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Bird tracks from Liaoning Province, China: New insights into avian evolution during the Jurassic-Cretaceous transition

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Abstract

Tracks of shorebird-like species from a small outcrop in the upper part of the Tuchengzi Formation at Kangjiatun, in the Beipiao area, Liaoning Province, may be the oldest bird tracks known from China. Formerly considered Late Jurassic in age, new fission track dates give an age of 145.9 Ma for ash beds associated with dinosaur track-bearing beds from the middle part of the Tuchengzi Formation outcrops at a nearby locality. Thus, the age appears to be close to the Jurassic-Cretaceous (Tithonian-Berriasian) boundary. The precise age of the bird track-bearing beds has not been determined, but is unlikely to be younger than about 139 Ma, based on dates for the upper part of the Tuchengzi Formation. Thus, the bird tracks, like the Tuchengzi ichnofauna in general, predate the famous Yixian Formation, which has produced a different avifauna.

The most distinctive tracks are here named *Pullornipes aureus* ichnosp. nov. and are tentatively assigned to the ichnofamily Koreanornipodidae. Other tracks from the same site appear to represent different ichnotaxa and therefore indicate the potential to find diverse avian ichnofaunas at this time. This record supports the evidence that East Asian avian ichnofaunas are the most diverse known during the Early Cretaceous.

Keywords: Bird tracks; Tuchengzi Formation; Liaoning Province; Early Cretaceous; Fission track dates

1. Introduction

Recently the Yixian Formation in the Beipiao area has become famous for yielding the fossils of feathered dinosaurs such as *Sinosauropteryx*, *Caudipteryx*, and *Protarchaeopteryx*, in association with a rich lacustrine fauna and flora including fish, amphibians, non-dinosaurian reptiles, birds, mammals, and many invertebrate and plant species. To date no vertebrate tracks have been reported from the Yixian Formation. However, an important track site was reported by Yabe et al. (1940) from the underlying Tuchengzi Formation near the village of Yangshan (Matsukawa et al., 2006).

Recent studies have revealed the presence of three bird trackways at a locality near the village of Kangjiatun, about 15 km northeast of Beipiao, and also about 15 km south southwest of the main Yixian feathered dinosaur locality (Fig. 1). According to the local geological maps, the locality represents an outcrop of the Tuchengzi Formation, which lies beneath the Yixian Formation (Hao et al., 1986). Other track sites reported from the Tuchengzi Formation in this region reveal abundant small theropod and bird tracks from the middle part of the formation (Wang et al., 1990; Zheng et al., 2001; Matsukawa et al., 2006).

Older reports claimed that the Yixian Formation contained a middle "Jehol" fauna that may be as old as Tithonian in age

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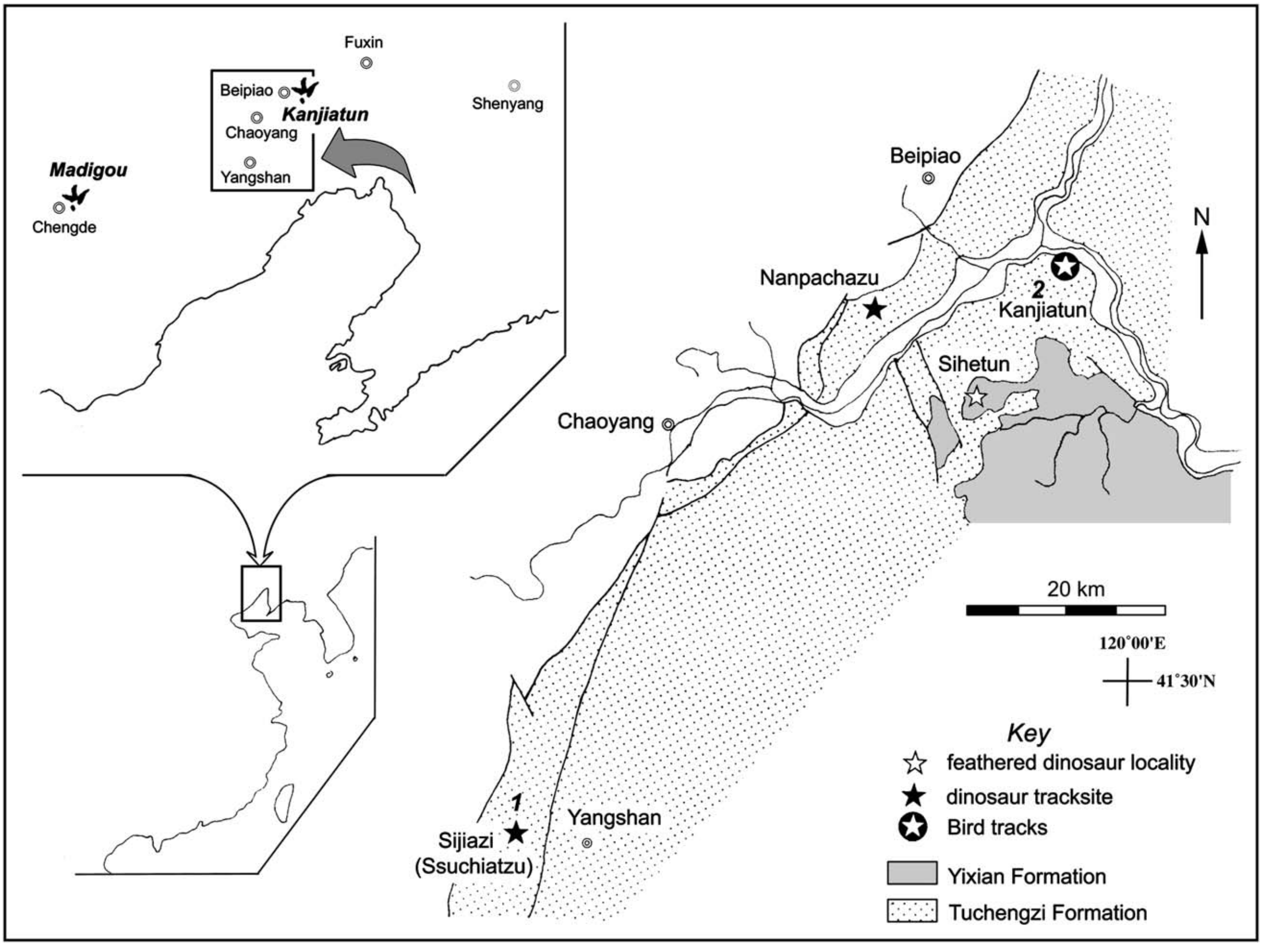

Fig. 1. Location map with detail of Beipiao-Chaoyang-Yangshan area showing the location of the Kangjiatun bird track site in relation to dinosaur track sites in the Tuchengzi Formation at Nanpachazu and Yangshan. The main feathered dinosaur locality at Sihetun is also shown, and the outcrops of the Yixian and Tuchengzi formations. The Madigou locality in Hebei Province is about 250 km east of Chaoyang. Compare with Figs. 2 and 3.

(Chen, 1999). Thus, the age of the underlying Tuchengzi Formation was generally inferred as older, i.e., late Middle–Late Jurassic (Pu and Wu, 1985; Wang et al., 1990; Zheng et al., 2001). However, more recent interpretations of the age of the Yixian formation suggest younger dates (124–123 Ma), suggesting a late Neocomian (Hauterivian-Barremian) age. Thus, the question arises as to whether the Tuchengzi Formation is also younger. Fission track dates obtained from the Tuchengzi Formation during the course of this study suggest an age of about 145.9 million years (Lockley et al., 2001b).

Since unequivocal bird tracks are not known from any pre-Cretaceous deposits, the bird tracks, which we assign to one or more shorebird-like taxa, probably suggest an earliest Cretaceous age, possibly Berriasian, based on the available dating. Only two other bird track sites, from Spain (Fuentes Vidarte, 1996) and British Columbia (McCrea et al., 2001), have been assigned such an early Berriasian age.

