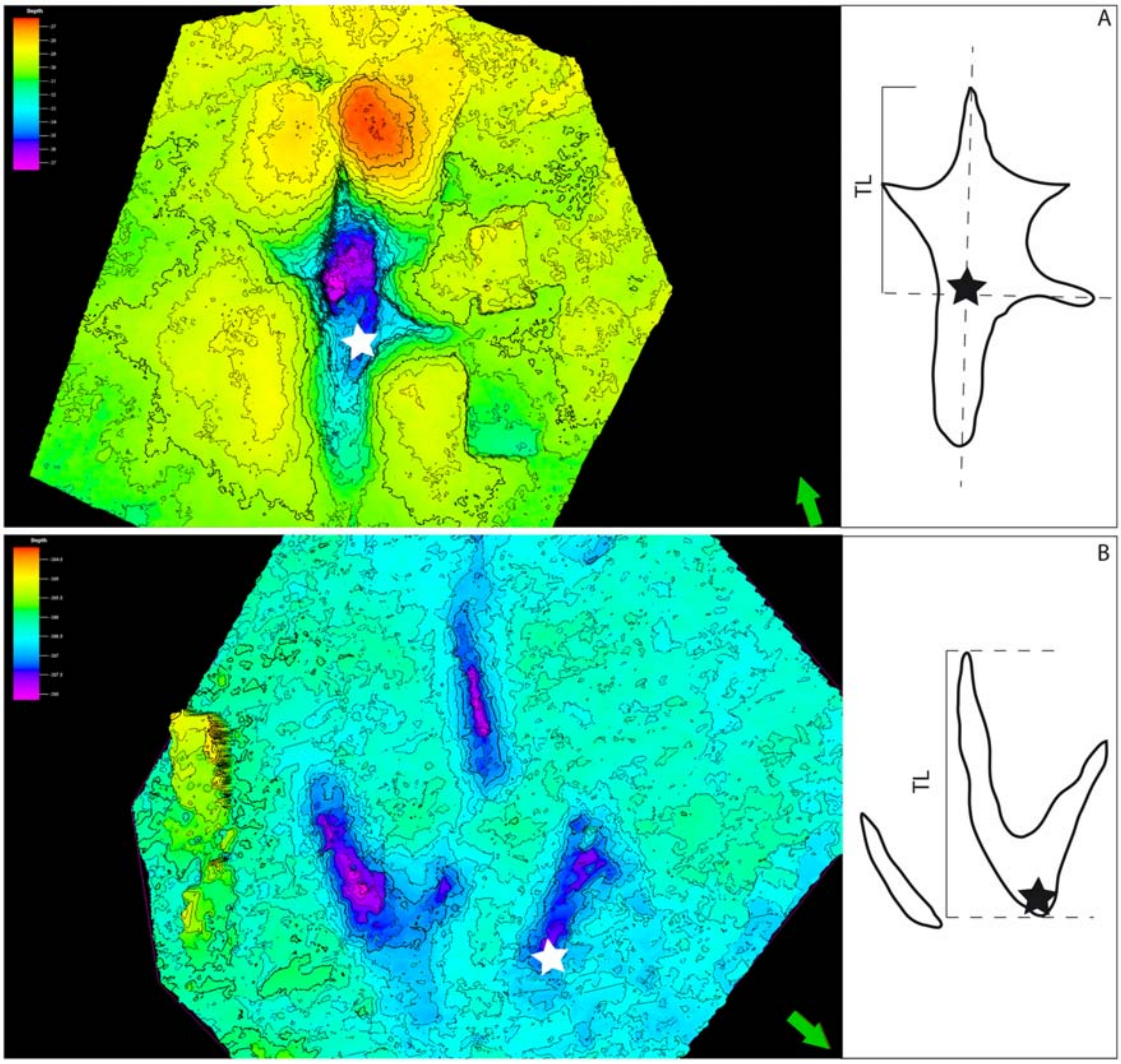

Figure 5. Standards for measuring track length (TL) and depths (black and white stars). A) TL excludes the elongated metatarsal impression, and the depth is taken approximately were the phalanx 1 of metatarsal IV should be. B) In this case there is no metatarsal impression and the TL is easier to measure. Depth is taken in the same point for every track. Color scale green indicates the track layer, purple is the deepest point recorded and red is the highest point recorded.
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Materials and Methods

A complete digital model of the track-bearing outcrop was generated using a RIEGL LMS-Z420i long range 3D laser scanner capable of 5–10 mm resolution [22,23,42] (for three-dimensional El Frontal tracksite caption see Appendix S1). The three-dimensional surface of the tracksite El Frontal is available as a polygon file in the Supplementary Information. This overview scan was complemented with close-range photogrammetric models [27] of individual tracks (Appendix S2), produced from 10 to 20 photographs per track and processed using VisualSFM (http://ccwu.me/vsfm/) [43].

Four trackways (F17, F7, F5, and F4) spanning the site were studied in detail, comprising a total of 49 tracks (17, 17, 5, and 10 tracks from the respective trackways) (Fig. 4). These trackways were chosen for their high morphological variability and their proximity to each other, with the aim of reflecting any effect of spatial variation in substrate consistency. For each track, several metrics were measured from the photogrammetric models using both ImageJ software and Schlumberger package Petrel: track length (TL, measured from tip of digit III, excluding metatarsal pad when present), track width (TW), interdigital angles (II^III, III^IV, II^IV), displacement rim height (DR), maximum depth (D_{max}), and depth of the metatarsal pad impression (D_{mp}). The two

Table 1. Table with measurements taken for all the theropod trackways in the El Frontal.

TRACK	TL	TW	II^III	III^IV	II^IV	PL	SL
45.1	34.4	15.6	23.6	18.4		85.4	166.1
45.2	34	x	x	x		85.1	x
45.3	32.2	18.7	22.8	26.3		x	x
44.1	19.2	17.4	24.2	38.7		68.8	115.7
44.2	31.3	20	24.8	19		54.1	108.2
44.3	27.8	16.8	17.2	20.9		62	x
44.4	20.1	15.8	24.7	21.3		x	x
43.1	26	18.5	21.4	42.9		62.2	124.9
43.2	26	17.7	20.3	30		66	x
43.3	21	18.5	25.3	22.5		x	x
42.1	31	18.1	x	x		65.4	x
42.2	26.4	15	x	x		x	x
41.1	39	24.3	22.2	19.3		71.4	133
41.2	27.2	14.3	19.7	17		66.5	x
41.3	22	19.2	20.4	16.5		x	x
40.1	21	23.7	29.6	34.1		66.1	x
40.2	25	20.6	32.3	38.6		x	x
39.1	22.1	16.5	35.7	19.24		71.1	x
39.1	22.4	22.4	25.6	17.44		x	x
38.1	22.7	17.8	17	14.6		74.1	x
38.2	22	x	x	x		x	x
37.1	18.1	15.5	32.5	39.2		66.1	150.5
37.2	14.6	18	24.4	44		82.3	139.1
37.3	24.7	18.1	27.6	22.5		54.1	x
37.4	14.7	18.7	54.2	51.37		x	x
36.1	21	16.5	13.7	25.6		39.6	x
36.2	19.6	15.8	28.05	39.3		x	x
35.1	19.3	22.1	16.4	18.4		52	x
35.2	21.7	15	x	x		x	x
34.1	25	14	25.2	30.8		87.5	x
34.2	26.2	19.8	17.4	25.6		x	x
33.1	23.4	19.4	38.8	36.3		90.3	163.7
33.2	23.4	27.1	21.3	25.4		69.1	x
33.3	23.7	16.3	x	x		x	x
32.1	15.5	15.3	x	25.2		70.8	146.3
32.2	23	19.3	19.8	24.4		76.2	x
32.3	23.6	19	28.9	30.8		x	x
31.1	21.4	18.2	33.3	18.6		67.1	131
31.2	26.2	23.4	35.8	35.1		76.1	x
31.3	22.7	15.5	27.5	29.8		x	x
30.1	17.8	13.5	54.7	x		62.9	x
30.2	19.6	18.8	24.2	26.5		x	x
29.1	18.3	21.7	26.3	28.3		86.1	x
29.2	20.4	18.7	18.5	17.6		x	x
28.1	5.8	5.3	29.5	30.3		28	x
28.2	5.2	4.6	24.9	32.3		x	x
27.1	7.8	6.4	21.07	30.6		25.1	x
27.2	7.7	7.8	35.5	32.7		x	x
26.1	6	5	26.5	26.7		28.6	x
26.2	5.1	6.2	23.52	30		x	x
25.1	21	27	68.2	77.6		97.2	202
25.2	28.4	21.8	45.3	36.5		107	x
25.3	28.4	20.2	43.8	36.5		100.6	x
25.4	25.2	19	40.2	42.5		x	x
24.1	6.5	5.3	24.9	26.8		26.8	x
24.2	5	5.5	40.8	28		x	x
23.1	5.5	6.3	31.2	39.1		16.1	29.5
23.2	6.9	5.8	27.2	39.2		15.3	x
23.3	3.8	5	42	42		x	x
22.1	5.8	5	20.5	20.1		23.7	x
22.2	5	5.6	25.3	25		x	x
21.1	7	6.3	36.7	28.5		26.3	x
21.2	7	6.1	12.9	26.1		x	x
20.1	8.2	5.4	20	27.1		27.4	53.5
20.2	6.4	5.9	30.4	36.8		26.3	x
20.3	5.4	4.3	40.2	47		x	x
19.1	4.6	4.4	60.2	43		18.4	34.6
19.2	4	4.1	34.4	30		17.2	35
19.3	4.2	3.5	52.3	30.5		18	x
19.4	5.3	4.8	32.4	40.8		x	x
18.1	4.6	4.4	17.7	28.6		x	x
18.2	7.3	7.9	55.7	49.1		20.1	x
17.1	30	14.7	27.3	25.6		91	180
17.2	29	13.2	22.1	19.9		95	182
17.3	27	17.7	26.7	32.7		96	177
17.4	31	14.0	19.7	22.1		85	175
17.5	29	14.3	21.5	30.3		90	
17.6	27	11.876	30	37.2	76.8	100	195
17.7	26	12.881	28.4	25.1	68.9	94	193
17.8	32	13.333	31.6	31.3	54.2	98	213
17.9	27	14.465	24.6	28.6	57.5	115	222
17.10	32	14.165	24.7	26.6	46.3	108	193
17.11	34	14.712	26.4	27.3	48.3	88	178
17.12	31	13.535	18.9	26	52.3	98	200
17.13	30	16.311	22.6	27	48.4	103	198
17.14	29	16.078	19.8	25.8	51.4	100	198
17.15	32	14.307	32	35.7	54	100	197
17.16	27	12.819	27.3	30.9	68.8	94	
17.17	30	16.297				100	
16.1	10.9	10.3	46.7	36.5		33.5	62.4
16.2	12	9.1	29.8	42		30.2	61.8
16.3	12.2	10.9	37.9	35.7		33.9	x
16.4	12.3	10.6	36	35		x	x
15.1	8	9.1	35.6	30.6		48.8	x
15.2	10.3	8.7	28.7	42		x	x
14.1	12.7	10.2	26.7	36		44.8	x
14.2	13.4	9.8	30.4	32.1		x	x

Table 1. Cont.

TRACK	TL	TW	II^III	III^IV	II^IV	PL	SL
13.1	15.5	12.1	23.9	38.8		40.4	81.2
13.2	15.7	12.1	22.8	29.1		42.4	x
13.3	15.5	14.6	20.1	33.2		x	x
12.1	18.3	11.8	29.1	32.2		44.8	91
12.2	18.8	11.8	33.2	20.2		48.8	95.2
12.3	16.2	11.4	26.2	21.6		49.4	x
12.4	20.5	10.8	27.5	35.1		x	x
11.1	12	11.3	42.7	34.4		62	119.4
11.2	13.4	11.8	32.8	31.3		58.7	119
11.3	13.8	10.5	32.9	34.6		60.8	x
11.4	13	11.3	30.7	33		x	x
10.1	18.2	15.2	25.4	38.4		50	x
10.2	16.4	14.3	31	35.2		x	x
9.1	12.3	10.2	30.4	45		48.6	92.4
9.2	14.2	10.2	34.4	33.5		44.6	93.1
9.3	14.2	11.5	30	40.4		49.6	x
9.4	11.7	11.3	31.9	44.2		x	x
8.1	8.9	9	28.5	46.6		36.1	80.6
8.2	8.7	9.3	36.6	47.1		45	68
8.3	11.3	9.3	48.7	48.7		24.9	x
8.4	10	8.8	38.6	46.5		x	x
7.1	20	11.0	29.2	27.9	57.6	88	185
7.2	21	13.9	26.3	39.6	59.3	98	193
7.3	23	13.9	27.3	42.4	65.9	100	
7.4	22	10.2	26.1	35.7	55.7	95	181
7.5	22	11.1	x			95	176
7.6	24	10.1	25	18.6	47.1	93	167
7.7	25	11.0	41.4	36.3	58.3	84	174
7.8	25	9.5	22.2	22	53.6	82	184
7.9	26	11.4				94	
7.10	22	10				93	196
7.11	25	11.2	45.9	17.2	59.6	103	201
7.12	24	13.0	27.9	29.6	51.3	102	195
7.13	21	10.7	32.9	26.2	66.7	99	193
7.14	22	12.0	30.6	31.7	59.6	97	197
7.15	25	10.9	38.3	52.6	64.7	100	195
7.16	19	10.7	32.5	38	73.4	99	
7.17	25	11.0				99	
5.1	17	12.0	29	41.4	77.7	74	142
5.2	19	12.1	31.6	48	78.6	68	134
5.3	16	8.7	39.4	43.2	80.3	69	135
5.4	18	10.4	28.5	39.7	70	66	134
5.5	22	11.7				65	
4.1	23	11.0	36.2	28.4	67.1	106	207
4.2	26	10.3	39.7	40.8	85.9	103	204
4.3	26	9.7	38.7	34.6	66.8	101	202
4.4	27	14.0	52.2	42.4	72.2	103	204
4.5	30	11.0	34	24.5	58.6	105	202
4.6	23	12.6	45	30.1	73.8	102	201
4.7	26	11.0	31.2	23	51.3	100	204
4.8	22	12.6	37.6	35	70.7	100	200
4.9	24	12.2	36.4	38.7	61.8	103	
4.10	27	12.3	43	31.5	70.2	100	
3.1	5.6	5.5	42.1	45.8		25.5	50.5
3.2	5.4	5.5	44.3	43.5		25.2	50
3.3	6.2	6.1	30.2	53.3		24.9	x
3.4	2.9	5.3	38	25.3		x	x
2.1	42.08	33.05	57.12	34.74		103	
2.2	38.18	39.13	61.8	44.25		113	210
2.3	46.87	41.1	51.03	51.25			
2.4							
1.1	7.5	6.8	32.2	36.6		22.8	44.9
1.2	8.6	6.6	34.6	37		21.8	x
1.3	7.3	5.6	25.2	37.3		x	x

TL (track length); TW (track width); II^III (interdigital angel between II^III); III^IV (interdigital angle between III^IV); II^IV (interdigital angle between II^IV taken for trackways 17, 7, 5 and 4); PL (Pace length); SL (Stride length). All measurements in Table 1 are in CM.

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depth metrics were recorded, because many of the tracks show signs of post-formational sealing of the track walls around the digit impressions. Maximum depth is therefore interesting to note, but is of no use for comparisons between tracks (though it remains a useful metric in tracks where no sealing has occurred). The metatarsal pad, conversely, rarely suffers from such wall collapse due to the width of the impression, and so depth recordings from this homologous point between tracks can be comparatively informative. Unfortunately, the metatarsal pad is not always impressed. However, by recording both depth metrics where possible, an indication of the track morphology can be conveyed (Fig. 5A–B). Additionally, pace length (PL) and stride length (SL) were measured both in the field and using the whole-outcrop digital model. Statistical analyses on the 49 tracks refer to linear correlation and dispersion plots that interpolate track length (TL), depth (D) and displacement rim height (DR) parameters.

