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Well-preserved theropod tracks from the Upper Cretaceous of Hwasun County, southwestern South Korea, and their paleobiological implications

Min Huh [a,*], In Sung Paik [b], Martin G. Lockley [c], Koo Geun Hwang [d], Bo Seong Kim [d], Se Keon Kwak [d]

[a] *Faculty of Earth Systems and Environmental Sciences & Korea Dinosaur Research Center, Chonnam National University, Gwangju 500-757, Korea*

[b] *Department of Environmental Geosciences, Pukyong National University, Pusan 608-737, Korea*

[c] *Geology Department, University of Colorado at Denver, Denver, CO 80217-3364, USA*

[d] *Korea Dinosaur Research Center, Chonnam National University, Gwangju 500-757, Korea*

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Abstract

Abundant dinosaur fossils including footprints, eggs and nests, teeth, and bones have been found from the Cretaceous nonmarine deposits of Korea. Among them, dinosaur tracks are the most distinctive, and some tracksites are among the most famous in the world. Approximately 1500 well-preserved dinosaur footprints, including more than 60 trackways, have been excavated from the Cretaceous Neungju Group in a quarry in Seoyu-ri, Hwasun County, Jeollanam-do, South Korea. Unlike other dinosaur fossil sites in South Korea, most of the tracks found in the area belong to theropods, especially small-sized theropods. The tracks show significant variation in size, morphology, and divarication. On the basis of morphology and size, the theropod tracks have been classified into three types. The first type is characterized by its small size, wide divarication, and slender digits, which can be more closely compared to *Magnoavipes*. The second type shows slightly thicker digits than the first one and narrow toe impressions and is similar to *Ornithomimipus* or *Xiangxipus*. The footprints of the third type belong to large theropods and display distinct sharp claw impressions. The calculated body sizes of the dinosaurs vary between small theropods with an estimated hip height of 68.4–194.5 cm, and large theropods with a maximum estimated hip height of 260.9 cm. The variety of morphotypes and sizes of the footprints and the calculated body sizes indicate that different theropods with various gaits inhabited in the study area during the Cretaceous. On the basis of the speed and gait analyses, it is inferred that the small theropods in the area were trotting, while the large theropods were walking slowly. The fossil site also shows diverse gaits with unusual walking patterns and postures in some tracks.

Keywords: Cretaceous; Neungju Group; Theropod tracks; Gait habitude

1. Introduction

Since their first discovery in South Korea in the early 1970s, various dinosaur fossils, including fossils of footprints, eggs and bones, have been excavated and reported in the scientific literature (Chang et al., 1982; Yang, 1982; Kim, 1983; Lim et al., 1989, 1994, 2002; Lim, 1991; Lockley, 1991; Lockley et al., 1992, 1997; Yang et al., 1995; Huh et al., 1996, 1997, 1999, 2001, 2003a,b; Yun and Yang, 1997, 2001; Paik et al., 1998, 2001, 2004; Lee et al., 2000a,b, 2001; Paik, 2000; Park et al., 2000; Dong et al., 2001; Huh and Paik, 2001; Hwang,

* Corresponding author.
E-mail address: minhuh@chonnam.ac.kr (M. Huh).

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2001; Huh and Zelenitsky, 2002; Lee and Huh, 2002; Hwang et al., 2002a,b; Park et al., 2003).

These findings suggest that the Korean Peninsula was the preferred habitat of abundant dinosaurs. In Jeollanam-do Province, where Cretaceous deposits are widely distributed, various dinosaur fossils have been reported from Haenam, Boseong, and Yeosu. In the Seoyu-ri area in Buk-myeon, Hwasun County, different types of dinosaur footprints fossils were recognized in 1999 from a quarry inside the Hwasun Hot Spring Complex. Presumably representing the upper tier of the food chain, theropod bone and track fossils had generally been less frequently reported than those of herbivorous dinosaurs (Bakker, 1975; Lockley et al., 1983). At the Seoyu-ri site, however, footprints of theropods occur in very high concentrations. The Seoyu-ri site, with its abundant footprints, as well as its plant fossils, trace fossils and sedimentary structures such as sun cracks and ripple marks, provides interesting material for the study of the behavior of theropod dinosaurs and for studies in the field of paleoecology.

This research describes the theropod footprints found in Seoyu-ri, Hwasun, and examines their gait patterns.

2. Study area

The Seoyu-ri dinosaur fossil site belongs to the administrative district, Mountain 150-1, Seoyu-ri, Buk-myeon, Hwasun County, Jeollanam-do, and is located at the latitude of 35° 10′ 00″ and the longitude of 127° 05′ 30″ (Fig. 1). The area is included in the Hwasun Hot Spring Complex (Keumho Resort) in the northwest part of Hwasun-gun County, which is located on the southeastern slope of a mountain ridge that stretches out from Mudeung Mountain to the northeast (Fig. 1). The dinosaur footprints were found over a wide-ranging surface of a stratum that had been exposed through active excavation in a quarry inside the Hawsun Hot Spring Complex.

Several nonmarine, pull-apart sedimentary basins were formed in South Korea by the northward subduction of the Izanagi Plate during the Cretaceous (Chough et al., 2000). The Gyeongsang Basin is the largest one, consisting of a 9000-m-thick sequence of deposits assigned to the Gyeongsang Supergroup in which innumerable dinosaur tracks occur (Lim et al., 1994; Huh et al., 2003a; Lockley et al., 2006). In the western part of the Gyeongsang Basin, several subordinate basins including the Haenam and Neungju Basins are present (Chough and Chun, 1988; Lee, 1999; Chough et al., 2000). The Neungju Basin containing the Seoyu-ri tracksite consists of tuffs, lava flows, tuffaceous conglomerates, and epiclastic deposits. Most of the volcanic rocks are acidic and their K-Ar ages were provisionally determined as Late Cretaceous (Huh and Paik, 2001; Huh et al., 2001). The Neungju Basin is thus time-correlated with the Yucheon Group of the Gyeongsang Basin.

The Seoyu-ri track-bearing deposits belong to the Jangdong Tuff overlying the Manweolsan Tuff and underlying the

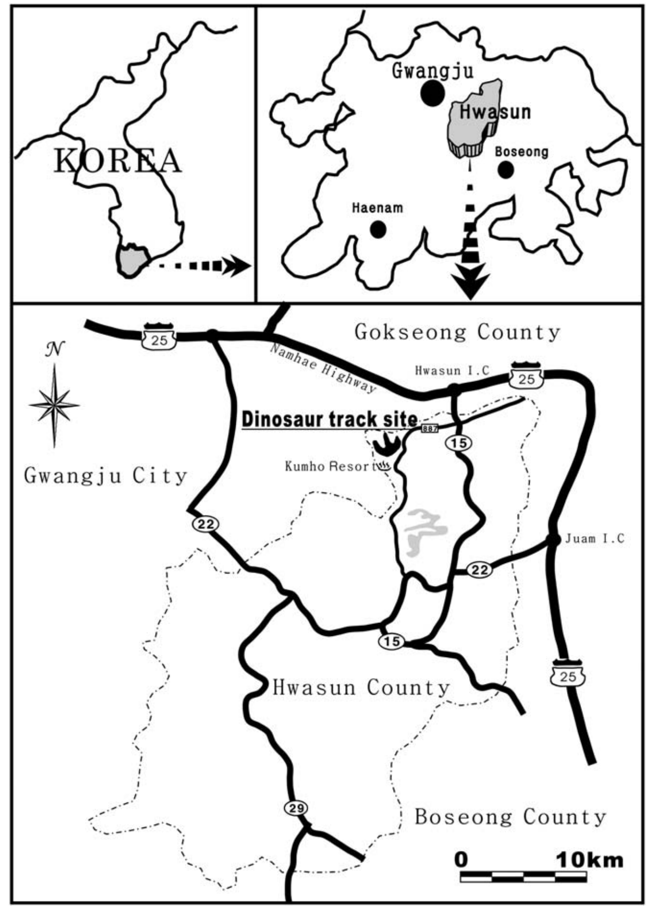

Fig. 1. Location map of the study area, Hwasun County, southwestern South Korea.

Yeonhwari Formation and the Jeokbyeok Tuff. The sedimentology of these units has yet to be studied in detail. We therefore present a brief overview of the lithologies found in approximately 25 m of section in the study area (Fig. 2) and a more section of the sedimentary profile at sites associated with three important levels (L1, L4 and L5: Fig. 3). The Jangdong Tuff consists of tuffs, tuffaceous sandstones, and epiclastic deposits. The dinosaur track-bearing deposits are composed of interbedded medium-grained sandstone-mudstone, interlaminated fine-grained sandstone-siltstone-mudstone, graded tuffaceous sandstone, planar- to cross-laminated fine-grained sandstone to siltstone, interlaminated silty mudstone-mudstone, chert, and lenticular-bedded conglomerate (Figs. 2, 3). Interbedded medium-grained sandstone-mudstone and interlaminated fine-grained sandstone-siltstone-mudstone beds dominate these deposits, and dinosaur tracks mostly occur in the interlaminated fine-grained sandstone-siltstone-mudstone.

