



# UNIVERSITÀ DEGLI STUDI DI PADOVA

Sede Amministrativa: Università degli Studi di Padova

Dipartimento di GEOSCIENZE

SCUOLA DI DOTTORATO DI RICERCA IN: SCIENZE DELLA TERRA  
CICLO XXI

## **ICHOLOGICAL RESEARCHES ON THE UPPER JURASSIC DINOSAUR TRACKS IN THE IOUARIDÈNE AREA (DEMNAT, CENTRAL HIGH-ATLAS, MOROCCO)**

**Direttore della Scuola:** Ch.mo Prof. Gilberto Artioli

**Supervisore:** Ch.mo Prof. Paolo Mietto

**Dottorando :** Matteo Belvedere



*“Look at this!”* said he. *“By George, this must be the trail of the father of all birds!”*

An enormous three-toed track was imprinted in the soft mud before us.

A. CONAN DOYLE, *The Lost World* (1912)



# ACKNOWLEDGEMENTS

---

Many people have to be thanked for helping me in this project.

First of all, I thank my supervisor, Paolo Mietto, who gave me the opportunity to carry out this PhD project, with fruitful discussions and always supporting me in following new approaches. His guidance and experience, as well as the constant encouraging during the last three years allowed me to complete the thesis in this short period.

Sincere thanks to all the authorities of the Demnat region, from the Commune chief to the Gouverneur of the Azilal Province, that gave me the permissions for the field work. A warm thank to the AESVT of Demnat, and especially to Mohamed Chaouki and Mohamed Essoufi, that friendly looked out for the relationships with the local authorities and for the logistic organization of the last field trips. This project would not have been finished without their precious help. The same warm thank goes to Simohamed Benhimou from Taghbalout, for the help in the field work during the first campaign but, above all, for supporting and helping in the worst days of the second campaign.

Thanks to Nour-Eddine Jalil, Marrakech Cadi Ayyad University, for the help in the organization of field trips and the relationships with the M’Goun Geopark direction.

Thanks to all the other friendly people I met in Demnat and in the Iouaridène villages, especially to the very friend Hamid.

A very best thank to Christian A. Meyer, Naturhistorisches Museum Basel, for sharing his ichnological knowledge and material on the study area, and for the helpful discussion debated during the last two years.

The same sincere thank to Shinobu Ishigaki, Hayashibara Museum of Natural Sciences Okayama, for the friendly sharing of its huge amount of unpublished sketches of the Iouaridène footprints and for the encouraging in the end of the project.

Thanks to Martin Whyte and Mike Romano for hosting me some days in Sheffield, and for allowing me to see the original material of the Middle Jurassic Yorkshire coast tracks, especially the *Deltapodus* footprints. The discussions regarding this last ichnogenus have been extremely useful for the identification of some tracks I’ve studied.

A thank to all the technicians of the Department; a great thank to Stefano Castelli for the “innovative” structure we built to digitalize the plastic films, and for the further elaboration of the photos, and to Maria Luisa Perissinotto (Maui) for the help in the field, and above all, for the help in casting and moulding footprints with silica rubbers and fibreglass: how many smelling hours we spent!

The same warm thank to Stefano Girardi and Fabio Remondino, Fondazione Bruno Kessler, for introducing me to the 3D world, and especially for having made the footprints digital model.

A special friendly thank to Marco Avanzini who taught me what dinosaur footprints are, gave me access to his huge reference library, and that never refused to discuss or help me.

Thanks to Fabio Petti, who involved me in the project of the 3D modelling, and who became a trustworthy friend.

A friendly thanks to Remmert Schouten, who allowed me to spend a couple of months at the

University of Bristol, always supporting and helping me. Thanks to him also for introducing me to Nour-Eddine. Thanks to Mike Benton for hosting me at the Earth Science Department of the University of Bristol. Thanks to Pam and Colin who gave me a roof and a warm bed during the time spent in Bristol, and above all their special friendship.

Thanks to Natalia Bevilacqua, and to CTS s.r.l., for the enthusiastic help in testing and choosing the best silica rubber to make casts in the field.

A special thanks to the Carabinieri of Montebelluna and to the ROS of Padova for taking care of the baggage, containing most of the plastic sheets drawn during the last field trip, lost at airport. This project would have been much poorer if those had data lost.

This project would not have been finished in time without the help of many undergraduate students that made their stage survey with me the Iouaridène area; thanks to Alice, Davide, Gigi, Irene, Maura, Nausicaa, Nicola, Sofia. Thanks to Anna, Lisa, Maui, Anna (another one), and to my brother Riccardo, for the unbounded help during the last field trip. Anna needs to be thanked again for the time spent in the discussion on the sedimentology of the site.

These three years in Padova wouldn't have been so nice and easy without the friendships of the other PhD students and researchers who shared not only the working life, but also enjoyed the social life outside the university: Ale, Anna, Chiara, Guido, Jacopo, Lisa, Manuel, Marco, Nereo, Renata.

A special thanks to my flat-mates, Ale Moro e Chiara, for all the nice time, the nice beers, and nice wines the time spent in our flats.

Thanks to the Jurassic Foundation for partially supporting the project.

Finally, I wish to thank my family for the constant support, and physical help as well, during all the period of my PhD.

The last thanks goes to Mara, for her love and the endless patience which allowed me to go beyond the hardest part of this doctorate.

# CONTENTS

---

<b>RIASSUNTO</b>	<i>p.</i>	3
<b>ABSTRACT</b>	<i>p.</i>	5
<b>1 INTRODUCTION</b>	<i>p.</i>	7
1.1 Geographical setting		
1.2 History of the site		
1.3 Aim of the work		
<b>2 METHODS AND TERMINOLGY</b>	<i>p.</i>	12
2.1 Labelling and Illustrating Tracks		
2.2 Ichnological Terminology		
2.3 Evaluation of Locomotion Speeds		
2.4 Principal Component Analysis		
2.5 Landmark Analysis		
<b>3 SEDIMENTOLOGY AND STRATIGRAPHY</b>	<i>p.</i>	25
3.1 Paleogeographical setting		
3.2 Geological setting		
3.3 Facies analysis		
3.4 Stratigraphical correlations		
3.5 Paleoenvironmental reconstructions		
<b>4 ICHNOLOGY OF THE IOUARIDÈNE ICHNOSITE</b>	<i>p.</i>	35
4.1 Group 1 – Tracks and Trackways of supposed Quadruped Dinosaurs		
4.1 Group 2 – Tracks and Trackways of Biped Dinosaurs		
4.3 Group 3 – Non-dinosaurian Traces		
4.4 Tracks and Trackways Analysis and Distribution		
4.5 Trackways Directions and Locomotion Speeds		
4.6 Distinctive Tracks and Trackways		
<b>5 INTERPRETATION AND ICHNOTAXONOMY</b>	<i>p.</i>	65
5.1 Ichnotaxonomy of Group 1		
5.2 Ichnotaxonomy of Group 2		
5.3 Tracking the Trackmaker		
<b>6 MULTIVARIATE STATISTICS</b>	<i>p.</i>	81
6.1 Principal Component Analysis		
6.2 Landmark Analysis		
<b>7 CONLCUSIONS</b>	<i>p.</i>	91
<b>REFERENCES</b>	<i>p.</i>	95
<b>APPENDICES</b>	<i>p.</i>	107
Appendix 1 - Tridactyl tracks measurements table		
Appendix 2 - Tridactyl trackways measurements table		
Appendix 3 - Group 1 measurments table		
Appendix 4 - Sauropod trackways measurments table		





# RIASSUNTO

---

Il sito Giurassico Medio/Superiore di Iouaridène è noto in letteratura fin dal 1937, ma, nonostante i numerosi lavori pubblicati, la sua icnocenosi non è mai stata studiata in dettaglio.

L'obiettivo di questa tesi di dottorato è quello di dare la prima completa descrizione icnologica dei vari morfotipi presenti nel sito di Iouaridène, estremamente importanti non solo per la ricostruzione della fauna a dinosauri locale, ma anche per risolvere i problemi relativi alla datazione del sito, ancora incerta, e la relativa distribuzione degli icnotaxa.

Questo scopo generale è stato perseguito utilizzando differenti discipline, dalla sedimentologia, all'icnologia alla morfometria geometrica, per citarne alcune. Questo perché le orme non sono soltanto dei resti fossili, come possono esserlo i resti ossei, ma derivano da complesse interazioni tra il piede dell'animale e il sedimento. Queste interazioni sono così strettamente correlate che spesso lo stesso dinosauro può lasciare impronte anche molto diverse tra loro solo a causa delle diverse caratteristiche del terreno su cui sta camminando.

L'alternanza ciclica di peliti rossastre e livelli siltoso/arenaceo fini più consolidati che caratterizza la formazione di Iouaridène, insieme alle caratteristiche di continuità degli affioramenti nell'area di studio, hanno permesso di seguire i livelli improntati per circa 4-5 km, dando la possibilità di riconoscere un paleoambiente di piana alluvionale costiera, in clima semi arido, soggetta a cicliche fasi di inondazione dovute o a piccole ingressioni marine o a variazioni climatiche stagionali.

Durante quattro campagne sono stati rilevati 21 livelli ad impronte, il più alto numero di livelli mai registrato nell'area. Un gradissimo numero d'impronte è stato rilevato con metodologie tradizionali e, gran parte di queste, circa un migliaio, erano sufficientemente ben conservate da permettere di essere misurate.

Sono stati identificati 12 morfotipi, divisi in tre gruppi, che testimoniano una fauna dominata da teropodi ma dove erano presenti anche sauropodi di enormi dimensioni oltre ad altri animali, dinosauri e non. Tra questi tipi meno abbondanti, tuttavia, è stata effettuata la più significativa delle scoperte icnologiche dell'area: la prima testimonianza in Africa dell'icnogenere *Delta-podus*. Questo ritrovamento ha notevoli ripercussioni non solo sulla distribuzione globale di questo gruppo di stegosauri, ma anche sulle ricostruzioni paleogeografiche dell'area tetidea nel Giurassico Medio e Superiore.

Per la prima volta è stato sistematicamente calcolato il *Trackway Ratio* per lo studio delle impronte di sauropodi. Il metodo si è rivelato molto utile non solo per quantificare il *gauge* delle piste di sauropodi, ma anche per comparare piste dominate dalle impronte delle mani con quelle simili e molto più note di *Breviparopus taghbaloutensis*. Il dato che ne deriva permette di immaginare un *trackmaker* dello stesso tipo per entrambi i morfotipi.

Tra le impronte tridattile, il gruppo maggiore è rappresentato da impronte con affinità "megalosauriana", generalmente organizzate in piste e con un grado di conservazione che può variare anche di molto lungo la stessa pista. Il ritrovamento di un così grande numero di queste impronte, nonostante la loro posizione tassonomica sia ancora discussa e lontana da una soluzione definitiva, permette comunque di supportare l'età Giurassico Superiore del sito.

L'elevatissimo numero di impronte tridattile rilevate ha consentito di testare, applicati all'icnologia, alcuni metodi statistici e morfometrici.

La *Principal Component Analysis* è stata effettuata su un dataset comprendente tutte le impronte tridattile del sito. Il test ha messo in luce le difficoltà di questa metodologia nel discriminare tra i vari morfotipi riconosciuti dall'analisi icnologica, almeno con le variabili applicate. Utilizzata, invece, per confrontare due o tre gruppi di impronte, la PCA si è rivelata molto più attendibile.

La *Landmark analysis*, la cui ultima applicazione all'icnologia risale a più di dieci anni fa, e solo a titolo esplorativo, è stata utilizzata con le impronte del sito di Iouaridène per quantificare quali variazioni nella forma dell'impronta siano dovute a reali caratteristiche anatomiche dell'autopodio del dinosauro e quali invece siano imputabili a caratteri extramorfologici.

Successivamente il metodo è stato applicato per testare l'attendibilità delle classificazioni tassonomiche finora proposte per le impronte "megalosauriane", mostrando che, a dispetto della confusione regnante nel gruppo, alcuni raggruppamenti possono essere individuati. Tuttavia, per avere un certa attendibilità tassonomica la *Landmark analysis* deve essere effettuata su molti più campioni, e possibilmente su fotografie o, meglio ancora, modelli tridimensionali digitali, in modo da annullare l'errore e la soggettività dei disegni schematici che costituiscono il maggior dato presente in letteratura.

# ABSTRACT

---

The Middle/Upper Jurassic Iouaridène site has been known and studied since 1937, but no complete report of its ichnocoenosis has ever been carried out so far.

The aim of this thesis is to give the first complete ichnological description of the Iouaridène morphotypes, meaningful not only for the understanding of the local dinosaur fauna but also as help in solving the age problems of the site and the related global distribution and evolution of ichnotaxa.

This general aim is pursued joining different disciplines from sedimentology to ichnology, to geometric morphometrics. This is because dinosaur tracks are not only biological objects such as fossil bones, but are rather derived from the complex interactions between the foot of the animal and the sediment. These interactions are so strictly related that the same individual can leave different traces only on account of the features of the ground it is walking on.

The Iouaridène formation, with its cyclic alternation of reddish mudstones and more consolidated silty/fine-sandy levels, together with the nature of the outcrops allowed to follow the trampled layer for 4-5 km and gave the possibility to carry out the paleoenvironmental reconstructions of what a costal flood-plain was, cyclically flooded by rapid marine incursions, or seasonal inundations

21 track-bearing layers were mapped during four field campaigns, the highest number of trampled levels ever recorded for the area. A very large number of footprints were surveyed with traditional methodologies, and most of them, around a thousand, were sufficiently preserved to be examined. 12 morphotypes, arranged in three groups, are here reported, describing a theropod-dominated fauna, but where very large sauropods and other dinosaurs were present as well. Few traces of non-dinosaurian animals were found too.

Among the less abundant types it the more important paleontological discovery of the site has been made: the first African *Deltapodus*. This evidence has great consequences on the global distribution of this stegosaurian ichnotype and on paleogeographical reconstruction of the tethyan area as well.

For the first time, a systematic evaluation of the Trackway Ratio (TR) has been carried out during the analysis of sauropod tracks. Furthermore, this method was successfully used to compare the manus-dominated trackways with the similar and well known *Breviparopus taghbaloutensis* tracks. The quantitative data derived from the TR permitted to determine the same tracemaker for both the morphotypes.

Among tridactyl footprints, a very large number of “megalosaurian” tracks have been recorded, mostly arranged in trackways, and with a preservation grade that could vary a lot also across the same trackway. These findings, even if the ichnotaxonomy of this group of footprints is under debate and far from a definitive solution, allow to confirm the Upper Jurassic age of the Iouaridène ichnosite.

The large number of tridactyl footprints recorded permitted to test the application of some statistical and morphometrics methods to ichnology.

*Principal Component Analysis* was carried out on all tridactyl footprints, highlighting the difficulty of this method to discriminate between many morphotypes. However, if applied to compare few groups of tracks, PCA showed a good reliability.

*Landmark analysis* was tried only as an explorative technique for the shape analysis, more than ten years ago. In the Iouaridène site it has been used again to study which features of tridactyl tracks are due to the morphology of the autopodium and which are extramorphologies within the same trackway.

Then the method has been used to try to check the reliability of the proposed taxonomies for the “megalosaurian” tracks, showing that certain groups could be individuated. Nonetheless, to be used significantly for ichnotaxonomical purposes, this method requires a larger number of samples, preferably photographs, or, better, 3D digital models, which can go beyond the errors and subjectivity that affect the schematic drawings present in literature.

# 1 INTRODUCTION

Although fossil footprints were the first discovery of dinosaur remains, and the study of fossil footprints gives more and more information on the locomotion, on the behaviour, and on the original faunal composition, it is only since the last 30 years that they have become an appreciated scientific discipline.

Nonetheless tracks and trackways have always been described, that is, many sites have been known for many years.

## 1.1 GEOGRAPHICAL SETTING

The Iouaridène ichnosite is located in the Moroccan central High-Atlas, around 150 km East of Marrakech, and about 15 km South-East of the city of Demnat (Fig 1.1A). The site is placed on the western boundary of the Iouaridène valley that can be easily reached from Demnat through the road that goes to the Imi'n'Ifri natural bridge. This road continues then to the village of Taghbalout, where it turns into a carriage track.

The ichnosite develops roughly North-South, and extends from the surroundings north of the village of Aït Mimoun to the village of Tirika (Fig. 1.1B). The southern tracks outcrop more or less in front on the village school.

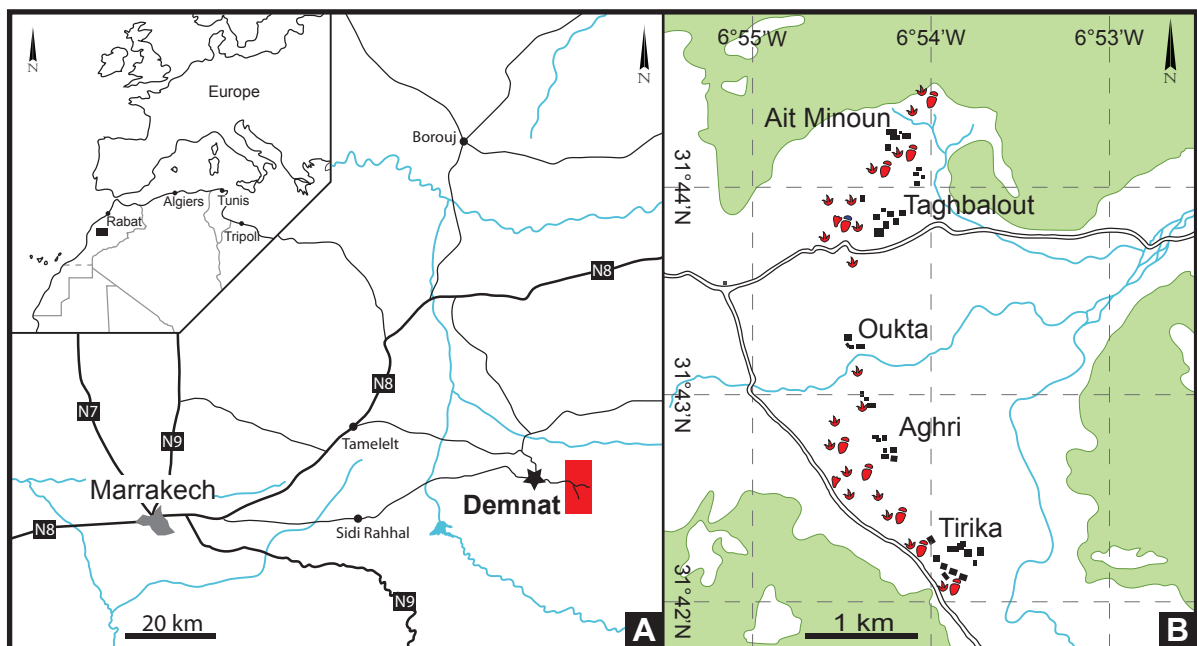


Fig. 1.1 – A: location map of the study area; B: map of the Iouaridène site; the footprints indicate the main track sites.

## 1.2 HISTORY OF THE SITE

The Iouaridène ichnosite appeared for the first time in a scientific report in Plateau et al. (1937). In this paper the site was considered interesting for the tridactyl footprints, supposed to be made by *Megalosaur*, and that was the main types described also in the following works. Lapparent (1942, 1945), and Lapparent and Zbyszewski (1957) described other tridactyl footprints, noticing, among the other things, the “megalosaurian” affinity on the tracks and their similarities with the Portuguese footprints from Cabo Mondego, Roch (1939) gave the first detailed description

of the “*couches rouges*” outcropping in the Iouaridène area, and Termier (1942) besides a more detailed description of the formation, supported the possibility expressed by Lapparent (1942) that the age of the formation could also have been Cretaceous (“*il n’y a aucune raison de se limiter au Dogger et au Lias.*”). Also Choubert et al. (1956) working on the “*couches rouges*” of the region proposed a lower Cretaceous age for the site.

Then, the site was forgotten for about 25 years, and reached new importance with the work of Dutuit and Ouazzou (1980), where the authors describe very large sauropods tracks naming this new footprints *Breviparopus taghbaloutensis*. This ichnotaxon, even if never formally emended, was considered valid in many following paper and was used by Farlow (1992) as perfect example of narrow gauge tracks.

Afterwards, new sedimentological and stratigraphical works were carried out (Jenny et al., 1981 a, b; Jenny and Jossen, 1982; Jenny, 1985) giving a Middle Jurassic age to the track-bearing layer.

But it is especially the large work of Ishigaki in the second half of the 1980s that starts to describe properly the tracks (Ishigaki, 1985a, b, c, 1986, 1988) raising the notoriety of the site, mainly for the description of manus-only and manus-dominated tracks that were interpreted as made by swimming sauropods (Ishigaki, 1989).

Then, during the 1990s a sort of silence covered the site, but since the 2001 new works have begun to be carried out.

Nouri et al. (2001), in a brief report examined some semi-plantigrade theropod tracks from the southern part of the site (Tirika). Meyer and Monbaron (2002), after a field campaign in the area, stated that the manus dominated tracks of Ishigaki (1989) were the misinterpretation of shallow tridactyl footprints or were not present in the site. A reply to this affirmation has recently been published by Ishigaki and Matsumoto (2008), in which the authors admit that while one trackway was misinterpreted (Detk MLXXIX in this work; see 4.6.8), the others described exist and were not found by the Swiss researchers.

Dalla Vecchia (2005) gives a brief description of the sedimentology of the site and shows black and white photographs of some of the most accessible tracks of the site.

Charrière et al. (2005) carried out new stratigraphical investigations on the area; the main result achieved regarding the ichnosite is the dating, based on palynomorphs and ostracods, to the Upper Jurassic (?Oxfordian-Kimmeridgian) of the track-bearing levels.

Then in the latest years Nouri (2007), in his doctoral dissertation, described some of the tracks present in the site, but without a systematic survey of the whole site. Boutakiout et al. (in press) summarize some of the discoveries expressed also in Nouri (2007).

### 1.3 AIM OF THE WORK

Since its discovery, also considering the latest and more in-depth works (Nouri 2007, Boutakiout et al. in press), the Iouaridène ichnosite has never been systematically studied.

The main aim of this work is, then, to give the first complete description of this ichnosite. To achieve this goal many geological and paleontological aspects have been carried out:

- ♣ Sedimentological and stratigraphical study of the track-bearing layers, and paleoenvironmental reconstruction;
- ♣ Systematic survey of the site and mapping and description of the tracks discovered, with the identification of type of tracks (e.g. true track, underprints, undertracks, overprints);
- ♣ Analysis and review of the *B. taghbaloutensis* reference tracks and related footprints;
- ♣ Description and relevance of the trackway gauge evaluated with the Trackway Ratio (Romano et al., 2007) for both manus and pes tracks;
- ♣ Interpretation of manus-only and manus-dominated sauropods tracks;
- ♣ Ichnotaxonomy of all the tracks, and distinction between trackmakers: sauropods, stego-

saur, theropods, and possible ornithischians; non-dinosaurian tracks.

- ⤴ Analysis of the ichnodiversity and implication for the paleoecology of the area;

Moreover, the large amount of tracks examined allows to test different statistical methods:

- ⤴ Principal Component Analysis was used to discriminate among different morphotypes, using several morphometric measurements
- ⤴ Landmark analysis was firstly tested to highlight the morphological variation within the same tridactyl trackway. Furthermore the method has been used to try to divide in smaller morphological groups the tracks with “megalosaurian” affinities.





## 2 METHODS AND TERMINOLOGY

This chapter illustrates the definitions and the terminology used in this work, and the way of collecting and analyzing data as well.

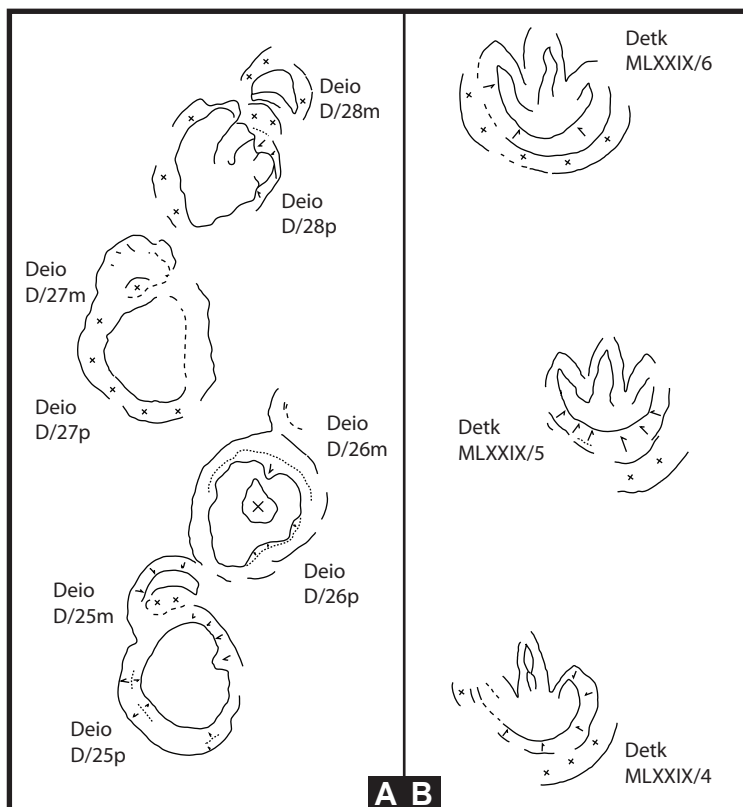
### 2.1 LABELLING AND ILLUSTRATING TRACKS

#### 2.1.1 Labelling tracks and trackways

Tracks and Trackways are labelled sequentially. Two acronyms have been used: Deio and Detk standing for Demnat Iouaridène and Demnat Tirika. The first one refers to tracks and trackways examined in the northern part of the site, around the villages of Taghbalout and Aït Mimoun. The second one refers to the tracks discovered in the southern part of the site, around the villages of Oukta, Aghri, and Tirika. The boundary between the two areas is the road that cuts more or less EW the ichnosite (Fig. 1.1B).

Roman numerals have been used to label trackways and isolated footprints, while Arabic numbers indicate the single footprints. The only exception are the sauropod parallel tracks and trackways surveyed close to a small river and named Deio LavA to LavE. This is due to avoid the repetition of already used numbers, because the trackways were named on a following time and not directly on the fields. Numeration of tracks generally starts from 1, but in some cases, when further surveys discovered other tracks, these have been labelled with negative numbers. Sauropods manus and pes have been distinguished adding a “m” or “p”, respectively, after the track number (Fig. 2.1).

The level of provenance has not been indicated in the track label, but is always reported in the descriptions.



**Fig. 2.1** – Schematic trackways explaining how tracks and trackways were numbered and illustrated; A: sauropod track (Deio D); B: theropod track (Detk MLXXIX).

### 2.1.2 Illustrating tracks and trackways

An objective representation is basic for the documentation and study of tracks and trackways. However it is usually quite difficult to obtain. Outline drawings tend to be over-simplified and subjective, while photographs are dependent on the illumination angle. Moreover, photographs that are not taken perpendicular to the surface can deform the morphology of the footprints.

#### Outline drawings

This method has the great benefit of highlighting the main representative characteristics of the footprints. On the other hand, this method is highly influenced by external factors, (e.g. illumination angle, the surface position, depth of the track, etc.) as well as by the interpretation of the researcher. Moreover, there is the difficulty of representing sharp margins which are usually drawn more rounded (Thulborn, 1990)

Nonetheless, this method is commonly used by ichnologists because it allows to survey large tracksites and also to maintain the actual relationships between the tracks of a trackway.

All the tracks have been sketched on transparent thick plastic films; the continuous line defines the inner footprint. In the few cases when the walls are not vertical between the inner and external track line, drawn with thick dashes, some arrows have been drawn indicating the gradient of the wall. When the outline of the footprint is not clear the line is dashed (Fig. 2.1).

The rims are drawn with a continuous line with “+”. Arrows indicate the gradient of rims when they are asymmetric or when this gradient is notable, like in sauropods tracks (Fig. 2.1). In these last cases the crests of the rims are marked with a dashed line.

#### Photographs

Besides the outline drawings all the tracks have been photographed (since July 2007 with a Fujifilm Finepix S5000, after with a Fujifilm Finepix S5700). Not all the trackways could be photographed entirely. For some of them a photo-mosaic was made; for the others just a general overview photo was taken.

Photographs give more objective information on the tracks, even if the details and also the morphology are highly influenced by the illumination angle that, if not appropriate, could flatten or exaggerate the relief (Ishigaki and Fujisaki, 1989; Thulborn, 1990; Gatesy et al., 2005a).

All the photographs have been taken at daylight, so they could suffer of inappropriate lighting (e.g. clouds, time of the day, presence of vegetation, etc.). However, the photographs of the footprints have been taken with the best conditions possible for that day.

#### 3D acquisition: Laserscanner and Photogrammetry

To go beyond the subjectivity and inaccuracy of the traditional methods, during the last 20 years many techniques of digital acquisition of footprints have been developed and tested.

Much progress in 3D acquisition techniques has been made over recent years, from the Moiré Topography applied to *Eubrontes* tracks by Ishigaki and Fujisaki (1989), to the latest laser scanner techniques applied to large surfaces (Bates et al., 2008a, b; Meyer and Thuring, 2006), inaccessible outcroppings (Avanzini et al., 2008), or to complete ichnosites (Marty et al, 2007), as well as to single footprints or tracks' portions (Hurum et al., 2006; Petti et al., 2008; Belvedere and Mietto, submitted).

During the development of the Moroccan project I was involved in the testing some of these new methodologies for the acquisition of dinosaur footprints. In the Coste dell'Anglone ichnosite (NE Italy) a triangulation laserscanner and also a photogrammetric technique were tested on the field. The results of these tests have been recently published in Petti et al. (2008). These

methods were applied also to digitize the fibreglass casts of two Moroccan specimens attributed to *Deltapodus* (Belvedere and Mietto, submitted).

## 2.2 ICHNOLOGICAL TERMINOLOGY

Vertebrate ichnology suffers from non-codified lexicon, and there is not always consensus about the terminology and the meaning of the terms used by the authors. Most of the terms used by ichnologists follow the definition of Leonardi (1987) and Thulborn (1990). However, to avoid ambiguity, the nomenclature used in this work is here defined and explained.

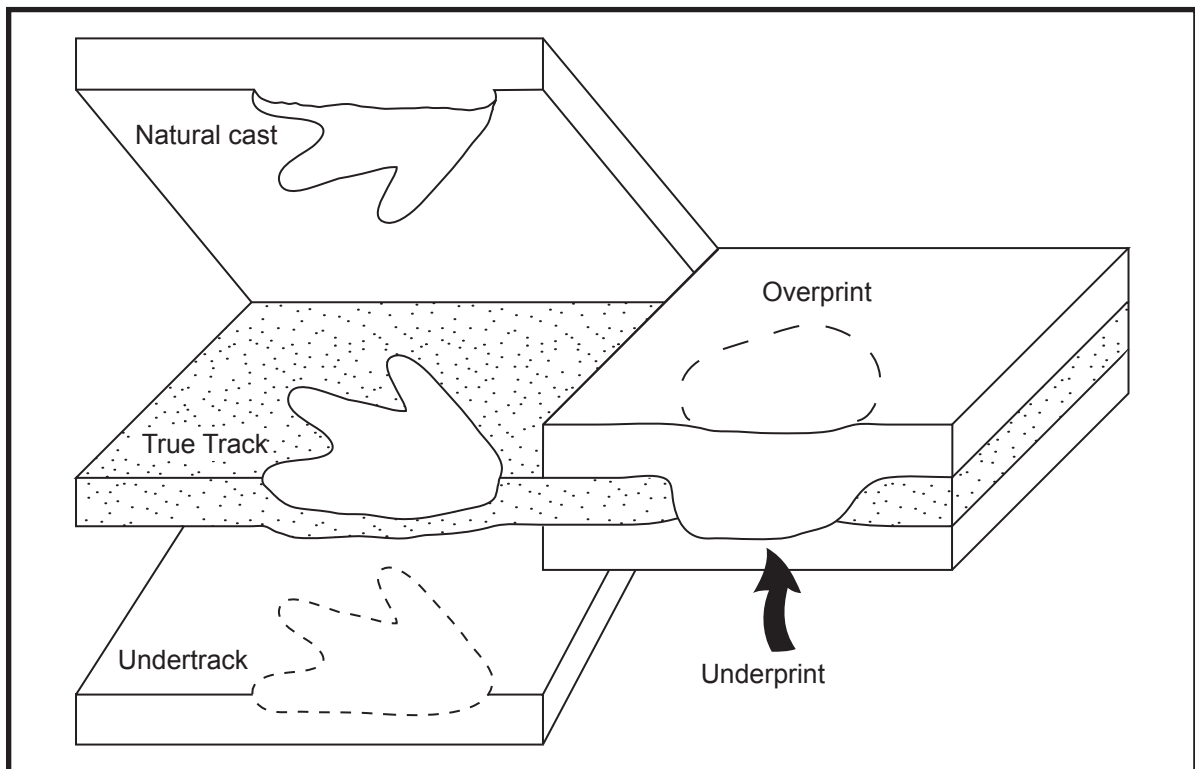
### 2.2.1 General terms

#### Displacement rim

Sediment rim that could surround the footprint, is always higher than the tracked surface. It is produced when an animal walk on a soft or plastic ground that displaces under the pressure of the foot (Fig. 2.1).

#### Footprint (track, print)

“The impression, partial or complete, of the autopodium of a tetrapod in the substrate” (Leonardi, 1987). Here it is intended as concave epirelief leaved on the top of a surface (Fig. 2.2). The term is used in a generic sense, without differentiating the nature of the track (e.g. underprint, true track, ecc..).



**Fig. 2.2** – Schematic drawing of preservation and nomenclature of tracks. (Redrawn and modified from Lockley, 1991b).

#### Ichnofauna

“A fauna whose composition is indicated (wholly or largely) by the traces of the activity of its components” (Leonardi, 1987).

**Ichnocoenosis (ichnocoenose)**

“An assemblage of fossil traces representing the activity of an association of leaving organisms” (Leonardi, 1987). To be used properly it has to refer only to the ichnological association from the same level.

**Megatracksite**

“A regionally extensive single surface, or very thin package of beds, that is track-bearing or track-rich over a large area, on the order of hundreds to thousands of square kilometres” (Lockley 1991b, 1997a, b).

An example of megatracksites is the Mid-Late Jurassic “Moab Megatracksite” which extends for about 1000 km<sup>2</sup> (Lockley 1991b).

**Morphotype**

A group of tracks which presents morphological affinities. It does not necessarily include tracks left by the same tracemaker.

**Overprint (overtrack)**

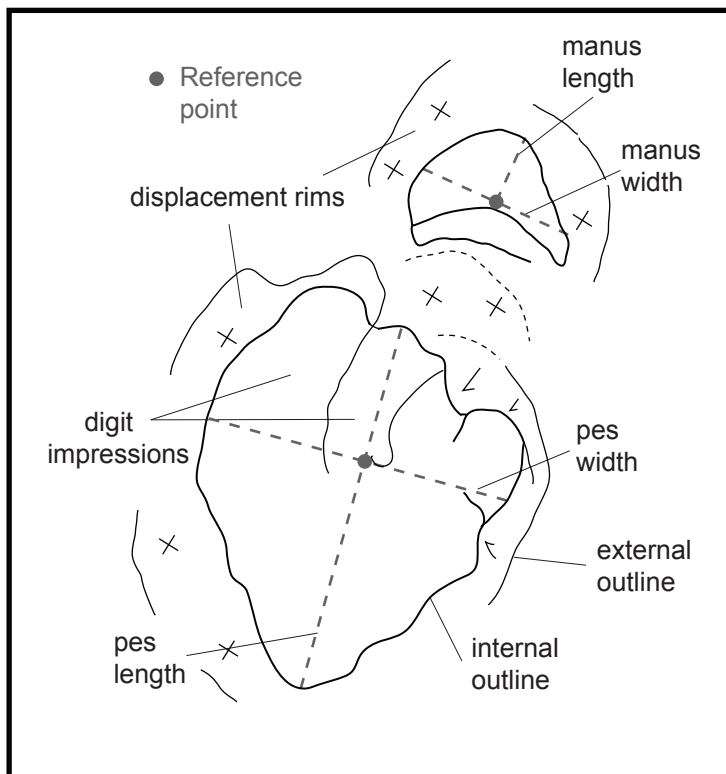
Depression that mirrors the presence of a footprint in the underlying level (Fig. 2.2). It forms in the sediment infilling of the true tracks. Usually very vague and faint. (Sarjeant 1988, Thulborn 1990).

**Ichnite (ichnofossils)**

Any kind of trace fossils, holding footprints, trackways, nests, hollows, burrows, etc.

**Footprint outline**

The **external** outline of the track is marked by the displacement rims or, if absent, by the upper limit of the print walls. The **internal** outline defines the actual limits of the true tracks (Figs. 2.3, 2.4). The definition of both the outlines is closely related to the preservation of the track.



**Fig. 2.3** – Schematic sauropod manus-pes couple explaining the parameter measured.

**Track preservation**

It refers to the detail that can be observed on the footprints. It is described qualitatively by adjectives, from very poor, when only a rough outline occurs, to excellent, when all the morphological characteristics (e.g. claw marks, pad impressions, etc...) are evident.

**Trackway**

A series of at least three successive footprints left by the same animal on the move (Fig. 2.5). Two consecutive footprints are not usually considered a trackway, but allow to extrapolate the direction of the trackmaker (Leonardi, 1987).

**Trackmaker (tracemaker)**

“The animal that produced the trackways by means of active contact with the substrate” (Leonardi, 1987).

**True track (actual track)**

The track emplaced on the actual tracked surface (Lockley 1991b). The term is used here sensu Lockley and Hunt (1995) and Lockley and Meyer (2000) as a clear track that is well-preserved, visually clear and not deformed by overprinting (Fig. 2.2).

**Underprints**

True tracks leaved on a level under the exposed surface (Fig. 2.2). These are formed when the substrate is firm enough to allow the foot to penetrate and leave a trace. If the substrate is split open at successively deeper layers the footprint will be found to be less and less complete (Thulborn, 1990).

**Undertrack (transmitted prints, ghost prints)**

It forms when the foot does not penetrate in a laminate and plastic substrate but compresses the deeper levels (Fig. 2.2). The impact of the foot is transmitted through a succession of sediment layers to form a stack of casts and moulds (Thulborn, 1990).

**2.2.2 Track parameters****Track length and width**

Width and length are measured on the inner outline and should correspond to the actual sizes of the foot. Measurements were taken in different ways for quadrupedal or tridactyl bipedal tracks.

*Quadrupedal*: the pes length (Pl) is measured along the footprint axis; the width (Pw) is roughly measured perpendicular to the length, in the wider point of the track. Manus length (Ml) is taken from the anterior to the posterior outline midpoint; the width (Mw) is measured perpendicular to the length on the larger point. Usually the width is more strictly connected with the actual manus dimensions because it is less deformed by the overlapping of the pes (Fig. 2.5B).

*Bipedal*: the length (Fl) is measured from the most anterior point of digit III to the rear of the footprint, more or less along the axis of the track. It can include the “heel” or the metapodium impression. In this last case, when possible, the length without the metapodium has also been measured, to make the sizes of the track comparable also with non-elongated footprints too. The width (Fw) is measured between the tips of the digits II and IV (Fig. 2.5A).

**Index of track size**

This parameter, introduced by Thulborn (1990) is based on the length and width of both pes and

manus, and is expressed in the same metric unit.

$$IS = (\text{length} \times \text{width})^{0.5}$$

It can be calculated both for pes (IPS) and manus (IMS) using the proper measurements.

### Heteropody

This parameter is valid only for quadrupedal tracks. It is defined by difference in area between manus and pes. It is usually given as a pes/manus-ratio. In this work it is not calculated but only estimated.

### Digital axis

This parameter is considered for bipedal tracks. It is the axis that separates the digits in two symmetrical halves (Fig. 2.4). Generally it passes through the digit tip, but if the digit is bended it could also follow a different path.

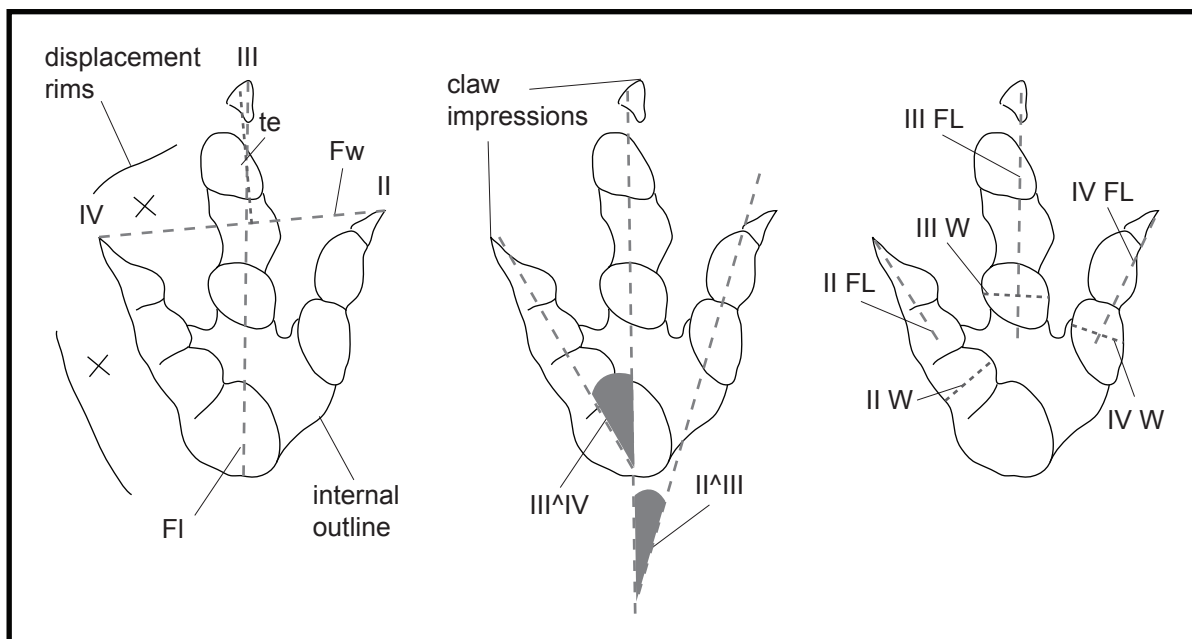
### Digits width and lengths

Also these parameters are considered for bipedal tracks only.

*Digit width* has been measured for all the digits, but because of the differential preservation grade and of the morphology of the footprints it has been difficult to maintain a constant technique for measuring. Generally it was measured on the inner outline at about the half of the digit free length, and perpendicular to the digital axis.

*Free digit length* (Leonardi, 1987): this is the measurement of the segments that joins the extremity of the digit to the midpoint of adjacent hypices. For digits II and IV, lacking adjacent digits, the intersection of the digital axis with the perpendicular junction to the hypex has been considered (Fig. 2.4).

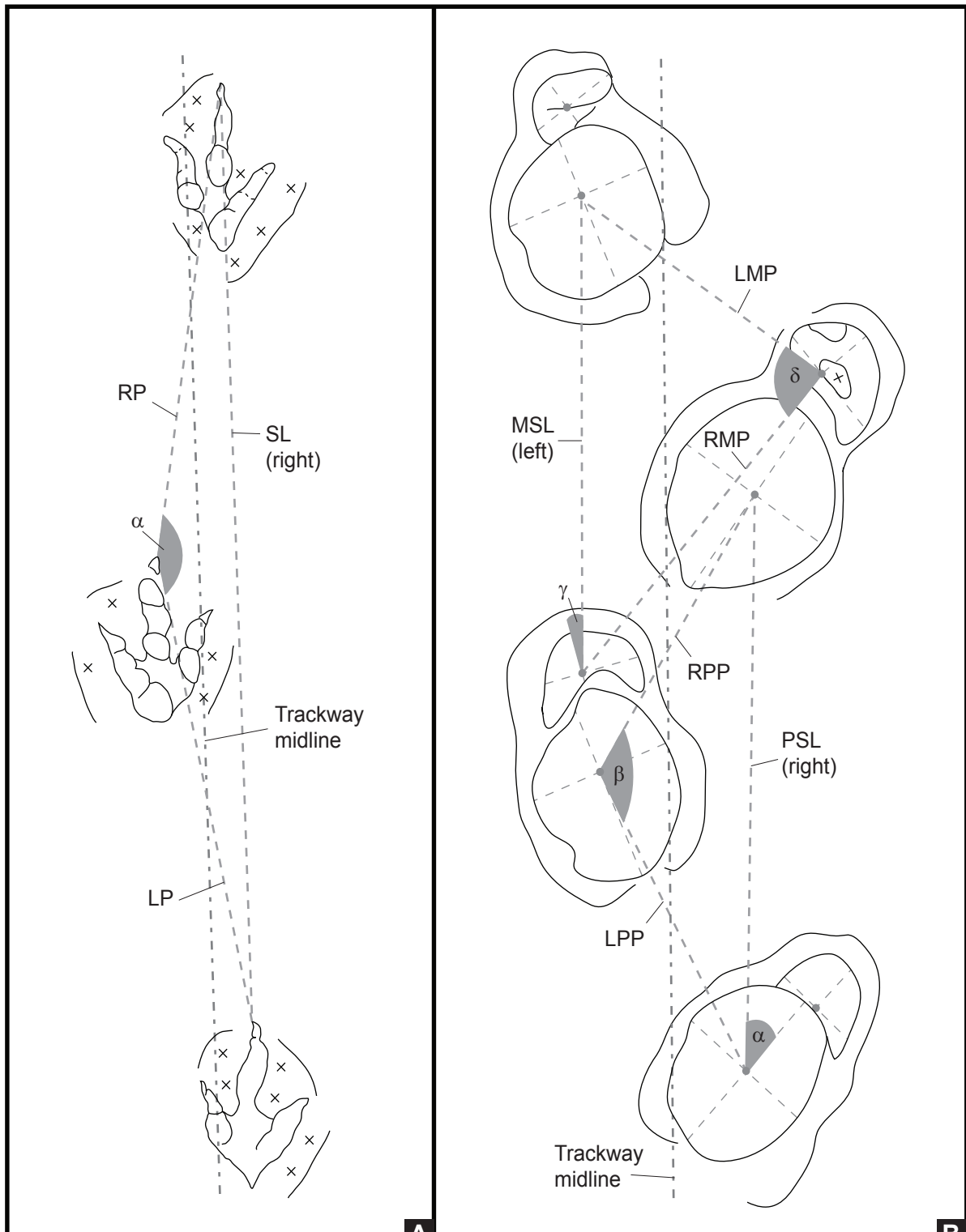
*Length of the phalangeal portion* (Leonardi, 1987): this length measures, along the digital axis, the segment that joins the extremity of the digit with the corresponding mid-point of the metapodial-phalangeal pad (Fig. 2.4). This parameter has been measured only for those tracks which have sufficient preservation, where the phalangeal pad impressions are maintained.



**Fig. 2.4** – Schematic tridactyl footprint explaining the parameter measured; *FL*: Foot Length; *Fw*: Foot Width; *te*: Toe Extension (Weems, 1992);  $II^{\wedge}III$ : interdigital divarication angle between digits II and III;  $III^{\wedge}IV$ : interdigital divarication angle between digits III and IV; *II FL*: digit II Free Length; *II W*: digit II Width; *III FL*: digit III Free Length; *III W*: digit III Width; *IV FL*: digit IV Free Length; *IV W*: digit IV Width.

### Interdigital divarication angles

This measures the angle between digital axes (Thulborn, 1990). The *total divarication angle* is defined as the sum of the interdigital angles between digits II and III, and III and IV (Fig. 2.4).



**Fig. 2.5** – Schematic trackways explaining the parameter measured. A: tridactyl trackway; LP: Left Pace length; RP: Right Pace length; SL: Stride Length;  $\alpha$ : Pace Angle; B: sauropod trackway. LPP: Left Pes Pace length; RPP: Right Pes Pace length; PSL: Pes Stride Length;  $\alpha$ : Pes rotation;  $\beta$ : Pes pace angle; RMP: Right Manus Pace length; LMP: Left Manus Pace length; MSL: Manus Stride Length;  $\gamma$ : Manus rotation;  $\delta$ : Manus pace angle.

### Digitigrades

Common position of the feet during motion for most biped dinosaurs, with the digits spread out flat on the ground and the metapodium that has no or partial contact with the ground (Thulborn, 1990). As results, often footprints often carry the impression of digits and of the most distal part of the metapodium.

### Plantigrade

Position of dinosaurs' feet during the motion where the metapodium entirely touches the substrate, leaving more elongated tracks. (Thulborn 1990)

## 2.2.3 Trackway parameters

### Stride length

This is the distance covered by an animal during one complete cycle of limb movements. (Thulborn, 1990). It is measured as the distance between the reference points of two consecutive footprints left by the same foot (e.g. left-to-left pes)(Fig. 2.5).

### Pace length

This is defined as the distance between reference points in two successive tracks (e.g. left-to-right)(Fig. 2.5). In very narrow trackways it corresponds rightly to the half of the stride length (Thulborn 1990).

This definition corresponds to the “oblique pace” of Leonardi (1987).

### Pace angulation

It corresponds to the angle between two consecutive paces, and gives an approximation of the gauge of the trackway. It is measured directly from the trackway (Fig. 2.5) and not with the cosines law from pace and stride lengths as illustrated in Thulborn (1990).

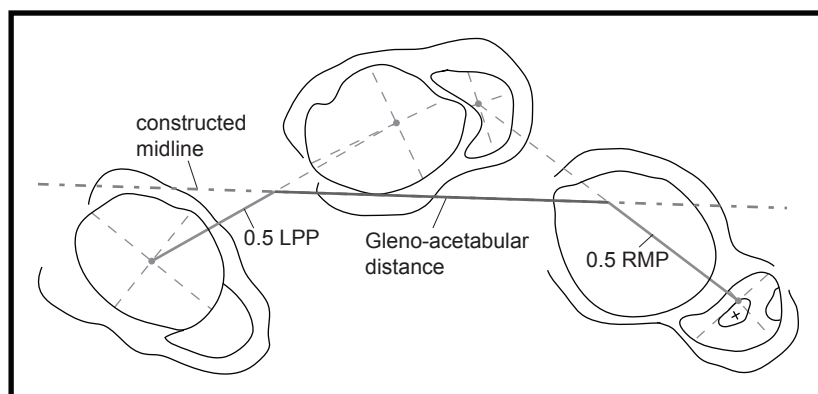
### Footprint rotation

This is the angle between the principal axis of the footprint and the trackway midline (Fig. 2.5). When the footprint is rotated outward it shows a *positive* rotation while when rotated inward the rotation is *negative* (Demathieu, 1970; Leonardi, 1987; Lockley, 1991b). However, certain authors (Haubold, 1971; Thulborn, 1990) consider it in the opposite sense.

In this work the rotation is always expressed as outward or inward and never as positive or negative, to avoid misinterpretation of the terminology.

### Glenoacetabular distance

This parameter can be measured only from sauropod footprints, and it is an indication of the body size. It is measured from the midpoint of the line connecting two consecutive pes tracks and the midpoint of the line connecting the next two manus tracks (Fig. 2.6), and, from an



**Fig. 2.6** – Schematic sauropod trackway illustrating how the gleno-acetabular distance is measured. The midline is constructed intercepting the midpoint of the pace of two subsequent pes (0.5 LPP) and manus tracks (0.5 RMP). The distance between the two midpoints, measured along the constructed midline, is the gleno-acetabular distance

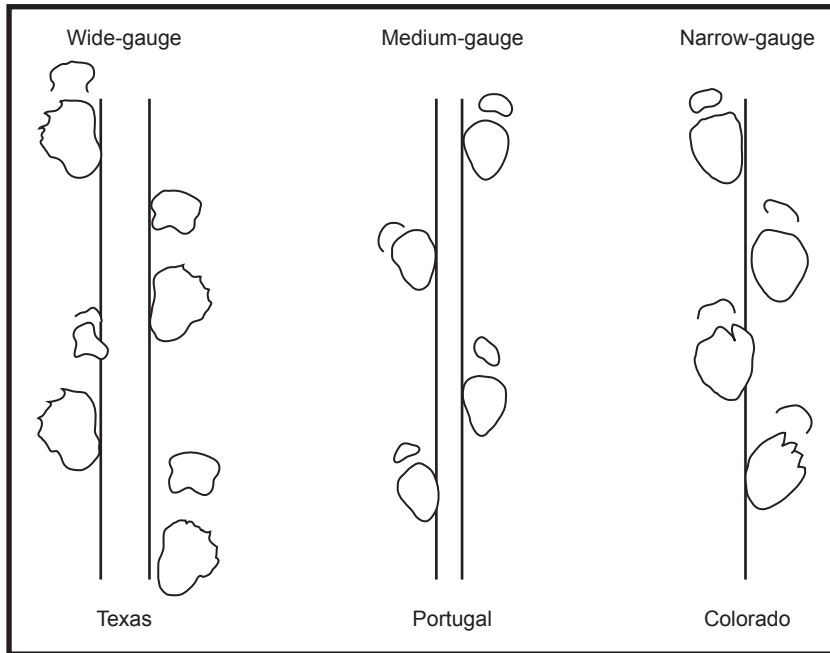


anatomical point of view, it corresponds to the distance between the centre of the shoulder joint and the centre of the hip joints.

