

First report of the small bird track *Koreanaornis* from the Cretaceous of North America: implications for avian ichnotaxonomy and paleoecology

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ABSTRACT

Although body fossils of shorebirds and shorebird-like species are extremely rare from the Cretaceous, rapid increase in the discovery of bird footprint sites provides valuable alternate evidence to help fill gaps in the story of the early evolution of shorebird-like species. Newly discovered bird tracks from the Albian-Cenomanian Dakota Formation in northeastern Utah represent the first report of the ichnogenus *Koreanaornis* from North America and only the second report of bird tracks from this formation. These tracks are not attributable to *Aquatilavipes* as previously claimed. Three well-preserved trackways are described and provisionally referred to *Koreanaornis* cf. *hamanensis* (Kim). However, a review of the ichnotaxonomy of shorebird ichnites reveals that this ichnotaxon also closely resembles the Miocene ichnospecies *Avipeda sirin* (Vyalov). This latter comparison points to the need for a thorough evaluation of the similarity between Mesozoic and Cenozoic avian ichnotaxa, which may be over-split in some cases and under-differentiated in others.

The new material helps distinguish ichnogenus *Koreanaornis* from the larger bird track *Aquatilavipes*, which is more abundant and widespread in North America. In some cases *Aquatilavipes* has been incorrectly used as a catch-all ichnogenus both in North America and Asia. The Dakota Formation stratigraphy at the tracksite indicates that the track makers lived in a marginal marine paleoenvironment. However, despite the widespread distribution of such facies, often replete with dinosaur tracks, the bird track record of the Dakota Formation, and the Cretaceous of the western USA remains relatively sparse in comparison with other areas such as east Asia.

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1. Introduction

Despite the rapid increase in discovery of Cretaceous bird tracks in recent years, especially in East Asia (Lockley, et al., 1992, 2006a,b, 2007a; Yang et al., 1995; Li et al., 2002a,b; Kim et al., 2006; Zhang et al., 2006) reports are still comparatively scarce in North America. In fact all well-confirmed reports of Cretaceous North American bird tracks are confined to the western part of the continent, and the majority occur in Canada (Currie, 1981; McCrea et al., 2001). Prior to the discovery described herein only five Cretaceous sites had been reported from the western USA (Mehl, 1931; Robison, 1991; Lockley et al., 2001, 2004; Wright et al., 2006). These are all associated to varying degrees with the coastal plains of the area

broadly defined as the Cretaceous Western Interior Seaway region (Lockley and Hunt, 1995). With one exception (Mehl, 1931) none of these sites had yielded clear trackways, thus hampering complete ichnological description of diagnostic characters. Comparative analysis is further hampered by the incompleteness of many other existing samples and descriptions.

The first fossil bird tracks ever reported from the Mesozoic were those named as *Ignotornis mcconnelli* from the upper Albian to lower Cenomanian Dakota Group, near Golden, Colorado (Mehl, 1931). The type locality was subsequently re-studied and additional topotype material discovered (Lockley et al., 1989, 1992, 2007b, 2009; Lockley and Hunt, 1995; Lockley and Rainforth, 2002). Despite the presence of at least 20 trackways, only one (the holotype) has been illustrated and described (Lockley et al., 2007b). Until recently (Kim et al., 2006) the ichnogenus was unknown outside the type locality.

Koreanaornis hamansensis (Kim, 1969), from the Lower Cretaceous of Korea, was only the second bird track reported from the

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Mesozoic. This ichnogenus received no attention from ichnologists until more material was discovered in Korea (Lockley et al., 1992). Until the present study the ichnogenus had not been identified in North America, and no trackway had been described.

The third bird track reported from the Mesozoic, *Aquatilavipes swiboldae* (Currie, 1981), was found in Aptian deposits in Canada. Since its discovery, its recognition at several localities makes it appear more typical of North American ichnofaunas than either *Ignotornis* or *Koreanaornis*. For example, tracks reported from Early Cretaceous deposits of the same age (Barremian–Aptian) in the Lakota Group of South Dakota were assigned to *Aquatilavipes* (Lockley et al., 2001). A newly discovered site in the Cedar Mountain Formation of Utah (Wright et al., 2006) also yields bird tracks that have not yet been named. Other known Lower Cretaceous sites are all in Canada (McCrea and Sarjeant, 2001; McCrea et al., 2001), although many have yet to be described in detail.

Thus, many of the western North American sites are associated with upper Lower Cretaceous (Barremian to Albian) deposits. Only one site is from the Berriasian (McCrea et al., 2001) and a few others have been reported from younger Cenomanian through Maastrichtian deposits (Robison, 1991; McCrea et al., 2001; Lockley and Rainforth, 2002; Lockley et al., 2004).

The purpose of this paper is to describe new shorebird tracks that were recovered from a locality near Dinosaur National Monument (DNM): Fig. 1. They were discovered at a relatively inaccessible cliff top location (N 40° 28' 25.6", W 109° 22' 26.2": Fig. 2) while the senior author was conducting an undergraduate field project (see acknowledgements). Two slabs with original tracks were collected, and repositated at Dinosaur National Monument as specimens DINO 17873A and 17873B. Replicas of these specimens in the Dinosaur Tracks Museum, University of Colorado at Denver have the prefix CU. The tracks, which were initially assigned to a new ichnospecies of *Aquatilavipes* (Anfinson et al., 2004) are, for the reasons elaborated below, more appropriately assigned to the ichnogenus *Koreanaornis*. Ideally one should refer new finds to an appropriate existing ichnotaxon wherever possible, and avoid introducing new ichnotaxa for material that is not clearly diagnostic of novel and previously-undescribed morphology. The naming of fossil bird tracks is already complex due to the number of ichnotaxa that are based on incomplete, inaccessible or poorly preserved specimens.

