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"OFF-TRACKING" - LIKE PHENOMENON OBSERVED IN THE TURNING SAUROPOD TRACKWAY FROM THE UPPER JURASSIC OF MOROCCO

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ABSTRACT

A turning trackway of a large sauropod dinosaur was discovered from the Upper Jurassic Iouaridène Formation in the Central High Atlas Mountains, Morocco. Its turning angle is 56° to the left. It is remarkable that the manus prints are imprinted outside of the pes trackway at the turning point. The gap between the trackway midlines of manus and pes imprints reaches its maximum width at the very point of turning. Other sharp turning trackways of large sauropods previously discovered from Utah and Switzerland present similar gaps between the two midlines. However, such gap is not recognized in the turning small sauropod trackway from Croatia, or in the fossil turning proboscidean trackway from Japan. A turning trackway of a modern Asiatic elephant presents a similar gap but in opposite mode. The appearance of the gap might be analogous to the "off-tracking" phenomenon observed in turning four wheel vehicles. Gleno-acetabular distance, steering ability of the hindlimbs, position of body mass and the existence of long neck and long tail may affect the appearance of the phenomenon. The analysis of this phenomenon in the turning trackways of quadrupedal animals would be useful for investigating the kinematics of extinct animals.

Key words: trackway, sauropod, off-tracking, turn, Jurassic, Morocco

石垣　忍・松本幸英　(2009)　モロッコ国上部ジュラ系より産出した竜脚類の方向転換した行跡に見られる「外輪差・内輪差」様の現象．福井県立恐竜博物館紀要 8：1–10.

モロッコ国高アトラス山脈中の上部ジュラ系イウアリデン層から大型竜脚類が方向転換した行跡化石が発見された．転回角は左へ 56° である．この行跡の特徴は，方向転換点において，後足印の行跡の外側に前足印が印跡されていたことである．前足印の行跡軸と後足印の行跡軸との間のずれは方向転換の中心のところで最も大きかった．大型竜脚類の方向転換した行跡化石は米国ユタ州とスイスからも報告されており，いずれの行跡にもこのようなずれが見られる．しかし，クロアチアから発見された小型竜脚類の方向転換した行跡化石や日本から発見された長鼻類の方向転換した行跡化石にはこのような現象は見られなかった．現生アジアゾウの方向転換の行跡の場合は，ずれは見られたが，ずれの方向が逆だった．こうした前足と後足の行跡軸のずれは，四輪自動車の方向転換時に見られる「外輪差・内輪差」と呼ばれる現象の現われと同様であると考えられる．後肢による身体方向の制御能力，窩臼長（肩関節と腰関節間の距離），体の重心の位置，長い首と長い尾の有無が，この現象の発現に影響すると考えられる．印跡動物の方向転換を示す足跡におけるこの現象の分析は絶滅動物の運動解析に有用である．

INTRODUCTION

Trackway analysis is one of important keys to reconstructing the locomotion of the extinct animals. Productive ichnosite yielding various trackways of one morphotype of footprint provides an excellent research area to investigate the variation of walking manner of the specific trackmaker. The Iouaridène Basin in the High Atlas Mountains, Morocco is one of important sites, yielding many sauropod and theropod trackways. First report on the Iouaridène ichnosite was made by Plateau et al. (1937). The site has been frequently mentioned by later authors (e.g., Roch, 1939; Bourcart et al., 1942; Lapparent, 1942, 1945). From the ichnosite, Dutuit and Ouazzou (1980) described and named the large sauropod footprint *Breviparopus taghbaloutensis*. Ishigaki

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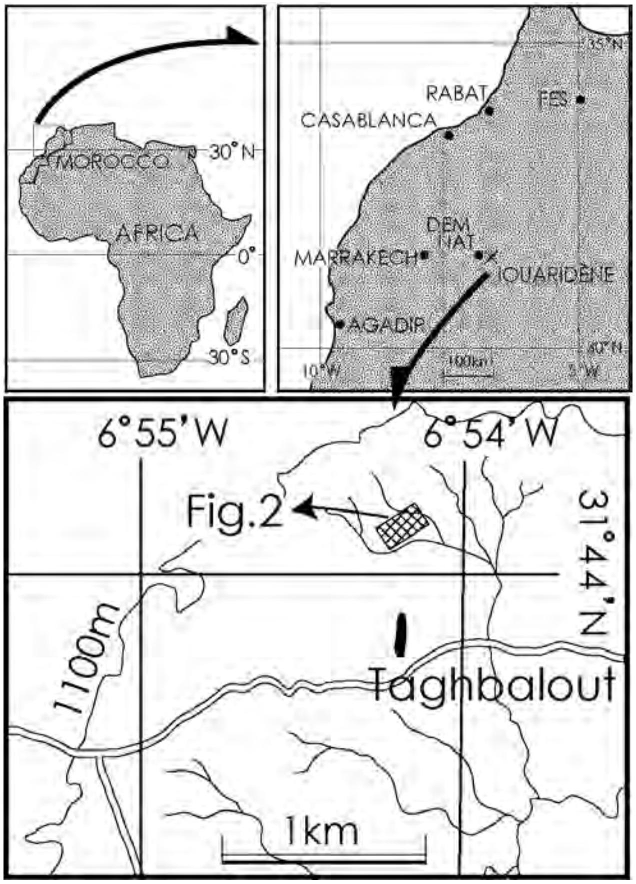

FIGURE 1. Locality map of Iouaridène ichnosite. Meshed part denotes the area covered by detailed outcrop map of Fig. 2.

