

INTERPRETING BEHAVIOR FROM EARLY CRETACEOUS BIRD TRACKS  
AND THE MORPHOLOGY OF BIRD FEET AND TRACKWAYS

By

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B.S., Lake Superior State University, 2007

Submitted to the Department of Geology and the Faculty of the Graduate School of  
the University of Kansas  
In partial fulfillment of the requirements for the degree of  
Master of Science

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## ABSTRACT

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Bird tracks were studied from the Lower Cretaceous Lakota Formation in South Dakota, USA, and the Lower Cretaceous Haman Formation, South Korea. Behaviors documented from the Lakota Formation included: (1) a takeoff behavior represented by a trackway terminating in two subparallel tracks; (2) circular walking; and (3) the courtship display high stepping. Behaviors documented from the Haman Formation included: (1) a low-angle landing in which the hallux toe was dragged; (2) pecking and probing behaviors; and (3) flapping-assisted hopping during walking. The invertebrate trace fossil *Cochlichnus* was associated the avian tracks from the Lakota Formation. No traces of pecking or probing were associated with *Cochlichnus*. The invertebrate trace fossils *Cochlichnus*, *Arenicholites*, and *Steinichnus* were found associated the bird tracks from the Haman Formation. Probe and peck marks associated with the avian tracks and trackways from this Formation may indicate interactions between the birds and the invertebrates that produced the traces.

The distal end of the avian tarsometatarsus affects the angle of divarication of the toes and, therefore, how tracks and trackways will be produced. The greater the arc angle of the trochlea of the tarsometatarsus, the smaller the angle of divarication between the toes. This correlation is true only for anisodactyl birds as the zygodactyl

foot structure has a much greater angle of divarication and, therefore, a more complex arrangement of trochlea. The relationship between the angle of divarication and the arc angle of the trochlea can be used to retrodict the tarsometatarsal morphology and avian morphotype of the fossil tracks and trackways. There is no correlation between stride length and limb length or digit three length in birds; however, weak correlations exist between functional leg length and posture. Weak correlations also exist between avian functional leg length (divided by stride length) as compared to arboreality, method of locomotion, and method of feeding.

## ACKNOWLEDGEMENTS

In the process of completing this thesis, there have been breakthroughs and confusions, complications and achievements, and perhaps most important of all, the stimulation of new ideas for future research, and new hypotheses into the evolution of birds based on both anatomy and trace fossils. These could not have been done without the support and encouragement of many people. My mentor, Larry D. Martin provided a constant sounding board for any new ideas or hypothesis and helped further my interests in avian hindlimb anatomy and evolution. My co-chair, Stephen Hasiotis, assisted me with his in-depth knowledge of ichnology and sedimentology, as well as his tireless editorial aid. Dr. Rick Devlin was always ready to offer advice and direction whenever I asked. Dr. David Burnham of the University of Kansas also provided an excited and enthusiastic ear for any ideas and discussions pertaining to this thesis, and was kind enough to assist me in my field work in South Dakota. Time after time, Mark Robbins, collection manager of the Ornithology division of the University of Kansas Natural History Museum and Biodiversity Research Center, took hours out of his day to assist me in looking through ornithology collections to complete my research. The staff at Black Hills Geologic Institute was extremely helpful, patient, and took time out of their busy schedules to aid me during field work. Ali Nabavizadeh provided a sympathetic ear when things went poorly, and offered helpful advice and critical readings of the chapters within this thesis, and also accompanied me into the field. Reaching back further, I must thank the people who

steered me down this road to begin with, Dr. Thomas Allan of Lake Superior State University, who encouraged me, even as a young undergrad, to study ornithology, Dr. Lewis Brown, who first introduced me to paleontology and geology as a whole, and who first encouraged me to apply to graduate school for paleontology, and Dr. Gregory Zimmerman, who encouraged me throughout both undergraduate and graduate career. Thanks also to A. Feduccia, K. Bader, K. Zielinski, I. Matthews, R. Bramlette, J. Schmerge, D. Reise, A. Rosales, J. Retrum, N. Anderson, S. Knickerson, J. Cheng, and A. Sutton for everything ranging to excellent ideas to moral support. Funds were provided by: The University of Kansas Department of Geology, KUEA Panorama Grant, The University of Kansas Natural History Museum and Biodiversity Research Center, the Geological Society of America and by the University of Kansas General Research Fund allocation # 2301278. Thanks especially to the support—monetary, moral, and otherwise—of my parents, M. and K. Falk.

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## CHAPTER ONE. INTRODUCTION

This thesis provides a behavioral interpretation for two Lower Cretaceous bird tracksites and addresses the morphologic and anatomic variation in bird tracks and trackways. The thesis is divided into three manuscripts (chapters) and covers two main research areas—the Lower Cretaceous Lakota Formation of South Dakota, USA, and the Lower Cretaceous Haman Formation of South Korea (Chapter 2, 3). The third manuscript (Chapter 4) is on modern bird hindlimb anatomy that relates anatomical features surveyed from the University of Kansas Ornithology Collection to such diagnostic criteria as angle of divarication of the toes found in avian ichnofossils. The objectives of this thesis are to (1) interpret Early Cretaceous bird behaviors from examples of tracks and trackways; (2) examine the paleobiogeographic distribution of Early Cretaceous bird trace fossils and evaluate their geographic pattern with respect to early avian evolution; and (3) determine if there is any correlation between the angle of divarication and the different morphotypes of birds. Bird morphotypes may have a specific range of divarication angles that would help to identify potential tracemakers of Mesozoic and Cenozoic avian trace fossil.

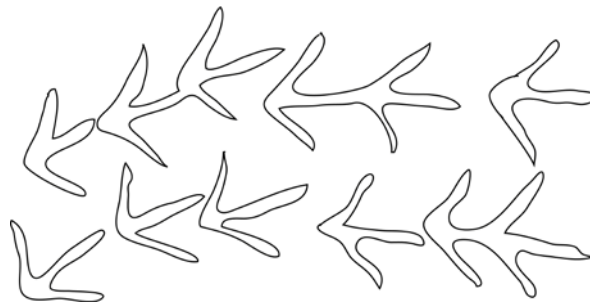
Fossil tracks have been known in the Western Hemisphere since the middle of the 19<sup>th</sup> century (Hitchcock, 1836). These were large tridactyl tracks, originally named *Ornithichnites* and thought to belong to giant birds. Later studies disputed this, as the New Red Sandstone is Lower Jurassic in age (Rainforth, 2005). The first

description of a fossil bird track—one that is still disputed today—was based on a single track found in the Dakota Sandstone of Ellsworth County, Kansas (Snow, 1886). Since that time, many localities containing bird tracks have been discovered worldwide, from Asia to North America (Lockley et al., 1992, 2006; Lim et al., 2000; Azuma et al., 2002; Anfinson et al., 2009). In the last 10 to 15 years, the number of known bird tracksites has greatly increased. This is due in part to a greater interest being taken in the subject, and also many new localities found in Asia.

The majority of avian ichnology research has been primarily concerned with distinguishing the tracks of birds from the tracks of dinosaurs. These studies focus on ichnotaxonomy—the classification of trace fossils—and overall description. While distinguishing criteria and classification are important, they overlook the primary purpose and greatest asset of ichnology: the fact that trace fossils—burrows, nests, borings, tracks, trackways and other traces—are the only direct record of organism behavior in the fossil record. The skeleton of a bird can tell us many things—if it was a wader or a bird of prey, if it depended more on flight or on walking—but the skeleton cannot always show what foraging methods the bird used, its courtship displays, or its interactions with other birds.

Bird tracks provide a great deal of insight into the life habits and evolution of the birds that created the trackways. Fossil trackways and traces are the only records of behavior that exist for extinct animals and plants; particularly for birds in that tracks can show evidence of flight, courtship, feeding and other behaviors. Bird tracks and associated traces can tell scientists not only about feeding behavior of the

bird, but also such potential courtship displays as high-stepping in charadriiform birds, which leaves very clear and precise types of traces (Fig. 1), ground-nesting behaviors, territorial displays, or even types of bathing, such as dust wallows. Nonsediment interactions include woodpecker holes, cracked seed pods, broken-open shells, and arthropod carapaces. Coprolites also should be considered an important type of avian trace, if the bird is the type to leave pelleted feces. Owl pellets are well-known fur-and-bone balls regurgitated by owls after partial digestion. Owl pellets have been reported from fossil sites as early as the Miocene (García-Alix et al., 2008) and are another important trace fossil left by birds. Most bird traces preserved in the fossil record are tracks and trackways, with some secondary features, such as dabble marks (Erickson 1967) or probe marks (Genise et al., 2009). Traces of flight are also preserved as takeoff and landing traces.

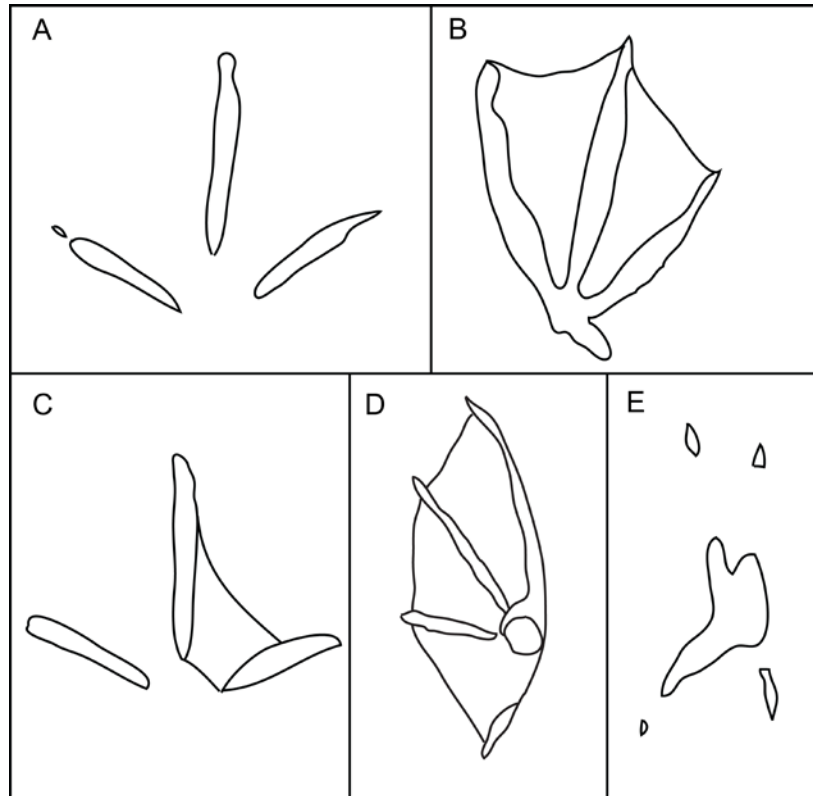


**Figure 1.** An example of a high-stepping courtship display of a Kildeer. Modified from Elbroch and Marks (2001). The overlapping, paired steps terminate in a pair of tracks that are much deeper and more defined than the rest of the tracks in this sequence, as is typical of high-stepping behavior.

The defining characters for bird tracks include the angle of divarication between toes II and IV (110–120°), the slenderness of the digit and claw impressions, the direction of curvature of the claws (away from the midline of the foot), foot length:foot width ratio, and track density (Lockley et al., 1992). Identification of tracks down to the ichnogenic and ichnospecific level involves a diverse and changing set of criteria that has changed over the past two decades. An excellent compendium of these historical criteria has been published by de Valais and Melchor (2008).

There are several different avian morphotypes. Anisodactyl is the most common foot configuration for birds, with toes II, III and IV facing forward, and toe I reflexed, if it is present (Fig 2A). There are several different kinds of webbed feet, including the most common type of webbing, palmate, in which toes II, III and IV are joined by skin (Fig 2B), to semipalmate where only two toes are joined by webbing that may be restricted to only the proximal toe surface (Fig 2C), to totipalmate, in which all four toes are bound together by webbing (Fig 2D). Zygodactyl tracks differ from the standard avian foot configuration by having two toes facing forward, and two toes facing backwards (Fig 2E). This gives the foot and footprints a distinctive appearance—called a “K-shape” in the literature (Elbroch and Marks, 2001)—which can be formed in two different ways. In ground-running cuckoos, such as the Greater Roadrunner (*Geococcyx californianus*), the straight line of this K is formed on the outside of the foot by toes III and IV. Owls such as the Great-Horned Owl (*Bubo*

*virginianus*) on the other hand, create the line on the inside of the foot, with toes I and II becoming the straight edge (Elbroch and Marks, 2001).



**Figure 2.** The different types of foot structures of birds and the tracks left by them.

A.) Anisodactyl. B.) Palmate. C.) Semipalmate. D.) Totipalmate. E.) Zygodactyl.

The earliest undisputed bird tracks are Berriasian in age (Early Cretaceous) and are interpreted as anisodactyl shorebird-like tracks (Fuentes Vidarte, 1996). Tracks of webbed-footed birds appear in the Aptian–Albian (late Early Cretaceous) (Lim et al., 2000, 2002; Kim et al., 2006) based on palynology studies (Kimura, 2000). Zygodactyl tracks are also known from a single locality in the Lower



Cretaceous Tianjialou Formation of northeastern China, which is Aptian–Albian in age (Li et al., 2005; Lockley et al., 2007).

Probe marks and peck marks are common traces associated with modern shorebird tracks and trackways. Certain types of perching birds exhibit similar types of behaviors, such as gaping, in which the beak is pressed into sediment and opened (Elbroch and Marks, 2001). Swallows and other perching birds also scrape mud off of river banks for nest materials. Other modern traces created by birds other than shorebirds include dust baths and certain types of nests (Elbroch and Marks, 2001).

The avian hind limb is different from the hind limb of any other animal. The femur articulates with the pelvis at an angle nearly parallel with the ground, and is splayed out from the body, with the splay angle varying between genera (Hertel and Campbell, 2007). The fibula is reduced to a thin splint and is fused to the tibia. The astragalus and calcaneum have fused to the distal tibia/fibula; this is the tibiotarsus. The tarsometatarsus is made up of the fused distal tarsal and the fused metatarsals (George and Berger, 1966). The distal end of the tarsometatarsus has a series of three trochlea that articulate with the toes. These trochlea can be either arched or straight, with a great deal of variation present in their appearance. The variation in this bone affects the angle of divarication of the toes.

The femur is bound to the abdominal wall with muscle (Heilmann, 1927; Gill, 1995). The femur is never vertical, as in theropod dinosaurs (Kaiser, 2007), instead projecting forward and slightly downward nearly parallel to the pelvis. The femur has little impact upon locomotion even in the most cursorially-adapted bird, the ostrich

(*Struthio camelus*). The femur abducts and adducts only at an angle of  $\sim 9.5^\circ$  (Rubensen et al., 2007). Therefore birds are not hip-driven locomotors, but rather knee-driven (Hutchinson et al., 2008). The knee joint becomes the pivot point for leg movement, and nearly all forward motion is supplied by the tibiotarsus-tarsometatarsus portion of the leg. The ankle joint effectively becomes the knee joint. This is unique among bipeds.

Ground locomotion among avian morphotypes varies. Some birds walk, others run, whereas others hop symmetrically or asymmetrically. Each method of locomotion would be preserved differently in the fossil record. The difficulty, however, lies with birds that walk and run. The transition between speeds in birds can be difficult to see in terms of stride and pace length (Verstappen et al., 1998, Farlow, 2000). Other indicators of speed could be a reduction in the angle of divarication between the toes (Elbroch and Marks, 2001, Genise et al., 2009), however angle of divarication can also vary due to sediment grain size (Currie, 1981). Speed and any transitions between pace will be very difficult to determine from the fossil record.

Mesozoic bird tracks are found worldwide (Lockley et al., 1992) and are generally holarctic, with a notable exception of an Argentinean locality from the Late Triassic?-Early Jurassic? (Melchor et al., 2002, 2006; de Valais and Melchor, 2008; Genise et al., 2009) and a Upper Cretaceous (Campanian) site also found in Argentina (Coria et al., 2002). Early Cretaceous bird tracksites are mainly from shorelines adjacent to freshwater settings (Lim et al., 2002), with few continental-marine transitional zone deposits (Anfinson, 2004). North American bird tracks are found in

environments that are interpreted as having been shorelines in humid climates (Lockely, 2001). Bird tracks in Asia are found in fluvial or lacustrine environments similar to those in North America (Lim et al., 2000). This indicates that these birds were likely shorebirds—in this thesis the term shorebird refers to the general gross morphology, habitat, and behaviors as being similar to modern *Charadriiformes*. Such tracks probably do not represent true Charadriiform birds, as the earliest evidence of that particular order does not appear in the fossil record until the Eocene (Feduccia, 1996).

North America has only three known ichnogenera of bird tracks (Anfinson, 2009). The first unquestionable bird tracks to be described from the Mesozoic were *Ignotornis mcconneli*, from the Dakota group of Colorado (Mehl, 1931). *Aquatilavipes* was the second North American avian ichnogenus to be discovered in 1981, from the Lower Cretaceous Gething Formation in British Columbia, Canada (Currie, 1981). There are several sites with tracks attributed to *Aquatilavipes* in North America, including a site in the Lakota Formation (Lockley et al., 2001). A third ichnogenus has recently been identified as *Koreanaornis* from a locality in Utah (Anfinson, 2009).

The avian ichnofaunas of Asia are much more diverse and abundant than those of North America. Nine ichnogenera have been described from China, Japan and South Korea (Anfinson et al., 2009). All three North American ichnogenera are present, as well as others that include *Jingdonornipes* (Lockey et al., 1992), and the webbed tracks *Uhangrichnus* and *Hwangsaniipes* (Yang et al., 1995).

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## **CHAPTER TWO. A BEHAVIORAL ANALYSIS OF BIRD TRACKS FROM THE LOWER CRETACEOUS LAKOTA FORMATION, SOUTH DAKOTA, USA**

*Currently in review as:*

Falk, A. R., Hasiotis, S. T., Martin, L. D. A behavioral analysis of bird tracks  
from the Lower Cretaceous Lakota Formation, South Dakota,  
USA: *PALAIOS*.

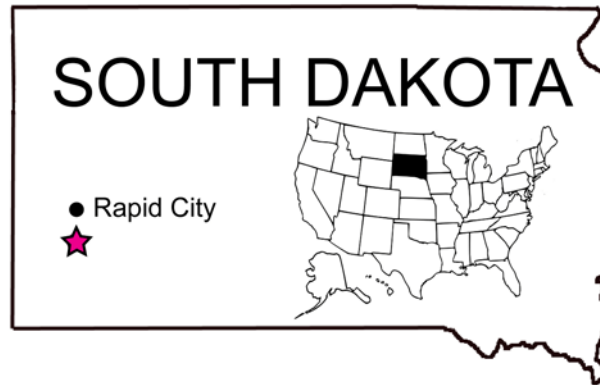
### **ABSTRACT**

Cretaceous bird tracks are known from both the eastern and western hemispheres. This study documents significant behaviors observed in the shorebird track morphotype from the Chilson Member of the Lower Cretaceous Lakota Formation near Hermosa, South Dakota. The tracks used in this study were previously described by Lockley et al. (2001) and assigned to *Aquatilavipes*, though no behavioral interpretations were made. The birds that produced the Lakota Formation tracks were most likely medium-sized, shorebirdlike ornithurine birds resembling the extant genus *Chadrius*, based on morphologic and behavioral interpretations. These tracks and trackways represent such behaviors as feeding, flight, and courtship. Invertebrate traces assigned to the ichnogenus *Cochlichnus* were found with the tracks. No avian feeding traces (e.g. probe or scratch marks) were found associated with the tracks. Behavior is an important factor in Mesozoic birds

because the criteria used to separate theropod and bird tracks overlap in some instances, including the angle of divarication. Many bird behaviors have the potential to be preserved as trace fossils, including locomotion and such feeding-related behaviors as circular or curvilinear walking or probe marks left by the beak of the bird, all of which can be used as proxies for body fossils that represent organisms at the class, ordinal, or family level. The Lakota Formation tracks as well as other Early Cretaceous ornithurine tracks and trackways suggest that shorebird-like ornithurines were widely distributed by the Early Cretaceous and likely represent an earlier origin of this group.

## INTRODUCTION

This paper interprets the behaviors of Early Cretaceous shorebird-like birds from a tracksite in the Chilson Member of the Lakota Formation near Hermosa, South Dakota (Fig. 3). The tracks and trackways, found on massive sandstone blocks, were originally described by Lockley et al. (2001) and assigned to *Aquatilavipes*, though no behavioral analysis was performed. The behavioral interpretations of these tracks and trackways presented here provide important clues to the evolution of early ornithurine birds and their paleogeographic distribution.



**Figure 3.** Locality map. Star indicates study site.

Bird tracks are present worldwide from eastern Asia to central North America by the Early Cretaceous (Lockley et al., 1992). Early Cretaceous bird tracksites are preserved mainly in freshwater deposits (Lim et al., 2002), with a few transitional-zone, track-bearing deposits deltaic deposits in South Korea (Anfinson, 2004). Early Cretaceous tracks are morphologically similar to modern tracks produced by the order Charadriiformes—shorebirds (Kim et al., 2006). Web-footed birds also appear by the Aptian (Kim et al., 2006) and have been attributed to birds that are morphologically similar to avocets, which are also in the Charadriiformes (Lim et al., 2002). It is possible to infer the behaviors of the Lakota Formation trackways based on the morphology of modern and ancient bird tracks, and the similarity of modern and ancient environments. The behavior of the Early Cretaceous birds represented by the Lakota Formation trackways, however, may not be identical to the behaviors of such modern shorebirds as sandpipers, curlews, and plovers. Note that in this paper, reference to the shorebird morphotype does not imply a relationship to the extant order of shorebirds Charadriiformes.

Previous studies of Early Cretaceous bird trackways have focused on morphometric measurements and ichnotaxonomy. Studies interpreting behavior from fossil bird tracks have been conducted on sites in the Eocene Green River Formation (Erickson, 1967; Yang et al., 1995). A recent study by Genise et al. (2009) observed modern shorebirds in ephemeral ponds in the mid-eastern Atlantic coast of Argentina and provide behavioral criteria for modern shorebirds that can be correlated to ancient tracks. Their study, however, does not extend to such breeding and courtship behaviors as the dancing of cranes or the high-stepping display in plovers (*Chadrius*) that produce distinctive track impressions and patterns (Elbroch and Marks, 2001).