### Trackway gauge

Following the definition of Farlow (1992) a sauropod trackway can be defined as *narrow-gauge* when “close or even intersecting the trackway midline” and *wide-gauge* when “well away from the trackway midline”. Meyer et al. (1994) introduces a middle-gauge definition, for those footprints falling in between the groups above (Fig. 2.7).

However this parameter is difficult to identify clearly on trackways without a quantitative approach. To solve this problem Romano et al. (2007) introduces the Trackway Ratio (see below for definition).



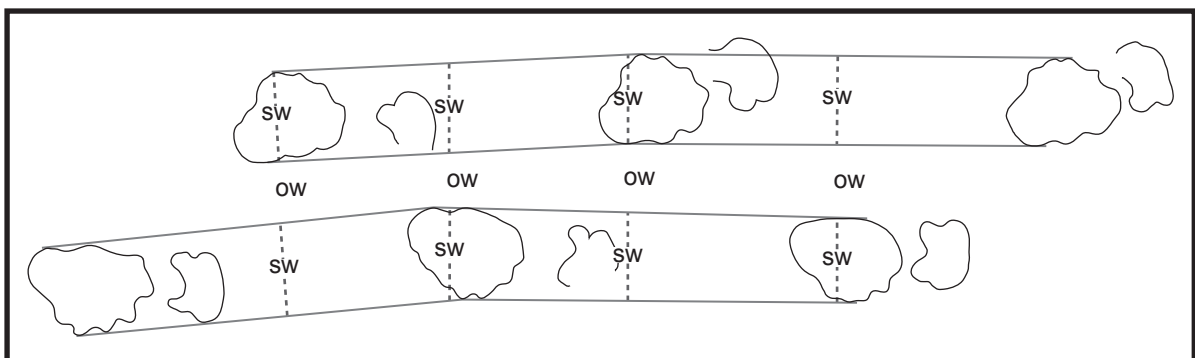
**Fig. 2.7** – Examples of “wide-”, “medium-”, and “narrow-” trackway gauge (Redrawn and modified from Meyer et al., 1994).

### Trackway ratio

This parameter, introduced by Romano et al. (2007), aims to quantify the gauge of sauropods trackways (Fig. 2.8).

$$TR = (\textit{side width} / \textit{overall width}) \times 100$$

It can be calculated both for pes (PTR) and manus tracks (MTR).



**Fig. 2.8** – Example of how Pes Trackway Ratio (PTR) is determined based on *Brontopodus birdi* trackway; *sw* = side width of pes tracks (measured transversely; left or right track, or mean of both); *ow* = overall width of trackway (measured between the outer margins of pes tracks of the left and right side) (Redrawn and modified from Romano et al., 2007, fig. 3A).

In this work both TR have been measured for the sauropods trackways giving for the first time the MTR for *B. taghbaloutensis*.

## 2.3 EVALUATION OF LOCOMOTION SPEED

Estimating the locomotion speed of dinosaurs is one of the most interesting topics based on dinosaur footprints. Thus, many are the works exploring the relation between dinosaur tracks and speed, looking for the best equation to describe it (e.g. Alexander 1976, Russell and Béland, 1976; Coombs, 1978; Thulborn, 1982, 1989, 1990; Thulborn and Wade, 1984, 1989; Weems, 2006).

### 2.3.1 Estimation of hip height

One of the most important parameters in determining the speed is the hip height. Unfortunately, this value is one of the most difficult to calculate because it depends on the definition of the hip height (Rainforth and Manzella, 2007). The height of the hip from the ground ( $h$  of Alexander, 1976) has been considered by different authors in different ways, indeed (Alexander, 1976; Thulborn, 1982; Thulborn and Wade, 1984; Henderson, 2003). However, Thulborn (1990), affirms that “these various dimensions are assumed to be roughly equivalent; they will greatly differ only in the largest dinosaurs”. It can be measured directly from the osteological remains, summing the lengths of the major hind limb bones.

While Alexander (1976) proposed a generic equation for the estimation of hip height ( $h = 4Pl$ ) Thulborn (1990) suggested many morphometrical ratios, derived from the cursory analysis of osteometric data, to predict the hip height from tridactyl tracks recognizing that different groups of dinosaurs have different ratios. No ratios are given for quadrupedal dinosaurs, even if a 5.9FL value, as for large ornithopods, is suggested.

Moreover, Thulborn (1990) introduced some allometric equations based on the assumption that the metatarsal III is equivalent to the phalangeal portion of digit III.

These last ratios have not been considered in this work because it was impossible to measure precisely the phalangeal portion of the digit III for the most of the footprints examined.

In this work we calculated the hip height using the following equations:

For sauropods:

- (1)  $h = 4Pl$  (Alexander, 1976)
- (2)  $h = 5.9Pl$  (Thulborn, 1989, 1990)

Determining the height of the shoulder of sauropods is more complex and no studies have been carried out so far. Thus, in this work, it has been calculated generically as  $h = 4Ml$  using the Alexander relation. Even if far from a demonstration, the speed calculated from manus and pes of the same trackway resulted comparable using the Alexander's relation (difference < 0.1 km/h).

For small tridactyls ( $Fl < 25$  cm):

- (3)  $h = 4.5Fl$  (Thulborn, 1989, 1990)

For large tridactyls ( $Fl > 25$  cm):

$$(4) \quad h = 4.9Fl \quad (\text{Thulborn, 1989, 1990})$$

### 2.3.2 Speed Equations

A descriptive approach to the speed of dinosaurs was introduced by Alexander (1976) Alexander et al. (1977) with the evaluation of the gait, which corresponds to the ratio between the stride length and the estimated hip height ( $S/h$ ). Thulborn (1990) deepened the concept discriminating three groups:

Walk  $S/h < 2.0$   
Trot  $2.0 < S/h < 2.9$   
Run  $S/h > 2.9$

Furthermore, Alexander (1976) derived an equation to estimate dinosaur speeds:

$$(5) \quad S/h \approx 2.3(v^2/gh)^{0.3}$$

$$(6) \quad v \approx 0.25g^{0.5}S^{1.67}h^{-1.17} \quad \text{for } S/h < 2.0$$

Where  $S$  = stride length;  $h$  = hip height;  $v$  = velocity;  $g$  = standard gravity.

Alexander (1976) and Alexander et al. (1977) suggested that this equation describes better the speed of a walking animal ( $S/h < 2.0$ ).

Thulborn and Wade (1984), starting from the formulas stated in Alexander et al. (1977) derived their equation for the trotting (Eq. 8) and running (Eq.7) dinosaurs:

$$(7) \quad v \approx [gh(S/1.8h)^{2.56}]^{0.5} \quad \text{for } S/h > 2.9$$

$$(8) \quad v \approx (Eq.6 + Eq.7)/2 \quad \text{for } 2.0 < S/h < 2.9$$

In this work equations 6, 7 and 8 are used for walking, running, and trotting dinosaurs, respectively. The Stride considered is the average of the trackway, because no evident differences between left and right paces have been recorded.

## 2.4 PRINCIPAL COMPONENT ANALYSIS

Principal Component Analysis (PCA) is a vector space procedure for finding hypothetical variables that accounts for as much of the variance as possible in a multivariate dataset (Hotelling, 1933; Jolliffe, 1986; Hammer and Harper, 2005). It is often used to reduce multidimensional datasets to lower dimensions for analysis, in which the components are orthogonal, linear combination of the original variables. The axes of maximal variance (principal components) can be interpreted and possibly identified.

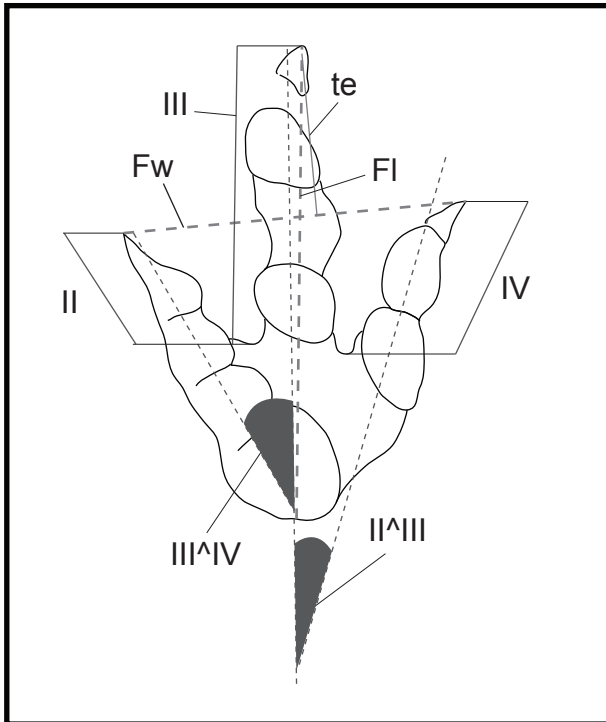
Each principal component (PC) is expressed by a vector (*eigenvector*) and associated to an *eigenvalue* (= magnitude of eigenvector) that indicates the relative proportion of overall variance explained by that component. Usually eigenvalues are converted into the percentage of their sum for each PC. The PC1 (main PC) is the component that bears the higher eigenvalue.

Usually most of the variation is expressed by the first two or three PC that can be also interpreted. It is uncommon, if not rare, that more than three PC could be interpreted, so the rest is often

considered as “noise” (Hammer and Harper, 2005).

Generally, in morphometrics, the variables are normalized before the PCA. The most common methods are the log-transformation and the normalization with respect to the variance. This last procedure is useful to reduce the dominance of variable with high variance and also to compare variables with different units (e.g. meters and degrees). PCA without the variance normalization is usually called *PCA on the variance-covariance matrix*, while PCA with variance standardization is called *PCA on the correlation matrix* (Hammer and Harper, 2005).

In this work the PCA has been carried out using PAST 1.86b<sup>®</sup> (Hammer et al., 2001), considering as variables the foot length (Fl) and width (Fw), the digits II, III and IV free length (II, III, and IV,



respectively), the toe extension (te) as defined by Weems (1992), and the interdigital angles II-III ( $II^III$ ) and III-IV ( $III^IV$ ) (Fig. 2.9).

The dataset was log-transformed. PCA was carried out using both variance-covariance matrices: the first one was used when the data considered were only linear measurements (centimetres); the second one when also the divarication (angular) values were taken into account.

**Fig. 2.9** – Schematic drawing of a tridactyl footprint showing the parameter considered for the PCA; *Fl*: Foot Length; *Fw*: Foot Width; *II*, *III*, and *IV*: Free Length of digits II, III and IV, respectively; *te*: Toe Extension (Weems, 1992);  $II^III$ : interdigital angle between digits II and III;  $III^IV$ : interdigital angle between digits III and IV.

## 2.5 LANDMARK ANALYSIS

Landmark analysis (Bookstein, 1991; Zelditch et al., 2004) is a branch of the Geometric Morphometry that allows the study of the shape outline of a given object by the comparison of homologous points.

A **landmark** can be defined as a point on each object that can be correlated across all the objects of the dataset. A landmark should be a homologous anatomical point that does not alter their topological positions relative to other landmarks, provides adequate coverage of the morphology, can be found repeatedly and reliably, and lie within the same plane (Zelditch et al., 2004). That ideally.

Bookstein (1991) presents a first classification of landmark:

*type I*: landmarks that occur where tissues or bones meet;

*type II*: landmark are defined by local property such as maximal curvature;

*type III*: landmarks occur at extremal points, or a constructed points such as centroids.

Dryden and Mardia (1998) defined a new classification of landmarks:

*Anatomical landmarks*: well defined points that are considered homologous from one species to the next;

*Mathematical landmarks*: defined on the basis of geometric properties such as maximum curvature or external points;

*Pseudo-landmarks*: constructed points between mathematical or anatomical landmarks.

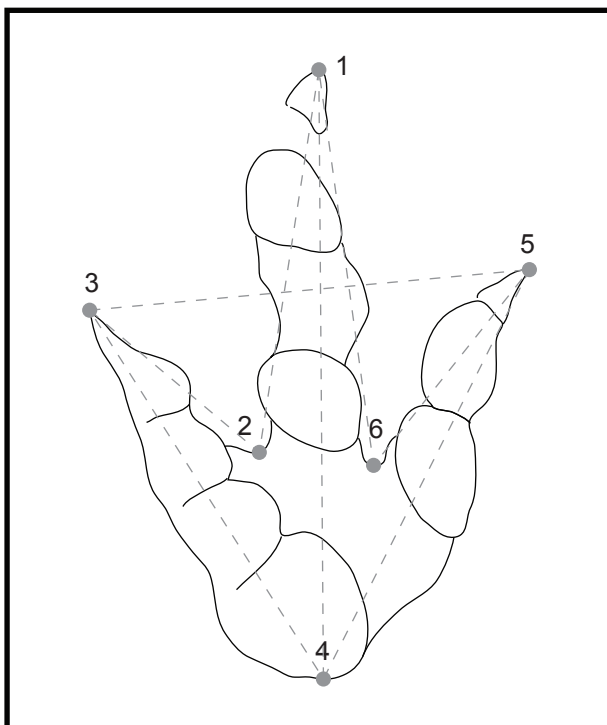
To align the landmarks the *Procrustes fitting* methods are used here; this allows to scale, rotate and translate the set of points before the following analyses (Dryden and Mardia, 1998, Hammer and Harper, 2005).

The visualisation of the deformation from one set of landmarks to another is called Thin-Plate spline (TPS) deformation (Thomson, 1917; Bookstein, 1991; Dryden and Mardia, 1998). It can be imagined as the deformation of a grid linked to the object landmarks. The transition from one shape to another is deforming the grid. The TPS produces figures that greatly aid in the interpretation of the shape changes, by displacing independently in x and y direction the landmarks positions. TPS is also the base for the following analysis on shape variations.

The decomposition of the deformation into components is known as *Principal* and *Partial warps* (Bookstein, 1991). Partial Warps (PW) especially provides the actual decomposed deformation to a given target, and can be considered as a mapping that represents directly displacements on the two main directions of the plane (it is a bivariate function) from any given point from the reference to the target. However, it must be considered that they are purely geometrical constructions not related to biological evidences.

The variation in distance between two shapes can be figured as a bending of the TPS and can be measured with respect to the “bending energy” involved in the transformation (Dryden and Mardia, 1998). The PCA of the bending energy can be regarded as the PCA of the TPS deformations from the mean to each individual shape. Each deformation can so be expressed as a set of PC, which are themselves deformations known as *Relative Warps* (RW) (Bookstein, 1991; Rohlf, 1993).

RW analysis, with respect to the bending energy, tends to emphasize the large scale deformations. To be noticed that RW are linear combinations of PW, thus there is no gain of information relative or partial scores to further multivariate analyses.



**Fig. 2.10** – Schematic drawing of a tridactyl footprint illustrating the landmarks placed; 1: tip of digit III; 2: hypex between digits III and IV; 3: tip of digit IV; 4: “heel” of the track, considered as the maximum curvature of the rear part; 5: tip of digit II; 6: hypex between digits II and III. The dashed line represents the links among landmarks used during the analysis.

In this work, landmark analysis has been applied to tridactyl tracks. Initially, as suggested in Rasskin-Gutman et al. (1997), the only paper on landmarks applied to tridactyl tracks, to compare the largest number of footprints possible, 6 landmarks have been chosen (Fig. 2.10): the base of the “heel”, considered as the maximum curvature of the rear part of the footprint, the tips of the three digits, and the two interdigital hypices. The landmarks used can then be classified as type III (Bookstein, 1991) or as mathematical landmarks (Dryden and Mardia, 1998).

The landmarks coordinates and analysis were carried out using the tps software (Rohlf 2008), particularly tpsUtil<sup>®</sup> 1.41 for data input, tpsDig<sup>®</sup> 1.40 for placing the landmarks, tpsRelw<sup>®</sup> 1.41 to visualize consensus, PW and RW, and tpsRegr<sup>®</sup> 1.31 for multivariate regression.

The landmarks were placed on drawings of the footprints and not on photographs mainly because photos were taken without checking the perfect perpendicularity between the surface and the camera. Moreover, for shallow

footprints, the illumination factor could notably influence the interpretation of the morphology and therefore the landmark positioning. At last, literature almost always provides drawings; using drawings for comparison is in some way aligning the two datasets, introducing, more or less, the same errors.

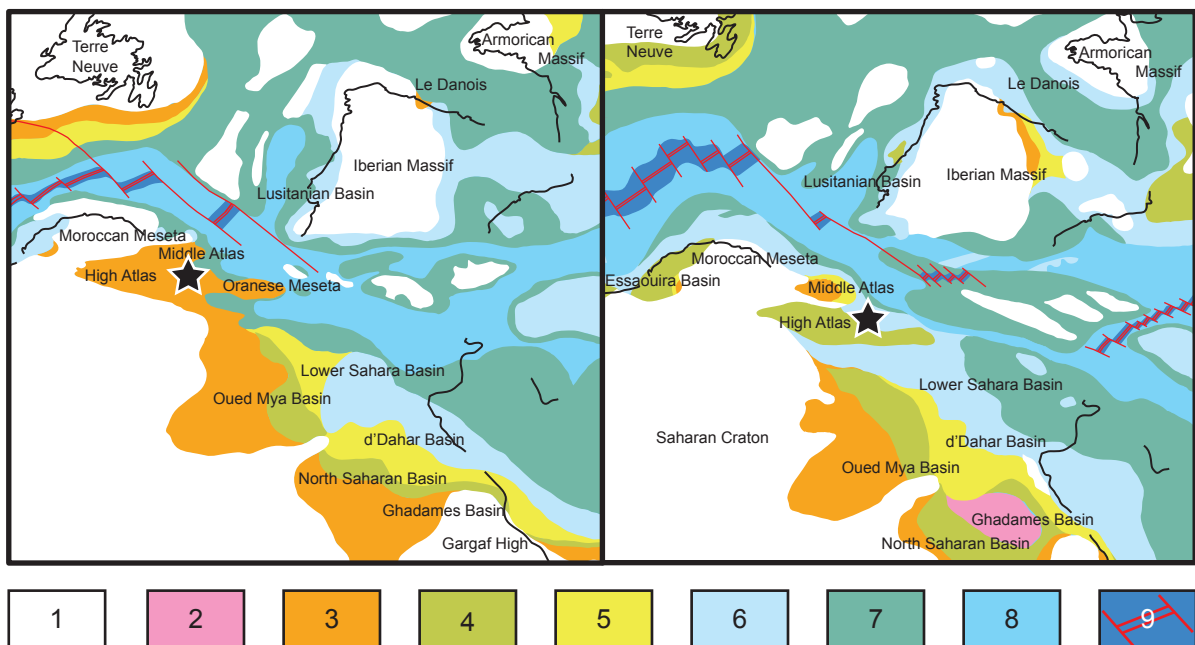
# 3 SEDIMENTOLOGY AND STRATIGRAPHY

## 3.1 PALEOGEOGRAPHICAL SETTING

During the early Middle Jurassic North Africa is characterized by a general tectonic and sedimentary instability (Elmi, 1996; Darcourt et al., 2000). The paleogeography is extremely articulated: deep basins and troughs, filled by marly sediments often interrupted by gravity flows, occur in the Middle- and High-Atlas; whereas carbonate platforms and sabkhas occur in the Northern Sahara and Moroccan Meseta. During the end of the Middle Jurassic (late Bajocian to Oxfordian) basins became less divided and underwent a more uniform marly sedimentation which preceded the edification of carbonate platforms or shallow-water environments.

In the Atlasic domain thick marls and turbidites registered a deepening peak during the Bajocian, while during the Callovian, fluvio-deltaic clays, silts and sandstones were widespread (Fig. 3.1A).

During Late Jurassic the “final differentiation stage” of Maghreb was reached (Elmi, 1996). The extension along a NE-ESE and SW-WSW trend, linked to the general divergence between Africa and Iberia, guided the settlements of deltaic complexes in the Rif basin and foreland (Cattaneo, 1991). Deltaic and coastal marine environments extended into the Atlasic and Saharan domains, with a constant and outstanding terrigenous input (Fig. 3.1B). Evaporitic intercalations are present in the various facies of the Sahara domain, but lithology and fossil record suggest a more humid climate than during the Early – Middle Jurassic period (Lefranc and Guiraud, 1990; Busson and Cornée, 1991).



**Fig. 3.1** – Paleogeographical map of the western Tethys; A: Middle Callovian; B: Early Kimmeridgian. Redrawn and simplified from Dercourt et al. (2000). 1: Exposed land; Hypersaline; 3: Eolian, fluvial, lacustrine, fluvio-lacustrine; 4: Shallow-water environments with fluctuating salinities; 5: Coastal marine, shallow marine (terrigenous); 6: Shallow marine (carbonatic); 7: Deeper carbonates, (hemi)pelagic oozes; 8: Deep marine; 9: Deep oceanic basins.

## 3.2 GEOLOGICAL SETTING

During Middle Jurassic to early Late Cretaceous, in the Atlasic domain (central and eastern High-Atlas and Middle Atlas) the continental “*couches rouges*” deposited, whereas the western area of the High-Atlas maintained a coastal-marine deposition, connected with the opening of the central Atlantic.

The stratigraphy of the area has been studied since the discovery of the tracks ichnosite (Plateau et al., 1937; Roch, 1939; Termier, 1942). But it is since the 1980s that this red bed succession has begun to be studied in detail and divided into various formations (Jenny et al., 1981a, b; Jenny, 1985).

In the Iouaridène valley three formations were recognized and logged, which have been recently reviewed by Charrière et al. (2005).

### **Guettioua Formation**

This formation is mainly composed by red to dark red conglomeratic to arenaceous beds alternated to varicoloured pelites. Fluvial channelization locally observed suggested a deltaic flood plain environment (Charrière et al., 2005). It is worth noticing that a hundred meters from the base of the succession, in the synclinal of Tilougguit, some sauropod bones were found (Monbaron and Taquet, 1981; Monbaron 1983), later interpreted as belonging to a new taxon: *Atlasaurus imelakei* (Monbaron et al., 1999).

### **Iouaridène Formation**

This formation was introduced by Jenny et al. (1981a) to describe the upper part of the Grès de Guettioua sensu Roch (1939). It is to be noticed that the type section is located exactly on the study area (as the formation’s name suggests). It is a thick formation (around 1000 m according to Charrière et al., 2005), divided into two members. The lower member is composed by an alternation of pelites and consolidated silt/sandstones, often pedogenized and topped with mud-cracks and symmetric ripple-marks. On that surfaces the dinosaur tracks object of this work occur. The upper member is more clayey and dark, with some dolomitic intercalations that gave a *Classopollis* palynological association.

Charrière et al. (2005) examined the first 250 m of the lower member, finding a Middle Jurassic *Porochara hians* at the base of the formation and, 60 meters above the main trampled layer (level 3 in this work), an assemblage of ostracods, *Porochara kimmeridgiensis* and, above all, *Dictyoclavator ramalhoi*. This association, for the authors, is without doubt Kimmeridgian (Charrière et al., 2005).

The Iouaridène ichnosite lays on the margin of the homonymous anticline. This affects the exposure, and above all the attitudes of the footprint-bearing strata.

### **Jbel Sidal Formation**

This formation tops the Iouaridène Fm. and is also the last formation that can be surveyed in the Iouaridène valley, where its type section is located.

It consists of arenaceous bars and lenticular conglomeratic levels separated by pelitic intervals. Where the top of the formation is preserved, some dolomitic levels are present, and it is possible to see a gradual transition to Aptian marine sedimentation (Charrière et al., 2005).

## 3.3 FACIES DESCRIPTION AND INTERPRETATION

In this work, a detailed sedimentological analysis of the track-bearing inferior member of the Iouaridène formation is carried out, in order to better understand the environment where these



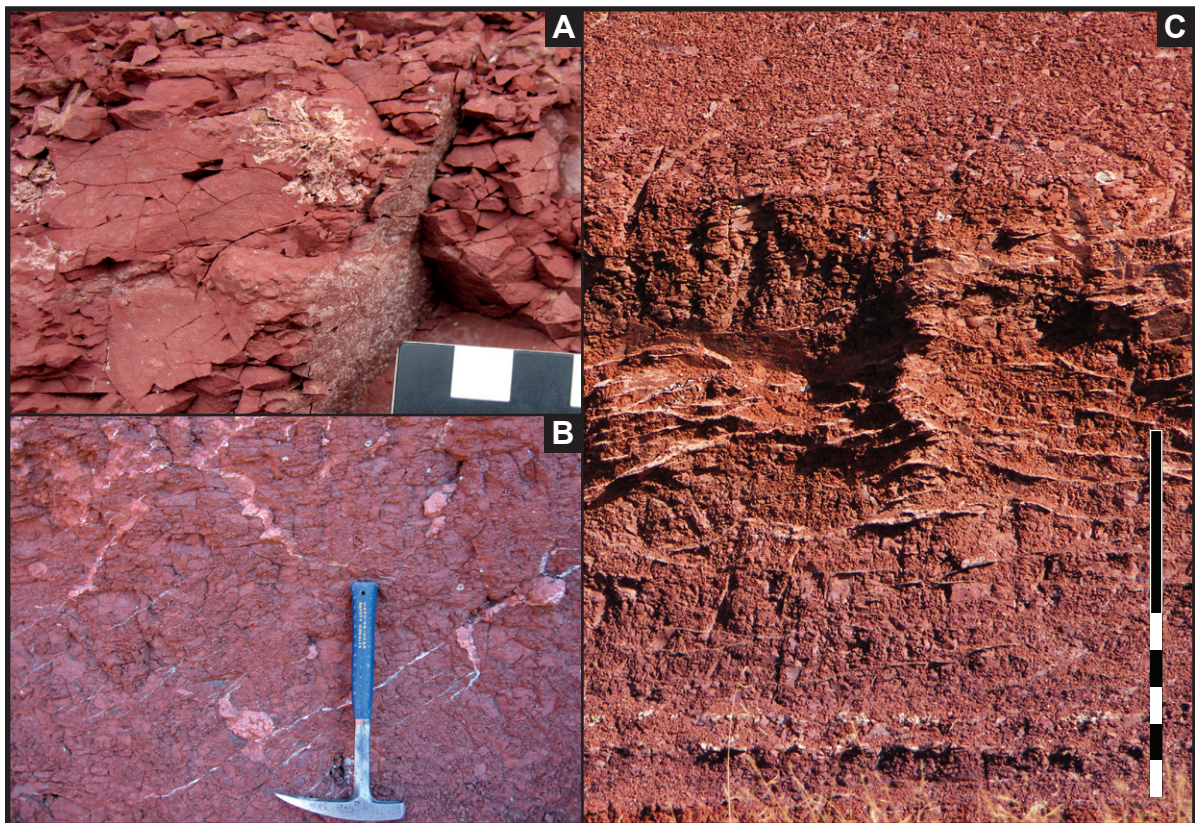
dinosaurs walked. Three facies associations have been distinguished and interpreted.

### 3.3.1 Facies association 1 – Floodplain mudstones

**Description:** most of the succession is represented by reddish (from brown to violet) siliciclastic mudstones (Fig. 3.2). These deposits are generally massive, but some vague planar bedding occurs locally. Evaporitic features occur all along the section. In the central part of the succession, evaporites are characterized by centimetric, radially developed, acicular crystals (Fig. 3.2A). In the upper part of the succession, close to the fluvial channels, evaporitic veins presenting concertina-like outlines (Fig. 3.2B), due to the compaction of mudstone (Massari et al., 1994), are observed, in places organized into sub-metric pseudoanticlinal structures (Fig. 3.2C). Except for evaporitic features, no other pedogenic features are generally observed.

**Interpretation:** the mudstones are interpreted to be accumulated on a low-gradient mudflat. The reddish-brown colour indicates that, after sedimentation, mudstones probably remained subaerially exposed, thus evolving under oxidizing conditions. The scarcely preserved lamination indicates that deposition occasionally occurred, under very low energy conditions. Reddish mudstones probably represent the very distal end members of river floods and were deposited as suspended load from waning flows in the lowest lying area of a distal dryland river system (Tunbridge, 1984; Aigner and Bachmann, 1989).

On the whole, the reddish mudstones were deposited as suspended load in a low-laying floodbasin, close to the transition between terrestrial and marine depositional environments, sporadically inundated, but commonly under subaerial conditions, as testified by mud cracks and pedogenic structures (pseudoanticline). Evaporitic structures are consistent with a prevalently arid climate.

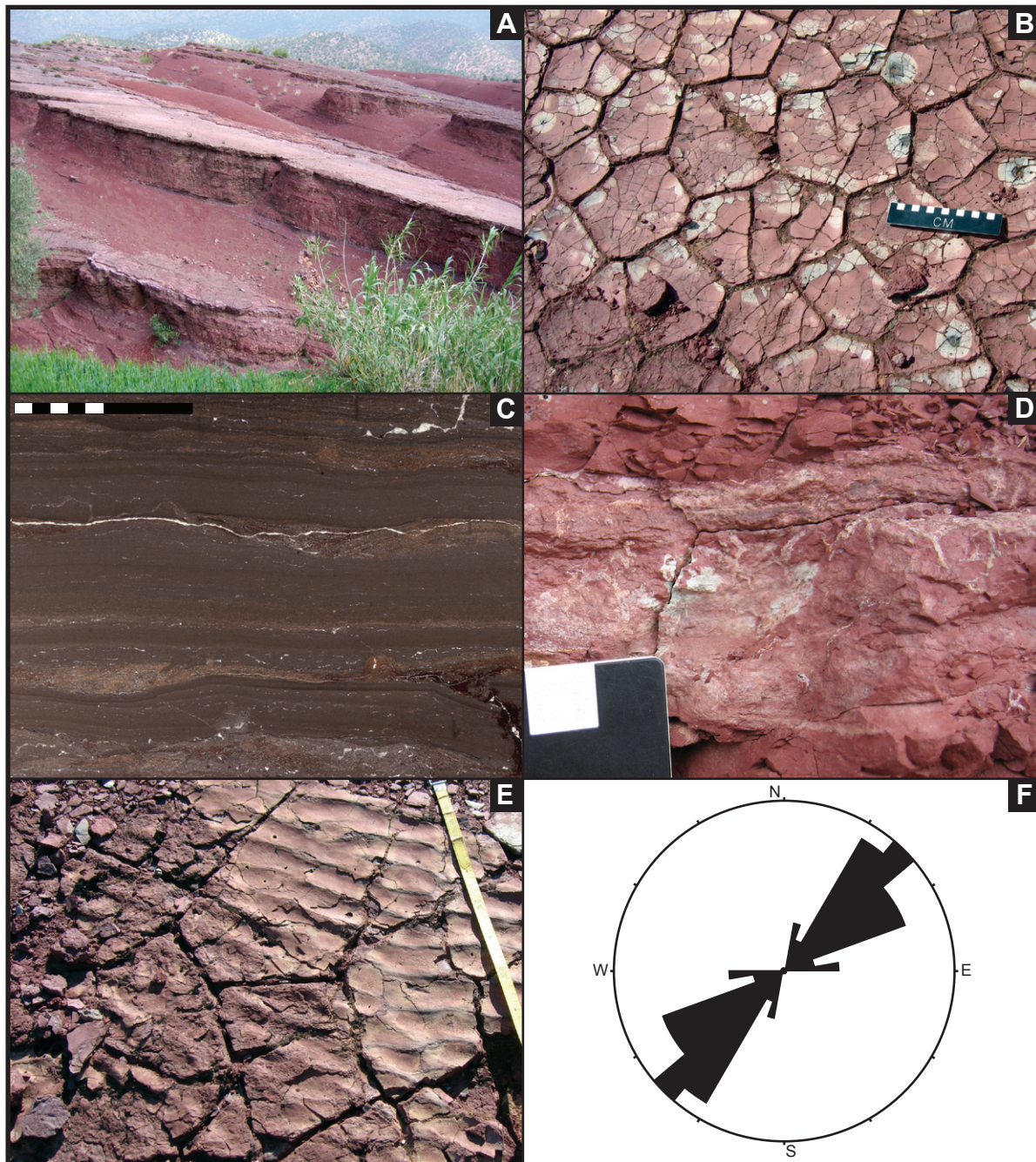


**Fig. 3.2** – A: evaporitic structure with radial growth. Scale 3 cm; B: evaporitic vein with concertina-like outlines due to mudstone compaction. Hammer for scale (33 cm) ; C: pseudoanticline structures sealed with evaporitic veins. Scale bar 50 cm.

### 3.3.2 Facies 2 – Carbonate-cemented levels

**Description:** mainly in the middle of the succession, centimetric to decimetric layers of highly consolidated, carbonate cemented, clays to very fine sandstones, are present, alternated to metric thickness of mudstones (Fig. 3.3A). The colour varies from gray-reddish to reddish, or sometimes ochre.

The finest, mostly clayey, sediments are almost always topped by spectacular mud cracks, with an average diameter of 10 cm (Fig. 3.3B). Small planar fenestrae, bird-eyes and algal lamination can be observed in thin-sections (Fig. 3.3C). Rare bioturbation occurs in these clayey to fine silty levels.

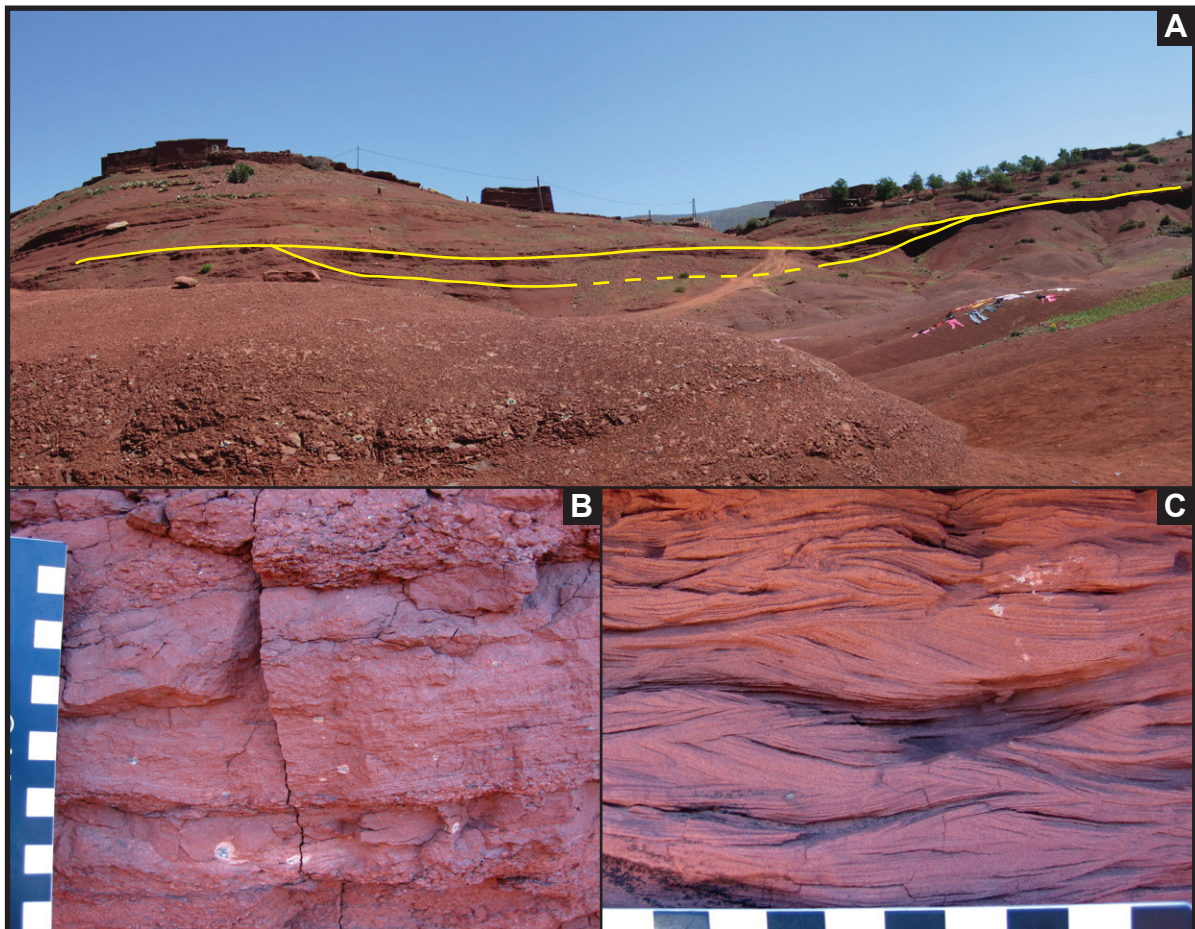


**Fig. 3.3** – A: Iouaridène Fm. outcrop at Ait Mimoun. The lighter levels are the most consolidated, the dark red layers are the mudstones. Note the cyclic alternation of mudstones and more consolidated and coarser levels. Each cycle measures about 2.5 m; B: mud cracks from a consolidated level. Scale 15 cm; C: thin-section of a consolidated bed. Fenestrae, planar-bedding and algal lamination can be noticed. Scale 1 cm; D: tiny root traces. Scale 2 cm; E: symmetric ripples topping a consolidated level. Scale 30 cm; F: rose diagram showing the directions measured on the crests of ripples. A NE predominant strike can be easily recognized.

The coarser, coarse silty to fine sandy, sediments generally show planar-bedding. These levels are often topped by symmetric ripples. These structures are generally small, with an average wave length of 28 mm, an average width of 24 mm, and an average height of 4 mm. The directions of the crests, measured on 42 ripples from different levels and different positions across the site, result generally orientated NE-SW (Figs. 3.3E, F). Small root traces occur sporadically (Fig. 3.3D) in these consolidated layers, but no other pedogenic features are present. Rare brackish water bivalves have been found on the bottom of the consolidated levels. Dinosaur footprints are present on the top of almost all the consolidated levels. The maximum depth of the tracks never exceeds 15 cm, also for those of very large sauropods. This testifies an early consolidation of the substrate that was firm enough to resist the load made by several tons-heavy dinosaurs. These highly coherent levels are cyclically alternated with floodplain mudstones (Facies association 1), topping cycles with an average thickness of 2.5 m.

**Interpretation:** The tabular consolidated levels, interrupting the normal fine clastic sedimentation, can indicate either small marine incursions or the presence of meteoric waters which allowed the precipitation of the carbonate cements by the mixing of marine and fresh waters (Bricker, 1971). Considering the sediment as a “beachrock” sensu Bricker (1971), that is, as the “sediment lithified in the intertidal plus sea spray zones, whether on high- or low-energy beaches, or even on broad tidal flats”, two hypotheses on the precipitation of the cement can be made: 1) simple chemo-physical precipitation due to evaporation and CO<sub>2</sub> loss; 2) precipitation from meteoric or marine waters when mixed with fresh waters.

The high frequency cyclicity recorded for this facies association is not sufficient to discriminate between the first and the second hypothesis, because both involve cyclic climatic or eustatic



**Fig. 3.4** – A: channel cross-section below the Aghri village. The yellow lines mark one of channel margins present in the area. Houses for scale; B: particular of normal graded bedsets with planar-bedding. Scale 14 cm; C: herring-bone cross-stratification occurring on the bars on the top of the section. Scale 10 cm.

variations. Mud cracks and the presence of footprints testify emersion phases of these beds; the small symmetric ripples give the evidence of shallow waters, but none of these data gives evidences for the origin of the inundations.

### **3.3.3 Facies association 3 – Fluvial channels**

**Description:** a channel-belt composed of 5 m thick and at least 100 m wide channels can be observed in the upper part of the section. Channels present an erosive base, generally cutting into the mudstones, or into the underlying channel. The infill of the channels is fining upwards, ranging from fine conglomerates (granules) to fine sandstones, and is arranged in decimetric bed-sets. Some very rare muddy intraclasts can reach centimetric size.

The beds are characterized by normal grading. Sandstones display planar lamination at the base to asymmetric, often climbing, ripples cross-bedding at the top.

The section is topped by metric medium to coarse sandstones, arranged into centimetric to decimetric beds and characterized by herringbone cross-bedding.

The small channel occurring at the base of the section is characterized by fine sandstones/siltstones and organized in laterally accreting bars.

**Interpretation:** the geometry of the channel-belt suggests a lateral migrating or switching system, with little accommodation space (Miall 1985). The prevalent fine sedimentation that characterizes the succession where the channels are encased suggests distal alluvial plain with reduced topographic gradients.

Normal grading and sedimentary structures (parallel- to ripple cross-bedding) is consistent with a decrease in the energy of transport within each bed-set.

Alternated horizontally stratified and climbing ripple cross-stratified sandstones may suggest oscillation between high-flow and low-flow conditions during a single depositional event (Hampton and Horton, 2007).

The herringbone cross-lamination highlights the presence of reversal current directions. The most probable explanation is a tidal influence along the channel, pointing out the extremely low gradient of the plain and the proximity to the coast (Massari and Neri, 1997).

## **3.4 STRATIGRAPHICAL LOGS AND CORRELATIONS**

During the field work detailed stratigraphical logs were measured (Figs. 3.5, 3.6) on the northern and southern margins of the site. The better outcrop conditions in this last part of the ichnosite allowed to log a long section and to individuate a larger amount of trampled levels in the northern part.

A correlation between these two sections was carried out (Fig. 3.7) using as marker levels the trampled surfaces and some more dark violet levels within the pelites, and above all the trample level 4, which has a typical whitish alteration colour easily recognizable all around the site.

It is evident that the two sections, located at around 4 km as the crow flies, can be perfectly correlated. The maximum discrepancies between homologous levels are less than one meter in thickness, and are localized in the area where the outcrops in the northern site are worst, that is, the discrepancies can be only due to less accurate measurements.

## **3.5 PALEOENVIRONMENTAL RECONSTRUCTION**

The depositional system investigated may be resumed as a low gradient area close to the coast line, characterized by an alluvial plain environment, cyclically interested by foodings.

On the whole, the red bed succession is characterized by continental fine-grained alluvial environment, with rare laterally migrating fluvial channels. The presence of fenestrae, and

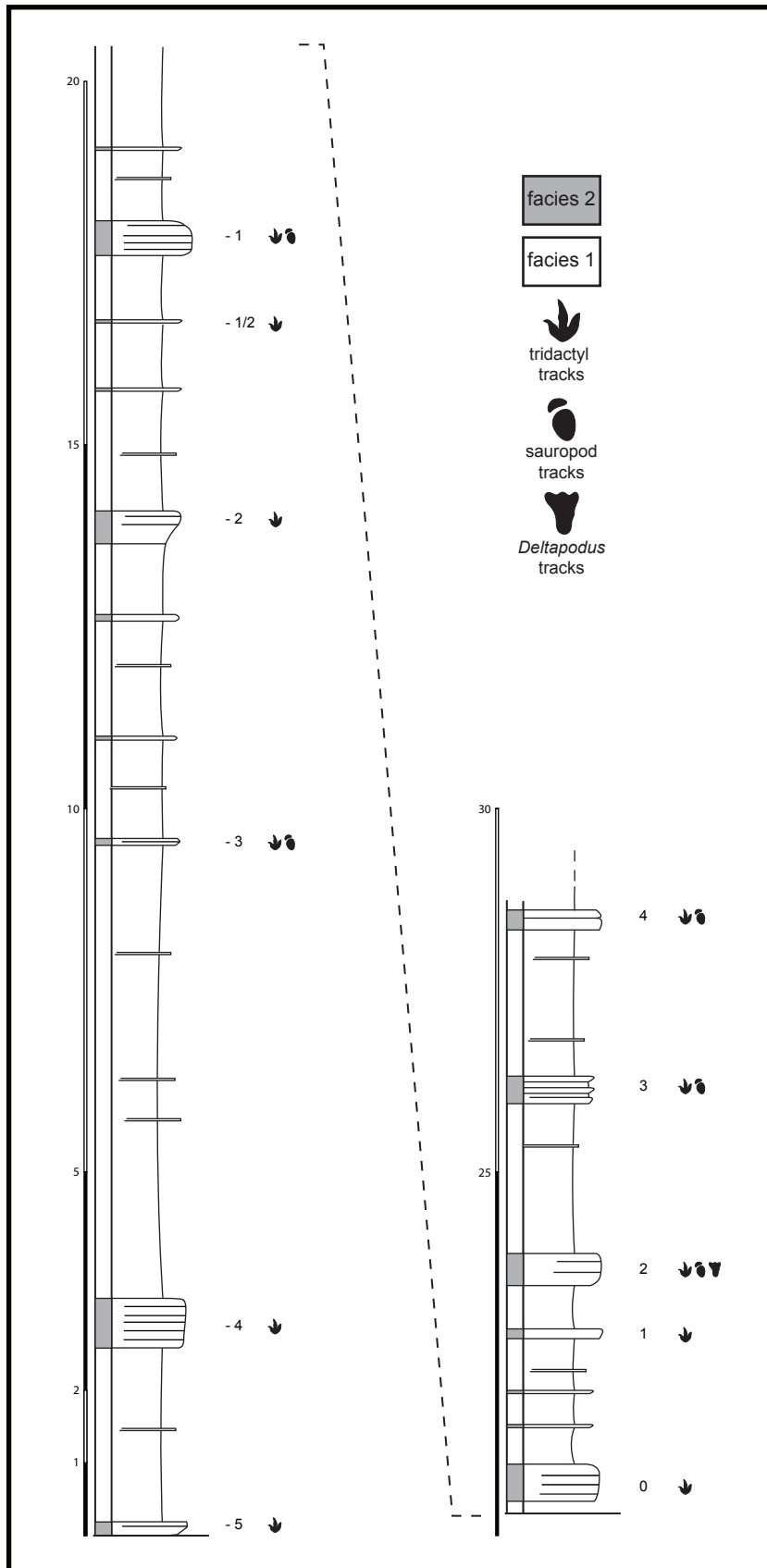
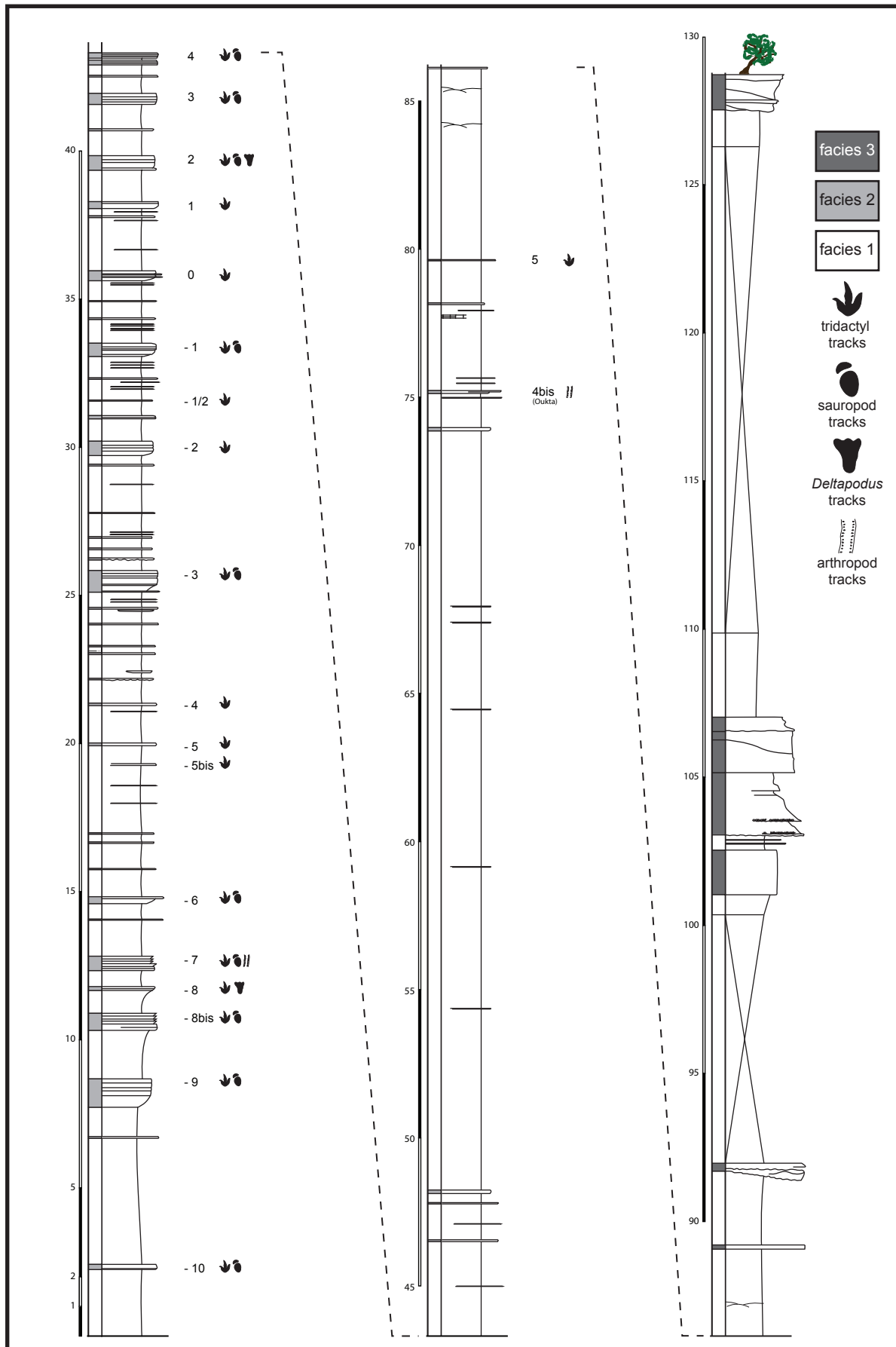
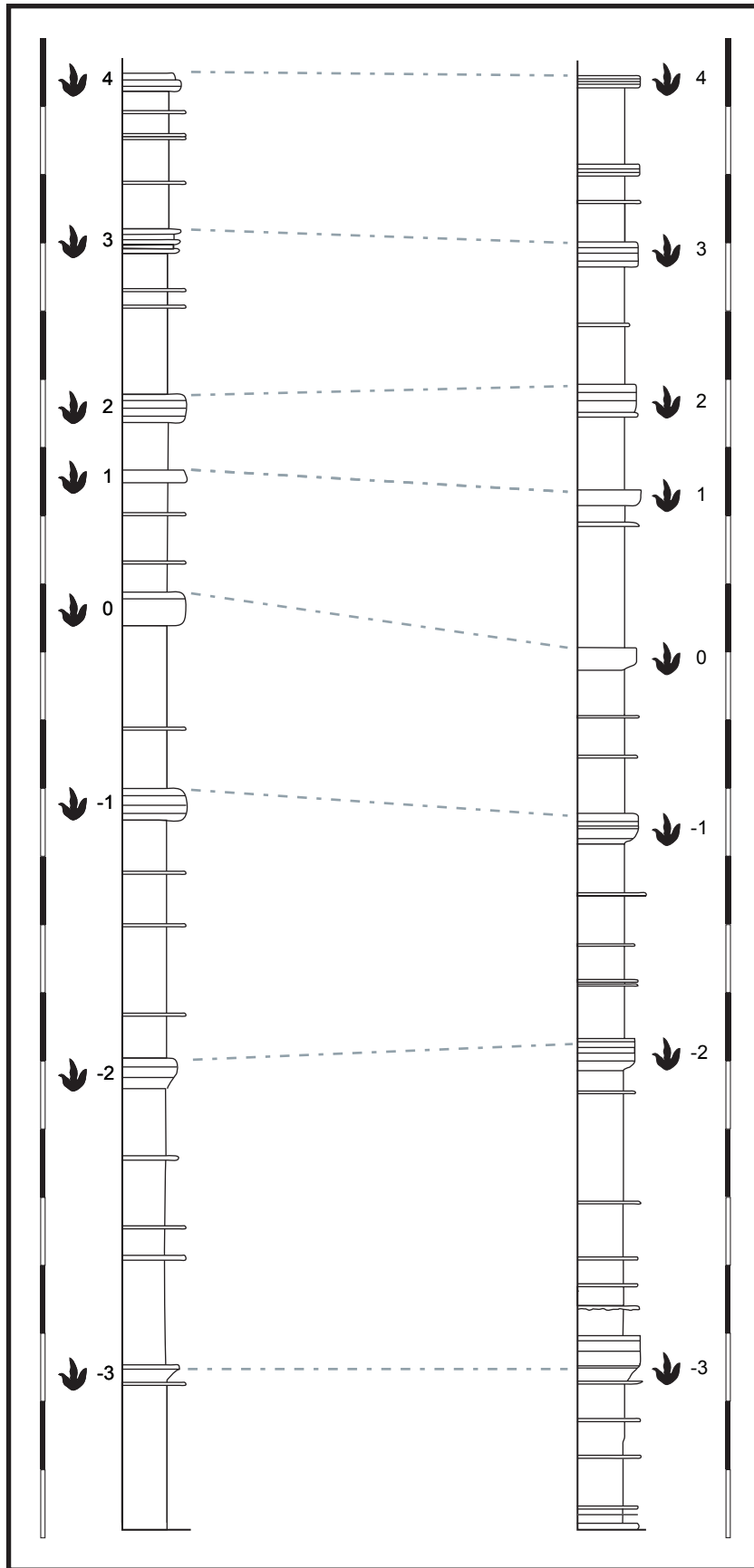


Fig. 3.5 – Stratigraphic log measured close to Aït Minoun (northern part of the ichnosite).