(1989) reported manus-only and manus-dominated sauropod trackways from the same site, which had led to the controversial wading sauropod hypothesis. Recently, Nouri (2007) and Belvedere (2008) reported many sauropod footprints of the site from different points of view.

In late 1980's to early 1990's, the authors discovered separately a trackway of a large sauropod making a left turn. The interesting feature of the trackway is that the manus prints are imprinted outside of the pes track path at the turning point.

Turning sauropod trackways are very rare all over the world and four trackways are known in the published literature to show sharp turning behavior. The sharpest turning trackway is from Copper Ridge, north of Moab, Utah, USA (Lockley, 1990, 1991). Three other sharp turning sauropod trackways were reported from Europe, such as Fenoliga, Croatia (Leghissa and Leonardi, 1990; Pavlovec and Gogala, 1992; Dalla Veccia, 1994; Mezga and Bajraktarevic, 1999), Lommiswil/Oberdorf site, Switzerland (Meyer, 1993; Lockley and Meyer, 2000) and Lagosteiros Bay, Portugal (Meyer et al., 1994).

The purpose of this paper is to describe the Moroccan turning sauropod trackway with comparisons to other known sauropod trackways, and to discuss the cause of the irregularity through comparing turning sauropod trackways with turning proboscidean trackways.

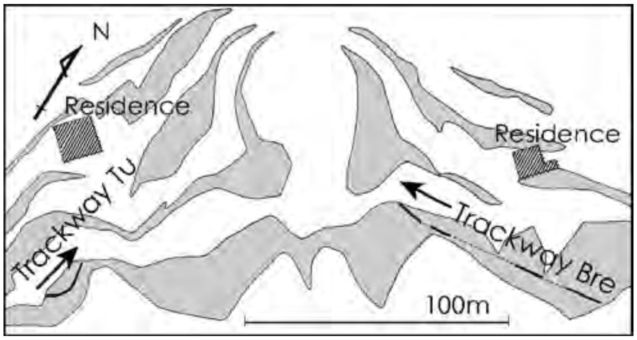

FIGURE 2. Outcrop map of northern part of Iouaridène ichnosite. Gray denotes outcrop of track-bearing bedding plane. Solid line denotes exposure of the trackway. Dotted line denotes eroded or covered part of the trackway. Arrows denote the orientation of the trackways. Trackway Bre: Reference trackway of *Breviparopus taghbaloutensis*, Trackway Tu: Turning trackway in this paper.

GEOLOGICAL AND GEOGRAPHICAL SETTING

The Iouaridène ichnosite is located in Central High Atlas Mountains, 10 km east of the town of Demnat, 105 km east of Marrakech, Morocco (Fig. 1). Footprints occur in the lower part of the Iouaridène Formation. The formation consists of terrestrial reddish pelitic sediments (Jenny et al., 1981; Jenny, 1985, 1988). Trackways are preserved on the hard fine sandstone beds. According to Jenny et al. (1981) and Jenny (1988), the age of the Iouaridène Formation is Middle Jurassic (Bathonian). However a recent study on charophytes and ostracods indicates that the age of the Iouaridène Formation is Upper Jurassic (Charrière et al., 2005).

The turning trackway (here abbreviated as Trackway Tu) was discovered in the northern part of the Iouaridène Basin by the authors (Fig. 2). The approximate latitude and longitude of the locality is 31°44'6″ N and 6°54'14″ W. The trackway was found on the uppermost horizons of footprint-bearing bedding planes. The famous reference trackway of *Breviparopus taghbaloutensis* of Dutuit and Ouazzou (1980) (here abbreviated as Trackway Bre) is on the same bedding plane (Figs. 6 Bre and A–D). The beginning point of the Trackway Tu is situated 148 m SW of the last footprint of the Trackway Bre.

ICHNOLOGY OF MOROCCAN TRACKWAYS

1) Turning sauropod trackway from Morocco (Trackway Tu)

