Bare-bones Paleontology: An Examination of the Systematic Methods Used in Vertebrate Paleontology and their Congruence with Avian Ichnotaxonomy

by

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ABSTRACT

Data used in the systematic paleontology of extinct vertebrates is limited to what can be collected from detailed comparisons of preserved anatomy. This restricts vertebrate paleontologists to those characters preserved on osteological specimens. Furthermore, parataxonomies such as ichnotaxonomy use different morphologic criteria for assigning tracks and trackways to ichnogeneric and ichnospecific levels. For taxa with no extant representatives, it is difficult to ascertain whether the osteologic characters used are consistent in their ability to discern among closely-related or morphologically-similar vertebrates. It is also difficult to determine the strength of congruence between osteology-based systematics and those taxonomic methods using criteria other than osteology data.

Phylogenetic relationships of higher-level taxonomic groupings using morphologic data on appendicular skeletal elements do not necessarily correlate with those relationships recovered using molecular data; while the genus-level groupings are (in the case of *Accipiter*, *Charadrius*, Ciconiidae, *Falco*, *Grus*, *Parapavo*, *Tringa*) retained by appendicular skeletal synapomorphies, similar groupings recovered by other morphologic phylogenetic analyses conflict with evolutionary hypotheses recovered by molecular phylogenies.

Regardless of the lack of congruence between molecular and morphologic phylogenies, there is increased osteologic information from the morphology of the distal tarsometatarus of Aves that can be used to increase the accuracy of avian ichnotaxonomy. Specifically, the plantar displacement of the trochlear surfaces of metarsals II and IV is greater in Aves than in non-avian theropods, even in avian taxa whose distal tarsometatarsal morphology shares convergent features with non-avian theropods, such as size.

Multivariate statistical analyses are demonstrated to be an additional tool to successfully test the relationships between avian osteomorphology and avian ichnotaxonomy. The statistically significant difference in the degree of plantar rotation in distal tarsometatarsals II and IV between Charadriidae and Scolopacidae, correlating with the significantly different digit splay in the footprints of these two families of shorebirds, demonstrates that osteomorphology and ichnomorphology can be used to increase the ichnotaxonomic resolution of Cretaceous-age avian footprints. It is likely that the differences in plantar displacement and torsion of metatarsals II and IV between avian and non-avian theropods, and its effects on the footprints of the respective trackmakers, will prove to be reliable synapomorphy-based characters that can be utilited in ichnotaxonomy to distinguish between the traces of large avian and small non-avian theropods.

PREFACE

The analyses and writing of papers submitted, appearing in revised format as Chapters 5—6, utilized some data provided by the second (RTM) and third (MGL) authors.

Chapter 4 has been submitted to Ichnos as: Buckley, L. G., R. T. McCrea, and M. G. Lockley. 2015. Birding by foot: a critical look at the synapomorphy- and phenetic-based approaches to trackmaker identification of enigmatic tridactyl Mesozoic traces. Ichnos 22(3–4):192–207. This manuscript was reviewed by B. Breithaut, S. Lucas.

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Chapter 6 is a compilation of research that has been published. Section 1 is published as Xing, L., L. G. Buckley, R. T. McCrea, M. G. Lockley, J. Zhang, L. Piñuela, H. Klein, and F. Wang. 2015. Reanalysis of *Wupus agilis* (Early Cretaceous) of Chongqing, China as a large avian trace: differentiating between large bird and small theropod tracks. PLoS ONE 10(5): e0124039. doi:10.1371/journal.pone.0124039

This research was conducted as part of an international research collaboration among vertebrate paleontologists (L. Xing, School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China; L. Buckley and R. McCrea of the Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia; M. Lockley of Dinosaur Tracks Museum, University of Colorado Denver, Denver, Colorado; L. Piñuela of the Museo del Jurásico de Asturias MUJA, Colunga, Spain; H. Klein of the Saurierwelt Paläontologisches Museum, Neumarkt, Germany). Chapter 6, Section 1 has been published as Xing et al. (2015), and was completed using data collected by members of the aforementioned research team. As the corresponding author I was responsible for data analysis, data interpretation, and manuscript composition. L. Xing was the coordinator of the field research for the data of this particular project. The Qijiang District Bureau of Land Resources, Chongqing, China provided funding for the field research.

Parts of Chapter 6, Section 2 were published in McCrea, R. T., L. G. Buckley, A. G. Plint, M. G. Lockley, N. A. Matthews, T. A. Noble, L. Xing, and J. R. Krawetz. 2015. Vertebrate ichnites from the Boulder Creek Formation (Lower Cretaceous: middle to ?upper Albian) of northeastern British Columbia, with a description of a new avian ichnotaxon, *Paxavipes babcockensis*, ichnogen. et, ichnosp. nov. Cretaceous Research 55:1–18. Original research on osteology correlations to ichnomorphology appearing in part of the cited manuscript was first designed, analyzed, and written as part of this thesis.

DEDICATION

I dedicate this work to the memory of my great-aunt, Ms. Molly Yvonne Gresley-Jones (1923–2010). Her life-long passion for natural history and education is my earliest memory, and her lasting impression.

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CHAPTER 1

INTRODUCTION

Data used to determine the systematic paleontology of extinct vertebrates is limited to using what can be collected from detailed comparisons of preserved anatomy. This mostly restricts vertebrate paleontologists to those characters preserved on osteological specimens. Despite these apparent restrictions, there are other sources for paleontological data that are available for study that can be utilized in conjunction with the hard-tissue data. These different sources of data, referred to as parataxonomies, can both compliment and advance traditional osteologic studies.

Taxonomies and Parataxonomies

Taxonomy is the branch of biology that concerns identifying, delineating, and naming organisms. Taxonomy is often used synonymously with the term alpha taxonomy, which addresses the process of delineating species, and beta taxonomy, which Mayr (1968) describes as the process of delineating taxonomic ranks higher than that of species. Parataxonomies, also known as parallel taxonomies, serve to classify organisms, parts of organisms, or traces of organisms into recognizable, discernable units (Krell, 2004). However, despite the issue brought forth by Krell (2004) that parataxonomic units are not ascribed formal names, this is not the case for parataxonomic units as they are used in paleontology. Parataxonomic names within paleontology are governed by the

International Code on Zoological Nomenclature (ICZN), just as the system governs the recognition and naming of body fossils.

Paleontologists have been using parataxonomies for centuries to describe fossilized phenomena that are not bones. Ootaxonomy is the classification of eggs, egg clutches, and eggshell structure, such as the description of the oogenus and oospecies *Montanoolithus strongorum* and the establishment of the oofamily Montanoolithidae (oofam., oogen., and oosp.; Zelenitsky and Therrien, 2008). Ichnotaxonomy is the classification of any traces of organisms, such as burrows, feeding traces, resting traces, footprints, and trackways. Ichnotaxa are given hierarchical names of ichnofamily (ichnofam.), ichnogenus (ichnogen.), and ichnospecies (ichnosp.) Each ichnotaxonomic system uses nomenclature (e.g., -*oolithus*, -*ipes*, etc.) that distinguishes it from taxonomies utilizing body fossils, and new ootaxa and ichnotaxa must be formally named in a peer-reviewed, academic publication. In short, parataxonomies follow the same system of checks and balances as does osteology-based taxonomy, and while parataxonomies do not seek to exactly mimic or reproduce osteology-based taxonomy (Lockley and Hunt, 2010), they do classify biologic phenomena in parallel to osteology-based taxonomy.

Regardless of the oversight given to the use of ichnotaxonomy, there is still some hesitation from paleontologists to use ichnotaxonomic data in conjunction with, or to expand on, osteology data. For example, the body fossil record of terrestrial vertebrates from Mesozoic deposits of western Canada (at the time of this writing) is restricted to deposits of the Upper Cretaceous (97 to 72 million years ago, McCrea et al., 2014). However, the vertebrate ichnofossil record is more complete, extending the presence of terrestrial vertebrates in western Canada back to 140 million years ago in Lower and Upper Cretaceous deposits from which no body fossils have yet to be recovered (McCrea et al., 2014). Utilizing the ichnofossil record, in conjunction with the body fossil record, can only serve to increase our understanding of the paleofaunal composition of the Cretaceous.

Paleobotany does not appear to have the same hesitation in using parallel taxonomies. Botanical and paleobotanical taxonomy is governed by the International Code of Nomenclature for Algae, Fungi, and Plants (also known as the Melbourne Code). The Melbourne Code recognizes the presence of forma, or form taxa, which are used to describe elements of a plant (bark, fruit, leaves, seeds, etc.) without them being associated with a complete specimen, with the recognition that these form taxa can be subsumed into higher level taxonomic ranks (genus, species, etc.) However, there is no provision in the International Code on Zoological Nomenclature, for example, for the ichnogenus *Tyrannosauripus pillmorei* (Lockley et al. 1994) to be subsumed into *Tyrannosaurus rex*, the likely trackmaker of *Tyrannosauripus*. One reason for this may be the lack of published material describing a vertebrate, such as a dinosaur, found preserved at the end of its trackway. This is in contrast to paleobotany, where a more complete fossil plant can be found to consist of several forma. As such, it is more difficult to reconcile ichnofossil with the body fossil of proposed trackmakers (Chapters 2, 4).

Ichnotaxonomy uses different morphologic criteria for assigning tracks and trackways to ichnogeneric and ichnospecific levels (Lockley 1999) than is used for body fossils (or osteotaxa). As previously mentioned, it often occurs that an ichnological record exists for a formation or a geographic region from which no body fossils have been described or discovered. Also, as is the case with avian fossils from the Lower Cretaceous deposits of China, there are many body fossils of avialians, but few body fossils that would be potential trackmakers for the shorebird-, wading bird-, and anseriform-analog avian ichnotaxa that are abundantly preserved in the Lower Cretaceous deposits of China (Chapters 4–6). It is possible that the body fossils of the actual trackmakers have not yet been described. It is also possible that the trackmakers have been described, but insufficient attention has been paid to the pedes of these specimens, and there has been no data collected that can be used to link the traces to the trackmakers.

While the osteological record provides the data for which paleobiodiversity is discussed, it in of itself is not a complete record. For example, there are many theropod taxa that were described from incomplete material (e.g., Bell et al., 2015) and disarticulated appendicular skeletal material without skull or pelvic bones (e.g., DePalma et al., 2015; although see Arbour et al., 2015 for how the type specimen of *Dakotaraptor steini* is a chimera). Extant birds provide an opportunity to examine how the data available from taxa known only from bones reconstructs paleobiological diversity, evolutionary relationships, and congruence between the diversity recovered from body fossils and that recovered from ichnological studies. An examination of the appendicular skeletons of exant birds that occupy foot-using niches (Charadriiformes, Falconiformes, Galliformes), analogous to those of non-avian theropods, will allow me to test the systematic strengths of osteologic characters of incomplete specimens consisting of appendicular skeletal material (Chapters 2–3). Vertebrate ichnology utilizes both synapomorphy- and phenetic-based methods for attributing vertebrate traces to trackmakers. The synapomorphy-based method (Carrano and Wilson, 2002), uses footprint features that correspond with osteology-based synapomorphies to identify potential trackmakers. The phenetic-based method, as described by Lockley et al. (2002), compares footprint and trackway features to both the osteology and paleogeographic ranges of potential trackmakers. For example, when identifying avians as a potential trackmaker for a trace, some of the phenetic-based features may also be synapomorphies, such as a posteriorly-oriented digit I (hallux) for Aves. However, some phenetic features are based on the overall similarity in size and shape to extant birds, and use footprint features that may not have been examined in depth for extant taxa to determine these features are restricted to Aves. However, while the data provided by vertebrate ichnofossils can significantly contribute to the anatomical, behavioral, and paleofaunal information available for a trackmaker, there is little consensus on the accuracy with which the diversity of vertebrate paleofauna can be reconstructed due to preservational variation, and how much biologic diversity is potentially lost due to possible convergence in morphology of the skeletal elements involved. To date there are too few synapomorphies that are both restricted only to feet and consistently preserved in footprints to be a practical method for attributing tracks to an avian trackmaker. There is still much more comparative ichnological and statistical work to be done to discern novel traits that can be used to delineate between the traces of large avian and small non-avian Mesozoic theropods.

This study aims to review the systematic concepts applicable to comparing biologic taxonomy to morphologic species concepts (Chapter 2); examine in a morphologic cladistic analysis a select number of extant avian taxa that have skeletal elements subject to morphologic convergence due to similarities or specializations in habitat (birds of prey, gamebirds, shorebirds, wading birds) to test the degree to which convergence masks biologic diversity (Chapter 3), and how this affects hypotheses of evolutionary relationships; practically examine the correlation between skeletal synapomorphies and parataxonomies (ichnology) in extant and fossil avians (Chapter 4); and to demonstrate that, with increased data analysis and investigation of the skeletons of extant avians, their traces, and the conditions that impact the preservation of this data, we can increase the accuracy with which we reconstruct avian paleofaunal assemblages in the Mesozoic (Chapters 5–6).

CHAPTER 2

FOSSIL SPECIES, SPECIES CONCEPTS, AND BARE-BONES SYSTEMATICS: CONGRUENCE AMONG POPULAR SPECIES CONCEPTS AND IMPLICATIONS FOR THE RECOGNITION OF VERTEBRATE SPECIES IN THE FOSSIL RECORD.

INTRODUCTION

Systematics and parasystematics of extinct vertebrates are limited to what data (osteologic or ichnologic, respectively) is preserved. The strength of the correlation between osteology-based systematics and those taxonomic methods using criteria other than osteology data is difficult to determine, particularly in taxa for which there are no extant representatives. What information can the osteologic specimens of extant taxa provide on the systematic strengths of osteologic characters considered diagnostic, and what additional information may be provided to non-osteology based taxonomies and parataxonomies from detailed examination of anatomical details that are not commonly the focus of systematic analyses? This chapter examines the extent to which different, and oftentimes disparate, species recognition concepts correlate and their applicability to the vertebrate fossil record.

