

# 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

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## ABSTRACT

There are a growing number of Early Cretaceous avian tracks and trackways from around the world, with Asia (China and Korea) having the largest reported number and diversity of Mesozoic avian traces to date, and these new discoveries are increasing the Early Cretaceous avian ichnodiversity of Laurasia. Here we report on a new Lower Cretaceous avian track locality in the Guanshan area, Yongjing County, Gansu Province, northwest China, and on a novel ichnospecies of *Koreanaornis*, *Koreanaornis lii* ichnosp. nov. *Koreanaornis lii* is distinct from other *Koreanaornipodidae* in that it possesses a consistently wider digit divarication than previously described tridactyl tracks, and possess a short, small, posteromedially oriented hallux that displays a different orientation than that seen in *Koreanaornis hamanensis*. The lack of linear and angular data reported for digit I traces of many avian ichnotaxa has the potential to give misleading results in multivariate statistical analyses. Also, the wide divarication of *Koreanaornis lii* causes the ichnotaxon to not group with other *Koreanaornipodidae* in multivariate analyses, but with *Ignotornidae*. Despite the results of the analyses, *K. lii* is morphologically distinct from these ichnotaxa. The results demonstrate that relying solely on multivariate statistical analyses without careful examination of footprint morphology will result in erroneous ichnospecies groupings. While new vertebrate ichnotaxa discoveries from Asia may support the hypotheses of the presence of a unique and endemic Asian vertebrate ichnofauna during the Cretaceous, the recent discovery of skeletal remains interpreted to be of a volant wading bird from the Early Cretaceous, and recent reports of tracks from volant avians, could suggest that flighted avians of the shore- and wading bird ecotypes could have had a Laurasian-wide distribution during the Early Cretaceous. However, strong convergence in foot morphology of shore- and wading birds suggests that avian ichnotaxa found in both present-day Asia and North America may have been made by birds endemic to eastern and western Laurasia during the Early Cretaceous.

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## 1. Introduction

The avian track record from the Early Cretaceous is fast growing. New reports of avian tracks from Australia (Martin et al., 2013), Utah, (Lockley et al., 2015), and British Columbia (McCrea et al.,

2015) are beginning to flesh out the relative (and likely artificial) paucity of Early Cretaceous bird tracks from around the world. However, to date the greatest diversity of Early Cretaceous bird tracks is from the Lower Cretaceous deposits of Asia (China, Korea; Kim et al., 2012; Lockley et al., 2012c).

All bird tracks in northwestern China are distributed in Lower Cretaceous (?Aptian – Albian) strata, the majority of which

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occurring in the Lanzhou–Minhe Basin of Gansu (Li et al., 2002), Chabu of Inner Mongolia (Li et al., 2009; Lockley et al., 2012a), and Wuerhe of Xinjiang (Xing et al., 2011, 2013). The avian tracksites of the Wuerhe area preserve a highly diverse avian ichnofauna, with tracks attributed to *Aquatilavipes* ichnosp., *Goseongornipes* ichnosp., *Koreanaornis* ichnosp., and *Moguiornipes robusta* (Xing et al., 2011). *Tatarornipes chabuensis* occurs at the Chabu area, as well as *Aquatilavipes* ichnosp. and *Koreanaornis* ichnosp. (Lockley et al., 2012c). Lockley et al. (2012c) proposed that the abundance eastern Asian Cretaceous terrestrial vertebrate ichnofauna (specifically the dinosaurian ichnofauna) was due to local endemism. It remains to be seen if this endemism is supported by the avian track record, as several avian ichnotaxa are reported from China, Korea, and North America which indicates the existence of a prolific avian fauna in Laurasia during the Early Cretaceous.

Here we report a new avian tracksite containing a novel avian ichnotaxon of *Koreanaornis* from the Guanshan area, Yongjing County, Gansu Province. The Lanzhou–Minhe Basin is located on the boundary between the Gansu and Qinghai Provinces (Fig. 1) encompassing an area of 11,300 km<sup>2</sup>, where abundant fossils of dinosaurs (e.g. You et al., 2005, 2006) and dinosaur-pterosaur tracks (Zhang et al., 2006; Xing et al., 2013) have been found. In the year 2000, collaborators from the Research Center of Paleontology of the Bureau of Geology and Resource Exploration of Gansu Province discovered a bird tracks exposed at Yanguoxia No.1 tracksite (the most representative tracksite at Yanguoxia area) from Yongjing County. At the same time, four additional bird footprints were found as well (Li et al., 2002). Subsequently more bird tracks were discovered at Shangpujia and Xiapujia Villages, Guanshan Township, Yongjing County (Fig. 1). However, these new tracks have not been scientifically described. In 2013, a research team led by the first author began a detailed study of these track sites. During this process, Xing LD, Lockley MG, Marty D and Peng C investigated the Xiapujia bird tracksite and documented the rest of the tracks (Fig. 2).

Li et al. (2002) originally reported the tracks from the Yanguoxia locality as similar to *Koreanaornis hamanensis* and *Aquatilavipes sinensis*. A detailed examination of these and additional specimens shows that the tracks, with slender digit traces, wide digit splay, and a small, posteromedially oriented hallux impression, are most similar in size and morphology to those ichnotaxa within *Koreanaornipodidae*.

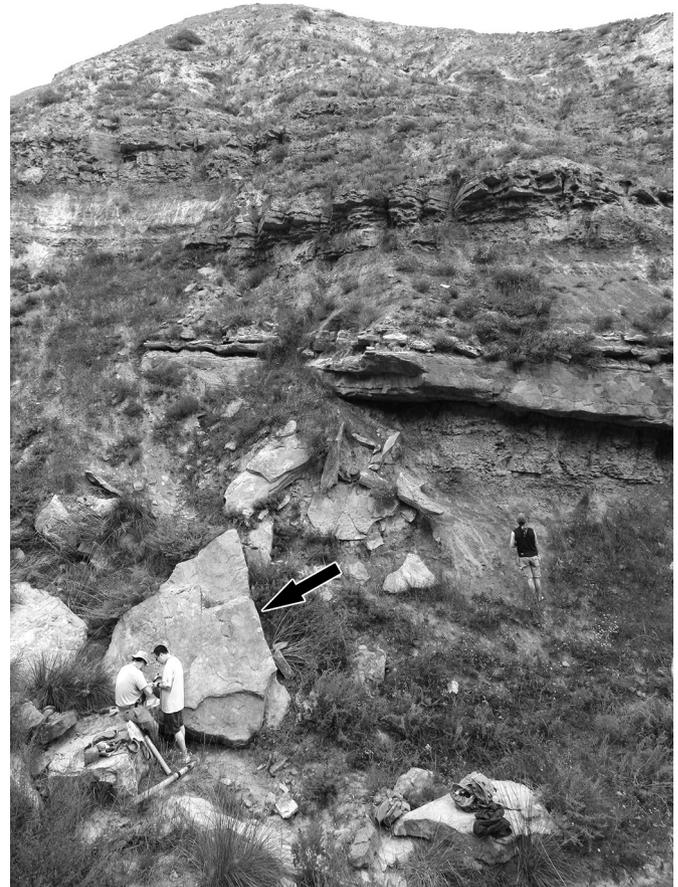


Fig. 2. Outcrop exposure of the Xiapujia bird tracksite in Gansu Province, central China. Arrow indicates the ex-situ slab on which the bird tracks were preserved.

### 1.1. *Koreanaornis* from Xiapujia and Shangpujia tracksites in the Gansu Province

*Koreanaornis hamanensis* was the second avian ichnotaxon named from the Mesozoic (Kim, 1969; Lockley et al., 2012a). The

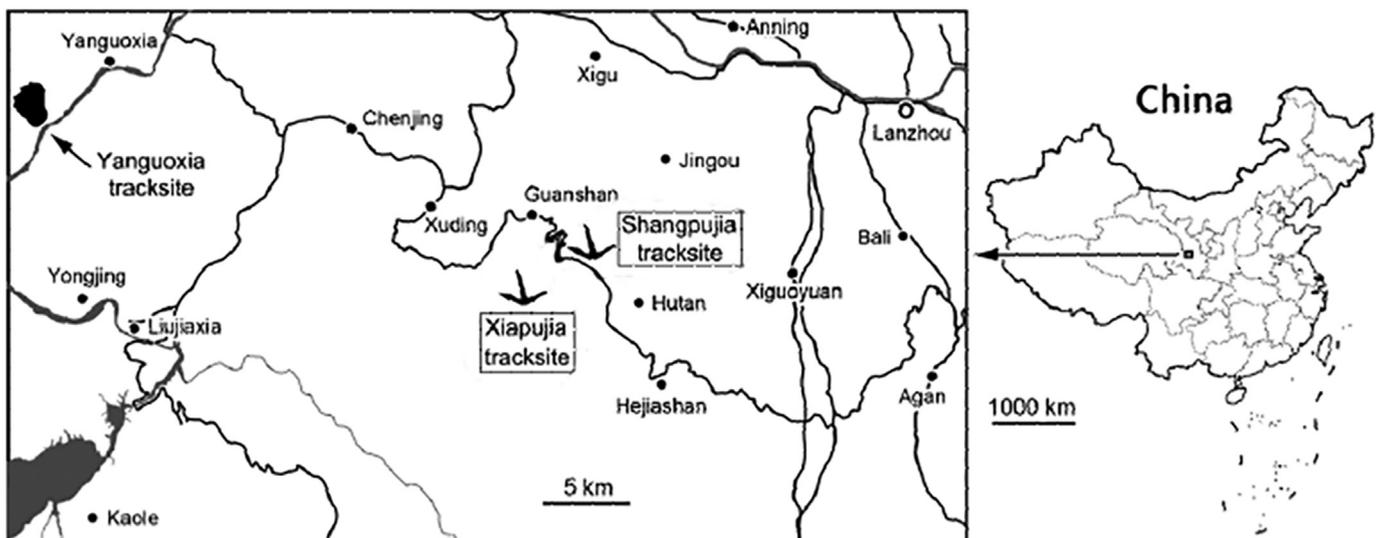


Fig. 1. Geographic location of location of the Xiapujia and Guanpujia bird tracksites from the Lower Cretaceous Hekou Group of Guanshan area, Yongjing County, Gansu Province.

initial description of *Koreanaornis hamanensis* did not differentiate it from other avian traces; although, at the time of description, *Koreanaornis hamanensis* was the second only avian ichnotaxon described from the Cretaceous, and the first diagnosis only became inadequate with the later discoveries of Early Cretaceous avian ichnotaxa. The diagnosis and description of *Koreanaornis hamanensis* was later emended by Lockley et al. (1992) to include more detailed information in characterizing the ichnospecies, including that the digit impressions are not joined proximally, the divarication between digit traces II–IV is between 105° and 125°, and that there is an inward footprint rotation in those tracks preserved in trackways. Lockley et al. (2006a) established the ichnofamily Koreanaornipodidae as traces that are small (2.5 cm–3.0 cm), functionally tridactyl but with an occasionally preserved small (although no length was specified) posteromedially directed hallux impression approximately 180° from digit IV trace, or, to follow the more conventional method of expressing digit I divarication, approximately 65°–90° from digit II impression, as calculated from a total divarication (divarication between digit traces II–IV) of 90°–115° for Koreanaornipodidae.