Polygonal desiccation cracks are common in the track-bearing deposits. Prismatic mudcracks are often observed and subaerial lenticular cracks (Paik and Kim, 1998) are present in places. Ripple marks are associated with desiccation cracks. They are mostly small scale wave ripples with sub-sinuous crestlines. Invertebrate body fossils are lacking in

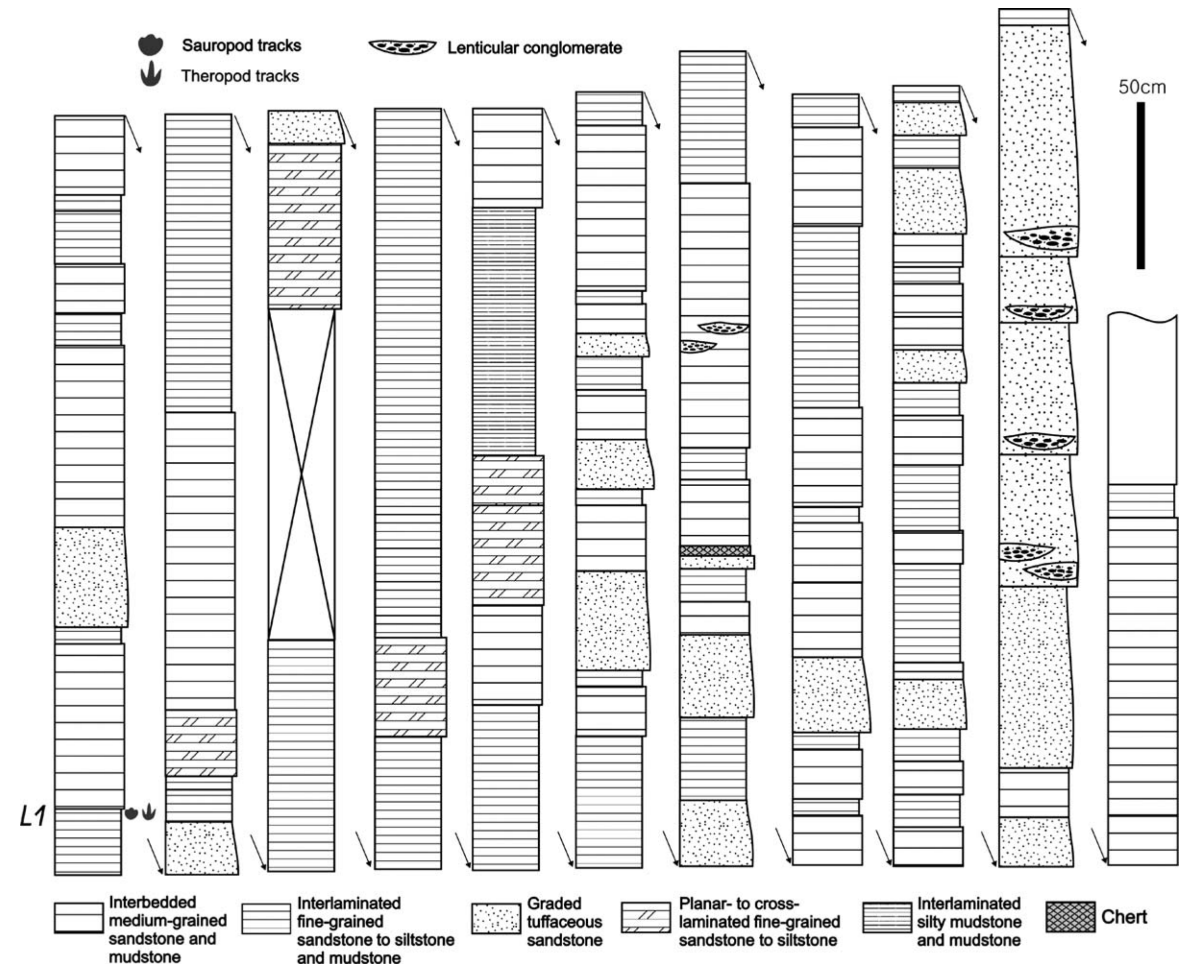

Fig. 2. Stratigraphic sections from the study area, Hwasun County.

the track-bearing deposits, and bioturbation features are very rare. Fragments of carbonized woods are scattered through some tuffaceous sandstone beds. Compared with the palustrine carbonate (pedogenic calcrete) development in the dinosaur track-bearing deposits of the Jindong Formation (Paik et al., 2001; Paik and Kim, 2003), calcretes are not associated with the Seoyu-ri track deposits (see Houck and Lockley, 2006, for further comments on terminology pertaining to various carbonate deposits).

The abundance of polygonal desiccation cracks and small scale wave ripples and the dominance of interlaminated beds of fine-grained sandstone-siltstone-mudstone produced by sheet flooding indicate that the Seoyu-ri track deposits are marginal to shallow lake deposits as is the case with the dinosaur track deposits of the Jindong Formation. Although the lack of carbonates and invertebrate bioturbation indicate that sedimentation rate of the Seoyu-ri track deposits was not low, the common presence of desiccation cracks and subaerial lenticular cracks suggest that alternating depositional and drying periods allowed for the preservation of the tracks. The frequent intercalation of tuffaceous deposits indicates that volcanic activity took place intermittently in the vicinity of the lake during deposition.

3. Dinosaur footprints

3.1. Occurrence

More than 1500 dinosaur footprint fossils were found at five levels (L1, L2, L3, L4, L5) in alternating beds of the sandstone, siltstone and mudstone strata (Figs. 2–11). Among these, 740 footprints form 61 trackways. The makers of these footprints were theropods, ornithopods and sauropods, but the occurrence of theropod footprints is statistically quite high compared to other dinosaur sites in South Korea, comprising 88% of the entire number of footprints. Theropod footprints smaller than 40 cm are most dominant in the study area. The majority of the trackways are also of small theropods, and they are well-preserved.

From L1 level 216 footprints were found that together comprise eight trackways. 205 of the 216 footprints belong to theropods; 199 have a length shorter than 40 cm. In addition

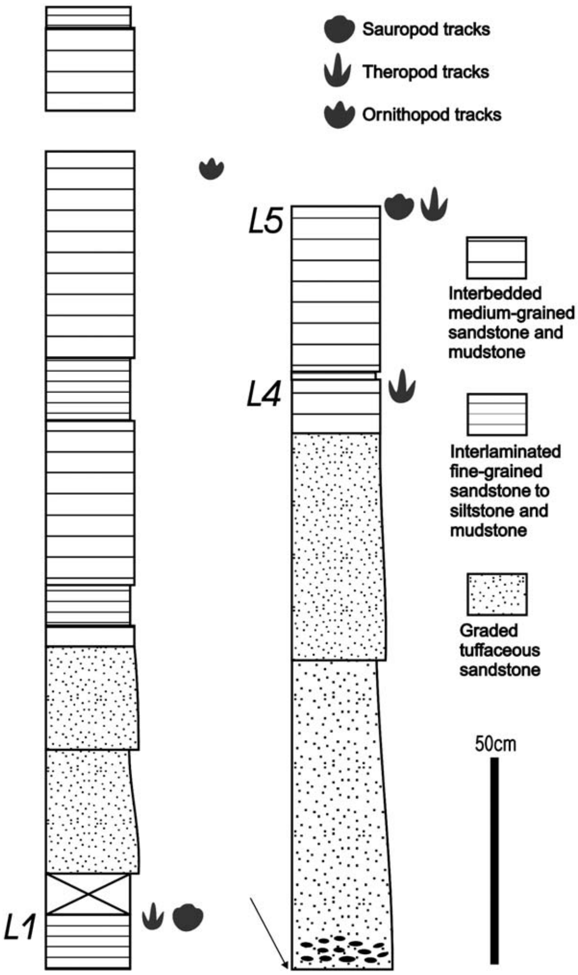

Fig. 3. Detail of stratigraphic sections showing dinosaur track-bearing levels L1, L4, and L5. Compare with Fig. 2.

to theropod footprints, more than ten sauropod footprints occur (Figs. 4, 8).

At L2 level, about 750 dinosaur footprints occur in a dense concentration (Figs. 5, 9). Theropod footprints comprise 73% (61% shorter and 12% longer than 40 cm). Ornithopods comprise 27% but make up 30% of the entire trackways. The length and width of the footprints vary from 11.5 to 56 cm, and 12 to 49 cm respectively, suggesting various different types of dinosaurs inhabited the area (Fig. 7).

At L3 level, 35 dinosaur footprints were found, including several indistinct ornithopod footprints, and one irregular theropod trackway. Preservation is generally good.

At L4 level, we found 129 irregularly distributed footprints. Of these, 124 are assumed to be of ornithopods and 5 of theropods.

At L5 level which is the highest we recorded at least 215 footprints with desiccation cracks. These include 173 theropod and 42 sauropod footprints (Figs. 6, 10). Approximately 24 trackways of theropod footprints were recognized in addition to poorly preserved isolated tracks.

Here we focus on the significance of the theropod footprints from the L1, L2, and L5 levels, where the footprints are well-preserved and the trackways relatively long.