2. Description of the Kangjiatun site and trackways

The Kangjiatun track site, known locally as the ‘‘Golden Chicken’’ site, consists of a small bedding surface of greenish, fine-grained, ripple-marked sandstone exposed in an area about 10 m long and 4 m wide (Figs. 2, 3). Latitude and longitude coordinates are: 41° 44′ 682″ N, 120° 56′ 429″ E. The bedding surface, which dips to the east at about 28 degrees, exposes three bird trackways (A-C). The longest (A) extends

Fig. 2. Photograph of the Kangjiatun bird track site looking south. North–south ripple crest trend runs parallel to strike. Compare with Fig. 3.

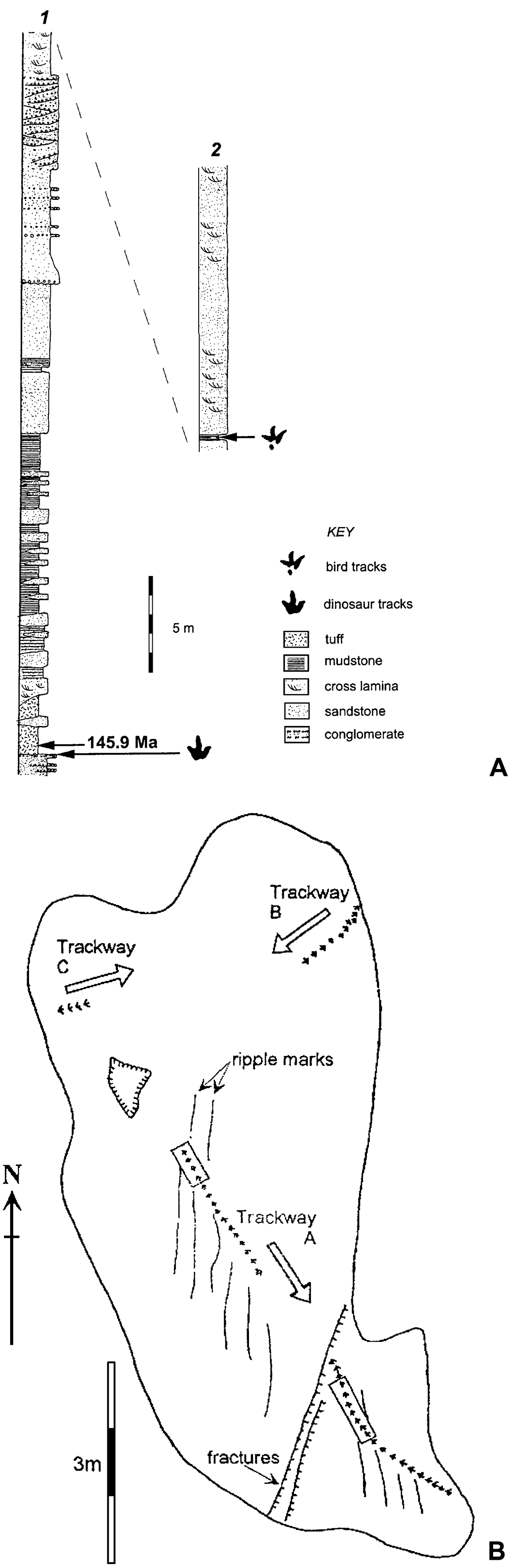

Fig. 3. A, simplified stratigraphic section for the Sijiazi site near Yangshan (1) where the fission track date was obtained and the Kanjiantun site (2); compare with Fig. 1. B, site map for Kangjiatun bird track site. Note location of trackways A–C (Figs. 5, 6) and N–S orientation of ripple marks; compare with Fig. 2. Boxes around tracks 1–4 and 30–36 in trackway A correspond to specimens CU 214.21 and CU 214.22, respectively. See text for details.

for about 6.5 m and consists of 34 footprints in a sequence that originally contained 45 consecutive footprints (Fig. 4). This large trackway runs in a southeasterly direction sub-parallel to the trend of ripple crests (Fig. 5). Trackway B consists of ten footprints oriented towards the southwest, and trackway C consists of only four footprints (Fig. 6). All trackways were traced (T463 and T464 in CU Denver tracings catalog), and 11 tracks from Trackway A were replicated, as described below.

2.1. Description of trackways

It is unusual to find Mesozoic bird track sites that reveal discrete trackways. Most track sites reveal high densities of tracks making it hard to discriminate consecutive footprints (trackways) made by individual animals (Currie, 1981; McCrea and Sarjeant, 2001). At the Kangjiatun site all three trackways are quite clear and separate from each other (Fig. 3). Trackway A, which originally consisted of 45 footprints, is only missing 11 tracks (16–26 inclusive) and thus may be the longest Mesozoic bird trackway sequence on record. (See Abbassi and Lockley, 2004 for a report of an Eocene trackway comprising a 46-footprint sequence with only five missing tracks.) Even trackway B, which consists of ten consecutive tracks, is also longer than most others previously reported from the Mesozoic (cf. Kim et al., 2006).

Trackway A consists of a series of 34 visible tracks (Figs. 3–5; Table 1) that originally made up two segments of a continuous 45 track sequence beginning with a right footprint (number 1) and ending with a right (probably number 45). The sequence is as follows: tracks 1–8 are well preserved

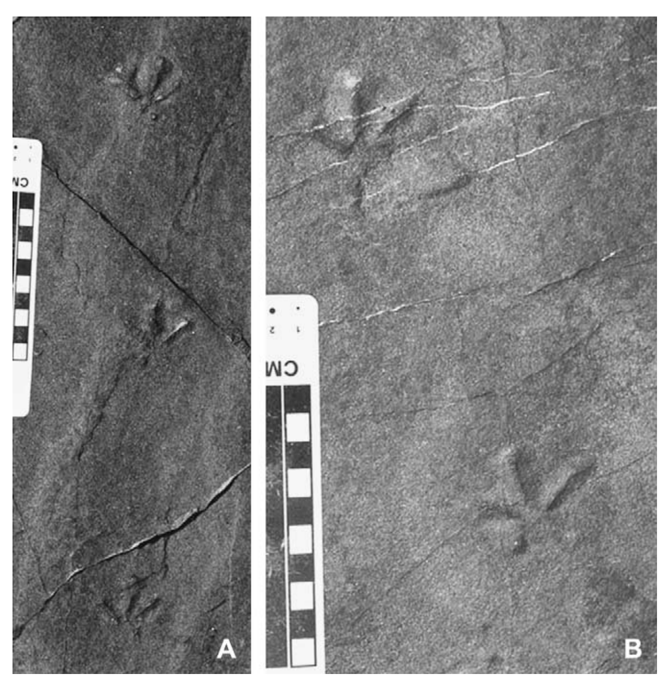

Fig. 4. A, photo of tracks 2–4 in Trackway A, corresponding to three tracks in specimen CU 214-21 from north end of trackway (see Fig. 3). B, photo of tracks 42 and 43 from south end of trackway A.