The total length of Trackway Tu is about 22 m. The middle

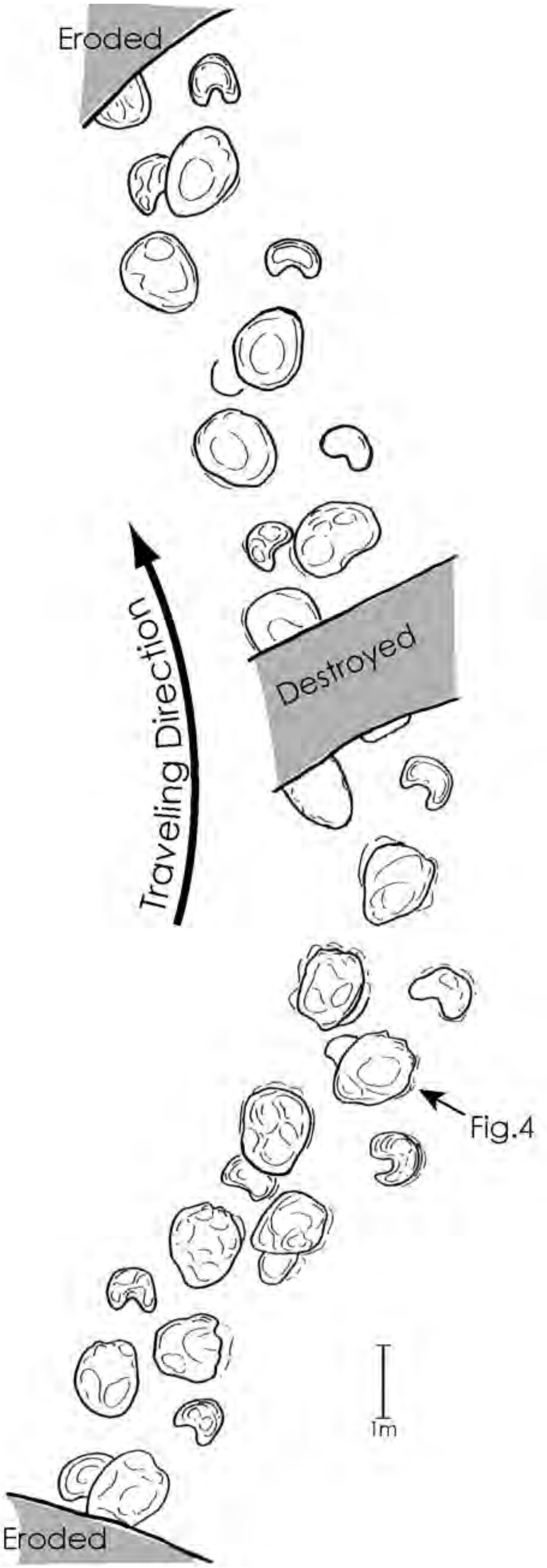

FIGURE 3. Drawing of Trackway Tu.

FIGURE 4. Photograph of the hind footprint (P7) of Trackway Tu. Photograph of P7 taken from right side oblique view. Arrows show digital-claw impressions.

part of the trackway, about 2 m in length, is damaged by small faults and erosion (Fig. 3). The trackway consists of 18 pes and 18 manus prints including some overlapped prints. 5 pes prints (P1, 10, 11, 12 and 18) are partially destroyed or covered with upper layer. Six manus prints (M0, 3, 4, 6, 14 and 16) are partially preserved, and one manus print (M8) is totally overlapped by pes prints. Two manus prints (M10 and 11) are not observable. The reconstructions of the whole trackway including missing parts are shown in Figure 5A and B.

The pes prints have an oval outline. Average footprint length and width are 115 cm and 95 cm, respectively. Three or four claw marks are recognized in the anterior rim of the well-preserved footprints (Fig. 4). The axes of pes prints are rotated outward. The rotation angle varies from 23° to 48°. The average rotation angle of left pes (32°) is smaller than that of right one (35°). The average depth of the pes prints is 5 cm.

The manus prints have a half-moon shaped outline. Average length and width is 42 cm and 68 cm, respectively. No claw impression is recognized in the manus prints. The axes of the manus prints rotate outward. The rotation angle varies from 25° to 50° showing outward rotation. On average, 28° for left manus prints and 36° for right manus prints. The depth of the prints is almost same as pes prints (5 cm). The distance between the center of manus prints and the center of pes prints is around 145 cm.

The orientation of the trackway begins with 41° (N41°E), and then changes to 345° (N15°W) at the middle point. Thus the trackway turned 56° to the left from the original direction. The maximum trackway width for the pes and manus is 205 cm and 210 cm, respectively. Trackway ratio of the pes print is around 50% based on the formula of Romano et al. (2007). Stride length of pes prints varies from 188 cm to 276 cm. The stride length increases after the turning point. The pace length of right prints is smaller than that of left ones. The ratio between the pace

