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Short communication

Lower Cretaceous avian tracks from Jiangsu Province, China: A first Chinese report for ichnogenus *Goseongornipes* (Ignotornidae)

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ABSTRACT

The Ignotornidae had a global distribution during the Cretaceous (Aptian – Cenomanian), but reports have been limited to North America, and localities in South Korea. Until recently, despite the high diversity of Ignotornidae described from Asia, no ichnospecies of Ignotornidae have been described from China. Here we report the first occurrence of Ignotornidae from the Lower Cretaceous of Donghai County, Jiangsu Province, China. Morphological and multivariate statistical analyses demonstrate that these functionally tetradactyl, semi-palmate bird tracks are most similar to *Goseongornipes* ichnosp. The apparent limited paleogeographical distribution of Ignotornidae from the Lower Cretaceous is likely artificial, and more exploration and documentation of Lower Cretaceous strata will increase our understanding of the extent of the global distribution of Ignotornidae.

1. Introduction

Abundant Cretaceous bird tracks have been found in East Asia, especially South Korea, such as the typical *Koreanaornis-Goseongornipes-Jindongornipes* assemblages (Kim et al., 2006; Lockley and Harris, 2010; Lockley et al., 2012a, b). These records shed light on patterns of bird-track diversity and abundance in the "middle" Cretaceous (Aptian–Cenomanian) of South Korea (Aptian-Cenomanian) and show that at least six distinct trackmakers for avian bird tracks.

The avian track record of Ignotornidae from South Korea is comparable with that from the Jehol Group (Barremian–lower Aptian, Sweetman, 2016), and from north-east China (Zhou and Wang, 2010). The latter yields thousands of bird skeletal fossils revealing the remarkable diversity of the Early Cretaceous avifauna. However, China just has a few reports of bird tracks from the Cretaceous Period, including a dense track assemblage in the Wuerhe district of Xinjiang which is dominated by *Koreanaornis* (Xing et al., 2011), and sporadic records from Sichuan (Zhen et al., 1994), Liaoning (Lockley et al., 2006a, b), Shandong (Li et al., 2005, 2015; Xing et al., 2010a) and Gansu (Xing et al., 2016).

The Yishu fault zone (along Zhucheng–Junan–Linshu–Tancheng) between the Shandong Province and the northern Jiangsu Province is part of the famous Tanlu fault zone from north-eastern China (Zhang et al., 2003). Yishu fault zone area has extensive outcrops of Jurassic–Cretaceous strata, bearing abundant dinosaur tracks (Xing et al., 2015). Bird tracks have been found from the Houzuoshan (Li et al., 2005, 2015) and Zhangzhuhewang sites (Xing et al., 2010a) within the Dasheng Group.

In 2016, a number of bird tracks were found in the Nanguzhai site (GPS: 34°36′23.34″N, 118°25′42.00″E) by Mr. Liu Yang from Donghai County (Fig. 1). In April 2017, the first author and Tang Y investigated the site and a detailed study of the track site was carried out.

1.1. Institutional abbreviations

MGCM, = Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; NGZ, Nanguzhai site, Donghai County, Jiangsu

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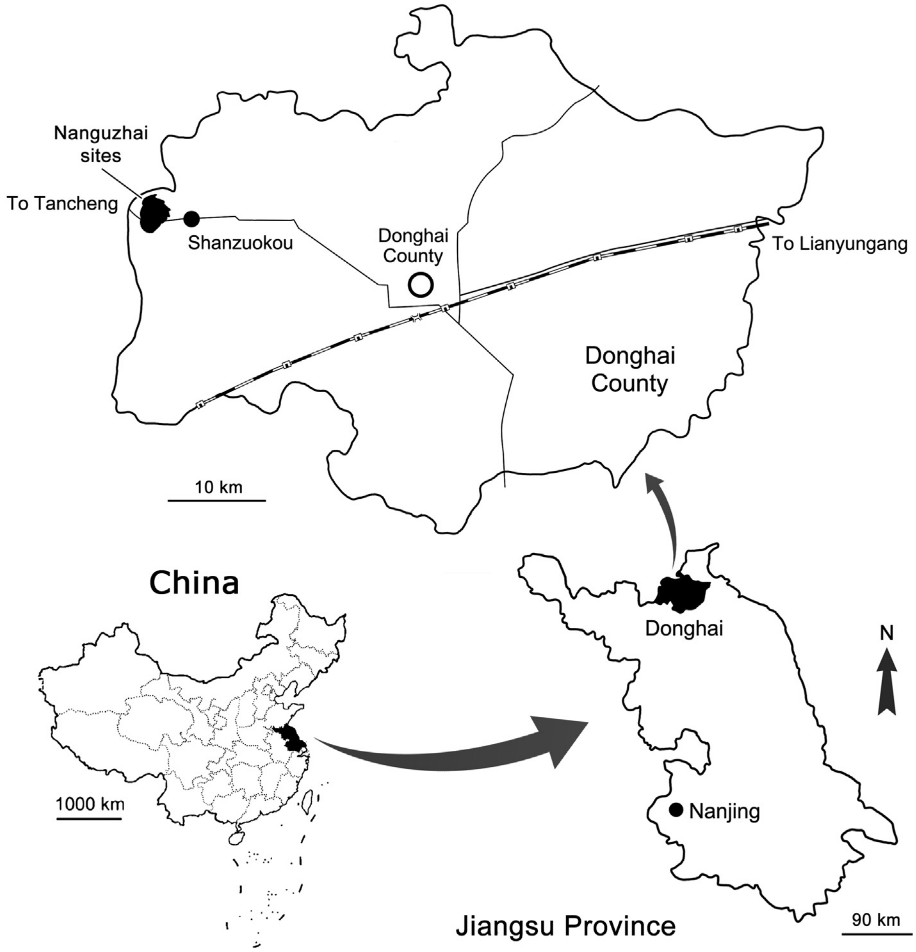

Fig. 1. Geographic map with the position of the Nanguzhai bird tracks locality (indicated by the footprint icon).

Province, China; ZDRC, = Zhucheng Dinosaur Research Center, Shandong, China.