2. Geologic setting

In the study area at the north end of Pipeline Road near the northwest corner of Dinosaur National Monument (Fig. 1) the Dakota Formation (Albian–Cenomanian) is ~32 m thick and

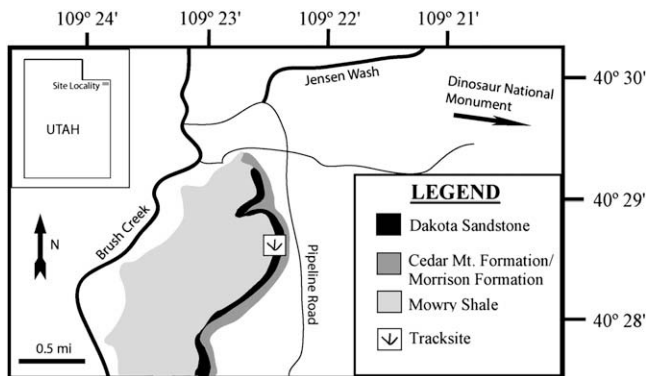


Fig. 1. Map of Utah and a detailed topographic map of the tracksite from the Dakota Formation at the north end of Pipeline Road near Vernal, Utah and Dinosaur National Monument. GPS coordinates: N 40° 28' 25.6", W 109° 22' 26.2".

unconformably overlies the fluvial deposits of the Cedar Mountain Formation and conformably underlies the major transgressive, offshore mudstones of the Mowry Shale, deposited in the Cretaceous Western Interior Seaway (Fig. 2). The Dakota Formation is a transgressive sequence comprising continental (fluvial) to marginal marine sandstone.

The track-bearing layers were found in the uppermost two meters of the Dakota Formation (Fig. 2), in a facies consisting of alternations of mm-thick fine rhythmic silt layers with sandstones about 10–20 cms thick. The footprints are preserved in current-ripple-laminated, fine-grained quartz sandstone capped by a very-fine silt layer. The fine silt layer suggests a period of standing water conditions perfect for preservation. The presence of invertebrate trace fossils implies that the avian trackmaker was active in an area with a potential food source. However there is no direct feeding evidence in the form of bill probe marks. The presence of two track horizons in such close proximity suggests that more tracks likely await discovery in the area.

3. Material and methods

Two track-bearing horizons that display a total of 18 separate footprint impressions were discovered. The lower footprint horizon was discovered approximately 60 cm below and 150 cm west of the upper track-bearing horizon. In this study we concentrate on describing the three well-preserved trackways from the upper horizon, from which two slabs (part and counterpart) were collected (Fig. 3). These specimens comprise three trackways, all of which contain tracks that are similar in general morphology and size to the type material of *Koreanaornis hamanensis* (Lockley et al., 1992). The presence of trackways with different orientations, plus slight size differences, suggests the presence of more than one individual. However, the lack of significant morphological differences, beyond those attributed to minor differences in preservation, suggest only one diagnostic trackmaker morphology: i.e., a shorebird-like track which we assign to *Koreanaornis*.

There are a total of three trace-bearing sandstone slabs associated with the site. Two of these display the positive and negative impressions of the same 10 tracks, (part and counterparts DINO 17873A and 17873B respectively). Of these 10 tracks, two are indistinct and the remaining eight tracks comprise three trackways (Fig. 3). Field relations between the part and counterpart slab were used to differentiate between the positive impression or mold (concave epirelief) and negative natural cast (convex hyporelief: *sensu* Häntzshel, 1975). This differentiation is otherwise difficult because the split between the part and counterpart did not lead to a clean break creating simple positive impressions and infilling casts. In places the fill from the upper layer (counterpart) adheres to impressions, giving the appearance of raised relief (i.e., convex epirelief). This may be in part due to suction effects on the original Cretaceous sediment and/or local compaction caused by the trackmaker (Lockley, 1991; McCrea and Sarjeant, 2001).

The third slab from the lower horizon, which still remains in the field, contains eight impressions. Of the eight impressions, seven are tracks that display a variable range of bird footprint morphologies, and one is a set of three parallel slash or scratch marks resembling *Characichnos* (Whyte and Romano, 2001). These marks look like swimming traces made by a tridactyl animal, possibly the *Koreanaornis* trackmaker (Fig. 4) or, more likely, some other creature (see Milner et al., 2006 and references therein for a recent discussion of swim tracks). There are three small mounds of sand directly behind each of the toe impressions that were pushed or scooped backwards as the animal's

