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The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): More evidence of high avian diversity in East Asia

Jeong Yul Kim [a], Sam Hyang Kim [a], Kyung Soo Kim [a], Martin Lockley [b,*]

[a] *Department of Earth Science Education, Korea National University of Education, Cheongwon, Chungbuk 363-791, Korea*
[b] *Geology Department, University of Colorado at Denver, Dinosaur Tracks Museum, PO Box 173364, Campus Box 172, Denver, CO 80217-3364, USA*

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Abstract

Tracks of web-footed birds and pterosaurs from the Lower Cretaceous (Aptian-Albian) Haman Formation of Changseon and Sinsu Islands, respectively (southern coast of Korea), represent the oldest records for these footprint types in Asia. The morphology of the bird tracks, with prominent posteriorly directed hallux impression, semi-palmate web, and small ratio of length to width is similar to *Hwangsanipes choughi* from the Upper Cretaceous (Cenomanian) Uhangri Formation. However, they about 20–25% smaller, and therefore much closer to the size of North American *Ignotornis* (size difference less than 10%). The development of the web appears intermediate in size between *Hwangsanipes* and *Ignotornis*. This leads us to infer a new ichnotaxon herein named *Ignotornis yangi*. This is the first Asian report of a named bird track similar to the type material of *Ignotornis* from North America.

Pterosaur tracks consist predominantly of clear impressions of tridactyl mani (length 9–13 cm) characterized by strongly asymmetric digit impressions that outnumber less-clear elongated pes traces by a ratio of about 10 to 1. Clusters of short digit impressions or parallel to subparallel scrape marks indicate incomplete pes traces probably made by swimming animals. The pterosaur tracks, here provisionally identified as *Pteraichnus*, represent the first record of this ichnogenus from Korea. The track maker represents a species quite different from the giant track maker represented by the ichnogenus *Haenamichnus* from the Cenomanian Uhangri Formation, but it is similar to recent reports of *Pteraichnus*-like forms from the Lower Cretaceous of China.

These new records shed light on patterns of bird-track diversity and abundance in the ‘‘mid’’ Cretaceous of Korea (Aptian-Cenomanian) and show that at least two quite distinct pterosaurian species existed during this time span with at least six distinct species of track-making birds. When combined with additional reports of bird track ichnotaxa from China, the picture emerges of a remarkably diverse Lower Cretaceous avifauna. Such diversity is consistent with the skeletal record for this region, though the types of birds represented by tracks are ‘‘shorebird-like’’ and therefore distinct from the skeletal avifauna, which consist of birds of the perching type.

The ability of tracks to record whole foot morphology including details of web and hallux configuration allows for fine discrimination of foot morphology and comparison with web-footed tracks from other regions and geologic time periods. As is the case with modern shore birds, Cretaceous tracks were probably mostly made by adults whose foot size as well as shape is probably indicative of the identity of the track maker at low taxonomic levels.

Keywords: Webbed bird tracks; Pterosaur tracks; Cretaceous; Haman Formation; Korea

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[*] Corresponding author.
E-mail address: Martin.Lockley@cudenver.edu (M. Lockley).

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1. Introduction

In recent years there has been an exponential increase in the discovery of bird and pterosaur tracks. The track record can be particularly instructive in adding information that is not otherwise available from the realm of body fossils. Especially in Korea there has been a significant increase in the rate of discovery of Cretaceous bird tracks with many additional reports from the Cretaceous of other regions including China, Japan, Israel, Spain, Canada, USA, and Argentina (Mehl, 1931; Avnimelech, 1966; Kim, 1969; Currie, 1981; Zhen et al., 1987; Lockley et al., 1992; Yang et al., 1995; Vidarte, 1996; Baek and Yang, 1997; Lockley and Matsukawa, 1998; Lim et al., 2000; Azuma et al., 2002; Coria et al., 2002). However, only a few webbed bird tracks including ten named and six unnamed ichnospecies have been previously reported from Cretaceous through Neogene strata (Table 1).

The purpose of this paper is to describe the new Changseon site in the Haman Formation (Fig. 1), from which 11 well-preserved trackways (comprising 80 footprints) of web-footed birds have been reported, and to provide a discussion of where these tracks fit into the morphological and ichnotaxonomic record of a rapidly expanding database of bird tracks from East Asia. We also describe the first *Pteraichnus*-like tracks (comprising at least three trackways and about 30 partial and complete tracks) from the Haman Formation of Sinsu Island (Fig. 1), and compare them with other pterosaur tracks from the Cretaceous of Korea and China.

2. Tracks of web-footed birds

Cretaceous web-footed bird tracks are known from at least seven separate geographical areas, four of which are found in Korea. The general localities of the Korean sites, in order of discovery are: western Goseong County (Lockley et al., 1992; this paper), Hwangsan Basin (Yang et al., 1995, 1997, 2003), Kyungnam (Baek and Yang, 1997; Yang et al., 1997) and the Changseon site described herein. There are two North American sites described from Colorado (Mehl, 1931) and Wyoming (Lockley et al., 2004), and one described from Argentina (Coria et al., 2002).

The ichnotaxa considered to represent web-footed birds are as follows: *Ignotornis mcconnelli* (Mehl, 1931) from Colorado, cf. *Ignotornis* Mehl, 1931 from Argentina (Coria et al., 2002) and *Sarjeantopodus semipalmatus* (Lockley et al., 2004) from Wyoming (Table 1). *Uhangrichnus chuni* and *Hwangsanipes choughi* (Yang et al., 1995) are known from the Uhangri Formation of the Hwangsan Basin in southwestern Korea, and the former ichnotaxon (*U. chuni*) is reported from the Kyungnam site (Baek and Yang, 1997). In this study we report well-preserved and extensive trackways of a new morphotype similar to the type material of *Ignotornis* from

Table 1
Record of webbed bird tracks

Age	Formation	Locality	Name	Reference
Pliocene	Bidahochi Fm	Arizona, USA	goose or goose-like tracks	Breed, 1973
Early Pliocene		California, USA	goose footprints	Miller and Ashley, 1934
Miocene (late Messinian)	Caños Fm	Almería, Spain	*Roepichnus grahami*	Doyle et al., 2000
Late Miocene	Copper Canyon Fm	California, USA	*Avipeda* ichnosp.	Scrivner and Bottjer, 1986
Miocene	Miocene fm	Rumania	*Anatipeda anas*	Panin and Avram, 1962
Oligocene	Lower Oligocene fm	Navarra and Zaragoza, Spain	heron-like or stork-like wading bird tracks	de Raaf et al., 1965
Late Eocene	Eocene fm	Trans-Pecos Texas, USA	*Charadriipeda becassi*	Sarjeant and Langston, 1994
Early Eocene	Green River Fm	Utah, USA	bird tracks	Moussa, 1968
Early Eocene	Green River Fm	Utah, USA	*Presbyorniformipes feduccii*	Yang et al., 1995
Paleocene	Fort Union Fm	Wyoming, USA	bird tracks	Johnson, 1986
Late Cretaceous (Maastrichtian)	Lance Formation	Wyoming, USA	*Sarjeantopodus semipalmatus*	Lockley et al., 2004
Late Cretaceous (Campanian)	Anacleto Fm	Neuquén, Argentina	cf. *Ignotornis*	Coria et al., 2002
Late Cretaceous (Cenomanian)	Dakota Sandstone	Golden, Colorado	*Ignotornis mcconnelli*	Mehl, 1931
Late Cretaceous (Cenomanian)	Uhangri Fm	Haenam, South Korea	*Uhangrichnus chuni* *Hwangsanipes choughi*	Yang et al., 1995
Early Cretaceous (Albian)	Jindong Fm	Goseong-Donghae, South Korea	*Uhangrichnus chuni*	Baek and Seo, 1998
Early Cretaceous (Aptian-Albian)	Haman Fm Haman Fm Haman Fm	Jinju, South Korea Jinju, South Korea Namhae, South Korea	tracks of web-footed birds *Uhangrichnus chuni* *Ignotornis yangi*	Lim et al., 2000 Baek and Yang, 1997 This study

Haman Formation outcrops on Changseon Island in the Kyongsang Basin (Figs. 1, 2).

