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[Original report]

Reconstruction of the low-heeled posture of *Tarbosaurus* based on an enigmatic V-shaped footprint of a large theropod

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Abstract

Well-preserved theropod footprints frequently exhibit an enigmatic V-shaped configuration, in which the rear of the impression of digit IV is positioned behind the impression of digit III. However, the interpretation of such footprints remains uncertain. The objective of this study was to use the pedal skeleton of *Tarbosaurus* and an enigmatic V-shaped footprint attributed to *Tarbosaurus*, which were found in the same Nemegt Formation (Upper Cretaceous) of the Bugin Tsav locality in Mongolia, to clarify how such footprints were printed. First, a flexibly articulated model of the *Tarbosaurus* pedal skeleton was constructed. Then, a pedal skeletal posture that created a sole outline closely resembling that of the footprint was determined. The pedal posture represented (1) touchdown of the most proximal IP joints and the more distal phalanges of digits II-IV, (2) metatarsals II-IV at a very low angle (<30°) to the ground, and (3) maximum adduction and plantar flexion of the fourth MP joint. Furthermore, experimental simulations revealed that the low inclination of the metatarsals was essential for the remarkable adduction of digit IV because of the skeletal structure of the heads of metatarsals II-IV.

Key words: Bugin Tsav, low-heeled posture, Mongolia, *Tarbosaurus*, theropod footprint

Introduction

Well-preserved theropod footprints frequently exhibit enigmatic V-shaped outlines (Hitchcock, 1858; Ishigaki, 1985, 1988; Demathieu, 1990; Thulborn, 1990; Avanzini, 1998; Lockley *et al*., 1996, 2003, 2007; Hunt *et al*., 2000; Gaston *et al*., 2003; Diedrich, 2004; Gierlinski *et al*., 2004; Clark *et al*., 2005; Ishigaki *et al*., 2009; Niedźwiedzki, 2011). These V-shaped outlines indicate incomprehensible positions of the digital impressions, in which the proximal end of the impression of digit IV is positioned behind the impression of digit III (Fig. 1). Furthermore, the following features can be observed: the proximal ends of three digital impressions are placed in a specific order (i.e., IV, II, and III) from back to front; the impressions of digits II, III, and IV have two, three, and four digital pad impressions, respectively; and the impressions of digit IV are often slightly convex laterally.

The interpretation of such footprints remains uncertain, particularly with regard to the pedal posture of the trackmaker. Footprints and body fossils are rarely found in the same formation at the same locality (Ishigaki *et al*., 2009), and therefore, it is often difficult to assign footprints to specific trackmakers and to reconstruct their pedal postures based on the footprints. However, there have been recent reports of discoveries in Mongolia of many dinosaur footprints in localities containing dinosaur body fossils (Currie *et al*., 2003; Ishigaki *et al*., 2009). For example, a *Tarbosaurus* skeleton and large theropod footprints, probably made by *Tarbosaurus*,

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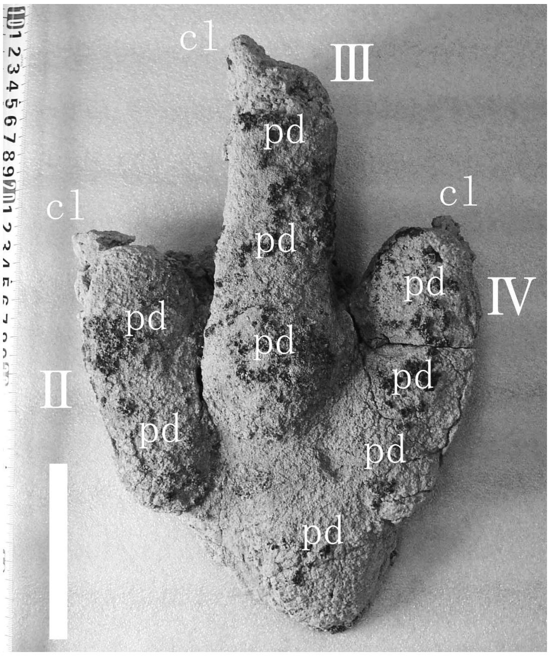

Fig. 1. Enigmatic V-shaped footprint of a large theropod from Shar Tsav, Mongolia (H.M.N.S. accession number 96-12-29). II-IV, digit II-IV impressions; pd, pad impression ; cl, claw impression ; scale bar, 10 cm.

Fig. 2. Map showing the location of Bugin Tsav, Mongolia.

were found in the Nemegt Formation (Upper Cretaceous) in the Bugin Tsav locality of Mongolia (Fig. 2) by the Mongolia-Hayashibara expedition (Suzuki and Watabe, 2000 ; Ishigaki *et al*., 2009 ; Watabe *et al*., 2010). This study reconstructed the pedal skeleton of *Tarbosaurus* in its touchdown phase based on a large theropod footprint attributable to *Tarbosaurus*, which has the rear of the impression of digit IV positioned behind the impression of digit III.

Materials and Method

Tarbosaurus skeleton

The large *Tarbosaurus* skeleton used for this study (Fig. 3, 4A, B) was excavated from the Nemegt Formation (Upper Cretaceous) at the Bugin Tsav locality by the Mongolia-Hayashibara expedition in 1995 (Suzuki and Watabe, 2000). The left pedal skeleton was prepared in the Hayashibara Museum of Natural Sciences (H.M.N.S.) of Japan (H.M.N.S. accession number 97-21-47 ; Matsumoto *et al*., 2010). A juvenile pedal skeleton of *Tarbosaurus* (H.M.N.S. accession number 2006-04-001) was used as a reference for the consideration of ontogenetic changes in the *Tarbosaurus* pes (Fig. 4D).

Footprints

The Bugin Tsav locality identified in this study includes the Bugin Tsav II locality of Ishigaki *et al*. (2009). The occurrence of large theropod footprints, assumed to be made by *Tarbosaurus*, have been reported from the Nemegt Formation in the Nemegt (Currie *et al*., 2003) and Bugin Tsav localities (Ishigaki *et al*., 2009). At other localities in the Nemegt Formation of Mongolia (e.g., Khermeen Tsav, Shar Tsav, and Yagaan Khovil), many other large theropod footprints have been found (Ishigaki *et al*., 2009 ; Watabe *et al*., 2010). These previous findings were used as references for selecting the clearest footprint (e.g., Figs. 1, 5F-G). Of the large theropod footprints found at the Bugin Tsav locality by the Mongolia-Hayashibara expedition (Fig. 5A-E), the best-preserved V-shaped example (H.M.N.S. accession number 2006-04-670) attributable to *Tarbosaurus* was used for this study.

