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New pterosaur tracks from the Hasandong Formation (Lower Cretaceous) of Hadong County, South Korea

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Abstract

In 2004, fifty new pterosaur tracks were discovered in the Hasandong Formation (Lower Cretaceous), South Korea. They are preserved as natural casts on the surface of an isolated dark grey mudstone block (70 × 50 cm). Manus and pes imprints are very small, averaging 25.6 mm and 25.7 mm long, respectively. The manus imprints (N = 25) are tridactyl and digit I, II, III are strongly asymmetric. Fully plantigrade pes imprints (N = 25) were left by elongate metatarsals with short four digits (the ratio of digit to whole pes length is 2.6). There is no trace of the 5th phalanx of the pes. As these features clearly distinguish the Hadong tracks from the type species of the ichnogenus *Pteraichnus*, we assign them to a new species, *Pteraichnus koreanensis*. They are stratigraphically the oldest pterosaur tracks in Korea and are distinguished by size and morphology from the two pterosaur ichnotaxa, *Haenamichnus uhangriensis* and *Pteraichnus* isp., previously reported from the Uhangri and Haman formations. *Pteraichnus koreanensis* is the smallest pterosaur track currently reported from Asia.

Keywords: Pterosaur tracks; *Pteraichnus koreanensis*; Early Cretaceous; Hasandong Formation; South Korea

1. Introduction

The first pterosaur trackway (*Pteraichnus saltwashensis*) was described from the Morrison Formation in 1957 (Stokes, 1957). Although it took approximately 40 years to confirm that *Pteraichnus* was indeed made by a pterosaur (Bennett, 1997; Lockley et al., 1995; Mazin et al., 1995; Unwin, 1997, 1999), the ichnologic record of Late Jurassic to Late Cretaceous pterosaurs has increased significantly in recent years (Lockley et al., 1995, 2001; Mazin et al., 1995, 1997; Wright et al., 1997; Garcia-Ramos et al., 2000; Calvo and Lockley, 2001; Fuentes Vidarte, 2001; Meijide Calvo, 2001; Meijide Fuentes, 2001; Hwang et al., 2002; Rodriguez-de la Rosa, 2003; Kim et al., 2006; Li et al., 2006; Zhang et al., 2006). Three pterosaur tracksites have been discovered so far in Asia, all in Cretaceous sediments. The first evidence of pterosaur tracks from Asia came from the Uhangri Formation (Upper Cretaceous) in Korea (Lockley et al., 1997) and was later named *Haenamichnus uhangriensis* (Hwang et al., 2002). They are currently the largest pterosaur tracks known world-wide. The two other occurrences are *Pteraichnus* isp., recently reported from the Haman Formation (Lower Cretaceous) in Korea (Kim et al., 2006), and cf. *Pteraichnus* from the Hekou Formation (Lower Cretaceous) in China (Li et al., 2006; Zhang et al., 2006).

In 2004, a new pterosaur tracksite was discovered in the Hasandong Formation (Lower Cretaceous), Korea (Fig. 1). It is the third occurrence of pterosaur tracks in Korea after *Haenamichnus* and *Pteraichnus* isp. The new pterosaur tracks are therefore an additional contribution to the growing database of pterosaurian ichnites in Korea as well as an important datum for Cretaceous pterosaur track sites, indicating that South Korea is of global importance in pterosaur ichnology. The new tracks are different in size and morphology from

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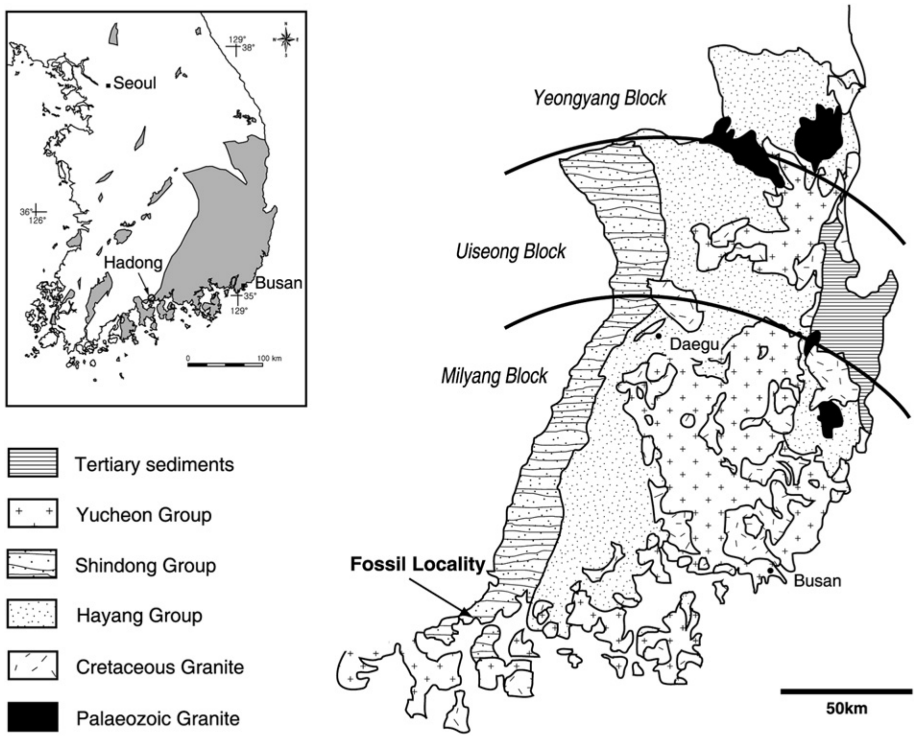

