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A Late Jurassic diverse ichnocoenosis from the siliciclastic Iouaridène Formation (Central High Atlas, Morocco)

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The Late Jurassic Iouaridène tracksite has been studied for decades and is well-known for the reference trackway of *Breviparopus taghbaloutensis*. These siliciclastic flood-plain deposits bear probably more than 1500 tracks, and at least 21 trampled levels: they yield tracks of medium to very large sauropods, possible stegosaurs and theropods. The first accurate description of the footprint association made by biped trackmakers is proposed herein. More than six hundred footprints and more than a hundred trackways has been mapped and analysed; this led to the definition of four tridactyl and two tetradactyl morphotypes, mainly produced by small to very large theropods, while probable small ornithopod tracks are also present. The bipedal footprint association is dominated by medium-large theropods, which are also the most abundant type. The taxonomical attribution of the morphotypes is made difficult by the poor preservation of many specimens. Furthermore, for the most abundant theropod tracks, those with "megalosaurian" affinity, there is also a complex ichnotaxonomical situation, that makes the attributions yet more challenging; however, it was possible to recognize the great affinity of the tridactyl specimens with the *Megalosauripus* tracks from the Iberian Peninsula and North America. Three-dimensional models were generated from the moulds of the best-preserved specimens to render a more detailed description and for easier access to the specimens.

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Key words: Late Jurassic, Morocco, Iouaridène Formation, dinosaur footprints, theropods, 3D modelling.

INTRODUCTION

The Iouaridène site was first reported by Plateau *et al*. (1937) indicating the presence of tridactyl footprints. Roch (1939) gave the first detailed description of the "couches rouges" outcropping in the Iouaridène area; de Lapparent (1942, 1945), and de Lapparent and Zbyszewski (1957) described other tridactyl footprints, noticing the "megalosaurian" affinity of the tracks and their similarities with the Portuguese footprints from Cabo Mondego. Termier (1942), besides a more detailed description of the formation, supported the possibility expressed by de Lapparent (1942) that the age of the formation might be Cretaceous ("...il n'y a aucune raison de se limiter au Dogger et au Lias."). Also Choubert *et al*. (1956) proposed an Early Cretaceous rather than Jurassic age for the site.

Dutuit and Ouazzou (1980) were the first to describe very large sauropod tracks, assigning them to the ichnotaxon *Breviparopus taghbaloutensis*. This ichnotaxon, even if never formally erected, was considered valid in many follo wing papers and was used by Farlow (1992) as a perfect example of a narrow gauge trackway.

Sedimentological and stratigraphical data presented by various authors (Jenny *et al*., 1981*a*, *b*; Jenny and Jossen, 1982; Jenny, 1985, 1988) indicated a Middle Jurassic age for the track-bearing layers.

The work of Ishigaki in the second half of the 1980s contained the first detailed description of the individual footprints (Ishigaki, 1985*a*, *b*, *c*, 1986, 1988). But it was the description of manus-only and manus-dominated trackways, interpreted as the evidence of swimming sauropods (Ishigaki, 1989) that got the attention of many ichnologists. Later, Nouri *et al*. (2001), briefly reported some semi-plantigrade theropod tracks from the southern part of the site (Tirika). Meyer and Monbaron (2002), after a field campaign in the area, concluded that the manus-dominated tracks of Ishigaki (1989) were a misinterpretation of shallow tridactyl footprints. In reply, Ishigaki and

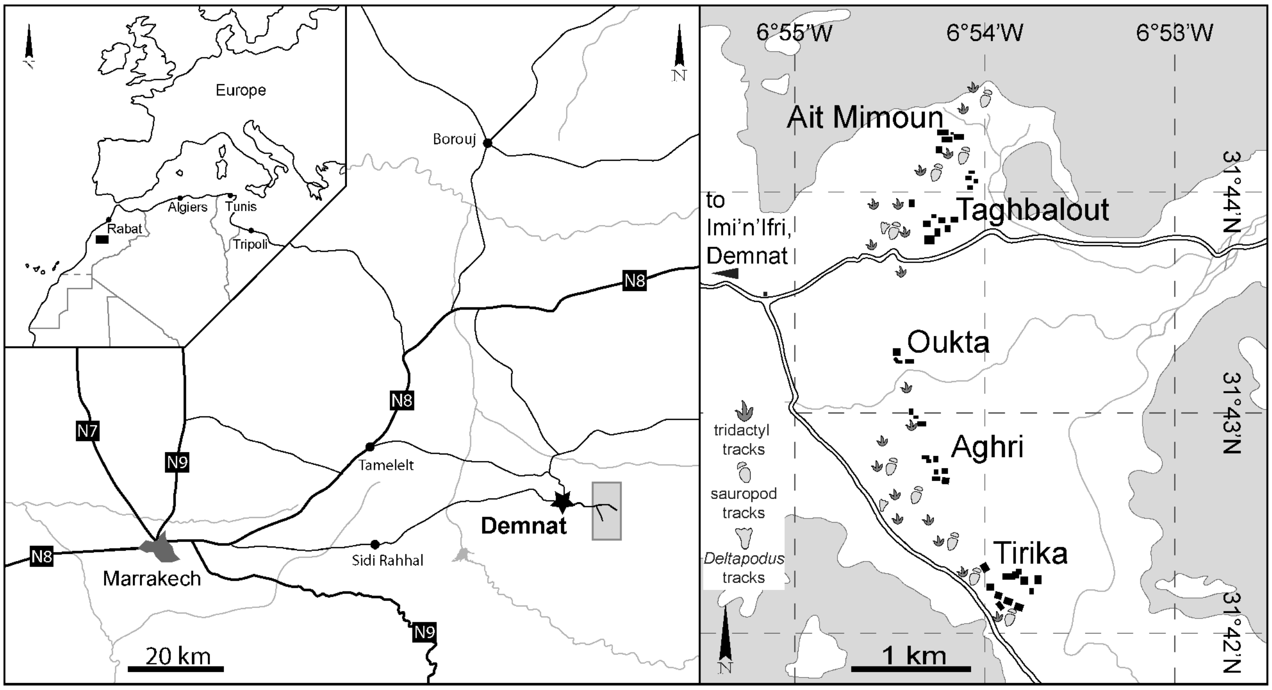

Fig. 1. Location of the Iouaridène locality

Tracks indicate the approximate location of the footprints and tracks of the tracksite

Matsumoto (2008, 2009*a*) recently admitted that whereas one trackway (trackway D in Ishigaki, 1989) was misinterpreted, the others described actually existed and were not found by the Swiss researchers. Dalla Vecchia (2005) gave a brief description of the sedimentology of the site and figured some of the most accessible tracks of the site. Charrière *et al*. (2005) assigned at least the higher part of the Iouaridène Formation, based on palynomorphs and ostracods, to the Late Jurassic (?Oxfordian–Kimmeridgian). This was later on confirmed by Haddoumi *et al*. (2009).

In recent years, a whole series of papers started the ichnotaxonomical renaissance of the Iouaridène basin. Belvedere *et al*. (2007) gave a brief description of the whole ichnofauna; Boutakiout *et al*. (2008*a*) reported a partial survey of the western part of the valley, listing the tracksites; Boutakiout *et al*. (2008*b*, 2009) analysed some very large theropod tracks, also reported in Belvedere (2008); Díaz-Martínez *et al*. (2009) studied some theropod tracks found close to the *Breviparopus taghbaloutensis* reference trackway and Belvedere and Mietto (2010) described the first African record of the ichnogenus *Deltapodus* Whyte and Romano, 1994. Belvedere and Mietto (2009) discussed the palaeogeographical importance of the importance of the track site. Ishigaki and Matsumoto (2009*b*) figured a trackway of a turning sauropod that was mapped back in 1980 which is now almost destroyed (trackway CI of Belvedere, 2008). Marty *et al*. (2010) compared the *B. taghbaloutensis* prints and trackways with coeval sauropod trackways from the Late Jurassic of Switzerland and considered *Breviparopus* a valid ichnotaxon, morphologically distinct from *Parabrontopodus*, though it needs to be formally re-described; and finally Boutakiout *et al*. (2010) updated knowledge of the site by adding information on track-bearing localities from the eastern part of the Iouaridène valley.

Today most of the historical part of the site has been mapped (February 2010) resulting in an estimated number of around 1500 footprints in the entire valley (Belvedere, 2008; Boutakiout *et al*., 2008*a*, in press). However, a part of the ichnofauna still awaited a detailed description The aim of this paper is to give a first thorough description of the ichnofauna assigned to bipedal animals of the Iouaridène site.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The tracksite is located in the Moroccan central High Atlas, 7 km from the Imi'n'Ifri natural bridge and around 15 km east of the town of Demnat. It is situated on the western flank of the Iouaridène syncline and can be easily accessed by road from Demnat to the Imi'n'Ifri natural bridge. The site stretches roughly in a north-south direction for about 6 km (Fig. 1), from the area north of the Ait Mimoun village (north) to the village of Tirika (south), corresponding to the area between the "yacimientos" (= localities) 4IGR and 31IGR of Boutakiout *et al*. (2009).