2. Geological setting

Cretaceous beds in Shuhe rift zone are divided into the Lower Cretaceous Laiyang Group, Qingshan Group and Dasheng Group, as well as the Upper Cretaceous Wangshi Group (Tan, 1923). The Dasheng Group, a lacustrine detrital deposit associated with a continental river system (Si, 2002), is mostly located within the Yishu rift basin (Shi et al., 2013). Despite controversy over the interpretation of the formations in the Dasheng Group (Li and Zhao, 1992; Si, 2002; Liu et al., 2003; Wang et al., 2013), it is widely accepted that the Dasheng Group comprises continental clastic rocks, including purple grey, purple red and dark purple polymictic conglomerate and fine sandstone occasionally interbedded with yellow green siltstone, and interbedded locally with volcanic rocks, primarily andesite and andesitic tuff. In sequences of the Dasheng Group, there are two large sedimentary cycles of fining-upwards sequences from bottom to top, reflecting periodic submergence alternating with exposure (Wang et al., 2013).

Kuang et al. (2013) completed a detailed description of the sedimentology and paleoenvironment of the study area, and considered the Dasheng Group is a set of alluvial fan facies–fluvial facies–lacustrine facies sediments; during the Tianjialou Formation to Mengtuan Formation, the Dasheng group area developed in the maximum lake flooding period in late Early Cretaceous. Kuang et al. (2013) also state that the Nanguzhai site tracks are found within thickly bedded delta front sandstones. Liu et al. (2003) divided the Dasheng Group from the base to the top into the Malanggou, Tianjialou, Siqiancun and Mengtuan formations. Xing et al. (2010b) considered that the Nanguzhai site belongs to the Mengtuan Formation. However, Kuang et al. (2013) considered these units to be different, but contemporaneous, facies. The Tianjialou and Mengtuan formations are a set of lacustrine facies deposits dominated by dark gray, yellow green, purple detrital rocks, occasionally mixed with dolomitic mudstones and micrite dolomite (dolomicrite). Based on the lithology of the Nanguzhai site, we interpret that the Nanguzhai site as belonging to the Lower Cretaceous Tianjialou Formation of the Dasheng Group. Kuang et al. (2013) considered that the Tianjialou/Mengtuan formations were formed in the late Aptian–Albian, about 110–100 Ma.

3. Methods and materials

Xing et al. (2010b) described diverse dinosaur tracks from Nanguzhai sites, including three small-sized *Parabrontopodus* isp. trackways (NGZ-T2 and T3), some large-sized sauropod tracks (roughly 50–60 cm long) and a theropod trackway. The bird tracks from Nanguzhai site have been collected. At least 29 natural cast bird tracks are found on a single rock slab (NGZ-B), with four consecutive tracks forming a single trackway NGZ-B1 and rest 25 are isolated tracks catalogued as NGZ-BI1–25 (Figs. 2 and 3; Table 1). The Nanguzhai locality described by Xing et al. (2010b)

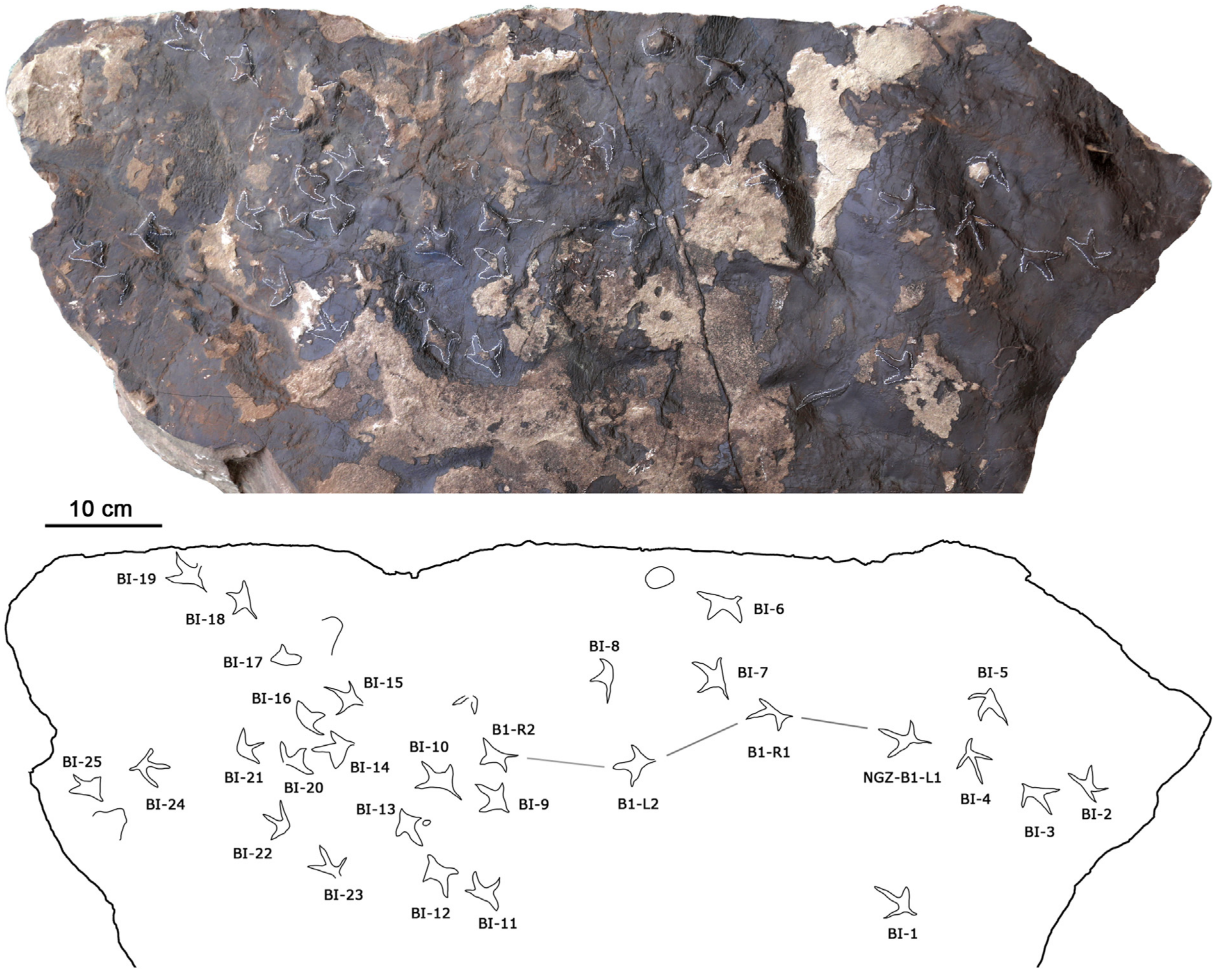

Fig. 2. Photograph and interpretative outline drawing of Nanguzhai bird tracks.