**Fig. 3.6** – Stratigraphic log measured close to Aghri (southern part of the ichnosite). The thickness measured is higher than in Ait Minoun (Fig 3.5) only for the more favourable outcropping situation. The scale is the half of Fig. 3.5.



**Fig. 3.7** – Stratigraphical correlation. The two sections outcrop about 4 km far on the crown flies.

evaporitic structures (e.g. crystallizations, veins, pseudoanticlines) confirm an arid or semi-arid climate.

The carbonate-cemented levels can be interpreted as temporary marine ingressions due to climatic or eustatic control, or as the result of meteoric waters controlled by climate. Only further geochemical analyses on the cements would allow to discriminate between these two origins of the carbonate, but they are beyond the aims of this work.

At present it is only possible to notice the parallelism between the ripple crests strikes and the dinosaur movement directions (Cap. 4.5), especially those of sauropods. This fact seems to be more consistent with the closeness to the shore-line, and so seems to confirm the marine ingression as cause for the carbonate precipitation. Nonetheless, it does not exclude the hypothesis of the presence of ephemeral ponds or lakes in a more proximal continental environment.



# 4 ICHNOLOGY OF THE IOUARIDÈNE SITE

---

The accurate surveying of the site, covered for about the 80% of its extension and on all its outcropping surfaces gives about 1000 of footprints. Most of them (~ 800) are tridactyl, followed by ~ 200 sauropod tracks, ~ 15 non-dinosaurian traces and only 2 stegosaurian footprints.

Most of the footprints are preserved as true tracks but also underprints and undertracks are present. Some tracks, especially of sauropods, are badly preserved so that no measurements or morphological attribution was possible. However, these footprints have been counted in the total amount of ichnites to obtain a more significant datum of the dinosaur association.

For descriptive purposes the traces of the Iouaridène site have been divided into three main groups basing on morphological and behavioural attributes. The groups have been furtherly divided into morphotypes, named mainly after morphological differences and listed in alphabetical order. The morphotypes represent types that differs from the other for at least two characteristics: length and shape of digits, interdigital angles, metatarsal impressions, etc...

Measurements tables on Appendices 1 to 4.

## 4.1 GROUP 1 – TRACKS AND TRACKWAYS OF SUPPOSED QUADRUPED DINOSAURS

The morphotypes included in this group are distinguished for both manus and pes shape, gauge, and, when possible, Trackway Ratio (Romano et al., 2007). The Trackway Ratio (TR) has been evaluated for both manus (MTR) and pes (PTR). In order to compare footprints with a different preservation grade, we calculate the TR following the suggestion of Romano et al. (2007) about the badly preserved tracks.

Manus position is quite variable among the prints of the same trackway and probably reflects more a gait attribute than an actual morphological character, as it appear from the Manus Track Ratio measured.

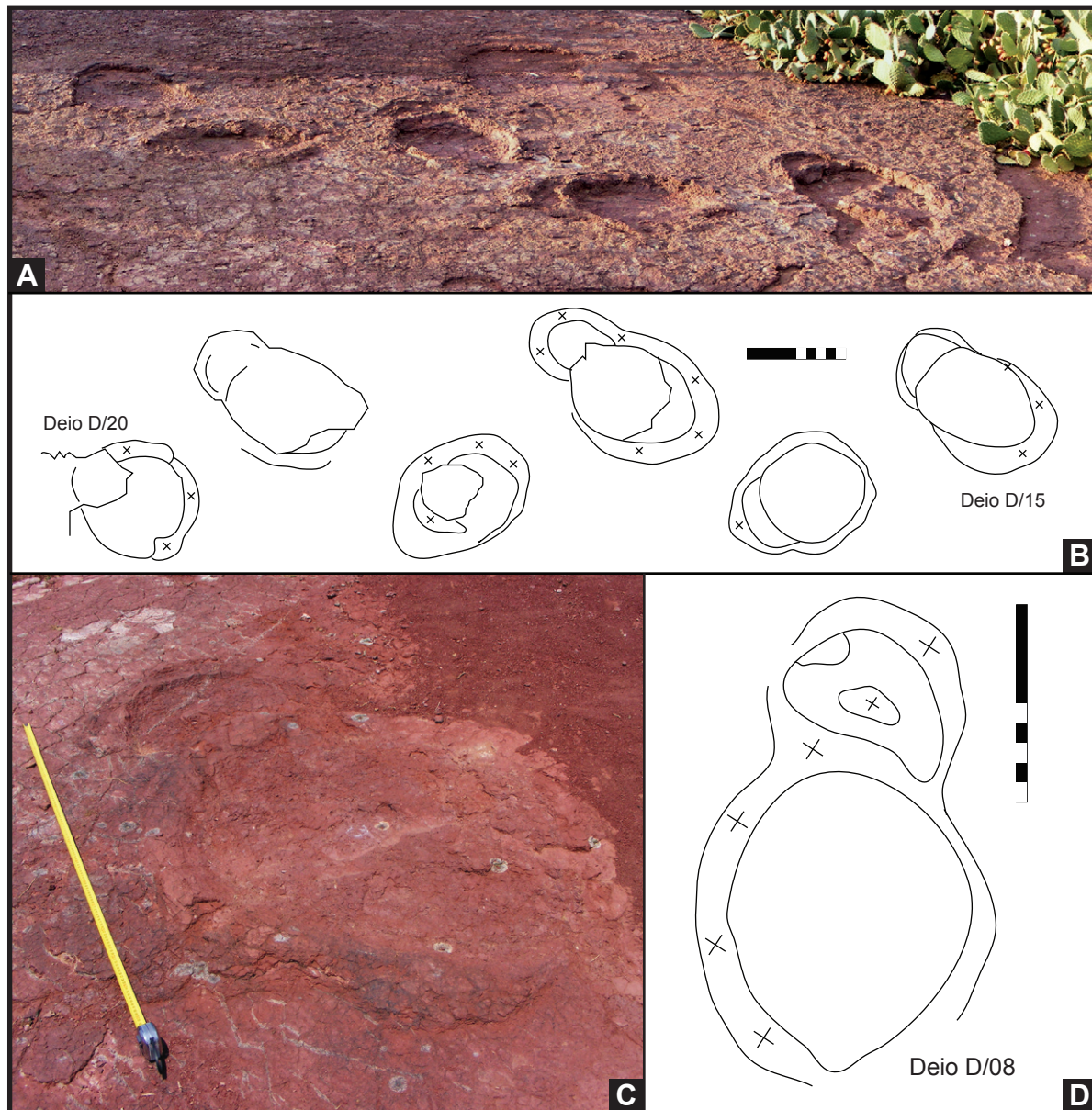
### 4.1.1 Morphotype 1A

It is the most frequent of the group, having been found on 10 out of the 20 trampled layers surveyed. It includes both manus and pes impressions. It is worth noticing that the reference trackway of the famous *Breviparopus taghbaloutensis* Dutuit and Ouazzou 1980 (Fig. 4.1) belongs to this morphotype. Most of the tracks seem to be preserved as underprints, but some true tracks can be found too, usually with a worse preservation grade.

The pes and manus descriptions are mainly made on the Deio D hind and forelimbs tracks and trackway, because it has the highest morphological details, one of the best grade of preservation, as well as because of its historical value, being it the *B. taghbaloutensis* reference trackway.

Pes prints are generally sub-oval to bell-shaped, elongated, very large (often more than 1 m long) and usually lacking digital or claw impressions. Only in one case (Deio D/28 in our survey), as also described by Ishigaki (1989, fig. 9.2 A–B) three poorly preserved, curved digital impressions are visible, but no claw mark is present.

Pes impressions are longer than wide, with the maximum width located in the middle, lightly anterior part of the footprints, with respect to the middle point of the pes elongation axis. The pes footprints are surrounded almost in all the specimens by displacement rims, more or less continuous, usually more pronounced in the antero-external part, and less developed or absent in the posterior and interior part of the track. In all the best preserved trackways an asymmetrical positive (outward) rotation of the pes has been recorded: e.g. in the *B. taghbaloutensis* reference trackway it is around 15° for the right pes, and around 30° for the left one.



**Fig. 4.1** – Example of morphotype 1B. A: photo of a portion of *B. taghbaloutensis* type trackway (Deio D/15 to D/20); B: schematic drawing of the portion figured above. Scale bar 1 m; C: photo of Deio D/08. The scale is 1.5 m; D: schematic drawing of Deio D/08. Scale bar 1 m.

Manus tracks are common in almost all the specimens studied. The footprints are often deformed by the proceeding pes tracks, so the shape varies from sub-circular, when undeformed, to crescent-shaped (horseshoe-shaped) when deformed. Their axis is consistent with the pes one, and the position, in relation with the midline, is more external. In some few cases the manus position is farther from the pes axis, and in one case, a poorly preserved undertrack (Deio XXXIX), it seems to be positioned across the midline, in the inner side of the trackway. Displacement rims are more developed anteriorly, but they can surround all the manus print, connecting with the rims of the pes tracks.

The gauge for the trackways of this morphotype is narrow. Direct measurement highlights that the gauge is not as narrow as expected following the literature, if we consider the inner outline of the footprints. However, considering also the displacement rim, the pes tracks cross the midline (Fig. 4.1). PTR is 50.2%, classifying the trackways as narrow-gauge; MTR is 34.1%.

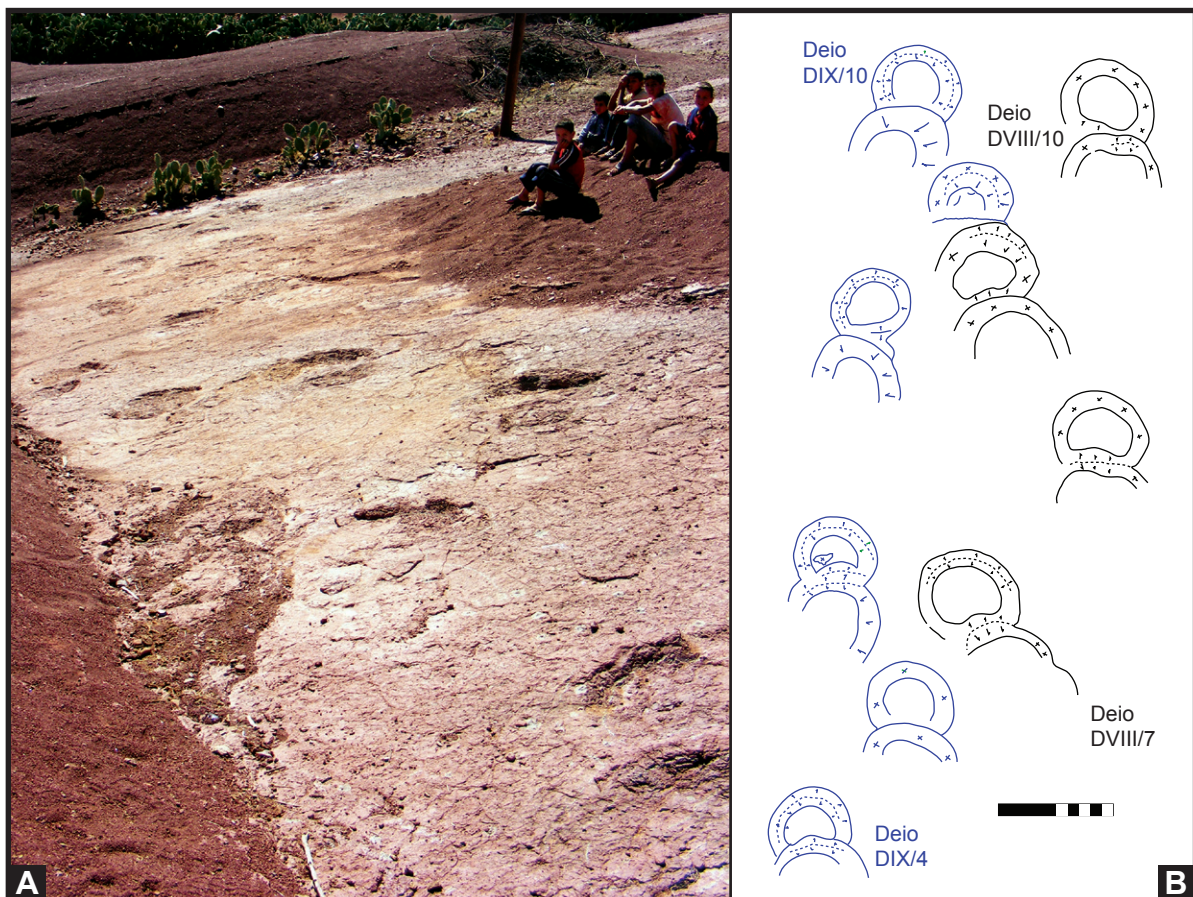
A probable small herd have been recorded in front of the school of Tirika, counting at least four parallel trackways with the same movement directions.

#### 4.1.2 Morphotype 1b

This morphotype is characterized by manus-only and manus-dominated sauropod tracks and trackways. Some of these have been also described by Ishigaki (1989), and recently this material has been reviewed by Ishigaki and Matsumoto (2008). To this known material some new trackways from the Aghri area have been added.

The shape of the manus is usually sub-circular, but in some cases it is more semi-circular (D-shaped) or crescent-shaped with a more rounded and regular anterior margin than the posterior. When not circular, the prints are wider than long. Displacement rims are present, usually in the anterior margin of the prints, but can also develop laterally, joining the posterior ones when present. In some cases, the manus tracks are so shallow that they can be only recognized by the occurrence of the rims.

In many trackways, partial or faint pes impressions are present. Usually they are very shallow and only the anterior part is impressed. Although some low displacement rims can be recognized, when the footprint is present, it is also possible to evaluate the relative manus position, which results antero-lateral (Fig. 4.2). The MTR for this morphotype is 36.4%.



**Fig. 4.2** – Examples of morphotype 1b. A: photo of a portion of the manus-dominated Deio DVIII and DIX trackways; B: schematic drawing of the portion of trackways Deio DVIII (blue outline) and DIX (black outline) illustrated on the right. Scale bar 1 m.

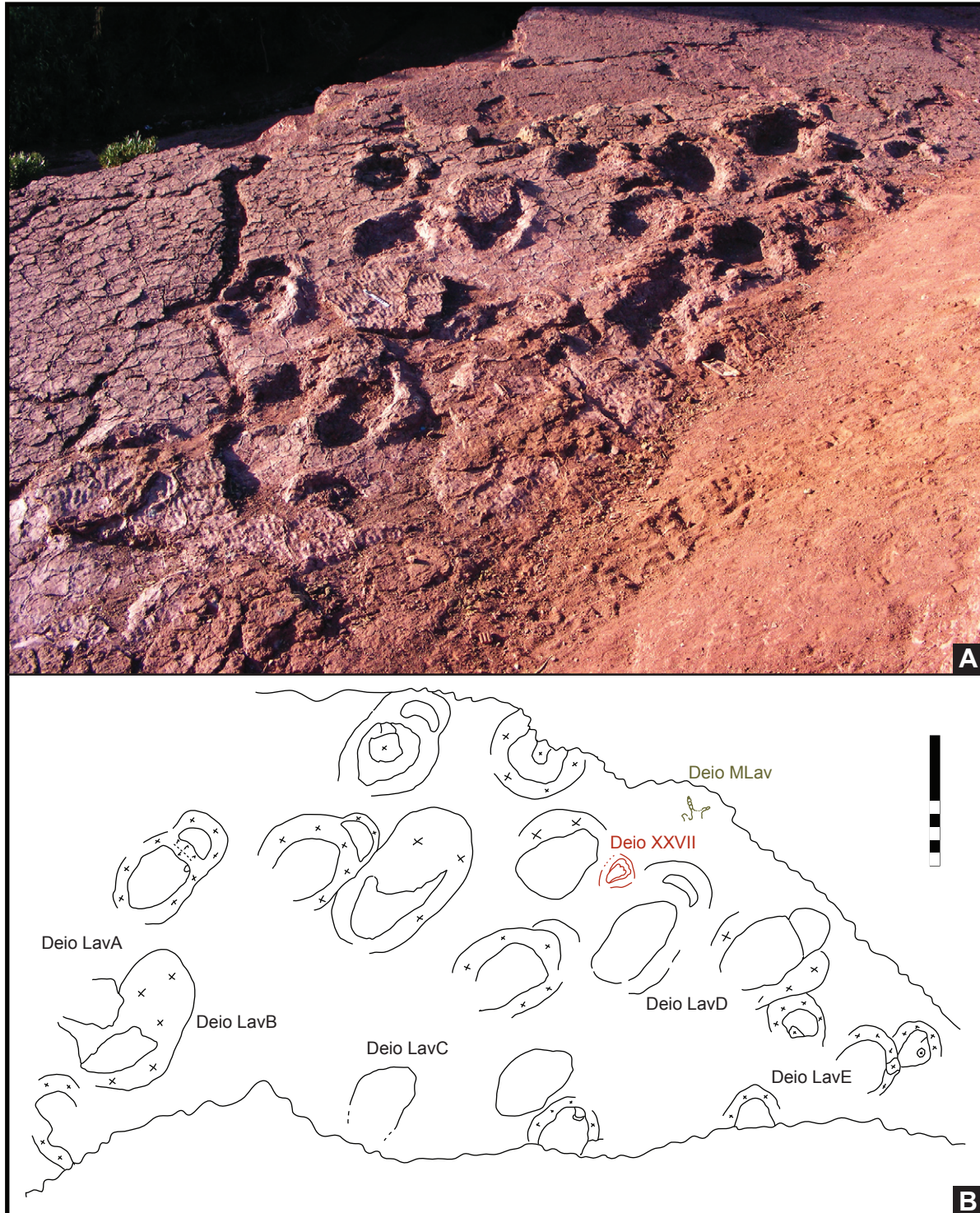
#### 4.1.3 Morphotype 1c

It is rarer than the previous one and occurs mainly on a single layer with at least five parallel trackways (Fig. 4.3). Other isolated couples of footprints occur northward with comparable estimated directions. This is the evidence of a probable herd of middle-size sauropods, in which all the individuals have more or less the same size. The only exception are the tracks of Deio LavB, but the poor preservation and the presence of the infilling layer which covers most of the

tracks, do not allow any further hypothesis.

The preservation is generally low and only one trackway (Deio LavA) is well enough preserved to allow proper descriptions.

The pes inner outline is sub-elliptical, longer than wide, with the widest portion of the footprint in the middle-anterior part of the footprints, with respect to the pes elongation axis middle point. No clear digit marks occur; only in the footprint Deio LavA/4 are present some depressions in the inner part of the footprints which can be interpreted as digit traces, but the preservation is too



**Fig. 4.3** – Morphotype 1c main outcropping surface. A: photo of the “lavatory” surface, where a small herd of mid-small sauropods outcrops. The name lavatory is due to the presence of a small wadi where the locals use to wash their clothes; B: schematic drawing of the same surface. Dark red outlines draw one of the morphotype 1d specimens (Fig. 4.4); dark green outlines draw a poorly preserved tridactyl track. Scale bar 1 m.

bad for any proof determination.

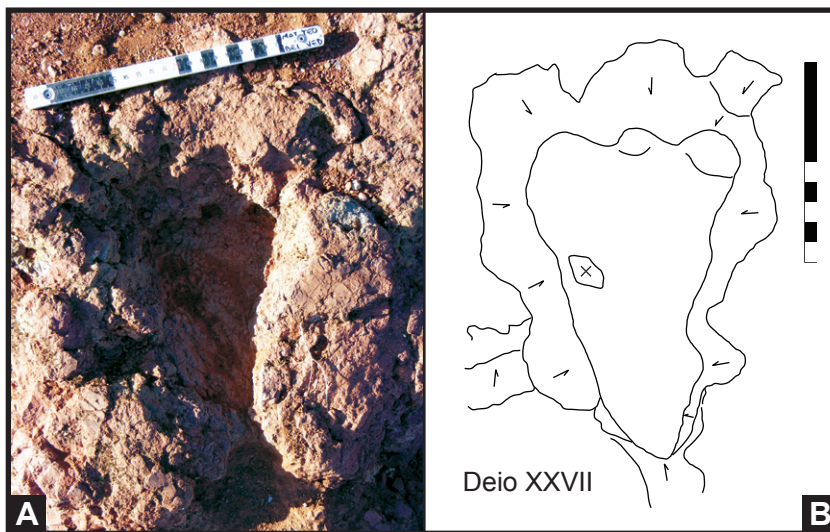
Manus prints are common, usually semicircular (D-shaped), wider than long, without other morphological details. They are generally positioned along the pes print axis, and do not show clear overlapping or deformation by the proceeding pes tracks.

Displacement rims are present all around the manus-pes couple. In the posterior part of the pes the rims are less developed or absent, while the thickest part is the antero-lateral exterior margin of the prints.

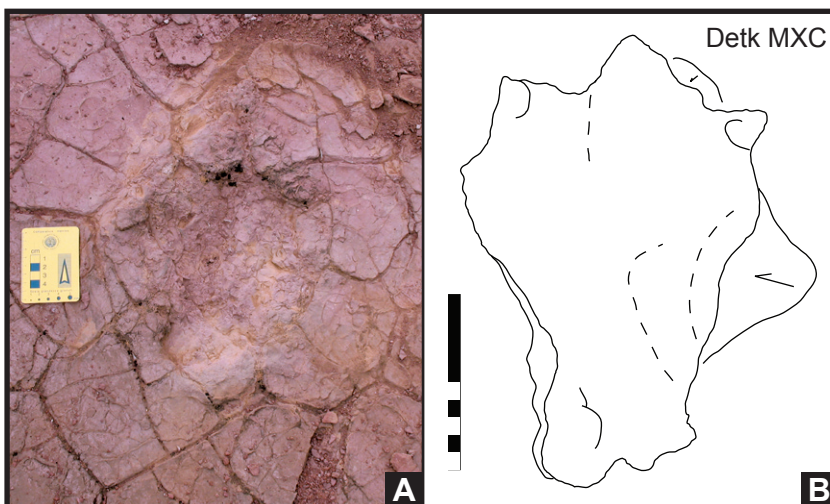
The PTR could be evaluated only on a single trackway (Deio LavA) and it is 44.7%. Following the ranking of Romano et al. (2007), this morphotype can be considered medium-gauge. The bad preservation, together with the small amount of tracks available for measurements, prevents from calculating a meaningful MTR.

#### 4.1.4 Morphotype 1b

This type (Figs. 4.4, 4.5) is the rarest in the whole dinosaurian ichnoassociation, counting only two specimens (Deio XXVII and Detk MXC). Despite the occurrence of only pes impressions, their plantigrady suggest a quadrupedal gait. Both the tracks are roughly sub-triangular, longer than wide, wider across the digits impression. Three short, blunt and rounded digits occur, having more or less the same sizes. The outline shows a concave and a convex side, present in both the specimens but more evident in Deio XXVII. In this print, deeper than the other, it is possible to notice the sub-vertical walls, deeper on the convex side of the track. Both the “heels” of the footprints are rounded, but the one of Deio XXVII is more tapered. Nonetheless, it is



**Fig. 4.4** – Example of morphotype 1b. A: photo of Deio XXVII. Scale 20 cm; B: schematic drawing of Deio XXVII. Scale bar 10 cm.



**Fig. 4.5** – Example of morphotype 1b. A: photo of Detk MXC. Scale 8 cm; B: schematic drawing of Detk MXC. Scale bar 10 cm.

not possible to discriminate if it is due to morphological differences or just to the preservation grade.

Despite the preservation differences between the two tracks, both the tracks show a less impressed digit on the more convex side of the print.

## 4.2 GROUP 2 – TRACKS AND TRACKWAYS OF BIPED DINOSAURS

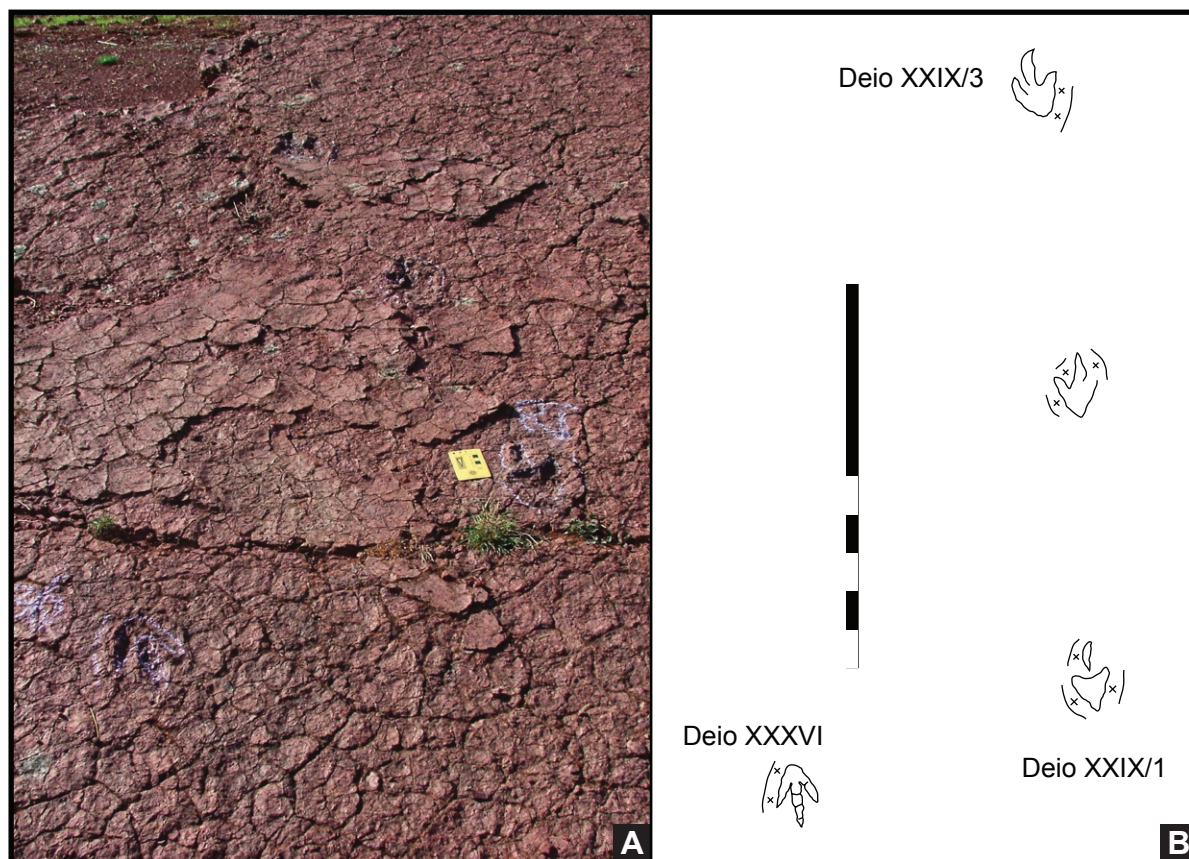
The second group is composed of tridactyl footprints that are the most common type in the site. Most of the tracks are arranged in trackways, more or less long, but can also occur as isolated footprints. In these cases the direction measured has been the digit III axis, according to the evidence that all the footprints rotations measured are very low ( $< 10^\circ$ ) or absent.

The preservation grade is very variable, and can change also among the footprints of the same trackway. The tridactyl footprints are mostly preserved as true tracks, but some probable underprints and transmitted tracks are present, too. In one case (Detk MXX) the tracks occur as overprints (Sarjeant, 1988; Thulborn, 1990) or track infillings (Lockley, 1991) and only in the last footprints of the trackway it is possible to see a partial true track. Displacement rims are common and usually more developed in the antero-external margin of the footprint.

### 4.2.1 Morphotype 2A

It is characterized by small tridactyl tracks ( $F_l < 20$  cm). Footprints are mesaxonic, longer than large ( $F_w/F_l$ : 0.74), and slightly asymmetric. Digit IV is always the longest and better defined, followed by digit III, and digit II; the width of all the digits is comparable with the digit III, which is slightly wider. With the exception of the footprints with bad preservation, claw marks are present in all the specimens (Fig. 4.6).

Interdigital II-IV angle is narrow, with the angle between digits II and III slightly narrower than



**Fig. 4.6** – Example of morphotype 2A. A: photo of the surface with Deio XXIX and Deio XXXVI. Scale 8 cm; B: schematic drawings of Deio XXIX and Deio XXXVI. Scale bar 1 m.

the one between digits III and IV.

A clear phalangeal formula was impossible to carry out, also in the best preserved footprints. Moreover, there is a notable variability in the “heel” shape. It is present in most of the footprints and can vary from tapered to rounded, while in some few tracks it is lacking. Because the changing of the heel shape have been noticed also into the same trackway, it is more probable that these variations are more related to substrate condition or kinematics than to anatomical features.

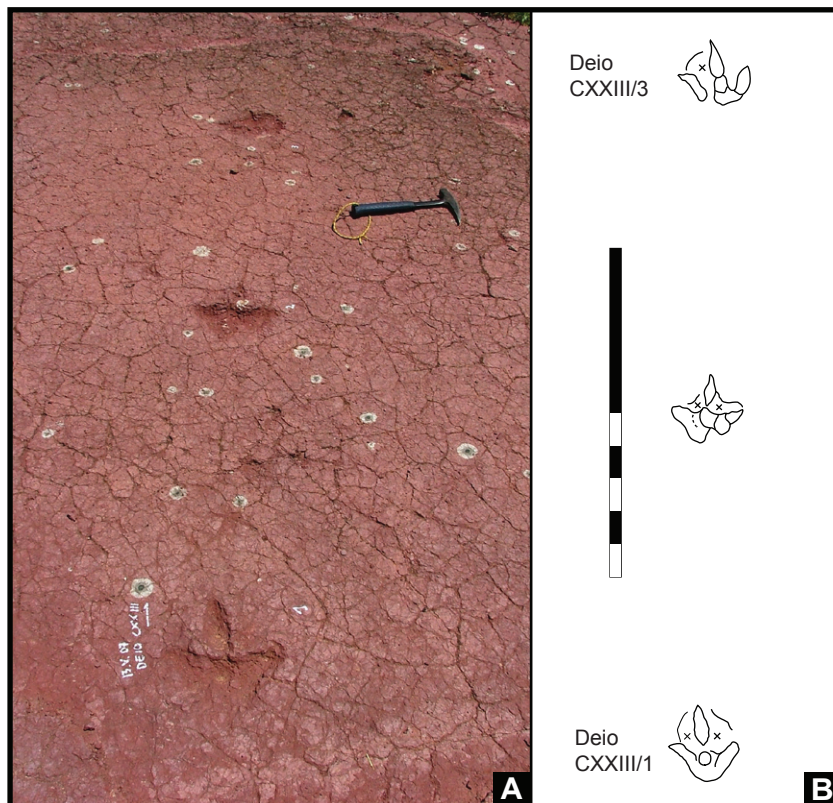
Long trackways are uncommon for this morphotype, which can be usually found as isolated footprints or arranged into short (< 5 footprints) trackways. The only long trackway present is Deio VII, composed of 21 almost continue tracks. All the trackways are always narrow, with the digits aligned or very close to the midline, and show a slight outward rotation (< 10°) of the footprint axis.

#### 4.2.2 Morphotype 2B

This type (Fig. 4.7) is quite rare in the site. The footprints size is middle-small. They are mesaxonic, slightly longer than wide (Fw/FI: 0.84), with a marked symmetry with respect to the digit III elongation axis. Digits have comparable lengths. Also the width is comparable between the three digits. Digits have a tapered termination but no claw impressions are present. Interdigital angle between digits II-IV is quite wide with a similar divarication between digits II-III, and III-IV. All the footprints have a rounded “heel”.

There are no well-preserved trackways. Pace measurements have been made on two aligned footprints, which probably belong to a trackway.

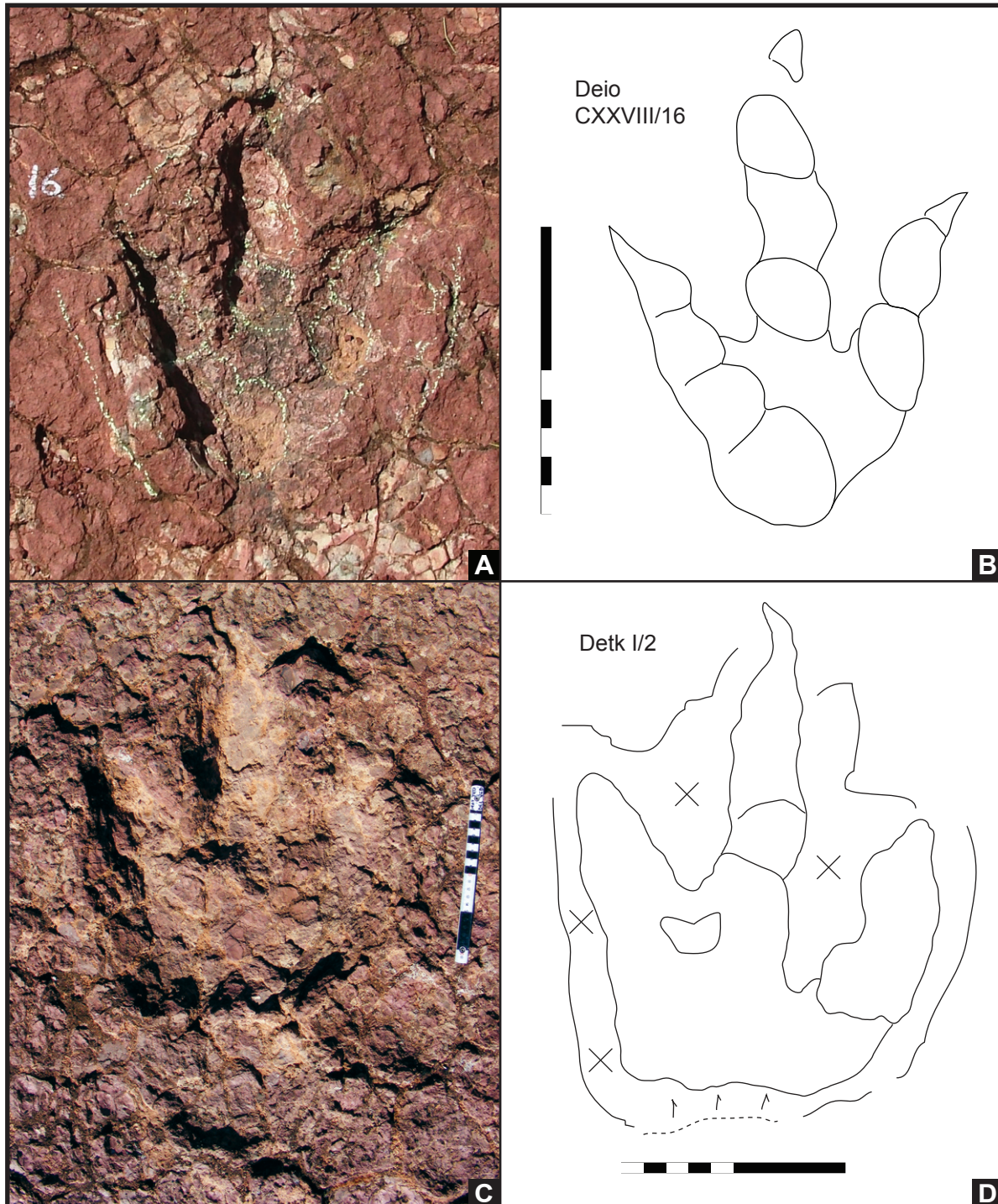
The general bad preservation of the specimens does not allow further descriptions. Although this type has great similarities with the previous one, and could be interpreted as its deformation, the symmetry on the footprints should be considered as morphological features which cannot be too much influenced by the substrate characteristics.



**Fig. 4.7** – Example of morphotype 2B. A: photo of Deio CXXIII trackway; B: schematic drawing of Deio CXXIII. Scale bar 1 m.

### 4.2.3 Morphotype 2c

This type can be diagnosed as large tridactyl asymmetric mesaxonid and is longer than wide (Fw/Fl: 0.75). Digits are well separated, with a phalangeal-pad impression formula 2-3-4, for digits II, III and IV, respectively. Digit IV is the longest and usually forms the rear of the footprint; its proximal pad is aligned with digit III axis. Digit III has a typical inward bending and has the longest free length. The width of digits, considering their free portion, is similar, but digit IV has a wider proximal pad. Claw marks are evident in all the digits, also in the most badly preserved tracks (Fig. 4.8).



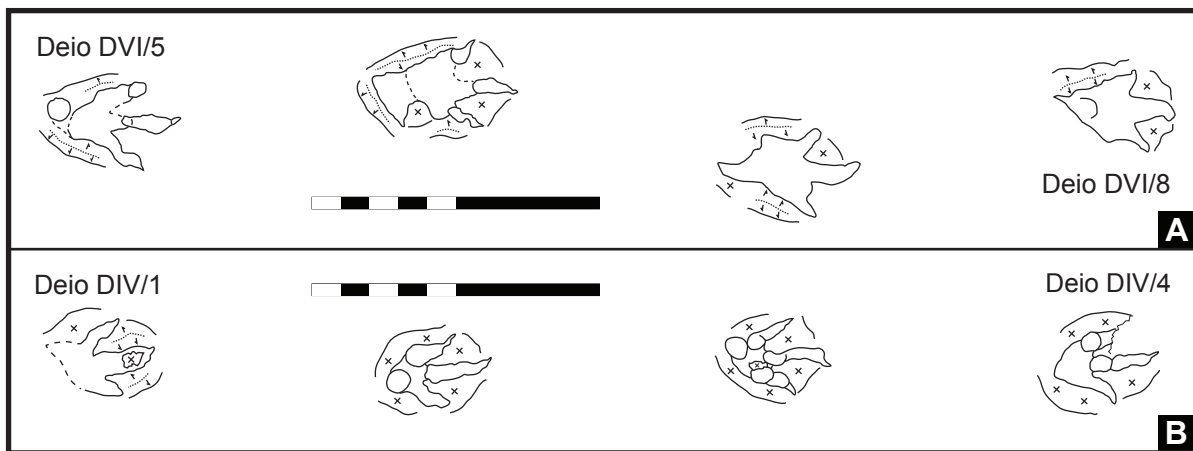
**Fig. 4.8** – Examples of footprints belonging to morphotype 2c. A: photo of Deio CXXVIII/16 showing, one of the best preserved tridactyl footprints; B: schematic drawing of Deio CXXVIII/16. Scale bar 20 cm; C: photo of Detk I/2, showing one of the bigger tracks of this morphotype, and the common preservation grade for this kind of footprints; D: schematic drawing of Detk I/2. Scale bar 20 cm.



The total interdigital angle is narrow ( $< 45^\circ$ ), with a clear asymmetry between the angle between digits II-III ( $17.2^\circ$ ) and the angle between digits III-IV ( $26.2^\circ$ ). Despite the lower absolute value of the II-III angle, it also presents the highest variability (from  $5.5^\circ$  to  $36.2^\circ$ ). This higher mobility cannot be explained only with extramorphological influences, and must be the result of anatomical characteristics of the trackmaker foot.

Trackways are very common in the record and show an irregular gauge, from very narrow to wide, without any relation with the stride length or the gait: trackways with the same footprints dimensions, comparable pace and stride length, comparable footprints rotation, left on the same level, have different gauges. This can be related to different tracemakers but no other evidence than the width of the trackway is present.

However, commonly the digit II crosses the midline. The rotation, with respect to the midline, is less variable but can change from narrow (around  $10^\circ$ ) to absent, especially in the narrower trackways (Fig. 4.9).



**Fig. 4.9** – Examples of trackways belonging to morphotype 2c. A: schematic drawing of a more wide-gauge trackway (Deio DVI); B: schematic drawing of a narrow-gauge trackway (Deio DIV). Scale bars 1 m.

#### 4.2.4 Morphotype 2d

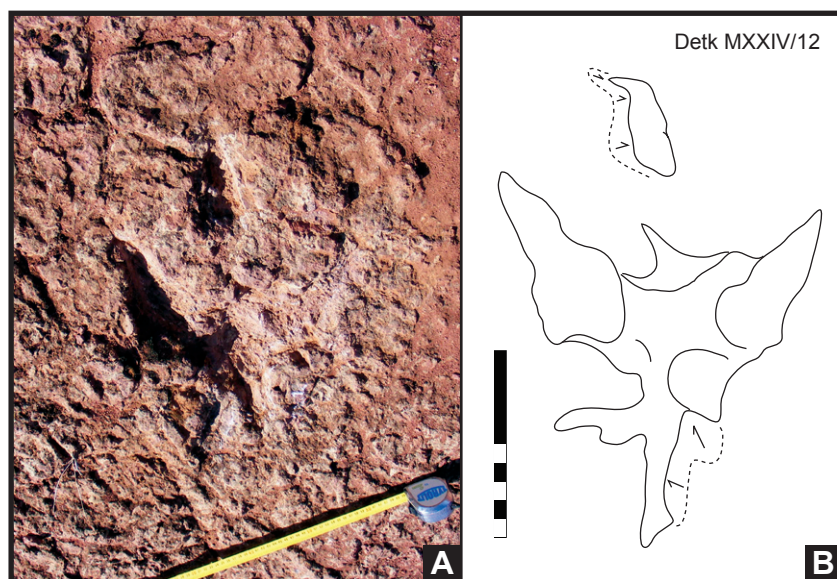
This morphotype occurs only in few tracks. Its peculiar characteristic is to be mesaxonic and tetradactyl, with a marked hallux and metapodium impressions. The proportions suggest that this impression is from a large part of the metatarsals. The shape of the footprints is asymmetrical, longer than wide, also not including the metatarsal portion, with four elongated and tapered digits. Digit IV seems to be the longest, followed by digit III, II and I. Often digit III is separated from the rest of the footprints by sediment infillings.

Interdigital angle between digits II-III is always narrower than the one between III-IV. Digit I is always directed laterally, through the trackway midline, with an average angle with digit II of  $73^\circ$ . The metatarsal impression is slightly interiorly oriented. Often the proximal portion of digit III is closed by mud-fillings or results less defined, but in most tracks the inward bending is evident (Figs. 4.10, 4.11).

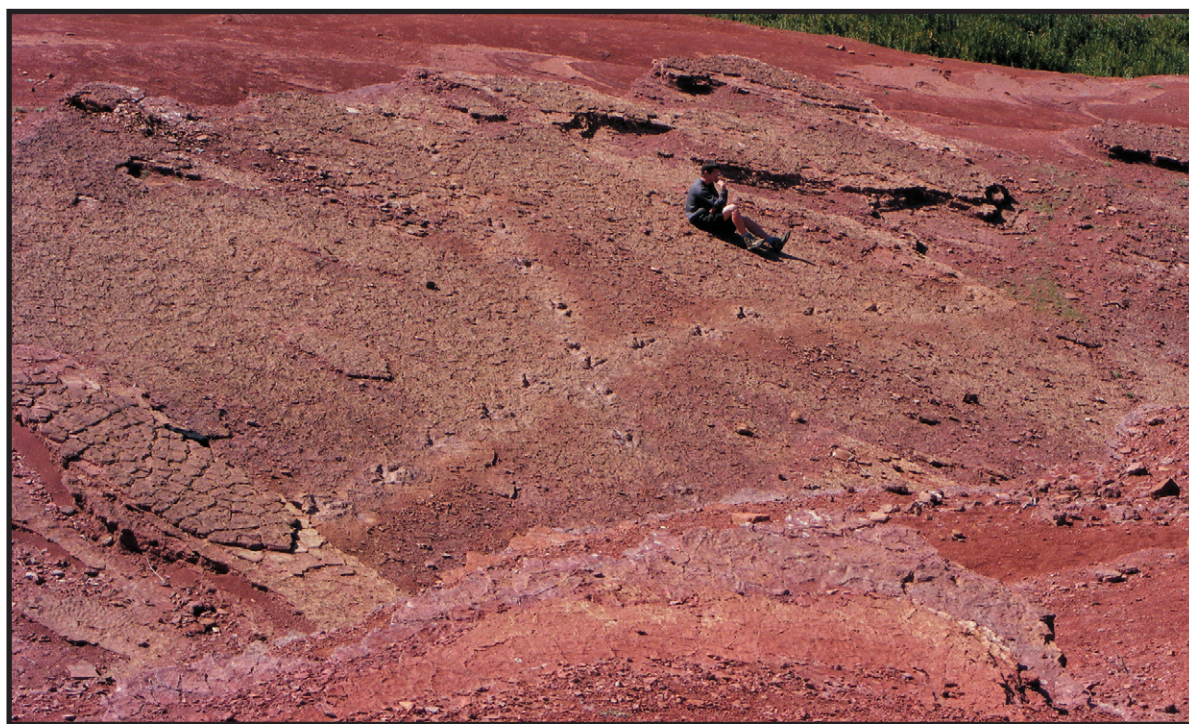
Only one long trackway (Detk MXXIV) has been found and shows relatively short paces with a continuous progression. The footprints are slightly rotated outward ( $< 10^\circ$ ), and the trackway gauge is quite narrow.

Detk MCIV seems to show the occurrence of both tridactyl and tetradactyl footprints, arranged in a trackway. There are no evidences of changing in the pace length, or in the depth of the footprints, but the poor preservation could have deleted some details.

No paired footprints or resting traces have been recorded. Thus, a simple slow-walking cause, as suggested in Day et al. (2002, 2004), is insufficient to explain these tracks. A substrate-related



**Fig. 4.10** – Example of morphotype 2D tracks. A: photo of Detk MXXIV/12; B: schematic drawing of Detk MXXIV/12. Scale bar 20 cm.



**Fig. 4.11** – Photo of the trackway Detk MXXIV, example of the morphotype 2D. Note the crossing with the theropod trackway Detk MXXV. Gigi for scale.

hypothesis is more probable: a soft, water-saturated ground could not only allow the sinking of the feet in the sediment, but could also influence the behaviour of the dinosaur.

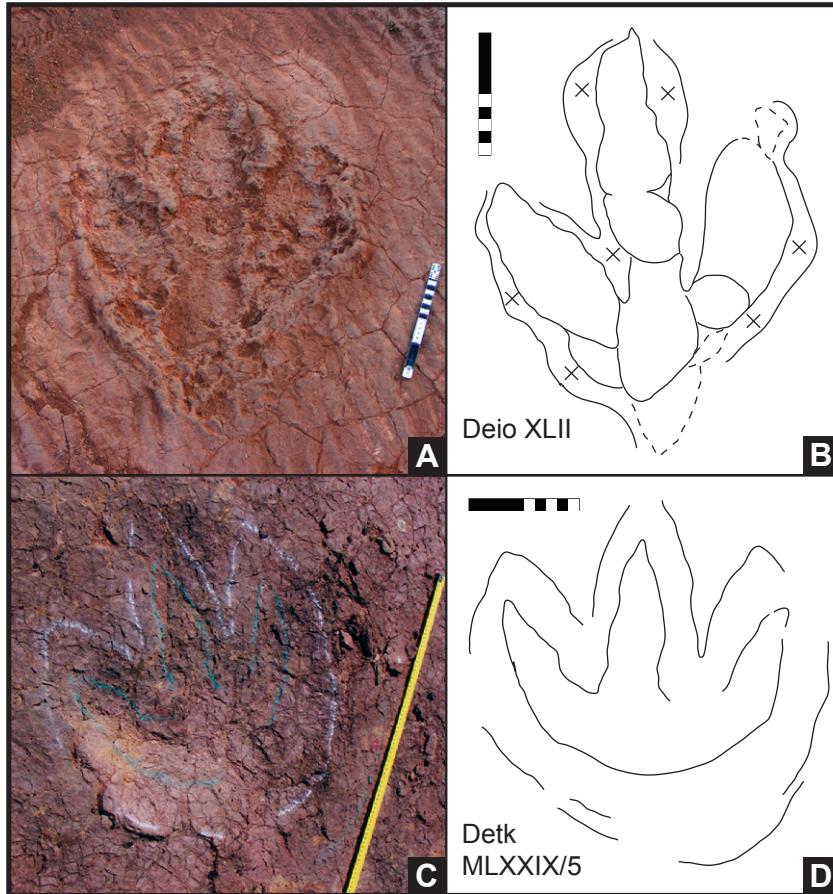
#### 4.2.5 Morphotype 2E

It is characterized by tridactyl, mesaxonic, very large footprints ( $> 45$  cm), usually slightly longer than wide ( $Fw/Fl$ : 0.86). Footprints are lightly asymmetrical, with well separated and long digits. Digit II is usually slightly shorter than digit IV, while digit III is long and straight. There are no evidences of pad impressions, except for Deio XLII, where three probable pads are visible in digit III. Claw impressions are rare, but in one specimen (Detk XVI) they occur clearly. Interdigital angle II-III is narrower, but very similar to the one between digits III-IV. The total interdigital angle is usually wide (more than  $55^\circ$ ). The rear of the footprints has a various

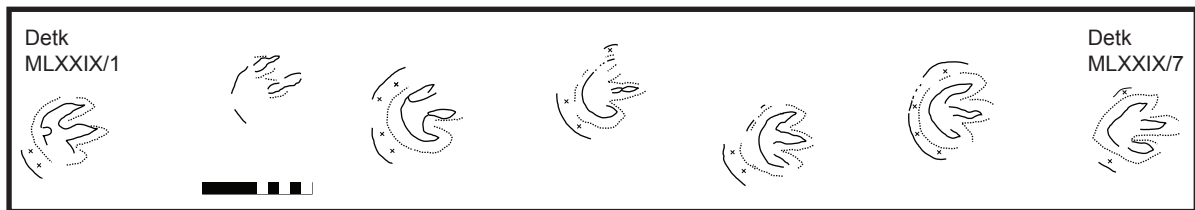
shape: from rounded to quite tapered (Fig 4.12).

Unfortunately, most tracks of this morphotype are badly preserved or preserved as undertracks or underprints, so that many details are missing and further descriptions cannot be made.

The unique 7-footprints-long trackway (Detk MLXXIX) examined shows short irregular paces (from 1.44 to 1.69 m), but there is no evidence of limping, being the pace irregularity distributed in both the pes tracks. Footprints are slightly rotated outward (Fig. 4.13).



**Fig. 4.12** – Examples of footprints belonging to morphotype 2E. A: photo of Deio XLII. Note the wonderful symmetric ripples; B: schematic drawing of Deio XLII; C: photo of Detk MLXXIX/5. Scale 75 cm. The white chalk lines were not drawn by me, but were already present when the trackway was discovered and photographed; D: schematic drawing of Detk MLXXIX/5. Scale bar 20 cm..



