Universitat Autònoma de Barcelona

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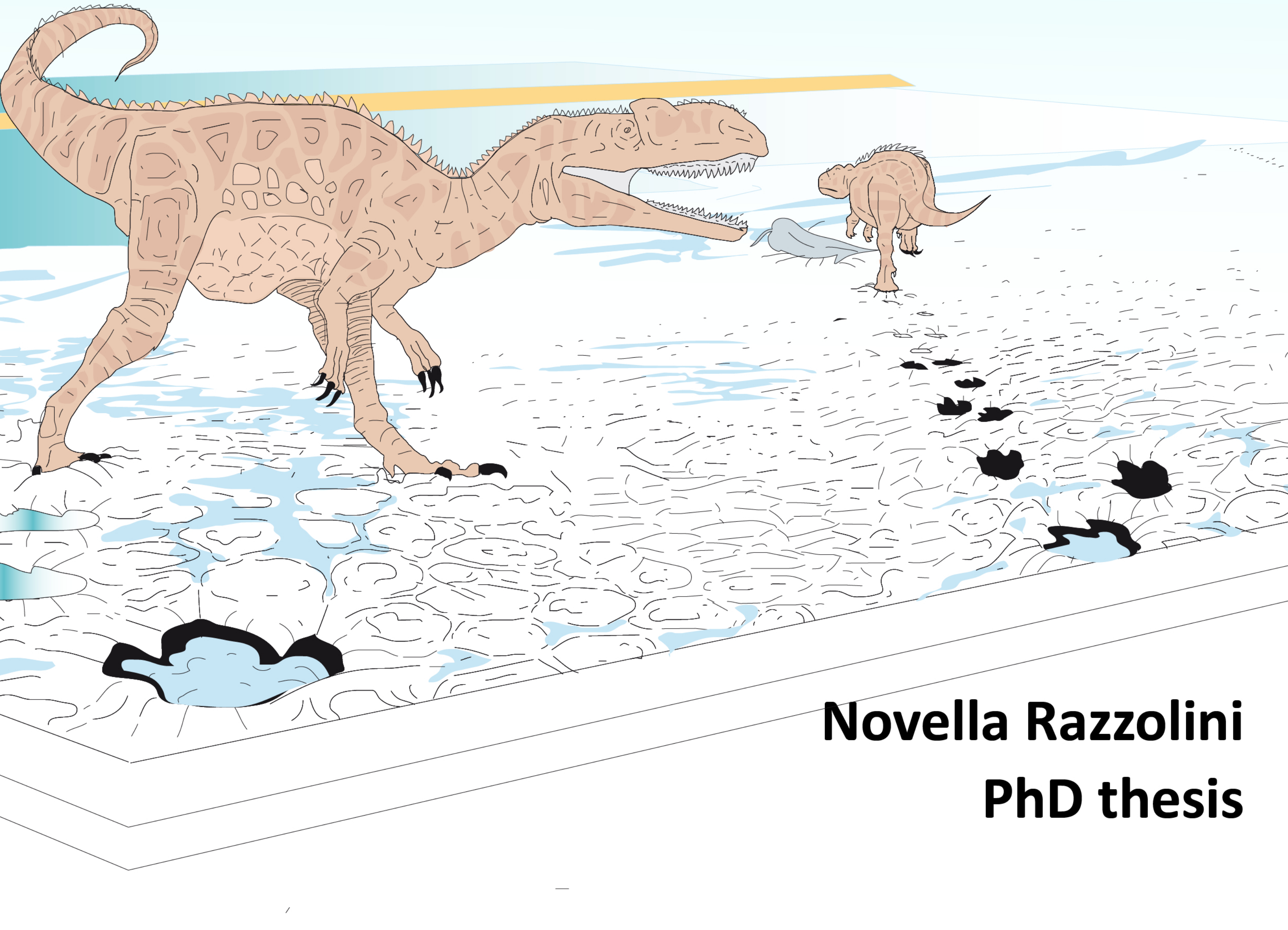

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**PhD thesis**

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PhD Thesis

Universitat Autònoma de Barcelona
Facultat de Ciències
Departament de Geologia

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Front cover illustration by Dr. Oriol Oms: reconstruction of Megalosaurids crossing tidal flats

# Morphological variation and ichnotaxonomy of dinosaur tracks: linking footprint shapes to substrate and trackmaker's anatomy and locomotion

Memoir presented by Novella Razzolini in order to apply for the degree of Doctor in Geology by the Universitat Autònoma de Barcelona, Departament de Geologia, complemented under the tutelage of Dr. Oriol Oms and the supervision of:

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- Dr. Bernat Vila i Ginestí, Institut Català de Paleontologia Miquel Crusafont

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*Actually, everything that can be known has a Number; for it is impossible to grasp anything with the mind or to recognize it without this*

Philolaus, greek pythagorean and presocratic philosopher

# CONTENTS

# ABSTRACT

# Abstract

The study of tridactyl dinosaurs tracks from a morphological perspective is here presented in the form of a new look and approach to the classic ichnology. The mechanisms that mostly control and affect track morphology during its formation have been thoroughly analysed, so that the ultimate goal is to provide extensive quantitative data to discuss the main foundation of morphological variation registered in individual tracks, trackways and large sets of trackways. The compendium of this PhD collected six different studies from distinct geographical (Spain, Portugal, Morocco and Switzerland) and geological frames (from Middle Jurassic to present) and the proposal of a preliminary approach in a laboratory controlled-experiment. This experiment aims to extrapolate and determine all parameters (water content, substrate properties and composition, grain size, porosity) intervening in the track formation process on heterogeneous substrates during the mechanical indentation of a vulture foot cast. The Cameros basin (NW Spain) offered two Early Cretaceous different scenarios for this thesis, the re-interpretation of a long ornithopod trackway on homogeneous substrate at the Barranco de La Canal tracksite and the new study of four previously unpublished theropod trackways inter-crossing a heterogeneous substrate at the El Frontal tracksite. The locality visited within the Argana basin (Morocco) provided neoichnological observations that are consider important for the identification of misinterpretations of ichnopathologies and sloping surfaces in the fossil record. These localities showed two different intra-trackway morphological variation patterns defined as alternate, which depends on the limb dynamics and foot anatomy of the trackmaker and continuous, which depends on the substrate consistency change along the tracking surface. The Lusitanian basin (Central-West Portugal) presented the previously known but unpublished Middle Jurassic quarry of Vale de Meios which underscores the importance of analyzing all types of track preservations in order to recognize the average morphology and that there should not be an assumption that vertebrate ichnotaxa are confined to specific ages or geographic regions. The Jura Carbonate platform (NW Switzerland) encompassed six Late Jurassic tracksites, which together with 49 trackways and 397 tracks provided the new and unpublished material for the description of a new ichnospecies and the discussion of track morphological variations, introducing the possibility that classic ichnoassociations might be the result of preservational variants of the same trackmaker. These two studies showed that when comparing multiple trackways on the same site or ichnoassemblage, taxonomical diversity and behavioural changes have to be considered together with substrate conditions and limb dynamics. 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.

## Resum

La present tesi presenta un estudi de les petjades tridàctiles de dinosaure a partir d'una perspectiva morfològica que representa una nova visió i aproximació a la icnologia clàssica. S'han analitzat en profunditat els mecanismes que principalment controlen i afecten la morfologia de les petjades durant la seva formació, amb l'objectiu final d'aportar dades àmplies i quantitatives per discutir el fonament principal de la variació morfològica registrada en petjades individuals, rastres i conjunts de rastres. El compendi d'aquesta tesi recull sis estudis diferents de diversos marcs geogràfics (España, Portugal, Marroc i Suïssa) i geològics (del Juràssic Mitjà a l'actualitat) i la proposta d'un enfocament preliminar en un experiment controlat de laboratori. Aquest experiment pretén extrapolar i determinar tots els paràmetres (contingut d'aigua, propietats i composició del substrat, mida de gra, porositat) que intervenen en el procés de formació d'una petjada en substrats heterogenis durant la penetració mecànica d'un motlle de peu de voltor. Per aquesta tesi la conca de Cameros (Nord-oest d'Espanya) ofereix dos escenaris diferents del Cretaci Inferior: la reinterpretació d'un rastre llarg d'ornitòpode sobre un substrat homogeni al jaciment amb petjades de Barranco de La Canal, i el nou estudi de quatre rastres inèdits de teròpodes creuant-se en un substrate heterogeni al jaciment de petjades d'El Frontal. La localitat de la conca de l'Argana (Marroc) ha proporcionat observacions neoicnològiques que es consideren importants a l'hora d'identificar interpretaciones errònies d'icnopatologies i superfícies en pendent en el registre fòssil. Aquestes localitats mostren diferents patrons de variació morfològica intrarastre definits com alternat, el qual depèn de la dinàmica de les extremitats i l'anatomia del peu de l'animal productor; i continu, el qual depèn de la consistència del substrat al llarg de la superfície on es produeixen les petjades. La conca lusitana (centre-oest de Portugal) conté la localitat ja coneguda però inèdita del Juràssic Mitjà de Vale de Meios, l'estudi de la qual destaca per la importància d'haver analitzat tots els tipus de preservació de petjades a l'hora de reconèixer la morfologia mitjana i el fet que no s'hauria d'assumir que els icnotàxons de vertebrats estan restringits a edats i regions geogràfiques específiques. La plataforma carbonàtica del Jura (Nord-oest de Suïssa) conté sis localitats amb petjades del Juràssic Superior, que juntament amb 49 rastres i 397 petjades, aporten el nou i inèdit material per a la descripció d'una nova icnoespècie i la discussió de les variacions morfològiques de les petjades, introduint la possibilitat que les icnoassociacions clàssiques puguin ser el resultat de variants preservacionals del mateix animal productor. Aquests dos estudis mostren que quan es comparen múltiples rastres del mateix jaciment o icnoagrupacions, s'han de tenir en compte la diversitat taxonòmica i els canvis comportamentals juntament amb les condicions del substrat i la dinàmica de les extremitats de l'animal productor. Les tecnologies tridimensionals han estat la base i l'eina per a totes les anàlisis quantitatives que s'han realitzat. Els escàners LiDAR han estat sempre un complement a la fotogrametria de curt abast per tal d'aconseguir els majors detalls morfològics i aportar una quantificació sistemàtica i precisa de la variació morfològica de les petjades.

# PART 1

## Introduction

# CHAPTER 1

## Structure of the dissertation and goals

# CHAPTER 1. STRUCTURE OF THE DISSERTATION AND GOALS

## Structure of the dissertation

The present thesis is structured as a compendium of publications organized as individual chapters divided in different conceptual parts. The Part 1 is the overall introduction of the dissertation, with a recollection of the work undertaken by contextualizing the studied sites from different geographical and geological scenarios and explaining the different materials and methods used for each tracksite (chapter 2).

The Part 2, entitled "Track morphological variation and interpretations" is the ichnological context of the research conducted in the thesis in which a historical background presents the general subjective approach in the interpretation of vertebrate tracks and the way of how objective two-dimensional and three-dimensional methods are progressively used to enhance the ichnological analysis (chapter 3). This part ends with chapter 4, which introduces the difficulty in the full understanding of the existing link between track formation and track morphology and presents the major factors that intervene in the determination of the final track shape.

Results are presented in Parts 3 to 5 as published papers (chapters 5, 7 and 9), submitted manuscripts (chapter 6), and under review research articles (chapter 8); all of them in Journals included in the Science Citation Index. Chapter 10 represents an in-progress work based on a laboratory-controlled experiment in which the cast of a vulture foot is mechanically and manually indented on heterogeneous substrates. Results of the present thesis are divided into three different parts according to what feature influenced the most in determining the final track morphology.

First results analyse the morphological variation produced in tracks under the influence of trackmaker's anatomy (Part 3); it presents two examples in which the foot anatomy of the trackmaker can be considered as coincident with the track morphology recorded when other parameters such as substrate and locomotion are adequately examined. In these circumstances, important evidence such as the inference of ichnopathologies on a dinosaur foot (chapter 5) and the establishment of a new ichnospecies (chapter 6) can be considered. Chapter 5 is centered in the quantification of the differences observed between the track morphologies produced by the right and left pes in an ornithopod trackway from the Early Cretaceous Barranco de La Canal-1 tracksite (La Rioja, NW Spain). A new parameter (Interdigital width, IDW) was developed exclusively for this case in order to quantify the qualitatively evident morphological difference in left tracks digit II with respect to
the contralateral counterpart. Chapter 6 presents new material from the Reuchenette Formation (Early-Late Kimmeridgian, Late Jurassic) of NW Switzerland in which a new ichnospecies of a large theropod dinosaur, *Megalosauripus transjurani*, is described. It is based on very well-preserved and morphologically-distinct tracks of several trackways from different tracksites and horizons, including

different preservational types.
Results of part 4 are focused on the influence of trackmaker's locomotion on the morphological variation observed in tracks. Two studies show how track morphologies inform on behavioral (chapter 7) and biomechanical (chapter 8) connotations. Chapter 7 presents the new Vale de Meios tracksite, from the Middle Jurassic of Portugal, in which sediment analysis and the environmental reconstruction together with the orientation of the large theropod trackways and the analysis of track preservation types give information on the trackmaker's behavior and identity. Chapter 8 presents a neoichnological study based on an extant bird trackway impressed on a slope of the river Issene in the Argana Basin (Western High Atlas, Morocco) and the variation of track morphologies according to the trackmaker's movement adjusting to that slope.
Lastly, Part 5 links the morphological variation of tracks to the characteristics of substrate. First paper included is based on data from the El Frontal tracksite (Early Cretaceous, Spain), a new site in which a gradient of medium to large track morphologies (from shallow to deep tracks) is preserved in a relatively small area, providing quantitative information on the relationship between depth of track, sediment consistency and water content (chapter 9). The last chapter (chapter 10) of the dissertation describes the preliminary approach used to study the production of tracks on layered heterogeneous substrates with different grain size and water content in a laboratory controlled experiment using the cast of a vulture foot. This chapter reports the results and shortcomings from three different experiments, two of which used manual indentation of the vulture foot while the third used a mechanical indentation.

Papers included are:

- Razzolini, N.L., Vila, B., Díaz-Martínez, I., Manning, P.L., Galobart, À., (2016a). Pes shape variation in an ornithopod dinosaur trackway (Lower Cretaceous, NW Spain): New evidence of an antalgic gait in the fossil track record. Cretaceous Research, V58, p125-134, doi:10.1016/j.cretres.2015.10.012. open access http://www.sciencedirect.com/science/article/pii/S0195667115300914 (Chapter 5).

- Razzolini, N.L., Belvedere, M., Marty, D., Meyer, C., Paratte, G., Lovis, C., Cattin, M. (submitted, October 2016). *Megalosauripus transjurani* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland. PLoS ONE (Chapter 6).

- Razzolini N.L., Oms O., Castanera D., Vila B., dos Santos V.F., Galobart À. (2016b). Ichnological evidence of Megalosaurid Dinosaurs Crossing Middle Jurassic Tidal Flats. Scientific Reports 6, 31494. doi:10.1038/srep31494 (Chapter 7).

- Razzolini, N.L. and Klein, H. (under review) Crossing slopes: unusual trackways of recent birds and implications for tetrapod footprint preservation. Ichnos Special Issue.(Chapter 8).

- 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. doi:10.1371/journal.pone.0093708 (Chapter 9).

## Goals

The leitmotiv accompanying the compendium of this four-year research is based on acknowledging that track morphology is a three-dimensional (3-D) ensemble that depends on multidimensional parameters such as foot anatomy, substrate dynamics (rheology) and limb kinematics as biomechanics and behavior. The main goal is to **study the track morphological variation in individual tracks and, especially, along single trackways and in set of trackways (ichnoassemblages and large tracksites)**. This involves the quantification of the multidimensional parameters already defined as concurring in track formation and also how much and what kind of variation they display along a trackway. To develop this goal, a "*super partes*" approach in the study of dinosaur tracks, directing and structuring the research according to the specificity of each tracksite is established. This allowed to formulate new hypothesis that aimed beyond the classic ichnological approach of documenting, describing and interpreting and rather incorporated the dynamic and three-dimensional view of tracks and trackways. All possible tools available, such as LiDAR scans, photogrammetry, computer programs, statistical analysis, concepts in rheology and sediment mechanics, ichnotaxonomy, neoichnology and engineering experiments are explored and considered as a single multidisciplinary ensemble that characterizes vertebrate ichnology. Tracksites from different areas (Spain, Portugal, Morocco and Switzerland) and ages (from Middle Jurassic to recent) are here presented under the perspective of deciphering track morphologies as objectively as current tools allow, by examining 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 presence, laboratory experiments).

The object of this thesis is centered in the **observation and quantification of the variation of track morphology according to foot anatomy, limb kinematics, locomotion and substrate behavior**. The analysis goes beyond the classic measurement of track and trackways parameters, by examining **how and why are the tracks in a trackway different**. If the shape and outline of fossilized tracks are stable along the length of a trackway, it is possible to consider limb kinematics and foot anatomy as a major determining factor of track morphology. Consistency of track morphology and geometry within a trackway also implies that substrate properties were consistent across the tracksite at the time of formation. For each case of study presented in chapters 5-10, the bias degree among locomotion, substrate and foot anatomy is defined by the interception of the three axes describing these variables, meaning that all the three variables are weighted and valued in order to define which one played the major role in track formation and in the determination of the final morphology.

This was possible through the evaluation of the potentiality of each site from LiDAR scans, photogrammetric models and three-dimensional reconstructions; taphonomical and sedimentological analysis to characterize the tracking surface and the type of substrate the trackmaker crossed; exhaustive morphometric measurements, ratios and statistical analyses on track geometries in order to discern how much of the morphology is directly caused by the trackmaker's foot anatomy and how much depends on the sediment and foot mechanics; reproduction in laboratory of 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.

# CHAPTER 2

## Account of work undertaken

**2.1 Motivation and background**

**2.2 Context of localities**

**2.3 Materials and Methods**

# CHAPTER 2. ACCOUNT OF WORK UNDERTAKEN

## 2.1 Motivations and Background

Dinosaur tracks from Spain and Portugal are well renowned worldwide and specific geological areas with tracks have been treated in detail in various PhD dissertations (Moratalla, 1993; dos Santos, 2003; Vila, 2010; Diáz-Martínez, 2013; Castanera, 2013; Piñuela, 2015). The great morphological diversity and the wide temporal range (from Middle Jurassic to Late Cretaceous) together with the increasing paleoecological, paleoethological and ichnotaxonomical interest encompassed by the tracksites lead some researchers to elaborate a declaration purpose of the dinosaur ichnites of the Iberian Peninsula as World Heritage in the UNESCO. Since 2008, the Mesozoic Research Group from the Institut Català de Paleontologia started a tight collaboration with researchers from the University of Manchester (United Kingdom) and they elaborated a great amount of ichnological data from numerous localities of the Iberian Peninsula (in areas of Spain and Portugal). The data were obtained thanks to the use of LiDAR laser-scan technology (Light Detection And Range), the highest resolution laser scanner at that time (almost ten years ago), which allowed three-dimensional digital reconstructions of the tracksites and the acquisition of accurate data.

Originally this thesis was conceived to take advantage of the laser scanner (LiDAR) data acquired during the digitization of the sites for the world heritage candidacy of UNESCO. Three of the sites presented in this thesis (chapters 5, 7, 9) were included in the IDPI project (Dinosaur Ichnites of the Iberian Peninsula), conceived to describe the tracksites to include in the world heritage candidacy (Fig.2.1). During the first year of the thesis (2012-2013), laser scans post-processing analysis was undertaken for these three tracksites. Two of them (Barranco de la Canal: chapter 5 and El Frontal: chapter 9), presented the laser scan 3-D reconstruction of the tracksites complemented with photogrammetric technique for high-resolution three-dimensional models of particular tracks. On the other hand, for the large quarry of Vale de Meios (chapter 7), laser scan of the tracksite could not be used due to resolution deficiency caused by adverse weather conditions and therefore two consecutive field campaigns (2014-2015) were organized to map the quarry.

The inclusion of three additional chapters in this thesis (Chapter 6, 8 and 10) was motivated by the need of a more accurate documentation of tracks morphologies by the use of new technologies that lead to objectively interpret their variations according to the regent parameters of foot anatomy, limb dynamics and substrate mechanics. Therefore, as a consequence of four months internship at the Naturhistorisches Museum of Basel (2016) visiting the collections of the Paleontologie A16 project, it was possible to obtain detailed 3-D photogrammetric maps of particular footprints and erect a new ichnospecies from the vast material (more than 300 tracks distributed in 49 trackways from 10 stratigraphical levels of

6 different tracksites) together with detailed analysis on three-dimensional photogrammetric models undertaken (chapter 6). Chapter 8 was born during the field trip organized in occasion of the First International Congress on Continental Ichnology (ICCI, Al Jadida, Morocco, 2015). The extant bird trackway observed on the slope of a river bank was a great example of how track morphology is strongly biased by substrate consistency and limb dynamics and how these two parameters are usually very complicated to quantify separately since the limb movement adjusts to a particular sediment and sloping condition. Lastly, Chapter 10 was motivated by the need to compensate the lack of (non-computer simulated) experiments on heterogeneous substrates, which are more realistic and similar to the fossil sediments where dinosaur tracks are found than homogeneous sediments. It also exemplifies the multidisciplinary research conducted by the PhD student, in the course of scientific-engineering collaboration with researchers of the Universitat Politècnica de Catalunya.

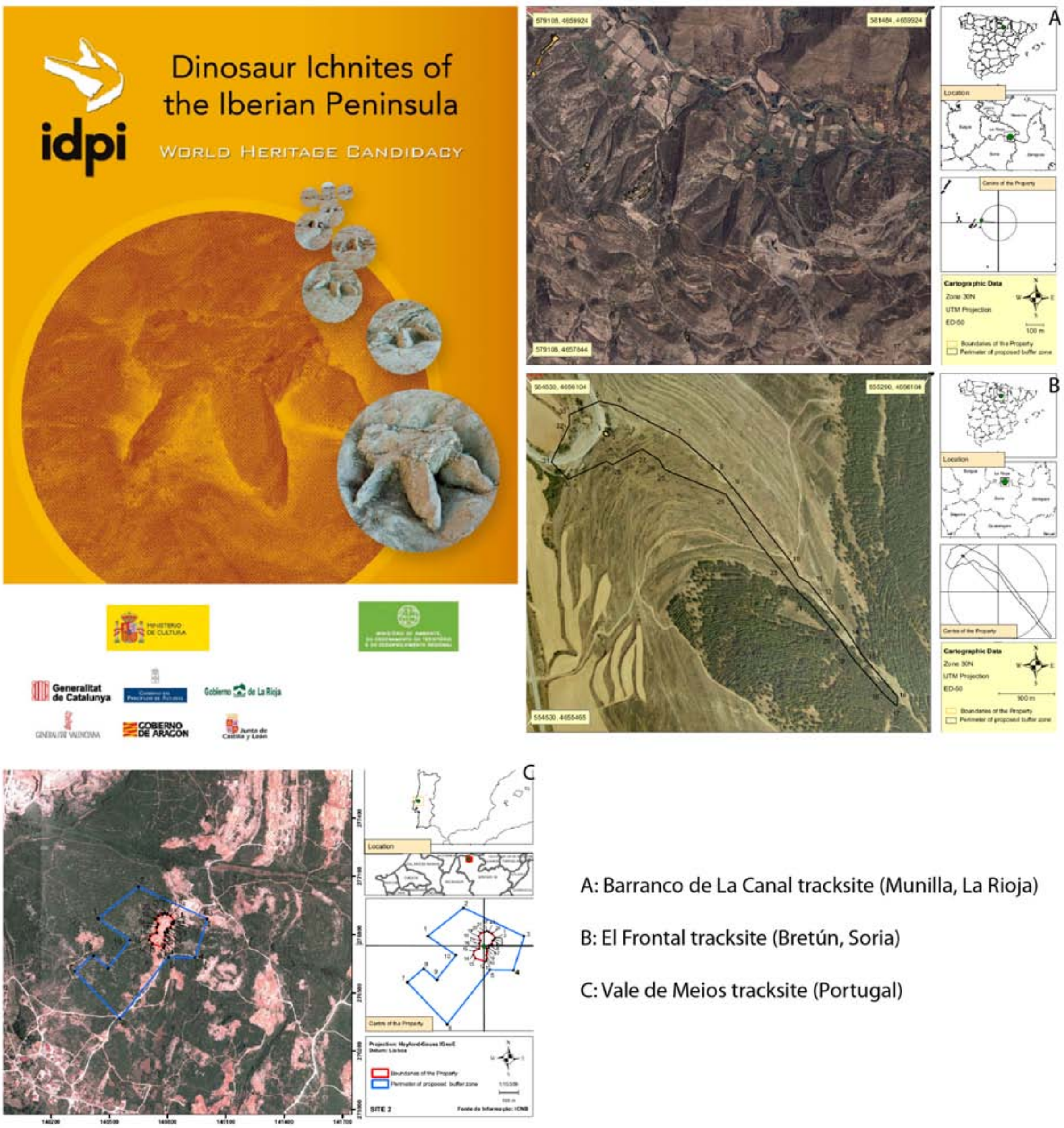



Figure 2.1. The Idpi declaration purpose of the dinosaur ichnites of the Iberian Peninsula as World Heritage in the UNESCO. Geo-localization of the Barranco de La Canal (A), El Frontal (B) and Vale de Meios (C) tracksites included in the Idpi project and in this thesis.

## 2.2 Context of localities

The material described in this PhD dissertation comes from localities (Fig.2.2) that can be organized into three different categories:

- Localities that have not been previously described: El Frontal (Spain), Issene river (Argana Basin, Morocco),
- Localities that have been previously mentioned in other PhD thesis regarding the same geological formations (Marty, 2008: Reuchenette Formation, NW Switzerland; dos Santos, 2003: Serra de Aire and Santo Antonio-Candeeiros Formations )
- Localities that have already been studied, but to which the present PhD provides a different approach: Barranco de La Canal (Spain; Casanovas et al., 1995).

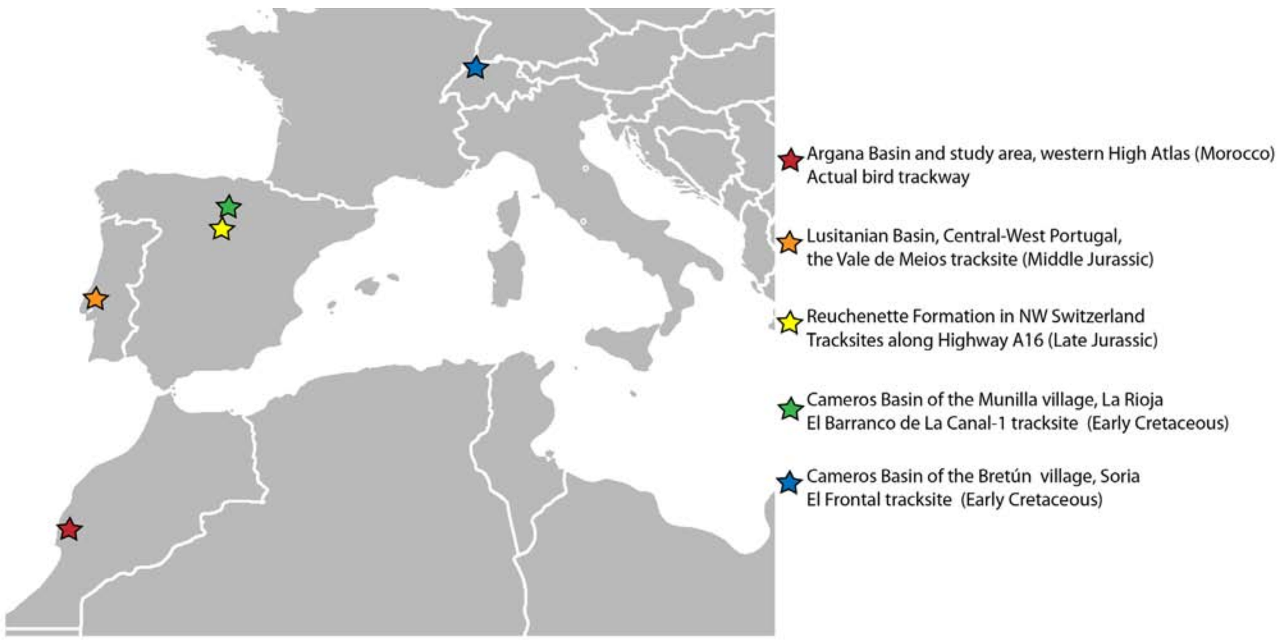



Figure 2.2. Geographical location of all the studied tracksites from Spain, Morocco, Portugal and Switzerland.

## Spain: the Cameros basin

### *Enciso Group: the Barranco de la Canal tracksite*

The Barranco de La Canal (BLC) tracksite is situated in northern-central Spain (Fig.2.3), in the part of the Cameros basin located in La Rioja region, close to the village of Munilla. The tracks are preserved on a silty sandstone slab of the Valdeosera-Traguajantes Unit, in the upper part of Enciso Group, in which sandstones, siltstones, marls and limestone are dominant (Hernandez Samaniego et al., 1990). The Enciso Group is among the most abundant in terms of dinosaurs tracksites (Díaz-Martínez, 2013). The middle and upper parts present a great variety of littoral and lacustrine deposits, evaporites and banks of limestones with diverse thickness, alternating with marls with desiccation cracks, fine grained siltstones and siltstones with ripples and hummocky cross-stratification. The palaeoenvironment of the Enciso Group has been reconstructed as a siliciclastic to carbonate mixed lacustrine system with occasional marine incursions (Doublet et al., 2003).The charophyte record suggested that the Enciso Group is early Barremian to middle Albian in age.

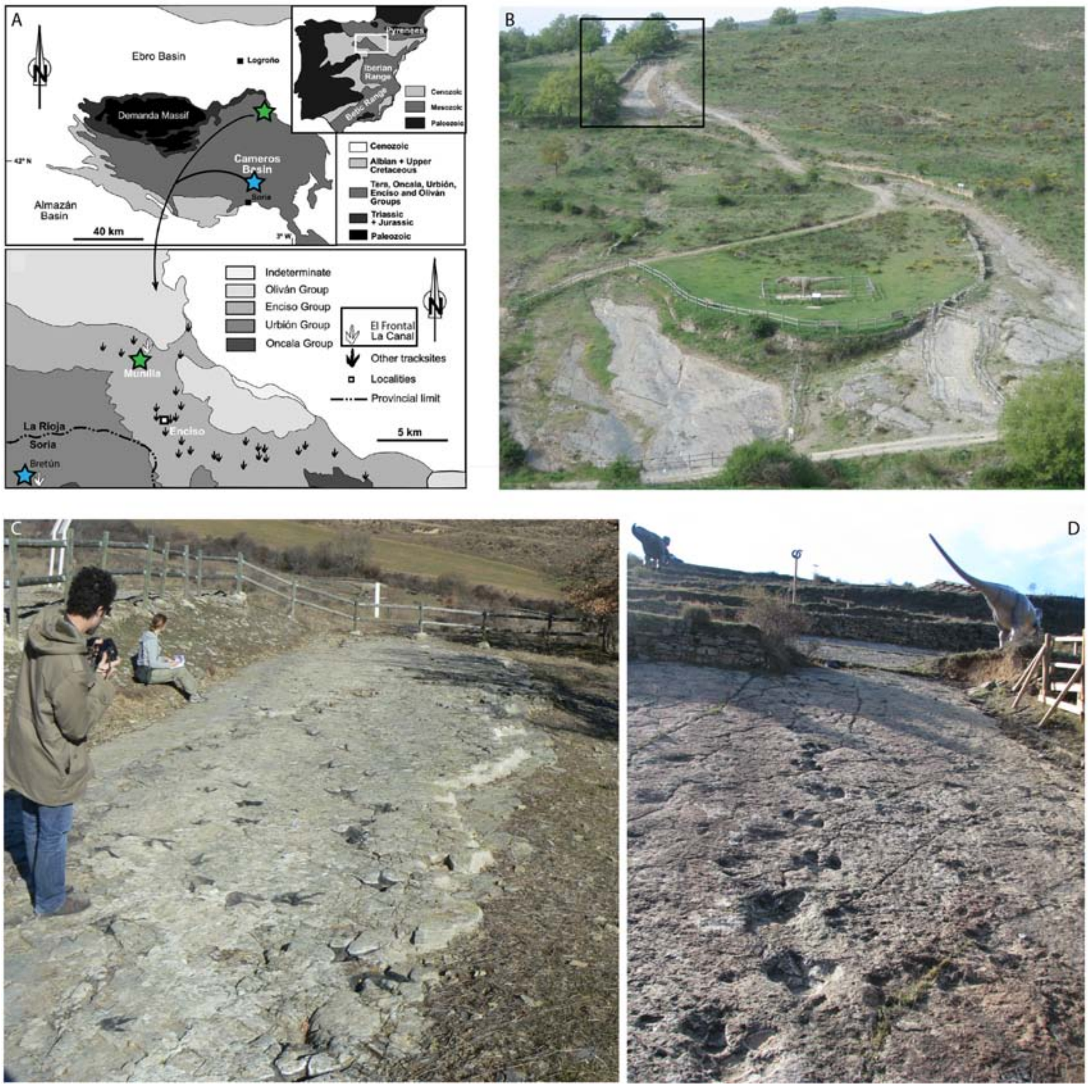



Figure 2.3. Geographical and Geological setting of the Cameros basin where the studied tracksites El Barranco de La Canal (Munilla village) and El Frontal (Bretún village) are located (A). Panoramic overview of other sites that outcrop together with the El Frontal site (B). Close-up to the El Frontal theropod tracksite (C). View of the ornithopod trackway at the Barranco de La Canal tracksite (D).

***Huerteles Formation (Oncala Group): the El Frontal tracksite***

The El Frontal site is found in the Cameros Basin (Soria, Spain), which is located north-west of the Iberian range (Fig.2.3). The sedimentation was dominantly continental as demonstrated by alluvial and lacustrine deposits (Gomez-Fernández and Melendez, 1994), but includes some sporadic marine incursions (Quijada et al., 2010, 2013). The tracksite falls in the DS-3 (depositional sequence) and belongs to the Oncala Group. It is subdivided into the Huerteles (which includes the El Frontal tracksite) and Valdelprado formations and dates to the Berriasian (Schudack and Schudack, 2009). The El Frontal tracksite is 150 meters apart from the outcrops of the Fuente Lacorte tracksite reported by Aguirrezabala and Viera (1980) and Sanz et al. (1997).

The lithology of the El Frontal tracksite is composed of 5 different layers that include intercalated organic rich gray siltstones mudstones and sandy-siltstones.

**Portugal: Lusitanian basin**

***Serra de Aire Formation: the Vale de Meios tracksite***

The Vale de Meios tracksite is found in the Middle Jurassic micritic limestones from the Maciço Calcário Estremenho (Limestone Massif of Estremadura, Lusitanian Basin, dos Santos, 2003), which encompasses the relief area of the central-west part of Portugal (Fig.2.4). The strata containing the analysed tracks were deposited in the eastern margin of the Protoatlantic Ocean, formed as a result of the rifting that started in the Midde Jurassic. 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. The barrier island environment is represented by the Santo António-Candeiros Formation, while the associated lagoonal and peritidal ones are represented by the Serra de Aire Formation (Azeredo et al., 2007). This last formation contains the Vale de Meios tracksite here reported, which is Bathonian in age after the occurrence of agglutinated foraminifera (Manuppella et al., 1985).

**Switzerland: Jura Mountains**

***Reuchenette Formation (NW Switzerland): the Chevenez-Combe Ronde and Courtedoux localities***

The studied material comes from 6 tracksites located about 6 km to the west of Porrentruy (Ajoie district, Canton Jura, NW Switzerland, Fig.2.5). Geologically, the studied tracksites belongs to the Tabular Jura Mountains and these area is located at the eastern end of the Rhine-Bresse transfer zone between the Folded Jura Mountains to the south and east and the Upper Rhine Graben and Vosges Mountains to the north. The studied trackways come from four different track-bearing laminite intervals, separated by shallow marine marls and limestones including massive nerinean limestones (Marty 2008; Comment et al. 2011) and they are part of the Reuchenette Formation (Thalmann 1966; Gygi 2000). It can be precisely dated with ammonites to the Tethyan Divisum to Acanthicum ammonite zones, i.e., late Early to early Late Kimmeridgian (Marty et al. 2003; Jank et al. 2006; Comment et al. 2011, 2015).

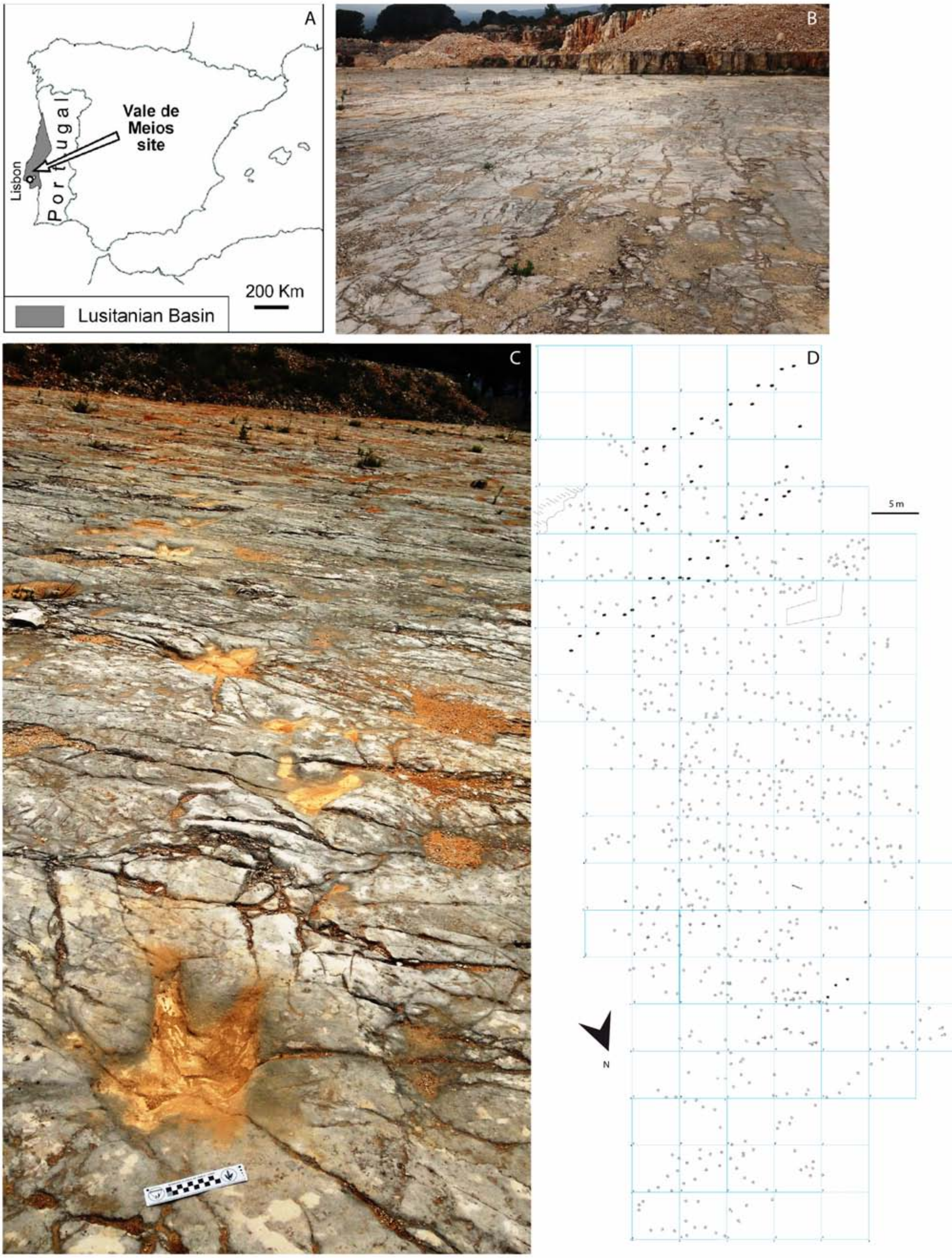



Figure 2.4. Geographical setting of the Vale de Meios tracksite in the Lusitanian basin (A). Overview of the whole active quarry of Vale de Meios (B). Detail of a trackway analysed in Razzolini et al., 2016b (C). Two-dimensional map of the studied quarry (D).

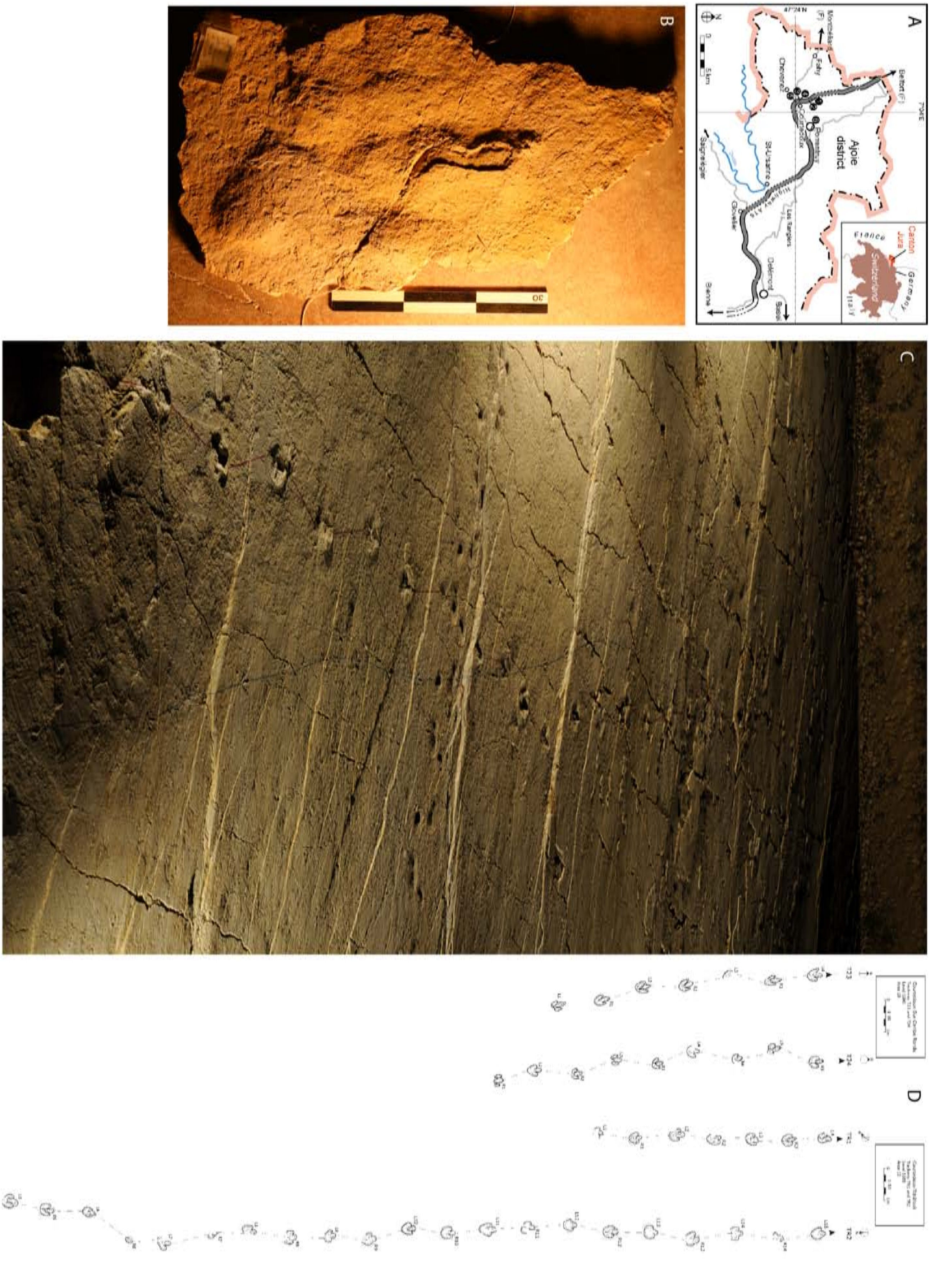


Figure 2.5 (previous page). Geographical setting of the Ajoie district in the Canton Jura (NW Switzerland) and the six Late Jurassic tracksites along Highway A16 ('Transjurane'). Numbers indicate the different tracksites: 1. Courtedoux—Béchat Bovais (CTD-BEB), 2. Courtedoux—Bois de Sylleux (CDT-BSY), 3. Courtedoux—Tchâfouè (CTD-TCH), 4. Chevenez—Combe Ronde (CHE-CRO), 5. Courtedoux—Sur Combe Ronde (CTD-SCR), 6. Porrentruy—CPP (POR-CPP) (A); detail of one paratype of *Megalosauripus transjurani* described in Razzolini et al., (submitted) (B); overview of one of the studied tracksites, Courtedoux—Béchat Bovais (C); four trackways from the same stratigraphical level but different tracksites Courtedoux—Tchâfouè and Chevenez—Combe Ronde (D).

## Morocco: Argana Basin

### *The Irerhi locality*

During a field trip in occasion of the First International Congress of Continental Ichnology (ICCI) 2015 in the Argana Basin, Morocco, we observed numerous trackways of small living birds (possibly *Limicola*), 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 and the trackway segment is recorded perpendicular to the 45º slope of the river bank (Fig.2.6).

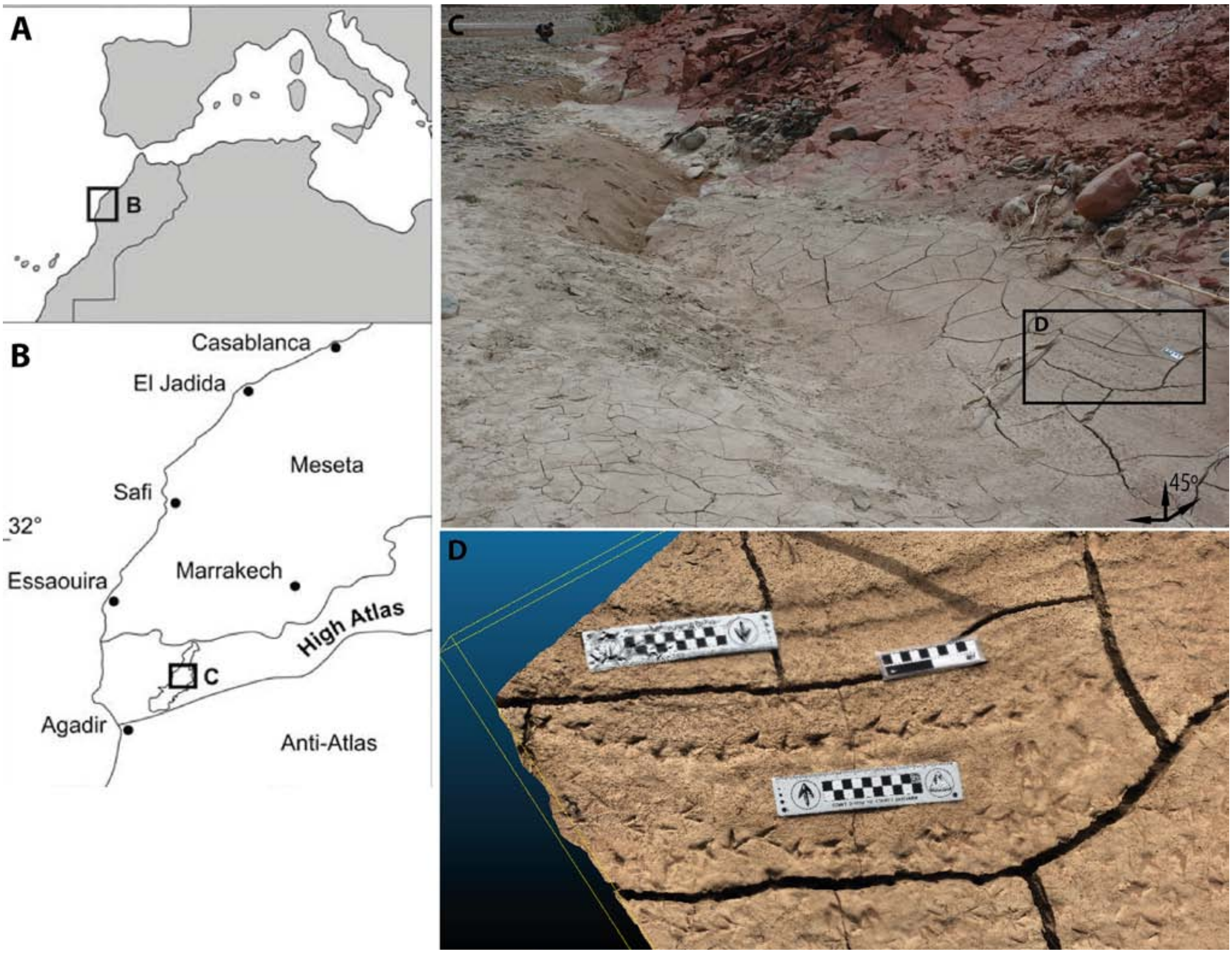



Figure 2.6. Geographical setting of the studied bird trackway. Position of the Argana Basin and study area in the western High Atlas of Morocco (A-B). Field aspect of the studied trackway, crossing a 45º sloping surface on a mud crack portion (C). Photogrammetric 3-D model of the studied bird trackway (D).

## 2.3 Materials and Methods

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. Because of the typology of the analyses undertaken and in order to obtain as much information on the track morphology as possible, different tools of quantification have been used to achieved this purpose. Documenting and digitizing techiques such as laser scans and close-range photogrammetry, together with morphometric parameters and ratios, statistical and sedimentary analyses have been used throughout this dissertation.

### LiDAR

Two complete digital models of the track-bearing outcrops El Barranco de La Canal and El Frontal (chapters 5 and 9) were generated using a long-range 3-D laser scanner LiDAR. The instrumentation used in both sites was a portable RIEGL LMS-Z420i 3-D laser scanner (Fig.2.7) and it was chosen because of its rapid spatial data acquisition (12,000 points/second in the spatial coordinates, xyz and intensity). The scanner uses a not dangerous near-IR laser, that has a range of 800 m and it can be powered by a 24 V or 12 V car batteries. A Panasonic Windows tough-book with the package RiSCAN PRO preinstalled allows the operator to acquire, view and process three-dimensional data in the field. The scanner counts on an attached camera (6.1 megapixel Nikon D100) that extracts RGB images and reflection information for the point cloud. A precise global positioning is required and given by Trimble PRO-XR Differential Global Positioning System (DGPS) (Bates et al., 2008; 2010).Multiple scanning (with an average of 10 scan stations and more than 20 million points for point clouds of chapters 5 and 9) provides more detailed 3-D shape information by eliminating shadows in the data caused by irregularities in the exposure surface (Bates et al., 2008; 2010). To avoid a null result, scans are taken from both perpendicular and oblique perspectives, with special regard to track depths that form features of negative relief on the scanned surface, giving a false impression. At each scan station, a panorama scan view of almost 2 million points obtained by the scanner is taken and coloured by the photographic images acquired from the wide angle of the camera. Then, the panorama view isobserved in the laptop through the software package RiSCAN PRO which gives a prototype to analyse, improve and correct. The outcrop is successively selected and multi-scanned at difference resolutions (from 0.01 m to 0.08 m point spacing) and from different angles. The result is a set of not heavy and small overlapping files that are much more manageable for later processing. Scan resolution is critical during fieldwork and data processing because it is when the size and the manageability of the data are decided. Hence, scans ought to be checked and processed on the laptop while still at the field. After the field photogrammetry, it was possible to construct high-resolution Digital Outcrop Models (DOM) of the tracksites with the help of modern digitalizing software (Geomagic® Studio 10 and Rapidform™ Inus Technology 2006) that superimpose field photos to the cloud of points captured by the laser-scanner. These are reverse engineering software that transform scan data and polygon meshes into accurate three-dimensional digital models to capture the exact geometry of the single points. Scans were exported from the RiSCAN PRO software to the Geomagic® one into *ASCII, *XYZ or *TXT formats. The raw point cloud data appeared as group of millions of black points because the light captured is altered. Thus, normals of every single raw point were reset. All files representing surfaces and trackways are imported into Rapidform™ softwareor Geomagic® Studio 10 to transform raw point clouds files from 2-D points into 3-D polygons. This process is called triangulation or polygonization of the scans and it consists on the connection of adjacent points with triangles using x, y and z coordinates. A surface is thus created from the point cloud by connecting points with triangles.


Figure 2.7. Close-up of the LiDAR methods with details of the portable RIEGL LMS-Z420i 3-D laser scanner and the attached camera (6.1 megapixel Nikon D100) (A); LiDAR functioning in the field while scanning the El Frontal tracksite (B).

## CRP-Close Range Photogrammetry

Every tracksite studied is supported by a close range photogrammetry that initially aimed to complement (such as in chapters 5 and 9) and then substitute (chapters6-8) the LiDAR laserscanner with a much higher-resolution for track and trackways morphological analysis.
Field photos were taken with:
- Canon Power Shot S5IS camera (focal length 35 mm, resolution 3264x2448) for Chapter 5 and 9;
- Canon 70D 20 Mpixel camera, equipped with a Canon 10-18mm STS or a Canon 18-135mm STS lens and a Canon ring flash (Macro Ring Lite MR-14 EXII) in order to eliminate the shadows generated by sunlight for Chapter 6;
- Canon PowerShotG12 camera (focal length 6 mm, 3648×2432 resolution) for Chapter 7; iPhone5s-camera (focal length of 35 mm with a resolution of 3264x2448) and with Nikon D70 (focal length 93 with a resolution of 3008x2000) for Chapter 8.
Point clouds and three-dimensional models were generated with:
-10 to 35 photos per track processed in Agisoft Photoscan standard version 1.1.4. build 2021software (http://www.agisoft.ru/) and colour maps with 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/) in Chapters 5-9.
-10 to 20 photographs per track and processed using VisualSFM (http://ccwu.me/vsfm/) and color maps three-dimensional models with Schlumberger package Petrel in Chapter 9.
Highest quality setting of the camera is required, the closer the camera is to the specimen, the higher will the final resolution of the model be. Every detail that is not in the pictures will not be in the final mesh. Move underneath and above the specimen to take photos. Take in-focus photographs. Aim for even lighting of the specimen to avoid shadows, ideally identical in all photographs. Move the camera in relation to the specimen (or vice versa) to create parallax; do not take panorama photos (many photographs from one camera position). Each point on the specimen must be well visible and in focus on at least two images. Take photographs with 40-60% overlap as rule of thumb. Avoid near-identical photographs. Overview photographs can be supplemented by close-ups, but much overlap is required. Take more photographs than necessary, because unsuitable photographs can later be excluded from model creation and replaced by others, and gaps can be closed.
All the works included in this thesis account with high-resolution photogrammetric models, created using VisualSFM (http://ccwu.me/vsfm/) and Agisoft Photoscan Pro (v.1.2.4 and v.1.2.5; www.agisfot.com, Fig.2.8), following the procedures of Falkingham, 2012 and Mallison and Wings (2014). The latest version of this software provides precise reports on the methodology, survey data, error and precision of the model. The accuracy of the models ranges between 0.1 and 0.03 mm. The scaled mesh, exported Stanford PLY files, were then processed in CloudCompare (www.cloudcomapre.com), where the meshes where accurately oriented though the generation of a plane intersecting the surface, in order to avoid imprecise alignment due to the roughness and irregularity of the surface, then it was possible to create accurate false colour depth-maps. The material need is very simple: scale bar along

the base (e.g., width) and height (e.g., length) of a track and a decent camera (cell phone also works). If camera settings and focal distance remain the same, hundreds of photo can be taken without refocusing, allowing for large areas (even entire tracksites) to be documented as part of one photogrammetric project. Therefore, anything that is on or over the surface will be modeled in 3-D and become part of the data set (i.e. sedimentary structures). In addition, unbiased, higher-level, mathematical analyses may be conducted on the 3-D data. Software algorithms can automatically quantify areas of surface curvature, roughness, slope, and other morphomet¬ric characteristics (Matthews et al., 2016; Wings et al., 2016).

### Morphometric parameters and ratios

Among classic ichnological measurements carried, I selected the following track and trackway parameters and ratios, based on a selection of works of previous authors (Leonardi, 1987; Thulborn, 1990; Marty, 2008; Lockley, 2009) and presented them in Fig.2.9.

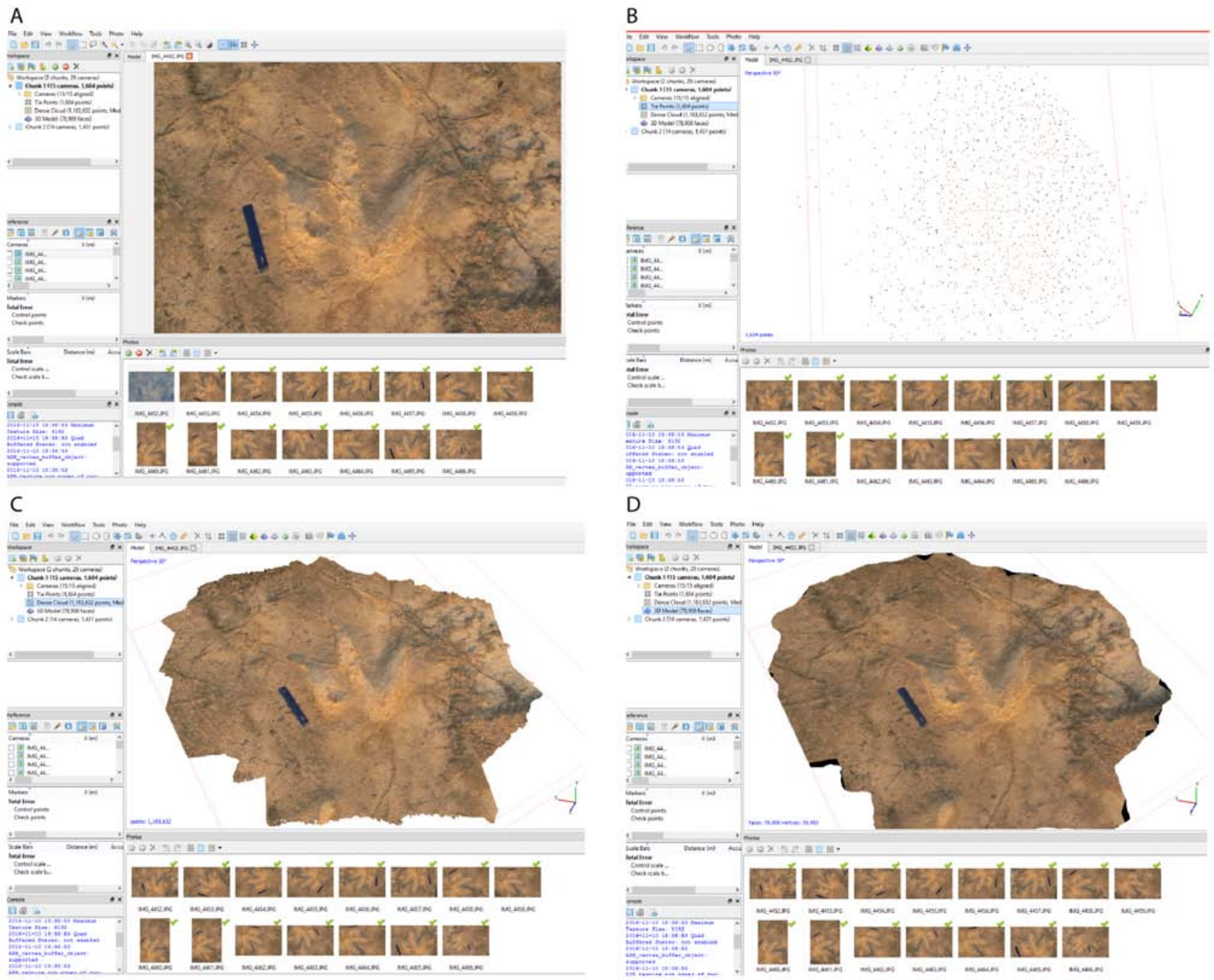



Figure 2.8. Steps to follow in Agisoft Photoscan software to create the 3-D mesh after undertaking photogrammetry on a theropod track (*Megalosauripus*). First step is to create a chunk with all the photos taken around the track (A); the software recognize the overlapping of the photos and creates tie points for the point cloud model (B); the software creates a dense cloud from the point cloud (C); it is now possible to build the three-dimensional mesh of the track (D).