Since the establishment of Koreanaornipodidae, two ichnotaxa ascribed to this ichnofamily were erected: *Pullornipes aureus* (Lockley et al., 2006b) and *Koreanaornis dodsoni* (Xing et al., 2011). *Koreanaornis* cf. *hamanensis* has been reported from the Cretaceous of China (Azuma et al., 2013; Lockley et al., 2015). Li et al. (2002) formally assigned the Yanguoxia tracks to *Avipeda*, but did not assign them to lower ichnotaxonomic levels. While the Gansu bird tracks are most similar in morphology to those of *Koreanaornis hamanensis* (as noted by Li et al., 2002), there are morphological differences that warranted a detailed comparison of the avian tracks from the Xiapujia and Shangpujia tracksites (hereon referred to as the “Gansu bird tracks”) to those of established Early Cretaceous avian ichnotaxa. Results of the comparison of the Gansu bird tracks to existing avian ichnotaxa demonstrate that the Gansu bird tracks are a novel ichnospecies of *Koreanaornis* (Figs. 3–5).

The purpose of this study is to describe the new ichnospecies of *Koreanaornis*, *Koreanaornis lii* ichnosp. nov., and to compare the new ichnospecies to other ichnospecies of Koreanaornipodidae and other similar-sized avian ichnotaxa from the Mesozoic in multivariate statistical analyses. The new ichnospecies is also discussed in the context of the hypothesis of local endemism in eastern Asian vertebrates of the Cretaceous.

## 2. Institutional abbreviations

GLSZP = Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of Gansu Province, China; SPJ = Shangpujia tracksite, Yanguoxia area, Gansu, China; XPJ = Xiapujia tracksite, Yanguoxia area, Gansu, China; GSGM = Geological Museum of Gansu.

## 3. Materials and methods

### 3.1. Footprint and trackway data collection

Footprint and trackway linear and angular data were collected (Table S1) as described in McCrea et al. (2015) (Fig. 6).

Data from the Gansu bird tracks were compared to published data of similar-sized bird tracks from the Early and Late Cretaceous: *Aquatilavipes izumiensis* (Azuma et al., 2002), *Aquatilavipes swiboldae* (Currie, 1981), *Archaeornithipus meijidei* (Fuentes Vidarte, 1996; although see Lockley and Harris, 2010, for why *A. meijidei* may be non-avian), *Barrosopus slobodai* (Coria et al., 2002), *Goseongornipes markjonsoni* (Lockley et al., 2006b), *Gyeongsangornipes lockleyi* (Kim et al., 2013), *Hwangsanipes chuni* (Yang et al.,

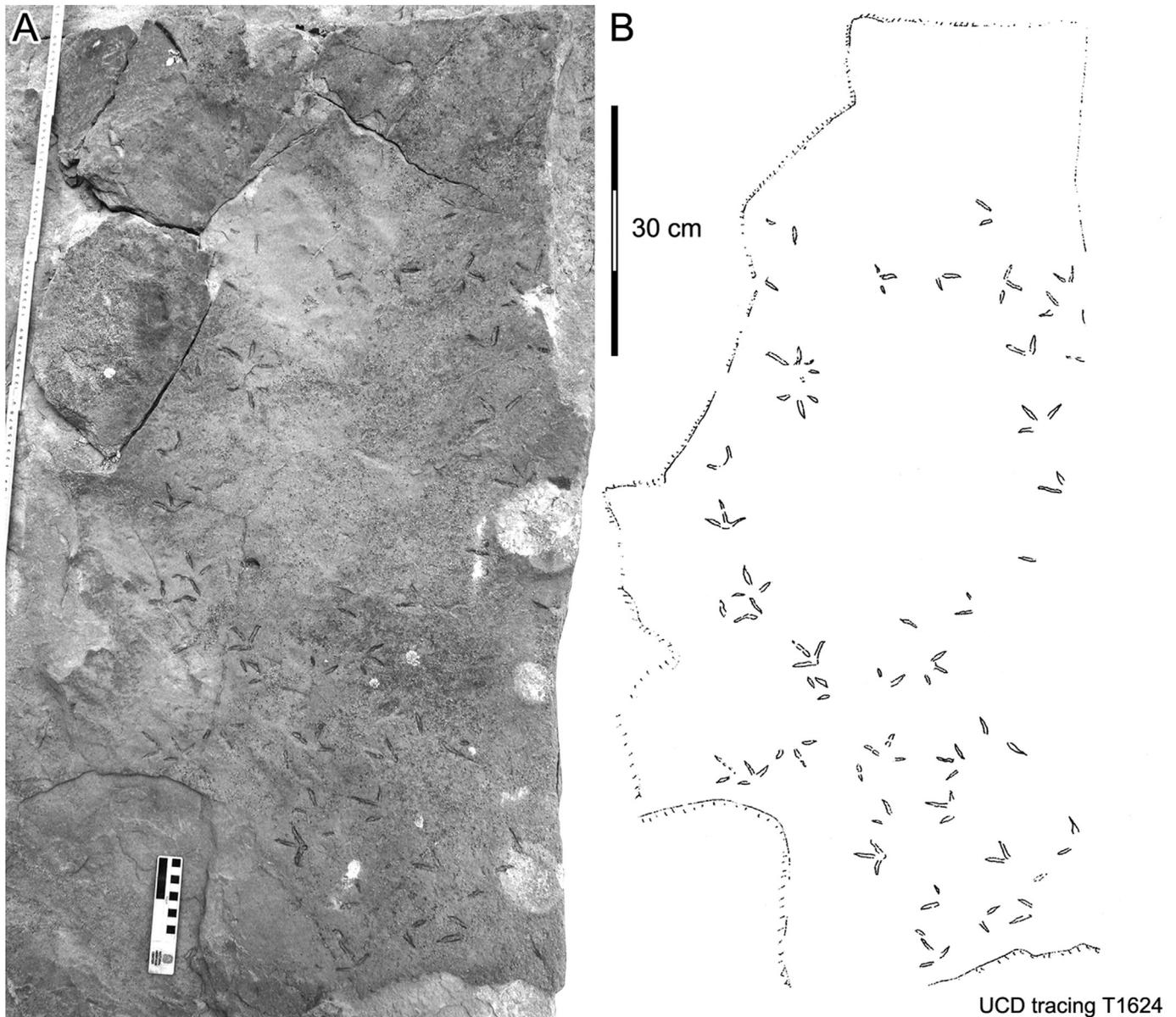
1995), *Ignotornis gajiensis* (Kim et al., 2012), *Ignotornis mcconnelli* (Lockley et al., 2009), *Ignotornis yangi* (Kim et al., 2006), *Jindongornipes kimi* (Lockley et al., 1992), *Koreanaornis dodsoni* (Xing et al., 2011), *Koreanaornis hamanensis* (Kim, 1969; Lockley et al., 2006a), *Pullornipes aureus* (Lockley et al., 2006b), *Morguornipes robusta* (Xing et al., 2011), *Paxavipes babcockensis* (McCrea et al., 2015), *Tatarornipes chabuensis* (Lockley et al., 2012a), and *Uhangrchnus chuni* (Yang et al., 1995). *Limivipes curriei* (McCrea and Sarjeant, 2001; McCrea et al., 2014) and *Wupus agilis* (Xing et al., 2015) were included in the initial analysis, but later removed as they are much larger than the aforementioned Cretaceous avian ichnotaxa, and their larger size tends to “push” smaller ichnotaxonomic groups together in morphospace and potentially masks informative ichnotaxonomic groupings. *Shandongornipes muxaia* (Li et al., 2005; Lockley et al., 2007) was not included because the zygodactyl trace is morphologically different from all the other anisodactyl traces under comparison.

### 3.2. Statistical analyses

Bivariate and multivariate analyses were performed on linear (FL, FW, DLII, DLIV, PL, SL) and angular (DIVTOT, PA) data using PAleontological STatistics (PAST) version 3.0 (Hammer et al., 2001). Digit maximum width (DW) data were also collected (Table S1), but were not used in the analyses. This metric was not often collected or reported in previous analyses and including DW in the multivariate analyses would introduce a large amount of missing data. Other data that were collected (Table S1) but were not used in the analyses were digit III length, and divarication angles between digits II–III and III–IV (DIVII–III; DIVIII–IV). This was done to compensate for the disparities in data collection and reporting for past studies of avian footprints. Digit III length is sometimes used as a proxy for footprint length, and in many instances divarication angles of digits II–III and digits III–IV are not reported. Data were log<sub>10</sub>-transformed and means were removed (Farlow et al., 2013) prior to analysis to reduce the effects of absolute size on the results. Analyses performed were discriminant analyses and multivariate analysis of variance (MANOVA). Discriminant analysis (DA) projects a multivariate data set down to one dimension in a way that maximizes separation between *a priori* separated groups: in this case, the *a priori* groups are ichnotaxonomic groups of footprints attributed to avian or theropod track-makers. The  $p_{\text{same}}$  between two *a priori* groups was determined using Hotelling's  $t^2$  test, the multivariate version of the  $t$ -test (Hammer et al., 2001; Hammer and Harper, 2006) to determine significance at  $p \geq 0.05$ . Three discriminant analyses were conducted: one including all Cretaceous avian ichnotaxa, and one with Limiavipedidae removed from the analyses. The third discriminant analysis was conducted after examining the Limiavipedidae removed results and observing that the Gansu bird tracks occupied a similar morphospace as that of Ignotornidae, and not that of Koreanaornipodidae.