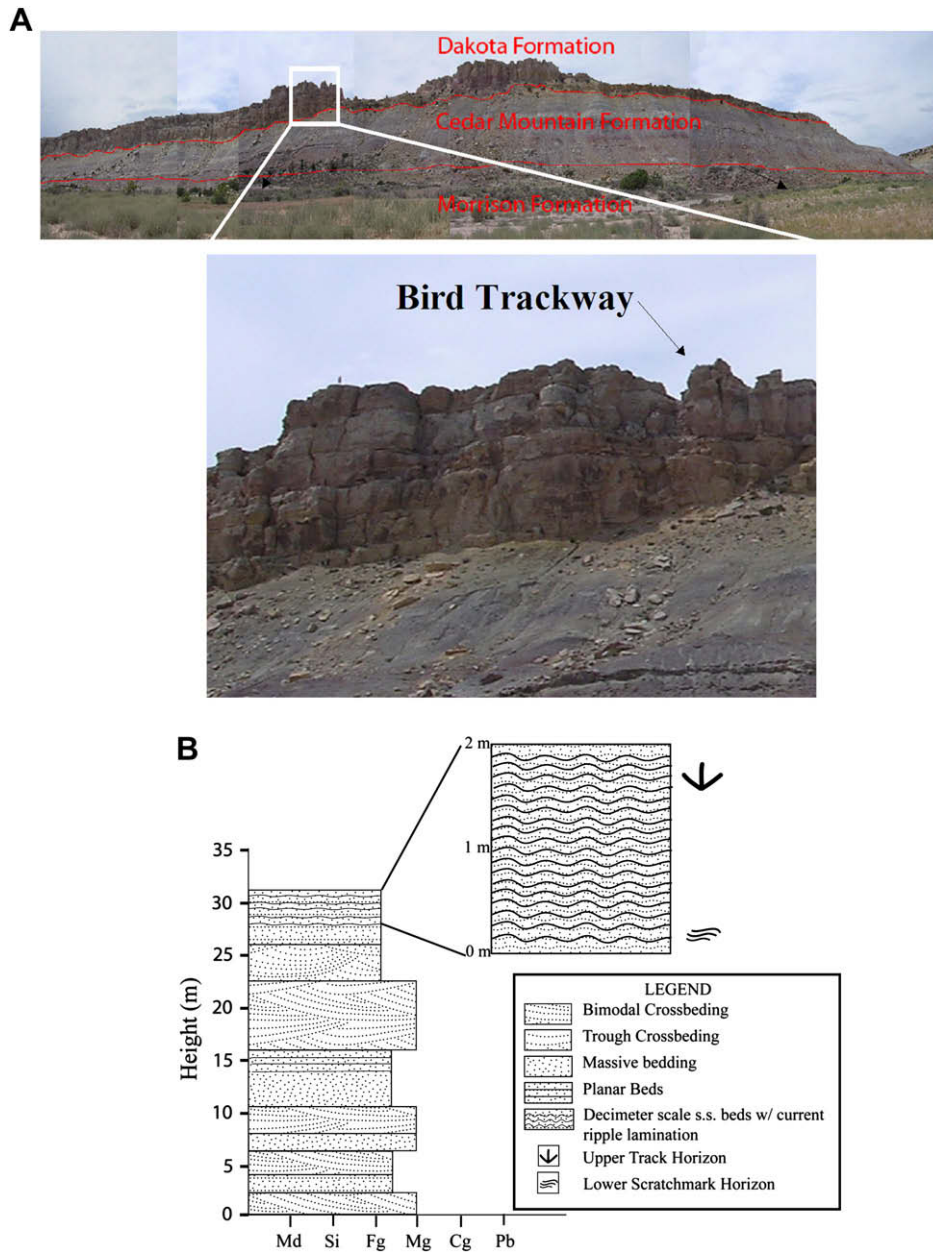


Fig. 2. Photograph (A) and corresponding stratigraphic section (B) of the Dakota Formation, which is approximately 32 m thick at the tracksite.

toes dragged through the sediment. The combination of bird tracks and swim scratch marks, along with the fine silt layers, support the interpretation that during deposition of the uppermost Dakota there was a fluctuation of water levels creating episodes of emergence and submergence.

Initial data on the tracks and their horizon was collected during fieldwork in the summers of 2003 and 2004. Paleoenvironmental analysis was undertaken through measuring a series of stratigraphic sections at six localities along the Dakota Sandstone outcrop at the north end of Pipeline Road, near DNM. The use of petrographic thin-sections further aided in the determination of the lithology as fine to medium grain quartz sandstone. The track data was compiled through drawings in the field and from analyzing pictures taken at the track site and at DNM where the slabs are repositied. The slabs were also replicated for the CU Denver Dinosaur Tracks Museum (DINO

17873a = CU 212. 31 and DINO 17873a = CU 212. 32). The specimens were also traced on clear acetate to facilitate production of accurate scale drawings (Fig. 3). All of the tracks were measured and tabulated (Table 1). The step, stride and pace angulations were measured from a series of four consecutive tracks, using the midpoint of each heel (Fig. 5). The angles of divarication are taken between lines drawn down the center of each digit. Width and length measurements are taken from the longest or widest part of the track. Digit divarications (often 110–140° or more in shorebirds) are important in distinguishing this type of avian trackmaker from small dinosaurs that have typical digit divarications much less than 90–100° (Lockley et al., 1992). Shorebird tracks are also typically wider than long whereas the reverse is true for non-avian theropod tracks, in which footprint lengths are usually greater than widths (Moratalla et al., 1988; Lockley et al., 1992; McCrea and Sarjeant, 2001).

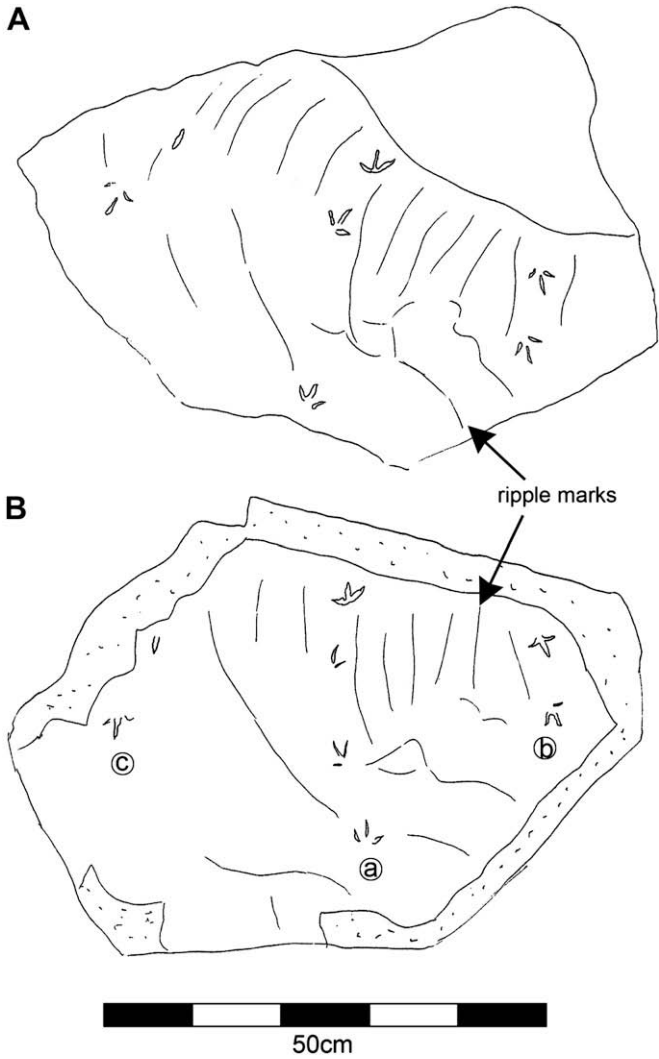


Fig. 3. The main trackbearing slabs (DINO 17873A,B) represent part and counterpart of three trackways. The central trackway (a) is the most complete.

4. Ichnological descriptions

4.1. Preliminary observations

A number of criteria affect the choice of ichnotaxonomic designation for the Utah trackways. These criteria are primarily morphological, as presented in the primary literature for given

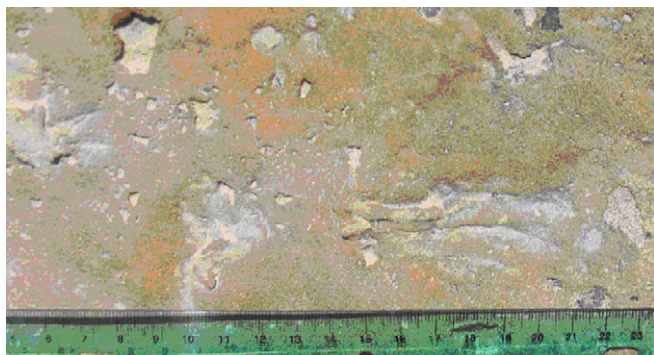


Fig. 4. The lower horizon showing one footprint (left) and swim scratch marks (right).

Table 1

Track measurements (length, width, digit divergences and steps) for trackways a, b and c from specimen DNM 17873a,b. Compare with Fig. 3.

