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Re-examination of manus-only and manus-dominated sauropod trackways from Morocco

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Manus-only and manus-dominated trackways of sauropods previously reported from the Iouaridène Basin of Morocco are relocated and re-examined. One trackway, interpreted as a manus-only trackway, was a misinterpretation of a poorly preserved trackway of a large theropod that walked in the opposite direction to that previously inferred. Two previously described manus-dominated trackways could be underprints. One previously described manus-only trackway and a newly discovered manus-only trackway could also be underprints. However, if the true imprinting surface is not identified, an "underprint origin" cannot be accepted as firm evidence that the footprints were imprinted on land, and a swimming or submerged sauropod might have left similar underprints under the contact layer. Kinematic investigations might help to reconstruct the origin of the trackway. The two manus-only trackways from the Iouaridène tracksite apparently show alternating pace lengths which suggests semi-galloping to galloping gait patterns by the trackmakers. Such a galloping gait pattern has never been reported from regular sauropod trackways, and it is unclear as to whether such a trackway pattern represents rapid locomotion. A partly submerged sauropod could perhaps register such galloping gait manus-only trackway patterns as a result of swimming behavior.

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INTRODUCTION

Manus-only and manus-dominated sauropod trackways have been a topic of discussion with relation to hypotheses of swimming sauropods. With regard to this topic, one of the authors (Ishigaki) first reported the discovery of two manus-dominated and two manus-only trackways of sauropods from the Iouaridène area in the High Atlas Mountains, 10 km east of the town of Demnat, 105 km east of Marrakech, Morocco (Ishigaki, 1989). He interpreted these trackways as imprinted on the sediment-water interface by a submerged swimming sauropod whose body and hindlimbs floated, causing only the manus to touch the substrate below the water. This submerged sauropod hypothesis had first been presented by Bird (1944), in which he interpreted a sauropod manus-only trackway from Texas. Ishigaki (1989) later interpreted four trackways from the Iouaridène Basin as further examples supporting Bird's hypothesis of swimming sauropods.

From late 1980's, manus-only and manus-dominated sauropod trackways were reported from many sites around the world (Pittman, 1989; Lockley and Santos, 1993; Lockley *et al*., 1994*a*, *b*; Santos *et al*., 1994; Lee and Huh, 2002; Vila *et al*., 2005; Lee and Lee, 2006). However, to interpret these abnormal trackways, an alternative explanation was presented. According to this explanation, they are undertracks imprinted in a terrestrial setting on the underlying sedimentary layers by the deeply sunk manus of the trackmaker while its pes sank relatively less into the substrate. In certain layers under the original footprint, only undertracks of manus prints are left, whereas there are no undertracks of pes prints on such layers (Lockley and Conrad, 1989; Lockley and Rice, 1990; Lockley, 1991; Lockley *et al*., 1994*b*). Vila *et al*. (2005) supported the undertrack origin of manus-only trackways with evidence from Spain, in which they showed an identical arrangement of manus prints in manus-only trackways and in a complete trackway (manus-pes sets) from the same tracksite. They regarded these as new evidence to support the underprint origin of manus-only trackways. Lee and Huh (2002) and Lee and

Lee (2006) claimed support for Bird's hypothesis with new evidence from Korea. However, Hwang *et al.* (2008) presented an alternative interpretation for the Korean trackways. Li *et al.* (2006) reported pes-dominated sauropod tracks and trackways from Gansu Province, China. They interpreted that these were made by swimming individuals in shallow water. Henderson (2004) used computer modelling to suggest that floating *Brachiosaurus* and *Camarasaurus* could have produced manus-only trackways. However, he also suggested that this would not have been a stable position for sauropods attempting to progress through deep water.

Meyer and Monbaron (2002) reexamined the Iouaridène site and reported that "The manus only trackways (swimming sauropods of Ishigaki) could not be found, all of the observed trackways consist of manus and pes sets. The presence of oscillation ripple marks on the track levels indicating a water depth of no more than 50 cm seriously questions Ishigaki's interpretation of swimming sauropods".