## 4. Geologic setting

The Lanzhou-Minhe Basin is a sedimentary basin with the widest and most extensive Cretaceous outcrops of the Longzhong Basin. The Lanzhou-Minhe Basin is a block-fault basin that has developed from the Middle Qilian Uplift Zone. The red clastic rocks that dominate the basin have been assigned to a single lithological unit, 3482 m thick, and have long been regarded as part of the Hekou Group (Bureau of Geology and Mineral Resources, Gansu Province, 1997; Chen, 2013; Chen et al., 2013) that is the Early Cretaceous in age (Tang et al., 2008). Without volcanic rock for accurate dating, Peng (2012) estimate that the age of the dinosaur bonebeds from the Lanzhou-Minhe Basin is probably earlier than or



**Fig. 3.** Holotype slab (GSGM-FV-00511) of *Koreanaornis lii*, ichnosp. nov. Replica under the same specimen number is deposited at the Geological Museum of Gansu. A, slab in the field, footprints traced to accentuate for photo; B, bird trackway map (outline drawing) of GSGM-FV-00511. Holotype trackway shown in Fig. 4.

equal to the Aptian–Albian period, according to the biostratigraphy information, such as the local documents of dinosaur and sporopollen.

The Guanshan area, Yongjing County, is situated at the east of the Lanzhou–Minhe Basin. The tracks were recovered from two layers: 1) at least two sandstone slabs with bird tracks were found on the side of the road of Shangpujia Village (GPS: 35°58′44.78″ N, 103°36′16.07″ E). The specimens have been collected and housed at GSLTZP. The original site has been destroyed by the road construction, and 2) hundreds of bird tracks were discovered at the dark purple-red medium thick bedded fine-grained sandstone, located at the valley of northwest of Xiapujia Village (GPS: 35°57′38.41″N, 103°34′44.88″E). The specimens are preserved at GSMG and in situ. The Hekou Group is divided into eight informal formation-level units (Zhang et al., 2006). The tracks of the Guanshan area come from the middle-lower part of the 5th informal formation-level unit, representing fluvial facies (Chen, 2013) (Fig. 2).

## 5. Ichnotaxonomy

Class Aves

Ichnofamily Koreanaornipodidae Lockley et al., 2006a

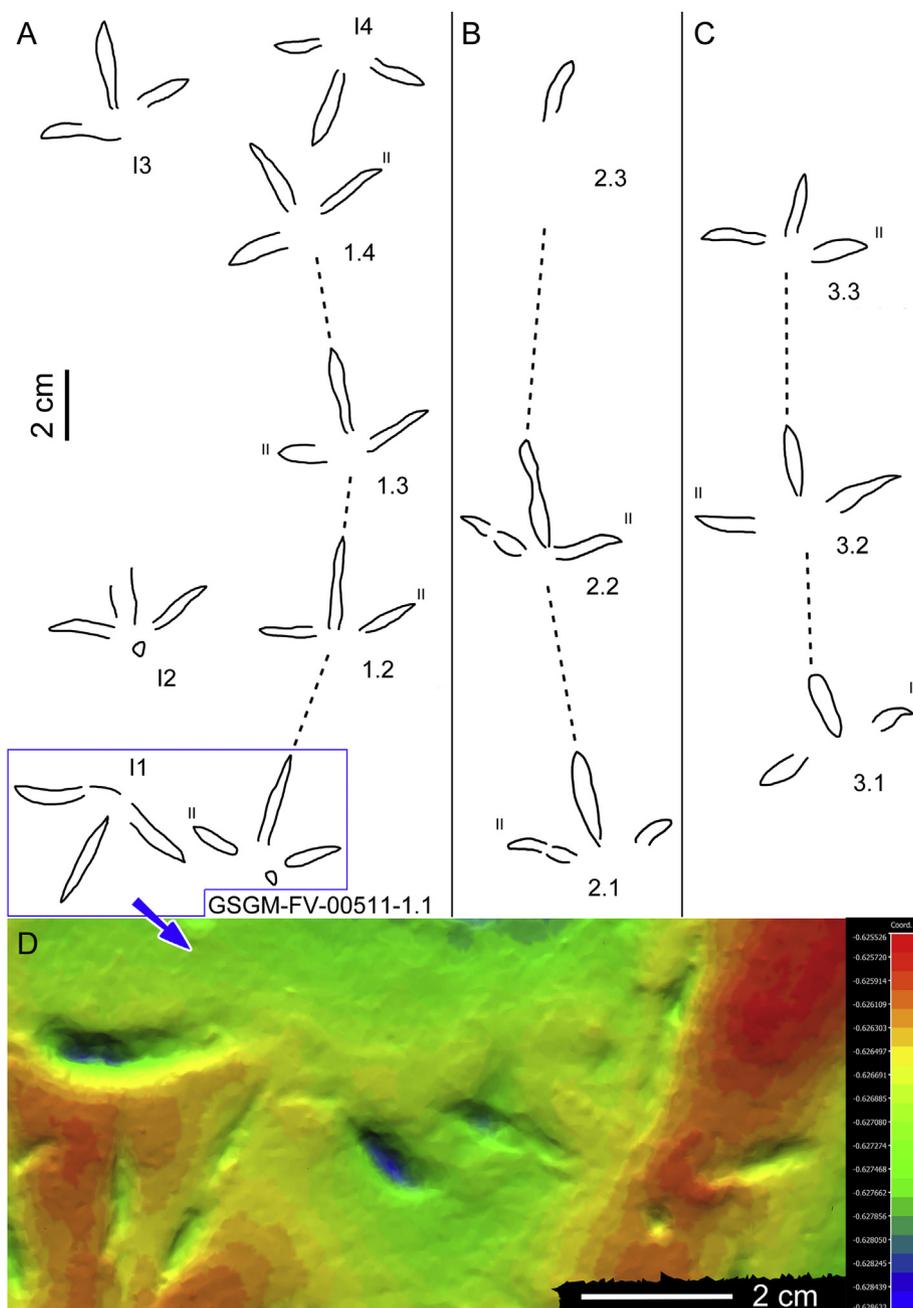
Ichnogenus *Koreanaornis*, Kim 1969; Lockley et al., 2012b

***Koreanaornis lii*** ichnosp. nov.

Figs. 3–5; Table S1

**Etymology.** The specific name is in honor of Dr. Da-Qing Li, a well-known geologist and paleontologist who has contributed substantially to the study of dinosaur fossils and tracks from Gansu, China.

**Diagnosis.** Small (FL ~ 32 mm, FW ~ 46 mm), sub-symmetrical, functionally tridactyl tracks with a consistently wide average digit II–IV divarication; lateral digit traces form a posterior margin (when preserved) that ranges from an obtuse angle to nearly perpendicular to the long axis of digit III impression; strong curvature of medial and lateral digit impressions away from digit III



**Fig. 4.** Holotype (GSGM-FV-00511) and paratype slabs (GSLTZP-S1) of *Koreanaornis lii*, ichnosp. nov., from the Xiapujia Tracksite. **A**, holotype trackway GSGM-FV-00511-1, showing holotype footprint GSGM-FV-00511-1.1, displaying a short, small, posteromedially-directed hallux. The hallux impression is not consistently preserved, and only occurs in three footprints out of the measured sample (footprints GSGM-FV-00511-1.1, footprint GSGM-FV-00511-1.2 figured, Table S1); **B**, paratype trackway GSGM-FV-00511-2; **C**, paratype trackway GSGM-FV-00511-3. Note the wide angle of the proximal track margin; **D**, photogrammetric image of holotype footprint GSGM-FV-00511-1.1 and footprint GSGM-FV-00511-1.2, showing the short, small posteromedially-directed hallux impression, wide proximal track margin, slender digit traces, and digit traces II and IV strongly curved away from digit III impression.

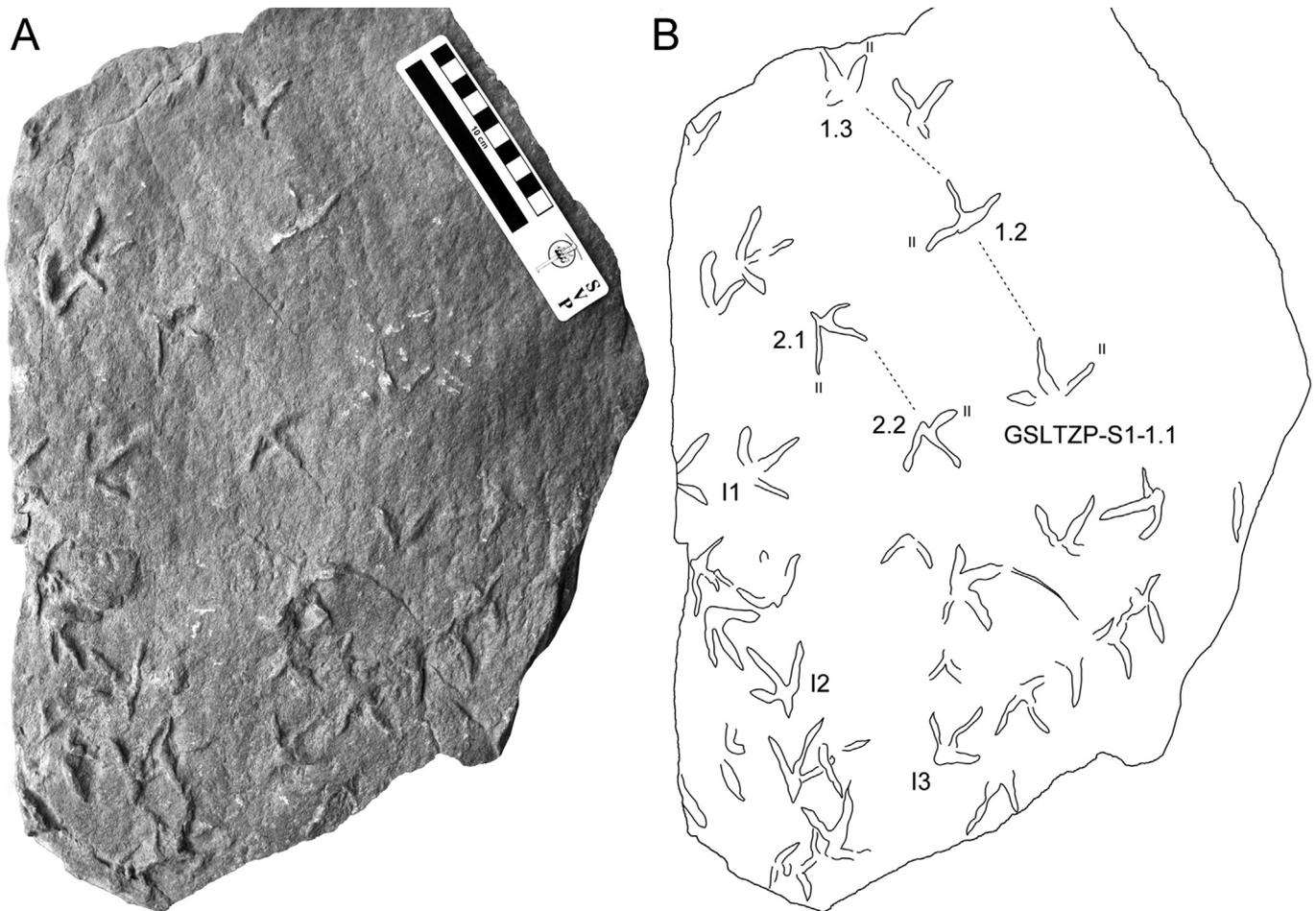
impression; inconsistently preserved, small posteromedially directed hallux impression less than one third of the length of digit III trace; digit divarication I–II between  $134^\circ$  and  $160^\circ$  (divarication II–IV between  $78^\circ$  and  $177^\circ$ ); footprints in trackway exhibit slight inward rotation.

