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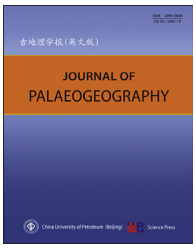

Biopalaeogeography and palaeoecology

A redescription of the ichnospecies *Koreanaornis anhuiensis* (Aves) from the Lower Cretaceous Qiuzhuang Formation at Mingguang city, Anhui Province, China

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Abstract The Cretaceous bird trackway originally labeled *Aquatilavipes anhuiensis*, in 1994, had previously been examined, photographed and replicated, but never described or illustrated in detail. However, it has been part of a widening discussion about the distribution of *Aquatilavipes* and *Koreanaornis* in China (and Korea). Here we illustrate and formally describe the holotype in detail and assign it to *Koreanaornis* (*Koreanaornis anhuiensis*) as informally proposed by previous authors. We also demonstrate that most authenticated reports of *Koreanaornis*, including the Anhui occurrence, are from the Lower Cretaceous, not from the Upper Cretaceous as previously reported.

Keywords Lower Cretaceous, Ichnospecies, *Koreanaornis*, *Aquatilavipes*, Qiuzhuang Formation, Anhui Province

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1. Introduction

At present, many Early Cretaceous bird tracksite reports come from China (Lockley and Harris, 2010; Lockley *et al.*, 2012a; Xing *et al.*, 2011, 2015, 2016) and Korea (Huh *et al.*, 2012; Lockley *et al.*, 2012b). The number of new ichnogenera is steadily growing. In addition to *Aquatilavipes* (Zhen *et al.*, 1994), the list now includes five recent additions: *Shandongornipes* (Li *et al.*, 2005), *Pullornipes* (Lockley *et al.*, 2006a), *Wupus* (Xing *et al.*, 2007, 2015), *Moguiornipes* (Xing *et al.*, 2011), *Tatarornipes* (Lockley *et al.*, 2012c), and *Uhangrichnus* which, by formal revision, is considered a subjective senior synonym *Dongyangornipes* following Buckley *et al.* (2016), *contra* Azuma *et al.* (2013). Korea has also proved a rich source of Cretaceous bird tracksites including ichnospecies belonging to eight avian ichnogenera, including six first named from Korea (Kim *et al.*, 2012, 2013; Lockley *et al.*, 2012b; and references therein). Together China and Korea have yielded the vast majority of important Cretaceous bird tracks making East Asia a "paradise" for birds (Kim *et al.*, 2012).

There were only two bird track records reported from China during 1990s, "*Aquatilavipes sinensis*" from Emei, Sichuan Province (Zhen *et al.*, 1994), and "*Aquatilavipes anhuiensis*" from Mingguang, Anhui Province (Jin and Yan, 1994). Jin and Yan (1994) named "*A. anhuiensis*" based on a single trackway, which is the only specimen presently referred to this taxon. The specimen was mentioned by Matsukawa *et al.* (2006, p. 20) as "bird tracks" from the "Mingguang" (*sic*) site, and traced (UCM 569), photographed and replicated by one of us (MGL), in 2001, for the University of Colorado Museum (UCM) collections as UCM 214.45. Lockley *et al.* (2008, 2012a) suggested that "*A. sinensis*" had more affinity to *Koreanaornis* (Kim, 1969; Lockley and Harris, 2010; Lockley *et al.*, 1992) than to "*Aquatilavipes*", and therefore reclassified it under the revised combination *Koreanaornis sinensis*. It is unlike *Aquatilavipes* in revealing a small hallux trace, and Lockley *et al.* (2013) also reclassified "*A. anhuiensis*" as *Koreanaornis anhuiensis*. We have since relocated the specimen allowing it to be described and illustrated here in detail based on independent examinations of the specimen more than a decade apart.

Jin and Yan (1994) did not mention geological setting or locality information in their brief paper describing the ichnotype of *K. anhuiensis*. Between 1999 and 2001, nothing was found during Sino–Japanese–American expeditions in Gupei Basin (also known as the Jiashan Basin) except for one potential site (32°58′38.16″N, 117°59′49.2″E; Matsukawa *et al.*, 2006) from which the specimen may have originated. In the following years, the first author and researchers from Anhui Geological Museum also failed to make any progress in this area. However, further study of *K. sinensis* specimen and geological investigation of the site in 2009 and 2017 have provided new information that necessitates a revision of this specimen.

