

A juvenile ornithopod tracksite from the Lower Cretaceous Haman Formation, South Korea

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ABSTRACT

A new dinosaur tracksite with footprints of non-adult ornithopods was discovered from the Lower Cretaceous Haman Formation (Albian), Gunbuk District, Haman County, South Gyeongsang Province of South Korea in 2018. The tracksite consists of 58 ornithopod footprints (seven short trackways and 26 isolated footprints) within three track-bearing horizons partially exposed on the small creek bottom. Lithofacies and sedimentary structures of the track-bearing horizons and overlying strata suggest a marginal lacustrine environment. All tracks are sub-symmetrical tridactyl and small- to medium-sized pes prints. They have wide, blunt, short digital impressions with a large, rounded heel pad impression. No manus print is observable in the tracksite. Tracks are generally longer than their width with a distinctly developed digit III. Trackways show the inward (negative) rotation of footprints. The morphological characteristics of the footprints are most likely attributable to ichnogenus *Caririchnium*. A relatively small pes size (lengths range from 13 to 27 cm) indicates that the trackmakers were juvenile to subadult ornithopods when compared with the contemporary large ornithopods in South Korea. The majority of the trackways show preferred orientations with trends of parallel to subparallel groupings on each surface, suggesting gregarious behavior. Notably, the tracksite consists exclusively of juvenile ornithopod dinosaurs, which is an uncommon phenomenon when compared to other ornithopod tracksites with age-mixed or large ornithopod footprints reported from other localities around the world. The absence of the adult ornithopod tracks may be interpreted as the spatial segregation of an ornithopod population based on their ages and the formation of juvenile-only communities without parental care.

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1. Introduction

Since dinosaur footprints were discovered for the first time in the Upper Cretaceous Jindong Formation in the early 1980s (Yang, 1982), South Korea has been noteworthy for numerous and diverse Cretaceous vertebrate ichnocoenoses (Lockley et al., 2012a). They include a variety of vertebrate trace fossils such as turtles, lizards, chorisoderans, crocodyliforms, dinosaurs, birds, pterosaurs, and mammals from the non-marine Cretaceous Gyeongsang Basin and other small sedimentary basins (Lee et al., 2000, 2001, 2020; Hwang et al., 2002; Huh et al., 2003, 2006; Lockley et al., 2006, 2012b, c, 2020; Lim et al., 2012; Kim et al., 2016; Kim and

Lockley, 2016; Kim et al., 2017a, b; Lee et al., 2018a). However, the first vertebrate ichnological study in South Korea began with the report of bird tracks (*Koreanaornis hamanensis*) from the Lower Cretaceous Haman Formation (Kim, 1969).

The Haman Formation belongs to the Hayang Group of the Cretaceous Gyeongsang Basin (Chang, 1975), producing various vertebrate trace fossils. Among them, bird tracks are the most abundant (Kim, 1969; Baek and Yang, 1997; Kim et al., 2006, 2012a; Falk et al., 2010, 2014; Kim et al., 2011). Tracks of pterosaurs (Kim et al., 2006; 2012b), theropods (Kim et al., 2008), and sauropods (Kim and Lockley, 2012) have been also found sometimes with well-preserved skin impressions of dinosaurs (Paik et al., 2010, 2017). However, ornithopod tracks are relatively rare when compared to their abundant trackways from the overlying Jindong Formation (Lee et al., 2000; Kim and Huh, 2018). To date, detailed ichnological information on ornithopods from the Haman

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Formation has been insufficient (Huh et al., 2003; Park and Lim, 2004; Yang et al., 2006). Fortunately, a new ornithopod tracksite was discovered from the Haman Formation, which is located in a small valley in Gunbuk District, Haman County, South Gyeongsang Province in 2018 (Fig. 1). The exposed surface of the outcrop is small (33 m² in total) but consists of a high density of footprints. The purpose of this paper is to report and describe this new ornithopod tracksite from the Lower Cretaceous Haman Formation, and to investigate the paleontological and paleoecological importance of this tracksite.

2. Geological setting

The Gyeongsang Basin is the largest terrestrial sedimentary basin in South Korea, which is located in the southeastern part of the Korean Peninsula. It is interpreted as a back-arc basin formed by the oblique subduction of the proto-Pacific (Izanagi) plate under the Asian continent (Chough and Sohn, 2010). The sedimentary beds of the Gyeongsang Basin are grouped in the Gyeongsang Supergroup, and subdivided into three major lithostratigraphic units: Sindong, Hayang, and Yucheon groups in ascending order (Chang, 1975).

The Haman Formation belongs to the middle to upper part in the Hayang Group (Chang, 1975) and lies between the underlying Silla Conglomerate and overlying Gusandong (Kusandong) Tuff with thicknesses ranging between 500 and 2600 m (Chough and Sohn, 2010). The Haman Formation is distributed over the Jinju Subbasin and the Daegu area of the Uiseong Subbasin. In the Jinju Subbasin, the Jindong Formation overlies the Gusandong Tuff and the Haman Formation while the Banyaweol Formation overlies the Gusandong Tuff and the Haman Formation in the area of Daegu (Chough and Sohn, 2010). The Haman Formation is typically characterized by the occurrence of purple mudstone and sandstone

(Um et al., 1983) and generally interpreted to be deposited in alluvial or fluvial settings with a semi-arid climate (Kim, 1969; Chough and Sohn, 2010; Paik and Kim, 2014). In some regions where the upper Haman Formation occurs, the typical reddish deposits are absent. Instead, lacustrine lithofacies formed by cyclic depositions of gray sandstone and mudstone with intercalating calcrite-bearing deposits have been reported, showing a similar aspect to the general lithofacies of the overlying Jindong Formation (So et al., 2007; Kim et al., 2018).

The new tracksite (Gunbuk Dinosaur Tracksite, GBDT) is represented by three track-bearing layers (Layer 1, 2, 3 from top to bottom) partially exposed on the small creek bottom (Fig. 2). All layers consist of dark gray mudstone with polygonal fractures on the surface. Between the upper two track-bearing layers (Layer 1 and 2), there is another layer exposed without any tracks (Layer A). This trackless layer contains symmetrical ripple marks that are not preserved in other track-bearing layers (Fig. 2B). The ripples occur in the southwestern part of Layer A with azimuths of 120°. Layer 1 (15 cm thick) and Layer A come into direct contact and Layer 2 is next to Layer A (4–5 cm thick) with a small groove between them. Layer 3 is located about 6 m southwest from Layer 2 (40 cm thick). Besides the track-bearing layers, reddish sandstone and mudstone beds overlie the track-bearing horizons. Two lithofacies (dark gray mudstone and reddish sandstone to mudstone) alternate in the section along the creek. Wavy bedding and symmetrical ripple marks are observed from the lower section of the reddish sandstone. In general, the sedimentary strata gently dip towards the southeast at an angle around 5°. Besides the dinosaur tracks, no fossils are found from the track-bearing layers except for cylindrical rhizoliths (6–8 mm in diameter) developed parallel to the bed in form of a horizontal branching network (Fig. 2C). The alternating lithofacies with the typical sedimentary structures such as wavy bedding, symmetrical ripple marks, and rhizoliths indicate that the

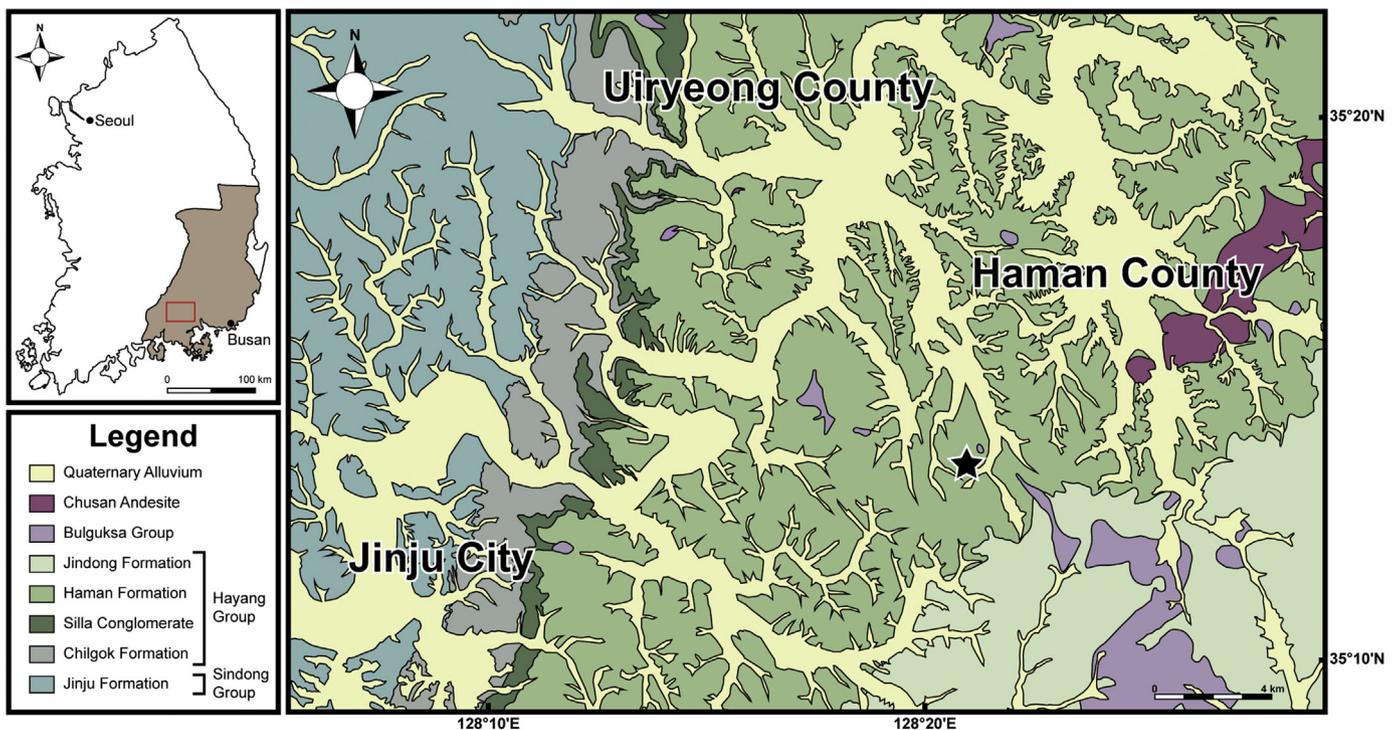


Fig. 1. Geological map of the study area and the locality of tracksite (Modified from Choi and Kim, 1963; Lee et al., 2018b). Brown region of South Korea (upper left) refers to the Gyeongsang Basin and the red square refers to the region of geological map (right). Black star in the geological map refers to the location of tracksite. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