3.2. Theropod footprints

3.2.1. Occurrence

The theropod footprints exhibit various shapes and sizes (Figs. 4–6), and we placed them into two groups, following the size categories suggested by Thulborn (1990): (1) a group of "small" abundant footprints with lengths of 25 to 30 cm, and (2) a group of "large" but less-common tracks with lengths longer than 40 cm (Fig. 7). Although the arbitrary foot length of 25 cm used by Thulborn (1990) to differentiate small and large tracks, may have limited statistical meaning, there does appear to be a natural break in the Hwasun sample, between these two size categories. Moreover it appears that the larger forms were rare (Farlow, 1993).

The small theropod footprints have a narrow length range from 16 to 24 cm. Although most of the tracks are tridactyl some appear didactyl (Figs. 4–6). Most of the footprints indicate a digitigrade, stance (Figs. 4C, 5D, 6C) and the trackways are narrow and straight with a pace angulation of 160–170°. Some trackways extend for about 50 m. The length of the large theropod footprints ranges between 42 and 56 cm without any distinctive trace of the metapodium.

The foot widths (FW) and lengths (FL) are mostly similar (FL/FW proportions between 0.9 and 1.1). However, the large theropod footprints exhibit a more elongated footprint shape with distinctive traces of s sharp claws (Fig. 7). The thickness of the digit impressions and the divarication angles are quite variable. In the case of the small theropods, two divarication ranges predominate (around 50°, and between 80 and 90°). Among the large theropods, the average divarication is 47.6° (Table 1) and the footprints are more close to a V shape.

3.2.2. Trackway description

Among the seven theropod trackways at L1 level (Fig. 8), six are long trackways composed of more than 30 footprints of small (foot length 18.6–22.4 cm), except for trackway D, which has a foot length of 56 cm. Trackway C contains 49 footprints. The trackways exhibit a typical theropod footprint shape with thin, tapering digits. Trackway orientations trends are variable but dominantly towards the north and northeast.

Trackway A is composed of 23 footprints with a stride range of 190–226 cm and relative stride lengths (stride length/hip height) between 1.9 and 2.7 (average 2.2: Table 2). This indicates an intermediate paced gait that is faster than walking but slower than running.

Trackway B is composed of 28 well-preserved footprints. The average pace of this trackway is 145.4 cm. The strides range between 232 and 393 cm. This indicates significant

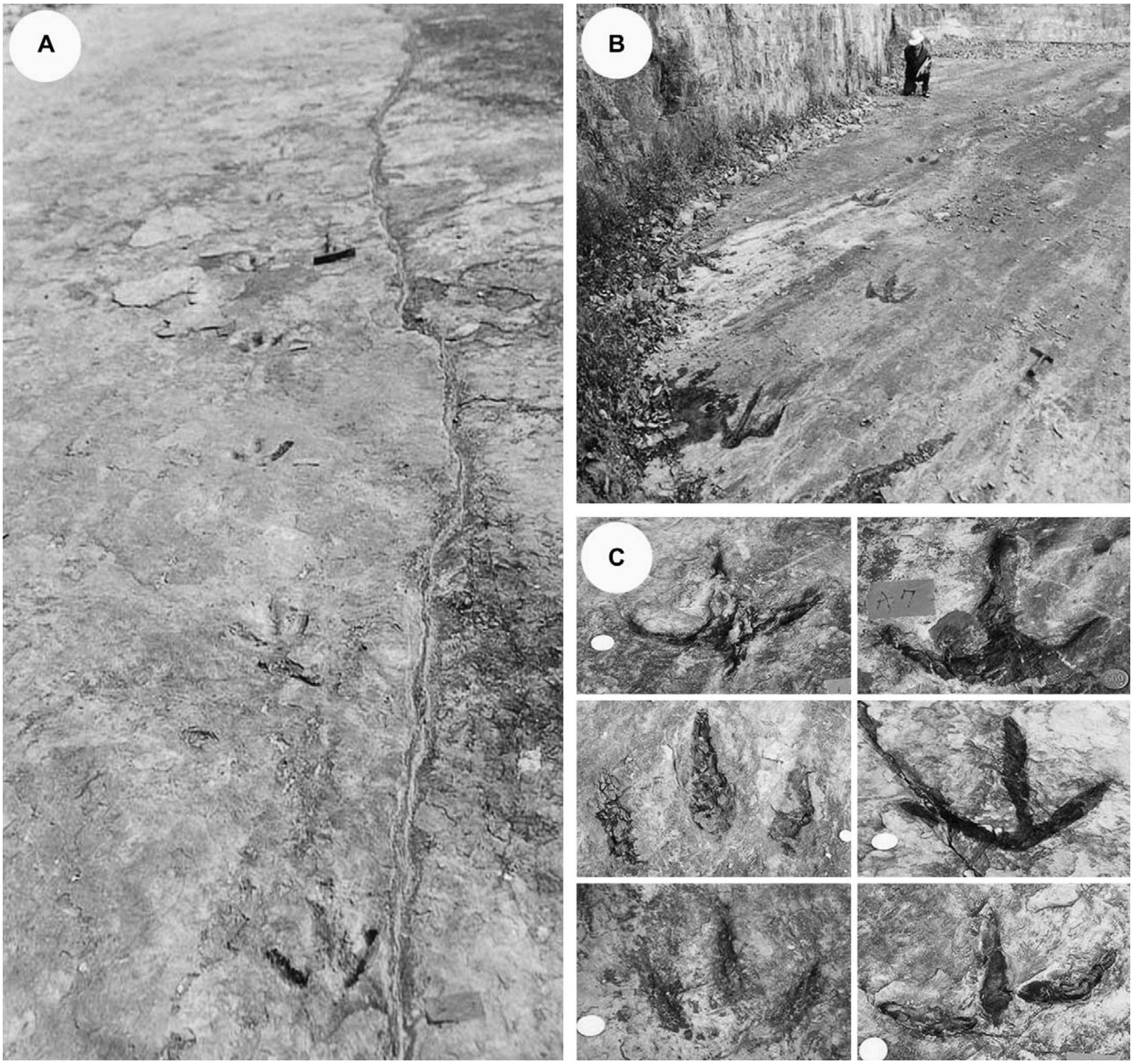

Fig. 4. Photographs of dinosaur tracks and trackways from level L1. A, well-preserved, long theropod trackway. B, trackway of large-sized theropod. C, diverse shapes of small theropod tracks.

changes in gait and speed. This trackway gradually increases stride lengths while proceeding. Initially the relative stride length is 2.3, which is considered trotting, then it increased to 3.9, indicating a running gait. The overall average is 3.2 (Table 2).

Trackway D is composed of six elongate footprints with distinctive spindle-shaped, V-shaped digits and a length of 56 cm. The total divarication is about 33°, which is relatively small compared to those of other small theropod trackways. Thus, the digits appear almost parallel to one other. The average pace of trackway D is 188.4 cm (range 174–202 cm). A striking characteristic of the trackway D is the alternation between long (L-R) and short (R-L) steps. Suggests another example of a limping dinosaur (Lockley et al., 1994; Moratalla et al., 1994).

Twenty-seven trackways averaging ten steps per trackway were recorded at L2 level (Fig. 9). Five represent large theropods and 22 represent small theropods. Large theropod footprint lengths vary from 42.0 cm to 55.5 cm and small theropod footprints between 14.9 and 35.0 cm (Table 1). The small theropod trackways are very narrow and most are tridactyl though some appear didactyl. Trackway directions are predominantly towards the southwest.

In the large theropod trackways, T4, T6, T12, T19 and T20, impressions of sharp claws are observed, and digit divarication is relatively low. Thus the footprint is V-shaped with digits almost parallel (Fig. 9). The relative stride length, between 0.9 and 1.6, indicates a slow gait (Table 1).