***Tracks parameters and ratios***

-Track length (TL): the length of a footprint is best measured along or parallel to the axis of the principal digit (Thulborn, 1990), which in the case of mesaxonic tracks (tridactyl tracks) is located parallel to the axis of digit III (middle digit). In this PhD thesis, track length was always measured from the maximum distal point of digit III (excluding claw marks where preserved) to the maximum proximal point of the first phalangeal pad of digit IV (PIV1) or the metatarso-phalangeal pad impression (when present). Moreover, it is specified when the track length includes or excludes the metatarsal-phalangeal pad and metapodium area (sensu Thulborn, 1990 p.81; Marty, 2008, p.37), where digit I impression (hallux) is preserved.
- Track width (TW): in this PhD thesis, it is measured drawing a line from the most anterior point of the tips of lateral digits II-IV (excluding claw marks, as in Marty, 2008, p.37). Differently to what suggested in Thulborn (1990, p.81), this measure is not necessarily perpendicular to the track length line.
- Track length and track width ratio (TL/TW): this ratio expresses the variation of the foot length with respect to its width and it is usually adopted to highlight a possible morphometric difference between theropods and ornithopods. Theropods tend to have >1 ratio, being these type of tracks longer than wide; while ornithopods display a ratio ≤1, being these tracks as long as wide. In this PhD thesis, this ratio is calculated for tracks of works presented in chapters 5-9.
- The anterior triangle (AT): this measurement has been proposed by Weems (1992) to examine the degree of mesaxony, that is how prominent digit III is in relation to digits II-IV. This measure defines the shape of the anterior triangle as illustrated in Lockley (2009). A strong mesaxony indicates a strong central tendency which create an acute triangle, while a weak mesaxony creates an obtuse triangle due to the sub-equal lengths of digits II-IV. Quantification of this parameter indicate the morphodynamic relationships between the degree of mesaxony and the shape of the tracks associated to different groups of dinosaurs. This parameter is measured from the distal point marks of digits II and IV, which may be variably preserved. The maximum height of the triangle (te) is measured, perpendicular to the transverse base of the triangle (TW) and expressed as the l/w ratio (AT l/w), following the definition of Lockley (2009) in Chapter 6 and 7.
- Interdigital angles (IDA): measured from the intercepting lines dividing the digits in halves (Chapters 5-9). These lines are also used as guides when measuring digit II, III and IV and pad PII1-2, PIII1-2-3and PIV1-2-3-4 lenghts (Chapter 6).
- Digit and pad widths: measured tracing a line at the point of greatest width perpendicular to the length axis of the digit impression (also Chapter 6).
New parameters introduced are relative to the quantification of the variation of track morphology according to the substrate consistency and therefore, general measurements on depth values were undertaken in Chapters 5, 8 and 9.
- Depth of the track was measured in the deepest point on the metatarso-phalangeal pad area and depth of the displacement sediment rims in Chapter 9; depth of digits II, III and IV (DII, DIII and DIV) were calculated in Chapters 5, 8 and 9 and the measure of the interdigital width recorded between digits II-III and III-IV impressions (IDW II-III and IDW III-IV) was introduced in Chapter 5.

***Trackways parameters and ratios***

Trackway parameters measured in Chapters 5-9 are measured following methodology in Thulborn, 1990 and Marty, 2008.

- Pace length (PL): in bipedal trackways, it is measured as the distance between corresponding points (such as the tip of digit III impression in right and left tracks) in two successive footprints (left-to-right and right-to left pace lengths). The ratio between short step and long step (Dantas et al., 1994; Lockley et al., 1994) is used as an index of limping behavior and irregular locomotion.
- Stride length (SL): in bipedal trackways, it is measured as the distance between corresponding points (such as the tip of digit III impression in right and left tracks) in two successive footprints made by the same foot (right-to right and left-to left distance).
- Pace angulation (PANG) is measured as the angle that forms between the measurements of two consecutive pace lengths (right-to left and left-to right lengths).
- Trackway gauge: (WAP/TL) expressed as the ratio between the width of the angulation pattern and the corresponding track length ratio as in Chapter 6.

***Trackmaker's anatomical estimations, parameters and ratios***

- Hip height calculation: always considered as an aproximation and estimation of the actual acetabular height of the trackmaker. This measurements uses Alexander's method (1976).
- Speed estimations following Alexander's formula (1976) in Chapters 5-8:

$$v(m/s)=0.25*g^{0.5}*SL^{1.67}*h^{-1.17}$$

**Statistical analysis**

Statistical analyses were conducted in chapters 5 and 9. Chapters 5 compared statistical differences in the pace lengths and in the averages of the interdigital width parameter (IDW II-III, III-IV) between right and left tracks through the two-paired samplestatistic analysis, suited to compare two population means, where there are twosamples in which observations in one sample (left pes morphologies)can be paired with observations in the other sample (right pes morphologies).

The statistical analyses on the 49 tracks carried in Chapter 11 refer to linearcorrelation 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, a graph for each analysed trackway were built using TL, PL (left Y axis) and depth measurements (right y axis).

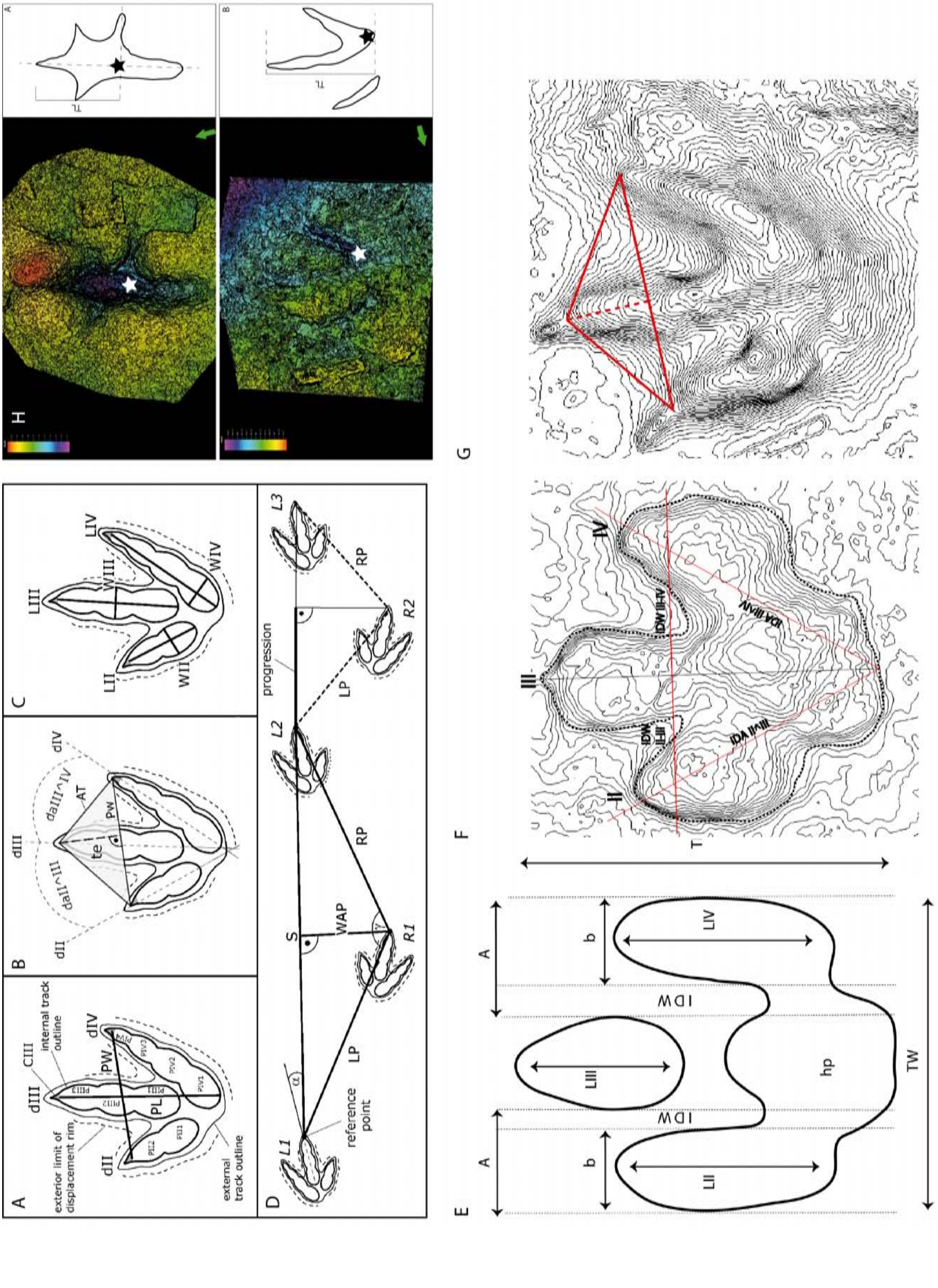

A
B
C
D
E
F
G
H
exterior limit of displacement rim
internal track outline
external track outline
reference point
progression
LP
RP
WAP
S
L1
L2
L3
R1
R2
LII
LIII
LIV
WII
WIII
WIV
IDW
TW
hp
AT
te

Figure 2.9 (previous page). Different measurement undertaken in this thesis. Outline drawing with complete information on the exterior limit of displacement rim (dot line), internal limit of displacement rim (continuous line) and internal track outline (bold line) (A). Measurements taken for the track: pes length (PL) and pes width (PW), measures of phalangeal pads when preserved (PII1, PII2, PIII1, PIII2, PIII3, PIV1, PIV2, PIV3, PIV4), anterior triangle ratio (te/PW), length and width of digits (A-C). Measurements taken for trackways: left pes (LP) and right pes (RP), stride (S) (D). Ideal representation of measurements taken in an ornithopod track: track length (TL), track width (TW), length of digits (LII, III, IV), heel pad (hp) and the new parameter interdigital width (IDW) (E). Left and right Caririchnium lotus tracks showing measurements of IDW and interdigital angle (IDA) taken on the isolines (contour lines) of height (Z coordinate) obtained from Paraview software every centimetre. To draw the track profile, one isoline was treated as an independent track contour line to use in the interdigital angle (IDA) and interdigital width (IDW) measurements (red lines) (F). *Megalosauripus* track displaying how is traced the anterior triangle AT (Weems, 1992; Lockley, 2009) (G). Three-dimensional depth models of theropod tracks showing where the maximum depth is measured in deep and shallow tracks (H).

## Sedimentological analysis

Sedimentological analyses were conducted for Chapters 7 and 9 (Fig.2.10).

For Chapter 7, three thin sections (sample numbers IPS87258, IPS87264, IPS87259 housed at the Institut Català de Paleontologia "Miquel Crusafont") were conducted on samples collected from the tracking surface and the infill of the tracks for sedimentological (microfacies) and environmental determinations.

In Chapter 9, four thin sections (sample number IPS-82477a-d housed at the Institut Català de Paleontologia "Miquel Crusafont") were undertaken to quantify lithology and mineral composition of the sediment collected from both the tracking and the undertrack surfaces.

Images of the polished thin sections were taken using light microscopy via a Leica DM 2500 photo-microscope.

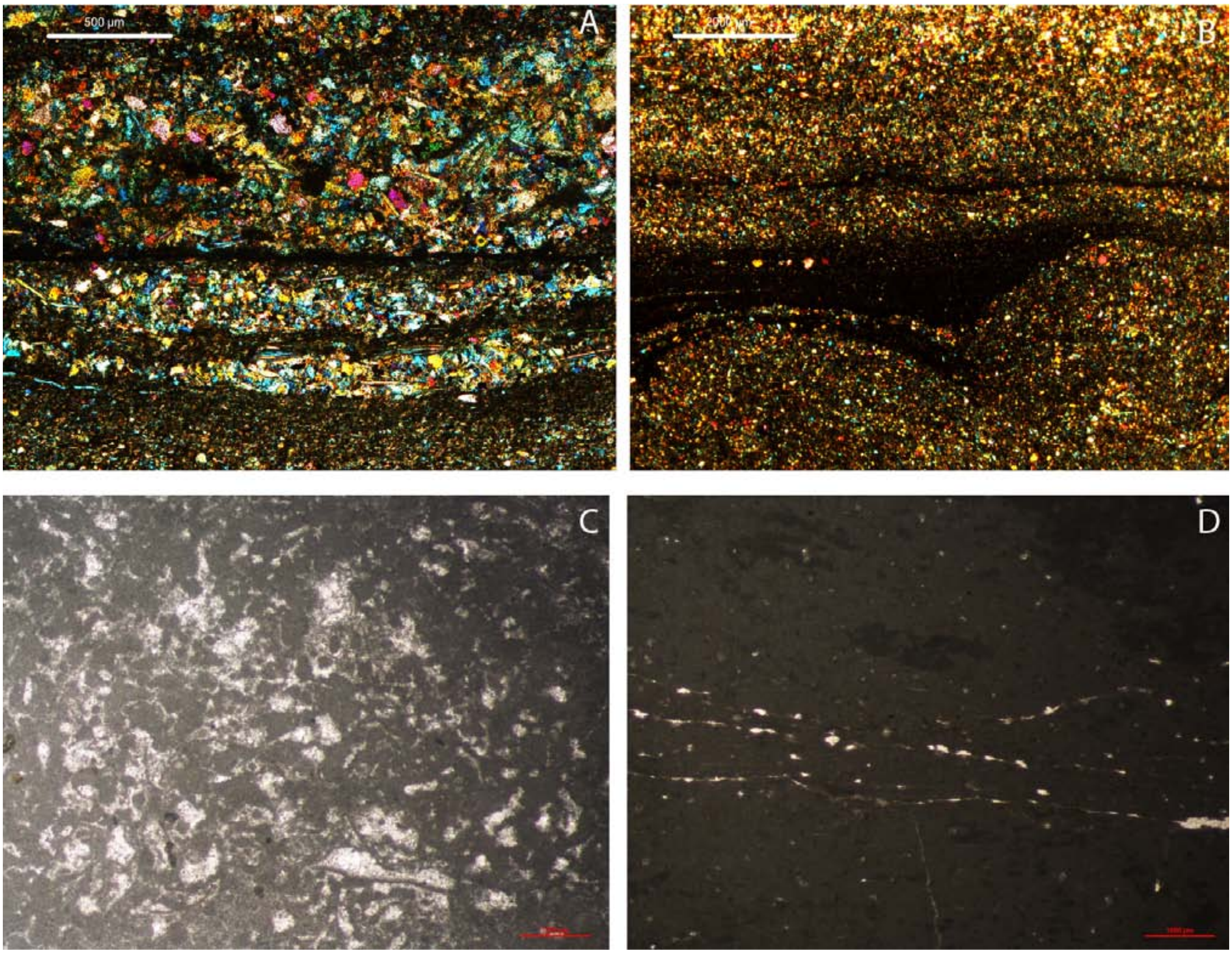



Figure 2.10. Thin sections from different tracksites (El Frontal and Vale de Meios). Sandstone intercalated by siltstone, mineral clays are abundant (.60%) (A); deformation structures (mud drapes) (B); massive limestone (C); and laminated limestone (D).

# PART 2

## Track morphological variation and Interpretation

# CHAPTER 3

## Ichnological context

### 3.1 Historical background

### 3.2 Documenting, describing and quantifying tracks

# CHAPTER 3- ICHNOLOGICAL CONTEXT

## 3.1 Historical background

Ichnology is a system of knowledge with a very well-defined nucleus (traditional ichnology) but with poorly defined borders (Baucon et al., 2012 ) and blurs in a vast gray area shared with other disciplines. The term "ichnology" has been in use for approximately 175 years, but it is only within the last 20 or 30 years that the importance of ichnology has been recognized with its tremendous potential for terrestrial biostratigraphy and biogeography, as well as for paleoecological and behavioral studies (Rainforth, 2005).

Edward Hitchcock is known as the father of ichnology after his description in 1836 of the first vertebrate tracks known from North America, even before the concept of dinosaurs was established in 1842. He established the tradition of vertebrate ichnotaxonomy (naming tracks), which he called Ornithichnology, the description of bird "footmarks". He named large Jurassic tracks from the Connecticut valley region as *Ornithoichnites*, implying that they were made by giant birds (Hitchcock, 1836). Nevertheless, the earliest published scientific account of fossil footprints dates to 1828, with a notice by William Buckland on footprints from the Permian of Scotland; these prints had been brought to his attention by Dr. Duncan, who elaborated on the matter in 1831. Owen (1842: p. 190) later named these prints *Testudo duncani*, marking perhaps the very beginning of vertebrate ichnotaxonomy and showing that the emphasis was on the producer (Lockley, 1991; Minter et al., 2007). In 1837, Hitchcock presents new findings of those "footmarks", under the general term of Ichnites, and classified 14 new species. Hitchcock's (1836-1865) classification of *Ornithichnites* into Leptodactyli and Pachydactyli (slender- and thick-toed respectively) is considered to be a taphonomic rather than biologic division (Rainforth, 2005).During the second half of the XX century, vertebrate ichnology expanded in North America, with the important findings at the famous Paluxy river (Bird, 1939, 1941, 1944, 1954), in South America (Leonardi, 1987) and in Europe (Lessertisseur, 1955; Khun,1958). In England, one of the most important contributions is produced by Sarjeant (1974) with the history of vertebrate footprints in the British islands.

From the beginning, morphology was of prime importance in establishing classifications and taxonomies of traces, and ichnology essentially adopts the same principles as standard body fossil taxonomy (Lockley, 2007). Linnaean binominal nomenclature has been applied to fossil footprints since 1836, andthe current rules regarding application and formulation of names are set forth in the International Code of Zoological Nomenclature (ICZN 1999). However, ichnotaxonomy has never had a clear published statement (nor consensus) of descriptive procedures to follow when naming a track. Sarjeant (1989) states that the fashion in which tracks are described and named should not be legislated too closely. He proposed some considerations to be borne in mind when describing vertebrate tracks (considering a complete trackway for defining a track morphology; undertaking a thorough bibliographic search before naming; the designation of a holotype; the photographic support and interpretative drawings; clear and complete measurements; unambiguous diagnosis and characterization of the track).

Modern ichnology is reshaped in the early 1950s, when Seilacher (1953) significantly contributed to the conceptual innovations on considering invertebrate trace fossils as manifestation of behavior, developing an ethological classification. This revolution is important because the overall potential of the multidisciplinary approach (i.e. sedimentology, rheology, ethology, biomechanics, osteological correlation) is finally unchained. In the 80s, a worldwide spread re-evaluation of the ichnofauna begins in the occasion of the First International Symposium on Dinosaur Tracks and Traces, convened in Albuquerque, New Mexico on May 22-24, 1986 (Gillette and Lockley, 1989). This congress was key for conveying and discussing core topics that determined the Vertebrate Ichnology Renaissance (Lockley, 1987). The issues enumerated during the congress are fundamental insights that blossom more than a century after the beginning of ichnology. Some of the main goals that have their origins in the conceptual and methodological consequences of this important breakthrough in dinosaur ichnology in the late 80s, lean especially on a multidisciplinary approach to expand the implication of an apparent simple morphology.

The concept of morphological variability (Fig.3.1) is introduced when ichnologists observed the morphological effects on tracks after and during the interaction of the foot of a moving animal with the substrate (Thulborn and Wade, 1989). Further, Farlow (1989) underscored 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. Ellis and Gatesy (2013) studied this dynamic process and noted that most foot-sediment and sediment-sediment interactions are rapid and hidden from view. The importance of the substrate as a controlling factor in the determination of track morphology is indeed recognized also through neoichnological observations (Scrivner and Bottjer, 1986; Marty et al., 2009) and through the analysis and discussion of structures such as metatarsal impressions (Kuban, 1989; Manning, 1999, 2008). At present, it is widely assumed that track morphology is determined by the track-maker and the substrate characteristics (Díaz-Martínez et al., 2009); it represents the interaction between a medium such as soils, sediment, or lithified materials and organism behavior (Hasiotis et al., 2007). For this reason, in recent years tracks are considered as dynamic fossils. In this regard, Baird's (1980) statement that "a footprint is not the natural mold of a morphological structure but is, instead, the record of that structure in dynamic contact with a plastic substrate" have triggered a new vision of the track morphology among vertebrate ichnologists. It is nowadays widely accepted that the substrate has a major loading in determining track morphology (Gatesy, 2003; Manning, 2004; Milàn and Bromley 2006, 2008; Marty, 2009) and moreover, substrate consistency is also quantified through computer simulated footprint recreation (Allen, 1997; Margetts et al., 2006; Jackson et al., 2009, 2010; Falkingham et al., 2010, 2011; Ellis and Gatesy, 2013). Hence, to understand the formation and preservation of (dinosaur) tracks, it is essential to understand the mechanics of soils, defined as any loose sediment deposit (Manning, 2004, 2008) and to understand what sediment deformation structures characterized the substrate at the time of track formation (Allen, 1982, 1989, 1997; Nadon, 2001).

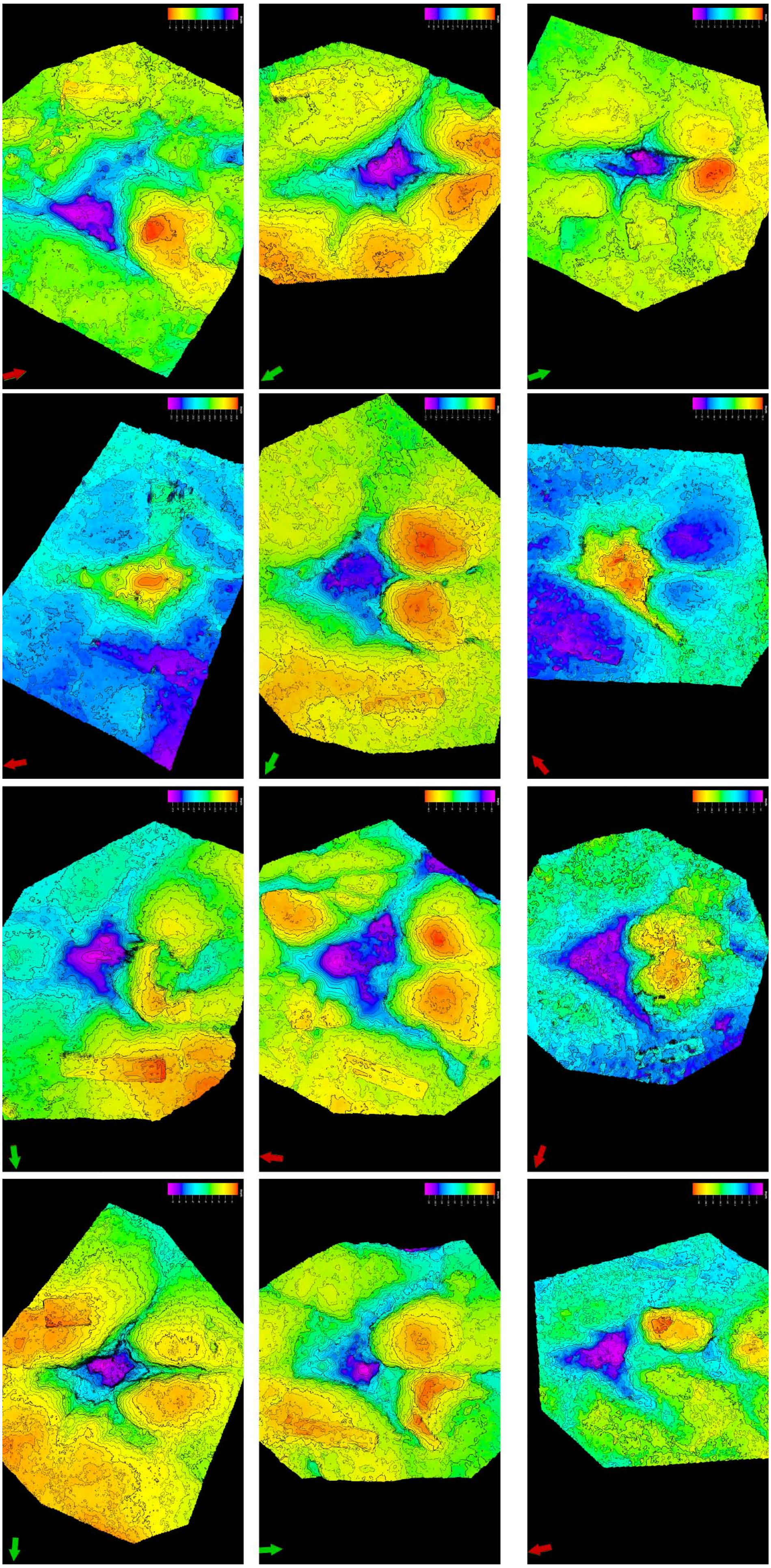


Figure 3.1. Morphological variability observed along the same trackway at the El Frontal tracksite.

Nevertheless, taking into consideration rheology and soil mechanics (Barnes, 2000; Craig, 2004) as the major response to a foot indention is still an entangled topic.
Baird (1957) stated that a trackway is not a simple record of anatomy. Instead, it is a record of how a foot behaves under a particular locomotive pattern as it makes contact with a particular substrate, introducing the concept of locomotion and limb dynamics of the trackmaker. The resulted morphology (footprint) is strictly linked to three factors: 1) foot anatomy, 2) animal locomotion/behavior, 3) substrate properties at the time of the indentation. Moreover, because of these co-dependent variables, the same animal on the same substrate but with a different behavior or a different locomotion pattern will very likely determinate a different track morphology.
Padian and Olsen (1984) were the first to assume a quantitative approach towards integrative morphological analysis of tracks. They proposed ternary diagrams with the three principal determinants of track morphology: anatomy of the foot, kinematics of the limb, and conditions of the substrate (Fig.3.2A). Any point within the triangle represents how the morphology has been influenced by each determinant. The second representation is given by a flow chart in which it is also highlighted how substrate conditions can influence kinematics, giving the track a morphology that is far from recalling the anatomy of the animal (Fig.3.2C). The fact that kinematics can distort the foot anatomy and that substrate can influence kinematics altering the final morphology is a fundamental concept that shows that reveling the trackmaker identity is not the main goal of ichnology. A more modern representation of this important concept is given by Minter et al. (2007, fig.1 p. 366), where they present a Venn diagram in which the variable relative influences on the morphology are behavior, producer and substrate (Fig.3.2B). More importantly, they stated that the contributions of the three factors on the morphology of different trace fossils are part of a continuum and that sometimes morphology is more influenced by, and reflective of, the producer, while in other occasions, it is more biased by, and reflective of, the behavior and substrate conditions. The latest representation and quantification is given by Falkingham (2014) who built a three-dimensional conceptual morphospace as dynamics, substrate and anatomy ultimately determined the 3-D morphology of the track (Fig.3.2D). The morphospace is composed by the variables dynamics (composed by kinematics and kinetics which encompass behavior), substrate (to consider as a suite of variables) and anatomy (preferred over the term producer).

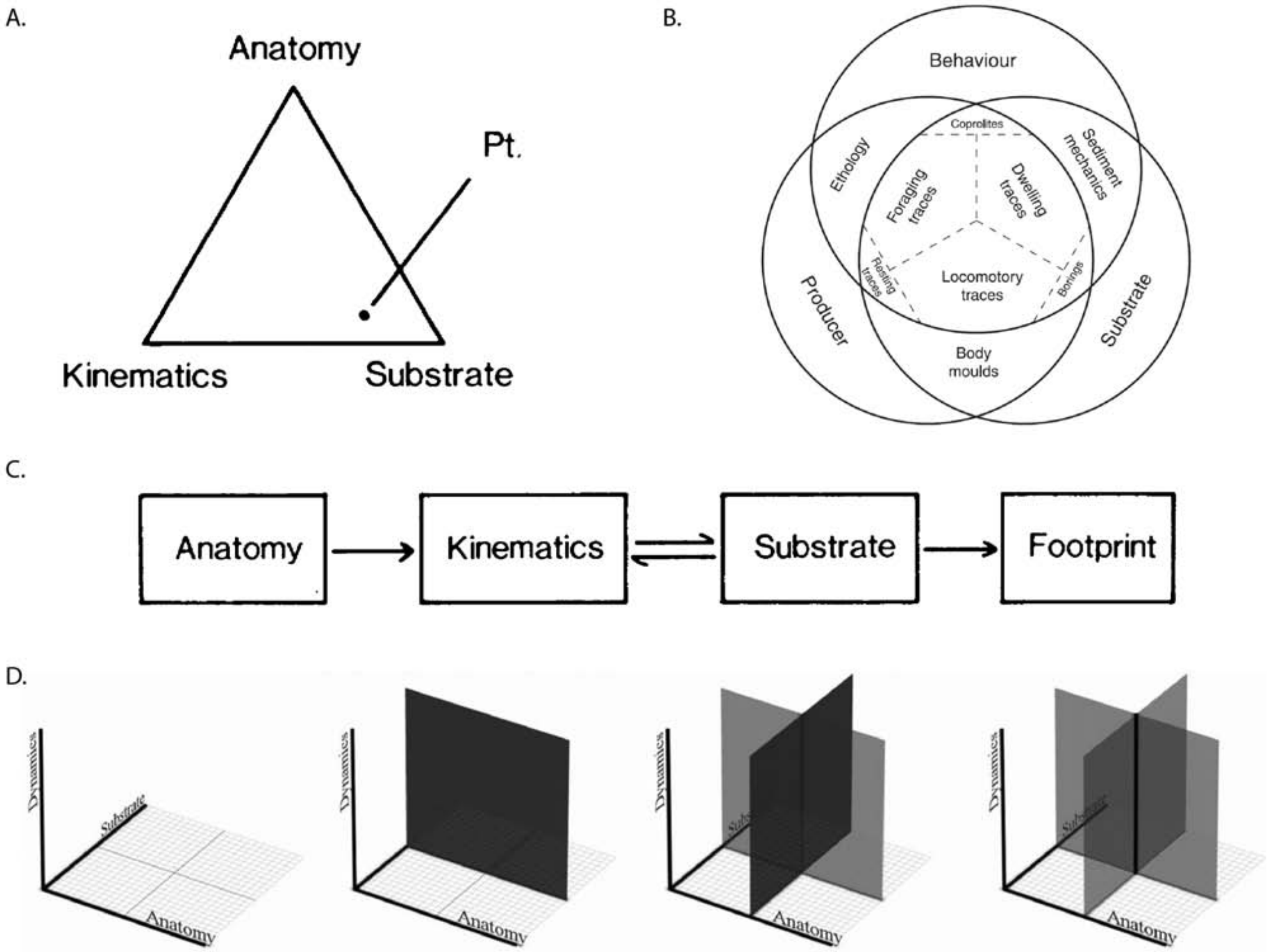



Figure 3.2. Different graphic representations of the three factors interacting during track formation and controlling track morphology. A) Ternary diagram after Padian and Olsen (1984); B) Venn diagram after Minter (2007); C) Flow chart after Padian and Olsen (1984); D) Conceptual morphospace after Falkingham (2014).

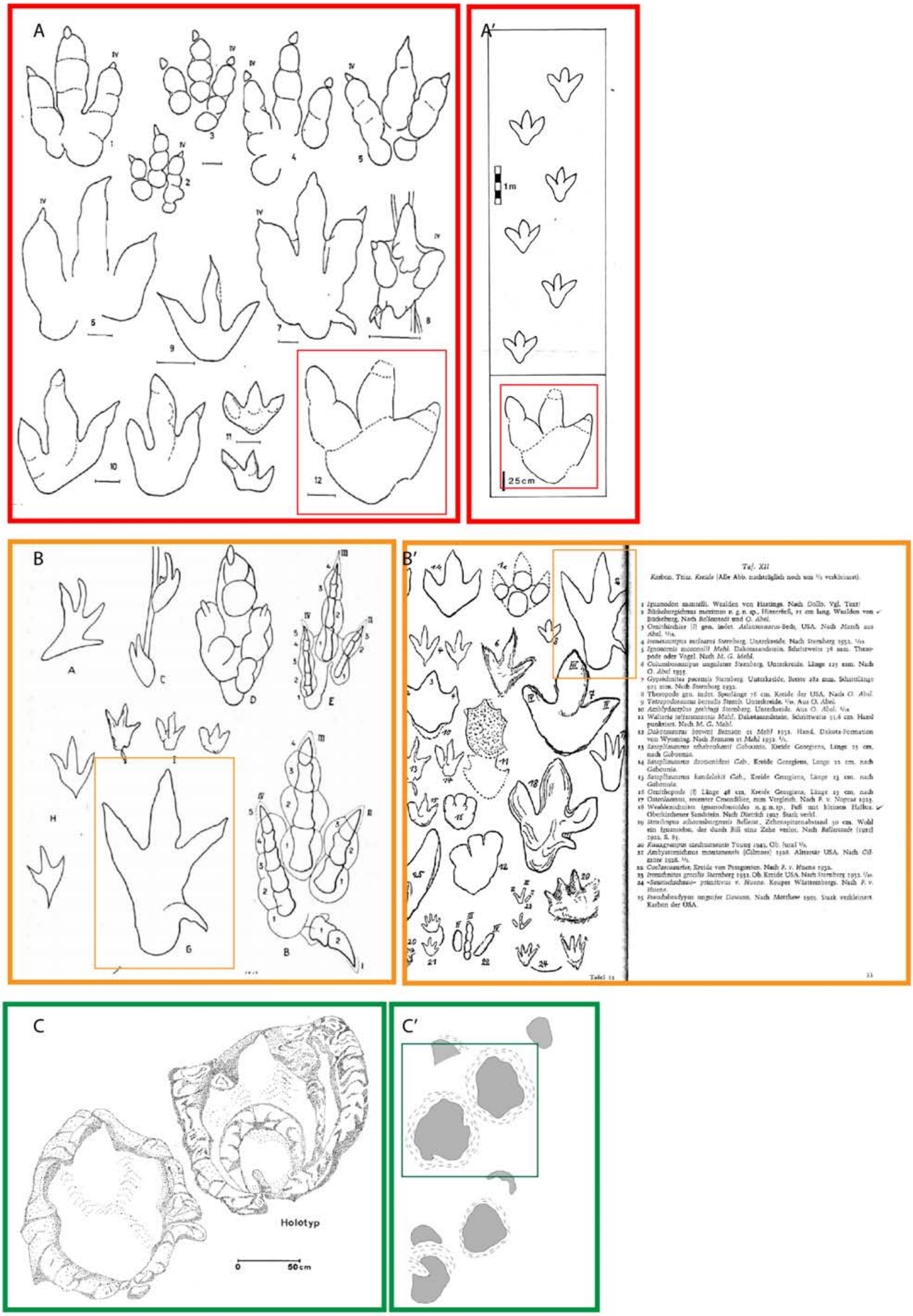
## 3.2 Documenting, describing and quantifying tracks

### *Two-dimensional data*

Historically, illustrations are sketches, outline drawings or silhouettes that give almost no relative data besides the size and shape, and depth information is lost. As shown in Thulborn (1990, fig.4.15), eight subjects represented the same track into eight different morphologies and this is very recurrent in literature, when publication after publication, the edited outline will eventually degenerate in some morphology that is far from recalling the original one. In fact, dinosaur ichnology remained almost exclusively a subjective and qualitative science, based on interpretations of track outlines and comparisons between them (Ballerstedt, 1905; Schuler, 1917; Nopsca, 1923; Peterson, 1924; Sternberg, 1932; Abel, 1935; Lull, 1942). Literature is rich in famous examples of coining new ichnotaxa based on a drawing and a statement of putative trackmaker with little or no information to support this assertion (see Fig.3.3). For instance, the ichnospecies T*yrannosauropus petersoni* (Haubold, 1971) was erected after seeing the drawings of a large trydactyl track from the Campanian of Utah presented in Peterson (1924) who illustrated various tracks implying that they could all be attributable to the same trackmaker (i.e., *Tyrannosaurus*). Lockley and Hunt (1984) have later shown that these tracks are instead of hadrosaurid origin. Another famous example is that of *Gigantosauropus asturiensis* (Mensink and Mertmann, 1984) from the Kimmeridgian of Asturias named after its putative trackmaker *Giganotosaurus* and later shown to be instead a sauropod track (Lockley et al., 2007). Other ichnotaxonomical confusions, the validity of which are still debated and unclear (Lockley, 1996; Lockley et al., 1998; Thulborn, 2001), are those of some of the most iconic dinosaur tracks presented in Lessertisseur (1955) who coined the terms *Megalosauripus* (p.115-116) and *Tyrannosauripus* (p.116) and Khun (1958) who erected the *Bueckeburgichnus maximus* ichnotaxon, on the same drawing presented for *Megalosauripus* in Lessertisseur (1955) (Khun, 1958 Table XII-2, p. 53). The fact that the same drawing of a track (Ballerstedt, 1905; Abel, 1935) can represent two different ichnogenera and ichnospecies is an expected result when parsimony and clear vision of what determines morphology is lacking.

Descriptions of the track morphology presented very few measurements of length, width and angles of the track, recording only two dimensions, initially by outline and/or shaded drawings, later accompanied by photographs and the core of the diagnosis was based on the qualitative description of the track (Falkingham, 2014). Two-dimensional drawings and photographs can generate problems in defining the actual morphology of the footprints, because their accuracy depends in part on the direction and intensity of incident light (Remondino et al., 2010). Even a monocular photograph, which is a highly detailed solution, often suffers from suboptimal lighting, which can cause misperceptions (Gatesy et

Figure 3.3 (next page). A) Red square, outline drawing of *Tyrannosauropus petersoni* after Haubold, 1971 (p.76) interepreted as a theropod track; A') *Tyrannosauropus petersoni* after Lockley and Hunt (1994) referred to hadrosaur tracks; B) *Megalosauripus* track in Lessertisseur 1955 (p.115); B') the same track referred as the type for the new ichnogenus *Buckeburgichnus maximus* coined in Kuhn, 1958 (p. 52); C) *Gigantosauropus asturiensis* in Mensink and Mertmann, 1984 (p.409); C') the same tracks reinterpreted as part of a sauropod trackway in Lockley et al., (2007).


A
A′
1m
25cm
B
B′
Taf. XII
C
C′
Holotyp
0
50cm

al., 2005) since the angle of illumination may considerably change the appearance of the track in the photograph (Sarjeant, 1989). The problem that originates from illustrating a track resides, on one side, in the subjectivity and perceptiveness of the drawer and on the other, in the determination and definition of track boundaries. The determination of the margin of a footprint can involve a problematical degree of subjective interpretation, compromising any quantitative analysis of footprint shape (Falkingham, 2016). This problem most drastically affects footprints that lack well-defined phalangeal pads, fade gradually into the surrounding sediment and/or show multiple edges (Sarjeant, 1975; Thulborn, 1990; Falkingham, 2010), which is the case in many deeper dinosaur tracks. Subjectivity equally affects both measurements and outline drawings, and both the size and shape of a footprint can differ considerably when separate approaches are employed (Lallensack et al., 2016). The dependence of a track to substrate deformation and limb dynamics, complicates the realization of the outline drawing to be faithful and reflective of the reality, mostly because it is a simplified, and sometimes, simplistic, two-dimensional representation of a complex three-dimensional structure. Nevertheless, the information about a track's surface morphology represents the basis of ichnological analysis and needs to be documented as objectively as possible (Marty, 2008). In order to succeed in this task, it is of pivotal importance to define the track extension, that is to say where does the true track begins and where does it end. This is not an easy task, especially when the surface is distorted and the track is surrounded by deformation zones and sediment rims. There are at least four possible measurements of the track length: 1) the base of the track, or direct track, in contact with the sediment (Gatesy, 2003); 2) the inflexion point (steep walls, Manning, 1999); 3) two opposite displacement rims; and 4) maximum deformation zone (MDZ, Manning, 2008). In tracks with no major complex deformation occurring, measuring the direct track will be closest to the size and shape of the track maker's foot, useful for palaeobiological interpretations such as speed, gait, and track maker identity (Falkingham, 2016). The best illustrative and thoroughly descriptive method to trace the overall morphology of a track is found in Marty (2008), in which a "continuous" line marks the exterior track outline, defined by the intersection of the track wall with the tracked surface. A "dotted" line marks the margin of displacement rims and it is located externally to the "continuous" line. Another "dotted" line is internally placed with respect to the "continuous" line and it marks the internal track outline (direct track, Gatesy, 2003). With this representation, sediment related features are well documented, retaining that kind of information relative to the foot-sediment interaction that would have been otherwise lost.

Proactive approaches that characterize modern ichnology, setting a huge difference with the previous track descriptions and reports, are the quantitative analysis of track parameters (measurements) and the quantification of track morphology. The first relates all possible measurements into morphometric ratios; the second objectively describes shapes. It has been already explained that the analyses of track morphology started as qualitative descriptions, presenting non-metrical ichnological parameters (Moratalla et al., 1988; Rasskin-Gutman et al., 1997) which are anatomical-autopodial traits the significance of which is based on their presence/absence, although their absence does not imply an actual lack of this feature in the animal's foot (Carrano and Wilson, 2001). These non-metrical characters usually refer to the presence/absence of claw marks, phalangeal pads, skin impressions and on the description of shapes, such as that of the heel pad (elongated, oval, rounded, “U”-”V” shaped) and the observable proportions of the track (wide, long, narrow, blunt). These sort of descriptions strongly depend on a subjective expertise and, in addition, they are difficult to compare and sometimes ambiguous among various researchers.

Moratalla et al. (1988) proposed metrical parameters (see Fig.3.4A), which are linear and angular measurements (track length and width, digit length and width, interdigital angles, interdigital distances) and introduced the concept of morphometric ratios, such as relating the track length to the track width, in order to quantitatively discriminate between theropods and ornithopods. The potential of this approach resides in possibility of looking to the range and distribution of these measurements (variables) individually or how any two variables relate to each other. This simple ratio marks the passage from a qualitative to a quantitative approach towards the description of track morphologies. The use of bivariate, factor and discriminate analysis and therefore the use of statistical methods to describe variability among observed, correlated variables in terms of a potentially lower number of unobserved variables called factors. The Factor Analysis undertaken in Moratalla et al., (1988) assembles the different parameters within abstract units (factors) correlating with a determinate informative degree, meaning that parameters such as width, length, angles can be highly, moderately or poorly significant. The Discriminate Analysis makes an estimation of parameters weighting in order to discriminate the sample into the two dinosaur groups (i.e. ornithopods and theropods) and in the bivariate analyses the sample distribution arranges according to the morphometrical indexes.

The statistical approach allows understanding the degree of significance of a determinate feature and therefore its implication according to its susceptibility to the animal’s locomotion and behavior and to the substrate nature. For instance, interdigital angles have been profusely demonstrated to be a very variable parameter, hard to interpret unequivocally (Olsen and Baird, 1986; Mortalla et al., 1988; Lockley, 2009) and hence should not be used as a diagnostic trait in ichnotaxonomy. This new method motivated various authors to find new measurements in order to evaluate, distribute and organize track morphologies. The introduction of morphometric ratios allows ichnotaxonomical revisions, potential decreasing ichnotaxonomical diversity, gathering together the morphological variations thanks to the

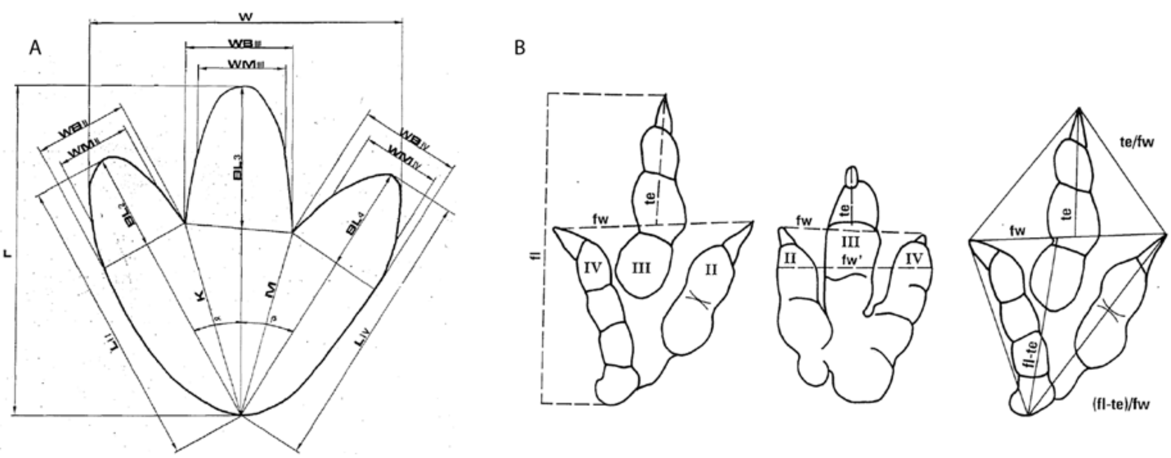



Figure 3.4. Morphometric ratios after Moratalla et al., 1988 (A) and Weems 1992 (B).

use of standard deviation (range of variability) and assembling shapes into numeric ranges with a more parsimonious approach. Weems (1992) introduction of the anterior triangle method for tridactyl tracks numerically describes the development of digit III (the height of the triangle) with respect to the width of the track (the base of the triangle), providing the index of mesaxony and considered as an important and intrinsic indicator of inter-taxon morphological variation (Fig.3.4B), a potential indicator of evolutionary relationships, ontogeny and allometry (i.e. GAE plexus in Lockley, 2009).
The next achievement in ichnological analyses is found in the quantification of the track morphological variability through geometric morphometric and landmarks-based approaches. This method analyses morphology by studying specific points placed on the track outline at strategic and shape-conservative positions. This method has been proved useful in ichnological studies (e.g. Rasskin-Gutman et al. 1997; Klein and Haubold 2003; Rodrigues and Santos 2004; Belvedere 2008; Clark and Brett-Surman 2008; Castanera et al., 2015; Lallensack et al., 2016) and it has been suggested that for tridactyl footprints, landmarks can be placed at the base of the heel, the tips of the three digits, and the two interdigital minima or hypeces (Rasskin-Gutman et al. 1997). The position of the landmarks has to be chosen carefully, avoiding highly variable zones in the track outline. In fact, high variability is usually recorded in the lateral hypex, the entire posterior margin of the heel region, and in the medial hypex (Lallensack et al., 2016); Castanera et al. (2015) have chose not to use the hypices as landmarks due to the possible variations in these points as a consequence of different substrate–foot interactions associated with the kinematics of walking (Manning 2004; Milàn 2006; Falkingham et al. 2009; Avanzini et al. 2012; Razzolini et al. 2014). If these variable points are included in the landmark analysis, the landmark shows high variance (Belvedere, 2008). Once the landmarks are placed, it is possible to create a mean shape through statistical analysis such as GPA (Generalized procrustes analyses, Lallensack et al., 2016) or TPS (thin plate spline, Castanera et al., 2015) that provides a best fit between the footprint shapes by translating, rotating and scaling, eliminating any information but the mere shape of the footprints. Geometric morphometric analysis is an excellent tool for creating an average shape and for quantifying morphological differences. The shortcoming of this technique is that it is applicable only in very well preserved and defined tracks and mostly, it is based on two-dimensional outlines, which is a simplification of the reality. Considering a track as a two-dimensional shape is very limited, because it excludes rheological and biomechanical factors from the morphological analysis.

***Three-dimensional data collection***

A step forward in quantitative ichnology is to use tools that capture the data in all three-dimensions. Ishigaki and Fujishaki (1989) noted the shortcomings of outline drawings and sketching based on the observation of dinosaur tracks because these are two-dimensional representations that do not point out the margins of the track with respect to the bedding plane, the depth, the inner relief and topography of the track. The Moiré topography method (see chapter 48 in Gillette and Lockley, 1989 for methodology) is the precursor of the photogrammetric method used in the articles of this thesis. It creates contour-like lines which spacing depends on the slope of the grating used to create lines and the distance of three different dimensions (distance between the grating and the track; distance between the camera and the grating; distance between the light and the camera, fig.48.4 in Ishigaki and Fujishaki, 1989). With the image that forms, it is possible to objectively create the outline of the profile of the inner relief of the track and quantify the depth of the track.

In the last few years GPS, close-range photogrammetry, and laser scanning, used also in other research fields (i.e. cultural heritage site documentation), provided new tools to easily analyze and measure tracks and trackways (Matthews and Breithaupt, 2001; Breithaupt et al., 2004; Petti et al., 2008; Bates et al., 2008; Remondino et al., 2009; Belvedere and Mietto, 2010, Falkingham 2012; Mallison and Wings, 2014). Advances in the field of laser technology have changed the face of three-dimensional data collection (Breithaupt et al., 2004; Chapman et al., 2012), especially in the build of topographic maps of particular tracksites, increasing the quantity of information due to the possibility of scanning inaccessible and vertical tracksites, such is the case of the Fumanya sauropod tracksite (Bates et al., 2008). The conservation and documentation of such sites requires new techniques to prevent the permanent loss of what is in many cases a finite natural resource. The term LiDAR (Light Detection And Range) first appeared in geoscience literature in the 1960s (Schuster 1970 and references therein) in relation to atmospheric aerosol studies. LiDAR (also known as ladar, optical radar, or laser radar) has grown in popularity since the 1960s and is now used in a variety of scientific, law enforcement, surveying, and construction applications (Bellian et al., 2005). LiDAR is by no means the first method that has been used to gather quantitative stratigraphic data. The use of laser scanners is especially useful for the protection of those fossil sites susceptible to weathering, erosion and destruction by other means such as quarrying or highway constructions (Marty, 2008). The potential to integrate LiDAR and photographic data (Breithaupt et al., 2004) and collect high-resolution quantitative data from footprint sites through remote surveying suggests that the method may provide a means to merge conservation with scientific exploration of heritage sites.

The LiDAR scanner has a range of 800 m, 80º vertical and 360º horizontal fields of view. The scanner emits a pulse beam of light that travels to a remote target; it bounces off that target and returns to the detector. The two-way travel time is divided in half and multiplied by the speed of light to calculate Z distance, while X and Y positions are calculated on the basis of the laser deflecting mirrors when the laser pulse leaves the scanner (Bellian et al., 2005; Bates et al., 2008). The high-resolution Digital Outcrop Models (DOM) of the tracksites is a powerful visualization tool and it functions as 3-D interactive database that preserve information about the site (Marty, 2008; Bates eta al., 2008; Castanera et al., 2013; Razzolini et al., 2014; Razzolini et al., 2016a) and would serve to evaluate the erosion degree. Also, this kind of models have been built as a tool to record the rate at which the physical specimens are being lost (Breithaupt and Matthews, 2001; Breithaupt et al., 2001; Breithaupt et al., 2004; Matthews et al., 2005; Matthews et al., 2006; Marty, 2008; Adams et al., 2010; Farlow et al., 2010). Laser scans are of great utility in the fast registration of three-dimensional data from huge surfaces that would need days of human work to be mapped. Nevertheless, the bigger the surface, the lesser detail there will be for the visualization of track geometry. However, in the majority of cases only the outline of a track is observed, with little depth perspective present (see Fig.3.5). Photo-texturing the model produces a much higher quality image in which the geometry of single tracks can be clearly seen (Bates et al., 2008).

An alternative to laser scans is the photogrammetry technique. Photogrammetry is the science of obtaining reliable measurements from photographs (images), i.e. it turns 2-D image data into 3-D information like digital models (Petti et al., 2008). Photogrammetry, or more strictly speaking stereophotogrammetry, is the derivation of 3-D information on points, lines and areas on objects or terrain from photographic image sequences (Mallison and Wings, 2014). It is a non-invasive technique that allows a three-dimensional preservation of a track, trackway and tracksite in a simple file format that can be shared and compared among all ichnologists. Most importantly, because a good primary photogrammetric data set does not weather and degrade with time, primary measurements can still be made from it long after the original surface is degraded (Mattews et al., 2016). In photogrammetry photographs taken with a digital camera are aligned, camera positions are calculated, and a point cloud is produced. Using multiple data collecting methods for the documentation of a tracksite has been shown to have extensive merits. Incorporating other documentation methods (e.g., LiDAR and

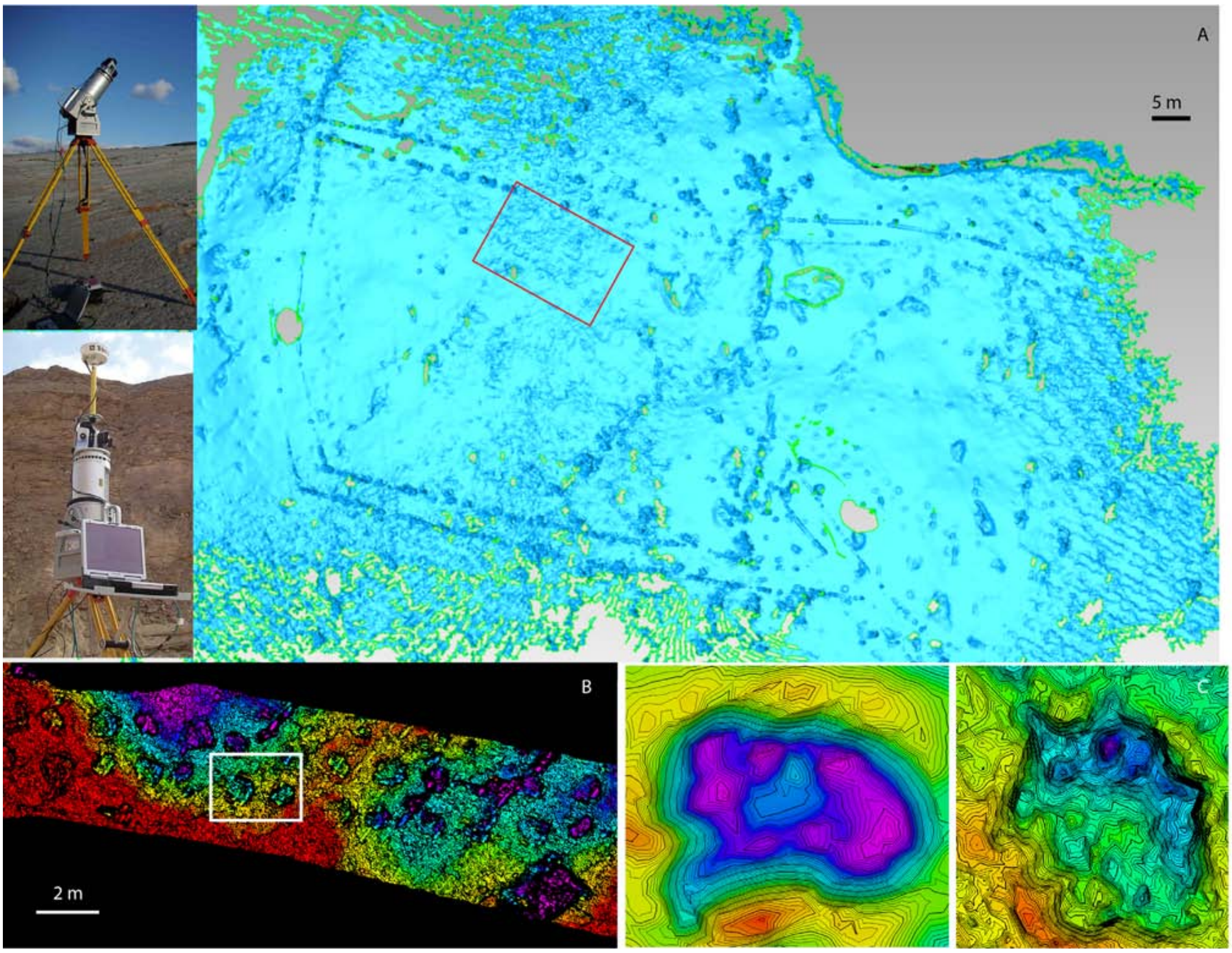



Figure 3.5. Laser scanner of the 40,000 m$^2$ Pedreira do Galinha quarry (Santos et al., 2009) in the Lusitanian basin (Portugal). Red square indicate a segment of one sauropod trackway (A). Detail of the fragment of the sauropod trackway depth 3-D map (B). Detail of a manus-pes set extrapolated from the laser scanner of the trackway, the resolution is lost when analysing track morphologies through laser scanner (C).