**Fig. 4.13** – Schematic drawing of Detk MLXXIX, the only long trackway preserved for morphotype 2E. Scale bar 1 m.

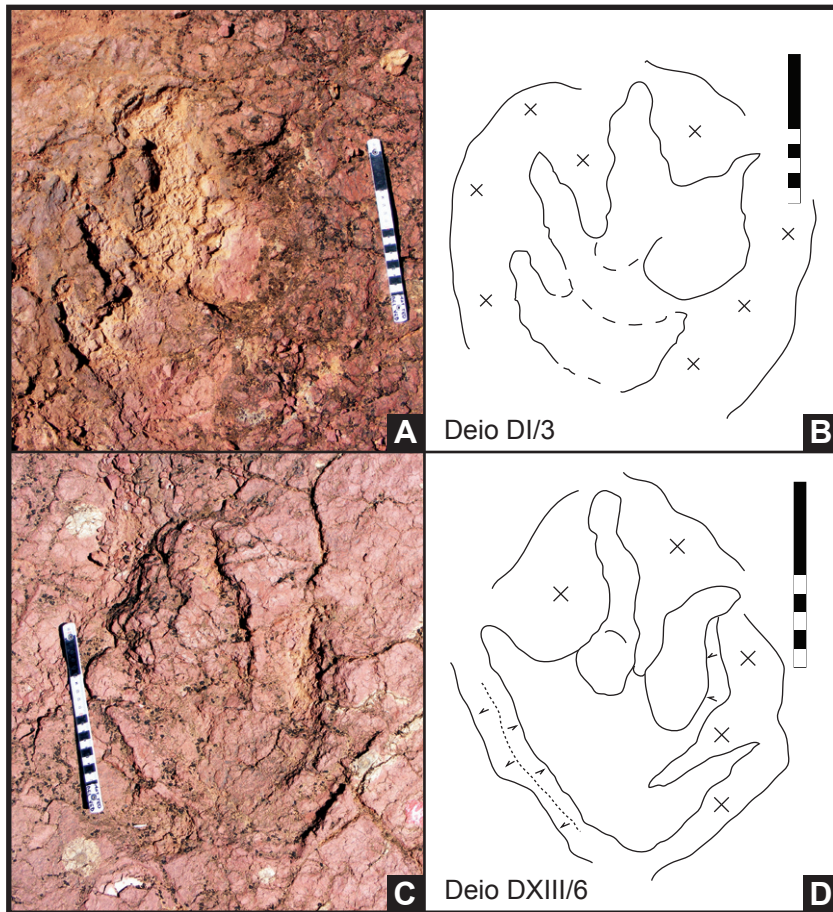
#### 4.2.6 Morphotype 2F

This asymmetrical, mesaxonic, and elongated morphotype is the second tetradactyl type of the ichnoassociation. Footprints are longer than wide, with 4 tapered digits. Digit IV is the longest, followed by digits III, II and I, but this interpretation is spoiled by the bad preservation of the specimens. The preservation grade does not allow a detailed measurement of other parameters. Nevertheless, some consideration can be made on the divarication, which is always narrower between digits II and III than between III and IV. Digit I is anteriorly directed, with a very narrow interdigital angle with digit II. Metatarsal impressions, where present, are broad and not elongated posteriorly as in morphotype 2D (Fig. 4.14).

Continuous trackways are missing, but footprints of this type occur in trackways bearing also footprints of the morphotype 2c. Thus, my opinion is that the impression of the digit I is

controlled by the characteristics of the substrate more than by the anatomy or behaviour of the trackmaker.

Furthermore, because of co-occurrence of the type 2F within trackways dominated by morphotype 2c, and also considering its rarity, this morphotype has been considered as part of the 2c type in the following distribution analysis.



**Fig. 4.14** – Examples of morphotype 2F footprints. A: photo of Deio DI/3; B: schematic drawing of Deio DI/3. Scale bar 20 cm; C: photo of Deio DXIII/6; B: schematic drawing of Deio DXIII/6. Scale bar 20 cm. No complete trackways of this morphotype are present.

### 4.3 GROUP 3 – NON-DINOSAURIAN TRACES

The last group includes those morphotypes that have not been produced by dinosaurs. It is the rarest group of the ichnoassociation and its morphotypes only occur in few levels and all in the southern area of the site.

#### 4.3.1 Morphotype 3A

A detailed morphological analysis of this footprint is prevented by the poor preservation. However, it is possible to give a general description. The morphotype only occurs with a small, shallow and faint print (Detk MLVII). It appears as a tridactyl track, with two larger and straight digits, and a shorter faint digit directed opposite to the other (Fig. 4.15A).

A second depression is present, with a morphology that can remind of the tracks above described, but the preservation is too poor for any further interpretation.

#### 4.2.2 Morphotype 3B

This morphotype represents the only invertebrate tracks found in the ichnosite. It usually appears as long hollow trails. The lateral parts of the tracks are generally deeper than the central. No

clear tail drags have been found inside the hollow. Size of the trails can vary in width from 5 up to 30 cm. In the level -7 at least 15 parallel trails are present; one of these furrow (Fig. 4.15) is overlapped by a tridactyl theropodian footprint (Detk MLXIV). Some tracks are cut by mud-cracks, so it can be said that they were left when the sediment was not dried. There are affinities with some arthropod deep traces, but no movement traces have been found, so any ichnological classification is impossible.



**Fig 4.15** – Examples of morphotypes 3A and 3B. A: photo of Detk MLVII. Scale 20 cm; B: Photo of Detk MLXIV, outcropping on level -7. Note that the footprint is cut by the arthropod trace. Scale 20 cm; C: photo of the parallel trails outcropping on level -7. The yellow square marks the position of Detk MLXIV.

#### 4.4 TRACKS AND TRACKWAYS ANALYSIS AND DISTRIBUTION

In this paragraph the tracks and trackways parameter both of quadrupedal and bipedal dinosaurs are analyzed.

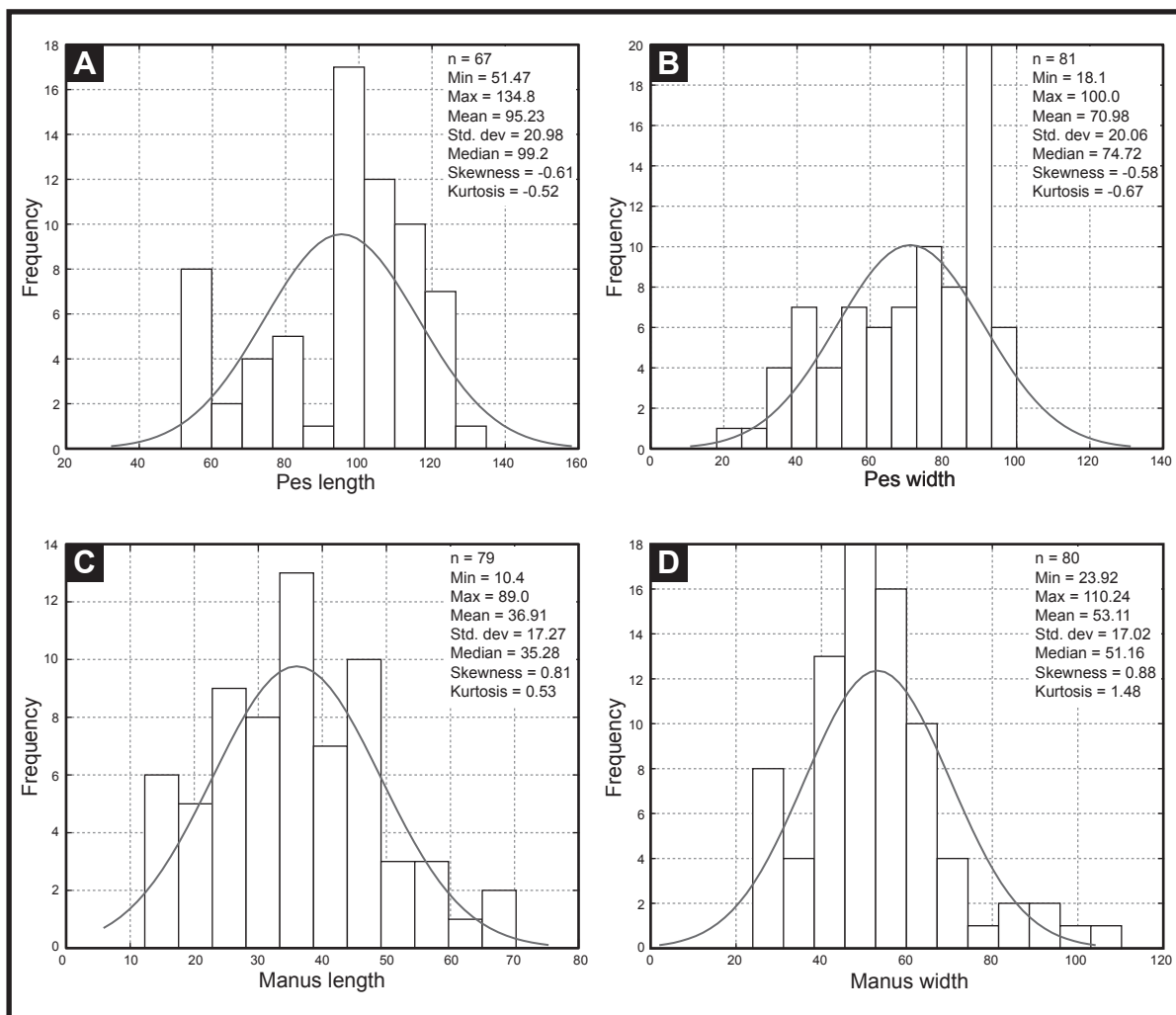
All the parameters, when possible, have been measured for each track and trackways. Nevertheless, the extremely poor preservation of some prints prevents any kind of reliable measurement, and some discontinuous trackways did not allow to obtain all the standard measurements.

#### 4.4.1 Group 1. Quadrupedal dinosaurs

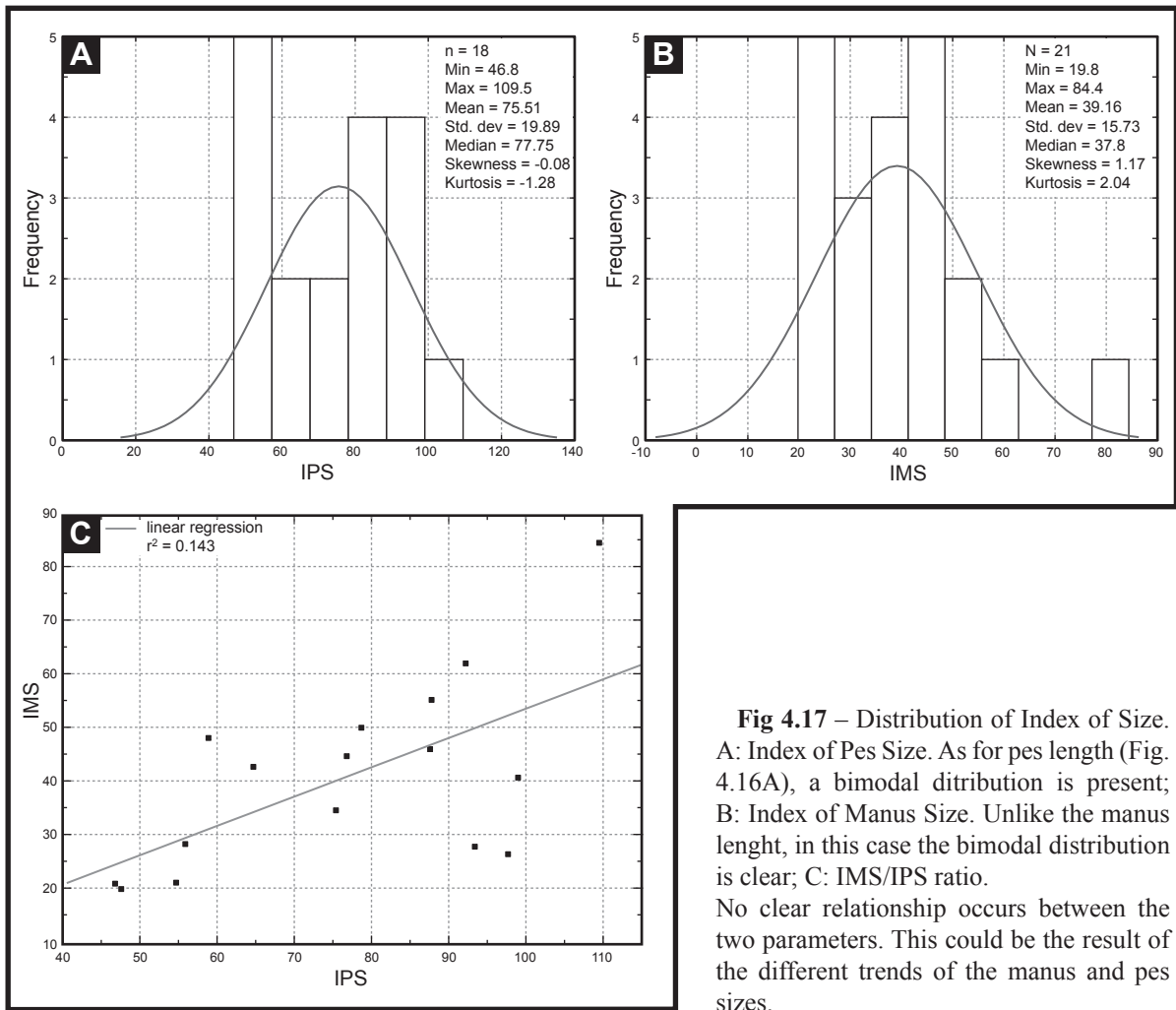
The size frequency and the index of track size distributions (Figs. 4.16, A-D) for both manus and pes impressions show a clear predominance of the large sauropod tracks, but with some distribution characteristics that need to be mentioned. In fig. 4.16B, the peak around 40 cm of pes width represents the tracks from the small herd which have almost all the same dimensions. Fig. 4.16C shows three distinct peaks, corresponding the smallest to the small-medium sauropods, and the other two to the *B. taghbaloutensis* tracks. These manus prints are split into two peaks, mainly because of the different grade of overlapping of the pes, which affects the manus apparent length. Looking at the manus width distribution (Fig. 4.16D), in fact, there is only one peak corresponding to the large sauropods, because this parameter is less affected by the deformation due to the pes.

The IPS (Fig. 4.17A) shows the clear occurrence of two size classes of sauropods, medium small (peak around 50 cm ) and large (peak around 90 cm), while the IMS (Fig. 4.17B) fits quite well the normal distribution with only one peak. It corresponds more or less to the tracks from, around the villages of Aghri and Tirika.

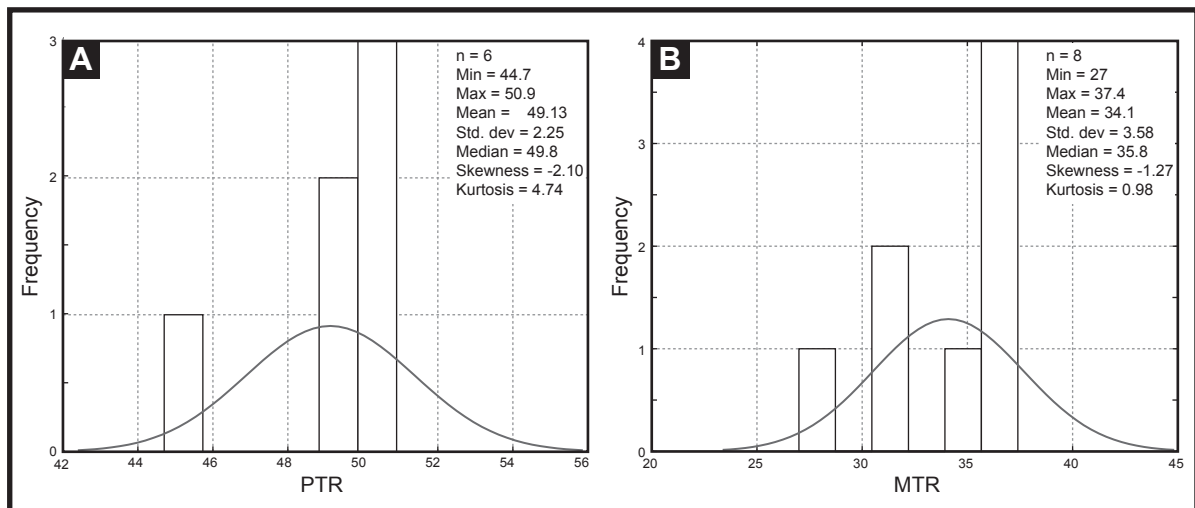
Also the IPS/IMS ratio has a Gaussian distribution, with only one peak, around 1.5, representing the very large and not overlapped manus tracks. The values larger than 3.0 represent the large but highly overlapped manus tracks.



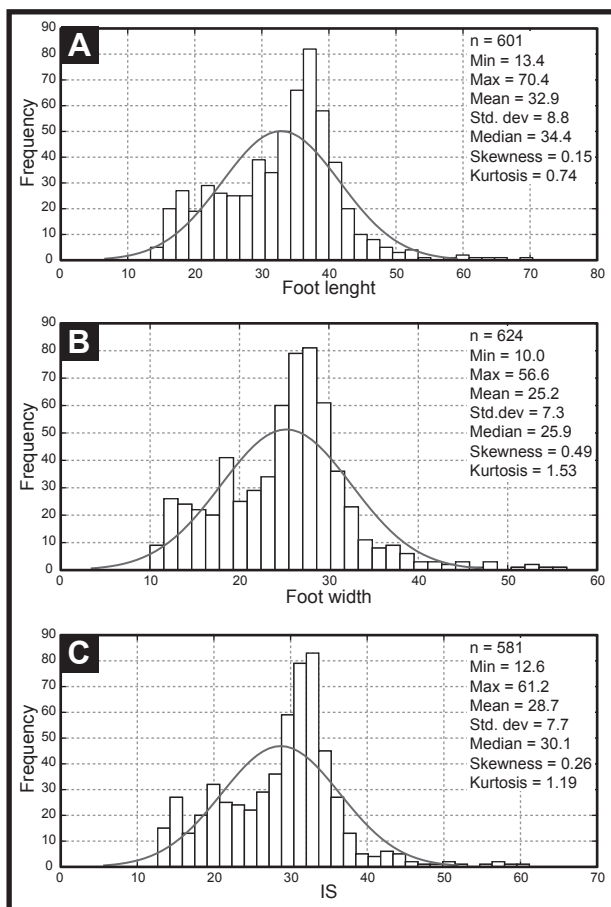
**Fig 4.16** – Distribution of sauropod manus and pes dimensions. A: pes length frequency. Note the clear bimodal distribution; B: pes width frequency. A bimodal distribution is evident, but less clear than in the pes distribution (Fig. 4.16A); C: manus length frequency; D: manus width distribution. In these last two cases the distribution is more normal, despite the different size of the tracks.



**Fig 4.17** – Distribution of Index of Size. A: Index of Pes Size. As for pes length (Fig. 4.16A), a bimodal distribution is present; B: Index of Manus Size. Unlike the manus length, in this case the bimodal distribution is clear; C: IMS/IPS ratio. No clear relationship occurs between the two parameters. This could be the result of the different trends of the manus and pes sizes.



**Fig 4.18** – Trackway Ratio distribution. A: Pes Trackway Ratio frequency. Despite the small amount of trackways available, two clear peaks are evident: the first, around 44.5%, represents the medium-gauge morphotype 1c; the second, around 50%, represents the narrow-gauge tracks of morphotype 1A; B: Manus Trackway Ratio frequency. Also this plot shows two peaks, but, unlike the previous one, the higher percentage (around 35%) represents morphotype 1A and 1B, whereas the narrower lower represent the morphotype 1c tracks.



Concerning the trackway gauges, the PTR divides into two clear classes (Fig. 4.18A), one around 45%, the other around 50%. The first identifies a middle-gauge trackways, the second narrow-gauge. Moreover, looking at which footprints correspond to the lower PTR, it represents the smaller sauropod tracks, while the narrower tracks are made by *B. taghbaloutensis* type.

The MTR distribution (Fig. 4.18B) is missing the smaller sauropod data because they were impossible to measure, that is, all the bars refer to *B. taghbaloutensis* type of footprints. Three groups can be pointed out, but all are wide-gauge and around 30%, wider than the PTR.

The difference between the two TR suggests a morphology of the sauropod with the forelimbs larger than the hindlimbs.

**Fig. 4.19** – Biped trackway sizes distributions. A: foot length frequency; B: foot width frequency; C: Size Index frequency. All the three parameter co nsidereer show a rough bimodal distribution, but without differing too much from the gaussian curve. This can indicate a extra-faunal

#### 4.4.2 Group 2. Bipedal dinosaurs

The size and the Index of track Size distributions (Figs. 4.19A-C) for the tridactyl footprints show a clear predominance of the large biped dinosaur. In Fig. 4.19A other peaks can be noticed at about 17 cm, corresponding more or less to the morphotypes 2A and 2B. Indeed, the peaks at 25 and 30 cm do not belong to different types, but represent different sizes of the main 2c morphotype.

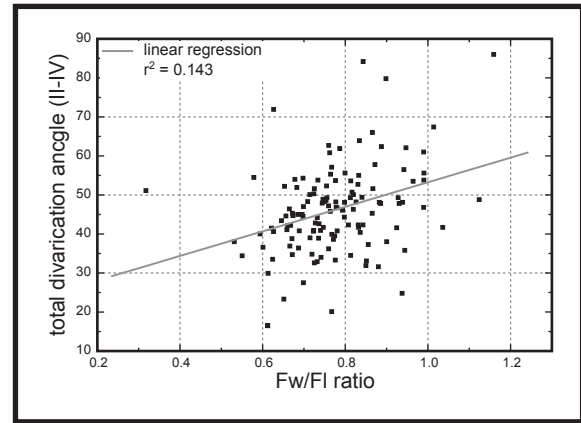
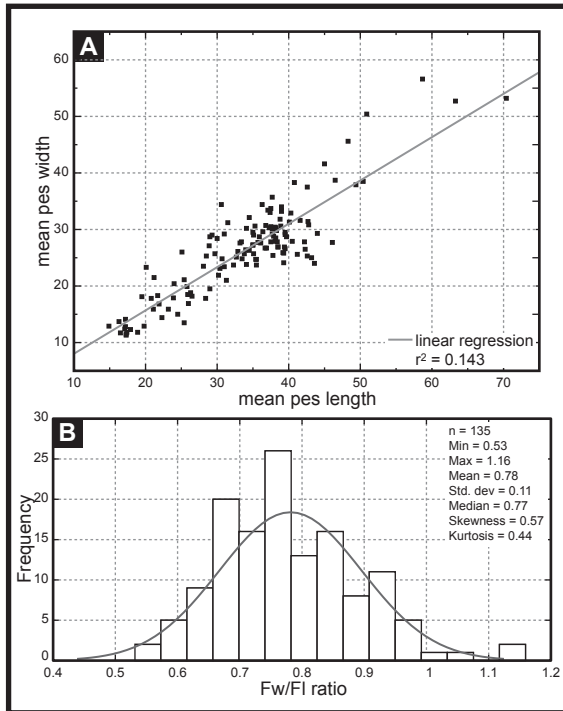
Fig. 4.20A shows the ratio between the pes length and width. The mean value for the ratio (0.78) is influenced by the larger amount of tracks of the morphotype 2c. The lower values correspond to the smaller footprints with narrower total interdigital angles.

The higher values (> 1) should be attributed to poorly-preserved tracks, where the actual length could not be measured properly. In the Fw/FI ratio frequency histogram (Fig. 4.20B) the peak around 0.95 is evident. This frequency can be explained by considering different causes: the dimensions of the tracks of the morphotypes 2B and 2E (see Detk MLXXIX description), and the preservation of certain tracks (e.g. Deio CXXX).

There are no other clear differences or separations resulting from these plots: this may indicate that the morphotypes are morphologically similar. However, for these plots only the mean values for each trackway have been considered, and this could have affected the resolution of the plot, mixing good and poor footprints. A solution could be that of considering only the best preserved footprints, but it goes beyond the aims of this work.

Fig. 4.21 plots the FI/Fw ratio against the total interdigital angles. Some tracks are missing from the record, because the angular values could not be measured. Even if the correlation is very low a broad trend could be found: the wider the divarication the wider the tracks (the higher is the Fw/FI ratio).





**Fig. 4.20 (left)** – A: plot of mean foot length (FI) against mean foot width (Fw) of all the tridactyl tracks of the Iouaridène ichnosite; B: distribution of the Fw/FI ratio for tridactyl footprints.

**Fig. 4.21 (above)** – Plot of the Fw/FI ratio against the II<sup>IV</sup> divarication angle. the correlation between the two variable is clearly very low.

This ratio is affected by the high variability of the total interdigital angle, which depends either on kinematics, or on extramorphological features, or on preservation factor. Nonetheless, this criterion is often used in literature to characterize tridactyl footprints (e.g. Thulborn 1990), and, if properly considered, it could help in the discrimination between theropodian and ornithischian bipedal tracks.

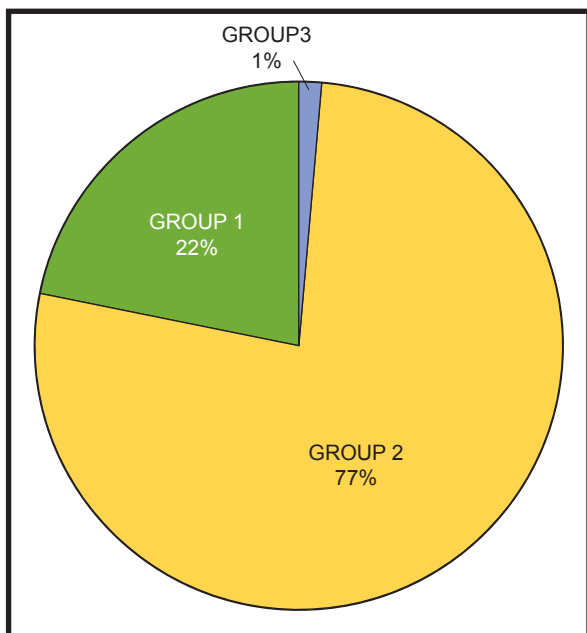
#### 4.4.3 Morphotypes relative abundances

The distribution of groups and morphotypes was carried out on the bulk of the tracks examined, but without considering the provenance layers. A layer-by-layer distribution would have been meaningless: whereas some levels are exposed for large surfaces, many other, especially in the lower part of the section, are visible in small and not continuous slabs, that is, not all the surfaces have the same exposure, so no comparison was possible.

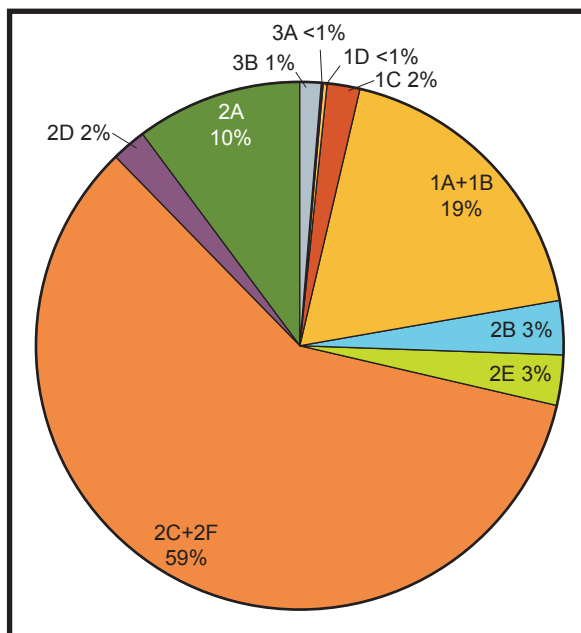
The group distribution (Fig. 4.22) highlights the predominance of the Group 2, the tridactyl footprints, against the other groups, covering more than three quarters of the total ichnoassemblage.

The relative distribution of the single morphotypes is shown in fig. 4.23. Morphotype 2F has been considered within the type 2c, because it almost always occurs in the same tracks of 2c tracks; the large sauropod tracks of morphotypes 1A and 1B are here considered together, because the manus-dominated tracks are considered related more to sedimentological features than to real anatomical differences.

Morphotype 2c is the most abundant of the site, covering the 59% of the entire association. The second more common type is the large sauropod of the morphotype 1A+1B with 19% of the association. The remaining fifth is shared by all the other groups (Fig. 4.23). It is worth noticing that the morphotype 1D, occurring with only 2 footprints, and covering something more than 0%, is one of the most notable findings in the site, as explained in Chapt. 5.1.6. Small tracks are generally poorly represented in the association (~12%), as well as the large tridactyl tracks (~4%); the non-dinosaurian tracks, counted as trail occurrence, are about the 1% only. The distributions within the single group are shown in Fig. 4.24A-C.



**Fig. 4.22** – Relative abundance of the groups singled out in the Iouaridène ichnosite. More than 3/4 (77%) of the ichnocoenosis is dominated by biped dinosaur; 22% is due to quadrupedal dinosaur; only the 1% corresponds to non-dinosaurian traces.



**Fig. 4.23** – Relative abundance of the morphotypes. More than a half (59%) is due to morphotype 2c and 2F, followed by morphotype 1A and 1B. All the other morphotypes account for less the 20% of the ichnocoenosis.

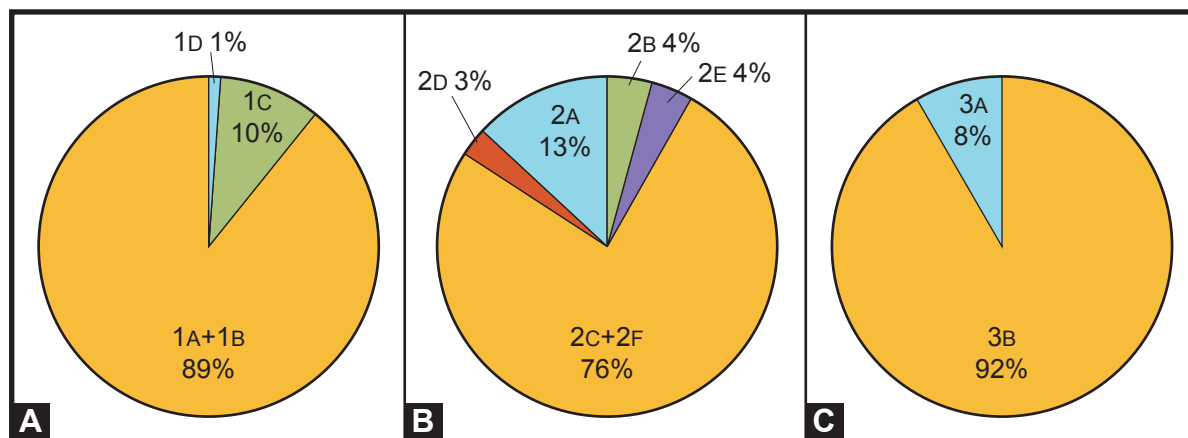
The small amount of tracks of light dinosaurs and of other small animals as well can be explained by the features of the substrate. As explained in Chapt. 3.5 the sediment was early consolidated by carbonate cementation. This, associated with a fast drying, made the surface firmer and allowed the preferential impression of heavier animal tracks.

In my opinion, this explanation fits better with the characteristics of the faunal assemblage which is completely lacking in tiny tracks, e.g. lizards, turtles, crocodiles.

### 4.5 TRACKWAYS DIRECTIONS AND LOCOMOTION SPEEDS

#### 4.5.1 Sauropod directions

All the sauropod trackways are essentially straight; some smaller turns are present in the longer trackways (e.g. Deio D, Chapt. 4.6.1) but are not relevant with respect to the main direction. The only evidence of turning sauropod is the track Deio CI: when it was relieved, the turning



**Fig. 4.24** – Plots showing the relative abundance of the morphotypes within each single group; A: Group 1; B: Group 2; C: Group 3.

was only supposed, because the preservation of the tracks after the bend is almost destroyed, but Ishigaki (pers. comm., 2008) who worked in the Iouaridène valley in the 1980s confirmed this hypothesis.

To determine the directions only those tracks occurring with at least two prints have been considered.

The rose diagram (Fig. 4.25A) shows the distribution of all the sauropod trackways. The main movement direction, considering the two opposite parallel directions, is NE-SW. Moreover, a S-heading peak is evident, which corresponds to the direction of the *B. taghbaloutensis* reference trackway and of the other similar tracks in the same area.

No interferences have been noticed between trackways, even in those belonging to the herds, and no crossings between sauropod trackways have been recorded.

#### 4.5.2 Biped directions

All the trackways are essentially straight, even if some turning can be seen in the longer ones. The only two exceptions are Deio VII and Detk XVII. The first one, left by a small theropod, has a small changing in the direction ( $\sim 30^\circ$ ). On the contrary, the second one, left by a large theropod, is the recorded of a  $90^\circ$  turning, made with only 7 tracks (see 5.6.11 for a detailed description).

Considering the low rotation of all the morphotype described, for isolated footprints the direction of the digit III axis has been considered as the movement direction.

Fig. 4.25B shows the direction of all the theropod tracks, from all the trampled layers. Main moving direction through NNW is evident. Excluding this main direction, the bipeds show an almost scattered moving distribution, even though a secondary main direction can be recognized ENE-WSW, parallel to the main sauropod direction shown in fig. 4.25A. No evidence of parallel bipedal trackways was recorded. Actually where many trackways are present, their directions are usually different from each other.

Crossing trackways have been recorded along the whole ichnosite, without any preferential area or direction. Interferences between tracks have been noticed and described track by track.

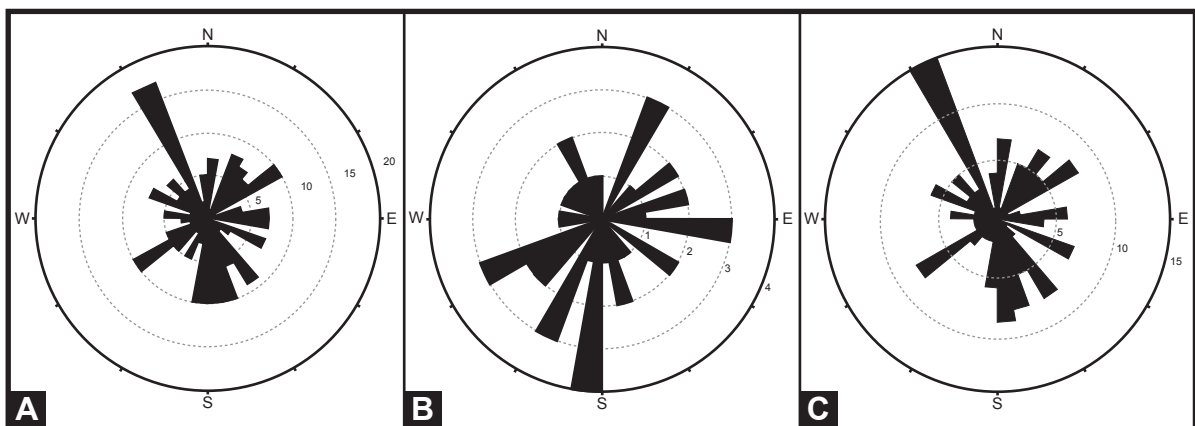


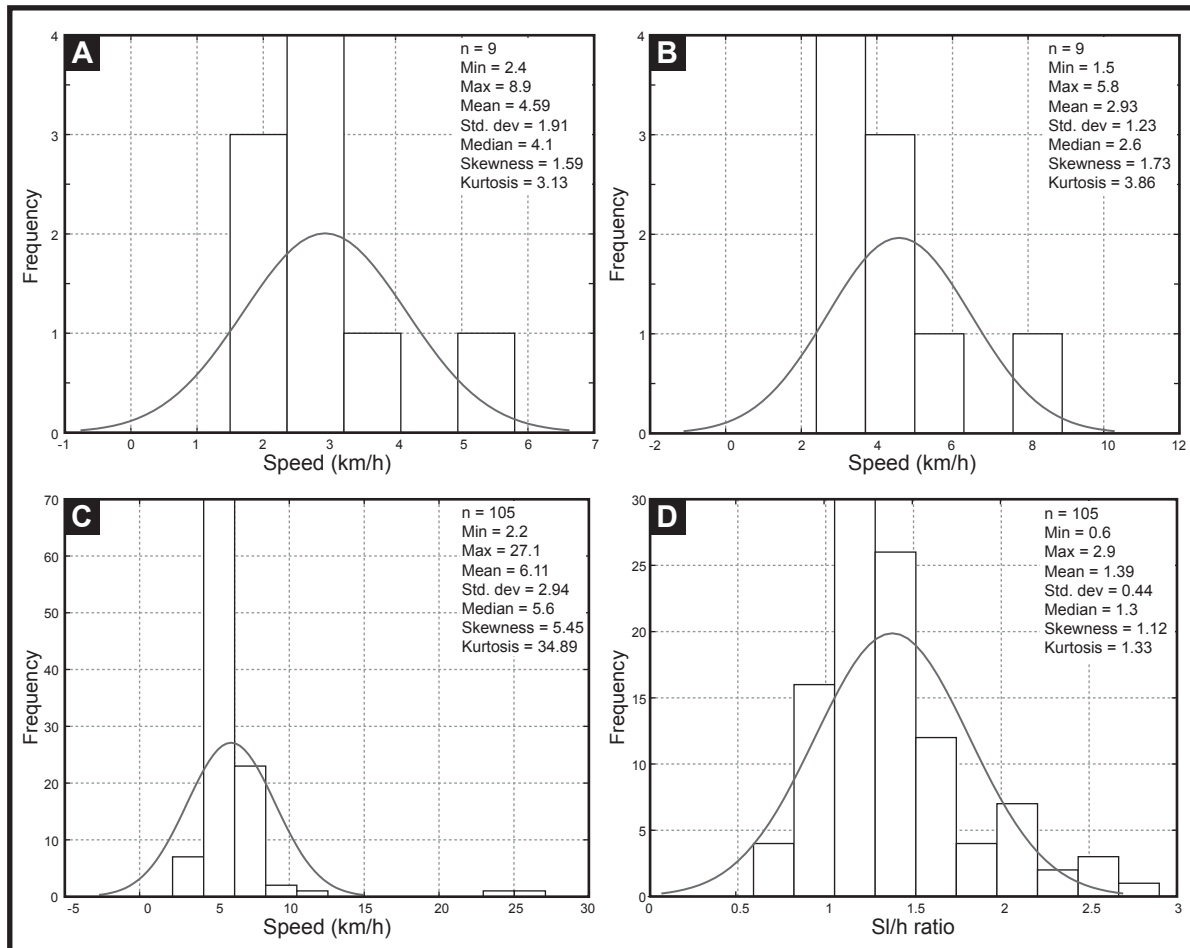
Fig. 4.25 – Rose diagrams showing dinosaur movement directions. All the directions have been corrected with the attitude. A: dinosaur movement directions; B: directions of bipeds; C: directions of sauropods.

#### 4.5.3 Sauropod locomotion speeds

The sauropod speeds (Appendix 4) have been calculated considering both the hip heights (eq. 1 and eq. 2) and using equation 6 (Chapt. 2.3 for explanations).

The velocities are usually around 4.0 or 2.5 km/h, considering hip height from eq. 1 and eq. 2

respectively. The slowest value is 2.4/1.5 km/h (Deio CI), but fits quite well the normal distribution. The maximum (Detk MLXXXVIII), on the contrary, is the only outlier of the distribution, with the extremely high value of 8.9/5.5 km/h (Fig. 4.27A, B). However, it has to be considered that this speed has been calculated on a manus-only trackway, by using the same equations than for the hindlimbs. However, the speed comparison calculated using the fore and hind limb of the same trackway gives according results, with a slightly higher speed for the hindlimbs. Then, also considering this value a bit higher than the actual one, it is one of the fastest for large sauropod.



**Fig. 4.27** – Speed and gait distributions. A: sauropod speeds, determined with the hip height derived by eq. 1; B: sauropod speeds, determined with the hip height derived by eq. 2; C: theropod speeds. The peak correspond to a slow speed (about 5 km/h), but higher values are present as well, with two specimens running faster than 20 km/h; D: SI/h distribution for trydactyls. Most of the specimens plot around 1-1.5, which corresponds to a walking gait. Few and rare are the very fast running dinosaurs, with a SI/h ratio higher than 3.

#### 4.5.4 Biped locomotion speeds

Values of speeds (Appendix 2) have been calculated with equations 6, 7 and 8 (see 2.3 for explanations), depending on the SI/h ratio, and with a hip height of  $4.5Fl$  for mean pes length smaller than 25 cm and  $4.9Fl$  for mean pes length higher than 25 cm, as suggested in Thulborn and Wade (1984).

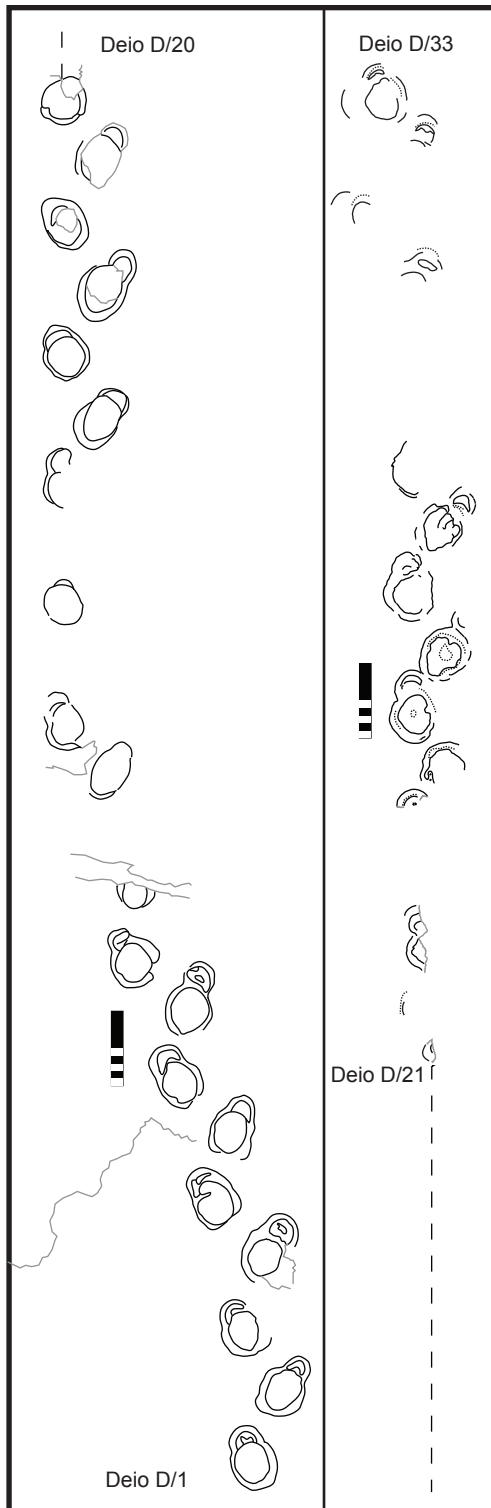
Fig. 4.27C shows the distribution of locomotion speeds for tridactyl tracks. Nonetheless, the range varies a lot from 2.2 km/h (Deio 28) to 27.1 km/h (Detk MXXVIII); most speeds plot in proximity of the mean (6.1 km/h). Only two outliers can be found (Deio XLI and Detk MXXXVIII) and represent the highest value of the tracksite.

The plot of the distribution of the SI/h ratio (Fig. 4.27D) also shows a peak around the value 2.0. This is mainly due to the small footprints ( $< 25$  cm), with the exception of Detk MXXXVIII,

which also represents the only record of non-walking large dinosaurs (morphotype 2c).

## 4.6 DISTINCTIVE TRACKS AND TRACKWAYS

In this paragraph detailed descriptions of some peculiar tracks and trackways of both the dinosaurian groups are reported.



**Fig. 4.28** – Schematic drawing of the Deio D trackway. Between tracks Deio D/20 and D/21 there is a 22 m gap. Scale bar 2 m.

### 4.6.1 *Deio D*

Here an update description of the *B. taghbaloutensis* trackway described by Dutuit and Ouazzou (1980) is given. The tracks occur as true tracks, on the surface of level 3. The general preservation is not excellent, but some morphological details can be recognized. The trackway lays on the trampled level 3, the main trampled level of the Taghbalout and Aït Mimoun area.

The trackway (Fig. 4.28) is composed by 33 tracks, and is long, non-continuously, about 86 m. There is a 22m gap between the tracks D/20 and D/21, due to the destruction of the trampled level. After this long gap the preservation is worse, and also the trackway continuity decreases. One right manus-pes couple and a pes are missing between the prints D/22 and D/23, while two other manus-pes couples are missing between D/29 and D/30. The direction, measured on the trackway midline, changes twice along the trackway ( $262^\circ$ ,  $250^\circ$ ,  $269^\circ$ ), while the stride length is almost constant. Pes rotations are asymmetric: the average rotation for the left pes tracks is  $15^\circ$ , while for the right ones is  $30^\circ$ , without notable changing close to the turns. The PTR is 50.1% and the MTR 33.7%.

Pes tracks are elongated, and the shape varies from elliptical to sub-triangular (bell-shaped). No digit impressions are present except for Deio D/28, where some four depressions, exteriorly bended, occur. No claw marks are present, and those illustrated by Ishigaki (1986, 1988, 1989) have been reinterpreted as dissection cracks dissecting the footprint outline. The maximum width of the track is usually in the middle of the pes elongation axis, but in the bell-shaped footprints it is positioned more anteriorly. Displacement rims are always present and are more developed on the anterior and external side of the tracks, while they are sometimes missing in the posterior (proximal) part of the pes print.

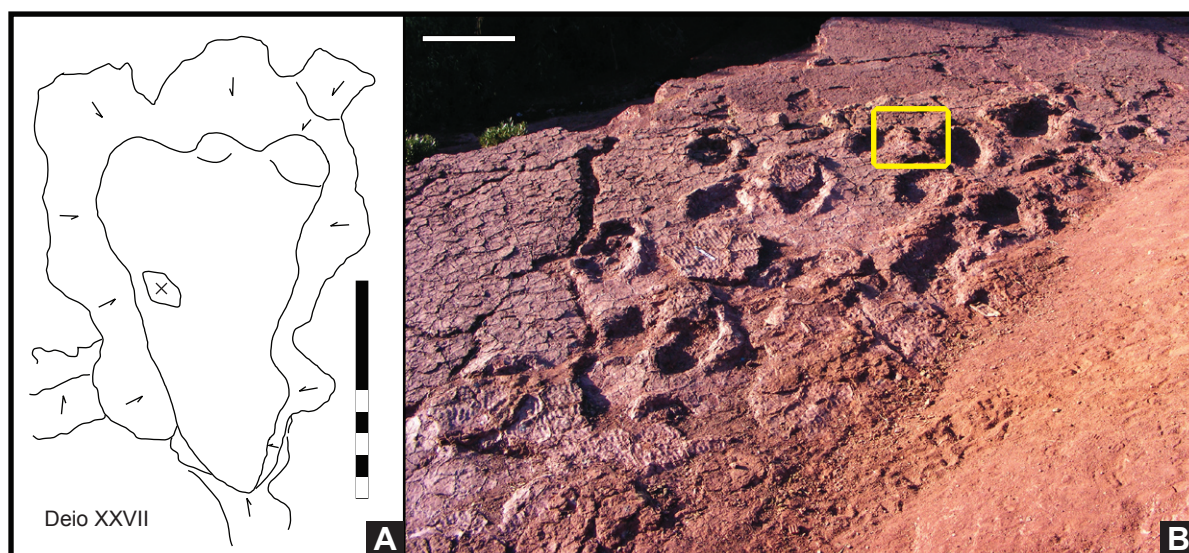
Manus tracks are always wider than long, crescent-shaped to semi-circular. The shapes have been probably deformed by the overlapping of the pes, which in one case (Deio D/16) almost covers the manus. No claw impressions or other morphological details are present. The position of the manus is almost always slightly more external with respect to the pes axis. Displacement

rims are common and well developed all around the tracks and, along the exterior margin, are connected to the pes rims without continuity solution.

#### 4.6.2 *Deio XXVII*

This specimen (Fig. 4.29A) was the first recognized of the morphotype 2D. It lays on the trampled level 2 of our survey, amid several parallel sauropod tracks (Fig. 4.29B). It is preserved as a true track, with sloping walls that make the exterior outline larger than the inner one. Thus, the external length is 209 mm and the external width is 156 mm, while the inner length is 166 mm and the inner width is 105 mm.

It is diagnosed as a triangular mesaxonic footprint, wider across the lateral digit impression, with one side slightly convex and the other slightly concave. On the concave side the wall is very steep, almost vertical, while on the other side it is less sloping. Three digits occur as short and blunt projections, the middle digit being the longest. A possible fourth digit impression could be found on the posterior part of the concave side of the footprint. No manus print has been found. A depth analysis has been carried out on 3D digital model, and showed an increasing of the depth from the rear to the front of the track.



**Fig. 4.29** – A: schematic outline sketches of Deio XXVII taken from actual footprints. Scale bar 10 cm; B: photo of the middle-small sauropod herd from trampled level 2. The yellow square indicates the position of Deio XXVII. Scale bar 1 m.

#### 4.6.3 *Detk MXC*

This specimen (Fig. 4.5) is the second footprint of the morphotype 2D, is preserved as underprint and outcrops in a small surface of the level -8, very close to the road to Tirika.

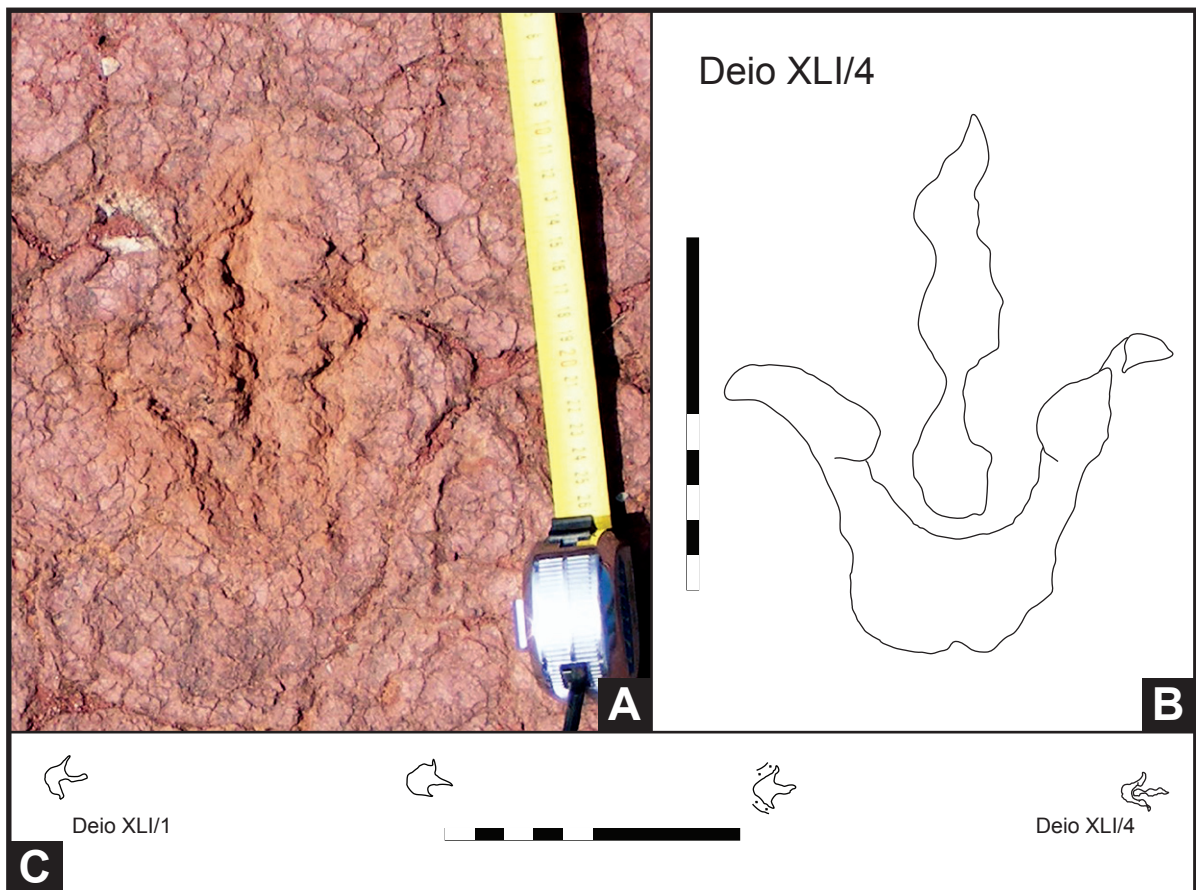
It is a shallow mesaxonic sub-triangular footprint, 257 mm long and 174 mm wide, larger anteriorly with three short and rounded digit impressions. The outline is more regular and less concave than Deio XXVII, and the “heel” is more rounded and deeply impressed. Also for this specimen, no manus print has been found. An in-depth study has been carried out on 3D digital model (Chapt.5.1.6; Belvedere and Mietto, submitted). Unlike in the previous track, in this case the depth is almost homogenous in all the footprints. However, it shallows more than the other specimen (Deio XXVII) approaching the concave side. These differences can be explained by the preservation affecting the two tracks: this footprint, preserved as underprint, bears less details than the previous one, left on a softer ground and preserved as true track.