Method

A flexibly articulated model of the pedal skeleton of *Tarbosaurus* was constructed using replicas of the original bones (Fig. 6) ; however, the skeleton of digit I was not reconstructed because the footprint does not contain its impression. Cartilage in the digital joints was not reconstructed either because the observed gaps between the articulated original phalanges of *Tarbosaurus* were very small (less than several millimeters) compared

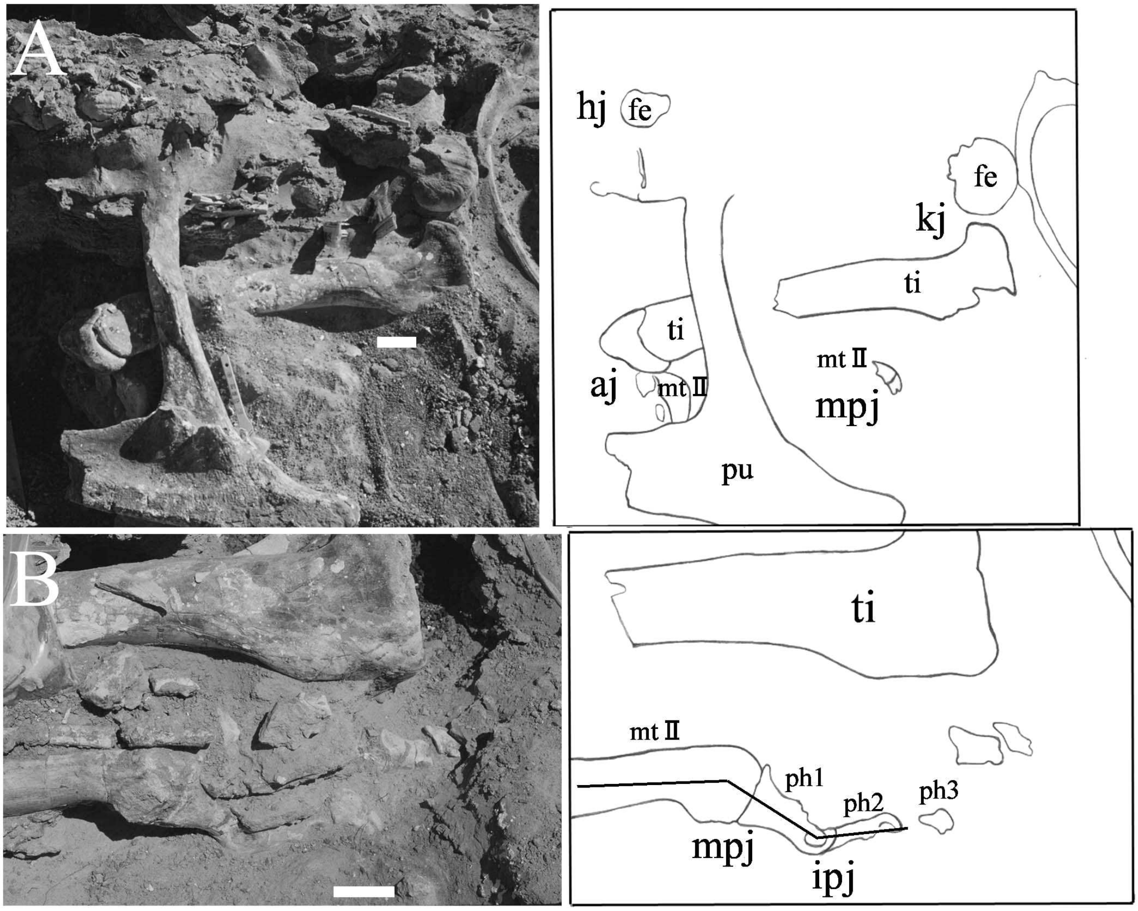

Fig. 3. Mode of occurrence of a large *Tarbosaurus* skeleton from the Bugin Tsav locality. A, medial view of left hind limb on the bed ; B, medial view of left pes on the bed ; left, photographs ; right, outline drawings of photographs ; pu, pubis ; fe, femur ; ti, tibia ; mt II, metatarsal II ; ph1-3, first to third phalanx ; hj, hip joint ; kj, knee joint ; aj, ankle joint ; mpj, MP joint ; ipj, IP joint ; scale bar, 10 cm.

Matsumoto Fig 3. Width 150 mm

with the phalangeal lengths, which controlled the results of this study. Then, a pedal skeletal posture with a sole outline similar to that of the enigmatic V-shaped footprint was simulated for various standing postures of the model. However, this examination presupposes that the digital impressions reflect grounded digital bones.

Descriptions

Tarbosaurus skeletons

The total body length of the *Tarbosaurus* used for the examination is estimated to be approximately 7 m. During excavation, the skeleton was found almost articulated in a posture with the head thrown back and the backbone arched. Its left articulated hind limb indicated the knee joint in flexion, the ankle joint in full dorsiflexion (extension), the second MP joint in plantar flexion, and the proximal IP joint of digit II in dorsiflexion (Fig. 3A, B). The gaps between the articulated phalanges were very small (less than several millimeters).