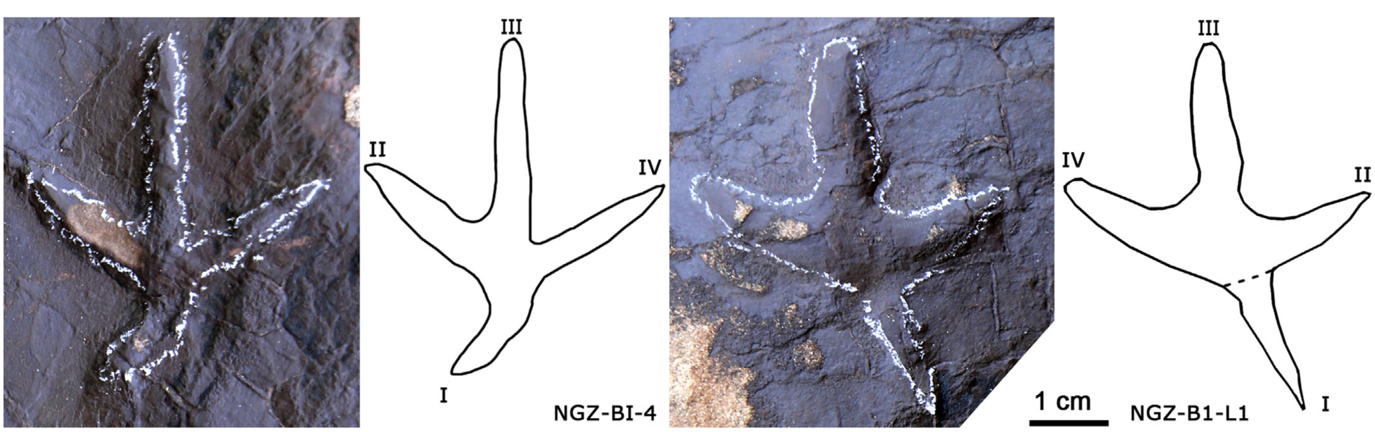

Fig. 3. Photograph and outline drawing of the well-preserved Nanguzhai bird tracks NGZ-BI-4 and NGZ-B1-L1.

includes sites I and II yielding isolated sauropod tracks and site III yielding sauropod and theropod tracks. Sites I and II are now totally destroyed by factory construction, as is the bird track site.

All tracks were examined by the first author (Xing L), and were outlined in chalk and photographed. All trackways and isolated tracks were traced on to transparent plastic acetate sheets. Using a combination of photographs and tracings, track maps of the trackway segments were produced.

Digit divarication (DIV), digit length (DL), digit width (DW), footprint length (FL), footprint width (FW), pace angulation (PA), pace length (PL), stride length (SL) and footprint rotation (R) were measured with the standard procedures established by McCrea et al. (2015) and Xing et al. (2016).

Multivariate statistical analyses (discriminant analysis, multivariate analyses of variance, MANOVA) were performed on linear and angular data from a modified version of the dataset published

Table 1
Measurements (in cm) of bird tracks from Nanguzhai site, Donghai County, Jiangsu Province, China.

Number	FL	FL'	FW	LI	LII	LIII	LIV	WI	WII	WIII	WIV	I-II	II-III	III-IV	PL	SL	R	PA
NGZ-B1-L1	3.12	4.75	3.72	1.75	1.58	3.12	2.63	0.57	0.56	0.50	0.55	107	69	54	11.43	23.04	24	156
NGZ-B1-R1	3.09	4.00	3.17	0.90	1.31	3.09	2.60	0.52	0.57	0.54	0.46	111	68	43	12.12	23.08	7	158
NGZ-B1-L2	2.79	3.72	3.60	1.12	1.72	2.79	2.43	0.77	0.54	0.71	0.70	123	67	53	11.40	–	–	–
NGZ-B1-R2	2.15	3.45	3.53	1.34	1.47	2.15	2.33	0.43	0.47	0.74	0.65	83	80	63	–	–	–	–
NGZ-BI1	3.45	4.32	3.34	0.86	2.04	3.45	2.20	0.29	0.68	0.52	0.45	119	52	54	–	–	–	–
NGZ-BI2	2.19	3.20	3.71	1.37	1.81	2.19	2.21	0.33	0.25	0.59	0.40	59	77	60	–	–	–	–
NGZ-BI3	2.90	3.65	3.54	0.62	1.69	2.90	2.75	0.42	0.46	0.55	0.55	119	59	46	–	–	–	–
NGZ-BI4	3.03	4.05	3.09	1.13	2.25	3.03	1.90	0.49	0.38	0.41	0.32	97	46	56	–	–	–	–
NGZ-BI5	2.36	2.92	4.12	0.55	1.96	2.36	3.06	0.56	0.35	0.70	0.70	104	58	49	–	–	–	–
NGZ-BI6	2.76	3.40	4.57	0.80	2.01	2.76	3.16	0.42	0.91	0.87	0.63	90	71	50	–	–	–	–
NGZ-BI7	2.89	4.43	3.60	1.53	2.11	2.89	2.24	0.54	0.58	0.70	0.52	98	55	55	–	–	–	–
NGZ-BI8	2.07	–	3.80	–	1.75	2.07	2.52	–	0.63	0.88	0.39	–	67	62	–	–	–	–
NGZ-BI9	2.84	3.84	3.17	0.98	1.98	2.84	1.93	0.59	0.70	0.74	0.60	117	56	57	–	–	–	–
NGZ-BI10	2.91	4.69	3.68	1.82	1.78	2.91	2.82	0.60	0.77	0.59	0.62	129	55	48	–	–	–	–
NGZ-BI11	2.26	3.88	3.21	1.66	1.88	2.26	1.95	0.77	0.58	0.63	0.52	135	55	62	–	–	–	–
NGZ-BI12	2.57	4.05	3.13	1.16	1.64	2.57	2.13	0.67	0.52	0.61	0.65	112	60	52	–	–	–	–
NGZ-BI13	2.50	3.72	2.56	0.87	1.46	2.50	1.75	0.59	0.56	0.69	0.69	109	57	56	–	–	–	–
NGZ-BI14	3.12	3.79	3.25	0.62	1.92	3.12	2.28	0.47	0.69	0.69	1.14	132	48	54	–	–	–	–
NGZ-BI15	2.84	3.81	3.08	0.75	1.85	2.84	2.12	0.55	0.40	0.59	0.44	133	49	57	–	–	–	–
NGZ-BI16	2.16	–	3.62	–	1.90	2.16	2.20	–	1.07	0.86	0.44	–	98	45	–	–	–	–
NGZ-BI17	1.84	–	2.65	–	1.46	1.84	1.42	–	0.79	0.64	0.97	–	70	59	–	–	–	–
NGZ-BI18	1.99	3.42	3.07	1.45	1.52	1.99	2.14	0.45	0.49	0.59	0.68	89	60	55	–	–	–	–
NGZ-BI19	2.97	4.41	–	1.42	–	2.97	2.59	0.71	0.45	0.78	0.70	126	48	51	–	–	–	–
NGZ-BI20	2.18	–	3.91	–	2.00	2.18	2.56	–	0.54	0.89	0.52	–	63	55	–	–	–	–
NGZ-BI21	2.33	–	3.36	–	2.10	2.33	2.13	–	0.60	0.29	0.52	–	47	57	–	–	–	–
NGZ-BI22	2.51	–	3.52	–	1.83	2.51	2.53	–	0.58	0.35	0.40	–	63	45	–	–	–	–
NGZ-BI23	2.71	3.19	3.46	0.43	1.70	2.71	2.46	0.59	0.32	0.48	0.45	110	64	49	–	–	–	–
NGZ-BI24	2.79	3.55	3.40	0.97	1.79	2.79	2.44	0.39	0.32	0.42	0.36	145	60	48	–	–	–	–
NGZ-BI25	2.38	3.39	2.95	0.93	1.56	2.38	2.24	0.56	0.89	0.39	0.67	116	66	38	–	–	–	–