As a result, the authors once more examined the data from the Iouaridène site. The purpose of this paper is to present the results of the reinvestigation and to discuss the swimming sauropod hypothesis.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Iouaridène Basin is a classic, well-known dinosaur tracksite (Fig. 1). Plateau *et al.* (1937) first described the site and it was mentioned frequently by later authors (Roch, 1939; Bourcart *et al.*, 1942; De Lapparent, 1942, 1945; Dutuit and Ouazzou, 1980; Jenny *et al.*, 1981*a*, *b*; Jenny, 1988; Ishigaki, 1989; Nouri, 2007; Belvedere, 2008). The site contains many theropod, sauropod, and some other footprints numbering about 1000 in total (Belvedere, 2008). The footprints are observed on reddish, consolidated, fine-grained sandstone beds with mud cracks. These track-bearing continental red beds belong to the lower member of Iouaridène Formation. It has been regarded as a Middle Jurassic (Bathonian) deposit (Jenny *et al.*, 1981*a*; Jenny, 1985; Jenny, 1988). A recent study on charophytes and ostracods, however, reported the age of the Iouaridène Formation as Upper Jurassic (Charrière *et al.*, 2005). Regarding sauropod footprints, Dutuit and Ouazzou (1980) described and named a large manus-pes set from the northern part of this tracksite as *Breviparopus taghbaloutensis*. The approximate latitude and longitude of the reference trackway of *Breviparopus taghbaloutensis* are 31°44'8"N, 6°54'6"W.

RELOCATION AND DESCRIPTION OF TRACKWAYS

One of the authors (Matsumoto) made a precise outcrop map of the northern part of the Iouaridène tracksite in 1991, the result of cooperative work supported by Japanese Overseas Cooperation Volunteers. He presented the map to the Moroccan Ministry of Energy and Mines. In the course of this work, Matsumoto relocated Trackways A, B, C of Ishigaki (1989) on the map (Fig. 2). The trackways are located in the northern part of the Iouaridène tracksite, north of the village of Taghbalout. Trackways A, B, C of Ishigaki (1989) and the long trackway of *Breviparopus taghbaloutensis* of Dutuit and Ouazzou (1980) are all on the uppermost footprint-bearing bedding plane.