To quantify the substantial intra-trackway depth and length variations, four graphs for trackways F17, F7, F5 and F4 were built using TL, PL (left Y axis) and depth measurements (right y axis). A sedimentological analysis (4 thin sections in total, IPS-82477a-d housed at the Intitut Català de Paleontologia ''Miquel Crusafont''-ICP) for layers 4 (undertracks) and 5 (tracking surface) was undertaken to quantify lithology and mineral composition of the sediment. Pictures of the four polished thin sections(Fig. 3A–F) were taken using light microscopy via a Leica DM 2500 photomicroscope.

Results

The El Frontal tracksite consists of a southwest-northeast orientated outcrop containing more than 200 tridactyl tracks and 45 trackways (see Table 1) [28–31], distributed along 185 m^2 surface area (Fig. 4). Track density is of more than one track/m^2, although tracks are not homogenously distributed (Fig. 4A–B).

We describe the position in the tracksite, spatial distance and possible interaction of trackways F17, F7, F4 and F5 with one

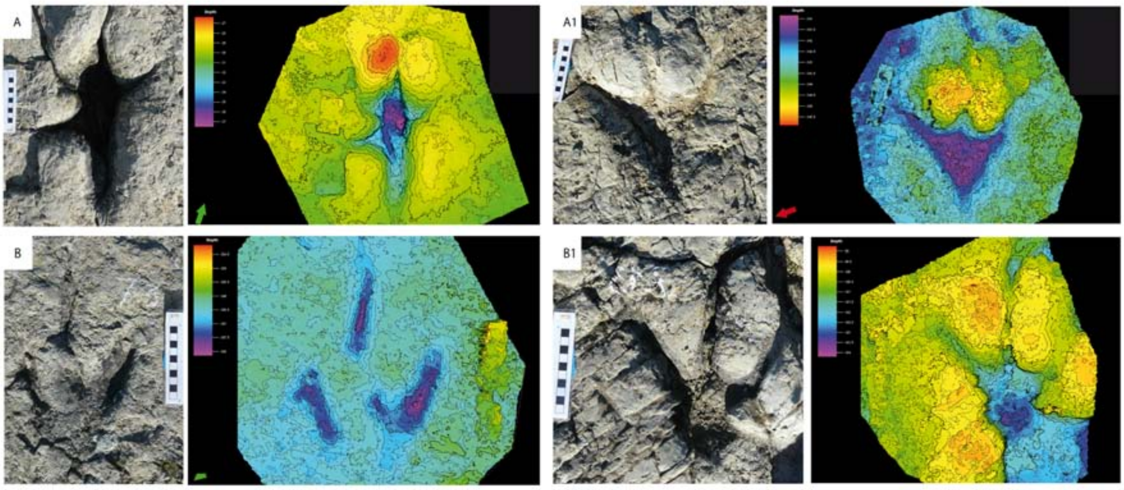

Figure 6. Morphological characterization of the El Frontal tracks. A) Morphotype A is track 17.2, A1) Variation of morphotype A, track 17.17, B) Morphotype B is track 7.3, B1) Variation of morphotype B, track 7.13. Color scale green and yellow indicates the track layer, purple is the deepest point recorded for depth and red is the highest point recorded for displacement rims.
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another. At the northeastern edge of the outcrop, the first tracks of trackway F17 are separated from those of trackway F7 by one meter (Fig. 4B). F17 crosses with trackway F7 (crossing area 1, Fig. 4B) at one meter from its origin. The crossing area includes tracks 17.4 and 7.4 (Fig. 4B), respectively, the former track overlapping the latter, and thus indicates the sequence of trampling. Trackway F17 turns east and aligns parallel to trackway F7 (Fig. 4B). They follow a north-northwest direction for about 10 meters. Trackway F17 finally crosses again with trackway F7 in a region that includes tracks 17.15 - 17.17 and 7.15 - 7.17 (crossing area 2, Fig. 4B). No overlapping of tracks is found in this area, although tracks are located very close to each other. Trackway F4 is parallel to but with an opposite direction to trackways F17 and F7, from which it is separated by 2 meters (Fig. 4B). Trackway F5 has a subperpendicular direction to trackways F17, F7 and F4, and intercepts trackway F4 at track 4.4 (crossing area 3, Fig. 4B) without evidence of overlapping.

1. Morphological Variation

Field observations and photogrammetric models (Appendix S2) revealed various intra-trackway morphotypes (Fig. 6). The morphological variation is exemplified by four different track shapes from the starting (17.2–7.3, Fig. 6A–B) and ending portions (17.17–7.13, Fig. 6A1–B1) of trackways F17 and F7. Track 17.2 in Figure 6A is characterized by being deep and poorly detailed with thin digital impressions (particularly Digit III), bounded by substantial displacement rims. In this regard, it is not uncommon to observe the exit hole *sensu* [45] p.39 of digit III. When digit III is long, and distinguishable, digits II and IV tend to be narrow due to wall collapse (e.g., tracks 17.1, 17.3, and 17.10; see three-dimensional model capture of El Frontal tracksite in Appendix S1). Conversely, when digit III is sealed and bounded by sediment ridges, impressions of digits II and IV are thicker (e.g., Tracks 17.17 and 5.2, Fig. 6A1, see Appendix S2). Track 17.2 (Fig. 6A) shows a deep central area and a deeply impressed and elongated metatarsal mark similar to that reported by Kuban [46]. Sometimes, tracks preserving impressions of digits II, III, and IV exhibit a posteromedially oriented hallux mark in the rear margin. Track 17.17 (Fig. 6A1) belongs to the same trackway as track 17.2, yet 17.17 lacks the hallux and metatarsal impressions which dominate the morphology of 17.2. On the other hand, track 7.3 (Fig. 6B) is a shallow track with a typical tridactyl appearance, digits II and IV usually well impressed, and digit III marked only in its distal part (eg., tracks 4.8 and 7.3, Fig. 6B, see Appendix S2 and Table 2). Track 7.3 shows very little extraneous substrate deformation. In the same trackway, track 7.13 (Fig. 6B1) is found, which differs substantially from 7.3, being considerably deeper and with displacement rims between digits II–III and III–IV. There is also a deep impression where the digits converge at the metarsal pad – an impression almost entirely absent from track 7.3. The tracks differ according to characters such as the presence/absence of hallux or metatarsus impressions, interdigital rims, mud collapse structures and pad impressions.

2. Quantification of Morphological Variation

The shape variation described above is reflected in changes in track parameters such as the measurable pace length (PL), track length (TL) and depth (D), and maximum height of the associated displacement rims (DR) (Table 2). This morphological variation is presented quantitatively in Figures 7–9.

The D versus DR graphic (see Table 2 and Fig. 7) shows the relationship between the depth (D) of the tracks, and the maximum sediment height of the associated displacement rims (DR) (Fig. 7). It shows that these two parameters are positively correlated (Pearson's correlation matrix r = 0.871 and Spearman's correlation matrix r = 0.820). Deeper tracks show the highest displacement rims between the digits.

The figure 8 shows considerable intra-trackway variation. More importantly, in deep tracks, measurable track length (TL) appears influenced by track depth. Thus, trackways F17, F7 and F5 show a wide range of values, displaying a very pronounced variability in both depth (D) and track length (TL) parameters (see Table 2). By contrast, tracks forming trackway F4 are more closely grouped, and the values are somewhat more conservative and consistent along the trackway. In trackway F17 (17 measurements), the D parameter ranges from 48 mm to 13 mm (mean: 31.5 mm,

Table 2. Table with measurements taken for all tracks belonging to trackways F17,F 7,F 5 and F4 of the El Frontal tracksite.

TRACKS	D	TL	PL	DR
7.1	0,18	20	88	0.700
7.2	0,18	21	98	0.320
7.3	0,17	23	100	0.320
7.4	0,9	22	95	0.917
7.5	0,8	22	95	0.600
7.6	0,8	24	93	0.710
7.7	0,7	25	84	0.8
7.8	0,18	25	82	0.75
7.9	1,3	26	94	0.64
7.10	1,4	22	93	0.6
7.11	1,5	25	103	0.7
7.12	2,1	24	102	0.782
7.13	2,25	21	99	1.709
7.14	2,1	22	97	0.9
7.15	2	25	100	0.8
7.16	1,9	19	99	1.189
7.17	1,2	25	99	0.553
average	1,16	23	95,35	
desvst	0,74	2,06	5,97	
max	1,9	25,06	101,32	
min	0,41	20,94	89,38	
17.1	3,18	30	91	1.582
17.2	4,8	29	95	4.179
17.3	4,32	27	96	2.951
17.4	3,1	31	85	1.132
17.5	2,9	29	90	2.267
17.6	2,8	27	100	1.771
17.7	2,6	26	94	1.432
17.8	2,6	32	98	1.679
17.9	2,9	27	115	1.965
17.10	2,7	32	108	2.256
17.11	3,1	34	88	2.332
17.12	3,5	31	98	1.879
17.13	3,8	30	103	2.277
17.14	4,7	29	100	2.653
17.15	3,1	32	100	2.331
17.16	2	27	94	2.014
17.17	1,3	30	100	1.511
average	3,15	29,59	97,35	
desv	0,88	2,27	7,29	
max	4,03	31,85	104,64	
min	2,27	27,32	90,06	
5.1	2,2	17	74	1.1
5.2	2,2	19	68	1.1
5.3	1,7	16	69	0.365
5.4	1,4	18	66	0.2
5.5	0,8	22	65	0.398
average	1,66	18,4	68,4	
desv	0,59	2,3	3,51	
max	2,25	20,7	71,91	
min	1,07	16,1	64,89	
4.1	0,5	23	106	0.35
4.2	0,6	26	103	0.593
4.3	0,7	26	101	0.574
4.4	0,7	27	103	0.798
4.5	0,9	30	105	0.8
4.6	1	23	102	1.01
4.7	1,2	26	100	1.02
4.8	0,66	22	100	0.987
4.9	0,69	24	103	0.617
4.10	0,8	27	100	0.781
average	0,78	25,4	102,3	
desv	0,21	2,41	2	
max	0,98	27,81	104,3	
min	0,57	22,99	100,3	

DR (depth rims); D (depth of the track); TL (track length); PL (pace length). For each measurement average (media), standard deviation (desv) and values with the maximum and minimum standard deviation (max and min) are calculated. All measurements in Table 2 are in CM.

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SD±0.88, Table 2). It is noteworthy that the highest values are in the tracks that show evidence of hallux and metatarsal impression marks. Depth in trackway F7 (17 measurements) displays a range of values from 1.7 mm to 22.5 mm (mean = 11.6, SD±0.74, table 2). In trackway F5 (5 measurements), depth ranges from 22 mm to 8 mm (mean = 16.6 mm, SD±0.59, table 2). Trackway F4 (10 measurements) shows a range from 5 mm to 12 mm in depth (mean = 7.8 mm, SD±0.2, table 2).

To quantify this substantial intra-trackway depth and length variations, four graphs for trackways F17, F7, F5 and F4 were built using TL, PL (left Y axis) and depth measurements (right y axis) (Fig. 9).

Figure 9 shows that: a) the pace length (PL) displays some variations, especially in trackways F17 and F7, b) the track length (TL) changes to a lesser extent than the depth parameter, and c) that the depth (D) is the most variable measurement. In particular, in F17, there is considerable variation in depth among the first few tracks, yet track length and pace length remain relatively consistent. Between tracks 17.4 (crossing area 1) and 17.9, TL and D both display a decrease of a 19% and 16%, respectively, while PL increases by 26%. From track 17.9 to 17.14, the PL decreases by 13% and D increases by 42%. From track 17.14 to track 17.17 (crossing area 2), D strongly decreases a 58%, while PL and TL do not show remarkable variations.

Between tracks 7.1 and 7.3, trackway F7 displays an increasing PL with constant D and TL. From track 7.4 to 7.8, PL slightly decreases, while D increases until track 7.7 to then decrease in track 7.8. From this point of the graphic, a remarkable increase in D (92%) is recorded from track 7.8 to track 7.13, but PL increases only by 17%. Finally, from track 7.14 to track 7.17 (crossing area 2), although PL and TL remain averagely constant, D strongly decreases by 43%. Trackway F5 displays a decreasing D (63%) from track 5.1 to 5.5, with an average constant PL and TL.

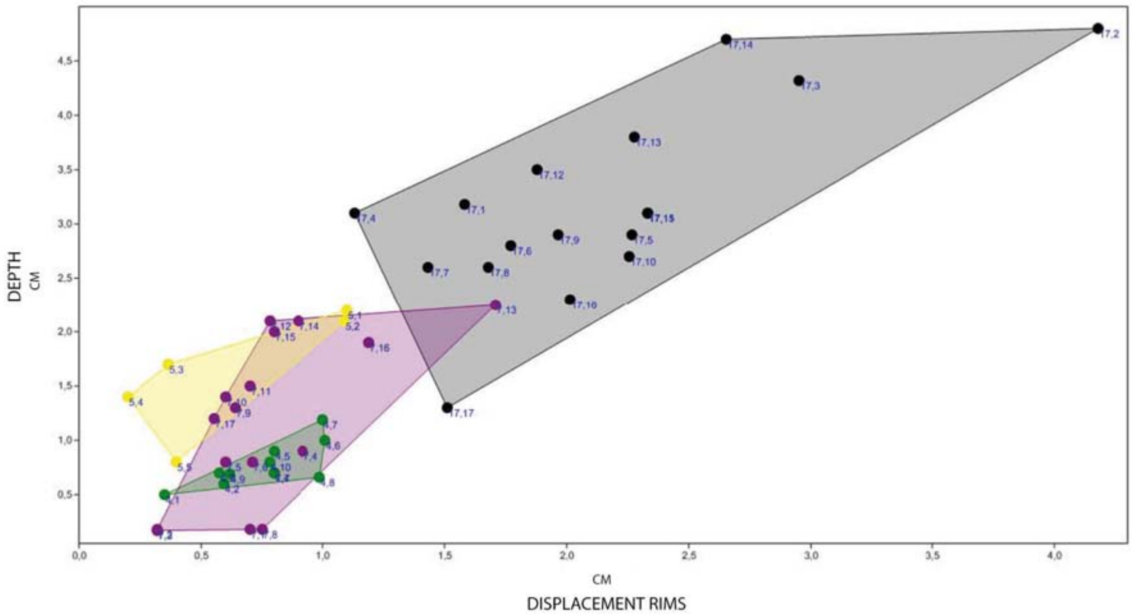

Figure 7. The linear correlation graphic of depth (D) vs displacement rims (DR) shows a positive correlation among these two values. Pearson's correlation matrix results in r = 0.871 and Spearman's correlation matrix in an r = 0.820. F17 (black colour), F7 (purple colour), F5 (yellow colour) and F4 (green colour). Units are in centimeters.
doi:10.1371/journal.pone.0093708.g007