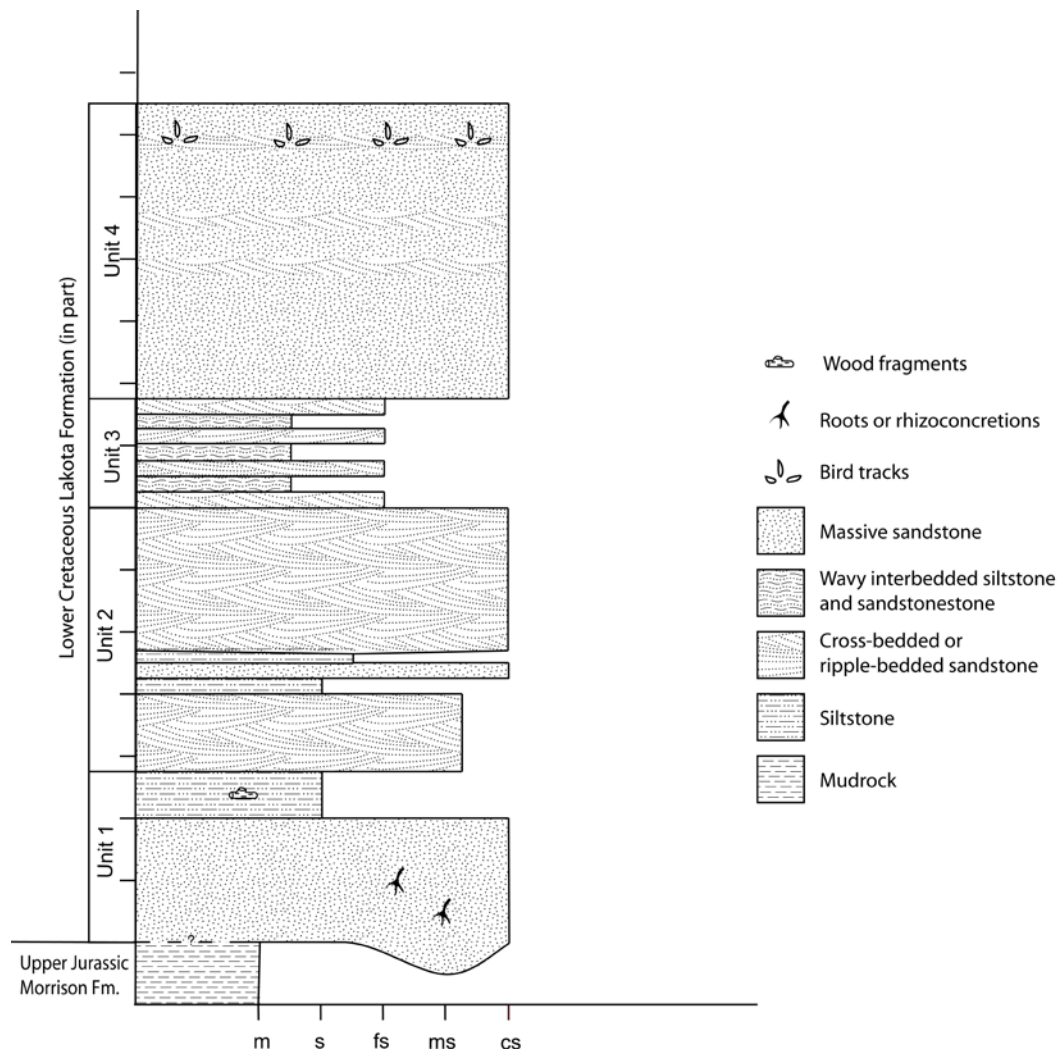
## GEOLOGIC SETTING

In the study area, the Lower Cretaceous Lakota Formation unconformably overlies the Upper Jurassic Morrison Formation (Dandavati, 1981). The Lakota Formation consists of three members in the southern and eastern Black Hills: the lower Chilson Member, the middle Minnewaste Limestone Member, and the upper Fuson Member. The Chilson Member is composed of sandstones that fine upwards into thick shale beds, and has been interpreted as a meandering river deposit, with broad channels and floodplains. The Minnewaste Limestone Member is a limestone that is lacustrine in origin, present only in the southern portion of the outcrops of the Lakota Formation. The Fuson Member is composed predominately of mudstones, and has been interpreted as a tidal inlet, tidal flat or marsh, depending on locality. The

Minnewaste Limestone Member outcrops only in the southern Black Hills (Dandavati, 1981).

The tracks and trackways used in this study come from the Chilson Member near Hermosa, South Dakota, in the extreme southeastern Black Hills (Fig. 3). This tracksite is on private property on large sandstone slabs that separated from a vertical cliff face and lay on the ground in various orientations. A stratigraphic section was measured to place the fallen bird-track-bearing block on the cliff face and determine original stratigraphic position (Fig. 4). The original stratigraphic position of the block was determined by comparing its thickness and bed forms with the *in situ* units.

The track-bearing horizon lies near the top of unit 4 (Fig. 4). Areas of cross-bedding and wavy bedding are clearly visible within the unit. The sandstone is fine to medium grained, rounded and well sorted with small, rounded and oxidized clay-clasts present. Within the massive sand are very small layers of finer material (fine sand or silt) present above the ripple-marked layers. These finer grained layers are extremely thin and are not readily visible on the cliff face. Small invertebrate surface traces (*Haplotichnus*) were noted on one of the ripple-marked layers below the track-bearing horizon. Soft-sediment deformation, especially just below the track-bearing horizon, is common.



**Figure 4.** Stratigraphic section of study site.

## METHODS AND MATERIALS

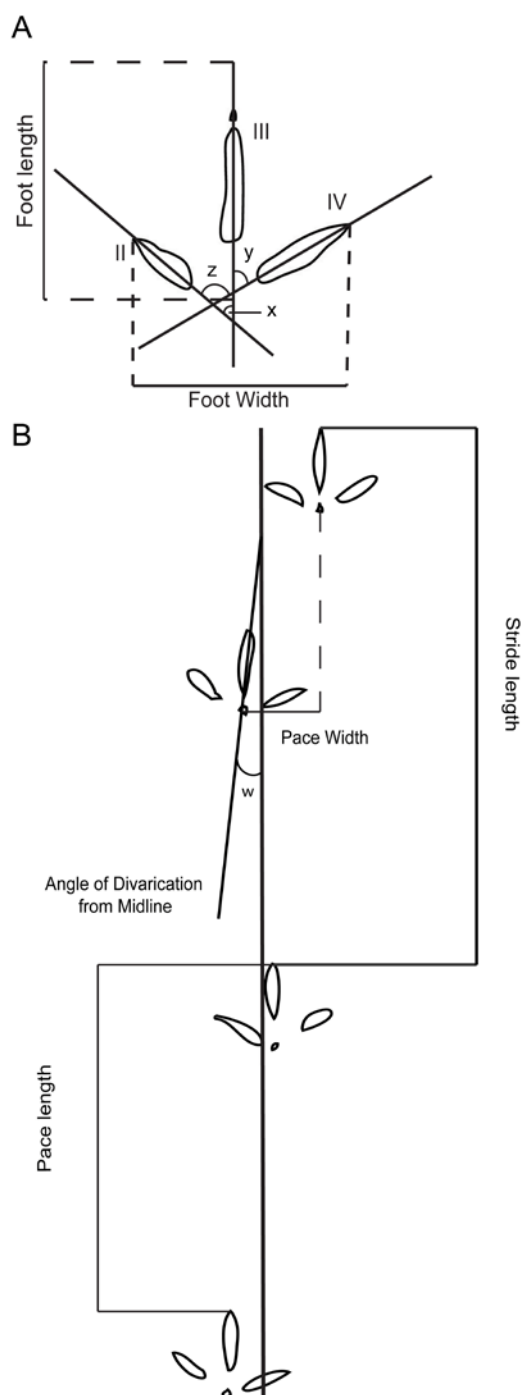
Bird tracks and trackways from the float block were molded as three separate peels (labeled A, B, and C) using two coats of thixotropic silicon mixed on site in a bucket. The first coat was a thin layer to cover the tracks and capture the fine detail. A second coat was applied to thicken and strengthen the original coat. The silicon

was allowed to cure for 24 hours before it was removed and returned to the University of Kansas Vertebrate Paleontology Division (KUVP 150474). In the lab, master casts from the original silicon peels was created by painting Dynacast<sup>®</sup> plastic on with a small brush. A total of 48 tracks were counted on the peels taken from the block with the majority of the bird tracks.

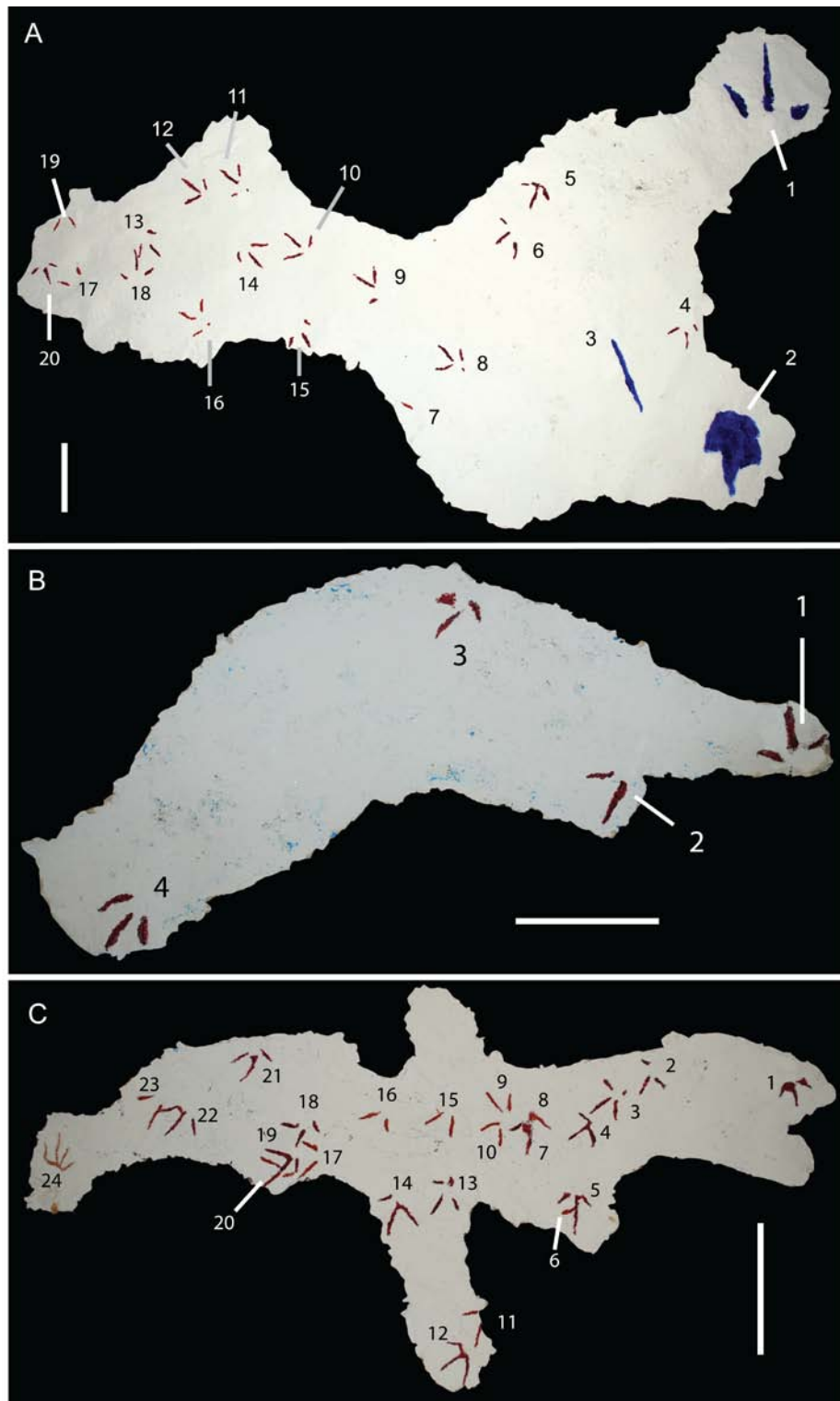
The tracks on the master casts and the peels were examined for such morphologic details as claw, pad, and skin impressions. The peels and casts were also closely examined for invertebrate traces and such bird-feeding traces as dabble marks and probe marks. A second set of casts for marking gross morphologic features of the tracks and trackways including angle of divarication, stride length, pace angulation, and digit length was produced from the peels (Fig. 5). The tracks on this set of casts were painted different colors to differentiate recognizable complete bird tracks, incomplete bird tracks, dinosaur tracks, and tracks of unknown origin prior to making measurements (Fig. 6). Foot width, foot length, and digit length and angle of divarication, stride length, pace angulation, and angle of divarication from midline (ADM) (Fig. 5) were established and measured by drawing on the casts with a felt-tip marker and straightedge. Bird tracks were distinguished from dinosaur tracks on the basis of divarication angle and foot length:foot width ratios (Currie, 1981; Lockley et al., 1992). Divarication angle was measured from the midline of each toe where the toe joins with the body out to the first joint; this prevents any rotation of the distal ends of the toes from having an effect on the angle of divarication. Foot width was measured from the distal end of toe II to the distal end of toe IV. Foot length was



measured from the base of the metatarsal pad to the tip of toe III. Digit length was measured from the base of the toe impression to the tip of the toe impression for each toe. Stride length and pace measurements followed Hasiotis et al. (2007). The behaviors that the tracks represent were determined using criteria from Elbroch and Marks (2001) and Genise et al. (2009).



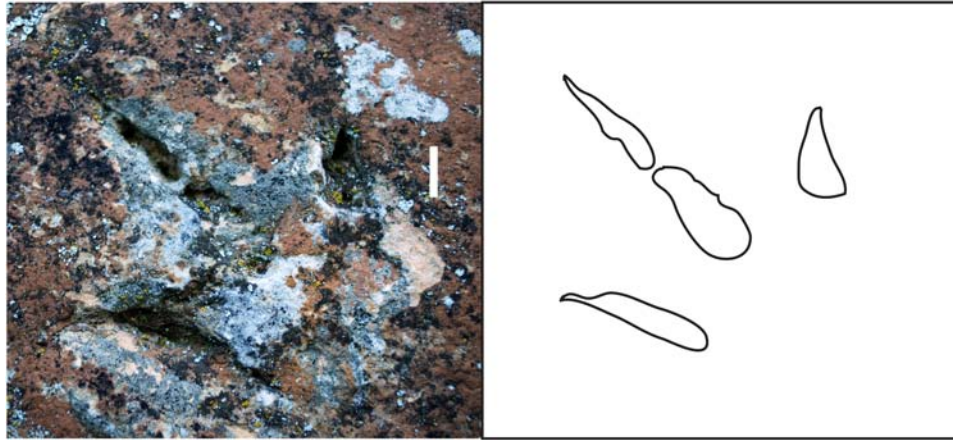
**Figure 5.** (Previous page) Morphologic measurements carried out on the plastic casts made from the silicon peels. A.) Single-track measurements. B.) Multi-track measurements.



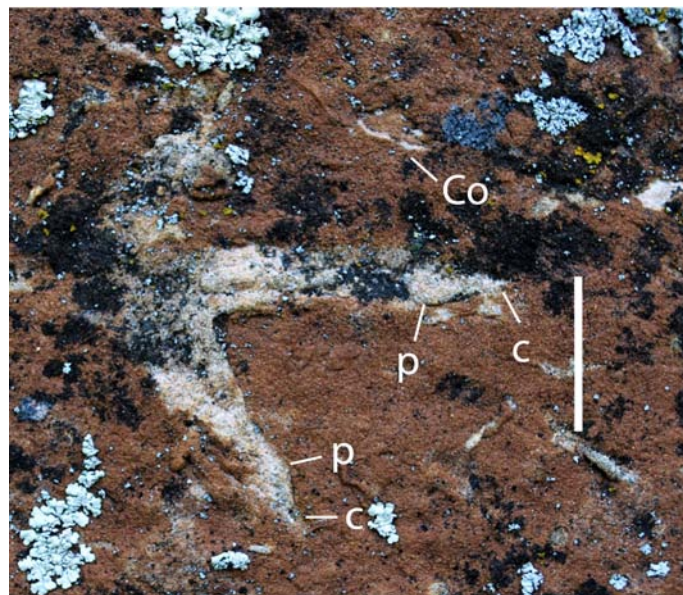
**Figure 6.** (Previous page) Photographs of the plastic casts, with the tracks painted with acrylic paint for clearer imaging. A.) Peel A, scale= 13 cm. B.) Peel B, scale= 12 cm. C.) Peel C, scale= 12 cm.

## RESULTS

Of the 48 the tracks studied on the peels, 3 were dinosaur tracks, 27 were complete bird tracks, 13 were partial bird tracks, and one track could not be identified (Table 1). All tracks are preserved in concave epirelief and were determined to be surface traces, because of the clear pad preservation in a theropod track (Fig. 7) and the clear claw impressions on several of the bird tracks (Fig. 8). The invertebrate trace fossil *Cochlichnus* was found on the rock surface from which peel A was taken (Fig. 8). One dinosaur track on Peel A was tentatively identified as a hypsilophodontid ornithopod dinosaur (Fig. 5A, track 2); the other tracks were a complete track and partial theropod track that could not be specifically assigned to any taxon (Fig. 6A, tracks 1, 3). Toe I is absent from all bird tracks present on each peel, indicating an elevated, reduced, or absent hallux toe. The metatarsal pad is lacking in the majority of tracks (Fig. 8).



**Figure 7.** Theropod track showing the clear outline of the pad. Scale=2 cm.



**Figure 8.** Typical bird track from the studied slab, showing lack of a metatarsal pad and toe I, and the clarity of claw impressions. Scale=2 cm. Note the *Cochlichnus* traces surrounding the track. Abbv.— p = pad c = claw, Co = *Cochlichnus*.

(in mm)								
Table 1								
Peel A								
Number	II-III (°)	III-IV(°)	II-IV(°)	FL (mm)	FW(mm)	II(mm)	III(mm)	IV(mm)
1	45	12	57	154*	135			
4	38	58	96	39*	45	11	25	19
5	39	75	111	42	49	22	33	24
6	85	65	150	33*	64	14	27	24
7	47	68	115	36	43	7	31	22
8	25	80	105	40*	48	18	33	29
9	65	58	123	45*	49	15	32	20
10	61	60	121	47	57	18	34	32
11	62	45	107	45*	53	11	39	20
12	34	63	97	47*	50	18	41	30
13	36	52	88	43*	47	15	27	22
14	39	46	85	42*	48	17	31	28
15	27	42	69	46*	46	11	26	16
16	46	60	106	42*	57	17	25	20
17	-	48	-	-	-	-	16	13
18	60	54	114	46*	52	12	34	17
19	-	65	-	-	-	-	21	16
20	52	70	122	35*	44	15	27	14
Peel B								
Number	II-III	III-IV	II-IV	FL	FW	II	III	IV
1	67	69	136	46	55	19	34	22
2	-	61	-	-	-	-	41	23
3	54	66	120	37	40	16	26	20
4	41	49	90	46	49	24	34	29
Peel C								
Number	II-III	III-IV	II-IV	FL	FW	II	III	IV
1	42	53	95	35	42	16	20	16
2	94	100	194	39*	47	8	28	19
3	52	83	135	43*	53	25	31	17
4	69	69	130	38	46	17	30	21
5	40	48	88	41*	43	16	40	20
6	67	-	-	35	-	20*	30	-

7	43	52	95	43	52	17	40	15
8	52	-	-	39*	-	22	31	-
9	-	39	-	-	-	-	32	24
10	83	-	-	-	-	23	23	-
11	-	65	-	-	-	-	30	20
12	44	57	101	37	53	20	30	29
13	59	46	105	45*	49	13	30	19
14	45	62	107	48*	57	28	34	18
15	-	53	-	-	-	-	25	23
16	76	-	-	-	-	28	26	-
17	71	-	-	-	-	31	21	-
18	50	78	128	40*	49	6	25	24
19	44	61	105	40*	49	19	29(est)	27
20	-	70	-	-	-	-	-	28
21	50	51	101	43*	50	22	34	20
22	50	32	82	45*	57	21	34	25
23	-	50	-	-	-	-	35	20

**Table 1.** Single-track measurements taken for all bird tracks used in the study. Track 1 on Peel A is the complete theropod track.

#### Peel A

Peel A is the largest peel and contains 17 complete and partial bird tracks (Fig. 6A). This peel was located in the lower right side of the block. Most tracks are either single or in pairs, rendering stride length, pace width, and pace length impossible to measure. The average angle of divarication between toes II and IV was 107.3°. The average foot length:foot width ratio of the avian tracks is 0.841. The theropod dinosaur track foot length:foot width ratio is 1.14.

The most interesting trackway is represented by tracks 8–12, which have an average stride length of 27.3 cm, a pace length of 13.1 cm, and terminate in a nearly

parallel pair of tracks, 4.5 cm apart. The average angle of divarication for tracks 8–12 is  $110.6^{\circ}$ . The pace length of tracks 11–12 is 6.2 cm, and the pace width is 4.5 cm, compared to an average 2.3 cm pace width of tracks 8–10. No tracks are present after the occurrence of these two tracks. The trackway represented by tracks 9–12 has an average ADM of  $3.5^{\circ}$ . Track 8, which appears to be turning into the straight-line trackway, has an ADM of  $14^{\circ}$ .

Tracks 13–15 also represent a fairly straight path. The stride length of tracks 13–15 is 30.5 cm. The angle of divarication for tracks 13–15 is  $80.7^{\circ}$ . These tracks have an average ADM of 22 cm, an average pace length of 17.8 cm, and an average pace width of 6.15 cm.

#### Peel B

Peel B is the smallest peel and has only four bird tracks, three complete and one partial (Fig 6B). The average angle of divarication for these tracks is  $54^{\circ}$ , and the average foot length:foot width ratio is 0.892.

#### Peel C

Peel C has the largest concentration of bird tracks, with 23 bird tracks: 13 complete tracks and 10 partial tracks (Fig 6C). Many tracks are either single or paired, making stride length a less-commonly used measurement; the most common measurements were pace length and pace width. There was also a single track that most likely represented an overprinted bird track; the track was not measured due to



the lack of clarity in the toe impressions. Overprinted trackways are represented by tracks 7–10 and 18–20, but were measurable to a certain extent. The average angle of divarication between toes II and IV for the whole peel is  $112.8^{\circ}$ . The foot width:foot length ratio is 0.832. Tracks 2–4 are a straight-path series with a stride length of 10.8 cm (Table 1). The average pace width is 0.85 cm, and the average pace is 5.55 cm, with an average ADM of  $10^{\circ}$ . The average ADM is highly skewed by the first track, which is  $27^{\circ}$ ; the others are  $0^{\circ}$  and  $3^{\circ}$ , respectively. Tracks 13–14 had no stride, and the pace is 6.8 cm. The pace width is 4.6 cm and the average ADM is  $1^{\circ}$ . Tracks 15–16 have a pace of 7.9 cm and the pace width is 2.6 cm. The average ADM is  $7^{\circ}$ . Tracks 5–6 are overstepping each other and directly in line, with toes III overlapping and the individual toe III impressions indistinguishable. Tracks 18–20 are very similar, but the tracks themselves are more pronounced and deeper in impression. Stride length, pace length, pace width and ADM were not measured on these tracks due to the difficulty in accurately separating the tracks and determining the midline, which may not be present.