Osteological Morphology in Differentiating Among Extinct Versus Extant Vertebrate Taxa

Comparing fossil vertebrate taxa to extant vertebrate taxa—There are many examples in vertebrate paleontology in which fossil taxa are compared with extant members of the taxonomic group in order to better understand both the morphology of the fossil specimen and the interrelationships within the higher taxonomic grouping. In 1969 a Pliocene woodpecker, *Paleonerpes shortii*, was described by Cracraft and Morony (1969) on a single tibiotarsus from Nebraska. Cracraft and Morony (1969) were able to distinguish between *P. shortii* and *Pliopicus brodkorbi* based on the smaller size and slender proportions of *P. shortii* tibiotarsus. The tibiotarsus of *Paleonerpes shortii* was compared to the tibiotarsus of other Cenozoic and Recent woodpeckers. *P. shortii* was thought by Cracraft and Moroney (1969) to represent an early stock of melanerpine woodpeckers in North America, although *P. shortii* is osteologically distinct from both melanerpine and extant woodpeckers. Another fossil bird taxon (*Uintornis*) previously thought to be allied with woodpeckers (Marsh, 1872) was tentatively reclassified as a cuculiform specimen (Cracraft and Moroney, 1969) based on re-examination of the tarsometatarsus.

From a different perspective of paleontological systematics, avian skeletal material and woodpecker allies, Mayr (2008) examines a new species of the genus *Zygodactylus*, a genus whose representatives were previously limited to a tibiotarsus and tarsometatarsus (Ballmann, 1969). Mayr (2004) analyzed a modified dataset (genetic and morphologic data) to determine the phylogenetic relationships of *Z. luberonensis*.The results revealed a Passeriformes + Zygodactylidae clade, which is supported by the close osteological similarity between extant passeriforms and extinct zygodactylids: this infers a possible closest relative to passeriforms (Mayr, 2004). Recent molecular phylogenies of birds shows that Passeriformes and Psittaciformes share a common ancestor (Jarvis et al., 2014)

These are two out of the many studies that utilize data from extant taxa to gain information on the morphology and relationships of fossil taxa. While the utility of using morphologic data for analyses such as phylogenetic analyses has been questioned (Scotland et al., 2003), it is the only way that fossil taxa can be compared with their extant counterparts (Wiens, 2004). There is one important consideration that is needed when interpreting results involving the comparison of fossil taxa with modern taxa. What certainty is there that a *biologically* distinct extant taxon and the component individuals can be confidently compared to a *morphologically* distinct fossil taxon and the component individuals? Does biological distinctiveness accurately reflect morphological distinctiveness? Are we attempting to compare *pommes* to *pommes de terre*?

Osteological systematic differences among extant taxa—Three notable studies address correlations between biologic and morphologic distinctiveness, and combined provide ambiguous interpretations of the utility of osteologic versus biological distinctiveness. Bever (2005a) tested the diagnostic utility of the ilium in fossil anurans by evaluating both continuous and discrete ilial characters commonly used to support species-level identifications for fossil species of *Bufo*. The analysis was conducted on dried adult or sub-adult specimens representing 27 extant species of North American *Bufo*. The study specimens were presumably (although this was not stated in the publication) identified using a combination of geographical, vocal, and coloration characters, none of which involve the use of osteologic characters. The osteologic characters traditionally used to identify fossil ilia of North American *Bufo* could not be used to unambiguously identify any of the 27 extant species of *Bufo* (Bever, 2005a).

While the focus of the implications of Bever's (2005a) study are specifically those revolving around Plio-Pleistocene herpetological faunal dynamics and stability (Bell and Gauthier, 2002), the study raises issues that have broad paleontological implications. One is the possibility that the characters used for species-level identifications of fossil organisms cannot be used to identify their extant representatives. Alternatively, the characters used to produce unambiguous species-level identifications for extant organisms may not do so for their fossil representatives, likely due to the lack of preservation of these characters. Yet, in the case of frogs, ilial characters are considered the best element upon which to produce unambiguous species-level identifications of fossil specimens due to their high rate of recovery in fossil collections and their large suite of morphological features (Bever, 2005a). This also raises the issue of using geographic location and temporal age of the specimen to refine a species-level diagnosis, when, arguably, the identification should be based on morphologic distinctiveness alone (Bever, 2005a). Bever (2005a) states that a morphology-only species-level identification should be based on characters that are unique when compared to all other known members of the group in question; characters established as derived on a phylogenetic tree should also be unambiguous, although this was not the case for the ilial characters of *Bufo*.

Bever (2005b) examined morphometric variation in *Canis latrans* (extant coyote) and *C. lepophagus* (Pleistocene coyote) in an attempt to establish the amount of morphologic variation present in cranial and dental characters of *C. latrans* and *C. lepophagus* and the degree of overlap resulting from interspecific character variation in morphometric space. Only cranial and mandibular characters were found not to overlap significantly for *C. latrans* and *C. lepophagus*, although it was noted that the dental characters were highly variable, and exhibited such a high degree of overlap that unambiguous species-level identifications for these two species were not possible (Bever, 2005b).

Both studies by Bever (2005a, 2005b) focused on using morphological discrete characters for unambiguous identification of fossil and extant specimens; each provides a different answer to the question whether biological discreteness equates morphological discreteness. Bever (2005a) revealed that *Bufo* skeletons of species-level grouping of *Bufo* identified using soft-tissue and habitat characters could not be replicated using skeletal characters alone. In contrast, Bever (2005b) was able to recover species-level classifications of both extant and fossil coyotes using osteological characters, and offer support for the presence of extant coyotes in the Pleistocene. Silcox (2014) suggested that paleontologists take a pragmatic approach to defining species in regards to what use paleontologists have for species.

I am assuming that what Silcox (2014) means by the present is the application and comparison of extant organismal data to the paleontological record. The present could also refer to the Biological Species Concept as being the one species recognition concept that is widely used for establishing extant species (Silcox, 2014). The assumption based on the former is addressed in the current analysis. The assumption based on the latter is also addressed in the current analysis with examination of the practical application of the Biological Species Concept to fossil organisms, despite the assumptions of morphologic discreetness being the equivalent of reproductive isolation.

The availability of extant vertebrate organisms, provides excellent models and case studies on how accurate morphologic discreetness is in determining reproductive isolation, and how the practical difficulties of reproductive isolation (i.e. hybridization, which is a common occurrence in many extant species of birds) and/or soft-tissue based morphologic groupings correlate with hard-tissue based morphologic groupings (Bever, 2005a).

Good osteologic characters and differentiating among morphologically similar taxa—Variation among individuals of the same species has the (often unstated) potential to be a source of variation in osteologic characters used to differentiate between closely related and similarly-sized taxa. Bochenski (2008) examined the occurrence of osteologic characters between *Podiceps cristatus* (Great Crested Grebe) and the *Podiceps grisegena* (Red-necked Grebe; Bochenski, 1994), the *Corvus corone* (Carrion Crow) and *Corvus frugilegus* (Rook; Bockenski and Tomek, 2000), and *Meleagris gallopavo* (Wild Turkey) and *Meleagris ocellata* (Ocellated Turkey; Bochenski and Campbell, 2006). Out of the 90 characters examined among all the taxa studied, only one character was found to be consistent in terms of its ability to correctly identify the species in question in each case (Bochenski, 2008). Bochenski (2008) presented her results from the standpoint of identifying zooarchaeology specimens using guidebooks. However, these results present caveats to the classical method of using, and coding (Wiens, 2001), characters. Those characters which are seemingly continuous, or have overlapping morphologies, contain data considered useful in phylogenetic analyses: characters considered fixed or continuous can be an artifact of sample size (Wiens, 2001). Given that many of the osteologic characters used for discriminating among species are subject to overlapping variation and abnormalities, Bochenski (2008) proposes that a taxonomically useful character has a presence frequency of at least 66% (two-thirds, or greater) on all specimens of a species in question: more important is that the researcher state the cut-off frequency used for the presence of the character(s) used. This is similar in concept to Mayr's (1935) 75% rule, where at least 75% of the specimens should be clearly identifiable to subspecies. That being said, Remsen (2010) numerically facetious when he predicted that 75% of subspecies of North American birds would fail Mayr's 75% rule. While subspecies can be argued as existing for convenience (Fitzpatrick, 2010), species are the fundamental unit of vertebrate taxonomy, regardless of the controversy surrounding the philosophy of their recognition. How one discipline of biology recognizes a species should strive to be testable and repeatable by any discipline in biology.

There are few studies that have examined the osteologic characters of species using a large enough sample size to fully document individual variation within character states (Wiens, 2001; Bochenski, 2008). Given the acknowledged intraspecific variation in useful osteologic characters, and the ambiguous results in identifying extant species when using osteologic characters considered useful for recognizing fossil species, it is necessary to examine *how* species are recognized, and to at least address the *a priori* assumptions that are used with species recognition concepts.

Fossil species as biologic or morphologic entities?

There are several problems in identifying fossil species as reviewed by Forey et al. (2004): fragmentary nature of fossils, lack of spatial and ontogenetic continuity, parataxonomies (such as ichnotaxonomy), and the creation of virtual species from computer reconstructions. Many fossil taxa are recognized using multiple lines of information, including geographic and temporal data. However, taxonomic discreetness is theoretically and ideally established based on morphologic discreteness within that specific geographic and temporal space (Bell and Gauthier, 2002; Bell et al., 2004, Silcox, 2014). As such, morphological discreetness, and the study of morphologic characters, is necessary for understanding the systematics of fossil organisms and their relationship to extant taxa (Wiens, 2004). However, when comparing fossil taxa that may have been defined using a variety of species concepts, it is crucial to compare species recognition concepts used in classifying extant organisms to the one species concept that is consistently used in vertebrate paleontology (the Morphologic Species Concept).

In relation to the use of parataxonomies, or the practice of sorting organisms into recognizable units (such as ichnotaxonomy in the case of trace fossils), Forey et al. (2004) state that parataxonomies are universally recognized as artificialbecause they often cross major biological boundariesand are not based on patterns of evolutionary descent. Parataxonomic groups such as vertebrate tracks and traces are recognized based on morphology, and in some cases on geographic distribution, and time. These are criteria often used for the identification of many fossil species known from skeletal remains (Bell and Gauthier, 2002; Bell et al., 2004). The alternative to using geographic and temporal criteria is to use unambiguous, non-overlapping characters to form ichnotaxonomic-level groupings of organisms: this is the same critique given for the identification of vertebrate skeletal remains (Bever 2005a). This means that vertebrate ichnospecies have the potential to be recognized based on the phenotypic cluster species concept of Mallet (1995), and that these ichnospecies groupings are no more artificial than those of skeletal fossil remains placed in species-level groupings based on morphology, or temporal and geographic range.

Species-level diagnosis of extant organisms is based on several different criteria, of which only one is morphologic distinctiveness (original biological species concept of Mayr, 1942, and in part the genotypic cluster species concept of Mallet, 1995). A species is also diagnosed when its representatives are ecologically (Van Valen, 1976), evolutionarily (Wiley, 1978; Cracraft, 1992) genetically (Paterson, 1982) or reproductively (Mayr, 1942; 1969) distinct (Coyne and Orr, 2004). The proposal and definition of each species concept is accompanied by the *a priori* assumptions supporting that the proposed species concept is the one that is universally applicable to most organisms (Miller, 2001).

Despite the claim by Miller (2001) that participants in the species recognition concept debate hold out hope for a universal species concept, it stands to reason that, depending on the organisms under study, some species concepts cannot be practically applied across all fields of biology. Morphologic discreteness as a basis for species recognition may not be realistic to those organisms that display a wide variety of morphologies on one individual (e.g. plant taxa, where cones and branches of the same tree should not be identified as different species), or are polymorphic and/or allopatric. An example of the latter is the geographic races of the British red grouse (*Lagopus lagopus scoticus*) which lacks the white winter plumage characteristic of its continental relative *L. l. lagopus* (Mallet, 1995).

The example raised in a study of extant *Bufo* (Bever, 2005a) raises the question: would specimens of a fossil vertebrate species, recognized based on unambiguous morphologic characters (morphologic species concept), be unambiguously identified as belonging to a discrete species based on the criteria and definitions of the species concepts commonly applied to extant vertebrates. Do the criteria and assumptions (both explicit and implicit) of different species recognition concepts categorize vertebrate individuals into species-level groups that are replicable or testable? When examining changes in vertebrate diversity over time and comparing species compositions of extinct and extant ecosystems, is it logical to compare fossil vertebrates with extant vertebrates, if the species recognition criteria used to create species-level groupings are different between fossil and extant organisms?

This chapter reviews the multiple species recognition concepts that are applied to extant and/or extinct vertebrate organisms, or those that are theoretically practical to apply to extinct vertebrates. Suggestions are offered for the recognition of fossil vertebrate species with as few assumptions as is practical, the reconciliation of differences between recognition of extant and fossil species, and a proposed alternative to a universal species recognition concept.

A BRIEF REVIEW OF SPECIES CONCEPTS AND RECOGNITION OF VERTEBRATE SPECIES

Coyne and Orr (2004) delivered a thorough treatment of multiple species recognition concepts. However, typological concepts that identify species based on the degree of morphologic (or genetic) difference were not treated in much detail. Coyne and Orr (2004) described the operational goals that species concepts are designed to fulfill: classify organisms in a systematic manner that is both testable and repeatable (although these last two criteria were not explicitly stated), classify organisms in such a way that corresponds to discrete entities as seen in nature, classify organisms in such a way that describes how discrete entities arise in nature, classify organisms in such a way that represents the evolutionary history of the organisms, and use a species recognition concept that applies to the largest number of organisms possible.

Mallet (1995) stated that a theory-independent definition of species that is not a concept would contradict many years of writings by Mayr and others. Mallet (1995:295-6) also stated that scientists need a definition for a species that is useful, however species are maintained and however they have come to be. Mallet (1995) distinguished between the fundamentally different questions of how to recognize from the questions regarding the origin of the species in question (evolutionary history) and process of speciation. Both of these latter concepts define species based on *processes* that affect species. Species need need to be defined independently of the processes that affect them to avoid circular reasoning (Mallet, 1995).

In the review presented here, species recognition concepts that have the potential to define extant and fossil vertebrate species are presented based on their operational assumptions of genetic similarity, phenotypic similarity, evolutionary lineage, and environmental associations. The following reviews of species recognition concepts should not be treated as comprehensive treatments, but rather a review of the applicability of these concepts and their assumptions as they apply to vertebrate species recognition, specifically the recognition of fossil vertebrates. Each review states the accepted definition of the species recognition concept, its applicability for identifying fossil vertebrates, and the assumptions applied to fossil vertebrate species by the use of that particular species recognition concept.