2. Geological setting

The Gupei Basin lies to the north of the Hefei Basin and is tectonically controlled by the extensional activities along the Tan–Lu Fault Zone like the Hefei Basin (Mercier *et al.*, 2007). The Yi–Shu Fault Belt extends from Shandong Province to Jiashan County in the north of Anhui Province with some Cretaceous graben basins developed along its extent. The Gupei Basin to the north of Jiashan County of Anhui Province is continuous with the Tancheng Basin in the south of Yi–Shu Fault Belt *via* Jiangsu Province (Zhu *et al.*, 2001).

Jin and Yan (1994) did not provide any geological background but only mentioned that "the fossil is found in Qiuzhuang Formation (formerly called Zhuxiang Formation) where plant fossils *Brachyphyllum*, *Otozamites*, *Suturovagina*, *Manica*, *Frenelopsis* with palynological assemblages dominated by *Schizaeoisporites* and other fossils such as bivalve *Sphaerium* had been discovered before, suggesting an early Late Cretaceous age" (Jin and Yan, 1994, p. 57).

However, Jin and Yan (1994) have confused some names of the formations. The Anhui Bureau of Geology and Mineral Resources (1987, 1988) considered that the Cretaceous sedimentary sequence of the Gupei Basin is divided into the Lower Cretaceous Xinzhuang Formation (formerly called Zhuxiang Formation), and Qiuzhuang Formation (formerly called Xiangdaopu Formation) and the Upper Cretaceous Zhangqiao Formation.

The Xinzhuang Formation is 1100 m in total thickness. The lower section of the Xinzhuang Formation mainly consists of gray purple conglomerate and gray yellow lithic sandstone interbedded with siltstone and mudstone. The upper section comprises yellow green medium-to fine-grained lithic sandstone, siltstone and mudstone interbedded with marlstone. This formation yields plant fossils (*Manica*, *Frenelopsis*, *Suturovagina*, and *Brachyphyllum*), bivalve (*Nakamuranaia chingshanensis*), conchostracan fossils (*Yanjiestheria* sp. and *Sinoestheria* sp.), and the ostracod *Cypridea* (*Cypridea*) *priva* Lubimova. Pollen of gymnosperms accounts for 81.3% of the palynological assemblage.