## DISCUSSION

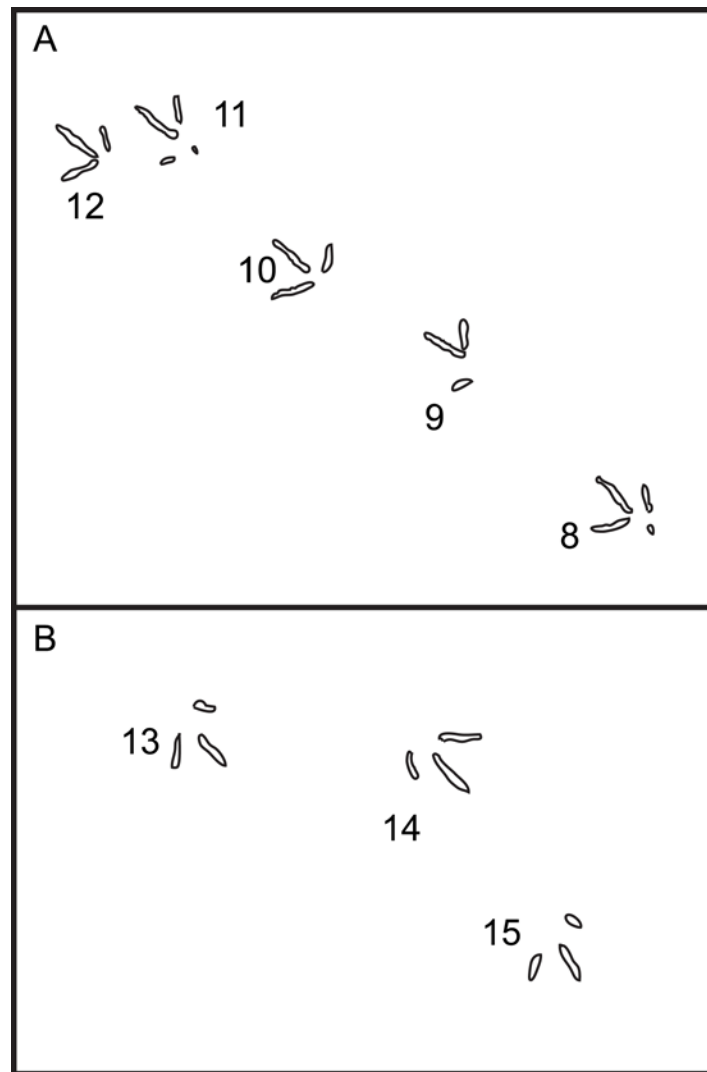
### Behaviors present

Many of the behaviors present on Peels A and C do not represent straight-line walking. No behavioral patterns can be interpreted from Peel B because of the small amount of tracks and their scattered affinity; however, the foot length:foot width ratio indicates that the tracks on Peel B are avian in origin.

Tracks 11–12 in trackway 8–12 on Peel A have a pace length of 6.2 cm—a much smaller pace length than the other tracks present—and a wider pace width than any of the other tracks in the trackway consisting of tracks 8–12. This, coupled with the fact that there are no tracks beyond the paired track, suggests that this trackway represents a takeoff trackway (Fig 9A). This trackway pattern is similar to the traces left by an extant bird that is standing still or taking off (Genise et al., 2009, fig. 7R, U). The terminal tracks of a takeoff trackway—termed *Volichnia* by Müller (1962)—are generally deeper than the other tracks present in the trackway (Genise et al., 2009); however, this can be difficult to determine, especially in the fossil record. Birds tend to have their feet nearly horizontal when taking off or landing (Genise et al., 2009). This is likely to prevent injury to the legs during landing or to get the greatest amount of upward force during the push off of the ground. During a running takeoff these paired tracks may not be present (Genise et al., 2009, fig. 7S). The presence of side-by-side tracks at the end of a trackway is a good indicator of flight.

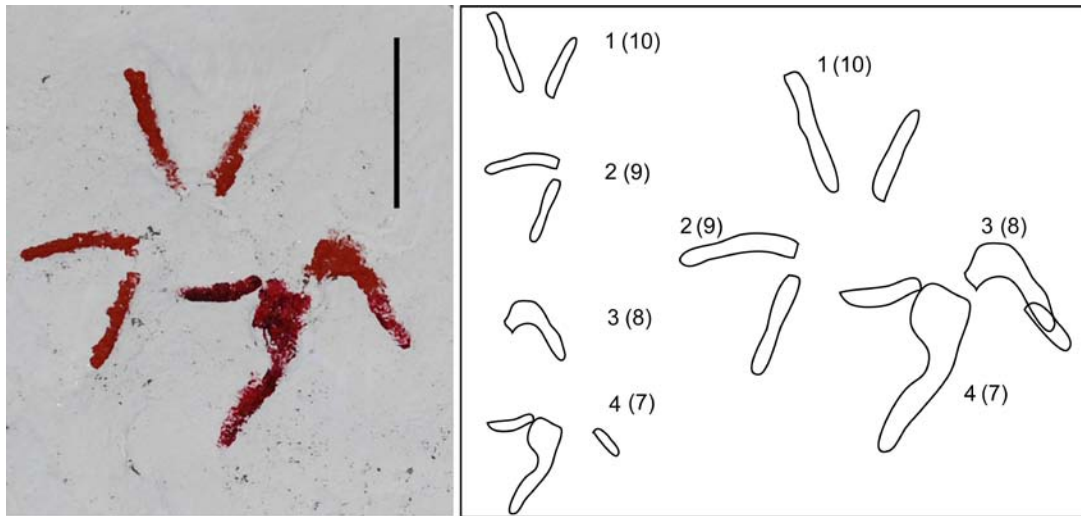
Tracks 13–15 (Fig 9B) on Peel A have a slightly longer stride length than the average stride of 8–12. If the stride length of the take-off tracks is excluded from the average stride length of tracks 8–12, the stride lengths of 8–12 and 13–15 are identical, with a value of 30.5 cm. The average angle of divarication is much smaller for tracks 13–15 (Table 1), and the average toe length is also much smaller for tracks 13–15; these measurements are indicative of running shorebirds (Elbroch and Marks, 2001; Genise et al., 2009). Stride length usually tells us about the relative speed at which an organism was moving; however, the stride length of birds does not always

differ with an increase or decrease in speed (Verstappen, 1998; Farlow, 2000). The reduction in the angle of divarication of tracks 13–15 suggests an increase in speed despite the fact that the stride length does not change significantly.



**Figure 9.** Schematic drawings of trackways composed of tracks 8–12 and 13–15 from peel A. A.) Outline of tracks 8-12. B.) Outline of tracks 13-15.

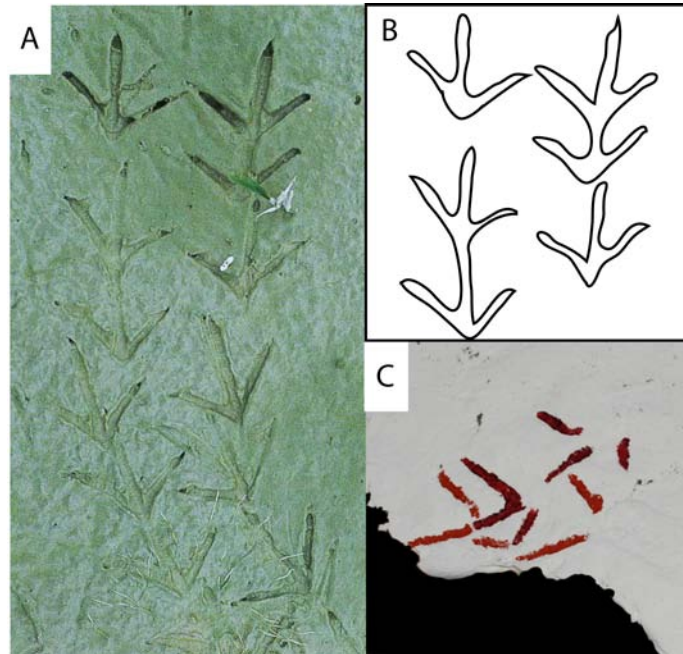
Tracks 7–10 on Peel C represent a series of overstepped tracks made by circular walking and one double-step (Fig. 10). The order of track production is not easy to distinguish due to poorer preservation, likely due to coarseness of the sediment. It is possible, however, to infer which track came first by determining whether it is a right or left foot and, therefore, where the missing toes should be located. Track 7 was likely the last track to be produced, as it is relatively the most complete track. Track 9 was likely the first track produced, as it is missing toe II. Track 10 followed, as toe IV is present and overlaps the position where the toe II of track 9 would have been placed. Track 9 is also missing toe II, however, and is overlapped by the complete track 7. Track 8 is difficult to determine, as it is almost entirely covered by track 7. The toe II of tracks 7 and 8 are nearly indistinguishable. Tracks 7–10 is interpreted as a circular feeding trackway, which is common foraging method of extant shorebirds and wading birds (e.g., Elbroch and Marks, 2001). These birds feed by making circular or back and forth movements while probing or sieving the sediment for small crustaceans or other invertebrates, which commonly results in overprinted tracks (e.g., Elbroch and Marks, 2001; Genise et al., 2009, fig. G).



**Figure 10.** Circular walking trackway from peel C. Tracks are numbered in chronologic order with track numbers in parentheses. Scale bar=4 cm.

On Peel C, tracks 18–20 represent an overstepped trackway produced in a different manner than tracks 7–10. This trackway was produced by a bird walking over its own tracks, and may preserve a type of shorebird courtship behavior that is seen commonly in plovers of the *Chadrius* genus, including the Killdeer (*Chadrius vociferous*), today (Fig. 11). This behavior is called high stepping, where the male bird approaches a female bird with short, stiff steps, raising the feet higher than normal (Elbroch and Marks, 2001). After a relatively short distance, the male then slams both feet down and leaps up into the air, resulting in noticeably clearer and deeper tracks (Fig 11A). In the case of tracks 18–20, 18 was produced first, then 19, then 20; the toe III of 19 was partially covered by the metatarsal pad of track 20. The trace of high-stepping as seen in the *Chadrius* plovers is a paired trace. The trace on Peel C has only one set of tracks present and is not paired (Fig 11C). It is possible

that this trackway was overstepped by a different bird, or the same bird re-walking its tracks. It is also possible, however, that the other foot was not preserved or had weathered off of the slab.



**Figure 11.** (Previous page) Examples of the courtship display high stepping and its fossil counterpart. A.) High-stepping display as seen in the Killdeer, *Charadrius vociferous* (photo from Elbroch and Marks, 2001). B.) Line drawing of A. C.) Traces from Peel C, interpreted as a potential high-step or similar courtship behavior.

No probe or drag marks are present on any of the peels. This may be due to preservation with respect to compaction or coarseness of the sediment. Most birds do not probe deeply into the sediment, and only those with the longest bills, such as Dowitchers and Curlews, can reach depths of  $> 4$  cm (Gill, 1995). Plovers and other

small shorebirds feed mainly by surface pecking or probing < 1 cm into the sediment (Gill, 1995).

The behaviors present on Peels A and C are consistent with our hypothesis of an avian origin for these tracks and trackways. Traces of flight are the greatest indicators of an avian tracemaker (Genise et al., 2009) and the presence of a trackway interpreted to represent a take-off also strongly suggests an avian origin. The ground-to-air takeoff necessary for this type of trackway suggests that the tracemaker was an ornithurine bird with a tri-osseal pulley system (Jenkins, 1993). The overstepping of tracks and the high-stepping display also indicate a shorebird-like tracemaker. Shorebirds and other birds are unique in their ground-based behavior. If a bird is on the ground, it is most likely for foraging, feeding, or courtship behaviors. These behaviors will be reflected in the tracks and trackways produced by the birds, as well as by associated traces of probing and scratching.

### Trackmaker Identification

Ornithurine birds that resembled medium-sized plovers from the genus *Chadrius* likely produced the bird tracks from the Lower Cretaceous Lakota Formation. These Early Cretaceous birds likely had similar feeding and courtship behaviors to such plovers as the Killdeer. These birds also had to have the complex flight mechanism necessary for takeoff from a flat surface. Ornithurine birds developed a highly modified dorso-lateral-facing glenoid to permit rotation of the wing back over the body and providing space for the downstroke of the wing

(Jenkins, 1993), allowing them to take off from a flat surface (e.g., pointbar or lake shoreline) without damaging their primary feathers at the wingtips. These tracks and trackways were likely not produced by early enantiornithine birds who had a poorly developed sternal keel (Zhou, 2002), or lacked one entirely (Zhang et al., 2004), indicating that they would be less capable of taking off from flat surfaces. Some enantiornithine birds also have a different foot structure than ornithurine birds, one more suited to arboreal living, in which toe IV is often reduced. This morphology should be prominent in their tracks and trackways (Lim et al., 2002), making them distinct from ornithurine tracks.

#### Paleobiogeographic and Evolutionary Implications of Early Cretaceous Bird Tracks

The presence of ornithurine bird tracks in the Early Cretaceous of North America (Currie, 1981; Lockley et al., 1992; Lockley et al., 2001; Anfinson, 2004) and throughout Asia (Lockley and Matsukawa, 1998; Azuma et al., 2002) show a worldwide distribution of these birds at this time. Many of these trackways were produced by shorebird-like birds (e.g., Currie, 1981; Lim et al. 2002; Anfinson, 2004; Lockley et al., 2006). This implies an early evolution of ornithurine birds (e.g., Martin, 1983) to facilitate this distribution or an earlier evolution of long-distance migration as part of the behavior of Early Cretaceous birds, which has not yet been proposed in the literature. Baker et al. (2007) suggested that the order Charadriiformes arose sometime in the Late Cretaceous based on molecular



phylogeny of modern shorebirds. It might be possible that the Lakota Formation avian tracks and trackways are closely related to the Charadriiformes.

Lower Cretaceous avian tracks and trackways are also important to understanding the early evolution of birds because they fill in the gaps that result from the lack of avian body fossils. Birds are divided into two major groups: the primitive Sauriurae and the more advanced Ornithurae (Martin, 1983). The most basal bird, *Archaeopteryx*, appears in the Late Jurassic of Germany (Feduccia, 1996) and belongs to the Sauriurae. The dichotomy between ornithurine and saurine birds would have happened very early in avian evolution (Martin, 1983). This dichotomy may have taken place before or during the breakup of Pangea in order to explain the presence of highly advanced-appearing shorebird tracks (Ornithurae) worldwide in the Early Cretaceous, assuming these that early birds were not capable of long distance or migrational flight behavior. Our supposition is supported by Feduccia (1996) and Martin (2004), whom suggested that the origin of birds extended back into the Triassic. The birdlike tracks described from Upper Triassic?–Lower Jurassic? deposits from Argentina by Melchor et al. (2002), Melchor and deValais (2006) and deValais and Melchor (2008) have been interpreted as birdlike theropods despite a high angle of divarication (115°), a reflexed hallux, and behaviors indicative of ornithurine birds, including locomotion, probing, and flight (landing traces). Alternatively the Argentinean tracks and trackways represent: (1) pseudosuchians (false reptiles) with foot and hindlimb morphology similar to shorebird-like ornithurine birds; (2) traces in rock units that are actually younger than Early Jurassic,

and more akin to Early or Late Cretaceous in age; or (3) may actually represent bird tracks and support an earlier evolution of birds in the Triassic. The latter case of trace fossils occurring earlier in the rock record than their respective body fossils is more common than originally thought and can be useful in reconstructing the evolution and radiation of a variety of continental and marine organisms (e.g., Hasiotis, 2003, 2004, 2008, and references therein).

## CONCLUSIONS

The bird tracks from the Lakota Formation were made by shorebird-like ornithurine birds. The behaviors interpreted from these tracks and trackways—evidence of flight, feeding and courtship—are consistent with this interpretation, as are the morphologic measurements including average angle of divarication and foot length:foot width ratio. The evidence of ornithurine birds worldwide in the Early Cretaceous implies either the evolution of long-distance migration or an earlier origin of ornithurine birds to permit dispersal.

## ACKNOWLEDGEMENTS

We thank the Black Hills Institute, Leon Thiesen and the landowner Dave Geary for access to the site and aid in fieldwork. We are grateful to Ali Nabavidazeh and David Burnham for assistance in the field. This paper is part of a Masters thesis conducted by ARF in the Department of Geology at the University of Kansas, Lawrence.

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### **CHAPTER THREE. A PRELIMINARY BEHAVIORAL STUDY OF EARLY CRETACEOUS BIRD TRACKS FROM SOUTH KOREA**

*Currently in review as:*

Falk, A. R., Hasiotis, S. T., Martin, L. D. A preliminary behavioral study of Early Cretaceous bird tracks from South Korea: *Geologica Croatica*.

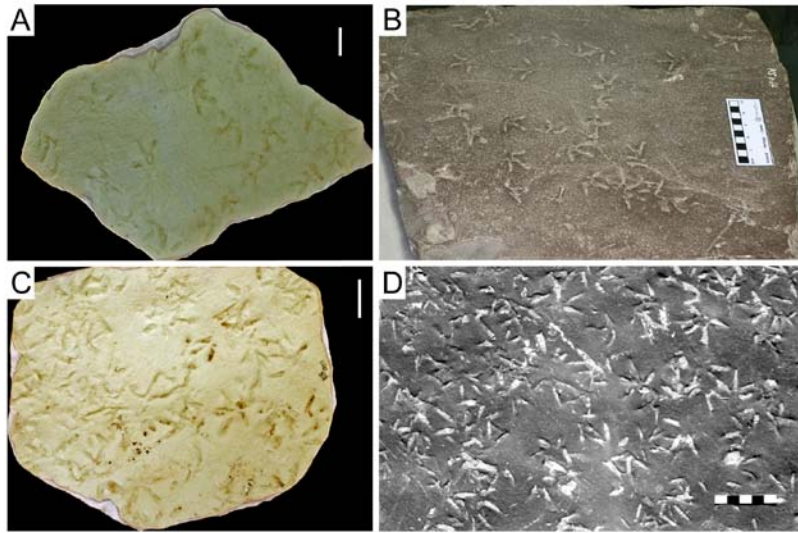
#### **ABSTRACT**

The bird track localities of South Korea are among the richest and most diverse avian tracksites in the world, but no behavioral studies have been conducted. This preliminary study interprets avian behaviors from casts (KS001 and KS064) from two localities in the Lower Cretaceous Haman Formation. The Haman Formation is Aptian–Albian in age, and contains the oldest known tracks of webbed-footed birds. It also contains thousands of tracks of small, shorebird-like ornithurines. Sixty-one non-webbed tracks were measured, with the cast, KS001, containing the majority of these tracks. The majority of tracks from KS001 are overprinted. Probing and pecking behaviors associated with feeding were interpreted from this cast. These behaviors may be associated with invertebrate trace fossils interpreted as those of insect larvae and annelids. Cast KS064 is different in that the number of overlapping tracks is greatly reduced, and individual trackways can be distinguished. Landing trackways are present on this cast including elongated hallux drag marks on several of the tracks. Hallux drags while landing represent a low-angle landing. One trackway with long hallux marks may represent some sort of pathology or injury as the hallux

impressions are found only on the right foot. Flapping-aided hopping is also present on KS064. These casts are a window into a much larger picture of an Early Cretaceous avian community in South Korea, with a greater opportunity for more study on Early Cretaceous avian behavior.

## INTRODUCTION

Early Cretaceous bird tracks from Asia are well known from China (Lockley et al., 2006; Zhang et al., 2006; Lockley, 2007), South Korea (Lim et al., 2000, 2002), and Japan (Azuma et al., 2002). These deposits are unique because of numerous, well-preserved tracks and the expanse of these track-bearing localities. The localities of the Haman and Jindong formations in Kyongsang basin, South Korea, have extensive outcrops and a high density of bird tracks. Thousands of bird tracks are exposed in three localities in the Haman Formation, making them among the largest bird tracksites in the world. Despite the expanse and number of tracks, no behavioral studies have been conducted. This paper provides a preliminary description of some of the behavioral aspects of Early Cretaceous bird tracks from Haman Formation (Fig. 12) and compares them to a modern analog, Killdeer (*Chadrius vociferous*) in the order Charadriiformes (shorebirds), which exhibit typical shorebird behaviors that may be similar to behaviors preserved in Lower Cretaceous deposits.



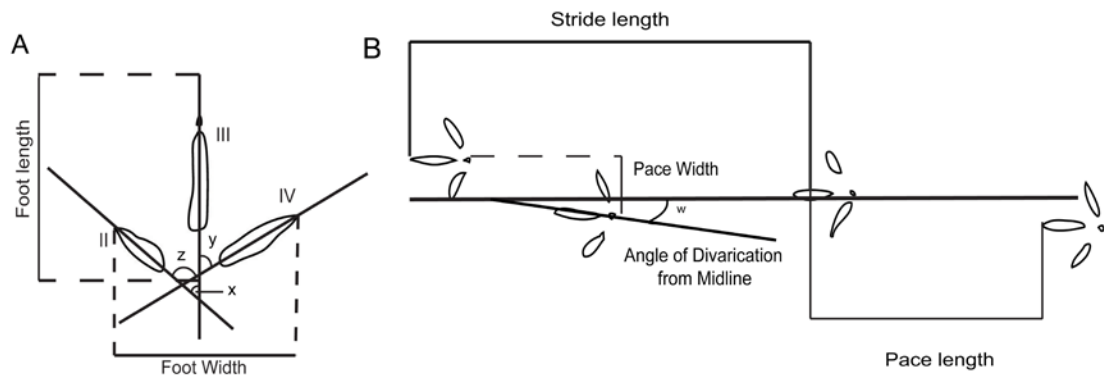
**Figure 12.** (Previous page) Photographs of the casts used, and corresponding photos of the slabs they represent. A.) KS001 B.) KS064

Here the term shorebird refers to an avian morphotype rather than the order Charadriiformes. Modern avian genera do not appear in the fossil record until the Eocene (Feduccia, 1996), and it is unlikely that the shorebirds present in the Early Cretaceous are the same shorebirds taxonomically.

Bird tracks from the Haman and Jindong formations consist of both webbed and non-webbed tracks (Lim, 2002). The webbed-footed tracks are interpreted as being similar to avocets (Charadriiformes), with the webbing restricted to the proximal portion of digits II–IV. These, along with other sites in South Korea (Kim et al., 2006), are the oldest webbed-footed bird tracks known (Lim et al., 2000, 2002).

## METHODS

The Cretaceous bird tracks used in this study come from two latex casts taken from the Haman Formation in South Korea (Lim et al., 2000). Jong-Doeck Lim from the National Heritage Museum in Daejeon provided the two casts (specimen numbers KS064 and KS001; Fig. 1) to the University of Kansas Vertebrate Paleontology division. These casts were photocopied and the tracks were individually numbered and outlined on the photocopies. Angles of divarication were measured between toes II and III, III and IV, and II and IV (Fig. 13). Foot length:foot width ratios were also measured and entered into an excel spreadsheet. Stride length, pace length and pace width were measured following Leonardi (1987) and Hasiotis et al. (2007). A total of 61 tracks were measured, 49 complete tracks and 12 incomplete tracks.



**Figure 13.** How to measure angle of divarication, stride length, pace length, pace width, and angle of divarication from the midline.

Plaster casts of tracks of the Killdeer taken from a floodplain near Lake Erie Metropark in Brownstown, Michigan, USA, in the summer of 2008 were used to compare modern shorebird track morphology and behaviors to the Early Cretaceous

tracks. The cast used measured 32 x 41 cm. Behaviors represented by the Killdeer tracks were recorded using a video camera, and temporal and spatial relations of the birds with respect to track production and position of the tracks to the grass line were documented. Foot length:foot width ratios were also measured from the cast.

Multitrack measurements (stride length, pace length, pace width, and angle of divarication from midline) were taken only on KS064. No multitrack measurements were taken on KS001 due to the high density of tracks on the casts that precluded the identification of individual trackways.