Abbreviations: FL: footprint length; FL': FL with hallux; FW: footprint width; LI, LII, LIII, LIV: digit lengths; WI, WII, WIII, WIV: digit widths; I-II, II-III, III-IV: angle between digits I and II, II and III, III and IV; PL: Pace length; SL: Stride length; R: footprint rotation; PA: Pace angulation.

by Buckley et al. (2016) of Cretaceous tetradactyl avian ichnotaxa *Hwangsanipes chouhi* (Yang et al., 1995), *Goseongornipes markjonesi* (Lockley et al., 2006a, b), *Ignotornis gajiensis* (Kim et al., 2012), *Ignotornis mcconnelli* (Lockley et al., 1992) *Ignotornis yangi* (Lockley et al., 2006a, b), *Koreanaornis dodsoni* (Xing et al., 2011), *Koreanaornis hamanensis* (Kim, 1969), *Koreanaornis lii* (Xing et al., 2016), and *Uhangrichnus chuni* (Yang et al., 1995) (Tables 2 and 3). *Dongyangornipes sinensis* (Azuma et al., 2013) is considered by Buckley et al. (2016) as a subjective junior synonym of *Uhangrichnus chuni*, based on the redescription of *Uhangrichnus chuni* by Lockley and Harris (2010) that included a description of a short posteriormedially directed hallux impression, and that the slight differences in webbing impressions and digit divarication are due to preservational variation (Buckley et al., 2016). *Uhangrichnus chuni*, although possessing a different webbing morphology (palmate) as compared to Ignotornidae (semipalmate), was included in the analyses based on similarities in overall size and digit morphology. *Gyeongsangornipes lockleyi*, although no hallux impression was reported (Kim et al., 2013) was also included in the analyses given the similarities in asymmetric semipalmate webbing and digit morphology. *Shandongornipes muxiai* (Li et al., 2005) was not included in the analyses as it is a highly distinctive zygodactyl ichnotaxon, and is distinct from other Cretaceous avian ichnotaxon that are anisodactyl in footprint shape. Ichnospecies of *Koreanaornis* (*Koreanaornis hamanensis, Koreanaornis lii*) were also included due to the presence (although somewhat inconsistent) of hallux impressions. However, *Koreanaornis* is morphologically distinct from Ignotornidae due to its relatively smaller size, consistent lack of webbing impressions, and relatively short hallux impression (Kim, 1969; Lockley et al., 1992, 2006a, b; Xing et al., 2016). *Jindongornipes kimi* was initially included in preliminarystatistical analyses, but was not included in the analyses described herein due to the tracks' larger size "skewing" the results, and the small sample size ($n = 2$). *Gruipeda vegrandiunus* (Fiorrillo et al., 2011) and *Sarjeantopus semipalmatus* (Lockley et al., 2004) were also excluded from the analyses due to the small sample size of the reported data. Linear data were first log-transformed, and the means for each measured variable were then removed from each linear and angular variable, as per Farlow et al. (2013). Multivariate statistical analyses were performed using Paleontological Statistics version 3.0 (Hammer et al., 2001). Data collection methods for each ichnotaxon used in the analyses can be found in the respective publications; however, details on measurement methodology for several of the ichnotaxa, as well as sample sizes, were summarized in Buckley et al. (2016).

4. Description of tracks and trackways

Small to medium-sized, sub-symmetric, functionally tetradactyl bird tracks with three widely splayed digits (II–IV) and a posteriorly directed hallux. The average length/width ratio of these tracks is 0.8 (range 0.5–1.0 cm) (Table 1).

79% of the tracks have well-developed posteromedially-directed halluces. Halluces are relatively shallow when compared to the depths of digits II–IV. Digit III is the longest digit; digit II is longer than the hallux, but can be slightly shorter than hallux in some tracks) but is consistently slightly shorter than digit IV in length. The average percentages of lengths of hallux as compared to digits II and III are 62% ($n = 22$) and 41% ($n = 23$), respectively. Digital pad impressions are absent. The tracks are longer than wide, with an average length/width ratio of 0.8. The divarication angles between digits II and III (62°, $n = 29$) are larger than those between digits III and IV (53°, $n = 29$).

The only trackway, NGZ-B1, contains tracks that are slightly semipalmate between digits III and IV. Compared to the extremely weak webbing between II–III, the webbing is more noticeable between digits III–IV. The average length:width ratio of the tracks within the trackway is 0.8 (range 0.6–1.0).

Table 2
Multivariate analysis of variance (MANOVA) results comparing Nanguzhai bird tracks to other described ichnotaxa of Ignotornidae, with hallux impression data included. With hallux impression data included, the only ichnotaxon the Nanguzhai bird tracks are not significantly from is *Goseongornipes* ichnosp (Kim et al., 2006). When hallux impression data are not included, the ichnotaxa the Nanguzhai bird tracks are not significantly different from are *Goseongornipes* ichnosp., *Gyeongsangornipes lockleyi*, *Koreanaornis dodsoni*, and *Koreanaornis lii*. Gates, Gates Formation Ignotornidae; Gos, *Goseongornipes* ichnosp.; *Goseongornipes markjonesi*; *Gyeongsangornipes lockleyi*; HwCh, *Hwangsanipes choughi*; KoDo, *Koreanaornis dodsoni*; KoHa, *Koreanaornis hamanensis*; KoLi, *Koreanaornis lii*; IgGa, *Ignotornis gajinensis*; IgMc, *Ignotornis mcconnelli*; IgYa, *Ignotornis yangi*; Nan, Nanguzhai bird tracks; UhCh, *Uhangrichnus chuni*.