Track number	Track length	Track width	Angle° II–III	Angle° III–IV	Angle° II–IV	Step a ¹ –a ²	Step a ² –a ³	Step a ³ –a ⁴
a ¹	2.7	3.3	70	41	111	9.6	11.0	7.5
a ²	2.5	2.7	66	45	111			
a ³	2.8	3.0	64	46	110	–	–	–
a ⁴	2.8	3.1	58	38	96	–	–	–
a mean	2.7	3.025	64.5	42.5	107°			a ¹ –a ⁴ = 9.37
b ¹	2.6	3.1	54	62	116	b ¹ –b ²		
b ²	2.7	3.1	60	43	103	7.9		
c ¹	2.9	3.1	79	59	138	c ¹ –c ²		
c ²	2.9	(3.2)*	65	–	–	10.7		
Grand mean	2.74	3.08	64.5	47.9	112.1	9.32	–	–

ichnotaxa (Mehl, 1931; Kim, 1969; Currie, 1981; Lockley et al., 1992, 2006a; Kim et al., 2006), with secondary considerations pertaining to size (also an aspect of morphology) and preservation. Paleogeography and age of trackmaker is also important to consider, though not considered relevant criteria in ichnotaxonomy.

Specimens DINO 17873A and B, herein referred to as *Koreanaornis* cf. *hamanensis* (Fig. 3) reveal footprints that are no more than 3.0 cm long and 3.5 cm wide (mean = 2.74 and 3.08 cm respectively; Table 1). By comparison the *Aquatilavipes* holotype (*A. swiboldae*) from Canada is 3.75 cm long and 4.67 cm wide: i.e. between 37 and 51% larger. The averages for the whole *Aquatilavipes* sample are 3.5 and 4.4 cm (n = 169 and 103 respectively; Currie, 1981). Paratypes of *A. swiboldae* may be as large as

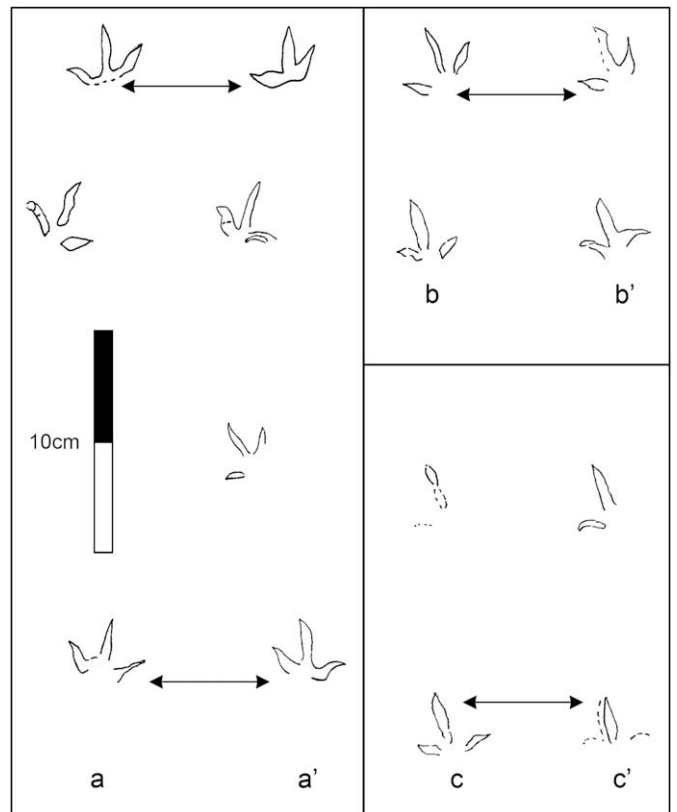


Fig. 5. Detailed drawings of the part and counterpart (natural mold and natural cast) of the three trackways (a–c) from specimen DINO 17873A and 17873B. Individual footprints are referred to as a¹–a³, b¹–b², and c¹–c² in text.

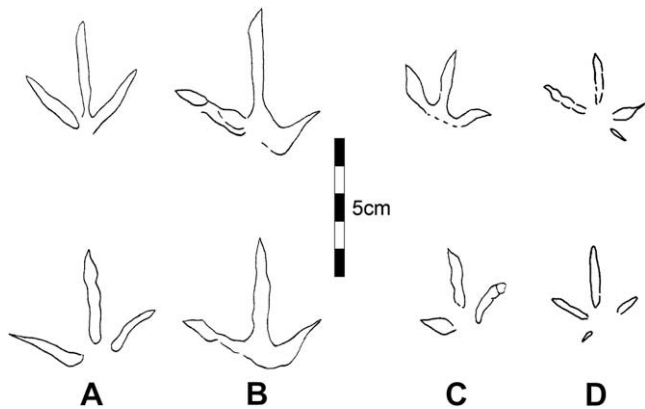


Fig. 6. Comparison between *Aquatilavipes* from Canada (A), South Dakota (B) and *Koreanaornis* from Utah (C) and Korea (D). A: after Currie (1981), B after Lockley et al. (2001), C after Fig. 5 (herein), D after Lockley et al. (1992). Note that *Koreanaornis* examples from Korea are rare examples of tracks where the hallux is preserved. The majority, including the type material do not show hallux traces.

4.5 × 5.3 cm, which is also the typical size of *Aquatilavipes* from the Lakota Group of South Dakota (Lockley et al., 2001; Fig. 6 herein). Only a few specimens from this large Canadian sample, of more than 200 footprints, are much smaller: i.e., less than 3.0 cm. The size variation is attributed to ontogeny by Currie (1981), but in our opinion might also be due to preservational variation and the possible admixture of more than one track type (ichnospecies). Preservational influences are also acknowledged by Currie (1981), who noted that within trackways made by the same individual size variation is not more than 10%. However, Currie (1981) did not illustrate individual trackways, and his measurements are of limited use for comparison suggesting only that step length averages 2.3 × foot length (compared with ~3.5 × foot length in the Utah sample: Table 1). Although they do not discuss size-variation in detail, most modern field guides dealing with shorebird tracks (Jaeger, 1948; Murie, 1974; Elbroch, 2001) note remarkable consistency in the size of tracks of any given species of shorebird. Size is considered a diagnostic character for modern bird track identification even though it is not generally considered a valid diagnostic character in paleoichnotaxonomy. Thus, we consider it very unlikely that the Utah and Canadian trackways were made by the same species.