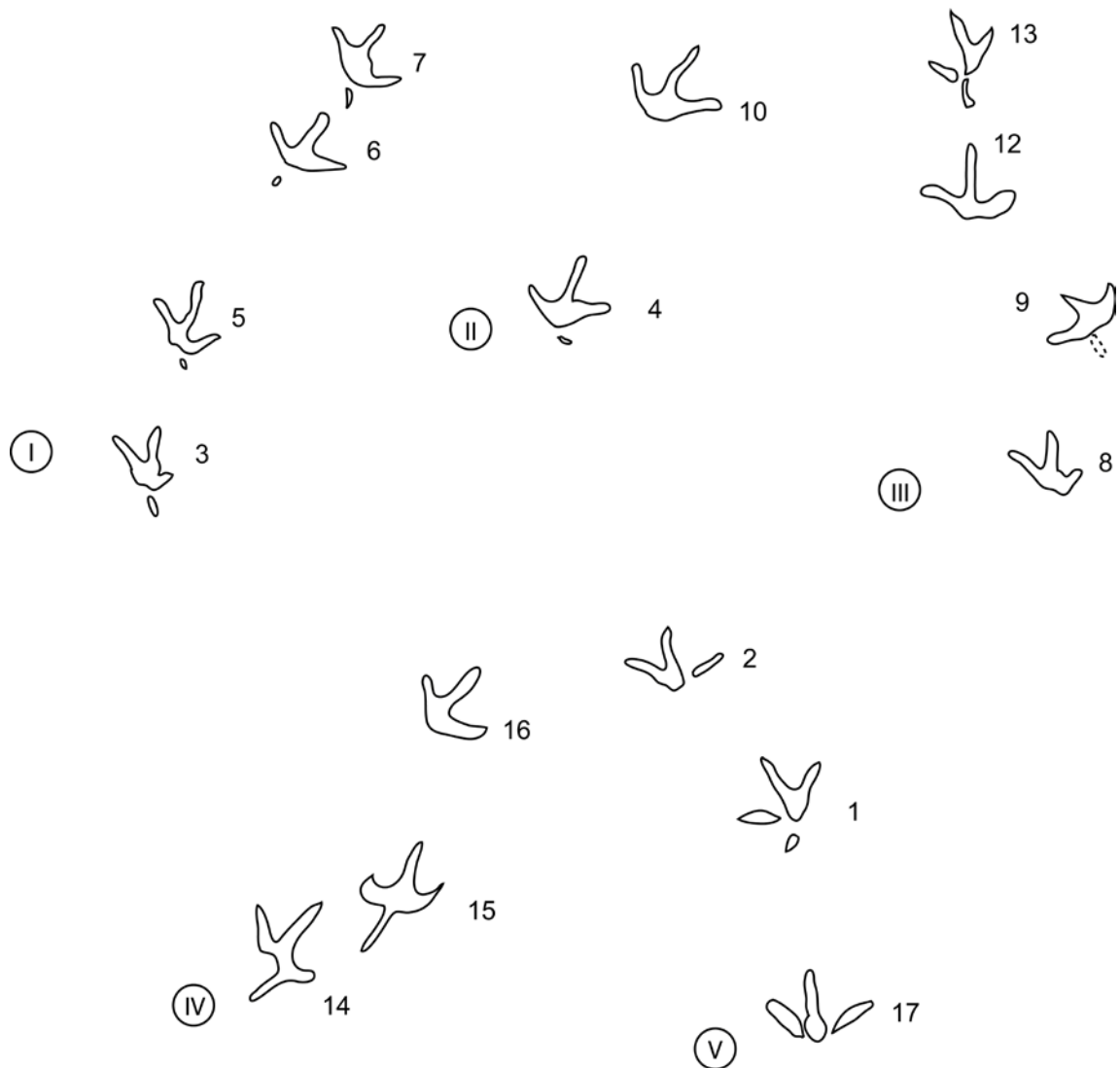
The patterns of the Korean bird tracks and their morphologies were compared to the patterns produced by specific behaviors of shorebirds recorded in a recent study by Genise et al. (2009). Their study of sandpiper behaviors was used primarily to examine the casts taken from the Haman Formation. The behaviors that the Korean tracks represent were also determined using criteria from Elbroch and Marks (2001) as a secondary source.

## RESULTS

Out of 61 tracks studied 14 tracks had hallux impressions. Five trackways were distinguished on KS064, which had a low density of tracks (4 tracks/10 cm<sup>2</sup>). No trackways were distinguished on KS001, however, it had the highest density of tracks (11 tracks/10 cm<sup>2</sup>).

### KS064

KS064 contains a total of 19 complete tracks. This cast contains only one overlapping track, track 17, which overlaps slightly with track 13. The average angle of divarication between toes II and IV is  $112^{\circ}$ . The average foot length:foot width ratio is 0.761. The majority of the tracks have hallux impressions; those tracks are 1, 3, 4, 5, 6, 7, 9, 13, 14 and 15 (Fig. 14).



**Figure 14.** Trackways on KS064.

Toe III is the longest toe on average, with a length of 18.7 mm. Toe II has an average length of 14.5 mm, and toe IV averages 16.97 mm long. Twelve tracks on this cast had hallux impressions, up to 15 mm long (Table 2).

Table 2 KS064														
			II- III	III - IV	II- IV	I	II	III	IV	FL	FW	FL:F W	Avg angle	
1	R	59	5 8	11 6		9	22	24	22	32	40. 7	0.786		112
			II- III	III - IV	II- IV	I	II	III	IV	FL	FW	FL:F W	Avg	
2	L	75	4 2	11 7	-		16	18.6	21	27	42. 5	0.632	II	14.33157 89
3	L	62	4 0	10 2	13	12.5	20	14	30.6	3	32.	0.947	Avg III	18.79473 6
4	R	60	5 2	11 2	-		11	22	17	30.7	31. 7	0.968	Avg IV	16.5
5	L	60	4 5	10 2	6	16	20	19	29.1		35. 2	0.826	Avg FL/F W	0.760594 7
6	R	70	6 2	13 2	-		15.5	19	17.5	24.6		0.702		
7	L	65	5 8	12 3	10	20.2	20.5	18	26.7		38. 1	0.700		
8	L	47	5 4	10 1	4	11	18	18.5	22.4		29. 7	0.754		
9	?	56	4 8	10 4	?	12	10.5	14.5	16		40. 4	0.396		
10	L	50	4 5		95	-	14.5	23	15	30.4	35. 6	0.853		
11	L	64	5 3	11 7	-		15	20.5	15	27	38. 7	0.697		
12	L	54	6 0	11 4	-		15	21.2	16.5	30.5	37. 3	0.817		
13	L	73	4 5	11 8	10	12	14.5	16	23.8		37. 2	0.639		
14	L	50	8 0	13 0	12	8.5	17.5	*	23.4		30. 7	0.762		
15	R	62	5 0	11 2	15	14	13.6	10	20.9		30. 7	0.680		
16	L	62	4 2	10 4	10	11.2	20	12*	26		27. 5	0.945		

17	R	60	5	12								0.534	
			0	0	-	17	18	20	23.5	44	21.	1	
18	R	47	5	97	-	9.5	12	9	19	5	0.882	7	
19	?					19.4	24.2	17.5	29.5	32	0.921	9	

# **KS00** **1**

			III	II-	-	II-	I	II	III	IV	FL	FW	FL:F		
			III	IV	IV								W		
1	L	51	9	14				9*	14.5	17.1	21	34.	0.608	Avg	114.5483
			7	8	-							5	7	angle	87
2	R	89	5	14				12	9.5	11.8	18.5	33	0.560	Avg	11.83142
			7	6	-								6	II	86
3	L	62	6	12				7	15	11	17	25	0.68	Avg	15.99230
			4	6	-							28.	0.734	III	77
4	R	72	6	14								28.	0.734	Avg	12.01034
			9	1	-			11.5	17.4	8.2	21.5	9	9	IV	48
5	L	56	4	10								28.	0.859	Avg	
			5	1	-			13	18.2	9	24.5	5	6	FL/F	0.75678
6	L	45	7	11									0.843	W	
			3	8	-			19	23	10.5	27	32	8		
7	L	64	4	11								24.	0.801		
			9	3	-			8.9	14.2	12.2	19.4	2	7		
8	R	54	5	10								30.	0.754		
			1	5	-			14	19.5	13.2	23	5	1		
9	R	78		13									0.6		
				3	-			10.5	15	22.2	19.2	32			
10	R	56	6	11									0.888		
			3	9	-			11.6	16	9	22.2	25			
11	R	-	7										-	-	
			9	79	-				9.5	8	19.2	-	-		
12	L	35	-	-	-			13.9	20	-	29	-	-		
13	L	69	-	-	-			7	12	-	15	-	-		
14	R	46	4							10.8		24.	0.979		
			1	87	-			9.8	17.5	*	24	5	6		
15	R	-	3										-	-	
			0	-	-				9	7.5	12.5	-	-		
16	R	78	-	-	-			13	12.5	-	-	-	-		
17	R	77	6	13									0.593		
			0	7	-			9.5	11*	11	19*	32	8		
18	L	42	-	-	-			9	13	-	22.4	-	-		
19	L	62	6	12									0.714		
			0	2	-			9	21	12	25	32	3		
20	R	45	5	10	6.			17	20.5	20.2	26.5	39.	0.681		
			9	4	5							8	2		
21	L	48	6	11									0.770		
			9	7	-			15.8	21.8	11.2	28.5	37	2		
22	L	44	7	11									0.794		
			0	4	11			14.5	22	13	27	34	1		



		II- III	III - IV	II- IV	I	II	III	IV	FL	FW	FL:F W
			4								0.973
23	R	38	8	86	-	11	14	10	18.5	19	7
24	L	62	-	-	-	8.2	11.8	-	19	-	-
			7	11							
25	R	38	9	7	-	7.4	14	-	20	-	-
			7					12.3			
26	R	-	2	-	-	-	18.5	*	-	-	-
			9	15							0.774
27	R	57	7	4	-	11	20.5	14	24	31	2
			5	12						25.	
28	R	70	8	8	-	11.2	15	8.5	23	5	0.902
29	L	53	-	-	-	12	15	-	19.5	-	-
			5	10						27.	0.656
30	R	51	3	4	-	9	11	10.2	18	4	9
			7	11							0.483
31	L	46	2	8	-	10	11	13.4	15	31	9
			6	10							
32	R	37	5	2	-	22	15.5	7*	31	31	1
			8	12			19.4			32.	0.757
33	L	48	0	8	-	12.2	*	11.8	24.4	2	8
34	L	63	-	-	-	9	15.4	-	19.5	-	-
			4								
35	L	-	2	-	-	-	15.2	12.5	19	-	-
			6	11			10.5		18.4		0.593
36	R	47	4	1	-	11	*	9.2*	*	31*	5
		37	5						23.8	32	0.743
37	L	*	9	96	-	?	11	11	*	?	8
			6	13						40.	
38	L	67	8	5	-	19.2	19.8	13.5	27	6	0.665
			4							26.	
39	L	42	5	87	-	10.2	23	13	24	4	0.909
			5								0.827
40	L	39	5	94	-	11.2	14.2	9.8	24	29	6
			6							28.	
41	L	20	1	81	-	13.5	21.2	13.5	31.5	5	1.105
			5			14.6					0.446
42	R	-	2	-	-	*	16.5	-	15*	-	4

**Table 2**—Measurements taken on KS001 and KS064.

Track 18 is the smallest track on the cast. While it does not have the smallest single measurement (for instance, track 9 has a smaller foot length), its combined

measurements show that it was significantly smaller than other tracks. It has the smallest foot width of any track, and the second-smallest angle of divarication (Table 2).

There are five discernable trackways on KS064. Trackway I consists of tracks 3, 5, 6, and 7. Trackway II consists of tracks 4 and 10. Trackway III contains tracks 8, 9, 12, and 13. Trackway IV consists of tracks 14, 15, and 16. Trackway V contains tracks 17, 1, and 2 (Table 3; Fig. 14).

<b>Table 3</b>						
KS064	(in mm)					
Trackway numbers	Stride length	Pace Length	Pace Width	Number	AOD from Midline	(in degrees)
3--7	(3-6): 145	(3-5): 57	(3-5): 19	1	10	
	(5-7): 126	(5-6): 85.5	(5-6): 4	2	5	
		(6-7): 41	(6-7): 4.5	3	22	
Trackway numbers	Stride length	Pace Length	Pace Width	Number	AOD from Midline	(in degrees)
4--10	-	82	1	4	0	
8--13	(8-12): 108	(8-9): 56	(8-9): 33	5	20	
	(9-13): 111	(9-12): 55	(9-12): 31	6	0	
		(12-13): 54	(12-13): 17	7	1	
14--16	85	(14-15):34	(14-15): 14.5	8	34	
		(15-16):51	(15-16):21.5	9	32	
17--2	153	(17-1): 85	(17-1): 28	10	0	
		(1-2): 55	(1-2) 31	11	-	
				12	17	
				13	3	
				14	2	
				15	11	
				16	3	
				17	35	

**Table 3.** Multi-track measurements taken on KS064.

Trackway I (Fig. 14) has an average stride length of 135.5 mm, an average pace length of 61.17 mm and an average pace width of 9.17 mm. The highest pace length is 85.5 mm between tracks 5 and 6, and the smallest pace width is 41 mm, between tracks 6 and 7. The largest pace width is 19 mm, between tracks 3 and 5 and the smallest is 4 mm between tracks 5 and 6. The average angle of divarication from midline for all tracks in this trackway is  $10.75^{\circ}$ .

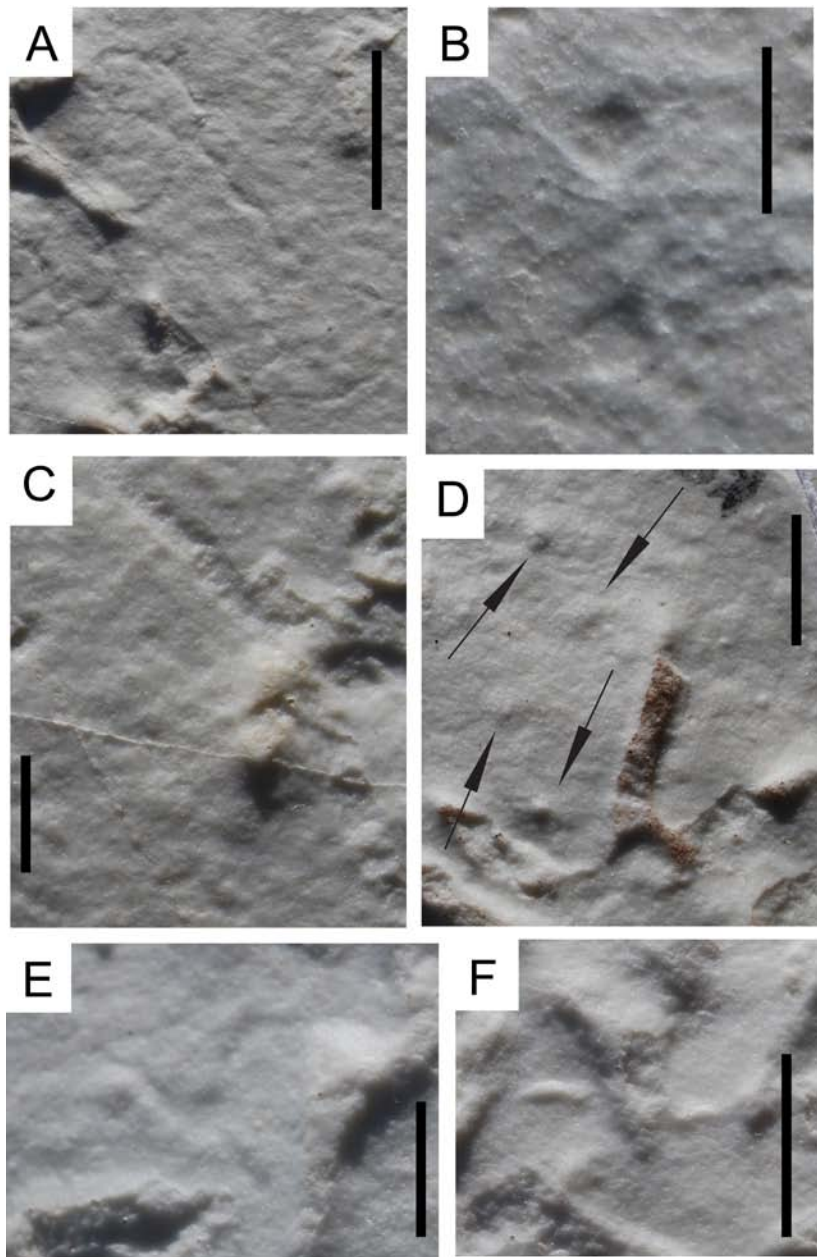
Trackway II (Fig. 14) has no stride length. The pace length is 82 mm and the pace width is 1 mm. The angle of divarication from the midline for both tracks is  $0^{\circ}$ .

Trackway III (Fig. 14) has an average stride length of 109.5 mm. The average pace length is 55 mm and the average pace width is 27 mm. The largest pace length is 56 mm between tracks 8 and 9, and the smallest is 54 mm, between tracks 12 and 13. The smallest pace width is 17 mm, between tracks 12 and 13, and the largest is 33 mm, between tracks 8 and 9. The average angle of divarication from the midline for all tracks in this trackway is  $21.5^{\circ}$ .

Trackway IV has a stride length of 85 mm, which is the smallest stride length present. The average pace length is 42.5 mm, and the average pace width is 18 mm. The average angle of divarication from the midline is  $5.3^{\circ}$ .

Trackway V has a stride length of 153 mm, which is the largest stride length present. The average pace length is 70 mm, the average pace width is 29.5 mm. The average angle of divarication from midline is  $16.7^{\circ}$ .

This cast has a variety of invertebrate traces alongside the avian tracks. Such invertebrate traces as *Cochlichnus*, *Steinichnus*, and *Arenicolites* indicate a high diversity of invertebrates present (Fig. 15A–C). In several cases (Tracks 5, 6, 7 and 9) the birds overstepped the burrows present. In one case, a *Cochlichnus* trail crosscuts a bird track (Track 11) (Fig. 15A). *Steinichnus* is preserved in concave epirelief, *Cochlichnus* is preserved in concave epirelief, and *Arenicolites* is preserved in convex epirelief.



**Figure 15.** Traces found on KS064 and KS001. A) *Cochlichnus* on KS064. Note the cross-cutting relations. Scale bar=2 cm. B) *Arenicolites* on KS064. Scale bar=1 cm. C) Bird track overstepping *Steinichnus* on KS064. Scale bar=1 cm. D.) *Arenicolites* on KS001 (arrows). Scale bar=1 cm. E.) Concave epirelief *Cochlichnus* on KS001.

Scale bar= 1 cm. F.) Convex epirelief *Cochlichnus* cross-cut by an avian track on  
KS001. Scale bar=1 cm.

### KS001

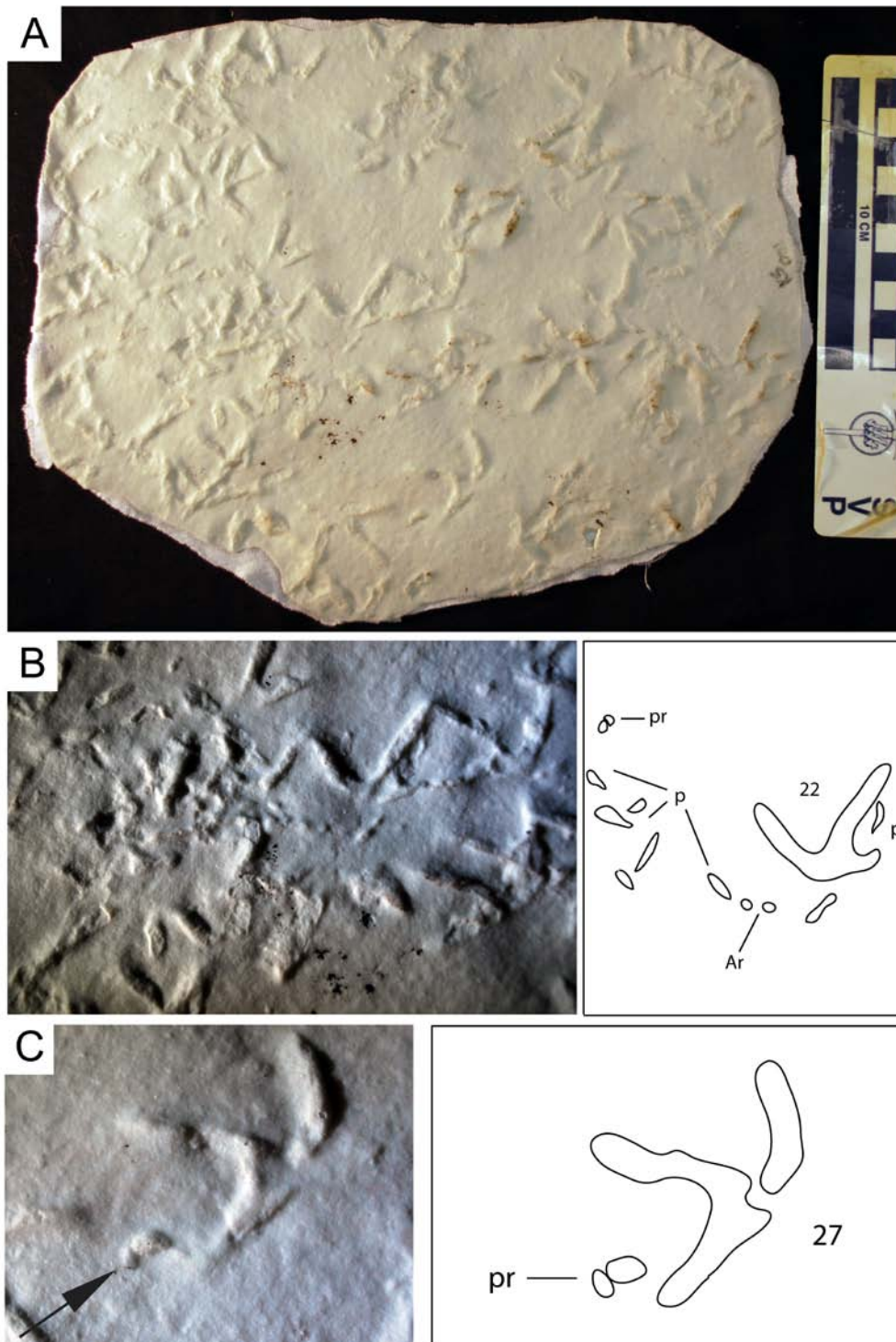
KS001 contains 42 tracks, 30 complete and 12 incomplete. The average angle of divarication for KS001 is  $113.98^{\circ}$ . Toe III is the longest toe on average (15.98 mm). Toes II and IV have averages of 11.96 mm and 12.16 mm, respectively. The foot length:foot width ratio is 0.757.

KS001 contains tracks with high angles of divarication (tracks 1, 2, 4, and 27) as well as tracks with angles  $< 100^{\circ}$  (Table 2). Tracks with an angle of divarication  $< 100^{\circ}$ , however, still have a foot length:foot width ratio  $< 1$ , except for track 41, which has a length:width ratio of 1.105. The smallest foot length:foot width ratio present is 0.446. Semipalmate tracks—tracks with partial webbing between two toes—are present (Figs. 12C, 16).



**Figure 16.** Schematic line drawing showing numbered tracks on KS001.

There are areas of dense concentrations of tracks (Fig. 17A). Among these dense concentrations of tracks are elongate convex marks that are 3–7 mm long and as much as 2 mm wide (Fig 17B). A teardrop-shaped mark is directly in front of toe II of track 27 (Fig 17C) and is separated into two portions, a smaller, circular portion and a larger, oval portion that are < 1 mm apart. Another, more oblong mark is directly behind track 5, and another is just in front of toe III of track 22. Also present are paired circular traces that are identical in diameter.

