Palaeogeography, Palaeoclimatology, Palaeoecology 293 (2010) 1–8

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Analysis of the acceleration phase of a theropod dinosaur based on a Cretaceous trackway from Korea

Bo Seong Kim [a], Min Huh [b,*]

[a] Mokpo Natural History Museum, 9-28, Yonghae-dong, Mokpo, Jeonllanamdo, 530-839, Republic of Korea
[b] Korea Dinosaur Research Center, Chonnam National University, 333 Yongbong-ro, Buk-gu, Gwangju, 500-757, Republic of Korea

ARTICLE INFO

Article history:
Received 20 May 2009
Received in revised form 29 March 2010
Accepted 14 April 2010
Available online 24 April 2010

Keywords:
Theropod locomotion
Accelerating phase
Cretaceous
South Korea

ABSTRACT

Well-preserved trackways of carnivorous dinosaurs belonging to small-sized theropods have been reported from the Cretaceous Neungju Group in South Korea. The site at Hwasun Seoyu-ri Quarry represents the most extensive and diverse theropod trackway ichnofauna in South Korea. Among them, one theropod trackway is unique in that it demonstrates that theropods were able to increase stride lengths to reach maximum speed, during the running phase. Fossilized track evidence of the acceleration ability of dinosaurs is scant. Despite this, the evidence shown in our findings suggests a theropod running near the limit of its capabilities and shows evidence of a temporary acceleration of speed while running.

1. Introduction

Dinosaur trackways provide direct clues to faunal diversity, individual and group behaviour, and allow for estimating locomotor posture, gait and speed. Since Alexander's methods (Alexander, 1976), or modifications (Thulborn, 1990) of them have been applied to many dinosaur tracks, trackways have been effectively used to assess the biomechanics of dinosaurian locomotion and, in some recent cases, offer new insights (Day et al., 2002, 2004; Henderson, 2003).

The Seoyu-ri Quarry site belongs to the Hwasun Hot Spring Complex (Keumho Hwasun Resort) which is located in the northwest part of Hwasun County (Fig. 1). The discovery of a dinosaur track site from the Cretaceous Neungju Group in Hwasun Seoyu-ri quarry, South Korea, is of considerable importance and value because of the numerous and varied sizes of theropod tracks and the ecological and biomechanical information that they provide (Huh et al., 2006).

The Gyeongsang Basin, assigned to the Gyeongsang Supergroup, is the largest non-marine basin formed during the Cretaceous in what is now South Korea. Several subordinate basins, including the Haenam and Neungju Basins, are also present (Chough and Chun, 1988; Lee, 1999; Chough et al., 2000; Huh et al., 2006).

The Neungju Basin contains the Seoyu-ri Quarry site, and comprises tuffs, lava flows, tuffaceous conglomerates, and epiclastic deposits. Trackway B (Fig. 2) occurs in interlaminated, fine-grained sandstone, siltstone, and mudstone strata (Huh et al., 2006).

This paper describes a unique theropod trackway found in Hwasun Seoyu-ri Quarry, and analyzes gait patterns to infer the trackmaker's locomotor capability.

2. Material and methods

Prior to this study, more than 1500 dinosaur footprints had been found at five levels (L1–L5) in alternating beds of the sandstone, siltstone and mudstone strata at the Hwasun Seoyu-ri Quarry (Huh et al., 2006, Fig. 2). At Level 1 (Fig. 2), 216 footprints were found, altogether comprising 8 trackways. The makers of these trackways were 6 small theropods (FL<25 cm), 1 large theropod (FL>25 cm) and 1 sauropod (Huh et al., 2006).

Among these, theropod trackway B (Huh et al., 2006, Fig. 8) is unique in that it shows that this theropod was able to increase stride length for acceleration during the running Phase. To obtain and analyze information from trackway B, it was necessary to measure and define typical observable dinosaur trackway parameters including: length of footprint (FL), width of footprint (FW), stride length (SL), pace length (PL) and pace angulation (PA) and the digit divarication angles (DD) defined as the interdigital angle between digit II and digits III, III and IV, trackway orientation (TO), and footprint rotation (FR), measured as the inward/outward direction of digit III, are also measured (Fig. 3). These trackway data were measured directly at the fossil site. Measurements could not be made for every footprint in Trackway B. Most measurements taken from each print of trackway B were made directly from the trackway, except for pace angulation. In the case of pace angulation, measurements of two successive paces (PL 1 and PL 2), and the stride length

* Corresponding author. Tel.: +82 62 530 0577; fax: +82 62 530 0578.
E-mail address: minhuh@chonnam.ac.kr (M. Huh).