Genetic Compatibility and Cohesion Assumptions

Biological species concept (BSC)—Coyne and Orr (2004) propose a modified version of the biological species concept (BSC) as a basis for delineating species-level boundaries. The biological species concept is attributed to Mayr's (1942) definition, which states that species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups (also see Mayr, 1969). Dobzhansky (1951) added to the definition and application of the biological species concept by providing a list of potential barriers to gene flow, or isolating barriers, defined by Coyne and Orr (2004) as biological features of organisms that slow or halt the exchange of genes with members of other populations. Coyne and Orr (2004) also noted that most of these barriers depend on genetic differences between populations, but that several are linked with morphologic, ethologic (behavior), and temporal incompatibility between representatives of two species based on reproductive incompatibility. Due to the difficulty of defining allopatric species using the biological species concept, Mayr (1969) redefined species as groups of interbreeding natural populations that are reproductively isolated from other natural populations. Given that Mayr (1969) initially dismissed the phenomenon of hybridization in the stated example of seeing no intermediates in birds in the observer's backyard, Coyne and Orr (2004) amend this definition of the biological species concept to characterize distinct species as two populations whose members experience substantial (but not always complete) reproductive isolation.

Original genotypic cluster species concept (GCSC)—Mallet (1995) put forth an alternative to the biological species concept that allows for both genetic and phenotypic recognition of distinguishable groups. For the purposes of this review of species concepts and fossil organisms the phenotypic component of Mallet's (1995) original genotypic cluster species concept is treated in a separate subcategory that addresses phenotypic data specifically (phenotypic cluster species concept), leaving the modified genotypic cluster species concept to address genetic data separately. Regardless of whether phenotypic or genotypic data is used, the original genotypic cluster species concept defines species solely by features used by researchers in their recognition (Coyne and Orr, 2004). This somewhat mitigates the criticism of circular reasoning said to be present for the BSC, as species cannot themselves be defined by interbreeding without confusing cause and effect if the applied theories of speciation involve a reduction in the ability to interbreed (Mallet, 1995). The modified genotypic cluster species concept as defined by Mallet (1995) suggested that a species is a *genetically* distinguishable group of individuals that has few or more intermediates when in contact with other genetically distinquishable groups (Coyne and Orr, 2004). As this species recognition concept deals with genetic data only, it is not a recognition concept that can be practically applied to fossil organisms.

Cohesion species concept (CSC), recognition species concept (RSC), and genetic species concept (GSC)—Miller (2001) lists two genetic, or internal cohesion, concepts that may be secondary attributes to assumptions of genetic similarity of the genotypic cluster species concept. One is the cohesion species concept of Templeton (1989), stating that a species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic mechanisms (1989). The second is the recognition species concept of Paterson (1993) stated a species is the most inclusive population of individual, biparental organisms with a common fertilization system1993. The genetic species concept (GSC) of Mayden (1997) as modified by Miller (2001) stated that species are delineated based on a measure of genetic differences, in which differences are assessed using methods varying from chromatography to sequencing (Miller, 2004. These species recognition concepts are testable for extant vertebrates, but are not testable for fossil taxa. These concepts require genetic data that is not practically obtained from most fossil organisms at this time. These *a priori* assumptions are associated with all genetic compatibility and cohesion concepts.

Applicability to fossil vertebrates—Concepts of genetic compatibility use the *a priori* assumption that organisms within a population are able to interbreed and retain their genetic compatibility, and that the organisms in question originate from an identical genetic lineage (Coyne and Orr, 2004). This is a problem with applying versions of the biologic species concept to the paleontological record, as there is a lack of a relationship between morphologic variation and reproductive isolation (Silcox, 2014). The biological species and the genotypic cluster species concepts are not applicable to fossil organisms (Benton and Pearson, 2001) without making the *a priori* assumption of genetic compatibility among the individual organisms representing the fossil species. The information remaining for fossil organisms includes their geographic location, their temporal location, and their morphology (Bell and Gauthier, 2002), so documenting interbreeding and quantifying the level of gene flow between two fossil organisms is not a practical option. However, Benton and Pearson (2001) direct our attention to evidence for a coincidence between morphologic and genetic differentiation (and presumably reproductive isolation) in studies of fossils, but also state that morphologic evolution does not always coincide with speciation.

Miller (2004) classified the genetic species concept of Mayden (1997) as a concept based on the compositional properties of specimens (Miller, 2001). In other words, Miller (2001) treated the morphologic, phenetic, and genetic species concepts as typological. If different species can be grouped based on a measure of genetic differences under the genetic species concept, then conversely members of the same species can be categorized based on a measure of their genetic similarity. Operationally there is little difference between the genetic species concept and the other species concepts that use the criterion of genetic compatibility as a proxy for genetic similarity. Regardless, the genetic species concept is only applicable to fossil organisms if a proxy for genetic compatibility is preserved with the organism.

Assumptions of the genetic compatibility and cohesion concepts when applied to fossil taxa

Assumption 1: Genetic distinctiveness is a proxy for morphologic distinctiveness—Genetic data is often applied to vertebrate paleontology studies in the form of total evidence phylogenies (Paton, 2003; Moyle et al., 2006) and comparisons of diversity between extinct and extant ecosystems (Bell and Gauthier, 2002). When comparing extant organisms (categorized into genetically discrete groups due to either direct samples of genetic data or inference of interbreeding activities) to fossil organisms (categorized into morphologically discrete groups due to unambiguous morphological characters; Bever, 2005a), there is an *a priori* assumption that genetic distinctiveness is congruent with morphologic distinctiveness (Forey et al., 2004). In other words, we assume that fossil species and extant species are equivalent operational taxonomic units, particularly when both fossil and extant taxa are included in a phylogenetic analysis (Silcox, 2014). Coyne and Orr (2004) state that a consistent correlation between a group of traits and reproductive compatibility can be used to show the concordance of [morphologic] characters and genes in the biological species concept, although they did not offer compelling examples for vertebrate organisms. Congruence between morphology and molecular data often appears as an unstated and/or unrecognized *a priori* assumption when comparing extant organisms to their fossil counterparts.

Several studies on extant vertebrate taxa directly test the congruence of morphologic and molecular species-level groupings. These studies are necessary, as cryptid species have the potential to be indistinguishable if only hard tissues (skeletal remains) are available (Silcox, 2014; however, see subsequent discussion for analyses of cryptic species of the kiwi, *Apteryx*). Turner et al. (2008) found that three sympatric morphs of pupfish are both morphologically and genetically distinct, although the evolutionary lineage of these pupfish predicted that reproductive isolation is unlikely. Evin et al. (2008) provided further support for congruence between morphologic and genetic distinctiveness in their reassessment of the taxonomic affinities of the *Myotis* species complex (*M. blythii, M. myotis*, and *M. punicus*) using geometric morphometric (morphologic) and genetic analyses. Both morphometric and genetic analyses recover the three groups of organisms as discrete species, but each analysis differs in how they interpret the relationships of the three species (Evin et al., 2008). The morphometric analysis showed a greater similarity between *M. myotis* and *M. punicus*, while the molecular phylogenetic analysis revealed a greater similarity between *M. blythii* and *M. myotis* (Evin et al., 2008). Regardless of the evolutionary interpretations, both morphology and molecular data recovered the organisms in their accepted species-level groupings.

Studies comparing morphologic and molecular data do not always provide congruent results. Tetrapod digits were interpreted by Sordino et al. (1995) as evolutionary novelties based on developmental molecular data, and skeletal information of the sarcopterygian *Panderichthyes*. Morphologic data gathered from computed tomography scans of *Panderichthyes* revealed the presence of distal radials, which allows the interpretation of digits as derived from the pre-existing radials of sarcopterygians (Boisvert et al., 2008). The identity of *Panderichthyes* was not in question in either of these studies; however, the information provided by molecular-developmental and morphologic data were incongruent. Smith et al. (2008) provided another example in fish, in that field identifications and morphology alone did not allow for species-level identifications within the southern ocean skate genus *Bathyraya*, whereas molecular analysis reveals a new species of skate in the Antarctic.

The taxonomy of bats also provides examples of incongruence between morphologic and genetic groupings. Griffiths (1982) addressed the history of the classification of New World nectar-feeding bats (Phyllostomidae: Glossophaginae). Glossophagines were originally distinguished by soft-tissue morphology of the rostral region (with the exception of the long narrow snout, which is skeletally controlled); however, the monophyly of Glossophaginae was called into question by subsequent studies of chromosomal, immunological, and skeletal data, none of which produced a taxonomic consensus. Conversely, systematics of the bat genus *Vampyressa*, while originally based on hard-tissue characters, does show consensus among systematic organizations based on morphologic-only and morphologic and mitochondrial DNA characters (Tavares et al., 2014). Morphologic differences may also correlate with genetic differences when those morphologies are related to dispersal of organisms. Morphology related to wing loading in bats shows that migratory bats with high wing loadings have less genetic structuring than low wing loading, non-migratory species (Burns and Broders, 2014). Cryptic extant and Pleistocene species of *Apteryx* (kiwis) also provide examples of incongruence between genetic- and morphologic-based species recognition concepts (see Discussion: Case Studies).

Assumption 2: Groups of organisms should be natural—One assumption explicitly stated for genetic compatibility concepts is that populations of organisms are *natural* (according to Mayr, 1942; Mayr 1969 for the biological species concept), or come into contact (the ideal scenario for the genotypic cluster species concept according to Mallet, 1995). Allopatric populations of the same species can speciate if the boundaries to gene flow remain intact, but will still be considered the same species if members of the two populations could produce viable offspring in sympatry.. Paleontologists observe the fossilized remains of natural populations at one point in time (although time-averaged deposits should be considered), both in terms of the organisms no longer being able to attempt interbreeding with allopatric populations, and in terms of the fossils themselves not amenable to transportation to a non-native paleogeographic location (Jaznoski et al., 2003).

Assumption 3: There is little to no gene flow between populations of two different species—A third assumption that is closely related to “natural” population assumption is that two populations experiencing little or no migration are considered separate species due to geographic isolation. An example given by Coyne and Orr (2004) is the extant species of cichlids occurring in African rift lakes. The males in these allopatric species exhibit different breeding colors (Turner et al., 2001) and it is unknown if these different species would be compatible in sympatry with their disparate coloration. Based on their morphologic dissimilarity and allopatric distributions these different populations of cichlids are considered distinct species under the biological species concept (Turner et al., 2001). This assumption should be testable for the study organism before using the biological species concept as a species recognition concept, and it is recognized by Miller (2001) that reproductive isolation is a secondary attribute of more robust concepts (i.e. genetic cohesion).

The genotypic cluster species concept allows for interbreeding between two allopatric populations of organisms to be considered the same species as long as the two populations do not form discrete groups (genetically) in sympatry (Mallet, 1995). Two species are recognized in the event that the two populations remain discrete clusters, regardless of the amount of gene flow between the two populations (Mallet, 1995). These assumptions should be testable or observable, both of which are not practical to observe from fossil organisms. Again, morphologic features (as stated by Forey et al., 2004) that are used as a proxy for genetic clustering are needed to assume either genetic compatibility or incompatibility in fossil taxa.

Morphologic Assumptions

Phenotypic cluster species concept—The phenotypic cluster species concept is a subcategory of Mallet's (1995) original genotypic cluster species concept. The phenotypic cluster species concept defines species as a morphologically distinguishable group of individuals that has few or no intermediates when in contact with other morphologically distinguishable groups (Coyne and Orr, 2004). Miller (2001) recognized three versions of Mayden's (1997) modified phenotypic cluster species concept. The morphologic species concept recognizes species as a group of organisms delineated from other such groups by essential morphologic attributes (Mayden, 1997). The morphologic species concept states that Group X is morphologically distinct from Group Y; therefore, groups X and Y represent different species. The phenetic species concept defines species where variation in a set of characters is less within a group than between groups (Mayden, 1997). The phenetic species concept states the amount of difference among all the members of Group X less than the difference observed when Group X is compared to Group Y. Groups X and Y are different species.

Applicability to fossil vertebrates—The morphologic and phenetic species concepts are the only species recognition concepts that can be practically applied to vertebrate skeletal material, if extant populations are considered as equivalent modern analogs to fossil populations of organisms (Benton and Pearson, 2001). That being said, there are issues surrounding the plasticity of morphology in vertebrates as it relates to phenotypic variation due to environmental influence (Gvozdík et al., 2008), ontogenetic change and polymorphism (Bever, 2005a). The most useful studies in paleontology are those that take ontogeny in to account when analyzing populations of fossil organisms (e.g. Buckley et al., 2011).

Assumptions of the morphologic species concepts when applied to vertebrate taxa

Assumption 1: Ecophenotypy and polymorphism are distinguishable from taxonomic phenotypy—Recognition that phenotypic expression can result in convergent morphologies based on similarity of habitat, behavior, or divergent morphologies due to polymorphism, is common in morphology comparisons of vertebrates. Livezey (1996) addresses the *Anser* and *Branta* species-complexes, and the debates as to whether the subgroups within these species-complexes are separate species or a polymorphic species. Evin et al.'s (2008) morphometric comparison of *Myotis blythii, M. myotis*, and *M. punicus*reveals *M. myotis* and *M. punicus* share several features of the posterior cranium and the rostrum. Evin et al. (2008) interpret the morphologic similarity as convergence due to similar feeding habits as molecular data shows that *M. myotis* and *M. punicus* are sister-species. Although all three species were distinguishable based on skeletal morphology alone, the incongruence between the molecular and morphologic groupings show that environment affects morphology in such a way that may potentially result in a single *morphologic* species classification for a group of organisms belonging to two different *biologic* species.

Another example is phenotypic variation in the tree frogs *Hyla arborea* and *Hyla savignyi* (Gvozdík et al., 2008). Gvozdík et al. (2008) found that, despite their species affiliations, the eastern Mediterranean populations of both species were closer to each other than to temporally coexisting populations from different regions, and that the local interspecific similarity is probably a common response to macroclimatic conditions. It is not known how these two biologically classified species would be categorized in the eastern Mediterranean if only their skeletons remained. Given that there has been little attention given to whether soft-tissue differences are congruent with hard-tissue differences, it is possible that these two species of *Hyla* would be, if known only from skeletons, considered the same species.