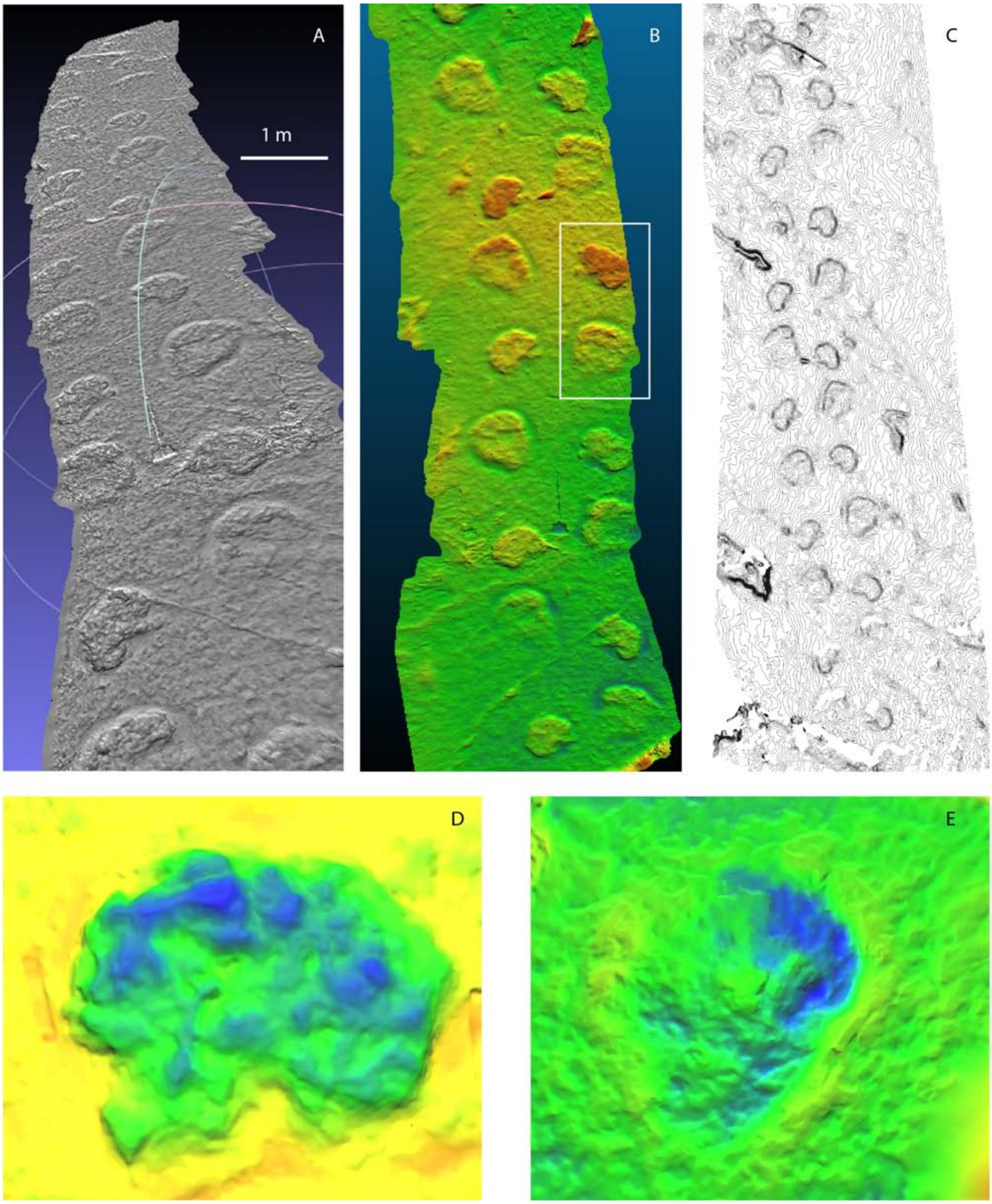
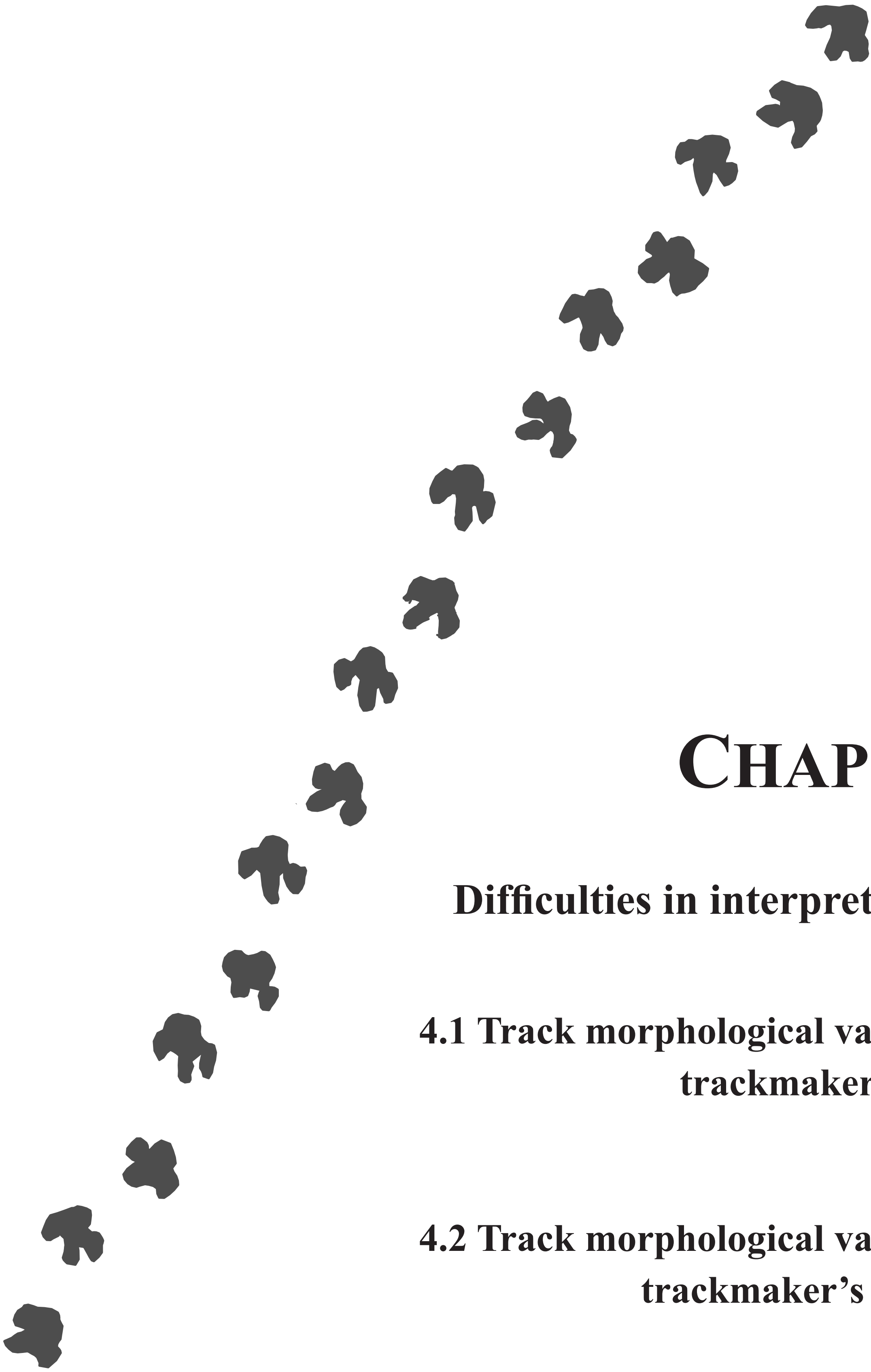



Figure 3.6. Photogrammetric analysis of the same sauropod trackway of figure 3.5 from the Pedreira do Galinha quarry. Details of the fragment of sauropod trackway after three-dimensional model is created in Agisoft Photoscan through photogrammetric analysis and visualization in freesoftware Meshlab (A), depth map in Cloudcompare (B) and contour lines in paraview (C). The manus and pes set show more morphological details through Close Range photogrammetric analysis (D).

traditional ichnological data collection, such as maps and tracings) with the photogrammetric data increases the value of the data set (Breithaupt and Matthews, 2001; Breithaupt et al., 2004; Matthews et al., 2006; Marty et al., 2010). Photogrammetric imaging was selected over field laser scanning as it was the most expedient and in terms of convenience, affordability, and time efficiency (Petti et al., 2008).
The use of photogrammetry in ichnology is not only a keep in step with technology fashion, but rather a *sine qua non conditio* for providing peers with objective tools that can be easily repeated and tested. Moreover, other researchers can follow step-by-step the whole methodological procedure, reducing the risk of multi-interpretation of one morphology for the sake of the parsimonious principle. Conversely, if only an outline of the track is offered, results depend on how the researcher took the measurements, which, although explained in material and methods section, is not always repeatable.
Up-to-date, there are at least 40 computer programs available that can create photogrammetric models, some of which are freeware software. The actual process of how photogrammetry works is explained in detail in Mallison and Wings (2014). Briefly, the creation of the 3-D model starts with the program that uses algorithms to find specific points on each image; these points from all images are compared with each other in order to find corresponding imaging parts (correspondence problem) through another algorithm that calculates the fundamental matrix that mathematically defines how the images parts are related. Next, these points are used to create a high-density point cloud that can be turned into a polygon mesh, which consists of triangles that connect the points. Color information can be included by directly taking the color of the various points from the photographs or by separately calculating a texture for the mesh.In summary, some of the most important points to be taken into account in order to assure the achievement of a high-resolution three-dimensional model are based on how a simple photograph is taken, since the quality of the pictures is key for the quality of the final model (Fig.3.6). The recently published "Dinosaur tracks: the next steps" book offers in chapter 2 an important contribution on the importance of the application of close-range photogrammetry for ichnology (Matthews et al., 2016). Some of the greatest advantages of using photogrammetry in vertebrate ichnology are the fact that track measurements (e.g., length, width, and depth), trackway parameters, morphology and overall geometry, substrate deformation and many other features can be derived from a well-constructed 3-D data set. Moreover, the 3-D surface derived from photogrammetry can be very precise and have submillimeter resolution and high morphometric fidelity. Photogrammetric ichnology is fundamental for objective morphological correlations and especially understanding the meaning of the ichnomorphologic characters, track formation, taphonomic, ontogenetic and behavioral implications.



# CHAPTER 4

## Difficulties in interpreting tracks

### 4.1 Track morphological variation and trackmaker's anatomy

### 4.2 Track morphological variation and trackmaker's locomotion

### 4.3 Track morphological variation and substrate

# CHAPTER 4. DIFFICULTIES IN INTERPRETING TRACKS

## 4.1 Track morphological variation and trackmaker's anatomy

Inferences on foot anatomy from fossil tracks are based on the definition of foot proportions and they are inevitably link to the search of the possible trackmaker. Extrapolating foot anatomy of the trackmaker from track morphology is quite utopian when all the variables concurring in the track formation and determination of the shape found in the fossil record are taken into account (Falkingham, 2014). Only basic aspects of manual and pedal orientation can be utilized to place generalized constraints on the locomotor characteristics of higher-level dinosaur taxa (e.g., Farlow et al., 1989; Gatesy et al., 1999). It is also true that a careful analysis of visible features preserved in the track can be useful in tracing the approach to be used in specific context of track analysis and identify those parameters that are more strongly concurring in the final track geometry (Fig.4.1).

Milàn (2006) in his experiments with living animals noticed that when placed on firm substrate, digit II of the emu was progressively less impressed and the interpad space between the proximal digital pad of digit II and the metatarsal pad often left no impression in the sand, indicating that the proximal part of digit II is held higher than in digits III and IV, resulting in didactyl morphology produced by tridactyl pes.

Baird's (1957, p.469) recommendation that “[t]he characters most diagnostic for the classification of footprints as such, as well as most useful for comparison with skeletal remains, are those which reflect the bony structure of the foot” is ideally correct. Some anatomical details, such as the number and relative positionof digits, digital pad impressions, and claw marks, if preserved, allow the derivation of thenumber and arrangement of phalanges (phalangeal formula). This information is essential in establishing the identity of the maker of a track. Thulborn (1990) and Lockley (1998) suggestion of "matching up" dinosaur footprint against trackmaker foot and its pedal osteology has a naive view when compared to the range of possibilities according to the stratigraphical record and skeleton finds, although it is sometimes used successfully (Romano et al., 2015; Romano and Citton, 2016). Osteometric ratios, the comparison of values of shape parameters estimated from footprints with values such as phalangeal ratios and free length of digits measured from skeletal material, carried out in Farlow and Lockley (1993) could be estimated for tracks with clear phalangeal nodes and they revealed a potential in the discrimination between early Mesozoic theropod tracks and more prosauropod-like or ornitisquian-like tracks. Olsen (1995) stated that ichnotaxa can be assigned to biological taxa only if they have shared derived characters of those taxa, with emphasis on phalangeal pad formula. Anyhow, the lack of features does not mean that the trackmaker physically and biologically lack this particular feature, although this is usually what transpires from descriptions of many tridactyl tracks, which diagnostic features are the lack of: phalangeal formula, digital pads, claw marks, "heel" pad. Lockley (1998)

raised the complex problem of the reconstruction of the fleshy part of the trackmaker foot by showing that predicting a footprint from the foot osteology is not straightforward. For instance, rhinoceros and elephants foot osteology indicate that they are digitigrade or unguligrade animals, but without the large fleshy pad available, tracks cannot be inferred correctly. For this reason Lockley (1998) proposed two methods for making correlation between foot anatomy (trackmaker) and foot morphology: 1) filling the gaps by reconstruction of fleshy parts; 2) matching tracks with trackmakers of similar size and geological age. Of course this approach is even more complicated when both small and large tracks are present in the same tracksite, meaning that the probabilities that the different sizes are due to ontogenetic growth or taxonomic diversity have to be thoroughly explored (Razzolini et al., 2016b; Razzolini et al., submitted), especially when different taxa are known to be present as skeletal record (Carrano and Wilson, 2001; Tithonian-Berriasian transition: Castanera et al., 2013).
Carrano and Wilson (2001) proposed a synapomorphic-based approach for the trackmaker identification by compiling a set of osteological synapomorphies that could be extrapolated from tracks and trackways. They also formalized and characterized phenetic correlation, which relies on the concept of similarity/dissimilarity between the track and the foot skeleton and coincidence correlation, which is based on stratigraphical and geographical information on osteological remains. Shortcoming of the former are that any variation in the track morphology is linked to a taxonomic variation, that convergences and parallelisms are not distinguished from homologies and that relationship between

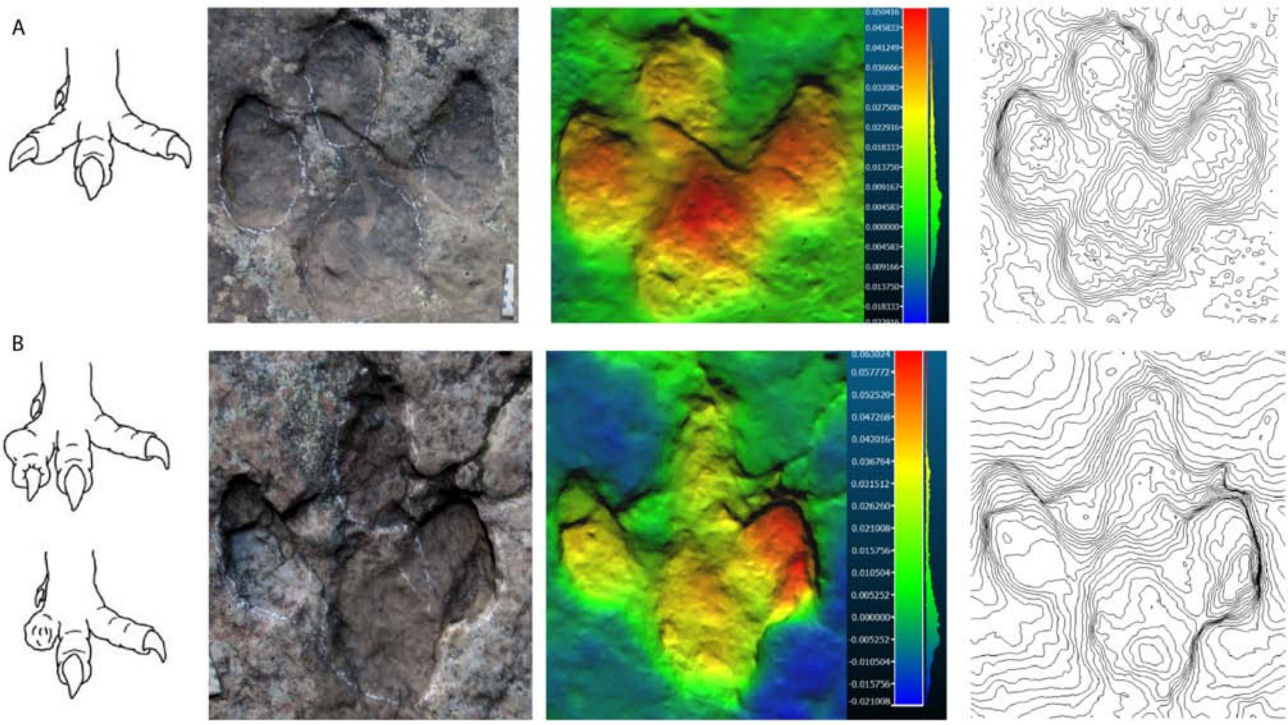



Figure 4.1. Example of two right-left tracks from the same trackway displaying morphological variation due to injury in digit II of left tracks. A) Right track with the normal ornithopod morphology with a homogeneous distribution of weight as shown by depth map of the three-dimensional model. B) Left track with an abnormal/pathological morphology showing a different disposition of digit II. Sketches of pes reconstructions modified from McCrea et al. (2015). Right and left tracks from Razzolini et al. (2016a).

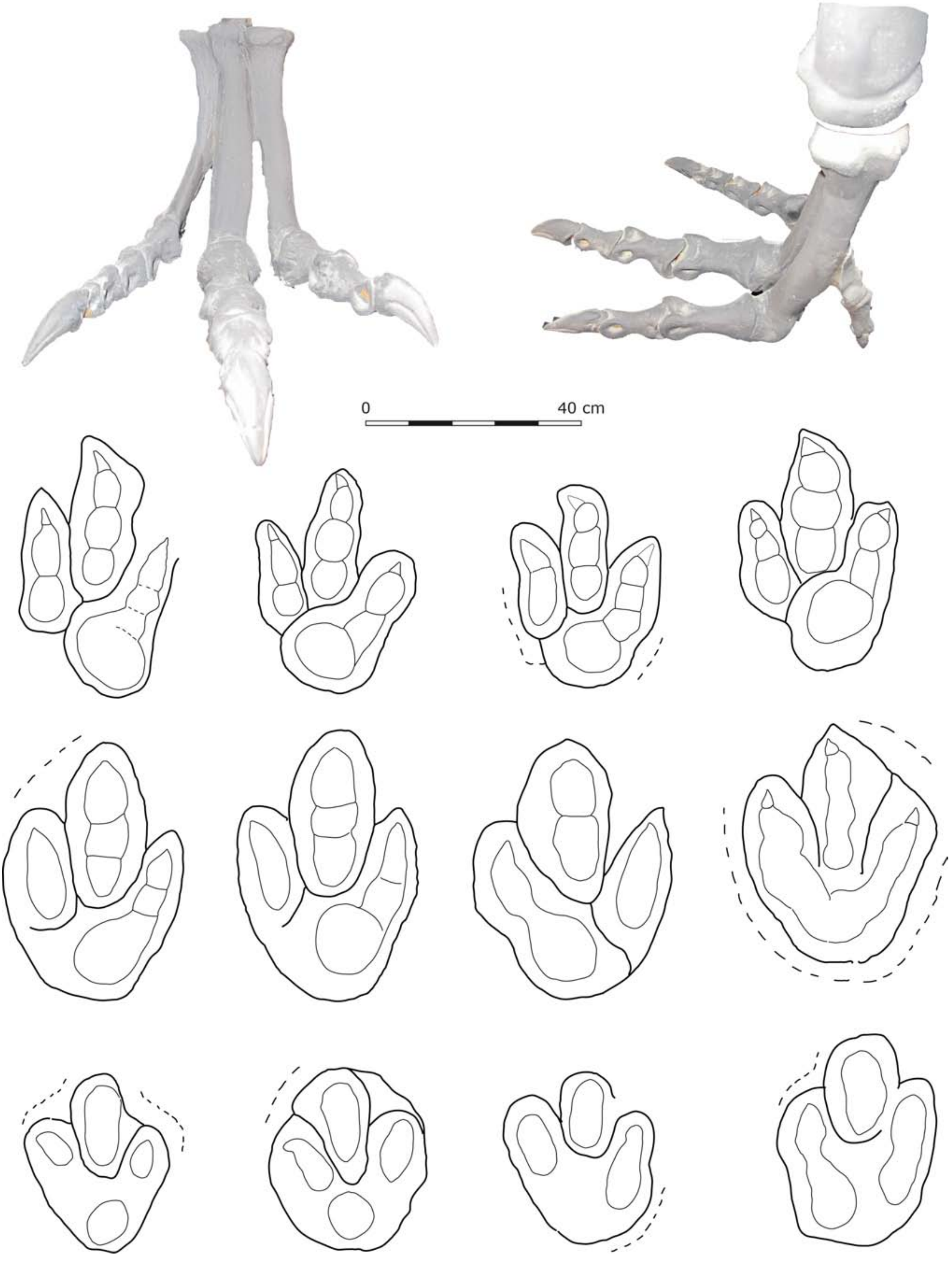



Figure 4.2. Track morphological variation and foot anatomy. Mounted pes of *Allosaurus* in the Museo Nacional de Historia Natural e da Ciencia (MUNAHC, Lisbon, Portugal) as an example of possible osteological correlation to *Megalosauripus transjurani* tracks (Razzolini et al., submitted) presented with some of the preservation variants observed. Example of correlation matching tracks with trackmakers of similar size and geological age (Lockley, 1998) and synapomorphic-based approach (Carrano and Wilson, 2001) with the observation of phalangeal pads disposition in both track and pes.

track-trackmaker is based only on primary features. The limitation of the latter is that it can only agree with currently established taxa abundances and distributions and moreover morphologically similar, geographically and geologically coincident animals cannot be distinguished using this type of correlation. Different tracks can represent the same taxa under different conditions as well as tracks belonging to the same ichnotaxon may represent different taxa (Farlow and Chapman, 1997; Farlow et al., 2000). By expanding Olsen (1995) statement, phylogenetic-based approach provide the best and primary mean of linking track and trackmaker (Carrano and Wilson, 2001). However, the biggest limitation of this approach (Fig.4.2) is the restriction of the synapomorphies only for those portions of the skeleton contacting the substrate (appendicular and pedal). Nevertheless, it is also suggested that the parameters used to describe tridactyl dinosaur footprints can often be used to provide a minimum estimate of the number of trackmaker taxa within an ichnofauna and that similarity in footprint shape is useful but not always a trustworthy indicator of phylogenetic relationships of trackmakers (Farlow et al.,2013, 2014). Moreover, the extent to which the makers of dinosaur footprints can be identified depends on the extent to which their foot skeletons can be told apart. Farlow et al. (2013) showed that methods such as principal component analysis and canonical variable analysis can be useful in discerning ground birds, non-avian theropod dinosaurs and ornithischians. They indicated that the ability to interpret few distinctive phalanges, digit lengths and other metrical parameter may be sufficient to allow a systematic interpretation between tracks and trackmakers. On the other hand, the most striking result is the great similarity in overall foot shape among very large theropods, regardless of their relationships. Farlow (2001) stated that three different taxa of large theropods (ceratosaurs, allosaurs and tryrannosaurs) could not be distinguished on the pedal phalangeal skeletons proportions, but the metatarsal lengths (Farlow et al., 2013) give more insights in the distinction. In fact, different metatarsal lengths would be reflected in the tracks as different projection of the length and positioning of the digits. Most recently, a new method based on a numerical scale that quantifies the quality of the preservation of dinosaur footprints has been proposed by Belvedere and Farlow (2016). The authors precise that by preservation they intend "the record of morphological features that can be related to the anatomy of the trackmaker's autopodium", restricting the application to morphological and taxonomical purposes only, independently from what caused these features (rheological-undertrack, biomechanical-deep tracks). High-score tracks (3: Table 6.1 in Belvedere and Farlow, 2016) can and should be used for making reliable identifications on the trackmaker.

## 4.2 Track morphological variation and trackmaker's locomotion

Incompetent substrates (that provide little or no resistance, soft sediment) usually preserve deep tracks (i.e. Kuban, 1989) which, according to Gatesy (2003), preserve two major features per digit: one produced on the way in and one produced on the way out. The digits enter and move forward when indenting the sediment. This forward movement into the sediment is the main difference with respect to the simple upward-downward indenting punch movement in sediment-controlled experiments (Allen, 1997), implying that limb (toes, digits, foot) dynamics inside the sediment can unravel much more information, although it is a highly complex system to deal with (Gatesy and Ellis, 2013; Falkingham and Gatesy, 2014). Up to date, the laboratory controlled experiments still excludes extraneous confounding factors such as time averaging, lateral sediment heterogeneity and post-formational factors (Falkingham et al., 2014). Limb dynamics (motions and forces) are known to play an important role in determining the morphology, including depth, of tracks.

***Locomotion and speed estimations from tracks***

While for understanding track formation, the study of this process should not be restricted to surface tracks but rather expanded to subsurface tracks (undertracks and transmitted tracks) with laboratory controlled experiments in order to gather all the properties of soil mechanics that oppose to the indention of the foot, speed estimations should be restricted to surface tracks and possibly well preserved true tracks because of the over/underestimations resulting from the application of this empirical formula. The speed at which a dinosaur was traveling is an important variable to assess if the potential of the 3-D preservation of tracks is to be fully utilized (Manning, 2008). The speed at which an animal travels directly affects the time a foot remains on the ground (duty factor) and the intensity and distribution of the load transmitted in that given time. Extrapolating the duty factor from fossil tracks is far too complicated and only a 3-D approach and track subsurface deformation could possibly shed light on this parameter.

Extrapolate locomotion information from tracks and trackways can offer only small inferences on gait and speed estimations and the vast majority of the biomechanical information is obtained from osteology and miology comparisons. Gatesy (1995) proposed six different categories for locomotor analysis: 1) Skeletal anatomy: the most traditional approach according to which data are collected from skeletal material and consists of qualitative and quantitative descriptions of bone shapes. 2) Limb posture: degree to which the limb is abducted, with limb abduction being the smallest angle between the femur or humerus and the sagittal plane of the body. In dinosaurs it can be estimated from skeletal remains and from the width of the trackways. 3) Limb-segment orientation: description of the position of individual limb elements during standing or at a single time in the stride cycle. 4) Limb kinematics: change of limb segment orientation through time. Data should reveal how the limb elements are actually moved during locomotion to propel and support the animal. 5) Muscular anatomy: information acquired in living animals by dissection and histology. 6) Neuromuscular control: analysis that addresses the control of limb muscles by the nervous system during locomotion. Of course this component is the most difficult to reconstruct, but it places important questions such as what muscles are generating the forces that control and mediate limb movement, how do various muscle interact and contribute to limb movement and are some muscles less important to locomotor behavior. From this categorization, it is clear that from tracks only limb posture and limb-segment orientation can be deduced, while the real interest, limb kinematics, can be only extrapolated by observing living animals. It has been remarked that estimating speed from footprints has a wide margin of error and footprints tell us little about how the whole limb or body moved, because of redundancy within the limb skeleton (Hutchinson and Gatesy, 2006). Anyhow, an enormous step-forward in the reconstruction of dinosaur locomotion was accomplished when Alexander (1976) published his (dimensionless) speed formula, which, based on the fact that the faster an animal moves, the longer its stride length, related the speed with the stride length and the body size of the animal, by observing living animals (for dinosaurs: v= 0.25g0.5*SL1.67*h-1.17). In ichnology, a stride length is the distance between two footprints from the same size (i.e. two right/left footprints in bipeds, two right/left pes/manus in quadrupeds), or, as explained in Thulborn (1990) the distance between corresponding points in two successive footprints of the same foot. Biomechanically, a stride is the distance covered by the animal during one complete cycle of limb movements (Thulborn, 1990), comprehending a stance phase and a swing phase (Hutchinson and Gatesy, 2006). Measuring the stride length is not complicated if the methodology is well defined and repeatability is confirmed.

Alexander's formula used a dimensionless number (Froude number) usually applied for continuum mechanics, which is the ratio between speed and stride length. Moreover he applied the Froude number in order to develop considerations based on physical (dynamic) similarity concept (see also Alexander, 1983, 1985; Vila et al., 2013). That is to say that Alexander's formula can predict that the movements of animals of geometrically similar forms (but of different sizes) will be geometrically similar only when they move with the same Froude number. Alexander's method allowed to display of at least three dinosaur gaits according to the stride length-hip height ratio called relative stride length (SL/h): walk (SL/h<2), trot (2>SL/h<2.9) and run (SL/h>2.9).

The estimation of the hip height is a very delicate issue. Bakker (1975) defined the relative hindlimb length as the sum of lengths of femur-tibia-tarsus and longest metatarsal and divided by the cube root of body mass. Alexander (1976) obtained a measurement of the hip height from the footprint length. The footprint length should be therefore 0.25*h (hip height measured from the ground) or else, the hip height measuring four times the footprint length (h=4*FL) because he considered that the metatarso-phalangeal joint would have rested on the ground, while the tarso-metatarsal one would have not. Thulborn (1981) and Thulborn (1982, 1984, 1990) proposed a series of insights on the definition and calculations of the hip height parameter. He proposed that the hip height should be the result of the combined lengths of femur, tibia and longest metatarsus plus a 5-9% increment to account for ankle bones and soft tissues at knee, ankle and sole. Moreover, Thulborn (1990) suggested a variety of methods to derive this parameter, such as geometry (trigonometry, which requires untestable assumptions on the angle of the gait of the dinosaur), morphometric ratios (derived from cursory analysis of osteometric data) and allometric equations (because the length of metatarsus is correlated to length of femur tibia and metatarsus) in which it is imperative the measurement of skeletal remains. Lockley et al. (1983) suggested that hindlimb/foot ratios and stride lengths estimates based on comparison with other animals should be based on comparisons with actual measurements of the footprint of the trackmaker (e.g. hadrosaur for Lockley et al., 1983).

The wide applicability of Alexander's method to all dinosaurs taxa, have encouraged many authors to use (Thulborn, 1981; Farlow, 1981; Farlow et al., 2000) and modify (Coombs, 1978; Demathieu, 1986; Weems, 2006) this formula to add information to trackways and highlight possible shortcomings of this empirical formula.

Coombs (1978) have offered a theoretical review of all the biomechanical constraints that might act during locomotion, proposing a system of four categories of running abilities, cursorial, subcursorial, graviportal and mediportal, to predict dinosaur running potential. The morphological correlates to cursorial habits included relatively long limbs, short limbs, hinge-like joints, digitigrade/unguligrade stance, symmetrical feet and characteristic of arrangement/presence of digits. Coombs (1978) underscored that considering the hip height (acetabular height) as four times the length of the footprint, as proposed in Alexander (1976), might underestimate the acetabular height of long-limbed and short-footed taxa, restricting the use of Alexander's formula only to estimate the speed at which a particular trackway was made and not to calculate top running speed of a dinosaur since the majority of morphological clues are not extrapolated from tracks but from bones. Farlow (1981) noticed that Alexander's formula gave rather low speed values and he reported a new Lower Cretaceous tracksite from Texas, in which dinosaur speeds achieved 12 m/s. Some authors have suggested that the movement of the limbs is similar to that of a pendulum (Hildebran 1974). Demathieu (1986) have developed the pendulum theory which, applied to the movement of limbs while walking, only furnishes low speeds where the muscular effort necessitated by the movement of the limb is minimal. It shows that the pendular speeds of animals, of moderate or large size, are situated within a relatively small range of variation, but it did not account for the shape and size of the body and for the different modes of alternation of limb during walk. Christian et al. (1999) have shown that estimations of speed using the natural pendulum frequency for stride lengths estimations seem less reliable for dinosaurs than speed estimates which are based on relations among stride length, hip heights, and speed (Alexander 1976) and calculations on bone strength (Alexander, 1985). Other authors (Rainforth and Mazella, 2006) graphed various combinations of skeletal measurements and ratios in order to determine if there was a single ratio of hip height: footprint length ratio and concluded that there is no simple relationship between hip height and footprint lenght and that metatarsal III is not a good indicator of footprint length (*contra* Alexander, 1976).

Henderson (2003) used sophisticated computer simulations to test Alexander's method of estimation of the hip height as the result of 4*FL (footprint length) and he added other morphometric methods that vary according to the size of the animal and the taxonomic group of the inferred trackmaker and allometric methods with size and taxon specific coefficients and exponents (Thulborn, 1989). The results shown that when Henderson's coefficient and exponents derived through morphometric and allometric formulae were applied to the computer models, the hip height suffered up to 84% of overestimation, resulting in the underestimation of the computed velocities. It was demonstrated that even with the finest technology and methodology available, the speed and hip height estimations presented in Alexander (1976) account for an error of the 10-20%, considered “not critical” for inferences from trackways.

Nevertheless, Manning (2008) pointed out that the assumption that a dinosaurs foot has a constant relationship to hip height (h) might be wrong because the h/FL ratio is unlikely to account for variation in geometry between dinosaur taxa (also noticed in Thulborn, 1990), it would have changed during growth (function of allometry, also commented in Thulborn, 1990) and mostly because this ratio assumes that the footprint length represents the actual animal’s foot length. The latter is an assumption that is tighten to considering a track as a substrate deformation and therefore only rarely representative of the pes of the trackmaker. When Manning (2004) defined the maximum deformation zone of a track (MDZ), he noticed also that in undertracks, the hip height estimation would be too high and the speed too low and conversely, if tracks are emplaced in a very firm substrate (with a minimum MDZ), the hip height would probably be underestimated causing an overestimation of the speed.

However, Alexander (2006) stated that the lack of living specimens and well preserved soft parts obliges to depend on doubtful assumptions and therefore, quantitative conclusions about dinosaurs locomotion must be interpreted very cautiously.

***Foot movement and experiments with living animals***

Thulborn and Wade (1989) noticed that a footprint may be always incomplete partly due to the mechanical response of the substrate properties to the indentation of the foot and partly due to the movement of the pes in the subsurface levels. They observed the morphological effects on tracks by deconstructing the interaction of the foot of a moving animal with the substrate into three phases called touch-down (T-phase), weight-bearing (W-phase) and kick-off (K-phase). In fossil footprints, these phases are not always appreciable, although some authors undertook vertical cross-sections on fossil slabs and could pinpoint the three phases (Avanzini, 1998) noticing furthermore that a progressive shift of the center of gravity is recorded by different functions of the digits in the different movement phases. Digit IV has a dominant function between the T-phase and the beginning of the W-phase; digit II is dominant during the T-phase and the whole W-phase; digit III is dominant during the end of W-phase and the whole K-phase and during propelling, it penetrates deeper.

Because of the necessity to cut fossil tracks in order to observe the different dynamic phases of the foot indenting the substrate, neoichnological experiments with living animals are pivotal to isolate, weight and account with the kinematic variable in analysing fossil tracks. William Buckland was the first to conduct a neoichnological experiment when he made walk tortoises and crocodiles on a soft, wet sand and soft clay in 1828 in order to address problematic of this experimental analysis, unveil the origin of track and compare results with fossil tracks. As early as in 1976, when the first biomechanical approach toward the study of fossil tracks was developed by Professor Robert McNeill Alexander, the observation of living animals played an essential role to extrapolate all sort of information extendable also to dinosaurs dynamics according to the principle of dynamic similarity. Neoichnological experiments are necessary in order to watch how the limb moves placing the foot in the sediment, how the foot is placed (entrance and exit, Gatesy et al., 1999) in the mud, sand, clay substrate, how the gait is affected by the limb movement and foot placement. Many experiments have been taken with salamanders and reptiles (McKee, 1944, 1947; Peabody, 1959; Brand, 1996) for comparison with Permo-Triassic tracksites, while for dinosaurs comparison (and especially small-medium bipedal dinosaurs) ratite birds such as *Rhea americana* (Padian and Olsen, 1989), *Struthio camelus* (Farlow, 1989) and *Dromaius novaehollandiae* (Milàn, 2003, 2006; Milàn and Bromely, 2006, 2008), have been widely used. Experimentation and functional morphology is based on the concept that "if the bones and articulations of two animals show no significant functional differences and their footprints match in all aspects related to kinematics of the limbs, the inference that those kinematics are fundamentally similar is strong" (Padian and Olsen, 1989). These authors carefully analysed the phalangeal pad configuration in the *Rhea* foot, which is of 3-4-5 phalangeal pads respectively for digits II-III-IV and noticed instead that the tracks did not show such configuration and usually due to the fact that pads cover the interphalangeal joints (also more swollen and visible in the track morphology) rather than the phalanges themselves. Experiments with emus have shown that the consistency of the substrate exercises a strong control on the track morphology and the amount of anatomical details preserved within it. Moreover, Milàn (2006) documented different morphologies of emu tracks produced with behavioral changing (e.g. tarsal-metatarsal impression when feeding on seeds) which were also observed in the fossil record (Kuban, 1989; Pérez-Lorente, 1993; Romano and Citton, 2016) and see Fig.4.3

The main difficulty of live experiments is the lack of control and repeatability because the animal is always unpredictable. Moreover, because all the primary factors that determine track morphology, such as the anatomy, the substrate consistency and more importantly, the foot dynamics (locomotor kinematics) are included simultaneously during the experiments, extrapolating which of these variables is the most biasing one is simply overwhelming.

### *Computer simulations for limb and foot kinematics*

The greatest advantage in computer simulations is that it is possible to isolate the effect of the variables of substrate (Falkingham et al., 2010, 2014; Sanz et al., 2015), foot morphology (Manning, 2004; Falkingham et al., 2010), the force applied through the foot (Falkingham et al., 2011; Bates et al., 2013, Morse et al., 2015) and the motion of the foot (Ellis and Gatesy, 2013; Falkingham and Gatesy, 2014). Each of these variables can be set with a fix value, while it is possible to alter the variable of interest and can be therefore be compared with fossil tracks (Sanz et al., 2015).

Gatesy et al. (2009) attempted the identification of biomechanically justifiable limb poses that large theropods (e.g. *Tyrannosaurus rex*) might have assumed when moving at constant speeds through the comparison of extant bipeds limb constraining positions.

Manning (2008) stated that the relative position of an animal's center of mass to the angle of the action of force acting on the foot results in the variation in the distribution of pressure over the sole of the foot during the step cycle. Therefore he wondered whether this variation in pressure could be the key to unlock the kinematic information of a track. This assumption was later analysed through digital image correlation (DIC) technique based on the fact that stress transmitted to the subsoil during animal walking has a dynamic and a static component (Shanz et al., 2013). By constraining foot geometry and constraining soil properties, these authors were able to determine the velocity of the elephant's foot at the time of contact with the subsurface and through FEA they were able to calculate the weight distribution in elephant limbs by relating the mass carried on single limb with the total mass of the animal. Bates et al.(2013) investigated the utility of footprints as indicators of habitual foot mechanics by correlating foot pressure and track depth through FE simulations and obtained valuable results for the understanding of pressure-depth correlation. They demonstrated that footprint geometry is highly dependent on the footprint depth and moreover, that the difference between shallow and deep tracks is linked to the understanding the variation of foot mechanics across different degrees of substrate consistencies.

Probably the best result for this understanding was obtained in Falkingham and Gatesy (2014) in which the three-dimensional movement of a guineafowl indending in a granular substrate were monitored by XROMM rays (Ellis and Gatesy, 2013). This experiment allowed the visualization of in vivo track formation both at the surface and subsurface levels for the very first time. In order to unveil the track formation, a track ontogenetic approach helps integrate both limb and substrate dynamics into the interpretation of track morphology. This research have underscored the fact that foot anatomy cannot be read directly from tracks because of all these factors, properties and variables concurring in track formation.

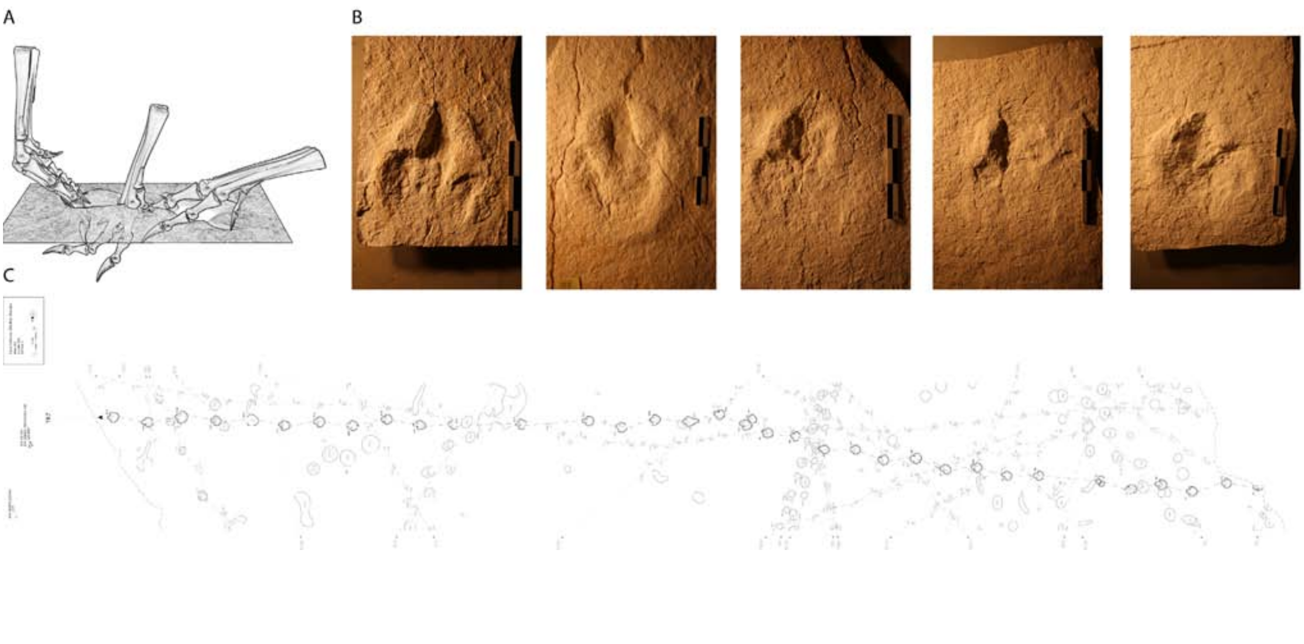



Figure 4.3. Foot morphology and limb-foot movement. A) Gatesy (2003)'s 3-D computer reconstruction of a theropod foot sequence of movements while indenting in a soft sediment. B) Morphological variation in some of the tracks preserved in the BEB-500 TR7 trackway (Razzolini et al., submitted) due to limb dynamics of the trackmaker changing gaits. Schematic drawing of the trackway BEB-500 TR7 (scale 1:50) of the Courtedoux—Béchat Bovais tracksite (NW Switzerland).

### 4.3 Track morphological variation and substrate

Tracks are a dynamic and interactive three dimensional ensemble between the foot and the substrate, adding rheology, or soil mechanics, as an important component in the morphological track analysis. Seilacher (1986) has suggested that a track is “an experiment in soil mechanics,” a chance to reconstruct the physical properties of the substrate over which the animal walked. Nadon (2001) noticed that the impact of feet and paws on unlithified sediments can be viewed as paleo-engineering tests of the substrate. Discussion about the biasing effect of substrate on the final morphology is a complex task that aims to disclose the ontogeny (formation) of the track itself.
In order to fully understand how a track is formed, laboratory controlled experiments based on the “indenter theory” and artificial substrates (Allen, 1989, 1997; Manning, 1999, 2004; Milàn and Bromely, 2006, 2008; Jackson et al., 2009, 2010) which have to include a deep rheological and substrate mechanics knowledge, computer simulations using finite element analysis, discrete element simulations and engineering methodologies (Falkingham et al., 2009; Falkingham et al., 2010; Falkingham and Gatesy, 2014) and neoichnological experiments (Padian and Olsen 1984; Brand, 1996; Farlow, 1989; Milàn, 2006; Marty et al., 2009) have been undertaken to isolate each variable and tentatively quantify its bias on the determination of the final track morphology. More recently, by taking advantage of high-performing computers, laboratory controlled experiments have been redrawn for computer simulations with engineering techniques that allow to isolate the individual effects of a particular variable of the substrate by systematically altering its value (Sellers and Manning, 2007; Gatesy et al., 2009; Falkingham et al., 2008, 2009, 2010; Ellis and Gatesy, 2013; Bates et al., 2013; Shanz et al., 2013; Falkingham and Gatesy, 2014). These computer simulation have been employed to study track formation, exploring subsurface deformation and the effects of varying load according to foot dynamics and body mass distribution. Some of these studies used Finite Element analysis in computer simulations demonstrating that “in order for a track to form, a substrate must not be too soft nor too firm (given homogeneity), and that the range of parameters in which the substrate was ‘just right’ was surprisingly small, and varied according to the trackmaker’s size and foot shape” (Falkingham et al., 2010, 2014), the so called “Goldilocks effect”. Recently, Falkingham et al., 2014 added more complex substrate models, simulating heterogeneous substrates (and therefore emulating the sediment where the fossil track record can be found) composed of multiple layers of different properties. Authors concluded that the range of parameters in which the substrate allows the formation of a track is highly dependent upon substrate properties (Falkingham et al., 2014).

***Rheology: grain size and water content***

A track ideally consists of a steeply inclined shaft caused by the indenter; a footprint or direct track *sensu* Gatesy, 2003 (direct contact of the pes with the grains) at the base of the shaft; a zone of deformed sediment (Loope, 1986; Scrivner and Bottjer, 1986; Allen, 1989; Manning, 2004; Marty et al., 2009) such as marginal upfold; a shaft fill (after the withdrawn of the indenter).

Isolating the properties that characterize a soil (*sensu* Craig, 2004) is pivotal for understanding that the consistency of a deformed substrate strongly depends on the water content and the texture (grain size, shape and sorting) of the sediment (Laporte and Behrensmeyer, 1980; Scrivner and Bottjer, 1986).
A major factor in determining the mechanics of the soil is the relative proportions of the particles that characterize a determinate soil and the voids among them (containing air or water). The relationship between the voids and the solids (particles) can determine a series of mechanical properties such as the porosity (ratio between the void volume and the total volume), the degree of saturation (water volume to total volume of voids) and the moisture content (ratio between weight of solids and weight of water). Grain size and water content are the constraints that determine the formation, preservation and the final morphology of a track.
The water content at the time of the impression, most strongly controls track morphology causing a big variety of track morphologies for any given trackmaker (Scrivner and Bottjer, 1986). These authors provided levels of water content in the soil to clarify how morphology changes in function of water content: 1) water-saturated sediment; 2) water-unsaturated sediment that tends to cling or adhere to the vertebrate hoof or foot; 3) moist or slightly damp sediment which shows the best preservation of tracks; and 4) dry sediment which is too hard to be deformed into an impression. When the sediment is quite saturated in water content, the edges of the tracks are often raised into rims and lack of internal structure impressions, such as pads; when the sediment is moist or water-undersaturated revealing a firm soil, tracks cannot penetrate deeply. Since water content is the most crucial factor for vertebrate track morphology tracks can be used to make conclusions about the sediment consistency at the time they were left (Allen, 1989; Scrivner and Bottjer, 1986; Manning, 2004;Marty, 2008; Marty et al., 2010; Jackson e al., 2010).
With all this in mind, water content and grain size and distribution in the media affecting track morphology, various authors have carried out laboratory-controlled experiments with indenters (artificial geometric punch penetrating the surface), with no limb kinematic involved (Allen, 1989, 1997; Manning, 2004; Jackson et al., 2009, 2010) and neoichnological experiments with living animals accounting also with the limb kinematic variable (Farlow, 1989; Brand, 1996; Milàn and Bromely, 2006, 2008; Marty et al., 2009) in order to understand which among the variables, plays a major role. By undertaking these experiments, the utility of rheology, the study of behavior and properties of different materials, for its comparison with fossil substrates and tracks is emphasized. With these experiments and especially with the vertical cuts, complex mechanical interactions between the substrate and the indented object are reveled.
By underscoring the fact that the properties and conditions of a substrate in which tracks are made also affect their formation, inhibiting or enhancing the animal's ability to traverse the substrate, and the gait adopted in some cases, (Milàn et al., 2004) carried vertical sections on dinosaur tracks from the Late Triassic lake deposits of Greenland, which allowed them to take a closer look to undertrack formation and other subsurface structures that form during track formation. Additionally, vertical cross sections clearly demonstrate the different appearances of three dimensionally and stress the importance of sediment properties in the final morphology of tracks (Milàn and Bromley 2006, 2008). Milàn and Bromley (2006, 2008) highlighted the intimate relationship between the properties of the substrate and

the morphology of the tracks, and cross sections are the tool to prove this connection. Cross sections analysis result significant because it informs on the sedimentological conditions at the moment when tracks were produced.

Comparison among different cross sections allows the recognition of similar sediment deformation structures. Characters such as displacement rims, maximum track depths, digital thinning and hallux impressions are features that may indicate that the original substrate conditions were different. Hence, it is inferable that changes in water content, and thus the firmness of the sediment, dramatically alter the appearance of true tracks (Milàn and Bromley, 2008).

***How is a track formed: surface and subsurface track in a layer perspective***

With the acquisition of a multidisciplinary and quantitative approach toward vertebrate ichnology, rheology and soil mechanics are explored as tools for the disclosure of the ultimate goal of ichnology: how is a track formed. Because one of the greatest limitations of studying track formation is that the foot-substrate interaction is hidden from the view and fossil vertebrate tracks are therefore studied after all the properties and mechanics controlling and driving these interactions already occurred, an understanding of laboratory-simulated tracks can assist in unravelling how fossil tracks are formed and the processes that subsequently altered them (Gatesy, 2003; Manning, 2004). Besides kinematics (limb movement), kinetics (foot load), anatomy and substrate properties, another factor that strongly alters the appearance of the track morphology is the preservation of the track itself. The phenomenon of undertracks, or subsurface tracks, accounts for the transmitted pressure of the trackmaker's foot down and outward to the surrounding sediment, deforming the lower levels. Hitchcock (1858) was the first to observe that a bird track from the Connecticut Valley, New England, could be found transmitted in successions at several different layers below each other, becoming larger downwardly and that several details that are absent at higher levels can instead appear in lower levels. For most of definitions, the distinction existing between true track and undertrack resides in a thin sedimentary layer, meaning that true tracks form in the uppermost layer, whereas undertracks form in deeper layers. Implications for the correct identification of an undertrack have been proved over the years with laboratory-controlled experiments. The pioneering work of Allen (1989, 1997) showed how substrate consistency and track morphology are tightly related and moreover, by vertically and horizontally cutting the experimental package (cross-sections) it was visible the motion and deformation of the substrate beneath the indenter.

***Laboratory-controlled experiments with artificial indenters***

In laboratory-controlled experiments, the formation of a track depends on the indentation of a static up and down movement of a structure (punch) in an elastic-plastic material, which is in turn physically responding to this indentation. This response provides a general mechanical model for track ontogeny and a basis for the assessment of track preservation in different sediment conditions (Allen, 1989, 1997). Allen (1989, 1997) used the simplest method: a vertical indentation and withdrawal of a cylindrical punch to form experimental tracks in plasticine.

The methodology followed by the first laboratory controlled experiments is based on plasticine markers with different templates piled in blocks (Allen, 1989,1997); a box to contain the laminated plasticine and a punch to which the force is applied. Over a period of a few seconds, a steady downward force was applied manually through the rod to the punch, the penetration of which was limited by an adjustable collar. One of the possibilities offered by this experiment is that these blocks can, after deformation, be dissected a layer at a time, affording insight into the progressive loss of anatomical detail downward through undertracks. Thanks to Allen's pioneering experiments (Allen, 1989), it was observed that the limb and foot cut a shaft into the sediment, creating an extensive zone of deformed sediment around and below the shaft; the degree of deformation increased with increased depth of penetration. The deformed zone comprised an axial downfold, in which downward-decaying undertracks were preserved, and a marginal upfold, with associated shear and fracture zones. Allen (1989) found that, where the sole of the foot was complex in shape, anatomical details, in the form of cross-folds (*sensu* Allen 1989), were preserved in the undertrack.

These experiments reproduce qualitatively all the essential features of real tracks (surface tracks, true tracks) and propose the "indenter theory" as an appropriate general

theoretical model for the first stage in track formation. Indeed his work have underscore the importance in discerning whether a tracks is a surface tracks or an undertrack in the fossil record. Anyhow, Allen (1989, 1997) did not account for the variation in the sediment water content and the sediment consistency, since the "soil" he used was a uniform, layered plasticine dough. The modeling experiments by Allen (1989, 1997) show clearly how cross sections of tracks in sediments of moderate cohesion are demonstrably different from naturally occurring soft-sediment deformation (Nadon, 2001).

Manning (2004) considered how the grain size, sorting, and permeability of sediment might control the subsurface track morphology and concentrated on the relationship between media moisture content and footprint morphology. More importantly, he has demonstrated that in sand media, there is a complex relationship between moisture content, medium density, and track preservation, called the moisture–density relationship. The important role that moisture content has in affecting (along with grain size) track morphology has been recognized before (Tucker and Burchette 1977; Scrivner and Bottjer 1986; Allen,1997). Manning's study (2004) generated and recovered well-defined subsurface tracks in both dry and saturated sediments, previously considered poor preservational media (Tucker and Burchette 1977; Scrivner and Bottjer 1986).

Other laboratory-controlled experiments (Jackson et al., 2009, 2010) recreated a colored-layered uniform sandy media (therefore reproducing a similar environment that dinosaurs walked) and used complex tridactyl morphologies as indenters. Moreover, they used different sediment consistencies, from dry (0% moisture content) to saturated (30% moisture content) with two moist states (10% and 20% moisture content) in between. The percentage moisture content of the saturated state (the mass of the water relative to the mass of the dry sediment; Barnes, 2000) was determined by weighing the sample before and after drying. To moisten the medium, the surface of each layer was sprayed with water during the construction process. The moisture content was estimated as the mass of water sprayed to each layer, as a percentage of the dry layer's mass, estimated from the known density and volume of each layer (Jackson et al., 2009, 2010). Results of these experiments shown that the moist states (10% and 20% moisture content) represented the optimal sediment for surface track preservation, in which track morphology is most accurately preserved. Poorer preservation of track morphology was evident in dry media due to the lack of moisture or in saturated media (30% moisture content) due to higher pore-water pressure. Extremes of moisture content prevent track formation either because the medium is too loose, or too liquid (Laporte and Behrensmeyer, 1980; Platt and Hasiotis, 2006).

Laboratory controlled simulations and neoichnological experiments (Milàn and Bromely, 2006, 2008; Milàn, 2006; Marty et al., 2009) have quantitatively demonstrated that track morphological variability is strictly dependant over the content of water in (laminated) homogenous sediments. The most important results of these experiments are that in firmer cement blocks, the morphology of the true track (surface track) shows a gradual increase in the horizontal dimensions, which were wider and longer than the surface track, corroborating the fact that undertracks showed a steady degradation of the true track morphology in the underlying layers. On the other hand, in nearly liquefied substrate, the true track is strongly distorted by the dynamic removal of the foot, showing collapse of wet cement in the surface, but retaining a closer resemblance to the anatomy of the emu foot in the undertracks layers.

Such approaches are well suited for documenting the distortion of interfaces between layers, but are unable to discern the displacement of sediment within each layer (Gatesy, 2003).

Shortcoming for laboratory controlled experiments is that the artificially indented object (punch, Allen, 1989, 1997) or more realistic foot models (Manning, 2004; Jackson et al., 2010) and severed feet (Milàn and Bromely, 2006, 2008) follow a stiff upward-downward movement, which is not comparable to the complex dynamic movement of the foot and the importance of the angle of indentation of the pes in the sediment. Because of the complexity in the movement of the pes inside the sediment, experiments using simple indenters models (Allen, 1997; Manning, 2004; Milàn and Bromely, 2006, 2008; Jackson et al., 2009; 2010) are not completely accurate in describing and isolating the effects of foot motion inside the sediment. Moreover, the vast majority of recorded tracks are impressed into unconsolidated, polyphase sediments that range from clay-mineral or lime muds to siliciclastic or bioclastic-ooid sands, and to laminated mixtures in between (Allen, 1997).

***Subsurface tracks and deep tracks:a particle-based dynamic perspective***

The depth of a track, when observable (cross sections), can display the history of the movement of the pes (Avanzini, 1998; Gatesy, 1999; Milàn et al., 2004; Milàn, 2006; Milàn and Bromley, 2006, 2008) inside the non-visible sediment. For instance, various authors have observed that in saturated sediments (wet sands, muds, cements) the track walls collapse over the digit impressions after uplifting of the foot, leaving a track consisting of a triangular 'heel' area and an oval hole where digit III left the sediment (Avanzini et al., 1998; Gatesy et al., 1999; Milàn, 2006). Tracks imprinted in this kind of sediment are not likely to reveal many details if fossilized because the sediment slowly flows together after the foot has been lifted. However, even if the footprint at the surface is collapsed and hardly

recognizable, experimental work by Milàn and Bromley (2006) has demonstrated that the footprint in such cases can be well preserved as an undertrack in the sediment layers just beneath the true track.
The depth to which a track enters the sediment can provide vast information, being a direct result of the weight, duty factor, and limb kinematics of the animal as well as of the substrate or sediment consistency (Falkingham et al., 2010). Depth study might demonstrate that the shape of the foot is an important factor that influences the depth to which the sediment is indented. Pronounced track depths could mean that the substrate is quite moist and this might have significant biomechanical implications to what it may concern balance and walking stability of the track-maker (Moratalla, 1993, Avanzini et al., 2011).
Deep tracks represent one extreme of a continuum of track morphologies caused by a gradient of substrate consistencies (incompetent mud) and in these cases, footprint morphology is usually distorted, lacking anatomical details (Fig.4.4). These tracks are more useful if analysed as the result of limb kinematic on a particular substrate consistency (Gatesy et al.,1999; Nadon, 2001; Razzolini et al., 2014, Razzolini and Klein, under review). On the other hand, shallow tracks may represent relatively accurate molds of plantar anatomy, that reveal where the foot was placed but very little about how the foot was placed (Gatesy et al., 1999; Gatesy, 2003) and therefore, in this specific situation almost no information on limb kinematics can be extrapolated and foot anatomy insights can be exploited. With all this, shallow tracks should be interpreted cautiously, bearing in mind that a shallow track is not synonym of a true track (weathering, erosion, Marty, 2008) and that a true track is not synonym of a plantar anatomy representation (Gatesy et al., 1999).
Gatesy (2003) noted that defining surface tracks as the surface layer of sediment on which the dinosaur walked is not always applicable, particularly in reference to the Greenland tracks made in very soft mud (Gatesy et al., 1999). Gatesy (2003), devoted part of his studies to isolate the grains and particles connecting with the trackmaker's foot, forming what he calls "direct track" and he designates track features as direct or indirect manifestations of foot contact. A deep track not only implies that the digits cut through the layers beneath until the foot finds a sufficiently firm layer to prevent a further sinking, but also that all these layers are being deformed by the pressure exerted by this foot. This phenomenon is explained when the ratio of penetration depth to layer thickness is high enough. This insight is very important because of the implication when dealing with undertracks, usually considered poorly-preserved true tracks due to weathering and therefore not usable for the track-maker recognition. However, the variation in depth/thickness ratios makes a definition of true tracks founded on layers entirely arbitrary (Gatesy, 2003). Such grain-based perspective is a magnifying glass that meticulously discerns between direct and indirect track features according to a distinction between the surface that contacted with the foot. Therefore, a pre-track and post-track surfaces are present. The former is a planar surface that will be altered by the track formation into the depressed, elevated, and fractured features of the post-track surface. Direct features are those that form when the foot is in direct contact with the grains of the pre-track surface, indirect features are indirectly moved by the indentation of the foot into the sediment layers but are never touched by the foot skin, meaning that are formed by grains that have been moved by other grains.

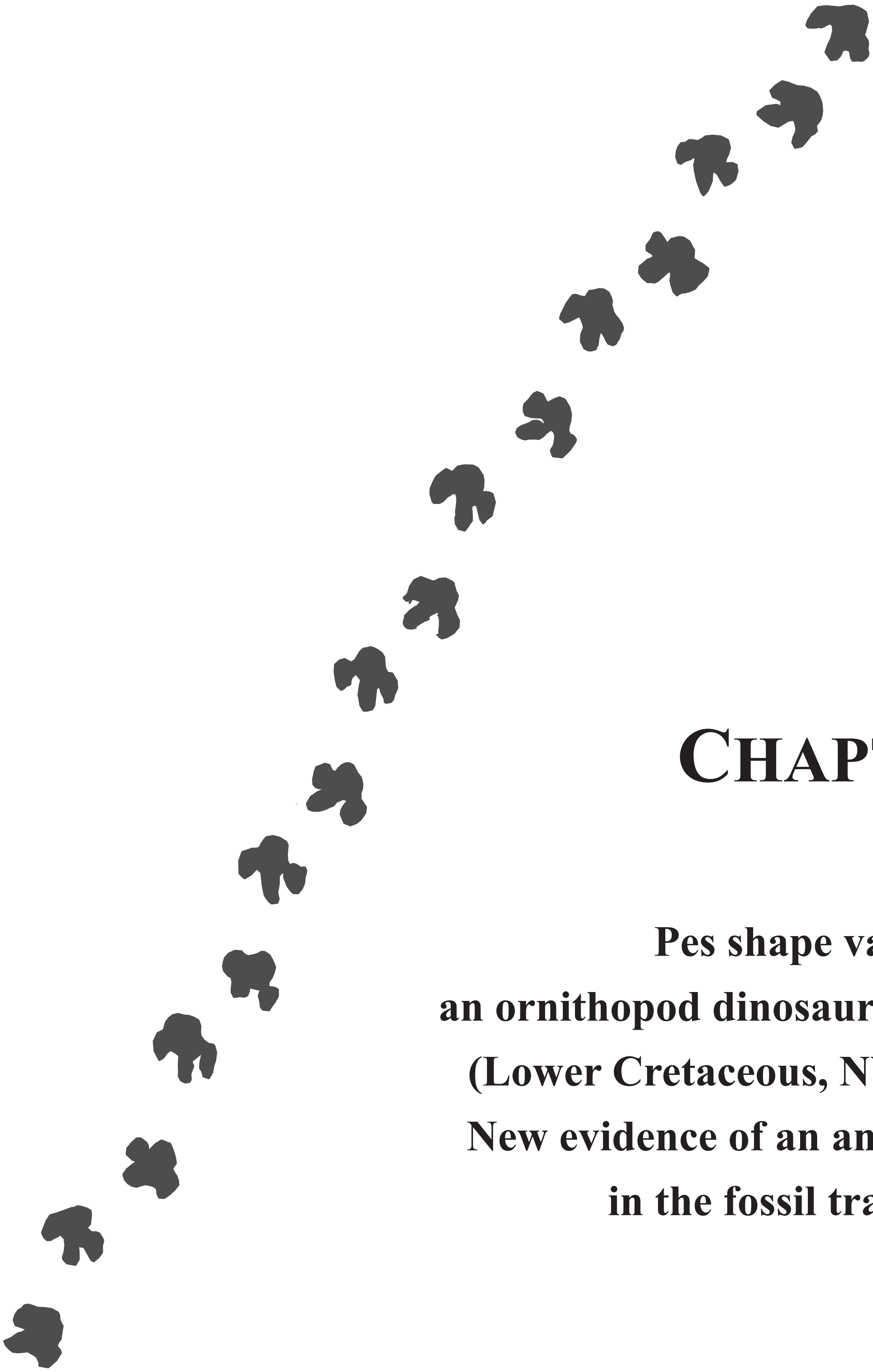
Figure 4.4. Foot morphology and substrate. Theropod track morphologies presented in the El Frontal tracksite (Soria, Spain: Razzolini et al., 2014) varying within a very limited area (<200 m$^2$) due to the presence of a transversal heterogeneity of the sediment conditions.