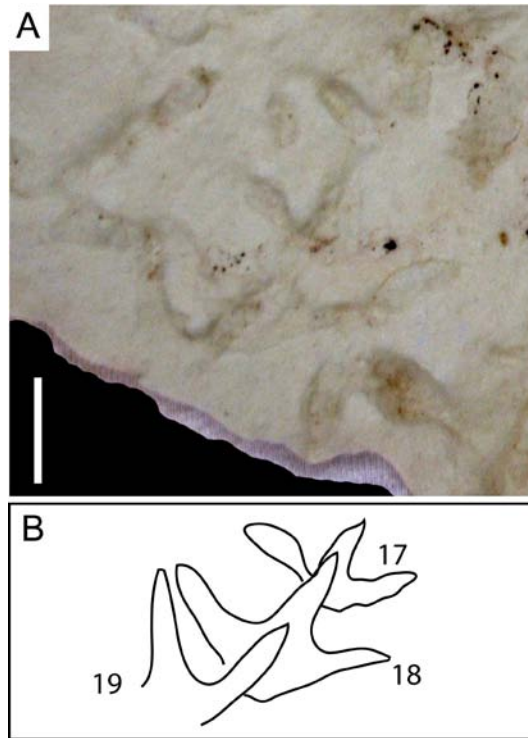


**Figure 17.** Probe and peck marks on KS001. A.) Traces interpreted to be clusters of peck marks. B.) Individual probe marks.



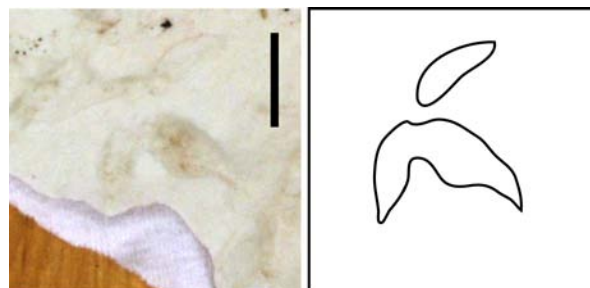
Only two tracks have hallux impressions, track 20 and track 22 (Fig. 16). The hallux on track 20 is 6.5 mm long; the hallux on track 22 is 11 mm long. Both tracks that had hallux impressions were larger than average, with some of the largest toe III measurements (20.5 mm and 22 mm, respectively) and largest foot width of all tracks measured (track 20, 39.8 mm). A third track—track 14—that is much smaller than 20 or 22 has a potential hallux mark as well, but it is in close proximity to another toe mark from a separate footprint (interpreted as a toe III imprint) and is 17 mm long and, therefore, has been assigned to that partial track as toe II (Fig. 16).

On KS001, many tracks are overstepped, an occurrence that is nearly absent on KS064. For example, tracks 16, 17, and 18 are overstepped (Fig 18). It is evident from the clarity of the toe II impression on track 18—where it overlaps with the metatarsal pad and toe III of track 17—that it was the last track in this sequence to be laid down.



**Figure 18.** (Previous page) Tracks 16-18 of KS001, showing details of overstepped tracks and identification of which track came first.

There are other tracks on this cast that have strange anomalies that cannot be attributed to overstepping. Track 10 (Fig. 19) has a bulbous impression in the center of its toe that is 9.5 mm wide. The widest toe on KS001 is on track 21, and it is only 7 mm long at its widest point. This bulbous toe III is not seen elsewhere on the cast.



**Figure 19.** Track 10 of KS001 showing bulbous toe III.

There are invertebrate traces present alongside the avian traces on this cast. *Arenicolites* is preserved in convex epirelief and found associated with bird tracks (Fig. 15D). *Cochlichnus* is preserved as both convex epirelief and concave epirelief (Fig. 15E–F). In one instance, a track is overstepping a *Cochlichnus* trace (Fig. 15).

## DISCUSSION

There are distinct differences in track morphology and behavior between the casts from KS064 and KS001. The most noticeable difference is the variation in number of tracks between the two casts. KS064 has only 19 tracks, whereas KS001 has 42, which may be indicative of (1) a different microenvironment or microhabitat varying in moisture or food availability, (2) a variation in the number of birds present, or (3) different species or genera of tracemakers with different behavioral patterns. The majority of the tracks on KS064 have hallux impressions, whereas only two tracks on KS001 have hallux impressions. In modern shorebirds, many sandpipers and their relatives have reflexed halluxes. Some plovers, on the other hand, have lost their hallux entirely and, therefore, will never show a hallux impression (Elbroch and Marks, 2001). The fact that there are tracks both with (larger tracks) and without hallux impressions (smaller tracks) present on the same cast in the same area indicates, therefore, that two different types of tracemakers were present, likely representing two different bird genera.

The tracks of KS001 are more numerous and were often overstepped. The overstepping made them more difficult to measure and distinguish than the tracks from KS064, and made distinguishing trackways impossible. Some tracks on KS001 had semipalmate webbing between toes II and III, such as track 8 (Fig. 16), whereas semipalmate webbing was not present on the tracks from KS064. This webbing is extremely restricted to the proximal one-third of the toe, and is not always preserved.

The bulbous impression on toe III of track 10 on KS001 (Fig. 19) may be indicative of some type of pathology or growth on the left outside of the toe. This bulbous toe III, however, is not seen elsewhere on the cast and, therefore, may indicate some type of probing or gaping behavior that was subsequently overstepped by the same tracemaker or a different tracemaker. Probing results when the beak is pressed straight or nearly straight into the sediment and is drawn back in the same direction (Elbroch and Marks, 2001). Gaping occurs when the bird presses its beak into the sediment and opens it, leaving a wider impression (Elbroch and Marks, 2001). The hole produced by one of these behaviors, when overstepped, resulted in a deformed track impression of toe III.

Overall, the tracks of KS001 are greater in number, smaller, and generally lack hallux impressions. The few tracks that have a hallux on KS001 look very similar to hallux-bearing tracks on KS064 and may represent a similar or identical tracemaker. KS001 tracks overlap with much greater frequency than the tracks from KS064, and show more evidence of feeding and foraging.

### Behaviors present

Trackway I on KS064 (Fig. 14) likely shows asymmetrical hopping gait or a flapping-aided hop with normal steps. Tracks 3 and 5 have a pace length of 57 mm. Tracks 5 and 6 have a pace length of 85.5 mm, and increase of nearly 30 mm. Tracks 6 and 7 have a pace length of 41 mm, which is short than that between tracks 3 and 5. This variation in pace length is most likely produced by a hopping behavior. Ground-based bird locomotion consists of three major types of movement: running and walking, hopping, and asymmetrical hopping. Hopping and asymmetrical hopping leave noticeably different trackways than walking or running tracks (Elbroch and Marks, 2001). Trackway I is unique, however, in the placement of the feet. Track 3 represents a left foot, and track 5 represents a right. At this point the bird left the sediment surface. Upon landing, the right foot fell first (track 6) then the left (track 7). This type of asymmetrical hopping is not commonly seen in birds that utilize this locomotion (e.g., American Crow, Elbroch and Marks, 2001). This strongly suggests that the hopping behavior was assisted by flapping, to allow the bird to become sufficiently airborne, and is associated with a walking trackway, not an asymmetrical hopping trackway.

Tracks 9 and 13 (trackway III), 14, and 15 (trackway IV) on KS064 (Fig. 14) have exceptionally long hallux impressions. Dragging of the hallux likely produced the long hallux impression. Long hallux impressions in trackways have previously interpreted as part of landing behaviors associated with flight (Genise et al., 2009). In trackway III, tracks 9 and 13 are both impressions of the right foot. The impressions

of the left feet of this trackway lack hallux impressions. Perhaps the hallux impressions in the right foot tracks only suggest an injury to one of the legs, forcing the bird to compensate for or shift its weight to the right side. Interestingly, the right foot impression is also of trackway III is also turned in slightly to the left, implying that there very well may have been an injury to this foot or leg. Trackway IV (tracks 14–16) is interpreted as a landing trackway in which a bird landed at a low angle relative to the ground, dragging the first toe for a short distance during landing. The pace length of tracks 14–15 is much smaller than that of 15–16. Birds tend to have their feet nearly parallel when landing to avoid injury; the greater pace length of tracks 15–16 represents the bird taking its first step after landing.

The tracks of KS001 show two types of feeding behaviors—traces interpreted to be probe marks and peck-mark clusters. The clusters of elongate marks (Fig. 17B) and their association with trackways are similar to the clusters of probe marks seen in sandpipers in their distribution (Elbroch and Marks, 2001); however, while sandpipers constantly probe in between clusters of probes (Elbroch and Marks, 2001), there is little evidence for continuous probing in the traces on KS001, and their traces are often rounder in shape. These elongate marks could be considered traces of pecking rather than probing, as probe marks are generally circular (Elbroch and Marks, 2001) and may be associated with invertebrates traces on KS001. Such traces can be produced by insect larvae or annelids (Hasiotis, 2002). During pecking, the motion of the beak is not only down into the sediment, but also back towards the body in a scraping motion. Modern pecking marks can be up to 10 mm long, though

the length is usually variable, and the width can be as great as 5 mm (e.g., Frey and Pemberton, 1987, Fig. 12). The length of modern peck marks is consistent with the marks from the Haman Formation, which are 3–7 mm long. The Haman Formation marks, however, are much thinner, only up to 2 mm wide. The difference between the two traces is a result of variation in the manner of sediment-beak interaction. During probing, the beak can be closed, open slightly, or open wide; if the beak is closed tightly, the depression created would be oval or circular and would not have any separation between the upper and lower mandible marks. If the beak is open slightly, as much as 2 mm of sediment may be present between the upper and lower mandible mark. If the beak is open wide, the area of sediment between the upper and lower mandible mark may be much greater. The peck-mark clusters on KS001 cannot be identified as belonging to any specific trackway.

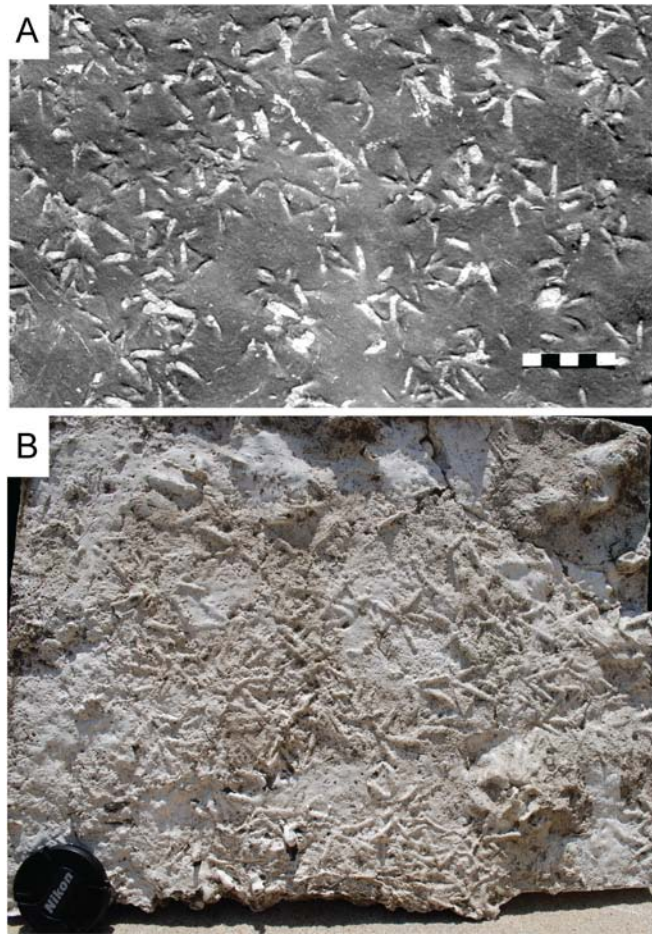
The presence of both individual probe marks and clusters of pecking marks may indicate two separate foraging styles and, therefore, separate species. Structures interpreted to be fossil probe marks were noted from the bird tracks of the Santo Domingo Formation (Genise et al., 2009); however they are difficult to determine from photographs and may be the openings of U-shaped burrows assignable to *Arenicolites*.

The presence of invertebrate traces, crosscutting and crosscut by the avian tracks suggests that these organisms were interacting with the sediment in the same period of time. The invertebrate traces on KS064 are preserved in both convex and concave epirelief, which suggests that the invertebrates were both on the surface of

the sediment and below the sediment surface. The invertebrate traces of KS001 are also preserved in both convex and concave epirelief. Given the prevalence of peck and probe marks on KS001, it is likely that the birds were hunting for the invertebrates whose traces they had overstepped.

The smaller tracks on KS001 overstep and overlap each other in many cases (Fig. 20A). This is very similar to the pattern seen in many shorebirds, for example, the Killdeer (Fig. 20B). This type of pattern can be made in a short period of time, and by a surprisingly few birds. Two Killdeer can fill a 32 x 41 square cm area with tracks in 45 minutes to 1 hour while foraging for food, actively feeding, and defending their territory from other birds. Such behavior observed in extant birds indicates that tracks on KS001 and KS064 may not be indicative of a large number of birds, but rather as few as two individuals defending their territory and foraging for food.





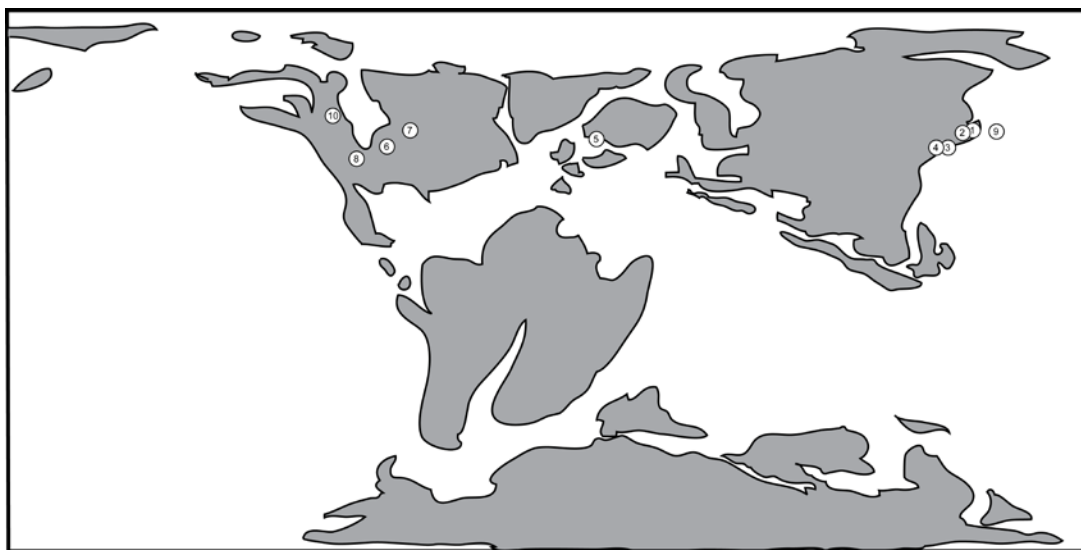
**Figure 20.** Photographs comparing KS001 to a plaster cast of modern *Charadrius vociferous*. A.) Photograph of the slab KS001 (photo courteously of Jong-Deock Lim). B.) Photograph of a 32x41 cm plaster cast of *C. vociferous* tracks.

#### Implications for avian diversity and dispersal

Recently, tracks assigned to the ichnogenus *Koreanaornis* have been discovered in North America (Anfinson, 2009). There are two other North American Cretaceous avian ichnogenera, *Ignotornis* and *Aquatilavipes*; *Ignotornis* is also found in Korea, and *Aquatilavipes* is found in China and Japan as well as in Korea (Lockley

et al., 2006). The bird track localities in Asia are, as a whole, much more diverse and numerous than the bird track localities in North America; this has been speculated to be due not to preservational bias but the paleoecology of these areas (Lockley et al., 2006).

The presence of all three North American avian ichnogenera across the Pacific Ocean in Asia has several implications for the early evolution and dispersal of birds. The epicontinental seas that covered most of Europe were a significant barrier between North America and Asia by the Early Cretaceous (Fig. 21). The Pacific Ocean was wider than today's Pacific by a significant distance. The ichnologic evidence implies that, at the very least, similar families or genera of birds existed on the separate continents at the same time. This pattern can be explained by using either dispersal or migration.



- |  |   |   |
|--|---|---|
| 1. Lim et al., 2000; 2002- <i>Koreanaornis</i>     | 5. Fuentes Vidarte, 1996- <i>Archaeornithipus</i> | 9. Azuma et al., 2002- <i>Aquatilavipes</i> |
| 2. Kim et al, 2006- <i>Ignotornis</i>              | 6. Mehl, 1931- <i>Ignotornis</i>                  | 10. Currie, 1981- <i>Aquatilavipes</i>      |
| 3. Lockley et al, 2006- <i>Pullornipes</i>         | 7. Lockley et al., 2001- <i>Aquatilavipes</i>     |   |
| ( <i>Koreanornipodidae</i> ); <i>Aquatilavipes</i> | 8. Anfinson et al., 2009- <i>Koreanaornis</i>     |   |
| 4. Lockley et al., 2007- <i>Shandongornipes</i>    |   |   |

**Figure 21.** (Previous page) Paleogeographic map showing potential localities of Early Cretaceous bird trackways. Modified from Northern Arizona University's paleoglobe project.

Based on paleogeographic reconstructions, dispersal for early avians may have been accomplished overland during the Early Jurassic, while the Atlantic Ocean was still relatively small and shallow. Alternatively, early ornithurine birds could have dispersed at high latitudes and worked their way down the coasts. Evolutionarily, it is likely that the split between the more advanced ornithurine birds and the more primitive birds of the subclass Sauriurae happened near the base of avian evolution (Martin, 1983); this split is thought to be in the Late Triassic-Early Jurassic (Feduccia, 1996; Martin, 2004). The Lower Cretaceous bird tracks found thus far have been interpreted as those of ornithurine birds; therefore, the Ornithurae had a worldwide distribution by the Early Cretaceous. This implies that the evolution of birds did not occur in the Late Jurassic, with the appearance of *Archaeopteryx*, but rather much earlier, as primitive avians would not have the capability to disperse across wide bodies of water.

As an alternative hypothesis, the ornithurine birds of the Early Cretaceous may have evolved long-distance migration. Today's long-distance migration is based on seasonal patterns (Steadman, 2005), whereas Cretaceous avian migration may have been based around wet-dry seasons, or seasonal variation in sunlight, for example, in polar regions. Some highly specialized species of birds such as the Bar-

Tailed Godwit travel 10,000 km without stopping for a rest (Newton, 2008). A detailed comparative study of the anatomy of Early Cretaceous ornithurine birds and modern-day long-distance migrants would show if Early Cretaceous ornithurine birds were capable of making such long, involved flights.

## CONCLUSIONS

This study is a preliminary analysis of two casts from the Lower Cretaceous Haman Formation of South Korea. Behaviors interpreted include feeding and foraging behaviors, landing, and walking with flapping-assisted hopping. Elongate, thin marks are interpreted to be pecking marks associated with trampled areas that represent feeding with surface scraping of the sediment. Asymmetrical paired oval depressions are interpreted as probe marks that represent surface and subsurface feeding. Ichnogenera of invertebrate traces associated with the bird tracks include *Cochlichnus*, *Steinichnus*, and *Arenicolites*. These invertebrate traces crosscut and are crosscut by the bird tracks. It is likely that the probe and peck marks on KS001 are a result of the birds searching for the invertebrates that produced those traces. The South Korean Lower Cretaceous tracksites likely contain more clues to the behaviors typical of shorebird-like ornithurine birds, and should be studied in greater detail in the future.

## ACKNOWLEDGEMENTS

We are thankful to Dr. Jong-Deock Lim of the National Heritage Museum in South Korea for donating the casts and for access to photographs. This paper is part of a masters' thesis conducted by ARF. ARF was supported by the University of Kansas Department of Geology, the University of Kansas Natural History Museum and Biodiversity Research Institute Panorama small grant competition, and the Geological Society of America.

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## **CHAPTER FOUR. A MORPHOLOGIC CRITERION FOR DISTINGUISHING BIRD TRACKS**

*Currently in review as:*

Falk, A. R., Martin, L. D. and Hasiotis, S. T. A morphologic criterion for distinguishing bird tracks: *The Journal of Ornithology*.

### **ABSTRACT**

There are few anatomical criteria that distinguish bird tracks from dinosaur tracks. The angle of divarication is one such criterion. A total of 186 bird tarsometatarsi were sampled to test the hypothesis that the morphology of the distal end of the tarsometatarsus influences the angle of divarication of the toes. Skeletal limb anatomy was also studied for correlations between methods of locomotion (hopping, skipping or walking), stride length, and morphotype (shorebirds, wading birds, perching birds, zygodactyl birds, birds of prey, ground foragers, webbed-footed birds, and syndactyl birds). Analysis shows that the larger the trochlea arc angle, the smaller the angle of divarication. The trochlear arc angle and the angle of divarication also correlated with such avian morphotypes as shorebirds, waders, ground foragers, and perching birds. Correlations between limb proportion, locomotion, stride length, and morphotype were difficult to determine and ambiguous. Weak correlation was found between avian functional leg length and posture; weak correlations were also found between avian functional leg length (divided by stride length) as compared to arboreality, method of locomotion, and method of feeding.

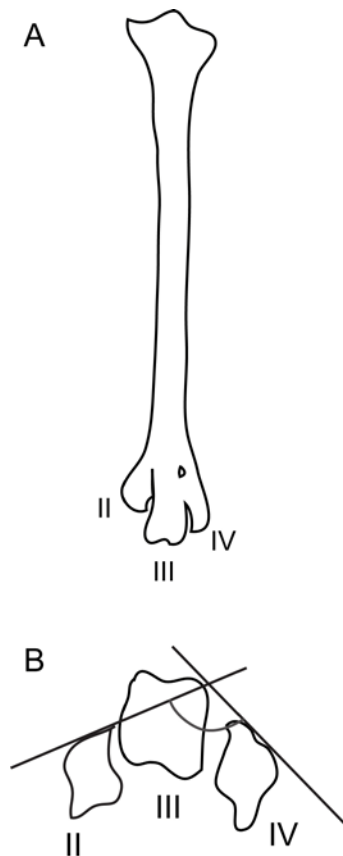
## INTRODUCTION

There has always been some difficulty in distinguishing the tracks of Mesozoic birds from those of small theropod dinosaurs (Lockley et al., 1992). The first tridactyl tracks discovered were given the name *Ornithichnites* by Hitchcock (1836), as he thought they belonged to giant, extinct birds. Lockley (1992) was the first to establish a set of easily definable criteria for distinguishing bird tracks from dinosaur tracks. Although many of the criteria selected were subjective—overall resemblance to modern bird tracks and slender digit and claw impressions—they included one very important criterion: angle of divarication. Lockley (1992) stated that the divarication angle of birds will, in general, be 110–120°, whereas the angle of divarication in theropod dinosaurs will always be <100°. This angle of divarication has been the criteria upon which studies have based their interpretations.

The purpose of this paper is to determine if tarsometatarsal morphology influences the angle of divarication in the foot of birds and bird tracks. Tarsometatarsi of eight different avian morphotypes were examined: shorebirds, wading birds, perching birds, zygodactyl birds, birds of prey, ground foragers, webbed-footed birds (palmate and totipalmate birds), and syndactyl birds (partly fused toes). This paper also examines leg morphology and locomotor patterns in extant birds to retrodict bird anatomy and lifestyle from Mesozoic and Cenozoic tracks and trackways.

The tarsometatarsus in ornithurine birds results from a fusion of distal tarsal III of the ankle and metatarsals II–IV of the foot. In enantiornithine (e.g., *Iberomesornis*) and Saurine (e.g., *Archaeopteryx*) birds, this structure fuses from

proximal to distal (i.e., ankle to toes). In modern birds (Ornithurae), those bones fuse from distal to proximal (Martin, 1983). The distal articular surface of the tarsometatarsus is formed by three trochlea, where toes II, III, and IV articulate (Fig. 22). Toe I, the hallux, is articulated to the tarsometatarsus by a splint-like metatarsal I further proximal on the bone. The extensor *digitum longus*—the muscle that flexes the toes—is the main muscle in this distal area of the tarsometatarsus and extends from the tarsometatarsus onto the digits (Cracraft, 1971; Verstappen et al., 1998).