Assumption 2: Species should be recognized in sympatry—Both the phenotypic cluster and genetic cohesion species concepts are often criticized by opponents because their assumptions work the best in sympatry and cannot be tested in allopatry (Coyne and Orr, 2004). Based on the definitions of Mayden (1997), morphologic and phenetic species concepts do not rely on discrete clusters of organisms in sympatry to diagnose species.

Evolutionary Lineage Assumptions

Evolutionary species concept (EvSC) and phylogenetic species concepts (PSC)—The evolutionary species concept states that a species is a single lineage of ancestor-descendant populations or organisms, and that these populations or oganisms maintain their identity from other lineages, as each lineage has its own evolutionary tendencies and historical fate (Wiley, 1978; modified by Coyne and Orr, 2004). A similar concept is the phylogenetic species concept. Miller (2001) lists three separate lineage-based concepts that are specializations of the original evolutionary species concept. With each lineage species concept are increasing levels of reliance on phylogenetic analyses in recognizing species-level groupings.

The Hennigian species concept recognizes species as reproductively isolated natural populations or groups of natural populations that originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation (Meier and Willmann, 2000). Wheeler and Platnick (2000) used the diagnosable species concept to define a species as the smallest group of populations or lineages diagnosable by a unique combination of character states (Wheeler and Platnick, 2000). The monophyletic species concept of Mishler and Theriot (2000) states that a species is the least inclusive taxon recognized in a formal phylogenetic classification, and organisms are grouped into species because of evidence of monophyly (Mishler and Theriot, 2000).

Applicability to fossil vertebrates and assumptions when applying to vertebrate taxa—Miller (2001) strongly supported the use of the evolutionary species concept as the “ultimate concept many of the operational approaches seem to be aiming to uncover” (2001:1) because it simultaneously describes both the identity of the species and the process of speciation in terms of evolutionary history. However, Miller (2001) also noted that most applied biologists would consider that a good species should be reproductively isolated from other species, and that morphologic differences can be used to diagnose or recognize different species. Therefore, unambiguous, non-overlapping morphologic characters (Bever, 2005a) that have the potential to identify organisms to species-level groups need not always reflect evolutionary history (Coyne and Orr, 2004). While the various evolutionary species concepts do attempt to consider morphologic variation over time (which is not explicitly stated in the biological species concept), the recognition of species as operational taxonomic units becomes somewhat arbitrary as all life forms are part of one lineage (Simpson, 1961). Cladistic solutions to delineating species (Ridley, 1989) still rely on organisms first being categorized into operational taxonomic units prior to a cladistics analysis, introducing circularity.

In contrast with Miller (2001) and Cracraft (1987), species recognition concepts should be used to identify non-overlapping, unambiguous groups of organisms without the requirement of how those unambiguous groups came to be (Silcox, 2014). Evolutionary history should be determined once the discrete biologic/morphologic groups have been identified to avoid circularity. Organisms often only represent the end products of whatever evolutionary processes formed the end products, as hypothesized by a phylogenetic analysis. As with the reproductive isolation and genetic cohesion concepts, the evolutionary and phylogenetic species concepts define species as part of a process (evolutionary history) and use the same processes to identify the species.

The strength of parsimony and/or maximum likelihood analyses in species recognition is for testing species-level groupings of morphologically similar organisms. Each individual behaves as a terminal taxon in these analyses, and where each individual has, to some extent, been identified as part of an operational taxonomic unit. Beresford and Cracraft (1999) use this method to test species-level groupings of populations of African robins. Using this method, Cracraft et al. (1998) test the genetic distinctiveness of subspecies-level groupings within tigers (see Discussion). The phylogenetic cluster approach to testing morphologic discreetness and morphologic similarities was recently used in dinosaur systematics. Tschopp et al. (2015) treated name-bearing type specimens of Diplodocidae and (relatively) complete referred specimens as operational taxonomic units within a parsimony phylogenetic analysis using 477 morphologic characters to resolve the systematic relationships of specimens of controversial and/or poorly known nominal species. Approaches such as that of Tschopp et al. (2015) do employ phylogenetic species concepts, but it should be noted that the resolved phylogenies first involved organisms that clustered based on increasing exclusivity of shared morphologic character states. In other words, morphology-based groupings of Diplodocidae were tested using a cladistics approach.

Ecological species concepts (EcSC) - The ecological species concept by Van Valen (1976) defines species as a lineage (or closely related set of lineages) that occupies an adaptive zone minimally different from that of any other lineage in its range, and that evolves separately from outside its range (Van Valen, 1976). This species concept incorporates habitat information to the lineage-based species recognition concepts, and the same critiques for the evolutionary and phylogenetic species concepts apply to the ecological species concept.

CASE STUDIES OF EXTANT AVIAN SPECIES AND THE SPECIES RECOGNITION CONCEPTS

Avian fossil species are recognized using the morphologic species concepts using hard tissues, while recognition of extant bird species is based on external morphologic characters (coloration), distinct vocalization patterns (Beresford and Cracraft, 1999; Alström et al., 2008), and recently molecular data (Barker et al., 2004), to distinguish among higher level taxa and to test species and subspecies relationships (Alström et al., 2008). The existence of multiple species recognition concepts adds to the debate of what characters delineate an extant species of bird; if different categories of characters do not provide consistent or reproducible results in recovering groups of organisms considered by one recognition concept as a good species, the conditions under which these extant species are recovered as such must be explicitly stated.

Apteryx

The study of kiwis (*Apteryx* species) and their conservation provides an excellent example of discordant morphologic and genetic differences, and has direct applicability to the recognition of fossil taxa. Currently there are five recognized species of *Apteryx*, which are divided into two morphologic groups; the five species are recognized based on DNA analyses (Shepherd et al., 2013). The little spotted kiwi (*Apteryx owenii*) is the only species of *Apteryx* that is considered distinguishable using hard tissue morphology (Worthy, 1997) based on its smaller size relative to co-occurring species, and the other spotted kiwi, the great spotted kiwi (*Apteryx haastii*) (Shepherd et al., 2013). The brown kiwi morphological group (Shepherd et al., 2013) has a complex systematic history. Early publications on *Apteryx* biology and conservation deal with the *Apteryx* species groupings by distinguishing the two species of spotted kiwi (*Apteryx haastii*, *Apteryx owenii*) and considering the species of brown kiwi (*Apteryx australis*) as one species containing within it three subspecies (*Apteryx australis australis*, *Apteryx australis lawryi, Apteryx australis mantelli*) (Baker et al., 1995). Worthy et al. (2013) used *A. australis lawryi* (Steward Island brown kiwi, which otherwise does not appear often in the comparative literature) in their comparisons with *Proapteryx micromeros*. *Apteryx australis lawryi* also appears in Worthy's (1997) analysis of South Island, New Zealand Late Quaternary fossil material, but the analysis of the skeletal material did not extend beyond the overall lengths and widths of pelvic limb elements. It is likely that many analyses of *A. australis* do not consider or indicate the probable subspecies. *Apteryx rowi(i)*, the rowi brown kiwi, appears in the literature in 2003, but is not formally named by Burbridge et al. (2003). To date, the recognized species of *Apteryx* (*A. australis*, *A. haastii*, *A. mantelli*, *A. owenii*, *A. rowii*) are recognized based on genetic analyses (Shepherd et al. 2013). Burbridge et al. (2003) considered that the specialized ecology of kiwis exhibits a strong stabilization selection on morphological characters, contributing to their cryptic morphology.

Baker et al. (1995) found that two morphologically cryptic species were combined in the brown kiwi (*Apteryx australis*) species (although recognized in previous studies as subspecies), whereas Burbridge et al. (2003) recognize three cryptic species within the brown kiwi. Baker et al. (1995) also note that, because the little brown kiwi and the brown kiwi hybridize successfully (it was not stated if these offspring were viable, only that hybridization took place), the biologic species concept of reproductive isolation does not successfully apply when differentiating these species. Baker et al. (1995) also detail the morphological differences among the different populations of *Apteryx*; however, the morphology used is limited to soft-tissues (plumage, epidermal tarsal scutes, facial bristles; table 2). The analyses performed on morphological data related to skeletal elements of *Apteryx*, at this time, only serve to reinforce the untested hypothesis that skeletal remains of *Apteryx* are too cryptic to be of use in distinguishing among species.

Hindlimb element lengths (femur, tibiotarsus, tarsometatarsus) group the five species of kiwi into what Shepherd et al. (2013) refers to as two morphologically distinct groups (small spotted kiwi, and the great spotted kiwi with the brown kiwi morphologic group). However, it should be noted that there was no examination of the morphology of hindlimb elements beyond element length. Only the bones of the adult little kiwi are considered morphologically distinct enough to identify to species level and that identification is based on size, whereas the adult specimens of the four largest species of kiwi overlap considerably in both size and shape characters (Worthy, 1997; Shepherd et al., 2013). Despite Worthy and Holdaway's (1993) hypothesis that hindlimb length-width comparisons may be useful in distinguishing among the large species of kiwi, the Worthy (1997) and Shepherd et al. (2013) studies revealed that analyses using only hindlimb element lengths, and hindlimb element proximal, distal, and midshaft widths are not sufficient to distinguish among the larger species of kiwi. In a paleontological framework, where an analysis of shape characters entails a detailed comparison of the bones of the species in question, basic length and width measurements are oftentimes not sufficient criteria for distinguishing among species (e.g. see Tshopp et al., 2015, for a detailed analysis of skeletal anatomy of sauropods). Neither the Shepherd et al. (2013) nor the Worthy (1997) studies present a description or analysis of detailed osteomorphology of kiwi hindlimb elements, so it is unknown if there are any osteomorphologic characters other than those based on relative size that can be used to identify large kiwis to species level.

Bird remains are often assumed to be too difficult to identify to species on the basis of morphometric criteria: the most diagnostic characters are cranial, and the cranium is rarely recovered (Barnes et al. 2000). However, the specimens used by Barnes et al. (2000) were refered to as bone fragments rather than complete or partially complete skeletal elements. The elements used in their study were sufficiently complete to allow them to be identified as humeri and a tibiotarsus or metatarsus (indicated by tib-met in table 1 of that study). It is possible that there is incongruence in technical language in the use of "fragment" between archaeology and paleontology; what might be considered "fragmentary" in zooarchaeology may contain useful osteomorphologic data in paleontology. Barnes et al. (2000) do not image the skeletal remains sampled for DNA sequencing, so the completeness of the elements is uncertain. Resolving species-level taxonomy using skeletal elements, in this example of geese, is not often the focus of phylogenetic studies: higher-level phylogenetic studies using DNA hybridization do not include many anseriform taxa (Livezey, 1996).

Fossil specimens (those specimens older than the Pleistocene *Apteryx* spp. that no longer contain genetic material that can be reliably tested) do not have the ability to be tested for correlation between groupings based on morphological and genetic similarity. There are key differences between how the zooarchaeology specimens and the extant specimens are analyzed in the aforementioned examples as compared to the analysis of paleontology specimens. Examination of skeletal characters of paleontology specimens involves a detailed comparison of the sizes and shapes of not only the gross anatomy of the skeletal elements, but of the sizes and shapes of articular surfaces, cotlyae, cristae, ementiae, fossae, foraminae, processes, tubercles, tuberositae, and sulci. The zooarchaeology studies did not examine elements beyond basic length and width measurements. Exceptions to this generalization are the studies by Bochenski (1994)

Tomek and Bochenski (2000), Bochenski and Campbell (2006), which were conducted within the framework of the morphologic species concept and involved detailed osteomorphological examination. The only study on comparative osteomorphology of *Apteryx* is of the description of *Proapteryx micromeros* (Worthy et al., 2013) from the Early Miocene deposits of Central Otaga. The study did not address the skeletal characters among the different species of *Apteryx*, although the authors were able to differentiate between *Proapteryx* and *Apteryx* using several characters of the femur and quadrate (Worthy et al. 2013). Studies such as these suggest that skeletal elements are not diagnostic because they overlap in both size and shape characters (Shepherd et al., 2013, citing Worthy, 1997). However, suggesting that skeletal remains are too ambiguous to provide species-level identifications, when detailed morphologic comparisons have not been completed, is inaccurate at best, misleading at worst. Further study into skeletal characters of *Apteryx* may reveal that the skeletal characters of *A. australis* are distinct enough to distinguish among the cryptic species. These characters may also reveal a grouping of operational taxonomic units that either agree or conflict with the currently accepted species groupings.

DISCUSSION

Multiple species concepts and the International Code of Zoological Nomenclature

The International Code of Zoological Nomenclature accepts the establishment of new taxa at the familial, generic, and specific levels using a variety of criteria: Article 13.1.1 states that new names published after 1930 must be accompanied by a description or definition that states, in words, characters that are purported to differentiate the taxon, and recommends that the authors should provide a clear summary of the characters that differentiate the new nominal taxon from related/similar taxa in languages used in the regions relevant to the taxa diagnosed (Recommendations 13A and 13B). This is the only specific criteria given for what constitutes a character: Recommendations 13A and 13B can be interpreted such that the characters in question can be used to differentiate among taxa within that particular field of study of the taxon in question. In the naming of new taxa in vertebrate paleontology, vertebrate paleontologists, by the nature of the preserved material, use the morphologic species concept (phenotypic cluster species concept of Mayden, 1997) for establishing familial, generic, and specific nominal taxa.

What happens when taxa established using morphologic characters are not recovered, or are further refined and subdivided taxonomically, using genetic characters? Unlike traditional biologic/morphologic-based taxonomies and parataxonomies (such as ichnotaxonomy), there is no provision in the International Code of Zoological Nomenclature for concurrent taxonomic groupings. This situation is seen with the species-level taxonomy of *Apteryx*: morphologic (and geographic) characters support three morphologic species of *Apteryx*, whereas genetic characters support five species. At this time, genetic-based species level groupings of *Apteryx* are considered the most accurate reflection of the biology and evolutionary history (and will be generally considered the most accurate reflection of their biology and evolutionary history until more thorough studies on skeletal characters of *Apteryx* are completed) of the species in question, and the genetic-based species-level groupings of *Apteryx* are now accepted in the literature over the previous morphology/population based groupings. Refined and/or amended species-level groupings using genetic characters are an expected outcome of increasingly available data, and testing morphology-based species-level groupings using genetic information has occurred for many avian taxa. However, species-level groupings for vertebrates based on genetic and/or soft-tissue characters should be examined to determine if there are skeletal differences congruent with their species-level groupings. Given the large number osteology specimens available for such testing for extant vertebrate species, there is surprisingly little testing of the congruence between osteomorphologic species-level groupings and soft-tissue based groupings. Until analyses such as these are completed in more taxa and with greater rigor, the question of whether skeletal-bases taxa are congruent with biologic taxa will remain unanswered.