However, by ichnological convention it is morphology, not size, that is the main criteria for distinguishing ichnospecies. The following morphological considerations indicate that the Utah tracks are similar to *Koreanaornis hamanensis*, from the Lower Cretaceous of Korea (Kim, 1969), but unlike *Aquatilavipes*. Digit divarication angles for *Koreanaornis* (Table 1), indicate II-III > III-IV whereas the opposite is characteristic of *Aquatilavipes* (II-III < III-IV). The inward rotation of the foot axis (digit III) in *Koreanaornis*, is typical of many modern shorebirds and ancient shorebird-like track makers, but the degree of inward rotation, if any, is unknown in *Aquatilavipes* (Currie, 1981). Ideally such rotation angles can only be measured confidently in trackways with three or more consecutive footprints (Peabody, 1955; Sarjeant, 1989).

Re-description of *Koreanaornis hamanensis* by Lockley et al. (1992) demonstrated that, in a minority of cases, topotypes of the ichnospecies preserves a small medially directed hallux trace. A hallux trace has never been reported for *Aquatilavipes*. The absence of this feature in most *Koreanaornis* tracks may be the result of variable preservation and the inherently small size of the hallux. Thus, a hallux trace is not a consistent, morphological feature, nor was it included originally in the formal description of the ichnospecies (Kim, 1969). At present however, the rare occurrence of

hallux traces provides an additional, albeit sporadically-preserved criterion for differentiating *Koreanaornis* from *Aquatilavipes*.

Neither *Koreanaornis* nor *Aquatilavipes* have well-defined or well-constrained spatial or temporal distributions. This is in part because *Aquatilavipes* has been used as a catch-all ichnogenus in reference to small bird tracks from a number of Asian bird track localities, and partly because the exact age of these localities is poorly known. For example, tracks named *Aquatilavipes sinensis* (Zhen et al., 1995) from Sichuan Province are probably a junior synonym of *Koreanaornis hamanensis* (Lockley, 2007a; Lockley et al., 2008). The discovery of similar tracks in Shandong Province and elsewhere makes it necessary to re-evaluate the differences between *Koreanaornis* and *Aquatilavipes* in order not to create false impressions of their distributions. It appears the reason *Koreanaornis* has, until now, only been reported from Korea, is that the type was discovered at a time when there was little interest in vertebrate ichnology, and so it was only known locally. By contrast *Aquatilavipes* was reported by an internationally-known paleontologist (Currie, 1981) at a time when interest in ichnology was much greater. Consequently *Aquatilavipes* was subsequently identified in Asia, but *Koreanaornis* was not identified in North America or elsewhere. While failure to identify *Koreanaornis* in Sichuan may be interpreted as an oversight, partly rectified by the preliminary identification of *Koreanaornis* elsewhere in China (Lockley et al., 2008), the failure to identify the ichnogenus in North America, until now, appears to be a legitimate reflection of its absence at other known sites on this continent.

4.2. Formal descriptions

Class: AVES

Ichnofamily Koreanornipodidae (Lockley et al., 2006a)

Ichnogenus: *Koreanaornis* (Kim, 1969)

Koreanaornis cf. *hamanensis*

Material: trackway a consists of 4 consecutive footprints preserved on sandstone slab DINO17873B (negative impression) and corresponding counterpart DINO17873A (positive impression) showing only three corresponding tracks (Figs. 3 and 5). Of the tracks, footprint a³ (left foot) has the best detail and best pad impressions on the digits. Both trackways b and c on slabs DINO 17873A and 17873B (Figs. 3 and 5) consist of only two consecutive footprints.

Description. Trackways of a small bird with tridactyl feet averaging about 2.7 cm long and 3.0 cm wide. Digit divarications average 64.5°, 42.5° and 107° for II-III, III-IV and II-IV respectively. Step varies between 7.5 and 11.0 cm. Stride varies from 18.3 (a²–a⁴) and 20.0 cm (a¹–a³). Digit III shows inward rotation relative to trackway midline (22°–32° for tracks a³ and a² respectively).

Comparative ichnology. Although our main objective is to demonstrate that *Koreanaornis*, rather than *Aquatilavipes*, is the best designation for the Utah specimens, further comparisons are necessary for more complete analysis. Recent work by one of us (S. H. Kim) in the Haman Formation has revealed abundant bird tracks attributed to *Koreanaornis hamanensis* and other ichnospecies that also represent small shorebird-like taxa (Kim et al., 2006). These will be described in detail elsewhere. However, given that no trackway of *Koreanaornis* consisting of more than three footprints has ever been illustrated, we include a representative example herein (Fig. 7) to allow comparison with the Utah specimen. A replica of this specimen (CU 214.134) is deposited in the Dinosaur Tracks Museum collections at the University of Colorado (Denver).

As noted below, other small shorebird tracks resembling *Koreanaornis* are known from Mesozoic and post-Mesozoic deposits. For example, *Barrosopus* from the Upper Cretaceous of Argentina (Coria

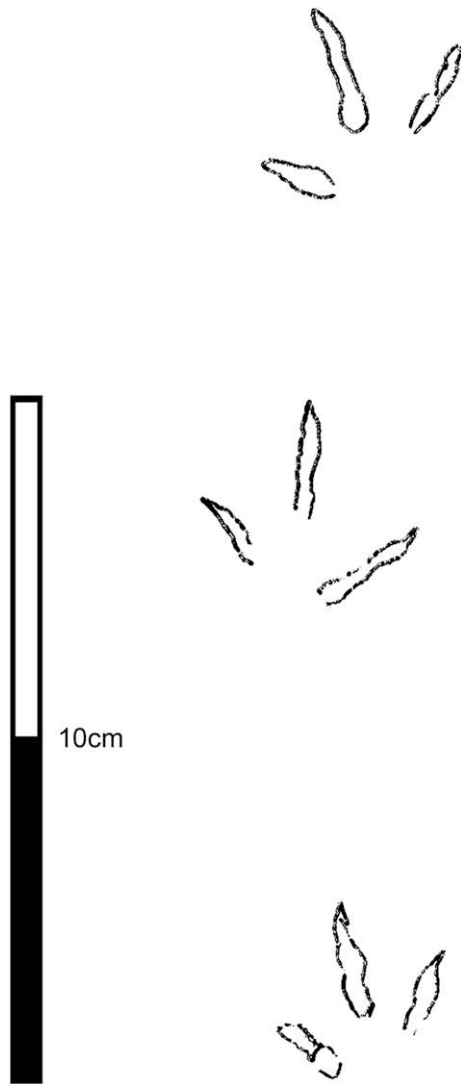


Fig. 7. *Koreanaornis* trackway from the Haman Formation, Cretaceous Korea (CU 214.134).