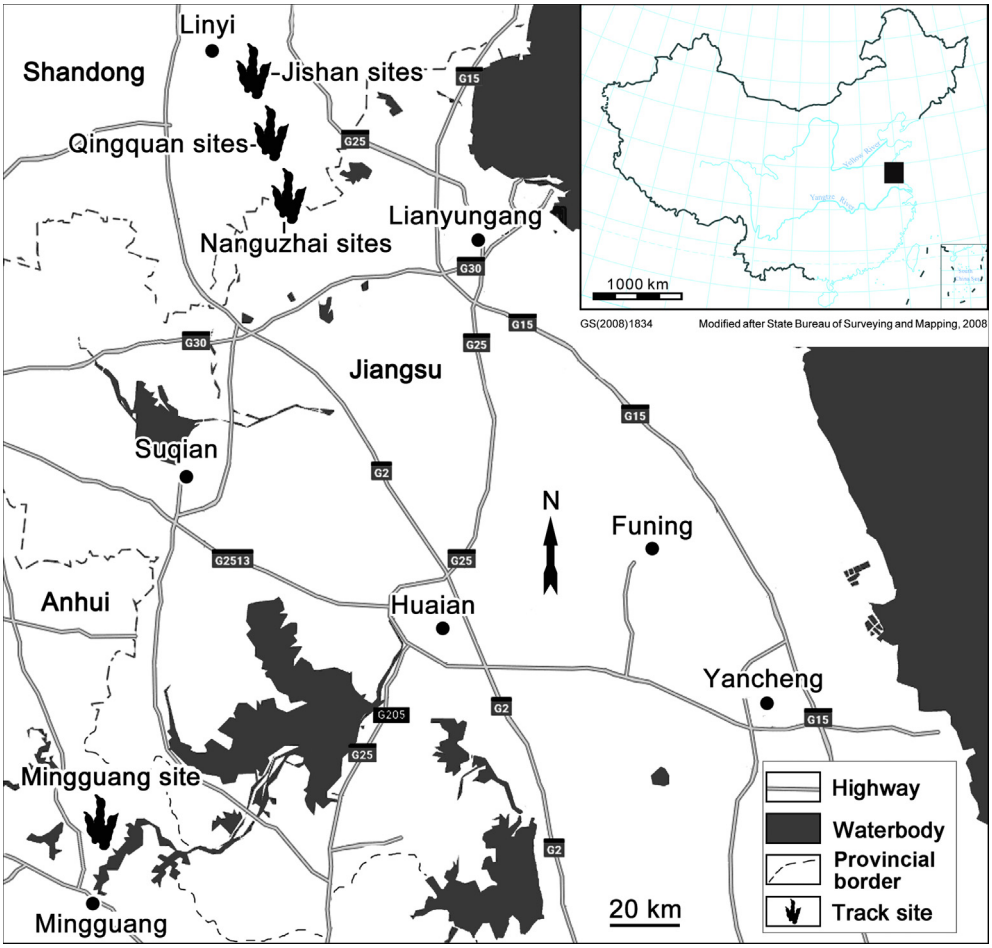

Fig. 1 Geographical setting showing the location (footprint icon) of the Mingguang bird site in Anhui Province, and dinosaur sites in Shandong Province, China.

The largest proportion of pollen gymnosperms accounts is Pinaceae (25%), and secondly, *Classopollis* (18.6%). Most spores are attributable to *Lygodiaceae* (Anhui Bureau of Geology and Mineral Resources, 1987, 1988; Li and Jiang, 1997; Tu and Xiang, 1989).

The Qiuzhuang Formation crops out mostly in the Gupei and Hefei basins. The lower section is constituted of interbedded fine lithic sandstone, arkose sandstone and siltstone, intercalated with calcilutite and sandy mudstone. The lower part of the upper section is made up of interbedded gray purple thick-bedded sandy conglomerate and fine-grained lithic arkose, and the upper part of the upper section is made up of interbedded dark purple silty mudstone and gray brown fine-grained lithic arkose. The total thickness is 2192 m, 900 m of which lies in the Hefei Basin and mainly crops out as brown and brownish gray silty mudstone, of which the upper part is interbedded with medium- to fine-grained sandstone that contains gypsum. The Qiuzhuang Formation is in conformable contact with the Xinzhuang Formation and preserves similar plant fossils. In the palynological assemblage found in the Qiuzhuang Formation, spores account for 52.3%, and most of them are *Schizaeoisporites* (41.6%), and angiosperm pollen accounts for 3.6%—6.1%. The ostracod *Cypridea* (*Pseudocypridina*) *aversa* and a few specimens of the bivalve *Sphaerium* can also be found in this formation (Anhui Bureau of Geology and Mineral Resources, 1987, 1988; Li and Jiang, 1997; Tu and Xiang, 1989).

Despite controversy over the geologic age of the Xinzhuang Formation (some authors proposed a Late Jurassic age (Zhang *et al.*, 2009)), the age of the Qiuzhuang Formation (Xiangdaopu Formation) is certainly the Early Cretaceous (Tu and Xiang, 1989; Zhang *et al.*, 2009; Zhu *et al.*, 2012). Zhu *et al.* (2012) suggested that the Xinzhuang Formation is Berriasian—Hauterivian in age, the Maotanchang Formation (volcanic rocks) is Barremian—Aptian, and the Qiuzhuang Formation is Albian based on crustal deformation kinematics and $^{40}Ar/^{39}Ar$ dating. These formations are contemporaneous with the Dasheng, Qingshan

Table 1 Measurements (in cm) of the bird tracks from Mingguang site (Fig. 1), Anhui Province, China.

Number	FL	FL′	FW	LI	LII	LIII	LIV	I—II	II—III	III—IV	PL	SL	L/W
AGB2882-1	2.32	—	4.06	—	2.14	2.30	2.20	—	61	77	—	—	0.6
AGB2882-2	2.76	3.49	3.12	0.76	1.55	2.68	2.10	101	51	61	5.33	—	0.9
AGB2882-3	<3.16	—	—	—	—	—	—	—	—	—	7.55	13.30	—
AGB2882-4	2.62	3.02	3.93	0.75	2.35	2.6	2.17	—	66	57	6.01	—	0.7
AGB2882-5	2.65	3.46	3.10	0.76	1.85	2.67	1.86	105	77	40	—	—	0.9
Mean	2.59	3.32	3.55	0.76	1.97	2.56	2.08	103	64	59	6.30	13.30	0.8

Abbreviations: FL = Footprint length; FL' = Footprint length with hallux; FW = Footprint width; LI, LII, LIII, LIV: Digit lengths; I—II, II—III, III—IV: Angle between digits I and II, digits II and III, digits III and IV; PL = Pace length; SL = Stride length; L/W = FL/FW.