Species recognition concepts and fossil vertebrates: universal concept or multiple concepts?

Comparing representatives of an extant species (as defined by the biological species concept, or a morphologic species concept using soft-tissue characters) to a fossil representative of a similar species (as defined by the morphologic species concept) requires that both concepts can be applied interchangeably to the taxa in question. It must also be considered that there is potential for incongruent results between using an (osteo)morphologic species concept and those concepts that use characters not readily preserved in the fossil record. Benton and Pearson (2001) state that paleontologists assume an osteology-based species concept is in line with the biological species concept. By inference, very few analyses have been completed to test the level of congruence between their morphologic- species and suitable extant (biological) species.

In analyzing species of African Robin, Beresford and Cracraft (1999) found that there was congruence between species-level groupings using each genetic and external morphologic character, but there was no test for congruence with skeletal characters. Alström et al. (2008) found that genetically-similar subspecies of the Spotted Bush Warbler formed groupings that are similar to those groupings based on linear measurements of morphologic characters, although neither genetic- nor morphologic-based groupings could recover the five subspecies recognized based on color and vocal characters.

Is there a species concept that has practical applicability to both extant and fossil vertebrate taxa? Fossil vertebrate data (to date) rarely provides the same data in terms of completeness (as the data reflect the whole biology of the organism) and abundance, as is available for extant species. Acceptance of the first premise should logically result in acceptance of the second premise: there is no one species recognition concept that is applicable, in the strictest sense of its application, to both extant and extinct species. It should come as no surprise that the only species recognition concepts available to paleontologists (with the exception of those studying fossil and sub-fossil material young enough to preserve genetic material, given the current technology) with the least amount of untestable assumptions as possible are the morphologic species concepts (Benson and Pearson, 2001) (Table 2.1).

CONCLUSIONS

Comparing apples to potatoes: pommes (extant species) to pommes de terre (fossil species)

One cannot simply assume that morphologic species groupings correlate 100% to those species-level groupings that are biology-based (Benton and Pearson, 2001): morphologic species groupings will not perfectly reflect the biologic diversity of a paleoecosystem. The total number of species identified from a paleoecosystem will more accurately reflect the morphologic diversity, as suggested by the Bush Warbler results of Alstöm et al. (2008). Missing characters from the lack of preservation (or rare preservation) of external morphology, molecular, behavioral, and small-scale habitat data, data from fossil vertebrates will not reflect the same level of biologic diversity seen in extant ecosystems.

This is not to say that one-to-one comparisons cannot or should not be made between fossil and extant vertebrate diversities: the comparisons will simply require a great deal of additional analyses to compare extant vertebrate biologic species (apples) to fossil vertebrate morphologic species (potatoes). The large amount of data available for delimitation of extant species provides excellent opportunities to determine the level of congruence between osteological characters and all other soft-tissue characters. This will mean detailed osteological comparisons of morphologically and genetically extant species. Delineating extant species using the same information available with fossil species will provide more accurate comparisons between extant and fossil vertebrate diversity and ecosystem analyses, and will provide data for hypotheses testing congruence among multiple species recognition concepts. This future work will enable us to work towards the goal of a universal species concept (Miller, 2001); however, as suggested by Silcox (2012), a universal species concept may not be practical at this time. This is not to say that one should not strive towards better understanding fossil species as biologic species. Testing the congruence between osteomorphologic species-level groupings and biologic species groupings will allow us to determine, to what extent, the morphologic species we observe in the terrestrial vertebrate fossil record reflect the extant biologic diversity with which we are most familiar.

Table 2.01 Summary of species recognition concepts and the practicality of their application to the recognition of fossil species.

Species Concept	Definition (Coyne and Orr, 2004; Miller, 2001)	Assumptions for fossil organisms	Vertebrate paleontology application?
Biological species concept (BSC)	Species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr, 1942; 1969).	1. Morphologically dissimilar organisms do not interbreed. However, the BCS also describes a process of speciation and recognizes a species as a process and an entity. 2. Morphologic discreteness is a reliable proxy as a barrier to gene flow. 3. Morphologically similar individuals in allopatric populations have no contact (i.e. through migration).	No (Benton and Pearson, 2001), unless testable morphological proxies are identified for interbreeding.
Genotypic cohesion species concept (GCSC)	A species is a genetically distinguishable group of individuals that has few or no intermediates when in contact with other such clusters (Mallet, 1995).	1. Morphologic discreteness is a reliable proxy for genetic discreteness. 2. Morphologic discreteness can be distinguished from phenotypic variation.	No, unless testable morphological proxies are identified for genetic similarity.
Phenotypic cohesion species concept (PCSC)	A species is a phenotypically distinguishable group of individuals that has few or no intermediates in sympatry with other such clusters (modified from Mallet, 1995).	1. Polymorphism can be distinguished from taxonomic phenotypy. 2. Ontogeny can be distinguished from phenotypic discrete clusters. 3. Phenotypic variation due to environmental effects can be distinguished from taxonomic phenotypy. 4. Species retain phenotypic discreteness in sympatry.	Yes, but may only be compared to other species identified using the PCSC or similar typological species recognition concepts.
Morphologic species concept (MSC)	A species is delineated from other such groups based on possession of essential morphologic attributes (Mayden, 1997).		
Phenetic species concept (PhSC)	A group is recognized as a distinct species when variation in a set of characters is less within a group than between groups (Mayden, 1997).		

Species Concept	Definition (Coyne and Orr, 2004; Miller, 2001)	Assumptions for fossil organisms	Vertebrate paleontology application?
Evolutionary species concept (EvSC) Phylogenetic species concepts (PSCs)	A species is a single lineage of ancestral descendant populations or organisms which maintains its identity from other such lineages (modified from Wiley, 1978). A phylogenetic species is a basal cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a pattern of ancestry and descent (modified from Cracraft, 1987), or A species is the smallest [exclusive] monophyletic group of common ancestry (de Queiroz and Donoghue, 1988; although see Wheeler and Nixon, 1990, for comments).	1. Species must first be identified using a different species recognition concept in order to avoid defining a species as both an entity *and* process (Coyne and Orr, 2004). A lineage is the evolutionary history of several organisms within the lineage, not a discrete biological entity. A species cannot be a lineage, only a representative of that lineage. 2. Phylogenetic/maximum likelihood *a priori* assumptions must be applied to discrete morphologic groups when determining lineage.	Yes, but not for the grouping of individuals into species-level clusters. Relationships of *a priori* designated species may be tested using evolutionary history concepts.
Ecological species concepts (EcSC)	A species is a lineage which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from other such lineages outside of its range (Van Valen, 1976).	1. Assumptions applied to evolutionary species concepts (see above). 2. Assumptions regarding allopatric species and biologic species concept (see above). 3. Convergent phenotypy due to environmental affects is distinguishable from taxonomic phenotypy. 4. Adaptive zones can be identified for fossil organisms.	No, as it is unlikely that, for the majority of the fossil record, the detail and resolution of preservation of local ecosystems is consistent enough for the EcSC to be applied practically.

CHAPTER 3

OSTEOMORPHOLOGY AND CLADISTIC ANALYSIS OF EXTANT AVIANS: DOES AN OSTEOLOGY-ONLY CLADISTICS ANALYSIS REPRODUCE THE TOTAL EVIDENCE PHYLOGENETIC TOPOLOGY OF ACCIPITRIDAE, GALLIFORMES, AND CHARADRIIFORMES?

INTRODUCTION

Classification of Extant Species of Aves

There are several taxonomic systems used to categorize extant species of Aves. Historically, taxonomic schemes for classifying familial, generic, and specific groupings within Accipitriformes, Charadriiformes, and Galliformes involve gross morphology (size, relative proportions, etc.) and characters highly dependent on the presence of soft tissue (plumage color and pattern, vocalizations), or behavior (timing of breeding, environmental preferences, etc.) Of these traditionally used characters, hard-tissue characters have the highest probability of fossilization.

Extant Aves as Model Taxa for Species Recognition Concepts for Extinct Theropoda

Extant Aves *are* Theropoda, and in studying extant Aves, we study the extant representatives of Theropoda, and given both the behavioral and morphological similarities between extant and extinct Theropoda, extant birds are the closest representatives available for examining Theropoda. Phylogenetic analyses on genetic data of extant Aves shows that it is possible for many of the extant groups (Charadriiformes, Charadrii, Lari) to have diverged in the Late Cretaceous, with the most recent common ancestor of Charadriiformes appearing around 93 Mya (Baker et al., 2007), a much earlier time than suggested by Paton et al. (2003) of 80 Mya. Many of the distinct skeletal features seen in extant Aves, particularly those groups which have early divergence times, may provide more information on the skeletal "discreetness" of avian- and small non-avian theropod taxa from the Mesozoic.

Paleontologists, in general, are limited to the use of the morphologic species concept (MSC), and specifically, an osteologic specialization of the MSC (an Osteologic Species Concept), where morphologic distinctiveness is based on hard tissue characters (Chapter 2). If extant species of Aves are examined as though the only data available for them is osteologic information (as with extinct species of Theropoda), would a cladistic analysis recover a topology with any similarities to those topologies recovered using myological, genetic, or a combination of data?

While there are an increasing number of complete specimens of Early and Late Cretaceous non-avian and avian theropods (e.g., *Archaeornitha* from the Early Cretaceous of China, Wang et al. 2015), there are many specimens of Theropoda that are described from incomplete skeletons, often lacking skull material (Bell et al., 2015). The plethora of skeletal specimens of extant Aves provides an opportunity to test if, using only elements from the appendicular skeleton, a cladistic analysis of a species of foot- and ground-utilizing birds (Charadriiformes, Ciconiiformes, Falconiformes, Galliformes) would recover the same evolutionary relationships recovered using different (molecular, Jarvis et al., 2015), or more complete (a combination of myological and osteological, Livezey, 2010) data. The accuracy of such an "incomplete" analysis will reflect the potential accuracy of similar fossil analyses.

Institutional Abbreviations: CVM, Cowan Vertebrate Museum, University of British Columbia, Victoria, British Columbia; **LACM,** Page Museum, Los Angeles County Museum, Los Angeles, California, USA; **RBCM,** Royal British Columbia Museum, Victoria, British Columbia, Canada; **UAMZ,** University of Alberta Museum of Zoology, University of Alberta, Edmonton, Alberta, Canada.

METHODS

Taxa and Specimens Analyzed

For the extant species, character state coding was done by examining the prepared skeletal elements of specimens in osteology collections. Specimens studied were collected between the 1940s–1980s. Species-level identifications of each extant specimen were presumably made using external morphological features (size, relative proportions, plumage, vocal cues), and was likely identified either at the time of collection or at the time the specimen was processed for the repository of the institution in question. Most extant specimens were either field collected, or were donated to institutions as wildlife salvage specimens. Fossil specimens from the La Brea Tar Pits (Pleistocene) were identified to generic and specific levels by comparisons of fossil material to skeletal material from extant specimens by staff of the George C. Page Museum at the La Brea Tar Pits. Given that many of the specimens excavated from the La Brea Tar Pits are disarticulated, separate elements were treated as individual specimens.

STUDY TAXA

Ardeiformes

Ardeidae

***Ardea herodias* Linnaeus, 1758 (Great Blue Heron)**—Great Blue Herons form a clade with other taxa historically considered to be typical herons (Vennesland and Butler, 2011). However, species of *Ardea* form a polytomy in phylogenetic analyses of osteologic characters (McCracken and Sheldon, 1998). Osteologic and molecular phylogenies of herons and egrets show little correlation. In the osteologic analysis *Ardea* spp. for a clade with species of *Tigrisoma*; whereas in molecular phylogenies species of *Ardea* are closest to *Bubulcus* (McCracken and Sheldon, 1998). Fossil specimens examined in present study: LACM F426, F503, K5154 (humerus); D9151, F850, K5123, K5124 (femur); F496, F561, G498, K3122 (tarsometatarsus).

***Botaurus lentiginosus* Rackett, 1813**—*Botaurus lentiginosus* forms a monophyletic group with other species of *Botaurus* in an analysis using only skeletal characters (McCracken and Sheldon, 1998). *B. lentiginosus* is considered a distinct species from the Old World herons based on morphologic data. Fossil specimens examined in present study: LACM F1111, G 4899, K2437, K5144 (tarsometatarsus).

Charadriiformes

Charadriidae

***Charadrius semipalmatus* Bonaparte, 1825 (Semipalmated Plover)**—*Charadrius semipalmatus* was originally differentiated from other species within Charadriidae by plumage and size. Systematics of *Charadrius* have been somewhat resolved by random amplified polymorphic DNA (Nol and Blanken, 2014). See description of *Charadrius vociferus* for summary on the relationships of Charadriidae. Specimens examined in present study: BCPM 12451, BCPM 17454, BCPM 23807, CVM 14485.

***Charadrius vociferus vociferus* Linneaus, 1758 (Killdeer)**—Early descriptions of *Charadrius vociferus* by Gordon (1892) describes the species as possessing two narrow black rings on chest, a chestnut-buff lower back and rump, and grey legs. Jackson et al. (2000) describe *C. vociferus* as the overall largest race (size) with brown upperparts (less grayish than other species of *Charadrius*), rufous edging on wing-coverts only, and moderately extensive in Basic plumage (color). Subspecies of *C. vociferus* are delineated by variations in plumage coloration. Members of the Charadriidae (lapwings, plovers, dotterels) form a polytomy with Haematopodidae in parsimony analyses of skeletal characters (Chu, 1995), while Sibley and Ahlquist (1990) show that Charadriidae is a monophyletic group in analyses of UPGMA (unweighted pair group method with arithmetic mean) groupings of DNA-DNA hybridization results. Specimens examined in present study: BCPM 9978, BCPM 10760, CVM 14428.