**Locality and horizon.** Lower Cretaceous (Aptian–Albian), middle-lower part of the 5th informal formation-level unit of Hekou Group, Guanshan area, Yongjing County, Gansu Province, China.

**Referred specimens.** Holotype slab GSGM-FV-00511; holotype trackway GSGM-FV-00511-1; holotype footprint GSGM-FV-00511-

1.1; paratype trackway GSGM-FV-00511-2; paratype trackway GSGM-FV-00511-3; paratype footprint-bearing slab GSLTZP-S1.

**Description.** Small (3.2 cm average length; 4.6 cm average width) tetradactyl tracks, with small (0.46 cm–1.07 cm,  $n = 3$ ) hallux impression inconsistently preserved, making the majority of the tracks appear functionally tridactyl; digit I trace relatively short compared to digit traces II–IV, average 0.73 cm (0.46 cm–1.04 cm range,  $n = 3$ ); digit traces II–IV do not connect proximally to a metatarsophalangeal pad; slender digit traces II–IV with preserved digital pads exhibiting (excluding ungual impression) 2–3–4 on



**Fig. 5.** Paratype slab (GSLTZP-S1) of *Koreanaornis lii*, ichnosp. nov. from the Shangpujia Tracksite. **A**, image of the track-bearing slab. The trackways and individual footprints show no consistent orientation with respect to ripple marks; **B**, trackway map of GSLTZP-S1. Trackways highlight the wide proximal margin.

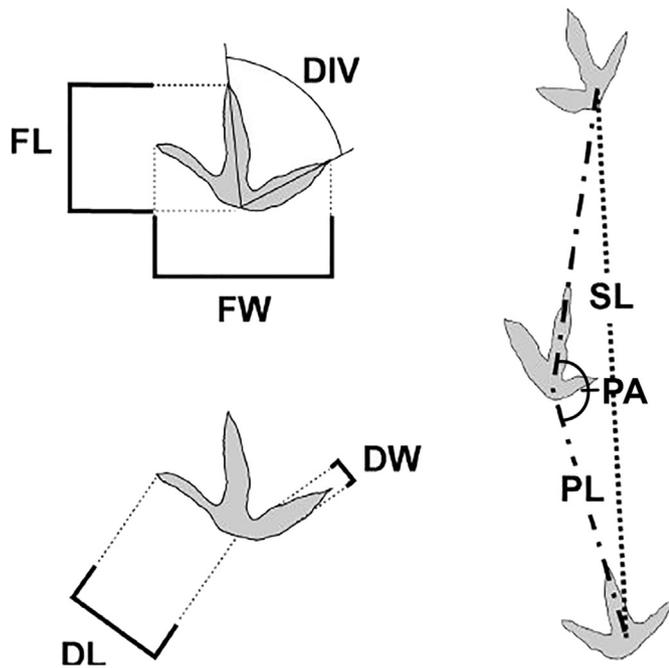
well-preserved specimens; digit trace splay high, with footprint length:width ratio average of 0.71 (range of 0.47–1.2). Digit II–IV divarication (total divarication) average  $137^\circ$  ( $78^\circ$ – $177^\circ$ ,  $n = 33$ ); divarication I–II high, average  $148^\circ$  ( $134^\circ$ – $160^\circ$ ,  $n = 3$ ).

**Remarks.** *Koreanaornis lii* ichnosp. nov. shares many features with *Koreanaornis hamanensis*, *Koreanaornis dodsoni*, and *Pullornipes aureus*. Tracks from *K. dodsoni*, *K. hamanensis*, and *P. aureus* are functionally tridactyl with slender digit traces that do not join proximally on most tracks, digit traces with indistinct digital pad impressions (although there are some tracks that do preserve distinct digital pads, see Fig. 4), and the occasional presence of a short, posteromedial directed hallux impression that is  $180^\circ$  from digit IV, a wide divarication ( $90^\circ$ – $115^\circ$ ) between digit traces II and IV, and webbing impressions consistently not preserved, even when digital pad impressions are preserved. Digit trace slenderness in *Koreanaornis lii* is more similar to *Koreanaornis hamanensis* (Kim, 1969; Lockley et al., 2006a; Lockley et al., 2012b) and *Pullornipes aureus* (Lockley et al., 2006b) than to *Koreanaornis dodsoni* (Xing et al., 2011).

Digit I–II divarication for *Koreanaornis lii* tracks is poorly represented at a sample size of three. The data available show that digit I–II divarication for *Koreanaornis lii* is  $148^\circ$  ( $134^\circ$ – $160^\circ$ ,  $n = 3$ ). However, the published range of total divarication (digit divarication II–IV) for *Koreanaornipodidae* (*Koreanaornis dodsoni*,

*Koreanaornis hamanensis*, *Pullornipes aureus*) is  $32^\circ$ – $170^\circ$  (average  $101^\circ$ ). The current diagnosis of the orientation of digit I trace for *Koreanaornipodidae* as  $180^\circ$  from digit IV trace, which provides an average digit I–II divarication of  $79^\circ$  ( $10^\circ$ – $148^\circ$ ). While one digit I–II divarication measurement of *Koreanaornis lii* ( $134^\circ$ ) falls within the range of digit divarication I–II published data for *Koreanaornipodidae*, two digit I–II divarication measurements ( $149^\circ$ ,  $160^\circ$ ) fall outside the range. The sample size of preserved digit I impressions is too small for *Koreanaornis lii* to propose an emendation of *Koreanaornipodidae* with regards to the diagnostic orientation of digit I impression, but it is enough to distinguish *Koreanaornis lii* from other ichnotaxa of *Koreanaornipodidae*.

*Koreanaornis* cf. *hamanensis* reported from Utah (Alfinson et al., 2009) display medial and lateral digit traces (digits II and IV) that curve strongly away from the digit III trace, as they do in *Koreanaornis lii*. However, none of the footprints from Utah possess an impressed digit I, so it is difficult to determine whether the Utah footprints are more similar to *Koreanaornis hamanensis* or *Koreanaornis lii*. For now, the Utah specimens are best left as *Koreanaornis* cf. *hamanensis* until more material is recovered. Li et al. (2002) also report avian footprints from Yanguoxia, Yongjing Country, Gansu Province, China, that are referred to either *Aquatilavipes* ichnosp. or *Koreanaornis* ichnosp. The Yanguoxia footprints lack a hallux impression so it is uncertain whether, if a hallux



**Fig. 6.** Schematic of linear and angular data collected (Table S1) for the Gansu bird tracks, *Koreanaornis lii* ichnosp. nov. These data were used in multivariate statistical analyses comparing *K. lii* ichnosp. nov. tracks to other Early Cretaceous bird tracks (Figs. 7, 8 and 10; Tables S2–5). DIV, digit divarication; DL, digit length; DW, digit width; FL, footprint length; FW, footprint width; PA, pace angulation; PL, pace length; SL, stride length. DW was not used in multivariate statistical analyses as it is not often collected metric in avian footprint studies. Figure modified from McCrea et al. (2015).

were to be impressed, digit divarication I–II would fall within the range of *K. hamanensis* or *K. lii*, or if a digit would impress at all. For now the Yanguoxia bird tracks remain unassigned to *Koreanaornis* ichnosp.

Tracks of *Koreanaornis lii* are morphologically most similar to those of *Koreanaornipodidae* given their slender digit traces, small, posteromedially directed digit I impression, and wide divarication. As such, they are assigned to the ichnofamily *Koreanaornipodidae*. Given their close morphologic similarity to *Koreanaornis hamanensis* (slender digit impressions, wide divarication, small but inconsistently preserved hallux impression), we concur that these footprints are an ichnospecies of *Koreanaornis*. The strong outward curvature of digit traces II and IV away from digit III trace is unique to this footprint morphology, warranting the erection of a novel ichnospecies of *Koreanaornis*, *Koreanaornis lii*.

## 5.1. Comparative ichnology

### 5.1.1. Comparison to *Aquatilavipes* and *Paxavipedidae*

*Koreanaornis lii* differs from *Aquatilavipes* (*A. swiboldae*, Currie, 1981; *Aquatilavipes izumiensis* Azuma et al., 2002) in that the lateral digit traces of *K. lii* that display a proximal margin (when preserved) that forms an obtuse angle; the proximal margins of tracks of *Aquatilavipes* ichnosp. are relatively more narrow than is observed in the proximal margin of footprints of *K. lii*. While this may be an artifact of substrate consistency, many of the tracks of *K. lii* lack a proximal margin. The difference in proximal margin morphology may indicate a difference in metatarsophalangeal morphology between the track-makers of *Aquatilavipes* ichnosp. and those of *K. lii*. *Aquatilavipes* ichnosp. is also reported to have a higher total (II–IV) divarication (average  $117^\circ$ , range  $71^\circ$ – $151^\circ$ ) than *Koreanaornipodidae* (average  $101^\circ$ ,  $32^\circ$ – $170^\circ$ ; Currie, 1981;

Lockley et al., 2006a). There is a considerable amount of overlap in total divarication between the *Aquatilavipes* ichnosp. and *Koreanaornis* ichnosp. so that the range of total divarication is not diagnostic. The overlap in ranges persists when the highest and lowest total divarication measurements for *Koreanaornipodidae* are treated as outliers (average  $101^\circ$ ,  $47^\circ$ – $150^\circ$ ). Also, no tracks of *Aquatilavipes* ichnosp. have been reported with a hallux impression, whereas footprints of *Koreanaornipodidae* are tetradactyl, even though the hallux impression is inconsistently preserved.