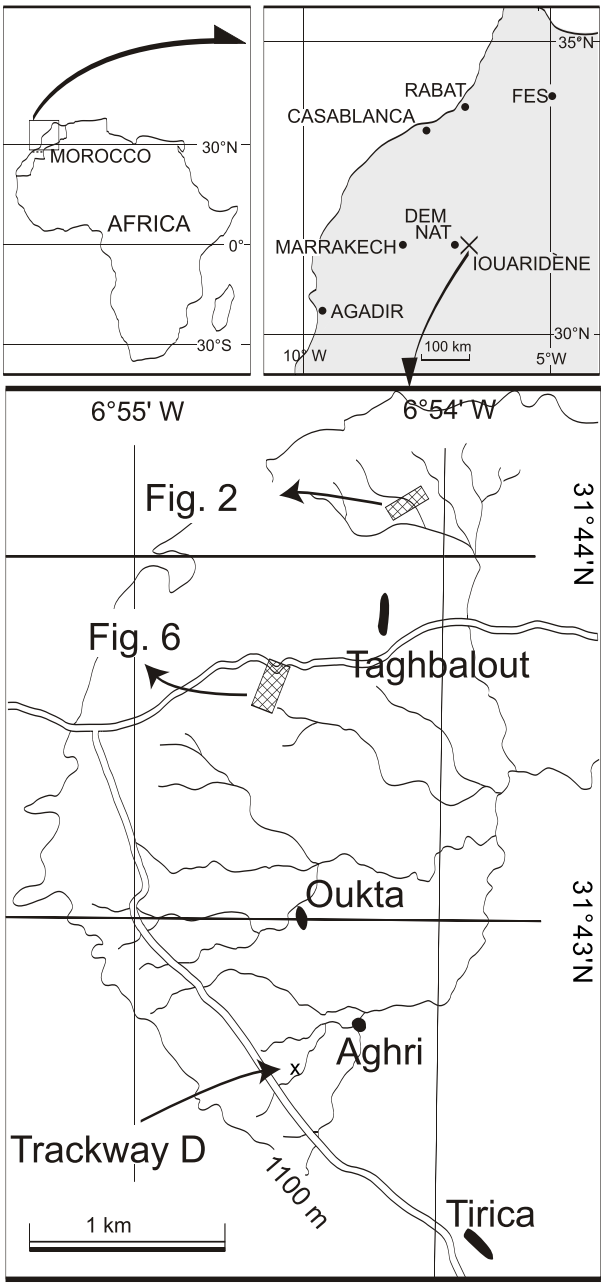

Fig. 1. Locality map of the Iouaridène tracksite

Meshed inset rectangles denotes the areas covered by detailed outcrop maps of Figures 2 and 6; the location of Trackway D is arrowed

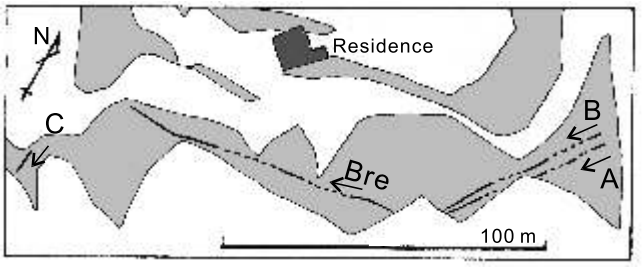

Fig. 2. Outcrop map of the northern part of the Iouaridène tracksite

Gray denotes outcrop of track-bearing bedding plane; continuous line denotes exposure of the trackway; dashed line denotes eroded or covered part of the trackway; arrow denotes the orientation of the trackways; A — Trackway A, B — Trackway B, C — Trackway C, Bre — Trackway Bre (= reference trackway of *Breviparopus taghbaloutensis)*

The distal segments of two parallel manus-dominated trackways (Trackways A and B of Ishigaki, 1989) have been relocated 18 m east of the proximal end of the long (89 m) trackway of *Breviparopus taghbaloutensis* abbreviated as Trackway Bre (Fig. 3 Bre, A and B). Trackways A and B of Ishigaki (1989) extend for more than 54 m. Ishigaki (1989) illustrated the distal 15 m of both trackway segments. The manus prints are almost always associated with the front part of pes prints (Fig. 3A and B). The manus prints have clear semi-circular to crescentic shapes outlined by the rims. In contrast, the pes prints are not clear, not very well outlined, shallower than manus prints, and only the anterior part is imprinted. The footprints are covered by massive mudstone without any clear internal sedimentary structures (Fig. 4).

The site location data given by Ishigaki (1989) for manus-only Trackway C was inaccurate. It has been relocated 36 m south-west of the distal end of the long *Breviparopus taghbaloutensis* trackway (Fig. 2). It is a very shallow trackway and the manus prints are not associated with anterior parts of pes prints (Figs. 3C and 5A, B).

Trackway D of Ishigaki (1989), which he interpreted as a manus-only trackway with dragging toe traces, has also been relocated 350 m SW of the village of Aghri at the location he originally reported (Figs. 1 and 7A, B).