The pedal skeleton, which is 950-mm long from the proximal end of metatarsal III to the tip of digit III, is completely preserved (Fig. 4A). Digits II-IV measure 350, 400, and 350 mm, respectively. The third MP joint and all the IP joints of the pedal skeleton are hinge joints. The second and fourth MP joints are condylar or ellipsoidal joints (Fig. 4B, C). The fourth phalanx at the end of digit III points slightly medially because the head of the third phalanx of digit III faces anteromedially (Fig. 4A). A line connecting the tips of digits II and IV passes

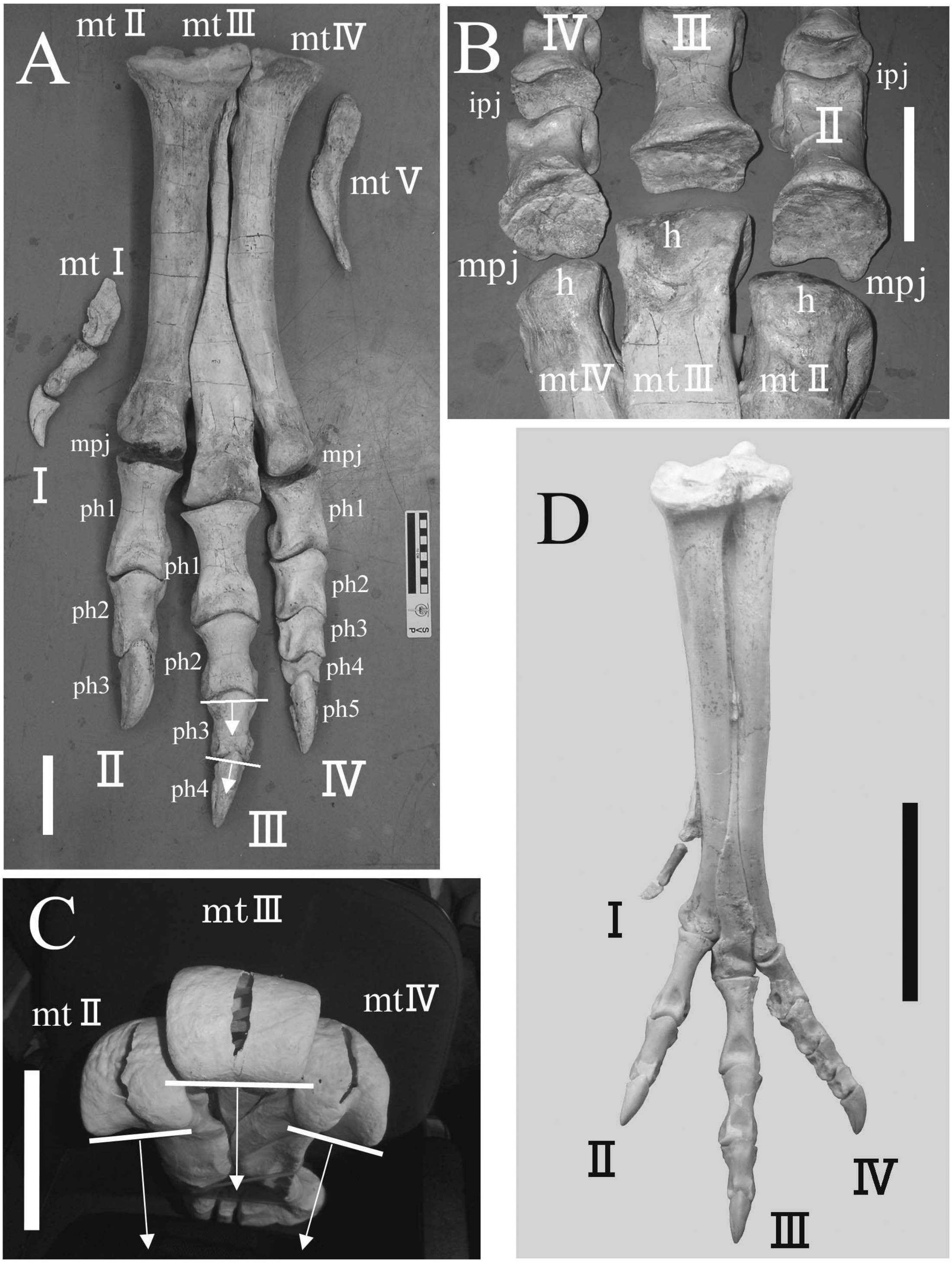

Fig. 4. Pedal skeletons of *Tarbosaurus*. A-C, adult left pes (H.M.N.S. accession number 97-21-47 ; Matsumoto *et al.,* 2010) ; D, dorsal view of a juvenile left pes (H.M.N.S. accession number 2006-04-001) with a restored third phalanx (ungual) of digit II ; A, dorsal view of articulated skeleton ; B, articular surfaces of MP and IP joints ; C, distal view of heads of articulated metatarsals II to IV (replicas) with the longitudinal slits on the heads, which are eyelets for the passage of elastic cords of a flexibly articulated model ; mt I-V, metatarsals I-V ; I-IV, digits I-IV ; ph1-5, first to fifth phalanx ; h, head ; mpj, MP joint ; ipj, IP joint ; arrows, directions of articular surfaces ; scale bar, 10 cm.