Paxavipedidae (*Barrosopus slobodai*, *Paxavipes babcockensis*) are distinguished from *Koreanaornis lii* (*Koreanaornipodidae*) by the consistent lack of digit I impressions (whereas *Koreanaornipodidae* occasionally preserve a short digit I; Lockley et al., 2006a), digit traces that are thick and connected proximally, and a larger divarication II–III than divarication III–IV (McCrea et al., 2015).

### 5.1.2. Comparison with *Ignotornidae* and *Gyeongsangornipes lockleyi*

It is necessary to compare the tracks of *Koreanaornis lii* with those Cretaceous avian ichnotaxa that possess a digit I impression. Tracks of *K. lii*, while possessing a small hallux impression, are different from other functionally tetradactyl avian tracks of *Ignotornidae* (*Goseongornipes markjonesi*, *Hwangsanipes choui*, *Ignotornis mconnelli*, *Ignotornis yangi*) in a number of characteristics. The hallux impression of *Koreanaornis lii* and other *Koreanaornipodidae* is small and so inconsistently preserved that, when present, the length is rarely reported. This is in contrast to the more consistently preserved hallux impression of *Ignotornidae*, where digit I trace is on average 13 mm in length (4 mm–30 mm) and is on average 35% of the length of digit III (15%–44%). Although tracks from extant avians with functional halluces do not consistently preserve digit I impressions (Buckley et al., 2015), the repeated presence (or absence) of digit I impressions in a sample of tracks is a reliable indicator of foot morphology. In this case, the longer hallux impression and its near-posterior orientation indicate that the track-makers of *Ignotornidae* have a pes with a digit I that was morphologically distinct from that of *Koreanaornipodidae* (short hallux, posteromedial orientation), and specifically, morphologically distinct from the track-maker of *Koreanaornis lii*.

The orientation of the digit I impression in *Ignotornidae* is on average  $145^\circ$  ( $105^\circ$ – $188^\circ$ ) from digit II. This range in digit I–II divarication does overlap the divarication between digits I and IV of  $180^\circ$  as used to diagnose *Koreanaornipodidae*. However, the consistently longer and preserved hallux impressions in *Ignotornidae* are different enough than those described in *Koreanaornipodidae* to not consider assigning the Gansu tracks to *Ignotornidae*. Also, all tracks currently assigned to *Ignotornidae* have repeated preservation of asymmetric webbing impressions between digits III–IV, whereas *Koreanaornipodidae* (including *Koreanaornis lii* ichnosp. nov.) lack both webbing impressions and the inward curvature of the medial and lateral digit traces that accompanies webbed tracks (e.g. *Uhangrichnus chuni*, Yang et al., 1995; *Geosangornipes lockleyi*, Kim et al., 2013). While preservation of webbing impressions can be influenced by depth of the footprint (see Falkingham and Gatesy, 2014), morphologic features such as the inward curvature of the medial and lateral digit impressions that occur consistently with the footprints of palmate birds is useful to distinguish among avian ichnotaxa.

Tracks of *Koreanaornis lii* are morphologically different from those of *Gyeongsangornipes lockleyi* in the consistent lack of webbing impressions: the *G. lockleyi* track-maker possessed distinct, consistently preserved asymmetric semipalmate webbing impressions (Kim et al., 2013, fig. 2), whereas *K. lii* tracks lack distinct webbing impressions. Also, the distal ends of the lateral digit traces (digits II and IV) of *G. lockleyi* curve towards the digit III

trace (Kim et al., 2013), which is often observed in footprints with extensive semipalmate or palmate webbing. In contrast, the medial and lateral digit traces of *K. lii* tracks generally curve away from the digit III trace.

### 5.1.3. Comparison with Cenozoic avian ichnotaxa

*Koreanaornis lii* has a stronger curvature of the medial (digit II) and lateral (digit IV) digit traces away from the digit III trace than is described for any other Cretaceous avian ichnotaxon. Outward curvature of the medial and lateral digit traces is comparable to Cenozoic ichnospecies of *Avipeda* (sensu Vialov, 1965). The holotype of *Avipeda filiportatis* (Vialov, 1965, pl. 15) displays outer digit traces whose distal ends curve away from digit III traces. However, based on the scale in Plate 15 (Vialov, 1965), these footprints are much larger (FL: approximately 10 cm) than those of *Koreanaornis lii*. Based on the images available, traces of *A. filiportatis* also appears to have well-impressed halluces (Vialov, 1966, pl. 32). The presence of hallux impressions is likely what prompted Sarjeant and Langston (1994) to reassign *A. filiportatis* to *Gruipepeda filiportatis*. *Avipeda phoenix* (Vialov, 1966, pl. 27) displays the obtuse to nearly straight proximal margin of the footprint, but the medial and lateral digit traces curve towards the digit III trace, rather than away from digit III. Figure 10 of Sarjeant and Langston (1994) show that one footprint in TMM 14500–25 (specimen of *Avipeda phoenix*, Vialov, 1966)

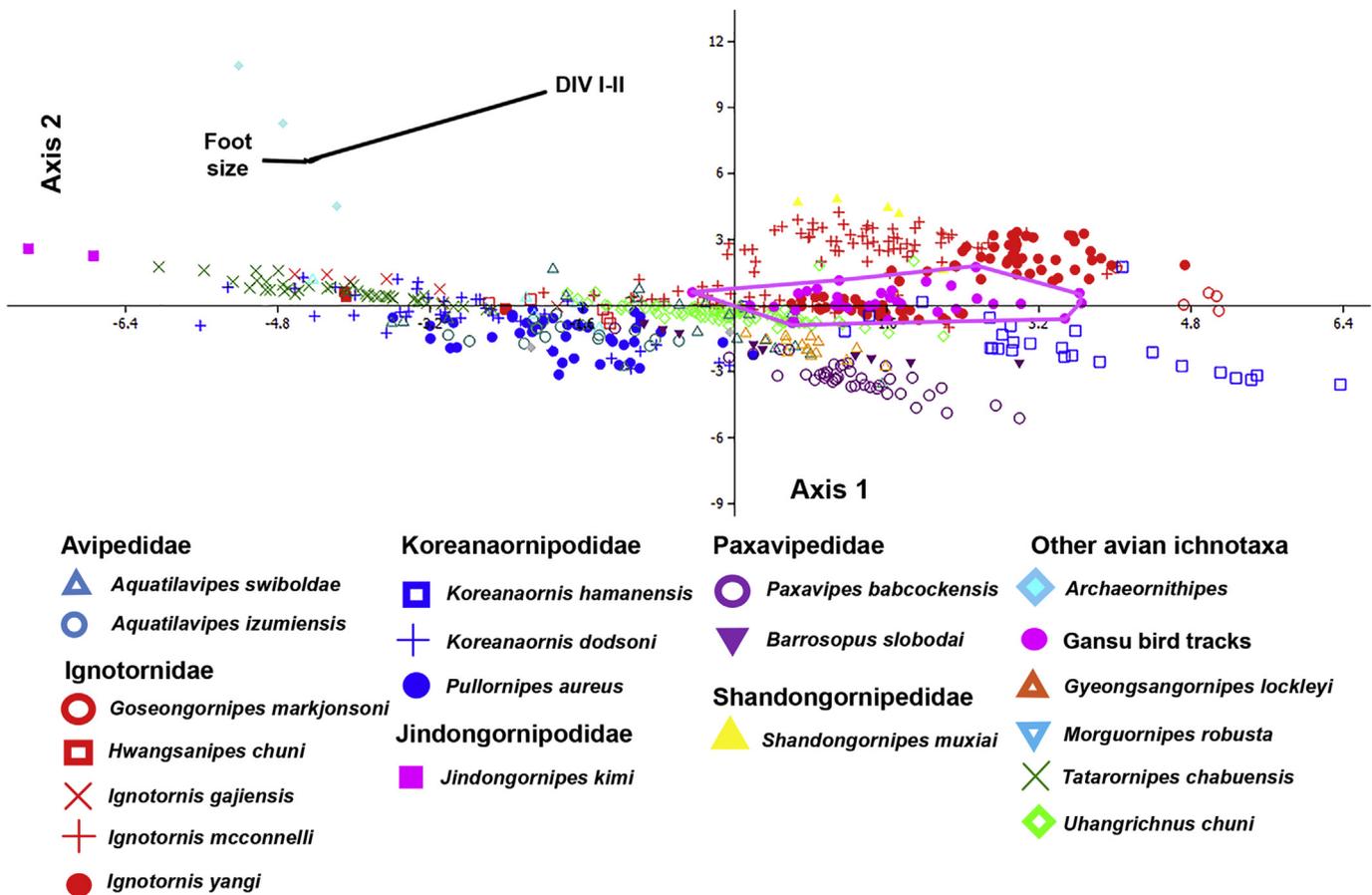
has an outward curving lateral digit trace. However, it is difficult to reconcile Sarjeant and Langston's (1994) interpretation of *A. phoenix* with the figures presented in Vialov (1966). A detailed examination of the physical specimen of *A. phoenix* is necessary to resolve this discrepancy. It is also not recommended that new ichnospecies be added to *Avipeda* while the ichnotaxonomy of small Cenozoic avian footprints remains unresolved.

## 6. Multivariate statistical analyses

Multivariate statistical analyses (discriminant analysis, multivariate analysis of variance) can be used to test the assignment of avian footprints to existing or novel avian ichnotaxa, as long as that assignment is first supported by the ichnomorphology (Buckley et al., 2016).