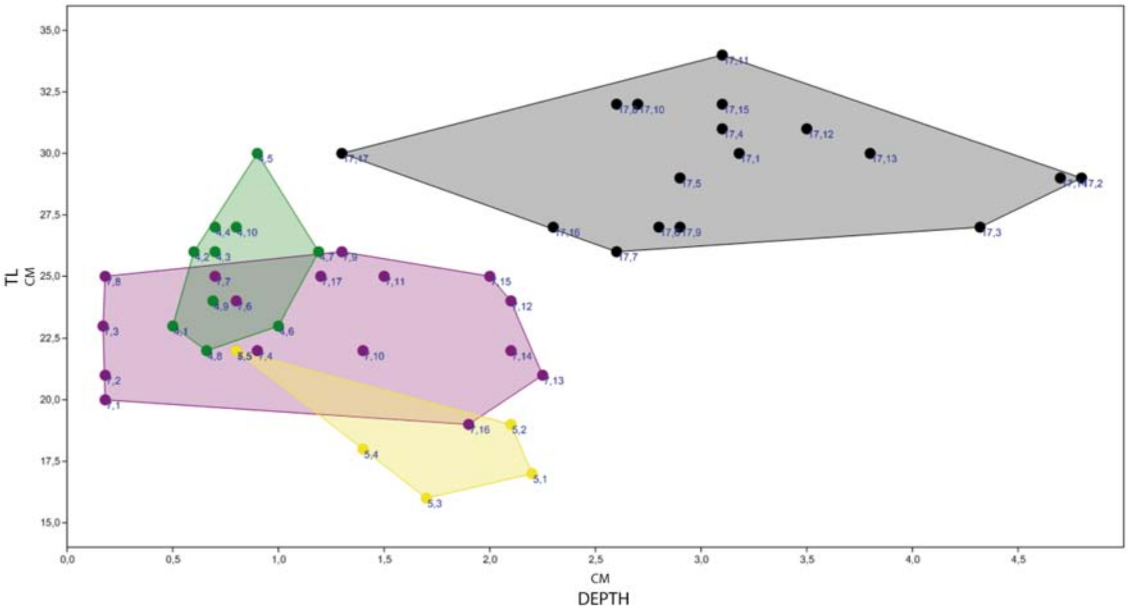

Figure 8. Dispersion graph of depth (D) vs track length (TL) shows a wide range distribution among the tracks of trackways F17, F7 and F5 (respectively black, purple and yellow colours) of the El Frontal tracksite. The most concentrated cluster in that of trackway F4 (green colour), in which values are quite consistent and only weakly vary along the trackway. Units are in centimeters.
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Figure 9. Quantification of the intra-trackway depth and length variations, four graphs for trackways F17, F7, F5 and F4 are built using TL, PL (left Y axis) and depth measurements (right y axis). Units are in centimeters.
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Trackway F4 shows an increasing D from track 4.1 to track 4.7 (58%), a variable TL (23% of variation) and a weakly decreasing PL (6%). From track 4.7 to track 4.10, D decreases quite abruptly (33%), while PL and TL do not display significant variations.

Discussion

The El Frontal site is an exceptional example of high within-trackway morphological variation. The final morphology of a track is determined by the shape of the track maker's foot, the dynamics of that foot, and the substrate conditions [4,47,48]. Within-trackway morphological variation cannot come from variations in foot anatomy, and therefore must originate from horizontal sediment heterogeneity, differences in limb dynamics, or a combination of the two.

The morphological variation of all tracks (Fig. 6 and Appendix S2) is highly influenced by the depth to which the animal sank. By observing the position of each track in the El Frontal tracksite (Fig. 4) and comparing the graphics with each other, it is noticed that similar depth trends are recorded for F4, F7 and F17, which are located parallel in the tracksite. Among trackway segments 4.6–4.10, 17.11–17.14 and 7.11–7.14, a progressive depth increase is recorded, while among trackway segments 4.5–4.1, 17.15–17.17 and 7.15–7.17 depth decreases. Trackways F17 and F7 differ in PL, TL and D values quite strongly (see Table 2), although they behave similarly along three different intra-trackway segments: between 17.2–17.8 and 7.4–7.8, depth decreases in both trackways, between 17.8–17.14 and 7.8–7.13 depth increases and finally, between 17.14–17.17 and 7.14–7.17 depth strongly decreases in both trackways (72% and 43% respectively). This last zone corresponds to the crossing area 2 (Fig. 4), in which trackways are closely located and, although displaying different absolute values of the parameters (Fig. 9), they present a similar trend in responding to the substrate (depth decrease).

Trackway F5, which crosses the site perpendicular to the other trackways, does not display any intra-trackway variation, or similar trends to those of F4, F7 and F17. Nevertheless, tracks 5.4 and 5.5 decrease depth values when approaching to the crossing area 2, where the general tendency is for tracks to be deeper (eg. F17 and F7).

It has been accepted for a long time that the depth to which a foot sinks is a determinant parameter in understanding the soil mechanics that control track formation [1,2,6,10,19–21,49]. The deep tracks at the El Frontal site represent part of a continuum that must have been produced on a laterally heterogeneous substrate (Figures 6 and 10). Hence, tracks change their morphology in accordance to their relative position along a substrate consistency gradient that persisted across the site (Figures 9 and 10). Scrivner and Bottjner [50] and Allen [51] suggested that there is a positive correlation between the foot penetration and the degree of deformation in a sediment. At the El Frontal tracksite, the D versus DR and D versus TL graphics (Figures 7 and 8) show a high difference of values for the 49 tracks considered in the sample as a whole and within single trackways. The dispersion graphics underpin the importance of substrate response with respect to track length and depth variations during the indention of the foot. If the substrate conditions of the El Frontal tracksite were uniform throughout the trampled surface, foot loads made by comparably sized animals moving in a dynamically similar fashion (see PL in Fig. 9) would have produced similar tracks (same track length and depth) along single and associated trackways. On the contrary, we observe that track depth

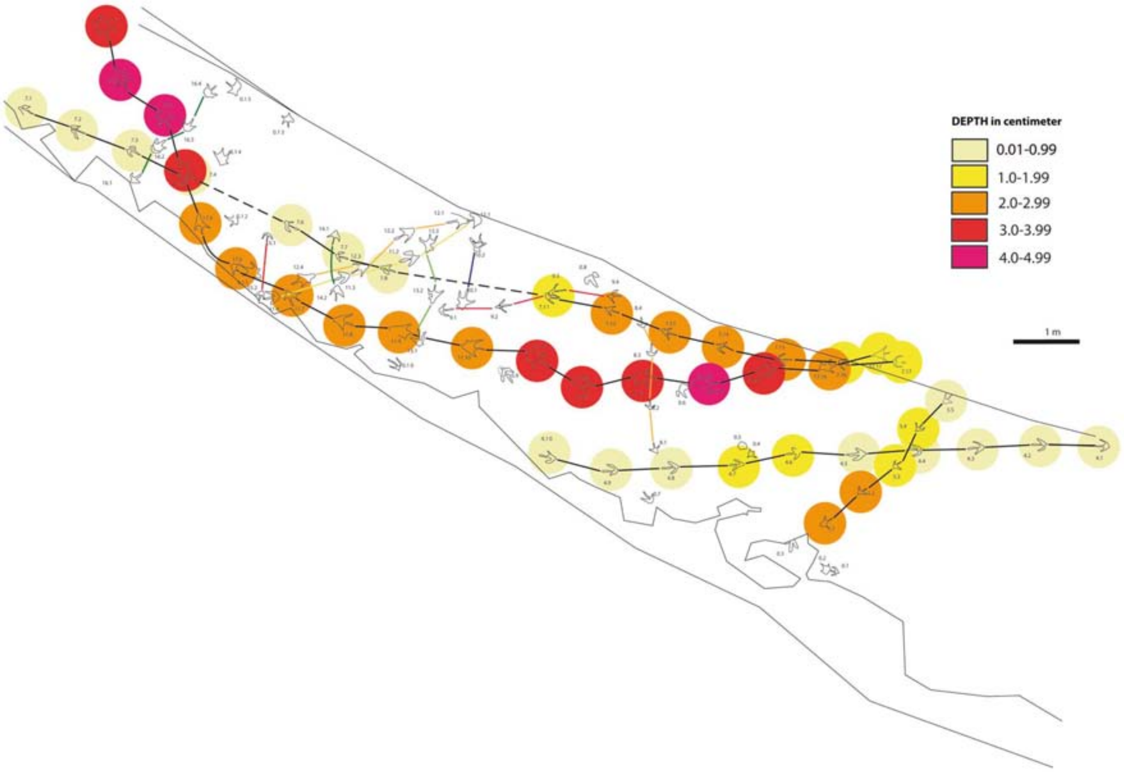

Figure 10. Morphological continuum of the tracks of the El Frontal tracksite. Color scale bar is based on depth intervals.
doi:10.1371/journal.pone.0093708.g010

and morphology are extremely variable both within a single trackway and the whole track sample (Fig. 9).

Tracks can be used to provide additional information on the conditions of the substrate at the time of track formation. Various works [1,8,10,20,52–54] underscored the fact that substrate properties such as consistency, sediment composition (e.g. proportion of clay minerals), grain size, texture, water content and rate of consolidation control and bias the resulting track morphology. The sedimentological analyses performed on the El Frontal site support with the idea that the original substrate was non-homogenous due to lateral changes in adjoining microfacies. Thin sections of layers 4 and 5 (Fig. 3D–F) reveal sedimentary structures (mud drapes and symmetrical ripples) that are usually found when the surrounding environment is characterized by interruptions in the continuity of water flows, such as the current produced in environments with tidal influence [37,38]. This implies that the energetic episodes are frequent, fluctuant and intermittent (Fig. 3D–F). A substrate with a higher water content offers more favourable conditions to produce deep tracks (Fig. 3A–C, 6A,B1). A drier substrate of firmer quartz dominant sandstone is more likely to have produced shallow tracks (Fig. 3A–B,6A1,B). The El Frontal tracks exhibit different depths and morphologies resulting from varying rheological conditions due to a lateral facies of changeable consistency, perpendicular to F17, F7 and F4, but parallel to F5, which is affected to a lesser extent.

Finally, in the current state of knowledge it seems difficult to assign any of the studied tracks to a particular group of tridactyl trackmakers, especially regarding the difficulties distinguishing between theropods and ornithopods in the Iberian Range during Berriasian times [33,55]. The presence of hallux marks and large steps might indicate a probable theropod origin [56], though they are not exclusive characters of this group. Several theropod ichnotaxa have been described in the Huérteles Formation: *Megalosauripus isp.* [57], *Kalohipus bretunensis* [58], "*Fillichnites gracilis*" [59] and *Archaeornitipus meijidei* [60]. Moreover, some grallatorid [61] and *Buckerburgichnus*-like tracks have been reported [62]. Inferences on possible ichnotaxa in the El Frontal tracksite are tangled by the morphological variability observed in the site. The substrate bias in the morphology prevents us from assigning any of the tracks to a particular ichnotaxon, and the strong substrate bias affects track morphology in such a way that it rarely correlates with real foot anatomy of the trackmaker. Interestingly, this study opens a new window into the interpretation of the aforementioned ichnotaxa in the Huérteles Formation and questions whether some of them might represent taphotaxa *sensu* [63].

Conclusions

The El Frontal tracksite displays a variety of tridactyl track morphologies and provides a valuable example of how track geometry might be dominantly affected by substrate conditions during formation, implying that rheology is the major factor in track formation. The photogrammetry models and depth analyses spotlighted that the deep and shallow tracks are part of a continuum of track morphologies and depths. Sedimentological analyses revealed that the site was a non-homogenous substrate that experienced lateral changes due to fluctuating and intermittent flow episodes in a fluvial-deltaic environment. The tracksite differentiation of substrate consistencies and the vast range of intra-trackway morphologies suggest that tracks were produced by similar trackmakers crossing the lateral gradient of heterogeneous substrate consistencies.

The presented analyses underline the influence of substrate on the final track morphology and length. The within-trackway variation highlights that ichnotaxonomic assignations of sediment-biased tracks should be avoided.

Supporting Information

Appendix S1 Caption of three-dimensional El Frontal tracksite. Scale bar 1 meter.
(TIF)

Appendix S2 Photogrammetry and depth analysis respectively undertaken with free software VisualSFM and Schlumberger package Petrel of the El Frontal tracksite. Tracks are disposed verticallly to underpin the intra-trackway morphological variation. Color scale green and yellow indicates the track layer, purple is the deepest point recorded for depth and red is the highest point recorded for displacement rims.
(TIF)

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Author Contributions

Conceived and designed the experiments: NLR BV DC PLF JLB JIC PLM AG. Performed the experiments: NLR BV DC PLF JLB JIC PLM AG. Analyzed the data: NLR BV DC PLF JLB JIC PLM AG. Contributed reagents/materials/analysis tools: NLR BV DC PLF JLB JIC PLM AG. Wrote the paper: NLR BV DC PLF JLB JIC PLM AG.