A small, 6.2-m-long theropod trackway, T2, consists of 7 tridactyl or didactyl, digitigrade footprints (Fig. 9). The

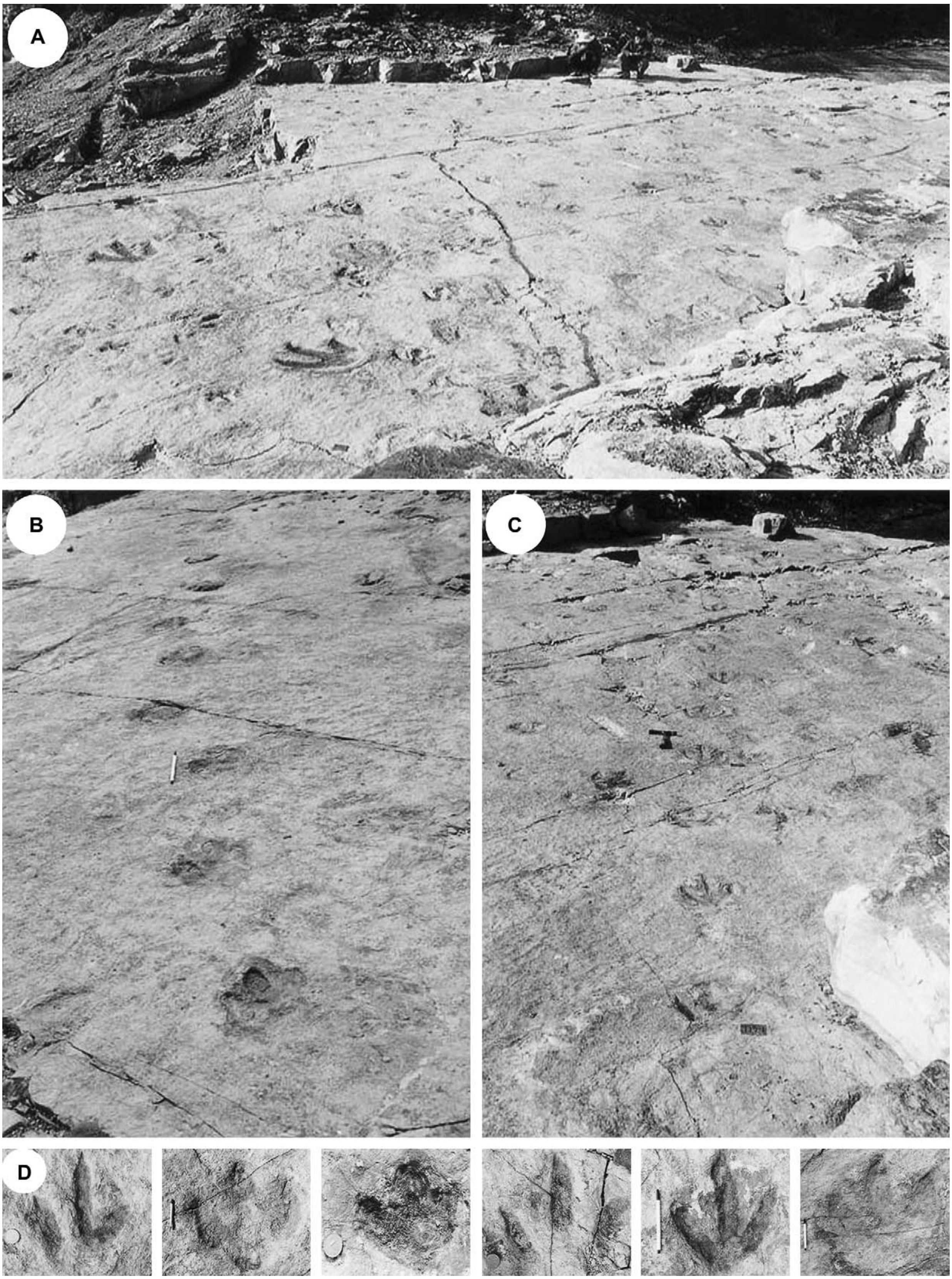

Fig. 5. Photographs of dinosaur tracks and trackways from level L2. A, overview of L2 tracksite. B, long, small-sized ornithopod trackway. C, long, well-preserved theropod trackway. D, diverse shapes of small theropod tracks.

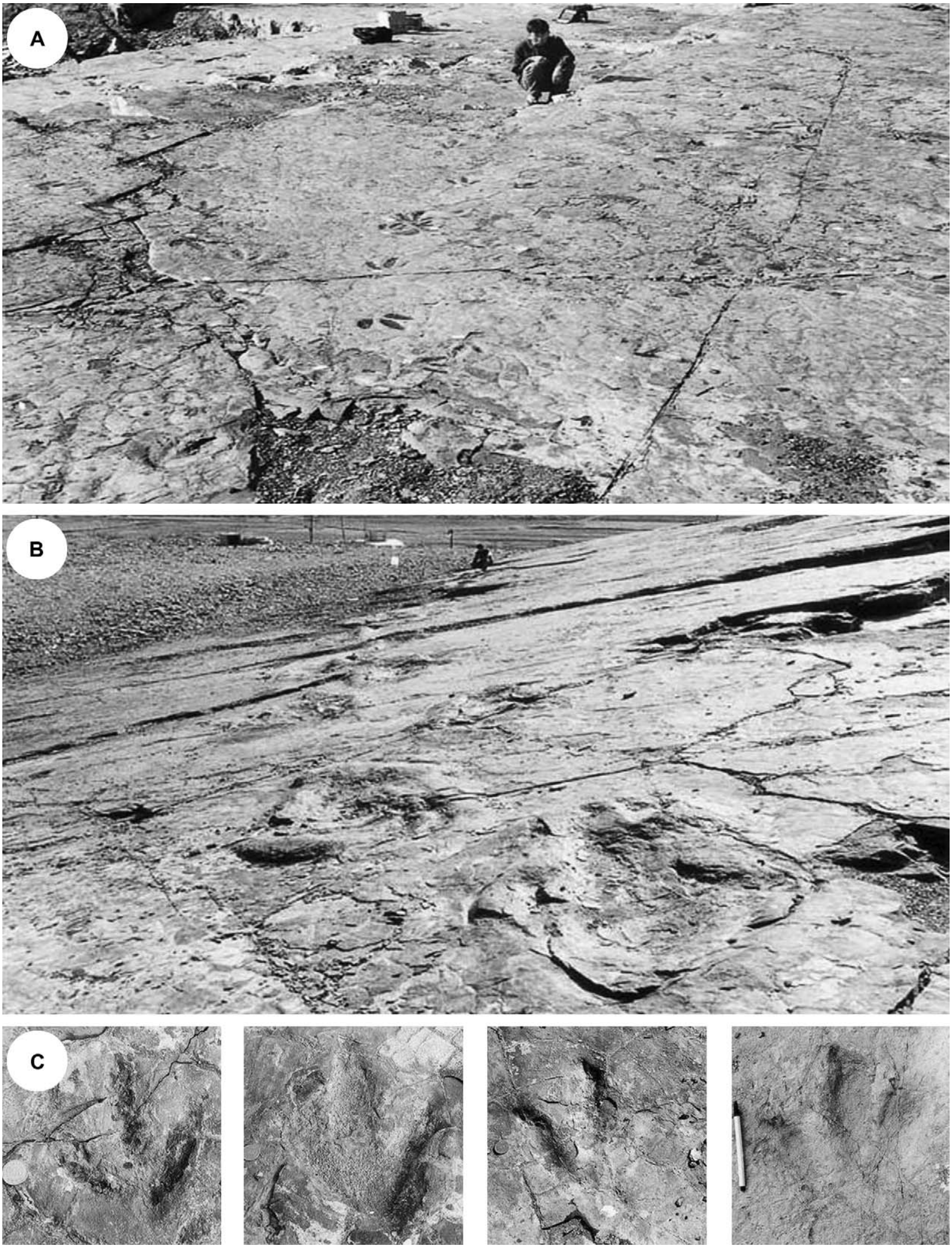

Fig. 6. Photographs of dinosaur tracks and trackways from level L5. A, long, well-preserved, theropod trackway. B, large-sized sauropod trackway. C, diverse shaped small theropod tracks.

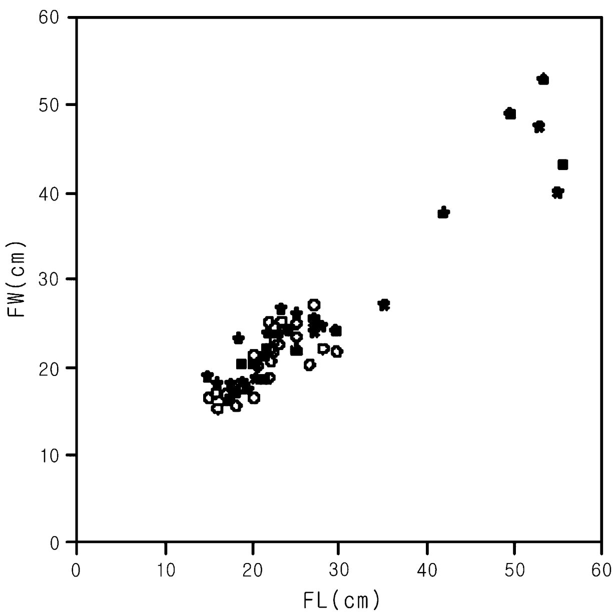

Fig. 7. Diagram showing the dimension of theropod footprints (■ = footprints from L1, * = footprints from L2, ○ = footprints from L5).

relative stride length of the trackway is 2.5, which indicates a quick trot, but the stride decreases somewhat as the trackmaker proceeds. Trackway T9 shows sharp claw impressions that curve outward, and during progression the total divarication and the depth of the footprints increased without any change in the stride or the gait. This suggests the substrate became softer in the direction of progression. Trackway T30 consists of a 9.5-m-long trackway of ten, mostly digitigrade footprints with claw impressions that tend to curve outward. Generally the strides are regular (relative stride length 3.2) indicating a running gait. The relative stride length of the small theropod tracks is about 2.0, thus, suggesting a trotting gait (Table 2).

Twenty-three small theropod trackways were recorded from the L5 level (Fig. 10). Footprint lengths range from 15.0 to 29.6 cm, and southeast orientations predominate.

