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Tracking Korea's Early Birds: A Review of Cretaceous Avian Ichnology and Its Implications for Evolution and Behavior

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Tracking Korea's Early Birds: A Review of Cretaceous Avian Ichnology and Its Implications for Evolution and Behavior

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Bird tracks are abundant and ubiquitous in many Cretaceous formations in Korea. To date, in order of discovery and description, the following six ichnogenera have been reported: *Koreanaornis, Jindongornipes, Uhangrichnus, Hwangsanipes, Ignotornis, Goseongornipes* and *?Aquatilavipes*. As more bird tracks are discovered it has become possible to amend descriptions of existing ichnotaxa to better understand track morphology (and ichnotaxonomic relationships), trackway patterns and associated feeding traces and gain further insight into the behavior and ecology. We review and re-evaluate the most important bird tracksites in Korea, with special reference to sites not previously fully or adequately described in accessible English language journals. We pay special attention to material from the Uhangri Dinosaur Museum, Haenam area, and the Gyeongsangnamdo Institute of Science Education, Gajin area, presenting revised descriptions, illustrations and information on *Uhangrichnus* and *Goseongornipes*.

Keywords Bird tracks, Cretaceous, Korea

INTRODUCTION

It is well-known that the Cretaceous of Korea has yielded a high abundance and diversity of bird tracks that is of historic importance to Mesozoic vertebrate ichnology (Kim, 1969; Lockley et al., 1992; Yang et al., 1995, 1997; Baek and Yang, 1997; Kim et al., 2006, 2012; Lockley and Harris, 2010; Huh et al., 2012). It is also well-known that most Cretaceous bird tracks, including those from Korea, are "shorebird-like." Although made mostly in lake shoreline settings, the trackmakers were presumably not members of modern shorebird groups because there is no evidence for such taxa in the Cretaceous, even though the track similarity strongly suggests convergence. Therefore, our primary goal is simply to differentiate ichnotaxa (morphotypes) and treat inferences about trackmaker identification, behavior and ecology as a secondary concern.

The shorebird-like trackmakers were small, lightweight birds that made relatively small tracks (footprint lengths ∼2 to ∼10 cm). In cases where they reveal diagnostic morphologies that form the basis of new ichnotaxa, one may conclude that "by definition" the tracks are well-preserved. However, the morphology of such shorebird-like tracks is generally simple, consisting, where there are no web, hallux or bill-feeding traces, of three narrow widely divergent digit traces. Thus, it is important not to overinterpret small morphological details by giving them undue ichnotaxonomic significance. As pointed out by Lockley and Harris (2010), it is evident that there has been little effort to compare Cretaceous and Cenozoic bird track morphologies in order to avoid unnecessary ichnotaxonomic splitting.

As demonstrated below, the Korean track samples are as important, if not more important, than any found in the Cretaceous, not just because of preservation but also because many of the formally named ichnotaxa are based on types associated with large samples, and moreover, the rate of new discoveries continues at a remarkable pace.

The purpose of this paper is to review what is currently known of Korean avian ichnology and to draw attention to important sites, some of which are described elsewhere in this volume for the first time. To do this we offer a historical perspective on the unfolding of bird track studies in the Cretaceous of Korea by reviewing the type of specimens, type localities and associated

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TABLE 1
Cretaceous avian ichnotaxa from Korea listed in chronological order of formal description, between 1969 and 2006. The list includes six ichnospecies accommodated in five ichnogenera (in ***bold***), of which one is assigned to the previously-named ichnogenus *Ignotornis.* The first-named ichnospecies of *Ignotornis* from the Cretaceous of Colorado is also listed. (* refers to a new ichnotaxon described in this volume: Kim et al., 2012)

Cretaceous avian ichnotaxa	Locality	References
Ignotornis mcconnelli	Colorado, USA	Mehl, 1931
Koreanaornis hamanensis	Korea	Kim, 1969
Jindongornipes kimi	Korea	Lockley et al., 1992
Hwangsanipes choughi	Korea	Yang et al., 1995
Uhangrichnus chuni	Korea	Yang et al., 1995
Ignotornis yangi	Korea	Kim et al., 2006
Goseongornipes markjonesi	Korea	Lockley et al., 2006
*Ignotornis gajinensis**	Korea	Kim et al., 2012
Aquatilavipes isp. indet.	Korea	Huh et al., 2012

topotype samples, many of which now form part of the network of Korean Natural Monuments.

TYPE AVIAN ICHNOTAXA FROM THE CRETACOUS OF KOREA

As summarized by Lockley and Harris (2010), there are six well-defined avian ichnospecies known from the Cretaceous of Korea (Fig. 1, Table 1), as well as a seventh reported elsewhere in this volume (Kim et al., 2012). With the exception of reports of six named ichnotaxa from China (Kim et al., 2012, table 4), one of which may be a synonym of *Koreanaornis hamanensis*, no other country has produced more than one formally named Cretaceous avian ichnotype.

ICHNOFAMILY KOREANAORNIPODIDAE Lockley et al., 2006

Koreanaornis hamanesis Kim, 1969

Koreanaornis hamanensis was only the second bird track formally named from the Mesozoic and the first named from Korea. It forms the basis of the ichnofamily Koreanaornipodidae (Lockley et al., 2006). (The first named bird track was *Ignotornis mcconnelli*, Mehl, 1931; see Table 1.) The *K. hamanenis* type locality was designated as Korean Natural Monument No. 222 in 1970. Kim (1969) designated Department of Geology, Seoul National University (DGSU) specimen 00158 as the holotype. Track-bearing beds exposed at the type locality illustrated by Kim (1969, pl. 2) expose a large sample of *K. hamanenis* topotypes in a protected part of Natural Monument No. 222 (Fig. 2). In addition to the bird tracks, the surface has a uniform distribution of distinctive symmetrical ripples that help to identify specimens originating from this locality. Herein, for the first time we illustrate a map of the *in situ* exposures from the type locality. As is clear from the map, at least 440 complete or partial tracks remain *in situ,* so the sample of topotype specimens is extensive.