### 6.1. Ichnofamilial comparisons

Discriminant analysis comparing the Gansu tracks (*Koreanaornis lii*) those similar-sized Cretaceous avian ichnofamilies reveals a rather unexpected result: despite the morphological differences in the hallux impressions of *Koreanaornis lii*, *Koreanaornipodidae* (*Koreanaornis hamanensis*, *K. dodsoni*, *Pullornipes aurea*), *Ignotornidae* (*Goseongornipes markjonsoni*, *Hwangsanipes chuni*,



**Fig. 7.** Discriminant analysis scatterplot of Early Cretaceous avian ichnotaxa similar in size to the Gansu bird tracks, *Koreanaornis lii* ichnosp. nov. Axis 1 is the divarication-size axis: as footprint size decreases, digit divarication increases with the largest contribution to variation contributed by divarication between digits II and III (DIVII–III). The data group *Koreanaornis hamanensis* (*Koreanaornipodidae*), and *Ignotornis mconnelli* and *Ignotornis yangi* (*Ignotornidae*), and *Paxavipedidae babcockensis* (*Paxavipedidae*) in a similar morphospace along Axis 1. *Gyeongsangornipes lockleyi* also groups in this morphospace and does not share morphospace with *Uhangrichnus chuni*, despite both ichnotaxa having strong webbing impressions; the webbing impressions of *G. lockleyi*, being asymmetric, is more similar to that of *Ignotornidae* than of *U. chuni*. Divarication has the highest discriminant loadings (Table S2). *Koreanaornis lii*, ichnosp. nov. does not group with either *Koreanaornis hamanensis*, or with the group formed by *Koreanaornis dodsoni* and *Pullornipes aureus*. *K. lii* groups closely with *Ignotornis mconnelli* and *Ignotornis yangi*.

*Ignotornis mcconnelli*, *I. yangi*) Paxavipedidae (*Barrosopus slobodai*, *Paxavipes babcockensis*), tracks of *K. lii* share a morphospace with some of both Koreanaornipodidae and Ignotornidae. The statistical comparisons also reveal that tracks of *K. lii* are most similar to the ichnofamilies Koreanaornipodidae, ( $p_{\text{same}} = 0.033$ ), Paxavipedidae ( $p_{\text{same}} = 0.251$ ), and the ichnospecies *Gyeongsangornipes lockleyi* ( $p_{\text{same}} = 0.242$ ).

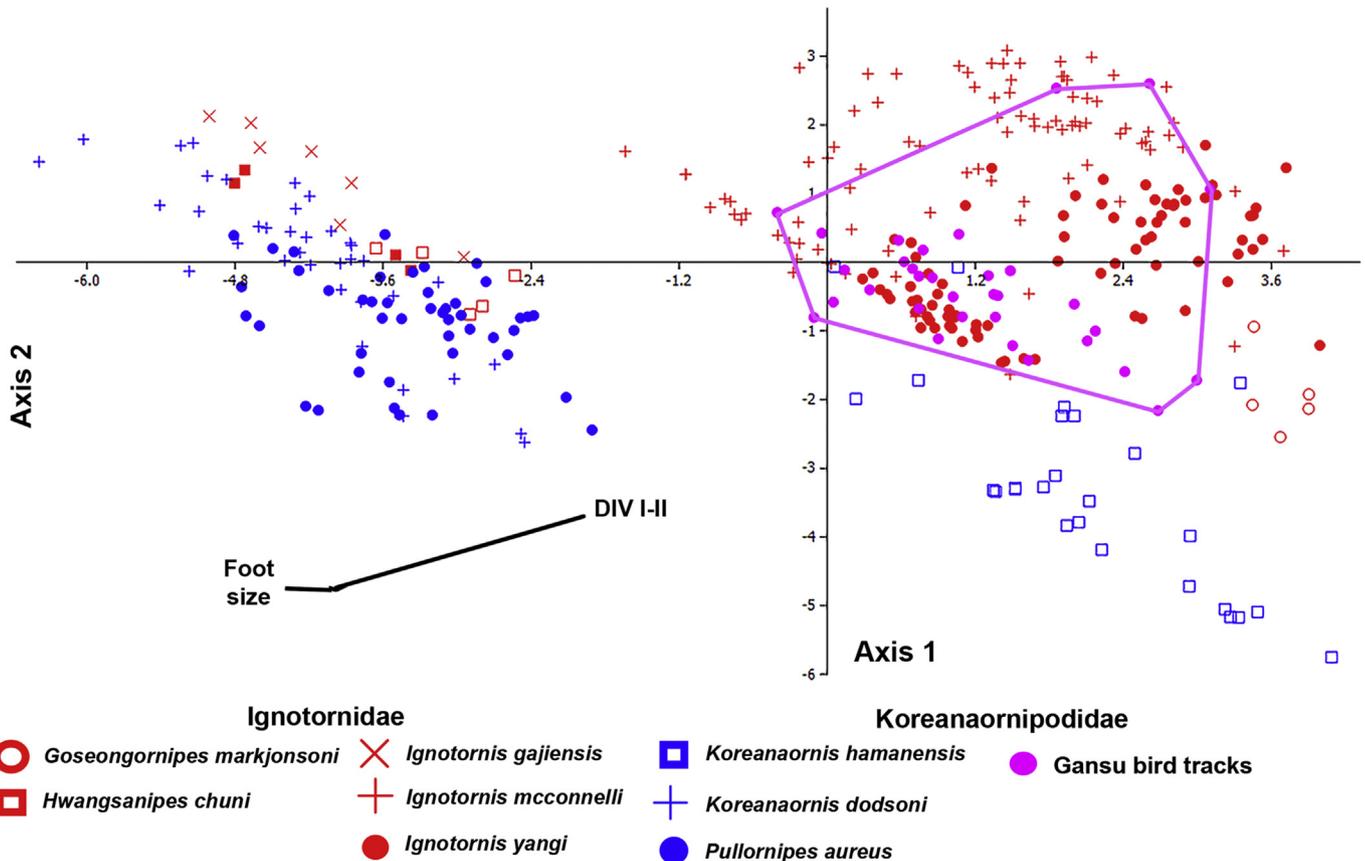
Examination of the multivariate analysis of variance (MANOVA) shows that tracks of *Koreanaornis lii* are statistically different from those of Koreanaornipodidae. Also, the discriminant analysis scatterplot shows that *Koreanaornis lii* tracks do not share a morphospace with any of the ichnospecies of Koreanaornipodidae (with the exception of one footprint of *Koreanaornis hamanaensis*) (Fig. 7).

### 6.2. Ichnospecies comparisons

Analysis of *Koreanaornis lii* (referred to in the analyses scatterplots and Supplementary Tables as Gansu bird tracks) with similar-sized avian ichnotaxa (Fig. 7, Tables S2–S4) shows that the *K. lii* shares a similar morphospace with *Ignotornis mcconnelli*, *Ignotornis yangi*, one footprint of *Gyeongsangornipes lockleyi*, and four footprints of *Koreanaornis hamanaensis* (Fig. 7). Discriminant analysis mistakenly identified tracks of *K. lii* as *Aquatilavipes swiboldae* (three tracks), *Barrosopus slobodai* (two tracks), and *Gyeongsangornipes lockleyi* (three tracks), and *Ignotornis mcconnelli* (two tracks) (Table S4).

Despite their similar groupings in morphospace, multivariate analysis of variance (MANOVA) does indicate that *Koreanaornis lii* is significantly different from *Goseongornipes markjonsoni* ( $p_{\text{same}} = 1.00 \times 10^{-10}$ ), *Ignotornis mcconnelli* ( $p_{\text{same}} = 5.71 \times 10^{-57}$ ), *Ignotornis yangi* ( $p_{\text{same}} = 0.003$ ), *Koreanaornis hamanensis* ( $p_{\text{same}} = 2.83 \times 10^{-25}$ ), and *Aquatilavipes swiboldae* ( $p_{\text{same}} = 0.014$ ). Despite the morphological differences, *K. lii* is not significantly different from *Aquatilavipes izumiensis* ( $p_{\text{same}} = 0.101$ ), *Gyeongsangornipes lockleyi* ( $p_{\text{same}} = 0.142$ ), or *Paxavipes babcockensis* ( $p_{\text{same}} = 0.577$ ) (Table S4).

A smaller discriminant analysis (Fig. 8) was performed separately on those ichnospecies that most closely grouped with the Gansu bird tracks in the small Cretaceous avian ichnotaxa analysis of Fig. 7 (*Goseongornipes markjonsoni*, *Hwangsanipes choughi*, *Ignotornis gajiensis*, *Ignotornis mcconnelli*, *Ignotornis yangi*), as well as Koreanaornipodidae (*Koreanaornis dodsoni*, *Koreanaornis hamanensis*, *Pullornipes aurea*). The tracks of *Koreanaornis lii* group along the Axis 1 (high divarication between digits I and II), along with tracks of *Koreanaornis hamanensis*, *Ignotornis mcconnelli*, and *Ignotornis yangi*. The difference between *Koreanaornis hamanensis* and *K. lii* is greater ( $p_{\text{same}} = 2.95 \times 10^{-25}$ ), than between the tracks of *K. lii* and *Koreanaornis dodsoni* ( $p_{\text{same}} = 5.73 \times 10^{-03}$ ), and *Pullornipes aureus* ( $p_{\text{same}} = 1.56 \times 10^{-03}$ ). Tracks of *K. lii* only share morphospace with two footprints of *K. hamanensis*: other than those two footprints, there is no overlap between the tracks of *K. lii* and the *K. hamanensis* group.



**Fig. 8.** Examination of the morphospace relationship between, *Koreanaornis lii* ichnosp. nov. (Gansu bird tracks), with Koreanaornipodidae and Ignotornidae. Axis 1 is the footprint size–digit I–II divarication axis. As footprints decrease in length, they increase in the size of DIVI–II. While ichnomorphologically similar to Koreanaornipodidae, and specifically the most similar to *Koreanaornis hamanensis*, the high divarication between digit traces I–II causes *Koreanaornis lii* to share morphospace with *Ignotornis mcconnelli* and *Ignotornis yangi*. However, while not sharing the same morphospace, *K. lii* is in a morphospace that is close to that of *Koreanaornis hamanensis*.