Trackway T1 is composed of 12 tridactyl, digitigrade footprints with thick claw impressions and digits that curve inward (Figs. 6, 10). The relative stride length is 2.1, which indicates a quick trotting gait (Table 2).

4. The gaits of the theropods

Measurements of theropod trackways from Hwasun Seyou-ri allow interpretation of trackmaker gait. As the methodologies and formulae applied in this examination are based on living animal morphology and behavior, it might be considered incautious to apply them to extinct dinosaurs. However, in the case of theropod dinosaurs, especially the small trackmakers with weights and body structures similar to living birds, satisfactory results can be expected (Coombs, 1978). Hip height was calculated using the formulae suggested by Alexander (1976), Lockley et al. (1983), Thulborn and Wade (1984), and Thulborn (1990, 1984). Likewise speed and gait (walking, or trotting or running) can be inferred (Alexander, 1976, 1977; Thulborn, 1982; Thulborn and Wade, 1984).

4.1. The sizes of the dinosaurs

To estimate the sizes of the dinosaurs that inhabited Hwasun Seoyu-ri in the Cretaceous, the hip height was calculated from the length of the footprint using the different formulae suggested by Alexander (1976), Lockley et al. (1983), Thulborn and Wade (1984), and Thulborn (1990). Then the average of the different numerical values was calculated. The hip heights estimated from the Hwasun Seoyu-ri footprints are 1.8–1.0 m for small theropods, and 2.6 m for the large theropods from the L1 level; 0.8–1.9 m for the small theropods and 2.0–2.6 m for the large theropods from the L2 level; and 0.7–1.4 m for the small theropods from the L5 level (Fig. 12).

4.2. Speed

Likewise the walking speed was estimated using an average value calculated from the formulae suggested by Alexander (1976), Lockley et al. (1983), Thulborn and Wade (1984), and Thulborn (1990).

The speeds for the theropod trackways from the L1 level are calculated to be between 7.6 and 17.4 km/h (average 11.3 km/h) for the small theropods, and 8.1 km/h for the single large theropod trackway. For tracks from the L2 level, the speed estimates are between 3.3 and 20.5 km/h (average speed 10.7 km/h) for the small theropods, and between 3.7 and 13.9 km/h (average 5.6 km/h) for the large theropods. For small theropod tracks at the L5 level, the speed estimates are between 3.6 and 13.9 km/h (average 8.2 km/h) (Table 2). Thus, small theropod speeds are generally faster than those estimated for larger theropods.

5. Discussion

5.1. Ichnotaxonomy of the Hwasun Seoyu-ri theropod trackways

One of the most prominent characteristics of the Hwasun Seoyu-ri site is that theropod footprints comprise 88% of the sample. This distinguishes the Seoyu-ri site from other dinosaur tracksites in Korea where theropod tracks are much rarer, for example the famous Jindong Formation sites (Lockley et al., 2006). In general, despite the current elevated interest in carnivorous dinosaurs, theropod fossils (both bones and footprints) are not normally dominant over those of herbivorous (e.g., sauropods and ornithopods) especially in Cretaceous. This is because theropods comprised the upper tiers of the food pyramid (Bakker, 1975; Lockley et al., 1983). In

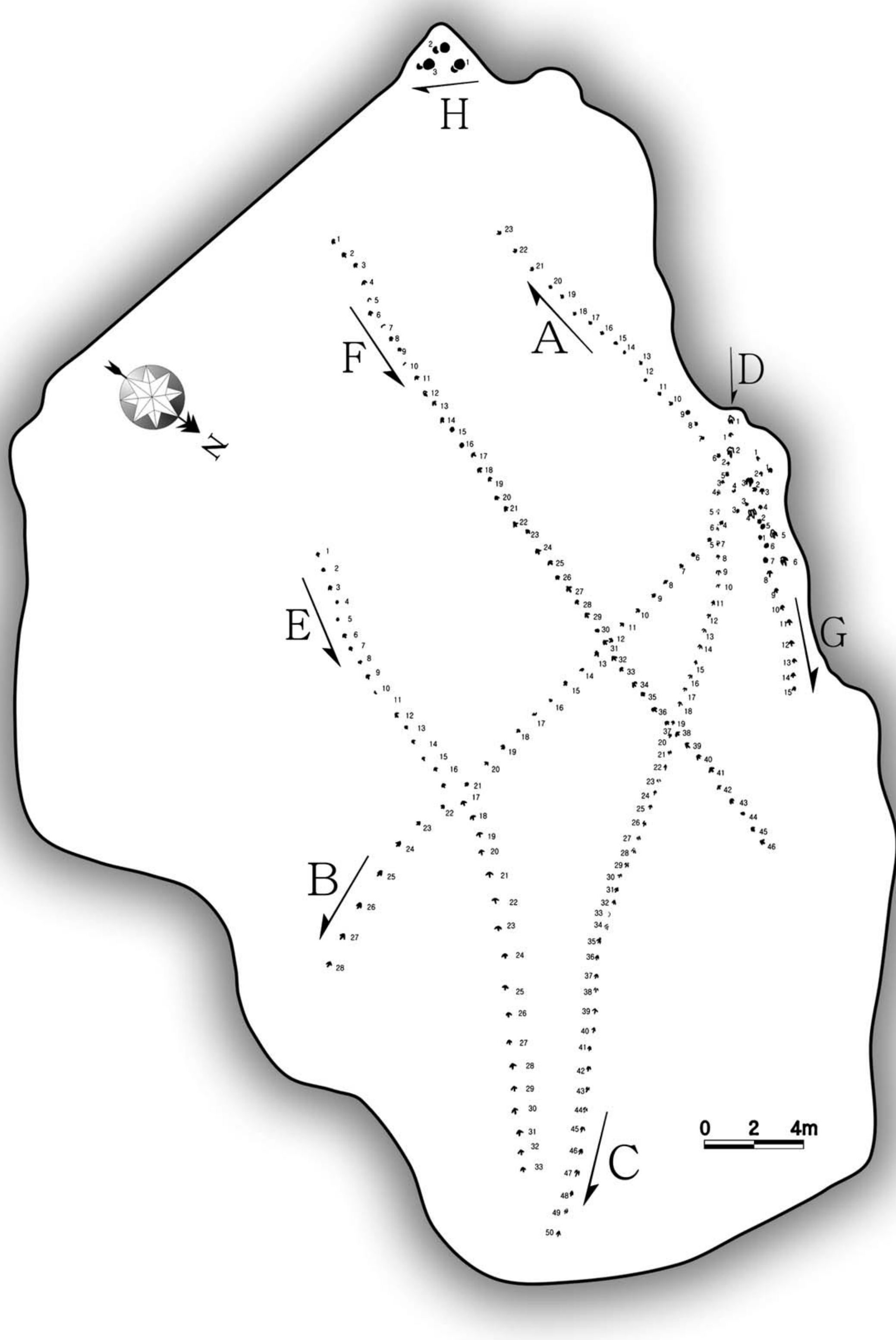

Fig. 8. Map showing distribution of eight dinosaur trackways (A–H) at level L1.

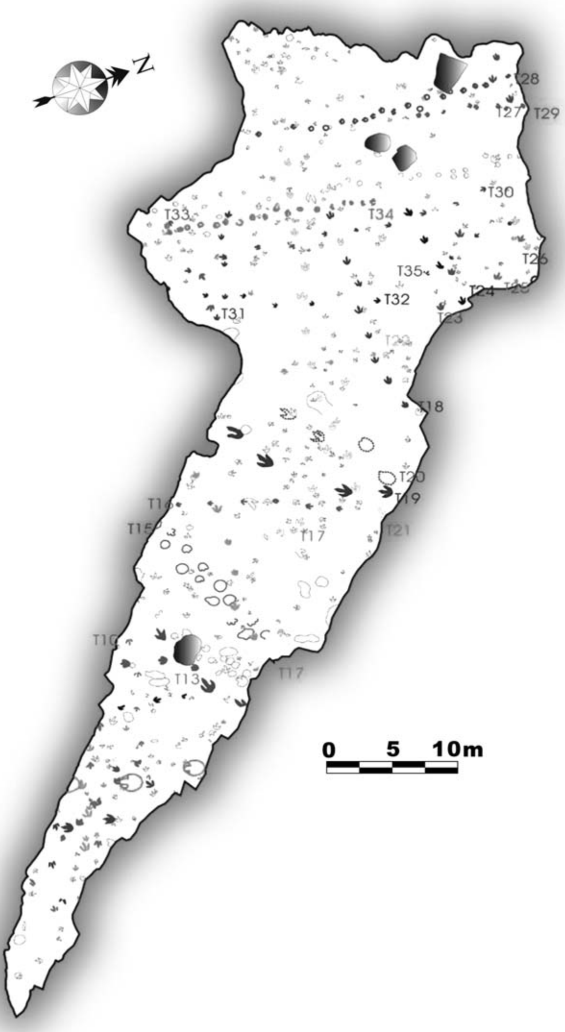

Fig. 9. Map showing distribution of multiple dinosaur trackways (T1–T35) at level L2.