The trampled levels are situated in the lower part of the Iouaridène Formation (Charrière *et al*., 2005) which consists of cyclic alternations of meter-scale red mudstones and decimetre-scale reddish carbonate-cemented mudstones to very fine sandstones, with mud-cracks. The surface of these layers, characterized by cyanobacterial lamination and traction structures (e.g., planar lamination), are associated with symmetrical ripple marks and mud cracks. Fluvial channels, with fining-upward sequences, climbing ripples and herringbone cross-stratifi-

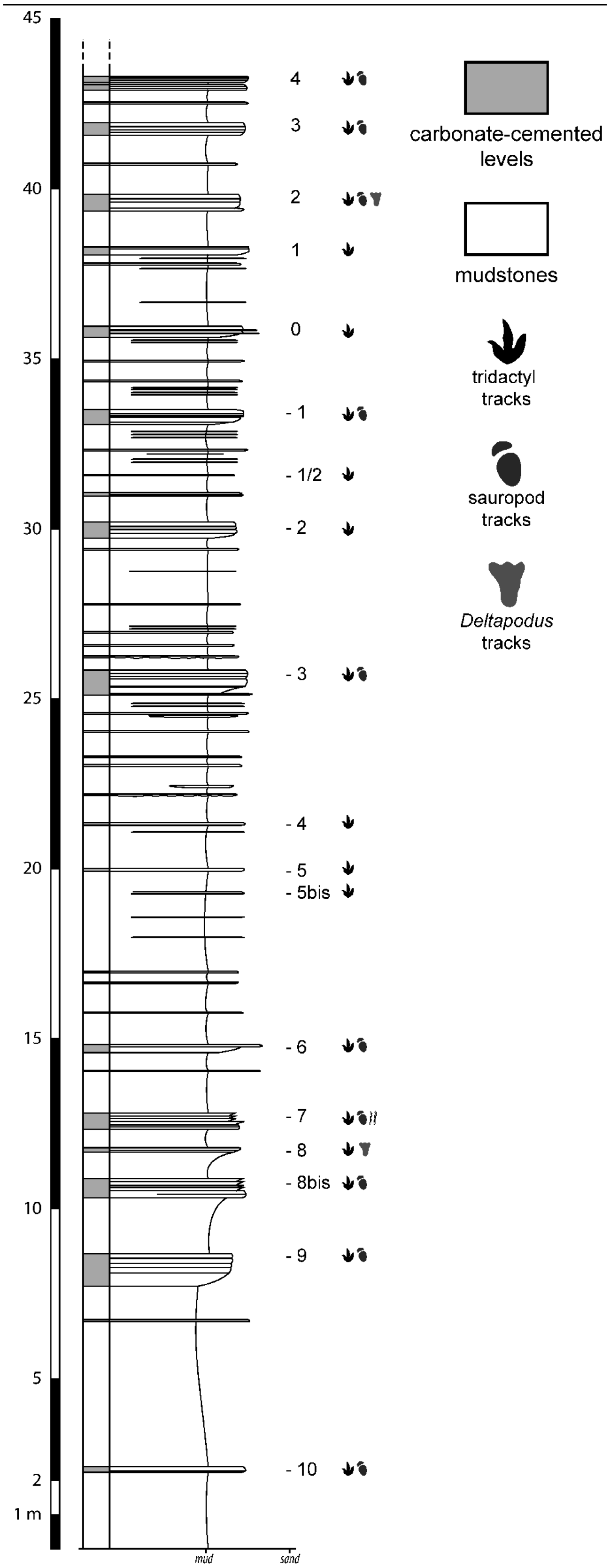

Fig. 2. Schematic stratigraphical log

The composite stratigraphical log illustrates part of the lower member of the Iouaridène Formation, i.e. 18 of the 21 trampled layers recognized (Belvedere, 2008)

cation, are present at the top of the sequence. The widespread occurrence of evaporitic minerals, concertina-like structures and small-scale pseudo-anticlines with evaporitic infillings suggest an arid or semi-arid palaeoclimate (Belvedere, 2008).

21 trampled layers were mapped within the section (Fig. 2); some of these levels can be followed throughout almost the whole site allowing a very accurate correlation of the track-bearing levels between the northern and southern end of the sites.

Different age assignations have been proposed for the Iouaridène Formation: Dutuit and Ouazzou (1980) rather vaguely designated it as Jurassic/Cretaceous; later it was more precisely dated to Bajocian/Bathonian (Jenny *et al*., 1981*a*, *b*,; Jenny, 1985, 1988; Nouri *et al*., 2001), although recent publications indicate an ?Oxfordian/Kimmeridgian age based on palynological and micropalaeontological data (Charrière *et al.*, 2005; Haddoumi *et al*., 2009); this dating is also supported by interpretation of the ichnological record (Belvedere *et al*., 2007; Nouri, 2007; Belvedere, 2008; Boutakiout *et al*., 2008*a*).

MATERIAL AND METHODS

Although several tracks show good morphological details (e.g., claw marks, phalangeal pad impressions, *etc*.), the general preservation is not excellent and often only the main outlines are visible. Most of the tracks are preserved as true tracks (*sensu* Lockley, 1991), but underprints (*sensu* Marty *et al*., 2009) or undertracks (*sensu* Thulborn, 1990; Lockley, 1991) are present too. All the measurements were taken in the field, or tracks were drawn on monofilm during the campaigns employing standard ichnological procedures and measurements (e.g., Leonardi, 1987; Thulborn, 1990), i.e., Fl indicates the foot length; Fw, the foot width; II-III, III-IV, II-IV the interdigital divarication angles between digits II and III, III and IV, II and IV, respectively.

The labels Deio and Detk, following Belvedere (2008), are acronyms for Demnat Iouaridène and Demnat Tirika and indicate the location of the footprints in the northern or southern part of the tracksite, in relation to the road that comprises a east-west transect of the site. The Roman numbers label trackways and isolated tracks, while Arabic numbers indicate the individual footprint.

Belvedere (2008) assigned morphotype 1 to quadrupedal or supposed quadrupedal dinosaurs, morphotype 2 to bipedal dinosaurs, and morphotype 3 to non-dinosaurian tracks; all the tracks presented in this paper belong to morphotype 2.

The most significant prints, except larger ones, were moulded with silicon rubber, then fibreglass casts were made for a replica of the actual print. The casts are stored in the Museo di Geologia e Paleontologia of the Università degli Studi di Padova (institutional abbreviation: MGPD).

The rubber moulds were digitised with a triangulation-based laser scanner (*NextEngine™ 3D Scanner HD*) with a resolution of 0.3 mm for the smaller tracks and with a 0.5 mm resolution for the larger ones; the raw data were acquired using the *NextEngine™ ScanStudio HD* software, while the subsequent data manipulation, contour lines and colouring were carried out with *Innovmetric Polyworks™*.