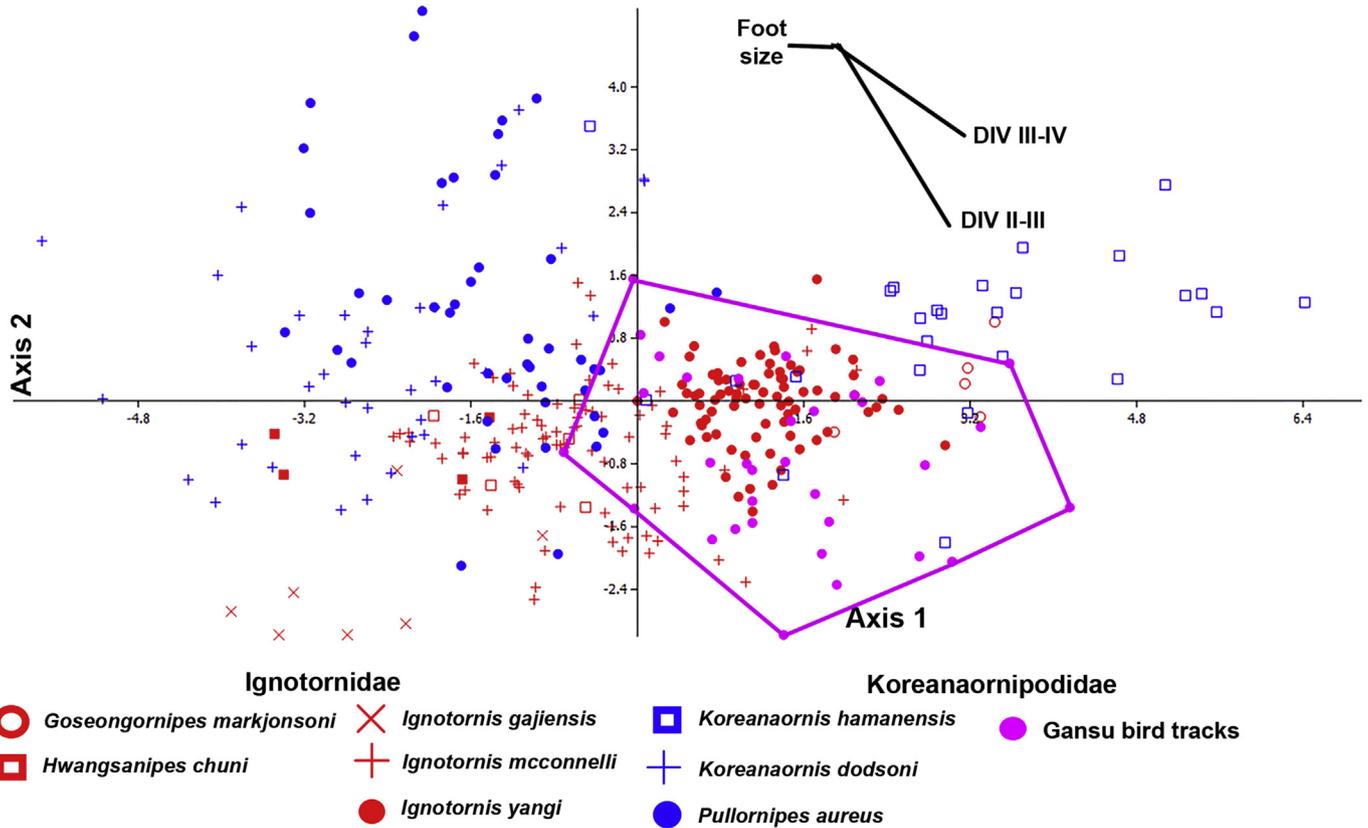
**Fig. 9.** Image of *Koreanaornis dodsoni* (Xing et al., 2011), showing the possible digit I impression. On closer examination, it is possible that the digit I impression (arrow) is in fact a partial invertebrate trace, such as that of *Arenicolites* ichnosp. Scale in centimeters.

6.3. Multivariate analysis discussion

Examination of the discriminant analyses results shows that the tracks of *Koreanaornis lii* occupy a similar morphospace to that of *Barrosopus slobodai*, *Gyeongsangornipes lockleyi*, *Ignotornis mcconnelli*, *Ignotornis yangi*, and *Koreanaornis hamanensis* (Fig. 7) due to the similarities in high divarication: all tracks have high digit II–III

and digit III–IV divarication values, and divarication between digits II–III and digits III–IV has the largest discriminant loadings (DIV-II–III and DIV-III–IV, Table S2). This analysis demonstrates a caveat of using multivariate analyses as a diagnostic tool: even morphologically distinct forms can share a morphospace and be considered statistically the same group when only considering measured variables. Examination of the morphology of the tracks shows inconsistencies with these statistical groupings. First, Paxavipedidae are morphologically distinct from Koreanaornipodidae (McCreary et al., 2015). Second, tracks of *K. lii* lack webbing impressions and medial and lateral digit trace curvature towards digit III trace that is seen in *Gyeongsangornipes lockleyi*, an ichnotaxon that the multivariate analyses groups closely with *K. lii*. Third, *Ignotornis* are morphologically distinct from the tracks of *K. lii* in that they consistently possess both asymmetric webbing impressions and a robust, posteriorly-oriented digit I trace, both of which are lacking in *K. lii*.

An interesting result of the targeted discriminant analysis (Fig. 8) was the separation between *Koreanaornis hamanensis* and the other ichnospecies of Koreanaornipodidae, *Koreanaornis dodsoni* and *Pullornipes aurea*. This result can be explained by the lack of data for digit I traces for these two ichnospecies. In other words, *K. hamanensis* separates from *K. dodsoni* and *P. aurea* based solely on the inclusion of digit I trace data in the analyses. It is also possible that the hallux impression reported for *Koreanaornis dodsoni* (Xing et al., 2011) is, in fact, an invertebrate burrow or a possible feeding trace (Fig. 9). Also, there is some uncertainty as to whether *Koreanaornis dodsoni* is distinguishable from *Koreanaornis hamanensis* (Lockley et al., 2012b); however, *Koreanaornis dodsoni* has thicker



**Fig. 10.** Discriminant analysis scatterplot showing the morphospace relationships of the Gansu bird tracks, *Koreanaornis lii* ichnosp. nov., with ichnospecies of *Ignotornidae* and *Koreanaornipodidae* when data from digit I (digit I trace length, digit divarication I–II) is removed from the analysis. Axis 1 is the still the footprint size-divarication axis; however, when footprint size decreases, there is a slight increase in divarication of digit traces II–III and III–IV. The overall pattern seen in Fig. 8 remains: *Koreanaornis lii* shares morphospace with *Ignotornidae*, and very little morphospace with *Koreanaornipodidae*, despite the ichnomorphological similarities between *Koreanaornis lii* with *Koreanaornis hamanensis*.

digit traces relative to *Koreanaornis lii*, *K. hamanensis*, and *Pullornipes aureus*.

A separate MANOVA and discriminant analysis were run comparing the tracks of *Koreananornis lii* to those of Icnornidae and Koreanornipodidae with digit I trace data removed (DLI, DIVI–II). The results were only slightly different than those obtained with digit I trace data included (Fig. 10, Table S5). Removal of the digit I trace data caused the ichnospecies clusters to show more overlap in morphospace. However, only seven footprints of *Koreananornis hamanensis* overlap with footprints of *K. lii*, and only six footprints of *Pullornipes aurea* overlap with footprints of *K. lii*. Removal of digit I trace data still resulted in tracks of *K. lii* sharing a morphospace with *Icnornis mcconnelli* and *Icnornis yangi*, despite their morphological differences.

This is not to say that digit I trace data should not be included in the multivariate analyses: the presence of a small (if inconsistently preserved) digit I trace is a diagnostic feature of Koreanornipodidae. Rather, the focus should be on reexamination of *K. dodsoni* and *P. aurea* to document the length and divarication of digit I traces instead of limiting analyses to the least common denominator of data reporting.

## 7. Discussion

### 7.1. *Koreanaornis lii* and *Koreanaornis dodsoni* as a distinct ichnotaxa

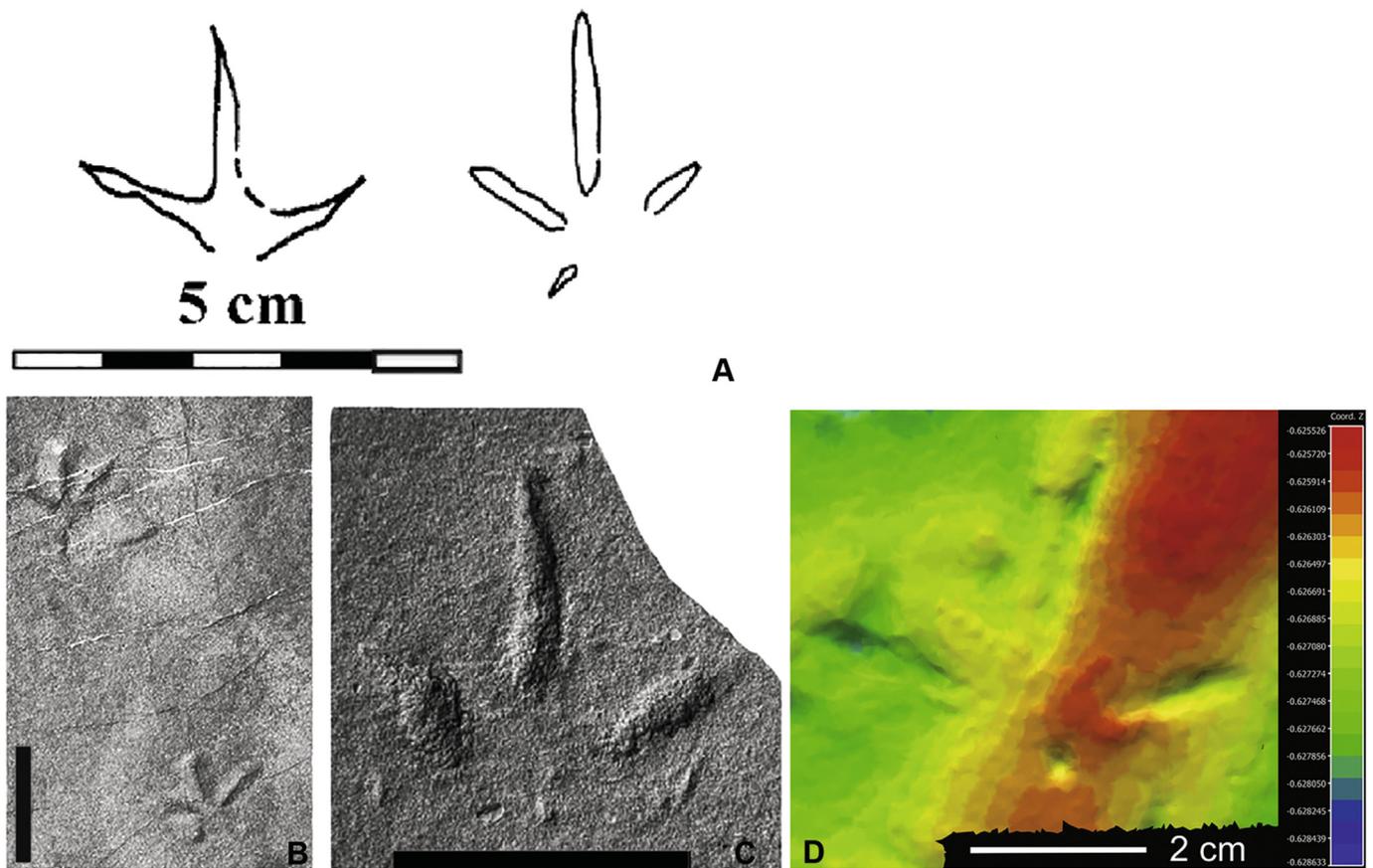
*Koreanaornis lii* is supported as a distinct ichnotaxon within Koreanornipodidae by the medial and lateral curvature of digit

traces II and IV, respectively. The inconsistent impression of a small, short digit I trace is the most similar to *Koreanaornis hamanensis*. The presence of the small hallux impression and the strong outward curvature of the medial and lateral digit traces separates *K. lii* from both *Koreanaornis dodsoni* and *Pullornipes aurea* (no hallux impressions, straight medial and lateral digit traces).