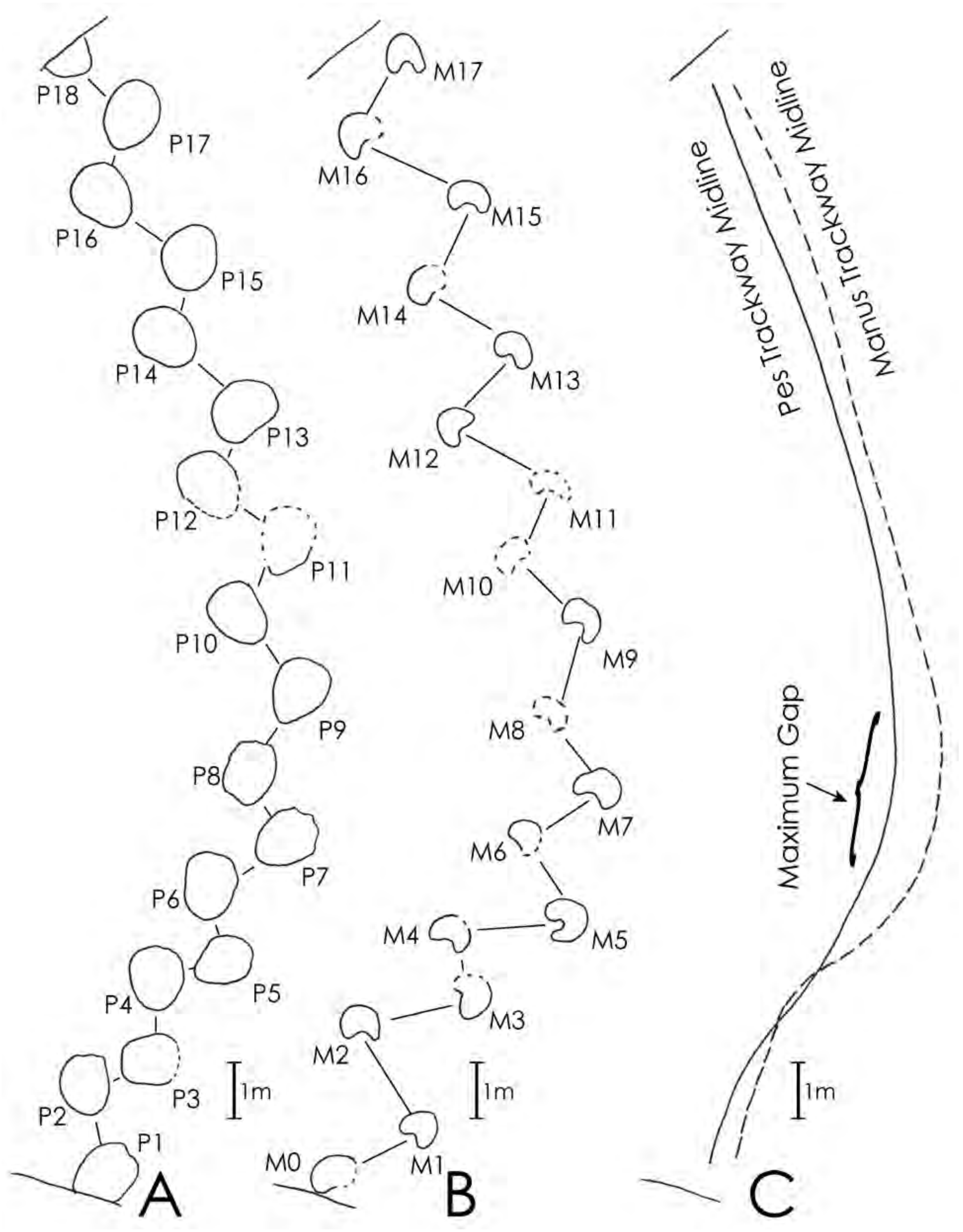

FIGURE 5. Reconstructed trackways and midlines of Trackway Tu. **A**, Reconstructed trackway of pes; **B**, Reconstructed trackway of manus; **C**, Trackway midlines of pes (solid line) and manus (broken line).

