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SHORT COMMUNICATION

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The oldest known tracks of web-footed birds from the Lower Cretaceous of South Korea

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Abstract We describe the oldest tracks of web-footed birds from the Early Cretaceous in South Korea. The tracks are characterized by a wide divarication angle and a long reversed hallux. The web is semipalmate and restricted to the proximal portion of the three forward digits. The tracks from the Early Cretaceous in South Korea are smaller than those of the Late Cretaceous, therefore confirming the trend of size increasing in the early evolution of birds as shown by skeletal fossils. The discovery of web-footed tracks with abundant non-web-footed tracks indicates that there was a considerable diversification of shore birds as early as the Early Cretaceous.

There has been a significant increase in discovery of fossil bird tracks, particularly in East Asia and North America. However, bird tracks from webbed feet are uncommon except for the famous Eocene *Presbyornis* trackways (Lockley et al. 1992). The oldest known tracks of web-footed birds have been from the Late Cretaceous, in Hwangsan Basin of South Korea, where two types are known (Yang et al. 1995). Here we report the discovery of tracks of web-footed birds from the Early Cretaceous in South Korea which represents the earliest record of shore birds with webbed feet. A relatively long, reflexed hallux is present, probably a holdover from arboreal ancestors. The webs are semipalmate and generally similar to avocets; they are restricted to the proximal portion of the three forward digits (i.e., between digits II–IV), and are smaller than those of most Cenozoic web-footed birds where webs extend to the ungual phalanges. Smaller, non-webbed tracks occur more abundantly in the same locality. The new findings indicate an unexpected diversification of early shore birds shortly after the radiation of land birds recently found in China.

Thousands of bird tracks, including some of web-footed species, have now been collected from the fluviolacustrine Early Cretaceous (Aptian-Albian) Haman Formation (shale facies) in the Kyongsang Basins of southwestern South Korea (Fig. 1). This is the largest exposure of Cretaceous strata in South Korea (Choi

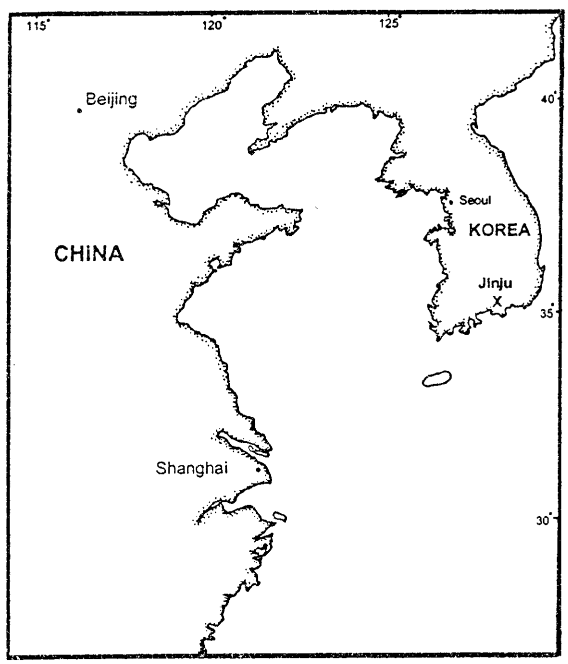

Fig. 1 Location of the Early Cretaceous web-footed bird track locality in Jinju, southeast South Korea

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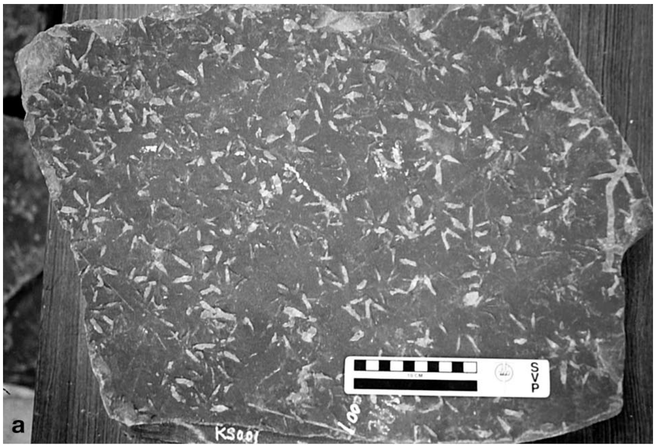