	IgMc	IgYa	IgGa	HwCh	Gos	GoMa	KoDo	KoHa	UhCh	GyLo	KoLi	Gates	Nan
IgMc		2.97×10^{-93}	3.09×10^{-03}	6.91×10^{-03}	5.30×10^{-24}	2.59×10^{-11}	1.50×10^{-65}	1.00×10^{-07}	2.16×10^{-29}	1.10×10^{-42}	4.29×10^{-61}	8.89×10^{-28}	9.30×10^{-56}
IgYa	2.97×10^{-93}		1.19 × 10-24	7.60×10^{-17}	6.89×10^{-03}	1.85×10^{-21}	3.53×10^{-17}	2.80×10^{-46}	6.91×10^{-93}	5.31×10^{-22}	3.89×10^{-08}	1.28×10^{-09}	9.51×10^{-10}
IgGa	3.09×10^{-04}	1.19×10^{-24}		Fail	Fail	Fail	2.74×10^{-13}	0.908	8.89×10^{-05}	1.68×10^{-04}	1.65×10^{-11}	0.037	2.13×10^{-10}
HwCh	6.91×10^{-03}	7.60×10^{-17}	Fail		Fail	Fail	1.19×10^{-08}	0.444	0.421	0.013	1.11×10^{-07}	0.435	1.09×10^{-06}
Gos	5.30×10^{-24}	6.89×10^{-03}	Fail	Fail		Fail	0.999	5.76×10^{-07}	8.40×10^{-22}	0.052	0.762	0.482	0.165
GoMa	2.59×10^{-11}	1.85×10^{-21}	Fail	Fail	Fail		1.57×10^{-11}	5.65×10^{-04}	1.53×10^{-12}	5.53×10^{-04}	5.37×10^{-10}	0.158	1.17×10^{-08}
KoDo	1.50×10^{-65}	3.53×10^{-17}	2.74×10^{-13}	1.19×10^{-08}	0.999	1.57×10^{-11}		4.31×10^{-27}	5.71×10^{-61}	1.10×10^{-12}	0.016	1.62×10^{-08}	1.93×10^{-07}
KoHa	1.00×10^{-07}	2.80×10^{-46}	0.908	0.444	5.76×10^{-07}	5.65×10^{-04}	4.31×10^{-27}		1.59×10^{-07}	9.17×10^{-15}	1.42×10^{-24}	1.77×10^{-09}	8.71×10^{-23}
UhCh	2.16×10^{-29}	6.91×10^{-93}	8.89×10^{-05}	0.421	8.40×10^{-22}	1.53×10^{-12}	5.71×10^{-61}	1.59×10^{-07}		4.40×10^{-41}	4.82×10^{-58}	1.09 × 10-28	1.72×10^{-54}
GyLo	1.10×10^{-42}	5.31×10^{-22}	1.68×10^{-04}	0.013	0.052	5.53×10^{-04}	1.10×10^{-12}	9.17×10^{-15}	4.40×10^{-41}		1.21×10^{-11}	1.08×10^{-04}	1.94×10^{-09}
KoLi	4.29×10^{-61}	3.89×10^{-08}	1.65×10^{-11}	1.11×10^{-07}	0.762	5.37×10^{-10}	0.016	1.42×10^{-24}	4.82×10^{-58}	1.21×10^{-11}		2.69 × 10-06	2.91×10^{-07}
Gates	8.89×10^{-28}	1.28×10^{-09}	0.037	0.435	0.482	0.158	1.62×10^{-08}	1.77×10^{-09}	1.09×10^{-28}	1.08×10^{-04}	2.69×10^{-06}		2.51×10^{-06}
Nan	9.30×10^{-56}	9.51×10^{-10}	2.13×10^{-10}	1.09×10^{-06}	0.165	1.17×10^{-08}	1.93×10^{-07}	8.71×10^{-23}	1.72×10^{-54}	1.94×10^{-09}	2.91×10^{-07}	2.51×10^{-06}	

Average maximum length including hallux impressions is 3.8 cm (range 2.9–4.8 cm), the value not including hallux impressions is 2.8 cm (range 2.2–3.1 cm); average maximum width is 3.5 cm (range 3.1–3.7 cm). Average divarication angle between digits II and IV is 124° (range 111°–143°). The average pace angulation is 157°. Pace length is about half of stride length. Tracks in the trackway exhibit slight positive (inward) rotation.

Wet and soft sediments might change the morphology of the track, and can produce tracks that display extramorphological distortion (digit edge collapse, drag marks, etc.) Well-preserved tracks, such as tracks NGZ-B1-L1 and BI-4, indicate that these tracks have slender digit impressions, but that wet and soft sediments resulted in some of the tracks appearing deeper, and made other tracks artificially appear wide due to soft sediment adhering to the plantar surface of the trackmaker's foot, as observed in tracks BI-6 and BI-17.

5. Comparison and discussion

The Dasheng Group Zhangzhuhewan site, which yields a small-sized *Parabrontopodus* isp trackway (Xing et al., 2010b) also preserves an isolated tetradactyl bird track (ZDRC.F3). The isolated tetradactyl bird track is 3.1 cm (with hallux) long, with a length (including hallux):width ratio of 0.8 and a large (121°) divarication angle between digit impressions II–IV. Xing et al. (2010b) suggested that ZDRC. F3 is different from other Mesozoic bird tracks from China, but that it is similar to the avian ichnotaxon *Jindongornipes* from the Lower Cretaceous Jindong Formation of Korea. Further analysis of ZDRC. F3 is difficult as there is only one specimen. Given the large disparity in size between *Jindongornipes* (8.0 cm footprint length with hallux) as compared to ZDRC. F3 and the specimens described herein, the Nanguzhai and Zhangzhuhewan site bird tracks are likely not *Jindongornipes*. However, ZDRC. F3 issimilar to the Nanguzhai bird tracks morphologically, and both are found within the Tianjialou Formation: it is likely they represent the same track type as *Goseongornipes* ichnosp.