During this reinvestigation, one of the authors (Matsumoto) discovered another manus-only trackway. The site of this new trackway (here designated as Trackway E) is located 243 m south of the vehicle road between Demnat and Iouaridène (Fig. 6). It is a very shallow trackway consisting of five impressions, and is partially eroded (Fig. 3E). It is difficult to determine whether these tracks are underprints or poorly preserved "true" prints (i.e., representative of the original surface affected by the trackmaker), because the bedding

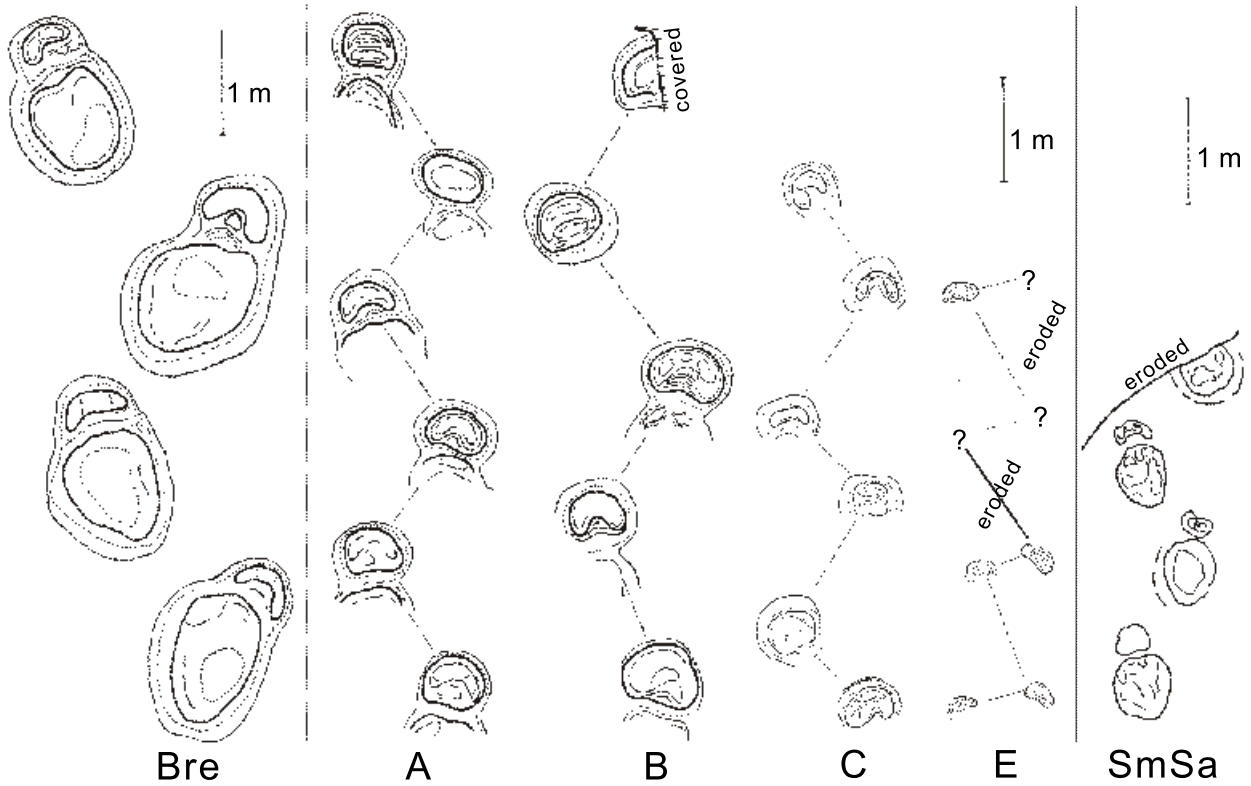

Fig. 3. Sketch of trackways

Bre — part of Trackway Bre (= reference trackway of *Breviparopus taghbaloutensis)*; A — part of Trackway A; B — part of Trackway B; C — Trackway C; E — Trackway E; SmSa — trackway of small sauropod from the Iouaridène tracksite; ? — denotes the eroded imprints

Fig. 4. Photograph of the manus-dominated Trackway B

Scale stick (behind the person) is 1 m; anterior part of pes prints are imprinted shallowly behind the manus prints

plane is covered by the previously mentioned massive mudstone. Trackway E belongs to 15 parallel short trackways of sauropods. The other 14 trackways are poorly preserved manus-dominated to complete (manus-pes sets) trackways. The footprint width of tracks in Trackway E is the smallest among those 15 trackways.