#### 4.6.4 Deio XLI

This trackway (Fig. 4.29) belongs to the morphotype 2A and lays on the level 1. The trackway is composed by four small complete footprints and a partial one. The footprints are mesaxonic, slightly asymmetric, always longer than wide ( $Fw/Fl = 0.77$ ). The poor preservation prevents precise measurement of the divarication angle, but in the best preserved tracks it is narrow ( $< 50^\circ$ ), with the angle between digits II and III always narrower than the one between digits III and IV. All the digits have tapered terminations, even if no clear claw impression is recorded. The digit IV is the longest, followed by digits III and II. However, the digit III has the longest free length. The width is almost the same for all the three digits. The rear of the footprint is rounded, and seems partially formed by the digit IV. No clear pad impressions have been found.

The trackway, even if short, is very notable. The rotation of the footprints is null and the tracks are aligned on the midline. Paces and stride are very long in relation with the pes length, testifying a high speed. The  $Sl/h$  ratio is 3.7, and the speed is around 23 km/h.

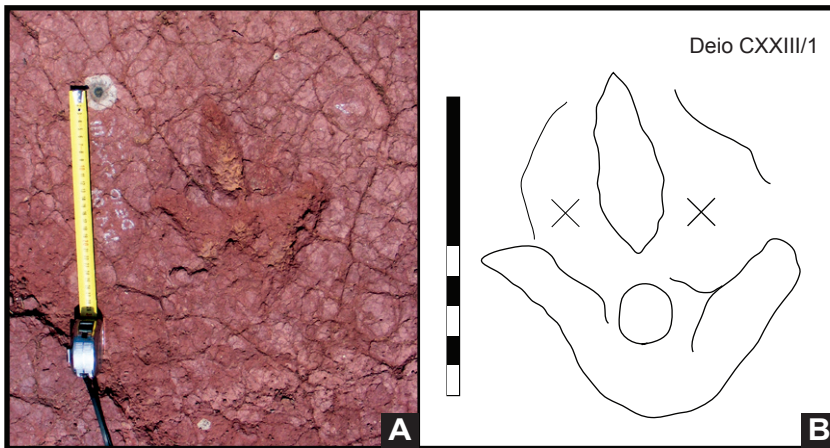
This is one of the few evidences of non-walking dinosaur, and, moreover, it is the trackway with the highest  $Sl/h$  ratio recorded for the entire ichnosite.



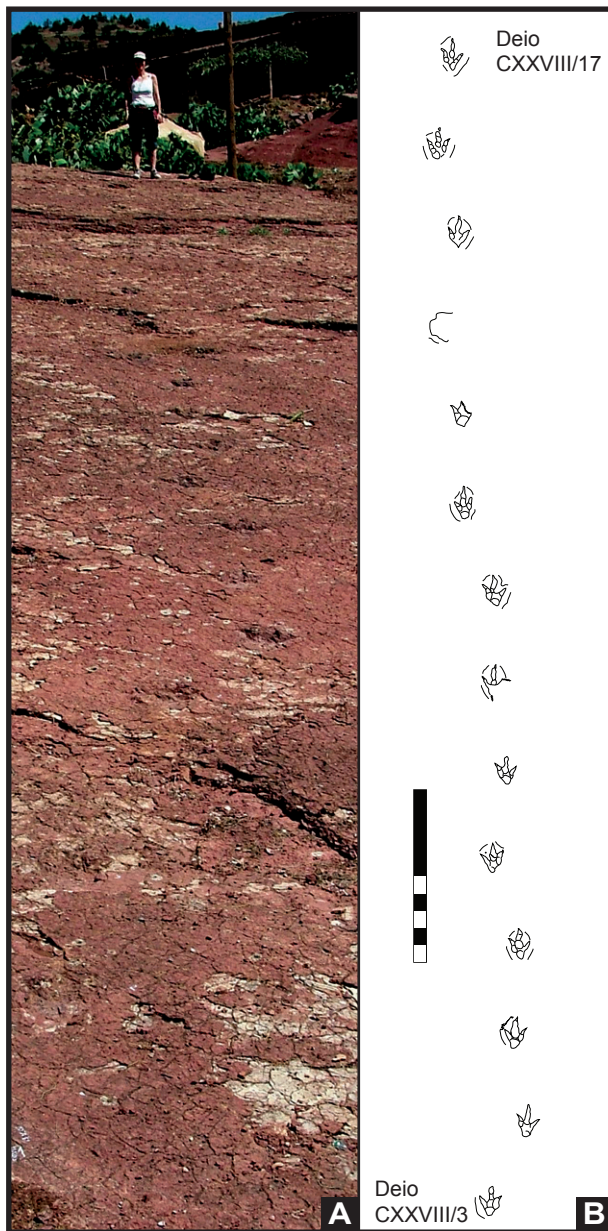
**Fig. 4.29** – A: photo of the small theropod footprint Deio XLI/4. Scale 25 cm; B: Schematic outline drawing of Deio XLI/4. Scale bar 10 cm; C: schematic drawing of the trackway Deio XLI. Note the very long pace strides with respect to the footprint size. Scale bar 1 m.

#### 4.6.5 Deio CXXIII

The footprints of this trackway (Fig. 4.30) are the more representative for morphotype 2B. Also these tracks come from the level 1. The tracks appear tridactyl, mesaxonic, as long as wide ( $Fw/Fl \sim 1$ ) with a high symmetry with respect to digit III. Digit III is the longest, but the difference with digits II and IV is slight, while the width is the same for the three digits. The total interdigital angle II-IV is wide ( $> 65^\circ$ ), with a high symmetry between the angles between digits II-III, and III-IV. The rear, when



**Fig. 4.30** – A: photo of Deio CXXIII/1. Scale 30 cm; B: schematic outline drawing of Deio CXXIII/1. Scale bar 20 cm.



**Fig. 4.31** – A: photo of the medium-large theropod trackway Deio CXXVIII, trackway taken from the same level, behind the first footprint; B: schematic outline drawings of a particular of Deio CXXVIII trackway (from Deio CXXVIII/3 to CXXVIII/17). Scale bar 2 m.

preserved, is rounded. No pad impressions have been found.

The trackway is composed only by three footprints, with a light external rotation ( $< 10^\circ$ ). The trackway (Fig. 4.7) is narrow, but the footprints are not aligned on the midline. The pace length is high with respect to the footprints size, even if the speed is lower than the one of Deio LXI.

#### 4.6.6 Deio CXXVIII

These tracks belong to the morphotype 2c, and represent one of the best preserved tracks of the entire ichnosite, even if the preservation varies a lot along the development of the trackway (Fig. 4.31). It lays on the trampled level 3.

The footprints are tridactyl and mesaxonic, longer than wide ( $Fw/Fl = 0.74$ ), with a clear asymmetry with respect to the digit III axis. The longest digit is the IV, whose proximal pad is aligned with the digit III axis and forms the rear of the footprint. Digit III has the longest free length and is characterized by a typical bending towards the inner part of the trackway. Digit II is the shortest and presents a certain mobility of its more distal part. Claw impressions occur in all the tracks. In the Deio CXXVIII/16 almost all the pad impressions are preserved, so that it is possible to determine the phalangeal formula: 2-3-4, respectively for digits II, III and IV. The total divarication angle is narrow ( $\sim 45^\circ$ ) with marked differences between the narrower angles between digits II-III ( $\sim 14^\circ$ ) and the wider between digits III-IV ( $\sim 31^\circ$ ). While the values of the angle between III-IV



have a low variability, the other can change more, from  $8.3^\circ$  to  $28^\circ$ .

The trackway is discontinuous and composed of 21 footprints. The highest gap is between Deio CXXVIII/17 and Deio CXXVIII/18 where three consecutive tracks are missing. The trackway is not straight but makes several small turns, even if a prevailing direction can be recognized. The gauge varies from middle to narrow, depending on the portion of the trackway considered, while the rotation of the footprints is always very low ( $< 5^\circ$ ) or absent.

The paces are usually short with respect to the size of the tracks, and the pace angle is usually close to  $180^\circ$ .

#### 4.6.7 Detk MXXIV

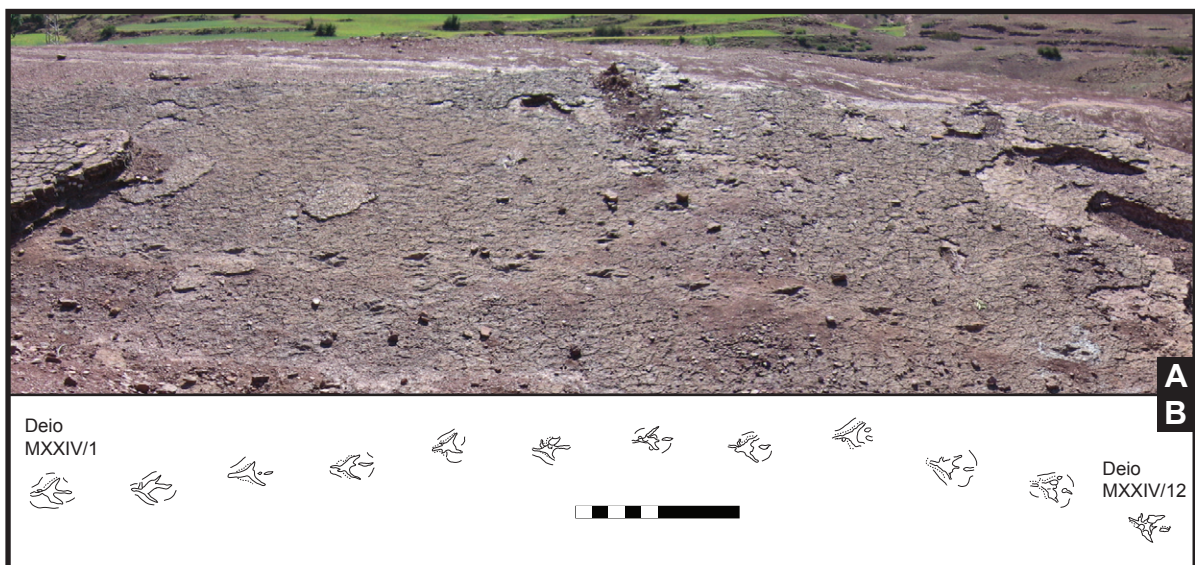
This trackway (Fig. 4.32) represents the best sample of the morphotype 2D, and lays in the level -3. Here the footprints show clearly the four digits and metatarsal impressions.

The tracks are mesaxonic, slightly asymmetrical, and, without taking into account the metatarsal impression, longer than wide. All digits are elongated and tapered. Digit IV looks the longest, followed by digits III, II and I, but the lacking in phalangeal pads does not give certainty for this assumption. The width of digits II, III, and IV is similar, while the hallux is always smaller. The digit III is often separated from the rest of the track by the collapse of the walls and the sediment filling; in two cases (Detk MXXIV/5 and MXXIV/9) digit III is completely filled by the sediment and can be “seen” only thanks to its lateral displacement rims. In every print where it is well defined, digit III shows a light inward bending.

The total divarication angle is wide ( $> 60^\circ$ ), with the angle II-III narrower ( $\sim 25^\circ$ ) than III-IV ( $\sim 39^\circ$ ). The hallux is always directed laterally, in some cases bending towards the anterior part of the footprint. It forms an average angle with digit II of about  $73^\circ$ . The metatarsal impression is straight and slightly angled ( $\sim 12^\circ$ ) towards the inner side of the trackway with respect to the digit III axis.

A careful analysis of the outline highlighted the presence of a less steep wall in the external side of the footprint. This could have been produced by a sliding of the pes, due to the soft and slippery substrate at the time of the impression.

The trackway is composed by 13 continuous footprints, with relatively short paces ( $\sim 1$  m), and also quite narrow-gauged. The footprints have a really small outward rotation ( $< 5^\circ$ ) for all the trackway length, also where some changing in the direction occurs. No evidences of changes in the pace lengths occur, neither in the turning portions.



**Fig. 4.32** – A: photo of the trackway Detk MXXIV; B: schematic drawing of the trackway Detk MXXIV. It is clear the intersection with Detk MXXV, directed to the top of the picture.

Displacement rims are present in all the footprints and are more developed around the external side of the track and in the anterior, around the digit III.

#### 4.6.8 Detk MLXXIX

Detk MLXXIX, laying on level 0, even if preserved with a poor detail, is the only representative trackway for the morphotype 2E, and it is composed by seven continuous and shallow footprints (Fig. 4.33). Before describing the tracks and the trackway, it is worth noticing that these tracks are probably preserved as underprints, if not as undertracks, producing the occurrence of two outlines: one internal, corresponding more or less to the actual footprint size, and one external. Measurements have been taken on the inner outline, to have more realistic data.

The tracks are mesaxonic, as long as wide (fw/fl ~ 0.9), with three well-separated, straight, and tapered digits. Digit II is usually shorter than the other two, while it is difficult to determine which is the longer between digits III and IV. The width is similar for all the digits. The footprints are fairly symmetric, with the interdigital angle between digits II and III (24.5°) a few degree narrower than the one between digits III and IV (29.5°). The total divarication is narrower than it appears at a first glance (~ 54°). Some phalangeal pads occur in the digit III of Detk MLXXIX/4. The rear of the footprints is always rounded, but this shape is probably the result of the preservation as underprint.



**Fig. 4.33** – A: photo of Detk MLXXIX. The shallow impressions and the inappropriate illumination conditions have made the tracks very difficult to identify. Lisa for scale; B: schematic drawing of Detk MLXXIX. Scale bar 1 m.

The trackway has very irregular and short paces, with respect to the very large size of the footprints. As irregular as the pace lengths are the rotations of the tracks: although it is possible to see a general low outward rotation, each footprint has a different angle.

A further note due on this trackway is that it was at the centre of a controversy between Ishigaki (1989, Fig 9.4) who interpreted it as a manus-only sauropods track, and Meyer and Monbaron (2002), who stated, correctly, that it was a tridactyl trackway.

#### 4.6.9 *Deio XLII*

This single footprint (Fig. 4.34) lays on the level -2, and is one of the largest present on the ichnosite. It is impressed on a very thin layer, topped by symmetric ripple marks. It is a trydactyl and mesaxonic track, longer than wide, with the rear part tapering. Digits are straight, with digit IV the longest, followed by digits III and II. The digit II seems to have a greater mobility with respect to the other. The interdigital angles are slightly different, with the II-III one narrower (25°). The total divarication is narrow.

Its importance consists in the morphological details, which are the best for the morphotype 2E.

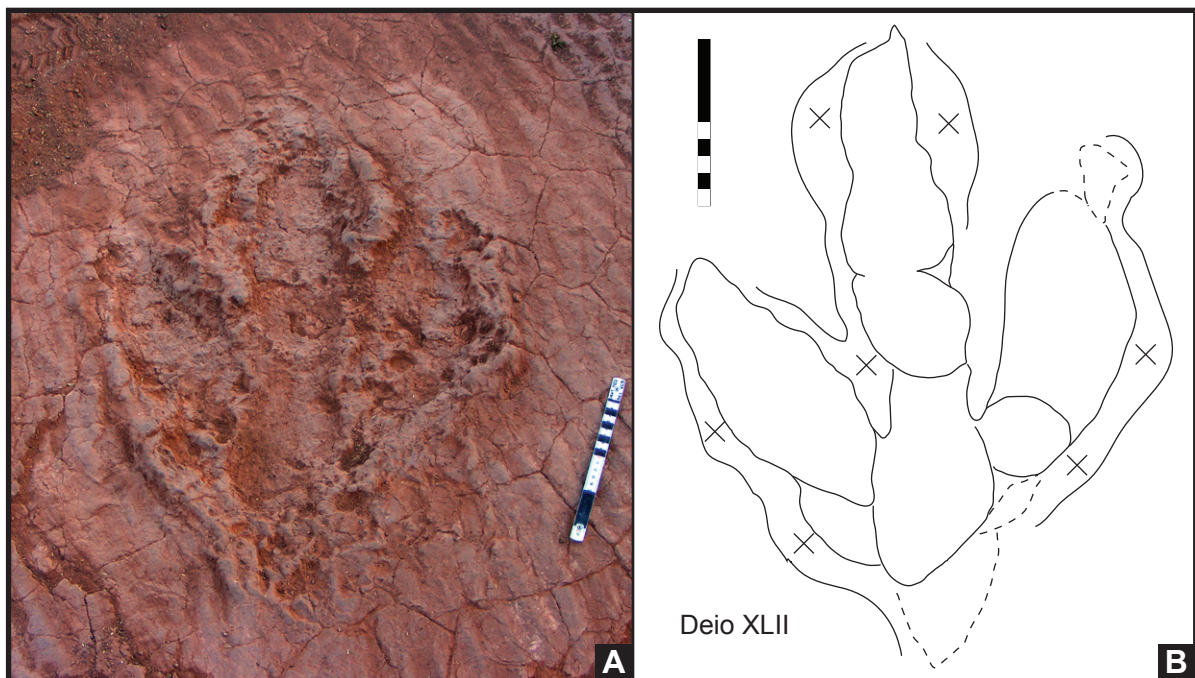


Fig. 4.34 – A: photo of Deio XLII. Notice the symmetric ripple marks crossing the surface; B: schematic drawing of Deio XLII. Scale bars 20 cm.

#### 4.6.10 *Deio DVI*

This trackways (Fig. 4.35) from level 2 correspond to the trackway 1Am2 of Nouri (2007), which is considered the type trackway for *Eutynichnium atlasichnus*.

The trackway is composed by 6 generally tridactyl, mesaxonic tracks. Digit III is always bended inward, and a light asymmetry is visible between the interdigital angles, with the II-III angle narrower than III-IV. The general preservation is poor and no clear morphological details are evident except for some phalangeal pad impressions in DVI/6. DVI/2 is elongated and has an impression that could be interpreted as a digit I print.

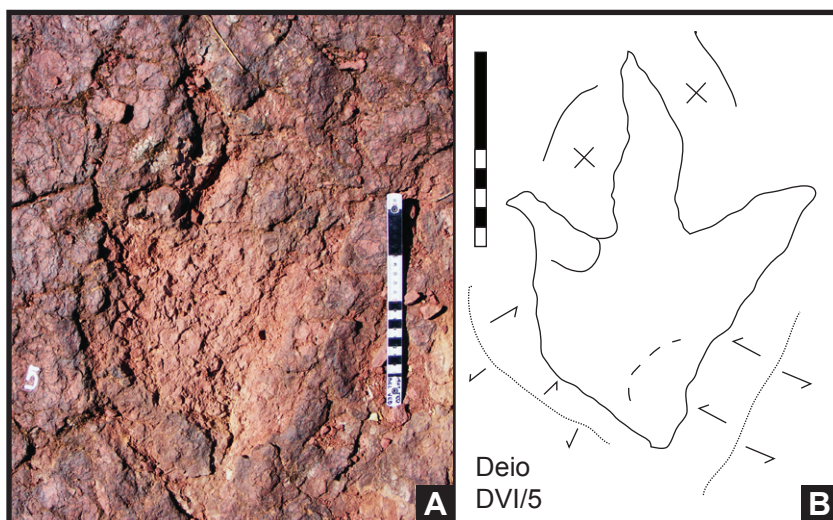
No other tetradactyl or supposed tetradactyl tracks can be recognized in this trackway.

The trackway gauge is quite wide, with the footprints touching the midline only with the digit II termination. Footprints are very slightly outward rotated.

A consideration is due to define the holotype of *E. atlasichnus*, defined on the footprint Deio



**Fig. 4.35** – A: photo of the Deio DVI trackway, proposed as type trackway for *E. atlasichnus* (Nouri 2007). Scale 14 cm; B: schematic drawing of Deio DVI. Scale bar 1 m.



**Fig. 4.36** – A: photo of this specimen proposed as holotype for *E. atlasichnus* (Deio DVI/5). Scale bar 20 cm; B: schematic drawing of Deio DVI/5; in my interpretation there is no first digit at all, that is, the footprint is here considered tridactyl. Scale bar 20 cm.

DVI/5 of this work (Fig. 4.36).

In my opinion, there is no evidence of the fourth digit as described in Nouri (2007), and generally the preservation of these trackways, but also of the other similar tetradactyl tracks described as topotypes, is too poor to institute a new ichnospecies. Moreover, if we consider the mess that reigns in the taxonomy of this group of theropod tracks, the institution of a new ichnospecies on such poor material would only increase the grade of confusion.



# 5 INTERPRETATION AND ICHNOTAXONOMY

---

In this chapter the morphotype will be compared with the known ichnogenera. However, when not definitely classifiable (e.g. the *B. taghbaloutensis* trackways), I prefer not to name the morphotypes, in order to prevent further confusion in the dinosaur ichnotaxonomy, especially that of tridactyls. However, to delineate the ichnoassemblage better, when possible, we illustrate the affinity of the trace to known ichnotaxa.

## 5.1 ICHNOTAXONOMY OF GROUP 1

### 5.1.1 *Sauropod classification criteria*

Besides the classical morphological measurements on the pes and manus tracks, Farlow et al. (1989) also introduced some trackway parameters in the description of the *Brontopodus birdi*. Then, Farlow (1992) proposed a classification of sauropod tracks based on the trackway gauge, suggesting that a trackway can usually be described as narrow-gauge or wide-gauge.

Meyer et al. (1994) and Lockley et al. (1994b) introduced a third category, the medium-gauge. They also affirmed that basing the classification only on the trackway gauge was premature, but they pointed out the value of studying gauge differences and heteropody. Nevertheless, in more recent works (Wilson and Sereno, 1998; Wilson and Carrano, 1999), heteropody was not considered a notable character in the phylogenetic taxonomy of sauropods.

However, Farlow (1992) himself and subsequently Wilson and Carrano (1999) inferred that the gauge variation could be made by different substrate characteristics, or to different locomotion speeds, or could be related to the skeletal morphologies.

Wright (2005), basing on some gauge variation occurring in some *B. birdi* trackway segments, recommended that sauropod tracks should be classified mainly on the morphology of manus and pes and only secondarily on the trackway gauge.

Moreover, to increase the degree of confusion, Lockley et al. (2002a), basing on evidences of titanosaurid trackways, highlighted the possibility that this group of sauropods could change from narrow- to wide-gauge during the ontogenetic growth.

Despite all these problems, the trackway gauge is commonly used for ichnotaxonomical attributions of sauropod tracks and in determining the trackmaker (e.g. Lockley et al 1994b, 2002a, b; Moratalla et al., 1994; Dalla Vecchia et al., 2000; Day et al., 2002, 2004; Avanzini et al., 2003; Marty et al., 2003; Moreno & Benton, 2005; Marty, 2008).

Nonetheless, recently Romano et al. (2007) introduced the Trackway Ratio, a new quantitative parameter to measure the trackway gauge. According to the authors' opinion that "quantitative definitions of the gauge terms would not only be useful in a descriptive sense but also would enable more meaningful comparisons to be made between trackways", the Trackway Ratio has been calculated for all the sauropod morphotypes of the Iouaridène ichnosite, both for manus (MTR) and pes (PTR). Here the TR, especially the manus track ratio, has been used not only in description but also to compare the manus-dominated trackways with the complete tracks.

### 5.1.2 *Review of Middle Jurassic/Cretaceous sauropod ichnogenera*

This paragraph reports the original descriptions of the three sauropod ichnogenera considered valid (Lockley et al., 1994b) for the Middle Jurassic/Early Cretaceous that will be compared to the Iouaridène morphotypes (Fig. 5.1).

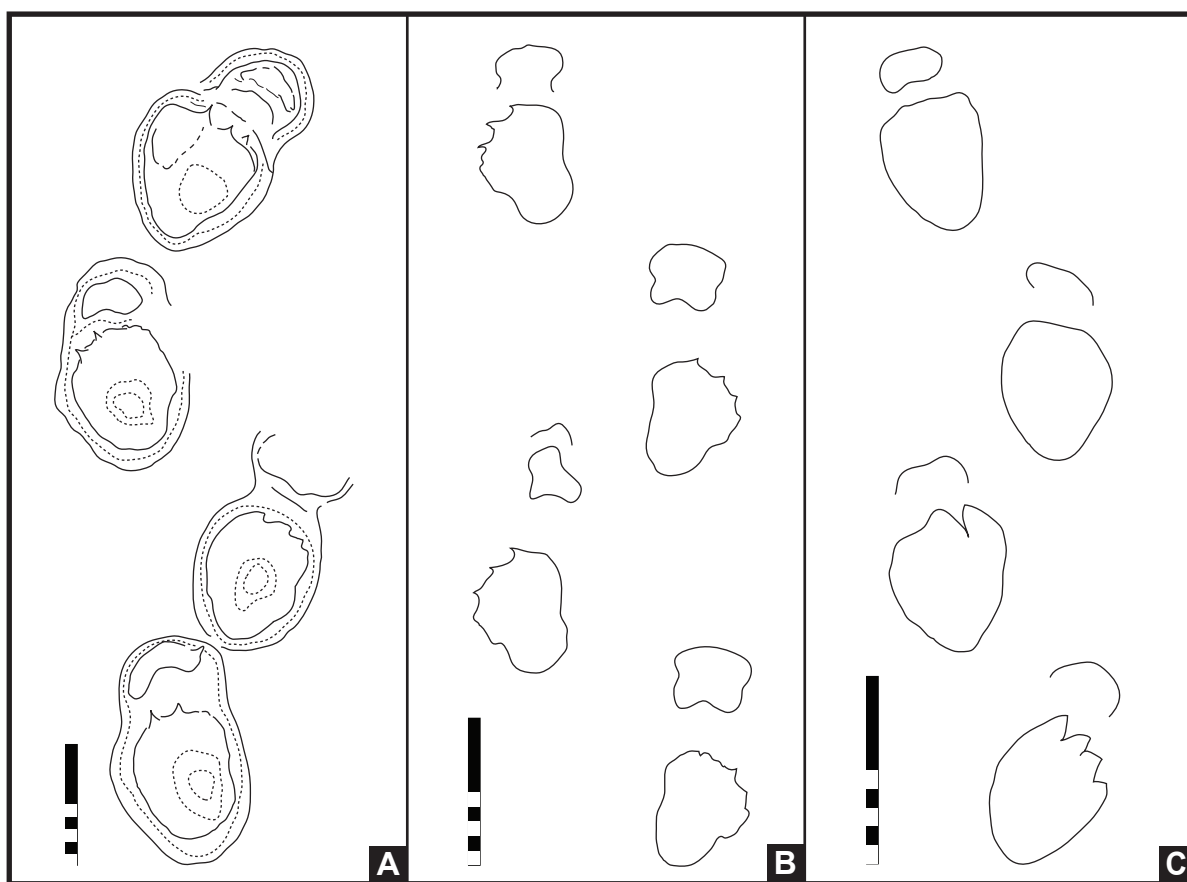
It is worth noticing that among the sauropod tracks considered there is the reference trackway

considered for *Breviparopus taghbaloutensis* Dutuit and Ouazzou 1980, and described in detail in paragraph 4.6.1.

### ***Breviparopus* Dutuit and Ouazzou 1980**

Firstly it is worth noticing that the authors gave this name to the tracks without any taxonomical aim, but just for descriptive purposes: “par simple commodité de désignation, et sans que cette appellation ait une quelconque valeur taxonomique, nous désignerons la piste et les empreintes du Sauropode de Taghbalout sous le nom de *Breviparopus taghbaloutensis*”. (Fig. 5.1A)

The description given for the ichnogenus is detailed, despite the period in which it was written: the tracks are described as having a very narrow posterior gauge, with the pes tracks crossing the midline and manus tracks with a larger gauge (“faible écartement des empreintes postérieures. Elles empiètent sur l’axe de la piste. Écartement plus grand des empreintes antérieures”); manus tracks are semicircular with any digital prints (“l’empreinte de patte antérieure est sensiblement en demi-cercle [...]. Aucun doigt n’est visible”) and positioned in front of the pes, partially overlapped by the posterior tracks (“l’empreinte laissée par le membre postérieur suit immédiatement celle du membre antérieur, le bourrelet antérieur de la première et le bourrelet postérieur de la seconde se confondant”). Pes tracks are sub-elliptical to triangular, with four digits impressions and claw marks (“l’empreinte de patte postérieure s’inscrit dans une figure géométrique intermédiaire entre le triangle à sommet postérieur et petit côté antérieur et l’ovale déformé s’effilant en arrière [...], on remarque aussi la présence d’encoches sur le bourrelet antérieur de l’empreinte postérieure, bourrelet qui témoigne ainsi de l’existence de griffes.”). Manu and pes tracks have parallel axes, rotated outward by 30° from the midline (“les axes des empreintes antérieure et postérieure sont sensiblement parallèles et font un angle de 300 environ avec celui de la piste”). Moreover, a pronounced heteropody is described (“La surface



**Fig. 5.1** – A: *Breviparopus taghbaloutensis*. Redrawn from Ishigaki’s original sketches (Ishigaki, pers. comm, 2008). Scale bar 1 m; B: *Brontopodus birdi*. Redrawn from Farlow et al. (1989). Scale bar 1 m; C: *Parabrontopodus mcintoshi*. Redrawn from Lockley et al. (1994). Scale bar 1 m.



d'empreinte postérieure est donc 3,6 fois plus grande que celle de l'empreinte antérieure”).

### ***Brontopodus* Farlow, Pittmann & Hawthorne 1989**

This ichnogenus is based on the type species *Brontopodus birdi*, the first ichnotaxon described considering also the trackway parameters (Fig. 5.1B). Thanks to the excellent preservation, the authors gave a very detailed description instituting this ichnotaxon:

“Sauropod ichnites of small to large size, known pes footprint length ranging 50 to over 100 cm. Manus footprint length and width about the same in well-preserved tracks; manus tracks clawless, somewhat U-shaped, with digit impressions I and IV slightly separated from the impression of the conjoined digits II-IV. Pes tracks longer than broad, with large, laterally directed claw marks at digits I-III (diminishing in size from I to III), a small claw, nail, or callosity mark at digit IV, and a small callosity or pad mark at digit V; digit marks IV and V only seen in well-preserved footprints. Manus tracks often (usually?) rotated outward with respect to direction of travel. Manus track medial to a line through pes track long axis, such that manus track centers are somewhat closer to the trackway midline than pes track centers. Trackway broad, with left and right manus and pes footprints often well away from the trackway midline; trackway width roughly 1-1.5 times pes track length. Outer limits of trackway defined by pes tracks. Manus-pes distance 0.5-1.2 times pes footprint length. Stride length roughly 2-5 times pes track length. Step angle generally 100-120°. Glenoacetabular length c. 3-4 times pes track length. Tail drag marks rare or absent.”

### ***Parabrontopodus* Lockley, Farlow and Meyer 1994**

This ichnogenus (Fig. 5.1C) is described by the type species of *P. mcintoshi*, and the description focuses heavily on the trackway pattern: “Narrow sauropod trackway of medium to large size (footprint length about 50-90 cm), characterized by no space between trackway midline and inside margin of pes tracks. Pes footprint longer than wide with long axis rotated outward. Pes claw impressions, corresponding to digits I, II and III show strong outward rotation. Manus tracks semicircular and small in comparison with the pes tracks (i.e. pronounced heteropody).”

#### **5.1.3 Discussion of Morphotype 1A**

The original reference material of the *B. taghbaloutensis* belongs to this morphotype, so the ichnotaxonomical assignment is certain (Fig. 5.2A). Nonetheless, besides the type material of the ichnospecies, many other tracks have been examined adding new information, especially regarding the shape and position of the manus. Manus track described in literature are more overprinted than supposed, and their actual shape, when preserved, is subcircular. Moreover the position of the forelimb prints can vary more than described by Dutuit and Ouazzou (1980) and Ishigaki (1985, 1986, 1988, 1989), but always with a gauge wider than the one for the hind limb.

Another morphological difference between the described genus and the Iouaridène material is the rotation angle. Dutuit and Ouazzou (1980) described an outward rotation of the footprints axes of 30°, but an asymmetry in the rotation has been noticed: around 30° for the left tracks and around 15° for the right.

The calculated PTR (50.2%) is wider than the one based on literature drawings computed by Romano et al. (2007), which is 51.48% or 53.54% using the drawings of Ishigaki (1989) or Thulborn (1990), respectively.

This can be easily explained because the published material refers almost exclusively to the best preserved and more narrow-gauge four tracks of the type trackway (Deio D/25 to Deio D/28), while this computation is based on all the available tracks of this type in the site. For the first time the MTR has been calculated giving a value of 34.1%.

The only other narrow-gauge ichnogenus known for this period is *Parabrontopodus*. Wright (2005) argued that instituting the taxon Lockley et al. (1994b) did not differentiate it from *Breviparopus*. Thus the new genus should be considered a juvenile synonym of *Breviparopus*. Here the differences are given between the two ichnogenera, which are both considered valid and not synonyms. Moreover, most differences concern the morphology of the tracks and not the trackway, so that also the suggestions of Wright (2005) in using trackways' parameter as taxonomical discriminator are respected.

The *Breviparopus* manus is subcircular while the *Parabrontopodus* is semicircular. Moreover, the manus in *Breviparopus* is more usually more external.

The average PTR for *Parabrontopodus* calculated on the Romano et al. (2007) data is 53.50 %, clearly narrower than the TR calculated for *Breviparopus*.

Recently Lee and Lee (2006) published some “*Parabrontopodus*-type” tracks from the Early Cretaceous of Korea with comparable sizes and pattern, but both MTR and PTR are sensibly narrower than those of *Breviparopus*.

#### 5.1.4 Discussion of Morphotype 1B

Sauropod manus-only and manus-dominated trackways are well known in the ichnological record of Middle/Late Jurassic to Maastrichtian, but no ichnotaxon has been instituted so far.

This morphotype differs from those described by Bird (1944; 1985) and Pittman (1989) for the manus morphology which is more similar to the tracks described in the Kimmeridgian of Portugal (Lockley et al., 1992c; Lockley and Santos 1993) and from the Aptian of Korea (Lee and Huh, 2002; Lee and Lee 2006).

The average MTR is 36.4%, comparable to the *B. taghbaloutensis* MTR (34.1%). Moreover, the sub-circular shape and the size are similar to those of the undeformed manus prints of the morphotype 1A. These considerations allow to suppose the same trackmaker for both the morphotypes.

There are two main hypotheses to explain the formation of these manus-only and manus-dominated tracks:

the first, introduced by Bird (1944) and drawn on by Ishigaki (1989) to explain some of the trackways of the Iouaridène ichnosite, supposes a “swimming” sauropod, which walks with its fore limbs while the hind legs were floating in the water and occasionally kick the ground;

the second hypothesis (Lockley and Conrad, 1989) suggests that the manus-dominated tracks are underprints, with a differential impression and preservation of manus and pes. The fore limbs would have sunk more in the sediment because the downward force is translated in the direction of the movement and, also, because of a smaller surface, causing a deeper deformation of the substrate than the hindlimbs.

In the Iouaridène ichnosite, the manus dominated trampled surfaces are often topped by symmetrical ripples that, as also suggested by Meyer and Monbaron (2002), could not form under the 3-4 m of water necessary for the sauropod to float.

Moreover, a detailed stratigraphic analysis shows that the trackways figured by Ishigaki (1989, figs 9.2 and 9.3) lay on the same layer, on a level few cm under the *B. taghbaloutensis* reference trackway.

In addition, on the same surfaces many other footprints of different types and sizes have been found.

Without excluding the swimming capabilities of sauropods, the only hypothesis to explain such a number of different tracks preserved together with manus-dominated is the one proposed by Lockley and Conrad (1989). Furthermore, the paleoenvironmental reconstruction of the site (par. 3.xx) does not allow the presence of the 3-5 m of water necessary to float such large

sauropods.

### 5.1.5 Discussion of Morphotype 1c

The morphological characteristics of this morphotype are different from those of the other sauropod of the site. The PTR is 44.7%, so it can be described as a medium-gauge sauropod (Fig. 5.2B).

It differs from *B. taghbaloutensis* not only because of the trackway gauge, but also for the shape of the pes and the shape and position of the manus, which in this type is not rotated laterally. Moreover the manus tracks gauge seems narrower than that of *Breviparopus*, even if the bad preservation prevents calculation of a meaningful MTR.

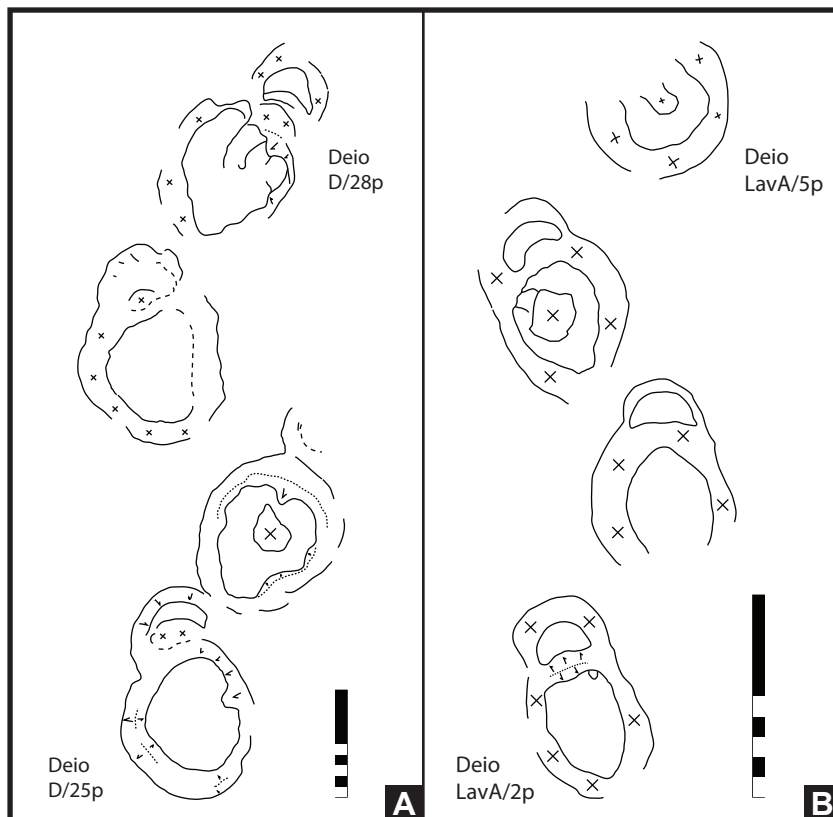
The main difference from *Parabrontopodus* is found in the trackway gauge. The manus and pes morphology are similar and in a preliminary interpretation they were described as *Parabrontopodus*-like (Belvedere et al., 2007).

The tracks and the trackways have features which are comparable with the footprints from Portugal figured in Meyer et al. (1994, fig. 4) to describe the medium-gauge trackway pattern. Similarities can also be found also with the tracks described from a herd of juvenile sauropods from the Late Jurassic of Portugal (Lockley et al., 1994a).

Actually most of the tracks of this morphotype occur within a herd bearing at least 5 parallel trackways, but no clear evidence of a juvenile ontogenetic state occurs.

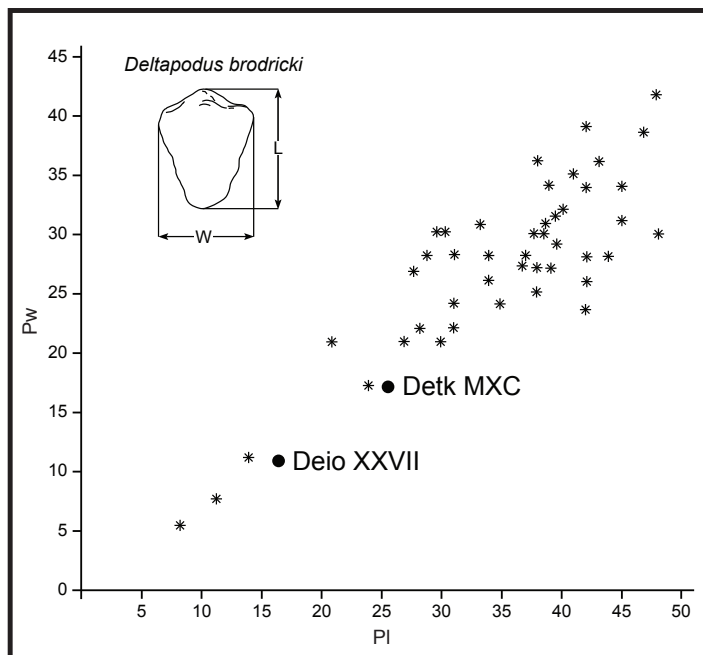
### 5.1.6 Discussion of Morphotype 1d

The morphological characteristics of this morphotype are close to the sauropods' but differ in that they are mesaxononic and three-toed.



**Fig. 5.2** – Examples of large and medium sauropod tracks and trackways. A: particular of a *B. taghbaloutensis* trackway. Scale bar 1 m; B: particular of Deio LavA trackway. Scale bar 1 m.

The only tridactyl and semi-plantigrade taxa for the Middle/Late Jurassic are those referred to stegosaurian dinosaur. Thus the two footprints have been compared with *Stegopodus* Lockley and Hunt 1998, and *Deltapodus* Whyte and Romano 1994. *Stegopodus*, occurring in the Upper Jurassic Morrison Fm of Utah, is characterized by three



**Fig. 5.3** – Scatter diagram showing plots of pes length (*Pl*) against pes width (*Pw*) for the 46 English specimens of *Deltapodus brodricki* (stars) and the Iouaridène specimens (dots). Redrawn from Whyte et al. (2007, fig. 13) and modified with new data.

long digits with well impressed phalangeal pads. The Iouaridène material is very dissimilar from *Stegopodus*, as it lacks the pad impression, and has very short and blunt digits.

On the contrary *Deltapodus* has short, blunt and rounded digits and no pad impression. The shape is usually sub-triangular, with a wide range of variation (Romano and Whyte, 2003, fig. 21), and in almost all the types there is a concave side on the inner part of the footprint.

The main characteristics of morphotype 1D are the sub-triangular shape, the occurrence of three blunt and rounded digits, and of a concave side in the outline. All these features are comparable with *Deltapodus*.

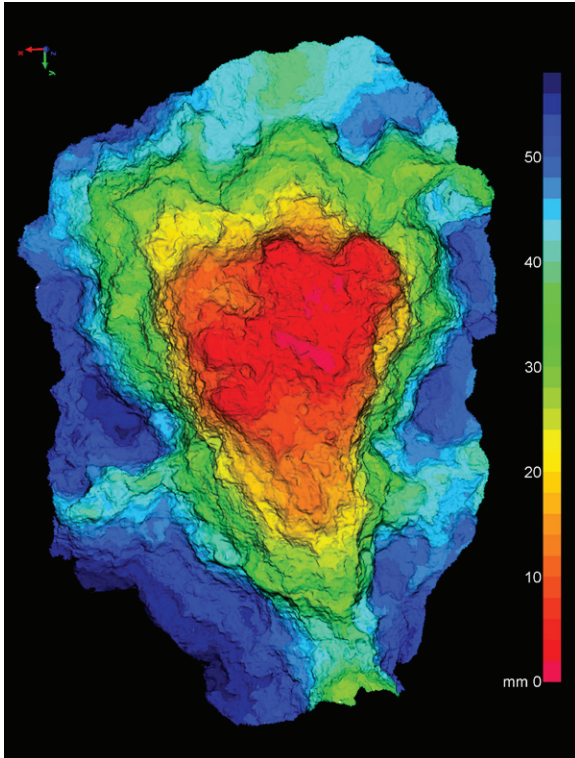
Then, the morphological measurements of the Moroccan specimens have been compared with the material by Whyte et al. (2007) and plotted in the same diagram (Fig. 5.3). The result is a definite alignment of the Moroccan specimens with the regression line of the English ichnofossils.

Despite the fact that other probable thyreophoran footprints have been mentioned in the Moroccan High-Atlas (Hadri et al. 2007), this is the first clear evidence of *Deltapodus* in Africa.

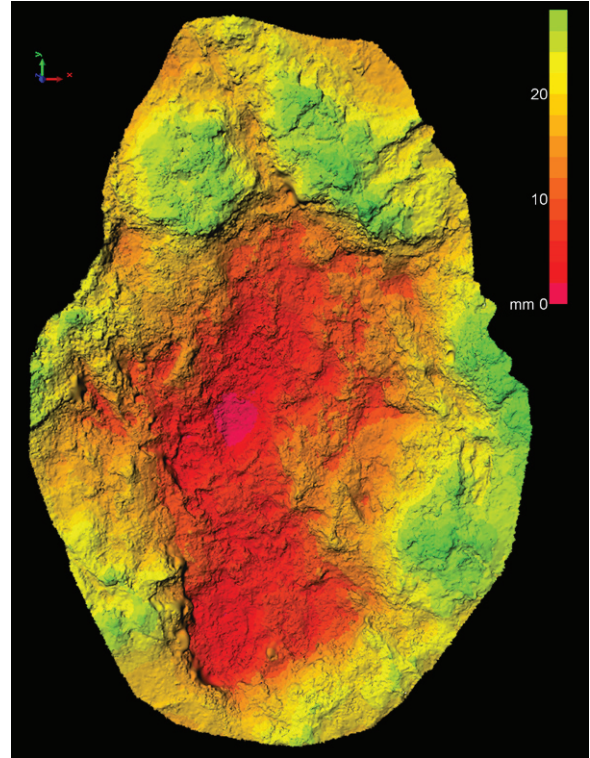
Thus, the fibreglass casts have been used to produce 3D digital models of the footprints. For the digitization of the footprints a triangulation-based laser scanner ShapeGrabber SG1002 was employed, while all the following elaborations were carried out with the Innovmetric Polyworks®, as previously done in Petti et al. (2008). For the investigated footprint area, we performed 5 scans at 0.3 mm resolution, which were then registered together achieving a final std of 0.11 mm.

From the digital models (Fig. 5.4, 5.5) it was possible to extract the contour-lines (Fig. 5.6) of the footprints and some cross sections. This allowed us to highlight the different depth-profiles of the two footprints. Detk MXC, being an underprint, has a more flattened base, with only a slight deepening through the anterior part (19 mm). On the other hand, in Deio XXVII the marked deepening can be easily noted: the total depth difference from the posterior to the anterior part is 56 mm.

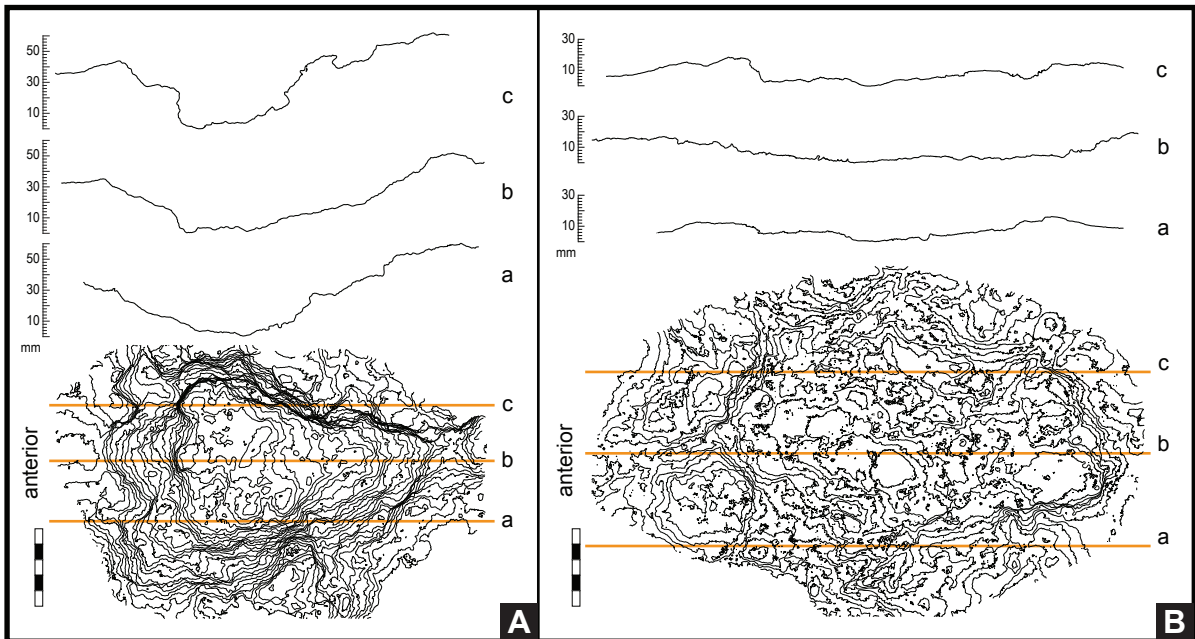
Until 2008 this ichnotaxon was known only from the Middle Jurassic of Yorkshire, but recently (Milàn and Chiappe 2008, in press) it has also been found also in the Upper Jurassic Morrison



**Fig. 5.4** – 3D model of Deio XXVII. The model is composed of colour-coded surface produced through dense point cloud data.



**Fig. 5.5** – 3D model Detk MXC. The model is composed of colour-coded surface produced through dense point cloud data.



**Fig. 5.6** – Contour lines of the specimens produced from the dense point cloud data. The lines step is 2 mm. A: Deio XXVII and cross sections parallel to the footprints axis; B: Detk MXC and cross sections parallel to the footprints axis. Scale bar 5 cm.

Fm of Utah. Other *Deltapodus* have been described from the Late Jurassic of Spain (Cobos et al. 2008; Garcia-Ramos et al. 2006, 2008) and also from Portugal (Mateus and Milan in press). This new record widens the geographical distribution of the ichnotaxon including, at least, Northern Africa, and highlighting similarities among the dinosaur ichnofauna of Iouaridène, western Europe and North America.

## 5.2 ICHNOTAXONOMY OF GROUP 2

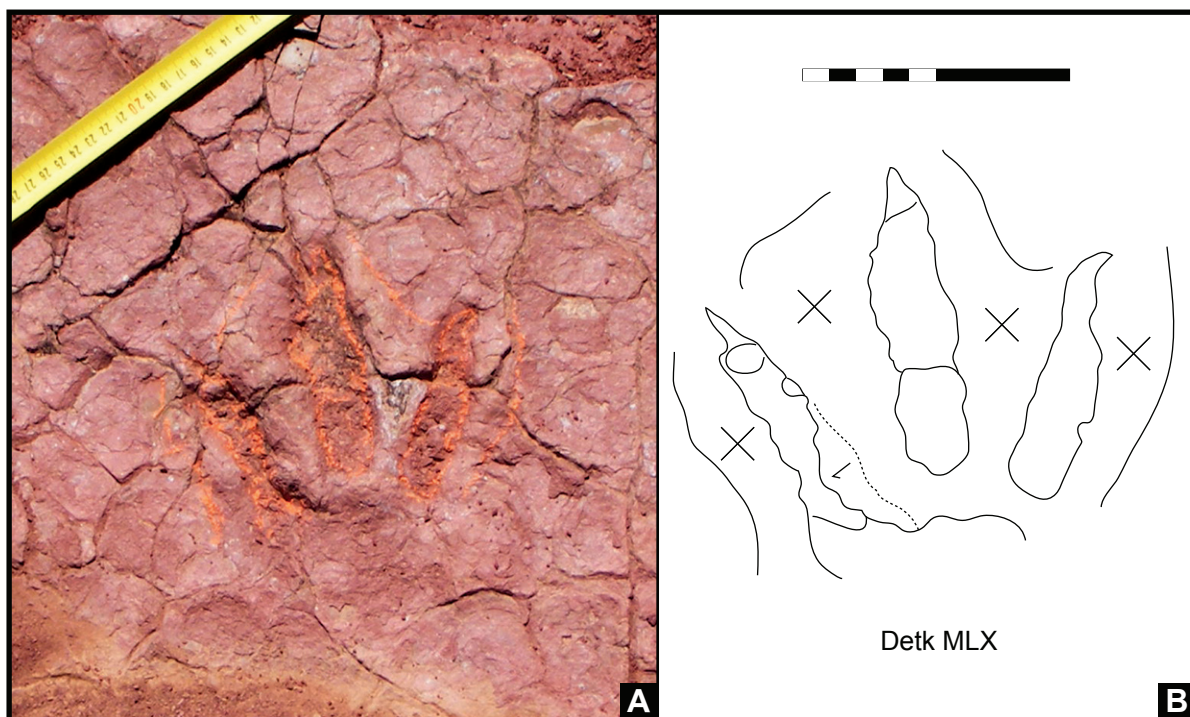
The situation of tridactyl ichnotaxonomy is even more chaotic than that of sauropods. Many ichnogenera and ichnospecies have been emended, but a complete, deep and objective revision is lacking. One of the most illustrative examples of this chaotic situation is the ichnotaxonomical position of the “megalosaurian” tracks explained in this chapter (5.2.3).