The track formation is the final product between the interaction of direct and indirect features, which is to say between the skin/sediment contact phase and between sediment/sediment phase (raised marginal ridges, radial fractures, concentric fractures, Allen, 1997; bourrelet, Thulborn, 1990).

Marty et al. (2009) showed that in recent microbial mat-covered tidal-flat environments, a wide range of morphologies of human footprints was formed. This variability depends on the water content, thickness and nature of the microbial mat and the underlying sediment. Nature, thickness and water content of the mat are crucial for its yield strength, plasticity, and its elastic limit. If the mat is broken or penetrated by the pressure of the foot, the nature and water content of the underlying sediment becomes the determining factor for footprint morphology, and either an underprint or a deep track is produced.

# PART 3

## Track morphological variation and Trackmaker’s anatomy



# CHAPTER 5

## Pes shape variation in an ornithopod dinosaur trackway (Lower Cretaceous, NW Spain): New evidence of an antalgic gait in the fossil track record

## AUTHOR'S CONTRIBUTION

Razzolini, N.L., Vila, B., Díaz-Martínez, I., Manning, P.L., Galobart, À., (2016).
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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, wrote the manuscript and prepared the figures and tables.

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# Pes shape variation in an ornithopod dinosaur trackway (Lower Cretaceous, NW Spain): New evidence of an antalgic gait in the fossil track record

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Trackways can provide unique insight to animals locomotion through quantitative analysis of variation in track morphology. Long trackways additionally permit the study of trackmaker foot anatomy, providing more insight on limb kinematics. In this paper we have restudied the extensive tracksite at Barranco de La Canal-1 (Lower Cretaceous, La Rioja, NW Spain) focussing on a 25-m-long dinosaur (ornithopod) trackway that was noted by an earlier study (Casanovas et al., 1995; Pérez-Lorente, 2003) to display an irregular pace pattern. This asymmetric gait has been quantified and photogrammetric models undertaken for each track, thus revealing distinct differences between the right and the left tracks, particularly in the relative position of the lateral digits II–IV with respect to the central digit III. Given that the substrate at this site is homogenous, the consistent repetition of the collected morphological data suggests that differences recorded between the right and the left tracks can be linked to the foot anatomy, but more interestingly, to an injury or pathology on left digit II. We suggest that the abnormal condition registered in digit II impression of the left pes can be linked to the statistically significant limping behaviour of the trackmaker. Furthermore, the abnormal condition registered did not affect the dinosaur's speed.



## 1. Introduction

The recognition of gait abnormalities in dinosaur trackways has been reported in both isolated tracks (Ishigaki, 1986, 1989; Mateus & Milàn, 2010) and trackways (Abel, 1935; Avanzini, Piñuela, & García Ramos, 2008; Dantas, Santos, Lockley, & Meyer, 1994; Lockley, Hunt, Moratalla, & Matsukawa, 1994; McCrea et al., 2014a,b; 2015). Previously published examples usually show the lack of a digit or a different value of homologous interdigital divarication angles (Avanzini et al., 2008). Palaeopathologies are more easily recognised in the osteological record (Anné et al., 2014; Rothschild & Tanke, 1992, 2005; Rega, Holmes, & Tirabasso, 2010; Tanke & Rothschild, 1997; 2002); ichnopalaeopathologies are much harder to identify because of the difficulty associated with discerning if anomalous features were due to physical abnormalities (i.e. injury, fractures, infections, deformations, swellings) were a function of unusual behaviour or merely a reflection of sediment rheology (Manning, 2004). Evidence for abnormal gaits come from trackways that display an alternating pes pace length pattern (Dantas et al., 1994; Lockley et al., 1994), although, many of these examples in literature may simply be unequal gaits of healthy animals (McCrea et al., 2015 and references therein). To date, several dinosaur trackway examples appear to correlate with a likely trackmaker limp to an actual cause, i.e., foot injury reflected in the narrow digit divarication (Abel, 1935; Avanzini et al., 2008; Ishigaki, 1986; Jenny & Jossen, 1982; Lockley et al., 1994 p. 194).

In this study we reanalysed an ornithopod trackway (Casanovas

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et al., 1995; Pérez-Lorente, 2003) recently assigned to *Caririchnium lotus* (Díaz-Martínez, Pereda-Suberbiola, Pérez-Lorente, & Canudo, 2015) from the Lower Cretaceous Valdeosera-Traguajantes Unit in the Enciso Group, NW Cameros Basin, Spain. Occurring with multiple other tracks on a horizon named Barranco de La Canal (BLC) by Casanovas et al. (1995) and Pérez-Lorente (2003), this trackway (BLC1) has been previously shown to include irregular pes pace length patterns. Casanovas et al., (1995) and Pérez-Lorente (2003) noted a shortening from left to right pes pace, but did not expand with any explanation of their observation. The aim of this study is to quantify the observations made by these earlier studies and interpret the possible cause for the recorded anomaly in the alternating pace lengths in the view of potential abnormalities to trackmaker limb kinematics. Furthermore, since these tracks have only previously been documented and described as 2-D track outlines, we provide the first 3-D evaluation of the Barranco de La Canal-1 tracks, permitting a comprehensive description of track morphologies through photogrammetric models that allow us to collect more accurate morphological information and provide evidence for the possible cause of the irregular pace lengths.

## 2. Geological setting

The Barranco de La Canal (BLC) tracksite is situated in northern-central Spain, in the Province of La Rioja, close to the village of Munilla (Fig.1). The Cameros Basin consists of a high-subsidence basin of the Iberian Rift System displaying several tectonic phases during the Mesozoic and Cenozoic (Más et al., 2002; 2011). During the Late Jurassic and Early Cretaceous, the basin consisted of a fluvio-lacustrine system in which siliciclastic and carbonate sediments were deposited (Más et al., 2002; Doublet, 2004). The tracks are preserved on a silty sandstone slab of the Valdeosera-Traguajantes Unit, in the upper part of Enciso Group, in which sandstones, siltstones, marls and limestone are dominant (Hernández-Samaniego et al., 1990). The Enciso Group is more than 2000 m thick with its lower part mainly formed by fluvial deposits (Clemente, 2010). The middle and upper parts present a great variety of littoral and lacustrine deposits, evaporites and banks of limestones with diverse thickness, alternating with marls with desiccation cracks, fine-grained siltstones and siltstones with ripples and hummocky cross-stratification. The palaeoenvironment of the Enciso Group has been reconstructed as a siliciclastic to carbonate mixed lacustrine system with occasional marine incursions (Doublet, García, Guiraud, & Menard, 2003). Doublet (2004), based on the charophyte record (*Atopochara trivolvis* var. *triquetra*; Kneuper-Haack, 1966; Schudack, 1987, and *Clavator grovesii* var. *lusitanicus*; Grambast-Fessard, 1980; Martín-Closas, 1991), suggested that the Enciso Group is early Barremian to middle Albian in age (Fig.1).

## 3. Material and methods

The site has a total surface area of 250 m$^2$ and preserves 64 tracks divided into 7 trackways and 9 isolated tracks (Casanovas et al., 1995). The present study concentrates on trackway BLC1 (following Casanovas et al., 1995 and Pérez-Lorente, 2003 nomenclature), which is composed of 31 consecutive tracks made by what has been interpreted as a large ornithopod. The 3-D digital outcrop model (DOM) of the tracksite was first generated using a RIEGL LMS1 Z420i long range LiDAR capable of 5–10 mm resolution (Bates, Manning, Vila, & Hodgetts, 2008) and post-processed in Geomagic® software (Fig.2). The digital outcrop overview was complemented with close-range photogrammetric models

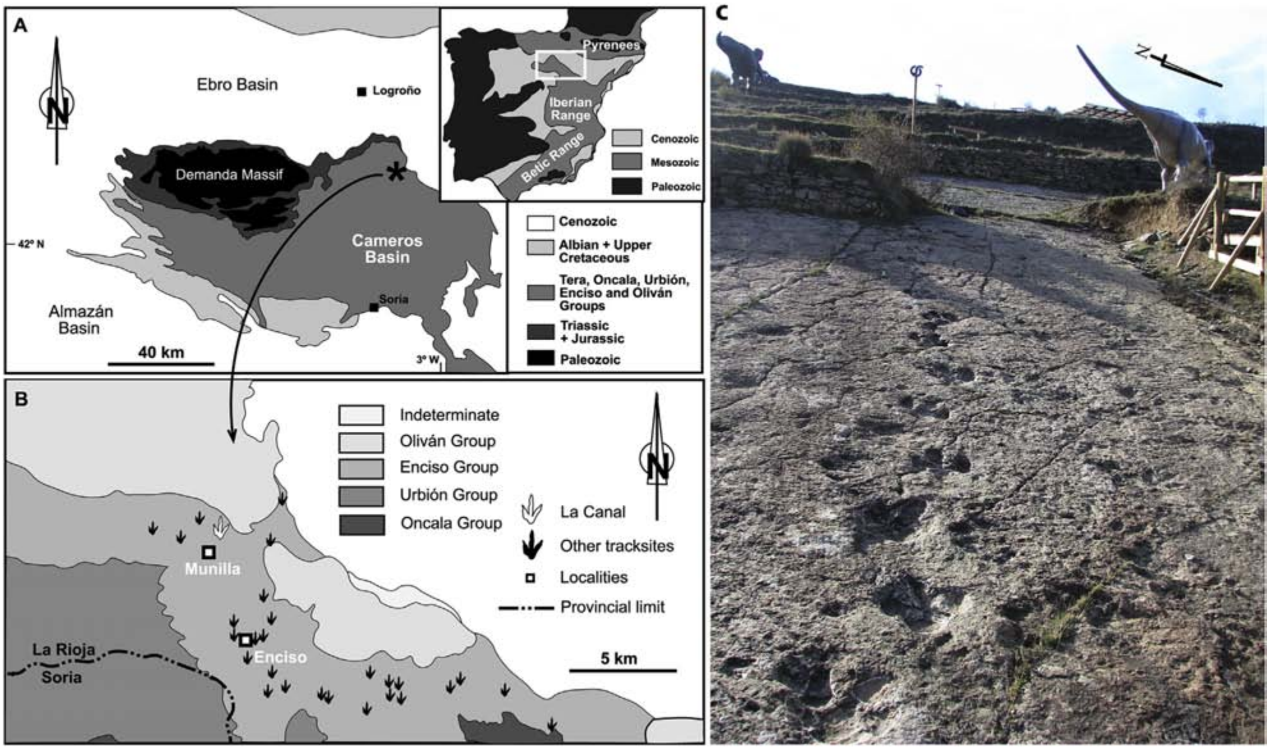



**Fig. 1.** A-B) Geographical and geological setting of the El Barranco de La Canal-1 tracksite from the Cameros Basin of the Munilla village, La Rioja, NW Spain. It belongs to the Enciso group. Geological map modified from Díaz-Martínez (2013). C) Field photo of the Barranco de La Canal-1 trackway with an overview of the tracksite.

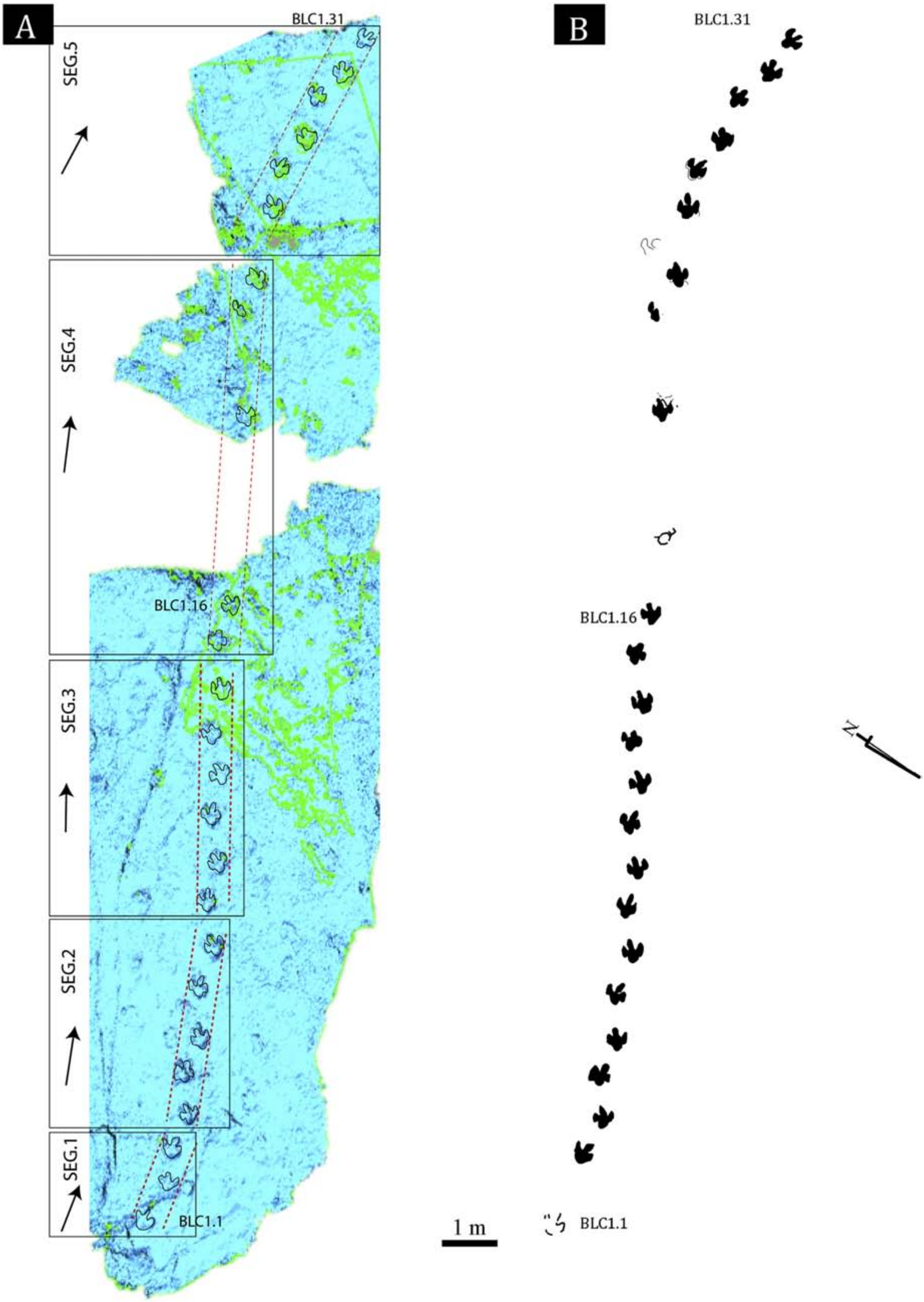



**Fig. 2.** A) Digital outcrop model (DOM)of the Barranco de la Canal-1 trackway (BLC1) obtained from post-processing the LiDAR scan raw data in Geomagic software. The BLC1 trackway is divided into 5 segments according to the slight change in the trackwaywidth and directional turnings. Segments are divided as follows: from 1) track BLC1.1 to track BLC1.3 and 70 cm wide; 2) track BLC1.4 to track BLC1.8 and 60 cm wide; 3) track BLC1.9 to track BLC1.14 and 60 cm wide; 4) track BLC1.15 to track BLC1.24 60 cm wide; 5) track BLC1.25 to track BLC1.31 and 95 cm wide. B) AutoCad drawing of the BLC1 trackway undertaken from the first field cartography made from a 10 × 10 m grid in the field (Pérez-Lorente, 2003). Scale bar 1 m.

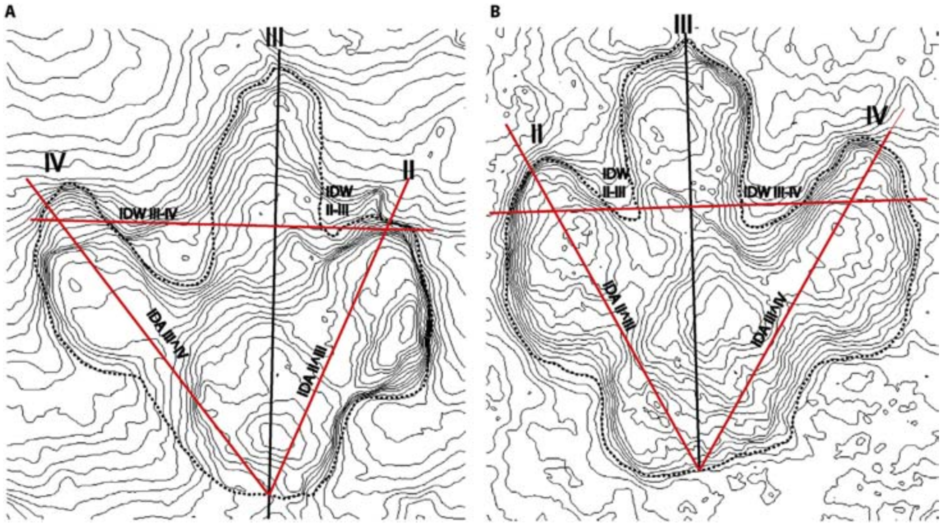



**Fig. 3.** Materials and methods explanation on:A)left track BLC1.9; B) right track BLC1.30. Isolines (contour lines) of height (Z coordinate) obtained from Paraview software every centimetre. To draw the track profile, one isoline was treated as an independent track contour line to use in the interdigital angle (IDA) and interdigital width (IDW) measurements (red lines). The IDW measurement (horizontal red line) was calculated by tracing the perpendicular segment (red line) to the track middle line (black line) and by accommodating it on the first isoline outside the hypexes. II, III, IV number of digit impressions; IDA II^III, III^IV: interdigital angle between II^III and III^IV; IDW II-III, III-IV, interdigital width between II-III, III-IV. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Measurements undertaken on right tracks from the BLC1 trackway of the Barranco de La Canal-1 tracksite. Abbreviations are as follows: TL: track length, TW: track width, PL: pace length, SL: stride length, IDA II^III: interdigital angle between digits II and III, IDA III^IV: interdigital angle between digits III and IV, DH: depth of the metarsodigital pad impression, DII: depth of digit II, DIII: depth of digit III, DIV: depth of digit IV, IDW II-III: index of the interdigital width between digits II and Table 1 III, IDW III-IV: index of the interdigital width between digits III and IV. Interdigital angles in degree and all other measurements are in centimetres.

| Right | TL | TW | PL | SL | IDA II^III | IDA III^IV | D H | D II | D III | D IV | IDW II-III | IDW III-IV |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BLC1.2 | 46.1 | 45.7 | 86.7 | | 0 | 35 | 4.4 | 3.3 | 3.2 | 4.9 | 3.2 | 12.0 |
| BLC1.4 | 30.3 | 29.3 | 90.0 | 178.7 | 35 | 36 | 4.3 | 3.0 | 3.5 | 2.2 | 3.3 | 2.2 |
| BLC1.6 | 45.3 | 38.3 | 107.7 | 175.1 | 0 | 32 | 4.5 | 3.8 | 4.1 | 3.1 | 2.9 | 7.7 |
| BLC1.8 | 43.5 | 40.3 | 102.1 | 198.5 | 0 | 28 | 6.1 | 4.2 | 5.0 | 5.6 | 3.3 | 7.4 |
| BLC1.10 | 33.3 | 39.7 | 102.5 | 183.5 | 0 | 30 | 3.0 | 2.3 | 2.7 | 3.1 | 4.3 | 4.8 |
| BLC1.12 | 39.9 | 40.6 | 96.7 | 185.9 | 0 | 31 | 2.2 | 2.4 | 1.5 | 2.2 | 2.5 | 7.2 |
| BLC1.14 | 45.0 | 40.8 | 102.6 | 174.8 | 0 | 28 | 3.1 | 2.9 | 2.6 | 2.1 | 2.7 | 2.5 |
| BLC1.16 | 38.4 | 39.7 | 76.5 | 192.1 | 0 | 34 | 4.2 | 3.0 | 3.3 | 1.5 | 5.1 | 2.5 |
| BLC1.22 | 40.2 | 41.3 | 96.7 | 186.0 | 30 | 35 | 4.0 | 3.1 | 3.3 | 2.8 | 2.5 | 2.7 |
| BLC1.24 | 47.2 | 39.3 | 104.0 | 173.4 | 0 | 30 | 2.9 | 2.6 | 3.4 | 4.3 | 2.9 | 7.7 |
| BLC1.26 | 50.6 | 43.8 | 107.7 | 165.8 | 0 | 30 | 2.7 | 1.6 | 1.6 | 1.7 | 3.8 | 3.4 |
| BLC1.28 | 39.8 | 38.3 | 105.6 | 187.5 | 0 | 38 | 3.6 | 2.8 | 3.2 | 2.8 | 2.1 | 2.8 |
| BLC1.30 | 43.3 | 42.4 | 99.6 | 188.0 | 0 | 37 | 3.8 | 3.4 | 2.5 | 2.7 | 3.3 | 4.1 |
| **AVERAGE** | **41.8** | **40.0** | **98.3** | **184.7** | **5** | **32** | **3.7** | **3.0** | **3.1** | **3.0** | **3.2** | **5.1** |

**Table 2**
Measurements undertaken on left tracks from the BLC1 trackway of the Barranco de La Canal tracksite. Abbreviations are as follows: TL: track length, TW: track width, PL: pace length, SL: stride length, II^III: interdigital angle between digits II and III, III^IV: interdigital angle between digits III and IV, DH: depth of the metarsodigital pad impression, DII: depth of digit II, DIII: depth of digit III, DIV: depth of digit IV, IDW II-III: index of the interdigital width between digits II and III, IDW III-IV: index of the interdigital width between digits III and IV. Interdigital angles in degree and all other measurements are in centimetres.

| Left | TL | TW | PL | SL | IDA II^III | IDA III^IV | D H | D II | D III | D IV | IDW II-III | IDW III-IV |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BLC1.3 | 41.1 | 38.2 | 92.1 | 171.4 | 19? | 28 | 5.5 | 4.1 | 4.0 | 6.1 | 2.5 | 7.4 |
| BLC1.5 | 46.3 | 35.9 | 92.1 | 193.6 | 24? | 32 | 7.0 | 2.4 | 3.2 | 6.1 | 3.0 | 11.3 |
| BLC1.7 | 47.6 | 40.9 | 97.3 | 192.8 | 17? | 32 | 2.9 | 3.1 | 2.5 | 3.2 | 1.9 | 6.1 |
| BLC1.9 | 46.2 | 35.9 | 89.7 | 185.7 | 13? | 31 | 4.8 | 7.0 | 3.3 | 3.4 | 2.1 | 6.6 |
| BLC1.11 | 43.1 | 35.4 | 91.2 | 180.4 | 16? | 30 | 4.5 | 4.7 | 3.2 | 3.6 | 1.8 | 7.9 |
| BLC1.13 | 41.5 | 36.2 | 83.6 | 183.3 | 18? | 31 | 4.2 | 3.8 | 2.9 | 4.3 | 2.0 | 4.5 |
| BLC1.15 | 40.8 | 39.7 | 93.7 | 192.0 | 16? | 32 | 4.3 | 5.7 | 3.6 | 5.0 | 1.9 | 4.7 |
| BLC1.21 | 36.9 | 40.1 | 84.9 | 185.0 | 14? | 35 | 4.0 | 3.2 | 2.4 | 2.9 | 1.6 | 8.0 |
| BLC1.23 | 41.1 | 37.4 | 91.1 | 177.9 | 18? | 32 | 5.2 | 4.2 | 3.6 | 3.9 | 1.5 | 6.7 |
| BLC1.25 | x | x | x | 181.4 | x | x | x | x | x | x | x | x |
| BLC1.27 | 41.2 | 39.0 | 89.7 | 184.5 | 19? | 32 | 2.7 | 2.0 | 2.2 | 2.5 | 1.6 | 5.7 |
| BLC1.29 | 39.3 | 37.2 | 92.8 | 188.3 | 19? | 42 | 3.0 | 3.5 | 0.5 | 1.9 | 1.4 | 6.4 |
| BLC1.31 | 30.3 | 41.2 | x | 191.8 | 19? | 34 | 2.3 | 2.6 | 1.8 | 2.0 | 0.9 | 4.6 |
| **AVERAGE** | **41.3** | **38.1** | **90.7** | **185.0** | **18?** | **32** | **4.2** | **3.9** | **2.8** | **3.7** | **1.8** | **7.4** |

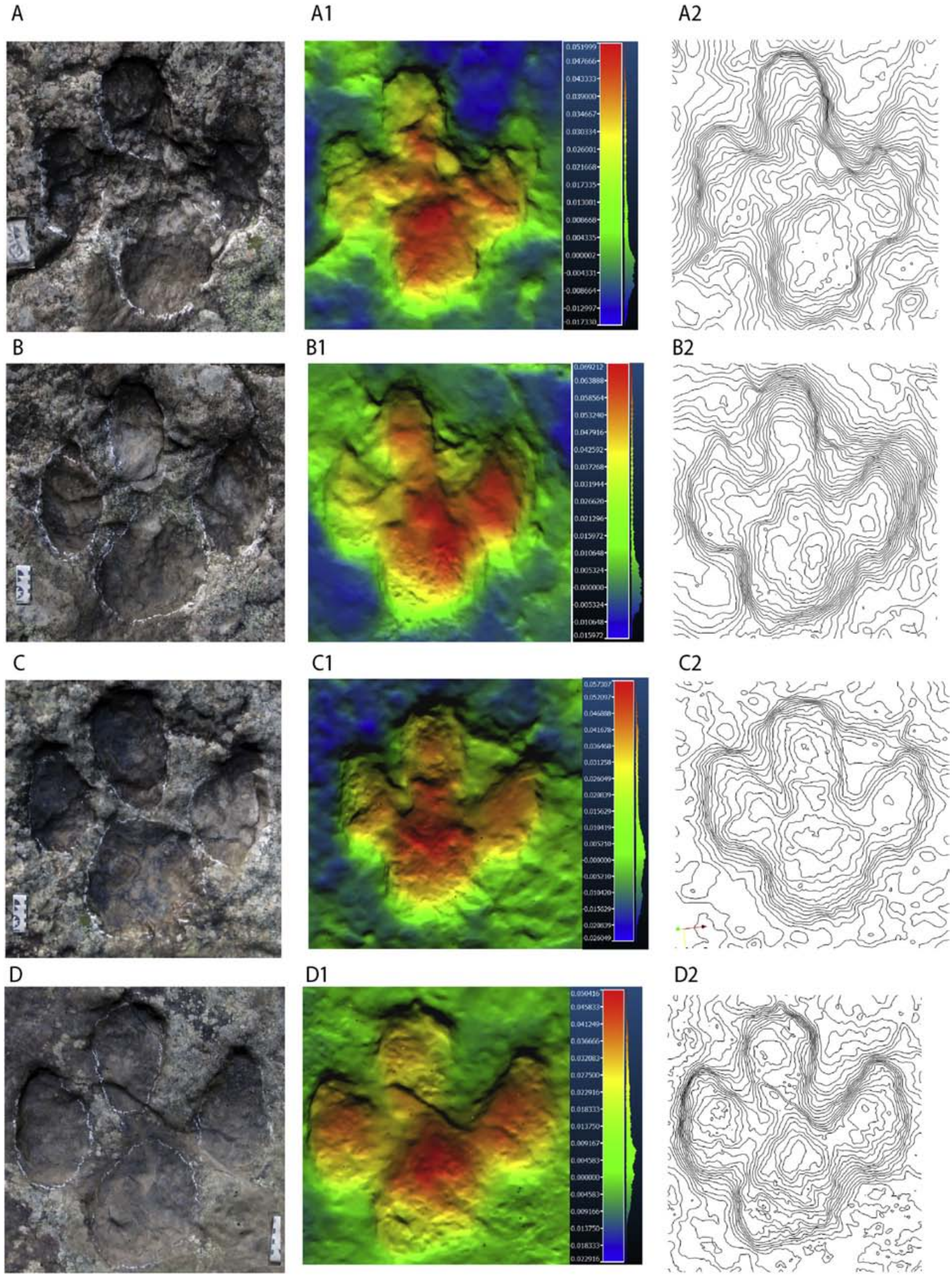
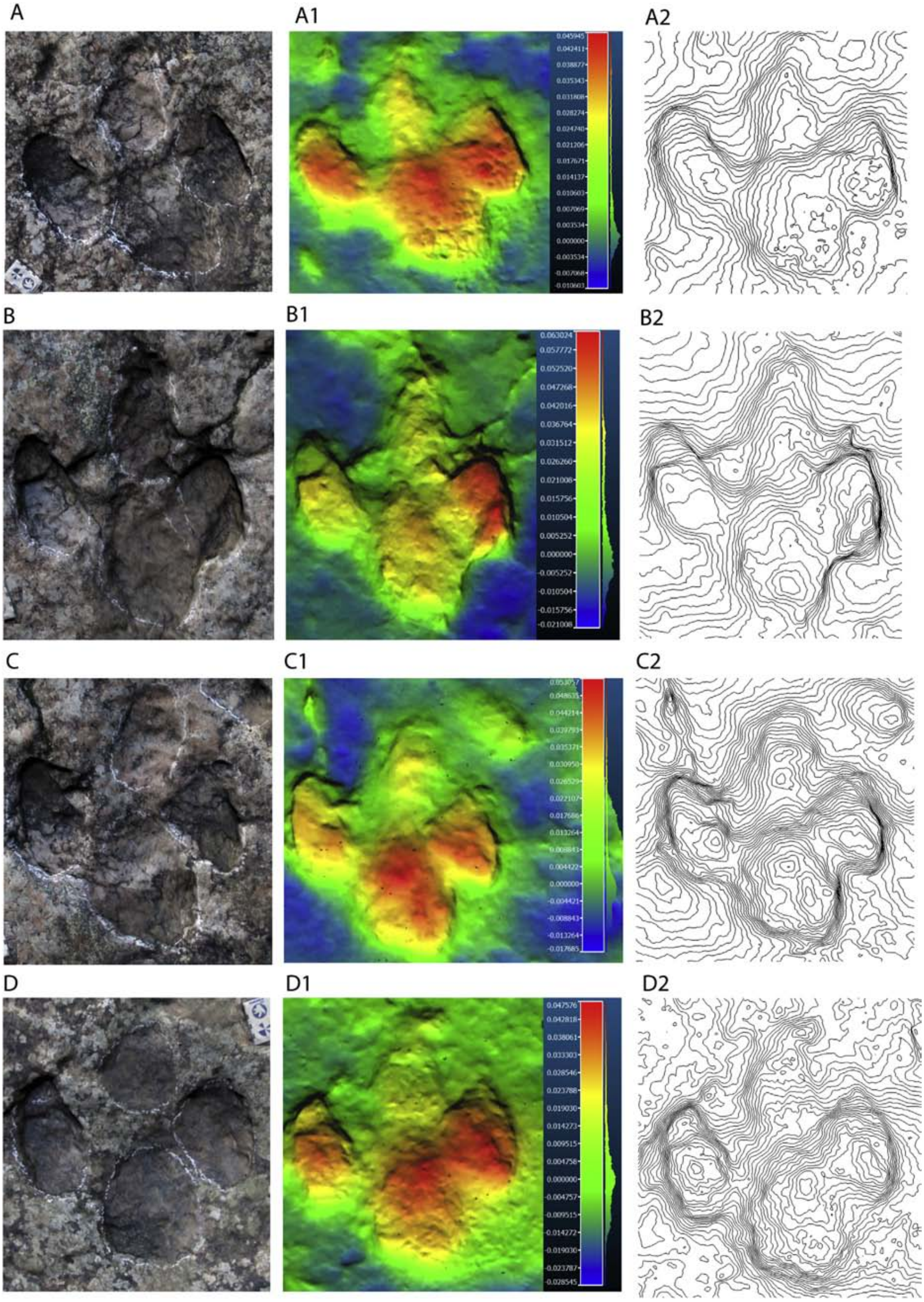



**Fig. 4.** Right tracks in A-D) Field photos of BLC1.6, BLC1.8, BLC1.28 and BLC1.30 respectively, scale bar 8 cm; A1-D1)height map of right tracks BLC1.6, BLC1.8, BLC1.28 and BLC1.30 respectively calculated in CloudCompare, colour scale bar in metres; A2-D2) Isolines of height (Z coordinate) of right tracks BLC1.6, BLC1.8, BLC1.28 and BLC1.30 respectively, generated using the free software Paraview. Each track displays a contour line every centimetre in order to provide a dense and objective outline of the right track morphologies. Tracks recall the *Caririchnium lotus* quadripartite and well discernible shape, with subparallel disposition and equal lengths of digits II and IV impressions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)


A
A1
A2
B
B1
B2
C
C1
C2
D
D1
D2

obtained from the best-preserved tracks (right: BLC1.6, BLC1.8, BLC1.28, BLC1.30; left: BLC1.7, BLC1.9, BLC1.11, BLC1.29).

Field photos were taken with Canon Power Shot S5IS camera (focal length 35 mm, resolution 3264 × 2448). Photogrammetry was undertaken following the general methodology explained in Mallison and Wings (2014) and terminology was used following Lockley, McCrea, and Buckley (2015). Point clouds were processed in Agisoft Photoscan standard version 1.1.4. build 2021software (http://www.agisoft.ru/) from a minimum of 10 to a maximum of 30 photos per track. 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 profile) 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 at a 0.25 cm distance according to maximum and minimum heights of the plane where tracks are. Pace length (PL), stride length (SL) and trackmaker velocity (Alexander, 1976) were estimated from the trackway DOM. The ratio of short/long pes pace length (*sensu* Lockley et al., 1994) was used as a numerical aid to compare the degree of gait irregularity. Track length (TL), track width (TW), interdigital angle (IDA) and a new parameter, interdigital width (IDW) were measured from 3-D models in Paraview 4.4.0. We developed the limping hypothesis on the basis of observation and quantification of an irregular gait in the BLC1 trackway. To test this hypothesis, we carefully examined each track in search of morphological clues. The left tracks were consistently deemed qualitatively different in the disposition of digit II with respect to that of right tracks. In this specific case of the BLC1 trackway, measurement of the interdigital angle between digits II-III impressions in left tracks was problematic due to the unclear orientation of digit II. Therefore, we developed a new parameter (IDW) exclusively for this case of the BLC1 trackway in order to quantify the qualitatively evident morphological difference in left tracks digit II impressions with respect to the contralateral counterpart. Although we acknowledge the confusion that may be generated by adding new parameters in the already established ichnological methodology (i.e., interdigital angles have been used as a diagnostic parameter with a large consensus), this parameter is simple to reproduce and is statistically significant in this restricted example. Unlike the interdigital angle parameter (IDA), the interdigital width (IDW) does not require knowledge of the orientation of the digits because it measures the separation between the medial/lateral edges of digit III and medial/lateral edges of digits II/IV. The IDW between digits II-III and III-IV impressions is determined by the perpendicular segment to the track middle line, found on the first contour line outside one of the hypexes (Fig.3). The higher the value of the IDW parameter, the bigger the interdigital distance. We restrict the use of the IDW parameter to this specific case of the BLC1 trackway to quantify the morphological differences that we observed qualitatively. To more broadly apply this parameter, future studies should further test the repeatability and reliability of this parameter in a more explicit methodological study, which is beyond the scope of the present work.

Relative depths of the metatarsodigital pad impression (DH) and digits II (DII), III (DIII), IV (DIV) digits impressions were calculated using Cloudcompare (v.2.6.1http://www.danielgm.net/cc/) in order to generalize the qualitative distribution within the track. Pace, stride lengths, track lengths, track widths, interdigital angles and interdigital widths were measured through ImageJ software (http://imagej.nih.gov/ij/). Statistical differences in the pace lengths and in the averages of the interdigital width parameter between right and left tracks were compared through the two-paired sample statistic analysis, suited to testing the hypothesis that the left pace length was consistently smaller than the right paired pace length and whether this difference might be linked to a cause. The test is used to compare two population means, where there are two samples in which observations in one sample (left pes morphologies) can be paired with observations in the other sample (right pes morphologies). Tracks BLC1.2, BLC1.26 and BLC1.31 were excluded because the corresponding paired tracks BLC1.1, BLC1.25 and BLC1.32 are either absent or preserved as partial prints in the tracksite. The statistical tests also took into account the 11 pairs of tracks (11 for the left and 11 for the right pedes impressions).

## 4. Results

The Barranco de La Canal-1 trackway (BLC1) measures 25 m in length and it is the longest trackway at the site. The trackway consists of 31 pes tracks, 25 of which are well preserved and could be measured (Tables 1 and 2). Manus tracks are observed in front of three of the pes tracks (BLC1.7, BLC1.11, BLC1.12).

Photogrammetric models undertaken on 25 out of 31 pes tracks of the BLC1 show a general well discernible morphology that fits the typical ornithopod track morphotype, which is mesaxonic, tridactyl with three stout and broad spreading toes ending in blunt hoof-mark toes and generally symmetric (*sensu* Pérez-Lorente, 2001; Thulborn, 1990). The tracks also display a quadripartite division corresponding to the pes anatomy (single pad print per digit and a subtriangular to rounded metatarsodigital pad impression). The common track shape is hexagonal because of the notches developing from the proximal parts of digits II and IV. The tracks are interpreted as true tracks because of the presence of clear blunt hoof marks in some of the tracks (e.g. track BLC1.16) and of the distinct outline of the entire track. The average track length (TL) and width (TW) range from 41.3 to 41.7 cm and from 38.1 to 40.0 cm respectively, resulting in a TL/TW index of ~1. The BLC1 tracks do not present evidence of sediment deformation such as displacement rims or mud collapse within the digits, although there is a low degree of homogenous erosion (probably current). The average pes stride length (SL) is 185 cm (for both sides of the trackway) and the average pes pace length (PL) is 94.5 cm ($n = 25$). However, the pace is uneven, 98.3 cm for the right-left pes pace length (range of 76.5–107.7 cm) and 90.7 cm for the left-right pes pace length (range 83.6–97.3 cm) (Tables 1 and 2). The "two-sample paired test" statistical analysis undertaken resulted in $t = 2516$; $p = 0{,}030596$ with 95% confidence level, therefore the left pace length was consistently smaller than the right paired pace length, showing a 81.8% of pace-shortening occurrence along the trackway (9 out of 11 paired paces) and displaying a 92% of gait irregularity (pace length ratio *sensu* Lockley et al., 1994). The BLC1 trackway can be divided into five segments that coincide with major orientation changes and variations in the external trackway widths (Fig. 2). Velocity estimations were calculated for each of these segments (Fig. 2) and resulted in: 1) 1.106 m/s; 2) 1.214 m/s; 3) 1.171 m/s; 4) 1.209 m/s; 5) 0.998 m/s following the Alexander's (1976) formula

**Fig. 5.** Left tracks in A-D) Field photos of left tracks BLC1.7, BLC1.9, BLC1.11 and BLC1.29 respectively, scale bar 8 cm; A1-D1)height map of left tracks BLC1.7, BLC1.9, BLC1.11 and BLC1.29 respectively calculated in CloudCompare, colour scale bar in metres; A2-D2) Isolines of height (Z coordinate) of right tracks BLC1.7, BLC1.9, BLC1.11 and BLC1.29 respectively, generated using the free software Paraview. Each track displays a contour line every centimetre in order to provide a dense and objective outline of the left track morphologies. Left tracks recall the *Caririchnium magnificum* or *C.* isp morphology, in which the metatarsodigital pad impression in laterally compressed and bigger in size. Digits II and IV impressions are divergently positioned and unequal in size and digit III is usually faintly impressed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(standard deviation ± 0.09).

Besides the statistically significant of pace length irregularity, morphological differences between right and left pes tracks were clearly observed in the BLC1 trackway. These include: 1) the shape of the metatarsodigital pad impression; 2) the degree of symmetry between impressions of digits II and IV (notch development); 3) the interdigital width (IDW) and interdigital angles (IDA), where measurable, between II-III and III-IV and 4) the depth distribution and values for metatarsodigital pad (DH) and impressions of digits II, III and IV (DII, DIII, DIV, see Tables 1 and 2 for measurements).

The shape of metatarsodigital pad impression in the right pes tracks ($n = 13$, Fig. 4, Table 1) is rounded to subtriangular, easily discernible in all tracks. It divides the track space into two even areas in which the antero-posterior length of the metatarsodigital pad impression equals that of impression of digit III. The notches that develop from the proximal parts of both impressions of digit II and IV toward the metatarsodigital pad impression region are very symmetric and consistent in all the right tracks, giving the impressions of digits II and IV an overall comparable geometry and morphology, being all three digit impressions straight-pointing (Fig. 4 A2-D2). Noteworthy features of right tracks are the subparallel orientation of digits II and III impressions (IDA range 0°–35°; IDW range 2.06–5.06 cm, Table 1) and the slight angulation and higher distance range between digits III and IV impressions (IDA range 28°–38°; IDW range 2.24–7.69, Table 1). Depth distribution appears qualitatively homogenous within the track. Maximum depths values are recorded in the metatarsodigital pad impression (range 2.2–6.1 cm), while digits II, III and IV impressions displayed the same average and range of depths (range 1.5–5.6 cm) (Fig. 4 A1-D1, Table 1).

The left pes tracks ($n = 12$, Fig. 5, Table 2) shape of metatarsodigital pad impression is laterally compressed and large, suboval in shape. Visually, it occupies more than half of the track area and it is antero-posteriorly longer thatdigit III impression. The notches developing from the proximal parts of both digits II and IV impressions toward the metatarsodigital pad impression region are not symmetrically organized. The notch that forms from digit II to the metatarsodigital pad impressions is steeper than the one that forms from digit IV impression and it is usually closer to the distal end of the metatarsodigital pad impression. Further important features of left tracks are the asymmetric arrangement and dissimilarity in shape and lengths of digits II and IV impressions, also evidenced by the divergence in the interdigital widths measurement. The interdigital angle between digits II and III impressions is not confidently measured since the arrangement and orientation of digit II impression is not clear also because of a more pronounced inward rotation of digit III impression (IDA range 13°–24°; IDW rage from 1.35 to 3.04). Interdigital angle range between digits III and IV impressions is similar to the right tracks one (IDA range 28°–42°), while IDW range is 4.53–11.31 cm (Fig. 5 A3-D3). Depth distribution and ranges within the left track are quite similar (DH range 2.3–7.0 cm, DII range 2.0–7.0 cm; DIII range 0.5–4.0 cm; DIV range 1.9–6.1 cm), (Fig. 5 A2-D2, Table 2).

In summary, the BLC1 trackmaker shows a 92% ratio of gait irregularity (*sensu* Lockley et al., 1994), corresponding to an 8% difference between the left-right (short) and right-left (long) consecutive steps in 81.8% of the footfalls, resulted in a statistical significance. Left tracks IDA II-III range (13°–24°) fall into the right tracks range (0°–35°), although this measurement is doubtful due to the unclear orientation of left digit II impression. Left and right tracks IDA III-IV range is very similar (20°–42°). More importantly, IDW for II-III and III-IV distances in left and right tracks were tested in the two-paired sample analysis and both resulted statistically significant in 95% of confidence level (two-paired sample test for IDW II-III: $t = 4.43$; $p = 0.0012$ and for IDW III-IV: $t = 3.36$; $p = 0.007$).

## 5. Discussion

The Barranco de La Canal-1 tracks are located in a decametric, fine-grained non-cohesive sandstone that lacks clear sedimentary structures (e.g., ripples, mud cracks, dunes). The tracks break the sandy layer and do not display sedimentary deformation structures, such as displacement rims, mud collapse, interdigital mud rims, which are often substrate-controlled features (Falkingham & Gatesy, 2014; Kuban, 1989; Razzolini et al., 2014; Scrivner & Bottjer, 1986). If erosion of the sediment is considered, it is simulated that tracks emplaced in a sufficiently deep sediment of homogenous composition and subjected to conditions of light and uniform erosion usually retain their basic dimensions and shapes (Henderson, 2006). Although it is true that a wide number of external factors that influence track morphology and the trackway quality can be either contemporaneous or post-depositional in origin (Schulp, 2002), a selective weathering on digit II impression of left tracks is unlikely in such a narrow trackway. The possibility that the BLC1 trackmaker was crossing different substrate consistencies throughout the tracksite, causing morphological changes according to the soil response (Dai et al., 2015; Manning, 2004; Milan & Bromley, 2006; Padian & Olsen, 1984) has also to be taken into consideration. Nevertheless, considering the sinuosity of the trackway, if the sediment was characterized by different consistencies, the track morphologies would uniformly or gradually display the bias caused by the trackmaker's trampling on the substrate (*sensu* Razzolini et al., 2014).

The Barranco de La Canal-1 trackway geometry shows that the right-left pace length is8% longer than the left-right pace length. This observation is usually quantified by the ratio of the average between short and long steps: the farther from the 1/1 ratio (equidimensional consecutive steps), the higher the degree of asymmetric movement. The alternating pes pace length noted and mentioned in Casanovas et al. (1995) and Perez-Lorente et al. (2003) is here quantified in a ratio of short/long pace length of 92%, such variation can be explained by an abnormal gait, such as a limping (Dantas et al., 1994; Ishigaki & Lockley, 2010; Lockley et al., 1994; Reineck & Flemming, 1997). However, left and right pes stride lengths in the BLC1 trackway show identical values for both sides (185 cm), despite the differences in the length of consecutive step (Tables 1 and 2). This stride length regularity is linked to a bipedal and narrow gait, since it is not usually visible in quadrupedal trackways (Lockley et al., 1994). Velocity variations calculated here for every turning segment in the trackway indicates that the animal was not significantly accelerating/decelerating along the trackway and that its locomotion was steady. Although we agree that trackmaker's behaviour can bias the trackway geometry, as shown by the recorded irregularities on pace lengths producing "anomalies" in the tracks that are not necessarily linked to a foot injury (McCrea et al., 2015), the noticeable difference on the placement of left digit II impressions with respect to the contralateral counterpart (Figs. 3–5) cannot be fully discarded as the causation of the irregular gait. The fact that limb dynamics (*sensu* Falkingham, 2014) is not playing a significant role in causing morphological differences recorded in right and left tracks is also shown through depth analyses, which resulted in similar values for both right and left tracks. Therefore, from our results, we believe that recorded significantly different morphologies on right and left tracks (left digit II impression placement with respect to the right digit II impression) depend on the foot anatomy of the trackmaker rather than being a consequence of the turnings and slight accelerations-decelerations recorded in the dynamic estimations.

The Barranco de La Canal-1 tracks have been identified as *Caririchnium lotus* (Díaz-Martínez et al., 2015), although, it is worth mentioning that Díaz-Martínez (2013) suggested that if the

Barranco de La Canal-1 right and left tracks were analysed separately, they could be easily assigned to different *Caririchnium* ichnospecies (*Caririchnium magnificum*, *C. lotus* and *C.* isp). Right pes tracks closely resemble those of *Caririchnium lotus* described by Xing, Wang, Pan, and Chen (2007; 2012).

Parameters such as the quadripartite subdivision of the track geometry, the subequal lengths and very similar morphologies of digit II and IV impressions and the subtriangular metatatarsodigital pad impression characterizing right tracks and more specifically, the shapes observed in tracks BLC1.6, BLC1.8, BLC1.28, BLC1.30 (Fig. 4), all agree with *C. lotus* assignation (Díaz-Martínez, 2013; Díaz-Martínez et al., 2015). The similar values of the interdigital widths and the homogenous depth distribution within the tracks point out the quadripartite and symmetrical large-ornithopod foot arrangement in the substrate (Lockley et al., 1994; Moratalla, Sanz, Melero, & Jiménez, 1989; Pérez-Lorente, 2003; Xing et al., 2007). On the contrary, left tracks do not display similarity between digit II and IV impressions as the statistically significant smaller values for the interdigital width parameter (digits II-III) pointed out, implying that digit II impression is closer to or overlapping that of digit III, displaying a different arrangement of digit II pad with respect the homologous on the right tracks. This dissimilarity in the distance between digit II-III impressions of the right and left pes tracks, confirmed by the statistical significance, suggests asymmetry in the pedal anatomy in the left pes. A similar scenario to the one we are proposing for the BLC1 tracks is found in the graphic scale of exostosis cases presented in Fig. 23 of McCrea et al. (2015), in which features characterizing the placement of the affected lateral digit involve interdigital width (short), interdigital angle (low) and digit length (small) parameters. Additional data such as the 92% degree of limping in the trackway (with the short step on the left side of the midline) also support an abnormal condition in the left digit II pad impression. This altered rhythm according to which the pes are placed along the trackway reveals a gait alteration, as it is shown by the 8% difference between right and left pes pace lengths.

Factors that can cause pathologies affecting morphology and locomotion have been recently dived into five categories (McCrea et al., 2015). We suggest that the abnormality in the left digit II pad belongs to the second category defined as a "biomechanical injury: defects due to physical damage to the body, possibly affecting the movement of the limp and its elements" (McCrea et al., 2015). The BLC1 trackmaker's injury was localized on its left digit II pad causing on the overall trackway geometry just a slight gait asymmetry (antalgic gait), small velocity changes and few differences in depth distributions within the tracks. A compensatory type of gait occurs where movement of the centre of gravity is such that there is an accommodation in the gait pattern to minimize muscle effort by the affected leg (Harrington, 2005).

Lockley et al. (1994) noted a trackway in which the shorter step was recorded on the opposite side to the supposed injured hind limb. On the contrary, in the Barranco de la Canal-1 trackway we suggest an antalgic gait for the individual, attempting to take less weight on the affected limb, shortening the duration of the support phase on the injured side (Harrington, 2005) and extending the pace length of the normal side. It would be mechanically coherent and convenient to have the shorter step (left-right) on the same side of the pedal injury (left digit II), since the right hind limb could still use all of its muscular strength to take the longer step (right-left).

## 6. Conclusions

A long trackway of *Caririchnium lotus* from the Barranco de la Canal-1 site (NW Cameros Basin, La Rioja, Spain) is here restudied using LiDAR and a photogrammetric-based approach. Previous work on the tracksite observed an asymmetric gait pattern in this 25-m-long trackway (Casanovas et al., 1995; Pérez-Lorente, 2003), which has been subject to in depth analysis for the first time and quantified in a 92% ratio of gait irregularity, corresponding to an 8% difference between the left-right (short) and right-left (long) consecutive steps in the 81.8% of the footfalls. Furthermore, 3-D photogrammetric models together with quantitative analyses undertaken on all the digital outcrop model point to a difference in the morphology of right and left tracks. These statistically significant differences refer to a distinct shape and placement of digit II impression with respect to digit III impression. The significant morphological and quantitative differences recorded between the right and left pes tracks suggest that an injury on the left digit II pad resulted in a pathology causing an antalgic limping behaviour. Moreover, it is also suggested that due to the low percentage in the discrepancy between consecutive steps, the pathological or abnormal condition inferred for digit II pad of the left track did not significantly affect the locomotion of the trackmaker. 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. The BLC 1 trackway adds new data on the occurrences of ichnopathologies in ornithopod dinosaurs, scarcely documented with respect to those relative to theropod dinosaurs.

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## References

Abel, O. (1935). *Vorzeitliche Lebenspuren* (pp. 1–644). Jena: Gustav Fischer.

Alexander, R. M. N. (1976). Estimates of speeds of dinosaurs. *Nature, 261*, 129–130.

Anné, J., Wogelius, R. A., Edwards, N. P., Tumarkin-Deratzian, A. R., Sellers, W. I., Bergmann, U. … Manning, P. L. (2014). Synchrotron imaging reveals bone healing and remodelling strategies in extinct and extant vertebrates. *Journal of the Royal Society of Interface, 11*, 20140277 http://dx.doi.org/10.1098/rsif.2014.0277.

Avanzini, M., Piñuela, L., & García Ramos, J. C. (2008). Theropod palaeopathology inferred from a Late Jurassic trackway, Asturias (N. Spain). *Oryctos, 8*, 71–75.

Bates, K. T., Manning, P. L., Vila, B., & Hodgetts, D. (2008). Three-dimensional modelling and analysis of dinosaur trackways. *Palaeontology, 51*, 999–1010.

Casanovas, M. L., Ezquerra, R., Fernández, A., Montero, D., Pérez-Lorente, F., Santafé, J. V. … Viera, L. V. (1995). El yacimiento de La Canal (Munilla, La Rioja, España). La variación de velocidad en función del tamaño del pie de los ornitópodos. *Zubía, 13*, 55–81.

Clemente, P. (2010). Review of the Upper Jurassic-Lower Cretaceous stratigraphy in western Cameros Basin,Northern Spain. *Revista de la Sociedad Geológica de España, 23*, 101–143.

Dai, H., Xing, L., Marty, D., Zhang, J., Persons, W. S., Hu, H. … Wang, F. (2015). Microbially-induced sedimentary wrinkle structures and possible impact of microbial mats for the enhanced preservation of dinosaur tracks from the Lower Cretaceous Jiaguan Formation near Qijiang (Chongqing, China). *Cretaceous Research, 53*, 98–109.

Dantas, P., Santos, V. F., Lockley, M. G., & Meyer, C. (1994). Footprint evidence for limping dinosaurs from the upper Jurassic of Portugal. *Gaia, 10*, 43–48.

Díaz-Martínez, I. (2013) (PhD thesis). *Icnitas de dinosaurios bípedos de La Rioja (Cuenca de Cameros, Cretácico Inferior): icnotaxonomía y aplicación paleobiológica* (Vol. 1, pp. 1–253). Universidad de La Rioja. xii + 632 pp, Vol. 2 (anexos).

Díaz-Martínez, I., Pereda-Suberbiola, X., Pérez-Lorente, F., & Canudo, J. I. (2015). Ichnotaxonomic review of large ornithopod dinosaur tracks: temporal and geographic implications. *PLoS One*. http://dx.doi.org/10.1371/journal.pone.0115477.

Doublet, S. (2004). *Contròles tectonique et climatique de l'enregistrement stratigraphique dans un bassin continental de rift: le bassin de Cameros*. Tésis doctoral. Inédito (pp. 1–512). Université de Bourgogne.

Doublet, S., García, J. P., Guiraud, M., & Menard, A. (2003). Wave dominated siliciclastic and carbonate sedimentation in a Lower Cretaceous lake (Cameros basin, northern Spain). *Journal of Iberian Geology, 29*, 11–30.

Falkingham, P. L. (2014). Interpreting ecology and behaviour from the vertebrate fossil track record. *Journal of Zoology, 292*, 222–228.

Falkingham, P. L., & Gatesy, S. M. (2014). The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences, 111*, 18279–18284.

Grambast-Fessard, N. (1980). Les charophytes du Montien de Mons (Belgique). *Review of Palaeobotany and Palynology, 30*, 67–88.

Harrington, I. J. (2005). Symptoms in the opposite or uninjured leg. In *Discussion paper prepared for the Workplace Safety and Insurance Appeals Tribunal, province of Ontario* (pp. 1–21).

Henderson, D. M. (2006). Simulated weathering of dinosaur tracks and the implications for their characterization. *Canadian Journal of Earth Sciences, 43*, 691–704.

Hernández-Samaniego, A., Ramírez Merino, J. I., Olivé Davó, A., Álvaro López, M., Ramírez del Pozo, J., Aguilar, M. J. … Meléndez Hevia, A. (1990). *Mapa Geológico de España a escala 1:50.000, Hoja 242, Munilla, Segunda Serie-Primera edición* (pp. 1–55). Hoja y Memoria: Instituto Tecnológico y GeoMinero de España.

Ishigaki, S. (1986). Dinosaur footprints of the Atlas mountains. *Nature Study, 32*, 6–9 (In Japanese).

Ishigaki, S. (1989). Footprints of swimming sauropods from Morocco. In G. G. Gillette, & M. G. Lockley (Eds.), *Dinosaur tracks and traces*. D.D. Gillette and M.G.Lockley (Eds.) Cambridge UniversityPress, 83–86.

Ishigaki, S., & Lockley, M. G. (2010). Didactyl, tridactyl and tetradactyl theropod trackways from the Lower Jurassic of Morocco: evidence of limping, labouring and other irregular gaits. *Historical Biology, 22*, 100–108.

Jenny, J., & Jossen, J. A. (1982). Découverte d'empreintes de pas de Dinosauriens dans le Jurassique inférieur (Pleinsbachian) du Haut Atlas central (Maroc). *Compte Rendu de l'Académie de Sciences, 294*, 223–226.

Kneuper-Haack, F. (1966). Ostracoden aus dem Wealden der Sierra de los Cameros (Nordwestliche Iberische Ketten). In *Beih. Geol. Jb* (Vol. 44, pp. 165–209).

Kuban, G. J. (1989). Elongate dinosaur tracks. In D. D. Gillette, & Y. M. G. Lockley (Eds.), *Dinosaur tracks and traces* (pp. 57–72). Cambridge University Press.

Lockley, M. G., Hunt, A. P., Moratalla, J., & Matsukawa, M. (1994). Limping Dinosaurs? Trackway evidence for abnormal gaits. *Ichnos, 3*, 193–202.

Lockley, M. G., McCrea, R. T., & Buckley, L. G. (2015). A review of dinosaur track occurrences from the Morrison Formation in the type area around Dinosaur Ridge. *Palaeogeography, Palaeoclimatology, Palaeoecology, 433*, 10–19.

Mallison, H., & Wings, O. (2014). Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques, 12*, 1–31.

Manning, P. L. (2004). A new approach to the analysis and interpretation of tracks: examples from the Dinosauria. In D. McIlroy (Ed.), *Geological Society,London, Special Publications: Vol. 228. The application of ichnology to palaeoenvironmental and stratigraphic analysis* (pp. 93–123).

Martín-Closas, C. (1991). *Els caròfits del Cretaci inferior de les conques periferiques del Bloc de l'Ebre*. Col·lecció de Tesis doctorals Microfitxades, numero 904 (pp. 1–581). Publicacions de la Universitat de Barcelona.

Mas, J. R., Benito, M. I., Arribas, J., Alonso, A., Arribas, M. E., Lohmann, K. C. … Omodeo, S. (2011). Evolution of an intra-plate rift basin: the Latest Jurassic-Early Cretaceous Cameros Basin (Northwest Iberian ranges, North Spain). In *Post-Meeting Field trips28th IAS Meeting, Zaragoza. Geo-Guías 8. Sociedad Geológica de España, Zaragoza* (pp. 119–154).

Más, R., Benito, I., Arribas, J., Serrano, A., Guimerá, J., Alonso, A. … Alonso-Azcarate, J. (2002). La Cuenca de Cameros: Desde la extensión Finijurásica –Eocretácica a la inversión terciaria-Implicaciones en la exploración de hidrocarburos. *Zubía, 14*, 9–64.

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

McCrea, R. T., Buckley, L. G., Farlow, J. O., Lockley, M. G., Currie, P. J., Matthews, N. A. … Pemberton, S. G. (2014a). A 'terror of tyrannosaurs': the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. *PLoS One, 9*, e103613. http://dx.doi.org/10.1371/journal.pone.0103613.

McCrea, R. T., Buckley, L. G., Plint, A. G., Currie, P. J., Haggart, J. W., Helm, C. W. … Pemberton, S. G. (2014b). A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus. *New Mexico Museum of Natural History and Sciences Bulletin, 52*, 5–93.

McCrea, R. T., Darren, H., Tanke, D. H., Lisa, G., Buckley, L. G., Martin, G. … Breithaupt, B. H. (2015). Vertebrate Ichnopathology: pathologies inferredfrom dinosaur tracks and trackways from the Mesozoic. *Ichnos, 22*, 235–260. http://dx.doi.org/10.1080/10420940.2015.1064408.

Milan, J., & Bromley, R. G. (2006). True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology, 231*, 253–264.

Moratalla, J. J., Sanz, J. L., Melero, I., & Jiménez, S. (1989). Yacimientos paleoicnologicos de la Rioja: Huellas de dinosaurios. *Gobierno de la Rioja y Iberduero*, 1–95.