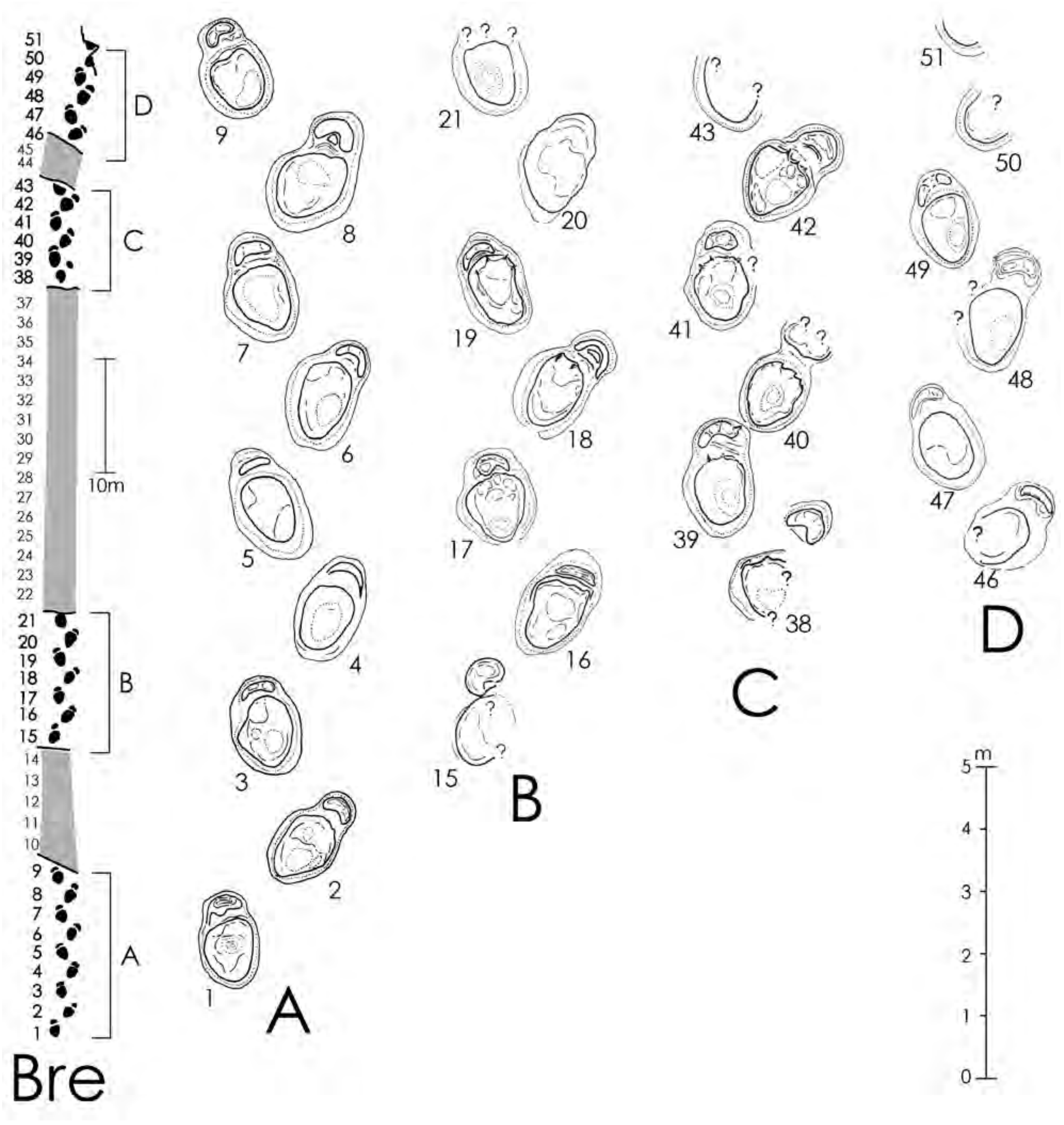

FIGURE 6. Drawing of Trackway Bre. Bre. Sketchmap of whole reference trackway of *Breviparopus taghbaloutensis*. A, B, C and D are the documented parts of the trackway. Numbers 1 through 51 denote the number of manus-pes sets from the beginning to the end of the trackway. **A**, **B**, **C** and **D**, Drawings of the exposed parts of the Trackway Bre.

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length of right and left pes prints is around 0.85. A similar pace ratio is also observed in the manus prints.

The trackway midlines of manus and pes are presented in Figure 5C. The manus midline is 42 cm right at the beginning point of the trackway, then 86 cm right around the turning point (around M7). It decreases to 40 cm in the end of the trackway (Fig. 5C).