### 5.2.1 Discussion of Morphotype 2A

These small tridactyl tracks, mesaxonic, with a slender digit III, narrow digital divarication and generally rounded “heel”, have similarities with many Middle Jurassic to Early Cretaceous ichnogenera: *Carmelopodus* Lockley et al. 1998a, *Wildeichnus* Casamiquela 1964, and *Irenichnites* Sternberg 1932. Another similar ichnogenus is *Skartopus* Tulborn and Wade 1984, from the middle Jurassic of Australia, but because of the large stratigraphical difference, it has not been discussed here.

*Carmelopodus* (fig 5.8) is described as “tridactyl sub-symmetric track of a biped, with digital pad formula 2-3-3 (for digits II, III and IV respectively) and well developed, distal claw impressions. Tracks almost as wide as long with wide digits divarication, especially pronounced between II and III. Trackway narrow with axis of digit III parallel to trackway axis. The description of the species *C. untermannorum* adds more information on the lacking of “any impression of a fourth proximal pad on digit IV in all ontogenetic stages” and on digit divarication angle larger “between digits II and III than between III and IV (average =28° and 47° respectively for first three tracks)”.

The description given by Sternberg (1932) for *Irenichnites* (fig 5.9) is quite schematic: “Functionally bipedal; tridactyle; digitigrade; digits well spread, not bound together by pad, and of uniform breadth throughout; claws blunt; digit II cut away from rest of foot; phalangeal pads faintly shown; heel impression not complete; tracks small; stride relatively long; trackway narrow.” Some more information came from the description of *I. gracilis*: “The heel pad is not



**Fig. 5.7** – A: photo of Detk MLX. Scale 15 cm; B: schematic drawing of Detk MLX. It represents the only specimen of morphotype 2A that do not present a rounded “heel”. Scale bar 10 cm.

completely developed; the impression of digit II is separate from that of the rest of the foot; the toes are of uniform breadth and terminate in blunt claws. The tracks are relatively short and broad. One shows faint impressions of phalangeal pads in digits III and IV. [...] All digits terminate in blunt claws, which are not deeply impressed. [...] The divarication varies somewhat, but in the central track of the series, which shows the best detail, the divarication of digits II and III is 38 degrees, of III and IV, 40 degrees.”

Marty (2008) describe a possible phalangeal formula 2-3-3 from observation on the holotype and other trackways, but the impressions are too faint to be surely interpreted.

Compared with *C. untermannorum*, the morphotype 2A has similar morphologies of digits even if it lacks in phalangeal pads. The slight subsymmetry is common but the digital divarication II-III is narrower than III-IV. Moreover, they differ in the morphology of the rear part of the footprint: *Carmelopodus* have no “heel”, with the three digits separated, while morphotype 2A has with only one exception (Detk MLX fig 5.7) a rounded rear. The lack of phalangeal pads in morphotype 2A does not allow for reconstruction of the phalangeal formula and the typical grallatorid one 2-3-4 cannot be excluded a priori.

Compared with *Irenichnites* the morphotype clearly differs in the relatively high divarication between digits II and IV and in the marked symmetry. Moreover, the original description specifies that the digit II is always separated from the rest of the foot. This characteristic, even if partially reviewed by Marty (2008, Figs. 5.44, 5.45), has never been noticed in morphotype 2A.

However, the asymmetry of the digit with respect to the median axis allows to exclude *Irenichnites*. The common presence of a “heel” rules out the classification as *Carmelopodus*, even if the morphotypes has many features in common with those ichnogenera. Then the absence of phalangeal pads does not allow to discriminate between the two taxa.

Moreover, even if *Carmelopodus*-like tracks were recognized in the Upper Jurassic of Switzerland (Marty, 2008) both the remaining ichnogenera are common of the Middle Jurassic and their presence in the Late Jurassic would have implications for ichnostratigraphy.

Meyer and Monbaron (2002) and Belvedere et al. (2007) assigned this morphotype to *Carmelopodus*, but I think that, lacking in detailed morphological characteristics, the type cannot be unambiguously assigned to any ichnogenus.

### 5.2.3 The megalosaurian tracks controversy

The controversy of the megalosaurian tracks began as soon as a megalosaurian track concept was born (Lapparent et al., 1951) as described in Lockley et al. (1996).

Lapparent and Zbyszewski (1957) discussing about the tridactyl tracks described by Gomes (1915-16) and named by Nopsca (1923) *Eutynichnium lusitanicum*, wrote: “il y a tout lieu de penser que les traces du Cap Mondego sont attribuables à *Megalosaurus pombali*, espèce de très grande taille d’après les vertèbres”, attesting the megalosaurian affinity to these kind of tracks.

Lessertisseur (1955) coined the name *Megalosauripus* (with “i”), considering the name given by Nopsca (1923) a nomen nudum. However, he did not provide any name for the species, neither did he designate a holotype, but instead figured a track from the Lower Cretaceous of Germany that he consider similar to the Portuguese footprints. Thus, despite the intentions of the authors, also *Megalosauripus* has to be considered a nomen nudum.

Kuhn (1958) highlighted this conclusion and formally instituted the German track as *Bueckeburgichnus maximus*.

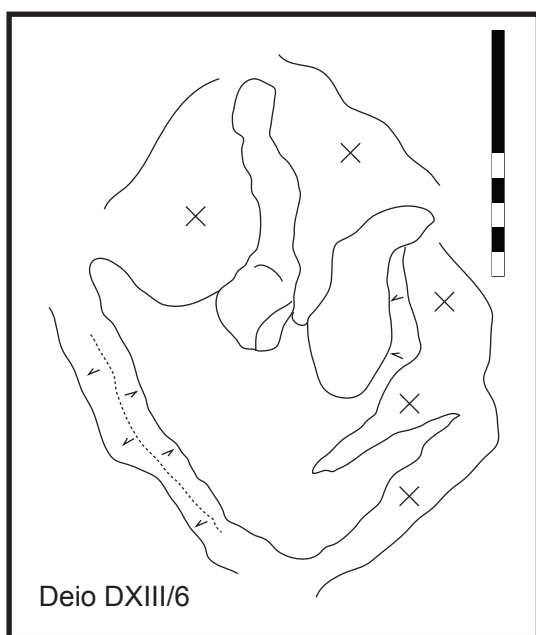
To add more confusion several papers, referring to large theropod tracks, published the name *Megalosauropus* (with “o”). The first ichnospecies described correctly was the Australian Lower

Cretaceous *Megalosauropus broomensis* (Colbert and Merrilees, 1967). Despite the validity of this ichnogenus and ichnospecies, other authors named the genus and instituted new species without referring to Colbert and Merrilees (1967), adding more uncertainty in the determination of the ichnogenus. These not valid ichnospecies are Late Jurassic *Megalosauropus teutonicus* (Kaefer and Lapparent, 1974), the Early Cretaceous *Megalosauropus* (?*Eutynichnium*) *gomesi* (Antunes, 1976) and the Late Jurassic *Megalosauropus uzbekistanicus* (Gabuniya and Kurbatov, 1982).

Further complications of the problems came from Haubold (1971), who accepted the ichnogenus *Megalosauropus* (with “o”) and suggested that the ?*Eubrontes titanopelobatidus* Shuler 1917 of the Upper Jurassic Glen Rose Fm. could be assigned to *Megalosauropus* (?*Eubrontes*) *titanopelobatidus*. Farlow (1987) considered this taxon a nomen nudum, but Lockley et al. (1996) affirmed that tracks of the same type from the same locality have been adequately described as ?*Eubrontes glenrosensis* (Shuler, 1935). Furthermore, Haubold (1971) erected a new ichnospecies from the Early Cretaceous of former Yugoslavia: *M. brinoensis*.

Finally Mensink and Mertmann (1984) assigned to large and small “Megalosauroida” the ichnotaxa *Gigantosauropus asturiensis* and *Hispanosauropus hauboldi* respectively. To be noticed that *Gigantosauropus* has been reviewed and reinterpreted as the footprints of a large sauropod by many authors (Thulborn, 1990; Lockley et al., 1994; García-Ramos and Gutiérrez Claverol, 1995; Leonardi, 1997; García-Ramos et al., 2002; Lires et al., 2001; Lockley et al. 2007) and thus a junior synonym of *Breviparopus* Dutuit and Ouazzou 1980 or *Parabrontopodus* Lockley et al. 1994 (Lockley et al. 2007).

At last, Lockley et al. (2000) tried a revision of the “megalosaurian” tracks. Considering *Megalosauripus* (with “i”) a nomen nudum, they adopted the name for the best preserved tridactyl tracks of the Late Jurassic, amending three related taxa in the base of the existing



**Fig. 5.8** – Tetradactyl footprint representing morphotype 2F. Schematic outline drawing of Deio DXIII/6. Scale bar 20 cm.

material: *Megalosauripus*, *M. uzbekistanicus* and *M. teutonicus*. Moreover they formally emend *Eutynichnium lusitanicum* described by Nopsca (1923). In this paper *Megalosauropus* (with “o”) is considered valid only for the Early Cretaceous tracks of Australia.

But Thulborn (2001) argued that some observations made by Lockley et al. (2000) are not correct; the main objection is that he does not consider *Megalosauripus* Lessertisseur 1955 a nomen nudum, and thus the following *Bueckeburgichnus maximus* Kuhn 1958 has to be considered a junior synonym. The relegation of *Megalosauripus* to such a characteristic form of track opens the possibility of a nomenclature review of the tracks thereto identified as *Megalosauripus*. However, this ichnotaxonomical revision is not carried out in the paper. Moreover Thulborn (2001) added that is not advisable to discriminate taxa on the basis on stratigraphic range because this can trigger a circularity in which the identification of

footprints is depended on the age and the stratigraphy is confirmed by the presence of determined the footprint.

The latest advance in this issue is given by Lockley et al. (2007). The paper reviews the Spanish ichnogenus *Hispanosauropus hauboldi*, which the authors consider a valid name and not a junior synonym of *Megalosauripus* (Lockley et al. 2000) or of *M. maximus* (Thulborn 2001). This important consideration derived from the fact that the revision proposed by Lockley et



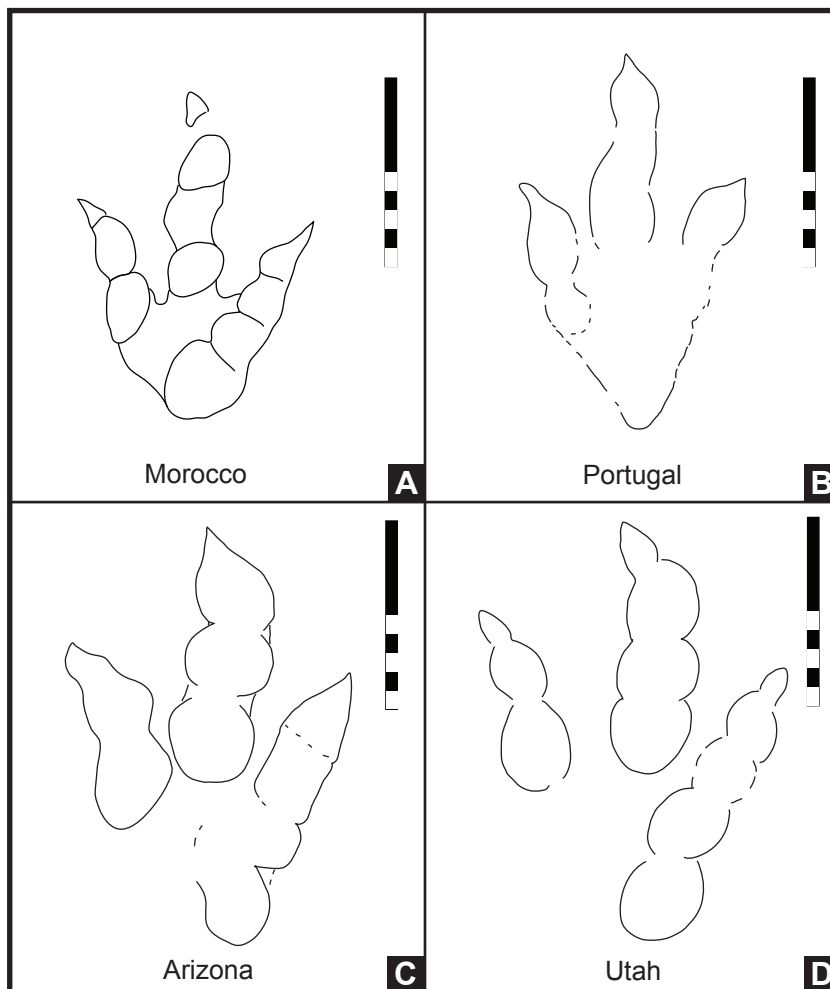
al. (2000) needs deepening, while the taxon described in Thulborn (2001) is morphologically different from *H. hauboldi*.

#### 5.2.4 Discussion of Morphotypes 2c, 2D and 2F

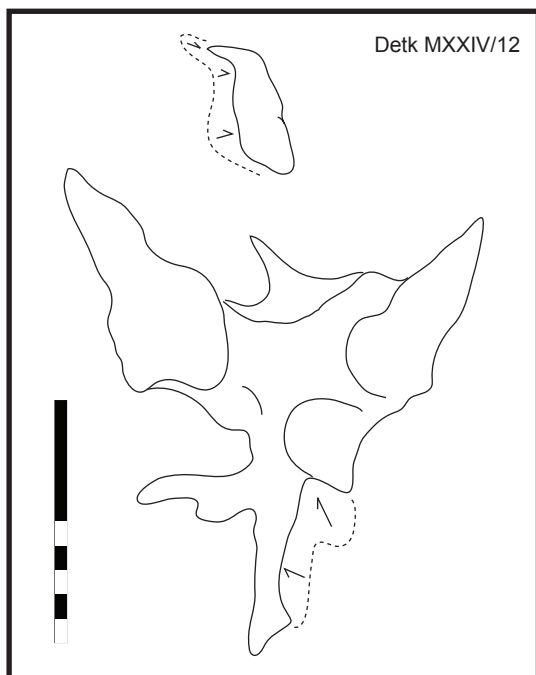
All the morphotypes 2c, 2D and 2F, which represent about half of the entire ichnoassemblage, have “megalosaurian” affinities. All their ichnotaxonomical discussion is treated in the same paragraph because it lays in the chaotic field of the megalosaurian tracks just described.

The tetradactyl **morphotype 2F** (Fig. 5.8) has great similarities with the *Eutynichnium lusitanicum* Nopsca 1923 amended in Lockley et al. (2000) especially as regards the morphology, position and orientation of digit I. Recently Nouri (2007) proposed a new ichnospecies for this morphotype: *Eutynichnium atlasichnus*. Even though the similarities between these tracks are close, and a generic broad classification can be made, the erection of new ichnospecies is in my opinion rash for two reasons: the first is that a great care is needed to add new species before the taxonomical position of ichnogenera of the “megalosaurian group” is cleared; the second is related to the preservation of the track considered as holotype by Nouri 2007 that is, in my opinion, too poorly preserved to be the comparison material for new species.

Even more complex is the ichnotaxonomical classification of the **morphotype 2c** (Fig. 5.9A). It has notable morphological similarities with the *Megalosauripus* described in Lockley et al. (2000, fig. 8), especially with the specimens from Arizona, Utah and Portugal (Fig. 5.9B-D). This last similarity was already noticed by Lapparent and Zbyszewski (1957). Nevertheless the morphological similarities with *Megalosauripus* sensu Thulborn (2001) are lower, mainly because the types described are tetradactyl and with a wider interdigital angle.



**Fig. 5.9** – Comparison between “megalosaurian” tracks. A: schematic drawing of Deio CXXVIII/16, reflected vertically to be a right footprint; B: *Megalosauripus* track from Portugal. Redrawn from Lockley et al. (2000); C: *Megalosauripus* track from Arizona. Redrawn from Lockley et al. (2000); D: *Megalosauripus* track from Utah. Redrawn from Lockley et al. (2000). Scale bar 20 cm.

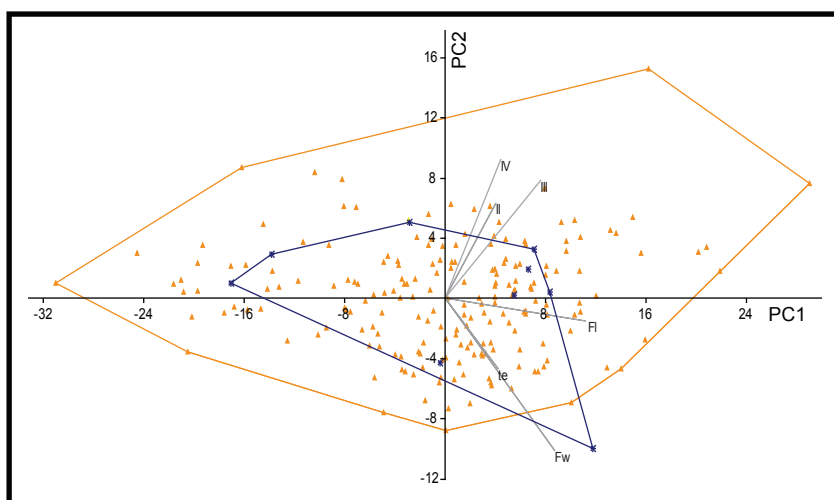


**Fig. 5.10** – Tetradaetyl track outline representing morphotype 2D. Note the different orientation of the first digit with respect to morphotype 2F (Fig. 5.8).

Those footprints of morphotype 2c that do not present phalangeal pad impressions greatly resemble the Asturian *Hispanosauripus hauboldi* Mensink and Mertmann 1984. Lockley et al. (2007) revised this ichnotaxon, designating a new paralectotype to substitute the lost holotype, and consider this name provisionally valid for the Spanish Late Jurassic tracks and for similar footprints of Europe named variously. Being aware that the megalosaurian origin of these tracks is only conjectural, the “megalosaurian” affinity of this morphotype is certain, as well as the similarities with the Late Jurassic North American and Portuguese *Megalosauripus* (sensu Lockley et al., 2000) and coeval Spanish *H. hauboldi*.

During the initial studies, **morphotype 2D** (Fig. 5.10) interpretation was unclear. So, to test the theropodian affinity of this genus a PCA was carried out using pes length and width, digits II, III and IV free length, toe extension (Weems, 1992) and the interdigital angles between digits II and III, and III and IV as variables.

Fig. 5.11 shows the score plot for the PCA comparing morphotype 2C and 2D tracks. the clear overlapping of the two groups can be observed. This result has been interpreted as derived from a common origin of the footprints. Thus, considering the clear belonging to theropods of morphotype 2c, also the 2D should have had a theropodian origin, which was not perfectly comprehended during the initial interpretation of the type.



**Fig. 5.11** – Score plot (PC1 vs. PC2) of the PCA made to compare morphotypes 2C (orange triangles) and 2D (blue stars). The overlapping between the two groups is clear. Further explanation in Chapt. 6.1.2.

After this test it was possible to compare this morphotype with the “megalosaurian” ichnogenera: the similarities with *B. maximus* (sensu Lockley et al., 2000) or *M. maximus* (sensu Thulborn, 2001) are numerous, indeed: not only the size and shape, but also the position and orientation of the digit I. The only clear difference, the shape of the metatarsal impression, wider and more aligned with the footprint axis, can be easily attributed to the substrate characteristics. A further note has to be given, even if it has poor taxonomical importance: *B. maximus* is recorded only in the Lower Cretaceous formations, while the Moroccan specimens are Late Jurassic.

Thus, in the absence of a definitive taxonomical position, and since there are some differences both morphological and stratigraphical with the more related ichnogenus, a deeper attribution is not advisable.

### 5.2.5 Discussion of Morphotypes 2B

This small tridactyl mesaxonid morphotype is preserved only with few and not well preserved specimens. Because of the high symmetry of the interdigital angles it has been compared with the ornithischian ichnogenus *Anomoepus* Hitchcock 1848. This taxon was described as “small (pes <20 cm), mostly bipedal and tetradactyl, but functionally tridactyl” (Olsen and Rainforth, 2003).

Despite the similarities with *A. scambus* Hitchcock 1848, neither manus tracks nor digit I impressions have been found.

This type has also similarities with *Moyenisauripus* Ellenberger 1974, but this ichnogenus has been recently reviewed and considered a juvenile subjective synonym of *Anomoepus* (Olsen and Rainforth 2003, Irmis, 2005).

Lockley et al. (1998) describe a new ornithopod ichnotaxon: *Dinehichnus socialis*. It is diagnosed as a “small- to medium-sized biped with footprints about as wide as long. Tracks quadripartite, symmetric and tridactyl with distinctive circular heel pad impression. Digit impressions consisting of single elongate oval impressions sometimes with tapered claw impression. Digit divarication (II-IV) averaging about 90°. Trackway narrow with pace angulation of about 155°. Negative (inward) rotation of digit III about 10-15° from trackway midline. Step length averaging a little more than three foot length”.

Compared with *Dinehichnus*, morphotype 2B shows many similarities in the tapering termination of the digits, in the proportion between length and width, in the high divarication angle. However, the Iouaridène specimens present always a rounded heel that is lacking in *Dinehichnus*, and show a slightly narrower interdigital angle. Furthermore, tracks are not quadripartite, having not separated digits. Trackways are narrow-gauge but no inward rotation has been noticed.

Thus, considering the general poor preservation and the differences noticed with comparable known ichnogenera, I prefer not to give any ichnotaxonomical attribution, but just to suppose a probable affinity to small biped ornithischian or small ornithopod ichnotaxa.

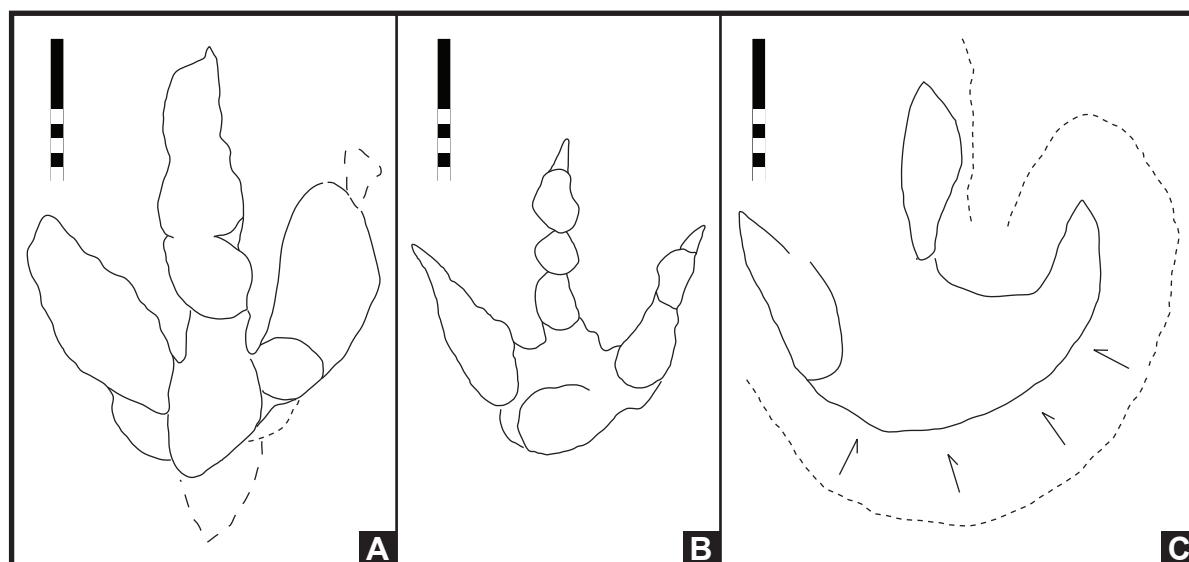
### 5.2.6 Discussion of Morphotypes 2E

These large tridactyl tracks (Fig. 5.17) are among the most difficult to classify of the site. This is mainly due to preservation-related features of these tracks, which are generally poorly preserved.

The first of these footprints discovered, Deio XLII, at first moment attributed to large ornithopods (Belvedere et al., 2007), having morphological similarities with a specimen from the Upper Jurassic of Portugal (Mateus and Milàn, 2008). The dimensions and shape of these tracks is also comparable with large ornithopod footprints discovered recently in the Late Jurassic of Yemen (Schulp et al., 2008; Schulp, pers. comm, 2008), but the trackway comparison shows a different rotation of the tracks: outward for the Moroccan specimen, inward for the Arabian. However, compared with the known large ornithopods ichnotaxa (*Iguanodontipus* Sarjeant 1988; *Hadrosaurichnus* Alonso 1980; *Caririchnium* Leonardi 1984), the similarities are not so clear. Furthermore, the discovery of other similar tracks and trackways, with tapered ending of the digits, if not with proper claw marks, suggests a theropodian origin for these tracks.

In addition, recently Ishigaki (2008, but also 1985c) recently illustrated some very large theropod tracks from the area near of the village of Oukta which are comparable with those of this morphotype for size and divarication angles.

A further evidence of the probable theropod affinities of this type comes from a recent paper by



**Fig. 5.12** – Examples of large tridactyl footprints of morphotype 2E. A: Deio XLII; B: Detk XVI; C: Detk MLXXIX/3. Scale bar 20 cm.

Manning et al. (2008) where a probable tyrannosaurid track from the Late Cretaceous of the US is described, having very similar morphologies and comparable dimensions.

However, no ichnotaxa are known with similar characteristics in the stratigraphic range of the site, so no classification can be carried out. Moreover, the material is so little, ambiguous, and poorly preserved that it cannot be used to erect a new ichnotaxon.

### 5.3 TRACKING THE TRACKMAKER

Generally it is not possible to determine the trackmaker from tracks, unless its remains are found at the end of the trackway, or associated to tracks, or in a close stratigraphic and geographic position.

Moreover, the record of dinosaur tracks and bones are not coincident, that is, many dinosaurs may be known only from bones because tracks are lacking, and vice versa. In addition, fossil footprints also preserve the traces of soft tissues, which are generally missing in the osteological record, and which are also difficult to reconstruct from the bones.

To further complicate the situation, the vertebrate ichnotaxonomy, besides being affected by various external factors, such as the sedimentological and mechanical features of the soil or the trackmaker behaviour, also lacks theoretical bases (Bertling et al., 2006).

#### 5.3.1 *Quadrupedal track maker*

##### **Sauropods (1A, 1B, 1D)**

In the last years many papers have tried to identify the trackmaker of sauropods prints. Most of them are based on the trackway gauge as described by Lockley et al. (1994) where is stated that the narrow- and wide-gauge have a stratigraphical meaning and that “narrow-gauge trackways are more common in the Jurassic than in Cretaceous deposits”.

Starting from this point, Wilson and Carrano (1999) stated that wide-gauge trackways were produced by wide-gauge sauropods. Because titanosauriforms appeared during the Late Jurassic (Upchurch, 1995), Wilson and Carrano hypothesized this group as a trackmaker of the wide-gauge tracks such as *Brontopodus*.

Following works (Day et al., 2002, 2004; Lockley et al., 2002a, b; Marty et al., 2003; Henderson, 2006) generally continued on this interpretation, attributing wide-gauge tracks to more derived sauropods (e.g. brachiosaurids and titanosaurids) and the narrow-gauge to more basal sauropods

(e.g. diplodocids).

In particular, the work of Henderson (2006), in which the determination of the trackmaker is made by modelling the walk of *Brachiosaurus* and *Diplodocus* and comparing their stability with narrow- and wide-gauge tracks, is based on some of the Moroccan tracks analyzed here, specifically on two different portions of the Deio D trackway. However, this work was based on the literature drawings of Dutuit and Ouazzou (1980) and Ishigaki (1985) where the size of the manus impression results smaller than in my survey. Moreover, the work does not take into account the semi- or subcircular manus tracks found on different tracks of the same morphotype. These considerations would affect the model used, and, also considering the wider gauge of the manus tracks, in my opinion, they make a more evolved trackmaker at least for *B. taghbaloutensis* less improbable.

Furthermore, the re-examination of the trackways record made by Wright (2005) and Romano et al. (2007) questioned the assumption that the wide-gauge trackways were more frequent in the Cretaceous. It results a more complex distribution of sauropods with respect to the trackway gauge than supposed by the osteological record. Then, gait style or ontogeny or sexual dimorphism origin for the trackway gauge cannot be excluded a priori (Lockley et al., 2002; Wright, 2005). These last two hypotheses could explain the presence of middle-small medium-gauge sauropod trackways on the site, dominated by large narrow-gauge tracks, especially considering the supposed larger size of track Deio LavB (Fig. 4.3).

Many authors (e.g. Salgado et al., 1997; Wilson and Sereno, 1998; Wilson and Carrano, 1999; Wilson, 2005) agree on the presence on sauropod manus and pes of a number of synapomorphies (e.g. presence and number of claw marks, digit impression pattern, etc...) that can be used for classification.

Both the large and the medium sauropod tracks of the Iouaridène site show no or very few morphological details. Three/four digits impressions and faint claw marks occur in few *B. taghbaloutensis* pes tracks, while a possible first digit impression occurs in the middle size pes impressions (Deio LavA/2p). Manus tracks always lack claw or pad impressions.

Wright (2005) stated that the presence/absence of claw marks may be a preservation artefact or be related to the behaviour of the trackmaker. Furthermore, in the Iouaridène site the co-occurrence of crescent-shaped to semi- or subcircular manus prints, often within the same trackway has been recorded. This could be related to the gait of the trackmaker which could have overimpressed or deformed manus tracks giving them a crescent-shaped, or, according to Marty (2008), to the behaviour of the trackmaker which could have varied from a semi-plantigrade to plantigrade manus posture.

The sauropods remains from the Moroccan area account three taxa: the Early Jurassic vulcanodontid *Tazoudasaurus*, the Middle Jurassic *Atlasaurus imelakei* and the Early Cretaceous diplodocids *Rebbachisaurus garasbae*. However, also excluding the vulcanodontid, no certain attribution can be made, firstly because no clear identification of the trackmaker group has been made (see above), secondly because the remains, especially those of *Rebbachisaurus*, are very few. Moreover, the assemblage of the bones of *Atlasaurus* seems to be not correct, and they could belong to more than one individual (Meyer, pers. comm., 2007)

### 5.3.2 Bipedal track maker

The trackmaker identification for tridactyl, and, generally, biped dinosaurs, is even worse than the one of sauropods. This is because tridactyl footprints have a conservative shape with reduced variation across the stratigraphical record. Moreover, the morphological details are strictly related to the preservation of the tracks, which in the Iouaridène site are high only in few cases.

Trackway gauge also has a minor importance than in sauropods, because of the higher mobility of the hindlimbs of biped animals, as testified by the occurrence within the same trackway of narrow- and wide- gauges. Thus, the tentative attribution is here carried out comparing the footprint morphology to the skeletal record of biped dinosaur from Europe and Africa in the Middle Jurassic to Early Cretaceous (Weishampel et al., 2004).

### **Small grallatorid theropod (2A)**

These tracks with long and narrow digits probably belong to a coelurosaurid trackmaker. The comparison with the pedal skeleton of the small mariraptorian *Ornitholestes* and *Coelurus*, both present in the Middle/Late Jurassic, shows some similarities: the longest digit is the IV followed by III and II. The angle II-III is reconstructed wider than III-IV. Finally the digit I is reduced, so that it cannot leave any impression if the dinosaur is not walking as plantigrade.

### **Probable ornithischians/ornithopods (2B)**

Because of the poor preservation no clear comparison with the osteological record is possible for this group of footprints. However, a tentative attribution could be made comparing the track morphology with those of the Mid/Late Jurassic small bipedal ornithischians and ornithopods known. Similarities occur with the North American and African (Tanzania) Late Jurassic *Dryosaurus*, but the III digit, in the pes osteological reconstruction, seems to be less extended with respect to the II and IV digit (Thulborn, 1990). Closer in morphology is also the pes of *Camptosaurus*, common in the Late Jurassic of North America and also Europe. This genus has been recently pointed out as the trackmaker of *Dinehichnus*, the closest ichnotaxon to the type 2B (Gierlinski and Sabath, 2008). This last genus has also been recorded in the Upper Jurassic Lourinha Formation of Portugal, where another small camptosaurid (*Draconix*) was also found (Mateus and Antunes, 2001).

### **“Megalosaurian” tracks (2C, 2D, 2F)**

This group, besides being the dominant in the site, is also the most difficult to attribute to a trackmaker. Although the theropodian attribution is certain, a more detailed classification is difficult to carry out, because the morphology of the pes is almost the same for all the theropod groups. *Ceratosaurus*, *Allosaurus*, *Lourinhanosaurus*, *Torvosaurus*, *Carcharodontosaurus*, *Spinosaurus*, *Megalosaurus*, probable basal tyrannosaurids (*Aviotyrannus*) are known from the Middle, but especially Late Jurassic of the surrounding areas, representing almost all the known infraorder of the Theropoda. Excluding for their size the spinosaurids and carcharodontosaurids, all the other taxa present comparable sizes with those of the Iouaridène tracks.

Also the occurrence of tetradactyl tracks is not useful. In my opinion, and according with Harris et al. (1996), the position and orientation of the first digit is not dependent on pes morphology, but is controlled by the characteristics of the sediment. However, also considering that morphotypes 2D and 2F have a different trackmaker, the distinction among the genera is practically impossible without the discovery of bone remains at the end of a trackway.

### **Large tridactyls (2E)**

As for the previous ones, this group is difficult to determine. Moreover, the lack of morphological detail due to the poor preservation makes the determination of the trackmaker simply speculative.

However, some consideration can be made about the size of the tracks. Using the equation 4 (Chapt. 2.3.1) the average hip height for this morphotypes could reach 3.4 m (Deio XLII). Such large theropods are represented in the Mid/Late Jurassic almost only by carcharodontosaurids and spinosaurids, but no pes bones are known from these taxa.

Thus, a suggestive interpretation of these tracks as a result of the transit of a large *Carcharodontosaurus* or *Spinosaurus*, is not to be excluded, but still far from a scientific demonstration.

# 6 MULTIVARIATE STATISTICS

One of the biggest problems with ichnology is the subjectivity of the interpretation. To avoid this, many ratios have been used during the years (e.g. Leonardi, 1987; Moratalla, 1988; Demathieu, 1990; Weems, 1992; Farlow 1997; Olsen et al., 1998). These methods considered only two variables per time, and only few have been a multivariate analysis of ichnological data.

In this work two methodologies have been tested on ichnology: one purely statistical (PCA), the other morphometric (Landmark analysis).

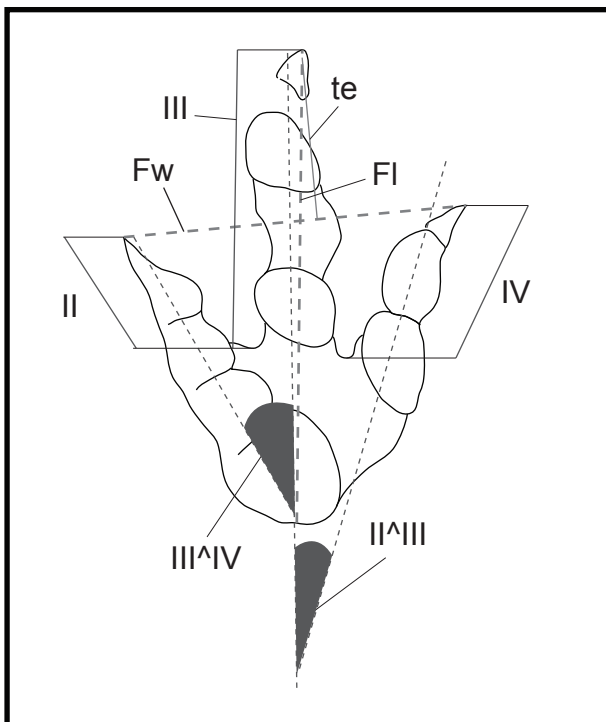
## 6.1 PRINCIPAL COMPONENT ANALYSIS

The Principal Component Analysis has been applied in this work to tridactyl footprints. The aim of this application was to test this multivariate statistical method for a discrimination among morphotypes.

### 6.1.1 PCA on the complete tridactyl record

Eight variables have been considered (Fig. 6.1): 1- foot length (*Fl*); 2- foot width (*Fw*); 3- digit II free length (*II*); 4- digit III free length (*III*); 5- digit IV free length (*IV*); 6- toe extension (Weems, 1992)(*te*); 7- interdigital angle between digits II and III ( $II^{\wedge}III$ ); 8- interdigital angle between digits III and IV ( $III^{\wedge}IV$ ).

The PCA was run using PAST 1.86b<sup>©</sup> (Hammer et al., 2001), and considering 6 or 8 variables per time. To compare the results with the ichnological subdivision of the tracks, the two PCA were run again giving a peculiar colour and sign to each morphotype.



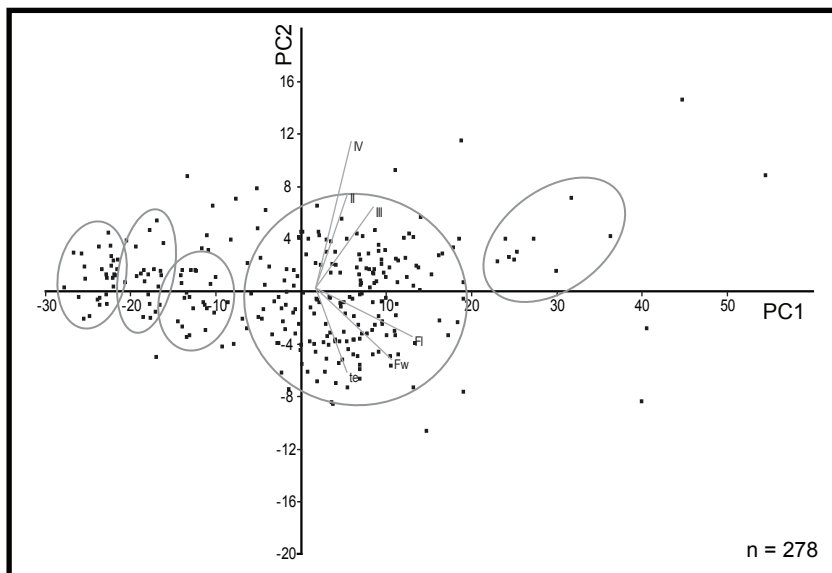
**Fig. 6.1** – Schematic drawing of a tridactyl footprint showing the parameter considered for the PCA; *Fl*: Foot Length; *Fw*: Foot Width; *II*, *III*, and *IV*: Free Length of digits II, III and IV, respectively; *te*: Toe Extension (Weems, 1992);  $II^{\wedge}III$ : interdigital angle between digits II and III;  $III^{\wedge}IV$ : interdigital angle between digits III and IV.

Firstly, six variables were considered (1 to 6 of the list above). These variables are all linear measurements made with the same unit of measurement (cm). This allows to run it without normalization using the *variance-covariance matrix* option given by the software.

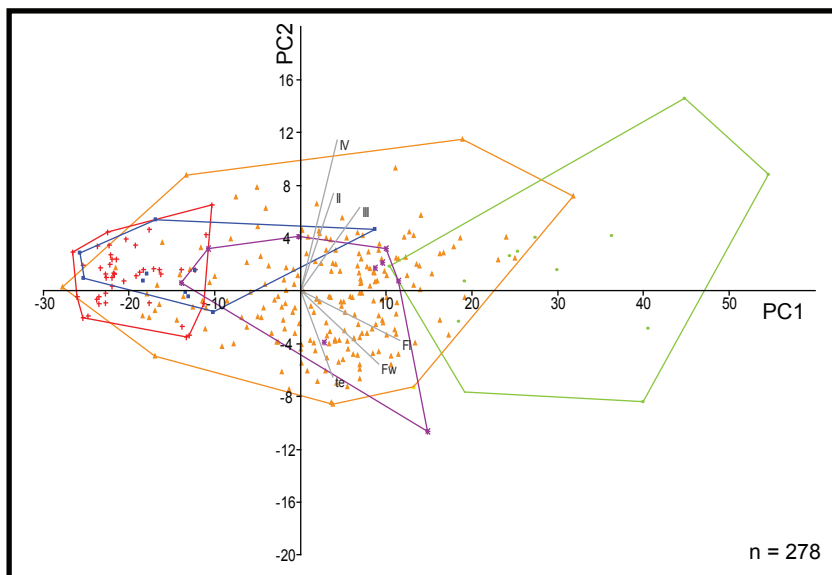
Fig. 6.2 shows the score plot, where it is possible to recognize roughly five different groups (grey circles).

However, when compared with the morphotypes defined on ichnological basis (Fig. 6.3), the matching between the groups is very poor; the only group having a coarse overlapping is morphotype 2c. This is not surprising, since this group counts alone more than a half of the object of the analysis.

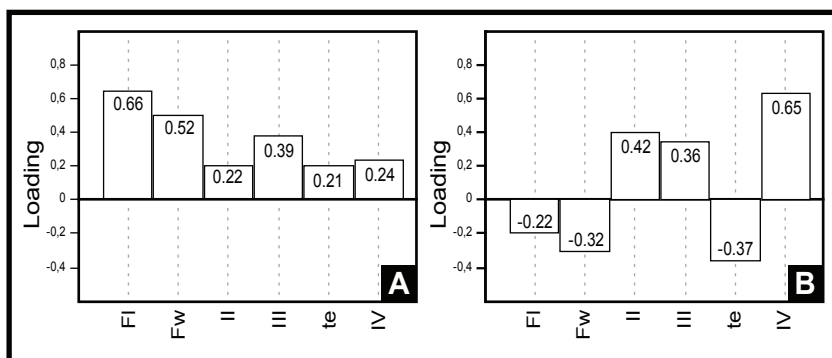
Fig. 6.4 shows the loading graphs, where it is evident that *Fl* and *Fw* account most of the variance of the PC1, while PC2 is more related to *III* and *Fw*.



**Fig. 6.2** – Score plot showing PC1 and PC2 of tridactyl tracks carried out considering six variables. Five groups can be roughly pointed out. PC1 = 84.6%; PC2 = 5.64%; PC3 = 5.1%; PC4 = 2.6%; PC5 = 1.7%; PC6 = 0.4%.



**Fig. 6.3** – Same score plot as in Fig. 6.2 showing also the recognized morphotypes. Compared with the groups highlighted in the figure above, no clear matching with the morphotypes is present. Red crosses: morphotype 2A; blue squares: morphotype 2B; orange triangles: morphotype 2C and 2F; purple stars: morphotype 2D; green circles: morphotype 2E.



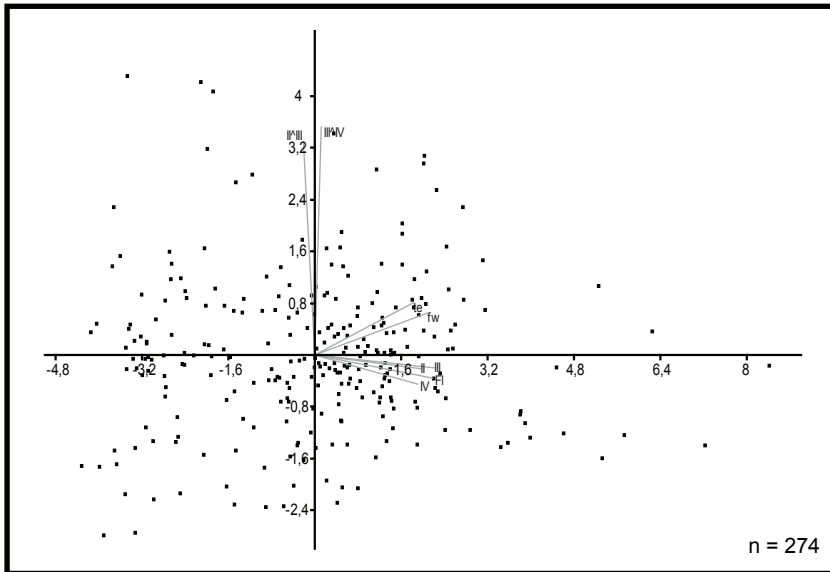
**Fig. 6.4** – Loading histograms for the main principal components of the analysis with six variables; the predominance of size in the PC1 is clear, while the PC2 is driven mainly by the free digit lengths. A: PC1 loadings; B: PC2 loadings.

Then, eight variables were taken into account to run the PCA, including also the interdigital angles, measured in degrees. As a consequence, it had to be carried out using the *correlation matrix*, which normalizes the variables dividing by variance.

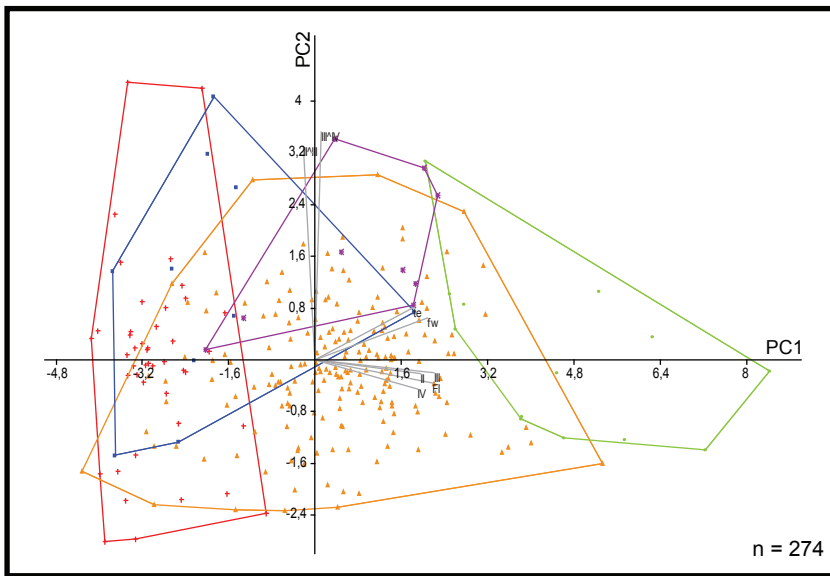
Fig. 6.5 shows the score plot for this PCA. The addition of the interdigital angles, instead of clearing the distinction between the groups, makes it more and more difficult to discriminate them. No notable groups can be pointed out, especially when considering the score plot with the morphotype, where almost all the types have overlapping (Fig. 6.6).

The loadings graph (Fig. 6.7) show that the PC1 is driven by the linear measurements (F1, Fw, II, III, IV, te), while PC2 is almost completely related to the interdigital angles (II<sup>^</sup>III, III<sup>^</sup>IV).

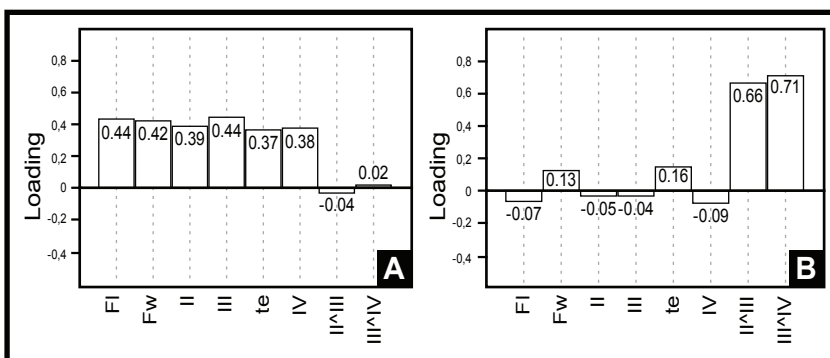




**Fig. 6.5** – Score plot showing PC1 and PC2 of tridactyl tracks carried out considering eight variables. Five groups can be roughly pointed out. PC1 = 58.1%; PC2 = 17.5%; PC3 = 9.8%; PC4 = 7.2%; PC5 = 3.1%; PC6 = 2.6%; PC7 = 1.1%; PC8 = 0.5%.



**Fig. 6.6** – Same score plot as in Fig. 6.5 showing also the recognized morphotypes. Red crosses: morphotype 2A; blue squares: morphotype 2B; orange triangles: morphotype 2C and 2F; purple stars: morphotype 2D; green circles: morphotype 2E.



**Fig. 6.7** – Loading histograms for the main principal components of the analysis with eight variables; PC1 is driven by linear measurement whereas PC2 is mainly related to the angular values of the interdigital divergations; A: PC1 loadings; B: PC2 loadings.

### 6.1.2 PCA between two morphotypes

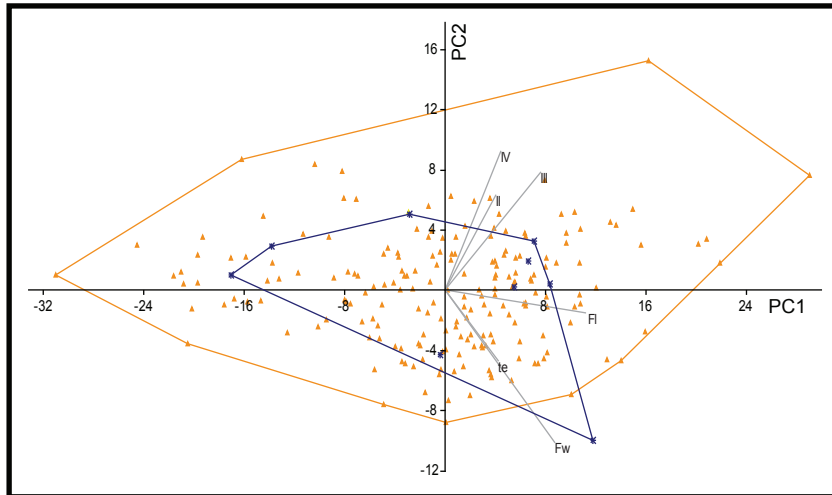
Despite the difficulties of PCA in discriminating among several groups, these methods have been used to quantify the analogies and differences between two discrete kinds of tracks.

These two morphotypes, 2c and 2d (Cap. 4.2.3, 4.2.4), are the evidence of tridactyl and tetradactyl footprints, respectively. The PCA was carried out to point out possible similarities that can testify the theropodian origin of morphotype 2d.

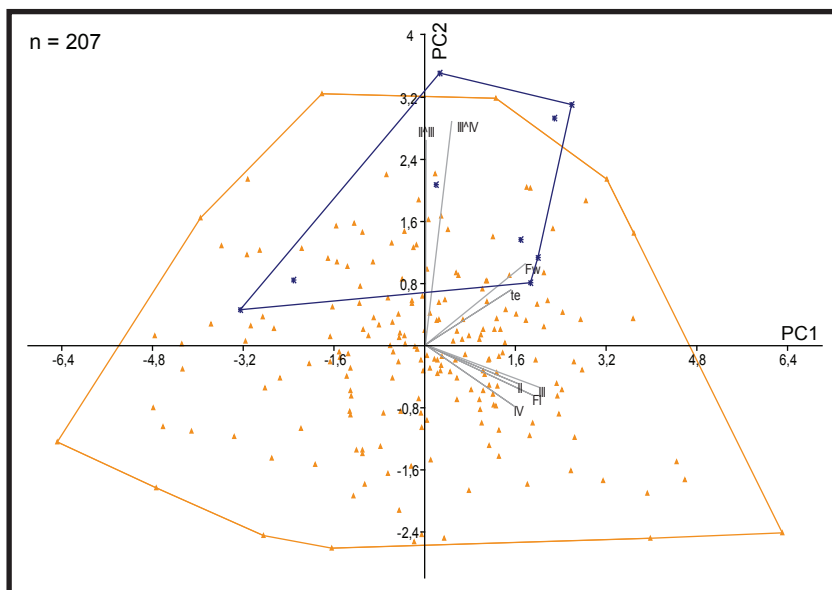
Sample procedures as above have been used for these analyses, but with a very different result. Both the score plots, generated from six (Fig. 6.8) or eight variables (Fig. 6.9), highlight the

relationship between these two groups. It is clear that morphotype 2D generally overlapped the 2C, and that only few points plot outside the 2C area. This is more evident on the 8 variable score plot (Fig. 6.9), and is mainly due to the generally higher interdigital angle measured on type 2D. However, this higher angle is more due to the behaviour of the dinosaur on a soft substrate rather than to actual morphology (Chapt. 4.2.4).