Ignotornidae (*Hwangsanipes choughi*, *Goseongornipes* isp., *Goseongornipes markjonesi*, *Ignotornis gajinensis, Ignotornis mcconnelli*, *Ignotornis yangi*, Buckley et al., 2016) has a global distribution. However, until recently, the ichnofamily was only reported from Colorado, USA (Mehl, 1931; Lockley et al., 2009), from sites in South Korea (Lockley and Harris, 2010; Kim et al., 2012; Lockley et al., 2012a, b), and from Canada (Buckley and McCrea, 2017). Increased investigation of Lower Cretaceous deposits, including this investigation, have begun to increase our knowledge of the distribution of Ignotornidae during the Early Cretaceous. Ichnospecies of *Goseongornipes* is smaller than ichnospecies of *Ignotornis*, and display less-pronounced webbing between digits III and IV than is observed in ichnospecies of *Ignotornis* (Lockley et al., 2009). Xing et al. (2011) described a single trackway, MGCM. H13 with 5 tracks from the Huangyangquan track site, Wuerhe district, Xinjiang, that may be referable to *Goseongornipes* ichnosp. However, the length of the tracks in trackway MGCM. H13 range from 3.8 to 4.4 cm. Limited specimen numbers and poor preservation make it difficult for specimens to be further analyzed.

Multivariate statistical analyses comparing the Nanguzhai bird tracks to other described ichnotaxa of Ignotornidae support the morphological similarities to *Goseongornipes* ichnosp (Table 2, Fig. 4). Multivariate analysis of variance (MANOVA) shows the Nanguzhai bird tracks to be significantly distinct from all other tetradactyl Cretaceous bird tracks with the exception of *Goseongornipes* ichnosp. ($p_{same} = 0.165$) when the hallux data are included in the analyses (Table 2). When hallux impression data are removed from the analyses (as halluces are not consistently preserved and may be artificially absent from a limited sample, Buckley et al.,

Table 3
Discriminant loadings of measured track variables for discriminant analysis comparing the Nanguzhai bird tracks to other Cretaceous tetradactyl bird tracks. Bird tracks that exhibit high values long Axis 1 have a high divarication between digit impressions II–III, while tracks that exhibit high values along Axis 2 have a high divarication between digit impressions I–II. The measured variables that contribute the most variation to the dataset are digit divarications I–II, II–III, and III–IV.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12
FL	−0.031	0.010	0.033	0.001	−0.005	0.002	−0.020	0.002	−0.003	−0.007	−0.010	−0.001
FW	−0.020	0.007	0.020	0.017	−0.014	0.004	0.018	−0.019	−0.014	−0.004	0.016	0.003
DLI	−0.005	0.001	0.012	0.006	0.016	0.008	−0.019	−0.007	−0.010	0.060	0.049	−0.022
DLII	−0.008	−0.002	0.006	0.031	0.003	0.016	0.003	0.004	−0.013	0.006	−0.014	0.002
DLIII	−0.012	0.009	0.042	0.001	−0.009	0.010	−0.018	0.003	−0.008	−0.007	−0.011	-2.95×10^{-05}
DLIV	−0.006	4.00×10^{-04}	0.001	0.010	−0.007	0.022	−0.015	−0.028	−0.023	−0.014	4.72×10^{-04}	0.003
DIVI-II	1.12	10.6	−1.85	−0.237	0.284	0.282	−0.427	1.73	−1.08	−0.607	−2.52	0.327
DIVII-III	2.46	−0.876	1.74	3.03	0.431	−6.69	−0.080	−2.21	−2.30	0.040	1.47	0.601
DIVIII-IV	1.88	−0.046	1.45	3.88	−0.402	0.981	0.954	−1.62	5.57	−1.90	2.71	−0.931
PL	−0.003	−0.002	−0.005	0.011	−0.058	−0.008	−0.019	0.009	−0.003	0.015	0.006	−0.029
SL	−0.003	−0.002	−0.006	0.011	−0.052	−0.005	−0.022	0.016	0.007	0.016	0.013	0.024
PA	0.147	−0.544	−1.97	2.1808	−1.62	−0.311	−2.25	7.88	−3.18	−5.84	6.59	−0.168

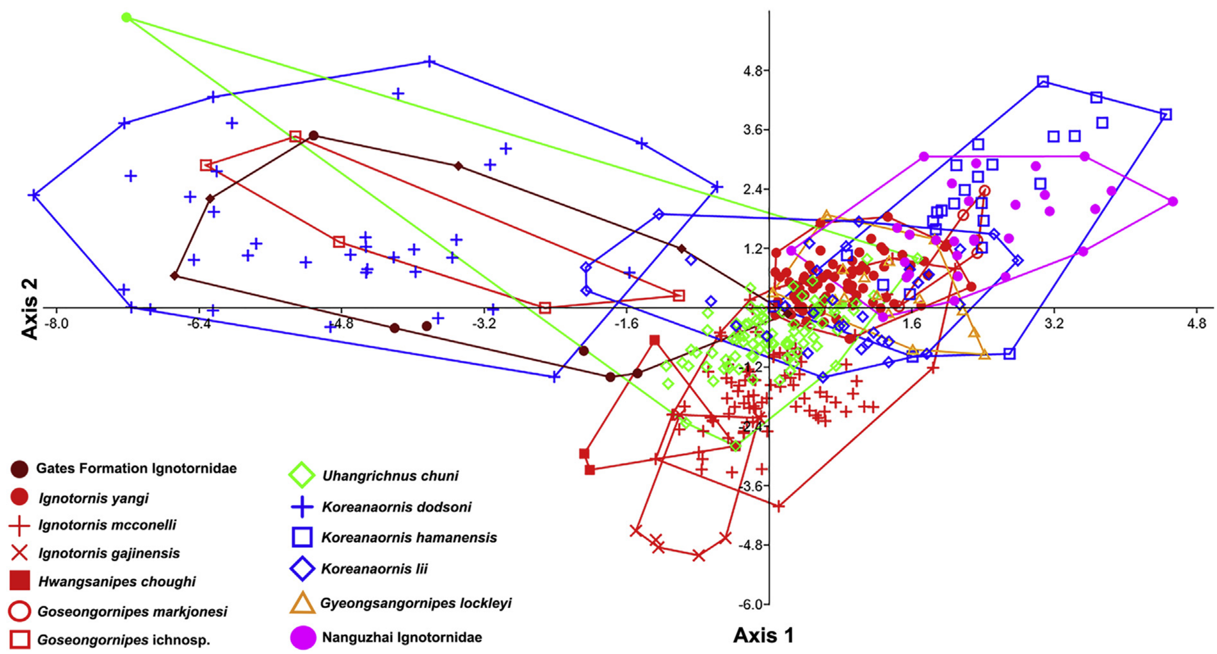

Fig. 4. Graphical results of discriminant analysis comparing the Nanguzhai bird tracks to described tetradactyl bird tracks from the Cretaceous Period. The Nanguzhai bird tracks, while grouping closely with *Koreanaornis hamanensis*, is morphologically distinct from all ichospecies of *Koreanaornis*. As indicated by the multivariate analysis of variance (MANOVA), the Nanguzhai bird tracks also group with *Goseongornipes* and *Gyeongsangornipes* (Table 2).