South Korea, at dinosaur sites such as Yeosu Sa-do and Haenam Uhang-ri in the Jeollanam-do area and Goseong and Masan in the Gyeongsangnamdo area, theropod fossils comprise as less than 5% of the entire sample (Huh et al., 1997, 2001, 2003a,b; Lee et al., 2000a,b; Hwang, 2001; Hwang et al., 2002a,b). By contrast at Hwasun Seoyu-ri, small theropod tracks comprise as much as 94% of the sample at level L1.

In the study area, various theropod footprints can be categorized into three morphological types. The first type has a wide digit divarication of 80–90° and slender digit impressions, like those of birds. They are relatively small (16–22 cm: Fig. 11a). This type of footprint is also observed at Yeosu Sa-do in Jeollanam-do province (Huh et al., 2003a,b), and is similar to *Argoides* (Lull, 1953; Hitchcock, 1985) from the Early Jurassic strata in Morocco (Ishigaki, 1986) and to unnamed footprints reported from the Lower Jurassic of Utah (Lockley and Hunt, 1995, fig. 4.12). However, *Argoides* is not a name that is commonly used and the type material may be an extra-morphological (i.e., preservational) variant of other well known forms such as *Grallator*, *Eubrontes*, and/or *Kayentapus* (Lockley and Hunt, 1995). Nonetheless slender-toed forms are known throughout the Mesozoic that owe their characteristics to primary morphology, rather than preservational distortion. Among these are *Magnoavipes* from the mid-Cretaceous (Lee, 1997; Lockley et al., 2001), which his first type of footprints resembles. This ichnogenus is usually a little larger on average than the Korean tracks, but not markedly so. This footprint type has also been found in the mid-Cretaceous of Israel (Avnimelech, 1966) where it has been attributed to a *Coelurosaurus*-like dinosaur. In comparison with early Jurassic dinosaur tracks which are mostly elongate, with low digit divarication angles, Cretaceous ichnofaunas reveal a number of gracile forms with wider feet (i.e., higher digit divarication angles). Lockley (1999) has suggested that there is a general morphodynamic trend towards widening of the foot in many of the more derived dinosaur clades. Thus, these footprints may indeed represent coelurosaurs that were derived forms that rose to prominence in the Late Jurassic and Cretaceous.

The second type of footprint has thicker digits and is slightly larger (20–28 cm), than the first type. It has narrow digit divarications ranging from 50 to 60° (Fig. 8b) and the claw impressions and trackway are also narrow. This type of footprint has been found at the Sa-do and Nang-do sites in Yeosu (Huh et al., 2001, 2003a,b), and is similar to *Ornithomimipus* from the Late Cretaceous of Canada (Sternberg, 1926), and to *Xiangxipus* from the Cretaceous of China (Zeng, 1982; Matsukawa et al., 2006).

The third type of footprint represents large theropods, with foot length greater than 40 cm, narrow digit divarications, around 50°, and distinctive claw impressions (Fig. 11c). Similar types occur at the Sa-do and Nang-do sites in Yeosu (Huh et al., 2001, 2003a,b). From a historical and ichnotaxonomic viewpoint Early Cretaceous theropod tracks are still poorly known (Lockley, 2000). Well-preserved tracks from North America have been named *Irenisauripus*, *Irenichnites*, and *Columbosauripus* (Sternberg, 1932) but have not been studied in detail since their original discovery more than 70 years ago. Tracks such as *Itsukisauropus* from the Lower Cretaceous Tetori Group in Japan (Azuma and Takeyama, 1991) may share very similar characteristics with this third type. The Hwasun Seoyu-ri theropod footprints are especially similar to the theropod footprints found in the Yeosu Sa-do area, and elsewhere in the region.

5.2. Discussion of gaits

The size (length) of small theropod footprints ranges between 14.9 and 35 cm, but mostly between 16.0 and 30.0 cm (Fig. 7, Table 1). The proportion of the foot length to the foot width varies little, from 0.9 to 1.1. The size

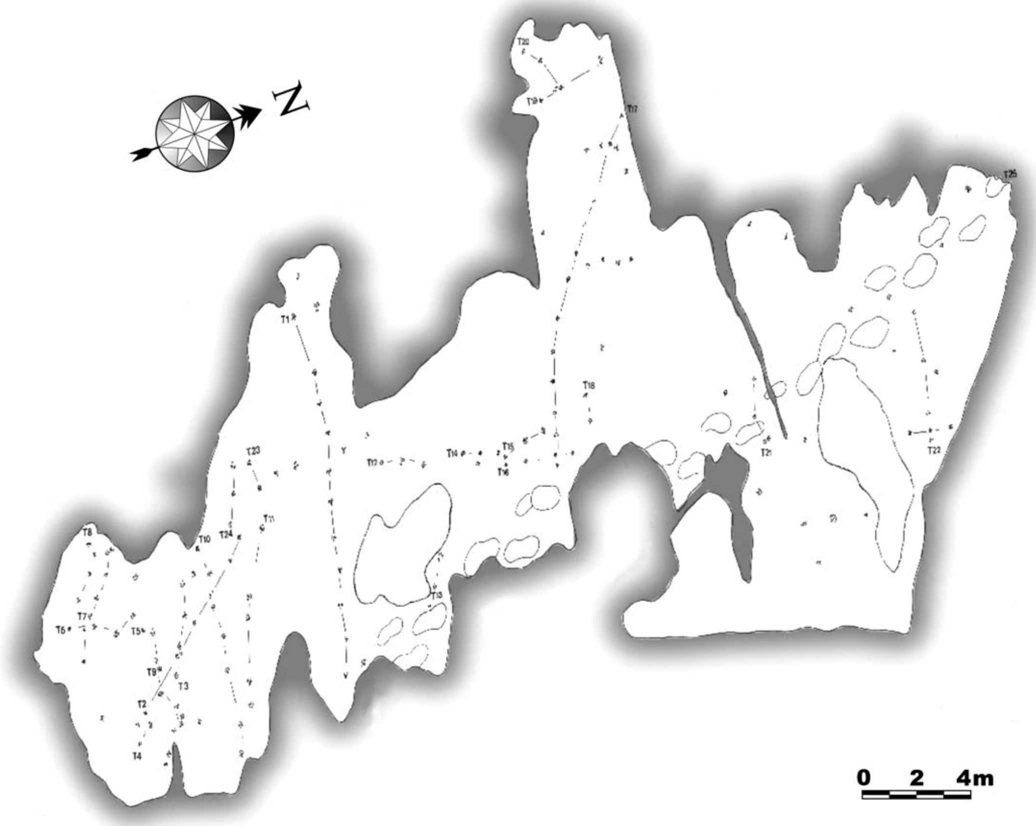

Fig. 10. Map showing distribution of multiple dinosaur trackways (T1–T24) at level L5.

(length) of the large theropod prints ranges from 42.0 to 56.1 cm and the FL/FW ratio (56.1/43.8) indicates a more elongate foot. Thus, the small and large theropods display distinctive differences in terms of the footprint shape and inferred body size, suggesting that the large and small theropods represented quite different theropod types. It is instructive to note that normally small theropod footprints are more elongate than larger footprints, especially in closely related forms such as *Grallator* and *Eubrontes* (Lockley, 1999; Olsen and Rainforth, 2003). Thus, the reversal of this general morphodynamic trend is likely to suggest that we are comparing two less closely related forms. As suggested above a small wider-footed form may represent a derived, rather than a primitive form.

The analysis of gait shows that the average relative stride length (SL/h) of the small and large theropods was 2.1 and 1.2 respectively. This suggests that the small theropods moved in a type of trot while the large theropods walked slowly (Table 2). This result conforms well with other interpretations which indicate that large theropods walked more slowly than small theropods (Coombs, 1978; Farlow, 1981). In the study area the small theropods indicate various gaits, including slow walking, trotting, and running, while the large theropod tracks only indicate slow walking. This interpretation is reinforced by calculating walking speed (locomotion speed), which for small theropods is mostly greater than 10 km/h, with some examples over 20 km/h, while the walking speed estimates for the large theropods ranged from 3.7 to 9.1 km/h.

In the case of accelerating trackway B, from the L1 level, the minimal relative stride length (2.3), indicates a speed of 11.5 km/h, increasing to a maximum relative stride length (4.2) and a speed of 25.7 km/h. This latter estimate is the highest speed calculated for the tracks from Hwasun Seoyu-ri. The speed is nevertheless lower than the maximum speed of living ungulates, humans, or ostriches (Farlow, 1981). A distance of 31 cm separates the minimum and maximum stride lengths in trackway B. Thus the animal accelerated to more than twice its initial speed in a relatively short distance. No distinctive changes in the shape of the footprints were recognized in the process of this transformation from trotting to running, but the lengths of the footprints associated with a stride longer than 300 cm were measured to be an average of 1.1 cm larger than those with a shorter stride.

In the case of trackway D from the L1 level, the left to right pace is on average 3.7 cm longer than the right to left pace. This slight differential is less than recorded for some ''limping'' trackways (Lockley, 1986; Lockley et al., 1994; Moratalla et al., 1994).