Lockley et al. (2012a) raise the possibility that *Koreanaornis dodsoni* (Xing et al., 2011) may not be distinct from *Koreanaornis hamanensis*. Morphologically, the relatively thicker digits of *Koreanaornis dodsoni* indicate a track-maker that has relatively thicker digit traces than the track-maker of *Koreanaornis hamanensis*, although it is possible that the relatively thicker digits could be the result of substrate consistency at the time the tracks were impressed. The discriminant and multivariate analysis of variance suggest that *Koreanaornis dodsoni* distinct from *Koreanaornis hamanensis* due to their similarities in a relatively lower DIVII–III and DIVIII–IV (Fig. 11). Until more samples are found, it is logical to consider that the morphological differences between *Koreanaornis dodsoni* and *Koreananornis hamanensis* represent ichnotaxonomic differences.

### 7.2. Avian diversity during the Early Cretaceous

The avian footprint record of the Early Cretaceous of China is steadily growing (*Aquatilavipes*, *Koreanaornis hamanensis*, *Koreanaornis lii*, *Pullornipes*, *Uhangrichnus*, *Shandongornipes*, *Tatarornipes Wupus agilis*; Xing et al., 2015; Lockley and Harris, 2010). At present, the majority of the track record of Early Cretaceous birds is from China (Lockley and Harris, 2010; Xing et al., 2011; Lockley



**Fig. 11.** Morphologic comparison of the ichnospecies of Koreanornipodidae. **A**, *Koreanaornis hamanensis* (Lockley et al., 2006a); **B**, *Pullornipes aureus* (Lockley et al., 2006a), scale = 2.0 cm; **C**, *Koreanaornis dodsoni* (Xing et al., 2011), scale 2.0 cm; **D**, *Koreanaornis lii*, ichnosp. nov., this paper. The thicker digits on *Koreanaornis dodsoni* distinguish it from *K. hamanensis*. The small hallux impression of *Koreanaornis lii* is similar to that of *Koreananornis hamanensis* (A) and *Pullornipes aureus* (B).

et al., 2012c; Huh et al., 2012), and Korea (Lockley et al., 2012a). The avian ichnological record, at present, shows little correlation with the known skeletal record of birds from the Cretaceous of China. No avian track specimens to date have been conclusively attributed to a confuciusornid or enantiornithine track-maker, and those tracks would, if recovered, be similar in morphology to those of extant scansorial avians (Buckley et al., 2015). New specimens of ornithomorph birds from the Early Cretaceous of China (Wang et al., 2015) suggest that a small wading bird with a digit III length (estimated total length of pedal phalanges III-1, III-2, III-3, and III-4) of approximately 18 cm–22 cm (measured from figures 3 and 4 of Wang et al., 2015) could be a possible track-maker for small bird traces with a present, if small, digit I impression. Not all extant birds with a digit I leave traces where the impression of digit one is preserved (Buckley et al., 2015). The morphology of the pedal unguis of *Archaeornithura* also supports the hypothesis of the specimen representing a shore- or wading bird: the unguis do not appear strongly curved as is seen in the enantiornithine birds, but are similar in gross morphology to those of extant shorebirds.

The track record of Early Cretaceous birds from China was dominated by those birds that occupied a paleoecosystem similar to that of extant shore- and wading birds (Falk et al., 2011). The comparative lack of avian track diversity in North America is likely artificial: the Early Cretaceous avian diversity gap is closing as more specimens are recovered (see McCrea et al., 2014 for avian specimens recovered and currently under description in western Canada) and described (Lockley et al., 2015; McCrea et al., 2015). There are similarities in the avian ichnofossils recovered from both Asia and North America. Unlike China, however, North America does not yet have many localities that produce well-preserved skeletal specimens of Cretaceous birds: skeletal records of birds from the Cretaceous of North America are mostly of fragmentary specimens. That *Archaeornithura* has well-preserved flight feathers with well-

developed alulae supports the hypothesis that the track-makers responsible for bird tracks from the Early Cretaceous were volant birds. Also, tracks from volant birds are documented from the Lower Cretaceous Eumeralla Formation (Albian) of Australia: one trackway is interpreted as the tracks of a large wading bird in the process of landing (Martin et al., 2013). This indicates that flighted shore- and wading birds were established during the Early Cretaceous.

It is possible that many of the avian ichnotaxa known from present-day Asia would have had similar representatives in present-day North America, and vice versa (Lockley et al., 2012c): for example, *Aquatilavipes* ichnosp. (Azuma et al., 2013) and *Koreanaornis* ichnosp. (Alfinson et al., 2009) are documented both in present-day Asia and North America (Table 1). During the Early Cretaceous, Laurasia would still be connected enough that volant shore- and wading birds, such as those attributed to the traces of Avipedidae, Koreanaornipodidae, Igotornidae, Limiavipedidae, and Paxavipedidae, would have had opportunity to access most of the continent. As there would have been no significant barriers inhibiting the spread of volant birds across Laurasia during the Early Cretaceous, it is not surprising that many of the ichnofamilies and ichnogenera (if not ichnospecies) are documented both from present-day Asia and North America. However, until skeletal material of the same species of volant shorebird and/or wading bird have been documented in deposits both in Asia and North America, it will be difficult to support a hypothesis that Mesozoic shorebirds engaged in long-range migrations, as is the case with extant shorebirds.

The pedes of shore- and wading birds show strong convergence based on their ecotypes (see Falk et al., 2011), and it is possible that the track-makers of these ichnotaxa did not have a global distribution. In other words, the traces *Aquatilavipes* ichnosp. and *Koreanaornis* ichnosp. found both in present-day Asia and North

**Table 1**  
Summary of avian ichnofamilies found between Asia and North America in the Early Cretaceous.

Ichnofamily	Ichnotaxon	China	Mongolia	South Korea	Japan	North America	South America
<b>Avipedidae</b>		X?			X	X	
	<i>Aquatilavipes</i> isp.	X?			X	X	
<b>Igotornidae</b>				X		X	
	<i>Goseongornipes markjonesi</i>			X			
	<i>Hwangsanipes choughi</i>			X			
	<i>Igotornis gajinensis</i>			X			
	<i>Igotornis mcconnelli</i>					X	
	<i>Igotornis yangi</i>			X			
<b>Jindongornipodidae</b>	<i>Jindongornipes kimi</i>			X			
<b>Koreanaornipodidae</b>		X		X		X	
	<i>Koreanaornis dodsoni</i>	X					
	<i>Koreanaornis hamanaensis</i>			X			
	<i>Koreanaornis cf. hamanaensis</i>					X	
	<i>Koreanaornis lii</i> ichnosp. nov.	X					
	<i>Pullornipes aurea</i>	X					
<b>Limiavipedidae</b>		X				X	
	<i>Limiavipes curriei</i>					X	
	<i>Wupus agilis</i>	X					
<b>Paxavipedidae</b>						X	X
	<i>Barrosopus slobodai</i>						X
	<i>Paxavipes babcockensis</i>					X	
<b>Shandongornipodidae</b>	<i>Shandongornipes muxiai</i>	X					
<b>Unassigned to ichnofamilies</b>	<i>Cyseongornipes lockleyi</i>			X			
	<i>Morguiornipes robusta</i>	X					
	<i>Tatarornipes chabuensis</i>		X				
	<i>Uhangrichnus chuni</i>	X					

Present-day continental distribution of avian ichnotaxa from the Early Cretaceous. While Asia (China, Korea) has the most number of avian ichnospecies, there are avian ichnofamilies (bold X) that are not restricted to one present-day continent. The presence of *Aquatilavipes* isp., *Igotornis* isp., and *Koreanaornis* isp. in Lower Cretaceous deposits of both present day Asia and North America indicates that these ichnofamilies and ichnogenera had a Laurasian-wide distribution during the Early Cretaceous. There is currently support for ichnospecies-level endemism in Asia for Early Cretaceous avian ichnotaxa; however, the trackmakers for these respective ichnogenera, especially if they were volant avians, may have not been restricted to these localities. The gaps in this table will be resolved as more exploration and documentation of Lower Cretaceous avian ichnites occurs.

America are the result of track-makers endemic to western and eastern Laurasia during the Early Cretaceous. As more skeletal and ichnological material is recovered both from Asia and North America, we will gain a better understanding of the diversity and distribution of Early Cretaceous shore- and wading birds.

## 8. Conclusion

*Koreanaornis lii* is a novel ichnospecies described from the Lower Cretaceous (?Aptian–Albian) Hekou Group in the Lanzhou–Minhe Basin of Gansu, northwest China. *K. lii* is distinguished by a proximal footprint margin that is obtuse to near perpendicular to the digit III trace, high digit II–IV divarication, and a small digit I impression with a digit divarication I–II between 134° and 160°. The multivariate statistical analyses reveal a caveat of relying solely on multivariate statistical analyses as a diagnostic tool: *K. lii* shares a morphospace with Igotornidae rather than Koreanaornipodidae, despite the morphological differences between the *K. lii* and all ichnospecies of Igotornidae. What hinders a more thorough comparison is the lack of consistent reporting of data of digit I traces of avian ichnotaxa. This new ichnospecies of *Koreanaornis* adds to the fast-increasing and unique high diversity of avian ichnospecies in China and Korea.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2016.06.005>.