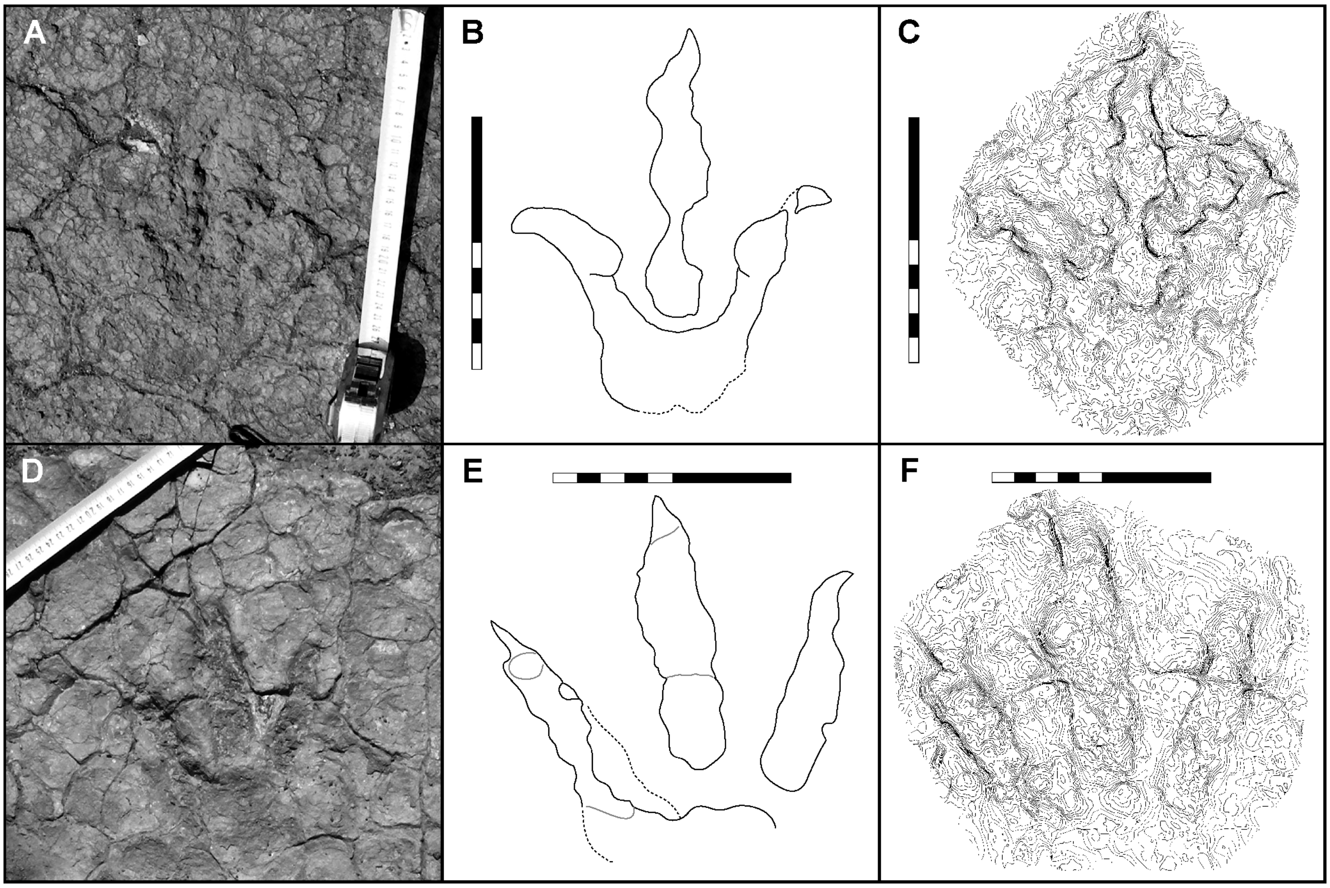

Fig. 3. Examples of morphotype 2A – *Carmelopodus* sp.

A – photo of the Deio XLI/1 (N 31°44.067', W 006°54.600'), scale bar 10 cm; **B** – schematic outline drawings of Deio XLI/1, scale bar 10 cm; **C** – contour lines of Deio XLI/1 generated from the 3D model data (supplementary file 1) with 0.5 mm equidistance between the lines, scale bar 10 cm; **D** – photo of the Detk MLX (N 31°42.368', W 006°54.340'), scale bar 10 cm; **E** – schematic outline drawings of Deio MLX, scale bar 10 cm; **F** – contour lines of Detk MLX generated from the 3D model data (supplementary file 2) with 0.5 mm equidistance between the lines, scale bar 10 cm; the continuous line draw the internal margin of the footprint, the dashed line the exterior margin, the grey lines the internal morphologies

DESCRIPTION

MORPHOTYPE 2A

This group (Fig. 3, supplementary files 1 and 2*) is characterized by tridactyl tracks with a foot length shorter than 20 cm, mesaxonic, longer than wide (average Fw/Fl: 0.74) and slightly asymmetrical. Digit IV is always the longest, followed by digit III and II; the width of digits II and IV is comparable with digit III, which is always slightly wider. Claw marks, or at least a clear tapering end of the digits, always present. The divarication angle II-IV is 47.3°, with II-III (20.3°) narrower than III-IV (27°). Phalangeal pads, even in the best-preserved footprints, are not well enough preserved to allow the determination of the phalangeal formula. Great variability occurs in the shape of the "heel": it is often present with a rounded or tapered shape, but, in a few cases, it is missing. These variations have also been noticed occurring in the same trackway, thus they are considered as extra-morphological features.

Long trackways of this morphotype are uncommon; generally the footprints are found isolated or arranged in short (<5 prints) segments. The only long trackway is Deio VII (N 31°43.200', W 006°54.533') that consists of 21 prints with only few tracks missing. The trackways are always narrow-gauged, with a slight outward rotation of the pes (<10°).

MORPHOTYPE 2B

This morphotype groups small to medium (average Fl <25 cm) tridactyl footprints, mesaxonic, slightly longer than wide (Fw/Fl: 0.84), with a marked symmetry in relation to the long axis of digit III and a generally rounded "heel" (Fig. 4, supplementary file 3*). All the digits have comparable widths and lengths, with digit III being by a slight amount the longest. No clear claw impressions are present, but most of the specimens present a tapering termination of the digits. Interdigital angle II-IV averages 58.3° with a similar divarication between II-III (28.2°), and III-IV (30.1°). Though pad impressions are ex-

* Supplementary files are available on website: www.gq.pgi.gov.pl

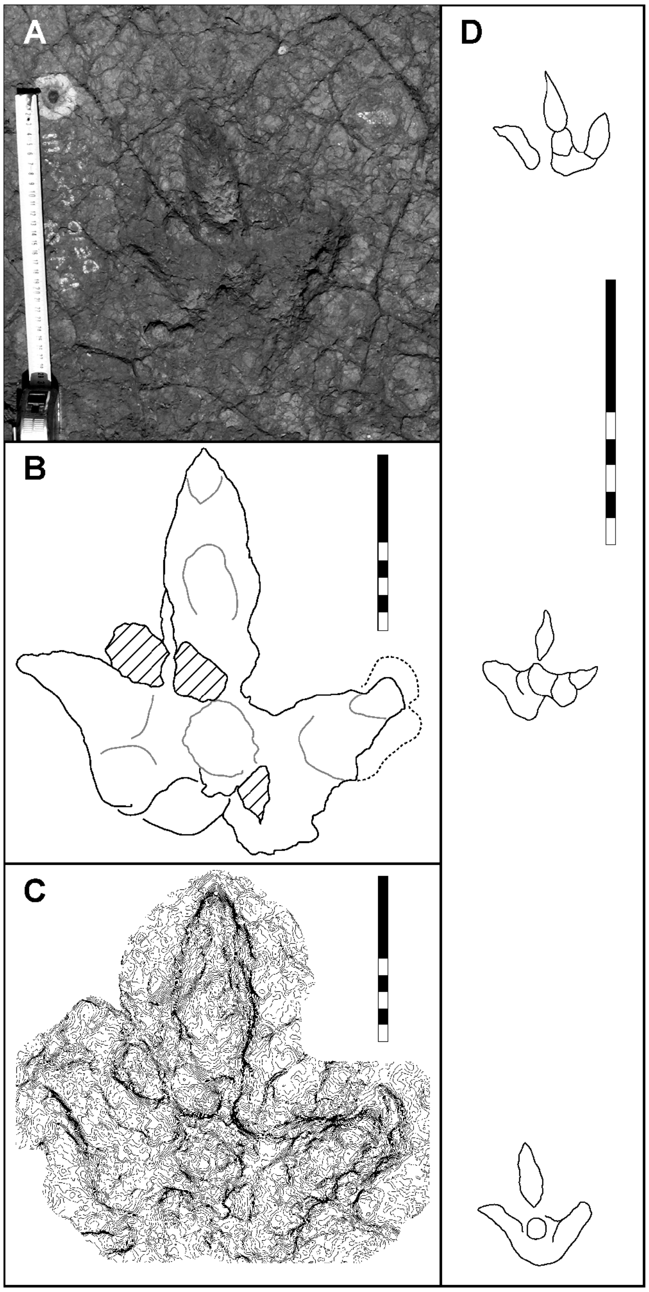

Fig. 4. Examples of morphotype 2B – *Dinehichnus* sp.

A – photo of the Deio CXXIII/1 (N 31°44.006', W 006°54.154'), scale bar 10 cm; **B** – schematic outline drawings of CXXIII/1, scale bar 10 cm; **C** – contour lines of CXXIII/1 generated from the 3D model data (supplementary file 3) with 0.5 mm equidistance between the lines, scale bar 10 cm; **D** – schematic outline drawing of Deio CXXIII, the best-preserved trackway for morphotype 2B; note the inward rotation of the pes prints, scale bar 50 cm; the continuous line draw the internal margin of the footprint, the long-dashed line the exterior margin, the dashed line the exterior margin, the grey lines the internal morphologies

tremely rare even in the best preserved specimens, in some tracks it is possible to observe the presence of the proximal pad of digit III (Fig. 4A–B). The analysis of the contour lines of the specimen Deio CXXIII/1 (Fig. 4C; N 31°44.006', W 006°54.154') highlighted the occurrence of other very shallow phalangeal pads in digits II, III and IV, otherwise not detectable.

Since there are no well-preserved or continuous trackways, stride length has been derived from pace measurements made on two aligned footprints, possibly belonging to the same trackway.

Unfortunately, the generally poor preservation of this specimens and the rarity of the morphotype do not allow further descriptions.

MORPHOTYPE 2C

This morphotype includes large (average Fl >30 cm), tridactyl, mesaxonic, asymmetric, longer than wide (Fw/Fl: 0.75) footprints (Fig 5, supplementary file 4). Digits are well separated with digit IV slightly the longest, whose proximal pad, aligned to digit III axis usually constitutes the "heel" of the footprint; digit III has a typical inward bending. The width of the digits, measured on their free portion, is similar. Claw impressions are very common on all the digits, even in the most poorly preserved tracks, and phalangeal pads occur quite commonly, allowing the reconstruction of a 2-3-4 phalangeal formula, for digit II, III and IV, respectively. The total divarication angle averages 43.4°, with a marked asymmetry between II-III (17.2°), and III-IV (26.2°). However, despite the lower average value of II-III, this angle also presents the highest variability, ranging from 5.5 to 36.2°: this higher mobility cannot be explained only as resulting from extra-morphological features, and has to reflect some anatomical characteristic of the trackmaker feet.