Matsumoto Fig.4. Width 150 mm

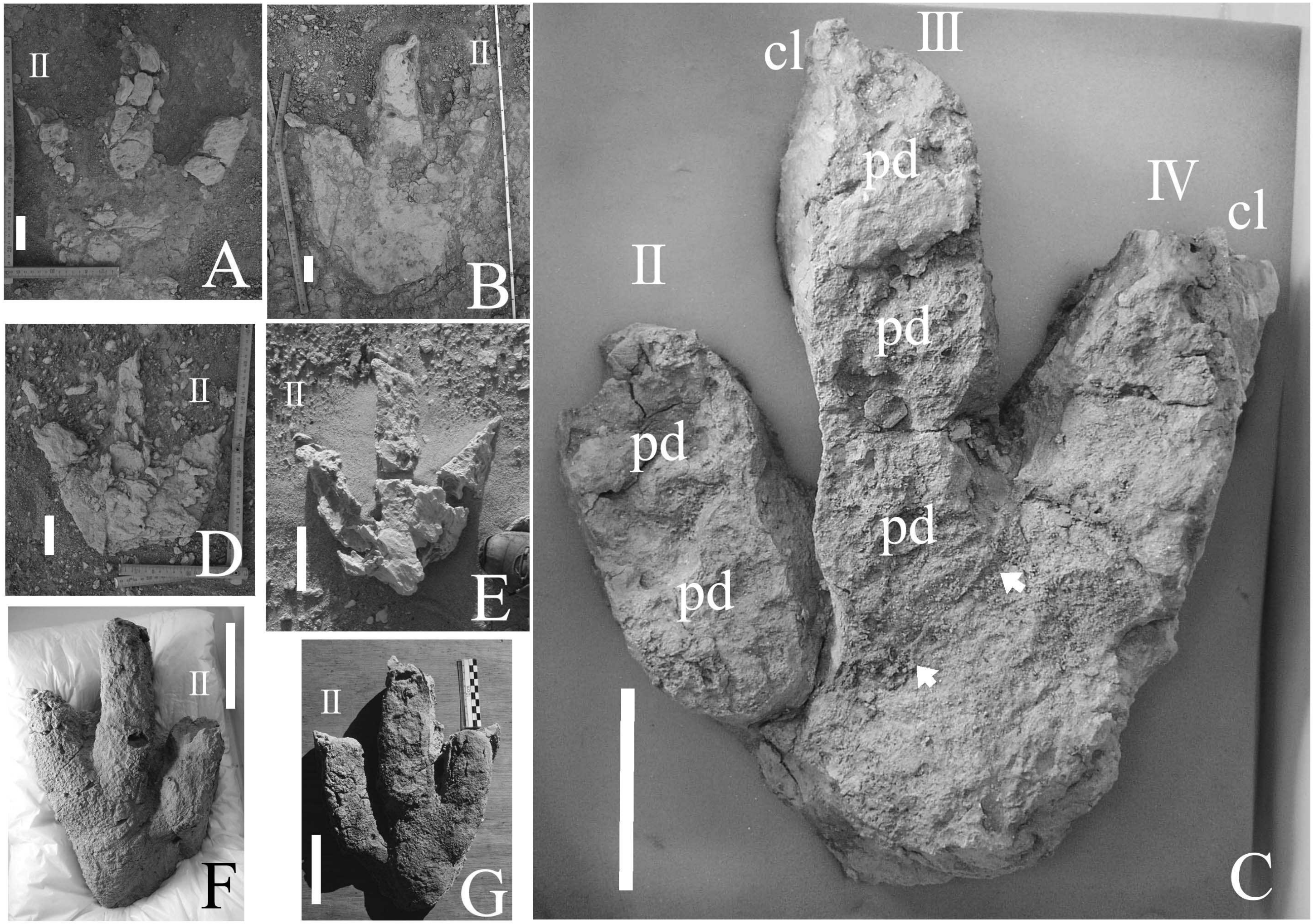

Fig. 5. Large theropod footprints from the Nemegt Formation of Mongolia. All are natural casts of footprints attributable to *Tarbosaurus*. II-IV, digit II-IV impressions ; pd, pad impression ; cl, claw impression ; scale bar, 10 cm ; A-E, footprints from Bugin Tsav ; F-G, footprints from Shar Tsav (H.M.N.S. accession number 96-12-30, no number) ; C, plantar view of the well-preserved left pedal cast used for the reconstruction of the pedal posture of *Tarbosaurus* (H.M.N.S. accession number 2006-04-670) ; arrows, the boundary between the impressions of digits III and IV. The impressions of digits III and IV indicate a V-shaped outline.

Matsumoto Fig. 5. Width 200mm

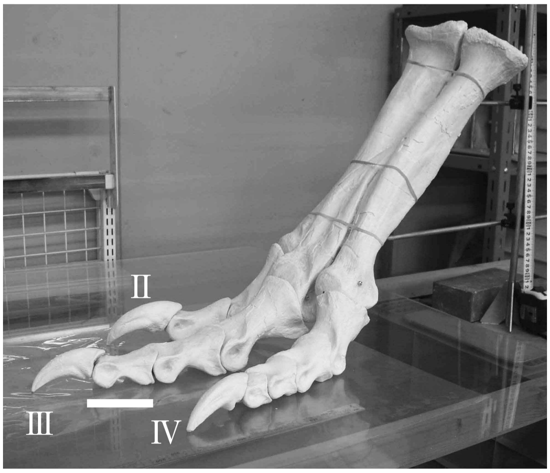

Fig. 6. Flexibly jointed replica of the left pedal skeleton of *Tarbosaurus*. Digit I is not reconstructed. II-IV, digits II-IV ; scale bar, 10 cm.

through the middle of the third phalanx of digit III. However, that of a juvenile pes skeleton, which is approximately 400-mm long, passes through the head of the second phalanx of digit III (Fig. 4D).

Footprint

The footprint used for the examination (Fig. 5 C) is an isolated natural cast of a tridactyl footprint 370-mm long, 280-mm wide, and 110-mm thick. The footprint indicates three digital impressions (digits II-IV). The impression of digit II is 180-mm long, 79-mm wide, and it has two digital pad impressions and no claw impression. If there were a claw impression almost as long as those of digits III and IV, the total length of the digit II impression would be approximately 210 mm. The impression of digit III is 250-mm long, 79-mm wide, and it indicates three digital pad impressions and a claw impression pointing anteromedially. The impression of digit IV is 280-mm long, 99-mm wide, and it has a claw impression and no digital pad impression because of poor preservation. The impression of digit IV is slightly convex laterally. Considering the length of the digit II impression with a restored claw impression as 100, the ratio of the lengths of the impressions of digits II, III, and IV is 100 : 119 : 133 (Fig. 7).

The impression of digit II is completely separated from that of digit III by a deep narrow groove. However, the impression of digit IV is set close to that of digit III and it forms a V-shaped outline with the digit III impression ; thus, their boundaries are not entirely clear. On closer inspection, a small perimeter groove linking together the two outlines