Padian, K., & Olsen, P. E. (1984). The fossil trackway *Pteraichnus*: not pterosaurian, but crocodilian. *Journal of Paleontology, 58*, 178–184.

Pérez-Lorente, F. (2001). *Paleoicnología: los dinosaurios y sus Huellas en la Rioja; apuntes para los cursos y campos de trabaja de verano. Cultural Joven Gobierno de la Rioja y fundación caja Rioja* (pp. 1–227). Fundación Patrimonio Paleontológico de La Rioja.

Pérez-Lorente, F. (2003). Aportaciones de los yacimientos de La Barguilla, Santisol y Santa Juliana (Hornillos de Cameros, La Rioja. España). In *Dinosaurios y otros reptiles mesozoicos en España, Pérez-Lorente, F. coord* (pp. 161–194).

Razzolini, N. L., Vila, B., Castanera, D., Falkingham, P. L., Barco, J. L., Canudo, J. I. … Galobart, À. (2014). Intra-trackway morphological variations due to substrate consistency: the El Frontal Dinosaur tracksite (Lower Cretaceous, Spain). *PLoS One, 9*, e93708. http://dx.doi.org/10.1371/journal.pone.0093708.

Rega, E., Holmes, R. B., & Tirabasso, A. (2010). Habitual locomotor behavior inferred from manual pathology in two Late Cretaceous chasmosaurine ceratopsid dinosaurs, Chasmosaurus irvinensis (CMN 41357) and Chasmosaurus belli (ROM 843). In *New perspectives on horned dinosaurs: The Ceratopsian Symposium at the Royal Tyrrell Museum* (pp. 340–354).

Reineck, H. E., & Flemming, W. B. (1997). Unusual tracks, traces, and other oddities. In *CaUL Farsch.-Inst. Senckenberg* (Vol. 20, pp. 349–360).

Rothschild, B. M., & Tanke, D. H. (1992). Paleopathology: Insights to lifestyle and health in the geological record. *Geoscience Canada, 19*, 73–82.

Rothschild, B. M., & Tanke, D. H. (2005). Theropod paleopathology: state-of-the-art review. In *The carnivorous dinosaurs* (pp. 351–365).

Schudack, M. E. (1987). Charophytenflora und fazielle Entwicklung der Grenzschichtenmariner Jura/Wealden in den Nordwestlichen Iberischen Ketten (mit Vergleichenzu Asturien und Kantabrien). *Palaeontographica Abteilung B, 204*, 1–108.

Schulp, A. S. (2002). The effects of tectonic deformation on dinosaur trackwaymorphology. Sargetia. *Acta Musei Devensis, Series Scientia Naturae, Deva, 19*, 27–32.

Scrivner, P. J., & Bottjer, D. J. (1986). Neogene avian and mammal tracks from Death Valley National Monument, California: their context, conservation and preservation. *Paleogeography, Paleoclimatology, Paleoecology, 57*, 285–331.

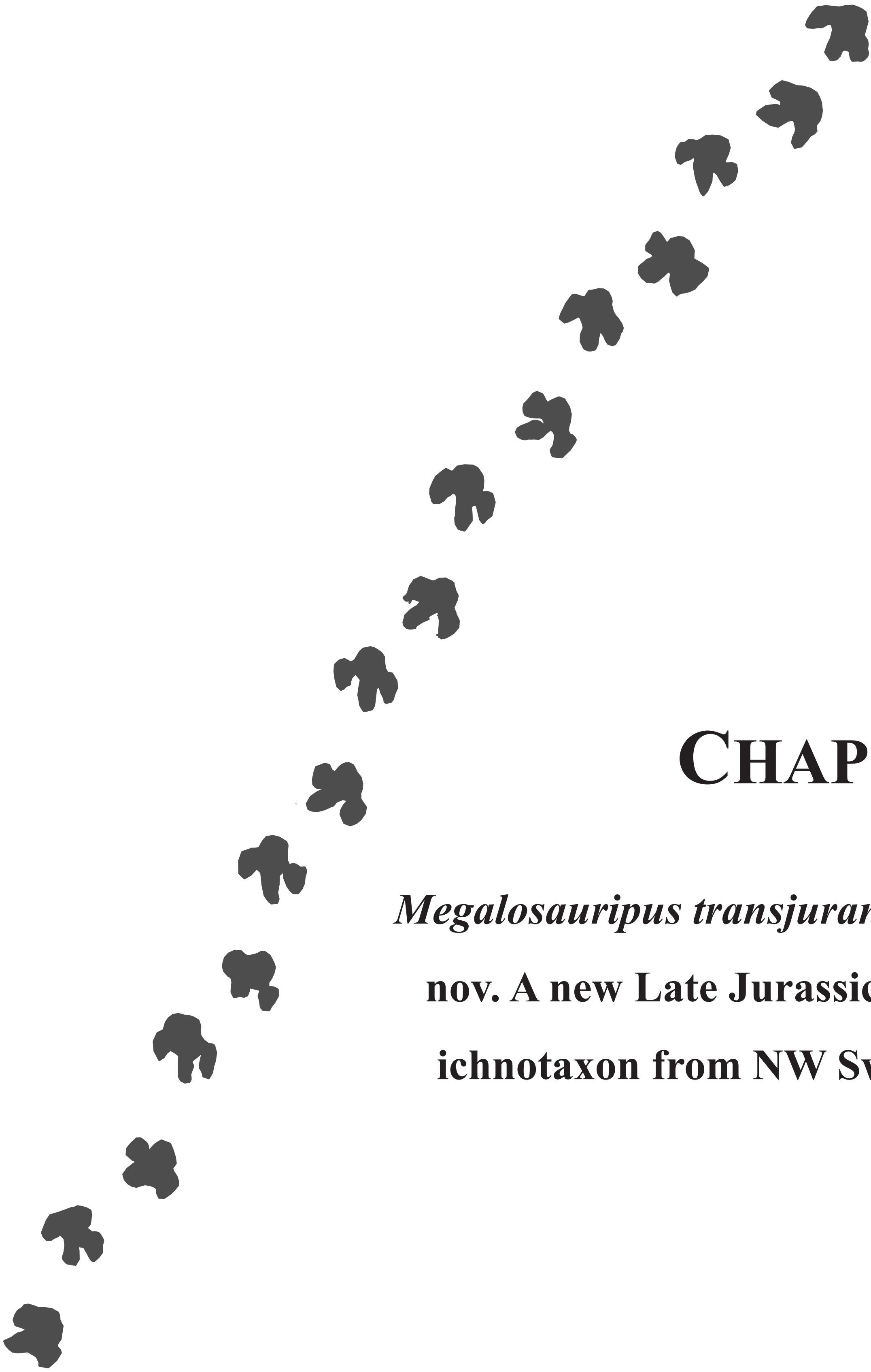
Tanke, D. H., & Rothschild, B. M. (1997). *Paleopathology. encyclopedia of dinosaurs* (pp. 525–530). San Diego: Academic Press.

Tanke, D. H., & Rothschild, B. M. (2002). Dinosores: an annotated bibliography of dinosaur paleopathology and related topics, 1838–2001. *New Mexico Museum of Natural History and Science*, 1–96. Bullettin 20.

Thulborn, T. (1990). *Dinosaur tracks* (pp. 1–410). London: Chapman and Hall.

Xing, L. D., Bell, P. R., Harris, J. D., & Currie, P. J. (2012). An unusual, three dimensionally preserved, large Hadrosauriform pes track from "Mid" Cretaceous Jiaguan Formation of Chongqing, China. *Acta Geologica Sinica, 86*, 304–312. English Edition.

Xing, L. D., Wang, F., Pan, S., & Chen, W. (2007). The discovery of dinosaur footprints from the middle Cretaceous Jiaguan formation of Qijiang county, Chonqing city. *Acta Geologica Sinica, 81*, 1591–1602 [in Chinese].



# CHAPTER 6

## *Megalosauripus transjurani* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland

## AUTHOR'S CONTRIBUTION

Razzolini, N.L. , Belvedere, M., Marty, D., Meyer, C., Paratte, G., Lovis, C., Cattin, M. *Megalosauripus transjurani* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland (Submitted to PLoSONE)

The author, N.L. Razzolini, measured and did the outline drawings of all the tracks, analysed the data, wrote the manuscript and prepared figures and tables and the electronic supplementary material.

TAXONOMIC DESCLAIMER

The name of the new ichnospecies described in Chapter 6 is not valid under the rules of the ICZN. The publication where it will be formally erected has been just submitted, and the name proposed here will be retained if possible.

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# Megalosauripus transjurani ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland

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| **Short Title:** | Megalosauripus tracks from the Late Jurassic of NW Switzerland |
| **Corresponding Author:** | Novella L. Razzolini<br>Institut Català de Paleontologia<br>Sabadell, Barcelona SPAIN |
| **Keywords:** | Tridactyl dinosaur track; track preservation; ichnotaxonomy; theropods; Kimmeridgian; Switzerland; photogrammetry; 3-D models; tidal flat |
| **Abstract:** | A new ichnospecies of a large theropod dinosaur, Megalosauripus transjurani, is described from the Reuchenette Formation (Early-Late Kimmeridgian, Late Jurassic) of NW Switzerland. It is based on very well-preserved and morphologically-distinct tracks (impressions) and several trackways, including different preservational types from different tracksites and horizons. All trackways were excavated along federal highway A16 near Courtedoux (Canton Jura) and systematically documented in the field including orthophotos and laserscans. The best-preserved tracks were recovered and additional tracks were casted. Megalosauripus transjurani is characterized by large tracks and notably an exceptionally large and round first phalangeal pad on the fourth digit (PIV1), that is connected with dIV and also forms the round heel area. Due to this combination of features, M. transjurani clearly is of theropod (and not ornithopod) origin. M. transjurani is compared to other Megalosauripus tracks and similar ichnotaxa and unassigned tracks from the Early Jurassic to Early Cretaceous. It is clearly different from other ichnogenera assigned to large theropods such as Eubrontes from the Late Triassic and Early Jurassic or Megalosauripus-Megalosauropus-Bueckeburgichnus and Therangospodus (oncalensis, pandemicus) tracks from the Late Jurassic and Early Cretaceous. A second tridactyl morphotype (called Morphotype II) is different from Megalosauripus transjurani tracks in displaying a subsymmetric, longer than wide (sometimes almost as wide as long), with blunt toes impressions and no evidence for discrete phalangeal pads and claw marks. Frequently, Morphotype II is found in association with M. transjurani trackways and it is also recognized in trackways that are assigned to M. transjurani. In these cases, Morphotype II recalls Therangospodus pandemicus morphology, suggesting that these Morphotype II tracks can be considered as an intra-trackway preservational variant and a morphological continuum of M. transjurani. Furthermore, a great similarity between Morphotype II recalling Therangospodus pandemicus and the tracks assigned to Megalosauripus isp. only on the ichnogeneric level because poorly-preserved, is observed. Therefore, it is suggested that in these cases, Therangospodus pandemicus may be actually the preservational variant of Megalosauripus ichnogenus. Consequently, the possibility that the Megalosauripus-Therangospodus ichnoassociation may have been previously misinterpreted is here discussed. On the other hand, long trackways that consistently exhibit Morphotype II features along the whole trackway (notably blunt digits, absence of phalangeal pads), are also observed and tentatively assigned to cf. Iguanodontipus? (former Therangospodus) oncalensis. These trackways are interpreted to be produced by a different trackmaker, likely an ornithopod dinosaur. The high frequency of large theropod tracks in tidal-flat deposits of the Jura carbonate platform, associated with small tridactyl and tiny to medium-sized sauropod tracks has important implications for the dinosaur community and for palaeoenvironmental and palaeogeographical reconstructions. As with most other known occurrences of Megalosauripus tracks, M. tranjsuriani is found in coastal settings, which may reflect their preference for expanded carbonate flats where food was abundant. |

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# *Megalosauripus transjurani* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland

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**Author contributions:**
N.L. Razzolini, M. Belvedere, D. Marty and C.A. Meyer contributed material/analysis tools, analysed the data, wrote the manuscript, prepared figures and/or tables, reviewed drafts of the manuscript
D. Marty, G. Paratte, C. Lovis, and M. Cattin conducted fieldwork, analysed the trackways in the field (trackway interpretation, parameter measurements), drew the site maps, prepared figures and/or tables, reviewed drafts of the manuscript

**Keywords:**
Tridactyl dinosaur track;track preservation;ichnotaxonomy;theropods;Kimmeridgian;Switzerland;photogrammetry;3-D models;tidal flat
**Running title:** *Megalosauripus* tracks from the Late Jurassic of NW Switzerland

**Summary statement**
Late Jurassic, well-preserved, large theropod tracks are described and figured in detail including low-angle light photographs, interpretative outline drawings, measurements, and 3D photogrammetric models of selected tracks. This new material is compared to known ichnotaxa (*Megalosauripus, Therangospodus, Iberosauripus*) from the Middle Jurassic to Early Cretaceous. The overall morphological difference warrants the erection of a new ichnotaxon *Megalosauripus transjurani*. Furthermore, a second large tridactyl morphotype is described and discussed in detail.

**Institutional abbreviations**
MJSN: Musée jurassien des sciences naturelles, Porrentruy, Canton Jura, Switzerland
PALA16: Paléontologie A16, Section d'archéologie et paléontologie, Office de la culture, Porrentruy, Canton Jura, Switzerland.
NMS: Naturmuseum Solothurn

**Abstract**
A new ichnospecies of a large theropod dinosaur, *Megalosauripus transjurani*, is described from the Reuchenette Formation (Early–Late Kimmeridgian, Late Jurassic) of NW Switzerland. It is based on very well-preserved and morphologically-distinct tracks (impressions) and several trackways, including different preservational types from different tracksites and horizons. All trackways were excavated along federal highway A16 near Courtedoux (Canton Jura) and systematically documented in the field including orthophotos and laserscans. The best-preserved tracks were recovered and additional tracks were casted. *Megalosauripus transjurani* is characterized by large tracks and notably an exceptionally large and round first phalangeal pad on

the fourth digit (PIV1), that is connected with dIV and also forms the round heel area. Due to this combination of features, *M. transjurani* clearly is of theropod (and not ornithopod) origin. *M. transjurani* is compared to other *Megalosauripus* tracks and similar ichnotaxa and unassigned tracks from the Early Jurassic to Early Cretaceous. It is clearly different from other ichnogenera assigned to large theropods such as *Eubrontes* from the Late Triassic and Early Jurassic or *Megalosauripus–Megalosauropus–Bueckeburgichnus* and *Therangospodus* (*oncalensis*, *pandemicus*) tracks from the Late Jurassic and Early Cretaceous. A second tridactyl morphotype (called Morphotype II) is different from *Megalosauripus transjurani* tracks in displaying a subsymmetric, longer than wide (sometimes almost as wide as long), with blunt toes impressions and no evidence for discrete phalangeal pads and claw marks. Frequently, Morphotype II is found in association with *M. transjurani* trackways and it is also recognized in trackways that are assigned to *M. transjurani*. In these cases, Morphotype II recalls *Therangospodus pandemicus* morphology, suggesting that these Morphotype II tracks can be considered as an intra-trackway preservational variant and a morphological continuum of *M. transjurani*. Furthermore, a great similarity between Morphotype II recalling *Therangospodus pandemicus* and the tracks assigned to *Megalosauripus* isp. only on the ichnogeneric level because poorly-preserved, is observed. Therefore, it is suggested that in these cases, *Therangospodus pandemicus* may be actually the preservational variant of *Megalosauripus* ichnogenus. Consequently, the possibility that the *Megalosauripus–Therangospodus* ichnoassociation may have been previously misinterpreted is here discussed. On the other hand, long trackways that consistently exhibit Morphotype II features along the whole trackway (notably blunt digits, absence of phalangeal pads), are also observed and tentatively assigned to cf. *Iguanodontipus*? (former *Therangospodus*) *oncalensis*. These trackways are interpreted to be produced by a different trackmaker, likely an ornithopod dinosaur. The high frequency of large theropod tracks in tidal-flat deposits of the Jura carbonate platform, associated with small tridactyl and tiny to medium-sized sauropod tracks has important implications for the dinosaur community and for palaeoenvironmental and palaeogeographical reconstructions. As with most other known occurrences of *Megalosauripus* tracks, *M. tranjsuriani* is found in coastal settings, which may reflect their preference for expanded carbonate flats where food was abundant.

## 1. Introduction

*Megalosauripus* can be considered as one the most widespread Late Jurassic ichnotaxon made by large theropods in Europe, America, and Asia. However, its correct assignement and validity has been highly debated in the the last twebty years [1-6]. This is especially because this ichnotaxon represents the typical shape of a large theropod foot (tridactyl, longer than wide, narrow), which is morphologically conservative and therefore difficult to characterize and distinguish.

*Megalosauripus* is known from Late Jurassic to Early Cretaceous deposits, although it has also been described from the Middle Jurassic of Asia, North America and Europe [3, 7-9].

The ichnotaxonomical entanglement started in 1955, when Lessertisseur [10] coined the name *Megalosauripus* referring to an illustration of a track from the German collection of Ballerstedt, [11] and reproduced in Abel, [12] assumed to have been left by a megalosaur dinosaur. Because this track was named after the purported trackmaker, and no proper ichnotaxonomical description was provided, this ichnogenus was declared a *nomen nudum* in Lockley et al. [1] and formalized as *Megalosauripus* ichnogen. nov. in Lockley et al. [3]. Interestingly, Kuhn [13] erected the new ichnogenus *Bueckeburgichnus maximus* on the same illustration indicated as *Megalosauripus* in Lessertisseur [10]. For this reason, Thulborn [5] stated that *Megalosauripus* LESSERTISSEUR 1955 should be considered as a senior synonym of *Bueckeburgichnus*. In addition to the debate about the validity of the ichnotaxon *Megalosauripus* (see Lockley et al. [3] vs. Thulborn [5]), it also turns out that many descriptions are based rather poorly-preserved material that is in dire need of revision (see also Lallensack et al. [14]). The purpose of this paper is to describe various new, and well-preserved large tridactyl tracks from the Late Jurassic of Highway A16 (NW Switzerland) from a morphological point of view. Here we follow the use of *Megalosauripus sensu* Lockley et al. [3] because of the morphological affinity of the studied material with the definition of ichnogenus and the emended description by Fanti et al. [6].

We focus on a large sample of mostly well-preserved, large tridactyl tracks and trackways from the Late Jurassic of NW Switzerland. All studied material has been excavated between 2002 and 2011 and systematically documented by the team "Palaeontology A16" on tracksites located on the future course of Swiss federal highway A16, also named 'Transjurane Highway', and on one tracksite located outside the Highway in Porrentruy. A part of the material described herein is assigned to the ichnotaxon *Megalosauripus*. Based on the difference of the new material (notably the very large and rounded first phalange on dIV), a new ichnospecies *Megalosauripus transjurani* is erected for the *Megalosauripus*-type large theropod trackways from Highway A16 and some additional sites in the Swiss Jura Mountains. Detailed differential diagnoses are provided to underline the difference between previously described ichnotaxa and *Megalosauripus transjurani.* The herein described *Megalosauripus* tracks fall into a size range between 35 to 45 cm and are thus much smaller than many other *Megalosauripus* tracks [3,15].

Apart from *Megalosauripus*-type tracks, the new material also contains large tridactyl tracks, named 'Morphotype II' by Marty [16] on the base of qualitative features that differenciate it from *M. transjurani* tracks. This morphotype is observed in both the same stratigraphical level of *Megalosauripus transjurani* (frequently) and in levels where *Megalosauripus transjurani* is absent. In the same levels of *M. transjurani,* some Morphotype II trackways preserve track morphologies that retain features observed in tracks assigned to *Megalosauripus (transjurani)*. While in other occasions, trackways assigned to *M. transjurani* can preserve some poorly preserved morphologies that are very similar to Morphotype II. In these cases, Morphotype II strongly recalls *Therangospodus pandemicus* [17] morphology or else a very poorly preserved track that can be assigned to *Megalosauripus* only on the ichnogeneric level.

Differently, when found in stratigraphical levels where *M. transjurani* is absent, Morphotype II is consistently observed along very long trackways that do not display morphological variability. In these trackways, Morphotype II recalls the diagnosis of *Iguanodontipus? oncalensis* (former *Therangospodus oncalensis* [17]), from the type locality of Fuentesalvo (Soria, Spain) recently revised and emended [18].

*Therangospodus pandemicus* [17] and *Iguanodontipus? oncalensis* [18] are both characterized by the lack of a discrete phalangeal pad formula and claw marks. In this study, the former is considered to be a preservational variant of *Megalosauripus* morphologies, as it is observed along trackways assigned to *M. transjurani*. The latter is interpreted as the consequence of a fleshy trackmaker foot, since its morphology is consistenly retained along very long trackways. The implications for these qualitative and quantitative observations are that *Therangospodus pandemicus* appears to be a preservational continuum of tracks assigned to *M. transjurani*, since it is not substantially different from poorly preserved *Megalosauripus* tracks and that trackways assigned to *Iguanodontipus? oncalensis* are likely produced by a different trackmaker (ornithopod) being these morphologies the consequence of a different foot anatomy rather than the product of different substrate conditions or limb dynamics.

Consequently, the *Megalosauripus–Therangospodus* ichnoassociation reported worldwide from various Middle to Late Jurassic tidal flat deposits and interfingering facies [3,7,17, 19-21], assigned to a variety of local names [3-5, 17] and interpreted as the presence of two ichnogenera and probably two different theropod trackmakers is here rediscussed.

## 2. General setting

### 2.1Geographical and geological setting

The studied material comes from one tracksite in Porrentruy (POR–CPP) and from five tracksites located about 6 km to the west of Porrentruy (Ajoie district, Canton Jura, NW Switzerland) on the course of Swiss federal highway A16 (Fig 1). The latter five tracksites are situated on a plateau between Courtedoux and Chevenez, and were systematically excavated level-by-level by the team PALA16 from 2002 until 2011 [16, 22-24]. Today all Highway A16 tracksites are (partially) destroyed and covered up by Highway A16, which was opened for to traffic in 2014. The POR–CPP (a.k.a 'Dinotec') tracksite is located in Porrentruy in the backyard of a technical school called 'CPP' and was discovered in 2011 during the construction of an additional building. A part of this tracksite (backyard) is now protected and accessible to the public [25].

The study area belongs to the Tabular Jura Mountains, and is located at the eastern end of the Rhine-Bresse transfer zone between the Folded Jura Mountains to the south and east and the Upper Rhine Graben and Vosges Mountains to the north. Elevation is around 500 m and bedding is (sub)horizontal and affected by normal faults created by several tectonic phases during the Cenozoic [26-28].

### 2.2 Stratigraphy and palaeogeography

The studied trackways come from three different track-bearing laminite intervals (named lower, intermediate and upper track levels), separated by shallow marine marls and limestones including massive nerinean limestones [16, 29]. The lower track levels are also referred to as levels 500–550, the intermediate track levels as levels 1000–1100, and the upper ones as levels 1500–1650 (Fig 2).

The track-bearing sequences form part of the Reuchenette Formation [32,33]. Fossil markers such as abundantly occurring ammonites assign the levels Cymodoce to Mutabilis (Boreal) respectively Divisum to Acanthicum (Tethyan) biozones, i.e., late Early to Early Late Kimmeridgian [22, 29-31, 34]. Some of these ammonites were found in layers very close to the dinosaur track-bearing levels, and the age assignement is also confirmed with ostracods [35].

The sediments of the Reuchenette Formation were deposited at the northern margin of the oceanic Ligurian Tethys on a large, structurally complex carbonate platform, e.g. [36-38]. This Jura carbonate platform was at a palaeolatitude of around 30° N, at the threshold between the Paris Basin to the northwest and the Tethys Ocean to the south and thus influenced by both the tethyan and boreal realms, e.g., [31, 34, 36, 37, 39]. During the Kimmeridgian, the climate of the Jura carbonate platform was semi-arid subtropical to Mediterranean with strong seasonal differences between prolonged, warm, dry summers and relatively short, wet winters, e.g. [40-45]. The presence of freshwater on the platform is corroborated by the occurrence of charophytes [46, 47] and hybodontid shark remains that display an unusual freshwater isotopic signal [48].

The recurrence of dinosaur tracks and emersive phases during the Late Jurassic support the hypothesis – at least during sea-level lowstands – of prolonged periods of emersion of the Jura carbonate platform, which would have connected the larger terrestrial landmasses of the London-Brabant Massif in the northeast and/or the Massif Central in the southwest [16, 47, 49, 50].

## 2.3 Sedimentology and palaeoenvironment

The track-bearing intervals are thinly-bedded, laminated, tabular and platy, marly limestones, which locally have a slightly stromatolitic appearance with intercalations of thin layers of calcareous marls [16]. Generally, the microfacies of the laminites is quite homogeneous and can be described as mudstone to wackestone *sensu* Dunham [51], or dolobiopelmicrite *sensu* Folk [52]; the most common biogenic sedimentary structures are (microbial) lamination and invertebrate burrows [16, 22].

The track-bearing laminites were deposited in inter- to supratidal flat or supratidal marsh palaeoenvironments, characterized by an exposure index higher than 60–90% [16]. This is indicated by macroscopic (stromatolitic lamination, desiccation cracks, wave ripples, invertebrate burrows) and microscopic (e.g., cryptmicrobial lamination, fenestrae, brecciation) sedimentological features [16, 22, 53]. Marty [16] suggested that this supratidal-flat palaeoenvironment was located several hundred meters away from the coastline towards the open marine realm or an internal lagoon, and that for most of the time was characterized by restricted and hostile conditions, which may have been interrupted by periods of rain or storm surges, and that during or rather at the end of such periods of wetting, dinosaur tracks were recorded.

The lower track levels (500, green band in Fig 2) have a thickness of about 0.6 m and contain at least 8 track-bearing track levels [16]. The intermediate track levels (1000, red band in Fig 2) with a thickness of around 1 m and at least 15 track-bearing levels are the track-richest interval, whereas the upper track levels are about 30-40 thick cm and contain only 2–3 track levels (1500, blue band in Fig 2). The lower track levels are suggested to represent one elementary sequence (Marty 2008), and the intermediate levels 1–2 elementary sequences of each 20 kyr. The sequence boundary Kim4 was placed in the intermediate levels by Colombié & Rameil [57] in fig. 10, but probably corresponds to the upper track-bearing levels [55], which again likely represent one elementary sequence.

## 3. Material and methods

### 3.4 Methodology

In the field, all trackways were excavated, labelled, and mapped at a 1:20 scale. The best tracks were collected on slabs and/or casted. Recovered slabs were stabilized and prepared, and polyester copies were produced. Laserscans with a resolution in the order of several mm and orthophotos with a resolution of around 2 mm were made of several of the studied track-bearing levels (e.g., BEB500, BSY1040, SCR1000). Additionally, selected tracks of the trackway BEB-500-T7 were scanned at a sub-mm resolution with a FARO Platinum Scanarm hand-scanner.

In 2016, measurements of original tracks and casted tracks (by NLR), and outline drawings on transparent Folex monofilm and vectorisation (with Adobe Illustrator) were made. Additionally, high-resolution photogrammetric models were generated from the collected specimens and the casts in the collection, in order allow a detailed documentation and morphological study.

Studied specimens numbers: MJSN BEB011-r58 (BEB500-TR7-L2, R2), MJSN BEB011-r54 (BEB500-TR7-R7), MJSN BEB011-r56 (BEB500-TR7-L10, R10, L11), MJSN SCR008-r131 (SCR1000-T18-R1), MJSN SCR008-r129 (SCR1000-T23-R1, L2, R2), MJSN BSY008-330 (BSY1035-T6-L2), MJSN BSY008-339 (BSY1040-T1-R1),MJSN BSY008-338 (BSY1040-T1-L2),MJSN BSY008-337 (BSY1040-T1-R2),MJSN BSY008-336 (BSY1040-T1-L3),MJSN BSY008-334 (BSY1040-T9-R3),MJSN TCH008-r2 (TCH1000-TR1-R2, L3, R3),MJSN TCH008-r4 (TCH1000-TR2-R9, L10, R10), MJSN TCH007-r72 (TCH1000-TR2-L12, R12, L13), MJSN TCH006-1348 (TCH1015-T1-L2), MJSN TCH006-1357 (TCH1015-T1-R3),MJSN TCH006-1366 (TCH1020-T1-R2), MJSN TCH006-1337 (TCH1020-T2-L1), MJSN TCH006-1355 (TCH1020-T2-R1), MJSN TCH006-1140 (TCH1020-T2-L2), MJSN TCH006-1137 (TCH1020-T2-R2), MJSN TCH006-1329 (TCH1025-T1-L4, TCH1025-T2-L1), MJSN TCH006-1023 (TCH1030-T1-R4), MJSN TCH006-1087 (TCH1030-T2-R2), MJSN TCH006-1022 (TCH1030-T2-L3), MJSN TCH006-1034 (TCH1030-T2-R3), MJSN TCH006-1024 (TCH1030-T3-L1), MJSN TCH006-1319 (TCH1030-T6-L1), MJSN TCH006-1317 (TCH1030-T7-L2).

All the collected and/or casted specimens, as well as the digital 3D data, are accessible at the PALA16 collections (Office de la Culture, 2900, Porrentruy, Switzerland) and will be transferred to the JURASSICA Muséum (Route de Fontenais 21, 2900, Porrentruy, Switzerland). No permits were required for the described study, which complied with all relevant regulations.

#### 3.4.1 Track & trackway parameter measurements in the field.

In the field, track (Fig3A) and trackway parameters (Fig 3D) were systematically measured following standard ichnological terminology e.g. [16, 67, 68]. All data,including mean and standard deviations per trackwayparameters, are provided in S1. The following abbreviations are used: PL: Pes Length; PW: Pes Width; PaL: Pace Length; SL: Stride Length; PA: Pace Angulation; WAP: Width of the Angulation Pattern.

For trackway parameter measurements, the distal end of the third digit (and not the tip of the claw) is used as reference point. Tracks directed outward with respect to the line connecting it with the consecutive track (the stride) have an outward (positive) rotation and those directed inward an inward (negative) rotation. For the quantification of trackway gauge (trackway width), the ratio between the width of the angulation pattern and the corresponding track length ([WAP/PL]-ratio) is used (see also [16, 56]). All studied theropod trackways have a [WAP/PL]-ratio< 1.0 and are thus narrow gauge. Therefore, trackways with a [WAP/PL]-ratio < 0.5 are considered as “very narrow gauge” whereas trackways with a [WAP/PL]-ratio > 0.5 (the minority of the trackways) are described as “comparatively wide” in comparison with the other trackways; they are still narrow gauge in as far that pes tracks intersect or touch the trackway midline.

Trackways as interpreted in the field were mapped and are illustrated by outline drawings exhibiting the distinct and essential characters of the tracks. In the trackway outline drawings, the internal track outline marks the actual imprint (impression) of the foot and defines the track dimensions (length, width), whereas the external track outline and the external limit of the displacement rim define the extramorphological features of the tracks (Fig 3A).

3.4.2 Track measurements in the collection (S1)

Detailed track measurements (phalanges, claws) were carried out on original material and casts (copies) of the holotype, paratypes and referred specimens stored in the PALA16 collection and this data is given in Table 1. Track (pes) length (PL) is measured from the maximum distal point of digit III (anterior point of PIII3, excluding the claw mark where preserved) to the maximum proximal point of the first phalangeal pad of digit IV (PIV1) or the metatarso-phalangeal pad impression when present (Fig 3A). Track (pes) width (PW) is measured between the tips of the lateral digits II and IV (Fig 3A); and not between the tip of the claw marks even if preserved.

The anterior triangle (AT), originally defined by Weems ([69], fig. 2), is measured between the distal ends of the three digits (Fig 3B) following Lockley [70], and not between the tips of the three claw marks as proposed by Weems ([69], fig. 2) because the claws are often variably preserved and/or mostly not preserved on all three digits. The maximum height of the triangle (te) is measured, perpendicular to the transverse base of the triangle (corresponding to PW) and its length/width-ratio ([te/PW]-ratio) is calculated following the definition of Weems [69], who called this ratio 'toe extension/foot width-ratio', used to characterize how much digit III projects anteriorly beyond lateral digit IV and medial digit II as expressed by polarity between strong mesaxony (strong central tendency) and weak mesaxony (weak central tendency) [70].

Interdigital angles (da) are measured from the intercepting lines dividing the digits in halves (Fig 3B). These lines are also used as guides when measuring digit II, III and IV lengths and widths (Fig 3C) and phalangeal pad (numbered from proximal to distal as in Fig 3A) PII1/2, PIII1/2/3 and PIV1/2/3/4 lengths. Digit and phalangeal pad widths are measured tracing a line at the point of greatest width perpendicular to the long axis (intercepting line) of the digit or phalangeal pad impression.

3.4.3 Calculation of locomotion speed (values in S1)

Calculation of locomotion speed (v) derives from the empiric relationship ($v \simeq 0.25 g^{0.5} SL^{1.67} h^{-1.17}$; SL = stride, h = hip height, g = acceleration of free fall) obtained by Alexander [71] and for the calculation of hip height the factor 4.9 is used: h = 4.9 x PL [68, 72]. Because of several shortcomings of this empiric relationship due to the estimation of hip height based on tracks and the *a priori* unknown precise trackmaker, e.g., [73, 74], as well as the unknown precise relationship between relative stride length (SL / h) and the Froude number ($speed^2$ / leg length x g) for dinosaurs

[75], speed calculations are considered rough approximations only [75, 76]. Nonetheless, Alexander's [71] method is at least informative providing an estimation for the magnitude of the locomotion speed of a dinosaur trackway and, more importantly, for the relative speed of a given sample of trackways.

3.4.4 Photogrammetry

The photogrammetric 3D models were obtained using a Canon EOS 70D, 20 Mpixel, camera, equipped with a Canon 10-18mm STS or a Canon 18-135mm STS lens and a Canon ring flash (Macro Ring Lite MR-14 EXII) in order to eliminate the shadows generated by sunlight. Models were created using Agisoft Photoscan Pro (v. 1.2.4 and v. 1.2.5; www.agisfot.com) following the procedures of Mallison & Wings [77]. The accuracy of the models ranges between 0.1 and 0.03 mm, and resolution is always submillimetric. Scaling and alignment was made in Photoscan Pro. The scaled mesh, exported Stanford PLY files, were then processed in CloudComapre (www.cloudcomapre.com), where the meshes where accurately oriented through the generation of a plane intersecting the surface, to avoid imprecise alignment due to the roughness and irregularity of the surface, then it was possible to create accurate false colour depth-maps. Rhinoceros (v. 5.12) was then used to create contour lines.

All photogrammetric and laserscanner 3D meshes used in this study, and the related quality reports, are available for download here: https://figshare.com/s/b8c2b0d532c6ece4bfaa (approximately 5 GB).

**4. Description and interpretation of tracks and trackways**

In the following descriptions, the studied tracks are identified and assigned to the later introduced *Megalosauripus transjurani* (see systematic palaeontology), to *Megalosauripus* cf. *transjurani* (metatarso-phalangeal pad PIV1 is appreciable, large and connected to digit IV, digits are well separated, at least one phalangeal pad per digit is discernible, and claw marks are preserved), to *Megalosauripus* isp. (digits are separated, heel pad not very well discernable, and morphometric parameters for tracks and trackway configuration typical for this ichnotaxon accordingly to the definition of Lockley et al., [3]), and to Morphotype II *sensu* Marty ([16]: p.135, tracks are subsymmetric, almost as wide as long, digits are not well separated, phalangeal pads are absent, digits II and IV are merged in the heel). The latter is discussed in greater detail in the chapter regarding preservational variability within the studied tracks.

The quality of the tracks varies a lot, but all the key specimens are amongst the best-preserved ones (preservation quality > 2.5 *sensu* Belvedere & Farlow [60]). A specific preservation value *sensu* Belvedere & Farlow [60] is indicated for the best-preserved tracks in the detailed descriptions below.

**4.1 Chevenez—Combe Ronde (CHE-CRO) tracksite: level 500**

**-Trackway CRO500-T43 (S2)**

**Description:** Five-tracks continuous trackway located in the northeasternmost part of excavation area 2, crossing three sauropod trackways. The total length of the trackway is of 4.4 m, [WAP/PL]-ratio is 0.2 indicating a very narrow-gauge. The mean rotation of the tracks is low, slightly outward (+5°) for the left and slightly inward (-5°) for the right pes tracks. The mean PaL is 96.5 cm for the left-right pace and 112.0 cm for the right-left pace, giving the trackway a slightly irregular configuration. Average SL is 207.3 cm, PA is 171º and speed estimation is 7.7 km/h. Mean PL is 30 cm and PW 27 cm. Identification of left and right tracks was not so obvious, because the trackway is indeed narrow, and because the tracks are subsymmetric in shape. The qualilty of the tracks falls in grade 1 [60]. Tracks are almost as long as wide and lack a differentiated phalangeal pad configuration. Lateral digits II and IV are connected in the heel area. DIII is separated from dII and dIV and has a clover-like shape.

**Interpretation**: Trackway configuration is reflecting a slight variability in the PaL and in the alternating pes rotation, which together with the very low [WAP/PL]-ratio suggest a trackmaker with a very narrow posture, which is not related to a faster gait, as the speed estimation is within the walking range.

### 4.2 Courtedoux—Béchat Bovais tracksite (CTD–BEB): level 500

**-Trackway BEB500-TR1 (S3)**

**Description:** Fifteen-tracks discontinuous, 18.5 m long trackway located in excavation area 1. It crosses eleven small tridactyl trackways and two sauropod trackways. It has a very narrow gauge as expressed by a [WAP/PL]-ratio of 0.2. Average PaL is 118.4 cm for the left-right pace and 114.1 cm for the right-left pace. Average SL is 230.5 cm, PA is 173º and speed estimation is 7.8 km/h. Mean PL is 34.3 cm and PW 30.1 cm. Quality of the tracks is of grade 2. Phalangeal pads are present in L2; claw marks occur in L3 and L4.

Identification of left and right tracks was not so obvious, because the trackway is narrow, and because the tracks are subsymmetric in shape. Tracks are almost as long as wide and lack a differentiated phalangeal pad configuration. Lateral digits II and IV are connected in the heel area.

**-Trackway BEB500-TR2 (S4)**

**Description:** Eighteen-trackscontinuous trackway located in excavation area 1 with a total length of 17.9 m. It crosses 18 smaller tridactyl trackways, two of which are subparallel to the studied trackway but with opposite direction, and three sauropod trackways. It has a comparatively wider gauge as expressed by a [WAP/PL]-ratio of 0.6. Average PaL is 106 cm for the left-right pace and 110 cm for the right-left pace. Average SL is 196 cm, PA is 149º and speed estimation is 6.4 km/h. Mean PL is 34 cm and PW 30.6 cm. Quality of the tracks is of grade 2. Tracks are almost as long as wide, with a very weak mesaxony. Phalangeal pads are present in R5; claw marks occur in R2, L5, R6, and L6. Trackway configuration is very irregular, with a marked sinusoidal and intermitent aspect caused by differences in pace lengths. This is especially visible in tracks L7 and R7, which are located besides each other and are here considered as 'standing-still' tracks. This rare record of 'standing still' tracks is expressed by a pair of parallel tracks, both showing a small inward rotation. Moreover, a decrease/increase in pace lengthsis visible before and after the standing tracks, indicating that the trackmaker was decelerating before and accelerating after stopping.

**-Trackway BEB500-TR3 (S3)**

**Description:** Fifteen-tracks continuous 14.5 m long trackway, located in excavation area 1. It crosses one sauropod trackway and twelve small tridactyl trackways. The gauge is very narrow as expressed by a [WAP/PL]-ratio of 0.3. Average PaL is 123 cm for the left-right pace and 124 cm for the right-left pace. Average SL is 242 cm, PA is 167º and speed estimation is 9 km/h. Mean PL is 32.6 cm and PW 28.5 cm. Quality of the tracks is of grade 2. Identification of left and right tracks isnot so obvious, because the trackway is narrow, tracks are sometimes alternatively outwardly and inwardly oriented, and because the tracks are subsymmetric in shape. Tracks are almost as long as wide and lack a differentiated phalangeal pad configuration. Lateral digits II and IV are connected in the heel area.

**-Trackway BEB500-TR4 (S3)**

**Description:** Eleven-tracks discontinuous trackway of 14.5 m length, located in excavation area 1. It crosses one sauropod trackway and twenty small tridactyl trackways. It has a very narrow gauge as expressed by a [WAP/PL]-ratio of 0.4. Average PaL is 95 cm for the left-right pace and 102 cm for the right-left pace. Average SL is 198 cm, PA is 160º and speed estimation is 5.3 km/h. Track length is 38.4 cm and track width is 27.7 cm. Quality of the tracks is of grade 1.5. The trackway is quite irregular due to the lack of some tracks. Tracks are almost as long as wide and lack a differentiated phalangeal pad configuration. Lateral digits II and IV are connected in the heel area.

**-Trackway BEB500-TR5 (S3)**

**Description:** 40-tracks discontinuous trackway, 34 m long, located in excavation area 1. It crosses 30 small tridactyl trackways and three sauropod trackways. It has a very narrow gauge as expressed by a [WAP/PL]-ratio of 0.4. Average PaL is 93.1 cm for the left-right pace and 94 cm for the right-left pace. Average SL is 181.9 cm, PA is 160º and speed estimation is 5.3 km/h. Mean PL is 29.6 cm and PW 25.2 cm. Tracks are almost as long as wide and lack a differentiated phalangeal pad configuration. Quality of the tracks is of grade 1.5. Tracks are very poorly preserved throughout the trackway, which has a marked sinusoidal configuration. However, phalangeal pads can be recognized in R1 and R11. Lateral digit impressions II and IV connect, forming a rounded/subrounded heel.

**-Trackway BEB500-TR7 (S3)**

**Description:** 35-tracks discontinuous, 42.8 m long trackway located in excavation area 1. It crosses seventeen small tridactyl trackways, six sauropod trackways and it is parallel to two other small tridactyl trackways. It has a narrowgauge as expressed by a [WAP/PL]-ratio of 0.5. Average PaL is 127 cm for the left-right pace and 126 cm for the right-left pace. Average SL is 244 cm, PA is 158º and speed estimation is 7.2 km/h. Mean PL is 40 cm and PW 47 cm. Quality of the tracks is of grade 2. Tracks are almost as long as wide, with a very weak mesaxony. Sometimes one pad per digit is recognizable, although the general shape strongly recalls morphotype II *sensu* Marty (2008). Trackway configuration is very irregular, with a marked sinusoidal and intermitent aspect caused by differences in pace lengths and directional changes. Tracks R9 and L10 are parallel, both showing a small inward rotation and are considered as 'standing-still' tracks. Moreover, a directional change is also visible right after the 'standing still' tracks, indicating that the trackmaker is milling on the tracksite along its course. Track L11 has a peculiar very elongated heel (metatarsal) impression.

**-Trackway BEB500-TR8 (S3)**

**Description:** 32-tracks discontinuous trackway located in excavation area 1. Total length of the trackway is 40.3 m. It crosses BEB500-TR7 (see above), ten small tridactyl trackways, two sauropod trackways, and it is parallel to three other small tridactyl trackways. It has a very narrow gauge as expressed by a [WAP/PL]-ratio of 0.3. Average PaL is 104 cm for the left-right pace and 106 cm for the right-left pace. Average SL is 206 cm, PA is 168º and speed estimation is 6.5 km/h. Mean PL is 34 cm and PW is 30 cm. Quality of the tracks is of grade 2. Tracks are almost as long as wide; phalangeal pads are present in R2, R3, R7, R12, L13, R13, L14, R14, L15, and L17; a single claw mark occurs only in dIII of R14.The heel area is poorly preserved.

### 4.3 Interpretation of trackways BEB500

Trackways TR1 to TR5, TR7 and TR8 (S3, S4), from the BEB500 level share common features in their track morphology. They are all almost as long as wide, subsymmetric, with robust and blunt toes; TR3, TR4, TR7 have no evidence for discrete digital pads and claws, whereas TR1, TR2, TR5 and TR8 sporadically show some phalangeal pad impressions and claw marks. Generally, the best-defined digit is digit III, which is separated from digits II and IV and has a slightly angular, trapezoidal (clover-like) shape with the maximum width located in the middle to anterior part of the digit. Digits II and IV, independently from the occurrence of phalangeal pad impressions, are less well-defined, more oval and more or less merged in a rather short, broad and rounded heel, without evidence for a postero-medial indentation on the heel, which is typically seen in theropod tracks and also *M. transjurani*.

Morphology in TR3, TR4 and TR7 (S3, S4) is consistent throughout the trackways and strongly recalls that of Morphotype II. Compared to *Megalosauripus* tracks, these tracks are wider (less slender) and less mesaxonic and they have a particular elongated trapezoidal shape of digit III and oval and blunt digits II and IV without evidence for impressions of phalangeal pads and claw marks. Generally, the sinusoidal or straight trackways are characterized by a narrow gauge where pes tracks intersect or touch the trackway midline. BEB500-TR7 (S4) shows a slightly wider gauge with tracks aligned in a zigzag fashion. Because speed estimations are all indicating slow moving trackmakers, and because tracks do not appear to be susceptible to a clear intra-trackway morphological variability due to changing substrate properties or kinematics, none of these trackways can be assigned to *Megalosauripus*. Instead, these trackways are tentatively assigned to *Iguanodontipus*? (formerly *Therangospodus) oncalensis* (*sensu* Castanera et al., 2013),

Trackways TR1, TR2, TR5 and TR8 (S3), on the other hand, present some intra-trackway morphological variations, due to the occasional occurrence of phalangeal pad impressions and claw marks. Because of these features, and considering also the overall morphology of these tracks, they are most likely preservation variants of *Megalosauripus* isp., even though they are also slightly similar to *Therangospodus pandemicus* (see discussion).

**4.4 Porrentruy—CPP (aka 'Dinotec', POR–CPP) tracksite: level 500**

**-Trackway CPP500-T1 (S5)**

Description: Discontinuous trackway with 8 tracks preserved within a total length of about 12 m, crossing two parallel trackways of small sauropods and one trackway of a medium-sized sauropod. Average PL is 37.4 cm and PW is 27.9 cm. IIIV divarication angle is 38°. The mean track rotation is low, slightly inward (-4°) for the left and slightly inward (4°) for the right pes tracks. It has a narrowgauge as expressed by a [WAP/PL]-ratio of 0.4. Average PaL is 80.5 cm for the left-right pace and 87.7 cm for the right-left pace. Average SL is 158 cm, PA 157º and speed estimation 3.8 km/h.

Several tracks but notably L8 are well preserved (grade 2.5), exhibiting slender and separated digits with phalangeal pads and three claw mark impressions. Several tracks (L6–L8) are protected *in situ* in a showcase in the schoolyard of the school 'Ecole des métiers techniques de Porrentruy' (CEJEF – Division Technique, DIVTEC).

Interpretation: Because this trackway exhibits phalangeal pads, claw marks, and rather slender and well-separated digits, it can be assigned to *Megalosauripus* isp. It is the only trackway on level 500 that can be clearly assigned to *Megalosauripus* and thus documents that Morphotype II trackways are associated with *Megalosauripus* tracks on the same level, even though not at the same site (ichnoassemblage) as at the CPP site no Morphotype II tracks were discovered on level 500. This implicates the following two hypotheses: (1) A distinct Morphotype II left by another tridactyl trackmaker co-occurs with *Megalosauripus*, or (2) Morphotype II tracks are preservation variants of *Megalosauripus* tracks, which are analysed in greater detail in the discussion.

**4.5 Courtedoux—Sur CombeRonde tracksite (CTD–SCR): level 1000**

**-Trackway SCR1000-T18 (S6)**

**Description:** Trackway T18 is discontinuous, with only 4 tracks preserved within a total length of 11.1 m. It is located in excavation area 2, crossing three sauropod trackways, one of which heading in the opposite direction. With a [WAP/PL]-ratio of 1.0 it has quite a comparatively wide-gauge for a bipedal tridactyl trackway.

The mean rotation of the tracks is low, strongly outward (+17°) for the left and slightly inward (-3°) for the right pes tracks. Due to the many missing tracks of the overall trackway, it was not possibleto calculate meanPaL, SL, and PA. Average PL is 27.2 cm and PW is 25.6 cm. Quality of the tracks is of grade 1. Tracks are almost as long as wide, with no clear heel area impressed, non-tapering digits, and notably dIII with a trapezoidal, clover-like shape and an overall symmetric aspect. Track morphologies are very variable along the trackway, with anatomical details only presenton the track R1.

**Interpretation:** Regarding the well-preserved track R2, this track recalls Morphotype II and an ornithopod morphology. However, there is not enough evidence to suggest an ornithopod trackmaker origin based on one single track only. The third digit may simply have indented deeper into the sediment, implying a sensitive influence of kinematics during track formation and which found its expression in this particular track morphology.

**-Trackway SCR1000-T23 (S7)**

**Description:** Seven-tracks continuous trackway located in excavation area 18, crossing a sauropod trackway moving in the same direction and almost parallel to an opposite-directed sauropod trackway. Total lenght of the trackway is of 8.4 m. It is narrow gauge with a [WAP/PL]-ratio of 0.3. The mean rotation of the tracks is quite low, parallel tothe midline for the left (0°) and slightly inward (-7°) for the right pes tracks. Average PaL is 133.5 cm for the left-right pace and 130.0 cm for the right-left pace. Average SL is 267.5 cm, PA is 165º and speed estimation is 8.2 km/h. Mean PL is 41 cm and PW 26.3 cm. Quality of the tracks is of grade 2. Tracks are elongated and narrow, with a pronouced mesaxony. Digits II and IV impressions display a low interdigital divarication angle. Tracks display one pad per digit, usually digit II and IV are not joint in the heel area, giving the track morphology an asymmetric aspect.

**Interpretation:** Trackway configuration is very regular with a straight disposition of the tracks on the midline, as underscored by the very small difference between right and left pace lengths, and the high pace angulation. Despite the absence of clear phalangeal pad impressions, track morphology is clearly that of a theropod and strongly recalls that of *Megalosauripus*.

**-Trackway SCR1000-T24 (S8)**

**Description:** Nine-tracks continuous trackway located in excavation area 18, is crossing three subparallel sauropod trackways withthe same orientationand one subparallel overlapping and oppositely-directed sauropod trackway. Total lenght of the trackway is of 10.2 m. It has a relatively wide gauge with a [WAP/PL]-ratio of 0.8. The mean rotation of the tracks is consistently inward with -7°for the left and -4°for the right pes tracks. Average PaL is 130 cm for the left-right pace and 123.3 cm for the right-left pace. Average SL is 247.6 cm, PA is 157º and speed estimation is 9.8

km/h. Mean PL is 31.6 cm and PW 28 cm. Quality of the tracks is of grade 2. Tracks are elongated, but mesaxony is not so pronounced. Only one pad per digit is discernableand lateral digit II and IV impressions are not joined in the heel area, giving the track morphology an asymmetric aspect.

**Interpretation:** Trackway configuration is quite irregular, with a "zig-zag" pattern and a clear inward rotation for both right and left tracks. Pace lengths are slightly different between the right and left sides. The wide disposition of the tracks with respect to the midline results in a pronounced pace angulation and comparatively high [WAP/PL]-ratio, despite a rather high speed estimation. This suggests a trackmaker with a wider posture. The general asymmetry of the track morphology due to the presence of a large PIV1 pad suggests an affinity to *Megalosauripus* cf. *transjurani*.

### 4.6 Courtedoux—Bois de Sylleux tracksite (CTD–BSY): levels 1005, 1010, 1015, 1020, 1025, 1035 & 1040

#### 4.6.1 Level 1005

**-Trackway BSY1005-T1 (S9)**

**Description:** Three-tracks continuous trackway located in excavation area 20. Total lenght of the trackway is of 2.7 m. The gauge is very narrow with a [WAP/PL]-ratio of 0.4. The mean rotation of the tracks is slightly outward rotated for two left pedes (5°), while the only right pes R1 appears to be aligned to the midline (no measurement available). Average PaL is 107 cm for the left-right pace and 83 cm for the right-left pace. Average SL is 221 cm, PA is 163º and speed estimation is 6.6 km/h. Mean PL is 37.3 cm and PW 21.5 cm. Quality of the tracks is between 2.5 and 3. Tracks are elongated and narrow, with a pronounced mesaxony. A clear phalangeal pad configuration is visible, with a formula 2-3-4 (for dII-III-IV) and claw marks ondIV in track L1. Lateral digits II and IV impressions are not joined in the heel area and digit II impression is isolated from digit IV and digit III, giving the track morphology an asymmetric aspect.

**Interpretation:** Trackway is too short in order to describe its configuration, although the alternating pace lengths pattern together with the low speed estimation and the moderate [WAP/PL]-ratio suggest that the trackmaker was walking quite slowly. Track morphology is very well preserved and the presence of a clear phalangeal pad configuration, with a special emphasis on the PIV1 phalangeal pad diameter (very wide) allow the assignement of these tracks to *Megalosauripus transjurani.*

**4.6.2 Level 1010**

**-Trackway BSY1010-T1 (S9)**

**Description:** Eight-tracks discontinous trackway located in excavation area 20. Total lenght of the trackway is 12.5 m. The gauge is very narrow with a [WAP/PL]-ratio of 0.4. The mean rotation of the tracks is slightly inward rotated for the left pes (-3°), while right pedes are slightly outward roataded (7º). Average PaL is 140 cm for the left-right pace and 132 cm for the right-left pace. Average SL is 270 cm, PA is 170º and speed estimation is 8.1 km/h. Mean pes length is 41.8 cm and track width 28.5 cm. Quality of the tracks is between 2 and 2.5. Tracks are elongated and narrow, with a pronounced mesaxony. A clear phalangeal pad configuration is visible only for one track (R5), with a formula 2-3-4 (for dII-III-IV) but no clear claw marks. For the rest of the tracks, only one pad per digit is discerned while lateral digits II and IV impressions are separated from one another and do not meet in the heel area. Phalangeal pad PIV1 is very wide and connected to digit IV, giving the track morphology an asymmetric aspect.

**Interpretation:** This trackway has quite a regular overall configuration as shown by the very small pace length difference between right and left sides. Track morphology is generally well preserved; although a clear phalangeal pad formula of 2-3-4 is only appreaciable in one track. Because of the connection of digit IV impression with the wide metatarsal-phalangeal pad (PIV1), this trackway belongs to *Megalosauripus transjurani*.

**4.6.3 Level 1015**

**-Trackway BSY1015-T1 (S9)**

**Description:** Two-tracks trackway located in excavation area 20. Trackway length is of 1.6 m. Trackway gauge cannot be determined because the presence of only two tracks. The mean rotation of the tracks is slightly outward rotated for the left pes (5°), while the right pes R1 appears to be aligned to the midline. PaL is 125 cm. Mean PL is 41.5 cm and PW 27.5 cm. Quality of the tracks is of grade 2. Both tracks are elongated and narrow, with a pronounced mesaxony. Lateral digits II and IV impressions are not joined in the heel area and digit II impression is isolated from digit IV. Despite the absence of clear phalangeal pad impressions, track morphology is clearly that of a theropod.

**Interpretation:** Trackway is too short to describe its configuration. The phalangeal formula of 2-3-4 for digits II-III and IV respectively is not discernible. Track morphology is characterized by one pad per digit, with PIV1 connected to digit IV. Moreover, the PIV1 phalangeal pad diameter is quite wide, allowing the classification of these tracks as *Megalosauripus transjurani.*

**4.6.4 Level 1020**

**-Trackway BSY1020-T1 (S10)**

**Description:** Five-tracks continuous trackway located in excavation area 20, crossing a sauropod trackwaywiththe same orientation. Trackway length is 6.1 m. It has a very narrow gauge with a [WAP/PL]-ratio of 0.4. The mean rotation of the tracks is outward for left tracks (13°) and right (2º) toa lesser extent. Average PaL is 137 cm for the left-right pace and 134.8 cm for the right-left pace. Average SL is 252.8 cm, PA is 167º and speed estimation is 7.2 km/h. Mean PL is 42 cm and PW 29.3 cm. Quality of the tracks is of grade 2. Tracks are elongated but not very narrow. Tracks show only one pad per digit and lateral digits II and IV impressions are separated from one onther and do not meet in the heel area, giving the track morphology an asymmetric aspect.

**Interpretation:** Trackway configuration is not very regular, although there's no significant difference in pace lengths between right and left sides. Trackway and footprint morphometric parameters and overall shape correspond to *Megalosauripus*, but because no further morphological details are preserved, the classification remains generic.

**4.6.5 Level 1025**

**-Trackway BSY1025-T1 (S11)**

**Description:** Eleven-tracks discontinuous and partial trackway located in excavation area 20. Trackway length is 17.2 m. The gauge is very narrow with a [WAP/PL]-ratio of 0.4. The mean rotation of the tracks is slightly outward rotated for the left pes (4°) and right pes (2º) tracks. Average PaL is 128.9 cm for the left-right pace and 135 cm for the right-left pace. Average SL is 263 cm, PA is 167º and speed estimation is 8 km/h. Mean PL is 40.6 cm and PW 26.1 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are elongated and narrow, with a moderate to pronounced mesaxony. A clear phalangeal pad configuration is appreciable in most of the tracks, with a 2-3-4 (for dII-III-IV) formula and claw marks indigit II and III of track R4. Lateral digits II and IV impressions are not joined in the heel area and digit II impression is isolated from digit IV (with the exeption of track L7) and digit III, giving the track morphology an asymmetric aspect.

**Interpretation:** This trackway has quite a regular overall configuration as shown by the very small difference in PaLbetween right and left sides. Track morphology is generally very well preserved, and aclear phalangeal pad formula of 2-3-4 for dII-III-IV is visible in the majority of the tracks. However, it is worth mentioning here that track morphology along this trackway is susceptible to pronounced variations with the presence of a continuum of morphologies from *Megalosauripus transjurani* over *Megalosauripus* isp. to morphotype II *sensu* Marty [16] in track LP7. However, because of the features of the best-preserved tracks, this trackway is assigned to *Megalosauripus transjurani*.

**-Trackway BSY1025-T2 (S11)**

**Description:** Eight-tracks discontinuous trackway located in excavation area 20. The trackway is 11.7 m long. The gauge is very narrow with a [WAP/PL]-ratio of 0.4. The mean rotation of the tracks is slightly outward oriented for the left tracks (3°) and in a greater extent for the right tracks (9º). Average PaL is 126.8 cm for the left-right pace and 128.5 cm for the right-left pace. Average SL is 254.8cm, PA is 166º and speed estimation is 7.3 km/h. Mean PL is 42.2 cm and PW 24.5 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are elongated and narrow, with a moderate to pronounced mesaxony. A clear phalangeal pad configuration is appreciable in most of the tracks, with a 2-3-4 (for dII-III-IV) formula and claw marks onall digits in track R1.

**Interpretation:** Trackway with a quite regular overall configuration as shown by the very small pace length differences between right and left sides. Track morphology is generally well preserved, the clear phalangeal pad formula of 2-3-4 is appreaciable in the majority of the tracks, even if track morphology is susceptible to some small changes along the trackway. Nevertheless, a wide and very well developed metatarso-phalangeal pad (PIV1) is quite consistently visible, and this is the diagnostic feature to assign this trackway to *Megalosauripus transjurani.*

**-Trackway BSY1025-T3 (S10)**

**Description:** Three-tracks continuous trackway located in excavation area 20, subparallel to an oppositely-directed sauropod trackway. The trackway is 2.6 m long. It has a narrow gauge with a [WAP/PL]-ratio of 0.3. The mean rotation of the tracks is outwardly rotated for left tracks (8°). Average PaL is 113 cm for the left-right pace and 121 cm for the right-left pace. Average SL is 233 cm, PA is 170º and speed estimation is 7.6 km/h. Mean PL is 36 cm and PW 29 cm. Quality of the tracks is between grades 1 and 2. Tracks have a weak mesaxony and display one thick pad per digit impression, and apoorly-preserved metatarso-phalangeal pad.

**Interpretation:** Trackway configuration is not very regular. Track morphometric parameters and overall shape definitely resemble *Megalosauripus* isp. but because no further morphological details are preserved, the classification should remain open.