Trackways are very abundant in the record, and present an irregular gauge, which ranges from very narrow to quite wide, independently of stride length or gait: trackways with the same footprint sizes, similar paces and strides, left on the same level, may have different gauges.

Despite this variability, trackways are generally narrow, with digit II crossing the midline; the pes rotation is less variable but can change from slightly outwards (<10°) to absent, especially in the narrower trackways.

Nouri (2007, trackway 3Am5) illustrated a large (Fl: 35 cm) ornithopod footprints (Fig. 6); the same tracks were recorded as Deio CXXX (N 31°44.000', W 006°54.078') by Belvedere (2008) but were interpreted as probable underprints of morphotype 2C.

MORPHOTYPE 2D

The footprints belonging to this morphotype (Fig. 7) are mesaxonic, asymmetrical, elongated, longer than wide (Fw/Fl: 0.79) and with 4 tapered digits. Digit IV is the longest, followed by III, II and I, however, this interpretation is obscured by the general poor preservation of the specimens; the other parameters cannot be reliably measured either because of the degradation of the prints. Nevertheless, some considerations can be made: the divarication angle II-III (18.2°) is always narrower than III-IV (28.2°), digit I is directed anteriorly, towards the distal part of the pes, and metatarsal impressions, where present, are broad and not very elongated posteriorly.

Morphotype 2D trackways are missing, but these footprints occur within trackways dominated by the morphotype 2B.

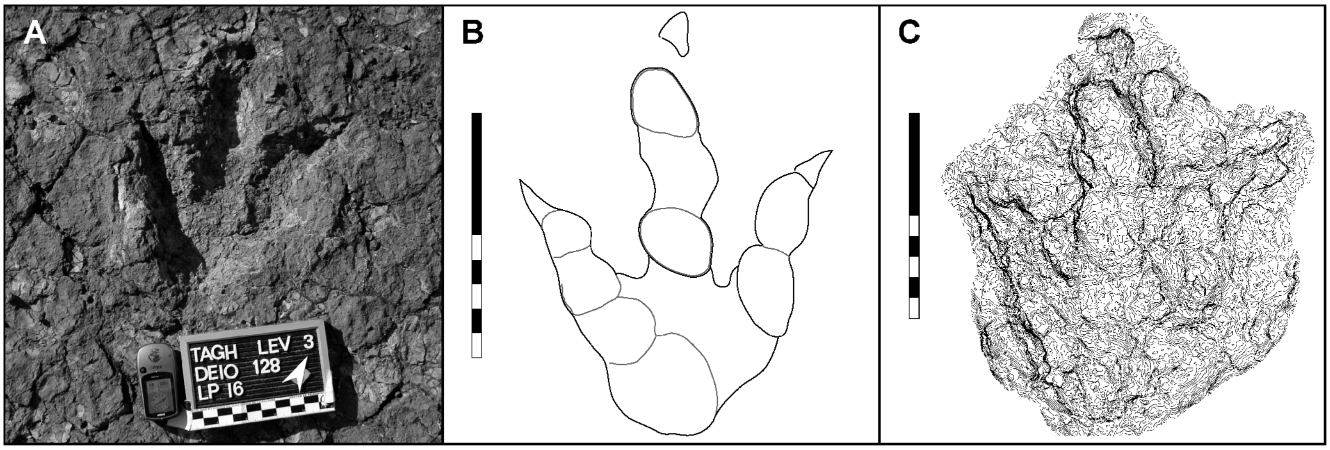

Fig. 5. Example of morphotype 2C – *Megalosauripus* sp.

A – photo of the well-padded Deio CXXVIII/16 (N 31°43.988', W 006°54.089'), scale bar 20 cm; **B** – schematic outline drawings of CXXVIII/16, scale bar 20 cm; **C** – contour lines of CXXVIII/16 generated from the 3D model data (supplementary file 4) with 1 mm equidistance between the lines, scale bar 20 cm; the continuous line draw the internal margin of the footprint, the grey lines the internal morphologies

MORPHOTYPE 2E

Although this morphotype has already been described in a recent paper by Boutakiout *et al*. (2009), we propose herein a new detailed characterization of the tracks, emending and revising the paper cited above.

Morphotype 2E includes the largest footprints present on the site (Fl from 41.6 to 78.3 cm; Fw from 33.6 to 63.8 cm). It is tridactyl, mesaxonic, usually slightly longer than wide (average Fw/Fl: 0.86), slightly asymmetrical, with well-separated and long digits (Fig. 8). Digit II is usually slightly shorter than digit IV, while digit III is long and straight. Clear phalangeal pads occur only in the best-preserved tracks and suggest a phalangeal formula of 2-3-4, for digit II, III and IV, respectively. Claw impressions are also common in the better preserved tracks; even if these impressions are missing, it is often possible to recognize a tapering termination of the digits.

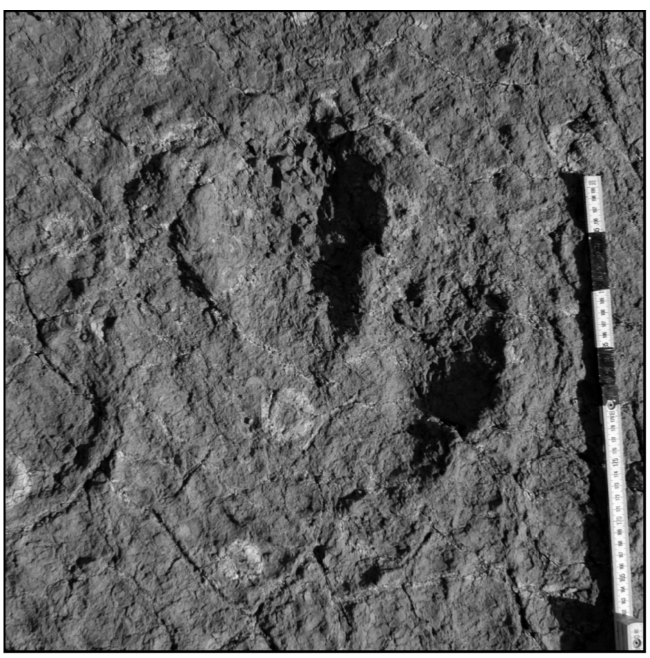

Fig. 6. Specimen Deio CXXX/2

Photo of the footprint Deio CXXX/2 (N 31°44.000', W 006°54.078'), scale bar 40 cm. This track has been interpreted as an ornithopod footprint by Nouri (2007) but in our opinion it is more likely an undertrack of type 2C theropod

The total divarication angle II-IV is usually wider than 50° and slightly asymmetrical, but it changes from track to track: II-III is always narrower than III-IV, even if the values are very similar. The heel can vary from rounded to quite tapered, but its shape is probably more related to preservation than to the actual morphology of the dinosaur foot.

The unique long trackway, consisting of seven consecutive prints (Fig. 8E), Detk MLXXIX (N 31°42.479', W 006°54.371') in Belvedere (2008), corresponds to the sauropod trackway D in Ishigaki (1989, fig. 9.4). It was reinterpreted by Ishigaki and Matsumoto (2008, 2009*a*), and corresponds also to the "yacimiento" 25IGR1 in Boutakiout *et al.* (2009). It consists of short irregular paces (from 1.44 to 1.69 m), but without evidence of limping, because the irregular paces apply to both left and right footprints. The footprints are very shallow, and it is worth noticing that these tracks are probably preserved as underprints, if not as transmitted undertracks (*sensu* Lockley, 1991) producing the occurrence of two outlines: one internal, corresponding more or less to the actual footprint size, and one, larger, external. In spring 2008, two of the authors (MB and PM) mapping Detk MLXXIX noticed that the outlines of the footprints were still highlighted with chalk. These outlines correspond to the figures published in Boutakiout *et al*. (2009, trackway 25IGR1). In our opinion this interpretation overestimates the size of the footprints (by about 20 cm), measuring the external margin of the footprints (Fig. 9). The trackway has very irregular and short paces when compared with the very large size of the footprints. Both the pace lengths and the rotation of the footprints are irregular: although it is possible to see a generally faint outward rotation, each footprint axis reveals a different angle. Pace and stride lengths are always short compared to the size of the footprints, varying from 1.19 to 1.74 m for pace, and from 2.35 to 3.38 m for stride.