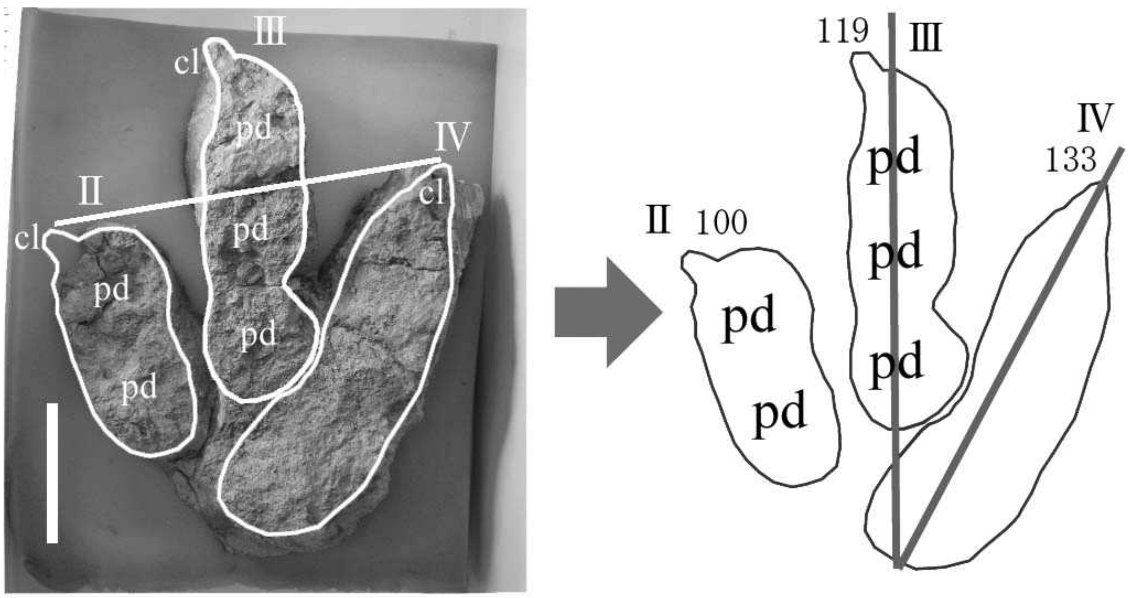

Fig. 7. Photograph and outline drawing of a natural footprint cast. II-IV, digit II-IV impressions ; bold straight lines, axes of digits III and IV ; pd, pad impression ; cl, claw impression ; numbers, ratio of lengths of digits II, II, and IV ; scale bar, 10 cm. The proximal portion of the digit IV impression is placed just behind the digit III impression, making a V-shaped outline.

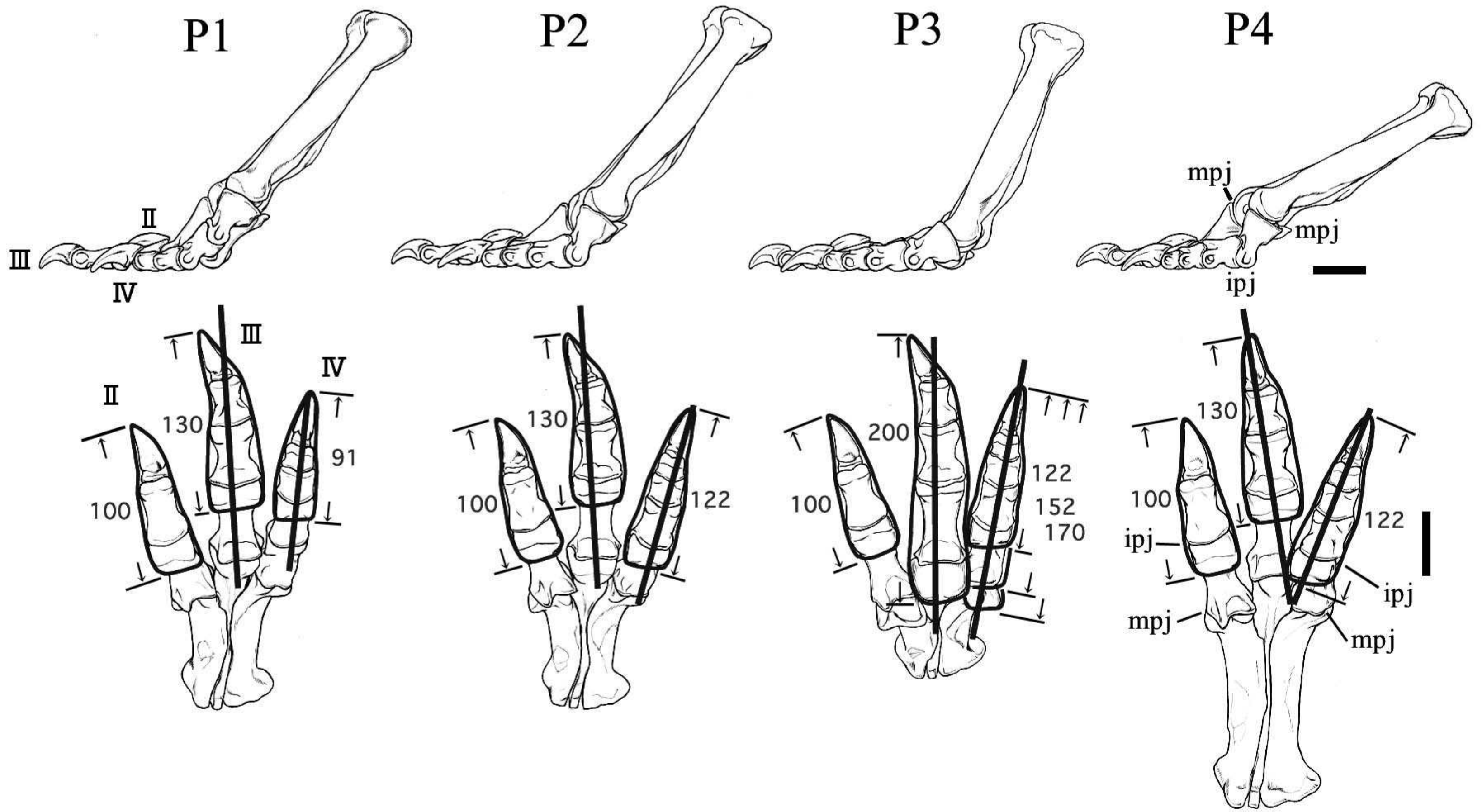

Fig. 8. Four different standing postures of the pedal skeleton and their corresponding sole outlines. P1-4, postures 1-4 ; upper, lateral views ; lower, plantar views ; II-IV, digits II-IV ; bold curved lines, outlines of the grounded sole parts of the skeleton ; bold straight lines, axes of digits III and IV ; mpj, MP joint ; ipj, IP joint ; arrows, portions of measurement ; numbers, ratios of lengths of grounded portions of digits II, III, and IV ; scale bar, 10 cm.

of the impressions of digits III and IV (Fig. 5C, arrows) can be recognized. The impression of digit IV indicates the maximum adduction (a movement bringing pedal parts closer to the axis of pes) of digit IV, and its proximal end is positioned just behind that of the digit III impression. The proximal ends of the three impressions of digits IV, II, and III are placed in that order from back to front. This footprint presents the features typical of the enigmatic V-shaped footprints.