***Pluvialis squatarola* Linneaus, 1758 (Black-bellied Plover)**—There has been much debate over the diagnostic characters of the skull and presence of digit I in differentiating species of plover (Paulson, 1995, and references within.) Specimens examined in present study: BCPM 17157; fossil specimen LACM K1125 (tarsometatarsus).

Scolopacidae

***Actitis macularia* Linnaeus, 1766 (Spotted Sandpiper, was *Tringa macularia*)**—Sometimes merged with *Tringa*, both plumage and multi-locus DNA studies indicate there are no subspecies (Reed et al., 2013, and references within). Specimens examined in present study: BCPM 23257.

***Calidris alba* Pallas, 1764 (Sanderling)**—The phylogenetic relationships of sandpipers is in need of a thorough examination. Mitochondrial DNA studies place *C. alba* within group of other *Calidris* including *C. minutilla* (Borowik and McLennan, 1999). The lack of a digit I caused Sanderlings to be placed within the monospecific genus *Crocethia* (Macwhirter et al., 2002, and references within); however, Livezey (2010) has noted that the presence of digit I is variable within *Calidris*. Specimens examined in present study: RBCM 18305.

***Calidris pusilla* Linnaeus, 1766 (Semipalmated Sandpiper)**—*Calidris pusilla* has an ambiguous placement within *Calidris* has ambiguous placement. *C. pusilla* was once considered a sister species of *C. mauri* (Western Sandpiper) based on its extensive interdigital webbing. Placement of *C. pusilla* as a sister species to *C. temminickii* (Temminck's Stint) is supported by both lacking rhythmically repeated calls (Miller et al., 1988; Hicklin and Gratto-Trevor, 2010). Specimens examined in present study: BCPM 10147, BCPM 17434, BCPM 18306, RBCM 23797.

***Tringa flavipes* Gmelin, 1789 (Lesser Yellowlegs)**—Nichols (1923) examined skeletons of *T. flavipes* and *T. melanoleuca* and determined that differences in the skull, sternum, pelvis, and hindlimbs may be related to differences in size and/or habitat. Nichols (1923) also concludes that, despite their superficial (plumage) similarity, the skeletal differences were enough to consider these two species as not closely related. Chu's (1995) strict consensus cladistics analysis shows that *T. flavipes* forms a polotomy with several species of *Tringa*, but does not show detailed relationships within *Tringa*. Specimens examined in present study: BCPM 11606, BCPM 23825, RBCM 17295.

***Tringa melanoleuca* Gmelin, 1789 (Greater Yellowlegs)**—Chu's (1995) parsimony analysis on skeletal morphology of Charadriiformes shows that *T. erythropus* is a sister species to *T. melanoleuca*, but that the *T. erythropus-T. melanoleuca* group forms a polytomy with other species of *Tringa*. Sibley and Alquist (1990) analysis DNA-DNA hybridization analyses show that *T. flavipes* and *T. melanoleuca* are sister species. As noted by Elphick et al. (1998), the relationships within Charadriiformes and within *Tringa* are complicated. Specimens examined in present study: BCPM 9943, BCPM 15429.

***Tringa solitaria* Wilson, 1813 (Solitary Sandpiper)**—*Tringa solitaria* was originally defined based on its geography and plumage coloration. Strict consensus of parsimony analyses shows that the relationships of species within *Tringa* are ambiguous (Chu, 1995). Specimens examined in present study: BCPM 16984, BCPM 17450, BCPM 17777, BCPM 23178.

Laridae

***Larus californicus* Lawrence, 1854 (California Gull)**—There has been little comparative work on *L. californicus,* other than comparisons of plumage to other species (and hybrids within the genus) of *Larus* (Winkler, 1996). Laridae, in the present analyses (with the exception of Baker et al., 2007), is usually treated at the familial level only: genera and specific-level relationships within Laridae are not examined. Stauch's (1978) analysis of skeletal characters presented Laridae (gulls) as sister taxa to skuas (Stercorariinae). Mickevich and Parenti (1980) examination of Stauch's (1978) analysis shows gulls as the sister taxa to *Rynchops* (skimmers). This relationship was also recovered in Baker et al.'s (2007) Baysian analysis of molecular characters of Charadriiformes, along with the recovery of Laridae as a monophyletic group. DNA-DNA hybridization analyses by Sibley and Ahlquist (1990) show that

Laridae is most closely related to Sternidae, a groups whose nearest clade are the skimmers. Chu's (1995) reanalysis, like that of Stauch (1978), shows that Laridae are closest to Stercorariidae (skuas). Specimens examined in present study: BCPM 11285, BCPM 12011, BCPM 12053, BCPM 15442.

Ciconiiformes

Ciconiidae—Phylogenetic analyses on skeletal characters of herons and storks shows that extant *Ciconia alba* and *Mycteria ibis* form a monophyletic group with other storks; however, the within-clade relationships of the species are not resolved (McCracken and Sheldon, 1998). This same grouping was also recovered in earlier osteologic and molecular analyses (McCracken and Sheldon, 1998, and references within). These analyses utilized mostly characters of the skull, and included four characters of the humerus and one of the tarsometatarsus (McCracken and Sheldon, 1998).

***Ciconia maltha*† Miller 1910 (La Brea Stork)**—Feduccia (1967) notes that there is variation in both size and osteologic characters of the scapulae (not examined in the current study) of *Ciconia maltha*. Fossil specimens examined in present study: LACM F347, K3030 (femora); F943, F945, K3153 (tibiotarsi); F357, K1025, K2154, K3156 (tarsometatarsi).

***Mycteria wetmorei*† Howard 1935 (Wetmore's Stork)**—Fossil specimens examined in present study: LACM K3528 (proximal tarsometatarsus).

Falconiformes

Accipitridae

Accipiter

***Accipiter cooperii* Bonaparte, 1828 (Cooper's Hawk)**—Size and color differences within *Accipiter cooperii* are correlated with geographic distribution. Whaley and White (1994) also note longer pes digit lengths in eastern populations and darker coloration in western populations. Specimens examined in present study: BCPM 22403, BCPM 23367.

***Accipiter striatus* Vieillot, 1807 (Sharp-shinned Hawk)**—Subspecies within *Accipiter striatus* are distinguished largely by coloration and geographic differentiation (Bildstein et al., 2000, and references within). Specimen examined in present study: BCPM 12155.

***Amplibuteo* (= *Morphnus*) *woodwardi*† Miller, 1911**—The specimen in question was originally described by Miller (1911) as a species of *Morphnus*. Campbell (1979) reassigned the type material of *Morphnus woodwardi* to the genus *Amplibuteo*. Fossil specimens examined in present study: LACM C6644, D2351, D3167, D4486, D4828 (tarsometatarsi).

***Buteogallus* (= *Wetmoregyps*; = *Morphnus*) *daggetti*† Miller, 1915**—Miller (1915) originally described *Morphnus daggetti* based on features of the tarsometatarsus, such as extreme elongation of the (tarsometa)tarsal shaft, weak distal trochlea that are set less obliquely on shaft, and an extreme reduction of the ratio of power arm to resistance arm (Miller, 1915). With the discovery of subsequent specimens, the specimens were given the generic reassignment of *Wetmoregyps* based on its size being equal to or greater than *Aquila*, an elongate tarsus, and the papilla of the tibialis anticus is placed relatively more proximal on the shaft (Miller, 1928). The tarsometatarsus is also described as having a superficial resemblance to *Urubitinga urubitinga*, but with a less excavated anterior face and with trochleae nearly equal in size and relative position (Miller, 1928).

Olson (2007) describes *Buteogallus daggetti* as 40% larger than extant *Buteogallus meridonalis* (Savanna Hawk) but (other than the difference in size) identical. Olsen (2007) describes the apparent absence of the impressio ligamentum collateralis laterali in *B. meridionalis* (Olson, 2007). While labelled in the analyses herein as "*Wetmoregyps*", all such specimens refer to *Buteogallus daggetti*. Fossil specimens examined in present study: LACM K5401 (femur); J9744 (tibiotarsus); D161, K5403 (tarsometatarsi).

Buteo

***Buteo jamaicensis* Gmelin, 1788 (Red-tailed Hawk)**—Several subspecies are recognized on the basis of plumage and (although unconfirmed at this time) size of tarsals, metatarsals, and phalanges. Molecular phylogenies reveal a confusing relationship of *B. jamaicensis* with other species of *Buteo* (Preston and Beane, 2009, and references within.) Specimens examined in present study: RBCM 22363, 22530.

***Buteo platypterus* Vieillot, 1823 (Broad-winged Hawk)**—Subspecies of *Buteo platypterus* are distinguished based on wingspan (size), geographic location, and coloration. Phylogenetic analyses (color patterns, karyotype, etc.) are conflicting in the closest *Buteo* to *B. platypterus*, with *B. lineatus* (Red-shouldered Hawk) and *B. swainsoni* (Swainson's Hawk) each being posited as the closest taxon to *B. platypterus* (Goodrich et al., 2014, and references within). Specimen examined in present study: RBCM 19916.

***Buteo regalis* Gray, 1844 (Ferruginous Hawk)**—Original description based on color, with chromosomal analyses showing that *B. regalis* is similar to *B. nitidus*, *B. jamaicensis*, *B. albicaudatus*, *B. magnirostris*, and *Parabuteo unicinctus*, but is not similar to *Buteo* species *B. swainsoni*, *B. buteo*, and *B. platypterus* (Bechard and Schmutz, 1995, and references within.) Based on chromosomal analyses, *Buteo* may not be monophyletic. Specimen examined in present study: BCPM 22247.

Falconidae

Falco

***Falco mexicanus* Schlegel, 1850 (Prairie Falcon)**—The original description of *Falco mexicanus* (as with the original descriptions of the majority of predatory birds) focuses on plumage coloration and habitat. Hybrids of *F. mexicanus* and *F. pergrinus* have been documented (Steenhof, 2013), although no note was made as to whether these offspring were viable. Specimen examined in present study: BCPM 10788.

***Falco perigrinus* Tunstall, 1771 (Peregrine Falcon)**—Subspecies of *Falco peregrinus* are distinguished on color variations of plumage (While et al., 2002.) Gordon (1892) describes *F. perigrinus* as bluish grey above, with a black crown and moustache, breast plumage as buffish and barred with brown. Specimen examined in present study: BCPM 10089.

Galliformes

Phasianidae

***Bonasa umbellus* Linneaus, 1766 (Ruffed Grouse)**—Approximately 15 subspecies of *B. umbellus* are currently recognized based on variations of plumage color and retrices length. Natal plumage of *B. umbellus* reveals an indistinct loral spot, with a majority of adults possessing 18 retrices. (Short, 1967; Rusch et al., 2000). Specimens examined in present study: CVM 10141, CVM 14123.

***Callipepla* (=*Lophortyx*) *californica* Shaw, 1798 (California Quail)**—Plumage color and pattern, vocal, and skeletal data support *Callipepla californica* as being sister species to *C.*

gambelii (Holman, 1961; Calkins et al., 2014). Fossil specimens examined in present study: LACM L182, L183, L186, L187 (femora); F8433 (tibiotarsus); L244, L247, L253, L254, L256 (tarsometatarsi).

***Dendragapus obscurus* Elliot, 1864 (Blue Grouse)**—After several separations and mergers, recent mitochondrial DNA analyses have determined that the Dusky Grouse (*D. obscurus*) and the Sooty Grouse (*D. fuliginosus*) are two distinct species: this separation is also supported by morphologic (color, retrices length and shape) and behavioral differences (Zwickel et al., 2005). Short (1967) noted that *Dendragapus* sp. has either 18 or 20 retrices: Zwickel et al. (2005) report that *D. fuliginosus* has 18 retrices, but it is not noted whether *D. obscurus* possesses 20 retrices. Blue Grouse is more closely related to the Sage Grouse than to Spruce Grouse (Zwickel et al., 2005). Specimens of *D. obscurus* examined in present study: CVM 14573, RBCM 23579.

***Falcipennis* (= *Canachites*) *canadensis* Linneaus, 1758 (Spruce Grouse)**—Distinguished from other species of Phasianidae by 16 retrices. While classified for many decades as two species (*Canachites canadensis* and *C. franklinii*), *Falcipennis canadensis* is distinguished from genus *Dendragapus* by lack of inflatable cervical sacs and natal plumage of *F. canadensis* most closely resembles that of *Lagopus lagopus* and *L. muta*, and adult *F. canadensis* have fewer retrices than *Dendragapus* (Short, 1967; Boag and Schroeder, 1992). Specimens examined in present study: CVM 3149, CVM 3151.

***Lagopus lagopus* Linnaeus, 1758 (Willow Ptarmigan)**—Natal plumage of *L. lagopus* is most similar to that of *Falcipennis* (Short, 1967). Species of *Lagopus* are documented as having 16 retrices (Short, 1967). *L. lagopus* is highly polytypic, with six subspecies in North America. Mitochondrial DNA phylogeny shows that *Lagopus* is monophyletic, with *L. lagopus* closest to

L. muta and *L. leucura* (Lucchini et al., 2001). Willow Ptarmigan frequently hybridizes with Rock Ptarmigan (Short, 1967), although no mention was made of whether these offspring were viable. Specimens examined in present study: CVM 14462, RBCM 23579, RBCM 23588, RBCM 23589.

***Lagopus leucurus* Richardson, 1831 (White-tailed Ptarmigan)**—There are five subspecies of *L. leucurus*, although their status is questionable (Braun et al., 1993). There is also less tarsal feathering than in *L. lagopus* (Short, 1967). Specimen examined in present study: RBCM 23579 (juvenile).

***Lagopus muta* Montin, 1781 (Rock Ptarmigan, also appears as *Lagopus mutus*)**— *L. muta* is highly polytypic with eight subspecies in North America. Given the early divergence dates of species of *Lagopus* (0.8-1.6 Mya), frequent hybridization of species within *Lagopus* was not unexpected (Lucchini et al., 2001). Specimens examined in present study: CVM 13393, RBCM 10157.