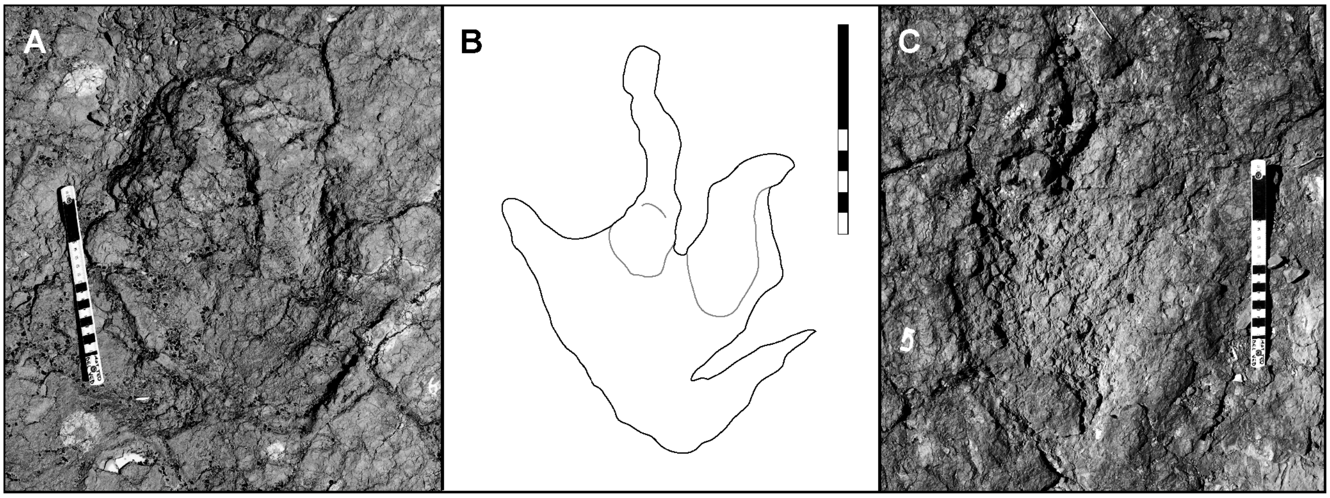

Fig. 7. Examples of morphotype 2D

A – photo of the tetradactyl Deio DXIII/6 (N 31°44.092', W 006°53.921'), scale 20 cm; **B** – schematic outline drawings of DXIII/6, the grey lines the internal morphologies, scale bar 20 cm; **C** – photo of Deio DVI/5, scale 20 cm, this footprint, 1Am2.5, has been proposed by Nouri (2007) as a holotype for the new tetradactyl ichnospecies *Eutynichnium atlasichnus*

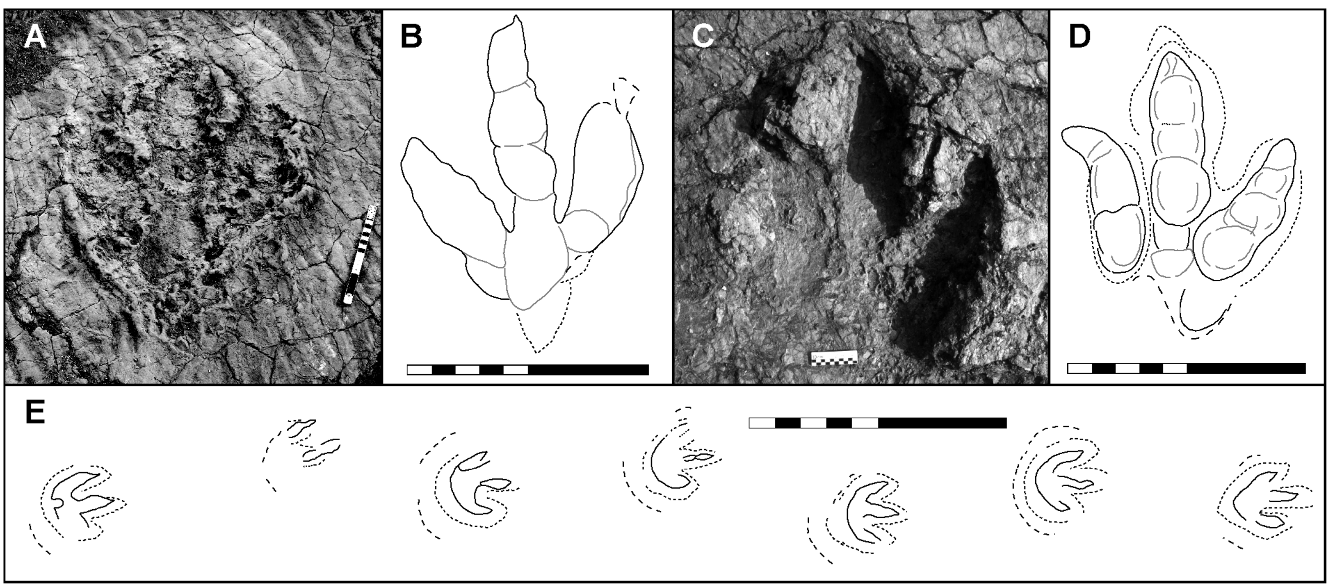

Fig. 8. Examples of morphotype 2E

A – photo of the Deio XLII (N 31°43.033', W 006°54.101'), scale bar 20 cm, note the marked symmetrical ripple-marks; **B** – schematic outline drawings of Deio XLII, scale bar 50 cm; **C** – photo of a very detailed true track outcropping close to Oukta, mapped by SI in 1984, probably corresponding to track 23IGR1.7 of Boutakiout *et al*. (2009), scale 10 cm; **D** – schematic outline drawing of the previous footprint, scale 50 cm. The continuous line marks the internal margin of the footprint, the dashed line the exterior margin, the grey lines the internal morphologies; **E** – schematic outline drawing of Detk MLXXIX (N 31°42.479', W 006°54.371'), the longest trackway for morphotype 2E, the longer dashed lines indicates the external margin of the displacement rims

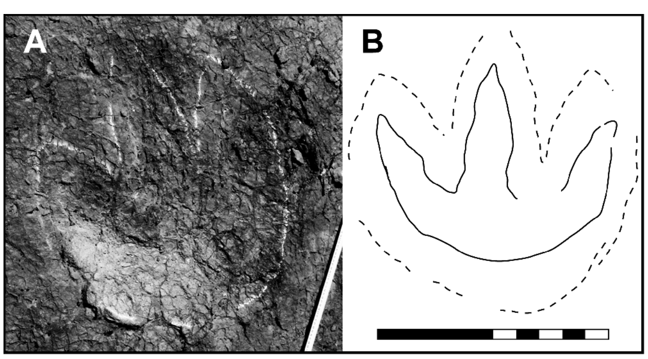

Fig. 9. Specimen Detk MLXXIX/5

A – photo of a very shallow and faint track Detk MLXXIX/5, probably preserved as underprint, no details can be observed, the white chalk lines were drawn by the Boutakiout *et al*. (2009) team and highlight the footprint's external margin, scale 30 cm; **B** – outline drawing of the same footprint, the inner and outer margins are clearly separated due to the preservation features, scale bar 50 cm