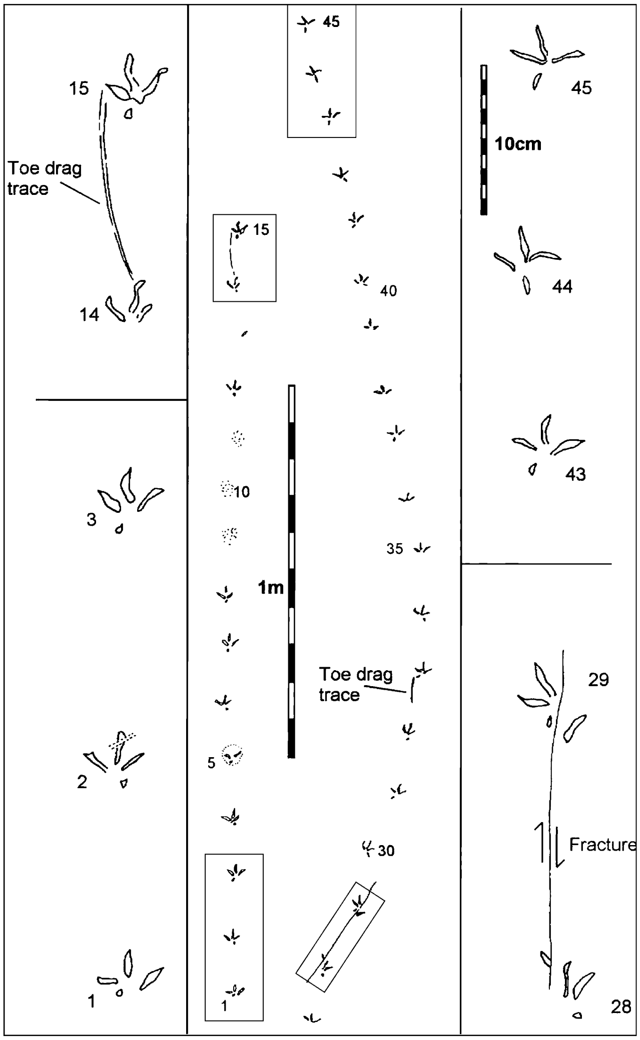

Fig. 5. Tracings of trackway A, in two segments (tracks 1–15 and 27–45), with details of tracks 1–3, 14–15, 28–29 and 43–45 all drawn to same enlarged scale (compare with Fig. 4). Note toe-drag traces and influence of fractures (see text for details).

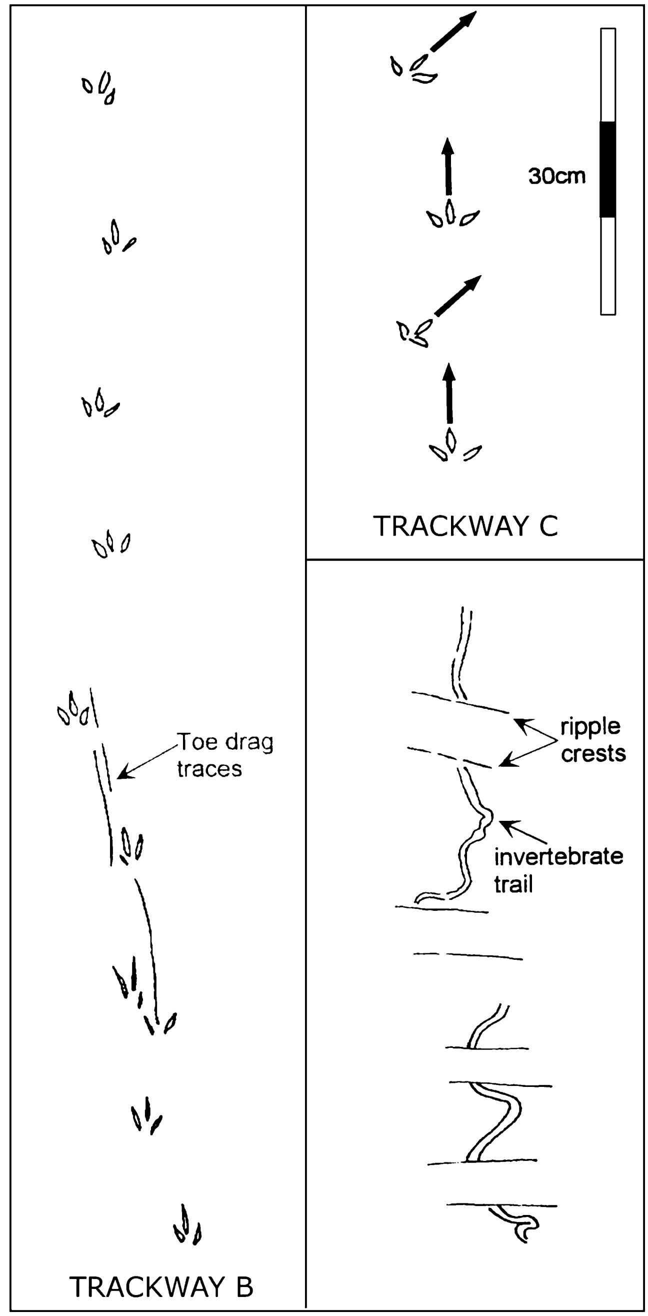

Fig. 6. Tracings of trackways B (left) and C (top right) and invertebrate trails (bottom left). Note toe-drag marks in trackway B (footprints 3–6). Note strong inward rotation of left footprints in trackway C.

and all are tetradactyl; 9–11 are poorly preserved and damaged; 12–15 are moderately well preserved and tetradactyl except for number 13, which is incomplete; tracks 16–26 are missing. The sequence from 27 through 45, situated east of a small north–south trending fracture (Figs. 3, 5), is complete, and all are tetradactyl except for 35–36 and 38–39. A small dextral fracture cuts through tracks 28 and 29. Although missing tracks in the sequence, after number 15, make it impossible to prove that the tracks east of the fracture resume the sequence with number 27; this inference is consistent with the regular spacing of footprints.

The footprints average about 4.1 cm long and 4.4 cm wide with an average step of 15.6 cm and average digit divarication of 115° and a slight inward rotation of digit III (Table 1). With the aforementioned exception of tracks 35–36 and 38–39 and incomplete track 13, all are tetradactyl, i.e., with a clear hallux impression. The hallux is short and directed medially (i.e., towards the trackway mid-line) more or less at 180° to digit IV. Toe-drag marks occur between tracks 14 and 15, and between tracks 32 and 33. Latex molds and plaster replicas of tracks 1–4 and 30–36 (corresponding to specimens CU 214.21 and CU 214.22, respectively) were deposited in the University of Colorado at Denver collections. An additional set of replicas was deposited in the Beijing Museum of Natural History.

Trackway B consists of ten consecutive tridactyl footprints beginning with a right and ending with a left. The trackway is somewhat irregular, consisting of small tridactyl tracks with toe-drag traces between track 3 and track 6 (Fig. 6; Table 2). The spacing between tracks 3 and 4 is very short and generally the divarication of digits is low, averaging about 56° in tracks

Table 1
Standard measurements for *Pullornipes aureus* (trackway A from Kangjiatun)

Trackway A												
No.	R/L	FL	FW	LII	LIII	LIV	II–III°	III–IV°	II–IV°	PL	SL	Rot°
1	R	3.3	4.7	1.5	1.9	2.3	82	50	132	15.1	32.7	2
2	L	3.9	4.3	1.9	2.3	2.1	49	56	105	17.7	32.5	10
3	R	4.6	4.8	2.1	2.4	2.3	45	42	87	14.8		25
4	L	4.0	4.7	3.1	2.5	2.4	39	80	119		31.5	15
5	R		4.7	2.0		2.3						
6	L	4.2	4.4	2.3	2.5	2.2	44	75	119	16.3	*28.8*	20
7	R	4.7	4.4	2.0	2.0	2.3	50	51	101	12.7		2
8	L	*3.9*	4.0	1.8	*1.2*	2.5	60	50	110			
12	L	4.1	4.2	1.6	2.8	2.3	40	40	80		28.0	1
13	R					2.0						
14	L	3.9	3.3	1.6	2.3	2.1	36	52	88	15.5		10
15	R	4.4	4.4	2.0	3.3	3.0	39	55	94			7
27	R		4.7	*1.3*	2.5	2.9	53	63	116	15.2	35.2	9
28	L	4.0		2.5	2.5		28			22	34.7	
29	R	4.5		2.2	2.6	2.5	49			14.7	32.0	
30	L	3.7	3.5	2.3	2.6	2.5	42	62	104	17.7	34.0	11
31	R	4.7	4.2	*1.4*	2.6	2.3	61	56	117	16.6	33.5	1
32	L	4.3	3.5	2.4	2.8	2.5	48	55	103	17	32.0	
33	R	4.5	4.9	2.3	2.7	2.5	77	64	141	15	32.2	1
34	L	3.7	4.5	2.5	2.3	1.9	56	84	140	17.2	31.3	2
35	R	3.9	4.6	1.9	2.2	2.5	53	70	123	14.2	32.3	
36	L		4.5	2.0	2.4	2.2	51	68	119	18.2	29.9	
37	R	4.0	5.1	2.0	1.8	2.4	70	56	126	11.2	30.0	5
38	L	3.6	5.1	2.0	2.1	2.4	64	61	125	18.4	31.4	
39	R		3.8	1.6	1.9	*1.5*	74	67	141	13	29.8	2
40	L	3.8	4.1	2.1	2.2	*1.6*	50	50	100	17	29.5	2
41	R	4.4	4.5	1.8	2.0	2.5	40	59	99	12.8	28.8	5
42	L	4.1	4.4	3.1	3.1	2.3	50	64	114	16.2	28.6	1
43	R	4.4	4.9	1.9	2.2	2.6	53	85	138	12.2	26.0	12
44	L	4.6	4.7	2.2	2.6	2.0	90	42	132	13.6		10
45	R	4.3	4.8	2.4	2.6	2.4	49	90	139			15
Mean		4.1	4.4	2.1	2.4	2.4	53	61	115	15.6	31.1	8
SD		0.3665431	0.4651193	0.3900041	0.3528231	0.2422339	14	13	18	2.4211889	2.3	7