Elsewhere in the Kyongsang Basin there have been additional reports of these and other bird tracks both from the Haman and overlying Jindong formations (Kim, 1969; Lockley et al., 1992; Baek and Yang, 1997; Lim et al., 2000, 2002). These include *Koreanornis* and *Jindongornipes*, both of which lack web traces. In addition to these reports, a new ichnospecies, *Goseongornipes markjonesi*, has been reported from the Jindong Formation (Lockley et al., in this issue; see Table 2 herein). As this species (*G. markjonesi*) also lacks any clear trace of webbing, none of the Jindong Formation bird tracks represent web-footed track makers. By contrast both the aforementioned bird tracks from the Uhangri Formation (*U. chuni* and *H. choughi*) represent web-footed species.

The material described herein from the Haman Formation at the Changseon site, while similar to *G. markjonesi*, evidently has better-developed semi-palmate webbing and a much longer hallux and must therefore be assigned to a different ichnotaxon. Although morphologically quite similar to *Hwangsanipes choughi* from the younger Uhangri Formation (Yang et al., 1995), the Changseon material is considerably smaller, with a less well-developed web, and has many features much closer to *Ignotornis mcconnelli* (Mehl, 1931), except that it is slightly larger (about 10%) with a somewhat larger web. This similarity was noted by Lim et al. (2002). It is important to compare all these tracks in order to see the size and shape differences (see Lockley et al., 2006, and Fig. 3 herein).

Five named and five unnamed ichnospecies of webbed bird tracks have been also reported from Paleogene and Neogene strata. They are unnamed webbed bird tracks (Johnson, 1986), *Presbyorniformipes feduccii* (Moussa, 1968; Yang et al., 1995), *Charadriipeda* (Panin and Avram, 1962, emended Sarjeant and Langston, 1994), heron-like or stork-like wading bird tracks (de Raaf et al., 1965), *Anatipeda anas* (Panin, 1965), and *Avipeda* ichnosp. (Scrivner and Bottjer, 1986), *Roepichnus grahami* (Doyle et al., 2000), goose footprints (Miller and Ashley, 1934), and goose or goose-like tracks (Breed, 1973).

3. Pterosaur tracks

Since the first discovery of pterosaur tracks named *Pteraichnus* from the Upper Jurassic Morrison Formation (Stokes,

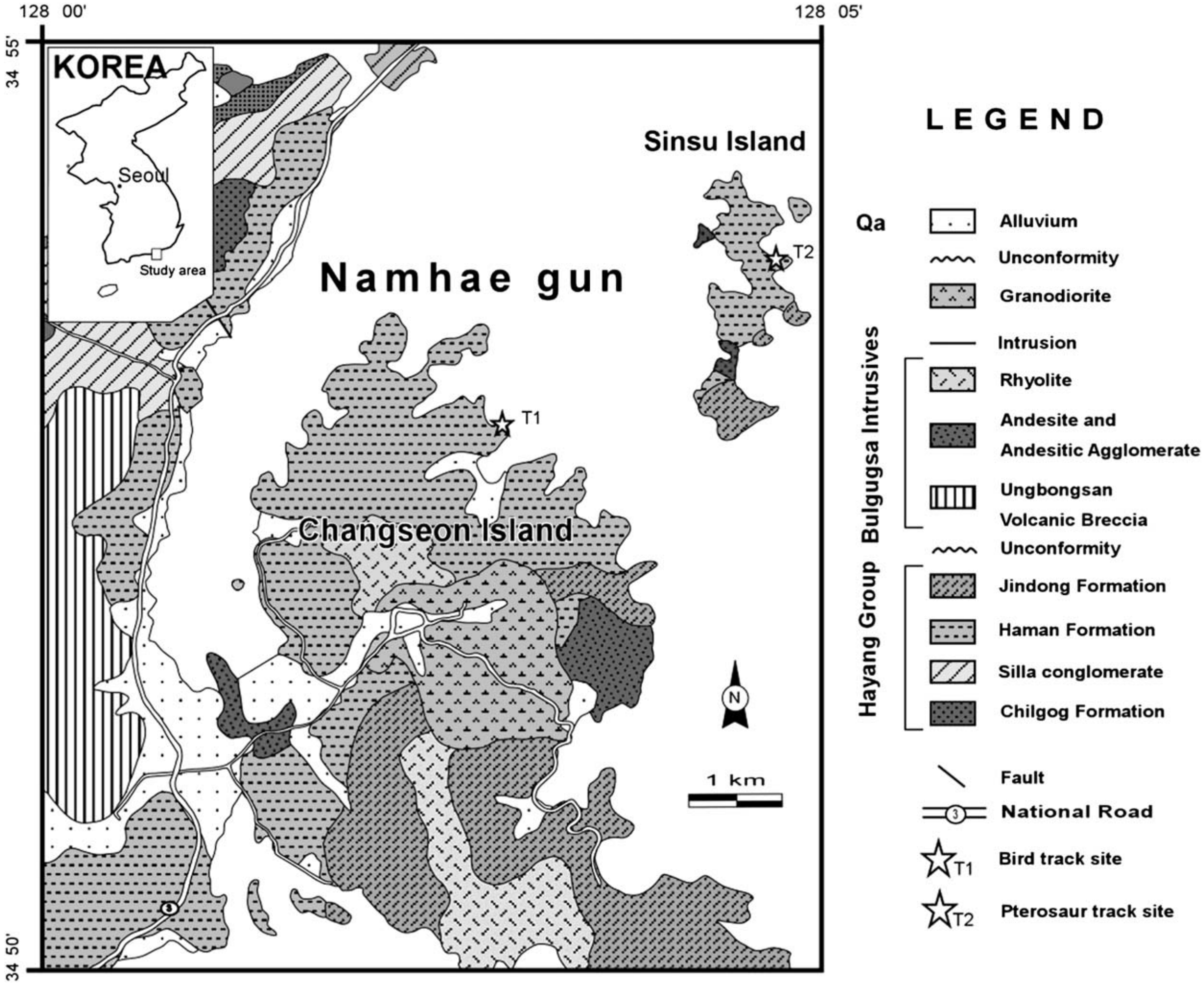

Fig. 1. Geologic map of the study area and bird and pterosaur track sites.