Kim (1969, figs. 17 and 18) included two photos of *K. hamanensis* in his description of the type material: the former figure showed details of three more or less complete tracks from specimen DGSU 00158; however, the complete slab was not illustrated. Lockley et al. (1992, p. 115) noted that Kim reported that the holotype was "misplaced when the Geology Department moved to a new location." However, a topotype slab was preserved at the new department location. This specimen, simply designated DGSU, which shows more than 40 complete and many additional partial tracks, was illustrated by Lockley et al. (1992, fig. 3) along with another topotype specimen (KPE 50001) that reveals at least 20 additional tracks. Both show the aforementioned, characteristic, symmetric ripple marks (Fig. 3).

Koreanaornis hamanensis is a very small ichnite. As described by Kim (1969) and confirmed by subsequent studies (e.g., Lockley et al., 1992), the third toe corresponding to footprint length is about 2.5 cm long. Kim did not identify any tracks with hallux traces. Although Lockley et al. (1992) observed that hallux traces are occasionally impressed, they also noted that they are always short and inconspicuous. The occasional presence of a hallux trace was noted in the emended description of the ichnospecies (Lockley et al., 1992), where it was also noted that trackways show inward (positive) rotation. Like Kim (1969), Lockley et al. (1992) agreed that digit divarication angles were in the range of 105–120º. Kim (1969) suggested that the tracks resemble those of modern plovers such as the Long-billed Plover (*Charadrius placidus*), the Little-ringed Plover (*C. bulius*) and the Kentish Plover (*C. alexandrinus*).

An important but hitherto unpublished thesis study (Kim, 2008) suggested that, based on consistent digit divarication patterns, there may be significant differences between *K. hamanensis* and another informally labeled ichnotaxon ("*K.* ichnosp. nov."). However, as the source of this name is an unpublished thesis and therefore not formally valid, the trival ichnospecies name is not committed to print here.

ICHNOFAMILY JINDONGORNIPODIDAE Lockley et al., 2006

Jindongornipes kimi Lockley et al., 1992

Jindongornipes kimi (Lockley et al., 1992) was the second avian ichnospecies reported from the Cretaceous of Korea. This distinctive ichnotaxon was discovered in 1991 in the Jindong Formation. The type specimen (KPE 50007) originates from

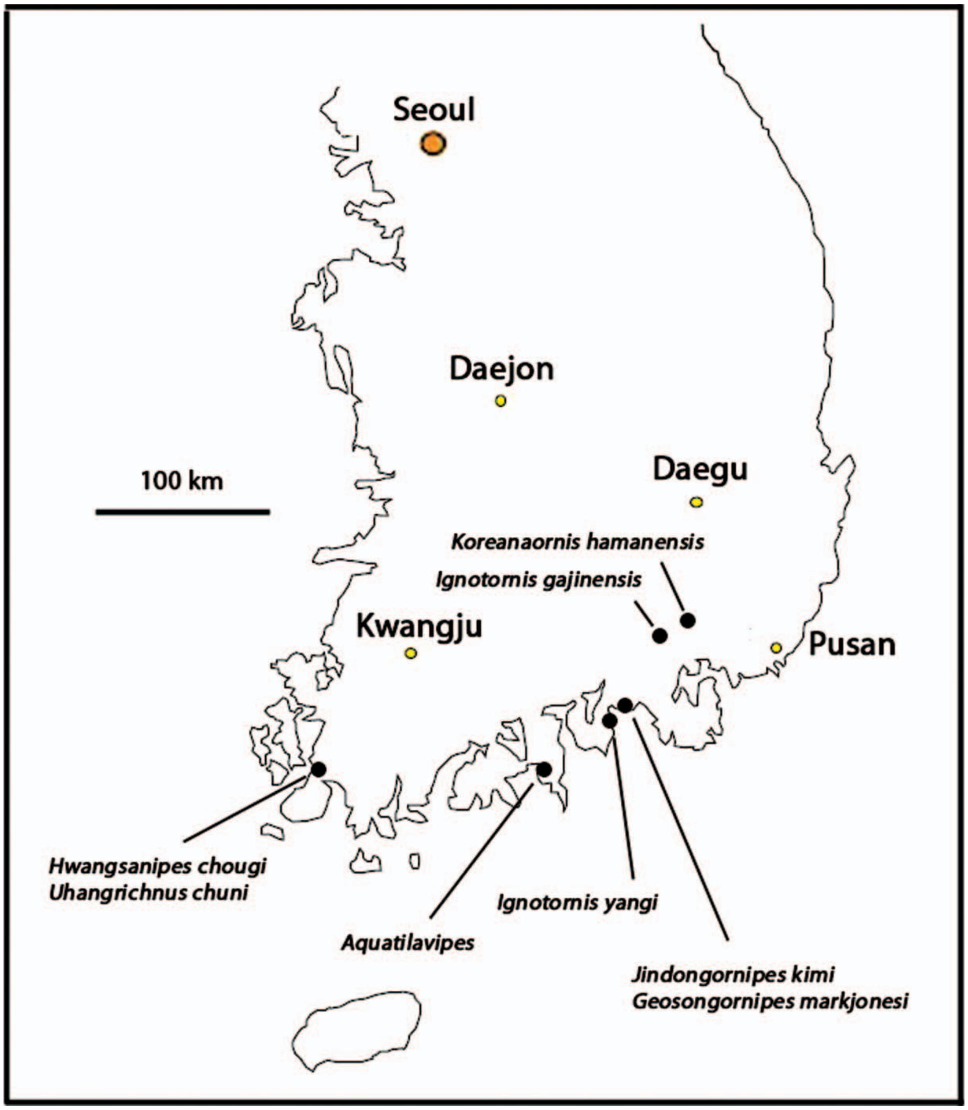

FIG. 1. Locality map, showing type localities for avian ichnotaxa mentioned in text. (Color figure available online.)

the type locality near Dukmeong village, Goseong-gun, which is in the area designated as the Goseong Tracksite (Natural Monument No. 411) within the Hallyo Haesang National Park area. The ichnospecies *J. kimi* occurs at several horizons in this area (Lockley et al., 1992, 2006) and is known from the formation in other areas.