FL and FW, foot width and length; L II, LIII, LIV, lengths of digits II, III, and IV; LII–LIII°, L III–IV°, LII–IV°, digit divarication angles; PL and SL, pace and stride lengths (measured toe-toe); Rot°, rotation of digit III axis relative to trackway midline.

1–6, widening to as much as 70° in track 8. Inward rotation of digit III is very slight (range 1–7°). Generally the trackway can be divided into two sections: the proximal, first-formed segment associated with short, irregular steps, narrow digit divarication and toe-drag marks; and the distal, later-formed segment consisting of longer, regular steps and no toe-drag traces. Measurements suggest that the track maker may have been accelerating speed (pace-length increases in length from 11.2–17.2 cm). The tracks are small, ranging from about 3.7 cm in length to 3.2 cm in width. Step length in the regular distal section ranges from 14–17 cm. The tracks therefore appear to be too small to have been made by the same individual that registered trackway A. This conclusion is also supported by the lack of hallux impressions in trackway B.

Trackway C consists of four consecutive tridactyl tracks that average about 3.4 cm long and 4.7 cm wide with strong inward rotation of digit III, especially in left tracks 2 and 4 in the sequence (Fig. 6; Table 2). The step length increases progressively from 11.1–12.7 to 15.5 cm. The trackway also shows an interesting asymmetry. The two right footprints (numbers 1 and 3) have lower digit divarication angles (averaging 98°) and only slight inward rotation (4–8°), whereas the two left footprints (2 and 4) have much wider digit divarications (123–135°) and stronger inward rotation (42–47°). Such asymmetry has been noted in certain dinosaur trackways, usually where there is a pattern of limping (i.e., alternating long and short steps). Based on size, lack of hallux traces and footprint rotation patterns it is unlikely that trackway C was made by the same individual that registered either trackway A or B.

2.2. Comparison of trackways

There are significant differences between the three trackways. The size differences indicate that different individuals register the trackways, and that only one track maker (A) had a hallux that left traces. Comparison of trackway A and B is complicated by the irregularity of trackway B, which shows considerable variation in step length, associated with toe-drag

Table 2
Measurements for bird trackways B and C from Kangjiatun

No.	R/L	FL	FW	LII	LIII	LIV	II–III°	III–IV°	II–IV°	PL	SL	Rot°
Trackway B												
1	R	4.2	2.5	2.1	3.3	2.3	23	24	47	11.2		7
2	L	3.5	3.2	1.9	2.3	2.4	29	25	54		14.2	6
3	R		2.8	*1.6*		2.3			51			
4	L	4	3	*1.6*	3.4	3.3	6	26	32	12.9	26.9	2
5	R	4	2.6	*1.2*	3	2.6	27	25	52	14.2	29.5	1
6	L	3.7	3.3	2	2.9	2.1	37	24	61	16.7	30.7	2
7	R	2.7	4	2.1	2.6	2	28	36	64	14.5	31.9	4
8	L	3.1	3.8	1.9	2.4	2	45	25	70	17.2	33.7	6
9	R	3.8	3.6	1.9	3	1.8	16	50	66	16.2		4
10	L	4	3.5	1.9	2.9	1.8	27	37	64			5
Mean		3.7	3.2	1.8	2.9	2.3	26	30	56	14.7	27.8	4
SD		0.4898979	0.5056349	0.2780887	0.3741657	0.4477102	11	9	11	2.2	7.1	2
Trackway C												
1	R	3.7	4.8	2.3	2.5	2.2	40	60	100	11.1	23.6	8
2	L	3.4	4.1	1.8	2.3	1.8	65	70	135	12.7		42
3	R	3.1	5.0	2.1	2.7	2.5	43	53	96	15.5	28.0	4
4	L	3.3	5.0	2.5	2.0	2.1	50	73	123			47
Mean		3.4	4.7	2.2	2.4	2.2	50	64	114	13.1	25.8	25
SD		0.25	0.4272002	0.2986079	0.2986079	0.2886751	11	9	19	2.2271057	3.1112698	22

Measured parameters as for Table 1.

marks, and lower digit divarication angles. However, A and B are comparable in showing toe-drag traces and relatively minor inward rotation of digit III. The short steps, narrow divarications, and toe-drag marks seen between footprints 1 and 6 in trackway B are likely a function of behavior and/or preservation. Possibly the track maker was emerging from a sub-aqueous or saturated substrate to an emergent and firmer area.

Comparison of trackways A and C reveal a much more pronounced inward rotation of the left foot of C (measured from the axis of digit III to the trackway C mid-line) which subtend a ''toe-in'' angle of 42–47°. This contrasts with the toe-in angles of only 4–8° for the right footprints (1 and 3), which are comparable to those found in trackway A. Given that track size and step (pace) lengths are similar in trackways A and C, we must interpret the significance of the asymmetric ''toe in'' of the left foot. If it was caused by injury, rather than an inherent toe-in gait seen in some shorebird or shorebird-like species, the gait difference can be explained away. However the lack of a hallux impression in trackway C must be taken as evidence of a morphological difference. Given that the tracks in trackway C are deeper and the digit impressions are broader, one can assume a softer substrate. Given this assumption it is hard to see how a hallux impression would show up in shallow but not in deep tracks if the track makers were the same species (or individual).

3. Other bird track sites from the Tuchengzi Formation

Bird tracks have also been reported from the Tuchengzi Formation at a locality named Madigou in Hebei Province. We traced and molded several specimens that originated from building stone quarries that were used to provide flagstone for the Summer Palace in Chengde. One specimen, illustrated here (Fig. 7), is housed in the Nanjing Institute of Geology and Paleontology. The specimen shows four consecutive tridactyl tracks in association with some possible arthropod traces. All other specimens consist of isolated tracks.

This specimen resembles *Aquatilavipes* because it lacks a hallux trace. The tracks average about 4.4 cm long and wide with a step of 11.5–12.0 cm. The trackway shows slight inward rotation. The trackway is not obviously similar to Trackway A from Kangjiatun, but bears some generalized resemblance to trackway C.

4. Systematic ichnology

4.1. General considerations

As noted in Matsukawa et al. (2006), bird tracks are very abundant in the Cretaceous of East Asia. The highest density of track sites is reported from Korea, where six ichnospecies have been named, including two in this issue of Cretaceous Research (Kim et al., 2006; Lockley et al., 2006). At least two additional ichnotaxa are also known from Japan and China. In the sections that follow we describe the new material from Kangjiatun and compare it with known bird tracks from East Asia and elsewhere.