(volcanic rocks) and Mengyin/Laiyang formations in the Yishu Graben and Jiaolai Basin, respectively.

3. Systematic ichnology

Koreanaornipodidae Lockley *et al.*, 2006b.
Koreanaornis Kim, 1969.

Type ichnospecies: *Koreanaornis hamanensis* Kim, 1969, Lockley *et al.*, 1992 emend.
Diagnosis: Small, tetradactyl bird tracks with small hallux impressions occasionally present. Digit traces typically separate (*i.e.*, not connected proximally). Claw traces variably present, slender, and obscure. Trackways exhibit inward (positive) rotation of the tracks. Tracks wider than long, with widths ranging from 2.5 cm to 4.4 cm. Divarication between digits II and IV averaging about 120° (Lockley *et al.*, 1992).

Koreanaornis anhuiensis n. comb (Jin and Yan, 1994). Lockley *et al.*, 2013.

Holotype: A complete natural cast of track from trackway with five steps cataloged as AGB2882-5 (GS VIII-4) from the Mingguang tracksite. The specimen is stored in the Anhui Paleontological Museum.
Paratypes: Track casts AGB2882-1—AGB2882-4 in the same trackway as the holotype stored in the Anhui Paleontological Museum.
Type horizon and locality: Qiuzhuang Formation, Lower Cretaceous. Mingguang tracksite, Anhui Province, China (Fig. 1).
Emended diagnosis: Small (footprint length ~33 mm, footprint width ~36 mm), sub-symmetrical, functionally tridactyl tracks by the following combination of characters: a consistently wide average digit II—IV divarication; consistently preserved, the midline of small hallux impression and digit III trace are aligned, and more than one third of the length of digit III trace; digit divarication I—II between 101° and 105° (Table 1; divarication II—IV between 112° and 138°).

Description (see Table 1 for reference): Small (3.32 cm average length; 3.55 cm average width) tetradactyl tracks, with small (0.75 cm—0.76 cm, n = 3) hallux impressions are consistently preserved, making the majority of the tracks appear functionally tridactyl. Digit I traces are relatively short compared to digit traces II—IV. Digit III is the longest digit, and digits II and IV are subequal in length. Digit II is broader than Digit IV. Digit traces II—IV connect proximally to a metatarsophalangeal pad. Digits II and III have two and three pads, respectively, and Digit IV pads are unidentifiable. Digit trace splay is high, with an average footprint length:width ratio of 0.8 (range of 0.6—0.9). The ratio of the length of the hallux impression to digit III is 1:3.5. Digit II—IV divarication (total divarication) is an average of 123° (112°—138° n = 4). The divarication of digits I—II is high (average 103°, range 101°—105°, n = 2). The AGB2882 trackway is incomplete. Based on AGB2882-4 and AGB2882-5, the tracks exhibit an outward rotation.
Remarks: In all five tracks, only AGB2882-1 does not have hallux impression and is oriented in a different direction from the other tracks, indicating a different trackmaker. AGB2882-2—AGB2882-4 may, however, represent the same trackmaker, which turned the foot in an unusual way to make the impression of AGB2882-1 (Fig. 2). AGB2882-3 has distinct drag or sliding traces and double imprints of digits III and IV. Hallux impression of AGB2882-4 shows a lateral sliding trace. The characteristics in the well-preserved AGB2882-2 and AGB2882-5 are similar. Diagnostic characters proposed by Jin and Yan (1994) include similarities with characters suggested by Currie (1981) and by Zhen *et al.* (1994) with the exception of shorter digits and a 128° digit divarication between II and IV. Both digit length and digit divarication of AGB2882 fall into the range of Koreanaornipodidae.
Discussion: It is important to note that *Koreanaornis* is different from *Aquatilavipes*, in size and other morphological features (Buckley *et al.*, 2016). When *Aquatilavipes* was first reported from China by Zhen *et al.* (1994), these authors were unaware of the