A line connecting the tips of the impressions of digits II and IV passes through a constriction between the two distal pad impressions of digit III, which was probably positioned under the center of the third phalanx of digit III (Fig. 7). This morphology of the footprint resembles those of the large *Tarbosaurus* pedal skeleton (Fig. 4A) and the *Tarbosaurus* footprint MPD 100F/12 reported from the Nemegt locality by Currie *et al*. (2003). Other large theropods—ornithomimids and therizinosaurids—are known from the Nemegt Formation ; however, compared with *Tarbosaurus*, digits II and IV of ornithomimids are shorter (e.g., *Gallimimus*, Osmólska *et al*., 1972), and digits II and IV of therizinosaurids are longer (e.g., *Alxasaurus* ; Russell and Dong, 1993). Therefore, it is inferred that the footprint was made by *Tarbosaurus*.

Results of examination

The ratios of lengths and positions of grounded portions of digits II, III, and IV of the skeletal model were compared with those of the impressions of digits II, III, and IV of the V-shaped footprint of a large theropod to determine a pedal skeletal posture with a sole outline similar to that of the V-shaped footprint. The results are outlined in the following.

Posture 1 (Fig. 8 P1)

In the posture in which all the IP joints of digits II, III, and IV touched down, except the most proximal one of digit IV, the grounded portions of digits II, III, and IV measured 230, 300, and 210 mm, respectively. Considering the length of the grounded portion of digit II as 100, the ratio of the lengths of the grounded portions of digits II, III, and IV was 100 : 130 : 91. Comparing this ratio with that of the lengths of the impressions of digits II, III, and IV of the footprint (100:119:133), the grounded portion of digit IV was found to be considerably short. Furthermore, in this posture, the grounded portions of digits III and IV were positioned mediolaterally and did not form a V-shaped outline.

Posture 2 (Figs. 6, 8 P2)

In the posture in which all the IP joints of digits II, III, and IV touched down and metatarsals II, III, and IV were inclined at approximately 60° to the ground, the grounded portions of digits II, III, and IV measured 230, 300, and 280 mm, respectively. The ratio of the lengths of the grounded portions of the three digits was 100 : 130 : 122. This ratio was more similar to that of the footprint (100 : 119 : 133) than that of P1. The proximal ends of digits IV, II, and III were placed in that order from back to front. This placement was the same as that of the footprint. However, in this posture, the third MP joint prevented the fourth MP joint being adducted because the third and fourth MP joints were positioned mediolaterally to each other. Therefore, the grounded portions of digits III and IV could not form a V-shaped outline.

Posture 3 (Fig. 8 P3)

In the posture in which all the IP joints of the three digits and the third MP joint touched down, the grounded portions of digits II, III, and IV measured 230, 460, and 280 mm, respectively. Exceptionally, when the substrate was as thick as the footprint, the grounded portion of digit IV could measure 350 or 390 mm. The 390-mm length included the fourth MP joint. However, as the fourth MP joint was positioned more proximally than the third MP joint, a very low metatarsal position was essential for the touchdown of the fourth MP joint on a thin substrate. The ratio of the lengths of the grounded portions of digits II, III, and IV was 100 : 200 : 122 (152, 170). Comparing this ratio with that of the footprint (100 : 119 : 133), the grounded portion of digit III was very long. Furthermore, the grounded portions of digits III and IV were mediolaterally situated and never formed a V-shaped outline.

Posture 4 (Figs. 8 P4, 9)

In this posture, all the IP joints of digits II, III, and IV touched down, metatarsals II, III, and IV were inclined at less than 30° to the ground, and the most proximal IP joint of digit IV was placed under the third MP joint by the maximum plantar flexion and adduction of the fourth MP joint. For this posture, the lengths and widths of the grounded portions of digits II, III, and IV were 230, 300, and 210 mm and 76, 82, and 75 mm, respectively. The ratio of the lengths of the grounded portions of the three digits was 100 : 130 : 122. This ratio was the closest of the four postures to that of the footprint (100 : 119 : 133). The proximal ends of digits IV, II, and III were placed in that order from back to front. This placement was the same as that of the footprint. In this posture, the third and fourth MP joints were anteroposteriorly positioned to each other, which allowed the fourth MP joint to be adducted to a maximal degree, and hence, the grounded portions of digits III and IV formed a V-shaped outline. However, the second MP joint could not be remarkably adducted and plantar-flexed. The adduction and plantar flexion at the fourth MP joint meant that the sole of digit IV had slight medial orientation.

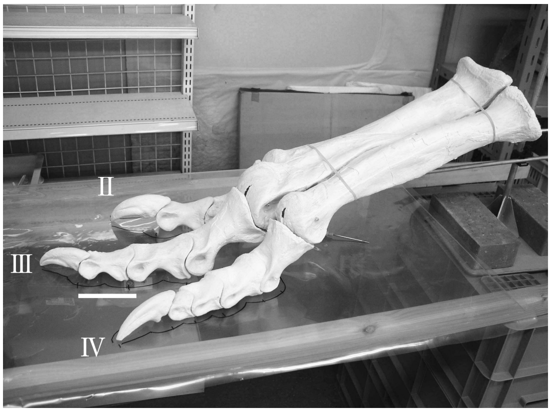

Fig. 9. Dorsolateral view of P4, a low-heeled pedal skeleton of *Tarbosaurus* reconstructed on the basis of an enigmatic V-shaped footprint of a large theropod. II-IV, digits II-IV ; scale bar, 10 cm.

Discussion

Reconstructed pedal posture and its mechanism

The four different standing postures of the *Tarbosaurus* pedal skeleton produced different sole outlines. Of the four sole outlines, only that of P4 closely resembled the footprint outline.

The ratio (100 : 130 : 122) of the lengths of the three grounded digits of P4 was compared with that (100 : 119 : 133) of the lengths of the impressions of digits II, III, and IV of the footprint. This revealed that the ratio (119) of the digit III impression is lower than that (130) of the grounded digit III of P4 by 8%, and that the ratio (133) of the digit IV impression is higher than that (122) of the grounded digit IV of P4 by 9%. The cause of the lower ratio of the digit III impression could be that the proximal end of digit III was blocked, and thus prevented from being printed more posteriorly, by the presence of digit IV placed close behind digit III. The higher ratio of the digit IV impression could be caused by the larger proximal impression of digit IV (width 99 mm) compared with the other digital impressions (width 79 mm). The digital pads of digit IV would have been bigger or printed on a larger scale than those of the other digits. In either case, of the four postures examined, the ratio of P4 is the closest to that of the footprint. In addition to ratio of the lengths of the three digits, the V-shaped placement of digits III and IV and the placement of the proximal ends of the three digits are analogous between P4 and the footprint. Therefore, the *Tarbosaurus* pedal posture, reconstructed based on the enigmatic V-shaped footprint, must have been the low-heeled P4 displaying the following three features :

Feature 1 : touchdown of the most proximal IP joints and the more distal phalanges of digits II, III, and IV (with the most proximal phalanges standing on their heads).