4.2. Systematic description

? Koreanornipodidae

The ichnofamily diagnosis for Koreanornipodidae is given by Lockley et al. (2006) and is based largely on the

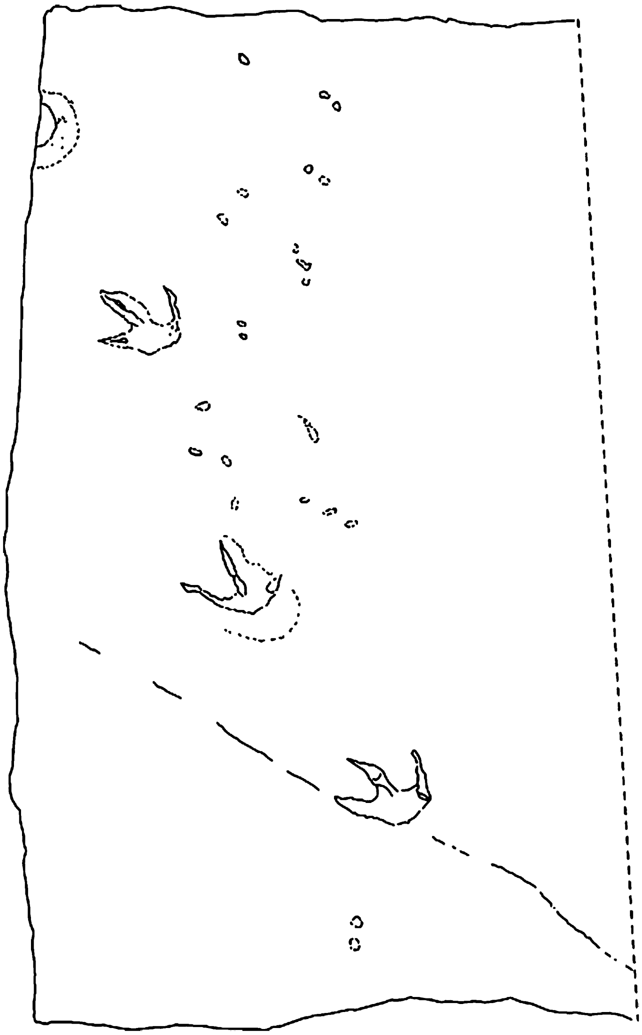

Fig. 7. Bird trackway (cf. *Aquatilavipes*) from the Tuchengzi Formation at the Madigou locality in Hebei Province. Several specimens that originated from building stone quarries were used to provide flagstone for the Summer palace in Chengde. Repository of specimen is Nanjing Institute of Geology and Paleontology, with replica in the University of Colorado at Denver, Dinosaur Tracks Museum. Tracks average about 4.4 cm long and wide. See text for details.

descriptions of *Koreanornis hamanensis* given by Kim (1969) and Lockley et al. (1992). *Koreanornis* is smaller (typically 2.5–3.0 cm wide) than the Kangjiatun trackway A. However, the morphology is similar, except for the larger hallux impression and the lesser degree of positive (inward) rotation in the Kangjiatun specimen. Our assignment of this specimen to Koreanornipodidae is tentative.

Pullornipes ichnogen. nov.

Diagnosis. Small subsymmetric functionally tridactyl track with wide digit divarication and small postero-medially directed hallux. Trackway narrow with only slight positive (inward) rotation.

Pullornipes aureus ichnosp nov.
Figs. 4–5

Derivation of name. Latin, *pullus*, chicken, *ornis*, bird, *pes*, foot, and *aureus*, gold.

Holotype. CU 212.21 and 212.22 plaster replicas of four consecutive footprints (1–4 and a further seven consecutive footprints (30–36) from the same trackway.

Type horizon and locality. Basal Cretaceous, Tuchengzi Formation, Kangjiatun, Liaoning Province, China (41° 44′ 682″ N, 120° 56′ 429″ E).

Description. Footprints tetradactyl and slightly wider than long (average 4.1 cm long and 4.4 cm wide; Table 1). Average digit divarication between II and III is 53.2° (range 28–90°); between III and IV is 61.0° (range 42–90°); between II and IV is 115° (range 88–141°). The hallux is short and directed medially (i.e., towards the trackway mid-line) more or less at 180° to digit IV. In all cases the hallux impression is separate from the impressions of digits II, III, and IV. These impressions in turn are mostly separate from one another but are more frequently connected between digits II and III than between III and IV. Trackway narrow: average step 15.6 cm and average stride 31.2 cm, with slight inward rotation of digit III.

Discussion. The length of the hallux impression is somewhat variable and tends to be shorter in the proximal part of the trackway (e.g., tracks 1–9) than in the distal part (e.g., tracks 40–45). This is probably due to the combined effects of interaction between gait and substrate. In most tracks there is no connection between the impressions of the four digits. The hallux impression (digit I) is always separate from the impressions of digits II, III, and IV, and only in a few cases is there a connection between digits II and III (which subtend the lowest average digit divarication angles). This pattern suggests that the distal end of the tarsus (tibiotarsus) was not in contact with the substrate, and that probably only the distal ends of the proximal phalanges made contact with the substrate. Similarly the proximal connection of the hallux to the tibiotarsus was presumably above the substrate so that only the distal hallux made impressions posterior to the impressions of digits II–IV. Toe-drag marks occur sporadically (between tracks 14 and 15 and between 32 and 33), but have no ichnotaxonomic utility. Their presence suggest that the track maker sometimes failed to lift its feet much above the substrate when taking steps.

5. Comparative ichnology

In recent years Mesozoic bird tracks have been found at many sites in Asia and North America, and they are also known from a few localities in Europe, Africa and South America (Lockley et al., 1992, 2006; Lockley and Rainforth, 2002; Kim et al., 2006). As noted by Greben and Lockley (1992), virtually all avian footprints in the fossil record are attributable to shorebird or wader-like species. In this section our main objective is to compare tracks from the Kangjiatun site with those known from other well-documented sites.

Owing to the fact that a short hallux is clearly present only in trackway A from the Kangjiatun site, we first compare this morphotype with other avian trackways that display an unequivocal hallux. Second, we compare trackways B and C, which appear to lack a hallux with similar trackways from other sites.

5.1. Trackways with hallux impressions

Cretaceous bird trackways with hallux impressions include *Ignotornis* from the Cenomanian of Colorado (Mehl, 1931; Lockley et al., 1992), *Koreanornis*, *Ignotornis*, *Jindongornipes*, *Goseongornipes*, and *Hwangsanipes* from the Cretaceous (Aptian-Cenomanian) of Korea (Kim, 1969; Lockley et al., 1992; Yang et al., 1995; Kim et al., 2006; Lockley et al., 2006), cf. *Ignotornis* from the Upper Cretaceous (Campanian) of Argentina (Coria et al., 2002), *Sarjeantopodus* from the Upper Cretaceous (Maastrichtian) of Wyoming and Colorado (Lockley et al., 2004), *Patagonichornis* from the Maastrichtian of Argentina (Leonardi, 1987, 1994), *Shandongornipes* from the Lower Cretaceous (Barremian-Aptian) of China (Li et al., 2005), and two additional unnamed morphotypes from the Maastrichtian of Wyoming (Lockley and Rainforth, 2002, figs. 16.14a, b, d; Lockley et al., 2004, fig. 15).