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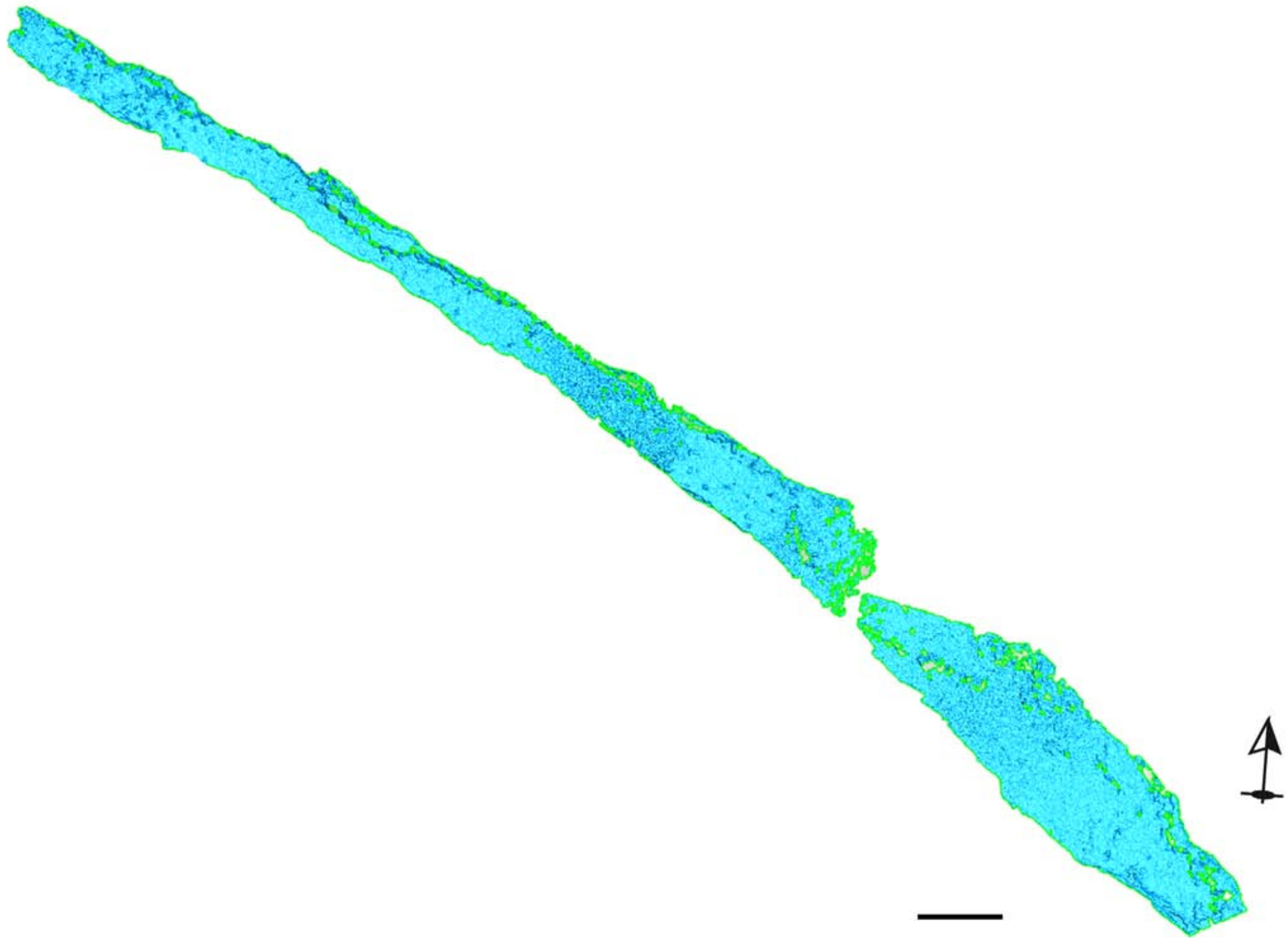
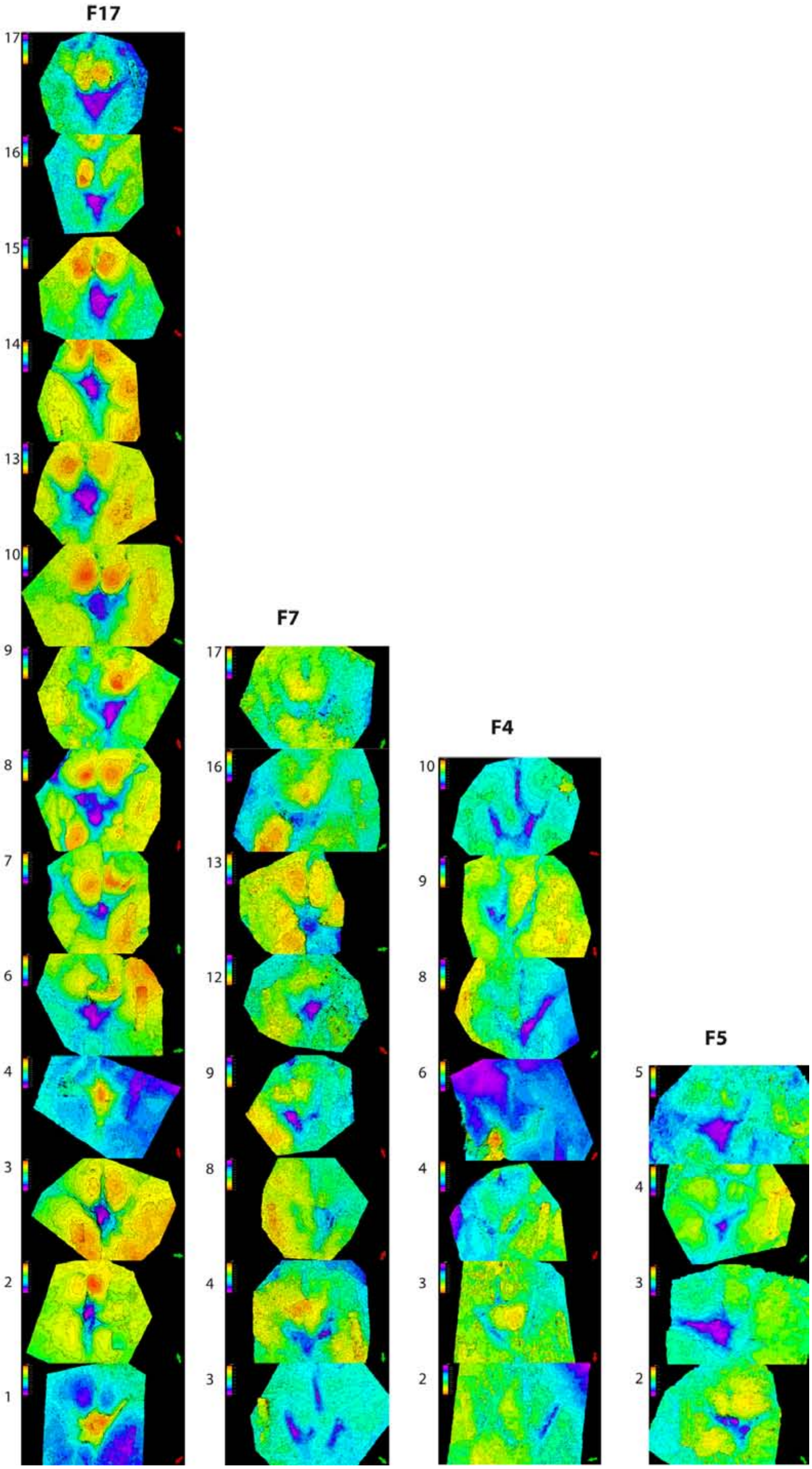


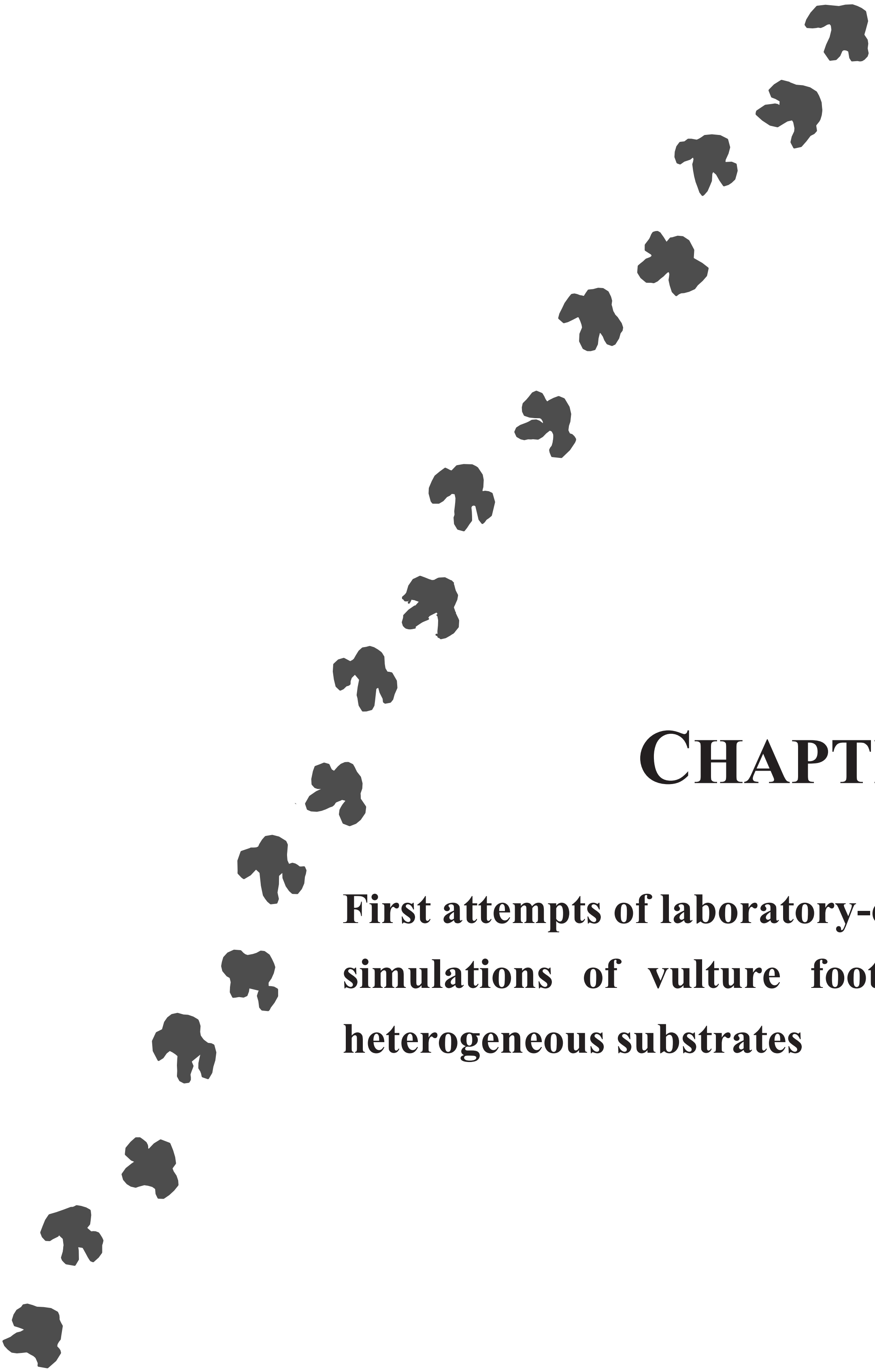
Appendix S1.

Caption of three-dimensional El Frontal tracksite. Scale bar 1 meter.
doi:10.1371/journal.pone.0093708.s001



Appendix S2.

Photogrammetry and depth analysis respectively undertaken with free software VisualSFM and Schlumberger package Petrel of the El Frontal tracksite. Tracks are disposed verticallly to underpin the intra-trackway morphological variation. Color scale green and yellow indicates the track layer, purple is the deepest point recorded for depth and red is the highest point recorded for displacement rims. doi:10.1371/journal.pone.0093708.s002



CHAPTER 10

First attempts of laboratory-controlled simulations of vulture footprints in heterogeneous substrates

CHAPTER 10. FIRST ATTEMPTS OF LABORATORY-CONTROLLED SIMULATIONS OF VULTURE FOOTPRINTS IN HETEROGENEOUS SUBSTRATES

Reasons for undertaking the experiment

Differently to other experiments, where uniform, homogeneous substrates have been usually adopted (coloured layered sand, Jackson et al., 2009, 2010; colored layered cement, Milàn and Bromley, 2006, 2008), the great majority of fossil substrate is characterized by the successive intercalation of heterogeneous substrates (i.e. sand, clay, silt, mud). In fact, it has been stated that the best setting for a track formation and preservation is one in which sediments are strongly heterolithic and rapidly aggrading (Nadon, 2001). Considering both cohesive (clays) and non-cohesive (sands) sediments is indeed more realistic for the parallelisms with fossil tracks. In fact, it has been underscored that the heterolithic nature of the strata is present in two typical depositional environments were tracks are usually found: intertidal and anastomosed fluvial systems. The first is characterized by fine grained and finely laminated layers subjected to tidal and dewatering events; the second is the product of suspended-load rivers in which the combination of fresh water and vegetation attract animals and the presence of mud for seasonal inundations (floodplains) offers an excellent condition for track preservation (Currie et al., 1991; Allen, 1997; Nadon, 2001).

Reconstructing heterogeneous substrates, or blocks of heterogeneous sediments in laboratory, considerably increases the difficulty in controlling the sediment response to the indentation of the foot and biases the final morphology of the track formed in a way that might be a closer representation of fossil track formation.

If a substrate is stratified with mechanically distinct layers (heterogeneous substrate), the depths and surface areas of present tracks can be used to infer the depth and mechanical properties of these layers at the time of track formation (Falkingham et al., 2011). Controlling mechanical properties for each typology of layered sediment and establishing different values of the relative moisture content (water presence percentage with respect to the weight of the sediment layer) to obtain different consolidation effects, potentially allows increasing the exactitude and veracity in the determination of the trackmaker.

During the last decade, experimental ichnology have produced important results, especially in those experiments carried out with computer simulations using Finite Element and biomechanical analysis (Falkingham et al., 2014; Falkingham and Gatesy, 2014). Foot anatomy and foot motion determine where, how and to what extent force is applied, while substrate governs the response to that force (Falkingham et al., 2011, 2014). Finite element analysis can be useful when simulating track formation over a range of different substrate parameters and trackmakers body masses and foot morphologies (ornithopod, sauropod and theropod dinosaurs foot geometry simulated in Falkingham et al., 2011).

In order for a track to form, the range of parameters in which the substrate is adequate to promote track formation in homogeneous substrates is very narrow (Falkingham et al., 2011). This range of parameters is called the "Goldilock effect". Because the main result of Falkingham et al., (2011) is that in homogeneous substrates, there is a very narrow range of shear strength values (how much stress is needed to obtain a permanent failure of the sediment) allowing the formation of observable surface tracks, independently from their track geometry, it means that most real tracks must form in mechanically heterogeneous substrates, or in relatively shallow homogeneous substrates underlaying a differently compacted sediment. Three years later, these authors have mitigated the narrow range of substrates where a track could form by adding more complex substrate models that simulated heterogeneous substrates composed by multiple layers of differing properties (vertical heterogeneity: Falkingham et al., 2014). Anyhow, this new range of possibilities of track formation still depends on a determinate range of potential of underfoot pressures (and trackmakers sizes) that can deform a substrate enough to form a track. Shortcoming of this computer simulation complex FE analysis on heterogeneous substrates relies on the artificial nature of these sediments that, although their properties are controlled and simulated, do not reflect real-world substrates and more importantly, it does not account for foot motion in the sediment.

In the paleo-engineering field of laboratory controlled experiments, substrates have been recreated in an ideal situation of relatively easy control on the variables of homogeneous sediment composition.

The proposition of this experiment of track formation on a vertical heterogeneous block of substrates, in which clays are intercalated with sands of two different grain size pretends to simulate the realistic environments of track-bearing outcrops.

The project consists in creating for the first time in laboratory the realistic situation of fossil substrates by modeling the heterogeneous stratification (intercalations of sands and clays) and in the proposition of an experiment to observe the change in the variables that control the sediment during track formation. Preliminary attempts have been made with a three-dimensional model of a vulture foot cast, manually indented in a box in which six successive layers of sands with two different grain sizes and clays, cement and different percentages of water content are layered. After the vulture pes is removed, the block is left to dry and then cut with a saw in order to observe the deformation beneath the foot indention. These first trials were undertaken to assure the possibility of cementation and vertical cross-cutting of the block before using the mechanical indentation. The last experiment is carried out in the laboratory by attaching the vulture foot to a mechanical punch with a determinate strength extrapolated from various papers (Bates et al., 2013; Falkingham et al., 2011).

These experiments are still very preliminary in their forms because we are still trying to understand whether it is viable or not the application of a more complex geometry. In fact, the future aim is to use real-size dinosaur pes and manus geometries (sauropod, ornithopod, theropod) of flexible material, obtaining three-dimensional casts with a moving capability that emulates that of the real foot (such as in fresh severed emu feet in Milàn and Bromley, 2006). In order to observe the degree of deformation caused in the under layered strata, the surface of indentation should be at least three times the length of the foot. This means that if a modeled pes measures 50 cm in length (which is a quite common measure in dinosaurs), the surface of the block of layers should be at least of 2.25 m^2.

Materials and methods and preliminary results

Experiment 1: 20% water content and manual indentation

Six substrate packages were prepared inside an opened box made of 5 plywood measuring 28 cm x 15 cm x 19 cm (length, width and depth). The plywood forming the base of the box was brushed with petroleum jelly in order to avoid difficulties when separating the block of sediments from the wood. The contact between lateral plywood and the base was isolated with modeling clay in order to avoid water leaking and therefore altering the final properties with respect to the initial ones. The lateral plywood were maintained together by a bar-clamp.

The six layers were prepared separately by adding 20% of cement to allow cementation of each layer and 20% of water measured from the total weight of the sediment and the cement added in each layer (Table 1).

1º) One layer of 600 grams of sand with grain size ranging between 1.2 mm and 0.5 mm mixed with 20% of cement (120 grams). This layer was sprayed with 20% of water with respect to the sum between sand and cement (720 grams), adding therefore 144 grams of water.

2º) One layer of 600 grams of clay mixed with 120 grams of cement and sprayed with 144 grams of water.

3º) One layers of 600 grams of sand with grain size lower than 0.5 mm, mixed with 120 grams of cement and sprayed with 144 grams of water.

This order of layers is repeated two times, resulting in six layers of medium-grain sand, clay, fine-grain sand, medium-grain sand, clay and fine-grain sand. The layers have a thickness of approximately 1.5 cm.

The tracking surface (last layer) was that of the fine-grain sand.

Because of the visible vertical heterogeneity, layers did not need any coloration and they can be distinguished on their natural color and grain size.