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doi:10.1016/j.palaeo.2010.04.020

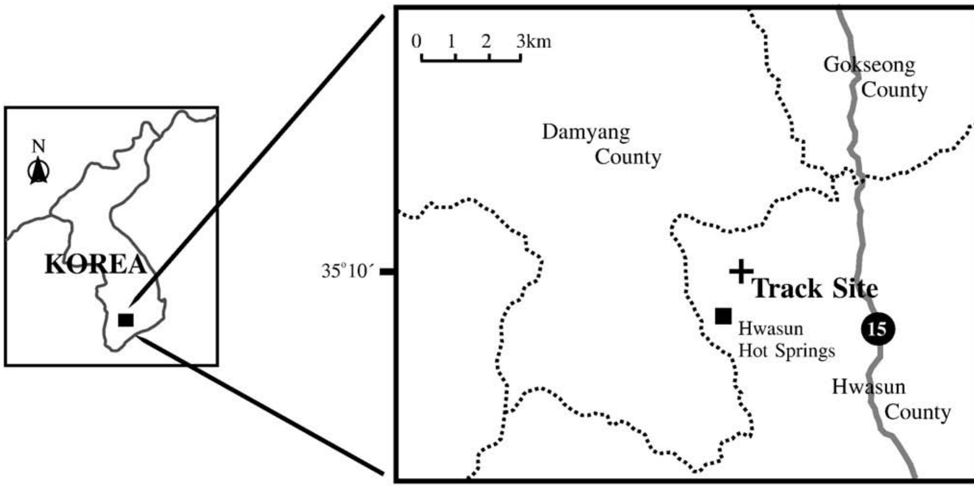


Fig. 1. Location map of the study area. The cross (+) indicates the location of the Hwasun Seoyu-ri Quarry, east of the city of Gwangju (Modified from Kim, 2002).

(SL) that they encompass, were made, from which pace angulation (PA) was calculated by the laws of cosines (Thulborn, 1990) — Eq. (1).

To indicate gaits and estimate absolute speeds of the track-maker of trackway B, dinosaur gaits were determined on the basis of relative stride length (SL/h), that is, the ratio of the dinosaur's stride length to its estimated height at the hip (h) was calculated, prior to estimating the absolute speeds of the dinosaurs (Thulborn, 1990). The stride length can be measured directly from the fossilized trackway, but, as noted below the dinosaur's height at the hip had to be estimated from the multiplying the length of its footprints by various factors that are based on known dinosaurian skeletal foot-limb length ratios (Thulborn, 1990).

Alexander (1976) found that living terrestrial vertebrates change from a walking gait to a trotting or running gait when SL/h reaches a value of 2.0, and suggested that the same was probably true for dinosaurs. In later studies of dinosaur locomotion (Thulborn, 1982; Thulborn and Wade, 1984), this observation was extended to define three dinosaurian gaits including: “walk” (SL/h<2.0), “trot” (2.0<SL/h<2.9), and “run” (SL/h>2.9). Relative stride length is not only an indicator of gaits, but also seems to be one of the best available criteria for appraising and comparing the locomotor performances of dinosaurs (Thulborn, 1984) (Table 1).

It is important that the hip height of the trackmaker is ascertained from the footprint (Rainforth and Manzella, 2007). Estimated hip height at the hip (h) is considered to be the most convenient measure of body size in bipedal dinosaurs (Thulborn, 1990) and is used when estimating relative speeds from trackways. There are various methods for estimating h from fossilized footprints and trackways (Avnimelech, 1966; Alexander, 1976; Lockley et al., 1983; Thulborn, 1984, 1989, 1990; Thulborn and Wade, 1984), and these various predictions are in fair agreement, especially for the smaller dinosaurs and for theropods in general (Thulborn, 1990). Nevertheless, allometric methods pertaining to the foot length in small dinosaurs (<25 cm) may be used as follows: $h = 3.06\text{FL}^{1.14}$ — Eq. (2) is used here, following the arguments of Thulborn (1990).

Since digit III is usually the longest in the theropod foot, the length of a footprint is best measured along or parallel to the axis of digit III (Thulborn, 1990). The foot length of a bipedal dinosaur should include the total length of digit III and the impression of the metapodium (Day et al., 2004). So calculating hip height by this method can be difficult due to the exaggerated length of the foot posterior to digit III (Thulborn, 1990; Day et al., 2004, Fig. 4). Digit III is measured through a convention proposed by Thulborn (1990, p. 83, Fig. 4.9; p.126, Fig. 5.10) relating to the position of the hypex.

Controversy may arise because the hypex length or the impression length of digit III (sensu Thulborn, 1990, Fig 4.9b) is generally less than the true length of the toe by observations of well-preserved theropod prints (Farlow et al., 2000). The proximal end of the digit III impression usually corresponds to the joint between phalanges 1 and 2, not the joint between phalanx 1 and the metatarsal (Farlow et al., 2000). Thus, using the hypex length of digit III or the entire footprint length to estimate hip height can potentially over- or underestimate the trackmaker's speed if the FL is measured incorrectly. Nevertheless, it is possible to measure the location of the hypex relative to entire foot length directly from every print when footprints occur in a single