None of these tracks are strikingly similar to trackways from the Kangjiatun site. Thus, as we are reluctant to assign Trackway A (*Pullornipes*) to any of these ichnotaxa at a low taxonomic level (ichnospecies or ichnogenus), we place it in this new ichnogenus. We can discount comparisons with *Ignotornis*, *Goseongornipes*, *Hwangsanipes*, and *Sarjeantopodus* because all have partial (semipalmate) web traces. The latter two ichnogenera (*Hwangsanipes* and *Sarjeantopodus*) are also too large to be close to *Pullornipes*, and the hallux is too prominent. Likewise, *Jindongornipes* and *Shandongornipes* are much too large and their halluxes too prominent, and posteriorly rotated, even though both lack web traces. This leaves only *Koreanornis*, which is significantly smaller than *Pullornipes* with a much smaller hallux that is only very rarely impressed. Nevertheless, the two are the closest in size among Cretaceous bird tracks with hallux traces and no web traces. The general configuration is sufficiently similar that we can consider the similarity significant for classification purposes. For this reason we consider that *Pullornipes* could tentatively be accommodated in the ichnofamily Koreanornipodidae as indicated above. However we should note that type, topotype and paratype *Koreanornis* show digital pad impressions in some cases (Lockley et al., 1992, 2006). Such traces are not seen clearly in *Pullornipes*.

5.2. Trackways without hallux impressions

Cretaceous bird trackways without hallux impressions include two species of *Aquatilavipes* from the Lower Cretaceous (Aptian and Albian) of Canada (Currie, 1981; McCrea and Sarjeant, 2001), a third species of *Aquatilavipes* from the Lower Cretaceous of China (Zhen et al., 1987, 1995), and a fourth species from the Lower Cretaceous (Berriasian-Valanginian) of Japan (Lockley et al., 1992; Azuma et al., 2002). There are many examples of *Aquatilavipes* or *Aquatilavipes*-like tracks known from other Lower Cretaceous localities in China (Li et al., 2002a,b; Lockley et al., 2001b, 2003), and North and South America (Lockley et al., 2001a, 2003; Coria et al., 2002). *Yacoriteichnus* and *Barrosopus* have also been reported from the Upper Cretaceous of Argentina by Alonso and Marquillas (1986) and Coria et al. (2002), respectively.

Archaeornithipus from the Berriasian of Spain (Fuentes Vidarte, 1996) has also been described as a bird track, though it is much larger than anything known from the Kangjiatun site, and could be of dinosaurian origin. Similarly *Magnoavipes*, a large tridactyl track from the Cretaceous (upper Albian-Cenomanian) of Texas, has been described as a bird track (Lee, 1997), although Lockley et al. (2001c) considered it to be a dinosaur track. Neither have significant hallux traces. Likewise *Aquatilavipes sinensis* (Zhen et al., 1995, pp. 117–119) is formally described as having "no hallux impression" though a single specimen illustrated by Lockley et al. (1992, fig. 6) and Lockley and Rainforth (2002, fig. 17.5b) was depicted with a "possible" short, posteromedially-directed hallux.

In trying to determine whether Kangjiatun trackways B and C are similar to others known from the Mesozoic, we face a difficult problem. Firstly trackway B appears quite variable, evidently owing to changing step length and preservational conditions. Similarly the preservation of trackway C is not good enough to determine whether the lack of a hallux, and inward rotation of the left foot are morphological characteristics of the track maker that sets it apart from maker of trackway A. Based on the visible differences discussed previously we consider that both trackway B and C would likely be attributed to *Aquatilavipes* or cf. *Aquatilavipes* if found in isolation. Only their association with trackway A (*Pullornipes*) raises questions about whether they are extramorphological variants of this hallux-bearing form. Likewise, the Madigou trackway (Fig. 5) is considered similar to *Aquatilavipes*.

Our measurements suggest that the maker of trackway B was smaller than the maker of trackway A and C. Also the length of the central digit (III) in trackway B is 20% longer than in trackway A and C. The digit divarication is much less in trackway B (mean about 56° as compared with about 114–115° for A and C). Low divarication values reduce the track width measurements and increase the track l/w ratio; however, these variables should not affect the overall track length or digit III length. It appears therefore, that the maker of trackway B had an inherently longer foot and longer digit III. Trackway B therefore, may belong to a different species of smaller track maker, which lacked a hallux.

6. Affinity of the track makers

Tracks that indicate a short hallux that is directed posteromedially, more or less along a line oriented a 180° from digit IV are reminiscent of those seen in modern Scolopacidae, a large family of shorebirds (Charadriformes) that includes the sandpipers, and the other large shorebird family (the plovers or Charadriidae) in which the hallux is usually absent.

However it is not possible to suggest with any confidence that the maker of trackway A was a member of the Scolopacidae, only that it had feet that were similar in morphology to representatives of this family. These families have not be identified in the Early Cretaceous.

7. Age of the Tuchengzi Formation

The Tuchengzi Formation underlies the Yixian Formation, currently famous for its feathered dinosaurs such as *Sinosauropteryx*, *Caudipteryx*, and *Protarchaeopteryx*. However, the age of the formation has been disputed. According to Hou et al. (1995), the Yixian Formation is probably Late Jurassic in age (about 147 Ma), a conclusion supported, at least for the lower part of the formation, by Lo et al. (1999a,b) based on a mean $^{40}Ar/^{39}Ar$ date of 145.3 (±4.4) Ma. These dates, however, are considerably older than the dates published by Smith et al. (1995) and Swisher et al. (1999), which are in the range of 122–124 Ma, but according to Hou et al. (1995), these dates may be compromised by thermal alteration of the samples. Chen (1999) also argues, on the basis of the evolutionary grade of the invertebrate faunas, for a correlation of the Yixian Formation and its "middle Jehol Biota" with Tithonian deposits such as the Solenhofen of Germany. Recent studies dispute these older dates and support Yixian dates in the range of 122–124 Ma (Smith et al., 2001; Swisher et al., 2002).

Recently, however, independent evidence for the age of the Tuchengzi Formation was obtained from fission track dates for the Yangshan dinosaur tracks locality (Fig. 3). The Yangshan dates indicate an age of about 145.9 Ma for the middle part of the formation, and can be compared with dates of 139.4 for the upper part of the formation (Swisher et al., 2002). A sample of volcanic ash was obtained from beds immediately overlying the track-bearing horizons in the Tuchengzi Formation at the Yangshan track site (Figs. 1, 3), which is considered to be part of the middle member of that formation (Wang et al., 1990; Zheng et al., 2001). This sample was subjected to fission track dating for titanite using the external detector method for uranium free muscovite (e.g., Naeser, 1976). Titanites of 75–250 μm were separated by conventional heavy-liquid techniques, mounted in PFA Teflon sheets, and ground polished to reveal a 4 π internal surface. Etching of titanite was carried out in aqueous alkali solution (50 M NaOH) at 130 °C for 140 min. The etched titanites were irradiated with standard glass (NIST-SRM612) covered by the muscovite detector at the graphite facility (Tc-Pn) of the Kyoto University Reactor, for which Cd ratios for Au are >2000. After irradiation the external detectors were etched by 46% HF for 12 min at 25 °C. The FT densities were measured at a magnification of 1000× under a dry 100× objective lens. Ages were calculated using the zeta calibration approach. We used a zeta value of 346.8 ± 10.0 determined dosimeter glass SRM612 using titanites from the Mount Dromedary Complex (Hurford, 1990).

Results of the FT dating are shown in Table 3. Ages were calculated for individual sample mounts. Uncertainties in the chronological data are quoted at 1 sigma. Each result passed the P (χ^2) test (Galbraith, 1981) at the 5% level, implying that the variability in the FT count data is limited to the inherent variability in the radiometric decay process and additional uncertainty derived from contamination of detrital grains can be ignored. The weighted mean age was 145.9 ± 4.8 Ma. The result assigns the ash bed to a point very near to the Jurassic (Tithonian) Cretaceous (Berriasian) boundary.

We recognize that the age of the ash at the Yangshan site may not be the same as the tracks at the Kangjiatun locality. However, based on the fact that both are referred to the Tuchangzi Formation, the Yangshan date is useful as an age indicator for this formation (Lockley et al., 2001a). Swisher et al. (2002) report dates obtained for the upper part of the Tuchengzi Formation. These include a date of 139.4 ± 0.19 Ma. The date is also fairly consistent with dates reported for the overlying Yixian Formation that range from $^{40}Ar/^{39}Ar$ dates of 145.3 (±4.4) Ma (Lo et al., 1999a,b); to 137.7 ± 7 Ma (Wang and Diao, 1984, cited in Smith et al., 2001); 124.6 (±0.3) Ma (Swisher et al., 1999); and 121.1 (±0.2) Ma (Smith et al., 1995). According to Smith et al. (2001), these latter two dates are the most reliable, and according to Swisher et al. (2002) the older dates reported by Lo et al. (1999a,b) for the Yixian Formation are unreliable.