Feature 2 : very low angle of metatarsals II, III, and IV to the ground (<30°).

Feature 3 : maximum adduction and plantar flexion of the fourth MP joint.

Furthermore, a comparison of P2 and P4 revealed a close relationship between Feature 2 (low inclination of the metatarsals) and Feature 3 (adduction of digit IV), and the mechanism relating them to each other. In P2, when the bundle of the three metatarsals rose up, the third MP joint prevented the fourth MP joint being adducted because the third and fourth MP joints were positioned mediolaterally to each other. Conversely, in P4, in which the bundle of metatarsals was tilted at an angle of <30°, the fourth MP joint could be adducted to a maximal degree because the third and fourth MP joints were positioned anteroposteriorly to each other. These experimental results for the two postures indicate that the adduction of digit IV was influenced by the angle of the metatarsals, which was caused by the skeletal structure of the metatarsals with the head of metatarsal III projected most distally (Fig. 4). Because of this structure of the pedal skeleton, the low inclination of the metatarsals was essential for the maximum adduction of digit IV. This mechanism is also applicable to other theropods because the most distally projecting head of metatarsal III is commonly seen in other theropod dinosaurs.

Relationship between pedal phalanges and digital pads

The lengths and widths of grounded digits II-IV of P4 measured 230, 300, and 280 mm and 76, 82, and 75 mm, respectively. The lengths and widths of the impressions of digits II-IV of the footprint measured 210, 250, and 280 mm and 79, 79, and 99 mm, respectively. These measurement results indicate that the three grounded skeletal elements of digits II-IV of P4 are almost the same size as the three impressions of digits II-IV. According to figures indicating the positional relationship between pedal bones and whole pes of ostrich, as illustrated by Matsumoto (2013), the length of the grounded bones of digit III is equal to 70% of the total length of the grounded pads and claw of digit III. Using this ratio, the sizes of the three grounded digital bones of the trackmaker of the footprint can be considered as 70% of those of the grounded portions of the three digits of P4. This means that the widths of the bones and pads of digits II-IV of the trackmaker were 53, 57, and 53 mm and 79, 79, and 99 mm, respectively. This estimation indicates that *Tarbosaurus* had relatively small digital pads on its digital bones because the digital pads of ostrich are two to three times wider than the digital bones (Matsumoto, 2013).

The shape of the groove between the casts of digits II and III of the footprint represents the nature of the substrate that used to be around the footprint. Because the groove is very deep and narrow, it is assumed that the substrate was very deep and sufficiently hard to maintain the shape and prevent subsequent deformation of the footprint. Therefore, it is considered unlikely that the cause of the narrow digital impressions is related to deformation of the substrate.

The digital skeletons of this large *Tarbosaurus* are very thick compared with those of other smaller theropods. If the pads of this *Tarbosaurus* were reconstructed with widths two to three times that of the digital bones, the vacant spaces between the three digits would be lost, and consequently, the movements of the three digits would be very limited. Therefore, it is reasonable to presume that a large *Tarbosaurus* with large pedal claws had smaller pads to preserve digital movements such as grasping. This presumption of small pads also reinforces the presupposition of the examination, whereby the digital impressions are considered to reflect grounded digital bones.

The positions of the recognized pad impressions of digits II and III correspond to those of the IP joints of digits II and III of P4.

Interpretation of P4

Feature 1 : The digital posture of *Tarbosaurus* with the most proximal phalanges standing on their heads and the remaining phalanges touching the ground is the same as that of ostriches (Muybridge, 1957; Matsumoto, 2013). As the musculus flexor perforatus digiti pedis tertii of ostrich inserts on the most distal portions of the body of the first phalanx of digit III and the stout plantar plate (plantar ligament) that covers the head of the first phalanx, the action of this muscle can cause the first phalanx to stand on its head and maintain this posture (Gangl *et al*., 2004 ; Matsumoto, 2013). Although the musculus flexor perforatus digiti pedis tertii of ostrich inserts on the first to fourth phalanges of digit IV, this muscle mainly inserts into and blends with the stout plantar plate that covers the head of the first phalanx. The action of this muscle can cause the first phalanx of digit IV to rise up on its head, and therefore, this digital posture is anatomically possible. This posture increases the distance between the hip joint and the ground. Such a posture means that ostriches, which have the heaviest bodies among birds today, are also the fastest flightless birds as well. Furthermore, the most proximal phalanges of ostriches' pedes stand on their heads and behave like motor vehicle suspension, reducing the load on the pedes during strenuous movement and generating strong vertical movement (Matsumoto, 2013). Therefore, the standing phalanges of *Tarbosaurus* could have acted in the same way as those of ostriches, which suggest that *Tarbosaurus* had a higher movement capability than other digitigrade and plantigrade dinosaurs.