**Figure 22.** Avian tarsometatarsus. A) The stylized tarsometatarsus of a bird, modeled after a Herring Gull (*Larus argentatus*). B) The distal end of the tarsometatarsus, looking down the long axis of the bone. Tangent lines indicate how to measure the

trochlear arc of the tarsometatarsus. These lines can intersect trochlea III—the line should touch the highest point of both condyles present. If only one condyle is present, the line should touch the highest point of the trochlea and cover as much of the surface of the trochlea as possible without intersecting the bone itself.

Few studies have been conducted on the functional morphology of the avian tarsometatarsi (Ostrom, 1979; Zhang, 2004, 2006). Studies of the hindlimb musculature of some avian taxa have examined the movement of toes and the general motion of the ankle joint (Berman, 1982, Cracraft, 1971, Verstappen et al., 1998). Ostrom (1979) hypothesized that the tarsometatarsus fused to compliment the complicated system of flexor muscles used to extend and retract the toes. Zhang (2004, 2006) studied the tarsometatarsus of modern raptors and Mesozoic birds, determining function (Zhang, 2004) and running statistical analyses to distinguish arboreal from terrestrial birds (Zhang, 2006). No study, however, has ever correlated the arc of the distal articular surfaces of the tarsometatarsus with the angle of divarication of the toes. It is this angle of divarication that translates itself into the tracks and trackways produced by birds.

The three trochlea that comprise the distal end of the tarsometatarsus vary in morphology and arrangement at the species level. Some tarsometatarsi have trochlea in a straight line, whereas others form an acute to an obtuse angle. No previous studies specifically document this variation across bird morphotypes, or its implication for the tracks and trackways produced by birds.

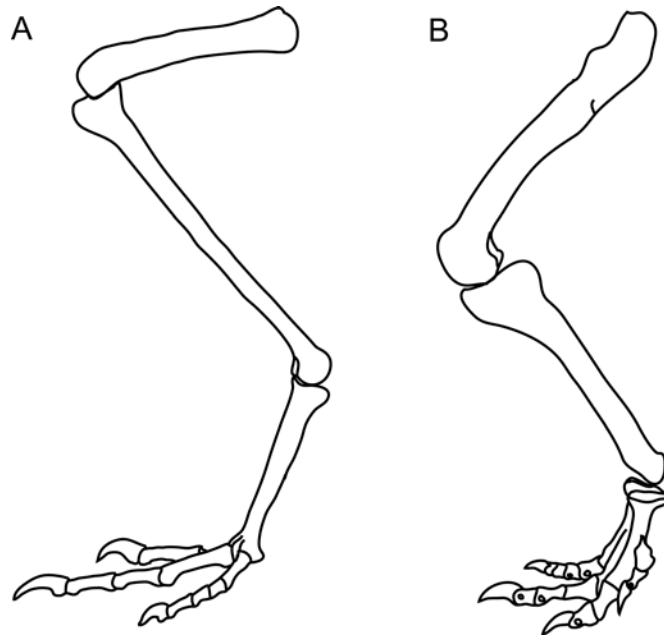
There are several different foot structures in birds (Proctor and Lynch, 1993). The most common arrangement of toes is called anisodactyl, where toes II, III, and IV face forward, and toe I (the hallux) is reflexed (i.e., posterior projecting). The next most common type is zygodactyl, with two toes aligned forward and two toes aligned backwards. There are two webbed-foot types, the most common webbed type is palmate, where toes II, III, and IV are bound by webbing, followed by totipalmate, where all four toes are bound together by webbing. Syndactyl arrangement is found in only a few families and is represented by the fusion or partial fusion of two or more toes.

## HIND LIMB ANATOMY AND METHODS OF LOCOMOTION IN BIRDS

It is possible to calculate acetabular (hip socket) height for the majority of bipeds and tetrapods based on the stride length of tracks (Hasiotis et al., 2007). Measuring the femur, tibia, and metatarsal height can also be used to calculate stride length. It may not, however, be possible to measure acetabular height for birds based on stride length because bird legs and their function are fundamentally different than other bipeds.

The femur of a bird is held nearly parallel to the body (Fig. 23A), rather than nearly vertical as in other bipeds (Kaiser, 2007). The functional leg is, therefore, composed of only two bones, the tibiotarsus and tarsometatarsus (Farlow, 2000). Rubenson et al. (2007) showed that the femur in ostriches, the most cursorial-adapted birds, moves in a restricted plane, abducting and adducting in a motion of  $\sim 9.5^\circ$ . In

theropod dinosaurs (Fig 23B), the functional leg consists of all three limb elements, and the femur is oriented nearly vertical with respect to the body (Farlow, 2000). Birds have a relatively shorter stride than dinosaurs, based on studies of trackways (Farlow, 2000).



**Figure 23.** A) A skeletal reconstruction of a bird leg based on a Turkey Vulture (*Cathartes aura*). B) Skeletal reconstruction of a ornithomimid dinosaur hindlimb.

The method of walking used by birds results in different trackways. Wading birds have very precise steps that often result in well-defined trackways with a narrow pace width and long stride length. Many webbed-footed birds waddle and produce trackways with a wide pace width, short stride length, and inward directed footprints. Perching birds and woodpeckers hop when on the ground; some perching birds (e.g., thrushes, blackbirds, some sparrows) alternate between walking and hopping

(Elbroch and Marks, 2001). Trunk-climbing birds also use hopping as they move up and down tree trunks (Norberg, 1981). While the methods of ground-based locomotion amongst birds are diverse, the primary method of locomotion for most birds is flight.

Fossil bird tracks are known from the Early Cretaceous worldwide (Lockley et al., 1992, 2001; Lockley and Matsukawa, 1998; Azuma et al., 2002; Anfinson, 2004). These tracks and trackways are interpreted to be shorebird tracks based on their overall similarity to tracks of extant shorebirds (Charadriiformes) and their overall environment of deposition, interpreted as river banks and other such water-margin environments as lakeshores, delta plains and tidal flats (Lim et al., 2002). Since shorebirds are the usual inhabitants of these environments today, it is reasonable to expect shorebird-like birds in similar environments 120 million years ago. Any morphometric criteria for distinguishing trackways of shorebirds from other birds, however, have not been available.

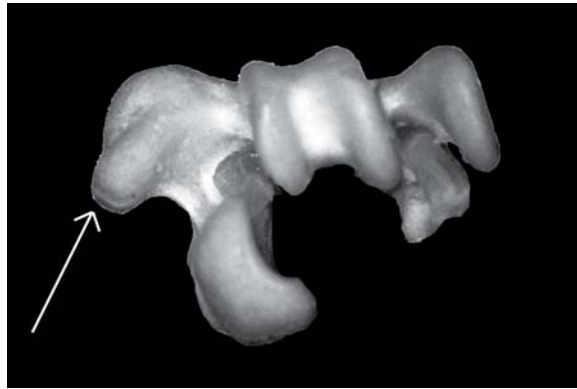
## METHODS

Several species of birds from each morphotype were selected from Elbroch and Marks (2001). Birds were separated into morphotypes based on habitat (wading, shorebird, bird of prey, perching, ground forager) or anatomy (web-footed, zygodactyl, syndactyl). These are used independent of taxonomic classification; therefore, shorebird does not necessarily mean the order Charadriiformes. Thirty-two species were selected, with the number of examples of their tracks measured varied

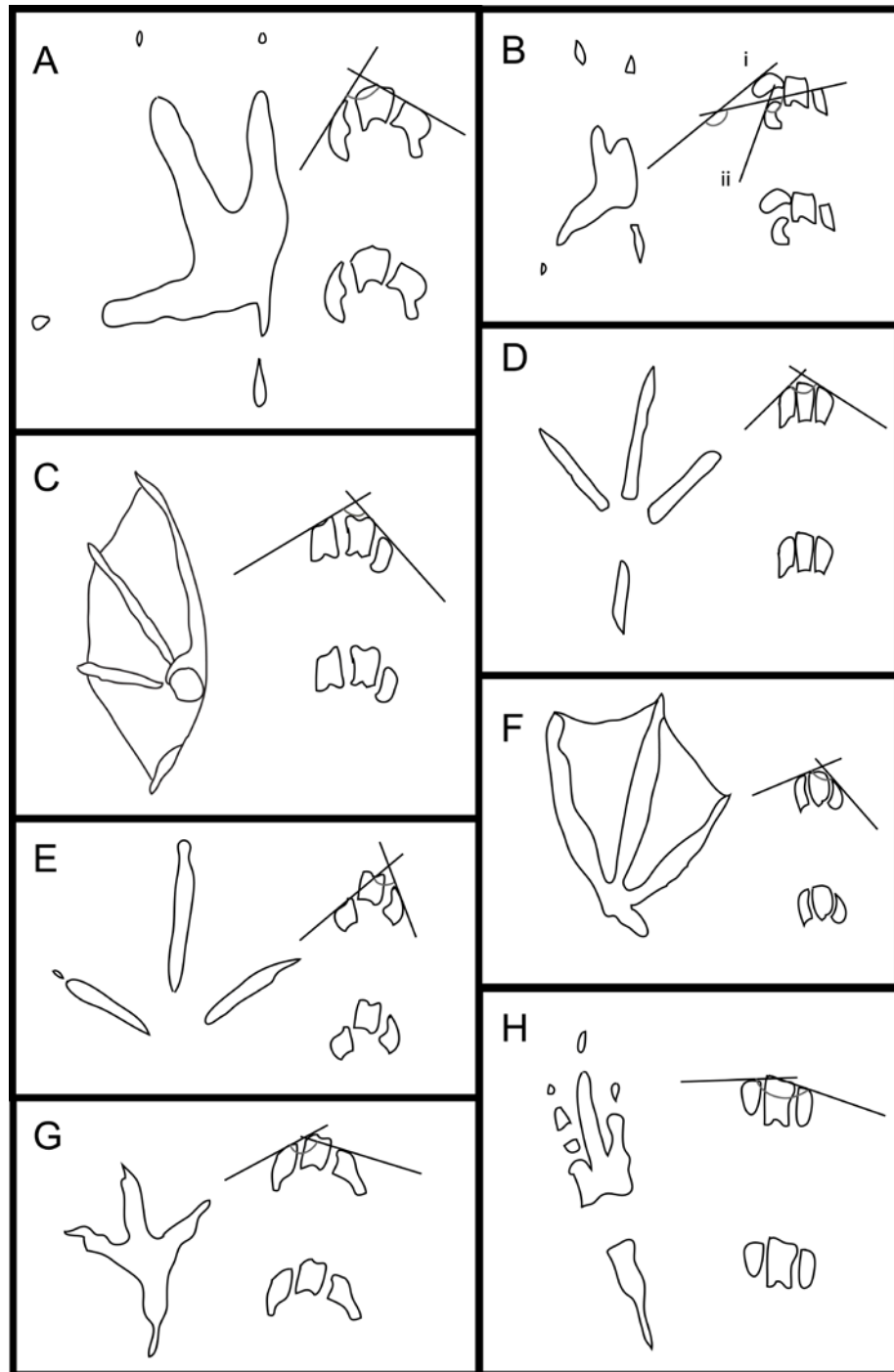
from two to eight. Skeletons of the species used in this study are from the University of Kansas Ornithology collections. Four to six individuals of each species were selected, except in the cases where there were fewer than four skeletons in the collections.

A total of 186 tarsometatarsi were measured. The distal ends of the tarsometatarsus from all morphotypes were impressed into thin slabs of clay to obtain a measurable image of the trochlea. The impression was made with the tarsometatarsus oriented vertically. These clay slabs were then laid on sheets of clear plastic and photocopied. The arc angle of the trochlea was measured on the photocopies by drawing tangent lines to the tops of the trochlear condyles II and IV (Fig 22B). The angle formed where the lines intersect is termed the trochlear arc angle. In the case of the Northern Flicker (*Colaptes auratus*) and the Pileated Woodpecker (*Dryocopus pileatus*), trochlea IV (Fig. 24) is composed of two separate trochlea (i.e., trochlea IV and *trochlea accesoria*). These were labeled i and ii, and measured individually (Fig 25). In some species the articular surface for digits II or IV was hard to distinguish, such as in the Great Horned Owl (Fig. 25A); therefore, the lines tangent to these condyles were approximated. Many species, especially birds of prey and zygodactyl birds, had a process extending from trochleas II or IV (Fig. 25A, G). This was not measured to determine the trochlea arc angle, as it is only a process of the external condyle of these trochlea.



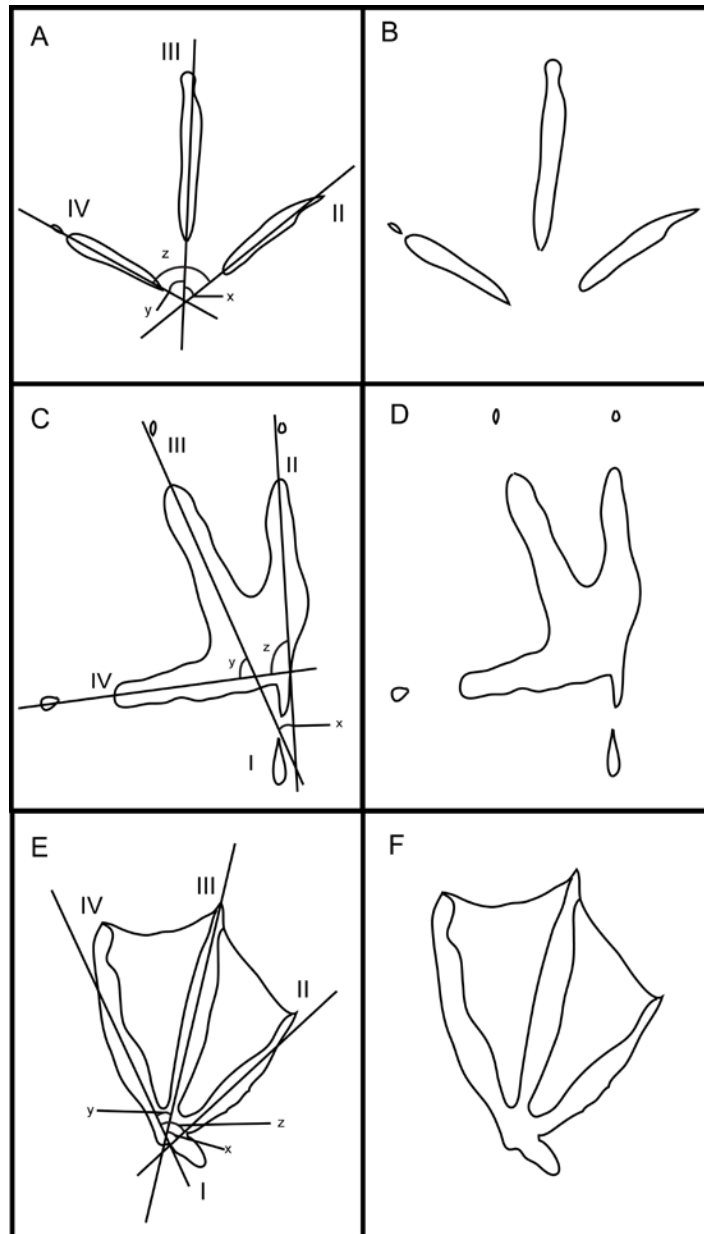


**Figure 24.** Distal end of a Pileated Woodpecker (*Dryocopus pileatus*) tarsometatarsus. Arrow points to the trochlea accessoria.



**Figure 25.** Distal ends of tarsometatarsi and tracks from each morphotype, including both types of zygodactyl tracks.

The angles of divarication of the toes were measured from illustrations in Elbroch and Marks (2001) and from modern tracks observed on the shoreline of Lake Erie at Lake Erie Metropark in Brownstown, Michigan, and the shoreline near the dam on Clinton Lake, in Lawrence, Kansas. Divarication angles were measured between toes II and III, III and IV, and II and IV (Fig. 26). The hallux was not measured. Angle of divarication is calculated from lines drawn through the midline of each toe to where the toe meets the metatarsal pad and follows the midline of the toe up to the first joint where it may diverge from the toe if necessary (Fig. 26E–F). Drawing the line in this manner prevents distal toe rotation from factoring into the angle and prevents the webbing in web-footed birds from having a pronounced effect on the angle of divarication, due to the way the toes curl inward (Fig. 26E, F). It has also been shown that sediment texture and moisture content can also impact the angle of divarication (Curie, 1981).



**Figure 26.** Measuring angle of divarication. A, B) Anisodactyl bird foot. C, D) Zygodactyl bird foot. E, F) Palmate bird foot. Angle of divarication ( $x$ ) between II and III, ( $y$ ) between III and IV, and ( $z$ ) between toes II and IV.

The arc angle of the trochlea for each species was averaged with no distinction made between left and right tarsometatarsi. The same was done for the angle of divarication of the toes. These measurements were imported into an Excel spreadsheet and graphed to determine any correlation between angle of divarication and trochlea arc (Fig. 27). Standard deviation for both arc angle and angle of divarication were calculated using the standard deviation function in Excel.

The relationship between the trochlear arc angle and the angle of divarication of the toes was applied to two tracksites from the Early Cretaceous in order to retrodict the arc angle of the trochlea from the angle of divarication of the toes. Tracks from the Lower Cretaceous Lakota Formation from South Dakota, USA and tracks from the Lower Cretaceous Haman Formation of South Korea were used in this practical application of these data gathered from this study.

Limb bones—the femur, tibiotarsus, and tarsometatarsus—from one species of each morphotype were measured in order to examine avian skeletal hindlimb anatomy and test for correlations with stride length, morphotype, and type of locomotion. These data were placed into an Excel spreadsheet and correlations between morphotype and limb bone ratios were determined. The formulas used were:

- 1) 
$$\frac{\text{femur} + \text{tibiotarsus} + \text{tarsometatarsus}}{\text{tibiotarsus} + \text{tarsometatarsus}}$$
- 2) 
$$\frac{\text{tibiotarsus}}{\text{tarsometatarsus}}$$
- 3) 
$$\frac{\text{functional leg length (tibiotarsus+tarsometatarsus)}}{\text{Median stride length}}$$

These formulae provide insight into the correlations between limb element length and bird morphotype, as well as any potential to calculate the acetabular height for each species in the study. Equation (1) is referred to as the avian functional leg length correlation, as it compares total leg length by functional leg length values. Equation (2) is a simple ratio that compares the tibiotarsus length to the tarsometatarsus length. Equation (3) is modified from Farlow (2000) and attempts to correlate functional leg length to median stride length. All measurements are in millimeters, and the results for equations (1) and (3) are in millimeters, whereas equation (2) results in a dimensionless number. Digit III was used originally in equation (3), and was considered a proxy for body size; however, this is a poor indicator (Farlow, 2000). In this study, digit III is replaced by the stride length as the divisor. Median stride lengths for the species used were taken from Elbroch and Marks (2001). Digit III was then placed back in equation (3) to determine if digit III was a reliable proxy for stride length.

## RESULTS

Trochlear arc varied from an average of 58° for the Willet (*Tringa semipalmatus*) to 175° for the Evening Grosbeak (*Coccothraustes yespertinus*) (Table 4). Standard deviation varied from 30.0 for the Northern Flicker (*Colaptes auratus*) to 2.6 for the Long-billed Curlew (*Numenius americanus*).

<b>Table 4</b>			
<b>Number</b>	<b>Trochlear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
1	72	1	118

2R	83.5	2	115
2L	91.5	3	118
3	64	4	118
4	85	5	139
		6	105
5	70	1	130
6R	93	2	109
6L	85	3	32
7R	91	4	117
7L	92	5	123
8	76	6	123
9	103	7	121
10	98		
11R	100	1	109
11L	86	2	86
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
12R	110	3	113
12L	100	4	98
13R	96	5	108
13L	110	6	111
14R	92		
14L	87		
15R	123		
15L	110		
16R	120		
16L	121		
17	107	1	79
18	139	2	80
19R	106	3	76
19L	112	4	83
20	139	5	81
		6	68
		7	78
		8	73
21	71	1	100
22R	91	2	123
22L	84	3	128
23	57	4	111
24	67	5	122

25	62	6	120
26	87		
27	153	1	58
28	158	2	63
29R	167	3	39
29L	163	4	52
30	164	5	40
31R	172	6	59
31L	160	7	47
32R	173	8	65
32L	176	9	53
33R	154*	1	56
33L	163*	2	49
34	160	3	58
35	149	4	68
36	171	5	57
		6	59
Number	Troclear arc angle	Track Number	Divarication angle
37R	76	1	135
37L	80	2	125
38R	76	3	125
38L	78	4	122
39R	84	5	120
39L	79		
40R	82		
40L	80		
41R	77		
41L	81		
42R	46	1	120
42L	60	2	112
43	68	3	110
		4	122
		5	110
		6	125
44R	76	1	98
44L	74	2	94
45R	78	3	136
45L	88	4	125
46R	77	5	91



46L	72	6	116
47R	87	7	97
47L	95	8	95
48R	71	1	124
48L	73	2	118
49R	65	3	116
49L	80	4	106
50R	59	5	112
50L	58	6	109
51R	70	7	129
51L	71		
52R	89	1	98
52L	83	2	102
53R	91	3	102
53L	90	4	108
54R	81	5	115
54L	84	6	104
55	175	1	50
56	162	2	58
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
57	170	3	39
58	174	4	45
59	175	5	44
60	168	6	40
		7	42
		8	42
61	167	1	50
62	120	2	50
63R	142	3	38
63L	142	4	69
		5	70
		6	59
64	167	1	58
65R	171	2	49
65L	173	3	70
		4	70
		5	52
		6	42

66	156*	1	42
67	147	2	37
68	120*	3	41
69	171	4	44
		5	46
		6	47
70R	177	1	52
70L	179	2	20
71	178	3	43
72	167	4	25
73R	175	5	50
73L	175	6	24
		7	49
		8	27
74	161	1	48
75	175	2	64
		3	54
		4	59
Number	Troclear arc angle	Track Number	Divarication angle
76R	119	1	85
76L	124	2	85
77R	112	3	93
77L	114	4	101
78R	105	5	97
78L	121	6	91
79	116		
80R	121		
80L	117		
81R	112		
81L	117		
82R	143	1	103
82L	149	2	125
83R	129	3	95
83L	128	4	103
84	128	5	99
85R	123	6	93
85L	141		
86R	129		
86L	146		

87R	110	1	91
87L	129	2	79
88R	110	3	85
88L	118	4	79
89R	115	5	81
89L	116	6	84
90	147	1	86
91R	122	2	95
91L	147	3	86
92R	129	4	90
92L	139	5	86
93R	133	6	84
93L	135		
94R	142		
94L	127		
95R	85	1	112
95L	96	2	104
96R	83	3	89
96L	79	4	95
97R	101	5	115
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
97L	98	6	109
98R	76		
98L	88		
99R	84		
99L	79		
100R	111	1	93
100L	114	2	52
101R	116	3	93
101L	124	4	93
102R	118	5	94
102L	117	6	94
103R	116		
103L	109		
104R	110		
104L	110		
105R	123		
105L	111		
106R	119	1	98