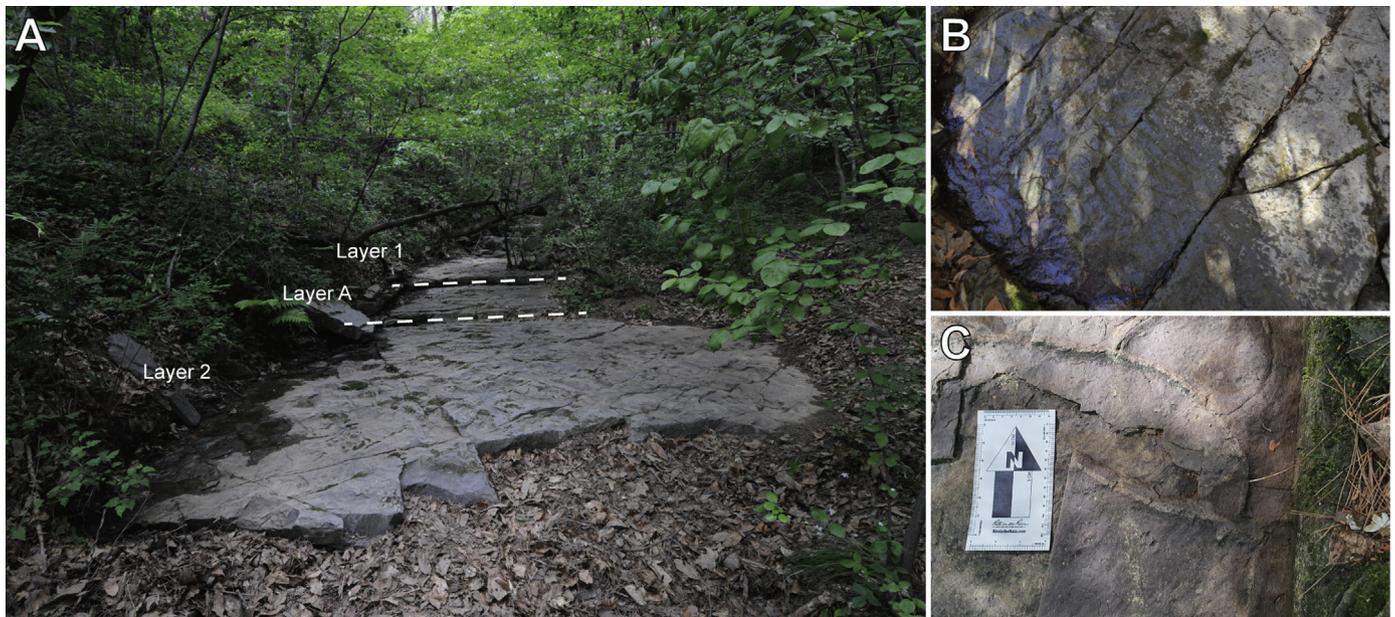


Fig. 2. Photos of the Gunbuk tracksite. A) Whole view of the tracksite to show Layer 1, Layer A, and Layer 2 from top to bottom. B) Layer A with partially preserved symmetrical ripple marks. C) Rhizolith traces from the strata above the uppermost track-bearing horizon.

tracksite was deposited in a marginal lacustrine environment with a fluctuating water level (Reineck and Wunderlich, 1968; Cohen, 1982; Paik and Chun, 1993).

The maximum depositional ages of the Haman Formation and the overlying Jindong Formation were dated to be 105.4 ± 0.4 Ma and 99.9 ± 0.7 Ma, respectively, by a recent U–Pb analysis of detrital zircons using SHRIMP and MC-ICPMS (Lee et al., 2018b). The Gusandong (Kusandong) Tuff is a key bed that is distributed over a wide range (200 km) between the Haman and Jindong formations. The eruption ages of the northern and the southern Gusandong Tuff (NKT and SKT) are 103.0 ± 1.2 Ma and 104.1 ± 1.3 Ma, respectively, by SHRIMP U–Pb analysis (Kim et al., 2013). Since the boundary between the Lower and Upper Cretaceous is placed in 100 Ma (Walker et al., 2013), the Haman Formation corresponds to late Albian in age.

3. Methods

The exposed surface was digitally mapped using photogrammetry to obtain 3D images of the whole track-bearing layers as well as the close-up images of the best-preserved footprints. The camera and the data processing software used in this study are Nikon D300 and Agisoft Photoscan (Metashape) Standard edition (Agisoft, 2014). After producing a single 3D model and a point cloud of each layer, a ply file was exported for post-processing using CloudCompare (version 2.10-beta; Girardeau-Montaut, 2016). CloudCompare was used to resize the model and to match the actual tracksite with the elimination of the unnecessary part, and to obtain the contour data of each footprint and the whole track-bearing layers. Outline drawings of the tracks and tracksite were drawn using the combination of a contour map and an image of the tracksite using Adobe Illustrator. Also, each track-bearing layers were photographed using a drone (MAVIC 2 Zoom) from above the surface.

The terminology used here follows the work of Lockley (2009), Castanera et al. (2013), and Lee et al. (2018c). Measurements were taken for the footprint length (L), the footprint width (W), the ratio of footprint length and width (L/W), the length of digits (II, III, IV),

divarication angles between digits (D(II–III), D(III–IV)), the anterior triangle length and width (AT l, AT w) and the ratio between them (AT l/w), the stride length (SL), the pace length (PL), the pace angulation (ANG), the azimuth of a track (azimuth), and the track rotation inside trackway (TR). The measurement procedures of Lockley (2009) and Castanera et al. (2013) were modified and used for the tracks and trackways (Fig. 3). The midpoint of the distal end of digit III was generally set as a reference point for measurement because digit III imprints show good preservation in most tracks, unlike a heel pad impression or other parts of footprints. However, due to the preservational inconsistency, we exceptionally designated the distal end of the heel impression as a reference point for Trackway 2E. Measurements of the footprints were created using Adobe Illustrator from the line drawings. Measurement of the surface area of the outcrops was calculated through the software ImageJ (Rasband, 1997). A rose diagram of the azimuth of tracks was plotted using GeoRose software (version 0.5.1; Yong, 2015).

4. Description

Except for Layer A, 58 footprints were mapped and measured from three track-bearing layers (Fig. 4). Seven trackways consisting of 32 footprints were identified on Layers 1 (GBDT-1A, 1B) and 2 (GBDT-2A, 2B, 2C, 2D, 2E), along with 26 isolated footprints from three track-bearing layers (Fig. 5A). Footprints on Layer 3 are all isolated tracks. All tracks are preserved as depressions of sizes ranging from 12.9 cm to 26.8 cm with an average 18.7 cm in length (Fig. 5B). Among the trackways, Trackway GBDT-1B consists of the smallest footprints with an average 16.6 cm in length while the largest ones with an average 22.2 cm in length belong to Trackway GBDT-2A. Due to the limited exposure of the outcrop surface, all trackways from the Gunbuk tracksite consist of only three to six consecutive footprints.