***Parapavo californicus*† Miller, 1910 (California Turkey)**—Described originally as a North American representative of the Asian peacocks, *Parapavo californicus* was later interpreted to be an intermediate form between *Agricharis* (Ocellated Turkey) and the peacock. Examination by Sushkin (1928) concluded that *P. californicus* is firmly within th meleagrines, and it may not be distinct from *Agricharis* based on examination of the tarsometatarsus, coracoid, and carpometacarpus. Fossil specimens examined in present study: LACM E7966 (humerus); E5309, E6048 (femur); E5261 (tibiotarsus); E5075, E5333, E6793, E6801, E7224 (juvenile), K1081 (juvenile) (tarsometatarsi).

Gruiformes

Gruidae

***Grus americana* Linnaeus, 1758 (Whooping Crane)**—The largest of the North American cranes, *Grus* is considered paraphyletic, although *Grus* and other gruiforms are traditionally united based on morphology of the lower legs (Fain et al., 2007; Urbanek and Lewis, 2015). Feduccia (1967) notes that there is variation in the size and osteologic characters of the skeletal material of Recent *G. americana*, and that the Recent material has no distinguishing characters from that of the fossil material. Feduccia (1967) made no mention of the nature of the variation of the osteologic characters. Fossil specimens examined in present study: LACM B8597, E7430 (femora); B5750 (tibiotarsus); F569, F651, F652 (tarsometatarsi).

***Grus canadensis* Linneaus, 1758 (Sandhill Crane)**—Fossil specimens examined in present study: LACM F654, G4878, G4882, K3137, K3138, K3140 (tarsometatarsi).

***Grus pagei*† Campbell, 1995**—Campbell (1995) compared specimens of cranes from Rancho La Brea to 14 complete and two partial skeletons of Recent *Grus canadensis*. The diagnosis of *Grus pagei* is based on characters of the cranium. *G. pagei* is described to be smaller than *G. canadensis* (and, by extension, *G. americana*, which is larger than *G. canadensis*), and skeletally different in the pelvic limbs in the femur (facies caudalis more flattened; condylus lateralis shorter anteroposteriorly, oriented at greater angle to the femur shaft), tibiotarsus (more lateral position of crista cnemalis, shorter; smaller facies articularis medialis; flattened directly distal to facies articularis medialis; narrow condylus medialis; both condyli medialis et lateralis shorter anteroposteriorly; trochlea cartilaginis tibialis sloping internad from condylus lateralis in distal view, deeper than condylus medialis), and tarsometatarsus (more rounded ementia intercondylaris; cotlya medialis deep and narrow, constricted; area intercondylaris deeper with stronger margins, compressed hypotarsus anteroposteriorly; distal metatarsal III trochlea more compressed anteroposteriorly with slight anterior rotation). Fossil specimens examined in present study: LACM F4636 (femur); F577, F1017, K3133 (tibiotarsi); F452, G4874 (tarsometatarsi).

Character Discussion: Pre-Analysis

Strauch (1978) and reanalyses–Strauch (1978) conducted a character compatibility analysis on 70 skeletal characters of 227 species of Charadriiformes. Three phyletic lines were recovered, which Strauch (1978) treated as suborders. The Scolopaci of Strauch (1978) contains the Jacanidae, Phalaropodidae, Rostratulidae, Scolopacidae, and Thinocoridae. Charadrii contain Lari and five other lineages (Burhinidae-*Pluvianus, Chionis-Pluvianellus* lineage, *Droma* lineage, Glareolidae lineage, and a lineage containing avocets, ibisbill, lapwings, oystercatchers, plovers, and stilts, respectively). Strauch (1978) selected an incomplete array of morphologic characters in their analysis. As is typical of such analyses, the majority of the osteologic characters were selected from the axial skeleton (cranium, vertebral column, sternum) and the pectoral and pelvic girdles (appendicular limbs, ilium, ischium, pubis). Characters 61–70 in Strauch (1978) are from the distal tarsometatarsus (61–63) and the hypotarsus, specifically the characters of the sulci tendinale and the hypotarsal canals of the hypotarsal ridges (64–70). There was no explanation given for the inclusion of only characters of the tarsometatarsus for the pelvic limbs. The character compatibility analysis of Strauch (1978) contained many of the features that were critiqued in later parsimony analyses: character states were ordered, and many characters were seemingly removed or ignored based on a mathematical algorithm (Mickevich and Parenti, 1980; Chu, 1995).

Chu (1995) reanalyzes Strauch's (1978) skeletal character phylogenetic analysis of Charadriiformes using a parsimony analysis. Chu (1995) chose not to follow the recommendations of Mickevich and Parenti (1980) as Chu (1995) found them to be flawed because they rejected too many characters that were found to be organizationally useful. Chu (1995) also conducted the analyses with a hypothetical ancestor, and with all of the character states unordered. Sandpipers were found not to be monophyletic, but were found in lineages similar (but not identical) to the systematics suggested by Lowe (1930). Both Strauch (1978) and Chu (1995) found lineages that clustered non-auk shorebirds into two groups: plover-like shorebirds and sandpiper-like shorebirds. Both Strauch (1978) and Chu (1995) found that containing avocets, ibisbill, lapwings, oystercatchers, true plovers, and stilts form a natural group; however, relationships within this group are unresolved and contain little consensus.

Phylogenetic works of Livezey and Zusi (2006) and Livezey (2010)—Characters of the distal tarsometatarsus were analyzed in detail by Livezey and Zusi (2006) and Livezey (2010). Characters 0436–0437 (Livezey, 2010) and character states for several characters in Livezey and Zusi (2006; see comments for character 121 below) address the relative lengths, positions, and orientations of the trochlear surfaces of metatarsals II and IV relative to that of metatarsal III. While these analyses did not extend to taxa outside of Aves, the character states describing the relative positions of the trochlear surfaces of metatarsals II and IV may be informative in discerning the tarsometatarsi of avian theropods from non-avian theropods. This may prove to be useful in discerning the traces of large avians from those of small non-avian theropods (Chapters 4, 6).

Cladistic Analysis

Parsimony analyses were performed in Mesquite version 3.03 (build 702). Characters are multistate and were analyzed as unordered. A hypothetical ancestor was included in the analysis as the outgroup. A second analysis was performed using *Rhea* as the outgroup (data from Livezey and Zusi, 2006), although the results were identical to those obtained using a hypothetical anacestor, and so were not included. The analysis was performed using a heuristic search (1000 saved trees, subtree pruning and regrafting). Both strict and majority rule (0.5 frequency, or only nodes supported by 50% of the saved trees retained) consensus trees were run on the 1000 shortest trees saved from the heuristic search. A separate analysis was conducted on the tarsometatarsi data only, after examination of the results of the more complete analysis revealed strong support for avian families from tarsometataral character states. Juvenile specimens of taxa were retained in the initial analysis. Where noted, male and female specimens that showed skeletal sexual dimorphism (i.e., *Parapavo carlifornicus*, where the bony spur is present on the tarsometatarsus of adult male specimens and is absent on adult female specimens) and the individual specimens were treated as terminal taxa (as in the specimen-level phylogeny of Tschopp et al., 2015) to test if ontogeny and/or sexual dimorphism had an effect on tree topology.

To determine the systematic utility of non-axial skeletal elements, analyses were restricted to the characters of the appendicular skeleton (humerus, femur, tibiotarsus, tarsometatarsus). The skeletal characters for the ingroup were selected and coded independent of previous analyses on shorebird (Stauch, 1978; Chu, 1995; Livezey, 2010) or avian (Livezey and Zusi, 2006) morphological characters. This was done for three reasons: to teach myself how to score characters for a cladistic analysis; to base the characters on observations from skeletons alone, and, after scoring these characters, to determine if there was consensus with the characters chosen in the present study and those selected by other studies (Livezey and Zusi, 2006; Livezey, 2010); and to test if skeletal characters of the hindlimb (femur, tibiotarsus) of a (relatively) limited number of taxa that have specialized use of their limbs (birds of prey, gamebirds, shore- and wading birds) would reproduce topologies seen in other morphologic phylogenetic analyses and those topologies of molecular analyses. In other words, does convergent morphology due to similarities in behavior and habitat affect cladistic analyses of avians?

CHARACTERS

Humerus

The character states of the humerus are not figured herein, as the focus of this section of the thesis is to analyze the possible masking effects of convergence in hindlimb elements in a phylogenetic analysis. However, the humerus was included in these analyses to observe any possible correlation between synapomorphic and autapomorphic character states of the humerus and those of the femur, tibiotarsus, and tarsometatarsus: such correlations provide the potential to examine character states related to behavioral strategies or habitat (hunting strategies, forest versus shoreline habitats, etc.)

001. Caput humeri: (0) not visible/indistinct; (1) slight swelling; (2) well-developed and rounded, oval; (3) well-developed and rounded, condylar; (4) large, encompasses almost entire proximal humerus; (5) well developed and oval, one side flattened.

Comment—Similar to characters 1349, 1351–1352 of Livezey and Zusi (2006). This study includes more differentiation among the variable presentation of the size of the caput humeri with respect to the dorsoventral width of the most proximal end of the humerus. In the taxa surveyed, invariably, Charadriiformes possess a caput humeri that is either rounded or oval, but encompasses less than half of the proximodistal width of the humerus, Falconiformes possess a caput humeri that is anteriorly flattened, and Galliformes possess a large caput humeri that nearly encompasses the entire proximal width of the humerus.

002. Sulcus ligamentosus transversus: (0) indistinct, absent; (1) weakly developed depression; (2) strongly developed, visible dorsoventral boundaries; (3) broad, cuts across entire proximal humerus; (4) boundaries posteriorly canal-forming; (5) strong yet restricted to half of the proximal width of proximal humerus.

Comment—Similar to characters 1431–1433 of Livezey and Zusi (2006).

003. Sulcus n. coracobrachialis: (0) indistinct/absent; (1) weak; (2) strong with well-developed borders; (3) wide with thinly developed borders.

Comment—Livezey and Zusi (2006) code this character as 1428, with character states represented as absent, present and represented by a sulcus et/aut canalis, or noncomparable. The present study also codes this character to address the proximodistal width of the demarcation for the sulcus n. coracobrachialis.

004. Tuberculum dorsale: (0) indistinct/absent; (1) weak mound; (2) strong mound, non-protruding; (3) strong and protruding mound or process; (4) ridge; (5) multiple projections; (6) protruding mound, yet flattened.

Comment—The tuberculum dorsale is described in character 1348 as part of a suite of morphologies that are coded en masse as absent or present by Livezey and Zusi (2006). It is also coded in character 1354 by the same authors as diminished, pronounced, or noncomparable. Character 1370 of Livezey and Zusi (2006) specifically codes the morphology of the tuberculum dorsale. The tuberculum dorsale is also mentioned in character state 1440(e) for the angulus caudalis corporis (a term erected by Livezey and Zusi, 2006). The tuberculum dorsale is coded in the present study to describe the variation in morphology, from diminished to a strong yet flattened mound, observed in the study taxa.

005. Impressio coracobrachialis: (0) absent, indistinct; (1) weak impression; (2) strong impression; (3) strong impression with a small defining ridge; (4) with border ridge and small tuberculum.

Comment—Similar to character 1361 of Livezey and Zusi (2006), but referred to as insertii m. coracobrachialis. In the present study, the tuberculum was observed in the Falconidae to accompany a small crista, unlike the character state 1361c (present, tuberculum, in absence of crista, Livezey and Zusi, 2006), and a strong crista without a tuberculum (character state 1361b, Livezey and Zusi, 2006).

006. Impressio coracobrachialis: (0) absent, indistinct; (1) short and wide; (2) long and thin; (3) long and wide.

Comment—There is no similar character coded by Livezey and Zusi (2006), but it is coded as part of the character states for character 1433 of Livezey and Zusi (2006; see comment below).

007. Impressio coracobrachialis: (0) absent, indistinct; (1) separate from sulcus ligamentosus transversus; (2) crista separating impression coracobrachialis from sulcus ligamentosus transversus; (3) continuous with sulcus ligamentosus transversus.

Comment—Similar to character 1433 of Livezey and Zusi (2006).

008. Facies bicipitalis: (0) not developed; (1) weakly developed crest; (2) well-developed crest.

Comment—There is not a similar character in Livezey and Zusi (2006) to 008 of this study; however, character state 1431b (Livezey and Zusi, 2006) describes the extent of sulcus ligamentosus transversus with respect to facies bicipitalis.

009. Intumescentia humeri: (0) continuous/indistinct from surface of proximal humerus; (1) distinct surface, smooth; (2) distinct surface, rugose.

Comment—Character 1429 of Livezey and Zusi (2006) codes the intumescentia humeri in terms of its convexity and concavity. Degrees of concavity would result in differing amounts of rugosity of the intumescentia humeri.

010. Crista bicipitalis: (0) not developed; (1) weakly developed, weak projection from the intumescentia humeri; (2) strongly developed, rounded distinct projection from the intumescentia humeri; (3) strongly developed, triangular process, weak posterior extension; (4) strongly developed, triangular, strong posterior extention.

Comment—Similar to character 1412 of Livezey and Zusi (2006).

011. Crista bicipitalis: (0) continuous (even if projecting) with intumescentia humeri; (1) distinct from intumescentia humeri.

Comment—Similar to characters 1403, 1413 of Livezey and Zusi (2006).

012. Tuberculum ventrale: (0) indistinct/absent; (1) small, weak protuberance; (2) strong protuberance, separate; (3) connected to crista bicipitis, strongly elongate; (4) connected to crista bicipitalis, short yet massive mound.

Comment—Several characters in Livezey and Zusi (2006) address the tuberculum ventrale, either specifically or as it is related to other structures (1357, 1359–1360, 1362, 1364–1369, 1388–1389). Character 1366 addresses its position relative to the fossa pneumotricipitalis (as do characters 1389 and 1416), and character 1367 addresses its orientation (ventral, proximal, posterior).

013. Fossa pneumotricipitalis: (0) not developed; (1) weakly excavated; (2) weak/small anteriorly, strong/large posteriorly, separated by diagonal crista; (3) weak/small anteriorly, strong/large posteriorly, separated by vertical crista; (4) strong, weak/no separating crista; (5) strong, distinct crista, equally strongly excavated; (6) singular, anterior fossa minute/weak.

Comment—Livezey and Zusi (2006) describe the fossa pneumotricipitalis as highly variable. Livezey and Zusi (2006) establish two terms to describe the variation they observed: the fossa pneumotricipitalis cingulus, and the fossa pneumotricipitalis totalis.