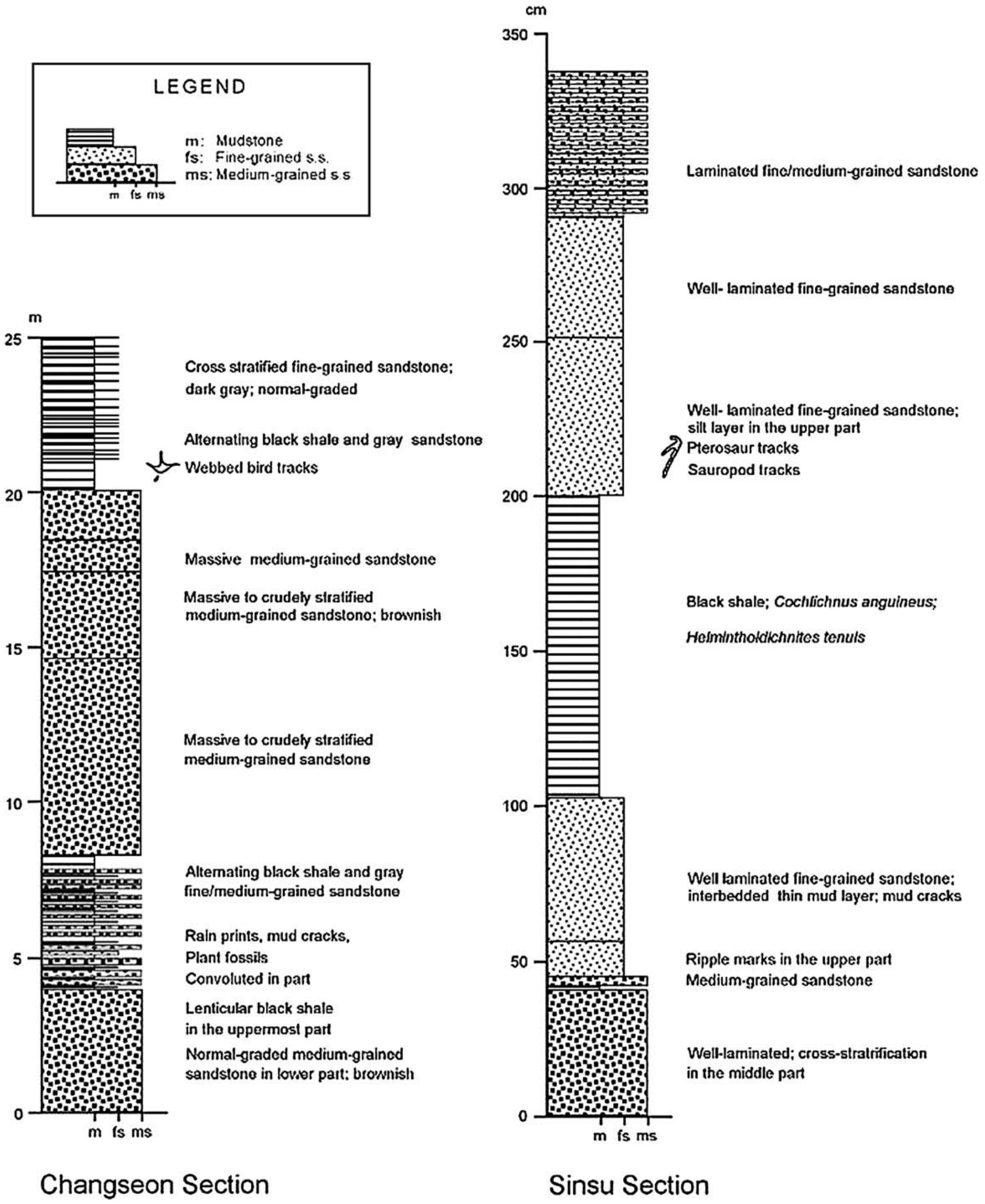

Fig. 2. Measured section of a portion of the Haman Formation on Changseon and Sinsu Islands showing webbed bird and pterosaur track beds.

1957), these tracks have been controversial. Padian and Olsen (1984) argued that *Pteraichnus* is attributable to a crocodilian (Unwin, 1989; Padian and Rayner, 1993; Padian, 1998, 2003). These arguments have been widely challenged by the discovery of a large amount of *Pteraichnus* material mainly from Europe and North America (Lockley et al., 1995, 1997, 2001a,b; Mazin et al., 1995, 1997, 2003; Wright et al., 1997; Calvo and Moratalla, 1998; Meijide Calvo and Fuentes Vidarte, 1999; Pascual Arribas and Sanz Perez, 2000; Garcia-Ramos et al., 2000, 2001; Calvo and Lockley, 2001; Hwang et al., 2002; Rodriguez de la Rosa, 2003; Billon-Bruyat and Mazin, 2003; Lockley and Wright, 2003; Sayao, 2003; Mickelson et al., 2004a,b).

The pterosaur tracks from Sinsu Island are therefore an additional contribution to a growing database on pterosaurian ichnites. They are of particular interest because of what appear to be a mix of manus-only and manus-dominated trackways with associated swim tracks. The functional morphology and lifestyle of pterosaurs has also been the subject of much discussion (Lockley et al., 1995; Bennett, 1997; Lockley and Mickelson, 1997; Unwin, 1997, 1999; Lockley and Wright, 2003; Mazin et al., 2003). Although trackways

Table 2
Bird and pterosaur tracks from Cretaceous formations in South Korea: ** refers to type material and first report, * refers to first report, pterosaur track ichnotaxa indicated in bold italics; see text for species names

Formation	Estimated age	Track type	Track size (length)
Uhangri	Cenomanian or younger	***Haenamichnus*** **	ca. 300 mm
		*Hwangsanipes***	ca. 80 mm
		*Uhangrichnus***	ca. 37 mm
Jindong	Albian	*Jindongornipes***	ca. 71 mm
		*Goseongornipes***	ca. 44 mm
		Koreanornis	ca. 22 mm
Haman	Aptian-Albian	*Jindongornipes*	ca. 71 mm
		*Ignotornis***	ca. 51 mm
		*Koreanornis***	ca. 22 mm
		Uhangrichnus	ca. 37 mm
		Pteraichnus *	ca. 100–120 mm

assigned to pterosaurs remain controversial in some quarters (Padian, 2003) it has become widely accepted that *Pteraichnus* morphologies are pterosaurian (Chatterjee and Templin, 2004).

4. Geological setting

The Cretaceous strata exposed in the southeastern part of Korea are referred to the Gyeongsang Supergroup (Chang, 1975). A nonmarine origin for the rocks of this supergroup has long been recognized from the occurrence of fossil plants (Yabe, 1905; Tateiwa, 1929), freshwater mollusks (Yang, 1975, 1978, 1979a,b), dinosaur footprints (Yang, 1982, 1986; Lim et al., 1989, 1994; Lockley et al., 1992), pollen and spores (Choi, 1985), and charophytes (Seo, 1985; Choi, 1987).

According to Chang (1975, 1982), the supergroup has been divided, in ascending stratigraphic order, into the Sindong (Berriasian–Barremian), Hayang (Aptian–middle Albian), and Yucheon Groups (upper Albian–Cenomanian) and the Bulgugsa Intrusives (Chang, 1982; Fig. 1). The Sindong Group consists mainly of alluvial fan, floodplain, and lacustrine deposits, the Hayang Group consists of floodplain and lacustrine sediments intercalated with minor volcanic ash beds (Um et al., 1987), and the overlying Yucheon Group consists of volcanic rocks.

The Hayang Group consists of, in ascending order, the Chilgog Formation, Silla Conglomerate, and Haman and Jindong formations. The Haman Formation rests conformably on the Silla Conglomerate and its thickness is estimated to exceed 1000 m. It is mainly composed of reddish shale and sandy shale and white to greenish and gray sandstones with minor intercalating tuffaceous and pebbly sandstone. They are metamorphosed into compact hornfels in the vicinity of the stock shaped granodiorite. The hornfels is tinged with a reddish color in the lower levels and with greenish gray color in the higher levels of the formation (Chi et al., 1983).

In the study area, the Haman Formation generally dips less than 20° SE and was intruded by the Bulgugsa Intrusives. Many dinosaur footprints and four kinds of bird tracks including *Koreanaornis hamanensis* (Kim, 1969; Lockley et al., 1992; Baek and Yang, 1997), *Jindongornipes kimi* (Baek and Yang, 1997), *Uhangrichnus chuni* (Baek and Yang, 1997), and unnamed webbed bird tracks (Lim et al., 2000) have been reported from the Haman Formation.

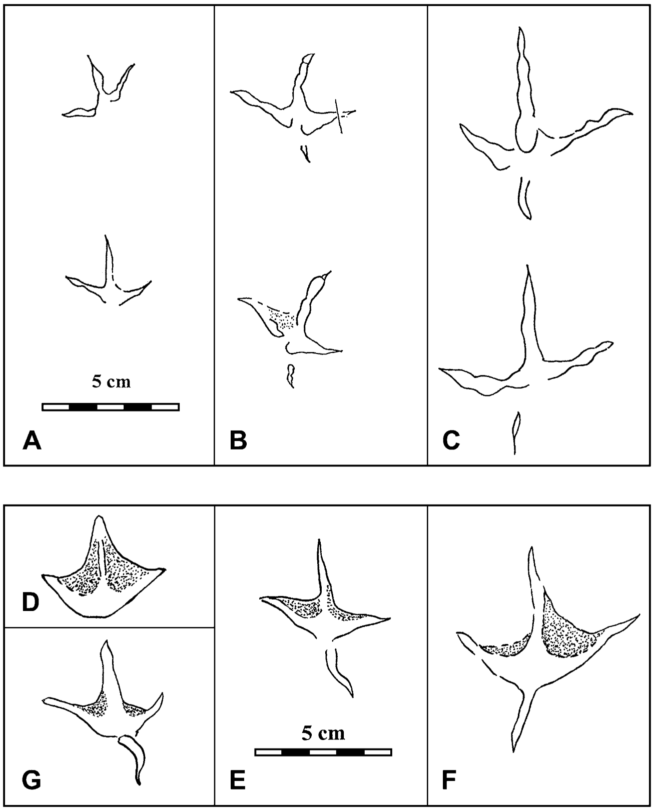

Fig. 3. Comparison of all named bird ichnospecies from the Cretaceous of Korea, all drawn to the same scale and arranged in increasing order of size from left to right (also broadly corresponding to increased hallux size). A, *Koreanornis hamanensis*, two tracks in sequence without hallux. B, two apparently consecutive tracks of *Goseongornipes markjonesi*. C, two separate tracks of *Jindongornipes kimi*. D, *Uhangriichnus chuni* type material. E, new *Ignotornis yangi* material from Changseon (compare with Lim et al., 2002, fig. 3). F, *Hwangsanipes choughi* type material. G, *Ignotornis mcconelli* type material. (A–C modified after Lockley et al., 2006; D and F modified after Yang et al., 1995).