**4.6.6 Level 1035**

**-Trackway BSY1035-T1 (S12)**

**Description:** Three-tracks continuous trackway located in excavation area 20, parallel to a sauropod trackway. The trackway is 3 m long. The gauge is narrow with a [WAP/PL]-ratio of 0.5. The mean track rotation is outward for the right pes (13°), butthis parameter is measured fromone track only, as the other two are too poorly preserved. Average PaL is 138 cm for the left-right pace and 139 cm for the right-left pace. Average SL is 275 cm, PA is 167º and speed estimation is 8.8 km/h. Mean PL is 40 cm and PW 26 cm. Quality of the tracks is between grades 1 and 2. Tracks are elongated and narrow, with a pronounced mesaxony. A clear phalangeal pad configuration is not appreciable, but all the digits are clearly separated from eachother and track R2 shows a largePIV1 connected to digit IV impression.

**Interpretation:** Trackway is too short to describe its configuration. The occurrence of very large PIV1 phalangeal pad impressions allows the classification of these tracks as *Megalosauripus* cf. *transjurani.*

**-Trackway BSY1035-T2 (S13)**

**Description:** Two-tracks partial trackway located in excavation area 20. Total lenght is of 1.9 m. Trackway gauge cannot be determined because the presence of only two tracks. Average PaL is 143cm. Mean PL is 43.5 cm PW 25 cm. Quality of the tracks is of grade 2. Tracks are very elongated and narrow, with a pronounced mesaxony. A clear phalangeal pad configuration is appreciable, with a 2-3-4 (for dII-III-IV) formula.

**Interpretation:** Trackway is too short to describe its configuration. Track morphology is very well preserved and the presence of clear phalangeal pads together with a very large PIV1 phalangeal pad assigns them to *Megalosauripus transjurani.*

**-Trackway BSY1035-T3 (S13)**

**Description:** Six-tracks discontinuous trackway, located in excavation area 20, subparallel to trackway T4 and crossing a sauropod trackway. Total length is 8.4 m. The gauge is narrow with a [WAP/PL]-ratio of 0.3. The mean rotation of the tracks is slightly inward rotated for the left pedes (-3°), while right pedes are aligned to the midline (0º). Average PaL is 114 cm for the left-right pace and 131 cm for the right-left pace. Average SL is 235.8 cm, PA is 167º and speed estimation is 6.9 km/h. Mean PL is 39.6 cm and PW 27.7 cm. Quality of the tracks is of grade 2. Tracks are elongated and narrow, with a moderate to pronounced mesaxony. A clear phalangeal pad configuration is appreciable in tracks L2 andR3, with a 2-3-4 (for dII-III-IV) formula.

**Interpretation:** Trackway with quite a regular and narrow overall configuration, despite some pace length differences between right and left sides. Track morphology is generally well preserved, digit impressions are always clearly separated from each other, and if visible the phalangeal pad formula is2-3-4. Because of the connection of digit IV impression with the wide metatarso-phalangeal pad (PIV1), this trackway belongs to *Megalosauripus transjurani*.

**-Trackway BSY1035-T4 (S13)**

**Description:** Three-tracks partial trackway located in excavation area 20, subparallel to T3. Total length of the trackway is 2.9 m. The gauge is narrowwith a [WAP/PL]-ratio of 0.3. Left tacks are slightly inward rotated (-3º). Average PaL is 122 cm for left-to-right pace and 126 cm for right-to-left pace; average SL is 243 cm; PA is 167º; speed estimation is not possible. Mean PL is 41.3 cm and PW 25 cm. Quality of the tracks is of grade 2. Tracks are very elongate and narrow, with a pronounced mesaxony. A clear phalangeal pad configuration is visibleindigit III in track L1 (3 pads). All tracks display a wide PIV1 pad impression.

**Interpretation:** Trackway is too short to describe its configuration. Track morphology is very well preserved and the presence of a large PIV1 phalangeal pad allows the classification as *Megalosauripus transjurani.*

**-Trackway BSY1035-T5 (S13)**

**Description:** Three-tracks discontinuous trackway located in the excavation area 20. Total length of the trackway is of 4.3 m. The gauge is very narrow with a [WAP/PL]-ratio of 0. Right tacks are slightly outward rotated (5º). Average PaL, measured for tracks R2-L3 is 118 cm, average SL is 268 cm. PA could not be measured. Speed estimation is 7.8 km/h. Mean PL is 43 cm and PW 27 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are very elongated and narrow, with a pronounced mesaxony. A clear 2-3-4 phalangeal pad configuration is visible in track R1, which also bears a claw mark in digit IV. All tracks display a wide PIV1 pad impression.

**Interpretation:** Trackway is too short and a track is missing to describe its configuration. Track morphology is very well preserved and the presence of a wide PIV1 phalangeal pad allows the classification of these tracks as *Megalosauripus transjurani.*

**-Trackway BSY1035-T6 (S14)**

**Description:** Two-tracks trackway located in excavation area 20. Total length of the trackway is 1.9 m. Trackway gauge cannot be determined because the presence of only two tracks. PaL is 150 cm. Mean PL is 40 cm and PW 22 cm. Quality of the tracks is of grade 2.5. Tracks are very elongate and narrow, with a pronounced mesaxony. A clear 2-3-4 phalangeal pad configuration for digits II-III-IV is exhibited in both tracks, which also bear a claw mark on digit III. All tracks display a wide PIV1 pad impression. Track BSY1035-T6-L2 preserved as a track fill (slab number BSY008-330) is one of the paratypes of the new ichnospecies and it exhibits fine details of pad and claw impressions in all three digits.

**Interpretation:** Trackway is too short to describe its configuration. Track morphology is very well preserved, with anatomical details of phalangeal pads in tracks R1 and L2. The presence of the wide PIV1 phalangeal pad connected to a padded digit IV is diagostic for the classification of these tracks as *Megalosauripus transjurani*.

**-Trackway BSY1035-T7 (S12)**

**Description:** Three-tracks partial trackway located in excavation area 20, crossing a sauropod trackway. Total length is 2.7 m. The gauge is narrow with a [WAP/PL]-ratio of 0.5. The mean rotation of the tracks is outward rotated for the right pes (2°), although this parameter is measured for one track only, as the other two are poorly preserved. Average PaL is 122 cm for the left-right pace and 113 cm for the right-left pace. Average SL is 230 cm, PA is 162º and speed estimation is 6.9 km/h. Mean PL is 38 cm and PW 26.3 cm. Quality of the tracks is between grades 1.5 and 2. Tracks are elongate and narrow. Track R1 does not have an impression of the heel area, but one pad per digit is appreaciable, L2 preserves only digits III and IV, R3 has a one pad per digit with digit II-III and IV clearly separated from one another and a wide PIV1 connected to digit IV impression.

**Interpretation:** Trackway is too short to describe its configuration. The large PIV1 phalangeal pad is diagnostic for *Megalosauripus* cf. *transjurani.*

**-Trackway BSY1035-T8 (S13)**

**Description:** Three-tracks partial trackway located in excavation area 20, subparallel to T3. Total length is of 3.1 m. The gauge is very narrow as expressed by a [WAP/PL]-ratio of 0.2. Right tacks are slightly inward rotated (-2º). Average PaL is 130 cm for left-to-right pace and 136.5 cm for right-to-left pace. Average SL is 265 cm. PA is 169º and speed estimation is 8.1 km/h. Mean PL is 40.7 cm and PW 22.7 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are very elongate and narrow, with a pronounced mesaxony. A clear phalangeal pad configuration is appreciable only for digit II in track L2 (2 pads), and digit III in track R2 (3 pads), which also bears a claw mark. All digit impressions are separated from one another, with a clear large PIV1 pad impression connected to digit IV impression.

**Interpretation:** Trackway is too short to describe its configuration. Track morphology is generally very well preserved and the phalangeal pad configuration for two out of three tracks, together with the presence of a largePIV1 phalangeal pad impression assign this trackway to *Megalosauripus transjurani*.

**4.6.7 Level 1040**

**-Trackway BSY1040-T1 (S15)**

**Description:** Seven-trackscontinuous trackway located in excavation area 20. Total length of the trackway is 8.2 m. The gauge is very narrow as expressed by a [WAP/PL]-ratio of 0.3. Both left and right pedes are outwardly rotated with 6º and 10º, respectively. Average PaL is 129.7 cm for left-to-right pace and 131 cm for right-to-left pace. Average SL is 258 cm. PA is 167º and speed estimation is 7.8 km/h. Mean PL is 40.5 cm and PW 24 cm. Quality of the tracks is of 2.5. Tracks are very elongate and narrow, with a moderate mesaxony. A clear phalangeal pad configuration 2-3-4 can be identified for digits II-III-IV ofall tracks. Claw marks are preserved on digit IV of track R1 (paratype slab number MJSN BSY008-339) and R4 and on digit II of track R2. All tracks display a wide PIV1 pad impression, which is connected to dIV impression.

**Interpretation:** Trackway configuration is quite regular, with a slight "zig-zag" pattern and a marked outward rotation for both right and left tracks. Pace lengths do not display any significant difference between the right and left sides. The [WAP/PL]-ratio suggests a trackmaker with a moderate narrow posture despite the relatively slow speed. These tracks are very well preserved and show all the key features (large PIV1 pad, phalangeal pad formula 2-3-4 and claw marks) of *M.*

*transjurani*. Therefore, BSY1040-T1-R1 (MJSN BSY008-339) was chosen as a paratype for *Megalosauripus transjurani*.

**-Trackway BSY1040-T7 (S9)**

**Description:** Eight-tracks discontinuous trackway located in excavation area 20, subparallel to trackway BSY1040-T8 (see below) and crossing severalsauropod trackways and trackway BSY1040-T9 (see below). Total length of the trackway is 21 m. The gauge is narrow with a [WAP/PL]-ratio of 0.5. The mean rotation of the tracks is on both sides slightly outwardly rotated (left 1º, right 1º). Average PaL is 125 cm for left-to-right pace and 131.5 cm for right-to-left pace. Average SL is 253.5 cm. PA is 172º and speed estimation is 7.9 km/h. Mean PL is 39.2 cm and PW 19.2 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are very elongate and narrow, with a moderate mesaxony. A clear phalangeal pad configuration of 2-3-4 is presentfor digits II-III-IV for all tracks. Claw marks are preserved on digits III and IV of tracks R2 and R9, on digits IV of tracks R4 and R5 and on digits II and III of track L9. All tracks display a wide PIV1 pad impression, which is connected to dIV impression.

**Interpretation:** Trackway configuration is quite regular, even though several tracks are missing. Pace lengths are slightly different between the right and left sides. Tracks are verywell preserved: all the diagnostic features for the assignation of these tracks to *Megalosauripus transjurani*, such as the presence of a large PIV1 pad, phalangeal pad formula 2-3-4 and claw marks, are discernable.

**-Trackway BSY1040-T8 (S16)**

**Description:** Six-tracks discontinuous trackway located in excavation area 20, crossing three sauropod trackways and trackway T7 (see description above). The gauge is narrow as expressed by a [WAP/PL]-ratio of 0.3. Total length of the trackway is 13.1 m. The mean rotation of the tracks could only be measured for right tracks and is outwardly oriented (+2°). Average PaL is 149.5 cm for left-to-right pace and 145.5 cm for right-to-left pace. Average SL is 304 cm. PA is 170º and speed estimation is 12.7 km/h. Mean PL is 33.7 cm and PW 18.9 cm. Quality of the tracks is of grade 2. Tracks are slightly longer than wide, with no clear heel area impressed and non-tapering digits with a trapezoidal (clover-like) shape and an overall symmetric aspect. Track morphology is characterized by one discernable pad for digit III, while digits II and IV impressions merge together in the posterior margin of the track.

**Interpretation:** Digit III is strongly indented into the sediment, and due to agreat deal of kinematics involved in track formation, these tracks recall Morphotype II and, more generally, ornithopod morphology. However, there is not enough evidence to suggest an ornithopod trackmaker origin and a preservational bias due to limb kinematics is suggested rather than a different trackmaker origin. In fact, trackway configuration parameters all point to a fast-moving trackmaker, with a highly digitigrade posture. High speed is a reasonable explanation of the merging lateral digits and the lack of a clear PIV1 impression.

**-Trackway BSY1040-T9 (S17)**

**Description:** Four-tracks discontinuous trackway located in excavation area 20, crossing trackway BSY1040-T8 (see above) and a sauropod trackway. Total length of the trackway is of 6.5 m. The gauge is narrow with a [WAP/PL]-ratio of 0.5. The mean rotation of the tracks is outwardly rotated for left tracks (2º), and inwardly rotated for right tracks (-4º). Average PaL is 125 cm for left-to-right pace and 131cm for right-to-left pace. Average SL is 260.5 cm. PA is 166º and speed estimation is 8.4 km/h. Mean PL is 38.8 cm and PW 23.9 cm. Quality of the tracks is between grades 1.5 and 2. Tracks are elongated, have massive digits and a moderate mesaxony. A clear phalangeal pad configuration 2-3-4 is appreciable for digits II-III-IV in track R3. Claw marks are not preserved. Track R3 displays a wide PIV1 pad impression, which is connected to digit IV impression. The other tracks are not well preserved but appear to display separate digit impressions. The overall track morphology is quite variable along the trackway.

**Interpretation:** Trackway configuration appears to be slightly irregular, with pace lengths slightly different between the right and left sides. The narrow gauge suggests a trackmaker with a fast-walking gait, as shown also by the pace angulation. Track morphology is very variable, with only one track well preserved. This track preservesa large PIV1 pad, a phalangeal pad formula 2-3-4, both diagnostic features for the assignation of the trackway to *Megalosauripus transjurani*.

**4.7 Courtedoux—Tchâfouè tracksite (CTD–TCH): levels 1000, 1015, 1020, 1025 & 1030**

**4.7.1 Level 1000**

**-Trackway TCH1000-TR1 (S8, S18)**

**Description:** Seven-tracks continuous trackway located in excavation area 12, crossing eight sauropod trackways and two small tridactyl trackways. Total length is 7 m. The gauge is very narrow with a [WAP/PL]-ratio of 0.1. The mean rotation of the tracks is outwardly rotated for left tracks (4º), and strongly inwardly rotated for right tracks (-16º). Average PaL is 118 cm for left-to-right pace and 120.4 cm for right-to-left pace. Average SL is 235.8 cm. PA is 171º and speed estimation is 7.3 km/h. Mean PL is 37.6 cm and PW 26 cm. Quality of the tracks is of grade 1.5. Tracks are slightly longer than wide and have a moderate mesaxony. Digit impressions are generally separated from one another, and in tracks L1, R2, L3 and L4 it is possible to distinguish the presence of a metatarso-phalangeal pad connected to digit IV. In tracks R1, L2 and R3, this distinction is not clearbecause ofthe merging of lateral digits II-IV in the heel area. Digit impressions do not preserve any phalangealpads.

**Interpretation:** Trackway configuration is quite regular and straight forward, and underlined by the high pace angulation and the narrow gauge of the trackmaker. Track morphometric parameters and overall shape are typical for *Megalosauripus*.

**-Trackway TCH1000-TR2 (S8, S19)**

**Description:** Twenty-one tracks, 25.6 m longcontinuous trackway located in the excavation area 12, crossing nine sauropod trackways and one small-sized tridactyl trackway and it is subparallel to two other small tridactyl trackways in two opposite directions. The gauge is very narrow with a [WAP/PL]-ratio of 0.1. The mean rotation of the tracks is outwardly rotated for both left tracks (+3º) and right tracks (+6º). Average PaL is 124.6 cm for left-to-right pace and 127.8 cm for right-to-left pace. Average SL is 251 cm. PA is 131º and speed estimation is 8.3 km/h. Mean PL is 37.1 cm and PW 27.3 cm. Tracks are almost as long as wide, with no clear heel area impressed and non-tapering digits with a clover-like shape and an overall symmetric aspect. Quality of the tracks is of 1.5. Track morphologies are very variable along the trackway. Digit impressions, generally separated from one another, are appreciable in tracks L5, R5, R7, L8, R12 and R14. In L10 lateral digits II-IV merge together in the poorly-preserved heel area, but digit III is still well separated and distinguishable. Another morphology is discernible for most of the tracks of this trackway in as far that all digits are merging in a coalesced clover-like shape. Digits impressions do not preserve any anatomical features (phalangeal pads, claws).

**Interpretation:** Quite irregular trackway. Poorly-preserved tracks are related to a 20º turnobviously affecting track morphologies of L6, R6 and L7. Despite the general intra-trackway variability observed, track morphometric parameters and overall shape reflect the definition of *Megalosauripus*, but because no further morphological details are preserved the classification remains generic.

**4.7.2 Level 1015**

**-Trackway TCH1015-T1 (S20)**

**Description:** Six-tracks discontinuous trackway located in excavation area 12, crossing seven sauropod trackways. Total lenght is 8.6 m. The gauge is narrow as expressed by a [WAP/PL]-ratio of 0.4. The mean rotation of the tracks is inwardly rotated for both left tracks (-6º) and right tracks (-10º). Average PaL is 139.3 cm for left-to-right pace and 140 cm for right-to-left pace. Average SL is 275.8 cm. PA is 176º and speed estimation is 10.6 km/h. Mean PL is 34.2 cm and PW 23.2 cm. Quality of the tracks is of grade 2. Tracks are very elongated and narrow, with a moderate mesaxony. A clear phalangeal pad configuration 2-3-4 is appreciable for digits II-III-IV for the majority of the tracks. Claw marks are preserved on digit III of tracks L3 and R3 and on digits III-IV of track L4. Tracks L2 (specimen MJSN TCH006-1348) and R3 (specimen MJSN TCH006-1357) exhibit fine details of pads and claws.

**Interpretation:** Trackway configuration is quite regular; pace lengths do not display any significant difference between the right and left sides. Track morphology is very well preserved, with a special remark to R3 (specimen MJSN TCH006-1357), in which all diagnostic features for the assignation of these tracks to *Megalosauripus transjurani*, such as the presence of a large PIV1 pad, phalangeal pad formula 2-3-4 and claw marks, are discernable.

**4.7.3 Level 1020**

**-Trackway TCH1020-T1 (S21)**

**Description:** Six-tracks discontinuous trackway located in the excavation area 12, with a relatively narrow gauge ([WAP/PL]-ratio of 0.5). Total length of the trackway is 6.6 m. The mean rotation of the tracks is outwardly rotated for both left (+7°) and right (+11°) tracks. Average PaL is 100.5 cm for the left-right pace and 107.3 cm for the right-left pace. Average SL is 205.1 cm, PA is 162º and speed estimation is 7 km/h. Mean PL is 32.4 cm and PW 25.1 cm. Quality of the tracks is of grade 2. Tracks are almost as long as wide. Digits impressions are well defined, with only one pad per digit appreciable, and lateral digit II and IV impressions do not merge in the heel area, giving the track morphology an asymmetric aspect.

**Interpretation:** Trackway configuration is quite irregular, with a 'zig-zag' pattern and a clear outward rotation for both right and left tracks. Pace lengths are slightly different between the right and left sides. The wide disposition of the tracks with respect to the midline results in a pronounced pace angulation, likley due to the relatively low locomotion speed. The general track morphology with the presence of a large PIV1 pad and well-separated and discernable digits suggest a *Megalosauripus* cf. *transjurani* affinity.

**-Trackway TCH1020-T2 (S22)**

**Description:** Seven-tracks discontinuous trackway located in excavation area 12, crossing a sauropod trackway and trackways TCH1020-T1 (see above, S21) and TCH1020-T3 (see below, S23). Total length is 10.6 m. It has a wide gauge, [WAP/PL]-ratio (0.6). The mean rotation of the tracks is inwardly rotated for both left (-9°) and right (-9°) tracks. Average PaL is 148.4 cm for the left-right pace and 139.3 cm for the right-left pace. Average SL is 283.5 cm, PA is 164º and speed estimation is 8.6 km/h. Mean PL is 42.8 cm and PW 30 cm. Quality of the tracks is of grade 2. Tracks are longer than wide. Digits impressions are well defined and separated from one another, with only one pad per digit appreciable and lateral digits II and IV impressions not merging in the heel area, giving the track morphology an asymmetric aspect, as exhibited in R1 (MJSN TCH006-1335) and L2 (MJSN TCH006-1140).

**Interpretation:** Trackway configuration is quite irregular, with a 'zig-zag' pattern and a clear inward rotation for both right and left tracks. Pace lengths are slightly different between the right and left sides. The wide disposition of the tracks with respect to the midline results in a pronounced pace angulation. The general track morphology with the presence of a large PIV1 pad connected to digit IV impression, and well-separated and discernable digits suggest a *Megalosauripus* cf. *transjurani* affinity.

**-Trackway TCH1020-T3 (S23)**

**Description:** Four-tracks partial trackway, located in excavation area 12, crossing trackway TCH1020-T1 and TCH1020-T2 (see above) and parallel to an opposite-directed sauropod trackway. Total length of the trackway is 4 m. The gauge is narrow ([WAP/PL]-ratio of 0.5). The mean rotation of the tracks is very outwardly oriented for both left (+12°) and right (+15°) tracks.

Average PaL is 135.5 cm for the left-right pace and 133.3 cm for the right-left pace. Average SL is 267 cm, PA is 176º and speed estimation is 8.7 km/h. Mean PL is 38.8 cm and PW23.3 cm. Quality of the tracks is of grade 1.5 but only two tracks are well discernible; the other two tracks are incomplete. Tracks are longer than wide, with no clear heel area impressed and non-tapering digits with a clover-like shape and an overall symmetric aspect. Track morphologies are very variable along the trackway and poorly-defined digits appear to be separated but not very discernable.

**Interpretation:** The tracks strongly recall ornithopod morphology but there is not enough evidence to suggest an ornithopod trackmaker origin based on two complete tracks only. These tracks represent a preservational morphotype that recalls Morphotype II *sensu* Marty, 2008), which will be discussed later. From the lack of clear pads defining the metatarsal-phalangeal pad region, it is not possible to identify these tracks as *Megalosauripus.*

**4.7.4 Level 1025**

**-Trackway TCH1025-T1 (S24)**

**Description:** Seven-tracks discontinuous trackway located in excavation area 12, crossing a sauropod trackway and trackways TCH1025-T2 (see below, S25, paratype). Total length of the trackway is 8.3 m. It has a comparatively wide gauge with a [WAP/PL]-ratio of 0.8. The mean rotation of the tracks is inwardly rotated for left (-1°) and outwardly rotated for right (+6°) tracks. Average PaL is 112.3 cm for the left-right pace and 130 cm for the right-left pace. Average SL is 231.3 cm, PA is 153º and speed estimation is 6.4 km/h. Mean PL is 40.4 cm and PW 29.4 cm. Quality of the tracks ranges between grades 1.5 and 2. Tracks are longer than wide and generally narrow. Digit impressions are well defined and separated from one another, with only one pad per digit appreciable and lateral digits II and IV impressions not merging in the heel area, giving the track morphology an asymmetric aspect visible in L4 (specimen MJSN TCH006-1329). When preserved, PIV1 is very well discernible, wide and connected to digit IV impression.

**Interpretation:** Trackway configuration is quite irregular, with a 'zig-zag' pattern. Pace lengths are quite different between the right and left sides. The wide disposition of the tracks with respect to the midline results in a pronounced pace angulation. The general track morphology with the presence of a large PIV1 pad, slightly connected to digit IV impression and well-separated and discernable digits suggest a *Megalosauripus* cf. *transjurani* affinity.

**-Trackway TCH1025-T2 (S25)**

**Description:** Three-tracks trackway located in excavation area 12, crossing theropod trackway TCH1025-T1 (see above). Total length of the trackway is 3.4 m. It has a relatively wide gauge as expressed by a [WAP/PL]-ratio of 0.9. The mean rotation of the tracks is registered only of left tracks and is a strong outward rotation (+18°). Average PaL is 142 cm for the left-right pace and 146 cm for the right-left pace. Average SL is 293.5 cm, PA is 162º and speed estimation is 11.3 km/h. Mean PL is 35.5 cm and PW 23.3 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are longer than wide and generally narrow. Digit impressions are well defined and separated from one another, with the typical phalangeal pad configuration of 2-3-4 (for digits II-III-IV) and claw marks in digits III and IV. The metatarso-phalangeal pad PIV1 is very well discernible, wide and connected to digit IV impression. This is especially true for track TCH1025-T2-L1, considered a paratype for the new ichnospecies (MJSN TCH006-1329).

**Interpretation:** Trackway configuration is slightly irregular, with a 'zig-zag' pattern. Pace lengths are quite different between the right and left sides. The general track morphology evidenced by the presence of a large PIV1 pad, connected to digit IV impression and well-separated and discernable digits assign this trackway to *Megalosauripus transjurani*.

**4.7.5 Level 1030**

**-Trackway TCH1030-T1 (S26)**

**Description:** Eight-tracks continuous trackway located in excavation area 12, parallel to an opposite-directed sauropod trackway and crossing trackway TCH1030-T3 (see below) and another sauropod trackway. Total length of the trackway is 9.7 m. The gauge is quite narrow ([WAP/PL]-ratio is 0.3). The mean rotation of the tracks is inward rotated for left (-4°) and outward rotated for right (+1°) tracks. Average PaL is 138.7 cm for the left-right pace and 129.8 cm for the right-left pace. Average SL is 264.4 cm, PA is 170º and speed estimation is 8.1 km/h. Mean PL is 40.5 cm and PW 28.6 cm. Quality of the tracks is between grades 1.5 and 2. Tracks are longer than wide, with no clear heel area impressed and non-tapering digits. Lateral digit impressions are almost not appreciable, with exeption oftrack R4 (MJSN TCH006-1023), which exhibits separated digits and a discernable PIV1 pad. Track morphologies are very variable along the trackway.

**Interpretation:** The track R4 (MJSN TCH006-1023) clearly respresents a *Megalosauripus* morphology allowing to classify this trackway as *Megalosauripus* isp. Most other tracks recall morphotype II, which in this case is a preservational variant of *Megalosauripus* tracks, related to variable substrate properties and/or trackmaker kinematics.

**-Trackway TCH1030-T2 (S27)**

**Description:** Five-tracks continuous trackway located in excavation area 12, subparallel to two sauropod trackways. Total length is 6.5 m. The gauge is very narrow with a [WAP/PL]-ratio of 0.1. The mean rotation of the tracks is outwardly rotated for both left tracks (+3º) and right tracks (+9º). Average PaL is 150 cm for left-to-right pace and 148 cm for right-to-left pace. Average SL is 301 cm, PA is 170º and speed estimation is 10.6 km/h. Mean PL is 37.9 cm and PW 23.7 cm. Quality of the tracks is between grades 2 and 2.5. Tracks are elongated and narrow, with a moderate mesaxony. A clear phalangeal pad configuration 2-3-4 is appreciable for digits II-III-IV inthe majority of the tracks. Claw marks are preserved on digits II-III of tracks L3 (MJSN TCH006-1022) and R3 (MJSN TCH006-1034). Track R2 (MJSN TCH006-1087) exhibits a wide PIV1 connected to digit IV impression. Tracks MJSN TCH006-1022 and MJSN TCH006-1087 are paratypes for the new ichnospecies.

**Interpretation:** Trackway configuration is quite regular, pace lengths not displaying any significant differences between the right and left sides. [WAP/PL]-ratio suggests a trackmaker with a narrow posture, that is moving relatively fast as expressed by the long SL. Track morphology is very well preserved, all the diagnostic features for the assignation of these tracks to *Megalosauripus transjurani*, such as the presence of a large PIV1 pad connected to dIV impression, a 2-3-4 phalangeal pad formula, and claw marks, are discernable.

**-Trackway TCH1030-T3 (S28)**

**Description:** Three-tracks discontinuous trackway located in excavation area 12, crossing theropod trackway TCH1030-T1 (see above) and three sauropod trackways. Total length is of 5.1 m. It has a very narrow gauge ([WAP/PL]-ratio of 0). The mean rotation of the tracks could only be measured for left tracks and results in an inward rotation (-12°). Average PaL is 146 cm, average SL 300 cm, and speed estimation is 10.8 km/h. Mean PL is 38 cm and PW 28.5 cm. Quality of the tracks is of grade 2. Tracks are longer than wide and narrow. Digit impressions are well defined and separated from one another. The metatarso-phalangeal pad PIV1 is well discernible, wide and connected to digit IV impression, well visible in track L1 (MJSNTCH006-1024).

**Interpretation:** Trackway is too short to properly describe its configuration. The general track morphology evidenced by the presence of a large PIV1 pad, connected to digit IV impression and well-separated and discernable digits suggest a *Megalosauripus* cf. *transjurani* affinity.

**-Trackway TCH1030-T4 (S29)**

**Description:** Two-tracks partial trackwaylocated in excavation area 12 and crossing TCH1030-T2. Total length of the trackway is 1.8 m. The gauge is not possible to calculate. Generally, the trackway is too poorly defined to be described. Quality of the tracks is between grades 1 and 1.5.

**Interpretation:** Trackway is too short to properly describe its configuration. The general track morphology is only discernible in track TCH1030-T4-R1, which shows that the track is longer than wide and narrow. These tracks are similar to *Megalosauripus* isp.

**-Trackway TCH1030-T5 (S28)**

**Description:** Two-tracks partial trackway located in excavation area 12. Total length of the trackway is 1.7 m. Trackway gauge cannot be determined because the presence of only two tracks. Average PaL is 125 cm. Mean PL is 34.8 cm and PW 27 cm. Quality of the tracks is of grade 2. Tracks are longer than wide and narrow. Track R1 is not very well preserved but displays a clear separation of digits. Track L1 is very well preserved, with digit impressions well discernible and separated from one another, with a claw mark on digit III, and the metatarso-phalangeal pad PIV1 well discernible, wide and connected to digit IV impression.

**Interpretation:** Trackway is too short to properly describe its configuration. The general track morphology with the presence of a large PIV1 pad connected to digit IV impression and well-separated and discernable digits suggest a *Megalosauripus* cf. *transjurani* affinity.

**-Trackway TCH1030-T6 (S30)**

**Description:** Two-tracks partial trackway located in excavation area 12. Total length is 1.5 m. Trackway gauge cannot be determined because the presence of only two tracks. Average PaL is 107.5 cm. Mean PL is 34.5 cm and PW 24.3 cm. Quality of the tracks is of grade 2.5. Tracks are very elongated and narrow, with a moderate mesaxony. A clear 2-3-4 phalangeal pad configuration is recognizable in all digits II-III-IV with a claw mark on digit III in track L1 (MJSN TCH006-1319).

**Interpretation:** Trackway is too short to define the configuration. Track morphology is very well preserved, and track L1 (MJSN TCH006-1319) is defined as the holotype of the newly-erected ichnospecies *Megalosauripus transjurani* (for more detailed descriptions see the diagnosis).

**-Trackway TCH1030-T7 (S31)**

**Description:** Three-tracks continuous trackway located in excavation area 12 with a very narrow gauge ([WAP/PL]-ratio of 0.2). Total length of the trackway is 3.4 m. Orientationcould only be measured for right tracksand resulted in an outward rotation (+4º). Average PaL is 137 cm. Average SL is 274.5 cm, with a PA of 173º and a speed estimation of 9.1 km/h. Mean PL is 38.8 cm and PW 22.5 cm. Tracks are very elongated and narrow, with a moderate mesaxony. A 2-3-4 phalangeal pad configuration is discernible for digits II-III-IV. Claw marks are visible for digits III-IV in track R1, and digit IV in track L2 (MJSN TCH006-1317), which is a paratype of *Megalosauripus transjurani*.

**Interpretation:** Trackway is too short to define itsconfiguration. [WAP/PL]-ratio suggests a trackmaker with a very narrow posture. Track morphology is very well preserved, especially in L2 (MJSN TCH006-1317), the paratype, with the presence of a large PIV1 pad and claw marks.

**5. Description of ichnoassemblages**

Large tridactyl tracks are quite a common element of the Ajoie ichnoassemblages, even though with 49 trackways they make up for only 19.4% of all documented tridactyl trackways and 10.3% of all documented dinosaur (tridactyl & sauropod) trackways.

Within both the lower and the intermediate track levels, only the lowermost main track level (i.e. level 500 and 1000, respectively) can be correlated between different sites. For instance, level SCR1000 can be correlated with TCH1000. Level CRO500 can be correlated with BEB500 and most likely also with CPP500, which, however, is located in Porrentruy about 5 km to the east of the CRO and BEB Highway A16 tracksites that are located only about 1.5 km from one another.

In most larger ichnoassemblages with large tridactyl trackways, several large tridactyl trackways were documented. Within these different ichnoassemblages they are associated with minute, small, and medium-sized theropod tracks, and with tiny ('baby'), small, and medium-sized sauropod tracks. However, in none of the ichnoassemblages are they associated with any of these size classes of theropod and sauropod dinsoaurs at the same time.

On the other hand, they are never directly associated with huge theropod and large sauropod trackways, even though at the BSY tracksite, trackways of both huge theropods and large sauropods occur on level BSY1050 only 10 cm above level BSY1040 with several trackways of large theropods.

Also on BSY1040, trackway T1 clearly overprints sauropod trackway S1. This is the only case where a large tridactyl trackway overprints a sauropod trackway and therefore clearly has passed by after the sauropod.

**(6) Systematic Ichnology**

Clade: Dinosauria OWEN [78]

Suborder: Theropoda MARSH [79]

Infraorder: Carnosauria HUENE [80]

Ichnosuborder: Carnosauripodoidei VYLOV [81]

Ichnofamily: Eubrontidae LULL [82]

Ichnogenus: *Megalosauripus* LESSERTISSEUR, [10] (*sensu* Lockley et al.[3])

**6.1 *Megalosauripus transjurani* ichnosp. nov.** (Fig 4)

**Etymology**: In analogy to Highway 16, also called 'Transjurane Highway'. All dinosaur track excavations prior to the construction of the highway were financed by 95% by the ASTRA (Swiss Federal Roads Authority), and herewith we want to acknowledge this important and unique contribution to Palaeontology in Switzerland. Trans from Latin meaning across, through or beyond.

Jura stands for the provenance (Jura Mountains, Jura Canton), and is derived from the Celtic/Gaulish word ‘Jor’ meaning forest or ‘mountains with forest’. The fossil-rich limestones of the Jura Mountains, which called Humboldt [83] ‘Jura Kalkstein’, are the basis of the name of the Jurassic Period [84, 85].

Holotype: TCH1030-T6-L1 (original specimen, collection no.: MJSN-TCH006-1319)

Paratypes: BSY1035-T6-L2 (original specimen, collection no.: MJSN BSY008-330), BSY1040-T1-R1 (original specimen, collection no.: MJSN BSY008-339), TCH1025-T2-L1 (original specimen, collection no.: MJSN TCH006-1329), TCH1030-T2-R2 (original specimen, collection no.: MJSN TCH006-1087), TCH1030-T2-L3 (original specimen, collection no.: MJSN TCH006-1022), TCH1030-T7-L2 (original specimen, collection no.: MJSN TCH006-1317).

Referres specimens: All referred specimens (tracks) are preserved as an original specimen. TCH1015-T1-L2 (MJSNTCH006-1348), TCH1015-T1-R3 (MJSN TCH006-1357), TCH1030-T2-R3 (MJSN TCH006-1034), BSY1040-T1-L2 (MJSN BSY008-338), BSY1040-T1-R2 (MJSN BSY008-337), BSY1040-T1-L3 (MJSN BSY008-336), BSY1040-T9-R3 (MJSN BSY008-334).

**Diagnosis**: Functionally tridactyl, asymmetrical track, clearly longer than wide ([PL/PW]-ratio ranges from 1.17 to 2.02, track length ranges from 35.5 to 44.5 cm, with a moderate mesaxony([te/PW]-ratio ranges from 0.35-0.73). Slender digits are well separated, often by small sediment ridges. Digit IV is the longest, followed by dIII and dII. Digit III is the widest, followed by dIV and dII. Tracks exhibit the typical theropod phalangeal pad formula of 2-3-4 corresponding to digits II, III and IV [68] in well-preserved tracks, while in slightly less well-preserved tracks, PIV3 and PIV2 are often not clearly discernible. PIV1 is very characteristic, as it has a circular (rounded) shape, it is the widest and largest phalangeal pad and is connected to the rest of dIV impression as it forms the round heel of the tracks. PIV1 is generally twice the width of the rest of dIV impression. Presence of well-marked and elongated claws, straight or sometimes inwardly/outwardly oriented on the tips of all three digits II-III-IV. Below digit II (between dII and dIV) a postero-medial indentation (notch) is well developed. Digit III impression is straight to sigmoidal; dII impression is generally inwardly oriented. Tips of dII and dIV can sometimes be on a line perpendicular to the long axis of dIII. Tips of digits II and IV can sometimes be on a line perpendicular to the long axis of digit III. In the majority of the analysed tracks, digit IV impression is the shallowest of the track, although sometimes the opposite also occurs (TCH1015-T1-L2 / specimen MJSN TCH006-1348; TCH1029-E1 / specimen MJSN TCH006-1321). There is no evidence for a digit I (hallux) impression.

Trackway configuration is generally quite regular; paces are subequal in length between the right and left sides, with no significant differences registered. Pace length ranges from 83 to 150 cm, pace angulation from 160º to 176º, and stride length from 235 to 301 cm. The gauge is variable with a [WAP/PL]-ratio of 0 to 0.5 indicating a trackmaker with a (very) narrow posture.

**Distribution:** Late Jurassic (Kimmeridgian)

**Type locality**: Courtedoux—Tchâfouè and Courtedoux—Bois de Sylleux tracksites, Ajoie district, Canton Jura, NW Switzerland.

**Type horizon**: Intermediate track-bearing levels [16, 24] of the Nerinean limestones *sensu* Jank [31, 34] of the Courtedoux Member [29] of the Reuchenette Formation [32].

**Age**: Tethyan Divisum to Acanthicum ammonite zones, late Early to early Late Kimmeridgian, Late Jurassic [22, 29-31, 34].

**Holotype**: Left pes track TCH1030-T6-L1 (MJSN TCH006-1319, Fig 5)

Description: Tridactyl, asymmetrical track with slender and well-segmented digits, with a phalangeal pad formula of 2-3-4 and with well-marked and inwardly-rotated claw marks. Digits are well separated, with well discernible sediment ridges between digits II-III and III-IV, and sediment displacement rims surrounding the track. The track is deep, especially digit IV, which is deeper than digits II digit III. The track is narrow, with asymmetric and low interdigital angles (29º for II^III and 22º for III^IV). The track is longer than wide ([PW/PL]-ratio= 1.5), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio= 0.58). Presence of wrinkle marks is due to growth of microbial mats, as also displayed by the well-laminated track-bearing layer. Two pads compose digit II. PII2 is longer and bigger than PII1 (proximal). There is a pronounced postero-medial indentation below the digitII impression. Digit III has a sigmoidal shape, and digit IV has four visible phalanges, wheras PIV1 is circular (well rounded), deep, and it is the largest phalangeal pad impression. It is also the deepest part of the track and forms the rounded heel of the track.

**Paratypes**

Left pes track TCH1030-T7-L2 (MJSN TCH006-1317, Fig 6)

Description: Tridactyl, asymmetrical track, slender and well-segmented digits, phalangeal formula 2-3-4 with well-marked and forwardly-directed claw marks. On digit II the claw mark is slightly inward oriented. Digits are well separated, with well-discernible sediment ridges between II-III and III-IV. The trac k is narrow, interdigital angles are asymmetric and low (9º for II^III and 21º for III^IV). The track is clearly longer than wide ([PW/PL]-ratio=1.85), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio=0.73). The track still preserves some track fillings. Digit II is composed of two pads, whereas PII2 is longer and bigger than PII1 (proximal). There is a pronounced postero-medial indentation below digitII impression. In digit III, PIII2 is longer than the proximal and distal pads. Digit IV has four clearly visible phalanges. PIV1 is well rounded, deep and large. It is the deepest part of the track. Furthermore, the IV digit impression is shallower than digitsII and III.PIV2 and PIV3 are not well discernible and not very big (marked as fused in S1). PIV2-3-4 are shallower than PIV1.

Right pes track BSY1040-T1-R1 (MJSN BSY008-339, Fig 7)

Description: Very shallow, tridactyl, asymmetrical track, with slender and well-separated digits. All phalanges, except for PIV3 and PIV2, are well discernible. Claw marks are slender and comparatively short, probably due to the firmness of the substrate, as reflected by the shallowness of the track. Presence of a pronounced postero-medial indentation below dII. Narrow track with asymmetric and low interdigital angles (5º for II^III and 14º for III^IV). The track is longer than wide (PL/PW=1.8), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio=0.6). The slab is characterized by a wrinkled surface ('wrinkle marks'), most likely due to the former presence of microbial mats [86, 87].

Left pes track TCH1025-T2-L1 (MJSN TCH006-1329, Fig 8)

Description: Tridactyl, asymmetrical track, with digits III and IV very well preserved and digit II in interference with track TCH1025-T1-L4 (preserved on the same slab MJSN TCH006-1329) and therefore not clearly discernible. Digits are well separated by very steep, pronounced and narrow sediment ridges between digits II-III, suggesting that sediment was squeezed between the two digits. Claws are forwardly directed forming shapes recalling isosceles triangles. Track is narrow, interdigital angle is asymmetric and low (6º for II^III and 20º for III^IV). The track is longer than wide ([PW/PL]-ratio=1.8), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio=0.51). Presence of wrinkle marks is due to the growth of microbial mats [86, 87], as displayed also by the finely-laminated track-bearing layer.

Right pes track TCH1030-T2-R2 (MJSN TCH006-1087, Fig 9B-E)

Description: Tridactyl, asymmetrical track, with slender and well-separated digits. Digits appear to be well impressed as the track shows a certain depth and digit IV impression is much shallower with respect to the other digits. All phalanges, apart from PIV3 and PIV2, are well discernible. Impression of PIV1 phalangeal pad is rounded and it measures 10 cm in diamater. Digits II-IV distal endings impressions are not aligned. Digits II-III impressions are inwardly rotated. Claw marks are slender and well developed, forming isoscele triangle shape in correspondance of digit II and scalene shapes for digit III impression. No claw mark is observed in correspondance to digit IV impression. The interdigital angles are asymmetric (18º for II^III and 30º for III^IV). The track is longer than wide ([PW/PL]-ratio=1.5), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio=0.6). The slab is characterized by a wrinkled surface (wrinkle marks), most likely due to the former presence of microbial mats [86, 87].

Left pes track TCH1030-T2-L3 (MJSN TCH006-1022, Fig 9F-I)

Description: Shallow, tridactyl, asymmetrical track, with slender and well-separated digits. All phalanges, except for PIV3 and PIV2, are well discernible. Impression of PIV1 phalangeal pad is rounded and it measures 10 cm in diamater. Digit IV impression is the shallowest. Digits II-IV distal endings impressions are slightly diverging from one another, meaning that they are not aligned. Digits II-III impressions are inwardly rotated. Claw marks are slender and well developed, forming scalene triangle shape in correspondance of digit II and isoscele shapes for digits III and IV impressions. The interdigital angles are subequal in divergence (19º for II^III and 19º for III^IV). The track is longer than wide ([PW/PL]-ratio=1.67), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio=0.58). The slab is characterized by a wrinkled surface (wrinkle marks), most likely due to the former presence of microbial mats [86, 87].

Left pes track BSY1035-T6-L2 (MJSN BSY008-330, Fig 10)

Description: Tridactyl, asymmetrical track fill, with slender and well-separated digits. Digits appear to be well impressed as the track shows a certain depth and the digit IV impression is somewhat shallower with respect to the other digits, although at least PIV1, PIV2 and PIV4 phalageal pad impressions are appreciable. Phalangeal pad impressions for all the digits are well discernible, except for PIV3. Impression of PIV1 phalangeal pad is rounded and very well developed and impressed, measuring 11.5 cm in diamater. Digits II-IV distal endings impressions are not aligned and digit II impression is slightly inwardly oriented, with a subparallel orientation with respect to digit III impression. Claw marks are slender and well developed, forming isoscele triangle shape in correspondance of digit II and inwardly oriented 'D-shape' for digit III impression. No claw mark is observed in correspondance to digit IV impression. The interdigital angles are subequal and narrow (10º for II^III and 15º for III^IV). The track is much longer than wide ([PW/PL]-ratio=1.8), the mesaxonic index is medium and not extremely pronounced ([te/PW]-ratio=0.5).

**Differential diagnosis** (Fig 11)

The major difference of *M. transjurani* with *M. uzbekistanicus* from the Late Jurassic of Turkmenistan and Uzbekistan [3, 6, 98] and *M. teutonicus* from the Late Jurassic (Kimmeridgian) of Northern Germany (Barkhausen tracksite; *Megalosauropus* in [96]; amended as *Megalosauripus* in Lockley et al.[3]) lies in the size of PIV1, which is twice the width of digit IV in *M. transjurani* and is much smaller in *M. uzbekistanicus* (comparable to the width of digit IV) and absent in *M. teutonicus*. The amended diagnosis for *Megalosauripus uzbekistanicus* of Fanti et al. [6] adds the presence of the hallux or digit I impression posteriorly and laterally oriented, which in all specimens of *M. transjurani*, independently of tracks depth, is always absent. *M.teutonicus* is characterized by deep tracks (10 cm), broad and short, deeply impressed digits, lack of any discrete phalangeal pad impressions and it is generally poorly preserved. All these features are clearly different from the shallow and well-defined *M. transjurani* features.

*Euthynichnium lusitanicum* from the Late Jurassic of Cabo Mondego, Portugal [99], amended in Lockley et al. [3] is considered very distinctive because of the small and slender anteromedially facing hallux impression, which makes the track tetradactyl with three large, non-tapering digits with no clear phalangeal pad impressions. All these characteristics are very different from *M. transjurani*. For similar reasons the tetradactyl *Boutakioutichnium atlasicus* from the Late Jurassic of Morocco [94] is also considered different from the studied tracks.

*Megalosauropus broomensis* from the Early Cretaceous of Australia [95, 100] is defined by a quite an atypical phalangeal pad formula of 3-4-5 for digits II-III-IV, which is absent in *M. transjurani*.

The taxonomic position of *Bueckeburgichnus maximus* from the Early Cretaceous of Northern Germany from the Wealden beds (Harrl-quarries near Bueckeburg [13]), was the subject of disagreements between Lockley [91] and Thulborn [5]. Although it is true that the concept of *Bueckeburgichnus maximus,* (redescribed in Lockley [91] as "large tetradactyl theropod track with a small hallux (digit I), digit II wide and well-padded, digit III parallel sided proximally but strongly tapering distally, digit IV narrow with traces of discrete digital pads"), differs greatly from *Megalosauripus transjurani*, it should be underscored that the amended diagnosis of Lockley [91] is based on a different specimen with respect to the original diagnosis by [13]. In fact, the holotype of *Bueckeburgichnus maximus* KUHN [13] is, as pointed out by Thuborn [5], the same specimen on which the taxon *Megalosauripus* was coined by Lessertisseur [10], who was referring to drawings by Ballerstedt ([11], fig. 4) and Abel ([12], fig. 120).

*Iberosauripus grandis* from the Jurassic-Cretaceous transition of the Iberian range [63] is rather poorly illustrated and the material poorly preserved. Based on the descriptions in Cobos et al. [63], and on our own personal observations, *I. grandis* differs from *M. transjurani* in the width of the track, almost as wide as long (PL/PW 1.2, table 2 in Cobos et al. [63]), the broadness of its digit impressions, the lack of a strongly developed PIV1, and the general symmetric aspect with lateral digits II and IV impressions subequal in length and a very weak mesaxonic index (0.3).

*Irenesauripus acutus* from the Aptian–Albian of Canada ([89], fig. 2, p.64) strongly differs from *M. transjurani* because of the very elongated, narrow and slender digits, larger interdigital angles, and absence of phalangeal pad impressions. This ichnotaxon is erected on a clearly compromised track due to rheological bias, which was left in a water-saturated sediment causing mud collapse and sealing of digit impressions after its formations.

*Irenichnites* [89] is clearly different from *M. transjurani* because the heel pad is not completely developed and the track is very broad and very small, the longest measure is of 15 cm.

*M. transjurani* lacks the sigmoidal digit III impression and exhibits much better-defined phalangeal pad marks with respect to *Hispanosauropus hauboldi* ([101], revised in Lockley et al.[4] and Avanzini et al. [102]) which is indicated as plantigrade. Although a clear and diagnostic description for this ichnogenus is not provided in these papers, it is indicated that at least some digit pad impressions are present in most examples, but they are usually not well defined [102].

*Asianopodus* from the Valaginian to Barremian of Japan [103] is diagnosed as small to medium-sized tridactyl, mesaxonic and subsymmetrical track with a distinct 'bulbous' heel impression, and Xing et al. [88] also reported *Asianopodus* from the Early Cretaceous of China displaying a well-developed and sub-rounded metatarsophalangeal pad located axially posterior to the axis of digit III. Despite some similarity with *Megalosauripus transjurani* regarding the metatarsophalangeal pad area (presence of a large PIV1)*, Asianopodus* is different because of the more central position of the metatarsophalangeal pad PIV1, giving the track a symmetrical shape and because of the clear separation of PIV1 with all digit impressions. As a quick clarification, Xing et al. ([88], fig. 6B, p. 310) figured a track as *Megalosauripus* isp., although this track is the type specimen of *Euthynichnium lusitanicum* (compare with Lockley et al.[3], fig.7).

*Jialingpus* from the Late Jurassic of China [104, 105] is similar to *M. transjurani* in resepct to the size of PIV1 but differs in the overall morphology since it displays a different phalangeal formula of 2-3-3-4 respectively for digits I-II-III-IV with two developed metatarsophalangeal pads that connect with lateral digits II and IV, and the presence of a hallux (dI) impression.

Huge (>70 cm) theropod ichnotaxa such as *Tyrannosauripus* from the Late Cretaceous of New Mexico [64], *Bellatoripes* from the Late Cretaceous of Canada [90] and some other large to huge unnamed tracks from the Late Jurassic of Portugal [106] and Morocco [93, 107] are not considered here, as they significantly differ from *Megalosauripus* and *Megalosauripus transjurani*. Huge to gigantic (PL > 50 cm) theropod tracks from Highway A16 that are significantly different from *M. transjurani* are currently under study [97].

**6.2 Other morphologies described**

The great amount of large tridactyl tracks and trackways uncovered on six different tracksites and ten different track levels on Highway A16 allowed classify a wide range of morphological variations registered on the different levels and even along the course of individual trackways (especially on levels 500, 1000, 1020, 1030 and 1040). For this reason, only the best-preserved tracks were classified in the new ichnospecies of *Megalosauripus transjurani*. Tracks that do not retain suffient diagnostic features to assign them to this new ichnospecies were addressed with three other 'morphological names': *Megalosauripus* cf. *transjurani, Megalosauripus* isp., and Morphotype II *sensu* Marty [16]. These three different morphotypes may occur on the same level and even along the course of a single trackway due to changes in substrate properties and/or kinematics of the trackmaker and this has important implications for the understanding and classification (ichnotaxonomy) of large tridactyl tracks. These aspects will further be commented in the discussion.

-*Megalosauripus* cf. *transjurani* (Fig 12A-H)

**Material:** Levels and Tracksites: SCR1000, TCH1020, TCH1025, TCH1030, BSY1035.

Trackways: SCR1000-T23, T24 (S7, S8); TCH1020-T1, T2 (S21, S22); TCH1025- T1 (S24); TCH1030-T5 ( 28); BSY1035-T1, T7 (S12).

This variation of the new ichnospecies is used when the track morphology is well preserved and the large and wide metatarso-phalangeal pad PIV1 is discernable and connected to digit IV, and when digits are well separated. However, not all the phalangeal pads and three claws are impressed and clearly discernible.

-*Megalosauripus* isp. (Fig 12I-Q).

**Material***:* Levels and Tracksites: TCH1000, BSY1020, BSY1025. Trackways: TCH1000-TR1, TR2 (Fig 12I-Q, and S18, S19); BSY1020-T1 (S10); BSY1025-T3 (S10), BEB500-TR1, TR2, TR5, TR8 (S3).

*Megalosauripus* isp. nomenclature is used when tracks reflect a limited preservational variation on the strict definition of this ichnogenus [3] and therefore when digits are separated and distinguishable from one another, heel pad (PIV1) is not very discernable, and morphometric parameters for tracks and trackway configuration are typical, such as tracks longer than wide, elongated, asymmetric, moderate mesaxony, notch developed between digit II and heel area impression, trackway configuration somewhat irregular. This classification is linked to a preservational variation of the *M. transjurani* track morphology linked to substrate consistency, limb kinematic and behavior of the trackmaker [108] rather than foot anatomy (different trackmaker).

-Morphotype II *sensu* [16] (Fig 12R-Y)

**Material***:* Levels and Tracksites: CRO500, BEB500, SCR1000, TCH1020, TCH1030, BSY1040. Trackways: CRO500-T43 (S2), BEB500-TR3, TR4, TR7 (S3, S4), SCR1000-T18 (Fig 12X, S6), TCH1020-T3 (S23), TCH1030-T1 (Fig 12RY, S26), BSY1040-T8 (S16).

Morphotype II is characterized by subsymmetric tridactyl tracks, most of them as wide as long but also with some specimens much longer than wide ([PW/PL]-ratio ranging from 1.18–1.72) and a moderate mesaxony ([te/PW]-ratio ranging from 0.45–0.58). Digits are not well separated as in

*Megalosauripus* tracks, especially the lateral digits II and IV, which are also typically merged in the heel without evidence for a postero-medial indentation below dII. Digits are tapered and rounded to slightly pointed, but no claw marks can be identified. Digit III impression is well separated from dII and dIV and blunt with a trapezoidal (clover-like) shape with the maximum width located in the medium to anterior part of the digit. It is short and forwardly directed, not sigmoidal. No phalangeal pads are discernible. All three digits are of about the same length. Tracks are usually inclined towards the digit III impression, which is the deepest one. Interdigital angles are roughly subequal. Displacement rims are often well developed, especially around digit III, sometimes they are present all around the track. There is no evidence for any manus tracks in association to the pes impressions. The [WAP/PL]-ratio ranges from 0.2 to 0.6, trackway configuration is quite variable, ranging from narrow and very straight to sinusoidal trackways displaying a 'zig-zag' pattern with outwardly rotated tracks and a wider gauge. Rare trackway patterns such as 'standing still' (pair of parallel tracks, commonly showing a small inward rotation, [109]) were documented. Intra-trackway stride lenghts range from 173 to 317 cm, pace lengths from 86 to 138 cm, pace angulation from 149º to 176º and speed estimations from 5.3 to 12.7 km/h.

## 7. DISCUSSION

### 7.1 **Other occurrences of *Megalosauripus*-type and other similar theropod tracks**

Ichnotaxonomy of medium-sized to huge theropod tracks, especially of those from the Late Jurassic and Early Cretaceous, is a complicated matter and has been debated in many different papers (e.g. Lockley, Thulborn etc). Many ichnotaxa have been discussed and reviewed by various authors, but, at the moment, there is no consensus about the validity or redundancy of many of these. It is outside the scope of the present paper to review all ichnotaxa of medium-sized to huge theropod tracks that are similar to the new ichnospecies *Megalosauripus transjurani*, Lockley et al. [4] pointed out that tracks named "*Megalosaurus"* from the Late Jurassic of Cabo Mondego, Portugal [110], named *Euthynichnium lusitanicum* in Lockley et al., [3] and problematic ichnotaxa such as *Megalosauripus* [3, 5 10] and *Megalosauropus* [96] have some potential relationship to *Hispanosauropus hauboldi* [101]. Avanzini et al. [102] noted that the relationship between *Hispanosauropus* and megalosaur tracks (*Megalosauripus*) is complex. However, Piñuela ([111], p.76) strongly suggested that *Hispanosauropus* should not be used anymore and should rather be included in the *Megalosauripus* definition [3], since the lacks of a holotype and the poor preservation of the designated topotype at la Griega tracksite. Nevertheless, it is of no surprise that all these ichnotaxa that describe relatively large to huge and massive Late Jurassic theropod tracks from the Iberian Peninsula and Western Europe are morphologically similar, and to some degree also to *Megalosauripus*. In addition, some theropod tracks of comparable size from Asturias were addressed with the binomen *Megalosauripus-Kayentapus* (figured and described in Piñuela, [111] fig. 9.1.7, p.87). These tracks are clearly different from the studied material, especially because of the lack of the diagnostic large and round PIV1 connected to dIV.

In the Jura Mountains, other so far unnamed large theropod tracks occur at the Kimmeridgian La Heutte II, Grenchenberg, and Glovelier—Côte du Crêt (GLO–CCR) tracksites in NW Switzerland, and at the Tithonian Plagne tracksite in France [112].

The trackway at the Glovelier tracksite was originally discovered in 1998 by G.-A. Beuchat [113]. It consists of six tracks that are poorly preserved, lack any anatomical details such as phalangeal pads or claw marks, and that are either strongly weathered and/or they are undertracks (pers. obs. 2016), so that they can at best be identified as tridactyl tracks of likely theropod origin, somewhat similar to Morphotype II *sensu* Marty [16], but clearly different from *M. transjurani*.

At the Grenchenberg, a trackway of a large theropod was discovered within this interval. This 3-m long trackway consists of four consecutive tracks with a mean length of 35 cm and a slightly-curved digit III. It is similar to the "robust morphotype" including the largest tracks of Highway A16 with a pes length of up to 80 cm [114]. From the La Heutte II tracksite Meyer & Hauser [115] described a single large theropod track that is longer than wide, has narrow interdigital angles, claw marks and pad impressions. However, based on fig. 3 in Meyer & Hauser [115], the digits have no pad impressions discernible, they are not separated and they are fused in a large and rounded heel area. Based on the figure and description of Meyer & Hauser [115], this track cannot be assigned to *Megalosauripus (transjurani)*, but a cast of the track is housed at the Naturmuseum Solothurn and is worth to be re-studied.

At Plagne (France), at least two trackways of medium-sized to large theropods are well preserved, but they are not yet published. Judging on personal observations (DM, 2012) both trackways labelled "PD" and "PG", respectively, are characterized by tracks with a PL of approximately 25-30 cm, well-separated digits with phalangeal pad impressions, and by the presence of a large PIV1 pad. These tracks can be assigned to *Megalosauripus* and maybe even *M. transjurani*, but this has to be confirmed by future studies.

The Late Jurassic Loulle tracksite in the French Jura Mountains exhibits an eight-step trackway of a huge theropod (LOU 20, mean PL=77 cm) that was tentatively assigned to *Megalosauripus* by Mazin et al. ([116], fig. 14). These authors stated that this trackway with an irregular gait exhibits asymmetric tracks with three well-separated digits, three claw marks, and a phalangeal pad configuration of 2-3-3 or -4 but that cannot be determined with confidence. Based on fig. 14 and descriptions in Mazin et al. [116] there is no evidence for a large PIV1 in connection with dIV and for this reason, and also because of their much larger size, these tracks are not similar to *M. transjurani*. Mazin et al. [116] have also described three trackways (LOU 05, LOU 06, LOU 13) with a PL between 21–24.3 cm, which they referred to *Carmelopodus*. However, these tracks also ressemble *Megalosauripus* because of their slender and well-separated digits with clear phalangeal pad impressions, but they are smaller than typical *Megalosauripus* tracks. Also, these tracks do not show evidence for a large PIV1 in connection with dIV and for this reason they cannot be assigned to M. *transjurani*.

Recently, Razzolini et al. [9] classified large theropod tracks (of up to 80 cm in pes length) from the Middle Jurassic Vale de Meios quarry from the Lusitanian basin of Portugal as *Megalosauripus* isp. Where preserved (e.g., track VMX.1 in [9], fig. 5), the phalangeal pad formula is 2-3-4 for digits II-III-IVbut these *Megalosauripus* tracks do not show the diagnostic large PIV1 pad of *M. transjurani* and are for this reason different (Fig 11).