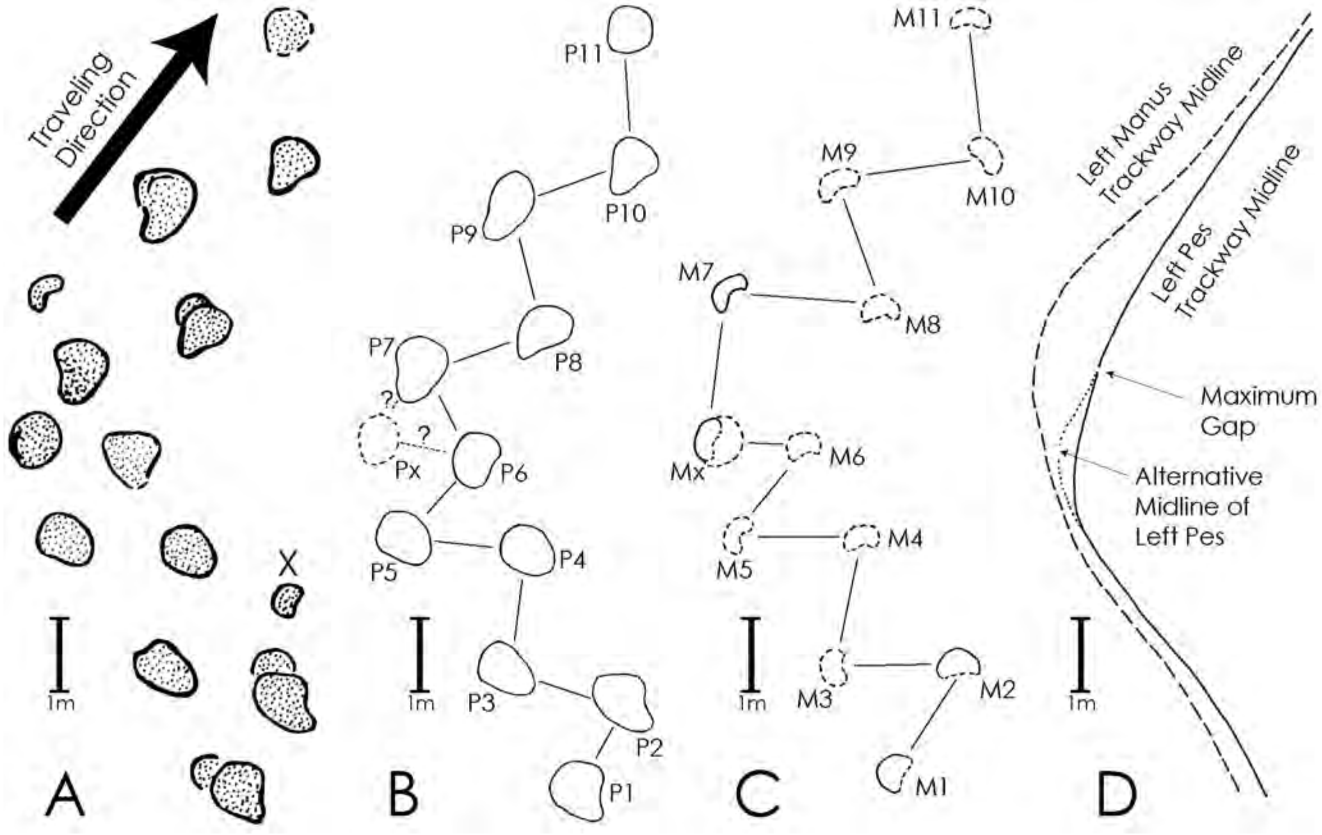

FIGURE 7. Turning sauropod trackway from Copper Ridge, Utah, USA. **A**, Turning trackway taken from original drawing of Lockley (1991), fig. 6.4. Footprint labeled as X is regarded as not belonging to the trackway; **B**, Reconstructed trackway of pes. Px could be a redundant imprinting of left pes. Dotted lines with interrogation marks are the possible reconstruction of pace, including Px; **C**, Reconstructed trackway of manus; **D**, Trackway midlines of left pes (solid line) and left manus (broken line). Dotted line denotes the alternative pes midline including Px footprint.

2) Comparisons to reference trackway of *Breviparopus taghbaloutensis* (Trackway Bre)

A whole sketch of the reference trackway of *Breviparopus taghbaloutensis* is presented in Figure 6 Bre, A, B, C and D. Trackway Bre extends 89 m, but nearly half of the trackway cannot be observed due to covering and destruction from erosion. The trackway is more or less straight and we estimate that it was comprised 51 manus-pes sets before the erosion (Fig. 6 Bre).

The morphologies of the footprints are identical to those of Trackway Tu in terms of overall shape, length and width, as well as claw impressions' shape and number at the anterior rim of well preserved pes prints. Depth of the footprints, absence of claw marks in manus prints, maximum trackway width of the pes and the manus and the value of the trackway ratio are also identical to those of Trackway Tu. Average outward rotation angle of the axis of pes prints is 17° in left pes print and 30° in right pes print. In manus prints, it is 20° in the left and 35° in the right print, respectively. The distance between the center of the manus and pes print is 88 cm, which is much smaller than that of Trackway Tu.

The average rotation angles of pes and manus are slightly smaller than those of Trackway Tu. The stride length is consistently 340 cm, which is much larger than Trackway Tu. Right pace length is smaller than that of left one. The ratio between them is 0.9. It is similar to that of Trackway Tu. The manus trackway midline is about 10 cm right of pes trackway midline.

ICHNOLOGY OF OTHER TURNING TRACKWAYS

1) Turning sauropod trackways from USA and Europe

One sharp turning sauropod trackway was described from the Morrison Formation (Late Jurassic) in Copper ridge, north of Moab, Utah, USA (Lockley, 1990, 1991, Fig. 7A). The turning angle is 66° to the right. Footprint length and width of pes

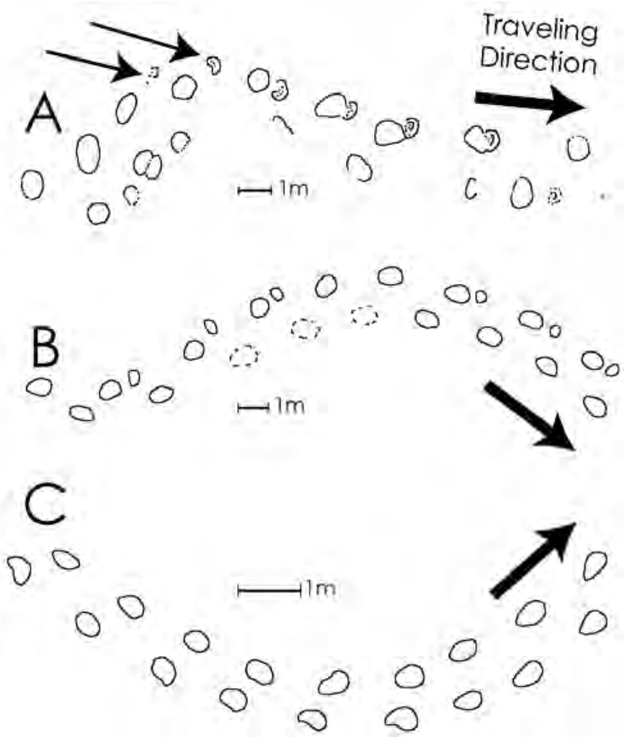

FIGURE 8. Turning sauropod trackways from Europe. **A**, Drawing of the turning part of the trackway from Lommiswil/Oberdorf site, Switzerland, redrawn from fig. 4 of Meyer (1993); **B**, Drawing of the turning part of the trackway from La gosteiros Bay, Portugal, redrawn from Trackway 2 in fig. 2 of Meyer et al. (1994); **C**, Drawing of the turning part of the trackway from Fenoliga, Croatia, redrawn from the fig. 3 of Mezga and Bajraktarevic (1999).