The webbed bird tracks described herein as *Ignotornis yangi* (Fig. 4) occur in the middle part of the Haman Formation (Figs. 1, 2), which consists of centimeter-scale rhythmic alternations of fine-grained siliciclastic sediment. In the measured section at the northeast of the Changseon Island the fine- to medium-grained sandstone frequently exhibits parallel lamination, cross-stratified lamination, convoluted bedding, flame structures, and ripple marks (Fig. 2). Fossil plants, raindrop imprints, and mud cracks are also observed on the bedding planes of the interbedded shale to mudstone.

Pterosaur tracks are found on the bedding surface of well-laminated fine-grained sandstone of the upper middle part of the Haman Formation in the Sinsu section (Fig. 2). The Sinsu section is mainly composed of well-laminated fine-grained sandstone, black shale, and fine- to medium-grained sandstone. Sauropod tracks, mud cracks, and ripple marks are

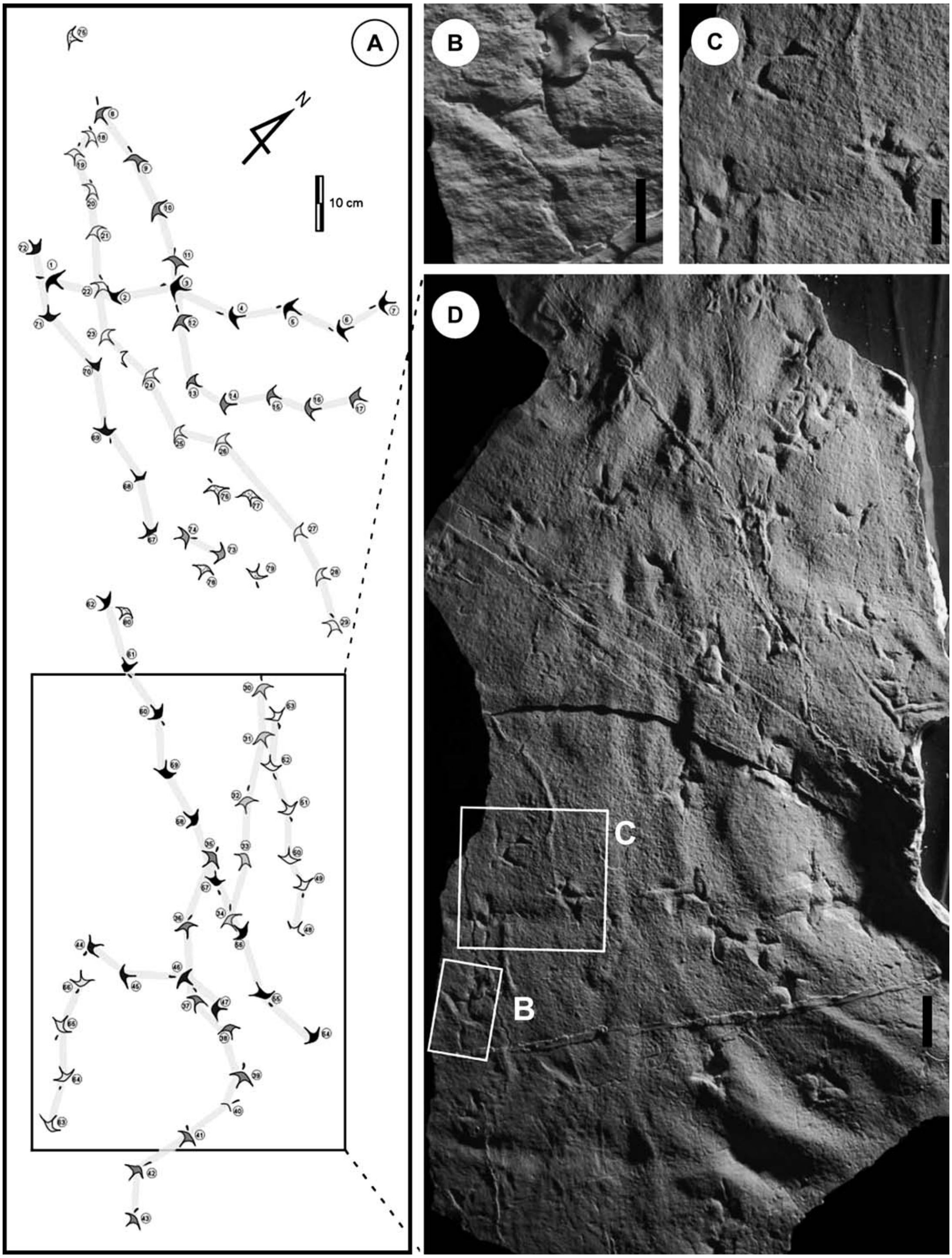

Fig. 4. The webbed bird tracks from the Haman Formation in the Changseon Island. A, map of *Ignotornis yangi* trackways; 11 trackways recognized shown in white, gray, and black are preserved as specimen number KNUE 040417. B–D, detailed photographs of *Ignotornis yangi* shown in A. Track number 66 shown in frame B is the holotype (compare with Lim et al., 2002, fig. 3). Scale bar in B and C represents 20 mm and in D, 50 mm.

observed on the fine-grained sandstone, and invertebrate trace fossils including *Cochlichnus anguineus* and *Helminthoidichnites tenuis* occur on the bedding surfaces of the black shale. Together with these footprints diverse invertebrate trace fossils, ripple marks, mud cracks, and raindrop imprints (Baek and Yang, 1997; Seo, 1997) provide evidence for a lakeshore environment (Lim et al., 2002).

5. Ichnotaxonomy

5.1. Systematic observations

The large increase in reports of Mesozoic and Cenozoic bird tracks has highlighted the need for revision of the ichnotaxonomy of fossil bird tracks. Fortunately the ichnotaxonomy at the ichnogenus and ichnospecies level is fairly straightforward, at least for Cretaceous tracks. However, organization at the supra-generic level has largely been ignored. For example Lockley et al. (1992) included most known Cretaceous bird tracks in the ichnofamily Ignotornidae. This preliminary classification is in need of amendment as it is now clear that we can draw well-defined distinctions between avian ichnotaxa on the basis of diagnostic features such as the presence or absence and the size and orientation of the hallux and the degree of web development (Fig. 3). The following observations suggest the direction such revisions should take.

We suggest restricting the definition of Ignotornidae to tracks that closely resemble *Ignotornis*, i.e., the type material (*I. mcconnelli*, Fig. 5) and forms like *Hwangsanipes* and the Changseon specimens (*I. yangi*) that have well-developed hallux impressions and asymmetric, semi-palmate webbing (Fig. 3E–G). Forms such as *Uhangrichnus*, which have fully developed web impressions (and no hallux) could easily be accommodated in their own ichnofamily, perhaps based on that ichnogenus. Likewise, non-webbed forms such as *Koreanornis* (Fig. 3A) and *Aquatilavipes* that lack well-developed web and hallux traces probably also belong in a separate ichnofamily. This was suggested by Sarjeant and Langston (1994), who placed *Aquatilavipes* in the ‘‘morphofamily Avipedidae’’ without reference to its previous assignment to the Ignotornidae (Lockley et al., 1992). However, since we amend this 1992 classification herein, the Sarjeant and Langston proposal is a step in the right direction of recognizing that *Aquatilavipes* belongs in a separate ichnofamily from *Ignotornis* (Lockley et al., 2006). Similarly, there are forms with intermediate length hallux impressions and no web traces such as *Jindongornipes* and *Goseongornipes* (Fig. 3B–C), now removed from Ignotornidae. In short, the diversity of Cretaceous bird tracks in Korea alone is sufficient to suggest at least three, perhaps four, broad morphological categories that merit serious consideration at the ichnofamilial level. These must be compared with those proposed by Sarjeant and Langston (1994) on the basis of Tertiary (Miocene and Late Eocene tracks) .