Fig. 1. Location map for the Lower Cretaceous Hadong pterosaur track locality in the Hasandong Formation, showing the Cretaceous basins including the Gyeongsang Supergroup.

the two ichnotaxa previously known, and they represent the oldest pterosaur tracks in Korea. They are of particular interest because they are the smallest pterosaur tracks yet reported from Asia. The purpose of this paper is to describe the new pterosaur tracks from the Hasandong Formation, Hadong County, Korea and to compare them with other pterosaur tracks from Asia and elsewhere. Finally, we discuss the likely identity of the Hadong track-maker.

2. Geological setting

The tracks described here are from the Hasandong Formation, the unit that forms the middle part of the Sindong Group, the lowermost group within the Gyeongsang Supergroup (Fig. 2). Diverse vertebrate ichnofaunas from the Gyeongsang Supergroup are well known internationally because they represent the largest concentration of Cretaceous vertebrate track sites reported from anywhere on the Asian continent (Lockley et al., 2006). They include abundant dinosaur tracks as well as bird and pterosaur tracks (Lee et al., 2001; Huh et al., 2003). Although body fossils are less well known compared to the vertebrate ichnocoenoses, the Hasandong Formation has yielded the most abundant vertebrate body fossils in the Gyeongsang Supergroup (Lee, 2003). Most bones occur as scattered, broken, and isolated pieces which had probably undergone long aerial exposure, transportation, and scattering on the floodplain before burial (Paik et al., 2001). To date, vertebrate faunas from the Hasandong Formation include *Sinamia* fishes (Yabumoto et al., 2006), trionychoid turtles, a protosuchian crocodyliform skull (Lee and Lee, 2005), a pterodactyloid pterosaur wing phalanx (Lim et al., 2002a) plus teeth (Yun and Yang, 2001), and dinosaurs. Dinosaurs include allosauroid (Park et al., 2000) and megalosaurid theropod teeth (Lim et al., 2002b), the sauropods *Pukyongosaurus millenniumi* (Dong et al., 2001), currently considered a *nomen dubium* (Upchurch et al., 2004) and *Chiayusaurus asianensis*, isolated camarasaurid and titanosaurid teeth (Lee et al., 1997), and ovaloolith-type dinosaur eggs (Yun and Yang, 1997).

Previously described vertebrate ichnofossils from the Hasandong Formation were dinosaur tracks, which have been found in the exposed bottom of the Gawha river channel near Jinju city (Lim et al., 1997) and along the coastal outcrops in Hadong County. Therefore, the Hadong pterosaur tracks are the first occurrence of non-dinosaurian ichnofossils in the Hasandong Formation.

The Hasandong Formation is characterized by red beds, including reddish and grey sandstone, reddish to greenish grey sandy mudstone, and dark grey shale. The Hasandong Formation shows alternating channel and interchannel sediments with floodplain deposits (Choi, 1986). Non-marine trace fossils from the Hasandong Formation, such as the ichnotaxa *Skolithos* and *Palaeophycus*, also indicate high-energy channel levee environments and low-energy floodplain settings (Kim et al., 2002). The formation is on average about 1200 m thick with strike between N30° ∼ 70°E and dip between 8° ∼ 20°SE, respectively.

The track site itself is an abandoned quarry next to the Hadong power plant, which used the rock as crushed stones. The quarry consists of about 5000 m^2 of exposure, representing the middle part of the Hasandong Formation (Fig. 3). The