Trackway C of Ishigaki (1989) and the newly discovered Trackway E reveals alternating short and long pace lengths, i.e. right and left pace lengths are different (Fig. 3C and E). In Trackway C the pace length from left to right manus print (average = 156 cm) is always longer than the right to left manus print (average = 110 cm). In Trackway E the pace length from right to left manus print (130 cm) is longer than the left to right manus print (average = 68 cm). The ratio between short and long pace is 71% (Trackway C) and 52% (Trackway E).

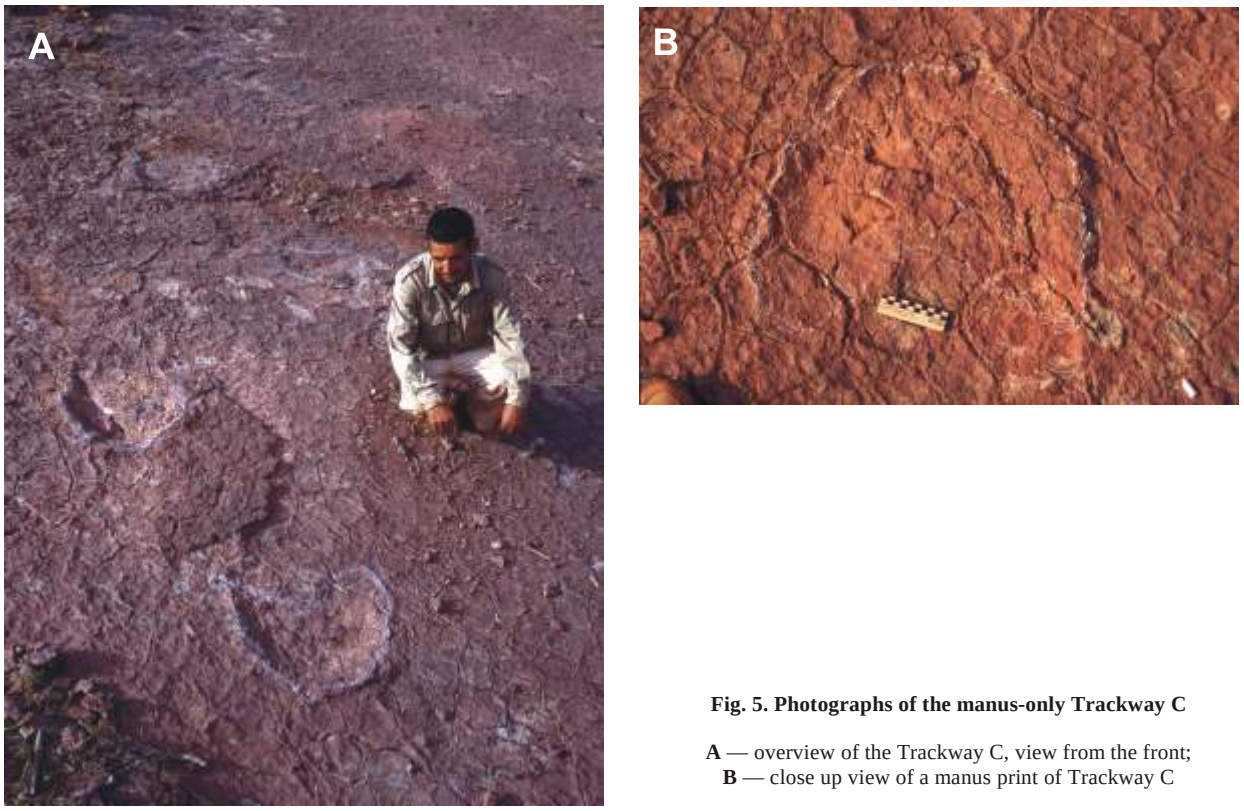

Fig. 5. Photographs of the manus-only Trackway C

A — overview of the Trackway C, view from the front;
B — close up view of a manus print of Trackway C