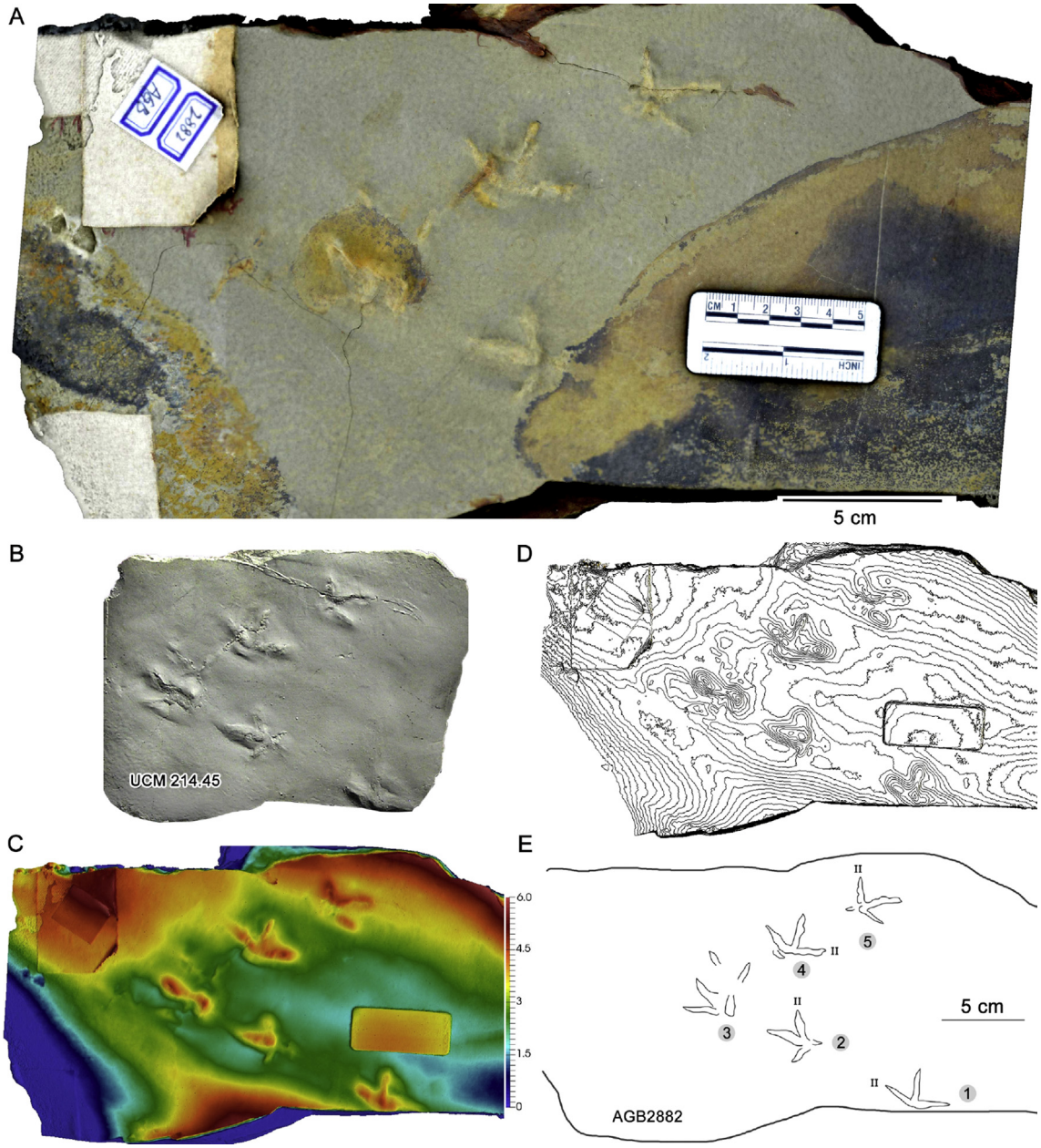

Fig. 2 Photograph (A), clean cast (B), 3D height map (warm colors are high, cooler colors are low) (C), contour map (D) and interpretative outline drawing (E) of *K. anhuiensis* AGB2882. A, C–E are in a same perspective. The rectangles in C and D are scale bar area from A.

original description of *Koreanaornis* from Korea (Kim, 1969). As a result, it was not until much later that it was recognized that such bird tracks, labeled as *Aquatilavipes* from China (Jin and Yan, 1994; Zhen *et al.*, 1994), were subjective junior synonyms of *Koreanaornis* (Buckley *et al.*, 2016; Lockley *et al.*, 2008, 2012a). However, it is still quite possible that *Aquatilavipes* may be found in China (Xing *et al.*, 2011).