Jindongornipes kimi is a distinctive large ichnospecies with a tetradactyl pes track up to 8.0 cm long (with hallux) and up to 7.5 cm wide. The long hallux is directed posteriorly (Fig. 4).

ICHNOFAMILY indet.

Uhangrichnus chuni Yang et al., 1995

Uhangrichnus chuni (Fig. 5) is a distinctive avian ichnospecies found in the Uhangri Formation in the area designated as the Haenam Tracksite Natural Monument No. 394. The tracks were first reported by Chun (1990) and formally named by Yang et al. (1995). *U. chuni* tracks reveal palmate web traces, which are equally well developed between digits II and III and between III and IV; see Kim et al. (2006, fig. 3) for comparisons between *Uhangrichnus* and semi-palmate forms such as *Ignotornis* and *Hwangsanipes*. The holotype of *U. chuni* is KPE 50101 (Yang et al., 1995, fig. 5) based on a large sample of isolated tracks, measured to give an average length (without hallux) and width of 3.70 cm (N = 85) and 4.58 (N = 70) cm, respectively. *U. chuni* co-occurs with the distinctive ichnospecies *H. choughi* described below. Both ichnotaxa were the first tracks with web traces reported from the Mesozoic.

According to an unpublished thesis study (Kim, 2008), another informally named ichnospecies of *Uhangrichnus* occurs

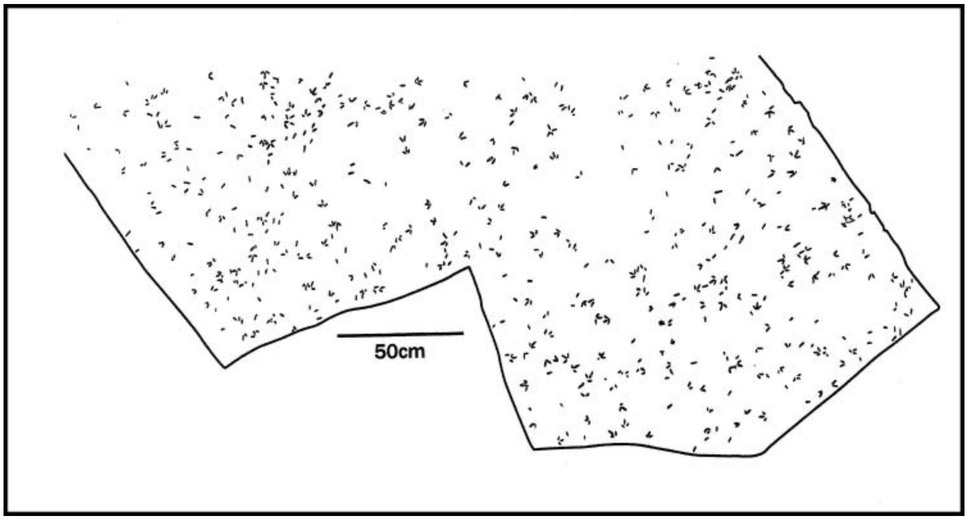

FIG. 2. Map of bird tracks *in situ* at *Koreanaornis hamanensis* type locality.

in the Haman Formation, labeled ichnotaxon ("*U*. ichnosp. nov."). However, as the source of this name is an unpublished thesis and therefore not formally valid, the trival ichnospecies name is not repeated in print here.

Although *U. chuni* was originally described without an example of a clear trackway and without evidence of a hallux trace, Lockley and Harris (2010, fig. 9C) illustrated a topotype trackway (Fig. 6) which shows both features, as well as the characteristic inward rotation. Thus the description of *U.chuni* can be emended as follows.

Uhangrichnus chuni emended
Referred material
Chun, 1990 p. 10a
"tracks of a bird with webbed feet" Lockley et al., 1992, fig. 9
Uhangrichnus chuni Yang et al., 1995, fig. 5
Uhangrichnus chuni Yang et al., 1997, figs. 3–5
Uhangrichnus chuni Lockley and Rainforth, 2002, figs. 17–12B
Uhangrichnus chuni Kim et al., 2006, fig. 3D
Uhangrichnus chuni Lockley, 2007, fig. 1D
Uhangrichnus chuni Lockley and Matsukawa, 2009, fig. 15D
Uhangrichnus Lockley and Harris, 2010, fig. 9C

***Emended description*.**

Small, functionally tridactyl track of a web-footed bird with small, postero-medially directed hallux trace sporadically preserved. Web configuration palmate (i.e., well-developed) and equally developed in hypicies between digits II and III and III and IV. Footprint, excluding hallux, wider (w) than long (l), averaging 3.70 and 4.58 cm, respectively (l/w = 0.81), but footprint length with hallux slightly longer than wide (l/w = 1.1; see Table 2). Trackway narrow with short step and stride (7.8 and 15.7cm, respectively) and strong inward rotation (mean 20°) of digit III relative to trackway midline (Fig. 6).

ICHNOFAMILY IGNOTORNIDAE Lockley et al., 2006, Emended Kim et al., 2006

Hwangsanipes choughi Yang et al., 1995

Hwangsanipes choughi is a distinctive avian ichnospecies found in the Uhangri Formation in the area designated as the Haenam Tracksite Natural Monument No. 394. The tracks were first reported by Seung Soo Chun in 1990 and formally named by Yang et al. (1995). *Hwangsanipes* tracks reveal partial web traces indicating a semi-palmate trackmaker somewhat similar

TABLE 2
Measurements for a *Uhangrichnus* topotype trackway with hallux traces

Track number	Length + hallux (cm)	Length (cm)	Width (cm)	Step (cm)	Stride (cm)	Rotation (°)
T 1	–	3.6	–	–		
T 2	–	3.5	4.3	7.7	15.5	30°
T 3	5.1	3.8	4.5	7.7	15.9	12°
T 4	4.9	4.0	4.8	8.1		18°
mean	**5.0**	**3.7**	**4.5**	**7.8**	**15.7**	**20°**