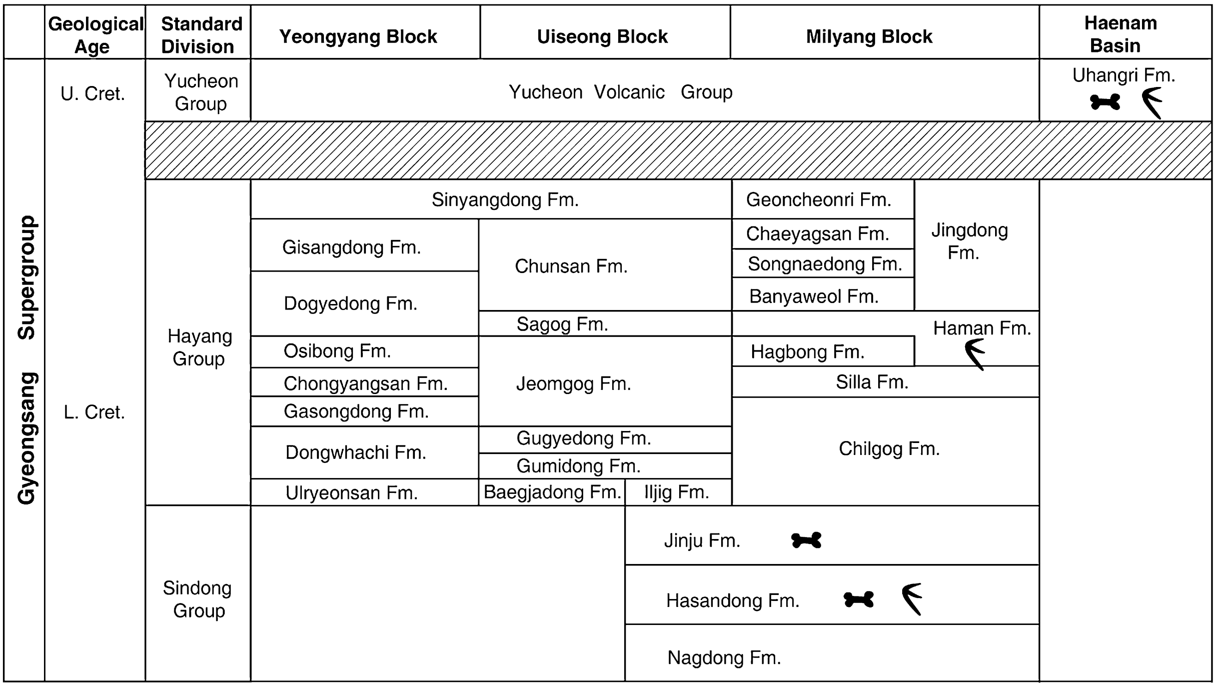

Fig. 2. Stratigraphic correlation of the Gyeongsang Supergroup with the pterosaur faunal horizons. pterosaur bones pterosaur tracks.

well exposed vertical section in the quarry is characterized by the alternation of light grey fine to medium sandstone and reddish massive mudstone associated with pebble-sized calcareous concretions. The pterosaur tracks were discovered in a dark grey mudstone bed in the middle part of the section. This bed also produces plant fossils (*Ptilphylum* sp., *Cladophlebis* sp., *Ruffordia* sp.) and various ichnofossils such as amphibian (?) and theropod dinosaur tracks as well as various invertebrate traces. This layer represents sediments thought to have been deposited in small swamps and/or marginal lakes associated with floodplains between channels. With body fossils, the ichnofossils clearly indicate that diverse vertebrate communities existed during the time of Hasandong deposition.

The age of the Hasandong Formation has been determined as Aptian to Albian by molluscan faunas (Yang, 1982) and as Hauterivian to Barremian by palynomorphs (Choi, 1985, 1989; Yi et al., 1994). The age of the Hasandong Formation was also regarded as Hauterivian on the basis of palaeontological and radiometric data (Chang, 1988). Recently, ion microprobe dating of a dinosaur tooth from the Hasandong Formation indicated a ^{238}U–^{206}Pb isochron age of 117 ± 18 Ma (Sano et al., 2002).

3. Systematic description

Order Pterosauria Kaup, 1834
Superfamily Pterodactyloidea Plieninger, 1901
Ichnogenus *Pteraichnus* Stokes, 1957
Ichnospecies *Pteraichnus koreanensis* ichnosp. nov.

Etymology. Named after Korea which yielded the holotype.

Holotype. Natural casts of manus and pes prints on a mudstone slab (70 × 50 cm) (KIGAM VP 200401: Korea Institute of Geoscience and Mineral Resources, Vertebrate Paleontology).

Horizon and locality. Hasandong Formation, Lower Cretaceous, an abandoned quarry next to Hadong power plant, Hadong County, South Gyeongsang Province, South Korea.

Description. The pterosaur tracks consist of 25 manus and 25 pes prints without tail trails, indicating quadrupedal locomotion. The tracks are preserved as negative depressions because they occur as natural casts on the underside of the mudstone slab (Fig. 4). The average manus length and width are 25.6 mm and 12.3 mm, respectively. The manus prints are asymmetrical, with three digit imprints. The digit I imprint is anterolaterally oriented and is the shortest (average length 10.7 mm). It is straight or slightly curved distally. The claw mark is not clear because there is rarely a clear differentiation between the prints of the claws and the digital pad. Digit II and III are oriented posterolaterally and appear rod-like. They end with a sharp mark that could represent a claw. The digit II imprint is straight and intermediate in length (average length 12.8 mm). The digit III imprint, the longest (average length 18.5 mm), is nearly straight or slightly curved distally. Divarication of digit I and III impressions ranges from 80° to 140° (average 116.2°); average digit divarication of digit I and II is 68.5°, which is approximately 21° greater than that between II and III (47.6°). The metacarpo-phalangeal joint depression is deeper than the digital impressions. There is no indication of digit impression IV, nor of webbing between the digits (Fig. 5).