106L	111	2	88
107R	129	3	95
107L	126	4	101
108R	120	5	79
108L	118	6	87
109R	116		
109L	109		
110R	108	1	82
110L	124	2	73
111	105	3	86
112R	102	4	85
112L	118	5	86
113R	124	6	84
113L	107		
114	89		
115R	85	2	112
115L	83	3	109
116R	86	4	102
116L	103	5	98
117R	85	6	100
117L	96		
118R	126		
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
118L	109	2	86
119R	120	3	88
119L	118	4	97
120R	135	5	100
120L	125	6	94
121R	125		
121L	125		
122R	128		
122L	124		
123R	119		
123L	121		
124	136	1	100
125	133	2	106
126R	131		
126L	134		
127R	131		

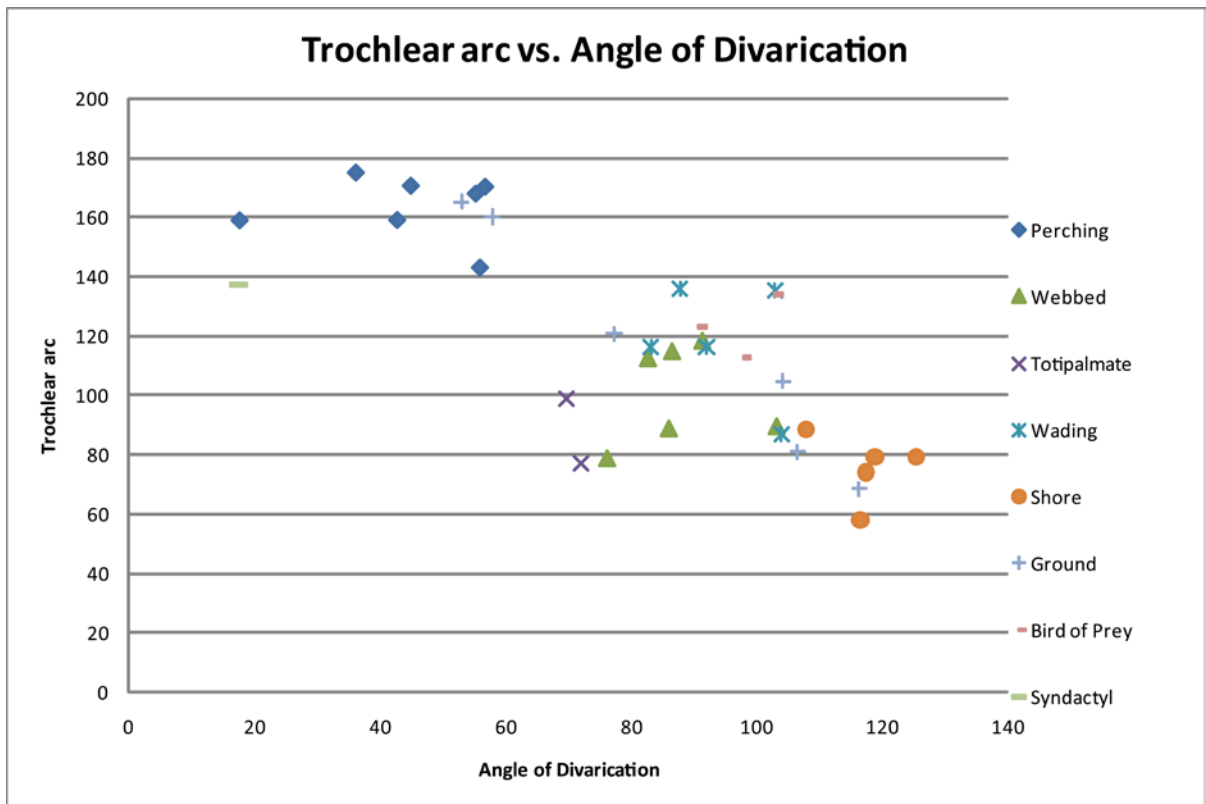
127L	118		
128R	136		
128L	131		
129R	151		
129L	136		
130R	114	1	91
130L	107	2	82
131R	108	3	101
131L	123	4	105
132	113	5	95
133	107	6	101
134R	114	7	122
134L	115	8	86
135R	65	1	62
135L	71	2	85
136R	67	3	75
136L	65	4	62
137	90	5	76
138R	94		
138L	86		
139R	75	1	104
139L	89	2	82
140R	72	3	76
140L	75	4	71
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
141R	105	5	92
141L	81	6	91
142R	88		
142L	106		
143R	97		
143L	90		
144R	98		
144L	90		
145R	81	1	89
145L	80	2	76
146R	61	3	71
146L	72	4	74
147R	87	5	63
147L	89	6	84

148R	77		
148L	83		
149R	79	1	73
149L	95	2	62
150R	92	3	77
150L	99	4	67
151R	108	5	69
151L	109		
152R	109		
152L	97		
153	90	1	101
154	98	2	76
155R	95	3	74
155L	102	4	105
156	93	5	97
157R	104	1	136
157L	85	2	130
158	109	3	124
159	114	4	142
160R	100	5	136
160L	107	6	146
		7	134
161R	93	1	127
161L	92	2	155
162	87		
163R	96		
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
163L	93		
164R	90		
164L	84		
165R	89	1	188
165L	104	2	176
166	100	3	205
167	89	4	213
168R	102	5	200
168L	89		
169R	90		
169L	91		
170	130	1	20

171R	123	2	15
171L	139		
172R	142		
172L	156		
173	134		
174Ri	114	1	187
174Rii	122	2	213
174Li	68	3	189
175Ri	148	4	197
175Rii	151	5	209
175Li	127	6	197
175Lii	142	7	180
176Ri	144	8	213
176Rii	160		
176Li	131		
176Lii	169		
177i	162		
177ii	180		
178i	143	1	143
178ii	174	2	135
179Ri	140		
179Rii	159		
179Li	134		
179Lii	155		
180i	145		
180ii	162		
181i	74		
181ii	98		
<b>Number</b>	<b>Troclear arc angle</b>	<b>Track Number</b>	<b>Divarication angle</b>
182	178	1	19
183R	171	2	11
183L	136	3	16
184	167	4	19
185R	139	5	19
185L	137	6	18
186R	177	7	14
186L	166	8	26

**Table 4.** (Previous page) Measurements of the angle of divarication and trochlear arc by species.

There is a strong correlation ( $r^2 = 0.60$ ) between trochlear arc angle and the angle of divarication, if the tracks of zygodactyl birds are removed (Fig. 27). With the zygodactyl tracks present,  $r^2 = 0.1882$ . The typical anisodactyl track has a highest average angle of divarication of  $119^\circ$  and an overall average of  $82.3^\circ$ . Zygodactyl tracks, however, can have an angle of divarication as high as  $213^\circ$  (Table 2). Divarication angle is the factor that skews the graph with respect to the zygodactyl tracks, as the arc angle measurements for these tracks are not that unusual.





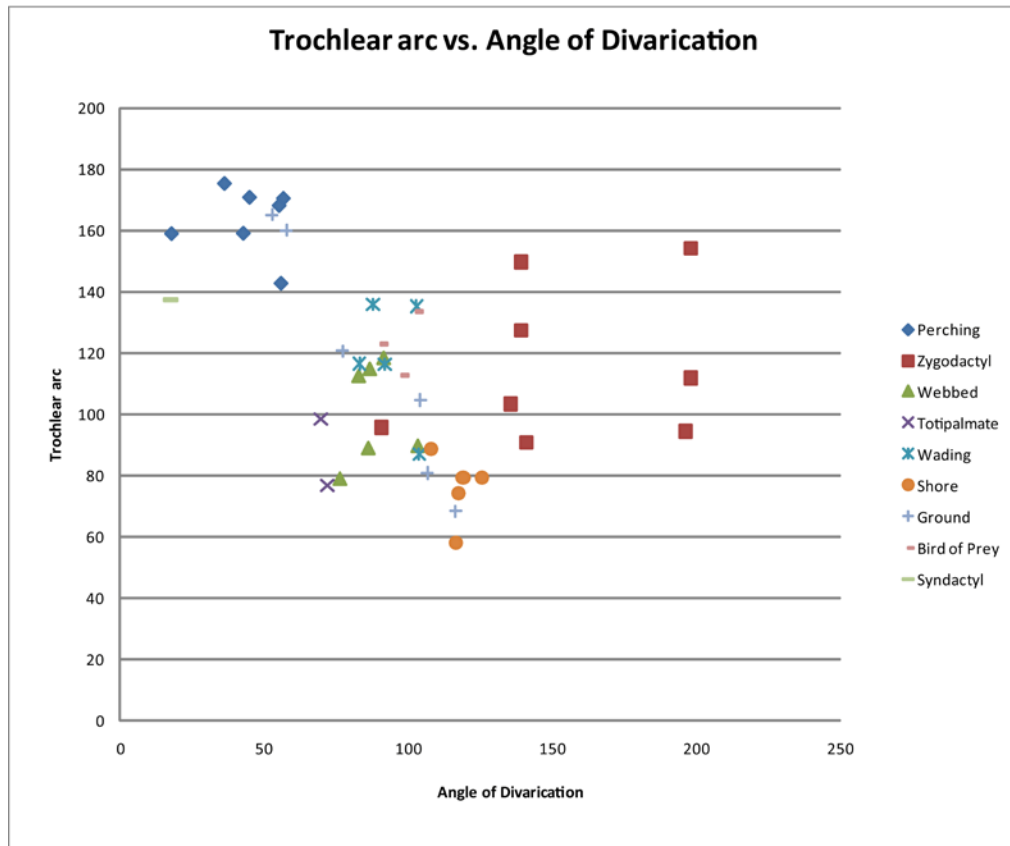
**Figure 27.** (Previous page) Graph showing the correlation between trochlea arc and angle of divarication, with the zygodactyl tracks removed.

Graphic representation of the measurement of angle of divarication vs. trochlear arc angle exhibits a variety of patterns. Perching birds and shorebirds form tight clusters (Fig. 27). Ground foragers are much more spread out along the trend line. Two of the ground forager measurements fall within the perching bird cluster: the American Crow (*Corvus brachyrhynchos*) and the Black-billed Magpie (*Pika pika*).

Angle of divarication in perching birds varies from  $17.75^{\circ}$  in the Blue Jay (*Cyanocitta cristata*) to  $56.8^{\circ}$  in the Spotted Towhee (*Pipilo maculatus*). Perching birds, including *C. cristata*, have very high angles of trochlear arc as well, with the morphotype average of  $163.5^{\circ}$  (Table 4).

Shorebirds have an average angle of divarication  $106.5^{\circ}$  and wading birds have an average angle of divarication of  $94^{\circ}$ . The trochlear arc angle for shorebirds and wading birds is  $75.83^{\circ}$  and  $118^{\circ}$ , respectively (Table 4). Only one individual of webbed-footed birds, the American Avocet (*Recurvirostra americana*), overlapped with the shorebird cluster. Totipalmate birds—birds that have all four toes joined by webbing—fall within the cluster of web-footed birds in terms of arc angle and angle of divarication (Fig. 27). These birds have similar swimming behaviors relative to the different genera of ducks and geese.

Zygodactyl birds generally lie outside the trend, except for the Great Horned Owl (*Bubo virginianus*), which lies in the middle of the webbed-footed bird cluster with an average angle of divarication of  $90.6^\circ$  and an average trochlear arch angle of  $95.6^\circ$ . The zygodactyl birds that had a split trochlea IV plotted well outside of the normal range (Fig. 28). In terms of trochlea IV, the first condylar region (i) had a smaller angle of arc than the second condylar region (ii). This difference between i and ii is more pronounced in *Colaptes auratus* than *Dryocopus pileatus*, with a difference of over  $40^\circ$ .



**Figure 28.** Graph showing the correlation between trochlea arc and angle of divarication with the zygodactyl tracks present.

### Limb length equations

The zygodactyl birds had an avian functional leg length value of 1.45 mm, indicating that they had similar leg proportions (Table 2). *Bubo virginianus* and the Red-tailed hawk (*Buteo jamaicensis*) also had similar values of 1.45 mm and 1.44 mm, respectively. The shorebird morphotype proxy, *Chadrius voiciferus*, had the smallest value, at 1.31 mm.

*Buteo jamaicensis* had the smallest tibiotarsus:tarsometarsus ratio, at 1.32. The highest was *Bubo virginianus*, at 1.94. Each morphotype showed varying values between these numbers, with no two morphotypes giving identical results (Table 5). Wading birds have a much smaller tibiotarsus:tarsometatarsus ratio than the short-legged webbed-footed birds (1.46 to 1.81, respectively, see Table 5), indicating a longer tarsometatarsus relative to the tibiotarsus.

<b>Table 5</b>		
<b>Equation</b>	<b>Species</b>	<b>Result</b>
	<i>Drycopus pileatus</i>	1.45
	<i>Cyanocitta christata</i>	1.38
$f = \frac{\text{femur} + \text{tibiotarsus} + \text{tarsometatarsus}}{\text{tibiotarsus} + \text{tarsometatarsus}}$	<i>Bubo virginianus</i>	1.45
	<i>Phalacrocorax auritus</i>	1.35
	<i>Butoroides virscens</i>	1.38
	<i>Buteo jamaicensis</i>	1.44
	<i>Colinus virginianus</i>	1.47
	<i>Anas platyrhynchos</i>	1.39
	<i>Charadrius vociferus</i>	1.42
	<i>Drycopus pileatus</i>	1.46
	<i>Cyanocitta christata</i>	1.37
	<i>Bubo virginianus</i>	1.94
$f = \text{tibiotarsus:tarsometatarsus}$	<i>Phalacrocorax auritus</i>	1.63
	<i>Butoroides virscens</i>	1.56

	<i>Buteo jamaicensis</i>	1.32
	<i>Colinus virginianus</i>	1.69
	<i>Anas platyrhynchos</i>	1.81
	<i>Charadrius vociferus</i>	0.769
	<i>Drycopus pileatus</i>	0.317
	<i>Cyanocitta christata</i>	0.284
functional leg length $f=(\text{tibiotalarsus}+\text{tarsometatarsus})$	<i>Bubo virginianus</i>	1.052
Stride length	<i>Phalacrocorax auritus</i>	0.843
	<i>Butorides virscens</i>	0.841
	<i>Buteo jamaicensis</i>	1.84
	<i>Colinus virginianus</i>	0.988
	<i>Anas platyrhynchos</i>	0.888
	<i>Charadrius vociferus</i>	2.327
	<i>Drycopus pileatus</i>	2.171
	<i>Cyanocitta christata</i>	3.275
	<i>Bubo virginianus</i>	2.297
functional leg length $f=(\text{tibiotalarsus}+\text{tarsometatarsus})$	<i>Phalacrocorax auritus</i>	1.549
Digit III length	<i>Butorides virscens</i>	1.995
	<i>Buteo jamaicensis</i>	1.637
	<i>Colinus virginianus</i>	2.429
	<i>Anas platyrhynchos</i>	1.982

**Table 5.** The equations listed in this study and their result by morphotype proxy.

For equation (3), on average, dividing the functional leg length by digit three increased the final quotient significantly. The exception to this is *Buteo jamaicensis*, whose values decreased between using stride length and digit III as the divisor, from 1.84 mm using stride length, to 1.637 mm using digit III. The species with the smallest value for functional leg length divided by stride length, *Cyanocitta christata*, increased to the largest value for functional leg length divided by digit III (0.284 mm to 3.275 mm).

### Practical application to Early Cretaceous bird tracks

The Lakota Formation tracks have an average angle of divarication of  $107^{\circ}$ . Their trochlear arc angle is estimated to be  $\sim 95^{\circ}$ . The average trochlear arc angle for the extant shorebirds measured in this study is  $\sim 75^{\circ}$ . The Lakota Formation tracks' estimated trochlear arc angle is smaller than most wading birds ( $\sim 118^{\circ}$ ) with the exception of the White Ibis (*Eudocimus albus*;  $87^{\circ}$ ). The average angle of divarication for the extant wading birds used in this study is  $94^{\circ}$ .

The bird tracks from the Haman Formation had an average angle of divarication of  $113^{\circ}$ . Their trochlear arc angle is estimated to be  $\sim 85^{\circ}$ . The average trochlear arc angle for the extant shorebirds used in this study is  $\sim 75^{\circ}$ , however the average trochlear arc angle measurements by species has a range of  $58\text{--}88^{\circ}$  (Table 4).

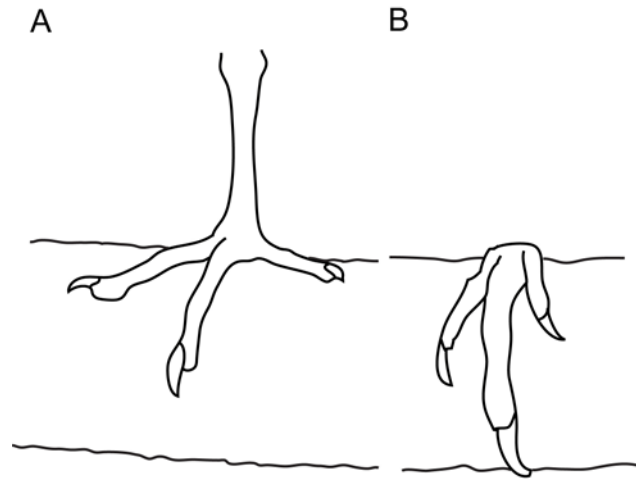
## DISCUSSION

The arc angle of the trochlea of the tarsometatarsus and the angle of divarication in birds have a strong correlation based on the high  $r^2$  value (without the zygodactyl tracks). The separate cluster of zygodactyl tracks indicates their unusually high angle of divarication. The exception to this rule, Great Horned Owl (*Bubo virginianus*), did not have a very high angle of divarication ( $90.6^{\circ}$ ). Other zygodactyl birds, however, including the Snowy Owl (*Bubo scandiaca*), have a much higher average angle of divarication, as high as  $198^{\circ}$  in *Colaptes auratus*. The reason for the difference between *B. scandiaca* and *B. virginianus* is difficult to explain, as both are

owls with similar foot structure. In owls, the straight edge of the K shape of the zygodactyl foot is formed by toes I and II, whereas in such zygodactyl cuckoos as the Greater Roadrunner (*Geococcyx californianus*) the straight edge is formed by III and IV (Elbroch and Marks, 2001). In woodpeckers, the formation of the K shape varies; for example, *Colaptes auratus* has a straight edge composed of III and IV, whereas I and II compose the straight edge in *Dryocopus pileatus*. There is no correlation between trochlear arc angle and angle of divarication in zygodactyl birds.

The trochlear arc angle has a significant effect on the angle of divarication in anisodactyl birds. In anisodactyl-footed birds, as trochlear arc angle decreases, the angle of divarication increases. Perching birds have the smallest angle of divarication, whereas shorebirds and waders have the largest angles of divarication. Perching birds have reduced the angle of divarication in order to cleanly and tightly grasp branches, which allows the toes to be brought close together at all times (Fig 29). Palmate birds were clustered away from the shorebirds and waders with a single exception, *Recurvirostra americana*, and this is likely because their limb proportions and behaviors are more like waders than other such webbed-footed bird as ducks and geese. Two ground-foraging birds fell within the cluster of perching birds on the scatterpoint graph; these were the American Crow (*Corvus brachyrhynchos*) and the Black-Billed Magpie (*Pika pika*). These are birds that could be considered, based on behavior either perching or ground birds, as they spend ~50 percent of the time perching in trees and other high objects, and ~50 percent of their time foraging on the ground. Based on phylogenetics, however, they must be considered perching birds

rather than ground-foraging birds, as they belong in the Passeriformes and have inherited the specialized hindlimb musculature that is typical of this order (Raikow, 1982).



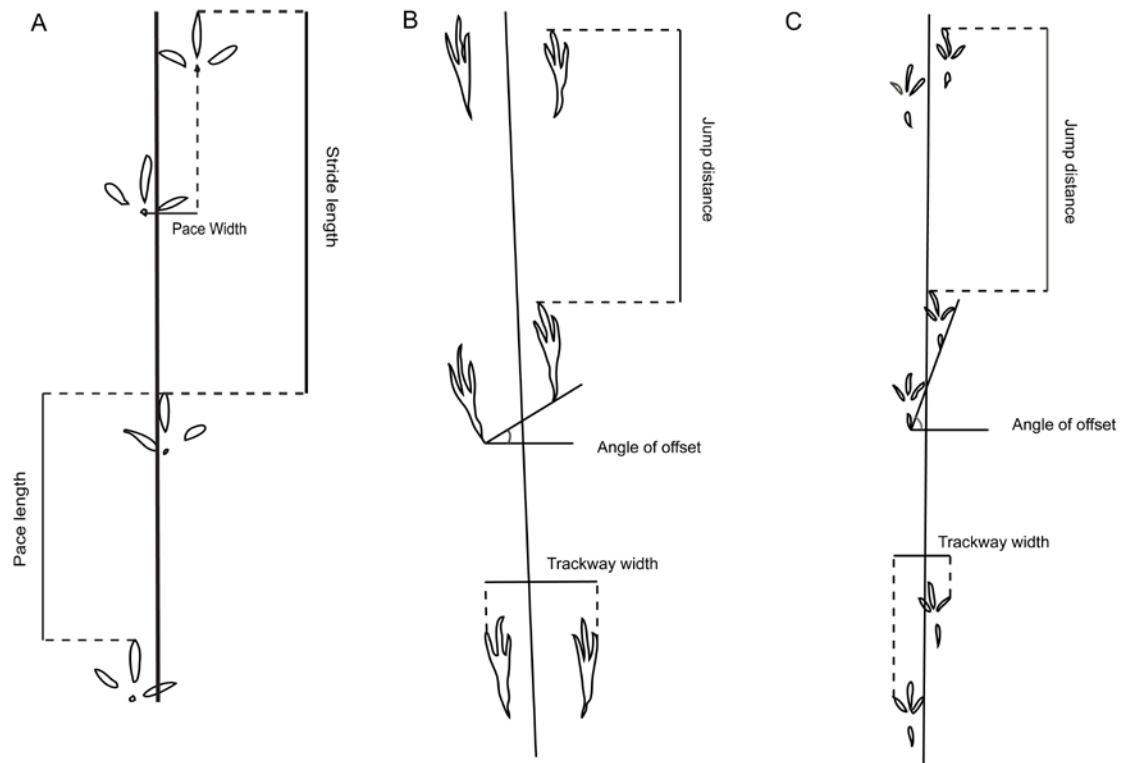
**Figure 29.** Comparison between a wading bird, the Black-crowned Night Heron (*Nycticorax nycticorax*) (left), and a perching bird, the Pine Siskin (*Carduelis pinus*) (right).

Correlating foot and limb anatomy to stride length and acetabular height in birds is problematic. It is difficult to tell from tracks when birds shift between walking and running (Verstappen et al., 1998; Farlow, 2000). Generally, footprints of a bird running may have a smaller angle of divarication between the toes (e.g., Elbroch and Marks, 2001, Genise et al., 2009). Birds have knee-driven locomotion, where forward movement during cursorial locomotion is produced at the knee, rather than at the hip joint (Hutchinson, 2009). This is opposite of many modern tetrapods

and all known bipeds, in which the femur is vertical or nearly vertical and is responsible for much of the forward movement (Kaiser, 2007).