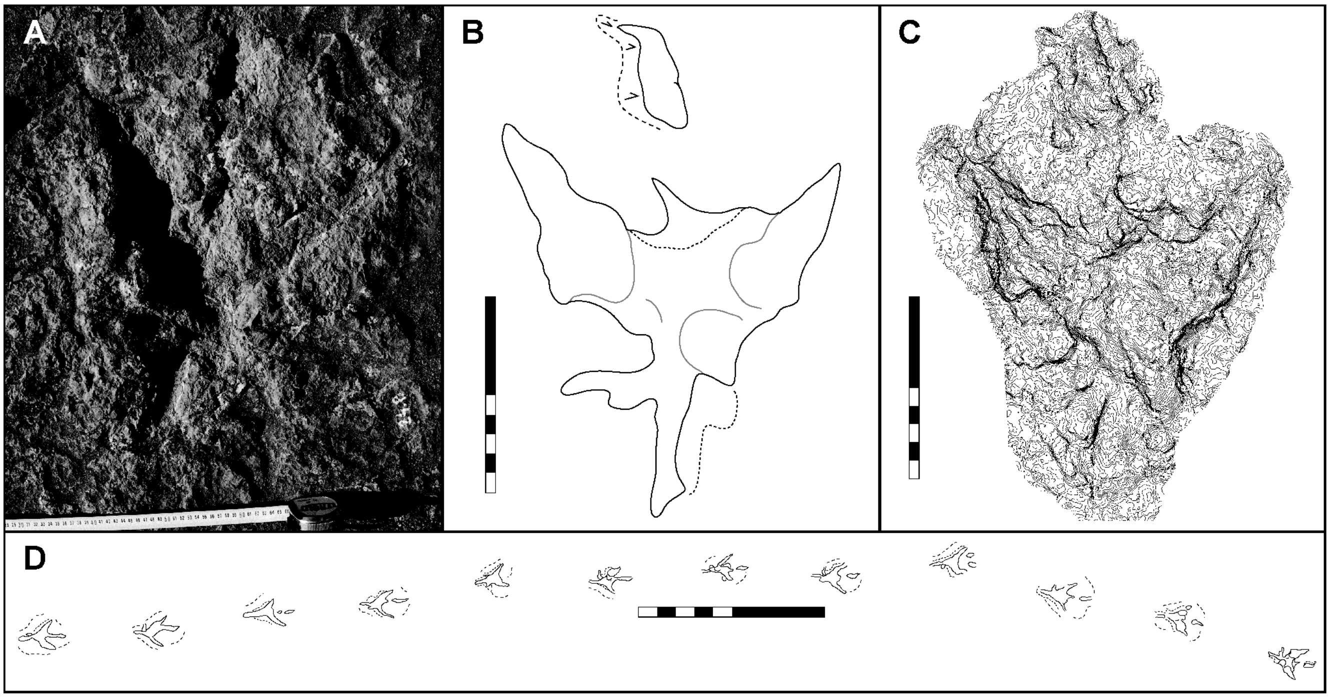

Fig. 10. Examples of morphotype 2F

A – photo of the tetradactyl footprint Detk MXXIV/12 (N 31°42.233', W 006°54.253'), scale bar 30 cm; **B** – schematic outline drawings of Detk MXXIV/12, scale bar 20 cm, the continuous line draw the internal margin of the footprint, the dashed line the exterior margin, the grey lines the internal morphologies; **C** – contour lines of MXXIV/12 generated from the 3D model data (supplementary file 5) with 1 mm equidistance between the lines, scale bar 20 cm; **D** – schematic outline drawing of Detk MXXIV, the longest trackway for morphotype 2F, scale bar 2 m, the dashed lines indicate the external margin of the displacement rims

varying from 1.19 to 1.74 m for pace, and from 2.35 to 3.38 m for stride.

MORPHOTYPE 2F

The peculiar characteristics of this mesaxonic and tetradactyl type are a marked hallux and metapodium impressions (Fig. 10, supplementary file 5); the proportions suggest that the latter are given from the large part of the metatarsal. The shape of the tracks is asymmetrical, longer than wide even without considering the metatarsal portion (estimated average Fw/Fw: 0.83), with four elongated and tapered digits. Digit IV seems to be the longest, followed by digit III, II and I, though digit III is often separated from the rest of the footprint by sediment infillings. The total divarication angle II-IV averages around 60 °, with II-III (25.4°) always narrower than II-IV (36.3°). Digit I is always laterally directed towards the trackway midline, with an average angle I-II of 73°. The metatarsal impression is slightly interiorly rotated.

The single long trackway, Detk MXXIV (N 31°42.233', W 006°54.253'), shows relatively short paces with a continuous progression. The footprints are generally parallel to the trackway midline and the gauge appears quite narrow. No paired footprints or resting traces occur, thus a simple slow-walking cause, as suggested by Day *et al.* (2002, 2004) is not sufficient to explain the tracks, but the substrate has also to be considered: a soft, water-saturated ground might not only have allowed the sinking of the pes to sink in the sediment, but could also have influenced the behaviour and the gait of the dinosaur.

ICHNOLOGICAL ANALYSIS

DISTRIBUTION, SPEEDS AND DIRECTIONS

Footprint sizes and the index of track size (IS, in Thulborn, 1990) were calculated to evaluate the composition of the ichnocoenosis of the Iouaridène site. All the parameters were measured for each footprint and trackway, even if the poor preservation of some footprints and the discontinuity of some trackways prevent reliable measurement. However, the amount of tracks (624) and trackways (105) measured is generally sufficient to obtain statistically significant data.

The analyses of track sizes and IS (Fig. 11A–C) illustrate a clear predominance of large (Fl: 30–40 cm) theropod dinosaurs; in Figure 11A the peaks around 17 cm roughly correspond to the average foot length of the morphotypes 2A and 2B, while the peak at 30 cm is not representative of a morphotype, but represents smaller specimens of the main type 2C.

The relative distribution, carried out on the bulk of the tracks identified, is shown in Figure 11D. The provenance layer was not considered in this distribution, since the level surfaces are not

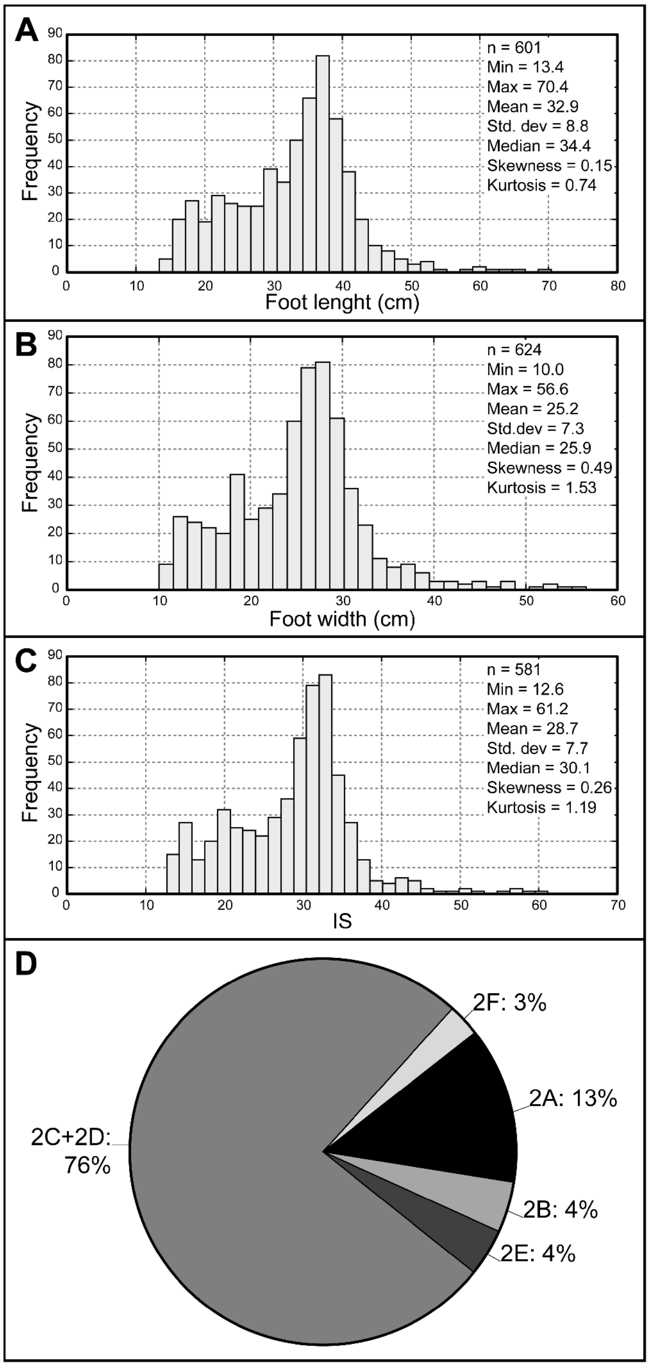

Fig. 11. Morphotype distribution and abundance

A – foot length frequency; **B** – foot width frequency; **C** – index of track size (IS) frequency, the three distributions are clearly not normal and several peaks can be pointed out, roughly indicating the distribution of the main morphotypes; **D** – percentage distribution of the bipedal morphotypes

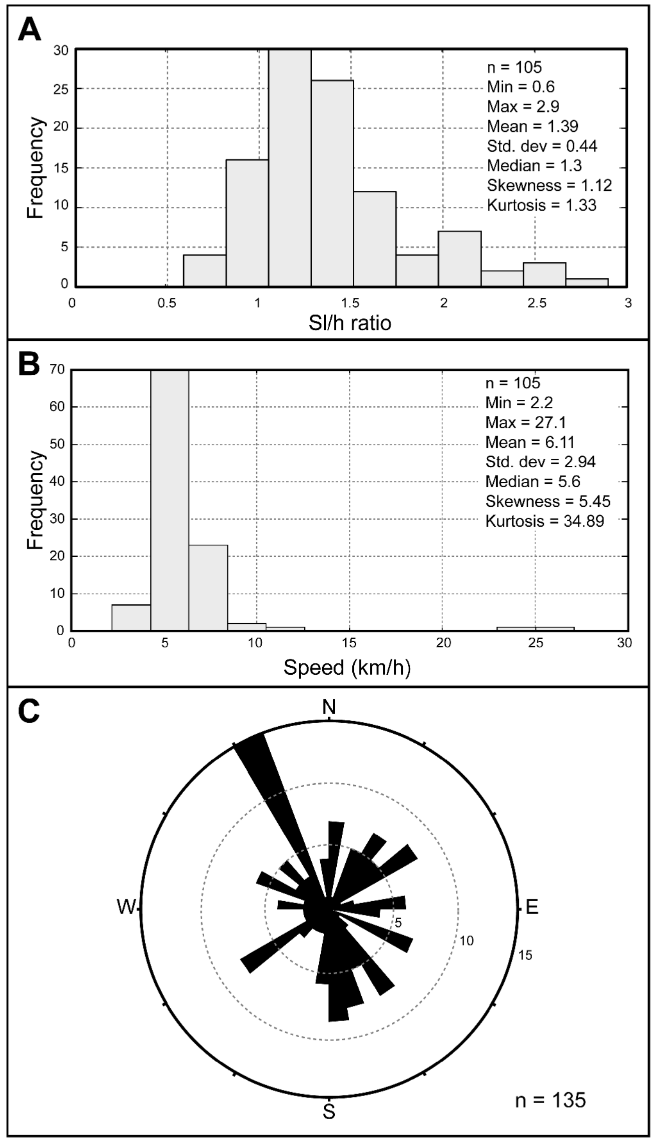

Fig. 12. Speed and directions

A – Sl/h ratio frequency; **B** – speed frequency, the peak corresponds to a slow speed (about 5 km/h), but higher values are present as well, with two specimens running faster than 20 km/h; **C** – rose diagram of walking directions

equally exposed. Morphotype 2D has been considered together with type 2C because it always occurs in type 2C trackways (see above). The size frequency diagram shows that the large type 2C+2D is the most abundant at the site (76%), followed by the smaller morphotype 2A (13%); morphotypes 2B, 2E and 2F represent together only 11% of the total distribution.