et al., 2002) is similar to the Utah specimen, but as *Koreanaornis* was named long before *Barrosopus*, *Koreanaornis* necessarily has priority. However, to the best of our knowledge there are no other well-described, named bird tracks from North America or elsewhere that are more similar to the Utah specimen than *Koreanaornis*. Indeed the only well-documented bird tracks from North America are *Ignotornis* (Mehl, 1931; Lockley et al., 2007b, 2009), *Aquatilavipes* (Currie, 1981) and *Sarjeantopodus* (Lockley et al., 2004). *Ignotornis* is easily distinguished from the Utah specimens (*Koreanaornis*) being twice the size, with robust digits, a pronounced hallux and an incipient semipalmate web between digits III and IV. The type of *Aquatilavipes* is significantly larger than Utah *Koreanaornis* (Fig. 6). Likewise *Sarjeantopodus* (Lockley et al., 2004) is also a large track with a well-developed semipalmate web trace incorrectly re-interpreted as an artifact by Falkingham et al. (2009).

5. Distribution of *Koreanaornis* and *Aquatilavipes* in space and time

As noted above *Koreanaornis* was previously known only from the Haman Formation of Korea (Kim, 1969) and the overlying

Jindong Formation (Lockley et al., 1992). However, if *Aquatilavipes sinensis* (Zhen et al., 1995) is correctly referred to *Koreanaornis* the latter form then also occurs in Sichuan Province, China. Likewise bird tracks discoveries in Shandong Province also suggest the presence of *Koreanaornis* elsewhere in China (Lockley 2007b; Lockley et al., 2008). The age of type *Koreanaornis* is probably Aptian–Albian (Matsukawa et al., 1998, 2006), and the age of the Shandong occurrence may be comparable (Barremian–Aptian) according to Li et al. (2005). However, as noted above the suggested Lower Cretaceous age of the Sichuan occurrence (Zhen et al., 1995; Lockley et al., 2007a; contra Chen et al., 2006) is uncertain. The Utah occurrence of *Koreanaornis* described herein is close to the Albian–Cenomanian boundary.

The type of *Aquatilavipes* (*A. swiboldae*) is known from British Columbia (Currie, 1981) and it is this ichnospecies that we use as the basis for our comparisons with *Koreanaornis*, because other species of this ichnogenus have not been described in comparable detail. Other occurrences of the ichnogenus *Aquatilavipes* (*sensu lato*) include the South Dakota site (Lockley et al., 2001) and sites in Japan (Lockley et al., 1992; Azuma et al., 2002) and China (Li et al., 2006; Zhang et al., 2006). The large ichnospecies *A. curriei* was named by McCrea and Sarjeant (2001) and *A. izumiensis* was described by Azuma et al. (2002). However, *A. curriei* is not at all similar to typical *Aquatilavipes* and should be transferred to another ichnogenus (McCrea personal communication). Although some Asian bird track identifications (e.g., *A. sinensis*, Zhen et al., 1995) have been questioned, *Aquatilavipes* and *Aquatilavipes*-like tracks, that have not been formally named, occur at other sites in China: i.e., in Inner Mongolia (Lockley et al., 2002).

North American *Aquatilavipes* tracksites all occur between the Barremian–Aptian and Cenomanian (Currie, 1981; Lockley et al., 1992, 2002; McCrea and Sarjeant, 2001; Azuma et al., 2002). However, although the ichnogenus or similar forms may occur in this interval in East Asia, (e.g., in Inner Mongolia: Lockley et al., 2002), elsewhere in the region the ichnogenus is reported as early as the Valanginian (Lockley et al., 1992; Azuma et al., 2002).

Existing evidence, therefore fails to draw any clear-cut distinction between the spatial and temporal distribution of *Aquatilavipes* and *Koreanaornis*. At present, the best possible conclusion is that *Aquatilavipes* is more widely distributed in space and time than *Koreanaornis*, especially in North America, but that both ichnogenera may co-occur in the upper Lower Cretaceous (~Barremian–Aptian). Given such uncertainty, the spatial and temporal distributions of both ichnospecies are too patchy to allow any firm biostratigraphic inferences.

6. Discussion

6.1. Naming small shorebird tracks

As summarized by Lucas (2007) Oleg Stepanovich Vyalov published a landmark, but problematic paper (Vyalov, 1965) in which he “proposed that all bird tracks be assigned to the single ichnogenus *Avipeda*” (Lucas, 2007, p. 113). This is clearly both impractical and unjustified on morphological grounds: i.e., bird tracks show considerable morphological diversity which, in the case of modern species, correlate with diagnostic morphological variation at the genus and higher taxonomic levels (Lockley et al., 2007c). Although Lucas (2007, p. 114) credited Vyalov with being conceptually ahead of his time and also affirmed that Vyalov’s ichnospecies were “correctly introduced in accordance with the International Code of Zoological Nomenclature” he noted that many of his illustrations are of poor or indifferent quality and lack scales. Thus, according to Lucas (2007) Vyalov’s ichnotaxonomic work, published in Russian, and dealing exclusively with Miocene tracks, is, like the tracks

themselves, rather inaccessible to English speaking ichnologists, and has not received the attention it deserves. As noted above a parallel can be drawn with *Koreanaornis* (Kim, 1969) which did not receive the attention it deserves, in part because the description of the ichnogenus *Aquatilavipes* (Currie, 1981) was more accessible.

The question arises as to whether *Koreanaornis* (or any other avian ichnotaxon) is synonym of *Avipeda*. Although several authors, working on Cenozoic bird tracks have attempted to re-evaluate Vyalov's ichnogenus, including *Avipeda*, and have labeled some small shorebird tracks with this name (Sarjeant and Langston, 1994; Sarjeant and Reynolds, 2001) they have ignored *Koreanaornis*. Thus herein, for the first time, we consider the possibility of synonymies between Cenozoic and Mesozoic shorebird tracks. The 1965 and 1966 ichnogenus named by Vyalov potentially have priority over ichnotaxa such as *Koreanaornis* which was named later (Kim, 1969). This would be especially true if *Koreanaornis* could not be distinguished on the basis of diagnostic morphological features. But until Vyalov's *Avipeda* types can be compared along side the types of *Koreanaornis*, no conclusions can be drawn.