Feature 2 : The inclination of metatarsals II-IV at <30° from the ground indicates *Tarbosaurus* had a very low posture. Because the enigmatic V-shaped footprint of *Tarbosaurus* is an isolated example, it is difficult to infer how *Tarbosaurus* could have moved in a low posture. However, the adoption of a low posture and motion in such a posture is assumed possible for large *Tarbosaurus* because many theropod footprints and trackways with impressions of the complete metatarsals, including footprints bigger than that of *Tarbosaurus*, have been reported (e.g., Hitchcock, 1858 ; Kuban, 1989 ; Pittman, 1989 ; Lockley *et al*., 2003 ; Thulborn, 2001 ; Romero-Molina *et al*., 2003; Nicosia *et al*., 2007; Stanford *et al*., 2007 ; Gierlinski *et al*., 2009 ; Milner *et al*., 2009 ; Wagensommer *et al*., 2012). In these footprints, two footprints of a trackway whose metatarsal impressions are higher than the bottoms of the digital impressions are included (Romero-Molina *et al*., 2003). The postures suggested by the two footprints indicate Feature 2. Osteologically, the knee joints of theropods have been reconstructed in bent positions, rather than in upright postures like those of elephants (Newman, 1970 ; Paul, 1987, 1998) because the knee joints of theropods such as *Tyrannosaurus* have thin femoral condyles that are thought to have been inserted and rotated between the tibia and fibula, as are those of the knee joints of birds. Femurs of theropods such as *Tyrannosaurus* and *Tarbosaurus* are arched and convex dorsally (Paul, 1998), similar to those of birds and tortoises, but unlike those of elephants. The arched femurs of theropods would be suitable for maintaining postures with subhorizontal positions. The proportions of the hind limbs of theropods such as *Tyrannosaurus* and *Tarbosaurus* indicate that they were subcursorial or cursorial animals similar to *Felis* and *Equus* (Coomb, 1978 ; Christiansen, 1998). Trackways with metatarsal impressions of theropods larger than *Tarbosaurus*, knee-joint structures restricting them to bent positions, arched femurs, and subcursorial or cursorial proportions of their hind limbs suggest that theropods had high capacity for exercise, which is consistent with a low posture of *Tarbosaurus*. Moving in a low posture needs greater limb strength than in an upright posture. Furthermore, the heavier the body weight, the more powerful the required limb strength. Therefore, a heavy body in a low posture needs powerful limb strength. However, the characteristics of "heavy body weight" and "low posture" are not easily compatible. Extant elephants, which have the heaviest bodies of terrestrial animals, always drink and sleep in an upright posture and lie down only when necessary (Katugaha, 1993). This postural difference between *Tarbosaurus* and elephants suggests that *Tarbosaurus* was more capable of changing its posture into a low position compared with elephants; it even suggests that *Tarbosaurus* might not have been so heavy for its size.

In the past, there have been few examples of low-angled metatarsal reconstructions based on theropod footprints (e.g., Gatesy *et al*., 1999). However, the results of the examination of *Tarbosaurus* highlight two other types of theropod pedal impressions that may also indicate that they had low postures. The first is the impression of digit I (e.g., Hitchcock, 1858; Gierlinski and Ahlberg, 1994 ; Lockley and Hunt, 1994 ; Lockley *et al*., 1998, 2004 ; Farlow *et al*., 2000 ; Lockley, 2000 ; Thulborn, 2001 ; Moratalla *et al*., 2003 ; Ishigaki *et al*., 2009 ; Nouri *et al*., 2011). For example, the theropod footprint *Tyrannosauripus pillmorei* (Lockley and Hunt, 1994), inferred to have been made by *Tyrannosaurus*, has a 17-cm-long impression of digit I that is connected to the impressions of the distal bodies and heads of metatarsals II-IV. The complete touchdown of digit I of the *Tyrannosaurus* skeleton, as reconstructed by Paul (1996, 1998), must have required low-angled inclination of its metatarsals. Digit I, which is positioned at the rear of birds' feet, is used for grasping, and it is miniaturized and more proximally positioned or lost among running birds (Komiya & Sugita, 2012). This is considered a structural adaptation of the pes for reducing the friction between digit I and the ground to make running easier. Therefore, touchdown of digit I, positioned at the rear of a theropod pes, might indicate an inefficient and unusual touchdown posture. The second type of impression is that of the metatarsal pad under the second or fourth MP joint (e.g., Thulborn, 1990; Olsen *et al*., 1998). As the second and fourth MP joints of theropod dinosaurs are more proximally positioned than the third MP joint, a low metatarsal position is essential for the touchdown of the second or fourth MP joint.

A low posture has the advantage of maintaining balance on substrates soft enough to retain footprints. Furthermore, when heels are positioned just above the substrate, it is easy to regain balance with a quick touchdown of the heels onto the substrate when slipping or losing balance. Because there are many normal footprints without an enigmatic V-shaped placement, the outlines of which are similar to that of P2 (e.g., Hitchcock, 1858; Demathieu, 1990; Thulborn, 1990; Lockley *et al*., 1996; Gierlinski *et al*., 2004), the low posture of theropods must have been a temporary position when walking on an unfirm substrate.

Feature 3: The adducted and medially shifted position of the impression of digit IV was caused by the maximum adduction and plantar flexion of the fourth MP joint. As this joint is a condylar or ellipsoidal joint, it is possible that the adduction of the joint was caused by tendon pull. While no notable adduction and plantar flexion occurred at the second MP joint, which is also a condylar or ellipsoidal joint, it was able to be adducted and plantar-flexed. However, in P4, the first phalanx of digit II was very long for the second MP joint to be adducted and plantar-flexed to its maximal degree. In general, manual and pedal digits are abducted by dorsiflexion (extension) and adducted by plantar flexion. In fact, this mechanism was the cause of the different adductions and plantar flexions at the second and fourth MP joints. In P4, as the adduction and plantar flexion at the fourth MP joint meant that the sole of digit IV had a slight medial orientation, digit IV can be convex laterally because of its plantar flexion. It seems that this mechanism could have been the cause of the slightly lateral convex impression of digit IV.

In P4, plantar flexion of the MP joints and dorsiflexion of the most proximal IP joints were seen. This is identical to the pedal posture of the original skeleton on the bed (Fig. 3B), and the low metatarsal inclination of P4 is consistent with the bent hind limb posture of the original skeleton on the bed. This postural similarity might be accidental; however, pedal postures similar to P4 have been observed among sitting birds (e.g., ostrich; Kokubo, 2001). As the pedal skeletons of *Tarbosaurus* and birds resemble each other osteologically, they could both be forced into similar postures by their skeletal structures and by tendon pulling. Therefore, P4 might be a characteristic posture for bent hind limbs.

Conclusions

The enigmatic V-shaped footprint of *Tarbosaurus*, in which the extremely adducted and medially shifted impression of digit IV lies behind the impression of digit III, suggests that the trackmaker was a *Tarbosaurus* in a low-heeled position with its metatarsals tilted at an angle of $<30°$ to the ground and the most proximal phalanges standing on their heads. The low inclination of the metatarsals was essential for the remarkable adduction of digit IV because of the skeletal structure with the most distally projecting head of metatarsal III. However, this mechanism is applicable to other theropods because the most distally projecting head of metatarsal III of *Tarbosaurus* is common in other theropod dinosaurs. Therefore, studies on other theropod dinosaurs, similar to this study of *Tarbosaurus*, are expected to be the subject of future research.

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