From the trackway analysis it was possible to estimate the gait and speed of the biped dinosaurs. The calculation of the gait followed the method of Thulborn (1990), whereas those relating to speed follow Alexander (1976) and Thulborn and Wade (1984).

The Sl/h ratio (Fig. 12A) illustrates a general, and expected, walking gait (mean: 1.39); the peaks correspond to the transition from walk to trot (around 2.0). The faster (>2.0), almost running animals were left by the morphotypes 2A and 2B (Fl <25 cm) and to the only fast trotting/trackway of morphotype 2C (Detk MXXXVIII; N 31°42.006', W 006°53.958'). As expected, the speeds are generally low and distributed around the mean value (Fig. 12B); only two faster outlayers can be pointed out, Deio XLI (N 31°44.067', W 006°54.600') and Detk MXXXVIII, both showing a high velocity (23.1 and 27.1 km/h, respectively), that is even more

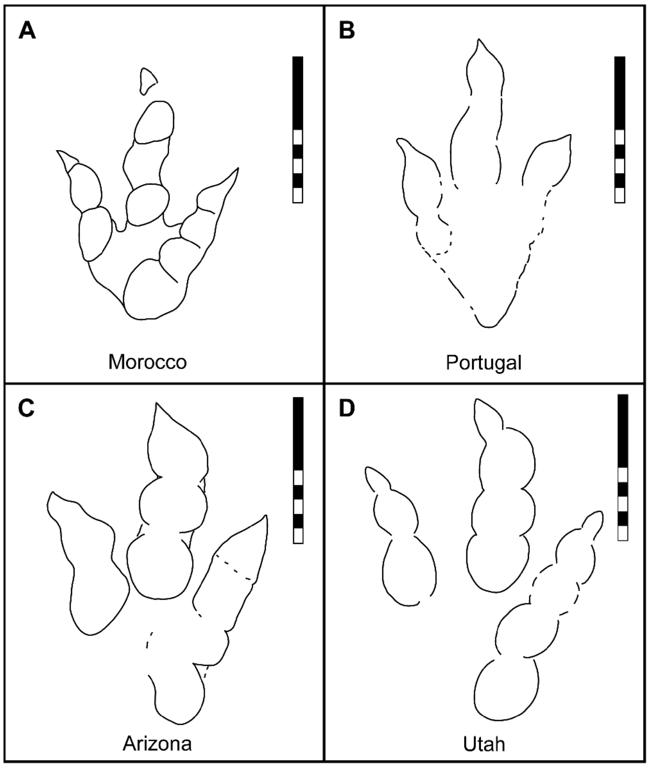

Fig. 13. Comparison of tracks with "megalosaurian" affinity

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, redraw from Lockley *et al*. (2000); scale bar 20 cm

impressive considering the small size of Deio XLI (Fl: 14.9 cm).

In Figure 12C the directions of the trackways and isolated tridactyl footprints (measured along the digit III elongation axis) are shown. A general scattered distribution of the direction is evident, with a main moving direction along a SSE–NNW axis; nonetheless, apart from this peak, it is worth noticing the occurrence of a roughly ENE–WSW direction, parallel to the main route of the sauropod present in the same levels (Belvedere, 2008).

ICHNOTAXONOMICAL INTERPRETATION

M o r p h o t y p e 2 A – Meyer and Monbaron (2002) and Belvedere *et al*. (2007) assigned this morphotype to *Carmelopodus* Lockley, Hunt, Paquette, Bilbey and Hamblin, 1998*a*. However, apart from the specimen Detk MLX (N 31°42.368', W 006°54.340'), illustrated in Figure 3D–F, all the other footprints present the impression of a generally rounded "heel", whereas the original description states the lack of "...any impression of a fourth proximal pad on digit IV in all ontogenetic stages..." (Lockley *et al*., 1998*a*). No clear phalangeal formula can be derived from the specimens studied, not even looking at the contour lines drawings generated from the 3D models, making uncertain the classification of this morphotype (apart of Detk MLX) as *Carmelopodus*.

Indeed, thee "heeled" tracks of this morphotype seem very similar to *Wildeichnus* Casamiquela, 1964; a comparable footprint was recently described by Gierliński *et al*. (2009) from the Middle Jurassic of Morocco, and classified as *Wildeichnus* sp., but it is not of comparable size to the analysed material. Thus, most of the type 2A specimens can be assigned to *Wildeichnus* sp., while Detk MLX can be considered as cf. *Carmelopodus* sp.

M o r p h o t y p e 2 B – because of the high symmetry of its interdigital angles this morphotype has been compared with *Anomoepus scambus* Hitchcock, 1845. This taxon was described as "...small (pes <20 cm), mostly bipedal and tetradactyl, but functionally tridactyl..." (Olsen and Rainforth, 2003). Despite some morphological similarities with *A. scambus*, the Moroccan specimens present some digital pad impressions, and do not have the inward rotation of the pes typical of that ichnospecies; moreover, neither manus tracks nor digit I impressions have been found, thus preventing a sure comparison of the morphotype with this ichnotaxon.

Lockley *et al*. (1998*b*) describes a new ornithopod ichnotaxon, lacking in manus impressions: *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." Compared with this ichnotaxon, the morphotype 2B shows many similarities in the tapering termination of the digits, in the proportion between length and width, and in the high divarication angle. However, it always presents a rounded "heel" lacking in the *D. socialis* description. Furthermore, the tracks are not quadripartite, since they do not have separated digits. Gierliński *et al*. (2009) describes a cf. *Dinehichnus* sp. from the Middle Jurassic of Morocco which presents a triangular "heel", less rounded but not dissimilar from the Iouaridène specimens. Thus, this morphotype is classified as cf. *Dinehichnus* sp.

M o r p h o t y p e s 2 C, 2 D, 2 F – these three morphotypes are discussed together, as their affinity is close to *Megalosaurus* tracks, although their ichnotaxonomical status needs further clarification. This uncertainty goes back to the assignation of *Eutynichnium lusitanicum* von Nopsca, 1923 to the theropod *Megalosaurus pombali* made by de Lapparent and Zbyszewski (1957), and became increasingly confusing in time with the revisions of several related new ichnotaxa: *Megalosauripus* (Lessertisseur, 1955; Lockley *et al*., 1996), *Bueckeburgichnus maximus* (Kuhn, 1958) *Megalosauropus* (Colbert and Merrilees, 1967; Keaver and de Lapparent, 1974; Antunes, 1976), *Gigantosauripus* (Mensink and Mertmann, 1984), *Hispanosauropus* (Mensink and Mertmann, 1984) *Irenesauripus* (Sternberg, 1932). Lockley *et al*. (2000) and Thulborn (2001) tried to solve the problem, but their interpretations are so different that the only ichnogenus that should be considered valid at the moment is *Hispanosauropus hauboldi* (Lockley *et al*., 2007, 2008). In this paper, we consider valid the *Megalosauripus sensu* Lockley *et al*. (2000), since it is completely different from *Bueckeburgichnus maximus*.