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prints, which we measured from the drawing, are about 85 cm and 65 cm, and the manus prints are roughly 30 cm and 56 cm respectively. Manus prints are often overlapped by pes prints.

We have reconstructed the manus and pes trackway from figure 6.4 and plate 4 of Lockley (1991). We have excluded one shallow print (X in Fig. 7A), which may not belong to the trackway. Eleven pes prints are recognized (Fig. 7B), but the depression labeled as "Px" is problematic. It could be a slipped footprint of left manus (Mx in Fig. 7C) or a redundantly printed left pes print before P7. Twelve manus prints have been reconstructed including an irregular print (Fig. 7C). The footprints labeled as "Mx" and M7 might have been made redundantly at abnormal locomotion.

The trackway midline of left manus and left pes prints are shown in Figure 7D. The dotted line represents the left pes trackway midline if the footprint Px is included as a print of pes. The left manus midline is 23 cm left from the left pes midline at the beginning point of the trackway, and then the gap increases after the print of P5 and M5 set. The maximum gap between two midlines is 90 cm at the point of M7. This maximum value does not change even at the dotted left pes midline. At the last footprint of the trackway, it decreases 23 cm, the same value at the beginning. (Fig. 7D).

Another sharp turning trackway of a large sauropod was reported from the Upper Jurassic (Kimmeridgian) Reuchenette Formation at Lommiswil/Oberdorf site, Switzerland (Meyer, 1993) (Fig. 8A). The turning angle is 61° to the right. Because the manus prints are not preserved completely, we could not reconstruct the whole trackway. However, at the very turning point, the left manus prints are located outside of the left pes midline (indicated with two thin arrows in Figure 8A).

Another sharp turning trackway was reported from the Late Jurassic carbonates in Lagosteiros Bay, Portugal (Meyer et al., 1994) (Fig. 8B). As the manus prints are not completely preserved at the turning point, the detailed analysis is not possible.

One turning trackway of a very small sauropod (40 cm in footprint length) was reported from the Cenomanian limestone bed in Fenoliga, Croatia (Leghissa and Leonardi, 1990; Pavlovec and Gogala, 1992; Dalla Veccia, 1994; Mezga and Bajraktarevic, 1999) (Fig. 8C). Mezga and Bajraktarevic (1999) interpreted that the manus prints are almost always overlapped by pes prints in this trackway.

2) Turning proboscidean trackway

To compare the turning behavior of other animals with sauropod, we chose proboscidean trackways because of their similarities of two different animals such as large bodies and long legs. Among proboscidean fossil trackways, turning trackways are very rare. There is only one report of a sharp turning trackway from Japan. This turning proboscidean trackway is from the trampled bed of the Osaka Group (Pleistocene) from the Ishikawa river bed, Tondabayashi, Osaka Prefecture, Japan (Tondabayashi-Ishikawa fossil research group, 1994) (Fig. 9A). The trackway is 8 m long and average footprint length is around 30 cm. Turning angle is 73° to the left. There is one irregular depression (beside footprint no. 7, indicated with thin arrow in Figure 9A) which is regarded as not belonging to the trackway (H. Taruno, personal communication, 2009). Thus, manus prints are always overlapped completely with pes prints. The trackway midlines of pes and manus are all same.

Okamura (2000) reported one trackway of a turning modern Asiatic elephant (Fig. 9B). In this trackway, manus prints are overlapped completely or partially by pes prints. The length of pes and manus imprints are 40cm. Turning angle is 21° to the right. There is no gap between trackway midlines of pes and manus imprints at the beginning and at the end of the trackway. But at turning point, manus trackway midline is at the right of pes one. It is the opposite direction of the gap compared with right turning trackways of large sauropods (e.g., Figs. 7A and 8A).