2015), the Nanguzhai bird tracks are not significantly different from *Goseongornipes* ichnosp. ($p_{same} = 0.99$), *Gyeongsangornipes lockleyi* ($p_{same} = 0.99$), *Koreanaornis dodsoni* ($p_{same} = 0.99$), and *Koreanaornis lii* ($p_{same} = 0.09$). The largest influence to the dataset are the measurements of digit impression divarications II–III and III–IV. Morphologic comparison of the ichnotaxa that are not significantly different than the Nanguzhai bird tracks reveals that the multivariate analyses should not be the sole tool for determining the identity of the Nangushai bird tracks. The Nanguzhai bird tracks are much smaller than *Gyeongsangornipes lockleyi* and do not demonstrate the same extent of webbing impressions. The size of the hallux impressions of the Nanguzhai bird tracks are different from those seen in ichnospecies of *Koreananornis*. When preserved, hallux impressions of ichnospecies of *Koreananornis* are consistently short, and much less than 25% of digit III impression length. Also, digit impressions of ichnospecies of *Koreanaornis* are consistently thin and lack any trace of webbing impressions between digit impressions III and IV.

A new ichnospecies of *Ignotornis* was reported from the Gates Formation (Lower Cretaceous, Albian) of western Canada (Buckley and McCrea, 2017), which is the first time since the initial description of *Ignotornis mcconnelli* (Mehl, 1931) that this ichnogenus has been described in North America. The Nanguzhai bird tracks are smaller (2.8 cm) in footprint length than the new ichnospecies of *Ignotornis* described from Canada (average 4.9 cm, Buckley and McCrea, 2017), and is also smaller than all reported ichnotaxa of Ignotornidae. The described ichnotaxa that are closet in size to the Nanguzhai bird tracks are *Goseongornipes markjonesi* with an average footprint length of 3.38 cm (Kim et al., 2006; Lockley et al., 2006a, b), and *Ignotornis yangi* (Lockley et al., 2006a, b) with an average footprint length of 3.26 cm.

6. Conclusions

Ignotornidae historically have had a Laurasian-wide distribution in Lower Cretaceous deposits, but are restricted to one locality in the United States, two localities in Canada, and to several localities in South Korea. This is the first report of Ignotornidae from China, demonstrating that the apparent restricted occurrences of Ignotornidae worldwide are likely artificial; reports of Ignotornidae will continue to increase with an increase in investigation of Lower Cretaceous deposits for small vertebrate tracks.

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References

Azuma, Y., Lű, J., Jin, X., Noda, Y., Shibata, M., Chen, R., Zheng, W., 2013. A bird footprint assemblage of the early Late Cretaceous age, Dongyang City, Zhejiang Province, China. Cretaceous Research 40, 3–9.

Buckley, L.G., McCrea, R.T., 2017. Avian traces of the Gates Formation (Early Cretaceous: Albian) of northwest Alberta and northeast British Columbia: first report of Ignotornidae in Canada. Canadian Society of Vertebrate Palaeontology. Vertebrate Anatomy Morphology Palaeontology 4, 12–14.

Buckley, L.G., McCrea, R.T., Lockley, M.G., 2015. Birding by Foot: A Critical Look at the Synapomorphy- and Phenetic-Based Approaches to Trackmaker Identification of Enigmatic Tridactyl Mesozoic Traces. Ichnos 22 (3–4), 192–207.

Buckley, L.G., McCrea, R.T., Lockley, M.G., 2016. Analysing and resolving Cretaceous Avian Ichnotaxonomy using multivariate statistical analyses: approaches and results. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: the Next Steps. Indiana University Press, Bloomington, pp. 259–309.

Farlow, J.O., Holtz Jr., T.R., Worthy, T.H., Chapman, R.E., 2013. Feet of the fierce (and not so fierce): pedal proportions in large theropods, other non-avian dinosaurs, and large ground birds. In: Parrish, J.M., Molar, R.E., Currie, P.J., Koppelhus, E.B. (Eds.), Tyrannosaurid Paleobiology. Indiana University Press, Bloomington, pp. 88–132.

Fiorrillo, A.R., Hasiotis, S.T., Kobayashi, Y., Breithaupt, B.H., McCarthy, P.J., 2011. Bird tracks from the Upper Cretaceous Cantwell Formation of Denali National Park, Alaska, USA: a new perspective on ancient northern polar diversity. Journal of Systematic Palaeontology 9 (1), 33–49.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1–9.

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., 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., Lockley, M.G., Seo, S.J., Kim, K.S., Kim, S.H., Baek, K.S., 2012. 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 (1–2), 28–42.

Kim, J.Y., Kim, M.K., Oh, M.S., Lee, C.Z., 2013. A new semi-palmate bird track, *Gyeongsangornipes lockleyi* ichnogen. et ichnosp. nov., and *Koreanaornis* from the Early Cretaceous Jindong Formation of Goseong County, Southern Coast of Korea. Ichnos 20 (2), 72–80.

Kuang, H.W., Liu, Y.Q., Wu, Q.Z., Cheng, G.S., Xu, K.M., Liu, H., Peng, N., Xu, H., Chen, J., Wang, B.H., Xu, J.L., Wang, M.W., Zhang, P., 2013. Dinosaur track sites and palaeogeography of the late Early Cretaceous in Shuhe rifting zone of Shandong Province. Journal of Palaeogeography Chinese Edition 15 (4), 435–453.

Li, Q.P., Zhao, F.J., 1992. The establishment and comparison of the Lower Cretaceous Dasheng Group in Shandong Province. Geology of Shandong 8 (2), 13–21.

Li, R., Lockley, M.G., Liu, M., 2005. A new ichnotaxon of fossil bird track from the Early Cretaceous Tianjialou Formation (Barremian-Albian), Shandong Province, China. Chinese Science Bulletin 50 (11), 1149–1154.