If the upper part of the Tuchengzi Formation is approximately 139.4 Ma and the tracks from the Yangshan area, dated as lying below a tuff that is 145.9 Ma, are from the middle member as suggested by Wang et al. (1990) and Zheng et al. (2001), then the age range of the middle and upper members falls within the latest Tithonian, Berriasian, or earliest Valanginian. Gradstein et al. (2004) give dates of 145.5 (±4.0) and 140.2 (±2.0), respectively, for the lower and upper boundaries of the Berriasian. Taken at face value, the Yangshan date is latest Tithonian, but very close to the Jurassic-Cretaceous boundary. However, the precise stratigraphic horizon from which the Kangjiatun bird tracks originate (i.e., the member

Table 3
Fission track analytical data of titanite seperates from the 527-1 tuff, Tuchengzi Formation, Yangshan

Sample Name	No. crys.	ρ_s (Ns) ($\times10^6$/cm^2)	ρ_i (Ni) ($\times10^6$/cm^2)	P (χ^2) %	ρ_d (Nd) ($\times10^5$/cm^2)	r	U ppm	Age (Ma) (±1σ)
527-①-1	23	2.364(3471)	1.012(1485)	50.3	3.592(3885)	0.894	34.6	144.0 ± 6.5
527-①-2	20	2.706(2798)	1.129(1167)	88.5	3.601(4256)	0.942	38.5	148.0 ± 7.1
Weighted mean = 145.9 ± 4.8								

Ages were calculated using NIST-SRM612 and the zeta value 346.8 ± 10.0. ρ, track density; N, total number of tracks counted. Subscripts: s, spontaneous; i, induced; d, dosimeter; P(χ^2), probability of obtaining χ^2 value for v degree of freedom (where v = No. crystals − 1) (Galbraith, 1981); r is correlation coefficient between ρ_s and ρ_i.

within the Tuchangzi Formation) is unknown, and the locality is some distance from the Yangshan dinosaur track sites. Nevertheless, an age of between about 145.9 and 139.4 can be inferred as a preliminary estimate.

8. Paleobiological and paleogeographical inferences

The most significant implication of the discovery of the Kangjiatun bird tracks is the evidence they give for the early appearance of shorebird-like species close to the Jurassic-Cretaceous boundary. Based on older correlations (e.g., Chen, 1999), the Tuchengzi Formation was considered as late Middle Jurassic or Late Jurassic. This would imply a pre-Cretaceous origin for shorebird-like species, or some similar avian group. Alternatively the formation is younger. Recent dating suggests that the Jurassic-Cretaceous boundary may be in the middle of the formation (Swisher et al., 2002). This indicates that all the tracks (*Pullornipes* and morphotypes B and C) are earliest Cretaceous in age. This is consistent with the fact that no unequivocal bird tracks have been reported from pre-Cretaceous strata, even though some bird-like tracks have been reported (Ellenberger, 1972, 1974; Lockley et al., 1992; McCrea et al., 2001).

If we use the tracks to estimate the age of this formation, we note that no shorebird or shorebird-like tracks have previously been reported in pre-Cretaceous rocks. The oldest known are *Archaeornithipus* (Berriasian of Spain) and unnamed *Aquatilavipes*-like tracks from the Valanginian of Japan (Lockley et al., 1992; Azuma et al., 2002). However, it was only relatively recently that any reasonably well dated shorebird or shorebird-like tracks were reported from Lower Cretaceous deposits (Lockley et al., 1992), and there is no reason to suppose that the Kangjiatun site is the oldest occurrence. Nevertheless based on existing dates and geological map correlations, this appears to be the oldest record currently known, with the possible exception of *Archaeornithipus* (Fuentes Vidarte, 1996).

Although a significant number of Lower Cretaceous birds have been reported from sites in Asia, Europe, and elsewhere, the abundance and diversity of shorebird-like species could not have been predicted with any confidence from the osteological record (Chiappe, 1995; Lockley, 1998). The track record suggests that in China there were at least two or three distinct forms (*Pullornipes* and cf. *Aquatilavipes*) present by earliest Cretaceous times. The latter form appears to become widespread in China during the Early Cretaceous. *Shandongornipes* also appears as a distinctive form in the middle of the Early Cretaceous, and by the end of this epoch (Aptian-Albian) there are at least a half dozen other ichnotaxa represented in South Korea (Kim et al., 2006).

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References

Abbassi, N., Lockley, M.G., 2004. Eocene bird and mammal tracks from the Karaj Formation, Tarom Mountains, northwestern Iran. Ichnos 11, 349–356.

Alonso, R.N., Marquillas, R.A., 1986. Nueva localidad con huellas de dinosaurios y primer hallazgo de huellas de Aves en la Formación Yacoraite (Maastrichtiano) del Norte Argentino. Actas, IV Congreso Argentino de Paleontologiá y Biostratigrafiá, Mendoza 2, 33–41.

Azuma, Y.A.Y., Tomida, Y., Currie, P.J., 2002. Early Cretaceous bird tracks from the Tetori Group, Fukui Prefecture, Japan. Memoir of the Fukui Prefectural Dinosaur Museum 1, 1–6.

Chiappe, L.M., 1995. The first 85 million years of avian evolution. Nature 378, 349–355.

Chen, P.J., 1999. Distribution and spread of the Jehol Biota. Paleoworld 11, 1–6.

Coria, R.A., Currie, P.J., Eberth, D., Garrido, A., 2002. Bird footprints from the Anacleto Formation (Late Cretaceous), Neuquén, Argentina. Ameghiniana 39, 453–463.

Currie, P.J., 1981. Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. Journal of Vertebrate Paleontology 1, 257–264.

Ellenberger, P., 1972. Contribution a la classification des Pistes de Vertebres du Trias: Les types du Stormberg d'Afrique du Sud (I). Palaeovertebrata, Mémoire Extraordinaire, 1–152.

Ellenberger, P., 1974. Contribution a la classification des Pistes de Vertebres du Trias: Les types du Stormberg d'Afrique du Sud (II). Palaeovertebrata, Mémoire Extraordinaire, 1–202.

Fuentes Vidarte, C.F., 1996. Primeras huellas de Aves en el Weald de Soria (España). Nuevo icnogenero, *Archaeornithipus* y nueva icnoespecie *A. meijidei*. Estudios Geologicos 52, 63–75.

Galbraith, R.F., 1981. On statistical models for fission track counts. Mathematical Geology 13, 471–488.

Gradstein, F.M., Ogg, J.G., Smith, A.G., 2004. A Geologic Time Scale 2004. Cambridge University Press, Cambridge. http://www.stratigraphy.org/chus.pdf.

Greben, R., Lockley, M.G.,1992. Vertebrate tracks from the Green River Formation, eastern Utah: implications for paleoecology. Geological Society of America, Rocky Mountain Section, Abstracts with Program 24, 16.

Hao, Y., Su, J.D., Yu, P., Li, Y., Li, N., Wang, H., Qi, S., Guan, H., Hu, X., Liu, W., Yang, L., Ye, Z., Shou, Z., Zhang, Q., 1986. In: The Cretaceous System of China, vol. 12. Geological Publishing House, Beijing, 301 pp.

Hou, L.H., Zou, Z.H., Martin, L.D., Feduccia, A., 1995. A beaked bird from the Jurassic of China. Nature 377, 616–618.

Hurford, A.J., 1990. Standardization of fission track dating calibration: recommendation by the Fission Track Working Group of the IUGS Subcommission on Geochronology. Chemical Geology Isotope Geoscience Section 80, 171–178.