DISCUSSION

The morphological features of pes and manus prints of

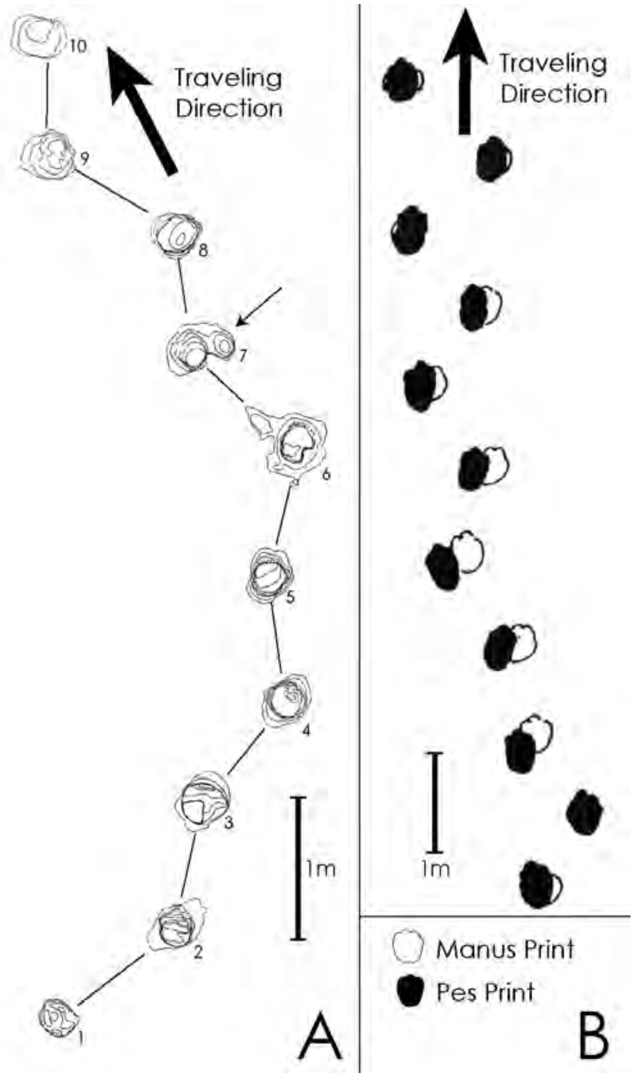

FIGURE 9. Turning proboscidean trackways. **A**, Turning proboscidean trackway from the Osaka Group (Pleistocene), Japan (Tondabayashi-Ishikawa Fossil Research Group 1994); **B**, Drawing of the turning part of the trackway of modern Asiatic elephant taken from Trackway No.13 in Okamura (2000 : p. 163).

Trackway Tu are the same as those of Trackway Bre. Therefore the Trackway Tu is assigned to *Breviparopus taghbaloutensis*. The important ichnologic feature of Trackway Tu is that the trackway midline of pes and manus imprints are different each other. The gap between them increases abruptly at the turning point (Fig. 5C). It is interpreted that originally the trackmaker had a walking habit such as the manus trackway midline was about 40 cm to the right from pes trackway midline. At the turning point, the manus trackway midline is situated about 46 cm more to the right, making an 86 cm difference. After the turn, it returns to normal. A similar phenomenon is observed in the turning trackway from Utah, USA (Fig. 7D), and from Switzerland (Fig. 8A).

In automobile engineering, the gap of the trace of the front and rear wheels at the turning point of a four wheel vehicle is known as “off-tracking.” This phenomenon occurs at the turning point of the vehicle (e.g., Abe, 2008). Mostly, the turn of the vehicle is controlled by front wheel steering angle. When a right turn is made, the trace of the front wheel is at the left of the trace of the rear wheel. With left turn, it is the opposite. The value of the off-tracking gap becomes larger in the case of longer vehicles and sharper turns. The direction of the off-tracking gap depends on which wheels steer. For example, a rear wheel steering forklift makes the opposite gap direction of off-tracking trace. When a forklift makes a right turn, the trace of front wheel is at the right of the trace of rear wheel.

We interpret that the large sauropod manus-pes trackway midline gap at the turning point is analogous to the off-tracking phenomenon of a turning front wheel steered vehicle. And from this basis, we also estimate that the walking direction of large sauropod is controlled mainly by forelimbs, not by hindlimbs.

From the same analogous points of view, we estimate that off tracking phenomenon becomes more apparent with animals that have long gleno-acetabular distance, such as large sauropods. The trackmaker of the Croatian material is a very small sauropod which has short gleno-acetabular distance compared to large sauropods. And also, we suggest that this small sauropod’s hindlimbs worked to steer the body together with the forelimbs. These might be the reasons why there is no clear off-tracking evidence in this material.

In the turning proboscidean trackways, off-tracking does not happen (Fig. 9A), or it happens in the opposite direction as with the case of forklifts (Fig. 9B). We interpret that proboscideans may have used a combination of front and hindlimbs to turn their bodies (Fig. 9A) or primarily hindlimbs (Fig. 9B).

Proboscideans have a large skull and a long nose just in front of their forelimbs. The center of mass is positioned at slightly anterior part of the trunk in proboscideans, and at the posterior part in large sauropods (Alexander, 1989). We estimate that less graviportal limbs are more suitable to steer the body while traveling. In large sauropods, the orientation of the body was mainly controlled by less graviportal forelimbs. In contrast, in proboscideans, less graviportal hindlimbs are also capable of controlling orientation.

Large sauropod dinosaurs had long forward extended necks, long tails suspended behind the body, and large body weight. Their body required themselves tremendous momentum to turn. Small sauropods which have relatively short necks and tails, as well as proboscideans with short necks and tails might have had physical ease when steering the body compared to large bodied sauropods. At the turning point, large sauropods might have had to overcome their bodies’ forward momentum in order to change direction. These differences may affect the appearance of the off-tracking phenomenon in the trackways.

Further study and comparison regarding the appearance of the off-tracking phenomenon in quadrupedal animal turning trackways would be fruitful in order to understand the kinematics of the animal. Especially the relationships between the position of the center of mass of each trackmakers and the usage of the limbs to steer the body are very important keys to investigating the locomotion. Simulation using physical methods of automotive vehicle dynamics would be useful to reconstruct the locomotion of extinct animals.

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