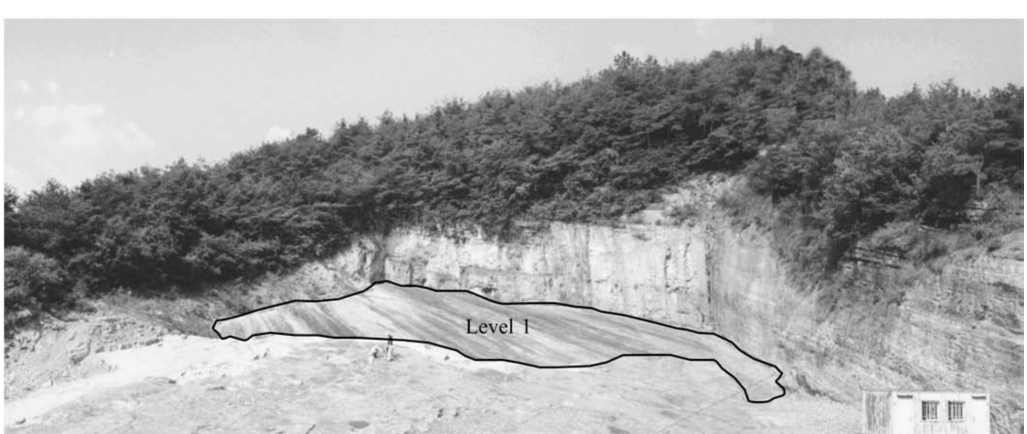


Fig. 2. Photograph showing Level 1 in the Hwasun Seoyu-ri Quarry.

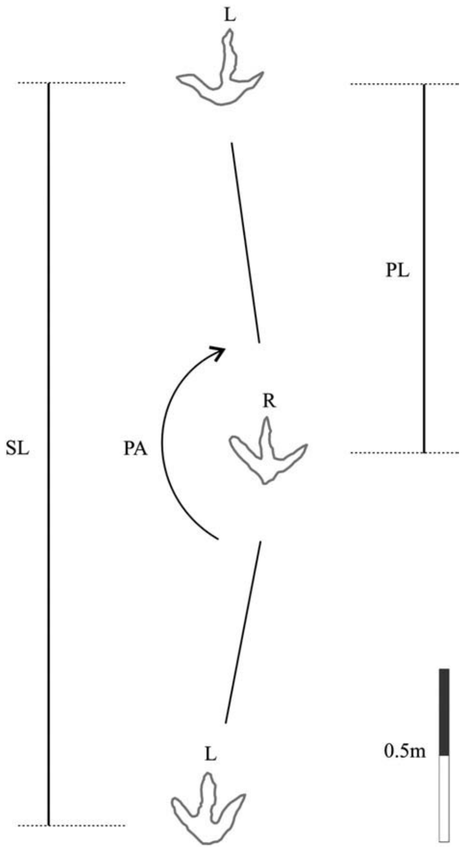


Fig. 3. An illustration of the Hwasun Seoyu-ri Quarry footprints comprising trackway B, identified as left (L) and right (R); PA, pace angulation; SL, stride length; PL, pace length (Adapted from Thulborn, 1990. Fig 4. 9, 11).

trackway (e.g. 28 in trackway B). This study yielded useful measurements using the two different estimates of foot length (the hypex and entire footprint) in order to bracket estimates of hip height.

There are several methods of estimating absolute speeds of dinosaurs, most of which are derived from Alexander's (1976) relationship between SL, h and V; $SL/h = 2.3(V^2/gh)^{0.3}$ (where SL = stride length, h = height at the hip, g = acceleration of free fall) — Eq. (3). These were used to calculate absolute speed for this section of trackway B. For running dinosaurs, the preceding relationship equation may be modified following Thulborn and Wade (1984) and Thulborn (1990) so that $V = [gh(SL/1.8\ h)^{2.56}]^{0.5}$ — Eq. (4). With SL/h between 2.0 and 2.9, the speed may be calculated as the mean of two estimates, using Eq. (3) and (4) (Thulborn, 1984, 1990). This equation does not seem to be seriously affected by variations in the consistency of the substrate (Thulborn, 1990). In these equations all linear measurements are in meters.

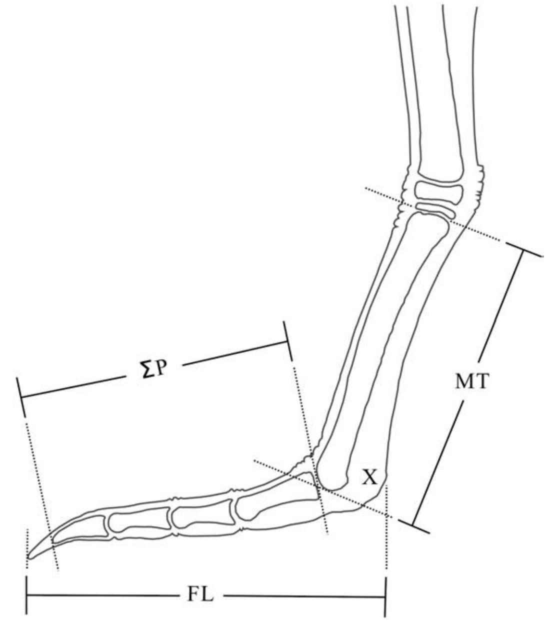


Fig. 4. Diagrammatic comparison of dimensions of the foot of a bipedal dinosaur. ΣP represents the sum of the lengths of phalanges in digit III. FL (footprint length) comprises ΣP together with claw sheath, joint capsules, base of the metatarsus and (perhaps) a fleshy 'heel' at point X. MT (length of metatarsus) is often about the same length as ΣP (Thulborn and Wade, 1984).