Another famous Middle Jurassic tracksite is that of Ardley Quarry (Oxfordshire, UK), which displays large tridactyl tracks indicated as *Megalosauripus*-like tracks in Day et al. [15, 117] and deeply analysed from a biomechanical and biological aspect in Mossman et al. [118]. The best-preserved tracks such as R20 of trackway T80 ([118], fig. 6) perfectly fit this ichnogenus classification because it exhibits well-separated, slender digits with claw marks, the average TL/TW index (1.40), the inward rotation of digit III and phalangeal pads possibly with a 2-3-4 phalangeal pad configuration for dII-III-IV, the PIV1 phalangeal pad connecting to digit IV impression and the postero-medial indentation developing from the posterior margin of digit II impression. Nevertheless, Ardley Quarry tracks are larger in size and the diagnostic PIV1 is not as developed as in *M. transjurani* and it is particularly small in the Ardley Quarry tracks.

Other tracks assigned to *Megalosauripus* from the Late Jurassic [93] and Early Cretaceous of Morocco [119], Arizona and Utah [3, 19], Poland [20], and Germany [14], and from the Middle Jurassic of Madagascar [120] and China [7] either display subequal phalangeal pads when preserved (Arizona, Utah, Germany, Morocco), lack a discrete phalangeal pad formula (Madagascar, England, Poland) or are too poorly preserved for a sound comparison (China).

To summarize, tracks from North America, Europe, North Africa and Asia that have been assigned to *Megalosauripus* ichnogenus differ from the new proposed ichnospecies *M. transjurani* described herein and the most diagnostic feature for *M. transjurani* certainly is the large and rounded PIV1 pad in connection with dIV.

In Lockley et al. [3], the smallest *Megalosauripus* tracks from North America, Central Asia and Europe have a PL of 39 cm, whereas the mean PL value is about 50 cm and the maximum 77 cm.

The English tracks published by Day et al. [15, 117] and some from Uzbekistan and Turkmenistan [6] are at the upper end of this size range. Generally, *Megalosauripus* track lengths from specimens from North America, Iberian Peninsula and Central Asia (Uzbekistan and Turkmenistan) are ranging from 40 cm to a maximum of 80 cm, while the material from Highway A16 ranges from 35.5 cm to a maximum of 45.5 cm. This size range is also encompassed in *Megalosauripus* isp. from the Late Jurassic–Early Cretaceous of China ([7]: PL=38.3 cm), Middle Jurassic of Portugal ([9]: PL 20-80 cm) and Madagascar ([120]: average PL=34 cm).

Although size alone should not be a criterion for ichnotaxonomic discrimination [120, 121], some tracksites (Vale de Meios tracksite, [9]; Tsisandro tracksite, [120]) display some track lengths values that are outliers (smallest track recorded in Vale de Meios, Portugal is of 22 cm) of the typical *Megalosauripus* size range (>50 cm).

It is not unsual to observe tracks retaining similar morphologies with different sizes [7, 9, 122, 123] because of different ontogenetic stages of the trackmakers [124], osteological convergence among different trackmakers or extramorphological factors biasing track morphology. On the other hand, it is noteworthy that among ten different stratigraphical levels analysed, the material clearly identified as *M. transjurani* has relatively small PL values compared to the other *Megalosauripus* tracks (see Fig 11I-O) and these are distributed over a narrow size-range (from 35.5 cm to 42.5 cm). The implications for this fact might be due to age-segregation distribution among these theropods [123, 125], perhaps concentrating larger theropod tracks (adult- individuals) attributable to *Megalosauripus* in other areas, leaving the tidal flat as the favoured environment for subadult and adult individuals confining the size of the footprint to a narrow range [15, 118].

The retention of similar track lengths and morphological features could be shrinking the trackmaker identification, to a middle-sized theropod.

### 7.2 Trackmaker identification for *Megalosauripus transjurani*

During the Late Jurassic, the taxonomic diversity of large theropods is quite high, including the famileis Allosauridae, Megalosauroidea, Ceratosauria and Coelurosauria. The osteological convergence and substantial overlap in phalangeal proportions of the theropod foot would not allow a lower level distinction among different theropod taxa.

In addition, the autopodium of all these theropods are very conservative concerning the functional morphology and the shape, and those features that could help with the indentification of the trackmaker, e.g. metarsal impressions and position and orientation of digit I [126], are not preserved in the analysed tracks. However, considering additional data such as the size and the provenance (considering both temporal and spatial distributions), a discussion on the skeletal remains of similar age as the *M. transjurani* tracks is attempted here. An identification of the large theropod trackmaker is not easy because of the scarcity of their skeletal remains in the Late Jurassic deposits of the Jura carbonate platform or surrounding areas. In the Swiss Jura Mountains, the body fossil record of theropods is scarce and only comprises an isolated allosaurid tooth from the Silberhöhle near Röschenz (Late Oxfordian, Canton Baselland; [127]); two isolated theropod teeth from the Solothurn Turtle Limestone (Late Kimmeridgian, Canton Solothurn; [128]), one of which is similar to dromaeosaurid teeth (Meyer & Thüring, 2003); and, finally, a large (total length of about 7 cm) theropod tooth from the Moutier sauropod bone assemblage (Early Kimmeridgian, Canton Bern) initially figured in [129], and attributed to *Ceratosaurus* [130].

In the French Jura Mountains, a couple of theropod teeth are known from the Damparis sauropod assemblage [131, 132] one of which is considerably large (total length of 11cm) and was attributed to *Megalosaurus insignis* by Lapparent [131]. Furthermore, several isolated, huge vertebrae are known from the Oxfordian of Plaimbois-du-Miroir, Doubs Department [133], corroborating the presence of a “very large theropod of uncertain affinity” [134], but these remains still lack any closer scientific description. However, the teeth from Damparis and the remains from Plaimbois-du-Mirroir are large enough to represent potential trackmakers from the Loulle quarry in the French

Jura Mountains [116]. The presence of megatheropods on the Jura carbonate platform during the Late Oxfordian and Kimmeridgian can now be confirmed by both the skeletal and track record.

Apart from those of the Jura Mountains, there are potential large theropod trackmakers known from the Late Jurassic in Europe and notably Portugal. These include members of the Ceratosauridae, Allosauridae, and Megalosauridae ('megalosaur' or 'megalosaurid'), e.g., [2, 3, 17, 91, 135-137].

*Allosaurus* specimens described from the Late Jurassic of Portugal and assigned to *Allosaurus fragilis* [138, 139] and *Allosaurus europaeus* [140] with an estimated hip height of 2.4 m seem plausible for having left tracks smaller than 50 cm in total length and covering the size range of *M. transjurani*. On the other hand, the largest *Allosaurus* specimens such as *Allosaurus fragilis* from the Cleveland-Lloyd Dinosaur Quarry with an estimated total body length of up to 12.5 [141, 142] and notably *Saurophaganax* [143] from the Late Jurassic Morrison Formation, USA were indeed too large and probably would have left tracks much bigger (PL > 50 cm) than *M. transjurani*. Ceratosauridae are also known from the Late Jurassic of Portugal [144]. *Ceratosaurus* with an estimated body length of around 5 m [145] is also a possible candidate for producing tracks ranging from 30 to 50 cm in pes length.

Megalosauridae or 'megalosaurs' are poorly understood, both in their anatomy and their phylogenetic affinities [146, 147], and Thulborn [5] stated, "there exists no definite conception of megalosaurs or of their tracks". However, *Torvosaurus* is a member of the Megalosauridae that apart from Colorado [148] is known from Portugal [106, 140]. Its body length ranges from 8-12 m, which is clearly too large for the studied tracks. Cobos et al. [63] have suggested that tracks classified as *Bueckeburgichnus*, *Hispanosauripus*, *Megalosauripus* were probably left by members of the Allosauridae. A recent paper [149] described a new large theropod *Wiehenvenator albati* from the Callovian of Germany, a derived megalosaurine megalosaurid closely related to *Torvosaurus*, which might be the only megalosaurid taxon to survive into the Late Jurassic. However, an allosaurid trackmaker seems much more likely for these tracks than a 'megalosaurid' trackmaker, which would have left larger tracks. There are larger (huge) theropod tracks discovered on the Highway A16 tracksites. However, these tracks are clearly different and will form another new ichnotaxon (under description).

**7.3 Interpretation and ichnotaxonomy of Morphotype II tracks**

Some of the studied tracks are classified as Morphotype II *sensu* Marty [16], characterized as subsymmetric, large, slightly mesaxonic, slightly longer than wide (sometimes almost as wide as long), with subsymmetric interdigital angles, and with blunt toes and without evidence for the impression of discrete phalangeal pads and claws. In the field, most (but not all) of these trackways were labeled as 'TR' trackways, because they were obviously different from other large '*Megalosauripus*-type', typical theropod trackways.

On four other different levels (1000, 1020, 1030 and 1040) from three different tracksites (BSY; TCH, SCR) Morphotype II tracks are associated with *Megalosauripus transjurani* (and/or cf. *transjurani* and/or *Megalosauripus* isp.). For instance, level 1000 can be correlated between the SCR and TCH tracksites, and here Morphotype II trackway SCR-1000-T18 is associated on the same level with *Megalosauripus* cf. *transjurani* SCR-1000-T23 and -T24 trackways, and with poorly-preserved *Megalosauripus* isp. trackways TCH-1000-TR1 and -TR2 (S8). On level TCH1020 Morphotype II trackway TCH1020-T3 is associated with the *Megalosauripus* cf. *transjurani* trackways TCH1020-T1 and -T2. Level BSY1040 is also characterized by the co-occurrence of Morphotype II (BSY1040-T8) and *Megalosauripus transjurani* BSY1040-T1, -T7 and -T9 trackways.

On level 1030, Morphotype II tracks even occur within trackways that can clearly be assigned to *Megalosauripus* (*transjurani*) and co-occur with *Megalosauripus transjurani* trackways TCH1030-T2 -T6 (holotype trackway of *M. transjurani*, Fig 5), and -T7. For instance, TCH1030-T1-R4 track clearly respresents a *Megalosauripus* but most other tracks recall Morphotype II (S26). This case is a preservational variant of *Megalosauripus* tracks, related to variable substrate properties and/or trackmaker locomotion. This trackway is important because it exhibits how track morphology may change along trackway course with single tracks resembling different morphotypes or even different ichnotaxa.

Trackway TCH1000-TR2 is another interesting example: because of the preserved phalangeal pads and claw marks in some of the tracks, it is classified as *Megalosauripus* isp., despite the fact that along the 25-m long trackway, tracks show different morphologies, some of which strongly recall Morphotype II (e.g. TCH1000-TR2-R9, L10, R10). Another example is trackway BSY1040-T8, which has the highest stride lengths (> 3 m) and speed estimation (12.7 km/h) of all studied trackways. In this trackway, tracks with altered morphology where the merging lateral digits and heel area is not discernable, resemble Morphotype II tracks. Further, digit III is strogly indented into the sediment, indicating that the trackmaker was moving fast, with a high digitigrade posture causing the merging of lateral digits and the lack of a clear PIV1 impression. Accordingly, Morphotype II tracks occurring in these trackways are also interpreted as preservation variants of *Megalosauripus* (*transjurani*) tracks.

However, in some of the other cases, especially when not both morphotypes occur along a single trackway, it is more difficult to unambiguously assess if a given Morphotype II trackway is a preservation variant of *Megalosauripus* or not, as they also resemble *Therangospodus pandemicus*. Lockley et al. [17] described *T. pandemicus* as medium sized, elongated asymmetric tracks (therefore longer than wide and not as long as wide) having digital pad impressions without creases separating discrete phalangeal pads, but which, when appreciable, suggest a 2-3-4 phalangeal formula; claw marks sometimes preserved; and trackway configuration quite similar to *Megalosauripus* (narrow trackway, variable step lengths and high 170º pace angulation). Or in other words, the diagnosis of *Therangospodus pandemicus* and *Iguanodontipus? oncalensis sensu* [17, 18] is entirely based on the lack of those features that are diagnostic for *Megalosauripus*, i.e. oval digital pads not separated into discrete phalangeal pads, no rotation of digit III, no separation on the proximal margins of the digits by a hypex.

Gierliński et al. ([150], p. 445) reported a tridactyl track from the Toarcian of Poland with more distinct phalangeal pads, but stated that they were ‘‘not sure if *Therangospodus* should be distinguished from *Megalosauripus*". A very important consideration in Gierliński et al. [150] is that they have noticed that "diagnostic features separating them (=*Therangospodus* vs. *Megalosauripus*) are entirely extramorphological and subject to growth and behavioral changes or potentially influenced by the substrate nature, so they may not reflect real taxonomic differences". Piñuela [111] also pointed out that because of the resemblance of *Therangospodus* (*pandemicus*) with altered and poorly-preserved specimens of *Megalosauripus*, this might at least in some cases be indicative, that *Therangospodus* (*pandemicus*) is the product of a morphological variation of the *Megalosauripus* ichnogenus. This would favour the interpretation of Morphotype II trackways as preservation tpyes of *Megalosauripus transjurani* or *Megalosauripus* in general, rather than assigning them to *Therangospodus* (*pandemicus*) or another new ichnotaxon. On the other hand, Fanti et al. [6], although noticing that some of the weathered *Megalosauripus* tracks are similar in overall morphology to *Therangospodus* (*pandemicus*), but larger in size, concluded that *Megalosauripus* and *Therangospodus* tracks preserved at the Khodja-Pil-Ata site (Turkmenistan) represent two distinct and valid ichnotaxa.

On the contrary, on level 500 (the lowest track level) at the CRO and BEB tracksites, Morphotype II tracks systematically occur along several trackways (CRO500-T43, BEB500-TR3, -TR4, -TR7, S2-4) without their morphology being susceptible to a high degree of intra-trackway variability. Thereby, some of the trackways of BEB500 are very long and exhibit more than 40 tracks per trackway. Notably, the consistent morphology suggests that these Morphotype II tracks are not preservational variants of *Megalosauripus*, but more likely were left by a different trackmaker.

On level BEB500, several trackways (BEB500-TR1, -TR2, -TR5, -TR8) with Morphotype II tracks that are most likely preservation variants of *Megalosauripus*-type tracks occur, even though they are also slightly similar to *Therangospodus pandemicus*. Furthermore, a single trackway assigned to

*Megalosauripus* isp. occurs on level 500 of the CPP tracksite. This indicates that Morphotype II trackways may be associated with *Megalosauripus*-type trackways.

Marty [16] stated that Morphotype II trackway CRO500-T43 shares both ornithopod and theropod characteristics, and is most similar to the ichnotaxon *Therangospodus* (but cannot unambiguously be assigned). It clearly differs from *Megalosauripus* (*sensu* [3]), and that it may have been left by a trackmaker with a well-padded, fleshy foot. Accordingly, Morphotype II tracks could also be addressed as '*Therangospodus*-type' tracks.

*Therangospodus oncalensis* was first informally introduced by Moratalla [151] in his thesis on dinosaur tracks from the Early Cretaceous of Spain, and later formally described by Lockley et al. [17]. The latter authors emended the description of *Therangospodus* as: "medium-sized, elongate, asymmetric theropod track with coalescend, elongate, oval digital pads, not separated into discrete phalangeal pads. Trackway narrow with little or no rotation of digit III long axis from trackway axis". Lockley et al. [17] regarded the lack of distinct, separate digital pads (robust digits without sharp termination) as a diagnostic feature of *Therangospodus oncalensis* and as evidence for a fleshy foot.

Gierliński et al. [150] noticed that Lockley et al. [17] have enriched the concept of 'megalosaur' tracks, restricting the name *Megalosauripus* to the tracks with distinct phalangeal pad impressions and *Therangospodus* for tracks lacking phalangeal pads distinctly imprinted. Barco et al. [21] also pointed out that the preservation of the *T. oncalensis* tracks from the Fuentesalvo tracksite (Early Cretaceous, Spain) is slightly variable, but the existence of a single tapering pad (narrower in the proximal and distal areas and wider in the centre) on each toe is observed in all of them; in the best-preserved ones, a rounded pad, corresponding to the heel, can be seen.

Castanera et al. [18] recognized the affinity of *Therangospodus oncalensis* with ornithopod tracks and they re-described it as *Iguanodontipus? oncalensis* declaring the former name *Therangospodus oncalensis* a *nomen nudum*. Díaz-Martínez [152], in his ichnotaxonomic review of large ornithopod tracks, also considered the trackmaker of *Therangospodus oncalensis* as an ornithopod dinosaur, but he considered *Therangospodus oncalensis* as a junior synonym of *Iguanodontipus burrey* ([152]: p. 25). Interestingly, trackway CRO500-T43 [16] was included in the bivariate analysis of medium-sized tridactyl tracks carried out by Castanera et al. [18], who pointed out its similarity with *I.? oncalensis.* Accordingly, this evidence suggests that at least some of the studied Morphotype II trackways can be assigned to an ornithopod trackmaker and that instead of '*Therangospodus*-type' tracks they are better addressed as either *I.*? *oncalensis* (*sensu* [18]) or *I. burrey sensu* [152].

**7.4 Trackmaker identification for Morphotype II tracks**

Trackmaker identification of Morphotype II is even more complicated than usually, as even within the same morphotype there are differences that can affect the interpretation. For these reasons, the identification of the trackmaker will be discussed grouping the tracks that present or lack phalangeal pads and/or claw marks.

BEB500-TR5, TR7, TR8 and CRO500-T43 lack most morphological features (e.g., phalangeal pads), and this lack is considered diagnostic for *Therangospodus oncalensis* [17]. However, the absence of a feature does not necessarily imply that the trackmaker's foot anatomically lacks this feature (i.e. phalangeal pads, claw marks), as the absence of a feature could also be related to substrate properties, kinematics, and/or taphonomical and preservational reasons (see also [55]).

Taking into accout these possible preservational issues, CRO500-T43 and the BEB500 Morphotype II trackways display a consistent morphology without marked intra-trackway variability, indicating that they were left by a different trackmaker than the *Megalosauripus* tracks, or in other words, these trackways are not poorly-preserved *Megalosauripus* trackways. However, the trackmaker cannot unambiguously be identified as a theropod or ornithopod dinosaur, even though the latter scenario (ornithopod) might be favoured because the trackways are tentatively assigned to *Iguanodontipus? oncalensis sensu* [18]. Accordingly, this would be the first evidence for the possible presence of ornithopod dinosaurs on the Jura carbonate platform.

The presence of a medium-sized to large sized ornithopod trackmaker during the Late Jurassic (Kimmeridgian-Tithonian) is supported by the skeletal record of the Iberian Peninsula [66,153-156], England [157] and North America (Morrison Formation, [158, 159]) that indicate the presence of both Ankylopollexia and Dryomorpha for non-Iguanodontoidea ornithopod. While skeletal remains of the hypsilophodontid *Othnielia* from the Kimmeridgian-Tithonian are quite abundant in the Morrison Formation [158], Late Jurassic records of hypsilophodontid orontihopods are scarce and few osteological remains were found in Portugal [153, 154]. Moreover, ornithopod dinosaurs are expected to leave smaller tracks (upto 25 cm) compared to those of level 500 (PL = 27-40 cm). Anyhow, the high degree of morphological convergence of the foot osteology beween medium-sized theropods and ornithopods from the Late Jurassic complicates a clear trackmaker assignment [14, 18, 160].

Morphotype II trackways from other levels (SCR1000-T18, TCH1020-T3, TCH1030-T1, BSY1040-T8), which present more morphological details, especially claw marks, are interpreted as preservational variants of *Megalosauripus* (*transjurani*). Therefore, they can be assigned more confidently to a theropod trackmaker, likely the same of *M. transjurani*, although it is not possible to refine the identification.

Even with a lot of available material, the present case of the Morphotype II tracks shows the difficulty to distinguish between poorly-preserved theropod tracks and (poorly-preserved) tracks that were left by ornithopods.

### 7.5 *Megalosauripus–Therangospodus* ichnoassociation

The *Megalosauripus–Therangospodus* ichnoassociation is known from various deposits around the world ranging in age from the Middle Jurassic to the Early Cretaceous, and it is characterized by the co-occurrence of these two ichnogenera both attributed to theropods [7, 17, 19-21]. Lockley & Mickelson [19] stated that in all cases of *Megalosauripus–Therangospodus* co-occurrences, tracks are associated with facies that represent the "interfingering of coastal dunes with flat, evenlybedded-argillaceous marginal marine sands", and Lockley et al [17] have suggested that the *Megalosauripus–Therangospodus* ichnoassociation has some potential utility for biostratigraphic correlations on a global scale.

In the present study, we have looked in detail at the intra-trackway variability and concluded that in the case of Morphotype II tracks of the intermediate track levels (1000, 1020, 1030, 1040) this variability is related to differences in substrate properties and/or kinematics, rather than addressing this variability as two different ichnotaxa (*Megalosauripus*, *Therangospodus*). This is also indicated by the presence of this variability along single trackways (intra-trackway variability). Therefore, we assume that in the intermediate track levels all Morphotype II tracks are poorly-preserved *Megalosauripus* (*transjurani*) tracks.

On level 500, on the other hand, Morphotype II tracks systematically occur along several single and considerably long trackways. These trackways are not considered as preservational variants of *Megalosauripus (transjurani)*, but as tracks tentatively assigned to *Iguanodontipus*? *oncalensis (sensu* Castanera et al. 2013), likely left by an ornithopod trackmaker.

Consequently, none of the Morphotype II tracks can be addressed as '*Therangospodus*-type' tracks indicating that the *Megalosauripus–Therangospodus* ichnoassociation is not present in Late Jurassic carbonate tidal-flat palaeoenvironments of the Jura carbonate platform (Ajoie, NW Switzerland).

The studied material shows that Morphotype II tracks (or '*Therangospodus*-type' tracks*)* and poorly-preserved *Megalosauripus* tracks often cannot clearly be distinguished and thus may be confounded with one another. Therefore, in the case of the *Megalosauripus–Therangospodus* ichnoassociation, it should be considered that inter- and intra-trackway morphological variability may represent a preservational continuum of one ichnotaxon rather than the presence of two different ichnotaxa. Accordingly, this may also question the occurrence of this ichnoassociation elsewhere if preservation variants of *Megalosauripus*-type tracks were misidentified as *Therangospodus* (*pandemicus*) tracks.

## 7.6 Palaeoecological inferences

The frequency of *Megalosauripus* (*transjurani*) trackways in the Ajoie ichnoassemblages indicates that large theropods were commonly present in tidal-flat environments of the Jura carbonate platform and represent a quite common and typical element of this ichnoassemblage. Within the Ajoie ichnoassemblages, *Megalosauripus* (*transjurani*) is associated with tiny ('baby'), small, and medium-sized sauropod, and minute, small, and medium-sized theropod tracks. Moreover, huge (i.e. PL > 50 cm) theropod tracks are rare in this ichnoassemblage and, when preserved, they never co-occur (on the same level) with *M. transjurani*. Generally, several *Megalosauripus* (*transjurani*) trackways head in similar directions as sauropod trackways and at least one trackway overprints ('follows') a small sauropod trackway. In an open, flat and easily-overviewed tidal-flat palaeoenvironment with harsh or no vegetation cover, sauropods, and notably the smaller animals, were exposed to a severe predation hazard.

As most other known occurrences of *Megalosauripus* tracks, *M. tranjsuriani* is found in coastal tidal-flat deposits, likely reflecting the preference of the trackmakers for broad, flat areas, with abundance of food (other dinosaurs, fishes, invertebrates) and good hunting possibilities (as also seen in Razzolini et al. [9]).

The level 500 is the only level where Morphotype II tracks are likely assignable to *Iguanodontipus*? *oncalensis* and together with these ornithopod trackways, *Megalosauripus* tracks also occur.

In this context, it was suggested and supported that *Therangospodus* is a morphological continuum and preservational variation of *Megalosauripus* tracks. Morphotype II tracks that clearly differ from other morphological variations of *Megalosauripus* (*transjurani*) are qualitatively similar to *Iguanodontipus? oncalensis*, identified as medium-sized ornithopod in Castanera et al.[18], and not theropod as in [17].

For this reason, the *Megalosauripus*-*Therangospodus* ichnoassociation does not indicate two similar-sized theropod trackmakers. The possible presence of ornithopods has important implications for the interpretation of the dinosaur community on the Jura carbonate platform. Apart from one track produced by a large ornithopod from the Late Jurassic of Portugal [66, 111, 160] have recently reported four parallel trackways of medium-sized and robust ornithopods from the Late Jurassic of Asturias (Spain), which constitute the first formal ornithopod trackways known from the Late Jurassic of Europe (the one described in [161] is a theropod track; see also [14]). This fact clearly reinforces the possibility of having both large theropods and ornithopods trackways in the Ajoie ichnoassamblages, as discussed for the *Megalosauripus-Therangospodus* ichnoassociation.

**7.7 Palaeo(bio)geographical implications**

The widespread and rich dinosaur track record of the Jura Mountains indicates that large parts of the Jura carbonate platform were emergent during several and prolonged time periods allowing the development of a soil [162] and vegetation cover [163-166], freshwater sources [47], and *in situ* dinosaur populations [16, 167]. This is further supported by the frequency of large theropod tracks and points to a 'faunal exchange corridor' for the exchange (on geological time spans) of dinosaur faunas between further south (Iberian Massif – Massif Central) and further north (Rhenish Massif – London-Brabant Massif) [16, 49, 50]. Skeletal remains of *Allosaurus fragilis* [138] indicate land bridges over the North Atlantic [169] and via Portugal, because of dinosaur remains with Morrison Formation affinity [140, 144, 154]. Such faunal exchanges are supported by the presence of large theropod tracks (with a similar morphology) in the Late Jurassic of France (*Megalosauripus*), N Germany (*Megalosauripus*), Morocco, Portugal (*Euthynichnium*), and Uzbekistan (*Megalosauripus*). All these observations are in strong contrast to ideas about insular dwarfism of sauropod dinosaurs during the Late Jurassic in Northern Germany [14].

**8. Conclusions and outlook**

- Based on very well-preserved and rich material including trackways with several well-preserved tracks exhibiting substantial anatomical details, *Megalosauripus transjurani*, a new ichnospecies of a large theropod dinosaur is erected and described in detail.
- *M. transjurani* is easily differentiated from previously-named ichnotaxa by the presence of a pronounced, large and well-rounded proximal pad on dIV. This feature does not occur in any of the many minute, small, and medium-sized tridactyl trackways documented on Highway A16 tracksites.
- It is further characterized by a clear 2-3-4 phalangeal pad formula,
- All trackways assigned to *M. transjurani* fall into a narrow size range with a mean PL ranging from 35.5 to 42.5 cm. This indicates a large predator as trackmaker, but by far not the largest theropod known from the Late Jurassic.
- An allosaurid theropod is considered as the most likely trackmaker for *Megalosauripus transjurani*.
- Amongst the large theropod tracks that cannot be assigned to *Megalosauripus* (*transjurani*), a second morphotype (Morphotype II *sensu* [16]) is recognized.
- Most of Morphotype II trackways (including all from the intermediate track levels) are most likely preservation variants of *Megalosauripus* tracks, supported by trackways exhibiting both morphotypes along their course.
- Trackway CRO400-T43 and several considerably long trackways on level BEB500 systematically show Morphotype II tracks without any evidence for typical *Megalosauripus* features (such as phalangeal pads). These trackways are tentatively assigned to *Iguanodontipus? oncalensis* (*sensu* [18]) which is considered to have been left by an ornithopod rather than a theropod trackmaker. Accordingly, this is probably the first evidence forornithopod dinosaurs on the Jura carbonate platform.
- Trackways of both *Iguanodontipus*? *oncalensis* and *Megalosauripus* occur on level 500 of the lower track levels, but they do not occur within the same ichnoassemblage (site).

Nonetheless, this would indicate the coeval presence of large carnivorous and herbivorous bipedal dinosaurs on the Jura carbonate platform.

- Due to the lack of *Therangospodus* (*pandemicus*) tracks in the Ajoie ichnoassemblages the *Megalosauripus–Therangospodus* ichnoassociation can not be confirmed for the tidal-flat deposits of the Jura carbonate platform.
- The studied material shows that Morphotype II tracks ('*Therangospodus*-type' tracks) and poorly-preserved *Megalosauripus* tracks often can not be clearly distinguished and thus may be confounded with each other. Consequently, the *Megalosauripus–Therangospodus* ichnoassociation is not easy to identify and may have been misinterpreted previously.
- The frequent presence of *Megalosauripus* (*transjurani*) trackways in the Ajoie ichnoassemblages indicates that large theropods were common in tidal-flat environments of the Jura carbonate platform.
- Within the Ajoie ichnoassemblages, *Megalosauripus* (*transjurani*) is associated with tiny, small, and medium-sized sauropod, and minute, small, and medium-sized theropod tracks.
- Within the Ajoie ichnoassemblages huge (i.e. PL > 50 cm) theropod tracks are rare and never co-occur (on the same level) with *M. transjurani*.
- *Megalosauripus* (*transjurani*) trackways generally head in similar directions as sauropod trackways, and at least one trackway (BSY1040-T1) overprints ('follows') a small sauropod trackway.
- During the Late Jurassic, the Jura carbonate platform may have represented a 'migration corridor' for the exchange (on geological time spans) of dinosaur faunas between further south (Iberian Massif – Massif Central) and further north

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**References**

1. Lockley, M.G., Meyer, C.A. & Santos, V.F. dos 1996: *Megalosauripus*, *Megalosauropus* and the concept of megalosaur footprints. *In:* Morales, M. (ed.), *The continental Jurassic*, Museum of Northern Arizona, Flagstaff, 113-118.
2. Lockley, M. G. (1998) Philosophical Perspectives on Theropod Track Morphology: Blending Qualities and Quantities in the Science of Ichnology, Gaia 15, 279-300.
3. Lockley, M.G., Meyer, C.A. & Santos, V.F. dos 1998a: *Megalosauripus* and the problematic concept of megalosaur footprints. Gaia, 15, 313-337.
4. Lockley, M.G., Lires, J., García-Ramos, J., Piñuela, L., and Avanzini, M. (2007) Shrinking the world's largest dinosaur tracks: observations on the ichnotaxonomy of *Gigantosauropus asturiensis* and *Hispanosauropus hauboldi* from the Upper Jurassic of Asturias, Spain, Ichnos 14, 247-255.
5. Thulborn, T. 2001: History and nomenclature of the theropod dinosaur tracks Bueckeburgichnus and Megalosauripus. Ichnos, 8, 207-222
6. Fanti, F., Contessi, M., Nigarov, A. & Esenov, P. New Data on Two Large Dinosaur Tracksites from the Upper Jurassic of Eastern Turkmenistan (Central Asia). Ichnos 20, 54–71 (2013).
7. Xing, L. D., Harris, J. D., & Gierliński, G. D. (2011). Therangospodus and Megalosauripus track assemblage from the Upper Jurassic–Lower Cretaceous Tuchengzi Formation of Chicheng County, Hebei Province, China and their paleoecological implications. Vertebrata PalAsiatica, 49(4), 423-434.
8. Lockley, M., and Gierlinski, G. (2014). Jurassic tetrapod footprint ichnofaunas and ichnofacies of the Western Interior, USA. Volumina Jurassica,12(2), 133-150.
9. Razzolini, N. L., Oms, O., Castanera, D., Vila, B., dos Santos, V. F., & Galobart, À. (2016). Ichnological evidence of Megalosaurid Dinosaurs Crossing Middle Jurassic Tidal Flats. Sci. Rep. 6, 31494; doi: 10.1038/srep31494 (2016).
10. Lessertisseur, J. 1955: Traces fossiles d'activité animale et leur signification paléobiologique. Mémoires de la Société Géologique de France, 74, 150 pp.
11. Ballerstedt, M. (1905) Über Saurierfährten der Wealdenformation Bückeburgs,

Naturwissenschaftliche Wochenschrift Neue Folge IV. Band; der ganzen Reihe XX. Band; Sonntag, den 7. August 1905; Nr. 31, 481-485.
12. Abel, O. 1935. Vorzeitliche Lebensspuren. Gustav Fischer, Jena, 644 p.
13. Kuhn, O. 1958. Die Fährten der vorzeitlichen Amphibien und Reptilien. Bamberg: Verlagshaus Meisenbach.
14. Lallensack, J., Sander, P. M., Knötschke, N., and Wings, O. (2015) Dinosaur tracks from the Langenberg Quarry (Late Jurassic, Germany) reconstructed with historical photogrammetry: Evidence for large theropods soon after insular dwarfism, Palaeontologica Electronica 18.2.31A: 1-34.
15. Day, J.J., Norman, D.B, Gale, A.S., Upchurch, P. & Powell, H.P. 2004: A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. Palaeontology, 47/2, 319-348
16. Marty, D. 2008: Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez—Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. PhD Thesis, University of Fribourg. GeoFocus, 21, 278 pp.
17. Lockley, M.G., Meyer, C.A. & Moratalla, J.J. 1998b: *Therangospodus*: trackway evidence for the widespread distribution of a Late Jurassic theropod with well-padded feet. Gaia, 15, 339-353.
18. Castanera, D., Pascual Arribas, C., Razzolini, N., Vila, B., Barco, J.L. & Canudo, J.I. 2013: Discriminating between medium-sized tridactyl trackmakers: Tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). PLoS ONE, 8/11, e81830.
19. Lockley, M.G. & Mickelson, D. (1997). Dinosaur and pterosaur tracks in the Summerville and Bluff (Jurassic) beds of eastern Utah and northeastern Arizona. In: Anderson, O.J., Kues, B.S. & Lucas, S.G. (Eds.), Mesozoic Geology and Paleontology of the Four Corners Region. New Mexico Geological Society Guidebook, 48, 133–138.
20. Gierliński, G. y Niedzwiedzki, G. (2002). Dinosaur footprints from the Upper Jurassic of Blaziny,Poland. Geological Quarterly, 46, 463-465.
21. Barco, J.L., Canudo, J.I. & Ruiz-Omeñaca, J.I. 2006: New data on *Therangospodus oncalensis* from the BerriasianFuentesalvotracksite (Villar del Río, Soria, Spain): an example of gregarious behaviour in theropod dinosaurs. Ichnos, 13, 237-248.
22. Marty, D., Cavin, L., Hug, W.A., Meyer, C.A., Lockley, M.G. & Iberg, A. 2003: Preliminary report on the Courtedoux dinosaur tracksite from the Kimmeridgian of Switzerland. Ichnos, 10, 209–219.
23. Marty,D., Cavin, L., Hug, W.A., Jordan,P., & Lockley; M.G. & Meyer. Ch.A. 2004. The protection, conservation and sustainable use of the Courtedoux dinosaur tracksite, Canton Jura, Switzerland. Revue de Paléobiologie, Genève (2004) Vol. spéc. 9
24. Marty, D., Ayer, J., Becker, D., Berger, J.-P., Billon-Bruyat, J.-P., Braillard, L., Hug, W.A. & Meyer, C.A. 2007: Late Jurassic dinosaur tracksites of the Transjurane highway (Canton Jura, NW Switzerland): overview and measures for their protection and valorisation. Bulletin of Applied Geology, 12, 75–89
25. Marty, D., Waite, R., Hug, W.A. & Paratte, G. 2013: Fieldtrip to the Late Jurassic (Kimmeridgian) CPP dinosaur tracksite and nearby reference section Roche de Mars (Porrentruy, Ajoie district, Canton Jura). In: Koppka, J., Hostettler, B., Marty, D., Reisdorf, A., Waite, R., Hug, W.A., Paratte, G., Jaeggi, D., Becker, D. & Borer, P. (eds.), Exkursionsführer der Jahrestagung 2013 in Porrentruy (Kanton Jura, Schweiz) der Subkommission für Jurastratigraphie der Deutschen Stratigraphischen Kommission (DSK), 3–22.
26. Giamboni, M., Ustaszewski, K., Schmid, S.M., Schumacher, M.E. & Wetzel, A. 2004: Plio-Pleistocene transpressional reactivation of Paleozoic and Paleogene structures in the Rhine-Bresse transform zone (northern Switzerland and eastern France). International Journal of Earth Sciences, 93, 207–223.
27. Ustaszewski, K., Schumacher, M.E. & Schmid, S.M. 2005: Simultaneous normal faulting and extensional flexuring during rifting – an example from the southernmost Upper Rhine Graben. International Journal of Earth Sciences, 94, 680–696.

28. Braillard, L. 2006: Morphogenèse des vallées sèches du Jura tabulaire d'Ajoie (Suisse): rôle de la fracturation et étude des remplissages quaternaires. GeoFocus, 14, 224 pp.
29. Comment, G., Ayer, J. & Becker, D. 2011: Deux nouveaux membres lithostratigraphiques de la Formation de Reuchenette (Kimméridgien, Ajoie, Jura suisse) – Nouvelles données géologiques et paléontologiques acquises dans le cadre de la construction de l'autoroute A16 (Transjurane). Swiss Bulletin for Applied Geology, 16/1, 3–24.
30. Comment, G., Lefort, A., Koppka, J. & Hantzpergue, P. 2015: Le Kimméridgien d'Ajoie (Jura, Suisse): lithostratigraphie et biostratigraphie de la Formation de Reuchenette. Révue de Paléobiologie, 34/2, 161–194.
31. Jank, M., Wetzel, A. & Meyer, C.A. 2006: A calibrated composite section for the Late Jurassic Reuchenette Formation in northwestern Switzerland (?Oxfordian, Kimmeridgian *sensu gallico*, Ajoie-Region). Eclogae GeologicaeHelvetiae, 99, 175-191.
32. Thalmann, H.-K. 1966: Zur Stratigraphie des oberen Malm im südlichen Berner und Solothurner Jura. Unpublished PhD Thesis, University of Bern, 125 pp.
33. Gygi, R.A. 2000a: Integrated stratigraphy of the Oxfordian and Kimmeridgian (Late Jurassic) in northern Switzerland and adjacent southern Germany. Memoir of the Swiss Academy of Sciences, 104, 152 pp.
34. Jank, M., Meyer, C.A. & Wetzel, A. 2006a: Late Oxfordian to Late Kimmeridgian carbonate deposits of NW Switzerland (Swiss Jura): Stratigraphical and palaeogeographical implications in the transition area between the Paris Basin and the Tethys. Sedimentary Geology, 138, 237-263.
35. Schudack, U., Schudack, M., Marty, D. & Comment, G. 2013: Kimmeridgian (Late Jurassic) ostracods from Highway A16 (NW Switzerland): taxonomy, stratigraphy, palaeoecology, and palaeobiogeography. Swiss Journal of Geosciences, 106, 371–395.
36. Thierry, J. 2000: Early Kimmeridgian. In: Dercourt, J., Gaetani, M., Vrielvynck, B. et al. (Eds.), Atlas Peri-Tethys, Palaeogeographical maps — Explanatory Notes, 85–97.
37. Thierry, J. et al. (44 co-authors) 2000: Map 10: Early Kimmeridgian (146-144 Ma). In: Dercourt, J., Gaetani, M., Vrielvynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S. & Sandulescu, M. (Eds.), Atlas Peri-Tethys, Paris, palaeogeographical map.
38. Stampfli, Gérard M., and G. D. Borel. "A plate tectonic model for the Paleozoic and Mesozoic constrained by dynamic plate boundaries and restored synthetic oceanic isochrons." Earth and Planetary Science Letters 196.1 (2002): 17-33.
39. Ziegler, P.A. 1988: Evolution of the Arctic – North Atlantic and the Western Tethys. AAPG (American Association of Petroleum Geologists) Memoir, 43, 198 pp.
40. Hallam, A. 1984: Continental humid and arid zones during the Jurassic and Cretaceous. Palaeogeography, Palaeoclimatology, Palaeoecology, 47, 195-223.
41. Frakes, L.A., Francis, J.E. & Sykes, R.M. (eds.) 1992: Climate modes of the Phanerozoic. Cambridge University Press, Cambridge, 274 pp.
42. Ross, C.A., Moore, G.T. & Hayashida, D.N. 1992: Late Jurassic paleoclimate simulation – paleoecological implications for ammonoid provinciality. Palaios, 7, 487-507.
43. Weissert, H. & Mohr, H. 1996: Late Jurassic climate and its impact on carbon cycling. Palaeogeography, Palaeoclimatology, Palaeoecology, 122, 27-43.
44. Bertling, M. & Insalaco, E. 1998: Late Jurassic coral/ microbial reefs from the northern Paris Basin – Facies, palaeoecology and palaeobiogeography. Palaeogeography, Palaeoclimatology, Palaeoecology, 139, 139-175.
45. Rees, P.M., Noto, C.R., Parrish, J.M. & Parrish, J.A. 2004: Late Jurassic climates, vegetation, and dinosaur distributions. Journal of Geology, 112, 643-653.
46. Oertli, H.J. & Ziegler, M. 1958: Présence d'un Séquanien lacustre dans la région de Pontarlier (Département du Doubs). Eclogae Geologicae Helvetiae, 51/2, 385–390.
47. Marty, D. & Meyer, C.A. 2013: A bridge over troubled water – The continuous record of terrestrial vertebrates from the Oxfordian to the Berriasian in the Jura Mountains. 57$^{th}$Annual Meeting of the Palaeontological Association, 13.-16.12.2013, Zürich, Switzerland, The Palaeontology Newsletter, 84, p. 48.

48. Leuzinger, L., Kocsis, L., Billon-Bruyat, J. P., Spezzaferri, S., and Vennemann, T. (2015) Stable isotope study of a new chondrichthyan fauna (Kimmeridgian, Porrentruy, Swiss Jura): an unusual freshwater-influenced isotopic composition for the hybodont shark *Asteracanthus*. Biogeosciences 12, 6945-6954.
49. Meyer, C. A., Thüring, B. & Wetzel, A. 2006: The hitch-hikers guide to the Late Jurassic– Basement structures provide clues to dinosaur migration routes. Hantkeniana, 5, p. 38.
50. Meyer, C.A. 2011: The hitch-hikers guide to the Late Jurassic and early Cretaceous – Dinosaur tracks from the Swiss and French Jura Mountains in a sequence stratigraphic context. Dinosaur Track Symposium, 14.-17.04.2011, Obernkirchen (Germany), Abstracts Volume, p. 25
51. Dunham, R. J. Classification of carbonate rocks according to depositional textures. 108–121 (1962).
52. Folk, R.L. 1962: Spectral subdivision of limestone types. In: Ham, W.E. (ed.), Classification of carbonate rocks, AAPG (American Association of Petroleum Geologists) Memoir,1, 62-84.
53. Marty, D. & Pacton, M. 2009: Formation and preservation of Late Jurassic dinosaur track-bearing tidal-flat laminites (Canton Jura, NW Switzerland) through microbial mats. In: Billon-Bruyat, J.-P., Marty, D., Costeur, L., Meyer, C.A. & Thüring, B. (Eds.), 5thInternational Symposium on Lithographic Limestone and Plattenkalk — Abstracts and Field Guides. Société jurassienne d'émulation, actes 2009 bis, 56–58.
54. Colombié, C. & Rameil, N. 2007: Tethyan-to-boreal correlation in the Kimmeridgian using high-resolution sequence stratigraphy (Vocontian Basin, Swiss Jura, Boulonnais, Dorset). International Journal of Earth Sciences, 96, 567-591.
55. Marty, D., and Billon-Bruyat, J.P. Field-trip to the excavations in the Late Jurassic along the future Transjurane highway near Porrentruy (Canton Jura, NW Switerland). En 5th International Symposium on Lithographic Limestone and Plattenkalk: abstracts and field guides. Société jurassienne d'Emulation, 2009. p. 94-129.
56. Marty, D., Belvedere, M., Meyer, C.A., Mietto, P., Paratte, G., Lovis, C. & Thüring, B. 2010: Comparative analysis of Late Jurassic sauropod trackways from the Jura Mountains (NW Switzerland) and the central High Atlas Mountains (Morocco): implications for sauropod ichnotaxonomy. Historical Biology, 22/1-3, 109–133.
57. Marty, D., Falkingham, P. & Richter, A. 2016: Dinosaur track terminology: A glossary of terms. In: Falkingham, P., Marty, D. & Richter, A. (Eds.), Dinosaur tracks – Thenext steps. Indiana University Press, Bloomington, 399-402.
58. Marty, D., Strasser, A. & Meyer, C.A. 2009: Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: Implications for the study of fossil footprints. Ichnos, 16, 127–142.
59. Gatesy, S.M. 2003: Direct and indirect track features: what sediment did a dinosaur touch? Ichnos, 10, 91-98.
60. Belvedere M., & Farlow, J.O. 2016. A Numerical Scale for Quantifying the Quality of Preservation of Vertebrate Tracks. In: Falkingham, P.L., Marty, D. & Richter, A. (eds), Dinosaur tracks, the next steps. Indiana Unviersity Press, 92-99.
61. Lockley, M.G. & Hunt, A.P. 1995: Dinosaur tracks and other fossil footprints of the western United States. Columbia University Press, New York, 338 pp.
62. Lockley, M.G. & Meyer, C.A. 2000: Dinosaur tracks and other fossil footprints of Europe, Columbia University Press, New York, 321 pp.
63. Cobos, A., Lockley, M. G., Gascó, F., Royo-Torres, R., & Alcala, L. (2014) Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain), Palaeogeography, Palaeoclimatology, Palaeoecology 399, 31-41.
64. Lockley, M.G. & Hunt, P.A. 1994: A track of the giant theropod dinosaur *Tyrannosaurus* from close to Cretaceous/Tertiary boundary, northern New Mexico. Ichnos, 3: 213-218.
65. Lockley, M.G, Matsukawa, M., Sato, Y., Polahan, M., Daorerk, V. (2006a). A distinctive new theropod dinosaur track from the Cretaceous of Thailand: Implications for theropod track diversity. Cretaceous Research, 27, 139-145.

66. Mateus, O., & Milàn, J. 2008: Ichnological evidence for giant ornithopod dinosaur in the Upper Jurassic Lourinhã Formation, Portugal. Oryctos, 8, 47–52.
67. Leonardi, G. 1987: Glossary and manual of tetrapod footprint palaeoichnology. Publicação do Departemento Nacional da Produção Mineral Brasil, Brasília, 117 pp
68. Thulborn, T. 1990: Dinosaur tracks. Chapman & Hall, London, 410 pp.
69. Weems, R.E. 1992: A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia. In: Sweet, P.C. (Ed.), Proceedings of the 26$^{th}$ forum on the geology of industrial minerals, 119, 113–127.
70. Lockley, M.G. 2009: New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. Geological Quarterly, 53(4), 415–432.
71. Alexander, R. McN. 1976: Estimates of speeds of dinosaurs. Nature, 261, 129-130.
72. Thulborn, T. 1989. The gaits of dinosaurs. In: Gillette, D.D. & Lockley, M.G. (Eds.), Dinosaur tracks and traces, Cambridge University Press, Cambridge, 39–50.
73. Coombs, W.P. Jr. 1978: Theoretical aspects of cursorial adaptions in dinosaurs. Quarterly Review of Biology, 53, 393-418.
74. Rainforth, E. & Manzella, M. 2007: Estimating speeds of dinosaurs from trackways: a re-evaluation of assumptions. In: Rainforth, E. (ed.), Contributions to the paleontology of New Jersey (II) – Field guide and proceedings, Geological Association of New Jersey, XXIV Annual Conference and field trip, 12.-13.10.2007, East Stroudsburg University, Pennsylvania, USA, 41-48.
75. Alexander, R. McN. 2006: Dinosaur biomechanics. Proceedings of the Royal Society of London, Series B, 273, 1849-1855.
76. Hutchinson, J.R., Anderson, F.C., Blemker, S.S. & Delp, S.L. 2005: Analysis of hindlimb muscle moment arms in Tyrannosaurus rex using a three-dimensional musculoskeletal computer model: implications for stance,gait, and speed. Paleobiology, 31, 676-701
77. Mallison, H., & Wings, O. (2014). Photogrammetry in paleontology: a practical guide. Journal of Paleontological Techniques, 12, 1e31.
78. Owen, R. (1842). Description of the Skeleton of an Extinct Gigantic Sloth: Mylodon Robustus, Owen, with Observations on the Osteology, Natural Affinities, and Probable Habits of the Megatherioid Quadrupeds in General. R. and JE Taylor, sold by J. van Voorst.
79. Marsh, O.C. (1881). Principal characters of the American Jurassic dinosaurs. Part V. American Journal of Science, 21, 417–423.
80. von Huene, F. (1920). Systematische und genetische Betrachtungen über die Stegocephalen. Molecular and General Genetics MGG, 23(1), 209-212.
81. vylov 1988
82. Lull, R. S. (1904). Fossil footprints of the Jura-Trias of north America (Vol. 5, No. 11). The Society.
83. Humboldt, F.A.v. 1799: Ueber die unterirdischen Gasarten und die Mittel ihren Nachtheil zu vermindern. Friedrich Vieweg, Braunschweig, 346 pp.
84. Brongniart, A. 1829: Tableau des terrains qui composent l'écorce du globe (ou essai sur la structure de la partie connue de la terre). Strasbourg, Imprimerie F.G. Lerault, 435 pp.
85. Buch, L. von 1839: Über den Jura in Deutschland. Berlin, Druckerei der Königlichen Akademie der Wissenschaften, 87 pp.
86. Porada, H. & Bouougri, E.H. (2007). Wrinkle structures – a critical review. Earth Science Reviews, 81, 199-215.
87. Dai, H., Xing, L., Marty, D., Zhang, J., Scott Persons IV, W., Hu, H. & Wang, F. (2015). Microbially-induced sedimentary wrinkle structures and possible impact of microbial mats for the enhanced preservation of dinosaur tracks from the Lower Cretaceous Jiaguan Formation near Qijiang (Chongqing, China). Cretaceous Research, 53, 98-109.
88. Xing, L. D., Niedźwiedzki, G., Lockley, M. G., Zhang, J. P., Cai, X. F., Persons, W. S., & Ye, Y. (2014a). *Asianopodus*-type footprints from the Hekou Group of Honggu District, Lanzhou City, Gansu, China and the “heel” of large theropod tracks. Palaeoworld, 23(3), 304-313.

89. Sternberg, C. M., Dinosaur tracks fromPeace River, British Columbia. National Museum of Canada, Annual Report. 59–85 (1932).
90. McCrea, R. T. et al. A 'Terror of Tyrannosaurs': The First Trackways of Tyrannosaurids and Evidence of Gregariousness and Pathology in Tyrannosauridae. PLoS One 9, e103613, doi: 10.1371/journal.pone.0103613 (2014).
91. Lockley, M.G. 2000: An amended description of the theropod footprint Bueckeburgichnus maximus KUHN, 1958, and its bearing on the megalosaur tracks debate. Ichnos, 7, 217-225.
92. Whyte, M. A., Romano, M. & Elvidge, D. J. Reconstruction of Middle Jurassic Dinosaur-Dominated Communities from the Vertebrate Ichnofauna of the Cleveland Basin of Yorkshire, UK Ichnos 14, 117 –129 (2004).
93. Belvedere, M., Mietto, P., and Ishigaki, S. (2010) A Late Jurassic diverse ichnocoenosis from the siliciclasticIouaridène Formation (Central High Atlas, Morocco), Geological Quarterly 54, 367-380.
94. Nouri, J., Diaz-Martinez, I., and Pérez-Lorente, F. (2011) Tetradactyl footprints of an unknown affinity theropod dinosaur from the Upper Jurassic of Morocco.PLoS ONE 6(12): e26882.
95. Romilio, A., & Salisbury, S. W. (2011). A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity. Cretaceous Research, 32(2), 135-142.
96. Kaever, M., & Lapparent, A. F. d. (1974) Les traces de pas de dinosaures du Jurassique de Barkhausen (Basse Saxe, Allemagne), Bull. Soc. Géol. France (7) 16, 516-525
97. Marty, D., Belvedere, M., Razzolini, N.L., Lockley, M.G., Meyer, C.A., Paratte, G., Lovis, C., Cattin, M. (in press). The tracks of huge theropods from the Late Jurassic of NW Switzerland (*Jurabrontes curtedulensis* ichnogen. & ichnosp. nov.; Reuchenette Formation, Kimmeridgian): palaeoecological & palaeogeographical implications
98. Meyer, C.A. & Lockley, M.G. 1997: Jurassic and Cretaceous dinosaur tracksites from Central Asia (Usbekistan and Turkmenistan). International dinosaur symposium for Uhangri Dinosaur Center and Theme Park in Korea, The Paleontological Society of Korea, Special Publication, 2, 77-92.
99. Nopsca, F. von 1923: Die Familien der Reptilien. Fortschritte der Geologie und Paläontologie, 2, 210 pp.
100. Colbert, E. H., and Merrilees, D. (1967) Cretaceous dinosaur footprints from Western Australia, Journal of the Royal Society of Western Australia 50, 21-15
101. Mensink, H., and Mertman, D. (1984) "Dinosaurierfährten (*Gigantosauropus asturiensis* n. g. n. sp.; *Hispanosauropus hauboldi* n. g. n. sp.) im Jura Asturiens bei La Griega und Ribadasella (Spanien), N.Jb.Geol.Paläont. Mh. 7, 405-415.
102. Avanzini, M., García-Ramos, J.-L., & Piñuela, L. (2011) Late Jurassic footprints reveal walking kinematics of theropod dinosaurs, Lethaia 45, 238-252.
103. Matsukawa, M., Shibata, K., Kukihara, R., Koarai, K., & Lockley, M. G. (2005). Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. Ichnos, 12(3), 201-222.
104. Xing, L., Lockley, M. G., Klein, H., Gierliński, G. D., Divay, J. D., Hu, S. M & He, Y. P. (2014b). The non-avian theropod track *Jialingpus* from the Cretaceous of the Ordos Basin, China, with a revision of the type material: implications for ichnotaxonomy and trackmaker morphology. Palaeoworld,23(2), 187-199.
105. Zhen, S.N., Li, J.J., Zhen, B.M., 1983. Dinosaur footprints of Yuechi, Sichuan.Memoirs of Beijing Natural History Museum 25, 1–19 (in Chinese, with English abstract).
106. Mateus, O., & Milàn, J. (2010). A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. Lethaia, 43(2), 245-257.
107. Boutakiout, M., Hadri, M., Nouri, J., Díaz-Martínez, I., and Pérez-Lorente, F. (2009) Icnitas terópodas gigantes. Sinclinal de Iouaridène, Jurásico Superior. Marruecos, Libro de resúmenes. XXIV Jornadas de la Sociedad Española de Paleontología. Museo del Jurásico de Asturias(MUJA), Colunga, 15-18 de octubre de 2008 (Eds. J.I. Ruiz-Omeñaca, L. Piñuela& J.C. García-Ramos), 21-22.

108. Falkingham, P. L. (2014). Interpreting ecology and behaviour from the vertebrate fossil track record. Journal of Zoology, 292, 222e228.
109. Genise, J.F., Melchor, R.N., Archangelsky, M., Bala, L.O., Straneck, R. & Valais, S. de (2009) Application of neoichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: the Late Triassic–Early Jurassic? Santo Domingo Formation, Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology, 272(3), 143-161
110. Lapparent, A. F., & Zbyszewski, G. (1957). Les dinosauriens du Portugal (No. 2). Direction Générale des Mines et Services Géologiques.
111. Piñuela, L. 2016. Huellas de dinosaurios y de otros reptiles del Jurasico Superior de Asturias. Universidad de Oviedo, PhD thesis, 328 pp.
112. Mazin, J.M. & Hantzpergue, P. (2012). Late Jurassic dinosaur tracksites of the French Jura Mountains. 4th Symposium Georges Cuvier, 8.-12.10.2012, Montbéliard (France) Abstract Volume, p. 32.
113. Beuchat, G.-A. (1999). Grande découverte paléontologique sur le territoire communal. 78. Jahresversammlung der Schweizerischen Paläontologischen Gesellschaft Porrentruy, 1.-2. May 1999. Abstract Volume, p. 8.
114. Meyer, C.A., Thüring, B. & Marty, D. 2013. A reassessment of the first Late Jurassic megatracksite in Northern Switzerland. Abstracts In 11th Annual Meeting of the European Association of Vertebrate Palaeontologists Meeting Villers-sur-Mer p.52
115. Meyer, C.A. & Hauser, M. 1994: New sauropod and theropod tracksites from the Upper Jurassic megatracksite of Northern Switzerland. Gaia, 10, 49–56.
116. Mazin, J. M., Hantzpergue, P.& Pouech, J. (2016). The dinosaur tracksite of Loulle (early Kimmeridgian; Jura, France). Geobios, 49/3, 211-228.
117. Day, J.J., Norman, D.B., Upchurch, P. & Powell, H.P. 2002: Dinosaur locomotion from a new trackway. Nature, 415, 494–495.
118. Mossman, D.J., Brüning, R. & Powell, H.P. 2003: Anatomy of a Jurassic theropodtrackway from Ardley, Oxfordshire, U.K. Ichnos, 10, 195-207.
119. Belvedere, M., Jalil, N. E., Breda, A., Gattolin, G., Bourget, H., Khaldoune, F., & Dyke, G. J. (2013). Vertebrate footprints from the Kem Kem beds (Morocco): A novel ichnological approach to faunal reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology, 383, 52-58.
120. Wagensommer, A., Latiano, M., Leroux, G., Cassano, G., & D'Orazi Porchetti, S. (2012). New dinosaur tracksites from the Middle Jurassic of Madagascar: Ichnotaxonomical, behavioural and palaeoenvironmental implications. Palaeontology, 55(1), 109-126.
121. Lallensack, J. N., van Heteren, A. H., & Wings, O. (2016). Geometric morphometric analysis of intratrackway variability: a case study on theropod and ornithopod dinosaur trackways from Münchehagen (Lower Cretaceous, Germany). PeerJ, 4, e2059.
122. Getty, P. R., Hardy, L., & Bush, A. M. (2015). Was the Eubrontes Track Maker Gregarious? Testing the Herding Hypothesis at Powder Hill Dinosaur Park, Middlefield, Connecticut. Bulletin of the Peabody Museum of Natural History,56(1), 95-106.
123. Fiorillo, A. R., Hasiotis, S. T., & Kobayashi, Y. (2014). Herd structure in Late Cretaceous polar dinosaurs: A remarkable new dinosaur tracksite, Denali National Park, Alaska, USA. Geology, 42(8), 719-722.
124. Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikulásˇ, R., Nielsen, J.K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M., Uchman, A. (2006). Names for trace fossils: a uniform approach. Lethaia, 39, 265-286.
125. Myers, T. S., & Fiorillo, A. R. (2009). Evidence for gregarious behavior and age segregation in sauropod dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology, 274(1), 96-104.
126. Romano, M. & Citton, P. 2016. Crouching theropod at the seaside. Matching footprints with metatarsal impressions and theropod authopods: a morphometric approach. Geological Magazine, doi:10.1017/S0016756816000546.
127. Meyer, C.A. & Thüring, B. 2003: Dinosaurs of Switzerland. C.R. Paleovol., 2, 103–117.
128. Huene, F. von 1926: Die Saurierfauna des Portlandkalkes von Solothurn. Eclogae Geologicae

Helvetiae, 19, 584–603.
129. Greppin, J.G. 1870: Description géologique du Jura bernois et de quelques districts adjacents. Matériaux pour la carte géologique de la Suisse, 8, 357 pp.
130. Marty, D. & Meyer, C.A. 2012: From sauropods to cycads – The Late Jurassic terrestrial record of the Swiss Jura Mountains. In: Witzmann, F. & Aberhan, M. (Eds.), Centenary Meeting of the Paläontologische Gesellschaft – Programme, Abstracts, and Field Guides, 24.-29.09.2012, Naturkundemuseum Berlin, Terra Nostra – Schriften der GeoUnion Alfred-Wegener-Stiftung, 2012/3, 119–120.
131. Lapparent, A.F. de 1943: Les dinosauriens jurassiques de Damparis (Jura). Mémoire de la Société géologique de France, Nouvelle Série, 47, 1–21.
132. Buffetaut, E. 1988: Les restes de dinosauriens de l'Oxfordien supérieur de Damparis (Jura): preuves d'émersion sur place. Revue de Paléobiologie, 7, 301–306.
133. Pharisat, A., Contini, D., & Frickert, J. C. (1993). Early Jurassic (Lower Toarcian)''Ichthyosaurs''from Franche-Compte, France. Revue de Paléobiologie, Volume spécial, 7, 189-198.
134. Allain, R., & Suberbiola, X. P. (2003). Dinosaurs of France. Comptes Rendus Palevol, 2(1), 27-44.
135. Holtz, T.R.Jr., Molnar, R.E.&Currie, P.J.2004: Basal Tetanurae. In: Weishampel, D.B., Dodson, P.&Osmólska, H. (Eds.), The Dinosauria – Second Edition, California University Press, 71–110.
136. Tykoski, R.S. & Rowe, T. 2004: Ceratosauria. In: Weishampel, D.B., Dodson, P.&Osmólska, H. (Eds.), The Dinosauria – SecondEdition, California University Press, 47–70.
137. Carrano, M.T., Benson, R.B.J. & Sampson, S.D. 2016: The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Paleontology, 10/2, 211–300.
138. Perez-Moreno, B.P., Chure, D.J., Pires, C., Marques da Silva, C., Santos, V. dos, Dantas, P., Povoas, L., Cachao, M., Sanz, J.L. & Galopim de Carvalho, A.M. 1999: On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. Journal of the Geological Society, London, 156, 449–452
139. Malafaia, E., Mocho, P., Escaso, F. & Ortega, F. 2016: A juvenile allosauroid theropod (Dinosauria, Saurischia) from the Upper Jurassic of Portugal. Historical Biology, dx.doi.org/10.1080/08912963.2016.1231183.
140. Mateus, O., Walen, A. & Antunes, M.T. 2006: The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to the Morrison Formation. New Mexico Museum of Natural History and Science Bulletin, 36, 1–7.
141. Madsen, J.H. 1976: Allosaurus fragilis: a revised osteology. Utah Geological Survey Bulletin, 109, 163 pp.
142. Bybee, P.J., Lee, A.H. & Lamm, E.-T. 2006: Sizing the Jurassic theropod dinosaur Allosaurus: Assessing growth strategy and evolution of ontogenetic scaling of limbs. Journal of Morphology 267/3, 347-359.
143. Chure, D.J. 1995: A reassessment of the gigantic theropod Saurophagus maximus from the MorrisonFormation (Upper Jurassic) of Oklahoma, USA. In: Sun, A. &Wang, Y. (Eds.), Sixth Symposium on MesozoicTerrestrial Ecosystems and Biota, Short Papers. Beijing: China Ocean Press, 103–106.
144. Mateus, O. & Antunes, M.T. 2000: Ceratosaurus sp. (Dinosauria: Theropoda) in the Late Jurassic of Portugal. 31st International Geological Congress. Rio de Janeiro, Brazil
145. Gilmore, C.W. 1920: Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera Antrodemus (Allosaurus) and Ceratosaurus. Bulletin of the United States National Museum, 110, 1–154
146. Molnar, R. E. (1990). Problematic Theropoda:"Carnosaurs". The Dinosauria. University of California Press, Berkeley, 306-317.
147. Benson, R.B., Barrett, P.M., Powell, H.P. & Norman, D.B. 2008: The taxonomic status of Megalosaurus bucklandi (Dinosauria, Theropoda) from the Middle Jurassic of Oxfordshire, UK. Palaeontology, 51, 419-424.