Figure 13 clearly illustrates the similarities of the Moroccan tracks with the specimens from the Late Jurassic of Arizona, Utah, and Portugal described by Lockley *et al*. (2000, fig. 8) and assigned to *Megalosauripus* (*sensu* Lockley *et al*., 2000). Nevertheless, the morphological similarities with *Megalosauripus*

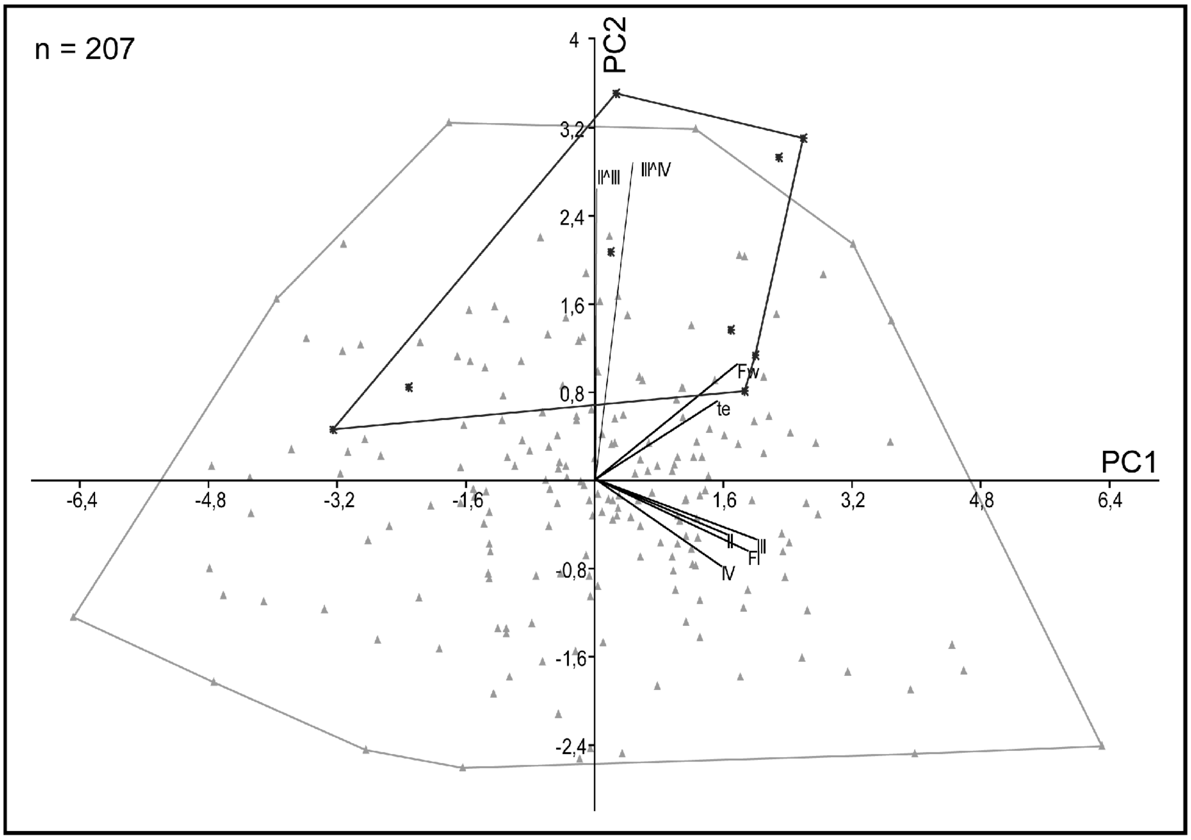

Fig. 14. PC1 *vs*. PC2 score plot of the comparison between morphotypes 2C and 2F (8 variables)

Gray triangles – morphotype 2C; black stars – morphotype 2F; PC1 = 47.6%; PC2 = 17.0%; PC3 = 13.7%; PC4 = 8.8%; PC5 = 5.1%; PC6 = 4.5%; PC7 = 2.2%; PC8 = 1.0%; Fl – the foot length; Fw – the foot width; II, III, IV – the free digit length of digit II, III and IV, respectively; te – the toe extension; II^III and III^IV – the divarication angle II-III and III-IV, respectively

(*sensu* Thulborn, 2001) are fewer, since the ichnogenus considered by the author as a new ichnotaxon is based on the revision of the tetradactyl *Bueckebeurgichnus maximus*. Those footprints that do not present phalangeal pad impressions greatly resemble the *H. hauboldi* from Asturias. Being aware that the megalosaurian origin of these tracks is only conjectural, the "megalosaurian" affinity of morphotype 2C is certain, as are the similarities with *Megalosauripus* (*sensu* Lockley *et al*., 2000) and *Hispanosauropus* (Lockley *et al*., 2007).

The same holds true for the tetradactyl tracks of morphotype 2D: the general morphology, especially the position and orientation of digit I, suggest great similarities with *Eutynichnium lusitanicum* von Nopsca, 1923, formally emended by Lockley *et al*. (2000). Nouri (2007) proposed a new ichnospecies, *Eutynichnium atlasichnus*, for this morphotype, but the proposed holotype (footprint 1Am2.5, Nouri, 2007) is too poorly preserved and deteriorated to be considered as the type material for this ichnotaxon. That track, mapped by Belvedere (2008) as Deio DVI/5 (N 31°43.988', W 006°53.921'), lies within a trackway sequence which shows some possible tetradactyl tracks, and does not preserve any undoubtedly digit I impressions (Fig. 7C). Type 2D tracks generally show very poor preservation and are always linked with tridactyl tracks. The impressions of digit I are interpreted here as having been controlled by the sediment rheology rather than by the anatomy or behaviour of the trackmaker.

These considerations, and the poor ichnotaxonomical status, does not justify the definition of a new ichnotaxon.

The tetradactyl morphotype 2F also shows some "megalosaurian" affinity, especially with *B. maximus* (*sensu* Lockley *et al*., 2000), in relation to the position and orientation of digit I, and the impression of the metapodium; however, the Moroccan tracks have a more slender and narrower metatarsal imprint. In order to verify the theropod origin of this generally poorly preserved ichnotaxon and also for testing its "megalosaurian" affinity we carried out a Principal Component Analysis with all the tracks of morphotypes 2C, 2D and 2F using *Past 1.86*© (Hammer *et al*., 2001). The eight parameters considered are the foot length and width, the free length of digits II, III and IV, the interdigital angle II-III and III-IV, and the toe extension (Weems, 1992). The score plot (Fig. 14) clearly illustrates that the types are perfectly correlated, with only a few footprints falling out of the type 2C group. Indeed, the type 2F has been considered together with 2C and 2D.

Thus, the "megalosaurian" affinity of all the three morphotypes can be affirmed, but it is possible to make an taxonomical classification only for morphotype 2C, that can be classified as *Megalosauripus* sp. (*sensu* Lockley *et al*., 2000).

M o r p h o t y p e 2 E – this morphotype has recently been taxonomically interpreted also by Boutakiout *et al*. (2009). However, we report here our interpretation which is broadly similar to that already cited. Despite a superficial resemblance to some known ornithopod tracks, the occurrence of clear claw marks in the best-preserved specimens questions this interpretation; because of their very large size, they have been compared to the largest theropod footprints known. The size of the specimen studied is similar to the one of *Tyrannosauripus* Lockley and Hunt, 1994. However, the Moroccan specimens are always tridactyl, whereas *Tyrannosauripus* is nearly tetradactyl, more robust in its morphology and was left by nearly semi-plantigrade animals.

Other large theropod footprints have been recorded from the Middle Jurassic of Oxfordshire (Lockley and Meyer, 2000; Day *et al*., 2002, 2004) and Yorkshire (Whyte *et al*., 2006) which show overall morphological and dimensional similarities of the pes.

Like the English specimens, the Moroccan footprints also show display general morphological similarities with the "megalosaurian" tracks from the same site, but no certain assignation can be made because of the peculiar straightness of digit III, and also due to the absence of the variable gait described for *Megalosauripus* (Lockley *et al*., 2000).

Theoretically a new ichnotaxon should be only established when enough well-preserved specimens are available. This is mandatory to understand the variability of the tracks, and to avoid error in identification. Even if these footprints probably belong to a new ichnotaxon, at least at the species level, the general poor preservation does not allow us to establish a new taxon.

SUMMARY AND CONCLUSION

1. The siliciclastic Iouaridène tracksite bears an extremely diverse track assemblage, dominated by diverse bipedal tracks consisting of large, middle and small theropods and probably also by small ornithopods. The lack of unequivocal large ornithopod tracks is noteworthy. Currently this is the most diverse ichnocoenosis from the Late Jurassic strata of Gondwana. It is quite similar to those of Spain (Asturias), Portugal and the Four Corners area of the USA (Belvedere and Mietto, 2009).

2. The prevalence of large theropods could reflect a real faunal distribution, or it may have been due to the rheological property of the substrate. Small tracks, indeed, are quite rare in the entire site and always shallow; this fact, together with the relatively shallow (<20 cm) tracks of huge sauropods (Belvedere, 2008; Marty *et al*., 2010), points to the tracks being made on firm ground.

3. The size of at least one trackway (25IGR1) measured by Boutakiout *et al*. (2009) was overestimated. Moreover, different trackways can rarely be linked as segments of longer trackways, based on the direction of movemen. Short and scattered segments cannot be considered part of a longer discontinuous trackway based only on moving direction, as the dinosaur would have had to walk only on a straight line, without any turns or changes in direction. Therefore, tracks 13IGR1 (Deio XLII in Belvedere's survey) and trackway 16IGR1 (not mapped by Belvedere) cannot be correlated because they are at least 2 km away from one another.

4. The availability of high-resolution 3D models of the footprints studied (see supplementary data) allowed a more detailed study. Therefore, the sharing of these data should become a common procedure in vertebrate ichnology, making the published data more objective and allowing better comparisons and/or revisions. Therefore ichnotaxonomical comparisons would become easier, helping to solve some of the systematic problems remain outstanding.

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