The high influence of the size on the main PCs does not affect too much these analyses because length and width of the two groups are strictly comparable.



**Fig. 6.8** – PC1 vs. PC2 Score plot of the comparison between morphotypes 2c and 2D carried out with six variables. The relationship between the two groups is evident. Orange triangles: morphotype 2c; Blue stars: morphotype 2D. PC1 = 69.6%; PC2 = 11.2%; PC3 = 9.9%; PC4 = 5.1%; PC5 = 3.3%; PC6 = 0.9%.



**Fig. 6.9** – PC1 vs. PC2 Score plot of the comparison between morphotypes 2c and 2D carried out with eight variables. Also adding more variable the relationship between the two types still evident. Orange triangles: morphotype 2c; Blue stars: morphotype 2D. PC1 = 47.6%; PC2 = 17.0%; PC3 = 13.7%; PC4 = 8.8%; PC5 = 5.1%; PC6 = 4.5%; PC7 = 2.2%; PC8 = 1.0%.

### 6.1.3 Conclusions

Principal Component Analysis, applied to a large number of tracks with large differences among them, is not able to clearly determine morphological groups. This is probably due to the strict relation between the main Principal Components and the size of the tracks. As a consequence, PCA is not suitable for this kind of analysis, at least with the variables chosen. Further trials with different variables (e.g. digit phalangeal length, digit width, etc.) could determine the reliability of this test to discriminate morphotypes, though these further variables are not common in the ichnological record, being preserved only in very well preserved tracks.

However, when applied to tracks with similar sizes, PCA is a suitable and reliable tool to mark analogies and differences, which allows to test in a quantitative way the relationships between known groups.

## 6.2 LANDMARK ANALYSIS

The application of Geometric Morphometric techniques to ichnology and to the ichnological record have received only very little attention in the past. Some applications were made on tridactyl (Rasskin-Gutman et al., 1997) and *Sauropodomorpha* (Rodrigues and dos Santos, 2002), but the works never went further on.

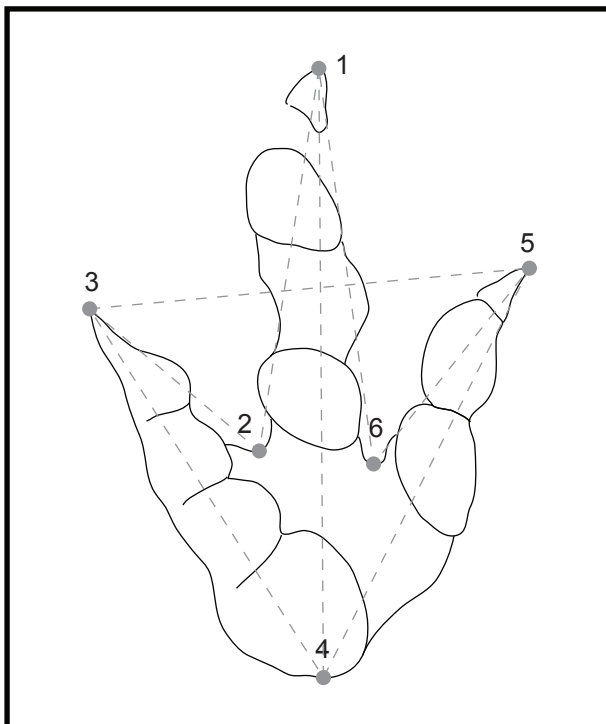
Here the Landmark analysis is used to identify with a quantitative approach what parameters of a tridactyl footprint are more reliable for ichnotaxonomy, that is, what parameters of the footprint are less affected by extramorphological features.

Moreover, this technique has been applied to ichnotaxonomy, trying to extrapolate some information from the literature data of the “megalosaurian” tracks.

### 6.2.1 Morphology vs. Extramorphology

To study the morphological variation on the footprints of the same individual it is necessary to choose a trackway with well preserved footprints without malformations.

The 21-footprints trackway Deio CXXVIII was selected among all the trackways mainly because of its good grade of preservation, which allowed to use 15 tracks (for the trackway description see Chapt. 4.6.6).



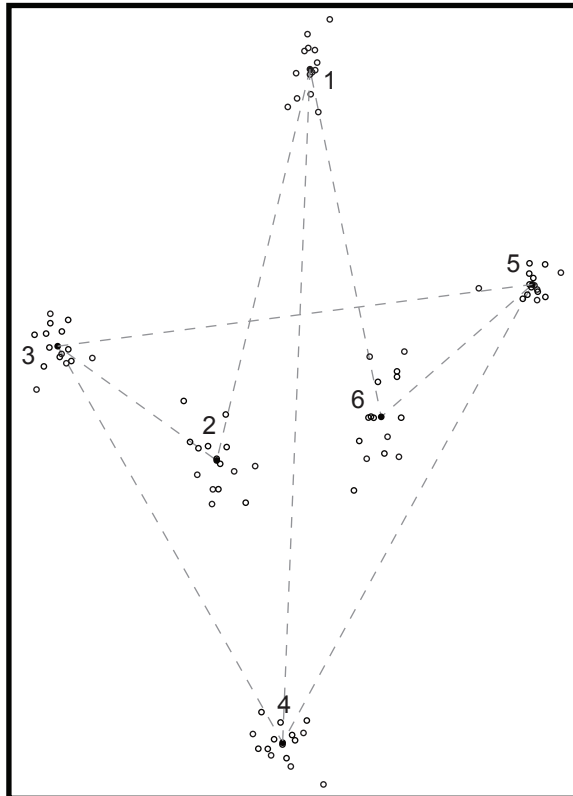
**Fig. 6.10** – Schematic drawing of a tridactyl footprint illustrating the landmarks placed; 1: tip of digit III; 2: hypex between digits III-IV; 3: tip of digit IV; 4: “heel” of the track, considered as the maximum curvature of the rear part; 5: tip of digit II; 6: hypex between digits II-III. The dashed line represents the links among landmarks used during the analysis.

Six landmarks have been placed on these footprints, following the suggestions of Rasskin-Gutman et al. (1997): 1- tip of digit III; 2- hypex between digits III and IV; 3- tip of digit IV; 4- “heel” of the track, considered as the maximum curvature of the rear part; 5- tip of digit II; 6- hypex between digits II and III (Fig. 6.10).

Due to the inherent characteristics of the materials analyzed, the landmarks placed are Type III (Bookstein, 1991) or mathematical landmarks (Dryden and Mardia, 1998), as already explained in Chapt. 2.5. To check the accuracy of the positioning of the landmarks, for certain tracks, the procedure has been repeated several times.

The footprints were all considered **left** pes tracks. The right ones were flipped using Adobe Photoshop®. The landmarks were placed on drawings of the footprints and not on photographs mainly because photos were taken without checking the perfect perpendicularity between the surface and the camera. The softwares used to determine the coordinates and for the following elaboration are listed in Chapt. 2.5.

The coordinates of all aligned specimens were used for thin-plate splines Relative Warp (RW) analysis (Bookstein, 1991; Rohlf, 1993). The Relative Warps (RW) analysis was performed with the scaling option  $\alpha=0$  (Rohlf, 1993), which gives each landmark the same weight, with the uniform component included (Rohlf and Bookstein, 2003).

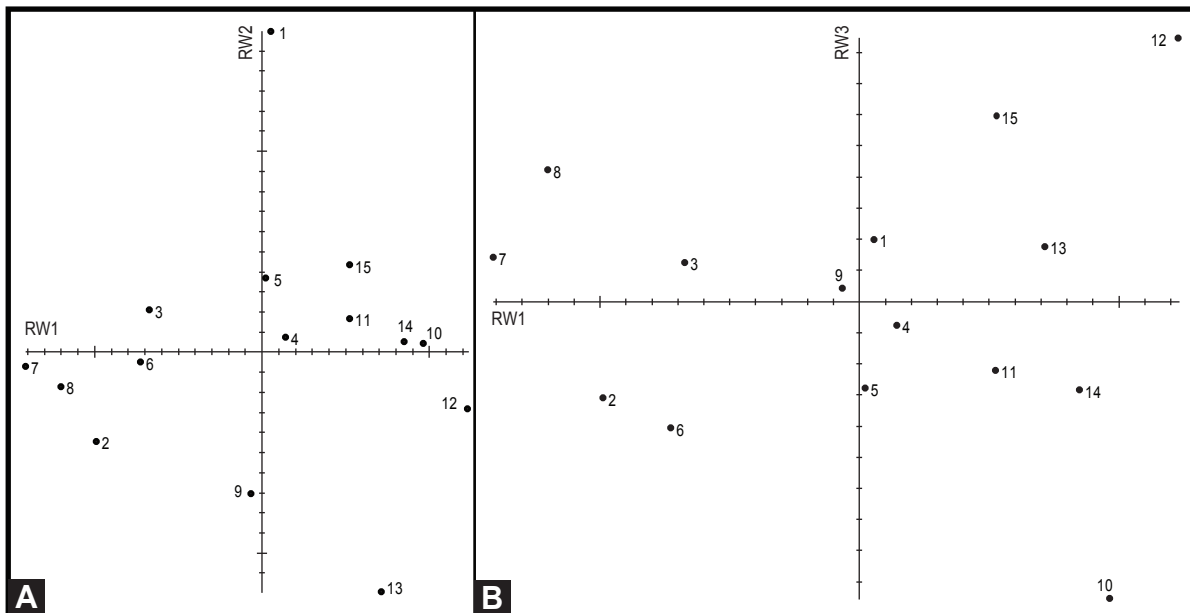


The *consensus* shows how the individual specimens plot in the same coordinate reference system. The superimposed drawing of the very well preserved Deio CXXVIII/16 track (Fig. 6.11) highlights how landmarks are distributed. Landmarks 3, 4, and 5 are distributed on a close area; landmark 1 plots are also not very disperse, but show a sort of alignment with the elongation axis of digit III; landmarks 2 and 4, in fact, show a large and scattered variability.

RW1 accounts for 44.02%, RW2 for 23.73%, RW3 for the 12.52%, while all the other warps are smaller than 10%. Therefore the 67.75% of the total variation is due to the only first two relative warps (Fig. 6.12).

Looking at what the first two RW are, it is clear that these two warps are mainly related to the position of landmarks 6 (RW1) and 2 (RW2), that is, the position of the hypices between digits II-III and III-IV, respectively.

**Fig. 6.11** – Consensus carried out on Deio CXXVIII tracks. Landmarks 1, 3,4, and 5 plots close to the centroid, whereas landmarks 2 and 6 are more scattered. Empty circles: individual landmarks; filled circles: centroids.



**Fig. 6.12** – Relative warps of the comparison among Deio CXXVIII tracks carried out with six landmarks. A: RW1 vs. RW2; B: RW1 vs. RW3. RW1 = 44.02%; RW2 = 23.73%; RW3 = 12.52%; other RWs = 10%.

### 6.2.2 Morphology vs. Extramorphology – Conclusions

The landmark analysis carried out on a trackway shows interesting results regarding what parts of the footprint morphology can be considered reliable. In particular, it is clear that the highest variation is due to the hypices position, whereas the other landmark influence is really low.

This high variance can be explained as the consequence of the interaction of the autopodium with the sediment.

Studies on the dynamics of the dinosaur walk (e.g. Avanzini, 1998; Milàn et al., 2006) and the analysis of 3D models of tridactyl footprints (Petti et al., 2008) highlight that the weight of the dinosaur is loaded on the digits and specially on the exterior part of the footprint (digits III and IV).

Thus, if the weight is loaded mainly on digits, hypices are a non-compressed area that can be more easily affected by deformations, such as small mud flows, walls collapsing, dragging, etc. This interpretation well explains also the higher variance of landmark 6, corresponding to the hypex between digits II and III: according to the dynamic analyses cited above, the inner side of the footprints should have been less loaded by the dinosaur weight, allowing a larger deformation.

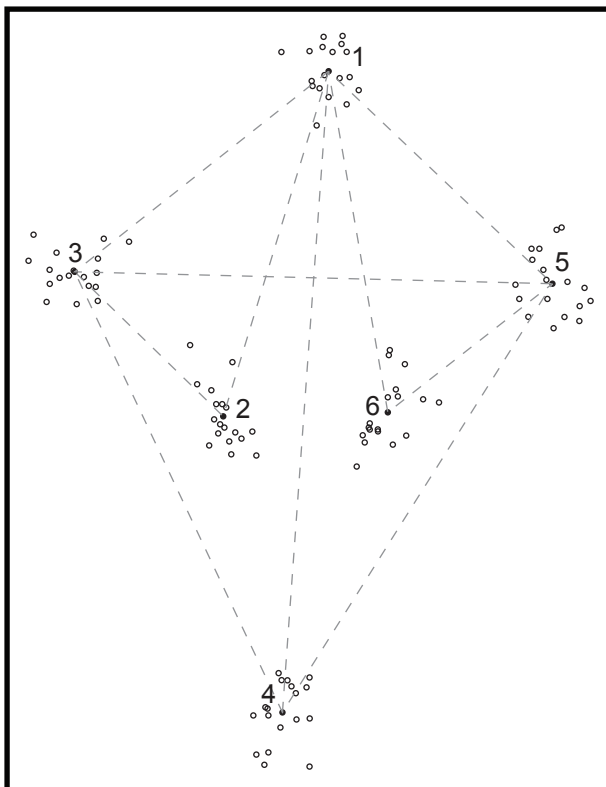
Then, despite their importance in describing footprint morphology, hypices, and related measurements, have to be cautiously considered, and should not be taken into account for ichnotaxonomy, at least for not exceptionally preserved tracks.

### 6.2.3 Application to “megalosaurian” ichnotaxonomy

Landmark analysis has been tried also on “megalosaurian” ichnotaxa, to verify if any relationship is present across the different ichnospecies and the ichnogenera proposed so far.

The same six landmarks used above were pointed in drawings taken from literature (Lockley et al., 2000, 2007; Thulborn, 2001; internet: <http://www.paleo.cc/paluxy/ovrdino.htm>) and also from the Iouaridène site (Deio CXXVIII/16 and consensus of Deio CXXVIII landmark analysis).

The same procedure as above was applied, that is, the coordinates of the aligned specimens were used for thin-plate splines Relative Warp analysis.



**Fig. 6.13** – Consensus of the comparison among “megalosaurian” tracks carried out with six landmarks. Landmarks 2 and 6 account the highest variations. Empty circles: individual landmarks; filled circles: centroids.

RW1 and RW2 have similar values, accounting respectively 30.93% and 30.13% of the total variation. The consensus (Fig. 6.13) shows that these RW are mainly driven by the landmark 2 and 6.

Having just above demonstrated how variable the position of hypices is, a new landmark analysis has been carried out considering only four landmarks: the three digit tips and the “heel”.

The consensus obtained from the new landmark analysis (Fig. 6.14) shows a cloud of points around the centroid of each landmark.

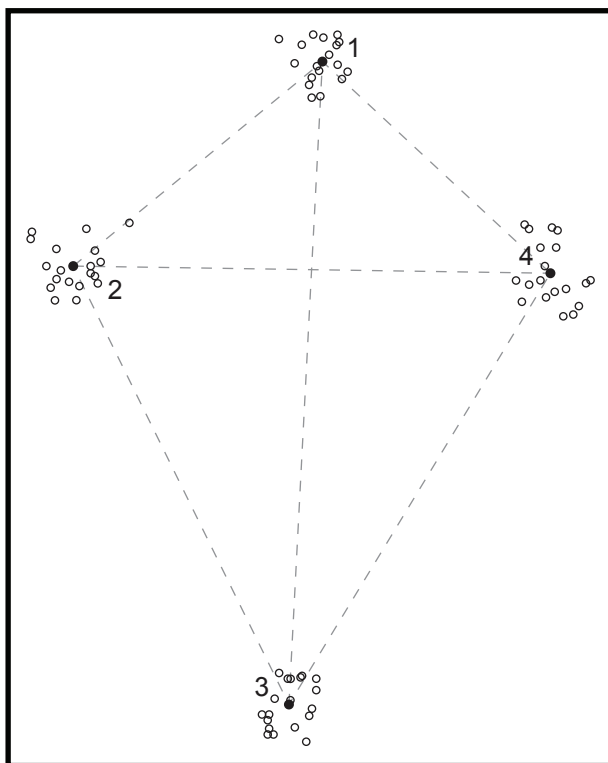
RW1 accounts for 47.99% of the total variation, RW2 for the 27.06%, RW3 for the 17.71% and RW4 for the 7.23%. These variations are mainly due to several factors and not to predominant variations in the shape of the track.

Looking at the score plot of the RW1 vs. RW2 (Fig. 6.15A) two main groups can be roughly pointed out: the first grouping the tracks numbered 2, 4, 5, 6, 7, 11, 14, the other grouping the tracks numbered 8, 9, 10, 15,

16,17, 19. The RW1 vs. RW3 score plot (Fig. 6.15B) shows a slightly different distribution of the tracks, with three clearer groups; nonetheless, a broader distribution, similar to the RW1 vs. RW2 plot can be distinguished along RW1.

### 6.2.3 Application to “megalosaurian” ichnotaxonomy – Conclusions

Looking at the groups pointed out from the score plots, it is worth noticing that the first group includes most of the *Megalosauripus* sensu Lockley et al. (2000) from North America, Turkmenistan and Spain, and some of the *H. hauboldi* (sensu Lockley et al., 2000, 2007), whereas the second group includes most of the *Megalosauropus* and *Megalosauripus* sensu Thulborn (2001), as well as the *B. maximus* both sensu Lockley 2000 and Thulborn 2001. It is interesting that the *Megalosauripus* track from Portugal (#3), having morphological similarities with the Moroccan specimens (#1, #2), in the first plot (Fig. 6.15A), does not plot in the same group. However, in the second plot (Fig. 6.15B) it is more closely related to the Moroccan specimens.



**Fig. 6.14** – Consensus of the comparison among “mega-losaurian” tracks carried out with four landmarks. Landmarks 2 and 6 have been depicted because of their high variability influenced the analysis. Empty circles: individual landmarks; filled circles: centroids.

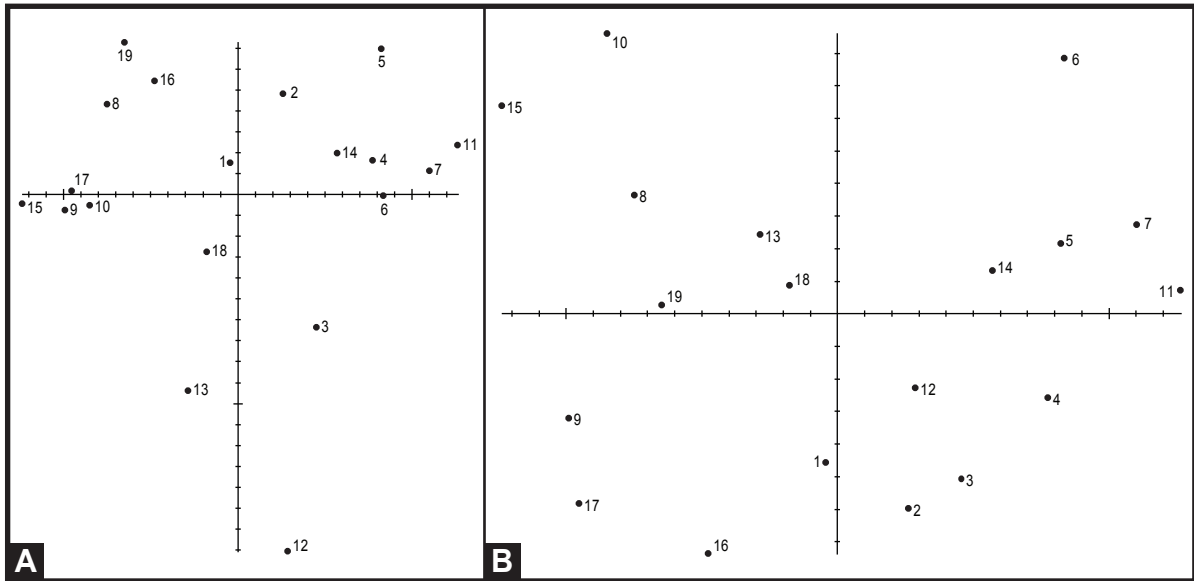
It is worth noticing that the Iouaridène specimens (#1, #2), even if coming from the same trackway, plot in different position. The cause of such a plot can be that landmarks of #1 were placed on a single footprint (Deio CXXVIII/16), whereas #2 is a virtual track derived from the consensus of the landmark analysis on Deio CXXVIII trackway.

Furthermore, the same specimen of “*M?*” *glenrosensis*, taken from two different drawings (#8 from Lockley et al., 2000; #9 from the internet, <http://www.paleo.cc/paluxy/ovrdino.htm>) plots in two different positions.

Thus, the different position of footprints made by the same dinosaur, and also of the same footprint taken from different drawings, introduces a new problem on the application of landmark analysis to ichnotaxonomy: how many reference specimens should be considered for a significant comparison? The best answer should be: as many as possible, possibly from photographs or, better, 3D digital models, taken from holotypes, top- and paratypes.

Unfortunately, for most of the dinosaur ichnological record so much information is not available; in fact, also the actual holotypes are often missing. In these cases, a solution could be to use the highest number of publications possible, including sketches and drawings made by different people, which could create a “virtual” number of different types of the same taxon.

Summing up, the Landmark analysis is a powerful tool also for solving the taxonomical problems, but need more improving to get significant results in comparing different footprints types. If applied systematically on the study of fossil tracks together with the 3D digital acquisitions, it could become a very useful technique to objectively describe the shape of a footprint.



**Fig. 6.12** – Relative Warps for the “megalosaurian” tracks; A: RW1 vs. RW2; B: RW1 vs. RW3. Two main groups can be roughly pointed out in both the plots. RW1 = 47.99%, RW2 = 27.06%, RW3 = 17.71%, RW4 = 7.23%.

Numbers represent the specimens analyzed: 1 = Deio CXXVIII/16 (original outline drawing); 2 = consensus of Deio CXXVIII trackway (Fig 6.9); 3 = Portugal *Megalosauripus* (Lockley et al., 2000, Fig. 8); 4 = Arizona *Megalosauripus* (Lockley et al., 2000, Fig. 8); 5 = Utah *Megalosauripus* (Lockley et al., 2000, Fig. 8); 6 = Turkmenistan *Megalosauripus* (Lockley et al., 2000, Fig. 8); 7 = Zambujal quarry (Portugal) *Megalosauripus* (Lockley et al., 2000, Fig. 4B); 8 = “*M.*” *glenrosensis* (Lockley et al., 2000, Fig. 5); 9 = “*M.*” *glenrosensis* (<http://www.paleo.cc/paluxy/ovrdino.htm>); 10 = *M. teutonicus* (Lockley et al., 2000, Fig. 5); 11 = Asturias cf. *Hispanosauropus* (Lockley et al., 2000, Fig. 4C); 12 = Asturias cf. *Hispanosauropus* (Lockley et al., 2000, Fig. 4D); 13 = Asturias *H. hauboldi* (Lockley et al., 2007, Fig 5C); 14 = Asturias *H. hauboldi* (Lockley et al., 2007, Fig 5A); 15 = *Megalosauripus* (Lessertisseur, 1955; Thulborn, 2001); 16 = *Bueckeburgichnus maximus* (Lockley et al., 2000, Fig. 2); 17 = *Euthynichnium lusitanicum* (Lessertisseur and Zbyszewski, 1957; Lockley et al., 2000, Fig. 1B); 18 = *E. lusitanicum* (Lockley et al., 2000, Fig. 3B); 19 = *H. hauboldi* (Lockley et al., 2007, Fig 5D).





# 7 CONCLUSIONS

## Paleoenvironment

The paleoenvironmental reconstruction identifies the site as coastal flood plain, with semiarid climate, where cyclic marine ingressions and/or flooding occurred, allowing the carbonatic cementation and so the preservation of the tracks. However, during the flooding water must have been not very deep, as it is evident from the frequent occurrence of symmetric ripples, which only forms in shallow waters.

This consideration makes the interpretation of the manus-only and manus-dominated tracks as traces of swimming sauropods baseless. The size of the tracks indicates a very large dinosaur, with a hip height higher than 4 m, that is, the inundation water should have been more than 4 m deep to allow the sauropod floating. But this hypothesis is not consistent with the sedimentological features of the facies analyzed.

Considering ripple directions, a main NE-SW strike is evident. This could be due to either the influence of main wind streams or to the coastal wave. There are no clear evidences of which of the two interpretations is correct, but the ripple strikes are parallel to the main directions of movement of the dinosaurs (Fig 7.1). This consistency seems to be more related to the presence of a close continuous shore line than with ponds or ephemeral lakes where the ripple could have formed.

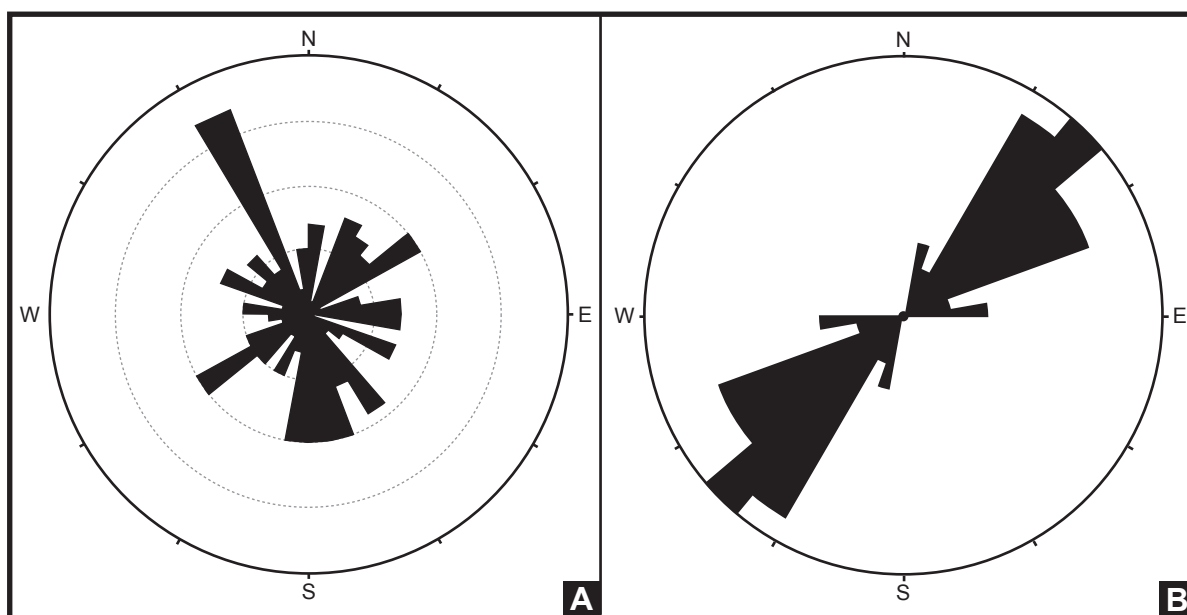


Fig. 7.1 – Comparison between dinosaur locomotion directions and symmetric ripple strikes; A: dinosaur movement directions; B: Ripple crest strikes.

## Statistical analysis

The large number of tracks surveyed and analyzed from the Iouaridène site allowed to test significantly Principal Component Analysis and Landmark Analysis applied to tridactyl footprints.

PCA, when applied to large number of different tracks, is not able to determine morphological groups consistent with the morphotypes described by ichnological features. This could reflect a limit of the method, or, more probably, the failure is due to an inappropriate or insufficient choice of variables. Further trials with different variables (e.g. digit phalangeal length, digit width, etc.), even if more affected by the preservation grade, could determine the reliability of

this test in the morphotypes discrimination.

However, when applied to tracks with similar sizes, the method turns out to be suitable and reliable, and points out analogies and differences. The methods allowed to recognize the theropod origin of the morphotype 2D, comparing it with the “megalosaurian” type 2c.

Landmark Analysis was firstly applied to a single trackway to determine if the chosen landmarks were reliable or not for a comparison between different tracks. The analysis pointed out that four of the landmarks (digits tips and “heel”) are good landmarks, being affected only by small variations along the trackway. Hypices, instead, showed a great and scattered variability, not dependent on actual morphological characteristics. Thus, despite their importance in the description of the footprint morphology, they cannot be considered as reliable landmark. Furthermore, in general, hypices have to be cautiously considered, and should not be taken into account for ichnotaxonomy, at least for not exceptionally preserved tracks.

Then the Landmark analysis has been used to draw a comparison between the “megalosaurian” tracks known from literature and those from the Iouaridène ichnosite. For this analysis, the hypices were not considered, and only four landmarks were taken into account. Despite the small number of points considered, the analysis stressed a division among these footprints. The tracks could be arranged roughly into two groups, which correspond more or less to the taxonomical distinctions made by Lockley et al. (2000, 2007) and Thulborn (2001). Thus, despite some problems regarding the quality of the drawing used to place the landmark emerged (Chapt. 6.2.3), the method showed a good potential in comparing unknown types with the known ichnotaxon, and it seems to be able to solve also ichnotaxonomical problems.

### **Paleoichnology, Paleontology and Paleogeography**

This study points out a highly differentiated dinosaur fauna, dominated by middle-large “megalosaurian” theropods followed by the large *B. taghbaloutensis* sauropods. Small dinosaur tracks, and other small non-dinosaurian traces are generally rare. Furthermore, tracks of the tinier and lighter animals (e.g. lizards, turtles, pterosaurs...) are missing. This is more easily explained by the sedimentological characteristics of the substrate than by an actual absence of these animals: the early hardening of the substrate, due to the early cementation, would not allow the impression of the traces of these lighter animals. Large theropod and also the large sauropod tracks are rarely deeper than 10 cm, also when occurring as true tracks.

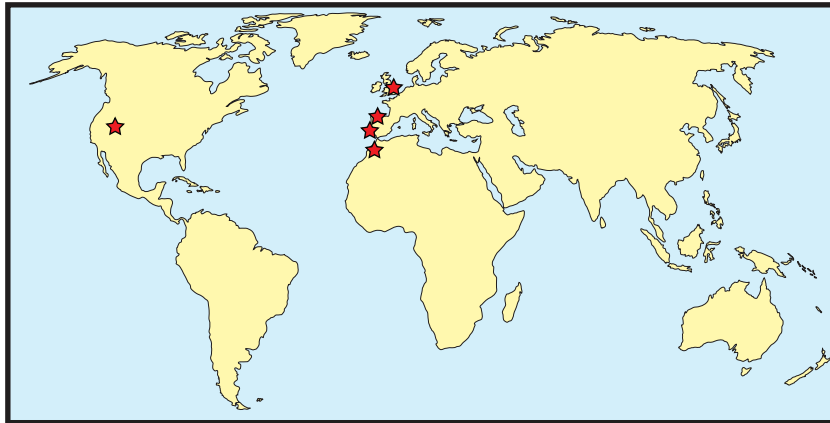
In the site the gregarious behaviour of sauropods is also highlighted, with the presence of two groups of parallel tracks, probably left by two herds consisting of the two main groups of sauropods. A certain parallelism has been noticed also among the manus-dominated tracks, but the data are too scattered to allow further interpretation. On the contrary, parallel theropod tracks can be considered missing.

Compared to other Upper Jurassic sites, the Iouaridène valley lacks ornithopod tracks of any size. As discussed in 5.2.6 the morphotype 2E has some characteristics that could remind of large ornithopod tracks, but no further analysis can be carried out.

The comparison made between the Late Jurassic dinosaurs bones remains (sauropods, theropods, stegosaurs, ornithopods) from the United States, Portugal and Tanzania (Mateus, 2006) shows similarities which allowed to hypothesize a connection between the northern and southern margin of the Tethys.

Ichnological comparison between the Late Jurassic ichnoassemblages of Asturias and western United States (Lockley et al., 2008) showed the same similarities.

Thus, considering the similarities of the “megalosaurian” tracks among Iouaridène, western US, Portugal, and Spain highlighted by the landmark analysis, and also the distribution of *Deltapodus* described above, the hypothesis of a land connection across the Tethys during the Middle to Late Jurassic seems to be more and more possible, and has to be taken into account for future paleogeographical reconstructions (Fig. 7.3).



**Fig. 7.2** – Global distribution of *Deltapodus*. Updated from Milàn and Chiappe (2008) including Moroccan occurrences.

### Ichnofacies

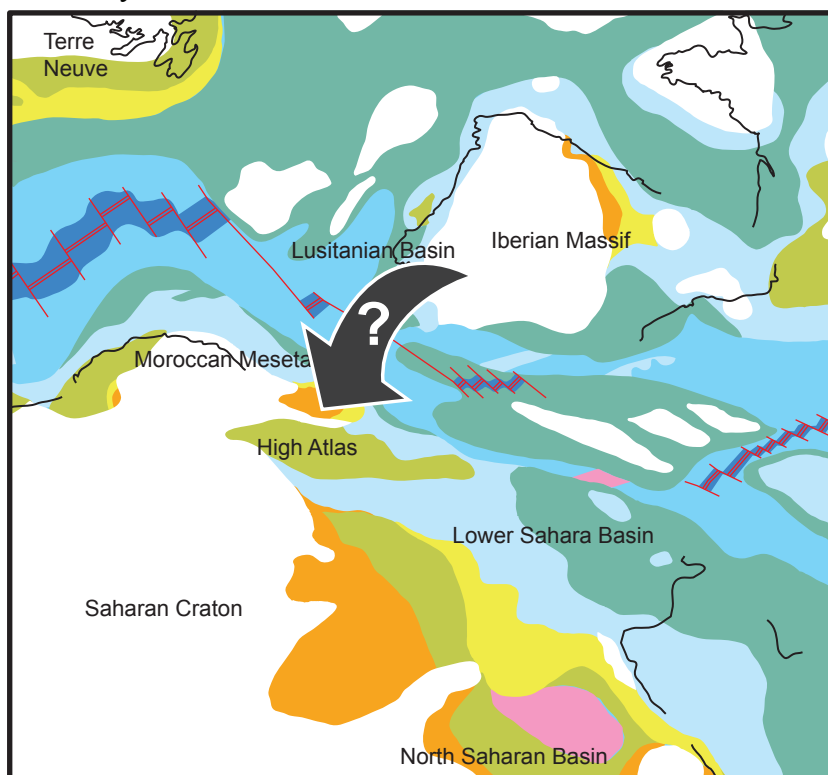
Considering the “new paradigm” ichnofacies (Lockley, 2007), there are two dinosaur ichnofacies: the *Brontopodus* and the *Grallator* ichnofacies. Hunt and Lucas (2007) updated the archetype of the *Brontopodus* ichnofacies, which describes a medium-high diversity ichnofauna (4-8 ichnogenera) in which the largest number of tracks are of terrestrial herbivores, with a lower presence of carnivore (> 10%). The stratigraphical range goes from Late Jurassic to Recent. The environments proposed are coastal plains, and clastic or carbonatic marine shore lines.

The *Grallator* ichnofacies archetype describes high differentiated ichnofauna (5-8 ichnogenera), with dominant tracks of avian and non-avian theropods. Tracks of bipedal and quadrupedal ornithischian, sauropods and herbivores mammals are also locally common. The stratigraphical range extends from Late Triassic to Recent. The environment proposed is lacustrine margin.

The *Grallator* ichnofacies is divided into four ichnocoenoses: 1- *Grallator* ichnocoenosis; 2- *Avipeda* ichnocoenosis; 3- *Jindongornipes* ichnocoenosis.

The same authors, in two previous works (Hunt and Lucas, 2006a, 2006b), named also a *Megalosauripus* ichnocoenosis, pointing out its possible biostratigraphic importance, at least for North America, being it close to the Oxfordian-Kimmeridgian boundary.

The analysis of the ichnocoenosis of the Iouaridène site dominated by bipedal dinosaurs, and



**Fig. 7.3** – Paleogeographic reconstruction of the Late Jurassic in the southwestern margin of the Tethys. Redrawn and modified from Dercourt et al., 2000.

particularly by medium-large “megalosaurian” theropods, describes very well the *Megalosauripus* ichnocoenosis. Thus, the Iouaridène ichnoassemblage can be described as one ichnocoenosis of the *Grallator* ichnofacies (sensu Hunt and Lucas, 2007). However, the definition of the inferred environment described on the archetype (Hunt and Lucas, 2007) is not completely applicable to the Moroccan ichnocoenosis. Indeed, the sedimentological analysis of the ichnosite gave a different paleoenvironment, even if continental (Chapt. 3.5).

### **Age of the site**

The application of Landmark Analysis allowed to compare in an objective way the Iouaridène “megalosaurian” tracks with very discussed literature record regarding this group. Though the solution of the problem, even with the use of geometric morphometrics techniques, is far, the Landmark Analysis stressed the similarities of the studied tracks with the Upper Jurassic *Megalosauripus* (sensu Lockley et al., 2000) from Portugal, Arizona and Utah, and the coeval *Hispanosauropus* from Spain.

Looking at other ichnological records, the occurrence of the *Breviparopus* ichnogenus out of Morocco has been recognized in the Upper Jurassic formations of Switzerland (Marty et al., 2003, fig. 5; Marty 2008) and Zimbabwe (Ait-Kaci Ahmed et al., 2004). Moreover, also the occurrence of *Deltapodus*, also in the Upper Jurassic layers of Portugal, has to be recorded.

Thus, the ?Oxfordian-Kimmeridgian age proposed by Charrière et al. (2005) seems the most probable for the site, being confirmed by micropaleontological data and by the ichnological record as well.

# REFERENCES

---

- AIGNER, T. and BACHMANN, G. 1989. Dynamic stratigraphy of an evaporite-to-red bed sequence, Gipskeuper (Triassic), southwest German Basin. *Sedimentary Geology*, **62**, 5-25.
- AIT-KACI AHMED, A., LINGHAM-SOLIAR, T. and BRODERICK, T.J. 2004. Giant sauropod tracks from the Middle-Late Jurassic of Zimbabwe in close association with theropod tracks. *Lethaia*, **37**, 467-470.
- ALEXANDER, R. McN. 1976. Estimates of speeds of dinosaurs. *Nature*, **261**, 129-130.
- ALEXANDER, R. McN., LANGMAN, V.A. and JAYES, A.S. 1977. Fast locomotion of some African ungulates. *Journal of Zoology*, **201**, 135-152.
- ALONSO, R.N. 1980. Icnitas de dinosaurios (Ornithopoda, Hadrosauridae) en el Cretácico superior del norte de Argentina. *Acta Geologica Lilloana*, **15**(2), 55-63.
- ANTUNES, M.T. 1976. Dinosaurios Eocretácicos de Lagosterios. *Ciências da Terra*, **1**, 1-35.
- AVANZINI, M. 1998. Anatomy of a footprint: bioturbation as a key to understanding dinosaur walk dynamics. *Ichnos*, **6**, 129-139.
- AVANZINI, M., FRANCESCHI, M., PETTI, F.M., GIRARDI, S., FERRETTI, P. and TOMASONI R. 2008. New Early Jurassic (Hettangian-Sinemurian) sauropodomorph tracks from the Trento carbonate Platform (Southern Alps, Northern Italy). *Studi Tridentini Scienze Naturali, Acta Geologica*, **83**.
- AVANZINI, M., LEONARDI, G. and MIETTO, P., 2003. *Lavinipes Cheminii* ichnogen., ichnosp. nov., a possible sauropodomorph track from the Lower Jurassic of the Italian Alps. *Ichnos*, **10**, 179-193.
- BATES, K.T., RARITY, F., MANNING, P.L., VILA, B. and HODGETTS D. 2008a. Three-dimensional modelling and analysis of dinosaur trackways. *Palaeontology*, **51**(4), 999-1010.
- BATES, K.T., RARITY, F., MANNING, P.L., HODGETTS D., VILA, B., OMS, O., GALOBART, À. and GAWTHORPE, R.L. 2008b. High-resolution LIDAR and photogrammetric survey of the Fumanya dinosaur tracksites (Catalonia): implications for the conservation and interpretation of geological sites. *Journal of the Geological Society of London*, **165**, 115-127.
- BELVEDERE, M., MIETTO, P. and MEHDI, M. 2007. Dinosaur track from the Upper Jurassic Iouaridène Formation (Demnat, Morocco). *Geoitalia 2007, Epitome*, **2**, 306. Rimini, Italy. 497 pp.
- BERTLING, M., BRADY, S., BROMLEY, R., DEMATHIEU, G., GENISE, J., MIKULÁŠ, R., NIELSEN, J., NIELSEN, K., RINDSBERG, A., SCHLIRF, M. and UCHMAN, A. 2006. Names for trace fossils: a uniform approach. *Lethaia*, **39**, 265-286.
- BIRD, R.T. 1944. Did *Brontosaurus* ever walk on land? *Natural History*, **53**, 61-67.
- BIRD, R.T. 1985. *Bones for Barnum Brown – Adventures of a dinosaur hunter*. Edited by Schreiber, V.T., Texas Christian University Press, Fort Worth, 225 pp.
- BOOKSTEIN, F.L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press, New York, 456 p.

- BOUTAKIOUT, M., HADRI, M., NOURI J., DÍAZ-MARTÍNEZ, I. and PÉREZ-LORENTE, F. In press. Prospecciones paleoicnológicas en el sinclinal de Iouaridène (Alto Atlas, Marruecos). Cuantificación de yacimientos y de icnitas. *Geogaceta*.
- BRICKER, O.P. (ed). 1971. *Carbonate cements*. Johns Hopkins Press, Baltimore and London, 376 pp.
- BUSSON, G. and CORNÉE, A. 1991. The Sahara from the Middle Jurassic to the Middle Cretaceous: data on environments and climates based on outcrops in the Algerian Sahara. *Journal of African Earth Sciences*, **12**(1/2), 285-105.
- CATTANEO, G. 1991. Evolution sédimentaire et paléogéographique du Jurassique supérieur et du Crétacé basal de l'avant-pays rifain oriental (Maroc). *Bulletin de la Société géologique de France*, **162**(1), 69-78.
- CHARRIÈRE, A., HADDOUMI, H. and MOJON P-O. 2005. Découverte de Jurassique supérieur et d'un niveau marin du marrémien dans les «couches rouges» continentales du Haut Atlas central marocain : implications paléogéographiques et structurales. *Compte Rendu Palevol*, **4**, 385-394.
- CHUBERT, G., FAURE-MAURET, A. and LEVÈQUE, P. 1956. Au sujet des grès de Guettioua et des empreintes de Dinosauriens de la région de l'Oued Rhzef (Atlas marocain). *Comptes Rendues de l'Académie des Sciences*, **243**, 1639-1642.
- COBOS, A., ROYO-TORRES, R., ALCALÀ, L., LUQUE, L. and ABERASTURI, A. 2008. Nuevos datos de las icnitas de dinosaurios en la Formación Villard el Arzobispo (Teurel). 25-26. In: RUIZ-OMEÑACA, J.I., PIÑUELA, L. and GARCÍA-RAMOS, J.C. (eds.), *Libro de resúmenes. XXIV Jornadas de la Sociedad Española de Paleontología. Museo del Jurásico de Asturias (MUJA). Museo del Jurásico de Asturias XVII*, Colunga, Spain.
- COLBERT, E.H. and MERRILEES, D. 1967. Cretaceous dinosaur footprints from Western Australia. *Journal of the Royal Society of Western Australia*, **50**, 21-15.
- COOMBS, W.P. JR. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quarterly Review of Biology*, **53**, 393-418.
- DALLA VECCHIA, F.M. 2005. Un viaggio geo-paleontologico in Marocco. *Natura nascosta*, **30**, 16-44.
- DALLA VECCHIA, F.M., TARLAO, A., TUNIS, G. and VENTURINI, A. 2000. New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia). Part I—Stratigraphy and sedimentology. Part II—Paleontology. *Memorie di Scienze Geologiche*, **52**, 193-292.
- DAY, J.J., NORMAN, D.B., UPCHURCH, P., GALE, A.S. and POWELL, H.P. 2002. Sauropod trackways, evolution, and behavior. *Science*, **296**, 1659.
- DAY, J.J., NORMAN, D.B., GALE, A.S., UPCHURCH, P. and POWELL, H.P. 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. *Palaeontology*, **47**, 319-348.
- DEMATHIEU, G.R. 1970. Les empreintes de pas de vertébrés du Trias de la bordure nord-est du Massif Central. *Cahiers de Paléontologie*, Éditions du Centre National de la Recherche Scientifique, Paris, 211 pp.
- DEMATHIEU, G.R. 1990. Problems in discrimination of tridactyl dinosaur footprints, exemplified by the Hettangian trackways, the Causses, France. *Ichnos*, **1**, 97-110.
- DERCOURT, J., GAETANI, M., VRIELYNK, B., BARRIE, R. E., BIJI-DUVAL, B., BRUNET, M.F., CA-

- DET, J.P., CRASQUIN, S. and SANDULESCU, M. (eds.). 2000. *Atlas Peri-Tethys, Palaeogeographical maps*. CCGM/CGMW, Paris, 269 pp., 24 maps.
- DRYDEN, I.L. and MARDIA, K.V. 1998. *Statistical Shape Analysis*. John Wiley & Sons, New York
- DUTUIT, J.M. and OUAZZOU, A. 1980. Découverte d'une piste de dinosaure sauropode sur le site d'empreintes de Demnat (Haut-Atlas marocain). *Mémoire de la Société géologique de France, Nouvelle Série*, **139**, 95-102.
- ELLENBERGER, P. 1974. Contribution à la classification des pistes de vertébrés du Trias: Les types du Stormberg d'Afrique du sud (II<sup>ème</sup> Partie: Le Stormberg Supérieur. I. Le biome de la zone B/1 ou niveau de Moyeni: Ses biocénoses). *Palaeovertebrata*, **141**, 1-147.
- ELMI, S. 1996. Stratigraphic correlation of the main Jurassic events in the Western Mediterranean Tethys (Western Algeria and Eastern Morocco). *GeoResearch Forum*, **1-2**, 343-358.
- FARLOW, J.O. 1987. A guide to Lower Cretaceous dinosaur footprints and tracksites of the Paluxy River Valley, Somervell County, Texas. *Geological Society of America, south-central section, 21st annual meeting, field trip guide-book*, Waco, Texas.
- FARLOW, J.O. 1989. Ostrich footprints and trackways: implications for dinosaur ichnology. In: GILLETTE, D.D. and LOCKLEY, M.G. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 243-248.
- FARLOW, J.O. 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal record. *Zubia*, **10**, 89-138.
- FARLOW, J.O., PITTMANN, J.G. and HAWTHORNE, J.M. 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal plain. 371-394. In: GILLETTE, D.D. and LOCKLEY, G.M. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 454 pp.
- GABUNIYA, L.K. and KURBATOV, V.V. 1982. Jurassic dinosaur tracks of Tashkurgan (Uzbekistan SSR). *Abstract of the scientific session, Tbilisi*, 20-22.
- GARCÍA- RAMOS, J. C. and GUTIÉRREZ CLAVEROL, M. 1995. La geología de la franja costera oriental de la depresión prelitoral de Oviedo—Caugas de Onís. 247-258. In ARAMBURU, C. and BASTIDA, F. (eds.), *Geología de Asturias*. Ed. Trea., Gijón, 312 pp.
- GARCÍA- RAMOS, J. C., LIRES, J., and PIÑUELA, L. 2002. *Dinosaurios. Rutas por el Jurásico de Asturias*. La Voz de Asturias, Lugones (Siero). 204 pp.
- GARCÍA-RAMOS, J.C., PINUELA, L. and LIRES, J. 2006. *Atlas del Jurásico de Asturias*. Ediciones Nobel, Oviedo, 225 pp.
- GARCÍA-RAMOS, J.C., PIÑUELA, L., RUIZ-OMEÑACA, J.I. and PEREDA SUPERBIOLA, X. 2008. Costas jurásicas frecuentadas por estegosaurios. 33-34. In: RUIZ-OMEÑACA, J.I., PIÑUELA, L. and GARCÍA-RAMOS, J.C. (eds.), *Libro de resúmenes. XXIV Jornadas de la Sociedad Española de Paleontología. Museo del Jurásico de Asturias (MUJA). Museo del Jurásico de Asturias XVII*, Colunga, Spain.
- GATESY, S.M., SHUBIN, N.H. and JENKINS, F.A. Jr. 2005. Anaglyph stereo imaging of dinosaur track morphology and microtopography. *Palaeontologia Electronica*, **8**, 10 pp. ([http://palaeo-electronica.org/2005\\_1/gatesy10/issue1\\_05.htm](http://palaeo-electronica.org/2005_1/gatesy10/issue1_05.htm)).
- GHOSH, P., SARKAR, S. and MAULIK, P. 2006. Sedimentology of a muddy alluvial deposit: Trias-

sic Denwa Formation, India. *Sedimentary Geology*, **191**, 3-36.

GIERLINSKI, G.D. and SABATH K. 2008. Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. *Oryctos*, **8**, 29-46.

GOLDRING, R. and SEILACHER, A. 1971. Limulid undertracks and their sedimentological implication. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **137**, 422-442.

GOMES, J.P. 1915-16. Manuscritos de Jacinto Pedro Gomes (publicação póstuma): descoberta de rastros de saúrios gigantes no Jurássico do Cabo Mondego. *Comunicações da Comissão do Serviço Geológico de Portugal*, **XI**, 132-134 (em “Manuscritos de Jacinto Pedro Gomes”). Publicacao postuma.

HADRI, M., PEREDA SUPERBIOLA, X., BOUTAKIOUT, M. and PÉREZ-LORENTE, F. 2007. Icnitas de posibles dinosaurios tireóforos del Jurásico Inferior (Alto Atlas, Goulmina, Marruecos). *Revista Española de Paleontología*, **22** (2), 147-156.

HAMMER, Ø. and HARPER D.A.T. 2005. *Paleontological data analysis*. Blackwell Publishing, Malden, 351 pp.

HAMMER, Ø., HARPER D.A.T. and RYAN, P.D. 2001. PAST: Palaeontological Statistics software package for education and data analysis. *Palaeontologica Electronica*, **4**(1), 9 p. [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm), accessed the 10.12.2008.

HAMPTON, B.A. and HORTON, B.K. 2007. Sheetflow fluvial processes in a rapidly subsiding basin, Altiplano plateau, Bolivia. *Sedimentology*, **54**, 1121-1147.

HAUBOLD, H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. In: KUHN, O. (ed.), *Handbuch der Paläoherpetologie — Encyclopedia of Paleoherpetology*, **18**, 124 pp.

HENDERSON, D.M. 2003. Footprints, trackways, and hip heights of bipedal dinosaurs – testing hip height predictions with computer models. *Ichnos*, **10**, 99-104.

HENDERSON, D.M. 2006. Burly gaits: centers of mass, stability, and the trackways of sauropod dinosaurs. *Journal of Vertebrate Paleontology*, **26**, 907-921.

HITCHCOCK, E. 1848. An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England. *Memoirs of the American Academy of Arts and Sciences*, 2d ser., **3**, 129–256.

HOTELLING, H. 1933. Analysis of a complex of statistical variables into principal components. *Journal of Educational Psychology*, **24**, 417-441, 498-520.

HUNT, A.P. and LUCAS, S.G. 2006a. Tetrapod ichnofacies of the Cretaceous. 61-67. In: FOSTER, J.R. and LUCAS, S.G. and SULLIVAN R.M. (eds), *Late Cretaceous Vertebrates from the Western Interior; New Mexico Museum of Natural History and Science Bulletin*, **35**, 410 pp.

HUNT, A.P. and LUCAS, S.G. 2006b. Tetrapod ichnofacies of the Upepr Jurassic Morrison Formation, western United States. 217-222. In: FOSTER, J.R. and LUCAS, S.G. R.M. (eds), *Paleontology and Geology of the Upper Jurassic Morrison Formation. New Mexico Museum of Natural History and Science Bulletin*, **36**, 249 pp.

HUNT, A.P. and LUCAS, S.G. 2007. Tetrapod ichnofacies: a new paradigm. *Ichnos*, **14**, 59-68.