Fig. 2 a) Unwebbed bird tracks in Jinju, southeast South Korea (KS 001). b) Picture of another specimen (KS 043) showing a dinosaur track preserved with much smaller unwebbed bird tracks

1986; Kim 1969) and has produced charophytes, algae, and plants, fresh water shells, estheriids, insects, tortoises, and dinosaurs. The dinosaur tracks are significantly larger than the bird tracks (Fig. 2).

Unwebbed bird tracks are probably referable to the ichnotaxon *Koreanaornis* (Baek and Yang 1997; Gatesy et al. 1999). The tracks are densely distributed ($1000/m^2$ in KS 001), suggesting species flocks (Fig. 2). Average length of those tracks is 26.2 mm (range 15.5–30.7 mm, $n=25$), and average width 34.3 mm (range 27.5–42.5 mm, $n=25$). The angle between the second and fourth digits averages 115.6° (range 95°–132°, $n=25$). The angle between the second and third digits averages 63.4° (range 47°–78°). The angle between the third and fourth digits averages 52.1° (range 42°–80°). The hallux is caudally directed, typical of bird tracks, and varies among individuals probably due to substrate (Gatesy et al. 1999) or activity variation. Average length of the hallux is 10.2 mm (range 4.8–20.4 mm, $n=19$). Individual trackways are difficult to recognize due to high density.

Webbed tracks comprise only a small proportion of the total bird tracks from the locality (Fig. 3). Average length of a footprint is 45.6 mm (range 41.5–49.5 mm, $n=4$) and average width 55.2 mm (range 49.7–61.3 mm, $n=4$). The angle between the second and fourth digits averages 122.2° (range 117°–127°, $n=4$). The angle between the second and third digits averages 58.2° (range 46°–67°, $n=4$). The angle between the third and fourth digits averages 64° (range 57°–74°, $n=4$). The angle between the second and third digits is slightly larger than that between the third and the fourth digits; the reverse is true in unwebbed bird tracks from the same locality. The hallux is well preserved in most of these tracks and is caudally directed. It is relatively long and slender (Fig. 3), with an average length of 13.0 mm (range 10.2–18.2 mm, $n=3$). The third digit is generally longer than the second and the fourth. The digital pads are relatively wide.

Fig. 3 The web-footed bird tracks in Jinju, southeast South Korea (KS 049)

The third digit is straight; the second and fourth digits are straight or slightly curved inward in different tracks. The distal ends of the digits terminate in short, slender claws. Tracks of web-footed birds are less densely distributed than the non-webbed tracks, suggesting individuals or small groups.

The web is connected mainly to the proximal portion of the three forward digits (i.e., between digits II–IV) as seen in avocets. Webbed feet occur in species of a variety of extant groups, such as Procellariiformes, Anseriformes, Sphenisciformes, Pelecaniformes, Phoenicopteriformes, Gaviiformes, and Charadriiformes. Most modern web-footed birds such as ducks have a more complete web, which extends nearly to the distal end of the forward digits. Early Cenozoic webbed tracks are nearly identical to those of most modern birds in this aspect (Fig. 4), but Late Cretaceous tracks are closer to Early Cretaceous ones in that the cranial margin of both web impressions between digits II and III and III and IV are distinctly concave cranially rather than straight or slightly concave (Yang et al. 1995). Therefore the web was restricted to the proximal portion of the foot and might represent a primitive condition in the evolution of web-footed birds. They were probably made by birds that waded in mud, wet sand,