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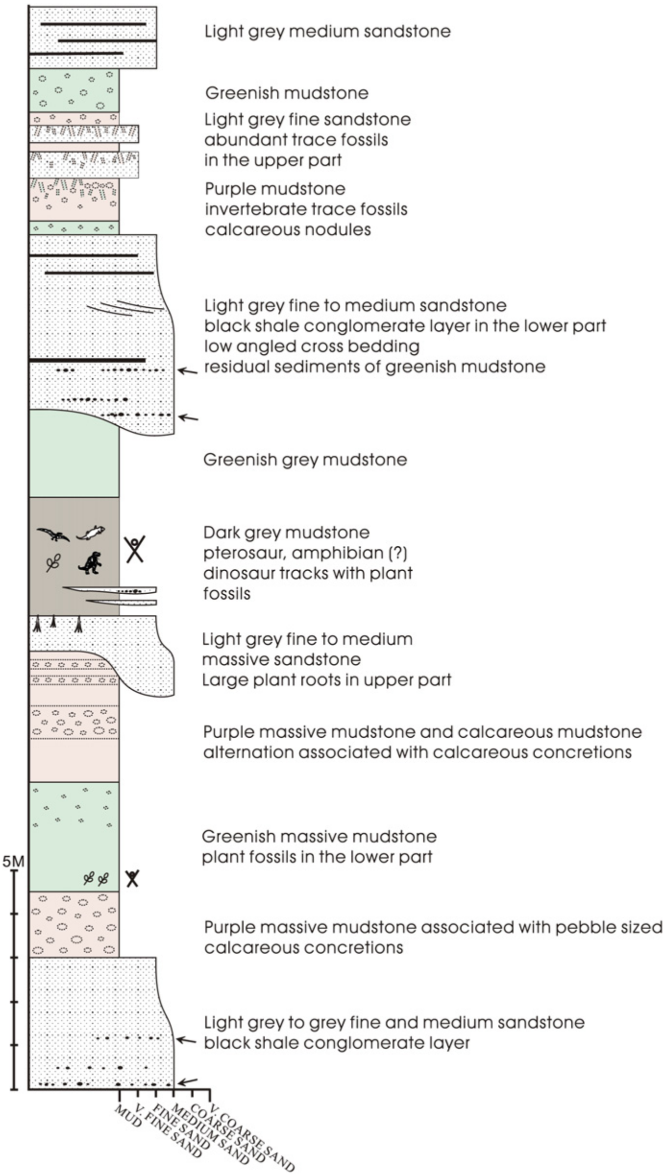

Fig. 3. Geological section of the site indicating the pterosaur track-bearing level associated with amphibian (?), theropod dinosaur footprints, invertebrate traces, and plant fossils.

The pes prints are triangular, elongate and fully plantigrade. They are tetradactyl with anterior claw marks. The average length and width of the pes impressions are 25.7 mm and 12.8 mm, respectively. Although the digit I imprint (average length 8.9 mm) is the shortest and the digit III imprint is the longest (average length 10.8 mm), the four digit imprints are roughly subequal in length (Table 1). The metatarsals are long and elongate, diverging moderately like the handle of a fork, and are always longer (average length 17.5 mm) than the digits. The heel is the deepest part of the prints, particularly at the metatarso-phalangeal joint. There is no preservation of an impression formed by a fifth metatarsal.

Most of the tracks are oriented in an apparently random pattern, including some overstepping imprints. This random orientation with high density suggests gregarious behavior (Mickelson et al., 2004), possibly suggesting that this group of pterosaur individuals was feeding together. Although the quality of impression of the autopod anatomy is not very good in some imprints, nevertheless three manus-pes print sets (track numbers 5-4, 6-49, 10-9) can be recognized as a trackway (Fig. 6). The trackway shows a clear quadrupedal gait pattern comprising manus and pes prints easily recognized by the distinctive print morphology. In this trackway, the pes print is anterior to the manus print and the latter is located further from the mid-line than the former. Manus prints show inward rotation of 15.5° on average. The stride length is 90.9 mm and the average pace length is 55.1 mm. The pace angulation is 108° and the gait-width is 30.2 mm. Pes prints show an average outward rotation of 19.3°. The stride length is 95.2 mm and the average pace length is 52.9 mm. The pace angulation is 126° and the gait-width is 22.7 mm. Therefore, the pace angulation and stride of the pes is greater than that of the manus. The inner trackway of pes imprints shows a clear ‘‘narrow gauge’’ pattern. Moreover, the narrow manus trackway and relatively short stride suggest that the animal's body was held semi-erect at low-velocity walking (Mazin et al., 2003).

Discussion. Although *Pteraichnus koreanensis* could have been produced by different taxa, we suggest that all the tracks were made by the same kind of animals at similar ages because all manus and pes imprints show a low amount of variability in size and morphology (Fig. 7). The small degree of variability could correspond to the interaction between track-maker dynamics and the substrate (Mazin et al., 2003), or to individual variation. Moreover, considering the small size and consistency of track depth in such a small area, the tracks were probably made in a short period of time. The possibility that the tracks represent juveniles and not adults cannot be excluded, but determining this is beyond the scope of this study.