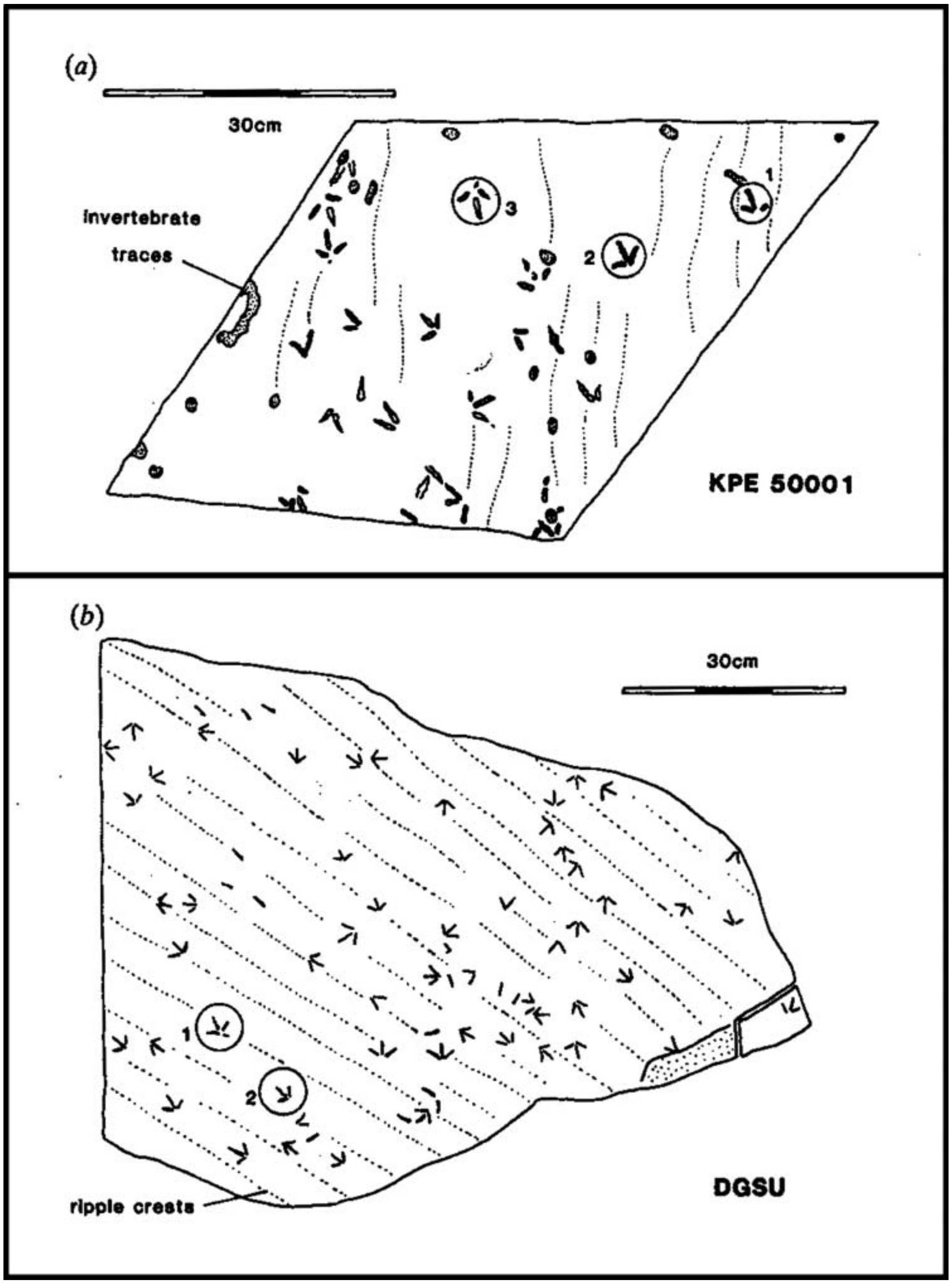

FIG. 3. *Koreanaornis hamanensis* after Lockley et al. (1992).

to *Ignotornis,* that is, with the web trace between digits III and IV more developed than between digit traces II and III. However, in comparison with *Ignotornis*, *Hwangsanipes* is larger with more developed web traces; see Kim et al. (2006, fig. 3) for comparisons. The holotype of *H. choughi* is KPE 50101 (Yang et al., 1995, fig. 6) is based on a sequence of four tracks (Fig. 7), of which three were measured to give an average length (without hallux) and width of 4.86 cm and 6.26 cm, respectively. *H. choughi* co-occurs with the distinctive ichnogenus *Uhangrichnus chuni* described above. Both ichnotaxa were the first bird tracks with web traces reported from the Mesozoic.

Goseongornipes markjonesi Lockley et al., 2006

Goseongornipes markjonesi was named by Lockley et al. (2006) to describe tracks intermediate in size and morphology between *Koreanaornis* and *Jindongornipes*. This distinctive ichnotaxon was discovered in the Jindong Formation in the

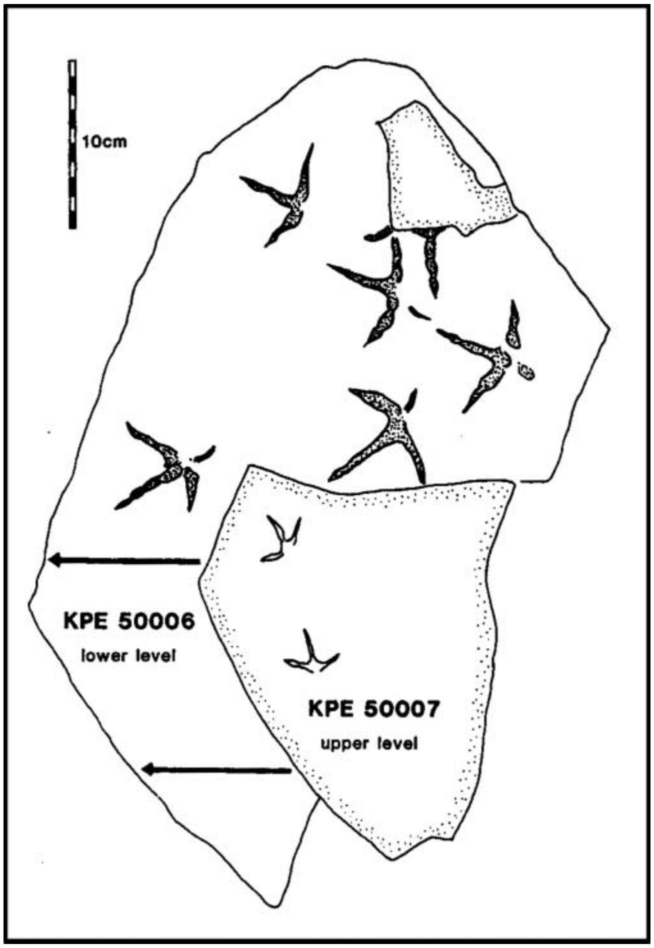

FIG. 4. *Jindongornipes kimi* after Lockley et al. (1992).