3. Results

3.1. Description of trackways

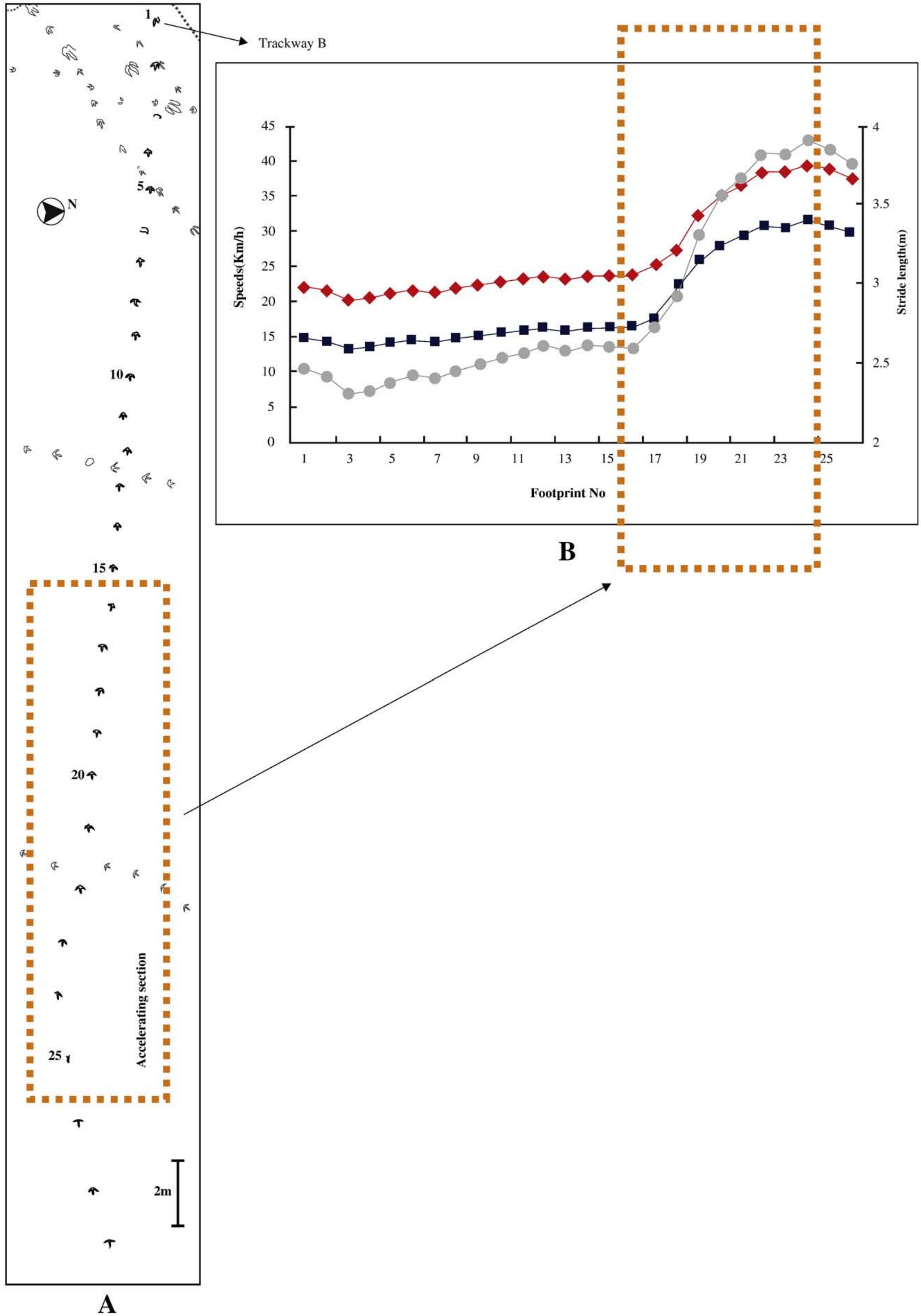
Trackway B is oriented in an east-west direction at Level 1 (Huh et al., 2006, p. 131, Fig. 8). It appears at the western edge of the quarry, and disappears under overburden in the eastern part of the site (Fig. 5). Most of the prints of trackway B are tridactyl, but some appear didactyl. The theropod trackways from L1 exhibits a typical V-shaped theropod footprint with thin, tapering digits (Huh et al., 2006). Huh et al. (2006) did not include photos of multiple tracks in trackway B as we do here (Figs. 6 and 7). Print lengths from trackway B measure 0.17 m to 0.24 m and average 0.21 m, while the print width measures 0.20 m. The average measurement for the length of digit III in trackway B is 0.16 m (Table 2). Digit III is the most likely to be completely preserved as it forms the main weight-bearing toe. Digits II and IV are often incompletely preserved. There are no clearly defined digital pads preserved in any of the footprints, and the prints from L1 are relatively shallow.

Some prints tend to point be rotated slightly inwards at approximately 10° medially from the midline of the trackway: this is defined as 'positive rotation' (Thulborn, 1990, p. 88). However, this is significantly less developed in the part of the trackway associated with an increase in stride. Overall, the shapes of footprints in trackway

Table 1
Summary of estimated maximum speeds of dinosaurian track-makers related to sizes, relative stride length based on trackways.