In a recent review of pterosaur ichnotaxa, Billon-Bruyat and Mazin (2003) reassessed *Pteraichnus* based on the discovery of new specimens from the United States and Europe and discussed the validity of several ichnospecies referred to *Pteraichnus*. Based on ichnotaxonomical principles, they concluded that only the type species *Pteraichnus saltwashensis* is valid. We admit that it is difficult to discriminate between ichnospecies based on print morphology and track pattern due to track-maker dynamics and variability resulting from interaction between the track-maker and the substrate. *P. koreanensis* is different from the type species *P. saltwashensis* in its small size and unique morphology as well as in stratigraphic occurrence and palaeogeographic location.

Since *Pteraichnus* was first named by Stokes in 1957, its diagnosis has been emended twice (Lockley, et al., 1995; Billon-Bruyat and Mazin, 2003). Although *P. koreanensis* meets the updated diagnosis of *Pteraichnus*, *P. koreanensis* differs from the type species. Firstly, *P. koreanensis* is approximately three times smaller than *P. saltwashensis* where the manus and pes lengths are 82.6 mm and 76.2 mm, respectively. The pes of *P. saltwashensis* is distinctly V-shaped with a sharply pointed heel (Stokes, 1957, fig. 2), which is quite different from the

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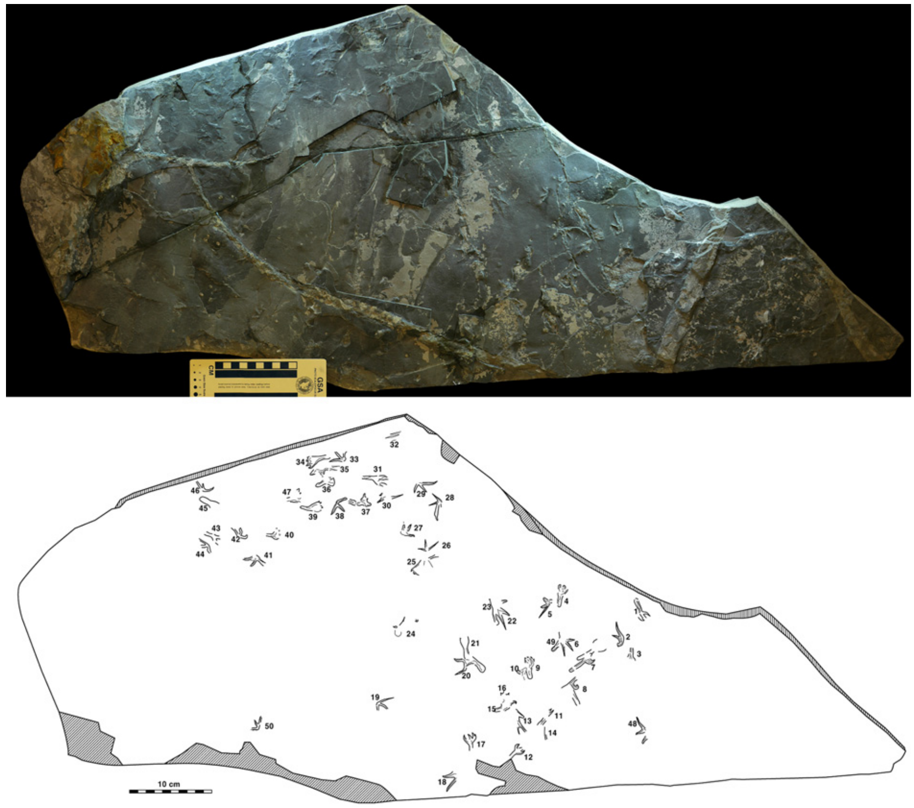

Fig. 4. Photograph and drawing of *Pteraichnus koreanensis* isp. nov. on the block.

long and elongate metatarsal impression, recalling the handle of a fork, in *P. koreanensis*. The divarication of the pes is greater in *P. saltwashensis* (40°) than it is in *P. koreanensis* (30°). The ratio of digit to whole pes length is 1.9 in *P. saltwashensis* while it is 2.6 in *P. koreanensis*. The pes angulation of *P. koreanensis* is greater (126°) than it is in *P. saltwashensis* (115°), but this is not a diagnostic feature allowing us to distinguish the two ichnospecies because it is not an ichno-anatomic but, rather, an ichno-dynamic feature. In addition, the long time interval and geographic distance between the Upper Jurassic Morrison Formation in North America and the Lower Cretaceous Hasandong Formation in Korea is unlikely to reflect the existence of only one species.