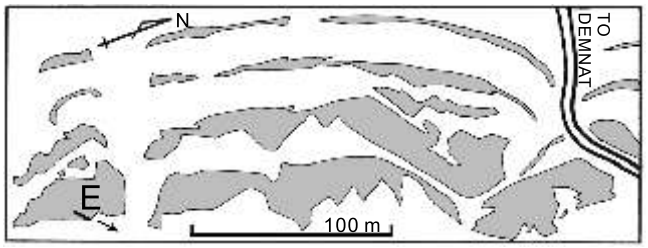

Fig. 6. Outcrop map of the central part of the Iouaridène tracksite and the location of Trackway E

Gray denotes outcrop of track-bearing bedding plane; continuous line denotes exposure of the trackway; arrow denotes the orientation of Trackway E

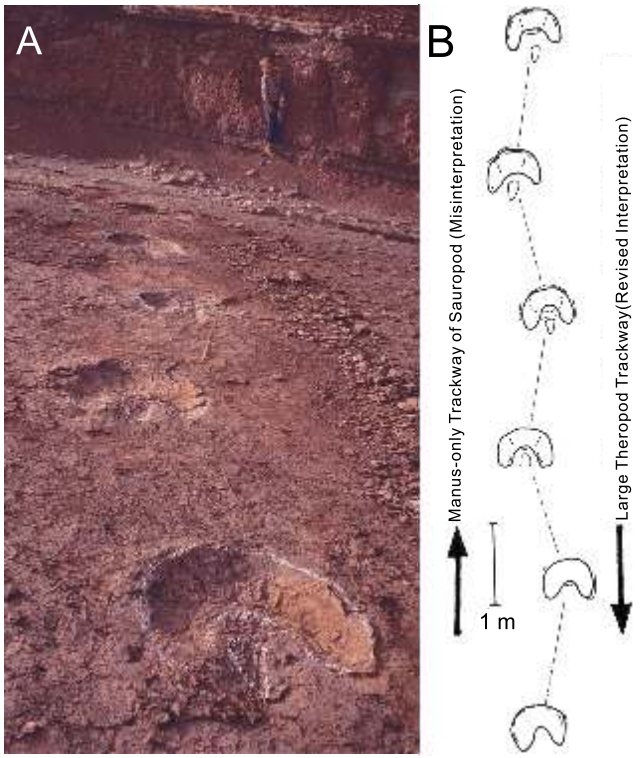

Fig. 7. Misinterpreted theropod Trackway D

A — photograph of Trackway D; scale stick 1 m;
B — misinterpreted drawing of Trackway D of Ishigaki (1989, fig. 9.4)

DISCUSSION

TRACKWAY D

Careful re-examination of Trackway D of Ishigaki (1989) reveals that it is not a sauropod trackway. It is a poorly preserved trackway of a very large theropod that walked in the opposite direction from that inferred by Ishigaki (1989) (Fig. 7A and B). The impressions of digit II, digit IV and digit-metatarsal joint part are deep in this trackway. However the digit III impression is shallow particularly in the proximal part. Ishigaki (1989) originally interpreted this shallow digit III impression as the dragging mark of the toe of a sauropod, and here we correct that misinterpretation. It is also obvious that the pace angulation of Trackway D (160°) is typical of theropods and not sauropods which typically have pace angulations of about 100°.