The track-bearing layers are located at the bottom of a small creek where the stream flows. The tracks must have been continuously washed out after subaerial exposure. Therefore, most of the tracks do not show detailed morphologies due to the eroded surface of the track-bearing layers. Nevertheless, some deeply

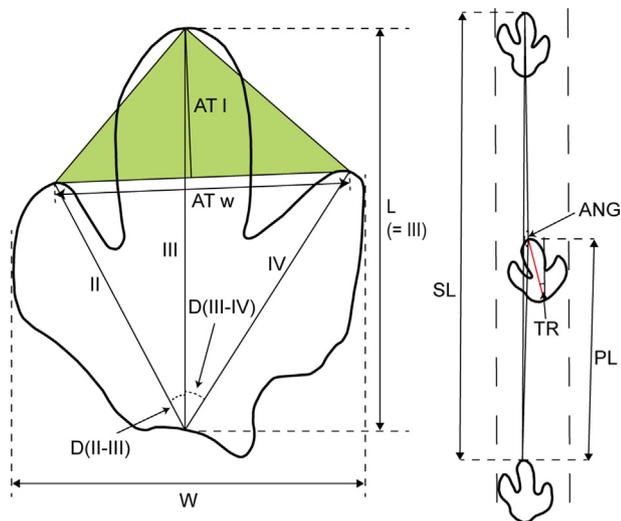


Fig. 3. Measurements taken from the individual tracks and the trackway segments (modified from Castanera et al., 2013). Green triangle refers to the anterior triangle of the track. Abbreviations: L = footprint length; W = footprint width; II = digital length of digit II; III = digital length of digit III (= L); IV = digital length of digit IV; AT I = anterior triangle length; AT w = anterior triangle width, D(II-III) = divarication angle between digits II and III; D(III-IV) = divarication angle between digits III and IV; SL = stride length; PL = pace length; ANG = pace angulation; TR = track rotation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

impressed tracks are exceptionally well preserved without big deformation. No manus tracks are observed in this tracksite. Pes prints are tridactyl with a sub-symmetrical outline, showing wide and short digits with blunt distal ends (Fig. 6). Tracks do not show distinct claw marks. Most tracks are longer than wide or similar in length and width (L/W ratio from 0.89 to 1.30) with one peculiar exception (1.61). Nonetheless, the average L/W ratios of the tracks are relatively consistent in the trackways, ranging from 1.01 to 1.18 (average 1.08; Table 1). The average divarication angle between digits II-III (D(II-III)) and digits III-IV (D(III-IV)) are 29.3° and 30.1°, respectively. However, these angles are more inconsistent between digits II-III than digits III-IV, ranging from 20.1° (GBDT-2C) to 36.2° (GBDT-1B). The average anterior triangle ratio (AT I/w) of the tracks is 0.43, showing that digit III is relatively enlarged than other digits. All tracks of the trackways show an inward (negative) rotation (mostly within 12°), but several tracks show a greater rotation than 20°.

The pace and stride lengths of all trackways vary from 54.6 cm and 107.9 cm (GBDT-2D) to 74.4 cm and 147.5 cm (GBDT-2B), respectively. The pace angulation ranges from an average of 152.5° (GBDT-2E) to 177.6° (GBDT-2A) with an average of 167.4°. Although half of the footprints are isolated and somewhat randomly distributed, the azimuths of tracks are quite concentrated around 120°–150° (Fig. 5C). Two trackways in Layer 1 (GBDT-1A, 1B) show the average azimuths of 143.4° and 141.4°, displaying almost parallel orientation while those of five trackways in Layer 2 (GBDT-2A, 2B, 2C, 2D, 2E are 33.3°, 123.8°, 39.6°, 136.5°, and 148.0°, respectively) are concentrated in two orientations that show near perpendicular orientation to each other (2A and 2C versus 2B, 2D, and 2E).

5. Discussion

5.1. Comparisons to neornithischian ichnotaxa (Fig. 7)

In South Korea, Cretaceous ornithopod tracks have been mainly discovered from the Late Cretaceous Jindong Formation of the

Gyeongsang Basin, South Gyeongsang Province (Lee et al., 2001; Huh et al., 2003; Lockley et al., 2006; Kim and Huh, 2018), including two ichnotaxa, *Ornithopodichnus masanensis* (Kim et al., 2009) and *Caririchnium kyoungsookimi* (Lim et al., 2012). However, Díaz-Martínez et al. (2015) declared *O. masanensis* as a nomen dubium and emended *C. kyoungsookimi* as *Hadrosauropodus kyoungsookimi*. Tracks originally reported as *Ornithopodichnus* were robust and slightly wide tridactyl tracks with a weakly developed digit III (Kim et al., 2009; Lockley et al., 2012b, 2014), which differ from the Gunbuk ornithopod tracks in morphology. *H. kyoungsookimi* tracks are diagnosed with small manus prints and large pes prints with bilobed 'heel' impressions, which is also different from the pes-only Gunbuk tracks with rounded 'heel' impressions. On the other hand, the Early Cretaceous ornithopod tracks have been occasionally reported from isolated small basins in South Korea. *Caririchnium yeongdongensis* (Kim et al., 2016) reported from the Lower Cretaceous Sainri Formation (Valanginian-Hauterivian) of the Yeongdong Basin, North Chungcheong Province has pes prints similar to the Gunbuk tracks, but its diagnosis mainly depends on the characteristics of manus prints. Therefore, a meaningful comparison cannot be determined between the two. In other cases, *Caririchnium*-type tracks discovered from the Lower Cretaceous Sanbukdong Formation of an unnamed small basin in the west of Gunsan City, North Jeolla Province also have morphological similarity to those of the Gunbuk tracks in general (Lee et al., 2018c). Unfortunately, detailed comparisons are difficult due to the poor preservation of tracks.

Tsukiji et al. (2018) reported ornithopod footprints from the Lower Cretaceous Kitadani Formation (Aptian) and classified them as *Caririchnium* sp. and *Amblydactylus* sp. mainly based on their L/W ratio and 'mesaxony' of tracks. Pes prints of *Caririchnium* sp. are similar to those of the Gunbuk tracks, showing a high AT I/w ratio (average 0.43), indicating that digit III is relatively enlarged than other digits. However, the Kitadani tracks include manus impressions occasionally. Unlike *Caririchnium* tracks, *Amblydactylus* tracks are wider than their length with a low AT I/w ratio (average 0.27), which differ from the Gunbuk tracks. Other ornithopod tracks from the Lower Cretaceous Tetori Group have been also reassigned recently as *Caririchnium* and *Amblydactylus* (Tsukiji et al., 2019).

Some small neornithischian ichnotaxa, such as *Anomoepus* (Olsen and Rainforth, 2003; Lockley and Matsukawa, 2009; Xing et al., 2017) and *Dinehichnus* (Lockley et al., 1998) show similarity with the Gunbuk tracks based on their small footprint size, inward rotation in trackways, and symmetrical, tridactyl pedal morphology. However, these Triassic to Early Cretaceous ichnogenera are easily distinguished from the Gunbuk tracks by having gracile and long digit impressions with relatively sharp claw marks, and a small and rounded metatarsophalangeal impression. Early Cretaceous *Neoanomoepus* is characterized by tetradactyl (occasionally preserved as tridactyl), slightly elongate pes and pentadactyl manus tracks (Lockley et al., 2009), showing no similarity to the Gunbuk tracks.

Ichnotaxonomically, the Gunbuk tracks well correspond to the diagnosis of ichnogenus *Caririchnium* such as the wide and short, blunt digits and rounded 'heel' pad impression that is wider than the proximal part of the digit III impression (Díaz-Martínez et al., 2015; Xing et al., 2015). All *Caririchnium* ichnospecies except for *C. lotus* from the Jiaguan Formation (Barremian-Albian) of China exhibit tracks wider than their length (Xing et al., 2007, 2015; Díaz-Martínez et al., 2015). At the ichnospecies level of *Caririchnium*, the 'heel' pad impression, longer than wide, was used as an autapomorphic character of *C. lotus* (Xing et al., 2007, 2015). Notably, ornithopod tracks discovered from the Lower Cretaceous Sanbukdong Formation are very similar to *C. lotus* in this respect (Lee et al., 2018c). Unfortunately, the Gunbuk tracks show morphological and