Four Lower Cretaceous *Pteraichnus* ichnospecies (*P. palacieisaenzi, P. cidacoi, P. manueli,* and *P. vetustior*) had been named from Oncala, Soria, Spain (Pascual Arribas and Sanz Pérez, 2000; Fuentes Vidarte, 2001; Meijide Calvo, 2001; Meijide Fuentes, 2001; Fuentes Vidarte et al., 2004a, b). However, all were regarded as *nomina nuda* because they were unavailable according to the ICZN and, furthermore, their minor differences were attributed to intra-ichnospecific variability (Billon-Bruyat and Mazin, 2003). Later, two new

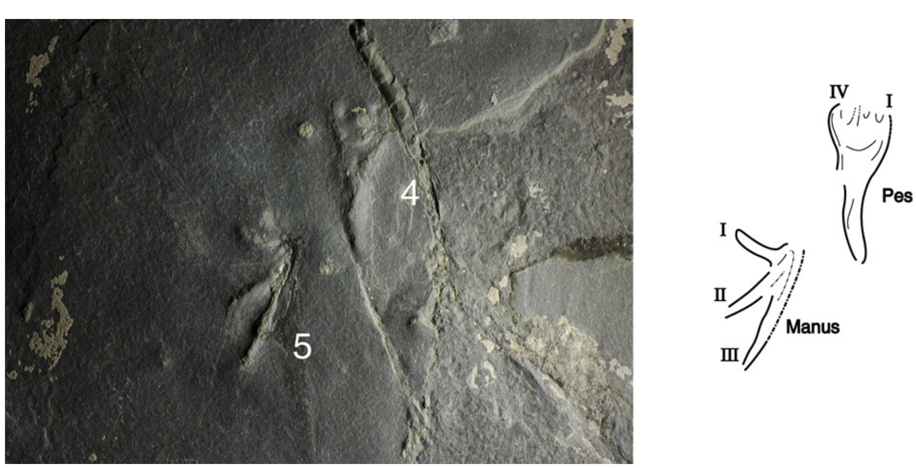

Fig. 5. Enlarged photograph and drawing of a complete right manus-pes set (number 4, 5).

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Table 1
Measurment (in mm) of *Pteraichnus koreanensis* isp. nov. form the Hasandong Formation in the Hadong site. Abbreviations: $T_{\#}$, track number; M/P, manus/pes; L/R, left/right; L, length; W, width; L/W, ratio of length/width; I, II, III, IV, length of digits I, II, III, IV; MT, metatarsals length; $D_{(I\text{-}II)}$, divarication between digits I and II; $D_{(II\text{-}III)}$, divarication between digits II and III; $D_{(I\text{-}III)}$, divarication between digits I and III

$T_{\#}$	M/P	L/R	L	W	L/W	I	II	III	IV	MT	$D_{(I-II)}$	$D_{(II-III)}$	$D_{(I-III)}$
1	P	R	21.4	12.5	1.7				7.4	12.9			
2	M	L	27.9	12.1	2.3	9.3	13.5	22.9			75	50	125
3	P	L								16.3			
4	P	R	23.6	10.9	2.2	9.5			10.8	15.2			
5	M	R	22.4	10.1	2.2	7.3	12.7	20.7			50	30	80
6	M	L	25.5	12.2	2.1	10.7	17.1	20.7			45	45	90
7	P	?	30.1	13.9	2.2			8.5	9.3	20.5			
8	P	?	28.7							22.7			
9	P	R	21.7	11.0	2.0	9.6	9.4	10.5	8.1	16.2			
10	M	R		12.3	0.0	8.7	9.6						
11	P	?	25.8	10.8	2.4			9.6		16.6			
12	P	?	25.0	12.8	2.0	8.2	8.3		9.7	17.9			
13	M	L	32.6			12.3	12.6	19.1					
14	M	?				5.9							
15	M	?					8.5						
16	P	?	25.9	14.7	1.8	8.1	8.7	11.8	14.7	20.6			
17	P	?	26.8	16.4	1.6	10.7	11.2	10.0	12.4	20.6			
18	M	R		16.8			13.4	18.1					
19	M	R	23.1	10.9	2.1	9.7	10.9	14.5			60	55	115
20	M	R	26.2	16.8	1.6	10.0	18.0	14.1					
21	P	R	24.9	8.9	2.8	7.8	7.9	8.2	10.0	15.6			
22	M	L	28.1	12.6	2.2	14.8	15.3	23.4			70	35	105
23	P	L	32.8	16.7	2.0	10.6		13.4	14.7	19.3			
24	P	?	30.4	14.6	2.1	9.9		12.4		19.2			
25	M	?	23.8	10.4	2.3	11.3	13.1	21.3					
26	M	L	27.9	15.1	1.8	11.7	17.0	20.2			70	65	135
27	M	R	24.1	13.9	1.7	12.0	14.5	16.0			65	35	100
28	M	R	29.7	16.6	1.8	15.2	16.6	23.0			65	65	130
29	M	R	29.2	13.7	2.1	13.8	14.0	19.9			70	50	120
30	P	?	32.3	16.2	2.0	8.4		12.2		21.2			
31	P	?	30.1	12.7	2.4	10.3	12.2	13.9	13.6	19.5			
32	P	?						14.4	12.4				
33	M	R	21.2	14.0	1.5	9.2	12.8	16.5			55	45	100
34	P	?	25.0	13.8	1.8	8.1	8.9	9.8	8.7	15.4			
35	M	?	29.1			13.9	12.5	20.0					
36	P	?	22.6	10.5	2.2	8.0		8.9	7.7	12.0			
37	P	?	25.0	13.1	1.9	8.5	8.1	10.0	7.0	16.7			
38	M	L	26.3	12.3	2.1	11.1	11.3	17.4			70	65	135
39	P	?	23.1	11.1	2.1	8.5	9.1	10.6	9.0	17.0			
40	P	?		11.2	0.0	8.3	8.7	9.1	8.6				
41	M	L	26.2	13.5	1.9	11.9	11.3	16.2			80	50	130
42	M	R	22.7	8.5	2.7	9.4	8.7	16.6			75	55	130
43	P	?	20.8	12.0	1.7		7.3		9.2	16.3			
44	M	L	19.2	11.1	1.7	7.9	7.2	11.5			100	40	140
45	P	?	20.7	10.1	2.0		7.9		8.9	14.4			
46	M	L	22.6	10.3	2.2	9.3	8.8	14.4			85	30	115
47	P	?	23.2	13.0	1.8	8.1	8.9	10.2		17.6			
48	M	L	27.9	11.7	2.4	11.8	14.3	21.9			60	55	115
49	P	L	25.5	14.1	1.8	8.7			11.1	19.5	70	40	110
50	M	L	21.2	11.6	1.8	10.0	12.5	18.3					
Manus in average			25.6	12.3	2.2	10.7	12.8	18.5			68.5	47.6	116.2
Pes in average			25.7	12.8	2.0	8.9	9.0	10.8	10.2	17.5			