TRACKWAYS A AND B

The authors could not find firm evidence supporting the concept that Trackways A and B are "true" prints formed subaqueously. We also did not find any counter-evidence to challenge the interpretation of shallow water depth (50 cm) associated with the track level as inferred from the oscillation ripple marks by Meyer and Monbaron (2002). The authors accept that they might be underprints. However, if they are underprints, the shallow water depth (50 cm) suggested by the ripple marks may not indicate the environment at the time of imprinting by the trackmaker. The true print horizon, then may have been at a certain level higher than the track-level. As mentioned before, Trackways A and B are covered by massive mudstone making it difficult to determine the "true" print horizon. Thus, we cannot estimate the water level at the time of imprinting with any degree of certainty.

The authors think it is difficult to completely deny the swimming hypothesis only on the basis that they are underprints, because a swimming or submerged sauropod might have left similar underprints. Vila *et al.* (2005) took a new approach to evaluate whether the trackway represents underprints or not. They compared patterns between a manus-only trackway and manus prints in complete (manus-pes sets) trackways. As the arrangement of manus prints in the manus-only trackway is identical with that of a complete (manus-pes sets) trackway from the same site, they judged that the manus-only trackway represents underprints of the complete trackway. Figure 8 shows the comparison of manus prints of sauropod trackways in the Iouaridène tracksite, taken from: the trackway of *Breviparopus taghbalouensis* (Trackway Bre); Trackways A, B, C, E in this paper; and a small, land-walking sauropod from the Iouaridène tracksite (SmSa). These trackways are all from the same or very similar horizons of the Iouaridène tracksite.

Manus prints of Trackway Bre, Trackway A, and Trackway B are similar in size and outline shape. However, the gauge of the manus trackway is wide in Trackway Bre, and narrow in Trackways A and B. They are not identical. It is therefore difficult to apply the logic of Vila *et al.* (2005) to regard Trackways A and B as unequivocal underprints of land-walking trackmakers of the type seen in Trackway Bre. However, if we disregard variation in size, there are no distinct differences between Trackways A and B, and general land walking manus trackways, such as that of Trackway SmSa. Consequently, the authors think that there is no firm evidence to prove that Trackways A and B were registered by submerged sauropods and we have insufficient evidence for aquatic ability of sauropods based solely on these trackways.

TRACKWAYS C AND E

Regarding manus-only Trackways C and E, the authors could not find firm evidence indicating that they are "true" prints, and we acknowledge that they might be underprints. For the same reasons as cited for Trackways A and B, we compared the arrangement of manus prints between those belonging to normal land-walking sauropod trackways (Trackways Bre and SmSa) and manus-only trackways (Trackways C and E). As a result, the manus arrangement of Trackways C and E is very irregular (Fig. 8). It is inferred that the walking patterns of Trackways C and E were very different from those of Trackways Bre and SmSa.

Sauropod trackways with alternating pace lengths exist amongst the regular manus-pes sets trackways that indicate land walking. But the ratio of short/long paces is greater than 80% in general. This contrasts with the more differentiated values recorded for Trackways C and E as 71 and 52% respectively. Literature research on published sauropod trackways tells us that such irregularity suggesting semi-galloping to galloping behaviour of the trackmaker has never been observed among normal land-walking sauropod trackways (e.g., Bird, 1944, 1985; Lockley, 1991; Farlow, 1992; Lockley and Meyer, 2000; Marty, 2008). Here we stress that the reference to a "galloping gait pattern" is primarily a descriptor for the alternating long-short paces, and does not imply rapid progression. Indeed speed estimates suggest walking speeds. From the kinematic point of view, the authors infer that submerged sauropods would be more likely to register such traces, because the graviportal stress generated by a galloping gait would be less in the water. Ishigaki (1989) claimed that the trackmaker of Trackway C floated its hindlimbs totally, while only the manus touched to the bottom. He also interpreted the alternating pace length of Trackway C as indicating a gallop with the rhythm of swimming strokes. The same interpretation could be applied to newly discovered Trackway E.

As Trackway E is one of the 15 parallel trackways, the authors think that there could be two implications.