Thus, the ichnofamilial classification of bird tracks is in need of further attention. Sarjeant and Langston (1994) attempted to bring order to the classification by elevating the ichnogenus categories of Panin and Avram (1962), based on modern bird family names (i.e., Gruipeda, Charadriipeda, Avipeda and Anatapeda) to the level of track-based morphofamilies. Thus, they proposed four: Gruipedidae, Charadriipedidae, Avipedidae, and Anatapedidae, based on Tertiary tracks (upper Eocene and Miocene). However, Sarjeant and Langston (1994) did not make reference to either the ichnofamily Ignotornidae or Trisaurpodiscidae named by Lockley et al. (1992) in the context of a review of Mesozoic tracks. We also note that the ichnological literature contains no clear statement about whether the categories ‘‘morphofamily’’ and ‘‘ichnofamily’’ imply any meaningful distinction.

This history raises two questions for future investigation: (1) is there any overlap between the original concept of Ignotornidae (Lockley et al., 1992) and the four morphofamilies proposed by Sarjeant and Langston (1994), and (2) are Mesozoic bird track morphologies sufficiently similar to Tertiary morphotypes to conform to a classification that was essentially derived from comparison of Miocene tracks with modern bird footprints? We can tentatively answer the first question by noting that further formal classification of Mesozoic bird tracks is necessary in order to better describe morphological variation at the familial level. Our revised and restricted definition of ichnofamily Ignotornidae should allow ichnologists to recognize some of the morphofamilies proposed by Sarjeant and Langston (1994) as useful, rather than rejecting them as synonyms of Ignotornidae and/or Trisaurpodiscidae.

5.2. Systematic descriptions

A total of 80 webbed bird tracks and 12 manus and about four recognizable pes tracks of pterosaurs from the Haman Formation of the Changseon and Sinsu Islands were mapped and measured (Table 3, Figs. 4, 6). Replicas of the specimens for this study are housed in the Department of Earth Science, Korea National University of Education, Chungbuk.

Ichnofamily Ignotornidae Lockley et al., 1992
Ichnogenotype *Ignotornis* Mehl, 1931 emend. Lockley et al., 1992 (Fig. 5 herein)

Emended diagnosis. Tetradactyl bird tracks showing prominent postero-medially-directed hallux impressions comprising about one third of total track length. Hypex between digits III and IV more anteriorly situated than hypex between digits II and III, with tendency for development of asymmetric, semi-palmate web that is more strongly developed between digits III and IV. Digit divarication between II and IV, wide usually averaging at least 110–120°. Digit pad impressions variable, but sometimes showing a 2-3-4 phalangeal formula corresponding to digits II, III, and IV. Step typically short with a strong tendency towards inward rotation.

Referred material. *Ignotornis mcconnelli* Mehl, 1931; *Hwangsanipes choughi* Yang et al., 1995; *Ignotornis yangi* ichnosp. nov. (this paper); unnamed specimen Lim et al. (2000, fig. 3) and Lim et al. (2002, fig. 3).

Ignotornis yangi ichnosp. nov.
Fig. 4.

Derivation of name. After Seong-Young Yang, Kyungpook National University, Taegu, South Korea, for his contributions to vertebrate ichnology in Korea.

Material. Silicon rubber mold and plaster replica of 80 tracks. Specimen number: Korea National University of Education (KNUE) 040417. Track number 66 (Fig. 4B) is designated as the holotype.

Description. Tetradactyl and anisodactyl bird footprints with postero-medially directed hallux impression and fine

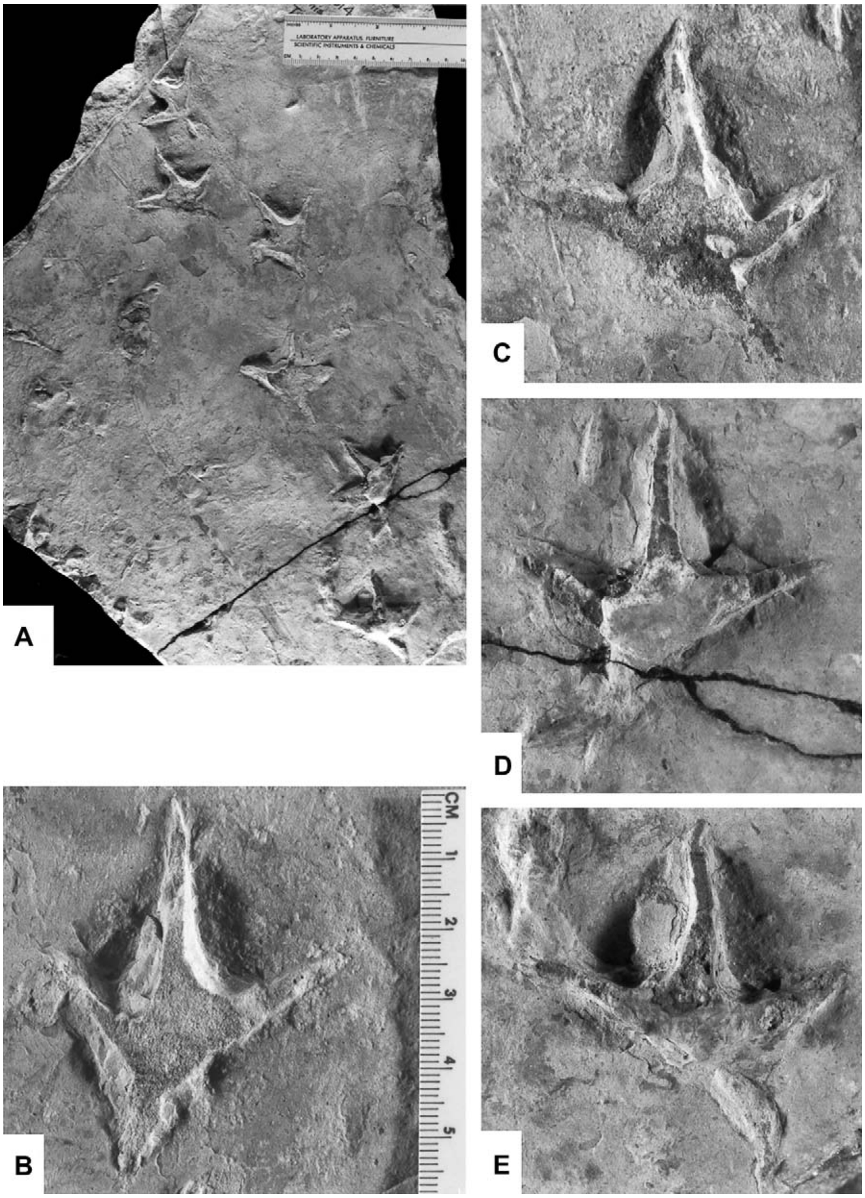

Fig. 5. A, the type specimen of *Ignotornis mcconnelli* from the upper Albian–lower Cenomanian of Colorado. B–E, respectively, detail of the fourth, fifth, second, and first tracks in the sequence, all at the same scale as B.

acuminate claw traces on all four digits, displaying semi-palmate webbing between digits II and IV. Web traces asymmetric, i.e., more developed in hypex between digits III and IV than between II and III. The average width of tracks is approximately 45 mm (range 38–51 mm), and the average length of tracks, excluding hallux, is 33 mm (range 28–37 mm) and with hallux is 51 mm (range 43–63 mm). Thus, the hallux comprises an average of 35% of track length. In the 11 trackways; the length–width ratio (excluding hallux) is 0.73 (range 0.64–0.78). The average angle of divarication between digits II and IV is 123° (range 115–130°). The angle between digits II and III averages 64° (range 50–79°) and the angle between digits III and IV averages 59° (range 45–70°).