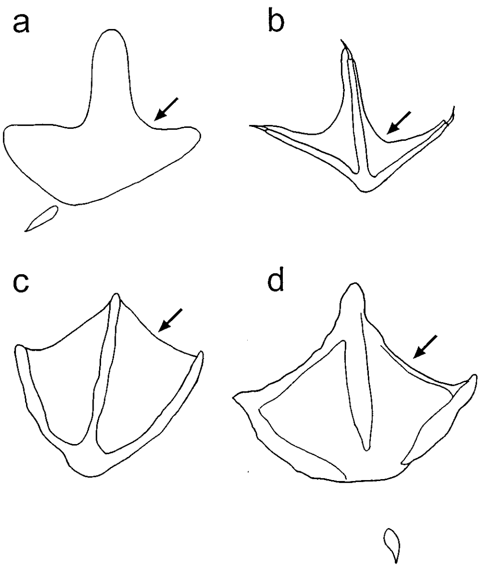

Fig. 4a–c Comparison of the webs. a) Early Cretaceous tracks in Jinju, southeast South Korea. b) Avocet (*Recurvirastra americana*), Division of Ornithology of University of Kansas Natural History Museum 49858. c) Trumpeter Swan (*Olor buccinator*). d) Bird track of a web-footed bird, possibly belonging to *Presbyornis*, from the Eocene Green River Formation, Utah (from Erickson 1967). *Arrow* cranial margin of the web. Not to scale

or shallow water to search for food and were only occasional swimmers.

The hallux of modern shore birds is either short or lost. In the Late Cretaceous webbed tracks, it is absent in one ichnospecies, *Uhangrichnus chuni*, but present in the other, *Hwangsanipes chuoughi* (Yang et al. 1995). The oldest shore (either marine or lacustrine) birds should retain a reversed hallux, as all Jurassic and Early Cretaceous arboreal relatives have one for perching. No dinosaur has a reversed hallux, as was recently confirmed (Gatesy et al. 1999; Norell and Makovicky 1997). The Early Cretaceous shore bird (lacustrine shore in this case) *Gansus* has a relatively long hallux. The impression of the caudally directed hallux of the webbed tracks from the Early Cretaceous of South Korea are also relatively long. It might already be lost in the maker of the Late Cretaceous *Uhangrichnus* tracks from southwest Korea.

The divarication angle between digits II and IV has been used as a criterion to distinguish bird tracks from dinosaur tracks (Lockley et al. 1992). Both web-footed and unwebbed bird tracks in this study show a wide divarication angle between digits II and IV (about 116° and 122°, respectively). However, examination of modern shore birds with webbed feet shows that the angle varies among different taxa, and in many cases (e.g., Trumpeter swan, Canada goose, and Glaucous gull) this angle is actually less than 90° (Murie 1954). We measured several shorebirds at the Natural History Museum of the University of Kansas. Some of the data of the angle between digits II and IV are as follows: *Fratercula corniculata* (Alcidae) 58°, *Larus argentatus* (Laridae) 80°; *Stercorarius pomarinus* (Stercorariidae) 52°; *Catoptrophorus semipalmatus* (Solopacidae) 84°. The tracks of small perching birds also have a narrow divarication angle between digits II and IV of less than 90° (Murie 1954; Smith 1982). We suggest that the divarication angle between digits II and IV is useful to distinguish unwebbed bird tracks from those of dinosaurs. The wide divarication angle of the webbed tracks from the Early Cretaceous of southeast South Korea is a distinctive feature of those tracks.

The webbed tracks described here are smaller than in most modern web-footed birds, and slightly smaller than those of the Late Cretaceous (Yang et al. 1995). It is noteworthy that size reduction was a general trend in early avian evolution from the Late Jurassic to Early Cretaceous (Zhou and Hou 1998), and the ancestor of shore birds was probably reduced in size as in their arboreal cousins *Cathayornis*, *Sinornis*, and *Chaoyangia* from the Early Cretaceous of China (Hou et al. 1996; Zhou 1995). *Enaliornis*, the best-known Early Cretaceous marine bird, is a hesperornithiform (Martin and Tate 1976) and had lobed feet. However, it is probably more interesting to compare *Gansus* (Hou and Liu 1984) from the Early Cretaceous of northwest China with the webbed tracks. *Gansus* was described as the oldest shore bird based on a completely articulated foot with elongated pedal phalanges and short claws. It has been suggested that *Gansus* had webbed feet, based on pointed extensor process at the base of the claws (Zhou and Hou 2000; R. Prum, personal communication). The *Gansus* foot is very similar in size to the webbed tracks, but *Gansus* has a relatively long fourth digit, and the reverse is true in the webbed tracks that have long third digits, excluding *Gansus* as a candidate for the trace maker.