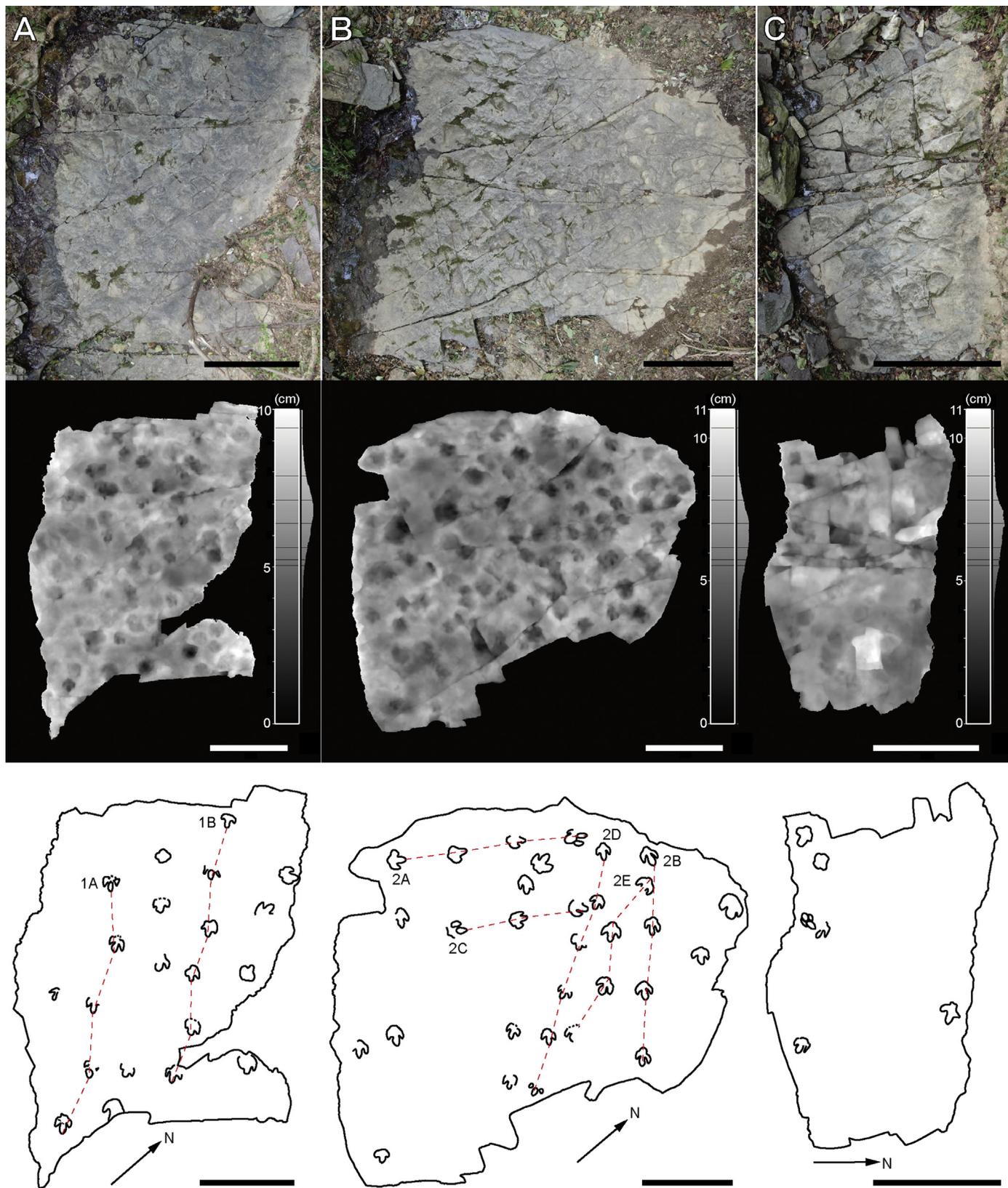


Fig. 4. Photographs taken using a drone from above the surface (upper row), 3D photogrammetric depth maps (middle row), and the schematic maps as line drawings (lower row) of track-bearing layers. A) Layer 1. B) Layer 2. C) Layer 3. Elevation scale on the depth maps are in cm. Scale bars are all 1 m in length.

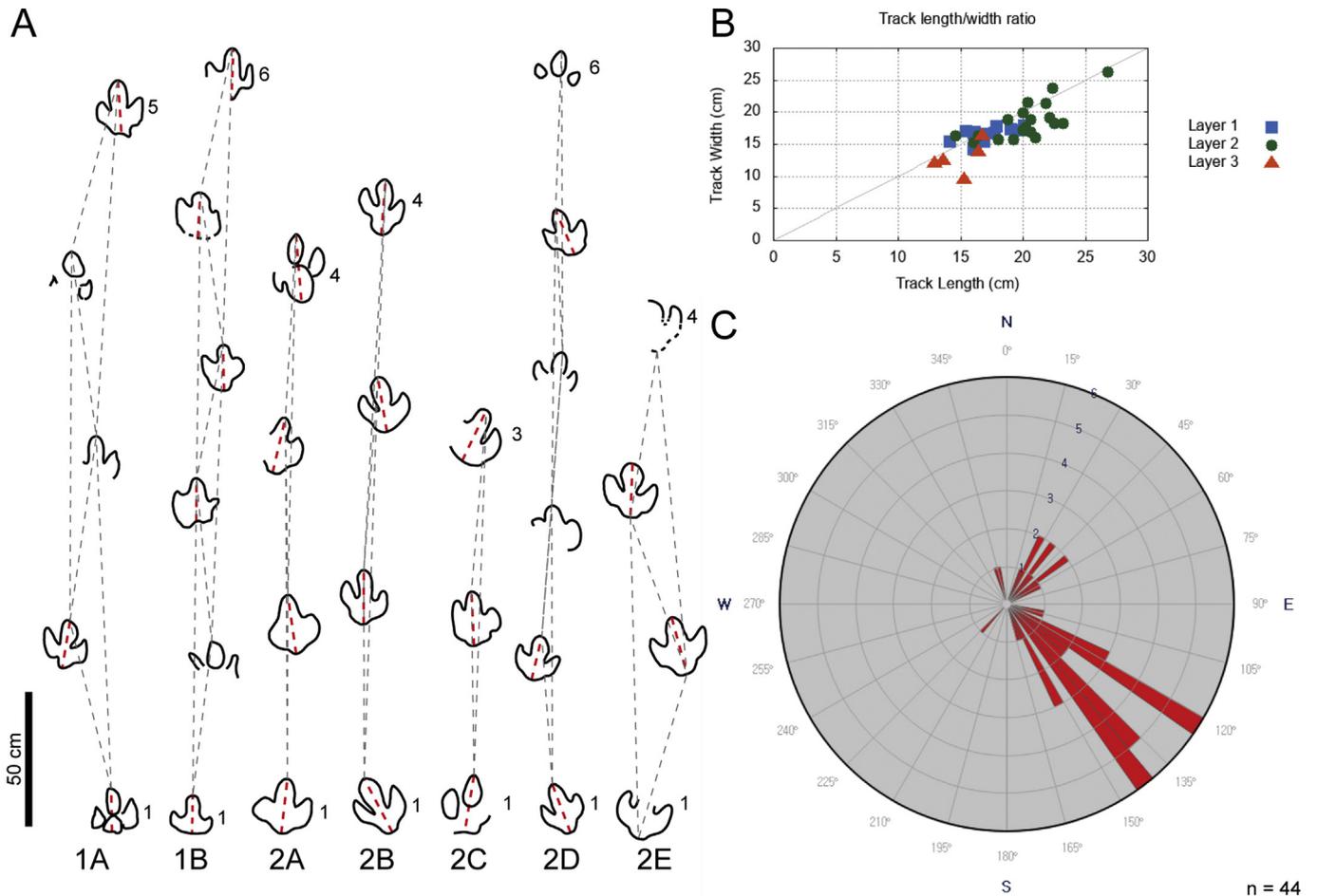


Fig. 5. Seven ornithod trackways with a bivariate plot of footprint length-width measurements and a rose diagram. A) Outline drawings of six trackways. Red dotted lines refer to the azimuths of individual tracks. Gray dotted lines refer to the stride and pace lengths of the trackways. B) Bivariate plot of track length versus width. C) Rose diagram plotting the azimuths of 44 individual tracks from three track-bearing horizons. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

preservational variation of the metatarsophalangeal dimension. Therefore, it is reasonable to conclude that they are assigned to *Caririchnium* isp.

5.2. Age and speed estimation

When Xing et al. (2007) reported *C. lotus* ornithod tracks from the Lower Cretaceous Jiaguan Formation of China, they subdivided them into three age groups according to track lengths: 37–40 cm (adults), 25–30 cm (subadults), and 19–23 cm (juveniles). Similarly, Matsukawa et al. (1999) subdivided footprints that belong to

Caririchnium leonardii from the Dakota Group (Albian-Cenomanian) of North America into three age groups corresponding to track lengths: 29.3–55.0 cm (adults), 21.7–29.3 cm (subadults), and 16.5–21.7 cm (juveniles). Most of the Early Cretaceous ornithod pes imprints found in South Korea also range from 20 cm to 50 cm in length (Kim and Pickerill, 2003; Lockley et al., 2012c; Kim et al., 2016; Lee et al., 2018c). Interestingly, all pes tracks of the Gunbuk site do not exceed 27 cm in length, clearly indicating that they were imprinted by the juvenile to subadult ornithod. Morphological consistency between adults and subadults of *C. lotus* (Xing et al., 2007) supports the immaturity of the Gunbuk trackmakers. There

Table 1
The average value (in cm) of seven ornithod trackways from the Gunbuk tracksite.

Trackway	L	W	L/W	II	III	IV	D(II-III)	D(III-IV)	Azimuth	SL	PL	ANG	AT I/w
GBDT-1A	17.8	17.0	1.05	12.7	17.8	15.1	29.8	31.4	143.4	133.8	67.3	159.9	0.50
GBDT-1B	16.6	16.4	1.01	12.7	16.6	13.6	36.2	30.7	141.4	111.3	56.3	163.1	0.37
GBDT-2A	22.2	20.4	1.05	15.3	22.2	17.2	29.3	29.3	33.3	134.1	67.6	177.6	0.52
GBDT-2B	20.9	17.8	1.18	15.9	20.9	17.1	26.4	26.6	123.8	147.5	74.4	177.0	0.41
GBDT-2C	20.8	17.7	1.14	17.5	20.8	16.0	20.1	28.4	39.6	135.9	68.0	174.5	0.32
GBDT-2D	17.9	16.0	1.13	14.1	17.9	13.6	30.6	31.6	136.5	107.9	54.6	174.9	0.40
GBDT-2E	20.9	20.5	1.01	16.9	20.9	18.2	32.7	32.5	148.0	119.9*	62.7*	148.0*	0.32
Average	19.6	18.0	1.08	15.0	19.6	15.8	29.3	30.1	–	127.2	64.4	167.9	0.41

Abbreviations: ANG = pace angulation; AT I/w = ratio of anterior triangle length to width; D (II-III) = divarication angle between digits II and III; D (III-IV) = divarication angle between digits III and IV; L = footprint length; L/W = ratio of footprint length to width; PL = pace length; SL = stride length; W = footprint width; II = digital length of digit II; III = digital length of digit III; IV = digital length of digit IV. * refers to the measurement value based on the presumptive track morphology.