1990s but not described formally until 2006. The type specimen (KPE 50010) originates from the type locality near Dukmeong village, Goseong-gun, which is in the area designated as the Goseong Tracksite (Natural Monument No. 411) within the Hallyo Haesang National Park area.

The type specimen shows two tracks, but it is unclear whether they are part of a trackway. Holotype measurements indicate a width of 4.2–4.5 cm and a length with hallux of 4.1–4.5 cm (without hallux 3.0–3.5 cm). Like *Ignotornis* and *Hwangsanipes, Goseongornipes* is semi-palmate but with only a slight web development in the proximal part of the hypex between digits III and IV. It is clear from preliminary study of large new samples that *Goseongornipes* is typical of shorebird-like trackways in showing strong inward rotation.

The discovery of large bird track assemblages in the Gajin area has added much to the sample of discrete *Goseongornipes* trackways (Fig. 8). It is now possible to identify many trackways that show progression over different substrates, with and without ripple marks and dinosaur tracks. Given the large size of the Gajin sample and the need for a thorough analysis, it is premature to present a revised description of the ichnospecies. Nevertheless, it is pertinent to note the following. The ichnospecies, originally illustrated by Lockley et al. (2006, figs. 9C and 20B, D) was also illustrated by Kim et al. (2006, fig. 3B), Lockley and Matsukawa (2009, fig. 15B) and Lockley and Harris (2010, fig. 9B). Lockley et al. (2006) also noted that specimen KPE 50005, previously illustrated as *Koreanaornis hamanensis* Lockley et al. (1992, fig. 12) was better designated as a paratype of *G. markjonesi* (Lockley et al., 2006, fig. 20D).

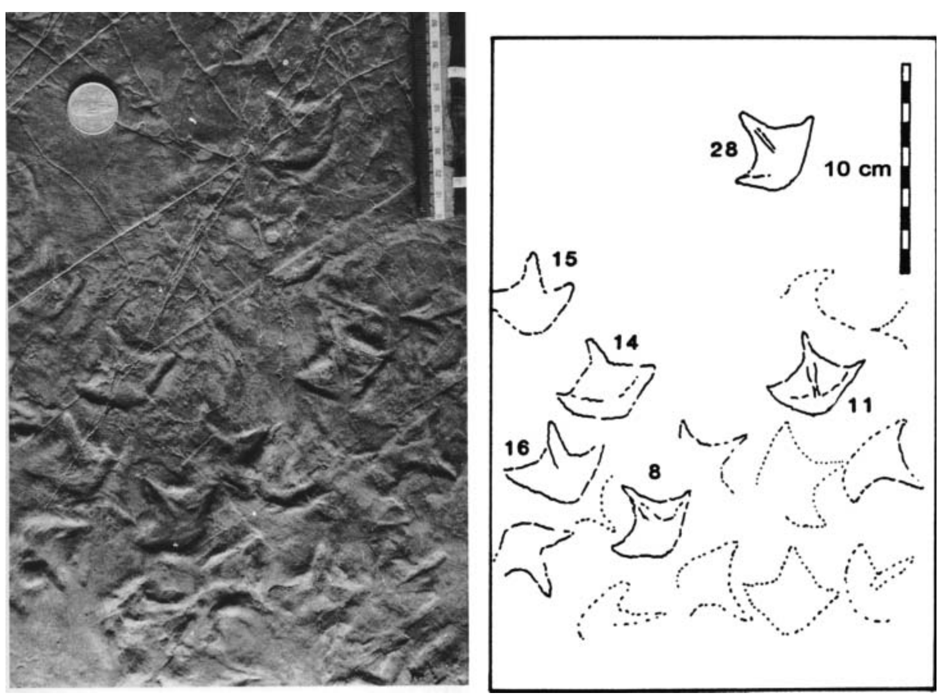

FIG. 5. *Uhangrichnus chuni* after Yang et al. (1995).

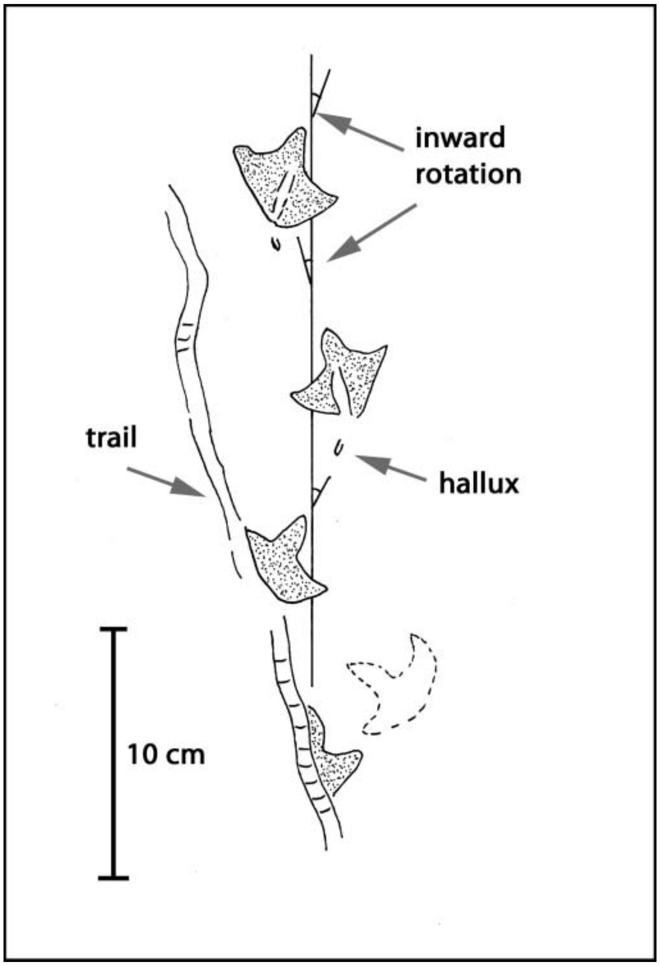

FIG. 6. *Uhangrichnus chuni* topotype trackway, modified after Lockley and Harris (2010, fig. 9C).