It is worthy of note that the Lower Cretaceous bird footprints, *Ignotornis mcconnelli* from the Colorado of the United States was correctly identified as bird tracks (Currie 1981). Furthermore, their remarkable similarity to the Early Cretaceous webbed tracks from South Korea suggests that it was another early webbed bird.

By the Early Cretaceous, birds had diverged into two fundamental clades. The Sauriurae, including Archaeopteryx, *Confuciusornis*, and the enantiornithine birds, predominated in arboreal and terrestrial niches. The Ornithurae probably occupied the water margin, where the unique resources reward animals that can quickly transverse large, open areas. One result was the modernization of the flight system in the ornithurine *Chaoyangia* (Early Cretaceous) at a time when enantiornithine birds were still primitive in many respects. Trackway evidence now shows that there was already a considerable diversification of birds with shore bird pedal morphologies at this time. The preservation of the bird's webs provides the most direct evidence for the coexistence of several types of shorebirds in the Early Cretaceous, which further reflects the successful opening of new ecological niches for the early ancestors of modern birds.

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References

Baek KS, Yang SY (1997) Preliminary report on the cretaceous bird tracks of the Lower Haman Formation, Korea. J Geol Soc Korea 34:94–104

Choi HI (1986) Sedimentation and evolution of the Cretaceous Gyeongsang Basin, southeastern Korea. J Geol Soc London 143:29–40

Currie PJ (1981) Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. J Vert Paleontol 1:257–264

Erickson BR (1967) Fossil bird tracks from Utah. Obser Sci Mus Minnesota 5:140–146

Gatesy SM, Middleton KM, Jenkins FA Jr, Shubin NH (1999) Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399:141–144

Hou L, Liu Z (1984) A new fossil bird from Lower Cretaceous of Gansu and early evolution of birds. Scientia Sinica 27:1296–1302

Hou L, Zhou Z, Martin LD, Feduccia A (1996) Early adaptive radiation of birds: evidence from fossils from northeastern China. Science 274:1164–1167

Kim BK (1969) A study of several sole marks in the Haman Formation. J Geol Soc Korea 5:243–258

Lee D-S (1987) Geology of Korea. Geological Society of Korea, Kyohak-Sa

Lockley MG, Yang SY, Matsukawa M, Fleming F, Lim SK (1992) The track record of Mesozoic birds: evidence and implications. Philos Trans R Soc Lond B Biol Sci 336:113–134

Martin LD, Tate J (1976) The skeleton of *Baptornis advenus* (Aves: Hesperornithifomes) Smithson. Contr Paleobiol 27:35–66

Murie O (1954) Field guide to animal tracks. Houghton Mifflin, Boston

Norell MA, Makovicky PJ (1997) Important features of the dromaeosaur skeleton: information from a new specimen. Am Mus Novit 3215:1–27

Smith RP (1982) Animal tracks and signs of North America. Stackpole, Harrisburg

Yang SY, Lockley MG, Greben R, Erickson BR, Lim SK (1995) Flamingo and duck-like bird tracks from the Late Cretaceous and Early Tertiary: evidence and implications. Ichnos 4:21–34

Zhou Z (1995) Discovery of Early Cretaceous birds in China. Courier Forschungsinstitut Senckenberg 181:9–23

Zhou Z, Hou L (1998) *Confuciusornis* and the early evolution of birds. Vertebr Pal Asiat 36:136–146

Zhou Z, Hou L (2000) The discovery and study of Mesozoic birds in China. In: Chiappe LM, Witmer L (eds) Mesozoic birds: above the heads of dinosaurs. University of California Press, Berkeley