Digit III longer than II and IV and straight or slightly curved. Length of digit IV is slightly longer than that of digit II. Digits II and IV are curved slightly inward (anteriorly) or straight. On the basis of the 11 identified trackways (T_1 to T_{11}), the pace length ranges from 75 to 115 mm, stride from 158 to 229 mm, pace width from 21 to 36 mm, and pace angulation from 139 to 161° in each trackway. The trackway pattern is of single tracks at regular intervals, in zigzag fashion or straight line, depending on the pace length or pace angulation, which can vary.

Discussion. *Ignotornis yangi* is quite similar to the type species *I. mcconnelli* Mehl, 1931, and to *Hwangsanipes choughi* (Yang et al., 1995). Indeed this similarity was noted by Lim et al. (2000). However both these latter species are larger, though the type *Ignotornis* (length 5.8 cm, width 5.1 cm) is significantly smaller than type *H. choughi* (length ca. 8 cm,

Table 3

Measurements (in mm) of bird tracks from Haman formation in Changseon Island

T	N	Wp	Lp	L/W	L'p	Ⅰ	Ⅱ	Ⅳ	La	Ra	$D_{\text{Ⅱ}\sim\text{Ⅳ}}$	$D_{\text{Ⅰ}\sim\text{Ⅱ}}$	Pace	Stride	Pa	Pw
$\mathbf{T}_{\text{Ⅰ}}$	1L	51	34	0.67	56	16	28	33	59	63	122	83	127	238	149	29
	2R	?	34	?	?	26	?	?	60	?	?	?	117	230	142	32
	3L	48	35	0.73	55	10	22	32	59	60	119	97	122	219	142	37
	4R	46	34	0.74	56	18	24	30	66	56	122	90	101	200	145	31
	5L	47	33	0.70	55	12	23	30	60	60	120	93	102	172	118	50
	6R	46	32	0.70	52	11	22	30	61	59	120	82	98			
	7L	48	33	0.69	58	13	23	31	60	58	118	92				
$\mathbf{T}_{\text{Ⅱ}}$	8R	48	35	0.73	59	19	26	29	72	54	126	76	112	217	163	17
	9L	49	37	0.76	58	17	24	32	77	52	129	80	107	214	180	4
	10R	45	35	0.78			23	30	67	65	132		104	213	161	19
	11L	51	36	0.71	54	17	23	31	75	53	128	80	115	232	180	6
	12R	47	36	0.77	60	15	24	30	62	60	122	112	119	180	137	34
	13L	38	28	0.74			22	22	60	70	130		75	150	125	36
	14R	38	29	0.76			23	20	67	60	127		93	155	135	25
	15L	40	29	0.73			24	25	68	65	133		75	152	130	25
	16R	40	31	0.78			24	23	60	65	125		92			
	17L	40	28	0.70			22	25	60	65	125					
$\mathbf{T}_{\text{Ⅲ}}$	18L	43	31	0.72	38	10	23	28	66	56	122	50	47	94	102	36
	19R	45	34	0.76	44	4	25	28	57	63	120	92	77	157	150	22
	20L	47	34	0.72	47	8	25	32	73	55	128	65	85	193	172	8
	21R	45	34	0.76			26	29	53	62	115		109	200	170	7
	22L	48	35	0.73	45	13	27	27	57	68	125	73	94	185	132	43
	23R	45	34	0.76			26	30	60	57	117		110	230	155	24
	24L	45	35	0.78			23	32	67	55	122		125	183	120	51
	25R	42	32	0.76			27	30	60	58	118		85			
	26L	43	31	0.72			25	26	65	55	120					
	27L	41	30	0.73			25	22	61	70	131		91	187	173	3
	28R	42	31	0.74			22	27	55	60	115		98			
	29L	43	31	0.72	48	8	24	30	55	50	105	77				
$\mathbf{T}_{\text{Ⅳ}}$	30R	46	35	0.76	45	9	22	30	60	59	119	90	106	210	133	40
	31L	47	32	0.68			25	32	60	58	118		124	220	151	30
	32R	47	35	0.75	56	15	26	28	64	56	120	85	106	220	168	13
	33L	45	35	0.78			23	30	63	52	115		115			
	34R	45	?	?	63	16	24	28	76	54	130	85				
$\mathbf{T}_{\text{Ⅴ}}$	35L	47	35	0.74	48	13	23	33	62	55	117	80	142	270	150	37
	36R	47	30	0.64	48	13	20	30	76	61	137	79	138	205	140	35
	37L	46	35	0.76	55	12	21	29	79	56	135	87	79	165	145	27
	38R	44	32	0.73			22	30	59	60	119		98	165	120	48
	39L	47	33	0.70	63	16	23	34	59	62	121	120	95	156	167	9
	40R	?	?	?	?	13	?	?	?	?	?	?	64	175	159	15
	41L	41	30	0.73	48	13	22	23	60	68	128	52	113	193	132	42
	42R	45	35	0.78	62	18	22	31	50	64	114	100	97			
	43L	45	30	0.67	48	9	23	25	75	55	130	85				
$\mathbf{T}_{\text{Ⅵ}}$	44L	47	35	0.75	45	8	25	29	58	62	120	78	74	182	148	25
	45R	46	35	0.76			23	30	70	56	126		115	184	138	33
	46L	45	32	0.71	48	15	25	25	73	66	139	78	81			
	47R	47	36	0.77			30	27	70	55	125					
$\mathbf{T}_{\text{Ⅶ}}$	48L	41	30	0.73			27	28	55	63	118		90	136	137	27
	49R	42	31	0.74	47	5	23	27	57	68	125	95	55	142	147	19
	50L	41	32	0.78			25	22	66	58	124		93	176	155	19
	51R	42	30	0.71	48	6	22	30	55	68	123	113	93	176	148	25
	52L	42	32	0.76	50	12	23	30	70	59	129	90	94			
	53R	42	30	0.71	47	10	23	25	57	63	120	79				
$\mathbf{T}_{\text{Ⅷ}}$	54R	48	35	0.73			26	30	68	63	131		120	243	150	32
	55L	47	34	0.72	53	12	26	29	77	45	122	90	130	234	180	13
	56R	43	30	0.70			20	27	70	54	124		99	225	175	12
	57L	47	33	0.70	46	6	22	30	60	47	107	110	126	223	164	14
	58R	45	34	0.76			25	23	68	56	124		100	203	150	23
	59L	45	34	0.76			23	30	59	56	115		111	215	150	28
	60R	41	30	0.73	52	8	26	30	64	56	120	110	104	225	157	23
	61L	45	35	0.78	46	12	?	?	67	62	129	92	127			
	62R	45	33	0.73			23	30	68	59	127					
$\mathbf{T}_{\text{Ⅸ}}$	63L	47	35	0.75			22	30	65	55	120		96	195	156	20
	64R	44	29	0.66	46	7	24	28	64	62	126	60	103	190	151	24
	65L	48	33	0.69	62	9	23	30	69	52	121	91	94			
	66R	45	32	0.71	48	12	23	27	63	63	126	88				
$\mathbf{T}_{\text{Ⅹ}}$	67L	44	31	0.71			25	25	65	60	125		100	204	155	23
	68R	?	30	?			?	24	?	65	?		110	225	156	25
	69L	48	33	0.69	51	8	23	33	68	55	123	90	122	240	148	33
	70R	42	31	0.74			25	23	61	59	120		130	245	164	19
	71L	43	32	0.74			26	25	68	58	126		119			
	72R	43	31	0.72			27	25	69	54	123					
$\mathbf{T}_{\text{Ⅺ}}$	73L	43	30	0.70			26	26	60	60	120		75			
	74R	40	31	0.78	43	8	23	29	68	58	126	92				
	75	48	35	0.73			25	30	56	64	120					
	76	47	33	0.70	47	8	23	30	73	51	124	90				
	77	47	35	0.75			24	34	72	50	122					
	78	48	33	0.69			22	32	74	51	125					
	79	40	30	0.75	48	12	23	27	52	68	120	85				
	80	38	27	0.71			18	25	70	60	130					
	M	45	33	0.73	51	12	24	28	64	59	123	86	102	197	150	25

N: Number of measurement, Lp: Length of pes, Wp: Width of pes, L/W: Ratio of Lp/Wp, L'p: Length of pes including hallux, Ⅰ, Ⅱ, Ⅳ: Length of digits Ⅰ, Ⅱ, Ⅳ, La: digital angle between left side digit and Ⅲ, Ra: digital angel between right side digit and Ⅲ, $D_{\text{Ⅱ}\sim\text{Ⅳ}}$: Divarication between digits Ⅱ and Ⅳ, $\mathbf{D}_{\text{Ⅰ}\sim\text{Ⅱ}}$: Divarication between digits Ⅰ and Ⅱ, P: Pace, S: Stride, Pa: Pace angle, Pw: Pace width, T: Trackways Ⅰ, Ⅱ, Ⅲ, Ⅳ, Ⅴand Ⅵ, L: left pes, R: right pes.