The ichnotaxonomic picture is further complicated by the work of Panin and Avram (1962) which has potential priority over Vyalov's work. Thus, the terminology of Panin and Avram (1962) has also been used by Sarjeant and Langston (1994), Sarjeant and Reynolds (2001) and Remeika (2001) also without reference to *Koreanaornis* and other Mesozoic ichnotaxa. For example, Panin and Avram (1962) described tracks attributable to the extant shorebird group Charadriiformes, which includes plovers and sandpipers, and named them as *Charadriipeda*. However, neither of the two ichnospecies they placed in this ichnogenus are similar to *Koreanaornis*: one (*C. recurvirostriodea*) has a well-developed web traces, between digits II and III and digits III and IV, and the other (*C. minima*) has a well developed hallux. These diagnostic features are not seen in *Koreanaornis* nor, according to Sarjeant and Langston (1994), are they characteristic of their amended definition of Avipedidae.

Thus, excluding *Charadriipeda*, we can focus on a consideration of ichnogenus *Avipeda* and the ichnospecies *Avipeda phoenix* and *Avipeda sirin* described by Vyalov (1960, 1965, 1966), and re-illustrated by Lucas (2007, p. 114). The former ichnospecies (*Avipeda phoenix*) was subsequently designated as the type species for ichnogenus *Avipeda* by Sarjeant and Langston (1994). Although Vyalov (1965) introduced the name *Avipeda phoenix* in 1965, and explicitly limited it to specimens described as up to 1.6 cm long, he did not designate or illustrate a holotype until 1966. Based on this explicit size limit, it could be argued that his intent was to exclude larger tracks from this ichnospecies. Indeed, he also named *Avipeda sirin* for a specimen illustrated in an earlier paper (Vyalov, 1960), and this ichnospecies has a middle digit 2.5 cm long, in the holotype, and more than 3 cm long in other specimens. Thus, Vyalov (1966) expanded the concept of ichnogenus *Avipeda* to include larger shorebird tracks. On the basis of this information, one might consider *Avipeda sirin* similar to *Koreanaornis hamanensis*. However, the *A. sirin* holotype has very wide digit divarication (~155° between II and IV) and appears to be a poorly preserved isolated footprint that is not part of a trackway. Thus, as already stressed, any suggestion of synonymy cannot be confirmed without a detailed comparison of the type material of both ichnospecies.

Vyalov's inclusion of many morphologically distinct and much larger tracks (up to 13 cm in length) in *Avipeda*, dilutes the concept of *Avipeda* to the point where it lacks any diagnostic morphological significance. For example, Vyalov included morphotypes in *Avipeda* which are obvious junior synonyms of ichnogenus such as *Ardeipeda* (a large heron track) named by Panin and Avram (1962) and discussed by Lockley et al. (2007c). Sarjeant and Langston (1994) considered *Avipeda* representative of a poorly-defined

'morphofamily' which they named Avipedidae. However, given Vyalov's original intent to have *Avipeda* cover "all" bird tracks, their designation of morphofamily Avipedidae (Sarjeant and Langston, 1994) is too vague and undiagnostic, even at the familial level, to have much meaning.

The implications of the preceding evaluation are complex but can be summarized as follows: 1) no serious attempt has previously been made to compare Cenozoic and Mesozoic shorebird tracks, and until this is done conclusive ichnotaxonomic inferences will be difficult, and at best tentative, as the following inferences indicate: 2) *Koreanaornis hamanensis* may be similar to *Avipeda sirin* in size, but the latter ichnospecies is too poorly known to allow useful comparison, without restudy of the type material which is currently inaccessible to the present authors: 3) the ichnotaxonomy of *Avipeda* is complex and in flux. While some authors have attempted to amend Vyalov's ichnogenus *Avipeda* (Sarjeant and Langston, 1994) and have named multiple new ichnospecies, others (Lucas, 2007, 113) have avoided "an analysis or revision of Vyalov's ichnotaxonomy." We agree with Sarjeant and Langston (1994) that revision is desirable, but note that the problems are complex, potentially ambiguous and unlikely to be resolved without a wide-ranging and comprehensive study of all avian ichnotaxonomic literature and specimens.

6.2. Affinity of the trackmaker

The morphological characteristics for identifying shorebird or shorebird-like tracks are: 1) gracile appearance with slender digit impressions, with indistinct pad impressions, but corresponding to a 2,3,4 phalangeal formula for digits II, III and IV respectively if present; 2) tracks wider than long, exclusive of hallux digit I (if present), with corresponding wide angle of divarication (typically about 110°–120°) between digits II and IV, but ranging from 100°–150° or more, with angle between digits II and III usually consistently different from the angle between III and IV where large samples are available for measurement; 3) small size, typically from about 2.5 to 7.5 cm 4) slender terminal claws. Although these characteristics show some variation, there are other characteristics that are typically more highly variable between different ichnotaxa, but consistent within a given ichnotaxon. These include: 5) presence or absence of a hallux, 6) orientation of hallux if present (posterior to postero-medial), 7) rotation of pes axis (digit III axis), which is often but not always strongly inwardly rotated by as much as 30–35°, 8) angular bend in digit II, 9) presence or absence of a proximal web traces between digits II and III and/or III and IV (semi-palmate condition). Usually the web is only incipiently developed between digits III and IV, and absent between digits II and III. As noted above, the presence of well-developed web traces easily distinguishes *Charadriipeda* from forms like *Koreanaornis*.

All shorebird-like tracks from the Cretaceous fall within a size range that is common among modern shorebirds. Indeed, many Cretaceous and Cenozoic tracks are almost indistinguishable from modern tracks. As noted by (Lockley et al., 1992) most tracks of this type were made in shoreline settings very similar to those frequented by modern trackmakers. In such settings high densities of tracks are common. For these reasons a Cretaceous-through Recent 'shorebird ichnofacies' has been defined (Lockley et al., 1994); see Doyle et al. (2000); Lockley (2007b) and Hunt and Lucas (2007) for further discussion of the vertebrate ichnofacies concept.