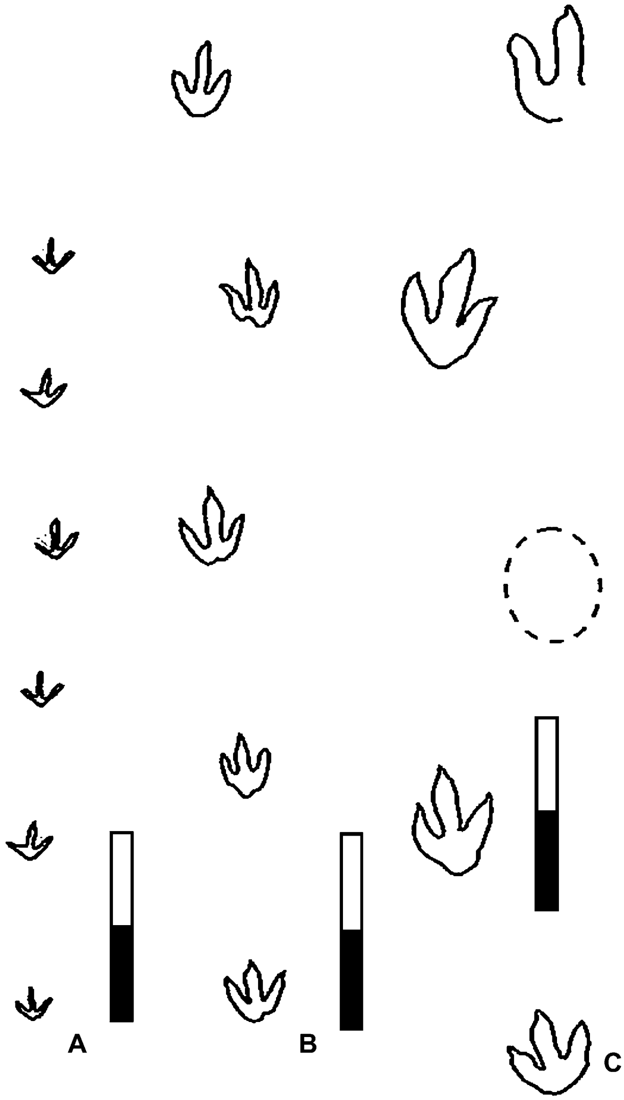

Fig. 11. Three types of theropod footprints from the Hwasun tracksite (scale bar represents 1 m). A, small bird-like footprints with narrow digits and wide divarication. B, medium-sized footprints with thick digits and narrow toe impression. C, large theropod footprints with distinct and sharp claw.

The theropod tracks from all three levels at Hwasun Seoyu-ri do not offer evidence of gregarious behavior. Orientations are mostly random (Figs. 4–10), and even in the few cases of parallel trackways, the types of footprints are different, indicating that they were formed by different theropod species.

6. Conclusion

More than 1500 well-preserved dinosaur footprints comprise more than 60 trackways, from the Cretaceous strata (Neungju Group) in Seoyu-ri, Hwasun-gun, Jeollanam-do, South Korea. Most of the footprints belong to theropods, and among them, small theropod footprints are predominant. Long trackways, mainly of small theropods, are concentrated at three levels (L1, L2 and L5).

The theropod footprints fall into three types. The first type characterized by its small size, wide digit divarication, and thin digits, is comparable to *Magnoavipes*. The second type has thicker digits and relatively narrow divarication, and is similar to *Ornithomimipus* and *Xiangxipus*. The third type, characterized by its distinctive impressions of sharp claws, is larger, longer than 40 cm, with narrow digit divarication, and can be compared with theropod footprints found at Yeosu Sa-do and Nang-do, and tentatively compared with theropod tracks from Canada (*Irenisauripus*, *Irenichnites* and *Columbosauripus*: Sternberg, 1932) and from Japan (*Itsukisauropus*).

Hip height estimates range widely, from 68.4 to 194.5 cm for the small theropods, to a maximum of 260.9 cm for the large theropods. The diverse shapes of the footprints suggest at least three types of theropod dinosaurs inhabited the study area.

The analyses of speeds reveal different gaits: slow walking, trotting, and running. The small theropods usually left trotting or running trackways, while the large theropod trackways indicate slow walking. Changes in the gait and speed of some animals indicate a flexible locomotor repertoire for several dinosaurs. The Hwasun County trackways also substantially change our perception of the abundance of theropods in the Korean track record, which elsewhere is dominated by the trackways of sauropods and ornithopods (Lockley et al., 2006).

The Seoyu-ri, Hwasun County, Jeollanam-do tracks are associated with deposits where there is a significant proportion of volcaniclastic material, as the lithologic unit names imply (e.g., Jangdong Tuff overlying the Manweolsan Tuff and underlying the Yeonhwari Formation and the Jeokbyeok Tuff). It is therefore interesting to note that well-preserved tracks occur in tuffs at other localities including the Cretaceous Jindong Formation to the west (Houck and Lockley, 2006). Other localities where dinosaur tracks are associated with volcanic ashes include the La Matilde Formation in the Jurassic of Argentina (Melchor et al., 2004). Similarly, tracks of various mammals and birds have been found in abundance in the so called Footprint Tuff in the ash rich Pliocene Laetoli beds of Tanzania (Leakey and Hay, 1979; Hay and Leakey, 1982).

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Table 1
Measurements (in cm) of theropod tracks from the study area (FL = foot length, FW = foot width, P = pace, S = stride, TDV = total divarication)

Trackway	FL	FW	P	S	Digit length			Ends span		Ends angle		TDV
					II	III	IV	II–III	III–IV	α	β	
Tracksite: L1												
A (Small theropod)	21.1	21.4	106	212	11.3	15.3	10.8	15	14.5	44.5	43.4	85.4
B (Small theropod)	20.7	20.4	145	291	11.1	15.6	11.3	14.6	15.1	44.6	47.3	91.2
C (Small theropod)	21.7	18.9	91.5	183	12.1	16.5	11.3	14.1	12.8	39.4	28.9	67.7
D (Large theropod)	56.1	43.8	188	367	31.7	37.9	30.3	25	21.9	17.3	10.4	33
E (Small theropod)	18.6	20.3	102	203	9.7	15	9.7	13.8	14.6	47.3	52.4	93.1
F (Small theropod)	21.2	22.3	95.1	190	10.4	14.5	10.4	15.6	15.6	47.7	49.4	104
G (Small theropod)	19.3	–	94.1	206	10.8	15	10	12.2	13.5	38.3	42.2	82.7
Tracksite: L2												
T1 (Small theropod)	25.8	22	124	–	11	19.3	11	15	14.5	30	25	50
T2 (Small theropod)	17.7	18	101	200	8.9	15.4	9.6	12.2	11.5	35.7	33.3	69.8
T3 (Small theropod)	23	24	120	–	13.5	22	13.3	14.5	16.5	19	27.5	46.5
T4 (Large theropod)	42	37.5	103	–	20.3	29.5	24	20.5	23	22.5	27.5	50
T5 (Small theropod)	35	27	112	223	17.7	26.3	17	19.3	18	29.7	33	65
T6 (Large theropod)	49.5	49	183	355	–	–	–	–	–	–	–	–
T7 (Small theropod)	17.9	17.5	84.5	169	7.6	12.5	169	11.7	11.7	37	41.6	78.6
T8 (Small theropod)	27.3	24.1	133	267	16	21.4	14.9	14.3	15.3	17.5	29.3	58.5
T9 (Small theropod)	18.5	23	98	–	10.2	14.3	9	14	12	43.3	39	84
T10 (Small theropod)	20.8	18.4	121	241	12.4	16.5	10.5	11	12	25	35.5	58
T11 (Small theropod)	25	26	120	–	15	21	15.3	15.5	15.5	28	32.5	60.5
T12 (Large theropod)	55.5	40	106	228	20	32	20.7	23.5	22.3	37.5	27.3	56
T14 (Small theropod)	26.8	25.6	121	238	11.6	17.4	12	16	15.6	37.2	32	69.2
T16 (Small theropod)	18.4	18	–	–	9.5	12.3	9.2	10.8	10.5	38.3	40	80
T17 (Small theropod)	24.2	24.6	131	262	13.6	20.8	15.7	16.1	16.1	27	27.5	53.7
T18 (Small theropod)	29.4	24.5	85.1	170	14.9	22	15.3	14.5	16	26.7	30.9	58.6
T19 (Large theropod)	53.5	52.7	124	–	28.3	38.3	26.7	27	28	26.8	27.7	53.3
T20 (Large theropod)	53	47.5	126	245	28.5	39.5	28	29	29.5	15.5	30	45.5
T21 (Small theropod)	27	25.6	117	234	13.6	20.7	14.7	15.3	15.1	24.7	28.7	52.3
T22 (Small theropod)	21.8	24	–	–	–	–	–	–	–	–	–	–
T23 (Small theropod)	23.5	26.5	132	164	17	24.7	16.3	17.7	16.3	33.3	30	63.3
T24 (Small theropod)	27.8	24.2	114	228	14.5	22.5	16	17.3	17.5	27.5	29.5	57
T30 (Small theropod)	14.9	18.8	106	211	10.9	13.7	10.7	11.8	11.4	33.6	30.6	64.1
T31 (Small theropod)	19.3	17.6	91	182	8.6	13.5	8.2	12.4	11.3	29.6	33	62.6
T32 (Small theropod)	15.9	18	106	208	10	14.6	11	12	11.4	40	31.4	71.4
T33 (Small theropod)	25	22	104	221	12.5	20	13	15	15	17.5	30	55
T35 (Small theropod)	17.3	16	112	222	9.5	12.1	8.6	11.6	11.5	30	25	55
Tracksite: L5												
T1 (Small theropod)	20.1	21.3	116	234	10.3	15.5	10.4	14.6	13.1	18.4	23.6	42.2
T2 (Small theropod)	17	16.6	130	267	9.3	12.6	8.7	11.9	10.7	37.7	34.2	72
T3 (Small theropod)	28.1	22	110	216	13.5	19.1	13.9	14.6	14.8	28.5	27.3	55.2
T4 (Small theropod)	20.3	21.8	–	–	–	–	–	–	–	–	–	–
T5 (Small theropod)	25.1	23.6	79	125	12.5	19	11	18	16.7	35	26.7	62
T6 (Small theropod)	22.8	22.4	93.8	167	11.7	17.3	11	17.3	15.5	45	43	93.7
T7 (Small theropod)	15.9	17	85	165	8.5	13.6	8	12.3	13.2	34.7	43.3	79.7
T8 (Small theropod)	20.1	20.1	100	198	12	16.8	10.5	14.8	14.9	27.6	30	55
T9 (Small theropod)	25.6	20.3	–	–	–	–	–	–	–	–	–	–
T10 (Small theropod)	21.6	18.3	103	206	9.8	16	8.9	11	12.3	20.8	16.8	39
T11 (Small theropod)	29.6	21.6	78	–	–	18.6	–	–	–	–	–	–
T12 (Small theropod)	27	27	–	–	–	–	–	–	–	–	–	–
T13 (Small theropod)	23	22.5	–	–	–	17.8	–	–	–	–	–	–
T14 (Small theropod)	15	16.5	83.5	164	9.5	11.5	11.7	12.5	10.5	47.5	21.7	53.4
T15 (Small theropod)	24.8	25.5	110	212	15.5	20.4	15.5	17.7	17.2	23.8	25	50
T16 (Small theropod)	16.2	15.3	83.8	172	9.4	12.3	9.2	10.6	10	29.4	23.1	52.2
T17 (Small theropod)	20.5	16.5	98.9	198	12.8	14	10.3	11.8	10.3	30	20	50
T18 (Small theropod)	17.5	16.3	–	–	–	14	–	–	–	–	–	–
T19 (Small theropod)	21.7	21.7	112	–	11	16.2	10.7	14.3	15.3	26.4	45	71.7
T21 (Small theropod)	22	21.2	115	221	11	14.7	11.3	14.3	15.2	22.5	38.3	60
T22 (Small theropod)	18.1	15.8	88	–	–	13.3	–	–	–	–	–	–
T23 (Small theropod)	21.8	24.8	–	–	–	–	–	–	–	–	–	–
T24 (Small theropod)	23.5	25	106	211	15.5	16	13	–	–	–	–	–