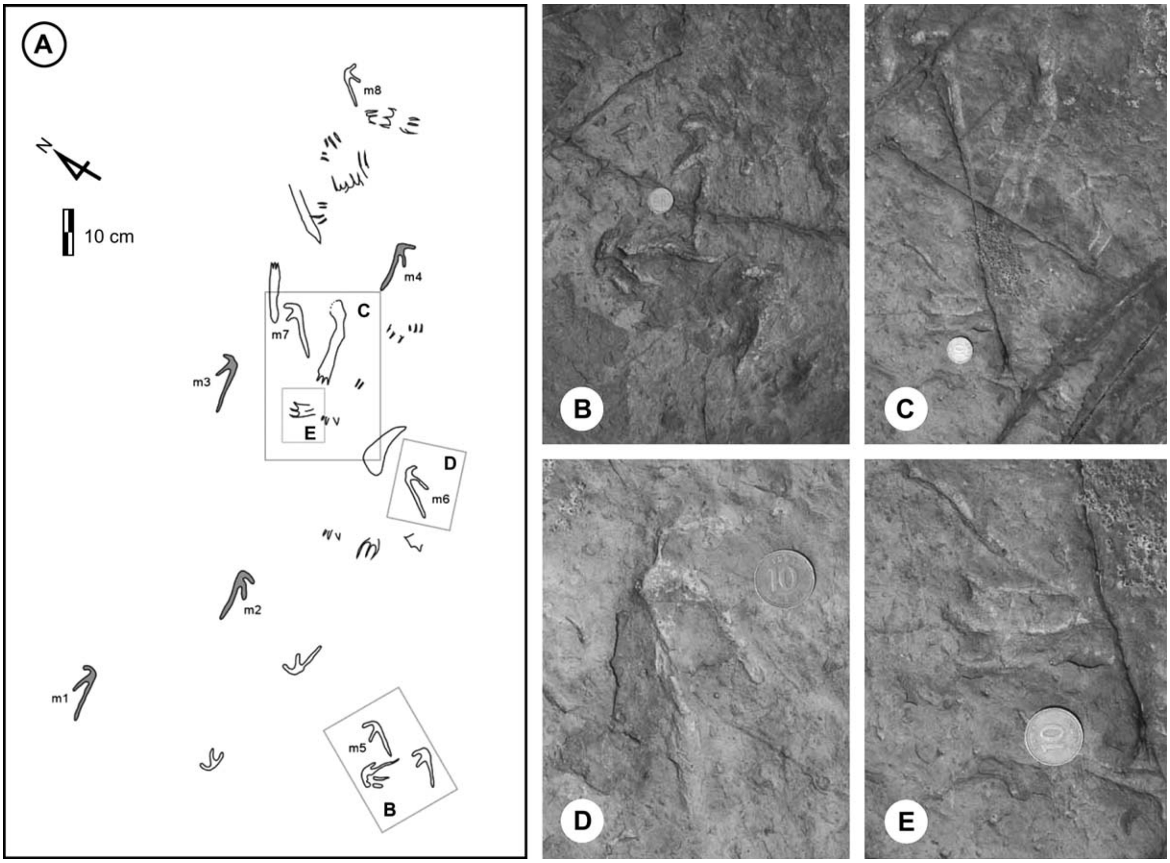

Fig. 6. The pterosaur tracks from the Haman Formation on Sinsu Island. A, map of *Pteraichnus*; two trackways recognized are shown in black (m 1 to m 4) and gray (m 5 to m 8). B–E, detailed photographs of *Pteraichnus* shown in A. Coin in B–E is 23 mm in diameter. Note that additional manus tracks and incomplete pes ''swim'' tracks indicate one or more trackways of other individuals.

mean width 6.26 cm; see Fig. 3). *H. choughi* also has a well-developed web between digits III and IV. In the case of *I. mcconnelli* in comparison with *I. yangi*, the webbing is only slightly developed in the proximal (posterior) part of the hypex between digits II and III and slightly more so in the hypex between digits III and IV (Fig. 5). This web asymmetry (II-III < III-IV) is typical of many semi-palmate shore birds. *U. chuni* is quite different from both these ichnospecies in all major characteristics including a greater asymmetry in the web configuration (Fig. 3).

Yang et al. (1995) erected and described *H. choughi* from the Cenomanian Uhangri Formation of the Haenam area of Korea on the basis of a trackway containing four footprints (only two of which are complete). Hence, the sample was rather small. Nevertheless the morphology of at least two of the tracks including web and hallux configurations is quiet clear (Fig. 3). Although our much larger sample consists of tracks that are significantly smaller (by about 25%), we nevertheless consider that the Changseon tracks are morphologically quite close to *H. choughi* and for this reason consider them similar at the ichnofamily level. However, given the aforementioned size and web shape differences, we consider that the tracks are significantly closer to *Ignotornis*, which is also closer in size (only 10% larger), also with a less developed web (Fig. 3). Although *H. choughi* is similar to *I. mcconnelli* Mehl, 1931, in general outline, on average it displays wider interdigital angles between digits II and IV. However, examination of tracks of modern shore birds with webbed feet shows that the angle varies among different taxa (Lim et al., 2000). Thus, though we provide divarication data, we consider its ichnotaxonomic utility only important to the degree that significant and consistent differences are found in comparisons between adequately large samples of different ichnotaxa with similar preservation.

Although the Changseon tracks are quite close in size to *U. chuni*, they are clearly different in having a hallux and a greater average divarication between the digits II and IV. Another obvious difference is that the web is highly developed and much more symmetric in *U. chuni* than in any of the other tracks recorded to date (Yang et al., 1995; Fig. 3 herein). The footprint length–width ratio, excluding the hallux, of *U. chuni* is greater than that of *H. choughi* as noted by Azuma et al. (2002).

Unnamed webbed bird tracks reported from the Haman Formation of Jinju area also show remarkable similarity to *I. mcconnelli* (Lim et al., 2000). Although it is difficult to compare our specimens of *I. yangi* with these unnamed webbed bird tracks because of poor preservation of the former, they appear to be similar in divarication between the digits II and IV. Thus we infer that, like the Changseon tracks, they may be assigned to *Ignotornis*.

We can compare the Changseon *Ignotornis* with *Goseongornipes markjonesi* (Lockley et al., 2006). Although both are similar in size (Fig. 3) it is clear that *G. markjonesi* has a much shorter hallux, comprising less than one quarter of footprint length, and little or no evidence of webbing. Thus, the newly discovered Changseon material cannot be assigned to this ichnogenus.

In the 11 Changseon trackways observed, most show a distinct pattern of single tracks placed at regular intervals. When making shallow tracks on an ideal substrate, the bird could move easily and therefore tended toward its natural trackway, i.e., normal walking, which is what we infer in this case. There is no evidence that the birds were hampered in their walking by a saturated or slippery substrate, or that the tracks are distorted by poor preservation. The asymmetry of footprints, i.e., slight differences in rotation of the tracks and divarication between the inner (II-III) and outer (III-IV) hypexes, is slightly different in the 11 trackways. However, tracks left by the same species in wet sand and in drier conditions while moving at different speeds may look different (Elbroch, 2001).