The majority of birds, including the Passeriformes and many of the Picidiformes, such as woodpeckers, do not walk; instead, they use two different methods of hopping—symmetrical hopping, in which the feet are held parallel, and asymmetrical hopping (also called skipping in Elbroch and Marks, 2001) in which one foot is held forwards relative to the other foot. Using the term stride when referring to modern birds is, thus, problematic. Elbroch and Marks (2001) address this issue by referring to the distance between pairs of hopping traces as strides. Using the term strides, however, can be misleading since stride refers to the measurement of a walking trace (Fig. 30). We recommend that the term jump distance be used to refer to pairs of tracks produced by hopping and that a variety of measurements be taken between the tracks to understand the motion produced by the trackmaker (Fig. 30B–C). Measurements taken would be similar to that outlined in Leonardi (1987) and Hasiotis et al. (2007).





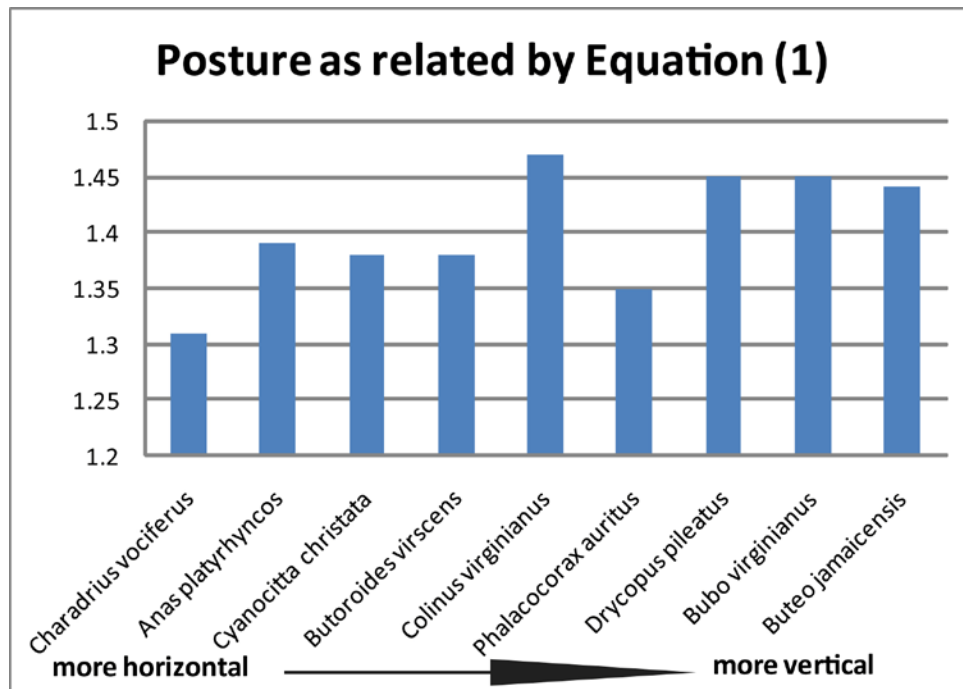
**Figure 30.** Measuring stride length and jump distance of bird trackways. A) Stride length in a walking bird. B) Jump distance in a symmetrically hopping bird. C) Jump distance in an asymmetrically hopping bird. Methods from Hasiotis et al. (2007).

### Equation results

Correlation between avian morphotype limb-bone elements is difficult to determine from the equations used. There is little similarity between the tibiotarsus:tarsometatarsus ratio and certain types of feeding behaviors. Hawks and owls, for example, are both highly specialized predatory birds. Their tibiotarsus:tarsometatarsus ratios, however, are completely different (Table 2).

Likewise, there is no clear distinction between differing types of locomotion and limb-bone elements.

The avian functional leg length correlation equation shows a potential relationship with posture (Fig. 31). *Dryocopus pileatus*, *Bubo virginianus* and *Buteo jamaicensis* all had values at or very close to 1.45; all of these birds have the same posture. Owls are known for their upright posture; it is one of the defining features that make an owl recognizable in the field. Hawks have a similar posture, and woodpeckers hold themselves vertical while climbing the sides of trees. Such birds as shorebirds and perching birds tend to have horizontal or slanted postures. This correlation may not be perfect, however, as the Northern Bobwhite, *Colinus virginianus* has a value of 1.47, and does not necessarily have an upright posture; while walking the posture is slanted, whereas the posture is upright while it is running.



**Figure 31.** Bar chart showing possible correlation of Equation (1) and posture. The species towards the left show a more horizontal posture, while the species towards the right show a more vertically-oriented posture.

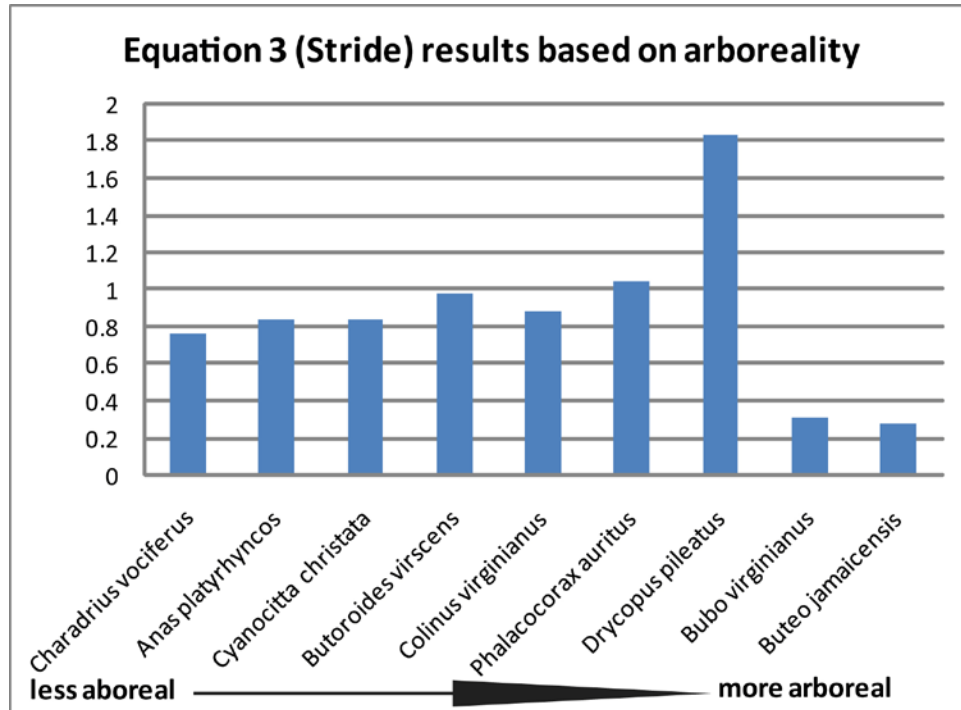
*Bubo virginianus* has the highest tibiotarsus:tarsometatarsus ratio (1.94), whereas *Buteo jamaicensis* has the lowest (1.32). This indicates that, despite having very similar predatory behaviors, their limb bone lengths are very different. The Blue Jay (*Cyanocitta cristata*) has a value of 1.37, and the only bird that has a lower value is *Buteo jamaicensis*; these birds are the only birds with values < 1.40, and use completely different methods of feeding. This ratio, therefore, does not correlate to method of feeding. This equation does not show a correlation with method of locomotion either, as *D. pileatus* has a value of 1.46, similar to the value of 1.42 of *Charadrius vociferous*. The tarsometatarsus:tibiotarsus ratio does not show any

correlations between morphotype, methods of feeding, or methods of ground-based locomotion.

Storer (1971) states that the tarsometatarsi and tibiotarsi must be nearly equal in length, else the center of gravity will shift and make squatting to roost or brood impossible. This, however, is the case only in cursorial birds with short toes and long legs. Birds that do not rely on running as their primary ground locomotion may have a higher difference between the bone lengths. *Buteo jamaicensis* and the Mallard, *Anas platyrhynchos*, are two examples from this study with the greatest difference between their tibiotarsal and tarsometatarsal length. These are birds that do not run often or well, if at all.

There may be a weak correlation between the different morphotypes when using known stride length as the divisor in the case of equation (3). Both types of predatory birds (birds of prey and zygodactyl predators) have the highest values for this equation (1.84 mm and 1.05 mm, respectively), whereas the perching bird proxy has the lowest value (0.284 mm). The perching and arboreal zygodactyl (woodpeckers) bird proxies (*Cyanocitta christata* and *Dryocopus pileatus*) both have very low values, 0.284 mm and 0.317 mm, respectively, which approximate 0.3 mm. In comparison, the birds that spend the majority of their time on the ground, such as the shorebirds and waders, have values of 0.769 mm and 0.841 mm, respectively. These results seem to indicate some correlation between the functional leg length and either arboreality (Fig. 32), stride length, or method of feeding behavior. These

relationships, however, should be studied in more detail before any definitive conclusions are made.



**Figure 32.** Bar chart relating Equation (3) to arboreality. Species towards the left are the least arboreal, while those towards the right are more arboreal.

When digit III is replaced into equation (3), no relationships are apparent (Table 5). There is no correlation of digit III to functional leg length, as all morphotypes are highly variable in their results. The variation in results between the two versions of equation (3), and the fact that some birds increase, whereas such others as *Buteo jamaicensis* decrease, demonstrates that digit III is not a feasible proxy for stride length.

The results indicate that the three equations used are not sufficient to understand how to measure acetabular height in birds from limb bones and trackways.

Acetabular (or pivot) height, cannot be easily determined for birds for multiple reasons. A bird's legs are held at constant angles (Kaiser, 2007). Even wading birds, which appear to be able to stand straight on one leg, actually have a slight bend between the tibiotarsus and tarsometatarsus. The leg is, effectively, never straightened due to the fact that the tibial condyles are on the front of the bone, not the base as with other bipeds, including theropod dinosaurs (see Fig. 23). The femur contributes very little to the motion of the leg, but it does contribute some motion (Rubenson et al., 2007), which will potentially affect the measurement for pivot point height. The best way to interpret pivot height in birds is to observe and measure height, angulation of joints and stride length, and to determine any correlations or discriminant functions that may assist in predicting height from trackways.

#### Fossil tracks and the trochlear arc angle

The Lakota Formation tracks had a trochlear arc angle ( $\sim 95^\circ$ ) intermediate between shorebirds ( $\sim 75^\circ$ ) and wading birds ( $\sim 118^\circ$ ). This result implies that birds that produced the Lakota Formation tracks had a foot morphology intermediate to the wading bird and shorebird morphotypes. This suggests that a separate intermediate morphotype may have been present in the Early Cretaceous of North America.

Their trochlear arc angle of the Haman Formation trackways was estimated to be  $\sim 85^\circ$ , which is above average for the extant shorebirds used in this study but still within the range of shorebird tarsometatarsi measured (Table 4). This indicates that shorebird-like ornithurine birds produced the Haman Formation trackways and is consistent with the behaviors interpreted from the tracks and trackways .

## CONCLUSIONS

Our study shows that a smaller angle of trochlear arc between the trochlea of the tarsometatarsus indicates a wider angle of divarication in the toes based on the correlation between the angle of divarication and the trochlear arch. This may have an evolutionary influence on the feet of wading and shorebirds. Such wide angles were most likely lost in perching birds to facilitate the grasping of limbs. The length of avian limb bones, however, and any correlation to method of locomotion, length of distance traveled between steps, method of feeding, or posture is much more difficult to determine and requires further research into the functional morphology of avian limbs and the function of the joints in living birds.

There is no apparent mathematical relationship that can confidently correlate stride length to leg length. More importantly, there is no mathematical relationship that can correlate stride length to digit III to leg length, or any combination thereof. This is especially important because: (1) the avian functional leg length differs from other bipeds in that it is knee-based, not hip-based, and (2) different birds have different styles of musculature that affect the way the leg is attached to the body, which is most evident in birds that spend much of its time foraging on the ground (e.g., pheasant) compared to a foot-propelled swimmer or diver (e.g., loon). In loons, the hindlimb musculature is extensive and complicated, binding not only the femur but also the tibiotarsus to the body (Heilmann, 1927; Gill, 1995). This allows only the tarsometatarsus to contribute to any walking motion and results in poor walking

abilities; however, it is excellent for swimming motion. Musculature, therefore, affects any type of morphometric equation dealing with limb length and stride length. If a mathematical relationship could be developed that correlates stride length to functional limb length, the position where foot-propelled divers plot on the line would be a major concern.

There are many possible evolutionary implications for the increase or decrease in trochlear arc angles in ornithurine birds. Birds that walk across soft media require a method to keep them from sinking into the mud. *Recurvirostra americana* and the flamingos have achieved this by evolving webbing between their short toes (Storer, 1971). Herons and other wading birds, however, evolved a different solution with elongated toes that create greater surface area (Storer, 1971). Similarly, a wide angle of divarication causes the weight of the bird to spread out over a larger area. The combination of wide angle of divarication and toe length has evolved to an extreme in the Jacanidae in the order Charadriiformes, which have exceptionally long toes and a wide angle of divarication; this allows it to walk across marshy ground and floating vegetation without sinking (Beletsky, 2006). This snowshoe effect, creating wider spaced toes, is a possible reason for the evolution of wider angles of divarication compared to other morphotypes of ornithurine birds. Early Cretaceous ornithurine birds lived in water-margin environments where the sediment was saturated. Spreading out the toes while walking across saturated mud would allow a bird to walk, run, or take off without having to pull its feet out of the mud. This type of foot



morphology, however, would not be useful for a perching bird as a wide angle of divarication would be a problem when perching in trees.

#### ACKNOWLEDGEMENTS

We are grateful to Dr. Mark Robbins of the University of Kansas for access to specimens. This manuscript is part of a Master's Thesis conducted by ARF. ARF was supported by the Panorama Small Grants Competition and the University of Kansas Department of Geology. J. Schmerge, D. Lobue, A. Rosales, and W. Jones of the IchnoBioGeoSciences (IBGS) Research Group contributed meaningful comments and insights that helped improve the manuscript. This investigation was supported by the University of Kansas General Research Fund allocation # 2301278.

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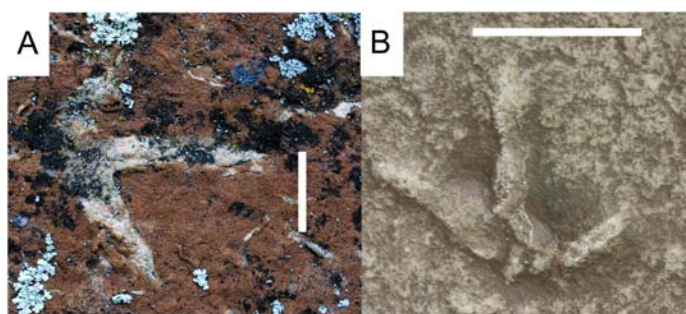
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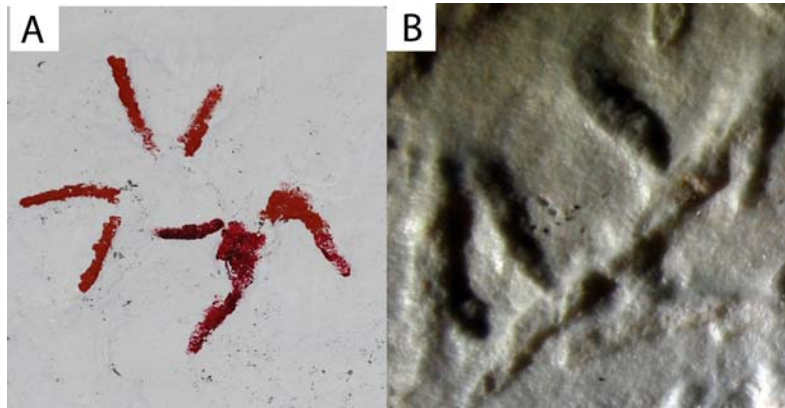
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## CHAPTER FIVE. SUMMARY AND CONCLUSIONS

The avian trace fossils from Lower Cretaceous deposits studied for this thesis exhibit similar styles of preservation. The tracks of the Lakota Formation (Chapter 2) are surface tracks rather than undertracks; undertracks are tracks where the foot deforms the layers of sediment layers underneath the interactive surface (Platt and Hasiotis, 2006). The tracks from the Haman Formation in Korea (Chapter 3) are also surface tracks, and are better preserved in terms of overall morphology; however, the Lakota Formation tracks have better-preserved claw and pad impressions (Fig. 33). The Lakota Formation tracks are more difficult to distinguish from each other in terms of overstepping, and it can be difficult to determine which track was laid down first. In the case of the Haman Formation tracks, overlapping tracks are generally easy to distinguish and easy to interpret (Fig. 34).



**Figure 33.** Comparison between the Lakota Formation tracks (A) and the Haman Formation tracks (B). Note the claw and pad impressions of the Lakota Formation track. (A) scale bar=2 cm. (B) scale bar= 3 cm.



**Figure 34.** Overstepped tracks from the Lakota Formation (A) and the Haman Formation (B).

The bird tracks from the Lakota Formation (Chapter 2) were made by shorebird-like ornithurine birds. These Early Cretaceous birds likely had similar feeding and courtship behaviors to such extant plovers as the Killdeer as no probe or peck marks were found associated with the tracks and trackways. These birds also had to have the complex flight mechanism necessary for takeoff from a flat surface based on the evidence of flight represented by a trackway terminating in nearly parallel tracks.

Behaviors interpreted from the Haman Formation tracks and trackways include feeding and foraging behaviors in the form of peck and probe marks, landing, and walking with flapping-assisted hopping. Ichnogenera of invertebrate traces associated with the bird tracks include *Cochlichnus*, *Steinichnus*, and *Arenicolites*, and these invertebrate traces crosscut and are crosscut by the bird tracks. It is likely that the probe and probe and pecking marks associated with these tracks and

trackways are a result of the birds searching for the invertebrates that produced those traces.

Avian hindlimb anatomy affects the morphology of the tracks and trackways produced by the bird. The trochlear arc angle of the tarsometatarsus correlates with the angle of divarication of the toes of anisodactyl birds (Chapter 4). There is no correlation between the arc angle of the trochlea and the angle of divarication of zygodactyl birds; this is most likely due to their foot structure in which two toes are pointed forward and two backwards, resulting in a high angle of divarication. The length of avian limb bones and any correlation to length of distance traveled between steps, method of locomotion, speed of the bird, or method of feeding is difficult to determine and requires further research into the functional morphology of avian limbs and the function of the joints in living birds.

There is no apparent mathematical relationship that can confidently correlate stride length to leg length. The avian functional leg length differs from other bipeds in that it is knee-based, not hip-based. Shifts between gaits are difficult to determine from the tracks and trackways of birds (Verstappen et al., 1998; Farlow, 2000). It is, therefore, likely that the trackway measurements related to calculating speed will not function for bird trackways and studies should instead focus on generalized behavioral interpretations. This is especially true for birds that use hopping as their primary means of ground-based locomotion, including the Passeriformes.

There are many possible evolutionary implications for the increase or decrease in trochlear arc angles in ornithurine birds. Birds that walk across soft media require a



method to keep them from sinking into the mud. Some birds, including the Avocets (Recurvirostridae), have achieved this by evolving webbing between their short toes (Storer, 1971). Wading birds have evolved a different solution with elongated toes that create greater surface area (Storer, 1971). Similarly, a wide angle of divarication causes the weight of the bird to spread out over a larger area.

Early Cretaceous ornithurine birds lived in environments where the sediment was saturated. Spreading out the toes while walking across saturated mud would allow a bird to walk, run, or take off without having to pull its feet out of the mud, making escape from predators much easier. This type of foot morphology, however, would not be useful for a perching bird as a wide angle of divarication would be a problem when perching in trees.

It is difficult to determine which came first in avian evolution; a high angle of divarication or a low angle of divarication. By the Early Cretaceous it is clear that a high angle of divarication is present in the ornithurine birds. The angle of divarication of *Archaeopteryx*, however, is much more difficult to determine as there are no known trackways of *Archaeopteryx*. A study of the arc angle of the trochlea of *Archaeopteryx* may assist in interpreting its life habits and indicate its angle of divarication of toes II and IV. Bird origins are most likely from the trees-down (Martin, 1983; Xu et al., 2003; Burnham, 2007) and, therefore, it seems likely that birds started with a small angle of divarication and a wide trochlear arc angle and evolved a wider angle of divarication as they moved into water-margin environments. A wide angle of divarication in Early Cretaceous ornithurine birds suggests that the

small angle of divarication in extant perching birds is a derived condition of the Ornithurae.

The angle of divarication between toes II and IV is an important measurement in the classification of fossil bird tracks. This thesis demonstrates that there is a correlation between the angle of divarication and the ecology and life habits of the bird. This may be useful in distinguishing avian ichnogenera, as well as shorebird-like birds from wading-like birds, and webbed-footed birds from other anisodactyl birds. Falkingham et al. (2008) discussed the issues with distinguishing webbed tracks from falsely-webbed tracks created by the slumping of sediment between the toes. The angle of divarication as it relates to morphotype of foot could be helpful in these situations; however, this study has shown that there is some overlap in the case of such webbed-footed birds as the American Avocet (*Recurvirostra americana*). Future studies could elaborate on the morphologic difference between the tracks of modern bird morphotypes and compare this to webbed-footed tracks in the fossil record.

It is possible to make interpretations on the hindlimb anatomy of the Early Cretaceous bird tracks from the Lakota and Haman Formations, based on the data from Chapter 4 that relates angle of divarication to the trochlear arc angle of different bird morphotypes. The Lakota Formation tracks have an average angle of divarication of  $107^{\circ}$ . Their trochlear arc angle is estimated to be  $\sim 95^{\circ}$ , which is higher than the average trochlear arc angle for the extant shorebirds measured in this study—  $\sim 75^{\circ}$ . The Lakota Formation trochlear arc angle is smaller than most wading birds ( $\sim 118^{\circ}$ ) with the exception of the White Ibis (*Eudocimus albus*;  $87^{\circ}$ ). The average angle of

divarication for the Lakota Formation tracks, however, is greater than those of the extant wading birds used in this study ( $94^{\circ}$ ; see Chapter 4, Table 4). The Lakota Formation tracks, therefore, likely had a trochlear arc angle ( $\sim 95^{\circ}$ ) intermediate between shorebirds ( $\sim 75^{\circ}$ ) and wading birds ( $\sim 118^{\circ}$ ). This result implies that birds that produced the Lakota Formation tracks had a foot morphology intermediate to the wading bird and shorebird morphotypes.

The bird tracks from the Haman Formation had an average angle of divarication of  $113^{\circ}$ . Their trochlear arc angle is estimated to be  $\sim 85^{\circ}$ , which is above average for the extant shorebirds used in this study but still within the range of shorebird tarsometatarsi measured ( $58\text{--}88^{\circ}$ , see Chapter 4, Table 4). This indicates that shorebird-like ornithurine birds produced the Haman Formation trackways.

The Early Cretaceous ornithurine birds were water-margin birds that likely lived in small-to-large flocks similar to modern shorebirds. They show typical shorebird feeding behaviors in probing the sediment, either singly or in clusters, and in the repetitive overlapping tracks and trackways including circular or curvilinear walking. Other behaviors indicate flight in the form of takeoffs and low-angle landings. The tracks tend to overlap, making directionality even more difficult to determine. Using these sets of criteria, other such trackways as *Trisauropodiscus* (Lockley et al., 1992) can be re-examined and perhaps re-interpreted based on behavior as well as morphologic evidence.

Mesozoic bird trackways may hold a wealth of information on the origin and early evolution of birds. Many tracksites have not been examined from a behavioral

aspect. Behavior can lend insight into specific morphotypes of birds present and social interactions between birds. Trackways and associated traces show evidence of flight and interactions between birds and prey species including insect larvae and annelids. By looking at the tracks of Mesozoic birds from both a taxonomic and behavioral standpoint, a more complete picture of the Early Cretaceous ornithurine bird community can be obtained.

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