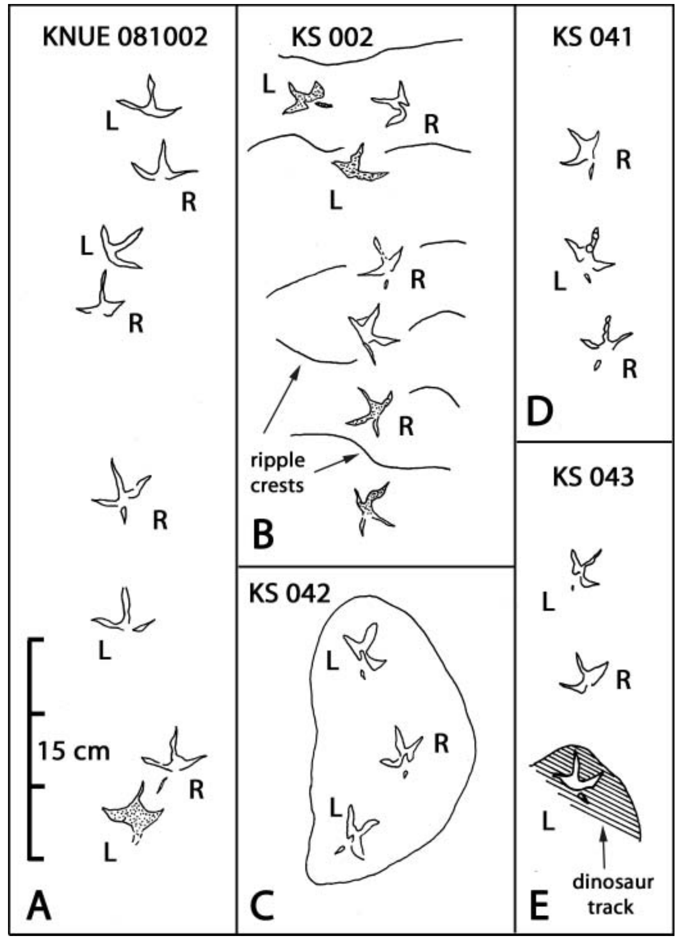

FIG. 8. *Goseongornipes* trackways after Kim et al. (2012).

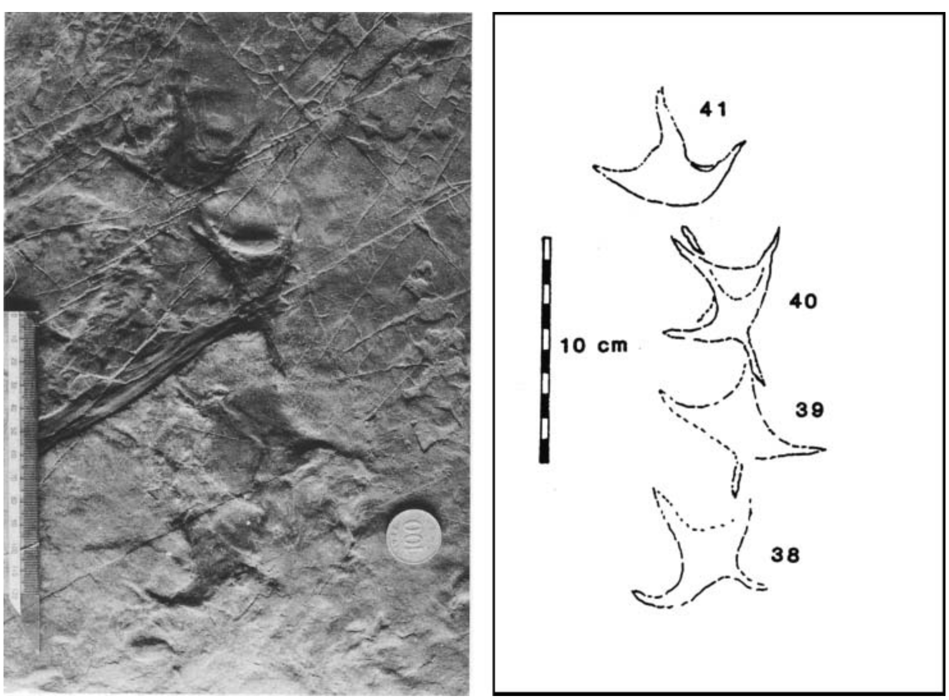

FIG. 7. *Hwangsanipes choughi* after Yang et al. (1995).