Track makers are interpreted as plover-like birds (Charadriiformes) because of their small size and high density of preserved tracks (Lockley et al., 1992). However, we should be somewhat careful in making comparisons between tracks of modern Charadriiformes, which includes gulls as well as plovers and sandpipers, and Cretaceous footprints. Certainly small tracks like *Koreanornis* (Kim, 1969) are similar to small plovers and sandpipers, which have a small hallux or no hallux at all. By contrast, both *Ignotornis* and *Hwangsanipes* have a well-developed hallux (comprising one third or more of track length). Similarly the webbing in both these ichnogenera is more pronounced than in most sandpipers and plovers, though it is convergent with patterns found in semi-palmated plovers. Lockley et al. (2004) recently reported the semi-palmated bird track *Sarjeantopodus semipalmatus* from the Maastrichtian of North America and noted that it is significantly larger than *Hwangsanipes*.

Ichnogenus *Pteraichnus* (Stokes, 1957)

Pteraichnus sp. (Lockley et al., 1995)
Fig. 6.

Material. Silicon rubber mold and plaster replica of tracks (specimen is KNUE 040176).

Description. General description as for ichnofamily Pteraichnidae (Lockley et al., 2001b). Manus elongate, tridactyl, strongly asymmetric between about 10 and 12 cm in length and 3–4 cm in width. Inferred digit impression I shortest, subtending an angle of about 86° relative to the trackway axis (anterior direction), with digit impression II intermediate in length, subtending an angle of about 139°, and digit impression III longest, slightly curved, and subtending an angle of 165–180°. Rare proximal traces of manus digit impression IV directed postero-medially opposite I (Lockley et al., 1995).

Pes: elongated impression with short digits and clusters of two, three or more short digit impressions or parallel and subparallel scrape marks or striations. The length and width of elongated pes impressions are up to 13.8 cm and 4.1 cm, respectively (Fig. 6D), but length may be somewhat exaggerated by sliding. Distal part of pes prints with digit impressions is occasionally observed. The widths of the clusters of short, parallel to subparallel, digit impressions are similar to those of elongated pes impressions. The distal extremities are often marked by traces of fine triangular claws that terminate sharply.

Two trackways consist of four consecutive manus sets: (m1–m4, Fig. 6A). In the larger trackway (black shading in Fig. 6A), manus to manus pace averages 477 mm (range 407–562 mm). Manus to manus stride averages 850 mm (range 770–911 mm). Manus to manus pace angulation averages 129° (range 123–138°) indicating a regular alternation of left and right manus footprints. Only one associated pes with outward rotation appears to be recognizable anterior to manus 3 (Fig. 6A). Exterior trackway width is about 257 mm and interior trackway width is about 168 mm in the two trackways. In the second trackway (gray shading, Fig. 6A) pes impressions are faint or absent. Other, smaller trackway segments are less complete with less regular alternation of steps, but, as in the clearer trackways, the pes track impressions are obscure or missing (Fig. 6A).

Discussion. The characteristic shape of manus impressions allow these pterosaur tracks to be assigned to *Pteraichnus*. Elongate pes impressions and clusters of short digit impressions that resemble swim tracks of pterosaurs (Lockley and Wright, 2003), closely associated on the same bedding surface, are also typical of this ichnogenus. Although *Pteraichnus* from Sinsu Island is about the same size as *P. saltwashensis*, the track is perhaps more similar to *P. stokesi* in that the pes tracks are rotated outward to a greater degree, and the manus digit impressions are wider relative to their length (Lockley et al., 1995). However, these differences may be due to preservation. The manus-dominated assemblage is also typical of pterosaur track assemblages (Lockley et al., 1995; Mickelson et al., 2004a). This has been explained by noting that in *Pteraichnus*, the manus prints tend to be more deeply impressed and better defined than pes prints because they reflect the anterior position of the center of mass in pterosaurs in quadrupedal stance (Lockley et al., 2001b).

Pterosaur tracks from the Aptian to Albian Haman Formation in the Sinsu Island represent the second oldest record of pterosaur tracks in Korea after *Haenamichnus* sp., which was reported from the Upper Cretaceous (Cenomanian) Uhangri Formation of Korea (Hwang et al., 2002).

Pteraichnus-like pterosaur tracks are also known from the Lower Cretaceous (Aptian) of Gansu Province China (Zhang et al., 2006). These tracks are all associated with a single trackway in which the average manus length is about 13–14 cm. For this reason the tracks are similar to those from Korea. However, the Korean tracks include some that are smaller (about 9 cm long) which are therefore the smallest pterosaur tracks currently reported from Asia. *Haenamichnus*, however, is much larger than any known pterosaur track with individual footprints up to more than 30 cm in length (Lockley et al., 1997; Hwang et al., 2002).

6. Discussion

The discovery in the Aptian-Albian Haman Formation of web-footed tracks in association with relatively small pterosaur tracks assigned to *Pteraichnus* has several interesting implications when seen in conjunction with other recent reports of bird and pterosaur tracks in Korea and elsewhere in East Asia. For example, as shown in Table 2, there are now three formations in Korea from which there are from two to four distinct bird track types. Two of these contain pterosaur tracks.

If the inferred ages of these three formations are correct, we recognize six bird tracks (ichnogenera) and two pterosaur ichnotaxa in an interval of time that spans about three stages across the Lower-Upper Cretaceous boundary (i.e., Aptian-Cenomanian). No other region reveals such a striking diversity of well-preserved bird track types in the mid-Cretaceous. In North America, for example, only three mid-Cretaceous avian ichnogenera are known from a relatively small number of sites representing a much greater time span (Mehl, 1931; Currie, 1981; Lockley et al., 2001a; McCrea and Sarjeant, 2001). Likewise in China where there are many bird tracks known, only two ichnogenera have been reported (Zhen et al., 1995; Lockley et al., 2006). We note that the Haman and Jindong formations occur in stratigraphic sequence and apparently share identical or indistinguishable examples of *Koreanornis* and *Jindongoripes* (Fig. 7). The Haman Formation differs from the Jindong Formation in exhibiting *Pteraichnus* and has not yet yielded *Goseongornipes*. The Uhangri assemblage is derived from a different geological basin and has revealed two ichnotaxa (*Uhangrichnus* and *Haenamichnus*) that are not known from the Jindong Formation. However, the report of *Uhangrichnus* from the Haman Formation suggests some overlap in the avian ichnofauna. Our interpretation of the Haman tracks as *Ignotornis* suggests that this ichnotaxon is present in the Haman Formation of the Jinju area as also suggested by Lim et al. (2000, 2002).

If we look at the shared avian and pterosaurian ichnotaxa relationships between the three formations with bird tracks, we note that the Haman ichnofauna is the most diverse. It yields five ichnogenera of which two are not found in the other two formations (Table 2, Fig. 7). Likewise the Uhangri Formation ichnofauna from the Haenam Basin reveals two out of three ‘‘indigenous’’ ichnotaxa. By contrast two of the three Jindong ichnogenera are shared with the Haman ichnofauna, thus stressing the close spatio-temporal relationship between these two successive formations in the same basin.

We tentatively suggest that a review of Chinese avian ichnofaunas in the Cretaceous is likely to suggest a different ichnofauna as suggested by currently named ichnotaxa (Zhen et al., 1995; Azuma et al., 2002; Lockley et al., 2006; Li et al., 2005). Thus, we pose the question as to whether there were differences in avifaunas between the continental margins and the continental interiors during the Cretaceous.

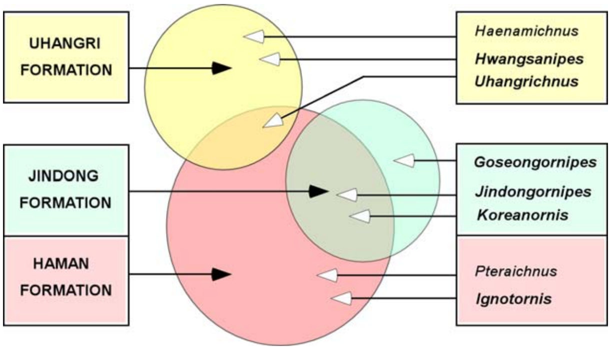

Fig. 7. Distribution of avian and pterosaurian ichnotaxa in the Haman, Jindong, and Uhangri formations. Note strong overlap between the ichnofaunas from the contiguous Haman and Jindong formations from the Kyongsang Basin. Note that the overlap is less between these two formations and the Uhangri Formation, which is associated with a different basin, the Haenam Basin.

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