HURUM, J.H., MILÅN, J., HAMMER, O., MIDTKANDAL, I., AMUNDSEN, H. and SAETHER, B. 2006. Tracking polar dinosaurs — new finds from the Lower Cretaceous of Svalbard. *Norwegian Journal of Geology*, **86**, 397-402.



- IRMIS, R.B. 2005. A review of the vertebrate fauna of the lower Jurassic Navajo Sandstone in Arizona. In: MCCORD, R.D. (ed.), *Vertebrate paleontology of Arizona*. Mesa Southwest Mus. Bull. **11**, 55-71.
- ISHIGAKI, S. 1985a. Dinosaur form the Atlas Mountain. *Nature Study*, **31**(10), 5-8. [In Japanese]
- ISHIGAKI, S. 1985b. Dinosaur form the Atlas Mountain. *Nature Study*, **31**(12), 5-7. [In Japanese]
- ISHIGAKI, S. 1985c. *Compte rendu d'activité 1984*. Unpublished Report, Ministère de l'Energie et des Mines, Rabat, 40 p.
- ISHIGAKI, S. 1986. Dinosaur form the Atlas Mountain. *Nature Study*, **32**(1), 6-9. [In Japanese]
- ISHIGAKI, S. 1988. Les empreintes de Dinosaures du Jurassique inférieur du Haut Atlas central marocain. *Notes et Mémoires du Service Géologique du Maroc*, **44**(334), 79-86.
- ISHIGAKI, S. 1989. Footprints of swimming Sauropods from Morocco. In GILLETTE, D.D and LOCKLEY, M.G. (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, 83-86.
- ISHIGAKI, S. 2008. *Take a walk with dinosaurs.-Excavation and research of dinosaur footprints*, Doshinsha, Tokyo, 40 p. [In Japanese]
- ISHIGAKI, S. and FUJISAKI, T. 1989. Three dimensional representation of *Eubrontes* by the Method of *Moiré* topography. In: GILLETTE, D.D. and LOCKLEY, M.G. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 421-425.
- ISHIGAKI, S. and MATSUMOTO, Y. 2008. Reexamination of manus-only and manus-dominant trackways of sauropod dinosaur from Middle Jurassic of Morocco. *Ichnia 2008 - Second International Congress on Ichnology, Abstract Book*, Crakow, Poland
- JENNY, J. 1985. Carte Géologique du Maroc à 1:100.000, feuille Azilal. *Notes et Mémoires du Service Géologique du Maroc*, **399**.
- JENNY, J. and JOSSEN, J-A. 1982. Découverte d'empreintes de pas de Dinosauriens dans le Jurassique inférieur (Pliensbachien) du Haut-Atlas central (Maroc). *Compte Rendu de l'Académie des Sciences de Paris*, **294**, II, 223–226
- JENNY, J., LE MARREC, A. and MONTBARON, M. 1981a. Les Couches rouges du Jurassique moyen du Haut Atlas central (Maroc): corrélations lithostratigraphiques, éléments de datations et cadre tectono-sédimentaire. *Bulletin de la Société Géologique de France*, (7), XXIII, 6, 627-639.
- JENNY, J., LE MARREC, A. and MONTBARON, M. 1981b. Les empreintes de pas de dinosauriens dans le Jurassique Moyen du Haut Atlas central (Maroc) : nouveaux gisements et précisions stratigraphiques. *Geobios*, **14**(3), 427-431.
- JOLLIFFE, I.T. 1986. *Principal Component Analysis*. Springer, New York, 487 p.
- KAEVER, M. and LAPPARENT, A.F. DE. 1974. Les traces de pas de dinosaures du Jurassique de Barkhausen (Basse Saxe, Allemagne). *Bulletin de la Société Géologique de France*, (7) XVI, 516-525.
- KUHN, O. 1958. *Die Fährten der vorzeitlichen Amphibien und Reptilien*. Verlagshaus Meisenbach, Bamberg, 64 pp.

LAPPARENT, A.F. DE and ZBYSZEWSKI, G. 1957. Les Dinosauriens du Portugal. *Memoria dos Servicos Geologicos de Portugal*, **2**, 1-63.

LAPPARENT, A.F. DE, ZBYSZEWSKI, G., ALMEIDA, F.M. DE and VEIGA FERREIRA, O. 1951. Empreintes de pas de Dinosauriens dans le Jurassique du Cap Mondego (Portugal). *Compte Rendu sommaire des Séances de la Société Géologique de France*, **1951**, 251-252.

LAPPARENT, A.F. DE. 1942. Dinosauriens du Maroc. *Compte Rendu sommaires de la Société géologique de France*, **5**, 28.

LAPPARENT, A.F. DE. (1945). Empreintes de pas de Dinosauriens du Maroc, exposées dans la galerie de Paléontologie. *Bulletin du Muséum National d'Histoire Naturel, Paris*, 2e sér., **XVII**(3), 268-271.

LEE, Y-N. and HUH, M. 2002. Manus-only sauropod tracks in the Uhangri Formation (Upper Cretaceous), Korea and their paleobiological implications. *Journal of Paleontology*, **76**, 558-564.

LEE, Y-N. and LEE, H-J. 2006. A sauropod trackway in Donhae-Myeon, Goseong County, South Gyeongsang Province, Korea and its paleobiological implications of Uhangri manus-only sauropod tracks. *Proceedings of the Goseong International Dinosaur Symposium, Journal of the Paleontological Society of Korea*, **22**, 1-14.

LEFRANC, J-P. and GUIRAUD, R. 1990. The Continental Intercalaire of northwestern Sahara and its equivalent in the neighbouring regions. *Journal of African Earth Sciences*, **10**(1/2), 27-77.

LEONARDI, G. 1984. Le impronte fossili di dinosauri. In: RUNZONI, GRAGGIO and GUART (eds.), *Sulle orme dei Dinosauri*, Venice, 165-186.

LEONARDI, G. 1987. *Glossary and manual of tetrapod footprint palaeoichnology*. Publicação do Departamento Nacional da Produção Mineral Brasil, Brasília, 117 pp.

LEONARDI, G. 1997. Problemática actual de las icnitas de dinosaurios. *Revista Sociedad Geológica. España*, **10**, 341-353.

LESSERTISSEUR, J. 1955. Traces fossiles d'activité animale et leur signification paléobiologique. *Mémoires de la Société Géologique de France*, **74**, 150 pp.

LIRES, J., PIÑUELA, L., and GARCÍA-RAMOS, J. C. 2001. Nuevos datos y reinterpretación del yacimiento jurásico de icnitas de dinosaurio de la playa de La Griega (Colunga, Asturias). In: MELÉNDEZ, G., HERRERA, Z., DELVENE, G., and AZANZA, B. (eds.), *Los Fósiles y la Paleogeografía. Publicaciones del Seminario de Paleontología de Zaragoza, XVII. Jornadas de la Sociedad Española de Paleontología*, **5**, 342-347.

LOCKLEY, M.G. 1991a. The dinosaur footprint renaissance. *Modern Geology*, **16**, 139-160.

LOCKLEY, M.G. 1991b. *Tracking dinosaurs: a new look at an ancient world*. Cambridge University Press, Cambridge, 238 pp.

LOCKLEY, M.G. 1997a. Megatracksites. In: CURRIE, P.J. and PADIANK, K. (eds.), *Encyclopedia of dinosaurs*, Academic Press, San Diego p. 417.

LOCKLEY, M.G. 1997b. The paleoecological and paleoenvironmental utility of dinosaur tracks. In: FARLOW, J.O. and BRETT-SURMAN, M.K. (eds.), *The complete dinosaur*, Indiana University Press, Bloomington, 545-578.

LOCKLEY, M.G. 2007. A tale of two ichnologies: the different goals and missions of inverte-

brate and vertebrate ichnotaxonomy and how they relate in ichnofacies analysis. *Ichnos*, **14**, 39-57.

LOCKLEY, M.G. and CONRAD, K. 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the Western USA. In: GILLETTE, D.D. and LOCKLEY, M.G. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 121-134.

LOCKLEY, M.G. and HUNT, A.P. 1995. *Dinosaur tracks and other fossil footprints of the western United States*. Columbia University Press, New York, 338 pp.

LOCKLEY, M.G. and HUNT, A.P. 1998. A probable stegosaur track from the Morrison Formation of Utah. In: CARPENTER, K., CHURE, D. and KIRKLAND, J. (eds.), *The Upper Jurassic Morrison Formation: an interdisciplinary study*. *Modern Geology*, **23**, 331-342.

LOCKLEY, M.G. and MEYER, C.A. 2000. *Dinosaur tracks and other fossil footprints of Europe*. Columbia University Press, New York, 321 pp.

LOCKLEY, M.G. and SANTOS, V.F. DOS 1993. A preliminary report on sauropod trackways from the Avelino site, Sesimbra region, Upper Jurassic, Portugal. *Gaia*, **6**, 38-42.

LOCKLEY, M.G., SANTOS, V.F. DOS, RAMALHO, M.M. and GALOPIM, A.N. 1992c. Novas jazidas de pegadas de dinosáurios no Jurássico Superior de Sesimbra (Portugal). *Gaia*, **5**, 40-43.

LOCKLEY, M.G., MEYER, C.A. and SANTOS, V.F. DOS. 1994a. Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. *Gaia*, **10**, 27-36.

LOCKLEY, M.G., FARLOW, J.O. and MEYER, C.A. 1994b. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia*, **10**, 135-146.

LOCKLEY, M.G., MEYER, C.A. and SANTOS, V.F. DOS. 1996. *Megalosauripus*, *Megalosauropus* and the concept of megalosaur footprints. 113-118 In: MORALES, M. (ed.), *The continental Jurassic*, Museum of Northern Arizona, Flagstaff, 608 pp.

LOCKLEY, M.G., HUNT, A., PAQUETTE, M., BILBEY, S.-A. and HAMBLIN, A. 1998a. Dinosaur tracks from the Carmel Formation, Northeastern Utah: implications for Middle Jurassic paleoecology. *Ichnos*, **5**, 243-338.

LOCKLEY, M.G., SANTOS, V.F. DOS, MEYER C.A. and HUNT A.P. 1998b. A new dinosaur tracksite in the Morrison Formation, Boundaty Butte, Southeastern Utah. *Modern Geology*, **23**, 317-330.

LOCKLEY, M.G., MEYER, C.A. and SANTOS, V.F. DOS. 2000. *Megalosauripus* and the problematic concept of megalosaur footprints. *Gaia*, **15**, 313-337. For 1998.

LOCKLEY, M.G., SCHULP, A.S., MEYER, C.A., LEONARDI, G., and KERUMBA MAMAMI, D. 2002a. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research*, **23**, 383-400.

LOCKLEY, M.G., WRIGHT, J.L., WHITE, D., JIANJUN, L., LU, F., HONG, L. and MATSUKAWA, M. 2002b. The first sauropod trackways from China. *Cretaceous Research*, **23**, 363-381.

LOCKLEY, M.G., LIRES, J., GARCÍA-RAMOS, J.C., PINUELA, 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.

MANNING, P.I., OTT, C. and FALCKINGHAM, P. 2008. A probable tyrannosaurid track from the Heel Creek formation (Upper Cretaceous), Montana, United States. *Palaios*, **23**, 645-747.

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. *GeoFocus*, **21**, 278 pp.

MARTY, D., CAVIN, L., HUG, W.A., MEYER, C.A., LOCKLEY, M.G. and IBERG, A. 2003. Preliminary report on the Courtedoux dinosaur tracksite from the Kimmeridgian of Switzerland. *Ichnos*, **10**, 209–219

MARTY, D., AYER, J., BECKER, D., BERGER, J.-P., BILLON-BRUYAT, J.-P., BRAILLARD, L., HUG, W.A. and MEYER, C.A. 2007. Late Jurassic dinosaur tracksites of the Transjurane highway (Canton Jura, NW Switzerland): overview and measures for their protection and valorization. *Bulletin for Applied Geology*, **12**, 75-89.

MASSARI, F. and NERI, C. 1997. The infill of a supradetachment(?) basin: the continental to shallow-marine Upper Permian succession in the Dolomites and Carnia (Italy). *Sedimentary Geology*, **110**, 181-221.

MASSARI, F., NERI, C., PITTAU, P., FONTANA, D. and STEFANI, C. (1994) Sedimentology, palynostratigraphy and sequence stratigraphy of a continental to shallow-marine rift-related succession: Upper Permian of the eastern Southern Alps (Italy). *Memorie di Scienze Geologiche*, **46**, 119-243.

MATEUS, O. 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru Beds (Tanzania): a comparison. 1-9. In: FOSTER, J.R. and LUCAS, S.G. (eds), *Paleontology and Geology of the Upper Jurassic Morrison Formation. New Mexico Museum of Natural History and Science Bulletin*, **36**, 249 pp.

MATEUS, O. and ANTUNES, M.T. 2001. *Draconyx loureiroi*, a new Camptosauridae (Dinosauria: Ornithopoda) from the Late Jurassic of Lourinhã, Portugal. *Annales de Paléontologie*, **87**, 61-73.

MATEUS, O. and MILÀN, J. 2008. Ichnological evidence for giant ornithopod dinosaurs in the Upper Jurassic Lourinhã Formation, Portugal. *Oryctos*, **8**, 47-52.

MENSINK, H. and MERTMAN, D. 1984. Dinosaurierfährten (*Gigantosauropus asturiensis* n. g. n. sp.; *Hispanosaurus hauboldi* n. g. n. sp.) im Jura Asturiens bei La Griega und Ribadasella (Spanien). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **7**, 405-415.

MEYER, C.A. and MONBARON, M. 2002. Middle Jurassic dinosaur tracks from Morocco - *Facts and Fiction*. 7<sup>th</sup> European Workshop on Vertebrate Palaeontology, Sibiu (Romania). *Abstract book*.

MEYER, C.A. and THÜRING, B. 2006. A marriage between geotechnique and paleontology: three dimensional visualization of a geological monument for scientific exploration and geotechnical conservation (Cal Orcko, Sucre, Bolivia). *4th Swiss Geoscience Meeting, 25.11.2006, Berne, Switzerland, Abstract volume*, 133-134.

MEYER, C.A., LOCKLEY, M.G., ROBINSON, J.W. and SANTOS, V.F. DOS 1994. A comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the Western United States: evidence and implications. *Gaia*, **10**, 57-64.

MIALL, A.D. 1985. Architectural-element analysis: a new method of facies analysis applied to

fluvial deposits. *Earth-Science Review*, **22**, 261-308.

MILÀN, J., AVANZINI, M., CLEMMENSEN, L., GARCÍA-RAMOS, J.C. and PIÑUELA, L. 2006. Theropod foot movement recorded by Late Triassic, Early Jurassic and Late Jurassic footprints. 352-364. In: HARRIS, J.D., LUCAS, S.G., SPIELMANN, J.A., LOCKLEY, M.G., MILNER, A.R.C. and KIRKLAND, J.I. (eds.), *The Triassic-Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin*, **37**, 610 pp.

MILÀN, J. and CHIAPPE, L.M. 2008. First American record of the stegosaurian ichnogenus *Delatapodus* from the Upper Jurassic Morrison Formation, Utah, USA. In: *52<sup>nd</sup> Annual Meeting of the Palaeontological Association. Abstracts*. Glasgow, Scotland.

MILÀN, J. and CHIAPPE, L.M. In press. First American record of the Jurassic ichnogenus *Delta-podus* and a review of the fossil record of stegosaurian footprints. *Journal of Geology*.

MONBARON, M. 1983. Dinosauriens du Haut Atlas central (Maroc): état de recherche et précision sur le découverte d'un squelette complet de grand Cétiosaure. *Actes Société jurassienne d'Emulation*, Porrentruy, 203-234.

MONBARON, M., RUSSELL, D.A. and TAQUET, P. 1999. *Atlasaurus imelakei* n.g., n.sp., a brachio-aurid-like sauropod from the Middle Jurassic of Morocco. *Compte Rendu de l'Académie des Sciences de Paris*, **329**, 519-526.

MONTBARON, M. and TAQUET, P. 1981. Découverte du squelette complet d'un grand Cétiosaure (Dinosaure Sauropode) dans le bassin jurassique moyen de Tilougguit (Haut-Atlas central, Maroc) - *Compte Rendu de l'Académie des Sciences de Paris*, **292/II**, 243-246.

MORATALLA, J.J. 1988. Nueva evidencia icnológica de dinosaurios en el Cretacico Inferior de La Rioja (España). *Estudios Geológicos*, **44**, 281-372.

MORATALLA, J.J., GARCIA-MONDEJAR, J., SANTOS, V.F. DOS, LOCKLEY, M.G., SANZ, J.L. and JIMENEZ, S. 1994. Sauropod trackways from the Lower Cretaceous of Spain. *Gaia*, **10**, 75-84.

MORENO, K. and BENTON, M.J. 2005. Occurrence of sauropod dinosaur tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*). *Journal of South American Earth Sciences*, **20**, 253-257.

NOPSCA, F. VON. 1923. Die Familien der Reptilien. *Fortschritte der Geologie und Paläontologie*, **2**, 210 pp.

NOURI, J. 2007. La paléoichnologie des empreintes de pas des dinosauriens imprimées dans les couches du Jurassique du Haut Atlas Central. *Unpublished Ph.D. dissertation*, Université de Rabat, Rabat, 240 p.

NOURI, J., PÉREZ-LORENTE, F. and BOUTAKIOUT, M. 2001. Descubrimiento de una pista semi-plantígrada de dinosaurio en el yacimiento de Tirika (Demnat. Alto Atlas central maroquí). *Geogaceta*, **29**, 111-114.

OLSEN, P.E. and RAINFORTH, E.C. 2003. The Early Jurassic ornithischian dinosaurian ichnogenus *Anomoepus*. 314-368. In: LETOURNEAU, P.M. and OLSEN, P.E. (eds.), *The Great Rift Valleys of Pangea in Eastern North America, Volume 2: Sedimentology and Paleontology*. Columbia University Press, New York, 248 pp.

OLSEN, P.E., SMITH, J.B. and McDONALD, N.G. 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate*

*Paleontology*, **18**, 586-601.

PETTI, F.M., AVANZINI, M., BELVEDERE, M., DE GASPERI, M., FERRETTI, P., GIRARDI, S., REMONDI-NO, F., and TOMASONI, R. 2008. Digital 3D modelling of dinosaur footprints by photogrammetry and laser scanning techniques: evaluation of the integrated approach at the Coste dell'Anglone tracksite (Lower Jurassic, Southern Alps, Northern Italy). *Studi Tridentini Scienze Naturali, Acta Geologica*, **83**.

PITTMAN, J.G. 1989. Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the Gulf Coastal Plain. In: GILLETTE, D.D. and LOCKLEY, M.G. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 135-153.

PLATEAU, H, GERMAN, G. and ROCH, E. 1937. Sur la présence d'empreintes de Dinosauriens dans la region de Demnat (Maroc). *Compte Rendu sommaires de la Société géologique de France*, **16**, 241-242.

RAINFORTH, E. and MANZELLA, M. 2007. Estimating speeds of dinosaurs from trackways: a re-evaluation of assumptions. 41-48. 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*, East Stroudsburg University, Pennsylvania, USA.

RASSKIN-GUTMAN, D., HUNT, G., CHAPMAN, R.E., SANZ, J.L. AND MORATALLA, J.J. 1997. The shapes of tridactyl dinosaur footprints: Procedures, problems and potentials. 377-383. In: WOLBERG, D.L., STUMP, E. and ROSENBERG G.D. (eds.), *Dinofeast International Proceedings*, Arizona State University.

ROCH, E. 1939. Description géologique des montagnes à l'Est de Marrakech. *Mémoires du Service des Mines et Carte géologique du Maroc*, **51**, 244 p.

RODRIGUES, L.A. and SANTOS V.F. DOS. 2002. Sauropod Tracks – a geometric morphometric study. 129-142. In: ELEWA A.M.T. (ed.), *Morphometrics. Applications in Biology and Paleontology*. Springer, New York, 263 pp.

ROHLF, F.J. 1993. Relative warp analysis and an example of its application to mosquito wings. in MARCUS, L.F., BELLO, E. and GARCIA-VALDECASAS, A. (eds.), *Contributions to morphometrics. Monografías del Museo Nacional de Ciencias Naturales*, **8**, 41-61.

ROHLF F.J. 2008. tpsUtil v. 1.41. Dept. of Ecology and Evolution, Stony Brook University. <http://life.bio.sunysb.edu/morph>.

ROMANO, M. and WHYTE, M.A. 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. *Proceedings of the Yorkshire Geological Society*, **52**, 361-369.

ROMANO, M., WHYTE, M.A. and JACKSON, S.J. 2007. Trackway ratio: a new look at trackway gauge in the analysis of quadrupedal dinosaur trackways and its implications for ichnotaxonomy. *Ichnos*, **14**, 257-270.

RUSSELL, D.A. and BÉLAND, P. 1976. Running dinosaurs. *Nature*, **264**, 486.

SALGADO, L., CORIA, R.A. and CALVO, J.O. 1997. Evolution of titanosaurid dinosaurs. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana*, **34**, 3-32.

SARJEANT, W.A.S. 1988. Fossil vertebrate footprints. *Geology Today*, **4**(4), 125-130.

SARJEANT, W.A.S., DELAIR, J.B. and LOCKLEY, M.G. 1998. The footprints of Iguanodon: a history and taxonomic study. *Ichnos*, **6**(3), 183-202.

- SCHULP, A.S., AL-WOSABI, M. and STEVENS N.J. 2008. First dinosaur tracks from the Arabian Peninsula. *PLoS ONE*, **3**(5), e2243.
- SHULER, E.W. 1917. Dinosaur track in the Glen Rose Limestone, near Glen Rose Texas. *American Journal of Science*, **4**(44), 294-298.
- SHULER, E.W. 1935. Dinosaur tracks mounted on the bandstand at Glen Rose, Texas. *Field and Laboratory*, **5**, 34-36.
- STERNBERG, C.M. 1932. Dinosaur tracks from Peace River, British Columbia. *National Museum of Canada Bulletin*, **68**, 59-85.
- TERMIER, H. 1942. Donnée nouvelles sur le Jurassique rouge a Dinosauriens du Grand et du Moyen-Atlas (Maroc). *Bulletin de la Société Géologique de France*, (5) XII, 199-207.
- THOMPSON, D'ARCY W. 1917. *On Growth and Form: A New Edition*. Cambridge University Press, New York.
- THULBORN, T. 1982. Speeds and gaits of dinosaurs. *Palaeogeography Palaeoclimatology Palaeoecology*, **38**, 227-256.
- THULBORN, T. 1984. Preferred gaits of bipedal dinosaurs. *Alcheringa*, **8**, 243-252.
- THULBORN, T. 1989. The gaits of dinosaurs. 39-50. In: GILLETTE, D.D. and LOCKLEY, M.G. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 454 pp.
- THULBORN, T. 1990. *Dinosaur tracks*, Chapman & Hall, London, 410 pp.
- THULBORN, T. 2001. History and nomenclature of the theropod dinosaur tracks *Bueckeburgichnus* and *Megalosauripus*. *Ichnos*, **8**, 207-222.
- THULBORN, T. and WADE, M. 1984: Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum*, **21**, 413-517.
- THULBORN, T. and WADE, M. 1989. A footprint as a history of movement. 51-56. In: GILLETTE, D.D. and LOCKLEY, M.G. (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge, 454 pp.
- TUNBRIDGE, I.P. 1984. Facies model for a sandy ephemeral stream and clay playa complex; the Middle Devonian Trentishoe Formation of North Devon, UK. *Sedimentology*, **31**, 697-716.
- UPCHURCH, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, **349**, 365-390.
- 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 26th forum on the geology of industrial minerals*, Virginia Division of Mineral Resources Publications, **119**, 113-127.
- WEEMS, R.E. 2006. Locomotor speeds and patterns of running behaviour in non-maniraptoriform theropod dinosaurs. 379-389. In: HARRIS, J.D., LUCAS, S.G., SPIELMANN, J.A., LOCKLEY, M.G., MILNER, A.R.C. and KIRKLAND, J.I. (eds.), *The Triassic-Jurassic Terrestrial Transition*. *New Mexico Museum of Natural History and Science Bulletin*, **37**, 610 pp.
- WEISHAMPEL, D.B., DODSON, P. and OSMÓLSKA, H. (eds.) 2004. *The Dinosauria. Second Edition*, University of California Press, Berkeley and Los Angeles, 833 pp.
- WHYTE, M.A. and ROMANO, M. 1994. Probable sauropod footprints from the Middle Jurassic

of Yorkshire, England. *Gaia*, **10**, 15-26.

WHYTE, M.A., ROMANO, M. and ELVIDGE D.J. 2007. Reconstruction of Middle Jurassic dinosaur-dominated communities from the vertebrate ichnofauna of the Cleveland Basin of Yorkshire, UK. *Ichnos*, **14**, 117-129.

WILSON, J.A. 2005. Overview of sauropod phylogeny and evolution. 15-49 In: CURRY ROGERS, K.A. and WILSON, J.A. (eds.), *The sauropods: evolution and paleobiology*, University of California Press, Berkeley and Los Angeles, 358 pp.

WILSON, J.A. and CARRANO, M.T. 1999. Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, **25**, 252–267.

WILSON, J.A. and SERENO, P.C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology, Memoir*, **5**, 68 pp.

WRIGHT, J.L. 2005. Steps in understanding sauropod biology — The importance of sauropod tracks. 252-280. In: CURRY ROGERS, K.A. and WILSON, J.A. (eds.), *The sauropods: evolution and paleobiology*, University of California Press, Berkeley and Los Angeles, 358 pp.

ZELDITCH, M., SWIDERSKI D., SHEETS, D.H. and FINK W. 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press, 443 p.



# APPENDICES

---

## APPENDIX 1 - TRIDACTYL TRACK MEASUREMENTS TABLE

Appendix 1 shows the measurements and morphotypes table tridactyl footprints of Group 2.

MORPH: morphotype; Fl: foot length (cm); W: maximum width (cm); I, II, III, IV FDL: digits I, II, III, and IV free digit length (cm); I, II, III, IV W: digits I, II, III, and IV width (cm); II, III, IV PPL: digits II, III, and IV phalangeal portion length (cm); II<sup>^</sup>III°: II-III interdigital angle (degree); III<sup>^</sup>IV°: III-IV interdigital angle (degree); II<sup>^</sup>IV°: total divarication angle (degree); Fw: foot width (cm); te: toe extension (cm); Fl MET: foot length including the metatarsal portion (cm); III<sup>^</sup>MET: angle between the III digit and the matatarsal axes (degree).

Red values indicate approximative measurement due to the preservation of the track.

Unmeasurable tracks are not listed here.





















## APPENDIX 2 - TRIDACTYL TRACKWAY MEASUREMENTS TABLE

Appendix 2 shows some mean values for trackways and notable tracks, including pace and stride values and derived measurements.

Fl: foot length (cm); Fw: foot width (cm); II<sup>^</sup>IV<sup>°</sup>: total divarication angle (degree); te: toe extension (cm); Pace: pace length, mean of left and right paces (cm); Sl: stride length, mean of left and right strides (cm); IS: index of track size (adimensional); h: hip height (cm); Sl/h: stride length/hip height ratio (adimensional); Speed: locomotion speed (km/h).

TRACKWAY	Fl	Fw	II <sup>^</sup> IV	te	Pace	Sl	IS	h	Sl/h	Speed
Deio I	42.2	27.8	41.1	14.0	118.0	234.0	34.3	206.8	1.1	5.0
Deio II	32.7	25.1	39.9	9.8	105.0	206.0	28.6	160.2	1.3	5.4
Deio III	37.4	33.0	48.1	13.9	106.0	210.0	35.1	183.3	1.1	4.8
Deio IV	44.0	29.3	36.9	13.9	124.0	247.0	35.9	215.6	1.1	5.2
Deio V	39.5	26.6	44.7	12.4	212.0	232.0	32.4	193.6	1.2	5.3
Deio VI	39.5	29.1	42.6	16.5	114.0	225.0	33.9	193.6	1.2	5.0
Deio VII	21.1	15.9	48.6	7.4	72.0	140.0	18.3	95.0	1.5	5.3
Deio VIII	39.2	25.9	42.1	13.5	118.0	235.0	31.9	192.1	1.2	5.5
Deio IX	22.3	14.4	43.4	7.6	62.0	124.0	17.9	100.4	1.2	4.0
Deio X	40.3	32.9	50.7				36.4	197.5		
Deio XII	17.9	12.3					14.8	80.6		
Deio XIII	17.2	14.1	50.1	5.4	51.0	102.0	15.6	77.4	1.3	3.9
Deio XIV	38.9	30.6	61.9	12.6	109.0	216.0	34.5	190.6	1.1	4.8
Deio XV	36.1	27.6	55.3	15.3	110.0	216.0	31.6	176.9	1.2	5.2
Deio XVI	34.1	30.2	47.8	13.9	125.0	251.0	32.1	167.1	1.5	7.2
Deio XVII	38.4	27.8	50.3	13.3	111.0	220.0	32.7	188.2	1.2	5.0
Deio XVIII	39.0	34.0	57.8	5.6			36.4	191.1		
Deio XIX	38.2	28.5	48.9	12.1			33.0	187.2		
Deio XXI	25.9	18.5	50.1	7.6			21.9	126.9		
Deio XXVI	21.7	18.3	84.2	8.6			19.9	97.7		
Deio XXVIII	58.7	56.6	53.5	19.8	92.0	182.0	57.6	287.6	0.6	2.2
Deio XIX	17.3	11.3	52.2	7.0	78.0	156.0	14.0	77.9	2.0	7.0
Deio XXX	38.1	27.9	44.2	12.6	122.0	243.0	32.6	186.7	1.3	6.0
Deio XXXI	31.0	29.2	56.5	11.4			30.1	151.9		
Deio XXXII	34.0	26.4	53.7	12.5	105.0	206.0	30.0	166.6	1.2	5.2
Deio XXXIII	34.5	26.3	60.8	12.6	100.0	202.0	30.1	169.1	1.2	4.3
Deio XXXIV	38.5	26.9	47.0	12.4	110.0	217.0	32.2	188.7	1.2	4.3
Deio XXXV	32.3	23.7	53.8	13.7	104.0	209.0	27.7	158.3	1.3	5.6
Deio XXXVI	16.5	11.7	48.3	5.8			13.9	74.3		
Deio XXXVII	38.3	29.8	46.8	13.1			33.8	187.7		
Deio XL	17.3	11.5	46.4	6.1	53.0	105.0	14.1	77.9	1.3	4.1
Deio XLI	14.9	12.9	66.0	7.1	124.0	247.0	13.9	67.1	3.7	23.1
Deio XLII	70.4	53.2	49.3	15.9			61.2	345.0		
Deio XLIII	35.1	29.0	48.2	9.1	119.0	243.0	31.9	172.0	1.4	6.6
Deio XLIV	37.3	30.3	49.3	11.2	104.0	196.0	33.6	182.8	1.1	4.3
Deio C	37.8	25.4	34.7	12.1	109.0	212.0	31.0	185.2	1.1	4.8
Deio CII	37.7	30.1	48.1	12.5	112.0	221.0	33.7	184.7	1.2	5.2
Deio CIII	39.4	26.9	51.9	16.8	109.5	219.0	32.6	193.1	1.1	4.8
Deio CIV	39.3	25.8	44.6	11.4	124.3	247.3	31.8	192.6	1.3	5.9
Deio CV	36.9	26.7	40.9	13.0	112.4	224.2	31.4	180.8	1.2	5.4
Deio CVI	34.5	32.1	47.8	9.9	102.3	204.1	33.3	169.1	1.2	5.0
Deio CVII	36.4	29.6	34.5	10.0	99.2	195.2	32.8	178.4	1.1	4.4
Deio CVIII	29.0	19.5	45.3	9.3	96.1	192.2	23.8	142.1	1.4	5.6
Deio CIX	26.5	18.2	36.4	8.4	92.3	181.9	22.0	129.9	1.4	5.6
Deio CX	33.8	25.7			101.4	197.7	29.5	165.6	1.2	4.9
Deio CXI	25.8	19.9	38.6	18.2	97.6	190.9	22.7	126.4	1.5	6.3
Deio CXII	17.1	12.4	32.6	4.2	75.9	151.2	14.6	77.0	2.0	6.6
Deio CXIV	37.7	29.2	39.5	11.6	107.2	210.2	33.2	184.7	1.1	4.8
Deio CXVI	46.1	27.7	36.6	13.6			35.7	225.9		
Deio CXVII	42.2	13.4	51.1	17.7	129.3	258.6	23.8	206.8	1.3	5.9
Deio CXVIII	41.6	31.6	47.2	11.5	119.0	235.0	36.3	203.8	1.2	5.1
Deio CXIX	24.0	20.4	31.9	8.9	96.6	193.9	22.1	108.0	1.8	7.8
Deio CXXI	35.7	27.7	33.3	12.4	128.8	238.0	31.4	174.9	1.4	6.2
Deio CXXII	42.6	25.3	40.0	15.5			32.8	208.7		
Deio CXXIII	21.2	21.5	67.4	10.8	102.0	203.3	21.3	95.4	2.1	10.9

Deio CXXV	29.7	25.7	45.3		101.9	199.5		27.6	145.5	1.4	5.8
Deio CXXVI	37.5	27.8	34.0	13.2	121.9	239.9		32.3	183.8	1.3	6.0
Deio CXXVII	35.1	25.7	32.9	10.0	116.5	230.3		30.0	172.0	1.3	6.0
Deio CXXVIII	35.5	24.7	45.0	12.4	104.9	208.5		29.6	174.0	1.2	5.0
Deio CXXIX	26.3	18.8	39.0	10.3	97.3	194.5		22.2	128.9	1.5	6.4
Deio CXXX	31.5	31.2	55.6	12.6	108.3	216.5		31.3	154.4	1.4	6.2
Deio DI	29.3	29.0	61.0	9.1	102.7	183.0		29.1	143.6	1.3	5.1
Deio DII	39.7	28.7	40.7	15.1	119.3	238.0		33.8	194.5	1.2	5.5
Deio DIII	39.5	29.5	41.7	12.3	128.0	256.0		34.1	193.6	1.3	6.3
Deio DIV	36.7	26.7	42.8	13.1	117.8	234.9		31.3	179.8	1.3	5.9
Deio DV	39.3	24.1	29.9	13.6	129.8	255.5		30.8	192.6	1.3	6.3
Deio DVI	38.2	30.3	46.2	13.6	118.6	233.8		34.0	187.2	1.2	5.6
Deio DVII	33.4	27.8	41.7	10.5	107.5	211.1		30.5	163.7	1.3	5.5
Deio DX	63.3	52.7	55.0	11.4	151.3	305.5		57.8	310.2	1.0	4.8
Deio DXI	35.0	29.5	42.3	13.3				32.1	171.5		
Deio DXII	19.8	12.9	23.3	5.7	56.2	112.4		16.0	89.1	1.3	3.9
Deio DXIII	35.0	27.3	46.7	11.7	106.7	199.9		30.9	171.5	1.2	4.8
Deio DXIV	38.8	31.8	46.3	13.3				35.1	190.1		
Deio DXV	18.9	11.8	33.5	6.2				14.9	85.1		
Deio DXIX	24.5	15.0	16.5	9.6	80.0	159.0		19.2	110.3	1.4	5.5
Deio DXXII	35.4	24.7	54.3	15.3	109.3	218.8		29.6	173.5	1.3	5.5
Deio DXXIV	16.3	13.7	49.4	6.7	78.9	157.8		14.9	73.4	2.2	7.1
Deio MI	38.5	26.9	27.5		124.4	248.8		32.2	188.7	1.3	6.1
Deio MIII	42.8	30.8	34.8	14.4	115.3	216.8		36.3	209.7	1.0	4.3
Deio MIV	48.3	45.6	35.8	15.6	145.0	287.2		46.9	236.7	1.2	6.0
Deio Mlav	20.1	23.3	86.0	12.6				21.6	90.5		
Detk I	49.4	37.9	20.1	16.0	148.2	297.4		43.3	242.1	1.2	6.2
Detk II	23.2	15.9	45.0		100.4	200.0		19.2	104.4	1.9	8.5
Detk III	35.5	23.7	42.2	12.5	109.8	213.0		29.0	174.0	1.2	5.2
Detk IV	25.4	13.5	38.0	7.7	120.7	240.6		18.5	124.5	1.9	9.5
Detk V	25.1	26.0	41.7	9.8				25.5	123.0		
Detk VI	43.6	24.0	34.4	13.0				32.3	213.6		
Detk VII	42.6	37.5	31.6	10.5	108.6	218.0		40.0	208.7	1.0	4.4
Detk VIII	35.0	27.2	48.2	7.1				30.9	171.5	0.0	
Detk X	21.9	16.8	57.1	8.8	95.0	190.0		19.2	98.6	1.9	8.4
Detk XII	35.9	28.7	55.6	11.8	124.7	250.0		32.1	175.9	1.4	6.7
Detk XIII	37.7	35.7	62.1	14.3	113.1	225.3		36.7	184.7	1.2	5.3
Detk XIV	31.0	23.4	52.3	23.3	104.2	206.6		26.9	151.9	1.4	5.8
Detk XV	17.2	12.8	47.9	6.7	68.4	135.0		14.8	77.4	1.7	6.3
Detk XVI	45.0	41.6	41.6	13.4				43.3	220.5		
Detk XVII	32.9	26.1	46.1	11.1	92.9	180.0		29.3	161.2	1.1	4.3
Detk XVIII	30.4	23.1	36.2	11.7	103.2	206.4		26.5	149.0	1.4	5.9
Detk XIX	38.1	30.4	44.3	13.7	134.0	270.0		34.0	186.7	1.4	7.1
Detk M	30.6	34.4	48.8	14.1	123.8	250.1		32.4	149.9	1.7	8.1
Detk MI	29.0	28.7	46.8	9.4	115.7	220.5		28.8	142.1	1.6	7.0
Detk MII	28.9	27.1	24.8	13.2				28.0	141.6		
Detk MIII	37.5	30.5	53.6	17.0				33.8	183.8		
Detk MVII	40.8	38.3	48.1	14.0	144.0	288.0		39.5	199.9	1.4	7.3
Detk MVIII	35.3	30.6	51.6	15.4	103.5	207.0		32.9	173.0	1.2	5.0
Detk MX	36.3	34.4						35.3	177.9		
Detk MXIV	28.1	23.5	40.4	12.0	110.9	220.0		25.7	137.7	1.6	7.2
Detk MXX	46.5	38.7			106.7	211.1		42.4	227.9	0.9	3.7
Detk MXXI	50.4	38.5	45.8	18.1	120.5	238.4		44.0	247.0	1.0	4.2
Detk MXXII	33.5	24.8	40.9	15.9	110.1	215.3		28.8	164.2	1.3	5.7
Detk MXXIII	31.3	21.0	38.8	12.0	115.0	228.6		25.6	153.4	1.5	6.8
Detk MXXIV	36.8	30.7	63.9	15.7	125.0	247.8		33.6	180.3	1.4	6.4
Detk MXXV	40.5	27.9	40.8	15.6	124.0	241.1		33.6	198.5	1.2	5.5
Detk MXXVI	23.9	17.9	48.3	8.4	99.3	180.8		20.7	107.6	1.7	7.0
Detk MXXVII	42.7	31.4	38.9	15.6				36.6	209.2		
Detk MXXIX	40.1	31.3	40.8	14.2	121.0	242.0		35.4	196.5	1.2	5.6
Detk MXXX	42.3	26.5	40.6	19.0				33.5	207.3		
Detk MXXXI	20.8	17.8	37.3	7.7	77.8	157.0		19.2	93.6	1.7	6.5
Detk MXXXIV	39.0	33.2	33.1	18.8	117.5	220.3		36.0	191.1	1.2	4.9
Detk MXXXV	28.5	25.3	62.4	12.0	94.9	182.2		26.9	139.7	1.3	5.2
Detk MXXXVIII	30.2	21.9	51.6	13.1	148.1	298.3		25.7	148.0	2.0	27.1
Detk MXLIV	25.4	21.1	52.7	9.5	100.7	199.6		23.2	124.5	1.6	6.9
Detk MXLV	43.2	25.0	54.5	13.3	130.2	256.7		32.9	211.7	1.2	5.7
Detk MXLVI	33.2	27.6	42.3	15.7	108.7	216.0		30.3	162.7	1.3	5.8
Detk MXLVII	37.5	33.7	79.8	24.1	100.0	200.0		35.5	183.8	1.1	4.4
Detk MXIL	28.4	17.8	71.9	10.6	103.9	207.3		22.5	139.2	1.5	6.5
Detk MLVI	30.0	28.4			112.0	225.0		29.2	147.0	1.5	7.0

<b>Detk MLXVI</b>	26.0	16.9		11.4				21.0	127.4		
<b>Detk MLXVII</b>	19.5	18.1	49.3	4.4	74.0	148.0		18.8	87.8	1.7	6.3
<b>Detk MLXX</b>	41.2	25.6	41.5	14.7				32.5	201.9		
<b>Detk MLXXVII</b>	34.1	23.8	44.5	14.4				28.5	167.1		
<b>Detk MLXXIX</b>	50.9	50.4	53.8	15.2	163.0	320.4		50.6	249.4	1.3	6.8
<b>Detk MLXXX</b>	17.4	11.8	54.0	7.6	76.5	152.7		14.3	78.3	2.0	6.8
<b>Detk MLXXXIV</b>	37.9	28.8	62.7	14.6				33.0	185.7		
<b>Detk MLXXXVI</b>	37.1	33.4	38.0	11.7				35.2	181.8		

### APPENDIX 3 - GROUP 1 MEASUREMENTS TABLE

Appendix 3 shows the measurements and morphotypes table for Group 1 tracks.

MORPH: morphotype; Pl: pes length (cm); Pw: pes width (cm); Ml: manus length (cm); Mw: manus width (cm). Red values indicate approximative measurements due to the preservation of the track. Unmeasurable tracks are not listed here.

TRACK NAME	PL	PW	ML	MW
Deio LavA/2	53.0	37.3	16.2	27.0
Deio LavA/3	55.4	41.3	15.7	32.2
Deio LavA/4	53.7	42.3	11.5	30.6
Deio LavA/5		41.1		
Deio LavB/1	113.9	55.4		
Deio LavB/2	121.1	64.9		
Deio LavC/1	56.3	42.5		
Deio LavC/2	59.3	36.4		
Deio LavC/3	63.8	39.2		
Deio LavD/1	70.1	38.3		
Deio LavD/2	78.8	40.0	10.4	28.5
Deio LavD/3	64.1	48.4	17.9	33.8
Deio LavE		38.6	27.2	23.9
Deio XI/1	108.6	77.8	12.3	53.1
Deio XI/3	118.3	90.4	12.7	57.2
Deio XXXVIII-XXXIX/1	99.0	70.8	56.6	46.8
Deio XXXVIII-XXXIX/2	102.9	73.3	25.8	55.6
Deio XXXVIII-XXXIX/3	115.4	73.9		
Deio C/10	112.1	92.0		51.5
Deio C/11		90.2		
Deio C/2	95.2	78.7	54.2	72.3
Deio C/3	108.4	83.1	66.7	70.6
Deio C/4	96.8	89.1		
Deio C/5	100.0	89.8	51.7	51.1
Deio C/6	94.2	75.8	70.2	66.2
Deio C/7	97.2	87.6		
Deio C/8	102.3	92.9	64.0	63.4
Deio C/9	94.4	82.3		
Deio D/1	110.6	91.4	30.0	56.2
Deio D/2	115.6	87.2	18.8	41.4
Deio D/3	107.6	80.4	14.8	48.6
Deio D/4	101.6	79.2	46.0	66.0
Deio D/5	117.2	92.8		
Deio D/6	110.2	87.8	33.8	51.2
Deio D/7	113.2	86.6	27.6	62.4
Deio D/8	124.4	98.8	43.8	71.8
Deio D/9	101.0	90.4		
Deio D/10		65.0		
Deio D/11	121.2	90.0		
Deio D/12	101.0	85.4		
Deio D/13	109.2	98.0		
Deio D/14	94.6			47.6
Deio D/15	123.0	87.4	32.0	62.8
Deio D/16	105.8	95.8	22.0	72.0
Deio D/17	134.8	95.0	41.0	50.6
Deio D/19	122.4	97.8	33.6	58.4
Deio D/20	104.0	92.0		
Deio D/24		92.8		
Deio D/25	102.6	83.6	16.6	53.4
Deio D/26	106.4	89.0		
Deio D/27	99.2	85.6	33.0	49.0
Deio D/28	111.4	91.4	22.8	48.8
Deio D/33	108.2	80.0		45.4

TRACK NAME	PL	PW	ML	MW
Deio DIX/1		50.6	35.9	40.9
Deio DIX/10			35.3	41.9
Deio DIX/11			37.3	53.9
Deio DIX/2			34.0	50.3
Deio DIX/3			30.4	40.4
Deio DIX/4		56.1	23.4	45.0
Deio DIX/5			37.9	43.2
Deio DIX/6		48.2	24.4	39.4
Deio DIX/8			35.5	46.2
Deio DIX/9				34.0
Deio DVIII/-1		59.9	39.0	44.1
Deio DVIII/-2		57.2	38.3	52.6
Deio DVIII/-3		56.2	46.4	27.3
Deio DVIII/1		62.9	19.0	54.2
Deio DVIII/2		0.8	43.7	62.5
Deio DVIII/3			31.4	61.0
Deio DVIII/6		71.7	44.5	58.9
Deio DVIII/7			45.4	54.3
Deio DVIII/8			35.4	55.2
Deio DVIII/9		66.6	33.8	55.6
Deio DVIII/10		61.0	40.2	49.7
Deio DXVIII/1			55.4	64.8
Deio DXVIII/2	93.5	72.8		
Deio DXVIII/3	111.6	77.6		
Detk DIX/1		74.7	45.3	55.3
Detk DIX/2	78.6	74.6	19.8	52.7
Detk DIX/3	81.0	72.2	16.9	110.2
Detk MLVII/1	51.5	43.9	13.1	
Detk MLXXXI/1		26.2	26.5	27.5
Detk MLXXXVI/1				90.0
Detk MLXXXVI/3			74.0	77.0
Detk MLXXXVI/4			74.0	102.0
Detk MLXXXVI/8	81.0	91.0		
Detk MLXXXVI/10			48.0	89.0
Detk MLXXXVI/11	120.0	100.0		
Detk MLXXXVI/12			79.0	86.0
Detk MLXXXVI/14			89.0	87.0
Detk MLXXXVI/15			75.0	91.0
Detk MLXXXVIII/1	97.0	90.0	15.0	51.0
Detk MXLI/1	76.4	71.6	36.2	48.4
Detk MXLI/2		62.6	32.4	42.0
Detk MXLI/3	57.0	52.0	26.4	27.4
Detk MXLI/4	59.8	55.2	26.8	32.2
Detk MXLII/1			40.0	57.8
Detk MXLII/2	74.8	56.4	47.0	24.2
Detk MXLII/3	69.6	59.4	47.4	39.4
Detk MXLIII/1	98.2		30.4	44.2
Detk MXLVIII/1	88.1	65.9	25.9	45.5
Detk MXLVIII/2	77.9	71.3	23.7	50.5
Detk MXXXII/1	94.0	79.8	37.2	47.0
Detk MXXXII/2	98.0	71.2	32.2	54.8
Detk MXXXII/5		79.4	54.6	63.4
Detk MXXXIII/1		58.8	44.8	41.0
Detk MXXXIII/2			47.2	49.0
Detk MXXXIII/3			50.2	66.4
Detk MXXXIII/4	93.2	74.0	42.8	59.0

## APPENDIX 4 - SAUROPOD TRACKWAY MEASUREMENTS TABLE

Appendix 4 shows some mean values for sauropod trackways, including both left and right pace and stride values, and derived measurements.

Pl: pes length (cm); Pw: pes width (cm); Ml: manus length (cm); Mw: manus width (cm); LPP: left pes pace (cm); RPP: right pes pace; LPSl: left pes stride length (cm); RPSl: right pes stride length; LMP: left pes pace (cm); RMP: right pes pace; LMSl: left pes stride length (cm); RMSl: right pes stride length; PTR: pes trackway ratio (%); MTR: manus trackway ratio (%); h (eq.1): hip height evaluated using equation 1 (m); h (eq.2): hip height evaluated using equation 2 (m); V (eq.1): locomotion speed evaluated considering the h (eq.1) hip height (km/h); V (eq.2): locomotion speed evaluated considering the h (eq.2) hip height (km/h); IPS: index of pes size (adimensional); IMS: index of manus size (adimensional); IPS/IMS: index of pes/index of manus size ratio (adimensional).

TRACKWAY	Pl	Pw	Ml	Mw	LPP	RPP	LPSl	RPSl	LMP	RMP	LMSl	RMSl
Deio XI	113.4	84.1	12.5	55.2	217.1	219.2	369.8				379.7	
Deio XXXVIII-XXIX	105.7	72.6	41.2	51.2	177.4	198.5	327.4		161.5			
Deio CI	100.1	86.2	61.4	62.5	145.5	149.2	217.4	236.7	193.5	206.8	236.0	259.4
Deio D	110.7	88.5	29.7	55.4	207.8	195.3	348.4	352.6	233.8	231.7	347.0	362.7
Deio DVIII		63.9	37.0	52.6					172.3	178.0	277.7	289.6
Deio DIX		48.2	33.1	43.1					135.5	135.3	211.9	238.9
Deio DXVIII	102.5	75.2	55.4	54.8					201.9			
Deio LavA	54.0	40.5	14.5	29.9	109.2	120.5	203.0	204.5	108.6	123.9	202.0	
DeioLavB	117.5	60.1										
DeioLavC	59.8	39.4										
DeioLavD	71.0	42.2	14.2	31.2		96.4				101.5		
DeioLavE		38.6	27.2	23.9								
Detk IX	79.8	73.8	27.3	72.7		175.3			175.5	198.3	318.8	
Detk MXXXII	96.0	76.8	41.3	55.7		178.6				204.4		
Detk MXXXIII	93.2	66.4	46.3	53.9					206.4	173.0	314.2	270.8
Detk MXLI	58.4	53.6	26.6	29.8	156.2	150.8	278.8	274.6	175.7	155.4	248.6	314.4
Detk MXLII	72.2	57.9	44.8	40.5					171.6		223.0	247.6
Detk MXLIII	98.2		30.4	44.2								
Detk MLVII	51.5	43.9	13.1	30.0								
Detk MLXVIII	83.0	68.6	24.8	48.0	161.9				164.1			
Detk MLXXIII		26.2	26.5	27.5								
Detk MLXXXVI	120.0	100.0	81.0	88.0					343.5	378.5	613.0	578.7
Detk MLXXXVIII	97.0	90.0	15.0	51.0								

TRACKWAY	PTR	MTR	h (eq.1)	h (eq.2)	V (eq.1)	V (eq.2)	IPS	IMS	IPS/IMS
Deio XI			4.5	6.7	4.4	2.8	97.7	26.3	3.7
Deio XXXVIII-XXIX			4.2	6.2	3.6	2.4	87.6	45.9	1.9
Deio CI	50.2		4.0	5.9	2.4	1.5	92.2	61.9	1.5
Deio D	50.2	27.0	4.4	6.5	4.1	2.6	99.0	40.6	2.4
Deio DVIII		36.1						44.1	
Deio DIX		36.5						37.8	
Deio DXVIII			4.1	6.1			87.8	55.1	1.6
Deio LavA	44.7		2.2	3.2			46.8	20.8	2.2
Deio LavB							84.0		
Deio LavC			2.4	3.5			48.5		
Deio LavD			2.8	4.2			54.7	21.0	2.6
Deio LavE								25.5	
Detk IX	49.4	36.6	3.2	4.7	5.0	3.2	76.8	44.6	1.7
Detk MXXXII			3.8	5.7			58.9	48.0	1.2
Detk MXXXIII		35.5	3.7	5.5	3.6	2.3	78.7	49.9	1.6
Detk MXLI	49.4	31.6	2.3	3.4	5.9	3.6	55.9	28.2	2.0
Detk MXLII	50.9	32.1	2.9	4.3	3.4	2.2	64.7	42.6	1.5
Detk MXLIII			3.9	5.8				36.7	
Detk MLVII			2.1	3.0			47.6	19.8	2.4
Detk MLXVIII			3.3	4.9			75.4	34.5	2.2
Detk MLXXIII								27.0	
Detk MLXXXVI		37.4	4.8	7.1	8.9	5.8	109.5	84.4	1.3
Detk MLXXXVIII							93.4	27.7	3.4