Most characteristics of *K. anhuiensis* match those of Koreanaornipodidae (Kim, 1969; Lockley *et al.*, 2006b), such as small, wide, sub-symmetric, functionally tridactyl tracks with slender digit impressions and wide (90°—115°) divarication angles between digits II and IV. The published range of total divarication (digit divarication II—IV) for Koreanaornipodidae (*Koreanaornis dodsoni*, *K. hamanensis*, *K. lii*, *Pullornipes aureus*) is 32° (probably affected by muddy sediment)—170° (average 101°). With the exception of *K. lii*, the diagnostic orientation of digit I for Koreanaornipodidae is 180° from digit IV, which provides an

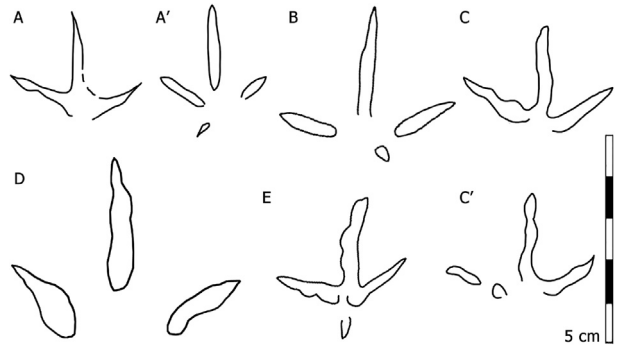

Fig. 3 Morphologic comparison of the ichnospecies of Koreanaornipodidae. A and A' – *Koreanaornis hamanensis* (Lockley *et al.*, 2006b); B – *Koreanaornis lii* (Xing *et al.*, 2016); C and C' – *Koreanaornis sinensis* (Lockley *et al.*, 2008, 2012b); D – *Koreanaornis dodsoni* (Xing *et al.*, 2011); E – *Koreananornis anhuiensis*.

average digit I—II divarication of 79° (10°—148°). Both divarications of *K. anhuiensis* are in this range.

K. anhuiensis shares many features with *K. hamanensis*, *K. dodsoni*, *K. lii* and *K. sinensis*. However, significant differences exist. For example, *K. hamanensis*, *K. dodsoni* and *K. lii* have digit traces that do not join proximally on most tracks, but digit traces of *K. anhuiensis* connect proximally to a metatarsophalangeal pad. Digit trace slenderness in *K. anhuiensis* is more similar to *K. hamanensis* (Kim, 1969; Lockley *et al.*, 2006b, 2012b), *K. sinensis* (Lockley *et al.*, 2008; Zhen *et al.*, 1994) and *P. aureus* (Lockley *et al.*, 2006b) than to *K. dodsoni* (Xing *et al.*, 2011). Furthermore, *K. dodsoni* is larger in size, probably due to some degrees of preservational bias (Fig. 3).

The hallux impressions of *K. anhuiensis* tracks are only known from two specimens. Based on AGB2882-2 and AGB2882-5, the midline of the hallux impression almost overlaps that of digit III, different from other Koreanaornipodidae tracks. More specimens, however, are needed to determine the taxonomic significance of this feature.

4. Conclusions

Koreanaornis is well known from tracksites in Korea. It was first discovered and named by Kim (1969) on the basis of abundant tracks from the Haman Formation (Aptian). Subsequently, the ichnotaxon was reported from the Jindong Formation (?Albian) of Goseong County (Lockley *et al.*, 1992) and other Korean localities (Kim, 2008). *Koreanaornis* was also recently described from the Early Cretaceous Tianjialou Formation (Barremian–Albian) Jishan tracksite in Shandong Province (Li *et al.*, 2005), on the basis of very small tracks (~2.5—3.0 cm wide and long). This occurrence indicates that *Koreanaornis* was also widely distributed in northern China in the late Early Cretaceous in addition to being abundant in Korea.

Based on the present knowledge, *Koreanaornis* is found in the late Early Cretaceous (Barremian—Albian) of China, as well as in deposits of broadly similar age in Korea (Lockley *et al.*, 2012b). This age range corresponds to the occurrence of *K. anhuiensis* from Anhui Province and supports the conclusion that it is inappropriate to consider these materials as Late Cretaceous (*contra* Jin and Yan, 1994).

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