Ichnotaxa or track-makers	h(m)	V(km/h)	SL/h	Gait	Source	Equation	Geological age
Ornithopods *Wintonopus*	0.29	22.7	5.0	Run	Thulborn and Wade (1984)	3.97MT1.16	Mid-Cretaceous
Ornithopods *Wintonopus*	0.49	28.2	4.9	Run	Thulborn and Wade (1984)	3.97MT1.16	Mid-Cretaceous
Ornithopods *Wintonopus*	0.54	29.4–29.9	4.9	Run	Thulborn and Wade (1984)	3.97MT1.16	Mid-Cretaceous
Theropod *Skartopus*	0.13	13.6–15.9	4.6–5.2	Run	Thulborn and Wade (1984)	3.06MT1.14	Mid-Cretaceous
Q94/48 Theropod	1.16	42.8[a]	4.9[a]	Run	Farlow (1981)	4FL	Cretaceous
Q94/48 Theropod	1.16	43.6	4.9[a]	Run	Farlow (1981)	4FL	Cretaceous
Theropod	1.92	24	2.9	Run	Irby (1996); Hutchinson (2005)	4FL	Jurassic
Trackway B	0.73	39.5	5.4	Run	Kim (2002)	3.06MT1.16	Late-Cretaceous
Trackway B*[b]	0.98	31.4	4	Run	Kim (2002)	3.06MT1.16	Late-Cretaceous

[a] Trackway identification numbers and estimates taken from Farlow (1981).
[b] Values of trackway B*'s h are estimated from the average FL (m) (km/h).



Trackway B
N
1
5
10
15
20
25
Accelerating section
2m
A
Speeds(Km/h)
Stride length(m)
Footprint No
B

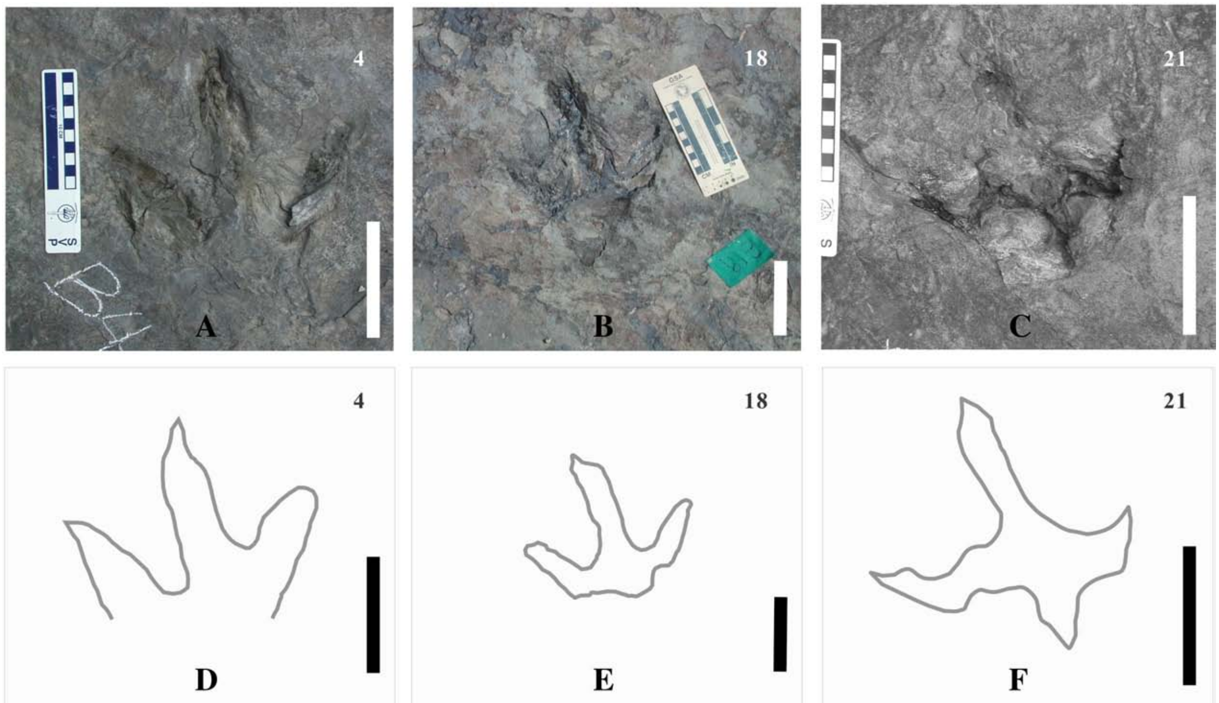


Fig. 6. A–C) Photographs of theropod tracks from trackway B from Hwasun Seoyu-ri Quarry. D–F) Sketch of footprints of trackway B, scale bar represents 0.1 m (Numbers in each photo indicate footprints from trackway B).

B show different degrees of interconnection between the digital impressions, including the total length of digit III and the impression of the metapodium (Day et al., 2004). The depth and clarity of the footprints tend to become shallower and more poorly defined along the trackway. This may be related to the amount of time that a foot remained on the ground during acceleration.