ichnospecies, *P. longipodus* (Fuentes Vidarte et al., 2004a) and *P. parvus* were added to the list of Oncala pterosaur ichnotaxa, and redescriptions of *P. vetustior* and *P. manueli* were provided (Fuentes Vidarte et al., 2004b). Among six ichnotaxa from Oncala, two ichnospecies, *P. manueli* and *P. parvus*, are similar to *P. koreanensis* in size. The manus and pes length of *P. manueli* are 25.3 mm and 21 mm, respectively (Meijide Calvo, 2001), but its manus is characterized by small divarication (54°) between digit I and III (Fuentes Vidarte et al., 2004b): this is different from that of *P. koreanensis*. *P. parvus* is even smaller than *P. manueli* (manus imprint 23 mm, pes 15 mm long). The manus of *P. parvus* is longer than the pes, and the metatarsus impression is not elongate but very wide. In addition, *P. koreanensis* is much smaller than other

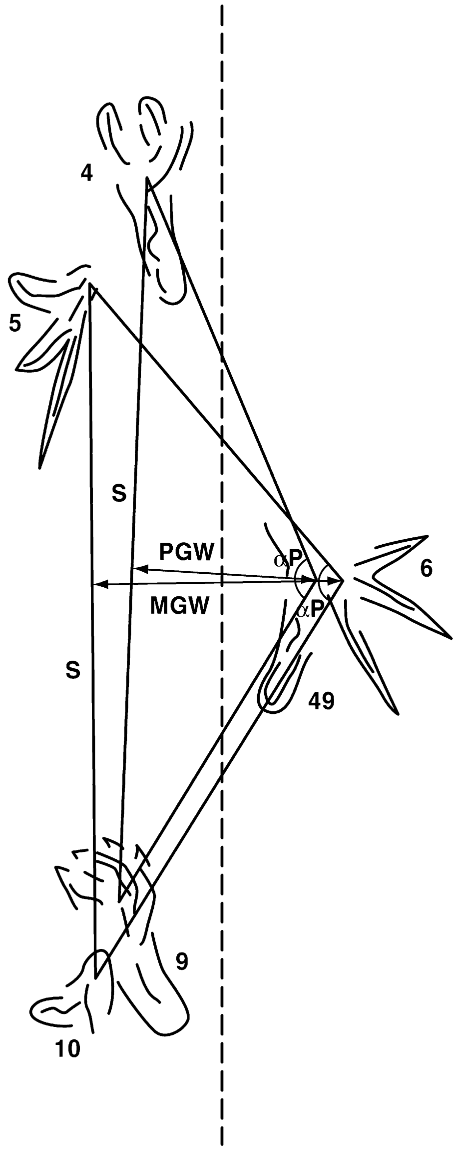

Fig. 6. A complete locomotion cycle of *Pteraichnus koreanensis* isp. nov. Abbreviations: αP, pace angle; MGW, manus gait-width; PGW, pes gait-width; S, stride.

Cretaceous pterosaur tracks such as *Purbeckopus* from England (Wright et al., 1997), and cf. *Pteraichnus* from the United States (Lockley, 1999), Argentina (Calvo and Lockley, 2001), and Mexico (Rodriguez-de la Rosa, 2003).

It is therefore reasonable to conclude that the Hadong pterosaur tracks represent a new Cretaceous ichnotaxon produced by a species as yet unrecognized from osteological remains.