MATERIAL	GRAMS	CEMENT TOTAL (GRAMS)/LAYER	RELATIVE WATER CONTENT(GRAMS)/ LAYER
SAND 1.2-0.5 mm	600+600	20%(600) 240	20% (600+120) 144
SAND <0.5 mm	600+600	20%(600) 240	20% (600+120) 144
CLAY	600+600	20%(600) 240	20% (600+120) 144

Table 10.1. Quantity of sediment, cement and water in grams for experiment 1.

The cast of the vulture (*Gyps fulvus*) foot measures 21 cm in length and 12 cm in width. This foot cast was made from a vulture foot and therefore it preserved all the anatomical details such as the phalangeal pads 1-2-3-2 for digits I-II-III-IV respectively and the scale covered skin (Fig.10.1). The vulture foot is tetradactyl (syndactyl) consisting of digits I, II, III and IV. Digit I, the hallux, is more posteriorly directed with respect to theropod footprints of similar size. The claws are pronouncedly curved and thin and they measure 2 cm for digit I, 3.7 cm for digit II, 3 cm for digit III and 2.9 cm for digit IV.

Figure 10.1. Vulture pes. Left, mounted vulture pes; right, detail of phalangeal pads, claw marks and skin impression.

Working with vulture foot is an advantage because ratites do not preserve the hallux (with the exception of the kiwi) and allows extrapolating information over the formation of hallux impressions. Nevertheless, we are still limited to the stiff upward-downward movement of the foot and cannot account for the variable of foot dynamic indenting the sediment, limiting wider inferences on hallux impressions.

The cast of the rigid vulture foot is manually impressed in the heterogeneous package because it was important to test if the chosen sedimentological succession allowed the deformation of the strata beneath the foot (Fig.10.2). After the foot is removed, the packages were left to dry during at least 10-15 days.

The block was then cut with an industrial saw perpendicular to the length axis of digit III with a spacing of 2 cm (Fig.10.3).

Main results from the vertical cross cuts are shown in Fig.10.3. The track emplaced in a 20% water saturated fine-grained sand (<0.5 mm) is well defined, showing high quality of anatomical details such as discrete phalangeal pad formula, claw marks represented as rounded indentations in correspondence to and separated from digits II and III (as the claw is arched) and as elongated impressions in correspondence to digits IV and I due to the stronger and unequal pressure applied. The skin impression is not preserved.

The first vertical cut (Fig.10.3A) was taken at half the length of digit III impression, which, in theropod

Figure 10.2. A)Track formed after manually indenting the vulture print in a 20% water saturated block of six layers of intercalated medium-grained sands, clays and fine-grained sands. B-D) different views of the six layers package after consolidation of the block of sediments (10-15 days approximately).

tracks, is usually the deepest area recorded. The manual indentation of the foot caused digit III to deform the first two layers (a: sand <0.5 mm and b:clays) to almost half their width, but the third layer from the top (c: sands between 1.2 mm and 0.5 mm) suffers no visible deformation and the same happens for the repetition of the heterogeneous layers underneath (a', b' and c', Fig.10.3A). The walls of digit III are very well defined, reflecting the deepening and shape of the digit and the upward displacement of the sediment (withdrawal rims as in figure 1 of Jackson et al., 2009). The deformation reflects the model of failure of general shear (downward) causing the upward displacement of the sediment, as described in Manning (2004).

The second vertical cut (Fig.10.3B) is taken at the base of the II phalangeal pad of the III digit (PIII2) and at the base of claw of digit IV (or the tip of digit IV). The undertrack formed in layer b (clay) appears to have received a stronger deformation, causing a higher raise of the marginal rims between digits II-III and III-IV. Moreover, the clay layer (b) slightly transmitted the pressure to lower layer c (medium-grained sands between 1.2 mm-0.5 mm) where digit III have penetrated but not in correspondence to the indentation of digit IV. This digit strongly compressed the clay level (b) to more than half of its width, causing a steeper track wall in the inner side of digit IV with respect to its external margin. Layer c was maintained unaltered beneath digit IV.

The third cut (Fig.10.3C) crossed the base of the first (proximal) phalangeal pad of digit III (PIII1), the II (distal) phalangeal pad of digit II (PII2) and the III phalangeal pad of digit IV (PIV3). Digit PIII1 walls are asymmetrical, showing a vertical wall on side toward digit II and a sloping wall on the side toward digit IV. PIII1 sinking appears quite shallow, causing a very low deformation on layer a and no transmission of pressure on the clay layer (b). A similar situation occured for PII2, which shows a wider and rounded section that caused a slight rise of the sediment rim in correspondence of the external margin of digit II. On the other hand, the deepest indentation is observed in PIV3 vertical cut, showing the almost complete deformation of layer a and the transmission of this pressure to layer b that halves its width. Layer c is maintained completely unaltered in this section.

From this vertical cuts it was observed that layer c (Fig.10.3A) composed by medium-grained sands, clearly absorbs too much deformation from the upper layers a and b (Fig.10.3A) and does not allow a further indentation of the track. Because of layer c, these tracks showed a relatively low degree of deformation with very small vertical deformations and very low depths of maximum deformation zone (Manning, 2004; Jackson et al., 2009).

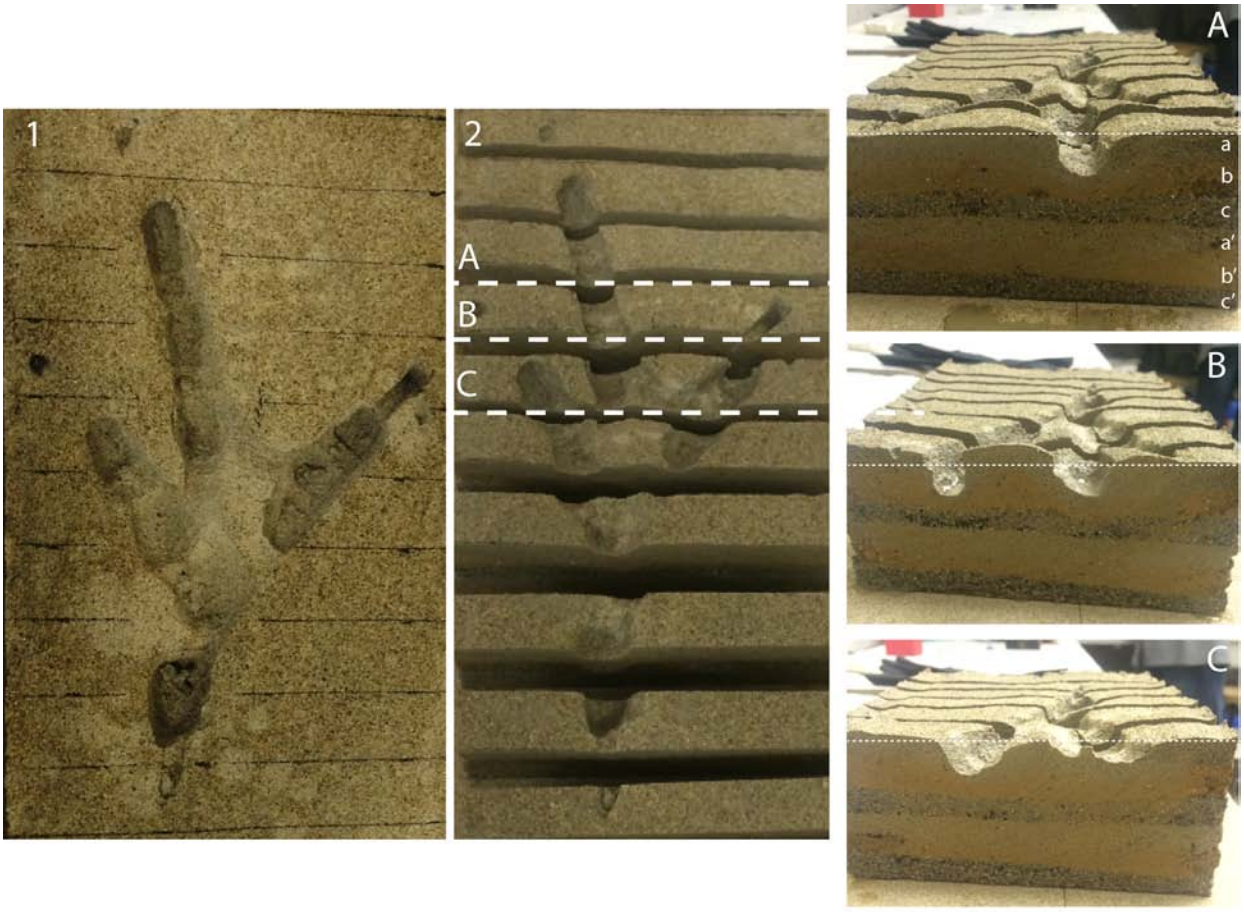


Figure 10.3. 1) Track produced in the fine-grained sand (<0.5 mm) representing the tracking layer. 2) Broken lines indicate the vertical cuts considered (A-C). A-C)Vertical sections through the heterogeneous package of layers showing the formation of undertracks along the subjacent horizons. Thin dotted lines in A-C shows the tracking surface.

Experiment 2: 40% water content and manual indentation

This experiments follows exactly the same procedure adopted for experiment 1. The relative water content changes from 20% to 40%, corresponding to 288 grams of water per layer (Table 10.2).

MATERIAL	GRAMS	CEMENT TOTAL GRAMS/LAYER	RELATIVE WATER CONTENT(GRAMS)/ LAYER
SAND 1.2-0.5 mm	600+600	20%(600) 120	40% (600+120) 288
SAND <0.5 mm	600+600	20%(600) 120	40% (600+120) 288
CLAY	600+600	20%(600) 120	40% (600+120) 288

Table 10.2. Quantity of sediment, cement and water in grams for experiment 2.

This experiment accounts for 40% of water saturation for each level of sediment (Fig.10.4). Jackson et al. (2009, 2010) have undertaken experiments ranging from 0% (dry) to 30% (saturated) underscoring that when the relative moisture content of water is of 30%, the cohesion is compromised causing a poorer preservation of the morphology of the track. While indenting the vulture foot in this saturated sediment, a water lamina was still present and resulted in a deep and deformed track (Fig.10.5). Digit impressions are wider and retained less discrete anatomical features. For instance, phalangeal pads are slightly discernable and claw marks appear to be strongly overestimated by the water saturation, while in the 20% water content block these were impressed as rounded sections separated from the digits because the convex surface of the claw did not contact with the sediment (Fig.10.3A), with the exception of digit II (Fig.10.3A,B).

A 40% moisture content implies a higher pore-water pressure and a higher degree of deformation due to the looser particles arrangement. This is observed in Fig.10.4C-E, in which some of the cement particles suspended in the 288 grams of water of the first layer separated and cemented in a new layer deposited on top of the fine-grained sands (<0.5 mm, layer a in Fig. 10.3A).

This implies that the sample was not correctly mix and vertical cuts were not undertaken for this block because deformation has not affected the layers beneath the foot due to the water lamina presence that acted as the tracking surface.

This experiment needs to be taken a second time in order to improve the methodology of mixing such a great amount of water with the cement and the sediment, preventing the cement particles to scatter and mix with water separately from the sandy layer. Moreover, although the morphology is altered by the increase of water presence (Fig.10.5A-D) in the package, the track shape is still well discernable and this is probably due to the fact that the newly formed layer (cement+water, Fig.10.4C) is finer than the fine-grained sand and it does not reflect the real saturated condition of the heterogeneous layers. In fact, the opposite situation is observed in Jackson et al. (2009, 2010) and Milàn and Bromley (2006, 2008), in which water saturated sediments (30%) display highly affected track morphologies. Another problem was found in mixing the water with the clay, which, due to their impermeability, take a long time to absorb the water and therefore a possible solution might be that of reducing the thickness of the layers by using less amount of sediments for each layer.

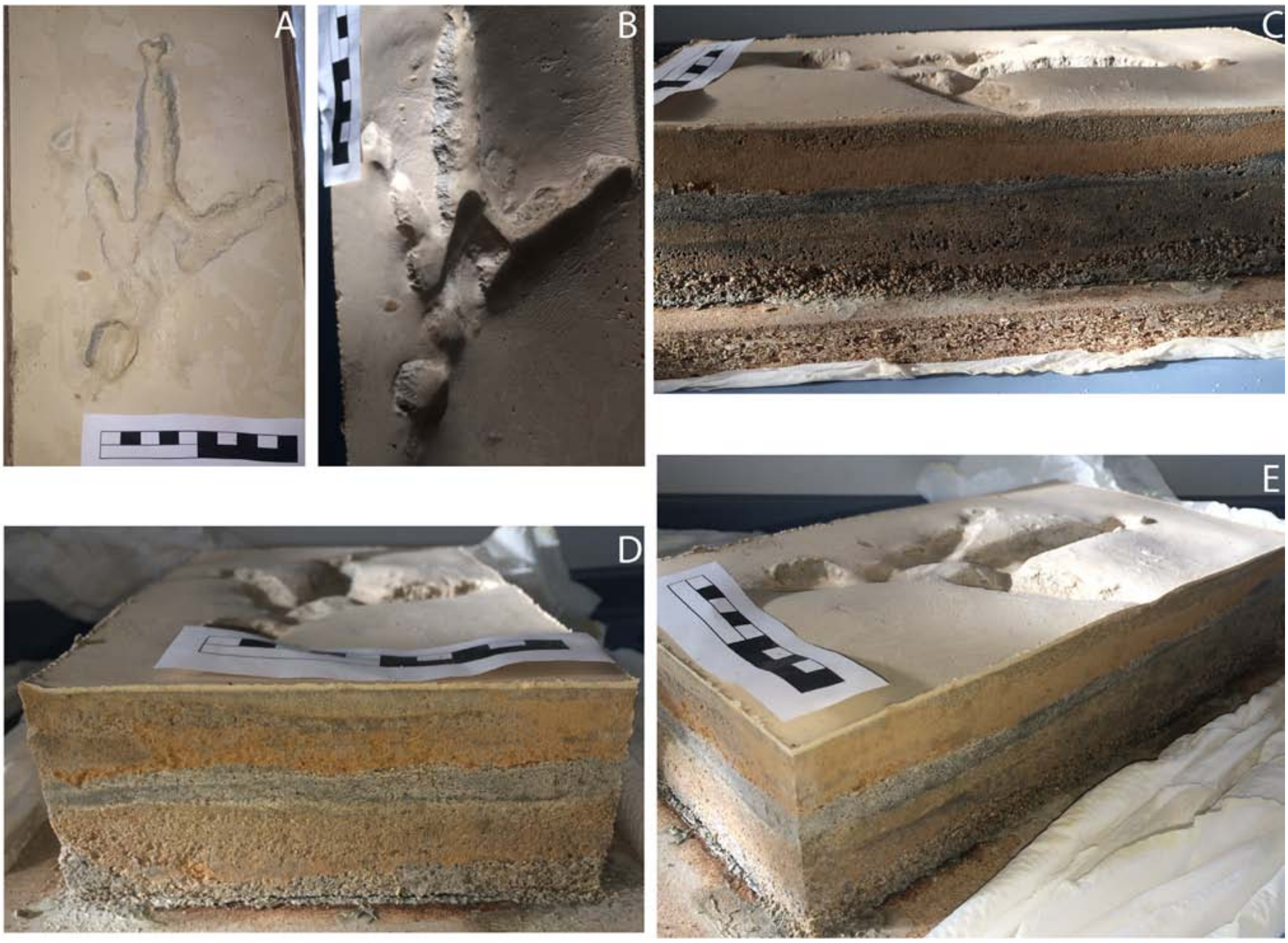


Figure 10.4. A-B)Track formed after manually indenting the vulture print in a 40% water saturated block of six layers of intercalated medium-grained sands, clays and fine-grained sands. C-E) Different views of the six layers package after consolidation of the block of sediments (20-25 days approximately).