3.2. Size and speed

The average value of hip height (h) of the maker of trackway B, calculated by the different formulae, is 0.9 m (Huh et al., 2006). Using an h value of 0.9 m, the estimated speed for trackway B, with a minimal relative stride length at 2.3, indicates a speed of 11.5 km/h. The maximum relative stride length of 4.2 indicates a speed of 25.7 km/h (Huh et al., 2006). However, Huh et al. (2006) miscalculated these speeds due to computational errors in calculating the speeds. Corrected computations, assigning the theropod an h value of 0.9 m, suggest speeds of between 15.1–33.6 km/h.

Despite the arguments concerning how to define the length of a fossilized footprints to predict reliable proportions of body size from fossilized trackway, it was clear that the use of FL for estimating speed from trackway B allows the use of the two different estimates of foot length to bracket estimates of hip height to interpret the trackmaker's locomotion.

By applying only the length of digit III, the average hip height value was calculated to be 0.73 m using Eq. (2). When using a hip height of only 0.73 m and the minimum relative stride length, the estimated speed during running for trackway B is 20.1 km/h (5.6 m/s) and the relative stride length of 3.2 is just over the trot-run transition speed. At maximum stride length, the maximum speed with a relative stride length of 5.4 is calculated to be 39.5 km/h (11.0 m/s) (Figs. 5 and 8).

Even when the entire pes length of trackway B is used (average FL are 0.21 m), it is then inferred that these dinosaurs used a trotting/running gait throughout the observable portion of trackway B (with a relative stride length >2.0) (Figs. 5 and 9).

3.3. Gait variation

The trackways of bipedal dinosaurs often show surprisingly narrow pace angulation, commonly in the range 160°–170°, and the left and right footprints often seem to fall in a single line, rather than in a zig-zag pattern (Thulborn, 1990). However, in rare cases there is evidence of wide- or dual-gauge locomotion in theropod dinosaurs (Lockley and Meyer, 2000; Lockley, 2001; Day et al., 2002).

Theropod trackway B is unique in that it indicates that this theropod increased stride length to accelerate its speed during the running/trotting phase, which extends for about 39.5 m before the acceleration section of this trackway, the tracks showed an irregular pace angulation within the range of 161°–180°. At the beginning of the acceleration phase, the prints of the hindfeet are arranged in a single line, with a pace angulation of 180°. Increasing stride length is shown to correlate with a pace angulation of 180° (Fig. 10).

Thus, as the animal increased their its speed, stride length increased and their its movement was more efficient with their its legs tucked under their its body nearer to the midline, in order to reduce energy loss and instability caused by pronounced lateral sway (Day et al., 2004).

3.4. Locomotion abilities

The Hwasun Seoyu-ri accelerating trackway offers new insights into bipedal dinosaur locomotor ability and suggests that this animal may have been running close to the limit of its capabilities associated with a temporary acceleration of speed while trotting/running.

The ability to use a fast, running gait with an unsupported phase is correlated with the animal's body construction (Thulborn, 1990). That

Fig. 5. A) Map showing distribution of trackway B in L1 at Hwasun Seoyu-ri Quarry (Adapted from Kim, 2002). B) Small theropod dinosaur of trackway B shows acceleration phase from Hwasun Seoyu-ri Quarry. Gray solid circle, stride length; blue solid square, estimated speeds using the average FL; Red solid diamond, estimated speeds using the average hypex.

Fig. 7. Photographs of theropod trackway B from Hwasun Seoyu-ri Quarry. Photo A indicates a typical narrow-gauge theropod trackway. Photo B indicates theropod prints depicting 'accelerating' phases.

small, running dinosaurs clearly used an unsupported phase on in registering this trackway may indicate stride-lengthening with relative stride length ranging from 3.2 to 5.4 (Using FL ranging from 2.5 to 4.0).

There is no certain evidence that any bipedal dinosaurs achieved a relative stride length much greater than 5.0, and it is difficult to imagine that they could sustain a running gait by doing so (Thulborn,

Table 2
Trackway B data from the Hwasun Seoyu-ri Quarry site of the Cretaceous of South Korea.

Trackway length:39.5 trackway width : 42 trackway orientation :N75W															
NO	L/R	FL	FW	PL	SL	FO	L.II	L.III	L.IV	II–III	III–IV	DD(α)	DD(β)	TDV	PA
1	L	17		121	248			15	11	12					180
2	R	20.5	20	126	243										180
3	L			117.5	232										171
4	R			115.8	234		13	15	10	12	14.5	35	50	85	180
5	L	20	22	119	240		11	18	13.5	16	15.5	50	40	90	180
6	R			120	244	10									180
7	L	22	20.5	122.5	242	15	10	18.5	11	19	17.5	40	40	80	171
8	R	19	17.5	120.5	247	5	9	16	10	12	16.5	40	50	90	180
9	L	21	19	126.5	251		10	19	11	16	16.5	45	40	85	171
10	R	19	21	126	255	10				13	16.5	45	55	100	168
11	L	23	19.5	131	258					16	16.5	40	45	85	180
12	R	20	19.5	125	263	10				15.5	15.5	45	55	100	168
13	L	23	19.5	140	259	10				13.5	15.5	38	47	85	161
14	R	18		123	263						12.5		32	32	168
15	L	21	23	140	262		13	17	13	13	14	40	52	92	171
16	R	18		123	261	10		14.5	9.5		15.5		52		180
17	L	17	21.5	139	275	10	18	13.5	12	15	13	41	52	93	180
18	R	23	20	136	294		12	16	9	14.5	16	43	52	95	180
19	L	19	18.5	158	333	10	7	14	10.5	14	14.5	56	44	100	180
20	R	21	18.5	173	358		11	15	10	14.5	13.5	49	41	90	180
21	L	20.5	19	180	370		9.5	14	10	12.5	13	41	52	93	180
22	R	23	22	189	385	10	12	18	14	18.5	16	47	51	98	180
23	L	21	22	186	384	10	9.5	18	14	17.5	14.5	56	39	95	180
24	R	24	23	188	393		12.5	15.5	11	15.5	18	48	55	103	180
25	L	21	18.5	205	387		8	15	12.5	14.5	12	41	40	81	180
26	R	20.5	21	181	378		12	16	10	13	15	44	41	85	180
27	L	22	22.5	194			11	7	13.5	16.5	14	49	51	100	
28	R	21.5	21				12	17	10	11.5	17	48	58	106	
Average		21.0	20.0	145.4	290.7		11.1	16.0	11.3	14.6	15.1	44.6	47.3	89.7	176.5