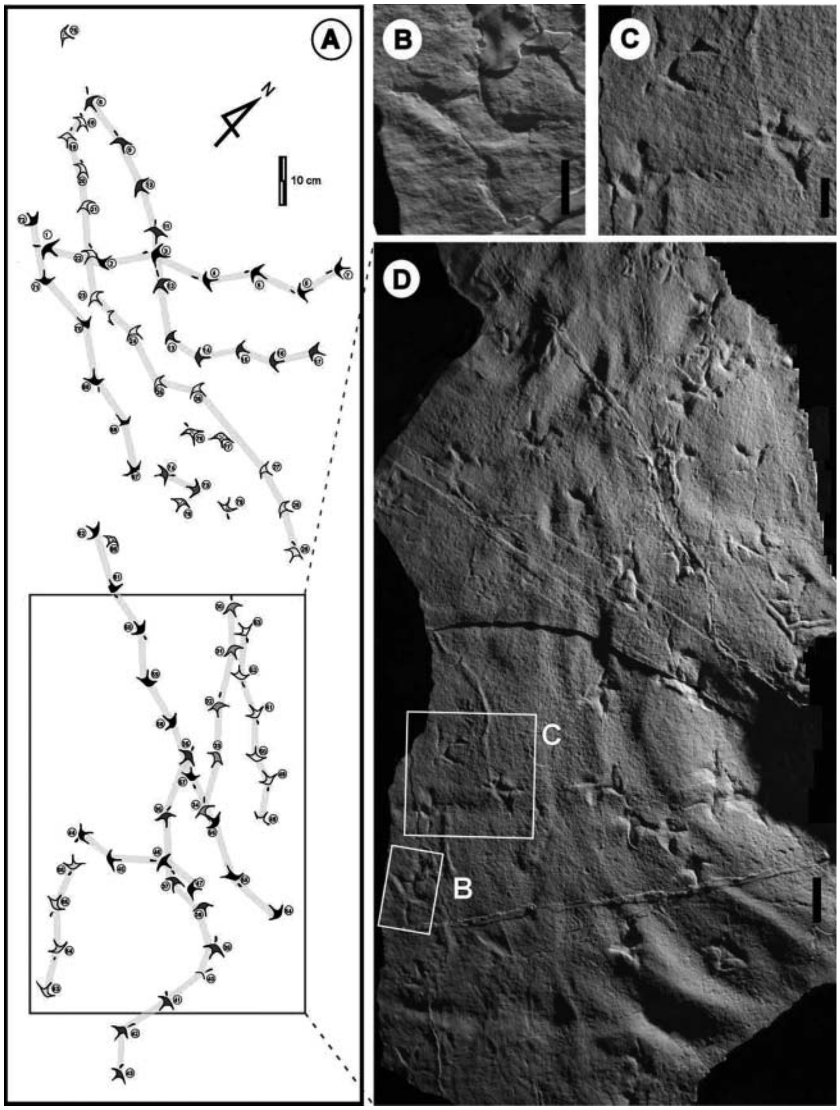

FIG. 9. *Ignotornis yangi* (Kim et al., 2006).

Ignotornis yangi Kim et al., 2006

Ignotornis yangi (Fig. 9) described by Kim et al. (2006) is the first example of an avian ichnospecies from Korea that has been assigned to an ichnogenus described from elsewhere. The type specimen (KNUE 040417) is from the Haman Formation of Changseon Island. *I. yangi* is significantly smaller than the type ichnospecies (*I. mcconnelli*) from Colorado and *Hwangsanipes choughi*. Although the size of *I. yangi* is similar to *Goseongornipes markjonesi*, the former ichnospecies has a better developed web trace between digits III and IV and a longer hallux trace.

Ignotornis gajinensis ichnosp. Kim et al., 2012

As noted elsewhere in this volume, where *Ignotornis gajinensis* is formally described (Kim et al., 2012), this newly identified ichnospecies is a tetradactyl semipalmate webbed track with a mean length, including prominent postero-directed hallux impressions, of about 6.75 cm and a mean width of about 5.54 cm. Other descriptive details need not be repeated here, but it is important to note that the ichnospecies is consistently associated with arcuate, parallel, double grooves attributed to sweeping movements of the bill from side to side. It is this distinctive morphological "feeding" trace that justifies erecting a new ichnospecies of *Ignotornis* based on a highly distinctive configuration of traces not seen in other avian ichnospecies (Fig. 10).

MORPHOFAMILY AVIPEDIDAE *sensu* Sarjeant and Langson 1994

Aquatilavipes isp. Indet.

Tracks assigned to *Aquatilavipes* are reported from the Haman Formation (Kim, 2008). Although this information has

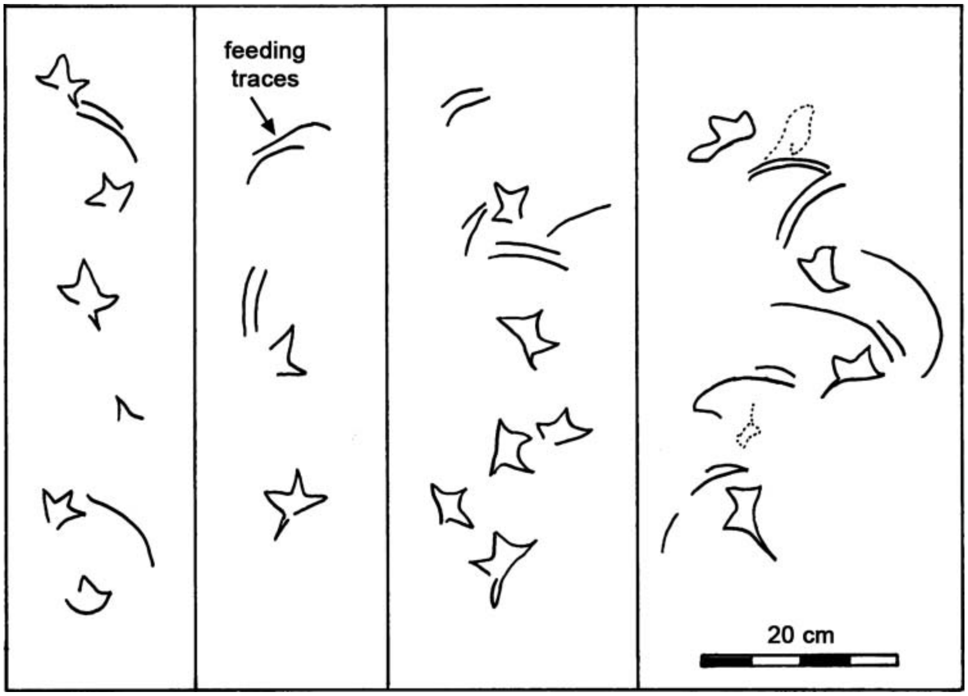

FIG. 10. *Ignotornis gajinensis* after Lockley and Harris (2010, fig. 11); see Kim et al. (2012).

been presented only in an unpublished thesis, it is consistent with other recent reports. For example, *Aquatilavipes* appears to be present in the small sample reported from Sado Island, the Yeosu Island archipelago (Huh et al., 2012). This tracksite is part of an unnamed Cretaceous formation within the area of Natural Monument No. 434 known as the Yeosu tracksite. There are historical problems associated with the differentiation of *Aquatilavipes* and *Koreanaornis*.