With the recent increase in the number of discoveries of shorebird-like tracks in the Cretaceous it is clear that there is considerable diversity of form among these early trackmakers. Many tracks such as *Koreanaornis* and *Aquatilavipes* are attributed to Charadriiform-like birds such as plovers and sandpipers (Currie,

1981; Lockley et al., 1992, 2006 a,b; Lockley and Rainforth 2002). Both groups typically lack a hallux, though a very short hallux may be present in some sandpiper species. Based on these criteria, *Koreanaornis* from Utah could well have been made by a small plover like species. Based on footprint size and lack of a developed hallux the trackmaker was a bird in the size range of a killdeer (*Charadrius morinellus*: foot length 2.5–3.0 cm) or a semipalmated plover (*Charadrius semipalmatus*: foot length 2.2–2.7 cm) both of which have strongly inwardly rotated tracks (Elbroch, 2001). These sizes also match *Avipeda sirin* (Vyalov, 1966; Lucas, 2007), and *Avipeda adunca* (Sarjeant and Langston, 1994). A few shorebirds have smaller feet. The sanderling (*Calidris alba*: foot length 1.6–2.2 cm) and the Piping Plover (*Charadrius melodus*, foot length 1.9–2.4 cm) have footprint sizes that approach those reported for *Avipeda phoenix* (Vyalov, 1966; Lucas, 2007). Larger *Aquatilavipes* from Canada and South Dakota more closely match the size of the tracks of the Black Bellied Plover (*Pluvialis squatarola*; foot length 3.5–4.1 cm) or those of the Black-Necked Stilt (*Himantopus mexicanus*; foot length 4.4–5.2 cm).

6.3. Paleoecology

Analysis of the Utah *Koreanaornis* cf. *hamanensis* tracksite clearly demonstrates that the trackmakers were small shorebird-like species that inhabited a marginal-marine coastal environment. From comparisons with other ancient and modern shorebird tracks it is clear that the trackmaker was comparable to the smallest known species. Observations of modern shorebirds indicate that they make abundant tracks in shoreline sediments while feeding (Frey and Pemberton, 1987). The abundant co-occurrence of bird and invertebrate traces suggests a possible feeding site. The trackmaker was active in a marginal marine environment where there was a rhythmic alternation of current activity and standing water leading to cyclic deposition. Such conditions were evidently favorable for producing fossil tracks. The slight variation in size of the tracks suggest there may have been more than one individual track maker in the upper horizon, and the presence of scratch or swim marks and other tracks on the lower horizon, indicates repeat animal activity, and the potential for further discovery and excavation.

Although the sample is small the distribution of the three trackways shows a discernable pattern: i.e. the central trackway goes in one direction and the two other that flank it on either side run in the opposite direction. This 'bimodal' distribution suggests back and forth activity along a shoreline. The trackways also run more or less parallel to the ripple crests.

Although Dakota Group vertebrate tracksites are widespread across many states (Utah, Colorado, New Mexico, Oklahoma, Kansas and Nebraska) in the western USA, only two bird tracksites are known out of a total of more than 65 recorded localities where dinosaur and other archosaur (crocodilian) footprints are common (Lockley and Hunt, 1995; Lockley et al., 2006c). These are the *Ignotornis* type locality (Mehl, 1931; Lockley et al., 2007b) and the '*Koreanaornis*' locality described herein. This suggests either that birds (i.e., shorebird-like taxa) were relatively rare in the Cretaceous of the area that is now the western USA, or that the environments where they may have been active were not conducive to track making or track preservation. Given that *Ignotornis* tracks are very common at the single locality where they occur (Mehl, 1931; Lockley et al., 2007b, 2009), it appears that preservational bias can not be invoked as a compelling explanation. Likewise, given the relatively intensive search for dinosaur tracks undertaken by ichnologists in the Dakota Group, the lack of bird tracksite discoveries is evidently not a function of lack of searching in these deposits. Thus, the rarity of bird tracks

may be a function of their ecological distribution during Dakota times. By comparison bird tracks are evidently somewhat more common in western Canada (McCrea et al., 2001; McCrea and Sarjeant, 2001), and very abundant in coeval Lower to 'mid' Cretaceous deposits in East Asia, both in Korea and China, where they occur in a variety of different depositional settings (Yang et al., 1995; Lockley et al., 2006a; Kim et al., 2006). In other well-studied regions such as Europe (Lockley and Meyer, 2000) and South America (Coria et al., 2002), the Cretaceous bird track record is even more impoverished than in the western USA. Indeed, in the case of Europe, purported bird tracks (Fuentes Vidarte, 1996) are unlike any shorebird footprints described from other regions and may be those of theropods (Lockley and Meyer, 2000). The question remains as to whether these differences reflect differences in avian paleobiogeography during the Cretaceous. We consider it prudent to infer that this is an open question and that the picture will likely change as more avian tracksites become known.

Based on current evidence, the diversity of bird tracks in the Dakota Group is low, comprising only two ichnotaxa. Even if we add in *Aquatilavipes* and extend the area considered to include the Western Interior Seaway (western USA), the diversity remains low in comparison with that recorded for the Lower to 'mid' Cretaceous record in East Asia (Matsukawa et al., 2006). However, excluding the Upper Cretaceous record, which is also sparse in the western USA (only ichnogenus *Sarjeantopodus*, Lockley et al., 2004 has been named), all three known avian ichnogenera from the Lower to 'mid' Cretaceous of North America (*Ignotornis*, *Aquatilavipes* and *Koreanaornis*) also occur in East Asia. None currently appear to be of precise biostratigraphic utility beyond suggesting an Early to 'mid' Cretaceous age.

7. Conclusions

- (1) A small shorebird-like track herein assigned to the ichnotaxon *Koreanaornis* cf. *hamanensis* (Kim, 1969) represents only the second report of avian tracks from the 'mid' Cretaceous Dakota Group. We therefore reject the previous suggestion that the tracks can be assigned to *Aquatilavipes* (Anfinson et al., 2004).
- (2) At least three sets of bird tracks, including those described herein (and Chinese and Canadian examples) had previously been incorrectly attributed to *Aquatilavipes*, suggesting that this ichnogenus is too often used as a catch-all ichnotaxon.
- (3) The tracks are similar to the Miocene tracks *Avipeda sirin* (Vyalov, 1966), but deficiencies in the description of that type material prevents any formal synonymy, without further detailed study.
- (4) Review of the literature on shorebird tracks reveals that there have been no serious attempts to compare avian ichnites between the Mesozoic and Cenozoic. This creates ambiguities of the type noted above (conclusions 2 and 3).
- (5) Despite yielding more than 60 vertebrate tracksites, bird tracks are comparatively rare in the Dakota Group, and in the Lower to 'mid' Cretaceous of western USA in general, especially in comparison with coeval deposits in East Asia. This is tentatively interpreted as reflecting real differences in paleoecology, rather than obvious preservational bias or lack of exploration.
- (6) The few bird track types known (3 ichnospecies) from the Lower to 'mid' Cretaceous of western USA are evidently the same as components of the more diverse east Asia avian ichnofaunas which contain as many as 9 valid ichnogenera, some with more than one ichnospecies.

- (7) There is currently little compelling ichnological evidence suggesting that Cretaceous bird tracks have any biostratigraphic utility.

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