148. Galton, P.M. & Jensen, J.A. 1979: A new large theropod dinosaur from the Upper Jurassic of Colorado. Brigham Young University Geology Studies, 26/1, 1–12.
149. Rauhut, O.W.M., Hübner, T.R. & Lanser, K.-P. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany: Implications for theropod evolution and faunal turnover in the Jurassic. Palaeontologia Electronica, 19.2.26A: 1-65.
150. Gierlinski, G., Niedzwiedzki, G., & Pienkowski, G. (2001). Gigantic footprint of a theropod dinosaur in the Early Jurassic of Poland. Acta Palaeontologica Polonica, 46(3).
151. Moratalla Garcia, J.J. (1993) Restos indirectos de dinosaurios del registro espan˜ ol: paleoicnologı´a de la Cuenca de Cameros (Jura´sico Superior-Creta´cico Inferior) y paleoologı´a del Creta´cico Superior. Universidad Complutense De Madrid PhD Thesis, 727p.
152. Diaz-Martínez, I., Pereda-Suberbiola, X., Pérez-Lorente, F. & Canudo, J.I. 2015: Ichnotaxonomic review of large ornithopod dinosaur tracks: Temporal and geographic implications, PLoS ONE 10/2, e0115477.
153. Rauhut, O. W. (2001). Herbivorous dinosaurs from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. Proceedings of the Geologists' Association, 112(3), 275-283.
154. Mateus, O. 2006: Late Jurassic dinosaurs from the Morrisson Formation (USA), the Lourinha and Alcobaça Formations (Portugal), and the Tendaguru beds (Tanzania): a comparison. In: J. R. Foster, J.R. & Lucas, S.G. (Eds.), Paleontology and geology of the Upper Jurassic Morrisson Formation, New Mexico Museum of Natural History and Science Bulletin, 36, 1–9.
155. Ortega, F., Escaso, F., Gasulla, J.M., Dantas, P., Sanz, J.L. (2006). Los Dinosaurios de la Península Ibérica. Estudios geológicos, 62 (1-2), 219-240.
156. Pereda Suberbiola, X., Ruiz-Omeñaca, J. I., Company, J. (2009). Primera descripción de restos esqueléticos de dinosaurio ornitópodo en la Formación Villar del Arzobispo (tránsito Jurásico-Cretácico): yacimiento de Cerrito del Olmo (Alpuente, Valencia). Geogaceta, 47 (3-4), 13-16.
157. Galton, P.M. 1980: Dryosaurus and Camptosaurus, intercontinental genera of Upper Jurassic ornithopod dinosaurs. Mémoires de la Société géologique de France nouvelle série, 139, 103-108.
158. Norman, D. B., Sues, H. D., Witmer, L. M., & Coria, R. A. (2004). Basal ornithopoda. The Dinosauria, 2, 393-412.
159. Carpenter and Wilson 2009
160. Piñuela, L., García-Ramos, J. C., Romano, M., & Ruiz-Omeñaca, J. I. (2016). First Record of Gregarious Behavior in Robust Medium-Sized Jurassic Ornithopods: Evidence from the Kimmeridgian Trackways of Asturias (N. Spain) and Some General Considerations on Other Medium-Large Ornithopod Tracks in the Mesozoic Record. Ichnos, 23(3-4), 298-311.
161. Diedrich, C. (2011) Upper Jurassic tidal flat megatracksites of Germany — coastal dinosaur migration highways between European islands, and a review of the dinosaur footprints, Palaeobiodiversity and Palaeoenvironments, 91, 129-155.
162. Waite, R., Marty, D., Strasser, A. & Wetzel, A. 2013: The lost paleosols: Masked evidence for emergence and soil formation on the Kimmeridgian Jura platform (NW Switzerland). Palaeogeography, Palaeoclimatology, Palaeoecology, 376, 73–90.
163. Van Konijnenburg-van Cittert, J.H.A. & Meyer, C.A. 1996: Plant remains from the Vellerat Formation (Oxfordian) of the Swiss Jura mountains. Eclogae Geologicae Helvetiae, 89/3, 1117–1136.
164. Allenbach, R. & van Konijnenburg-van Cittert, J.H.A. 1997: On a small flora with araucariaceous conifers from the Röschenz Beds of Court, Jura Mountains, Switzerland. Eclogae Geologicae Helvetiae, 90/3, 571–579.
165. Gee, C.T., Meyer, C.A. & Van Konijnenburg-Van Cittert, J.H.A. 2003: The first unequivocal sphenophytes from the Late Jurassic of northwestern Switzerland (Late Oxfordian Vellerat Formation) – palaeobotany and implications for facies interpretation. Courier Forschungsinstitut Senckenberg, 241, 97–109.
166. Philippe, M., Billon-Bruyat, J.-P., Garcia-Ramos, J.C., Bocat, L., Gomez, B. & Piñuela, L. 2010: New occurrences of the wood *Protocupressinoxylon purbeckensis* FRANCIS: implications for terrestrial biomes in southwestern Europe at the Jurassic/Cretaceous boundary. Palaeontology, 53/1,

201–214.
167. Meyer, C. A. (1993). A sauropod dinosaur megatracksite from the Late Jurassic of northern Switzerland. Ichnos: An International Journal of Plant & Animal, 3(1), 29-38.
168. Meyer, C. A. (2011). The hitch-hikers guide to the Late Jurassic and early Cretaceous–Dinosaur tracks from the Swiss and French Jura Mountains in a sequence stratigraphic context. Dinosaur Track Symposium, 14.-17.04. 2011, Obernkirchen (Germany). In Abstracts Volume (p. 25).
169. Brikiatis, L. (2016). Late Mesozoic North Atlantic land bridges. Earth-Science Reviews, 159, 47-57.

**Figure captions**

**Fig 1**.**Geographical settingof the Ajoie district (NW Switzerland)** and the three Late Jurassic tracksites along Highway A16 (‘Transjurane’). Inset shows location within Switzerlan(D) Numbers indicate the different tracksites: 1. Courtedoux—Béchat Bovais (CTD-BEB), 2. Courtedoux—Bois de Sylleux (CDT-BSY), 3. Courtedoux—Tchâfouè (CTD-TCH), 4. Chevenez—Combe Ronde (CHE-CRO), 5. Courtedoux—Sur Combe Ronde (CTD-SCR), 6. Porrentruy—CPP (POR-CPP).

**Fig 2**.**Chrono-, bio- and lithostratigraphic context of the Reuchenette Formation in the Ajoie district, Canton Jura, NW Switzerland** (modified from[16, 24, 29,30]. Four track-bearing intervals, named lower, intermediate, and upper (dinosaur track) levels, and track levels 600 have been identified within the Courtedoux Member (Nerinean Limestones, *sensu* [31]). All studied material comes from the intermediate (levels 1000–1100) and upper (levels 1500–1650) dinosaur track levels, details shown on inset on the upper right.

**Fig3**.**Methodology of track and trackway labelling and parameter measurements.** Note that the pictured tridactyl track does not correspond to *Megalosauirpus transjurani*, it is a schematical track with a typical theropod phalangeal pad configuration of 2-3-4 for dII-III-IV, respectively.
(A) Track length (PL) and width (PW), labelling of digits (d), phalangeal pads (P) and claws (C). The internal track outline corresponds to the (interpretation of the) actual impression of the foot. (B) Interdigital angles (da) and anterior triangle (AT). PW is the width and te the length (measured perpendicular to the width) of the anterior triangle, which in the present case has an obtuse angle for the the anterior apex indicating a low mesaxony. (C) Digit lengths (L) and widths (W). (D) Trackway parameters. Labelling of trackways always starts with L1; if L1 is missing R1 is the first number used. α is the rotation (in this case outward and thus a positive value) of the track (long axis) with respect to the next stride line. LP and RP are left and right pace, respectively; S is stride; WAP is width of the angulation pattern (measured perpendicular to the stride length; [16]), γ is pace angulation. The progression is a calculated value (with the Pythagors’s theorem) and it indicates the forward movement of the trackmaker in the direction of the trackway during one footfall (pace) [16]. Progression is only half of the stride in the case of completely regular trackways. The reference point for the trackway parameter measurements is on the tip of the third digit (without the claw where preserved).

**Fig4. Outline drawings of *Megalosauripus transjurani* footprints**.
(A) TCH1030-T6-L1, holotype. (B) BSY1035-T6-L2, paratype. (C) BSY1040-T1-R1, paratype. (D) TCH1025-T2-L1, paratype. (E) TCH1030-T2-R2, paratype; F TCH1030-T2-L3, paratype. (G) TCH1030-T7-L2, paratype. (H) BSY1040-T1-L2. (I) BSY1040T1-R2. (J) BSY1040-T1-L3. (K) BSY1040-T9-R3. (L) TCH1015-T1-L2. (M) TCH1015-T1-R3. (N) TCH1030-T3-L1. (O) TCH1030-T2-R3

**Fig5. Holotype of *Megalosauripus transjurani* TCH1030-T6-L1 (MJSN TCH006-1319).**
(A) Trackway representation. (B) Photo of the specimen. Scale 20 cm. (C) interpretative outline drawing. (D) contour-lines. Spacing 1 mm. (E) false-colour depth map. Depth measured in mm.

**Fig6. Paratype of *Megalosauripus transjurani* TCH1030-T7-L2 (MJSN TCH006-1317)**.
(A) Trackway representation. (B) Photo of the specimen. Scale 30 cm. (C) interpretative outline drawing. (D) contour-lines. Spacing 1 mm. (E) false-colour depth map. Depth measured in mm.

**Fig7. Paratype of *Megalosauripus transjurani* BSY1040-T1-R1 (MJSN BSY008-339).**
(A) Trackway representation. (B) Photo of the specimen. Scale 30 cm. (C) interpretative outline drawing. (D) contour-lines. Spacing 1 mm. (E) false-colour depth map. Depth measured in mm.

**Fig8. Paratype for *Megalosauripus transjurani* TCH1025-T2-L1 (MJSN TCH006-1329).**
(A) Trackway representation. (B) Photo of the specimen. Scale 20 cm. (C) interpretative outline drawing. (D) contour-lines. Spacing 1 mm. (E) false-colour depth map. Depth measured in mm.

**Fig9. Paratypes of *Megalosauripus transjurani* TCH1030-T2-R2 (MJSN TCH006-1087), TCH1030-T2-L3 (MJSN TCH006-1022).**
(A) Trackway representation. (B) sTCH1030-T2-R2 (MJSN TCH006-1087) photo. Scale 30 cm, C) interpretative outline. (D) contour lines. (E) false-colour depth map. Depth measured in mm. (F) photo. Scale 30 cm. (G) interpretative outline. (H) contour-lines. Spacing 1 mm. (I) false-colour depth map. Depth measured in mm.

**Fig10.Paratype of *Megalosauripus transjurani* BSY1035-T6-L2 (MJSN BSY008-330).**
(A) Trackway representation. (B) Photo of the specimen. Scale 30 cm. (C) interpretative outline drawing. (D) contour-lines. Spacing 1 mm. (E) false-colour depth map. Depth measured in mm.

**Fig 11. Outline drawings of the main large theropod ichnotaxa, all drawn at the same scale.**
Left tracks are mirrored as right footprints.
(A) Holotype of Megalosauripus transjurani (TCH1030-T6-L1); (B) *Asianopodus*, redrawn from [88]. (C) *Irenesauripus* redrawn from Sternberg,[89]. (D) *Tyrannosauripus pillmorei*, redrawn from Lockley and Hunt, [64]. (E) *Bellatoripes fredlundi*, redrawn from McCrea et al. [90]. (F) *Bueckeburgichnus maximus*, redrawn from Lockley [91]. (G) *Euthynichnium lusitanicum*, redrawn from Lockley et al., [3]. (H) *Iberosauripus grandis*, redrawn from Cobos et al. [63]. (I) *Megalosauripus uzbekistanicus*, redrawn from Fanti et al.[6]. (J) *Megalosauripus*-like, redrawn from Whyte et al.[92]). (K) Megalosauripus-like, redrawn from Day et al. [15]. (L) *Megalosauripus* from Arizona, redrawn from Lockley et al.[3]. (M) *Megalosauripus* from Utah, redrawn from Lockley et al., [3]. (N) *Megalosauripus*-like, redrawn from Belvedere et al. [93]. (O) *Megalosauripus*-like, redrawn from Razzolini et al.[9]. (P) *Boutakioutichnium atlasicus*, redrawn from Nouri et al. [94]. (Q) Holotype of *Hispanosauropus*, redrawn from Lockley et al.[4]. (R) *Megalosauropus broomensis*, redrawn from Romilio and Salisbury [95]; (S) *Megalosauripus teutonicus*, redrawn from Kaever and Lapparent [96]); (T) *Jurabrontes courtedoulensis* Holotype [96]

**Fig 12. Outline drawings of the different types of *Megalosauripus* cf. *transjurani* (A-H), *Megalosauripus* isp. (I-Q), and of Morphotype 2 (R-Y) all represented at the same scale.**
(A) SCR1000-T23-R1. (B) SCR1000-T23-L2. (C) SCR1000-T23-R2. (D) TCH1020-T1-R2;(E) TCH1020-T2-L1. (F) TCH1020-T2-R1. (G) TCH1020-T2-L2. (H) TCH1020-T2-R2. (I) TCH1000-TR1-R2. (J) TCH1000-TR1-L3. (K) TCH1000-TR1-R3. (L) TCH1000-TR2-R9. (M) TCH1000-TR2-L10. (N) TCH1000-TR2-R10. (O) TCH1000-TR2-L12. (P) TCH1000-TR2-R12. (Q) TCH1000-TR2-L13. (R) BEB500-TR7-L2. (S) BEB500-TR7-R2. (T) BEB500-TR7-R7. (U)

BEB500-TR7-L10. (V) BEB500-TR7-R10. (W) BEB500-TR7-L11. (X) SCR1000-T18-R1. (Y) TCH1030-T1-R4.

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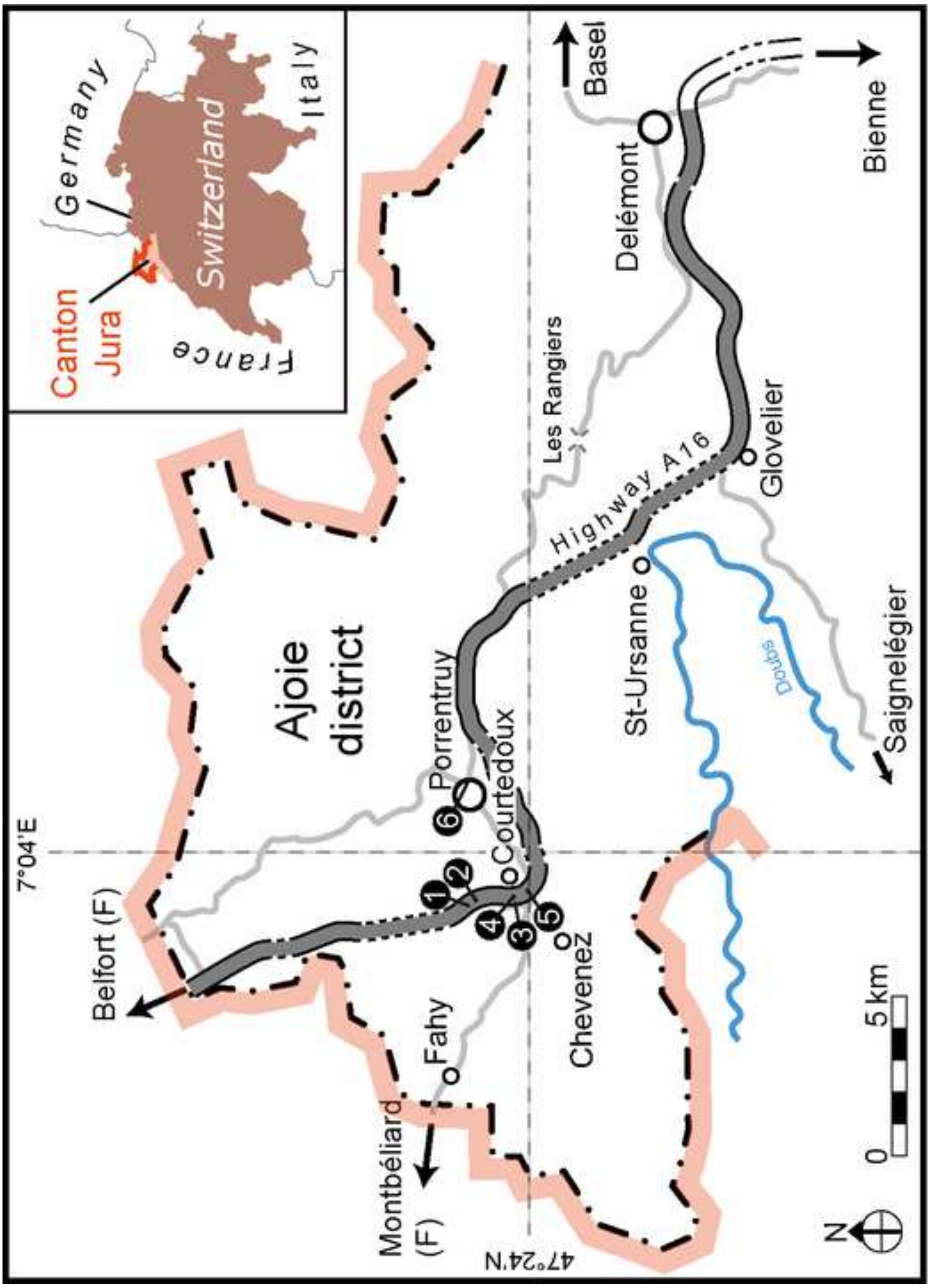


Figure 1

Figure 2

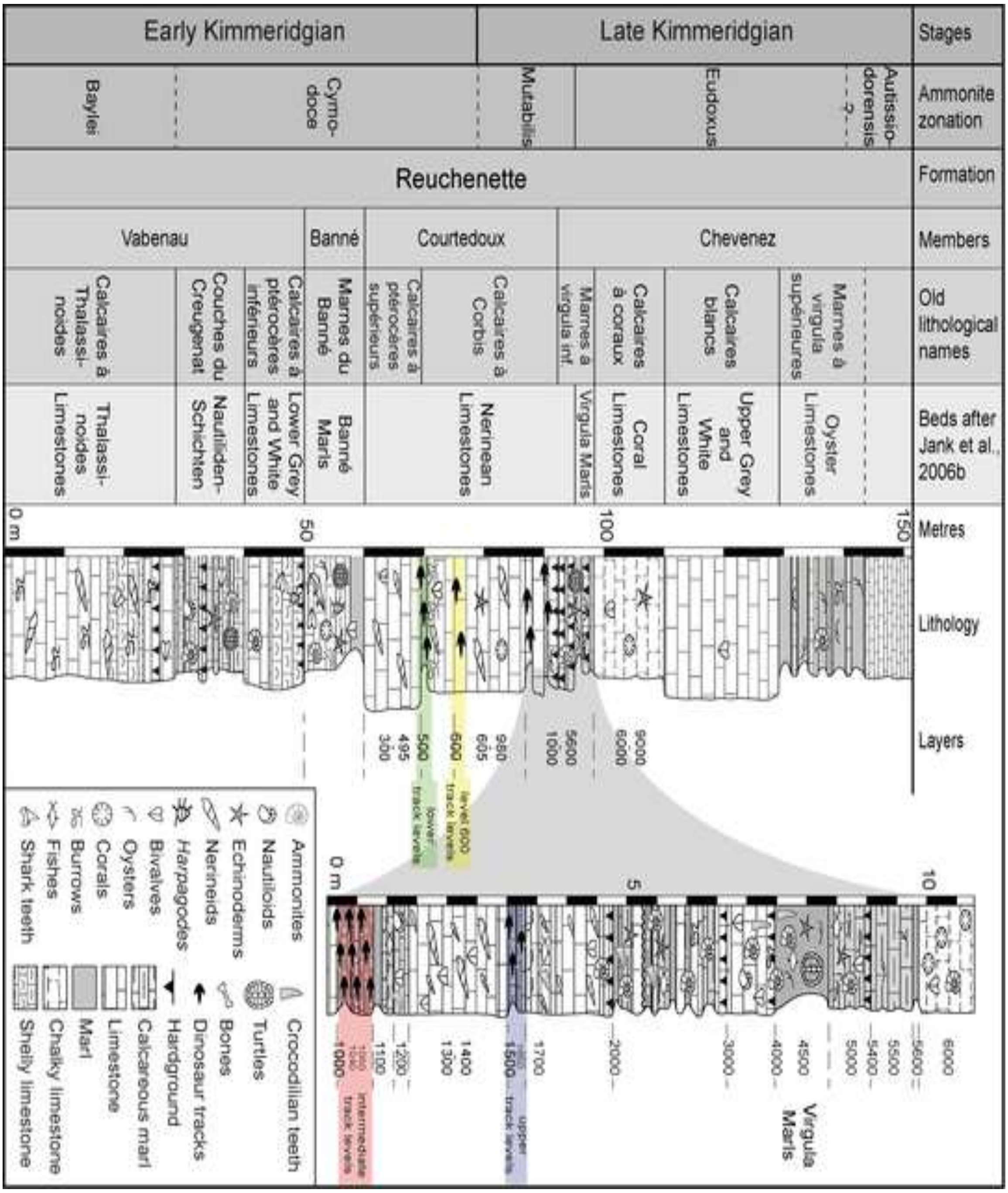


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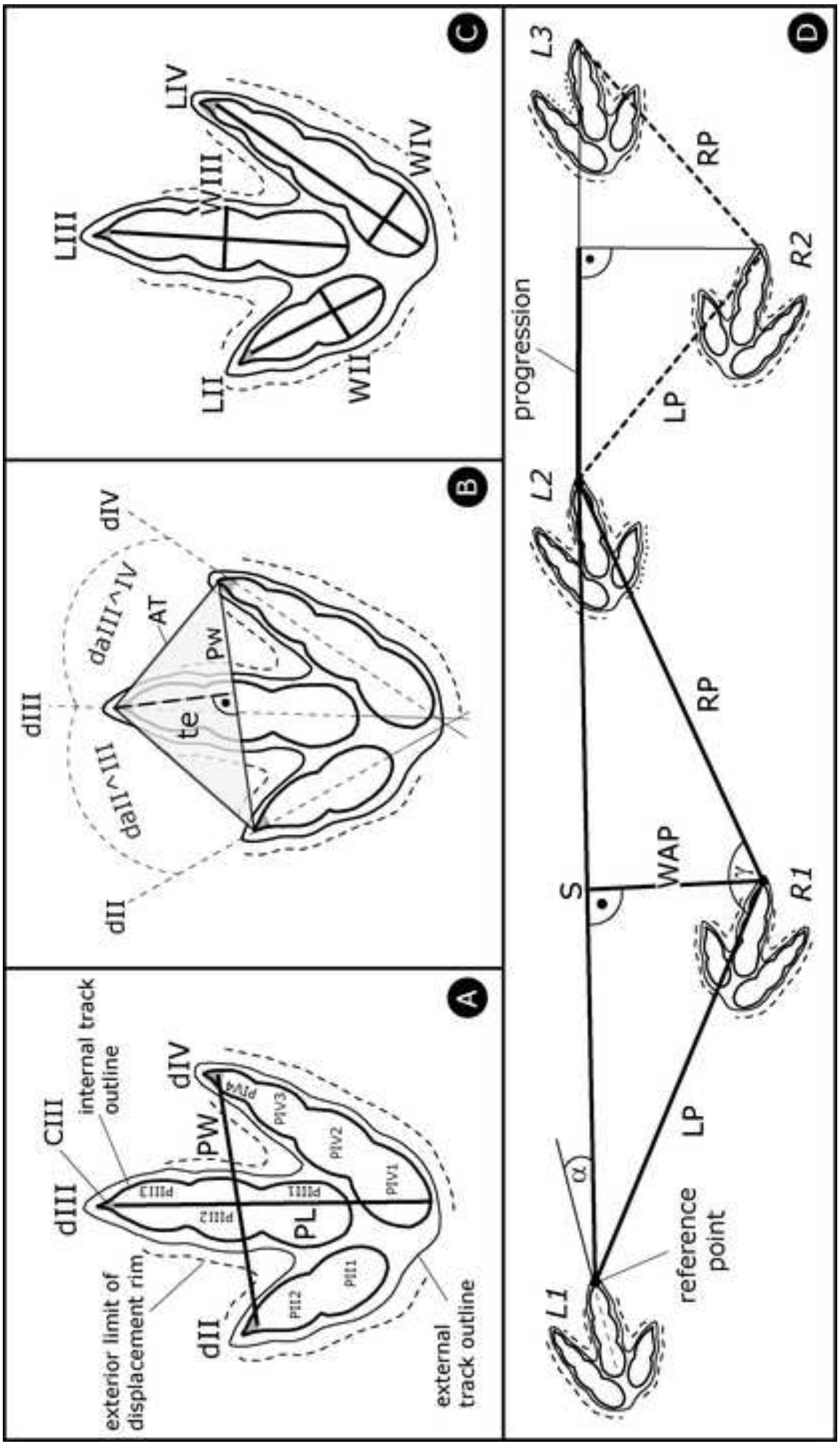
Figure 3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exterior limit of displacement rim
dII
dIII
CIII
internal track outline
PW
dIV
PL
external track outline
B
dII
daII^III
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te
PW
AT
daIII^IV
dIV
C
LII
WII
LIII
WIII
LIV
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LP
R2
RP
L3

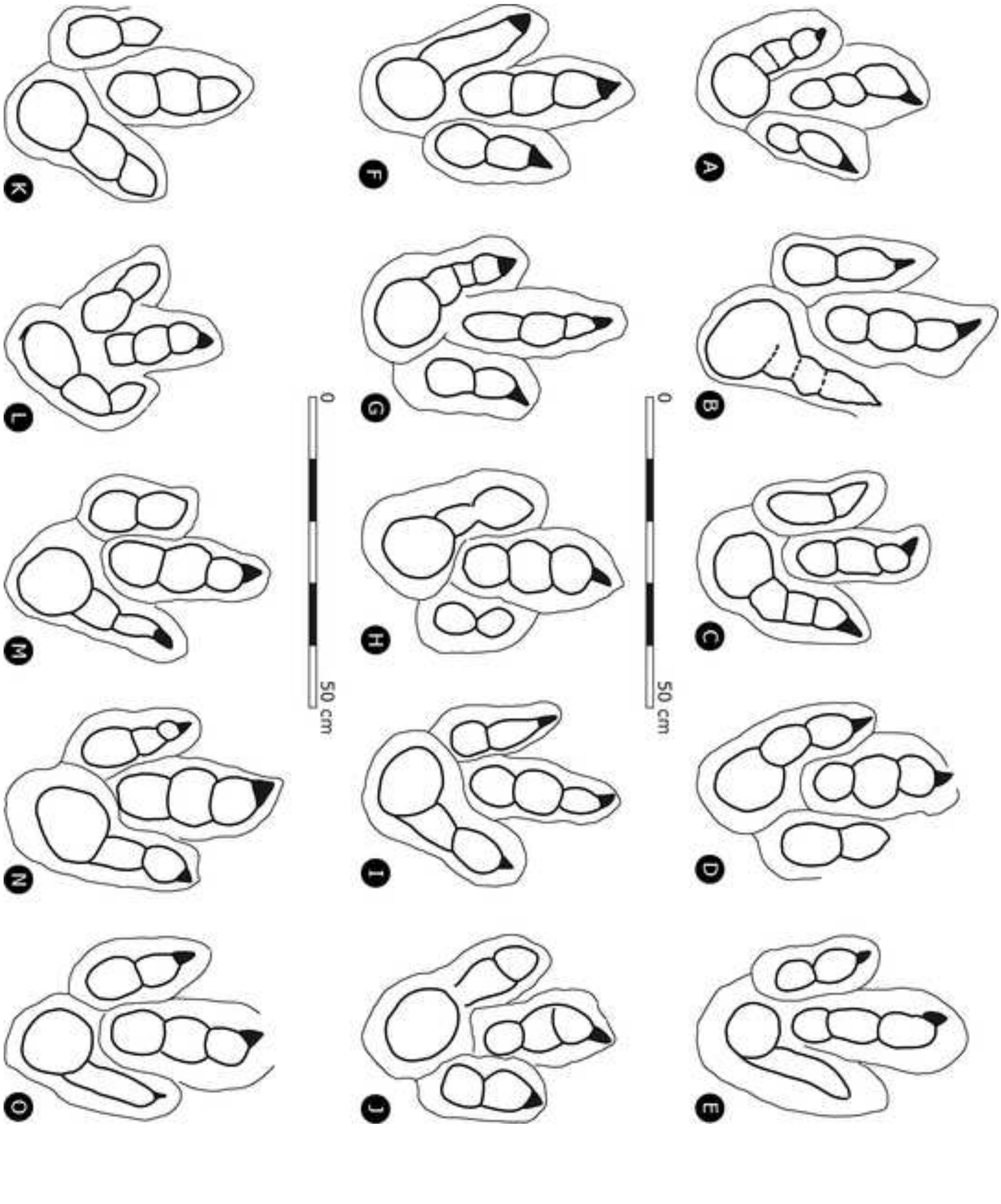
A
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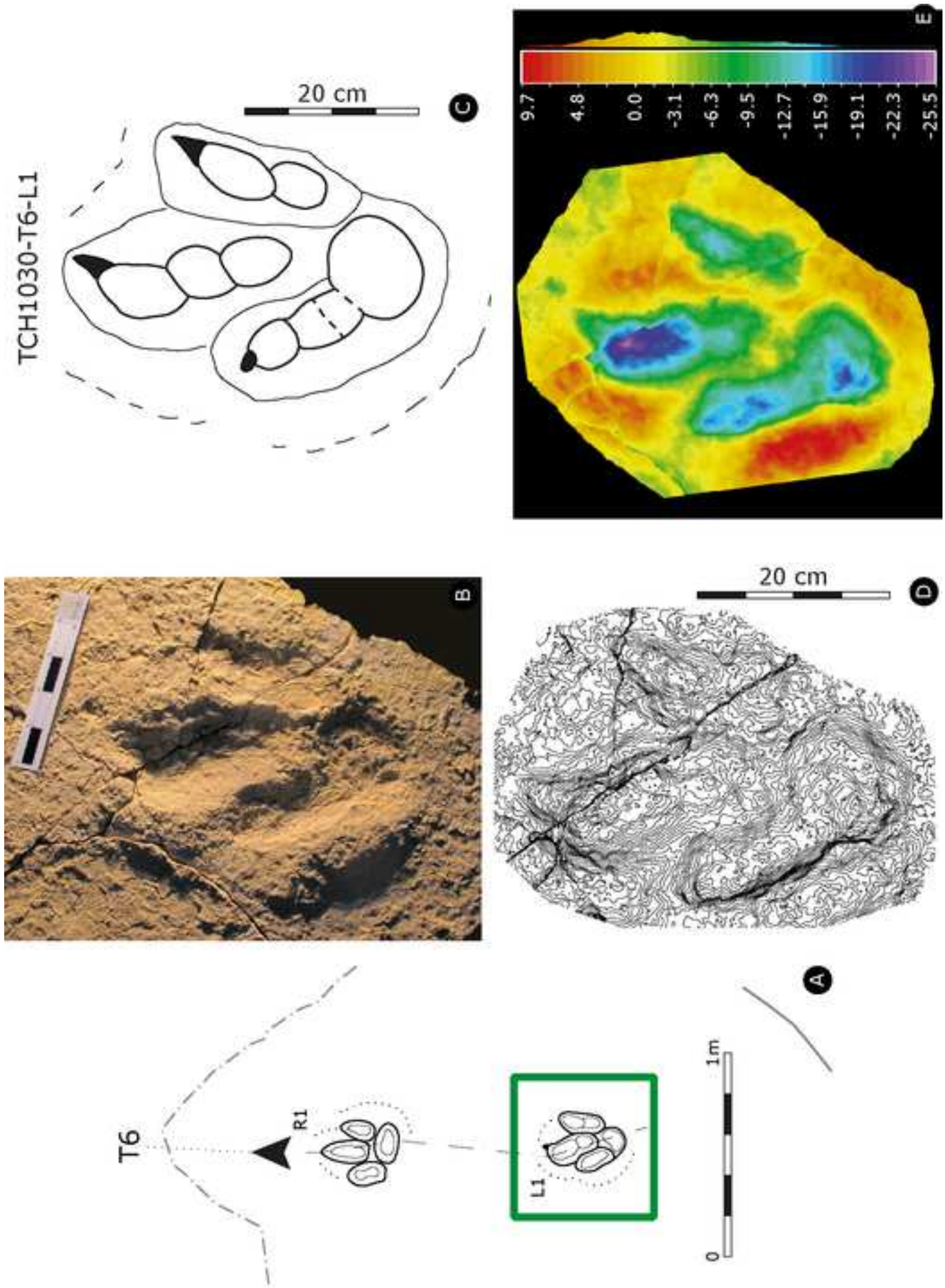
Figure 5



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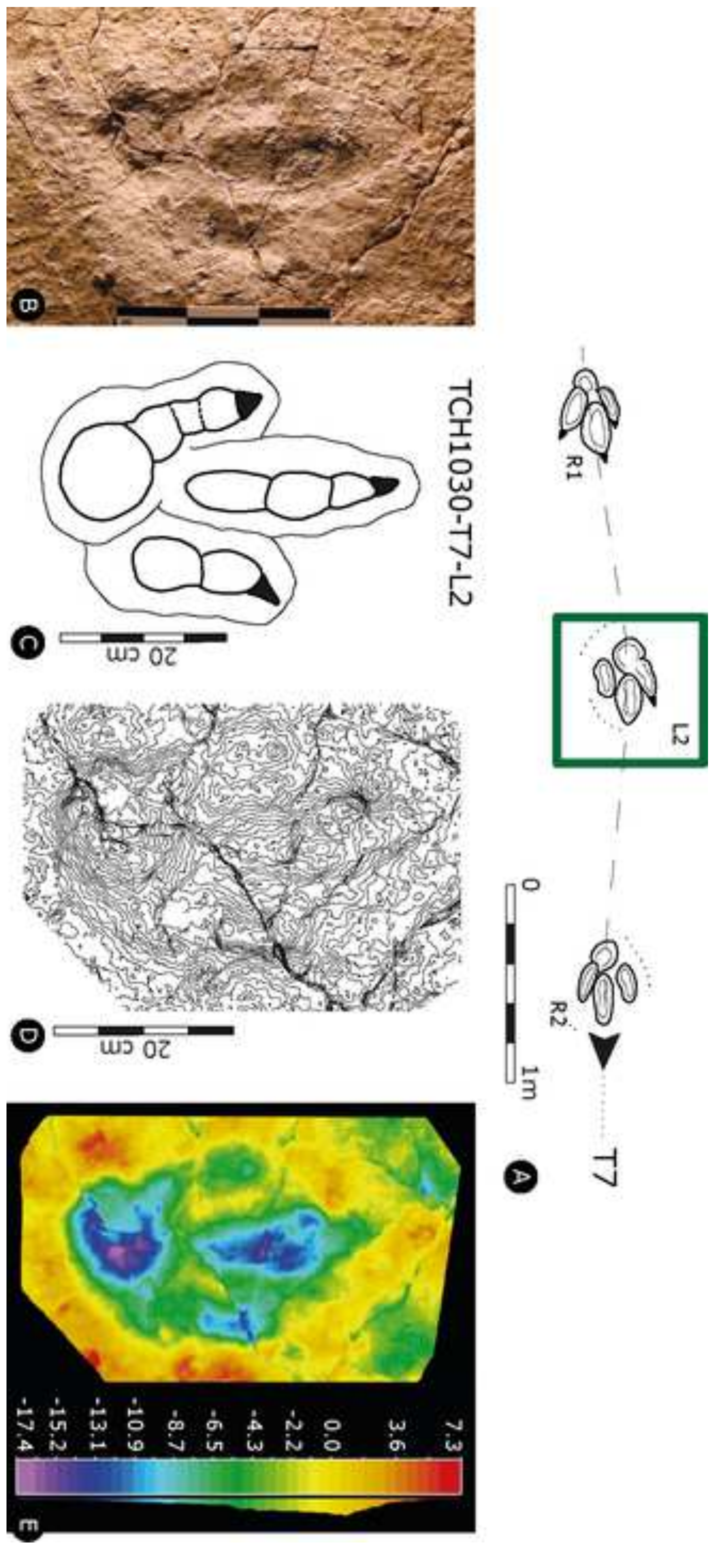


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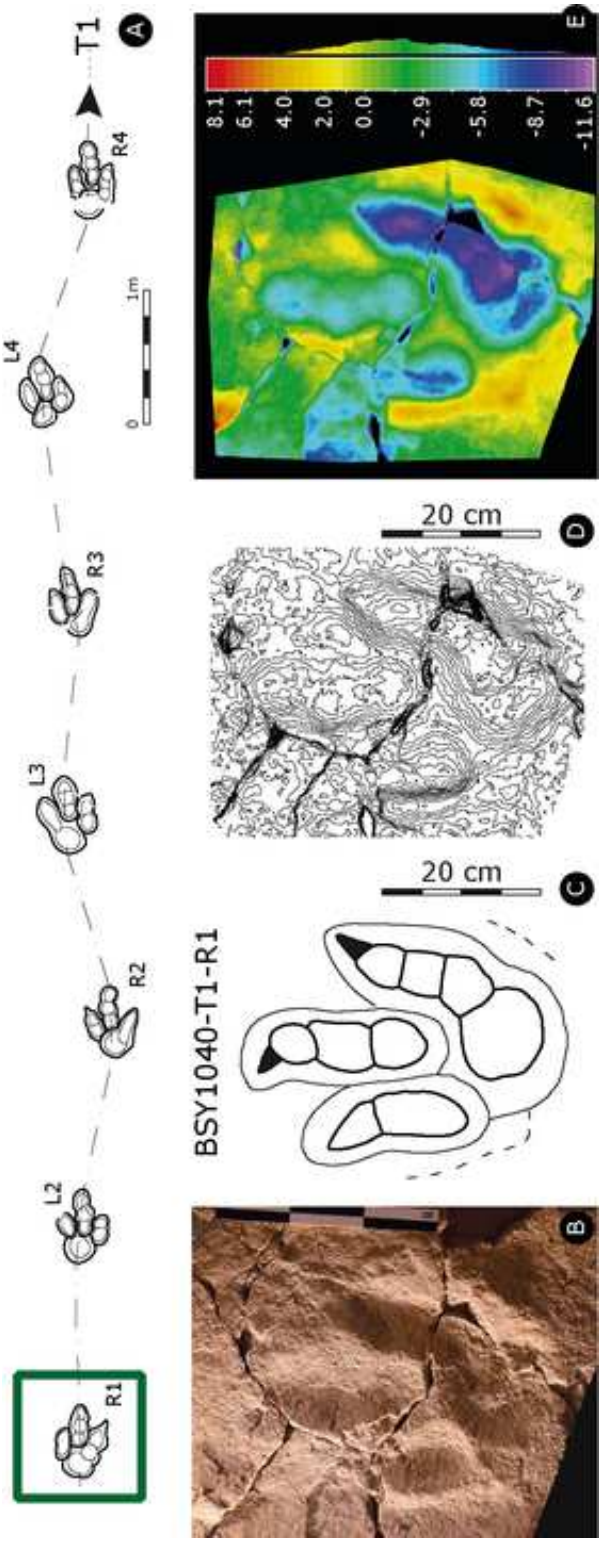
Figure 7



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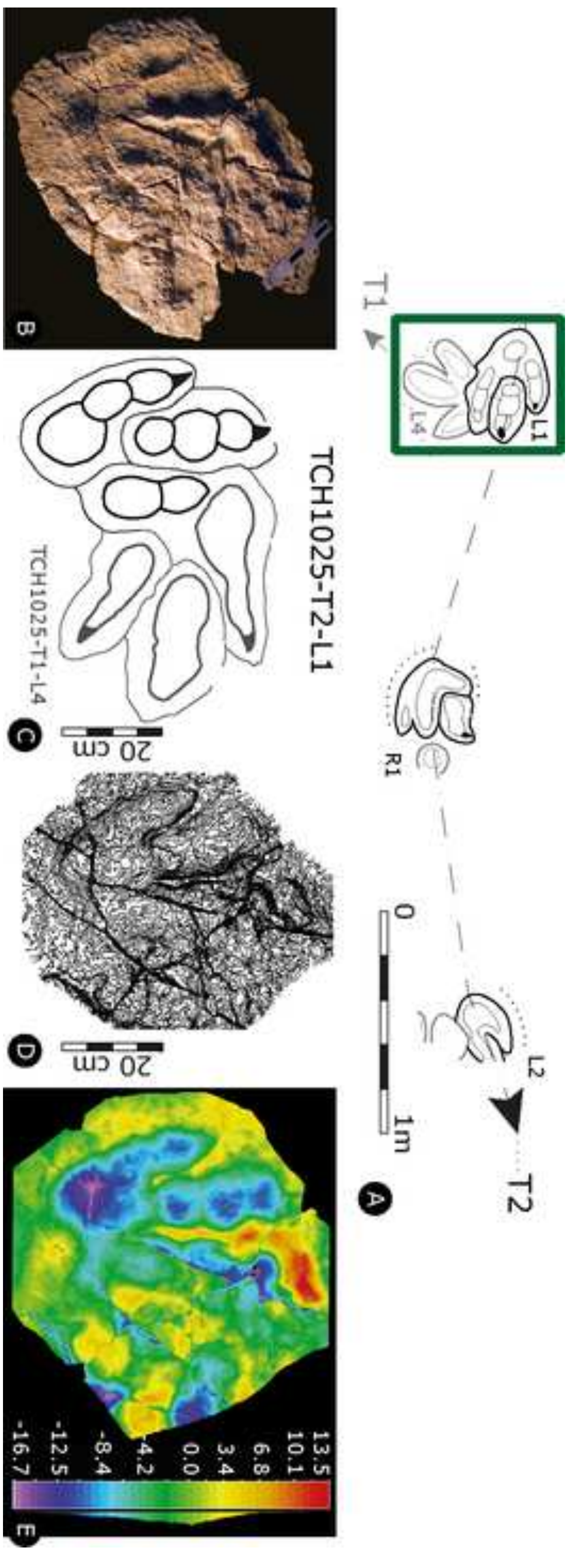


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Figure 9

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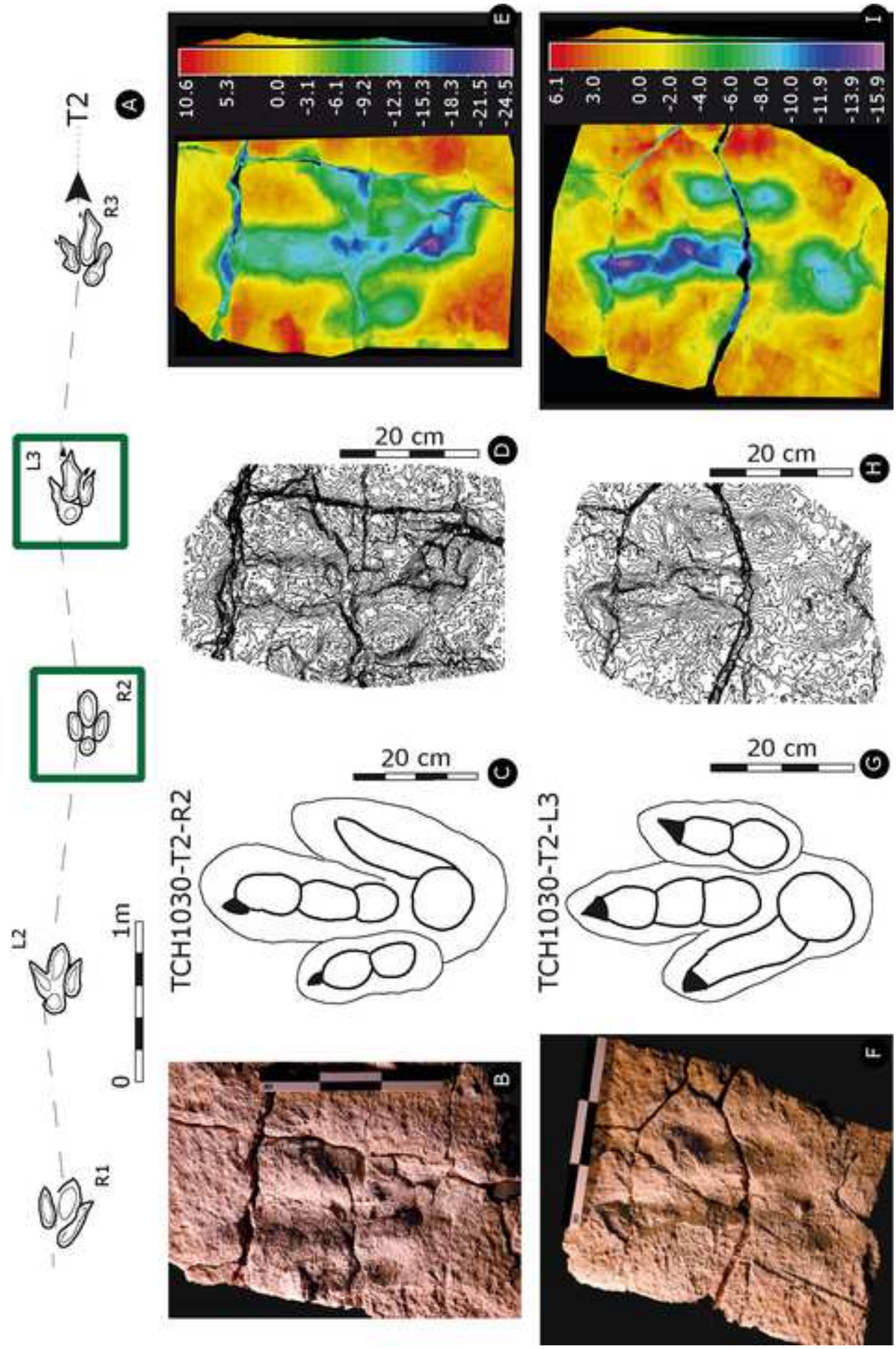

Figure 10

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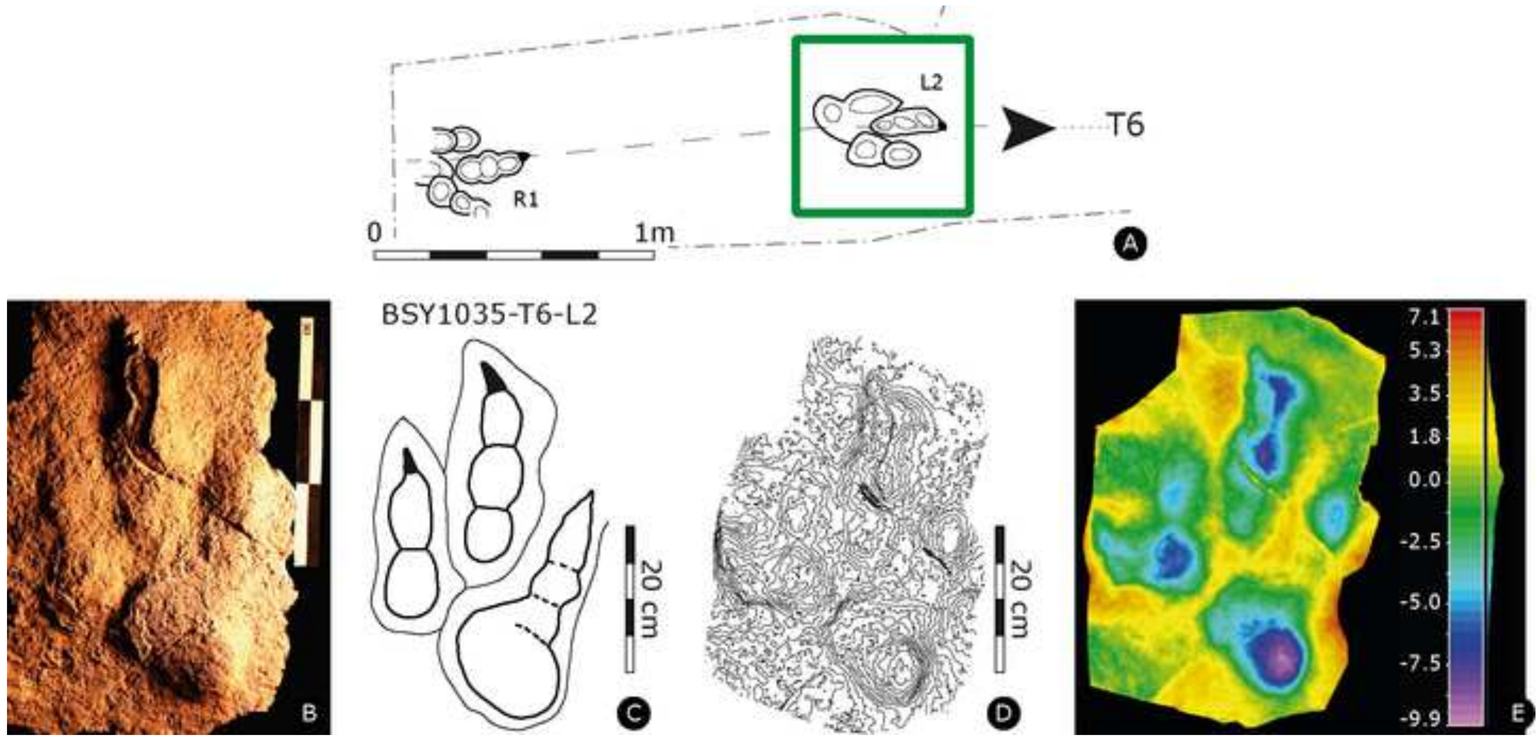


Figure 11



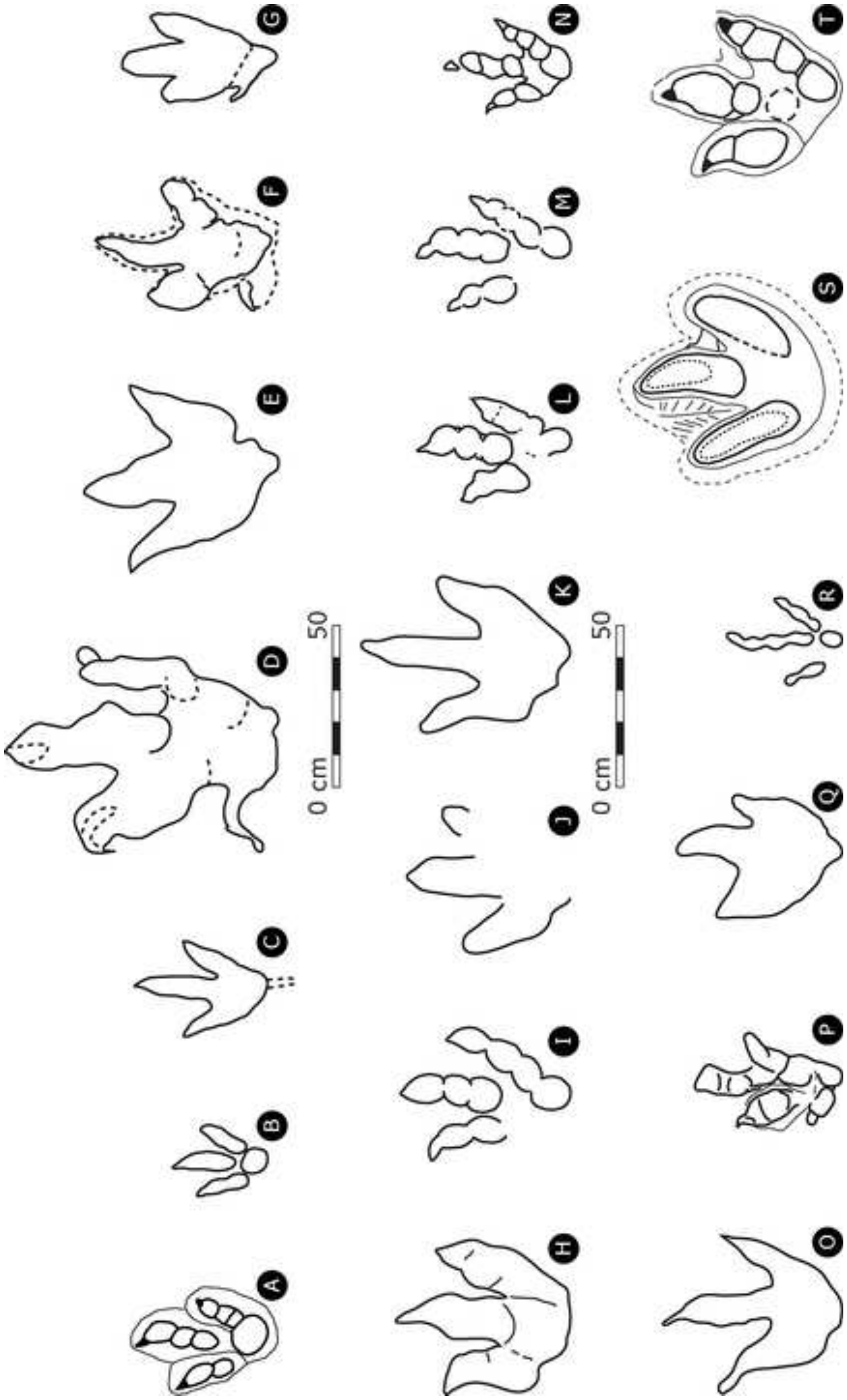
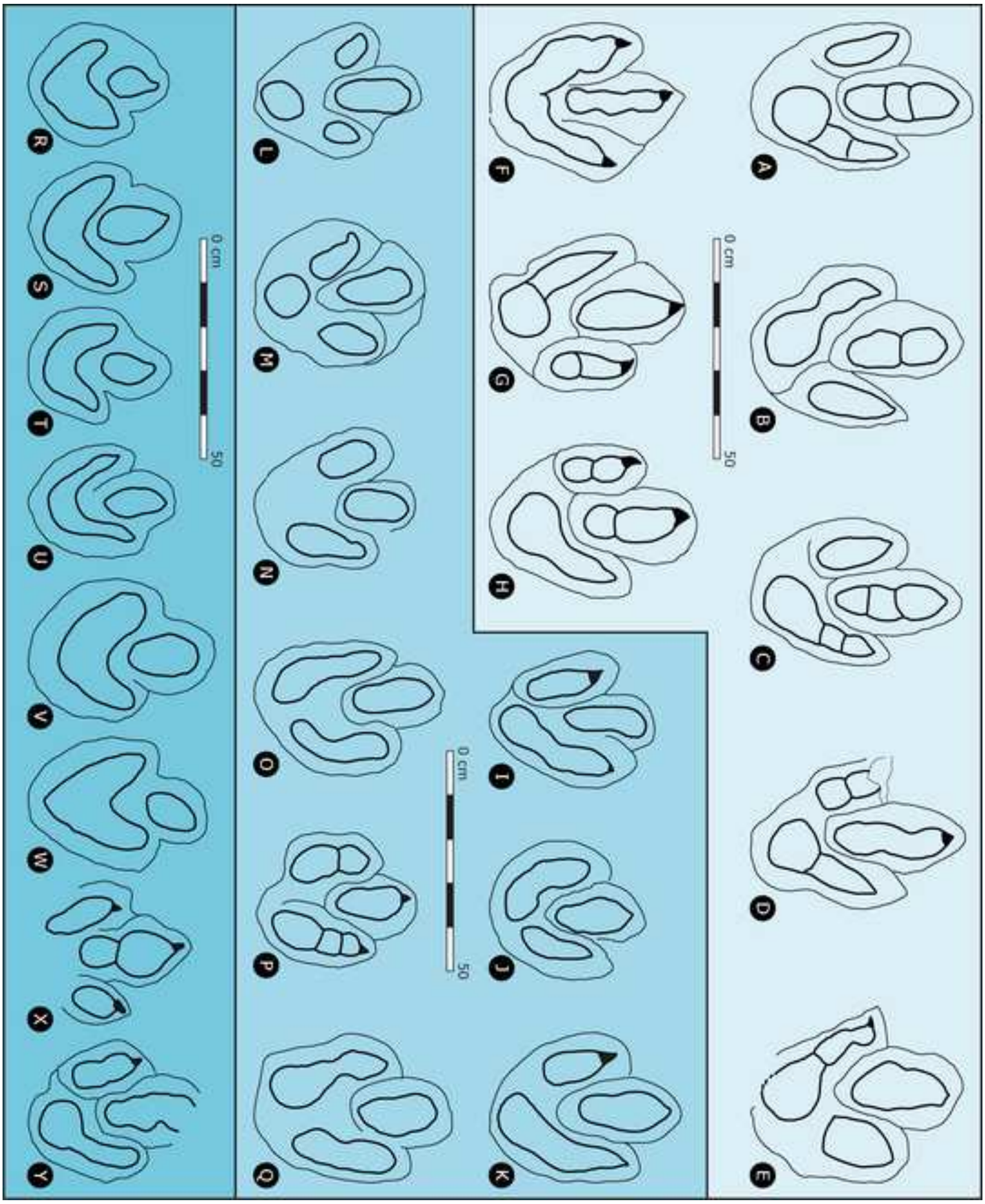


Figure 12

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