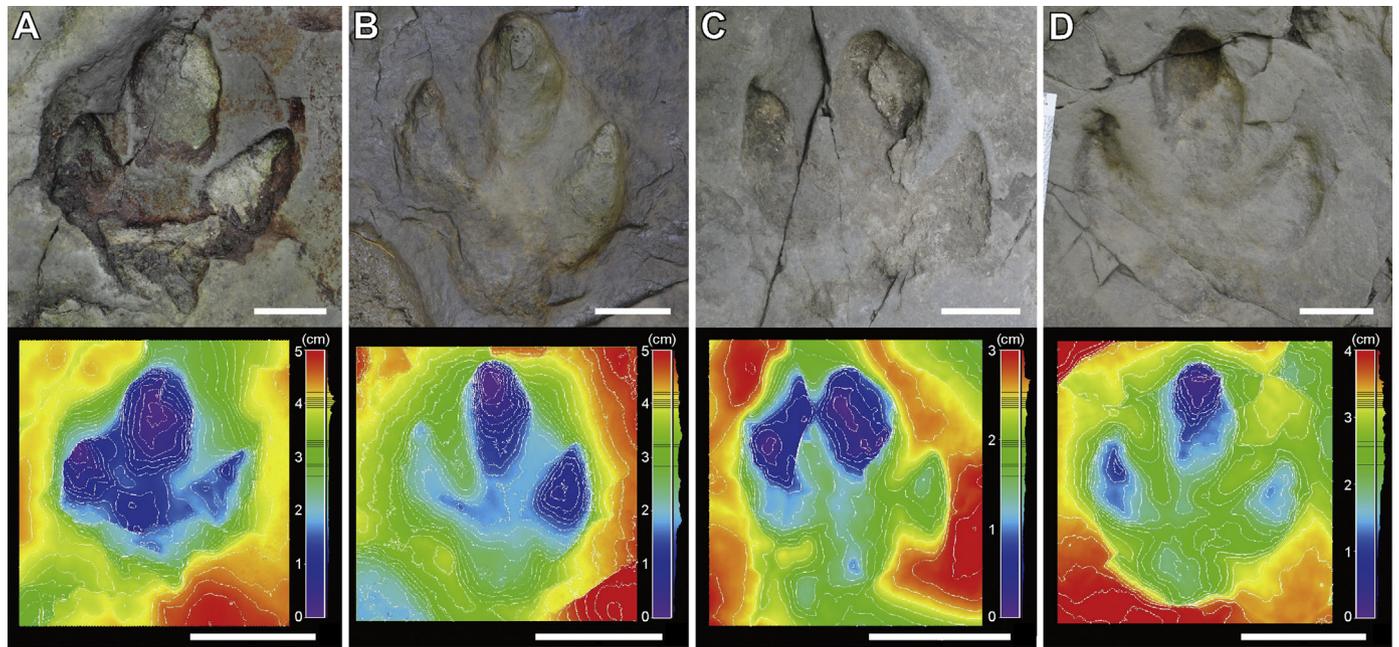


Fig. 6. Photos of the footprint (upper row) and 3D photogrammetric depth maps with contour lines (interval 2 mm; lower row). A) GBDT-1A-5. B) GBDT-2B-1. C) GBDT-1A-2. D) GBDT-2B-3. Scale bar on photos = 5 cm. Scale bar on depth maps = 10 cm. Elevation scale on the depth maps are in cm.

are no manus tracks observable from the Gunbuk tracksite. Although all manus tracks might be differentially eroded from the stream at the bottom of the valley, the probability is very low because most of the pes tracks are deeply impressed (average 2.7 cm, up to 5.3 cm). Therefore, it is reasonable to assume that the Gunbuk tracks were imprinted by bipedal animals.

Several formulas are being used for the estimation of size, locomotion speed, gait, and body length or mass of trackmakers from the measurements of the trackways and tracks (Alexander, 1976; Thulborn, 1982, 1989). In the estimation of the trackmaker's hip height, estimates for small ornithomorphs were used (hip height:

$h = 4.8L$; Thulborn, 1989). By following their formulas, the hip heights (h) of the trackmakers range from 79.7 cm to 106.6 cm with an average of 94.0 cm. The relative stride lengths (SL/h) vary between 1.20 and 1.56, implying that all trackways are imprinted by constant walking (Thulborn, 1984). Locomotion speed ranges from 3.8 km/h to 5.5 km/h (Table 2).

5.3. Locomotory pattern

Most of the Gunbuk pes tracks show centered and developed digit III impressions with a high AT l/w ratio, which is frequently

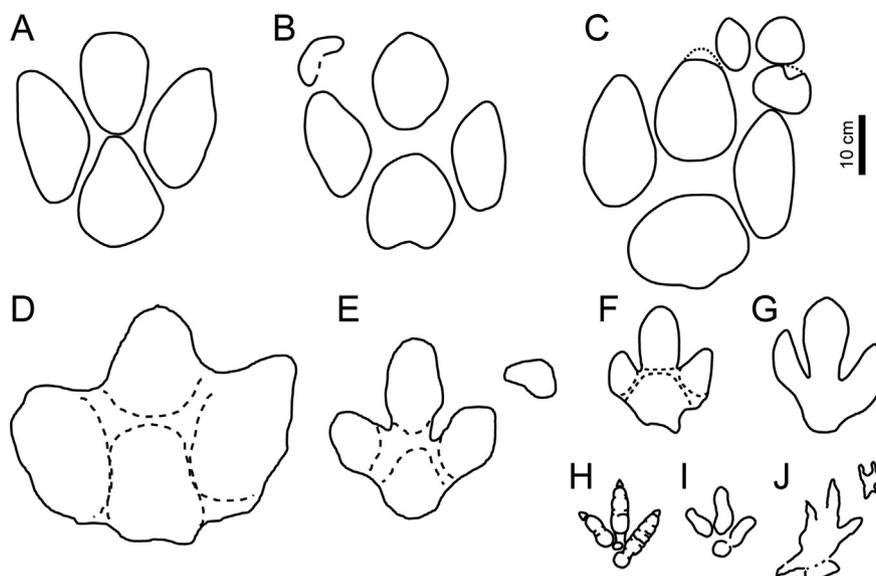


Fig. 7. Comparisons of Gunbuk tracks to the neornithischian ichnotaxa. A) *Caririchnium lotus* (redrawn from Xing et al., 2007). B) *Hadrosauropodus kyoongsookimi* (redrawn from Lim et al., 2012). C) *C. yeongdongensis* (redrawn from Kim et al., 2016). D) *Amblydactylus* isp. (redrawn from Tsukiji et al., 2018). E) *Caririchnium* isp. (redrawn from Tsukiji et al., 2018). F-G) Tracks from the Gunbuk tracksite (GBDT-1A-5 and GBDT-2B-1). H) *Anomoepus scambus* (redrawn from Olsen and Rainforth, 2003). I) *Dinehichnus socialis* (redrawn from Lockley et al., 1998). J) *Neoanomoepus perigrinatus* (redrawn from Lockley et al., 2009).

Table 2
Speed estimations of the trackways.

Trackway	Hip Height (cm)	Relative SL	Speed (m/s)	Speed (km/h)
GBDT-1A	85.6	1.56	1.53	5.49
GBDT-1B	79.7	1.40	1.22	4.39
GBDT-2A	106.6	1.26	1.19	4.27
GBDT-2B	100.4	1.47	1.49	5.36
GBDT-2C	99.7	1.36	1.31	4.72
GBDT-2D	85.8	1.26	1.06	3.83
GBDT-2E	100.3	1.20*	1.06*	3.80*
Average	94.0	1.36	1.26	4.55

* refers to the estimated values.

described to be 'mesaxonic' in purely geometric and dimensional terms (Lockley, 2009; Romano et al., 2020). Nonetheless, here we describe 'axony' in a functional term, as an axis that receives the greatest load during locomotion (*sensu* Leonardi, 1987; Romano et al., 2020).

Gunbuk tracks generally show deeper impressions in the digits than the metatarsophalangeal impression, meaning that the load was mostly supported by the digits. Some well-preserved tracks like GBDT-1A-5 or GBDT-2B-1 (Figs. 6A, B) show deep impressions on digits II and III, implying that the load was mainly supported by the centro-medial part of the pes (entaxonic) during the maximum load phase. However, the GBDT-1A-2 (Fig. 6C) exhibits deeper impressions on digits III and IV than other parts of the footprint, indicating that the weight was mainly supported by the centro-lateral part of the pes (ectaxonic) during the maximum load phase, and showing the opposite condition in which its locomotory pattern was not consistent even within one trackway from the point of view of the maximum load phase (Lallensack et al., 2016; Razzolini et al., 2016). Moreover, only the distal part of digit III is more deeply impressed (mesaxonic) in GBDT-2B-3 (Fig. 6D). Such an impression might represent the kick-off phase, when the tip of the third toe break through the surface of the substrate.

5.4. Juvenile gregarious behavior

The possible gregarious behavior of dinosaurs has been reported many times, such as multiple (sub-) parallel trackways, the congregation of eggs and nests, or the concentration of skeletons of a single or similar species (Ostrom, 1972; Horner and Makela, 1979; Currie, 1998; Kobayashi and Lü, 2003). Although there are many reports on multiple parallel ornithopod trackways in the world, most of them were imprinted by only adults or a mixed group of adults and juveniles (Carpenter, 1992; Matsukawa et al., 2001; Zhang et al., 2006; Xing et al., 2007, 2015; Kim et al., 2009; Lockley et al., 2012c; Fiorillo et al., 2014; Piñuela et al., 2016). Although evidence of the juvenile communities had been reported among various dinosaur taxa such as ornithomimids, sauropods, and ceratopsians based on their body fossils (Varricchio et al., 2008; Myers and Fiorillo, 2009; Zhao et al., 2013), the ichnological evidence for proving is relatively rare in ornithopod dinosaurs.