4. Identity of the *Pteraichnus koreanensis* ichnosp. nov. trackmaker

The taxonomic identification of a trackmaker depends on the diagnostic features preserved in the trackway integrated with skeletal data (Olsen, 1995; Carrano and Wilson, 2001). In addition to pterosaur tracks, pterosaur teeth and incomplete pterosaur bones have been found in Korea. The first pterosaur bone to be discovered was an incomplete possible wing phalanx (170 mm in length) found in the Uhangri Formation in 1997, and as yet undescribed. Other elements are an incomplete wing phalanx (247 mm in length) from the Hasandong Formation (Lim et al., 2002a) and three isolated teeth from the Hasandong and Jinju formations which are characterized by a curved, sharply pointed, long crown exhibiting fine striations (Yun and Yang, 2001). The discovery of pterosaur tracks in the Hasandong Formation is consistent with the report of two isolated pterosaur teeth from the same formation, but we cannot be certain whether the tracks were left by the same pterosaur taxon. In contrast to the fragmentary pterosaur bones and few teeth from Korea, abundant pterosaur taxa have been reported from the Jehol Group in Liaoning, northeastern China. Sixteen small to medium sized species have been described so far (Wang et al., 2005; Lü and Ji, 2006). It is reasonable to speculate that the candidate for *P. koreanensis* is among the Jehol pterosaur assemblage because the age of the Hasandong Formation is nearly equivalent to that of the Jehol Group (Swisher et al., 1999; He et al., 2004).

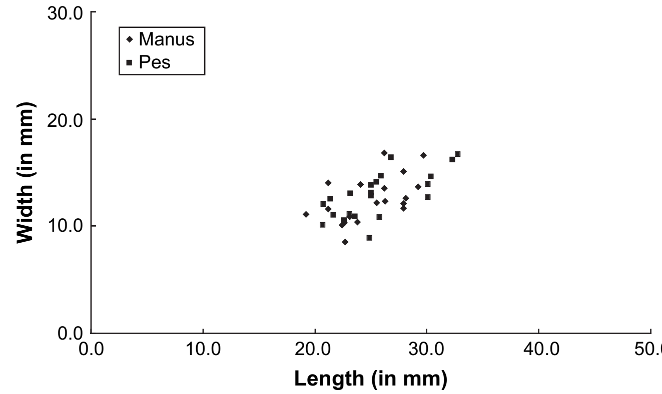

Fig. 7. Scattered diagram showing the relationship between length and width of manus and pes of *Pteraichnus koreanensis* isp. nov.

The Jehol pterosaurs include a wide range of taxa, including both basal and derived, and ranging from anurognathids to tapejarids. Among the small taxa comparable with the trackmaker of *P. koreanensis* are *Dendrorhynchoides curvidentatus* (Ji and Ji, 1998; Ji et al., 1999; Lü et al., 2006), in which the manus and pes lengths are less than 30 mm. However, it is basal anurognathid, rather than a derived pterodactyloid, and therefore could not be a candidate maker of *P. koreanensis* because a reduced pes digit V is a synapomorphy for Pterodactyloidea (Unwin, 2003). Except for an unnamed juvenile dsungaripteroid from the Jehol Biota (Kellner et al., 2006), all the pterodactyloids described so far from Asia are larger than the trackmaker that produced *P. koreanensis*. A new small pterodactyloid pterosaur may therefore have existed in East Asia during the Early Cretaceous, although it would be premature to draw this conclusion from tracks alone.

5. Discussion

Haenamichnus uhangriensis from the Uhangri Formation has the first pterosaur track named from Asia (Lockley et al.,

1997) and includes the largest pterosaur prints yet known (Hwang et al., 2002). In addition, both *Haenamichnus uhangriensis* and *H*. isp. have a rounded digit V impression. In their large size and presence of digit V impression, these tracks are very different from *P*. *koreanensis*. *Pteraichnus* isp., recently reported from the Haman Formation, is also distinguished from *P*. *koreanensis* by size and morphology (Kim et al., 2006). Finally, *P*. *koreanensis* is stratigraphically the oldest pterosaur tracks out of the three Korean formations (Fig. 2). A trackway (cf. *Pteraichnus*) has recently been reported from the Hekou Formation of Gansu Province, China (Li et al., 2006; Zhang et al., 2006), and is only the second reported pterosaur track occurrence in Asia after the Korean tracks. The Chinese tracks are larger than *P*. *koreanensis* and have prominent pedal digit V impressions. In Asia, Korea is therefore unique in the occurrence of at least three Cretaceous pterosaur ichnospecies.

It is interesting to note the congruence in size between tracks and osteological taxa. Small to medium sized pterosaurs and tracks are known from the Upper Jurassic, and in Lower Cretaceous strata, both pterosaur body fossils and tracks reached larger sizes (Hwang et al., 2002). However, although we do not yet have skeletal evidence, *P*. *koreanensis* and several other small pterosaur tracks from Spain indicate that some small pterodactyloid pterosaur species existed in the Early Cretaceous.

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