Figure 10.5. Evolution of absorption of water content on the tracking surface. A-B) After the track is impressed; C) After few days from impression, the sediment is still wet and plastic; D) complete cementation of the sediment block.

Experiment 3: 30% water content and mechanical indentation

For this experiment, the thickness of each layer was reduced by using less quantity of sediment. Instead of using 600 grams of sediment per layer, 200 grams are mixed with 20% of cement and 30% of water.

MATERIAL	GRAMS	CEMENT TOTAL GRAMS/TYPE OF SEDIMENT	RELATIVE WATER CONTENT(GRAMS)/ LAYER
SAND 1.2-0.5 mm	200+200	20%(200) 40	30% (200+40) 72
SAND <0.5 mm	200+200	20%(200) 40	30% (200+40) 72
CLAY	200+200	20%(200) 40	30% (200+40) 72

Table 10.3. Quantity of sediment, cement and water in grams for experiment 3.

This experiment was undertaken in the laboratory for rheological analyses of the UPC (Universitat Politècnica de Catalunya) as a trial for its viability and therefore only preliminary results that regard the process are presented (Fig. 10.6).

A perforation on top of and parallel to the axis of the tarsal-metatarsal bones of the vulture foot cast is applied to insert a screw that is attached to an adjustable collar for the indenter (vulture foot).

The rod was attached to an electromechanic press (50kN range) which applied an increasing compressive force to ident the vulture foot (Fig. 10.6A-D). The test was displacement-controlled and the force was measured with a load cell (2kN range).

A metal grid with 10-mm-squares was impressed onto the tracking surface the simulation so that the strain associated with track formation could be observed (Fig. 10.6E). The foot was indented progressively and constantly in the sediment blocks until it reached a maximum strength of 191.7N, which is the double of the vulture weight (10kg). Total depth reached by the indentation of the foot is of 13 mm (Fig. 10.6F).

More importantly, when data are plotted (Fig. 10.7) it is possible to observe how the sediment becomes progressively harder to deform with depth, meaning that more strength is needed in order to descent the foot with the same depth increment (strain hardening, Schanz et al., 2013). This indicates two facts: 1) the relative water content is high (and water is incompressible); 2) the water had no time to escape from the pores of the spaces between the particles of the sediment because the experiment was undertaken fast to simulate the vulture foot entrance.

The resultant graphic plot (Fig. 10.7) is a combination of the velocity of the experiment and the incompressibility of water, which was abundant in the heterogeneous package (30% water content each layer).

Foot morphology (Fig. 10.6G) is characterized by the impression of all phalangeal pads 1-2-3-2 for digits I, II, III and II and the presence of the tarso-metatarsal phalangeal pad impression symmetrically placed between digit II and IV impressions and in line with digit III impression, according to the syndactyl configuration of vulture foot. The only claw impression resulted from the 191.7N indentation strength is in correspondence of digit II. No other claw marks are impressed and this is probably due to the angle of penetration (how the foot is attached to the screw) and to the phalangeal pads, which prevent (and delayed) the indentation of claws in the sediment.

The resultant block composed by the six layers of alternated fine-grained sands, clays and coarse-grained sands needs to be cut perpendicular to digit III axis in order to observe the deformation pattern of the foot in the vertical cross-sections.

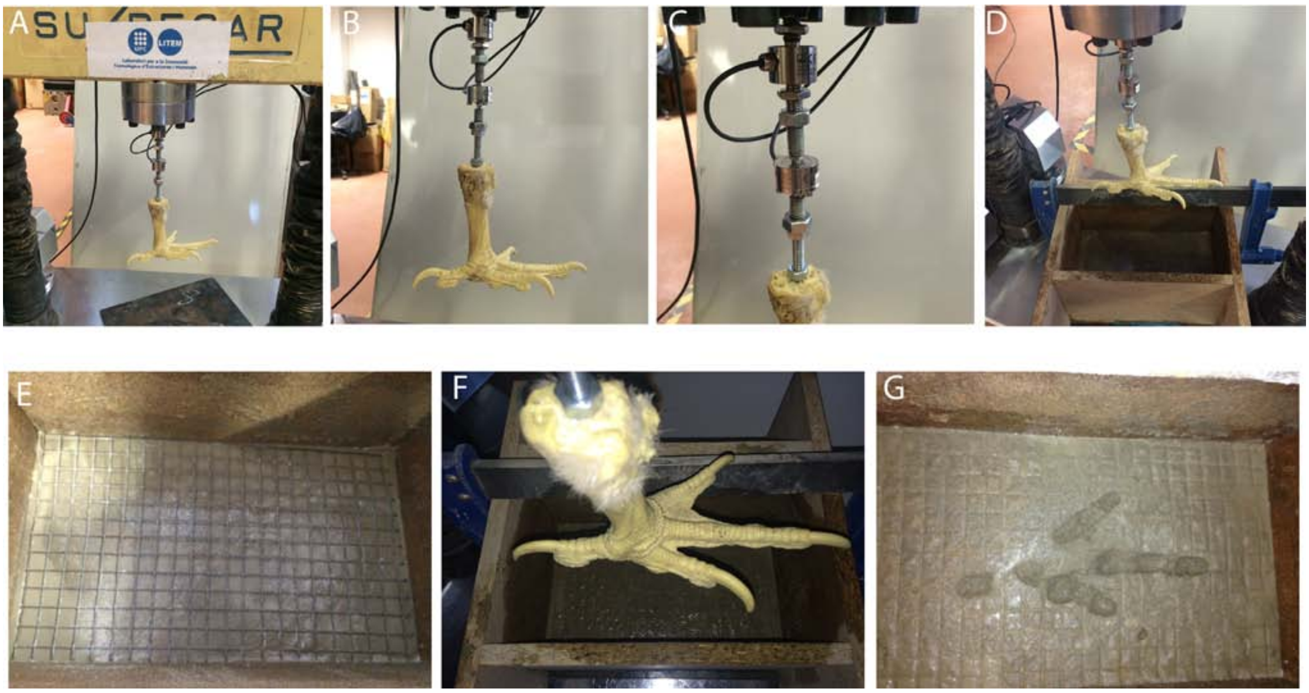


Figure 10.6. Experiment at the rheological laboratory of the UPC (Universitat Politècnica de Catalunya). A-D) electromechanical punch with the vulture foot attached and details of this attachment with a screw to the indentation collar. E) Square grid on the tracking surface composed of fine-grained sands, F) indentation of the foot on the package of sediments, G) final track morphology after 191.7N of strength applied and 13 mm of indentation.

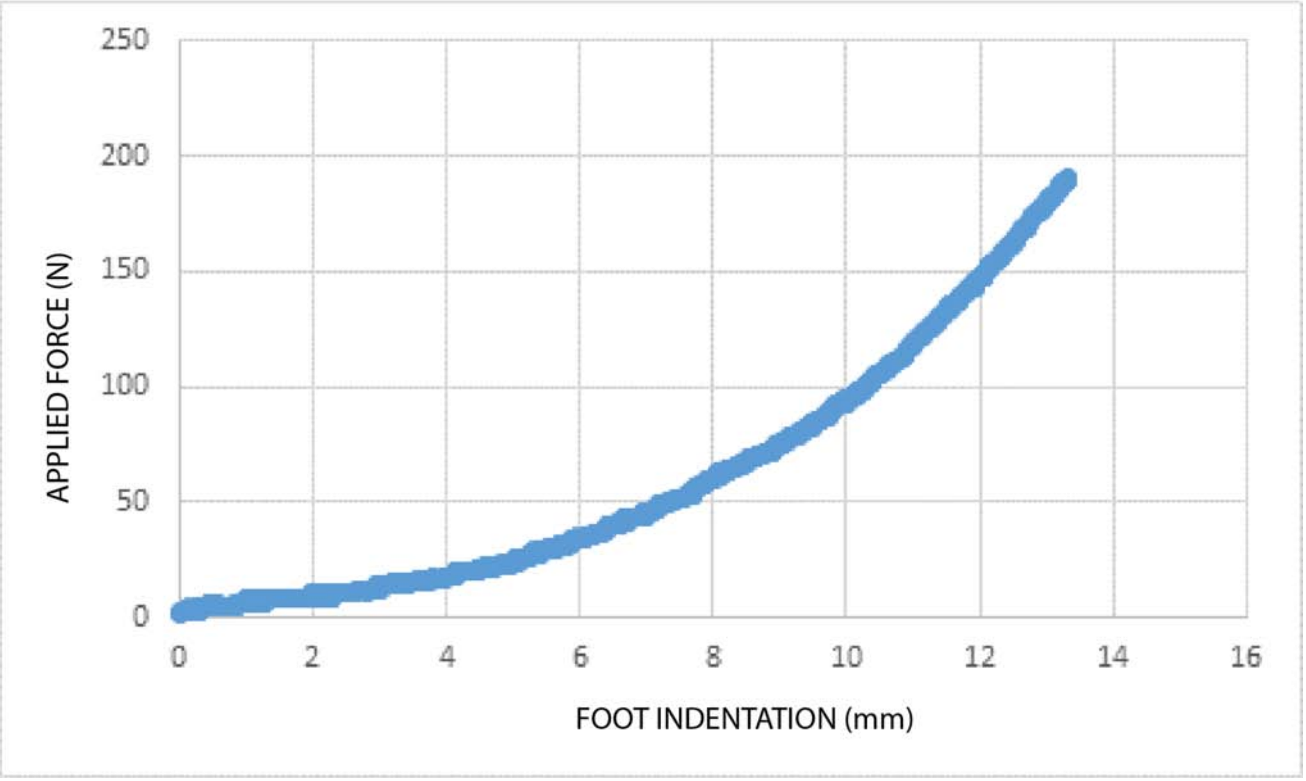


Figure 10.7. Plot of parameters of the foot descent (x axis) and the applied force (y axis) in the mechanical experiment on heterogeneous layers.

General considerations

Computer simulations have expanded the conditions in which tracks are formed by adding computer modeled surfaces that simulated the properties and variables found in heterogeneous substrates (Falkingham et al., 2014).

The experiments here described have been undertaken as indicative trials for viability of laboratory controlled experiments on heterogeneous non-artificial substrates. They are a first step on the characterization of track formation on heterolithic materials prepared with real sediments that want to simulate fossil substrates with vertical heterogeneity.

The three experiments undertaken have shown three different resultant morphologies (Fig.10.8). Morphologies in Fig. 10.8AB are the result of a manual indentation, while fig.10.8C is the result of the mechanical indentation. Several difficulties have been highlighted by these trials such as that cement properties are very complex to determine, clays difficultly absorbs the relative water content sprayed, coarse-grained sands almost display no deformation and compression under the foot indentation (so they will be likely removed from the future experiments), 40% water content causes a water lamina on the tracking surface that lasts days during which the cement particles scatter and mix with water forming a thin cement lamina which properties are not determinable.

The blocks need to be cut as in experiment 1 (20% water content) in order to observe the vertical cross

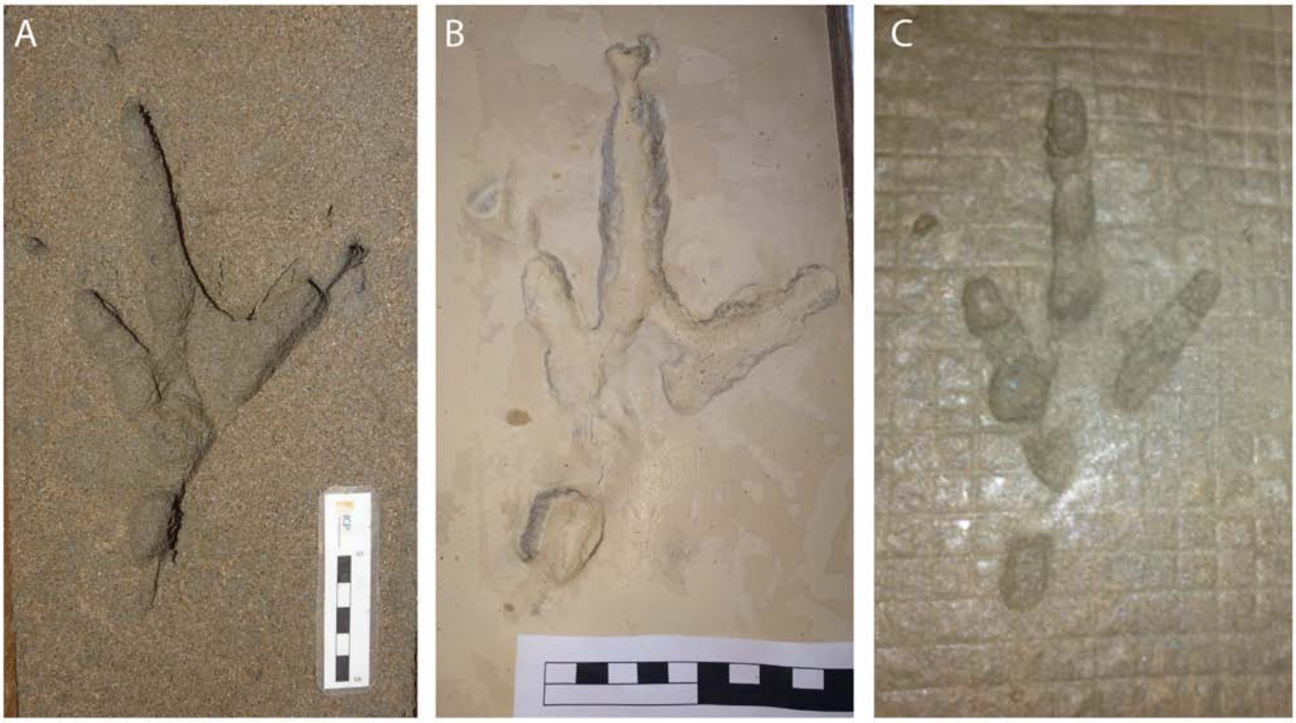


Figure 10.8. Resultant foot morphologies at A) 20% water content and 600 grams of sediment per layer; B) 40% water content and 600 grams of sediment per layer; C) 30% water content and 200 grams of sediment per layer.

sections and distribution of foot pressure in the layers underneath. Moreover, it is understood that in order to obtain significative results for heterogeneous substrates, properties for each sediment will need to be calibrated. For this, six experiments are programmed to isolate the properties for each sediment at a determinate water content:

1A) six layers of coarse-grained sands (200 grams/layer) with 20% of water content
1B) six layers of coarse-grained sands (200 grams/layer) with 40% of water content
2A) six layers of fine-grained sands (200 grams/layer) with 20% of water content
2B) six layers of fine-grained sands (200 grams/layer) with 40% of water content
3A) six layers of clays (200 grams/layer) with 20% of water content
3B) six layers of clays (200 grams/layer) with 40% of water content

Once each material is characterized with all its rheological and mechanical properties at different percentages of moisture content (shear stress, compressive stress, effective stress, apparent cohesion, shear strength, poisson ratio, young's modulus, angle of shearing resistance, internal friction) and parameters such as porosity, humidity, consistency limit and plasticity are determined, the sediments can be layered with vertical heterogeneity or each layer could be the result of mixture between sands and clays in an even more realistic perspective.

Experiments need to be taken with the mechanical indentation, since it is a quantifiable methodology that allows important insights on the progressive strain hardening of the soils with depth and water content and how these mechanical properties can affect the track formation.

The box containing the block of sediment packages should be larger, since this would reduce the confinement of soil allowing a deeper indentation of the foot and therefore a wider visibility of each layer deformation and soil response on the tracking surface.