Pérez-Lorente et al. (1997) reported three parallel small to medium-sized tridactyl trackways from the Les Cerradicas tracksite (Berriasian), Spain and interpreted them as gregarious behavior. However, the ichnotaxon and age of the trackmakers are uncertain. On the other hand, sixteen multiple trackways of small ornithopods (*Caririchnium*) were discovered from the Mosquero Creek tracksite, Mesa Rica Formation (early Upper Cretaceous), New Mexico (Lockley and Hunt, 1995). These trackways were hypothesized as herding at first and later were supported based on their distribution of speed and direction as well as the relationship between track size and relative stride length (Cotton et al., 1998). In South

Korea, at least six parallel trackways of small ornithopods (track length 12–15 cm) from the Upper Cretaceous Neungju Basin, South Jeolla Province were also interpreted as the herding of small ornithopods (Lockley et al., 2012b).

Gunbuk trackways can be subdivided into three groups based on their orientations: Group 1 (Trackways GBDT-1A and GBDT-1B), Group 2 (Trackways GBDT-2A and GBDT-2C), and Group 3 (GBDT-2B, GBDT-2D, and GBDT-2E). The average azimuths of Group 1 and Group 2 show the parallel orientation of two trackways (Table 1). Assuming that the lake shoreline did not dramatically change from the ripple azimuth of 120° on Layer A, Group 1 can be interpreted as moving side to side along the lake shoreline implying the herding of Group 1, while Group 2 might have moved away perpendicularly from the lake. In Group 3, trackways GBDT-2D and 2E seem to be crossing Trackway GBDT-2B at angles around 13° and 12°, respectively. These trackways can be also interpreted as moving along the lake shoreline. All cases above support the hypothesis that juvenile ornithopods were gregarious and moved as independent clusters after hatching until they joined herds of more mature animals (Currie and Sarjeant, 1979; Currie, 1983).

Cotton et al. (1998) argued that ornithopod trackways from the Mosquero Creek, Dakota Group show a negative correlation between footprint size and relative stride, indicating that smaller and larger animals reach similar locomotion speed as they move together. Trackway GBDT-1A shows larger footprints and longer relative stride length than those of GBDT-1B, indicating that the former simply walked faster than the latter. On the other hand, GBDT-2A shows larger footprints but shorter relative stride length than those of GBDT-2C, suggesting slow walking to lower the gap of moving speed between the two trackmakers (Table 2). Trackmakers of GBDT-2A and 2C were likely to be moving together, but the trackways at the Gunbuk tracksite are too short to obtain statistical significance. Therefore, this suggestion remains tentative.

5.5. Possible trackmaker

All footprints are sub-symmetrical tridactyl pes tracks, which can be interpreted as theropod or ornithopod tracks (Castanera et al., 2013). In general, theropod pes prints show a larger L/W ratio with narrower and longer digits than those of ornithopod footprints because theropods had the acuminate distal end of digits with sharp claws while ornithopods had the blunt distal end of digits and a rounded metatarsophalangeal ('heel') impression (Moratalla et al., 1988). All morphological characteristics of the Gunbuk tracks indicate that the trackmakers were ornithopods rather than theropods. Moreover, the strong negative rotation of tracks is one of the key characters in ornithopod trackways (Moratalla et al., 1992).

Considering only the size of footprints, small basal Early Cretaceous neornithischians such as jeholosaurids and parksosaurids might be possible candidates of the trackmakers. However, their tracks are more gracile than those of larger and derived ornithopods, having relatively slender and long digits with claw marks (Thulborn, 1994; Olsen and Rainforth, 2003; Gierliński et al., 2009). Most of the tracks from the Gunbuk tracksite have wide and short digits with the blunt distal end without claw marks, suggesting that more derived ornithopods with blunt toes are more reasonable to be considered as potential trackmakers.

Lee and Lee (2007) reported a maxillary tooth from the Lower Cretaceous Hasandong Formation (Aptian) that belongs to a derived iguanodontoid. Likewise, a derived iguanodontian *Fukuisaurus* and a basal hadrosauroid *Koshisaurus* (Kobayashi and Azuma, 2003; Shibata and Azuma, 2015) were discovered from the Lower Cretaceous Kitadani Formation (Aptian), Japan. A non-hadrosauroid iguanodontian *Equijubus* was also reported from the

Gonqpoquan Basin (Aptian), Gansu Province, China (You et al., 2003). In the Albian age, a derived iguanodontid *Altirhinus* (Norman, 1998), and basal hadrosauroids like *Probactrosaurus* (Rozhdestvensky, 1967; Norman, 2002) and *Penelopognathus* (Godefroit et al., 2005) have been reported from Mongolia and Inner Mongolia of China. Considering the temporal and paleogeographical distribution, the trackmakers of the Gunbuk tracksite were most likely attributable to juveniles to subadults of derived iguanodonts or basal hadrosauroids.

6. Conclusions

The Gunbuk tracksite provides a window into the Early Cretaceous ornithopod communities that lived in a marginal lacustrine environment of the Gyeongsang Basin in South Korea. Based on the footprint size and morphological characteristics, all tracks can be assigned to *Caririchnium* isp. Trackmakers are possibly juveniles or subadults of derived iguanodonts or basal hadrosauroids. Trackways generally show preferred orientations in subparallel directions, implying gregarious behavior of juvenile ornithopods moved along the lake shoreline. The total absence of adult footprints on three track-bearing horizons at the tracksite suggests that juvenile ornithopods occasionally formed juvenile-only clusters and moved independently from adult groups.

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References

Agisoft, L., 2014. Agisoft Photoscan (data analysis software). Standard version, from: <http://www.agisoft.com>.

Alexander, R.M., 1976. Estimates of speeds of dinosaurs. *Nature* 261, 129–130.

Baek, K., Yang, S., 1997. Preliminary report on the Cretaceous bird tracks of the Lower Haman Formation. Korea. *Journal of the Geological Society of Korea* 34, 94–104.

Carpenter, K., 1992. Behavior of hadrosaurs as interpreted from footprints in the "Mesaverde" Group (Campanian) of Colorado, Utah, and Wyoming. *Rocky Mountain Geology* 29, 81–96.

Castanera, D., Pascual, C., Razzolini, N.L., Vila, B., Barco, J.L., Canudo, J.I., 2013. Discriminating between medium-sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). *PloS One* 8, e81830.

Chang, K.H., 1975. Cretaceous stratigraphy of southeast Korea. *Journal of the Geological Society of Korea* 11, 1–23.

Choi, Y., Kim, T., 1963. 1: 50,000 Geological map of Uiryong Sheet. Geological Survey of Korea, p. 12.

Chough, S., Sohn, Y., 2010. Tectonic and sedimentary evolution of a Cretaceous continental arc-backarc system in the Korean peninsula: new view. *Earth-Science Reviews* 101, 225–249.

Cohen, A.S., 1982. Paleoenvironments of root casts from the Koobi Fora Formation, Kenya. *Journal of Sedimentary Research* 52, 401–414.

Cotton, W.D., Cotton, J.E., Hunt, A.P., 1998. Evidence for social behavior in ornithopod dinosaurs from the Dakota Group of northeastern New Mexico, USA. *Ichnos: An International Journal of Plant & Animal* 6, 141–149.

Currie, P.J., 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Palaeontologica Polonica* 28, 63–73.

Currie, P.J., 1998. Possible evidence of gregarious behavior in tyrannosaurids. *Gaia* 15, 271–277.

Currie, P.J., Sarjeant, W.A., 1979. Lower cretaceous dinosaur footprints from the peace River Canyon, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28, 103–115.

Diaz-Martinez, I., Pereda-Suberbiola, X., Perez-Lorente, F., Canudo, J.I., 2015. Ichnotaxonomic review of large ornithopod dinosaur tracks: temporal and geographic implications. *PloS One* 10, e0115477.

Falk, A.R., Hasiotis, S.T., Martin, L.D., 2010. Feeding traces associated with bird tracks from the Lower Cretaceous Haman Formation, Republic of Korea. *PALAIOS* 25, 730–741.

Falk, A.R., Lim, J., Hasiotis, S., 2014. A behavioral analysis of fossil bird tracks from the Haman Formation (Republic of Korea) shows a nearly modern avian ecosystem. *Vertebrata Palasiatica* 52, 129–152.

Fiorillo, A.R., Hasiotis, S.T., Kobayashi, Y., 2014. Herd structure in Late Cretaceous polar dinosaurs: a remarkable new dinosaur tracksite. Denali National Park, Alaska, USA. *Geology* 42, 719–722.

Gierliński, G., Niedźwiedzki, G., Nowacki, P., 2009. Small theropod and ornithopod footprints in the Late Jurassic of Poland. *Acta Geologica Polonica* 59, 221–234.

Girardeau-Montaut, D., 2016. CloudCompare (GPL Software) version 2.10-beta, from: <http://www.cloudcompare.org/>.

Godefroit, P., Li, H., Shang, C.-Y., 2005. A new primitive hadrosauroid dinosaur from the Early Cretaceous of Inner Mongolia (PR China). *Comptes Rendus Palevol* 4, 697–705.

Horner, J.R., Makela, R., 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282, 296–298.