Li, R., Lockley, M.G., Matsukawa, M., Liu, M., 2015. Important dinosaur-dominated footprint assemblages from the Lower Cretaceous Tianjialou Formation at the Houzuoshan Dinosaur Park, Junan County, Shandong Province, China. Cretaceous Research 52, 83–100.

Liu, M.W., Zhang, Q.Y., Song, W.Q., 2003. Division of the Cretaceous lithostratigraphic and volcanic sequences of Shandong Province. Journal of Stratigraphy 27 (3), 247–253.

Lockley, M.G., Harris, J.D., 2010. On the trail of early birds: a review of the fossil footprint record of avian morphological and behavioral evolution. In: Ulrich, P.K., Willet, J.H. (Eds.), Trends in Ornithology Research. Nova Science Publishers, Hauppauge, New York, pp. 1–63.

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 - B 336, 113–134.

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 (3–4), 229–249.

Lockley, M.G., Houck, K., Yang, S.-Y., Matsukawa, M., Lim, S.-K., 2006a. 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., Matsukawa, M., Ohira, H., Li, J., Wright, J., White, D., Chen, P., 2006b. Bird tracks from Liaoning Province, China: new insights into avian evolution during the Jurassic-Cretaceous transition. Cretaceous Research 27, 33–43.

Lockley, M.G., Chin, K., Houck, K., Matsukawa, M., Kukihara, R., 2009. New interpretations of *Ignotornis*, the first-reported Mesozoic avian footprints: implications for the paleoecology and behavior of an enigmatic Cretaceous bird. Cretaceous Research 30, 1041–1061.

Lockley, M.G., Lim, J.D., Kim, J.-Y., Kim, K.-S., Huh, M., Hwang, K.G., 2012a. Tracking Korea's early birds: ichnological insights into avian evolution and behavior. Ichnos 19, 17–27.

Lockley, M.G., Li, J., Matsukawa, M., Li, R., 2012b. A new avian ichnotaxon from the Cretaceous of Nei Mongol, China. Cretaceous Research 34, 84–93.

McCrea, R.T., Buckley, L.G., Plint, A.G., Lockley, M.G., Matthews, N.A., Noble, T.A., Xing, L.D., Krawethz, J.R., 2015. Vertebrate ichnites from the Boulder Creek Formation (Lower Cretaceous: middle to ?upper Albian) of northeastern British Columbia, with a description of a new avian ichnotaxon, *Paxavipes babcockensis* ichnogen. et isp. nov. Cretaceous Research 55, 1–18.

Mehl, M.G., 1931. New bird record from the Dakota Sandstone, of Colorado. The Geological Society of America Bulletin 42, 331.

Shi, W., Zhang, Y., Dong, S., Wu, L., Du, L., 2013. Tectonic deformation and formation and evolution of the Jiao-Lai Basin, Shandong: a case study of a deformation analysis of the Wangshi and Dasheng groups. Geological Bulletin of China 22 (5), 325–334.

Si, S.Y., 2002. Palynological assemblage from the Dasheng Group and its significance in Shandong Province. Journal of Stratigraphy 26 (4), 126–130.

Sweetman, S.C., 2016. A comparison of Barremian–early Aptian vertebrate assemblages from the Jehol Group, north-east China and the Wealden Group, southern Britain: the value of microvertebrate studies in adverse preservational settings. Palaeobiodiversity and Palaeoenvironments 96 (1), 149–167.

Tan, H.C., 1923. New research on the Mesozoic and Early Tertiary geology in Shandong. Bulletin of the Geological Survey of China 5, 95–135.

Wang, M.W., Kuang, H.W., Liu, Y.Q., Peng, N., Liu, H., Wu, Q.Z., Xu, J.L., Chen, J., Xu, H., Wang, B.H., Zhang, P., 2013. New discovery of dinosaur footprint fossils and palaeoenvironment in the late Early Cretaceous at Tancheng County, Shandong Province and Donghai County, Jiangsu Province. Journal of Palaeogeography Chinese Edition 15 (4), 489–504.

Xing, L.D., Harris, J.D., Wang, K.B., Li, R.H., 2010a. An Early Cretaceous Non–avian dinosaur and bird footprint assemblage from the Laiyang Group in the Zhucheng Basin, Shandong Province, China. Geological Bulletin of China 29 (8), 1105–1112.

Xing, L.D., Harris, J.D., Jia, C.K., 2010b. Dinosaur tracks from the Lower Cretaceous Mengtuan Formation in Jiangsu, China and morphological diversity of local sauropod tracks. Acta Palaeontologica Sinica 49 (4), 448–460.

Xing, L.D., Harris, J.D., Jia, C.K., Luo, Z.J., Wang, S.N., An, J.F., 2011. Early Cretaceous bird-dominated and dinosaur footprint assemblages from the northwestern margin of the Junggar Basin, Xinjiang, China. Palaeoworld 20, 308–321.

Xing, L.D., Lockley, M.G., Bonnan, M.F., Marty, D., Klein, H., Liu, Y.Q., Zhang, J.P., Kuang, H.W., Burns, M.E., Li, N., 2015. Late Jurassic–Early Cretaceous trackways of small-sized sauropods from China: New discoveries, ichnotaxonomy and sauropod manus morphology. Cretaceous Research 56, 470–481.

Xing, L.D., Buckley, L.G., Lockley, M.G., Zhang, J.P., Marty, D., Wang, Y., Li, J.J., McCrea, R.T., Peng, C., 2016. A new bird track, *Koreanaornis lii* ichnosp. nov., from the Lower Cretaceous Hekou Group in the Lanzhou-Minhe Basin, Gansu, Northwest China, and implications for Early Cretaceous avian diversity. Cretaceous Research 66, 141–154.

Yang, S.-Y., Lockley, M.G., Greben, R., Erickson, B.R., Lim, S.-K., 1995. Flamingo and duck-like traces from the Late Cretaceous and early Tertiary: evidence and implications. Ichnos 4 (1), 21–34.

Zhang, Y.Q., Dong, S.W., Shi, W., 2003. Cretaceous deformation history of the middle Tan-Lu fault zone in Shandong Province, eastern China. Tectonophysics 363, 243–258.

Zhen, S., Li, J., Zhang, B., 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan, China. Memoirs of the Beijing Natural History Museum 54, 105–120.

Zhou, Z., Wang, Y., 2010. Vertebrate diversity of the Jehol Biota as compared with other lagerstätten. Science China Earth Sciences 53, 1894–1907.