Being the geometry and the contact element analysis a complex manner and keeping in mind that the ultimate goal for these experiments is to capture the track distribution with depth and different materials, three-dimensional models are needed in order to reduce experimental exploration and to reconstruct the trackmaker's foot from its track within the different lithified layers through reverse engineer.

The exploration on the undertaken experiments is oriented, from a mechanical point of view, to the determination of the transmission of superficial deformations due to the indentation of a foot through a compressive block of layered sediments. They allowed the understanding of possible shortcomings from vertical heterogeneity (sands absorb a great amount of deformation) suggesting that next steps should rather consider mixing different sediment on the same layer, rather than extending homogeneous layers of different materials.

GENERAL DISCUSSION

GENERAL DISCUSSION

The basic element of study of this PhD thesis is the variation of track morphology. This element is controlled by three principal parameters: the foot anatomy, the limb dynamics and the substrate properties (Padian and Olsen, 1984; Minter et al., 2007; Díaz-Martínez et al., 2009; Falkingham, 2014). If the biasing degree of these parameters is unknown, which is usually the common case, the morphological description on the individual (isolated) track morphology might be reflecting the combination of substrate properties, limb kinematics and, finally, the foot shape.

The concept of morphological variability (Farlow, 1989; Farlow and Chapman, 1997; Gatesy et al., 1999) underscores the fact that the same animal can produce different track morphologies depending on the influences of the gait, of the trackmaker and the substrate conditions. The morphological variation has been principally analysed in individual tracks through geometric morphometric analyses (Belvedere, 2008; Castanera et al., 2015; Lallensack et al., 2016), laboratory controlled and neoichnological experiments (Allen, 1997; Manning, 1999; Milàn, 2006; Milàn and Bromley, 2008; Marty et al., 2009; Jackson et al., 2009, 2010) and complex computer simulations (Falkingham et al., 2008, 2011, 2014) with the main object to understand the relationship between the substrate parameter (i.e. substrate consistency) and final track geometry. A great deal of information on the foot anatomy and foot dynamics can be extrapolated from an individual track (Thulborn and Wade, 1989; Thulborn, 1990; Lockley and Hunt, 1994; Avanzini et al., 2008; Mateus and Milàn, 2008; Avanzini et al., 2011). In recent times, however, as stated by several authors (e.g. Allen 1997; Gatesy 2003; Manning, 2004; Milàn, 2006; Platt and Hasiotis 2006; Marty 2008; Falkingham et al. 2009, 2010; Jackson et al. 2009), sediment water content at the time of the track's formation is crucial, and strongly controls the track's morphology (Díaz-Martínezet al. 2005). Treating tracks as biogenic sedimentary structures, through an approach based on soil mechanics, may help understanding fossil tracks with a more complete perspective (Padian and Olsen, 1984; Allen 1989, Gatesy et al., 19999; Manning, 2004; Milàn et al., 2004; Milàn, 2006; Milàn and Bromley, 2006, Milàn et al., 2006; Minter et al., 2007; Schanz et al., 2013; Falkingham, 2014). Laboratory controlled experiments and especially computer simulations undertaken for individual tracks allow an almost complete control and prediction over the substrate variable on the track morphology. Computer simulations are run in order to generate a rheological model that simulates determinate substrate consistencies on ideal homogeneous (Falkingham et al., 2011) and heterogeneous substrates (Falkingham et al., 2014). Unfortunately, as already underscored in Part 2 of this thesis, shortcoming for laboratory experiments and computer simulations is the stiffness of the foot cast (with exception for Jackson et al., 2010). This rigidity of the indenter does not allow the realistic and dynamic interaction between the foot and the sediment. The preliminary structure traced for the rheological experiment proposed in this thesis (chapter 10), showed the importance of mixing different sediments on the same layer, rather than intercalating homogeneous layers of different materials. This would be a more likely representation of the sedimentological conditions encountered in fossil tracks

(Whyte and Romano, 2008; Wilson et al., 2009; Razzolini et al., 2014). The foot indenter should be a non-stiffed foot cast, which has to be always mechanically indented in a mixed heterogeneous substrate (sands and muds) with gradually increasing water content (from 0% to 40% water content). Track morphological extremes can be reproduced under controlled-experiments in which different water contents affect the shape of the track.

The quantification and qualification of long successions of tracks, complete trackways, enable the recognition of the morphological variability of tracks in the forms of intra-trackway and multiple-trackways (set of trackways) variations (Gatesy et al., 1999; Razzolini et al., 2014; Lallensack et al., 2016; Razzolini et al., submitted). In this regard, one of the difficulties encountered during this PhD thesis resided in discerning and isolating the most biasing factor in track morphology (foot anatomy, locomotion and substrate) not only on individual tracks but along single trackways and sets of trackways. Trackways can potentially reveal the cause of track morphological variation and the works conducted in the present thesis provide some proof examples. The results indicate that the track morphology in most cases is almost never consistently retained and it is always subjected to small, moderate or huge deformations. Since the trackways are composed by successive footprints produced by one trackmaker along a trampling surface, all the three main factors affecting the final shape of a footprint are involved in the process. For instance, when sediment deformation structures are observed along a trackway (chapters 7-9) or in some poorly-preserved trackways (such as levels 500 and 1000 described in chapter 6), any inference made from the footprint is very likely to be sediment-dependent. On the

	OBJECT OF STUDY	**TYPE OF VARIATION**	**FACTORS DOMINANTLY PRODUCING MORPHOLOGICAL VARIATION**
MORPHOLOGICAL VARIATION	INDIVIDUAL TRACKS	INDIVIDUAL VARIATION	Foot anatomy, limb dynamics, substrate
	TRACKWAYS	INTRA-TRACKWAY ALTERNATING PATTERN	Foot anatomy, limb dynamics
		INTRA-TRACKWAY CONTINUOUS PATTERNS	Limb dynamics, substrate

Table 1. Factors dominantly producing morphological variations observed in individual tracks and trackways.

contrary, if the shape and outline of fossilized tracks are stable and uniformly distributed along the trackway, it is possible to consider limb kinematics and foot anatomy as the determinant factors of the final track morphology, implying that the substrate properties are consistent throughout the tracksite or at least along the trackway. In fact, from the spatial succesion of track morphologies made by the same trackmaker (a trackway), a great information about the animal dynamics can be extrapolated (bipedal or quadrupedal conditions, gauge, pace and stride lengths, speed, accelerations and decelerations, gait, pace angulation, trackway width).

After the analysis of the morphological variation along complete trackways, I propose a theoretical classification based on observations along and among various trackways registered in tracksites and large ichnoassemblages. Morphological variation observed along single trackways results in several patterns, called intra-trackway morphological patterns. They can display an alternating pattern when substrate is a stable variable and a continuous pattern when substrate is a non-stable variable. In large ichnoassemblages containing multiple trackways, these morphological variation patterns can occur along a single trackway and among various trackways, meaning that behavioral and biological factors add up to the foot anatomy, substrate and limb dynamic ones.

The intra-trackway alternating pattern (Table 1, Fig.1A-B) is defined here as the morphological variation pattern in which tracks and/or trackway parameters (pace, stride) are differently preserved along a trackway with respect to its contralateral counterpart. For this scenario, sediment consistency and composition are usually considered homogeneous along the whole length of the trackway because the shape and state of preservation of the tracks are uniform in the respective sides of the trackway. In chapter 5, we re-examined an ornithopod trackway which was observed to display some irregularities in the gait by earlier authors (Casanovas et al., 1995; Pérez-Lorente, 2003). In the study, the typical short step:long step ratio (Dantas et al., 1994; Lockley et al., 1994) was backed up by statistical tests ("two-sample paired test") that quantified the significance of the track/paces alternating morphological variation. The observations on one sample (left paces and left tracks morphology) were paired with observations in the other sample (right pace and right tracks morphology). This test showed that the left pace lengths were consistently smaller than the right paired pace lengths, showing a 81.8% of pace-shortening occurrence along the trackway. Recognition of such abnormal and irregular gait (supported by new analyses on pace lengths) implied that an alternating, different, pattern existed between the footprint arrangement in both sides of the trackway. In addition, morphological differences in individual tracks from contralateral sides of long trackways are also typical of intra-trackway alternating pattern. When these differences are quantified and statistically significant, foot anatomy can be defined. For the ornithopod trackway, a new measurement (interdigital width, IDW, Fig. 3 of chapter 5) was introduced and proposed for quantify the qualitatively evident morphological difference in digit II impressions of left tracks with respect to the contralateral counterparts. In sum, the work of chapter 5 shows how trackway irregularity and paired-tracks qualitative differences resulted from both a dynamic factor such as a particular movement of the limbs producing right and left pes track morphologies and an anatomical factor, such as the consistently different position in digit II of left tracks from that of right tracks. It is a good example of how morphological variation is quantified to define a pattern in which anatomy and limb kinematics, rather than substrate conditions, are the main factors to produce the final shape of the footprints.

Another peculiar case of an intra-trackway alternating pattern is observed in chapter 8 under a completely different scenario, in which an actual bird () interacted with an unusual, tilted, wavy substrate. The slope traversed by the bird was a factor that strongly affected limb dynamics while walking the inclined surface up-hill and down-hill. Despite being the foot of -like birds tridactyl, the track morphology displayed an intra-trackway alternating "didactyl" pattern, with the left tracks showing only digits III and IV and the right tracks only digits II and III. The didactyl-looking tridactyl tracks foreshadow uncommon conditions that are here interpreted as the combination of a changing tracking surface (up-slope and down-slope) together with the adaptation of the limb movement adjusting to up-slope and down-slope and the foot indention on the up-slope and down-slope inclined surface. In this example, the substrate and the trackmaker (and thus, the foot anatomy) were known variables, and despite the bird was not directly observed walking, its limb dynamics and the structural disposition of the substrate (rather than its composition and consistency) seem to be the main factors affecting the final shape of the footprints. Interestingly, if the changing slope on an inclined surface was not detectable, such as in a fossil trackway, a pathological condition might be erroneously contemplated. When moving on an inclined surface, tracks might be susceptible to sediment collapse due to the angle of the slope, and track morphology is especially altered when moving up-hill. Moreover, in the trackway no irregular pace lengths are detected between right-left and left-right sides. Instead, overall decreasing (up-hill) and increasing (down-hill) values are recorded for pace, stride lengths and pace angulations, parameters that are all strongly related to the limb kinematics of the trackmaker, meaning that the animal limbs are adjusting to the changing slope. These changes in limb dynamics consequently cause track morphologies resulting from the angle and depth to which the bird indented the feet into the inclined surface, which is the reflection of the limb dynamics of the trackmaker adjusting "real time" to the changing slope (figure 4, chapter 8). In this chapter, substrate (sloping surface) together with the bird's limb kinematics are the factors that produced the morphological variation (an alternating didactyl morphology), meaning that limb dynamics and substrate become intrinsically linked (Falkingham, 2014) and co-vary together with the foot anatomy.

In these two case studies analysed, the intra-trackway alternating pattern is principally controlled by foot anatomy and limb dynamics, being this latter caused by an antalgic gait of the trackmaker and by a variation in the inclination of the tracking surface.

The intra-trackway continuous pattern (Fig.1C) can be defined as a morphological variation pattern in which tracks change their morphology in accordance to their relative position along a substrate consistency gradient that persisted across the trackway and the site. Gatesy et al. (1999), described a similar scenario meaning that shallow, intermediate and deep tracks that formed along a trackway strongly depend on the sediment consistency changes (dry, moist, wet). Chapter 9 of the present compendium exemplifies this pattern with a study focused on four long trackways crossing each other, that are characterized by a range of track morphologies considered as indicators of rheological conditions. The fact that these tracks belong to the same trackway indicates that their differences cannot be linked to variations in foot anatomy and therefore must originate from a combination of horizontal sediment heterogeneity and differences in limb dynamics (see also Wilson et al., 2009). Sedimentological analyses revealed that these consistency gradients reflected on the morphological continuum of tracks depend on the scarcity/abundance of chlorite minerals and sedimentary structures. In this type of scenarios, although some anatomical details can be impressed especially in water saturated sediment conditions (i.e. hallux impression), deep tracks are irrelevant for an ichnotaxonomical purpose but pivotal for biomechanical and substrate analyses (Gatesy et al., 1999; Cobos et al., 2016) and environmental reconstruction. In the study at El Frontal site, we underpinned the importance of the quantification of substrate response causing track length and depth variations during the indention of the foot. If the substrate conditions were uniform, foot loads made by animals of comparable sizes moving in a dynamically similar fashion would have produced similar tracks (Falkingham et al., 2011) along single and associated trackways. An intratrackway continous pattern implies that the wide range of track morphologies at the site results from similar trackmakers, or even the same one, crossing variable facies. Since many morphotypes described in literature may represent a morphological continuum of similar trackmakers in different substrate conditions, ichnotaxonomical assignments should be avoided in cases where a single trackway registers a continuum of tracks morphologies that depends on the consistency of a substrate.

One of the conclusions of the present thesis is the certainty that an intra-trackway morphological variation (alternating and/or continuous) produced by the same foot anatomy (one trackmaker) is discernable only when analyzing one trackway. When a large set of trackways is registered on a surface, such as in the ichnoassemblages presented in chapter 6 and in the large quarry of chapter 7, track morphology is indeed susceptible to variation that can be linked to a more complex range of biasing factors or to the multiple combination of them. The three principal factors (foot anatomy, limb dynamics and substrate consistencies) add on the possible presence of different trackmakers with different ontogenetic stages (and therefore, different foot anatomies). These taxa, in turn, may represent different behaviours (swimming: Ezquerra et al., 2007; Xing et al., 2016, courtship: Lockley et al., 2016, crouching: Romano and Citton, 2016) and different gaits (i.e. slow walking, fast walking). The conjunction of all these factors, registered among various trackways in the same tracksite or ichnoassemblage, inevitably produces a notable morphological track variation in the ichnoassemblage. Such track morphological variations require an extensive analysis in order to discern when the differences observed are linked to rheological factors, to the presence of various foot anatomies or to different limb dynamics of similar trackmakers.