Huh, M., Hwang, K.G., Paik, I.S., Chung, C.H., Kim, B.S., 2003. Dinosaur tracks from the Cretaceous of South Korea: distribution, occurrences and paleobiological significance. *Island Arc* 12, 132–144.

Huh, M., Paik, I.S., Lockley, M.G., Hwang, K.G., Kim, B.S., Kwak, S.K., 2006. Well-preserved theropod tracks from the Upper Cretaceous of Hwasun County, southwestern South Korea, and their paleobiological implications. *Cretaceous Research* 27, 123–138.

Hwang, K.-G., Huh, M., Lockley, M.G., Unwin, D.M., Wright, J.L., 2002. New pterosaur tracks (Pteraidnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea. *Geological Magazine* 139, 421–435.

Kim, B.K., 1969. A study of several sole marks in the Haman Formation. *Journal of the Geological Society of Korea* 5, 243–258.

Kim, J.-S., Cho, H., Kim, H.-G., Son, M., 2013. SHRIMP U-Pb zircon ages of the Gusandong (Kusandong) Tuff in the Cretaceous Gyeongsang Basin. *The Journal of the Petrological Society of Korea* 22, 235–249.

Kim, J.Y., Huh, M., 2018. *Dinosaurs, Birds, and Pterosaurs of Korea*. Springer.

Kim, J.Y., Lockley, M.G., 2012. New sauropod tracks (*Brontopodus pentadactylus* ichnosp. nov.) from the Early Cretaceous Haman Formation of Jinju area, Korea: implications for sauropods manus morphology. *Ichnos* 19, 84–92.

Kim, J.Y., Lockley, M., 2016. First report of turtle tracks from the Lower Cretaceous of Korea. *Cretaceous Research* 64, 1–6.

Kim, J.Y., Pickerill, R., 2003. Cretaceous nonmarine trace fossils from the Hasandong and Jinju Formations of the Namhae Area, Kyongsangnamdo, southeast Korea. *Ichnos* 9, 41–60.

Kim, J.Y., Kim, S.H., Kim, K.S., Lockley, M., 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): more evidence of high avian diversity in East Asia. *Cretaceous Research* 27, 56–69.

Kim, J.Y., Kim, K.S., Lockley, M.G., Yang, S.Y., Seo, S.J., Choi, H.I., Lim, J.D., 2008. New didactyl dinosaur footprints (*Dromaeosauripus hamanensis* ichnogen. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 262, 72–78.

Kim, J.Y., Lockley, M.G., Kim, H.M., Lim, J.-D., Kim, K.S., 2009. New dinosaur tracks from Korea, *Ornithopodichnus masanensis* ichnogen. et ichnosp. nov. (Jindong Formation, Lower Cretaceous): implications for polarities in ornithopod foot morphology. *Cretaceous Research* 30, 1387–1397.

Kim, H.J., Paik, I.S., Huh, M., 2011. Bird footprint-bearing deposits from the Cretaceous Haman Formation in the southern Gyeongsang Basin: occurrences, taphonomy and paleoenvironments. *Journal of the Geological Society of Korea* 47, 97–122.

Kim, J.Y., Lockley, M.G., Seo, S.J., Kim, K.S., Kim, S.H., Baek, K.S., 2012a. A paradise of Mesozoic birds: the world's richest and most diverse Cretaceous bird track assemblage from the Early Cretaceous Haman Formation of the Gajin tracksite, Jinju, Korea. *Ichnos* 19, 28–42.

Kim, J., Lockley, M., Kim, K., Seo, S., Lim, J., 2012b. Enigmatic giant pterosaur tracks and associated ichnofauna from the Cretaceous of Korea: implication for the bipedal locomotion of pterosaurs. *Ichnos* 19, 50–65.

Kim, J.Y., Lockley, M.G., Chun, H.Y., 2016. New dinosaur tracks from the Lower Cretaceous (Valanginian-Hauterivian) Saniri Formation of Yeongdong area, central Korea: Implications for quadrupedal ornithopod locomotion. *Cretaceous Research* 61, 5–16.

Kim, K.S., Lockley, M.G., Lim, J.D., Piñuela, L., Xing, L., Moon, H.W., 2017a. First report of lacertiform (lizard) tracks from the Cretaceous of Asia. *Cretaceous Research* 69, 62–70.

Kim, K.S., Lim, J.D., Lockley, M.G., Xing, L., Choi, Y., 2017b. Korean trackway of a hopping, mammaliform trackmaker is first from the Cretaceous of Asia. *Cretaceous Research* 74, 188–191.

Kim, H.J., Paik, I.S., Kim, S., Lee, H., 2018. Sedimentary facies, paleoenvironments, and stratigraphy of the Haman Formation (Early Cretaceous) in Sopo-ri, Hainan-gun, Gyeongsangnam-do, Korea. *Journal of the Geological Society of Korea* 54, 1–19.

Kobayashi, Y., Azuma, Y., 2003. A new iguanodontian (Dinosauria: Ornithopoda) from the Lower Cretaceous Kitadani Formation of Fukui Prefecture, Japan. *Journal of Vertebrate Paleontology* 23, 166–175.

Kobayashi, Y., Lü, J.-C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica* 48, 235–259.

Lallensack, J.N., van Heteren, A.H., Wings, O., 2016. Geometric morphometric analysis of intratrackway variability: a case study on theropod and ornithopod