Table 2
Estimated speed values of theropod tracks from study area (FL = foot length, H = height at hips, SL = stride, V = velocity)

Trackway	FL (cm)	H (m)	SL (m)	SL/H (m)	V (km/h)
Tracksite: L1					
A (Small theropod)	21.1	1	2.1	2.1	13.9
B (Small theropod)	20.7	0.9	2.9	3.2	17.4
C (Small theropod)	21.7	1	1.8	1.8	7.6
D (Large theropod)	56.1	2.6	3.7	1.4	8.1
E (Small theropod)	18.6	0.8	2	2.5	8.8
F (Small theropod)	22.4	1	1.9	1.9	8.3
G (Small theropod)	19.3	0.9	2.1	2.3	11.5
Tracksite: L2					
T1 (Small theropod)	25.8	1.2	2.5	2.1	24
T2 (Small theropod)	17.7	0.8	2	2.5	8.8
T3 (Small theropod)	23	1	2.4	2.4	16.5
T4 (Large theropod)	42	2	2.1	1.1	4.4
T5 (Small theropod)	35	1.7	2.2	1.3	5.7
T6 (Large theropod)	49.5	2.3	3.6	1.6	9.1
T7 (Small theropod)	17.9	0.8	1.7	2.1	7.1
T8 (Small theropod)	27.3	1.3	2.7	2.1	30.5
T9 (Small theropod)	18.5	0.8	2	2.5	8.8
T10 (Small theropod)	20.8	0.9	2.4	2.7	13.6
T11 (Small theropod)	25	1.2	2.4	2	9.9
T12 (Large theropod)	55.5	2.6	2.3	0.9	3.7
T14 (Small theropod)	26.8	1.3	2.4	1.8	9
T16 (Small theropod)	18.4	0.9	2.6	2.9	15.1
T17 (Small theropod)	24.2	1.2	1.7	1.4	5.6
T18 (Small theropod)	29.4	1.9	1.7	0.9	3.3
T19 (Large theropod)	53.5	2.5	2.5	1	4.5
T20 (Large theropod)	53	2.4	2.5	1.3	6.2
T21 (Small theropod)	27	1.2	2.3	1.9	9.2
T22 (Small theropod)	21.8	1	−	−	−
T23 (Small theropod)	23.5	1.2	1.6	1.3	5
T24 (Small theropod)	27.8	2.2	2.3	1	4.5
T30 (Small theropod)	14.9	0.8	2.1	2.6	9.3
T31 (Small theropod)	19.3	0.8	1.8	2.3	7.7
T32 (Small theropod)	15.9	0.9	2.1	2.3	11.5
T33 (Small theropod)	25	1.1	2.2	2	9.5
T35 (Small theropod)	17.3	0.8	2.2	2.8	9.9
Tracksite: L5					
T1 (Small theropod)	20.1	0.9	2.3	2.6	12.9
T2 (Small theropod)	17	0.8	2.7	3.4	12.9
T3 (Small theropod)	28.1	1.3	2.2	1.7	7.8
T4 (Small theropod)	20.3	0.9	−	−	−
T5 (Small theropod)	25.1	1.2	1.3	1.1	3.6
T6 (Small theropod)	22.8	1	1.7	1.7	6.9
T7 (Small theropod)	15.9	0.7	1.7	2.4	5.6
T8 (Small theropod)	20.1	0.9	2	2.2	10.8
T9 (Small theropod)	26.5	1.3	−	−	−
T10 (Small theropod)	21.6	1	2.1	2.1	13.9
T11 (Small theropod)	29.6	1.4	1.6	1.1	4.2
T12 (Small theropod)	27	1.3	−	−	−
T13 (Small theropod)	23	1	−	−	−
T14 (Small theropod)	15	0.7	1.6	2.3	5.2
T15 (Small theropod)	24.8	1.1	2.1	1.9	8.8
T16 (Small theropod)	16.2	0.7	1.7	2.4	5.6
T17 (Small theropod)	20.5	0.9	2	2.2	10.8
T18 (Small theropod)	17.5	0.8	2.2	2.8	9.9
T19 (Small theropod)	21.7	1	1.3	1.3	4.4
T21 (Small theropod)	22	1	1.8	1.8	7.6
T22 (Small theropod)	18.1	0.8	−	−	−
T23 (Small theropod)	21.8	1	−	−	−
T24 (Small theropod)	23.5	1.1	2.1	−	−

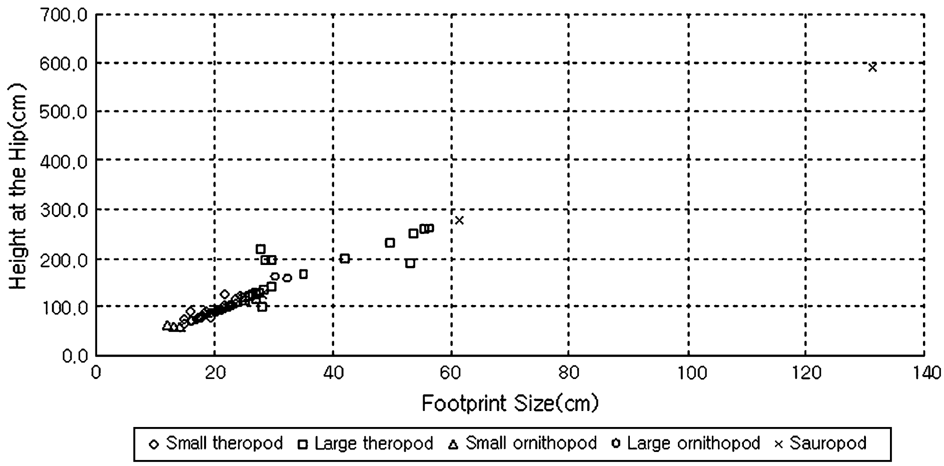

Fig. 12. Scatter diagram showing the ratio of hip height vs. footprint size from the Hawsun study area.

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