Different trackways preserved in the same tracksite or ichnoassemblage can contain multiple morphotypes that can be preserved along a single trackway, as an intra-trackway morphological variation, or among various contiguous trackways. This implicates that during the evaluation and interpretation of shapes variability, when the substrate has similar consistencies and compositions that encompass multiple trackways, one foot anatomy can produce a wide range of intra-trackway morphologies, while various foot anatomies (multiple trackmakers) can produce a wider range of morphologies that can be found along one trackway (intra-trackway pattern) but also recognized in sets of trackways. The presence of

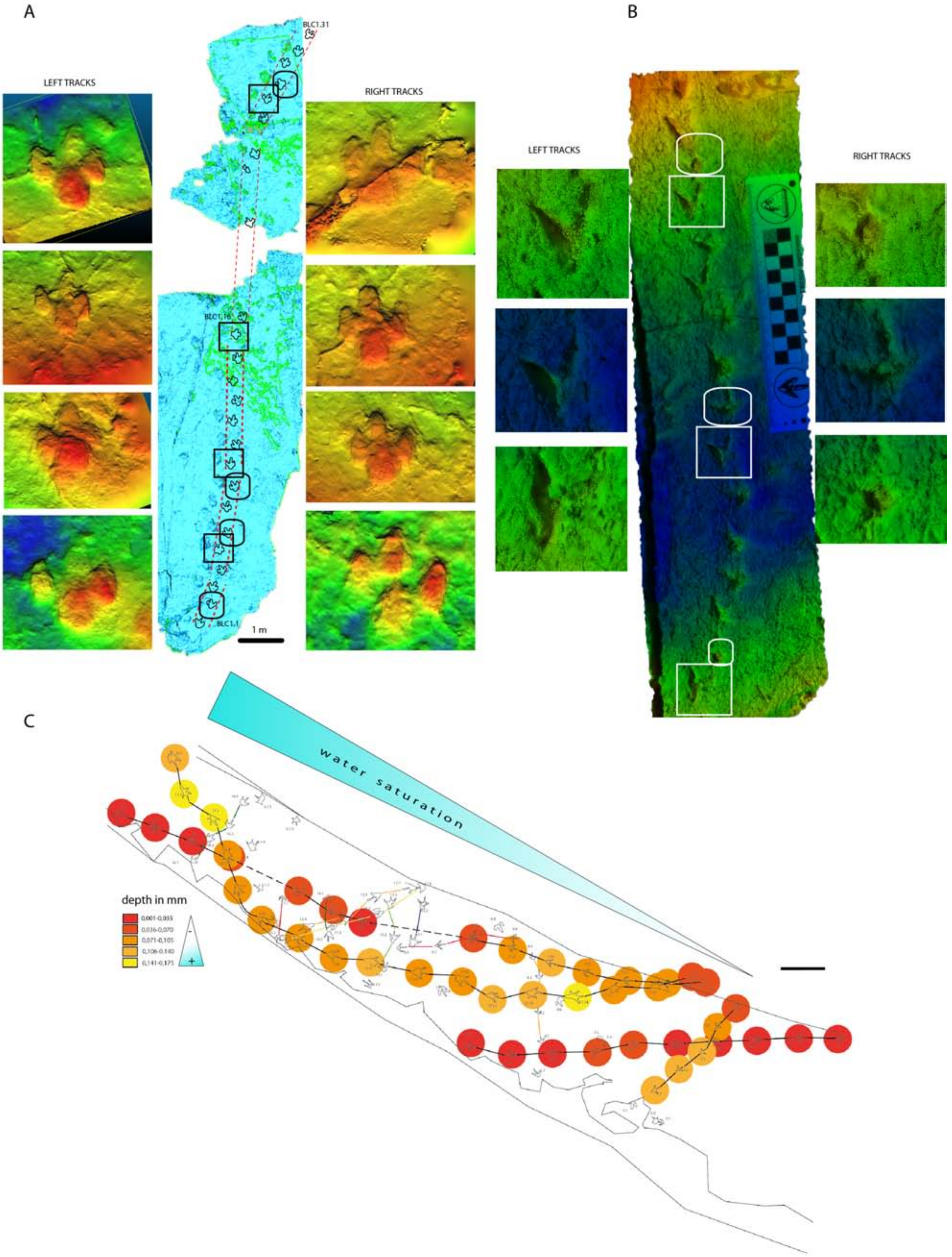


Figure 1. Intra-trackway morphological variation patterns observed. A) Alternating intra-trackway morphological variations due to a pathology (foot anatomy and limb dynamics); B) Alternating intra-trackway morphological variations due to sloping surface (limb dynamics and substrate); C) Continuous intra-trackway morphological variations due to lateral changes in substrate consistency.

multiple trackways opens the possibility of different trackmakers that may have produced similar track morphologies due to an anatomical convergence of foot anatomies (i.e. ornithopods and theropods) or to a similar locomotor dynamics of the trackmakers or to the combined or individual effects of each of the three principal factors intervening.

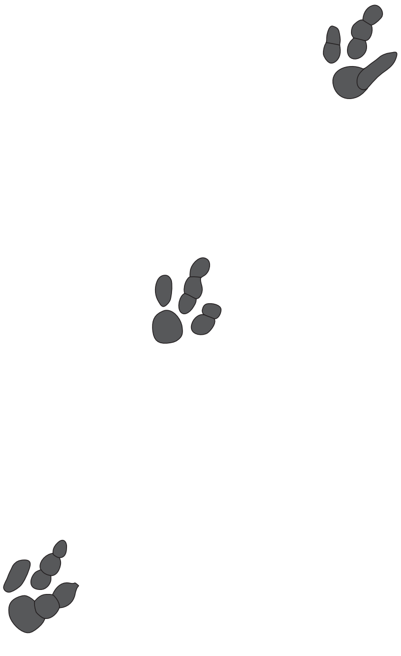
As an example, chapter 6 described two different track morphologies, one assigned to a new ichnospecies *Megalosauripus transjurani* and the other called Morphotype II (as in Marty, 2008). The latter morphology is sometimes found as an intra-trackway morphological variation of trackways assigned to *Megalosauripus transjurani* (or *Megalosauripus* isp., when poorly preserved). Under this scenario, Morphotype II tracks are considered to be the preservational variant of *Megalosauripus transjurani.* In other occasions, Morphotype II is consistently observed in long trackways that do not display other intra-trackway morphological variations. In this situation, the morphology consistently retained along a trackway can be produced by a different trackmaker, as thoroughly discussed in chapter 6. In the studied tracksite, the occurrence of (a) similar morphotypes that are intra-trackway preservational variants of a determinate foot anatomy and (b) morphotypes resulting from a consistently preserved morphology along the whole trackway length suggest that, besides those factors recognized as the principals in determining individual track morphologies, track morphological variation is constrained by taxic diversity in the ichnoassemblages (in that case, the possible co-occurrence of large theropods and ornithopods in the Late Jurassic tidal flats).

Differently to chapter 6, in which two different trackmakers are hypothesized for the ichnoassemblages of the Jura mountains (in spite that track length ranges are very narrow), chapter 7 contemplates the possibility that all the trackways of the analysed quarry were made by very similar trackmakers (in spite of the important track length range recorded both as intra and inter-trackways variations). In the Vale de Meios study, the exclusive assignment to *Megalosauripus* isp. for all the tracks of the quarry is based on the general morphology and morphometric ratios registered, irrespective of differences in the track lengths. In fact, it has been demonstrated that ichnotaxonomically meaningful comparisons are only possible when the influence of size is minimized (using ratios, Lallensack et al., 2016). Moreover, the intra-trackway track length variation discards the possibility that the quarry was crossed by a stock of taxonomically diverse theropods. When the average track morphology remains the same among tracks of different sizes, isolated small-sized tracks found within the quarry could be the reflection of a high variety of preservational modes (due to different stages of substrate consistencies) or to different ontogenetic stages of the trackmakers. These size differences, however, do no reflect taxonomically different trackmakers. Sediment analyses conducted in chapter 7 revealed that preservation of tracks could be strongly influenced by the tidal cycle, which produced preservations types such as modified true tracks and modified true tracks with mud collapsing through erosion and water saturation respectively, making any taxonomical diversity assumption very unparsimonious.

Finally and as a corollary, ichnogenera and ichnospecies should not be defined exclusively on the observed morphometric characters. Before defining a new shape, all the biasing factors (i.e. water content in the soil, type of sediment, firmness of the substrate, type of tracks preservations, limb dynamics, behaviour) that might have changed the original track morphology must be taken into consideration.

The recognition of the quantity of substrate influence in the determination of track morphology incentivizes a more parsimonious approach toward ichnotaxonomy, paying bigger attention to the morphologies that develop and change along a trackway. For this reason, photogrammetric analysis with the creation of high-resolution three-dimensional models for each track have been progressively preferred (or at least complemented) to the overall laser scan of the trackway and tracksite. The 3-D documentation is key for a deeper understanding and interpretation of dinosaur tracks and moreover, it is a great mean for sharing (objective) information of determinate track geometries, allowing the creation of digital type specimens. The models allow detailed measurements of depth values recorded for all the parts of a track, digit impressions, metatarsal-phalangeal pad impression, heel area, sediment rims, internal overtrack growth, claw impressions. More importantly, by measuring the depth for each digit impression, it is possible to compare where the indentation pressure (strain and stress) is applied the most and therefore extrapolate the distribution of weight, possible limb and foot adaptations to a substrate or to an injury.

GENERAL CONCLUSION



GENERAL CONCLUSION

The compendium of this PhD thesis collected six case studies from famous areas such as the Cameros basin (La Rioja and Soria regions in Spain), Lusitanian basin (central Portugal), the Jura Carbonate Platform (NW Switzerland) and the Argana Basin (Morocco) and it proposes the basis for a laboratory controlled-experiment on heterogeneous substrates in order to attempt the reproduction in laboratory of track formation by varying the substrate properties. Three-dimensional technologies have been the support and tool for all the quantitative analysis undertaken. LiDAR scans have been always complemented with a close range photogrammetry in order to give the highest morphological details and to provide a precise and systematic quantification of the track morphological variations recorded. With the years, close range photogrammetry have been enhanced and reached the laser scanner levels in terms of precision and reproducibility; photogrammetry of complete trackways and tracksites is progressively eased by free software that can process high definition three-dimensional models almost automatically, allowing various tracks and trackways to be processed at the same time in the same computer.

The geological and geographical diverse frames of the analysed tracksites allowed to develop, support and discuss a study under the perspective of objectively deciphering track morphologies by examining and isolating all concurring factors and quantitatively evaluate which had the major load among foot anatomy (trackmaker's identity and ichnotaxonomy), limb dynamics (locomotion and behavior) or substrate (environment, water consistency, slopes).

Tracks represent sedimentary distortions and the bias degree among dynamics, substrate and foot anatomy is defined by the interception of the three axes describing these variables. Each factor can vary independently or in conjunction to each other, such in the case of trackway analyses. Track morphology is always the result of substrate response to the foot indentation in particular sediment. Nevertheless, it is also possible to discern the degree of substrate biasing in the determination of the observed track shape. Morphological variations are shown to have different implications and controlling factors when considered in individual tracks, along a trackway and in multiple-trackways. In the intra-trackway alternating pattern, the sediment variable (substrate) can be less likely to be the main influence in determining the variation in track morphology. Foot anatomy and limb dynamics here play an almost equivalent role in the final track shape. In the intra-trackway continuous pattern identified in tracksites with a variable substrate consistency, both deep and shallow tracks are found along the same trackway. This pattern allows the identification of extreme and intermediate shapes that derive from variable water and sediment conditions. In large ichnoassemblages and quarries, where a large number of trackways is available for comparison, the occurrence of the same morphotype in multiple trackways can be due to a vast combination of factors that include taxonomical diversity and behavioural changes that add to substrate conditions, limb dynamics and biological diversity.

SUMMARY STATEMENTS

1. The long trackway of *Caririchnium lotus* from the Barranco de la Canal site (NW Cameros Basin, La Rioja, Spain) is restudied using LiDAR and a photogrammetric-based approach. The intra-trackway alternating pattern observed in this 25-m-long trackway has been subject to in depth analysis for the first time and a statistical quantification of gait irregularity. These data, together with the morphological and quantitative differences recorded between the right and left pes tracks, suggest an injury/pathology on the left digit II pad that may have caused the intra-trackway alternating pattern of morphological variations. This ornithopod trackway provides new insight to antalgic gaits and offers a more quantitative approach to the analysis of dinosaur track and trackway abnormal conditions.

2. The Jura Carbonate Platform (NW Switzerland, Late Jurassic) encompass abundant material including trackways with several well-preserved tracks exhibiting substantial anatomical details. This material allowed the proposition of the new ichnospecies *Megalosauripus transjurani*, large theropod tracks differentiated from previously-named ichnotaxa by the presence of a pronounced, wide and rounded proximal pad on digit IV impression. Amongst the large theropod tracks, a second morphotype is recognized sometimes as a preservation variant of *Megalosauripus transjurani* tracks and in other occasions, assignable to a different trackmaker, presumably an ornithopod.

3. The Vale de Meios limestone quarry (West-Central Portugal) is a key and unique reference for understanding the composition and distribution of the Middle Jurassic theropod fauna, especially due to both the ichnological and osteological record for this age being extremely scattered. Tracks and trackways from the whole tracksite are assigned to *Megalosauripus* isp. according to quantitative and qualitative analyses and comparisons undertaken. This ichnogenus occurrence, traditionally reported for the Late Jurassic Early Cretaceous, should therefore be expanded also to the Middle Jurassic. The directional analyses of trackways reveal that various individuals crossed a tidal flat in accordance to tide cycles, directing toward the barrier during low tide periods, probably for feeding purposes on exposed vertebrate.

4. The neoichnological study of an actual bird () trackway is proposed as an excellent scenario in which all the variables concurring in the determination of track morphology are known. The trackmaker and its foot anatomy are fixed parameters, the substrate is inclined and the up-hill and down-hill configuration of the portion where the trackway is impressed adds on the general inclination of the surface, causing a complex limb dynamics response and track morphologies that do not correspond to the trackmaker's foot anatomy and that produces an intra-trackway alternating pattern. This study documents the real time responses to the interaction of substrate consistency, inclination, environmental factors such as possible water activity indicated by water level marks and trackmaker kinematics adjusting to the complex terrain.

5. The new El Frontal tracksite is presented with a thorough quantitative description displaying a range

of tridactyl track morphologies that develop as an intra-trackway continuous pattern. This provides a valuable example of how track geometry during its formation is dominantly affected by substrate conditions. Moreover, the photogrammetry models and depth analyses spotlighted that the deep and shallow tracks are part of a continuum of track morphologies and depths. This study states the importance of the quantification of morphological variation, shown by correlation and dispersion graphics for track parameters and substrate response parameters (depth and sediment rims). The presented analyses underpin the influence of substrate on the final track morphology and length. The intra-trackway continuous morphological variation warns on ichnotaxonomic assignations on sediment-biased tracks.

6. The laboratory-controlled rheological experiment proposed is a preliminary base that needed to be set in order to recreate realistic heterogeneous conditions that simulate the formation of individual fossil tracks under different substrate-dependent variables.

FUTURE DIRECTIONS

The specificity and singularity of each tracksite, independently form the preservation status of the tracks requires a great deal of time for the analysis of all the concurring factors in determining track morphologies and detecting the range and degree of variations recorded. For this reason, the rheological experiment will be continued and tentatively formalized as a new laboratory-controlled example of track formation and morphological determination under heterogeneous conditions of mixed sediments with different water contents. This experiment will be carried on together with the Universitat Politècnica de Catalunya (UPC) according to the availability of its researchers and space. Other research analyses have started during my two-months internship at the Museu Nacional de História Natural e da Ciência (Lisbon, Portugal) have been carried on huge sauropod trackways (*Polyonyx gomesi*) from the Middle Jurassic of the Lusitanian basin. These trackways display a qualitatively different arrangement that needs to be evaluated under the perspective proposed for this PhD thesis. That is to say, morphologically different trackways can be produced by taxonomically different trackmakers (different foot anatomies), by similar trackmakers in different biomechanical situations, by similar trackmakers under different behavioral conditions. The ultimate goal is to accumulate a large set of three-dimensional models of hind-and forelimbs of the main Middle-Late Jurassic sauropods, in order to synapomorphically correlate the osteology to the tracks. Other research started during my internship at the PalA16 Office and the Naturhistorisches Museum (Basel, Switzerland) account for the extensive ichnotaxonomical analyses on huge (>50 cm) theropod tracks from the Late Jurassic of the Jura Mountains.
All the analyses will be always supported by photogrammetric techniques and by exploring new and specific software to use for track quantitative morphological analyses.

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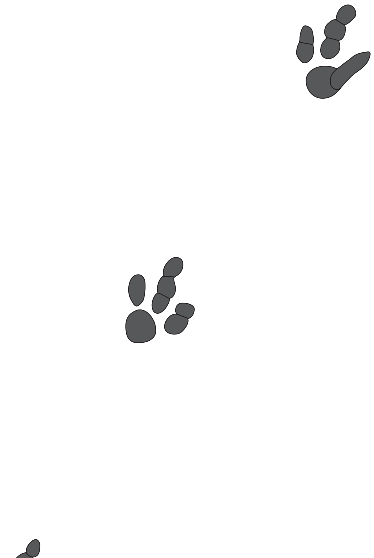

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