1. Trackway E was made by a small swimming sauropod which swam with a galloping rhythm. Because the animal was the smallest among 15 individuals, its floating hind limbs did not touch the sediment-water interface, whereas other larger trackmakers left complete or manus-dominated trackways. In this scenario, all 15 trackways could be undertracks or poorly preserved "true" prints. Whether they are underprints or not, however, does not affect this scenario.

2. Trackway E is composed of undertracks of a small sauropod which traveled with a galloping rhythm on land. All 15 trackways are then undertracks of land-walking trackmakers. Because the trackmaker of Trackway E was the smallest and the lightest among 15 individuals, it could leave only manus prints, which sunk into the mud more deeply, while other larger and heavier trackmakers left complete or manus-dominated underprints. However, given the lack of diagnostic information available, both interpretations are speculative.

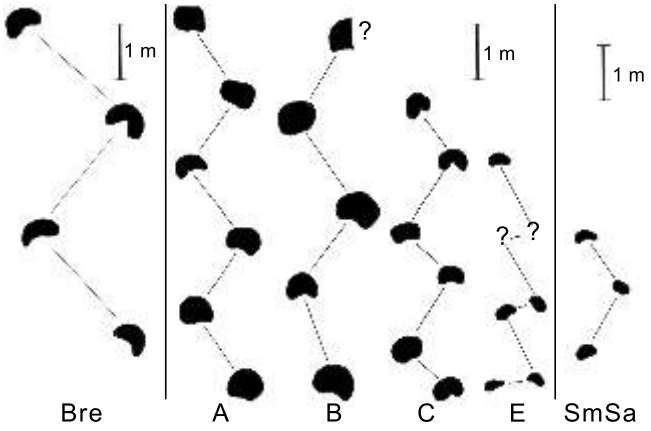

Fig. 8. Manus prints taken from trackways shown in Figure 3

Black part denotes manus prints. Bre — manus prints taken from part of Trackway Bre (= reference trackway of *Breviparopus taghbaloutensis*); A — part of Trackway A; B — part of Trackway B; C — Trackway C, SmSa — manus prints taken from the trackway of a small sauropod from the Iouaridène tracksite; ? — denotes eroded or covered imprints; scale bar = 1 m

From a sedimentological point of view, we could not find any persuasive evidence to support or refute either scenario. However, the authors think that the first interpretation is more likely, on the basis of kinematic reasoning.

SUMMARY AND CONCLUSIONS

Manus-only and manus-dominated trackways of sauropods reported by Ishigaki (1989) were relocated at the Iouaridène tracksite close to Demnat, Morocco. One of the trackways that Ishigaki (1989) interpreted as a manus-only sauropod trackway was a misinterpretation. It is a poorly preserved large theropod trackway, as indicated by the pace angulation.

A new manus-only trackway of a small sauropod suggesting a galloping gait pattern was discovered in the central part of the Iouaridźne tracksite.

It is often difficult to judge whether the imprints are underprints or not, from only the sedimentological observations in the field, especially when overlying layers are missing.

Manus-dominated tracks of Trackways A and B of Ishigaki (1989) could be undertracks. Manus-only tracks of Trackway C of Ishigaki (1989) and newly discovered Trackway E also could be undertracks. However, even if they are underprints, it is difficult to totally discard the swimming hypothesis solely on the basis of inferring that they are underprints, because swimming sauropods might have left similar manus underprints. In these cases, kinematic explanations may be applied to interpret

the trackways. If the manus-only or manus-dominated trackway configurations and the pattern of manus prints of complete trackways (manus-pes sets) are not identical, different interpretations are possible.

Trackway C of Ishigaki (1989) and newly discovered Trackway E have alternating pace lengths which suggest a semi-galloping to galloping style of locomotion of the trackmaker. Galloping gait tracks of sauropods have never previously been reported. The authors think that it was easier for sauropods to register such footprints in submerged conditions than in land-walking conditions.

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