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.Y., Kim, S.H., Kim, K.S., Lockley, M.G., 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 (1), 56–69.

Lee, Y.-N., 1997. Bird and dinosaur footprints in the Woodbine Formation (Cenomanian), Texas. Cretaceous Research 18, 849–864.

Leonardi, G., 1987. Glossary and Manual of Tetrapod Footprint Paleoichnology. Departamento Nacional da Produção Mineral, Brazil, 75 pp.

Leonardi, G., 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene). Companhia de Pesquisa de Recursos Minerais, Brazil, 248 pp.

Li, D., Azuma, Y., Arakawa, Y., 2002a. A new bird track site from Gansu Province, China. Memoir of the Fukui Prefectural Dinosaur Museum 1, 92–95.

Li, D., Zhang, J., Li, M., Lockley, M.G., Bai, Z., 2002b. Diverse dinosaur-pterosaur-bird ichnofaunas from the Cretaceous of Gansu Province China. Journal of Vertebrate Paleontology 22, 79A.

Li, R.-H., Lockley, M.G., Liu, M.-W., 2005. A new ichnotaxon of fossil bird track from the Early Cretaceous Tianjialou Formation (Barremian-Aptian) Shandong Province, China. Chinese Science Bulletin 50, 1149–1154.

Lo, C.H., Chen, P.-J., Tsou, T.-Y., Sun, S.-S., Lee, C.-Y., 1999a. Age of *Sinosauropterix* and *Confusciousornis* – ^{40}A-^{39}A laser single grain and K-Ar dating of the Yixian Formation, NE China. Geochimica 28, 405–409.

Lo, C.H., Chen, P.-J., Tsou, T.-Y., Sun, S.-S., Lee, C.-Y., 1999b. ^{40}A-^{39}A laser single-grain and K-Ar dating of the Yixian formation, NE China. Paleoworld 11, 329–338.

Lockley, M.G., 1998. The vertebrate track record. Nature 396, 429–432.

Lockley, M.G., Matsukawa, M., Li, J., 2003. Cretaceous bird tracks from China; their Cretaceous and global context. Journal of Vertebrate Paleontology 23, 72A.

Lockley, M.G., Yang, S.Y., Matsukawa, M., Fleming, F., Lim, S.K., 1992. The track record of Mesozoic birds: evidence and implications. Philosophical Transactions of the Royal Society of London 336, 113–134.

Lockley, M.G., Janke, P., Theisen, L., 2001a. First reports of bird and ornithopod tracks from the Lakota Formation (Early Cretaceous), Black Hills, South Dakota. In: Carpenter, K., Tanke, D. (Eds.), Mesozoic Vertebrate Life. New Research Inspired by the Paleontology of Philip J. Currie. Indiana University Press, Bloomington, pp. 443–452.

Lockley, M.G., Matsukawa, M., Wright, J., White, D., Li, J., 2001b. Bird tracks from near the Jurassic Cretaceous boundary, Liaoning Province, China. Journal of Vertebrate Paleontology 21, 73A–74A.

Lockley, M.G., Wright, J.L., Matsukawa, M., 2001c. A new look at *Magnoavipes* and so-called "Big Bird" tracks from Dinosaur Ridge (Cretaceous, Colorado). Mountain Geologist 38, 137–146.

Lockley, M.G., Nadon, G., Currie, P.J., 2004. A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, eastern Wyoming: implications for ichnotaxonomy. Ichnos 11, 229–249.

Lockley, M.G., Rainforth, E., 2002. The tracks record of Mesozoic birds and pterosaurs: an ichnological and paleoecological perspective. In: Chiappe, L., Witmer, L.M. (Eds.), Mesozoic Birds, Above the Heads of Dinosaurs. University of California Press, Berkeley, pp. 405–418.

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 (1), 70–101.

Matsukawa, M., Lockley, M.G., Li, J., 2006. Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: towards a synthesis. Cretaceous Research 27 (1), 3–21.

McCrea, R.T., Sarjeant, W.A.S., 2001. New ichnotaxa of bird and mammal footprints from the Lower Cretaceous (Albian) Gates Formation of Alberta. In: Carpenter, K., Tanke, D. (Eds.), Mesozoic Vertebrate Life. Indiana University Press, Bloomington, pp. 453–478.

McCrea, R.T., Lockley, M.G., Currie, P.J., Sarjeant, W.A.S., Pemberton, S., 2001. Avian footprint occurrences from the Mesozoic of Western Canada. Journal of Vertebrate Paleontology 21, 79A.

Mehl, M.G., 1931. Additions to the vertebrate record of the Dakota Sandstone. American Journal of Science Series 5 (21), 441–452.

Naeser, C.W., 1976. Fission track dating. US Geological Survey, Open-File Report 76–190, pp. 1–65.

Pu, R., Wu, H., 1985. Mesozoic sporo-pollen assemblages in western Liaoning and their stratigraphic significance. In: Zhang, L., Pu, R., Wu, H. (Eds.), Mesozoic Stratigraphy and Palaeontology of Western Liaoning 2. Geological Publishing House, Beijing, pp. 121–212.

Smith, P.E., Evensen, N.M., York, D., Chang, M.M., Jin, F., Li, J.L., Cumbea, S., Russell, D., 1995. Dates and rates in ancient lakes: ^{40}Ar/^{39}Ar evidence for an Early Cretaceous age for the Jehol Group, northeast China. Canadian Journal of Earth Sciences 32, 1426–1431.

Smith, J.B., Harris, J.D., Omar, G.I., Dodson, P., Hailu, Y., 2001. Biostratigraphy and avian origins in northwestern China. In: Gautier, J., Gall, I.F. (Eds.), New Perspectives on the Origin and Early Evolution of Birds: Proceedings of an International Symposium in Honor of John. H. Ostrom. Peabody Museum of Natural History, Yale University, New Haven, Connecticut, pp. 549–589.

Swisher, C.C., Wang, Y.-Q., Wang, X.-L., Xu, X., Wang, Y., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400, 58–61.

Swisher, C.C., Wang, X., Zhou, Z., Wang, Y., Jin, F., Zhang, J., Xu, X., Zhang, F., Wang, Y., 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new ^{40}Ar/^{39}Ar dating of the Yixian and Tuchengzi Formations. Chinese Science Bulletin 47, 135–138.

Wang, W., Diao, N., 1984. Geochronology of Jura-Cretaceous volcanics in west Liaoning, China. Scientific Papers, Geological International Exchange 5, 1–12.

Wang, W., Zheng, S., Zhang, L., Pu, R., Zhang, W., Wu, H., Ju, R., Dong, G., Yuan, H., 1990. Mesozoic Stratigraphy and Palaeontology of Western Liaoning 1. Geological Publishing House, Beijing, 168 pp.

Yabe, H., Inai, Y., Shikama, T., 1940. Discovery of dinosaurian footprints from the Cretaceous? of Yangshan, Chinchou: preliminary note. Proceedings of the Imperial Academy of Japan 16, 560–563.

Yang, S.Y., Lockley, M.G., Greben, R., Erickson, B.R., Lim, S.K., 1995. Flamingo and duck-like bird tracks from the Late Cretaceous and early Tertiary: evidence and implications. Ichnos 4, 21–34.

Zhen, S., Li, J., Zhang, B., Chen, W., Zhu, S., 1987. Bird and dinosaur footprints from the Lower Cretaceous of Emei County, Sichuan. In: First International Symposium, Nonmarine Cretaceous Correlations. Urumqi, Xingjiang, 37–38.

Zhen, S., Li, J., Zhang, B., Chen, W., Zhu, S., 1995. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan, China. Memoirs of Beijing Natural History Museum 12, 108–120.

Zheng, S.-L., Zhang, W., Ding, Q.-H., 2001. Discovery of fossil plants from Middle-Upper Jurassic Tuchengzi Formation in western Liaoning, China. Acta Palaeontologica Sinica 40, 67–85.