Ichnogenus *Aquatilavipes,* originally based on tracks from the Lower Cretaceous of Canada (Currie, 1981), is similar to *Koreananornis* in that it is a slender-toed, functionally tridactyl track that does not preserve a hallux trace in any hitherto described samples. (As noted above, no hallux was noted in the original description of *Koreanaornis*, and it was only later that a small hallux trace was recognized in a few footprints.) However, of more importance from an ichnotaxonomic viewpoint is the fact that *Aquatilavipes* is a larger track with greater maximum divarication angles that was originally described without reference to *Koreanaornis*. This meant that reports of *Aquatilavipes* elsewhere in Asia, for example, in Sichuan (Zhen et al., 1995), overlooked the need to compare tracks with *Koreanaornis*. For this reason, it has been suggested that the Sichuan tracks are similar to *Koreanaornis* (Lockley et al., 2008; Lockley and Harris, 2010). This does not mean, however, that *Aquatilavipes* does not occur in Korea or elsewhere in Asia, as reported by, for example, Azuma et al. (2002), based on Japanese material that was compared with *Koreanaornis*. More explicitly, Xing et al. (2011) have reported a new ichnospecies of *Koreanaornis* (*K. dodsoni*) from Xinjiang, China, although we consider that it is indistinguishable from *K. hamanensis*. Zhang et al. (2006) also reported *Aquatilavipes* from Gansu Province China. This issue is further discussed below.

DISCUSSION

In the last decade much has been written about bird tracks from the Cretaceous of Korea, and it is generally agreed that they all represent shorebird-like species. This interpretation fits well with the interpretation of the sediments in which they are found as lake-shore and lake basin deposits. It is also well-established that almost all the ichnospecies so far described are represented by large samples, sometimes impressed on multiple surfaces in high concentrations (see papers in this volume). From a strictly paleoecological point of view, it is not surprising that ichnologists have formally recognized a diversity of at least nine ichnotaxa in the Cretaceous of Korea. However, this ichnodiversity is not necessarily equivalent to the diversity of trackmakers because different trackmakers may have made similar tracks. Conversely, the same trackmakers may have made different tracks due to substrate variability or different behaviors.

It is easier to differentiate some morphotypes than others. For example, *Koreanaornis*, *Jindongornipes* and *Uhangrichnus* all appear quite distinct and are probably legitimately assigned to different ichnofamilies, as is currently the case. In contrast, *Ignotornis*, *Hwangsanipes* and *Goseongornipes* are more similar and assigned to the same ichnofamily. At the time *Koreanaornis* was discovered, there were no other similar Mesozoic bird tracks known, although this ichnotaxon could be compared with one or more of the *Avipeda* ichnospecies reported from the Cenozoic (see Lockley and Harris, 2010). As noted above, *Koreanaornis* was not properly compared with *Aquatilavipes* (Currie, 1981; Zhen et al., 1995), although later attempts to differentiate the ichnogenera have been published (Azuma et al., 2002; Lockley et al., 2008; Lockley and Harris, 2010).

An understanding of whether *Koreanaornis* is a monospecific ichnogenus or divisible into multiple ichnospecies is of importance in defining the composition and diversity of Korean bird track assemblages in a meaningful way. By assigning the Sichuan ichnotaxon *Aquatilavipes sinensis* to *Koreanaornis* (*K. sinensis* comb nov., *sensu* Lockley et al., 2011) and adding the new ichnotaxon *K. dodsoni* (Xing et al., 2011) to the list of ichnites assigned to this ichnogenus, *Koreanaornis* is rapidly becoming a complex ichnogenus at the ichnospecies level. This is to say nothing of the distinctions drawn by Kim (2008) in recognizing additional ichnospecies as yet not formally named. We consider that such finely drawn ichnospecies distinctions are only likely to prove useful if ichnologists can readily recognize the morphological characteristics on which such distinctions are based. If the distinctions are within the general range of variation in known *Koreanaornis* samples, they are likely to have no practical ichnotaxonomic utility.

It is noteworthy that there also are now three known ichnospecies of the ichnogenus *Ignotornis*, including two Korean forms, *I. yangi* (Kim et al., 2006) and *I. gajinensis*, the latter described in this volume based in part on distinctive feeding traces not associated with other ichnospecies (Kim et al., 2012). It is outside the scope of this review to enter into a detailed discussion of all the criteria that can legitimately be used to define and emend ichnospecies. However, as this review indicates, the addition of new material does much to improve our knowledge. For example, some ichnospecies were defined on the basis of isolated tracks or incomplete trackways. Such descriptions did not necessarily enter the literature as the result of a lack of material. On the contrary, as noted by Kim (2008), the high density of tracks has often made it impossible to find separate, unequivocally clear trackways. Nevertheless, new material and new observations have, in some cases, provided us with such clear trackways and significant new information. For example, in the case of some ichnotaxa, descriptions have been improved by adding previously unknown information about hallux traces, web traces, trackway configuration patterns (such as rotation angles) and feeding traces. All such features are an integral part of the trackway and may legitimately be used to improve or emend existing ichnotaxonomic descriptions.

In the future it is likely that further discoveries will supplement the new information presented herein. Even though there are at least four Korean research groups involved in serious scientific studies of Cretaceous vertebrate ichnology, the pace of discovery of new sites with abundant material challenges us to keep up with documentation of sites and to describe the new material consistently. Fortunately, these groups have worked collaboratively, as in this paper and volume. The aim of such collaboration is to strike a balance between oversight and "lumping" on the one hand and oversplitting (creating junior synonyms) on the other. In short, given the importance of bird tracks in the Cretaceous of Korea, it is useful to review all that is known "under one cover," as done here.

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