Measurements. These include: No, footprint number; L/R, indicates left and right prints; FL, footprint length; FW, footprint width; PL, pace length; SL, stride length; FR, footprint rotation; L.II, L.III, LIV, lengths of digit II, III, IV; II–III, III–IV, interdigital length between digit II and III, III and IV; DD(α) and DD(β), interdigital angle between digit II and III, III and IV; TDV, total divarication; PA, pace angulation. Measurements in metres(m).

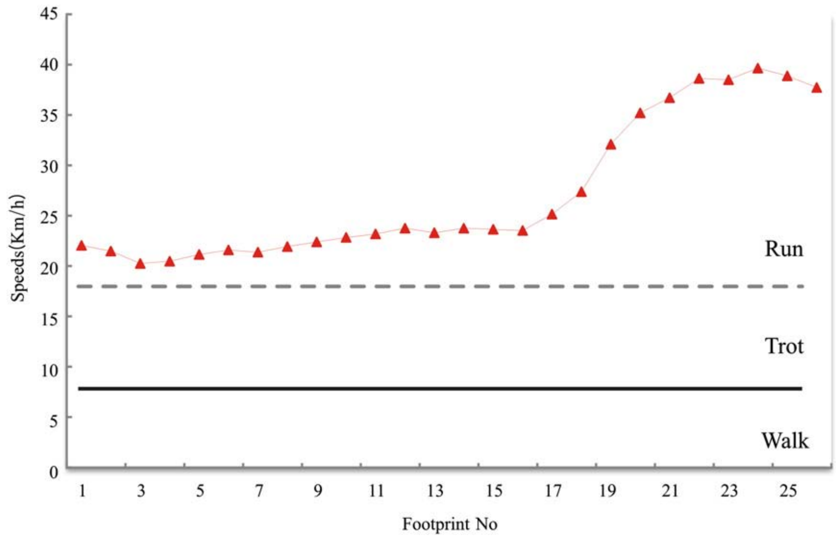


Fig. 8. Estimated speeds for acceleration phase of a single trackway from Hwasun Seoyu-ri Quarry (Hip height is estimated to be 0.73 m, using the average hypex). Each footprint was numbered sequentially. Horizontal lines defining gaits correspond to estimated speed.

1981, 1990; Thulborn and Wade, 1984). Our findings are in agreement with a maximum relative stride length limit for small, fast-running dinosaurs of about 5.0, although they which have also previously been recorded for ornithopods (Table 1, Thulborn and Wade, 1984; Thulborn, 1990).

In a study based on fossilized trackways of bipedal dinosaurs, Thulborn found dinosaur trackways favoured indicated walking gaits except in the case of data for the Lark Quarry site (Thulborn, 1984; Farlow et al., 2000). That the tracks of trotting or running dinosaurs are uncommon suggests that the preferred walking and running gaits represent energetic optima, and that the trot was a transitional gait of high energetic cost (Thulborn, 1984). Behaviourally, this trotting gait or slow running is used by those carnivores that hunt in packs or lie in ambush for unseen prey (Thulborn, 1984).

4. Discussions and conclusion

Alexander's (1976) methods has been used to estimate the gaits and speeds of dinosaurs from trackways since it was first introduced, and modifications (Thulborn, 1990; Henderson, 2003; Rainforth and Manzella, 2007) have been suggested. However, there seem to be some fundamental assumptions that have not been examined in a manner that considers both the skeletal structure and footprint morphology (Rainforth and Manzella, 2007). These criteria cannot be applied very easily to extinct animals such as dinosaurs because it is hypothetical and abstract that the quantification of trackway parameters could be estimated from directly measurable quantities of the trackway. These numbers are not biological laws or limits for the dinosaurs.

Despite the arguments concerning how to estimate reliable the quantification of trackway parameters, this study seems to be one of the best available guides to paleolontological interpretation for the behavioral implications of bipedal dinosaur locomotion.

The Seoyu-ri Quarry, Hwasun-gun, Jeollanam-do, South Korea contains one of the most important and diverse dinosaur track site in the world to document the biomechanics and evolution of theropod locomotion.