- dinosaur trackways from Münchheggen (Lower Cretaceous, Germany). PeerJ 4, e2059.
- Lee, Y.-N., Lee, H.-J., 2007. The first ornithopod tooth in Korea. Journal of the Paleontological Society of Korea 23, 213.
- Lee, Y.-N., Yang, S.-Y., Seo, S.-J., Baek, K.-S., Yi, M.-S., Lee, D.-J., Park, E.-J., Han, S.-W., 2000. Distribution and paleobiological significance of dinosaur tracks from the Jindong Formation (Albian) in Kosong County, Korea. Journal of the Paleontological Society of Korea, Special Publication 4, 1–12.
- Lee, Y.-N., Yu, K.-M., Wood, C.B., 2001. A review of vertebrate faunas from the Gyeongsang Supergroup (Cretaceous) in South Korea. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 357–373.
- Lee, H.-J., Lee, Y.-N., Fiorillo, A., Lü, J., 2018a. Lizards ran bipedally 110 million years ago. Scientific Reports 8, 2617.
- Lee, T.-H., Park, K.-H., Yi, K., 2018b. Nature and evolution of the Cretaceous basins in the eastern margin of Eurasia: A case study of the Gyeongsang Basin, SE Korea. Journal of Asian Earth Sciences 166, 19–31.
- Lee, Y.-N., Lee, H.-J., Han, S.-Y., Park, E., Lee, C.H., 2018c. A new dinosaur tracksite from the Lower Cretaceous Sanbukdong Formation of Gunsan City, South Korea. Cretaceous Research 91, 208–216.
- Lee, Y.-N., Kong, D.-Y., Jung, S.-H., 2020. The first possible choristoderan trackway from the Lower Cretaceous Daegu Formation of South Korea and its implications on choristoderan locomotion. Scientific Reports 10, 14442.
- Leonardi, G., 1987. Discussion of the terms and methods. In: Leonardi, G. (Ed.), Glossary and Manual of Tetrapod Footprint Palaeoichnology. Departamento nacional da produção mineral, Brasília, pp. 43–51.
- Lim, J.-D., Lockley, M.G., Kong, D.-Y., 2012. The trackway of a quadrupedal ornithopod from the Jindong Formation (Cretaceous) of Korea. Ichnos 19, 101–104.
- Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. Geological Quarterly 53, 415–432.
- Lockley, M., Hunt, A.P., 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. Columbia University Press, p. 338.
- Lockley, M., Matsukawa, M., 2009. A review of vertebrate track distributions in East and Southeast Asia. Journal of the Paleontological Society of Korea 25, 17–42.
- Lockley, M.G., Dos Santos, V.F., Meyers, C., Hunt, A.P., 1998. A new dinosaur tracksite in the Morrison Formation, Boundary Butte, southeastern Utah. Modern Geology 23, 317–330.
- Lockley, M.G., Houck, K., Yang, S.-Y., Matsukawa, M., Lim, S.-K., 2006. Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong County, South Korea: evidence and implications. Cretaceous Research 27, 70–101.
- Lockley, M.G., McCrea, R.T., Matsukawa, M., 2009. Ichnological evidence for small quadrupedal ornithischians from the basal Cretaceous of SE Asia and North America: implications for a global radiation. Geological Society, London, Special Publications 315, 255–269.
- Lockley, M.G., Huh, M., Kim, J.Y., Lim, J.-D., Kim, K.S., 2012a. Recent advances in Korean vertebrate ichnology: the KCDC comes of age. Ichnos 19, 1–5.
- Lockley, M.G., Huh, M., Kim, B.S., 2012b. *Ornithopodichnus* and pes-only sauropod trackways from the Hwasun tracksite, Cretaceous of Korea. Ichnos 19, 93–100.
- Lockley, M.G., Huh, M., Gwak, S.-G., Hwang, K.G., Paik, I.S., 2012c. Multiple tracksites with parallel trackways from the Cretaceous of the Yeosu City Area Korea: Implications for gregarious behavior in ornithopod and sauropod dinosaurs. Ichnos 19, 105–114.
- Lockley, M.G., Xing, L., Lockwood, J.A., Pond, S., 2014. A review of large Cretaceous ornithopod tracks, with special reference to their ichnotaxonomy. Biological Journal of the Linnean Society 113, 721–736.
- Lockley, M.G., Lim, J.D., Park, H.D., Romilio, A., Yoo, J.S., Choi, J.W., Kim, K.S., Choi, Y., Kang, S.-H., Kim, D.H., 2020. First reports of *Crocodylodus* from Asia: implications for the paleoecology of the Lower Cretaceous. Cretaceous Research 104441.
- Matsukawa, M., Lockley, M.G., Hunt, A.P., 1999. Three age groups of ornithopods inferred from footprints in the mid-Cretaceous Dakota Group, eastern Colorado, North America. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 39–51.
- Matsukawa, M., Matsui, T., Lockley, M.G., 2001. Trackway evidence of herd structure among ornithopod dinosaurs from the Cretaceous Dakota Group of north-eastern New Mexico, USA. Ichnos 8, 197–206.
- Moratalla, J.J., Sanz, J.L., Jimenez, S., 1988. Multivariate analysis on Lower Cretaceous dinosaur footprints: discrimination between ornithopods and theropods. Geobios 21, 395–408.
- Moratalla, J., Sanz, J., Jiménez, S., Lockley, M., 1992. A quadrupedal ornithopod trackway from the Lower Cretaceous of La Rioja (Spain): inferences on gait and hand structure. Journal of Vertebrate Paleontology 12, 150–157.
- Myers, T.S., Fiorillo, A.R., 2009. Evidence for gregarious behavior and age segregation in sauropod dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology 274, 96–104.
- Norman, D.B., 1998. On Asian ornithopods (Dinosauria: Ornithischia). 3. A new species of iguanodontid dinosaur. Zoological Journal of the Linnean Society 122, 291–348.
- Norman, D.B., 2002. On Asian ornithopods (Dinosauria: Ornithischia). 4. *Probatrosaurus*. Zoological Journal of the Linnean Society 136, 113–144.
- Olsen, P.E., Rainforth, E.C., 2003. The early Jurassic ornithischian dinosaurian ichnogenus *Anomoepus*. In: LeTourneau, P.M., Olsen, P.E. (Eds.), The Great Rift Valleys of Pangea in eastern North America. Columbia University Press, pp. 314–367.
- Ostrom, J.H., 1972. Were some dinosaurs gregarious? Palaeogeography, Palaeoclimatology, Palaeoecology 11, 287–301.
- Paik, I., Chun, J., 1993. Laminar calcrites, calcrite pisoids and ooids, and rhizoliths from the Gyeongsang Supergroup, Korea. Journal of the Geological Society of Korea 29, 108–117.
- Paik, I.S., Kim, H.J., 2014. Roll-up clasts in the Cretaceous Haman Formation, Korea: occurrences, origin and paleoenvironmental implications. Journal of the Geological Society of Korea 50, 269–276.
- Paik, I.S., Kim, H.J., Huh, M., 2010. Impressions of dinosaur skin from the Cretaceous Haman Formation in Korea. Journal of Asian Earth Sciences 39, 270–274.
- Paik, I.S., Kim, H.J., Lee, H., Kim, S., 2017. A large and distinct skin impression on the cast of a sauropod dinosaur footprint from Early Cretaceous floodplain deposits, Korea. Scientific Reports 7, 16339.
- Park, H.S., Lim, S.K., 2004. Dinosaur footprints from the Cretaceous Haman Formation at Nogok-dong, Buk-gu, Daegu City. In: Proceedings of the Korean Earth Science Society Conference 2004, 138–138.
- Pérez-Lorente, F., Cuenca-Bescós, G., Aurell, M., Canudo, J.I., Soria, A.R., Ruiz-Omeñaca, J.I., 1997. Las Cerradicas tracksite (Berriasian, Galve, Spain): growing evidence for quadrupedal ornithopods. Ichnos 5, 109–120.
- Piñuela, L., García-Ramos, J.C., Romano, M., Ruiz-Omeñaca, J.I., 2016. First record of gregarious behavior in robust medium-sized Jurassic ornithopods: evidence from the Kimmeridgian trackways of Asturias (N. Spain) and some general considerations on other medium-large ornithopod tracks in the Mesozoic record. Ichnos 23, 298–311.
- Rasband, W.S., 1997. ImageJ (image processing software) version 1.52a, from. <https://imagej.nih.gov/ij/>.
- Razzolini, N.L., Vila, B., Díaz-Martínez, I., Manning, P.L., Galobart, A., 2016. Pes shape variation in an ornithopod dinosaur trackway (Lower Cretaceous, NW Spain): new evidence of an antalgic gait in the fossil track record. Cretaceous Research 58, 125–134.
- Reineck, H.E., Wunderlich, F., 1968. Classification and origin of flaser and lenticular bedding. Sedimentology 11, 99–104.
- Romano, M., Citton, P., Avanzini, M., 2020. A review of the concepts of ‘axony’ and their bearing on tetrapod ichnology. Historical Biology 32, 611–619.
- Rozhdstvenskiy, A., 1967. New iguanodonts from central Asia. International Geology Review 9, 556–566.
- Shibata, M., Azuma, Y., 2015. New basal hadrosauroid (Dinosauria: Ornithopoda) from the Lower Cretaceous Kitadani Formation, Fukui, central Japan. Zootaxa 3914, 421–440.
- So, Y., Paik, I., Kim, H., Kim, S., 2007. Cyclic deposits in the Haman Formation (Cretaceous) of the Gyeongsang Supergroup at Sinsu Island, Sacheon, Korea: Occurrence and origin. Journal of the Geological Society of Korea 43, 1–19.
- Thulborn, R.A., 1982. Speeds and gaits of dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology 38, 227–256.
- Thulborn, R.A., 1984. Preferred gaits of bipedal dinosaurs. Alcheringa: An Australasian Journal of Palaeontology 8, 243–252.
- Thulborn, R.A., 1989. The gaits of dinosaurs. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, pp. 39–50.
- Thulborn, R.A., 1994. Ornithopod dinosaur tracks from the Lower Jurassic of Queensland. Alcheringa: An Australasian Journal of Palaeontology 18, 247–258.
- Tsukiji, Y., Azuma, Y., Shiraishi, F., Shibata, M., Noda, Y., 2018. New ornithopod footprints from the Lower Cretaceous Kitadani Formation, Fukui, Japan: ichnotaxonomical implications. Cretaceous Research 84, 501–514.
- Tsukiji, Y., Sakai, Y., Azuma, Y., 2019. Ichnotaxonomic revision of dinosaur tracks from the Lower Cretaceous Tetori Group, Japan. Memoir of the Fukui Prefectural Dinosaur Museum 18, 1–20.
- Um, S., Choi, H., Son, J., Oh, J., Kwak, Y., Shin, S., Yun, H., 1983. Geological and geochemical studies on the Gyeongsang Supergroup in the Gyeongsang Basin. Korea Institute of Energy and Resources Bulletin 36, 124.
- Varricchio, D.J., Sereno, P.C., Xijin, Z., Lin, T., Wilson, J.A., Lyon, G.H., 2008. Mud-trapped herd captures evidence of distinctive dinosaur sociality. Acta Palaeontologica Polonica 53, 567–578.
- Walker, J.D., Geissman, J., Bowring, S., Babcock, L., 2013. The Geological Society of America geologic time scale. GSA Bulletin 125, 259–272.
- Xing, L., Wang, F.P., Pan, S., Chen, W., 2007. The discovery of dinosaur footprints from the middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. Acta Geologica Sinica 81, 1591–1602.
- Xing, L., Lockley, M., Marty, D., Zhang, J., Wang, Y., Klein, H., 2015. An ornithopod-dominated tracksite from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, South-Central China: new discoveries, ichnotaxonomy, preservation and palaeoecology. PLoS One 10, e0141059.
- Xing, L., Abbassi, N., Lockley, M.G., Klein, H., Jia, S., McCrea, R.T., Persons IV, W.S., 2017. The first record of *Anomoepus* tracks from the Middle Jurassic of Henan Province, Central China. Historical Biology 29, 223–229.
- Yang, S., 1982. On the dinosaur footprints from the Upper Cretaceous Gyeongsang Group. Journal of the Geological Society of Korea 18, 37–48.

- Yang, S.-Y., Baek, I.-S., Kim, T.-W., Seo, S.-J., 2006. Dinosaur footprints from Haman Formation at Paegi Mountain, Gunbuk District, Haman County, South Gyeongsang Province. In: Proceedings of the Korean Earth Science Society Conference, 103-103.
- Yong, T., 2015. GeoRose (Rose diagram plot software) version 0.5.1, from. <http://www.yongtechnology.com/georose/>.
- You, H.-L., Luo, Z.-X., Shubin, N.H., Witmer, L.M., Tang, Z.-L., Tang, F., 2003. The earliest-known duck-billed dinosaur from deposits of late Early Cretaceous age in northwest China and hadrosaur evolution. *Cretaceous Research* 24, 347–355.
- Zhang, J., Li, D., Li, M., Lockley, M.G., Bai, Z., 2006. Diverse dinosaur-, pterosaur-, and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research* 27, 44–55.

- Zhao, Q., Benton, M.J., Xu, X., Sander, P.M., 2013. Juvenile-only clusters and behaviour of the Early Cretaceous dinosaur *Psittacosaurus*. *Acta Palaeontologica Polonica* 59, 827–833.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.104877>.