Trackway B, characterized by its small size (FL<25 cm), digitigrade posture, and thin and tapering digits, is tentatively assigned to the ichnogenus *Magnoavipes* (Huh et al., 2006). Among them, a single theropod trackway at Level 1 (i.e. L1) is unique in that it suggests that

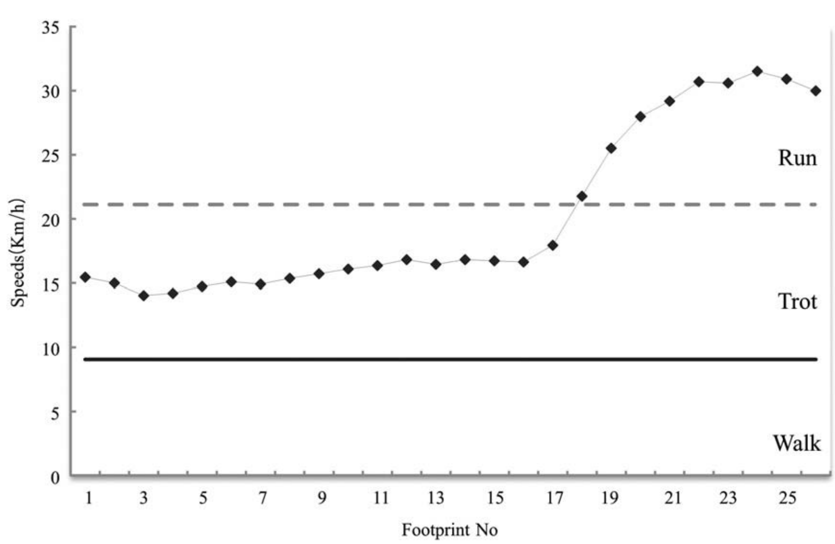


Fig. 9. Estimated speeds for acceleration phase of a single trackway from Hwasun Seoyu-ri Quarry (Hip height is estimated to be 0.98 m, using the average FL). Each footprint was numbered sequentially. Horizontal lines defining gaits correspond to estimated speed.

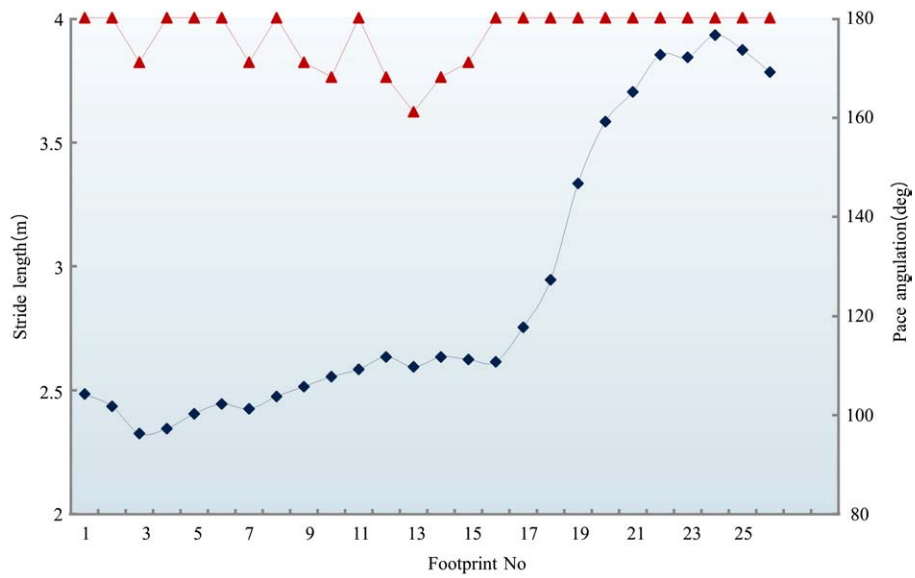


Fig. 10. Small theropod dinosaur trackway (FL <25 cm) shows acceleration phase of the "running" gait from Hwasun Seoyu-ri Quarry, South Korea (blue solid diamond = stride length; red solid triangle = pace angulation) (reproduced from Kim, 2002).

a small theropod (FL<25 cm) was able to lengthen stride in order to accelerate. At the beginning of the acceleration phase, the prints of the hindfeet are arranged in a single line, with pace angulation at 180°. No clearly defined track morphology changes are associated with the acceleration phase during the trotting or running stages.

Fossilized track evidence of the acceleration ability of dinosaurs is scant. Despite this, the evidence shown in trackway B provides new insight into the acceleration phase of small-to-medium bipedal dinosaurs, even if there is no obvious interaction or relationship with nearby trackways.

Acknowledgements

We thank Drs. James O. Farlow (Department of Geosciences, Indiana-Purdue University) and Martin G. Lockley (Dinosaur Tracks Museum, University of Colorado, Denver) for constructive criticisms of an early version of the manuscript. We also thank Donald Henderson (Royal tyrrell Museum of Paleontology, Alberta, Canada) and an anonymous reviewer of the manuscript for their constructive reviews and valuable comments. Finally, we thank the members of the Korean Dinosaur Research Center. This research was funded by a grant from the Korea Science and Engineering Foundation (KOSEF ROI-2008-000-20056-0) and partly supported by the BK21 project of the Korean Government.

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