The fossa pnuemotricipitalis cingulus, fossa pneumotricipitalis totalis, and subfossa ventrale et dorsale pneumatica are all recognized in the study taxa, but are here presented as they relate to the crus dorsale et ventrale. Similar to character 1421 of Livezey and Zusi (2006).

014. Fossa pneumotricipitalis: (0) continuous; (1) slight crista separated by crus dorsalis; (2) strong crista; (3) fully enclosed by crista.

Comment—Similar to character 1422 of Livezey and Zusi (2006).

015. Crus dorsale: (0) absent; (1) weak ridge and excavation; (2) strongly developed ridge.

Comment—Similar to character 1423 of Livezey and Zusi (2006).

016. Crus ventrale: (0) absent; (1) weak excavation; (2) strong excavation; (3) strong excavation, crista overlapping fossa.

Comment—Similar to characters 1404 of Livezey and Zusi (2006).

017. Tuberculum dorsale: (0) absent; (1) small protuberance, weak; (2) long low ridge; (3) strongly protruding; (4) small and strong.

018. Tuberculum dorasale: (0) continuous with deltopectoral crest; (1) long rounded ridge; (2) sharp distinct ridge; (3) restricted process/protuberance.

Comment—Characters 1371 and 1390 of Livezey and Zusi (2006) describe the degree of separation between the caput humeri and the tuberculum dorsale, and the relative position of the tuberculum dorsale with respect to the crista deltopectoralis.

019. Crista deltopectoralis: (0) absent; (1) weak ridge, slightly elevated from anterior surface of the shaft; (2) deltopectoral crest a long rectangular ridge; (3) deltopectoral crest a short rectangular ridge; (4) deltopectoral crest a long triangular ridge; (5) short triangular ridge.

Comment—Livezey and Zusi (2006) describe the crista deltopectoralis as comprising several different components of form. Livezey and Zusi (2006) code characters 1375–1403 and erect three new terms to describe the morphology of this structure. While it is possible to code for these characters in this analysis, only the general shape of the crista deltopectoralis and the associated structures were coded to avoid possible overweighting of the structure in the cladistic analyses.

020. Crista deltopectoralis, ala subtubercularis: (0) crista smooth; (1) crista point(s) with accessory protuberance, small, rounded; (2) protuberance large and squared, extends anteriorly; (3) crista with a rugose face; (4) protuberance posteriorly projecting; (5) crista with large triangular protuberance.

Comment—Livezey and Zusi (2006) establish a new term (ala subtubercularis) for character 1390 to differentiate between the tuberculum dorsale and the protuberance described in that character.

021. Facies cranialis: (0) no distinct features; (1) shallow, flattened face; (2) face with strong grooves or depressions.

Comment—Similar to characters 1405, 1429 of Livezey and Zusi (2006), which address the shape of facies cranialis.

022. Facies caudalis: (0) no distinct features; (1) shallow/flattened; (2) deeply excavated.

Comment—The morphology of the facies cranialis and the facies caudalis is addressed in character 1436 of Livezey and Zusi (2006), a multistate character with 11 character states. This character has been subdivided into two characters for the present study: one addressing concavities of the facies (Character 022), and a separate character describing the sigmoidal shape or bowing of the humeral shaft (Character 038).

023. Deltopectoral crest: (0) does not extend past humeral shaft; (1) extends past humeral shaft.

Comment—See comments on the treatment of the deltopectoral crest by Livezey and Zusi (2006).

024. Fossa m. brachialis: (0) weak/not developed; (1) small, shallow; (2) small, deep; (3) large, shallow, indistinct borders, extends up shaft; (4) large and deep, distinct borders; (5) large and shallow, sharp borders; (6) continuous with facies cranialis sulcus;

Comment—Similar to character 1456 of Livezey and Zusi (2006).

025. Processus supracondylaris dorsalis: (0) indistinct; (1) slight elevation or ridge; (2) ridge with distinct small protuberance; (3) ridge with large protuberance; (4) small proximally upturned flange; (5) large proximally upturned flange.

Comment—Similar to character 1467 of Livezey and Zusi (2006).

026. Epicondylus dorsalis: (0) indistinct/weak; (1) small and weak, slightly raised; (2) small but distinct protuberance; (3) large protuberance/process.

Comment—Livezey and Zusi (2006) address whether the processus supracondylaris dorsalis and the epicondylus dorsalis are connected in characters 1468 and 1469. This analysis addresses these two structures separately and does not code their connection, as no strong connection was observed in the study taxa.

027. Condylus dorsalis: (0) same size as condylus ventralis; (1) slightly larger than condylus ventralis; (2) much larger than condylus ventralis; (3) larger and proximally pointed

028. Condylus dorsalis: (0) diagonally (proximoposterior-distoanterior) oriented; (1) proximodistally oriented; (2) horizontally oriented.

029. Condylus ventralis: (0) rounded; (1) horizontally oriented, elongate; (2) proximodistally oriented, elongate.

030. Incisura intercondylaris: (0) flat, continuous with condyles; (1) weakly developed notch; (2) strongly developed groove.

Comment—Similar to character 1454 of Livezey and Zusi (2006).

031. Fossa olecrani: (0) wide, flat, shallow, continuous w sulcus humerotricipitalis; (1) depression, shallow, distinct from sulcus humerotricipitalis; (2) strongly developed with shallow sulcus humerotricipitalis, (3) strongly developed, deep, secondary sulcus.

Comment—Similar to character 1482 of Livezey and Zusi (2006). The character states recognize that, depending on the strength of the fossa olecrani, it can appear that there is no demarcation separating the sulcus humerotricipitalis and the fossa olecrani.

032. Epicondylus ventralis: (0) indistinct/absent; (1) small and weak, slightly raised; (2) small yet distinct; (3) large protuberance, rounded; (4) large protuberance, elongate; (5) secondary condyle.

Comment—Similar to character 1472 of Livezey and Zusi (2006).

033. Tuberculum supracondylare ventrale: (0) indistinct/absent; (1) slight swelling, anteriorly positioned; (2) slight swelling, more ventral on ventral condyle; (2) small, distinctly developed; (3) large swelling/mound; (4) large flange-like protuberance; (5) rugose surface; (6) slight protuberance, pit; (7) large protuberance, pit.

Comment—Similar to character 1481 of Livezey and Zusi (2006), but coded here to include the presence of a small pit directly present on the tuberculum in the analyses.

034. Process flexorius: (0) absent/indistinct; (1) small; (2) large; (3) large and elongate.

Comment—Similar to character 1479 of Livezey and Zusi (2006).

035. Humerus: (0) long, slender; (1) short, stocky.

Comment—Similar to character 1346 of Livezey and Zusi (2006).

036. Sulcus scapulotricipitalis: (0) indistinct; (1) defined by small processes; (2) defined by small, well-developed condyles.

Comment—Livezey and Zusi (2006) do not directly address the sulcus scapulotricipitalis.

037. Incisura capitis: (0) weak, indistinct; (1) shallow groove; (2) strong groove.

Comment—(Characters refer to Livezey and Zusi, 2006.) The presence of the incisura capitis is included in character 1348 describing several features of the humerus, and its presence, strength, and shape are detailed in characters 1355, 1356, and 1357, respectively.

038. Humerus: (0) straight; (1) bowed.

Femur

039. Caput femoris: (0) continuous with facies articularis antitrochanterica-iliac facet; (1) distinct facies articularis acetabularis; (2) facies articularis acetabularis separated from shaft by a constriction only; (3) constriction extends to facies articularis antitrocharterica, forming a full neck (Figure 3.01).

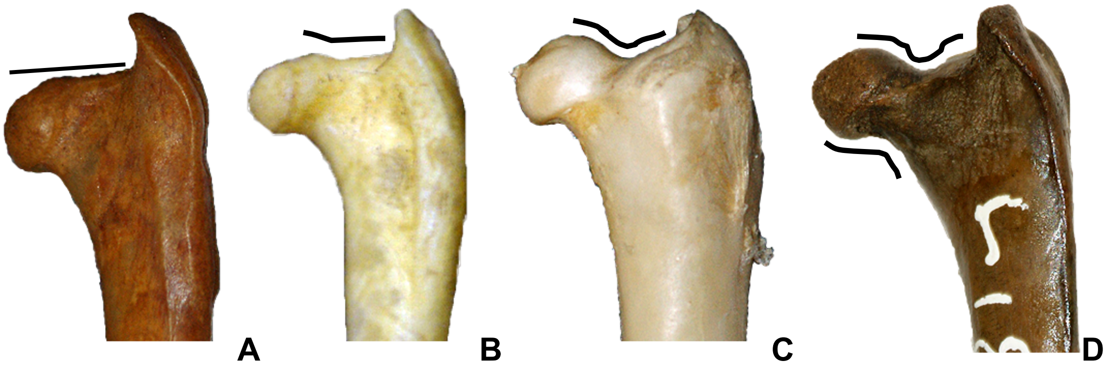

Figure 3.01: Character 039, caput femoris of the proximal femur. **A**, character state 1 (BCPM 10151 *Larus californicus*, anterior view); **B**, character state 2 (BCPM 15491 *Charadrius vociferus*, anterior view); **C**, character state 3 (BCPM 10141, *Bonasa umbellus*, posterior view); **D**, character state 4 (LACM L182 *Callipepla californicus*, anterior view). Specimens scaled to approximately the same proximal mediolateral length. These character states code the gradation from a caput femoris that is indistinctly delineated from the femoral shaft, to a caput femoris that is fully separated from the femoral shaft as a well-developed condyle.

Comment—Similar to character 1965 of Livezey and Zusi (2006), where the character states describe the shape as bulky, transversely elongate, or subspheroidal. Character 1966 (Livezey and Zusi, 2006) describes the mediolateral width of the (facies of the) caput femoris with respect to the rest of the extremitas proximalis femoris.

040. Facies articularis acetabularis: (0) in line or continuous with facies articularis antitrochanterica; (1) slightly elevated proximal to the facies articularis antitrochanterica; (2) strongly elevated and elongate (Figure 3.02).

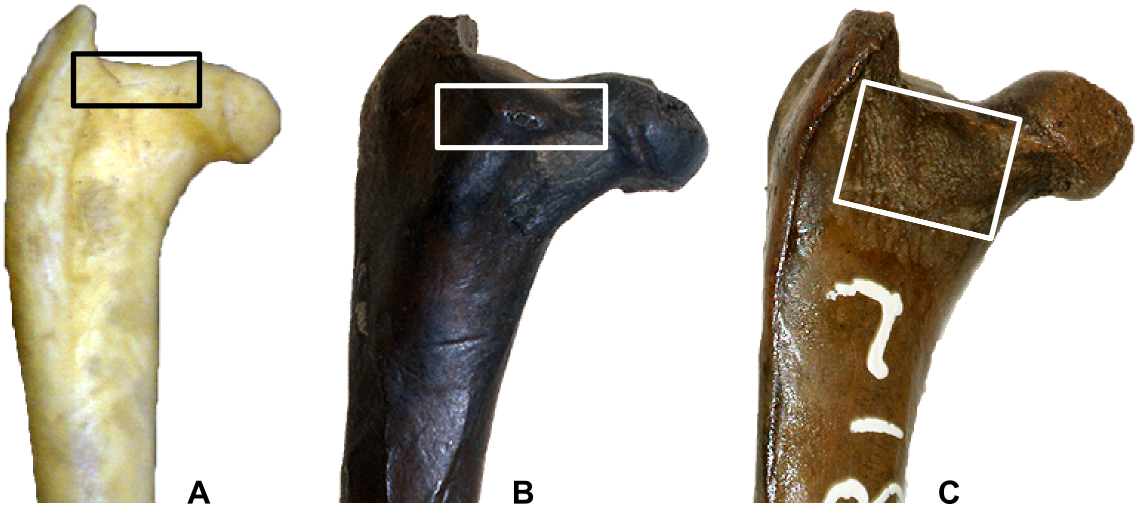

Figure 3.02. Character 040, facies articularis acetabulis of the proximal femur. **A**, character state 0 (BCPM 15491 *Charadrius vociferus*, anterior view); **B**, character state 1 (LACM E5309 *Parapavo californicus*, posterior view); **C**, character state 2 (LACM L182 *Callipepla californicus,* anterior view). Elements scaled to approximately the same proximal mediolateral length.

Comment—Similar to character 1968 of Livezey and Zusi (2006), whereas the characters in the present study are coded as relative positions rather than expressed as angles with respect to the proximodistal axis of the femur.

041. Fovea ligamentosus capitus: (0) absent or indistint; (1) shallow concavity; (2) deep concavity (Figure 3.03).

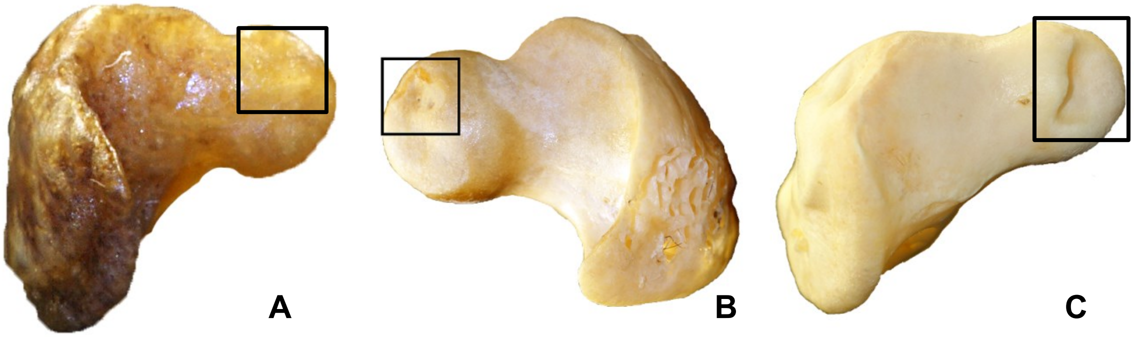

Figure 3.03. Character 041, fovea capitus of the proximal femur. **A**, character state 0 (RBCM 18305 *Calidris alba*); **B**, character state 1 (CVM 14573 *Dendragapus obscurus*); **C**, character state 2 (BCPM 02247 *Buteo regalis*). Proximal views. All elements scaled to approximately the same mediolateral length.

Comment—Similar to character 1971 (Livezey and Zusi 2006), but the present study includes character states that describe the variation observed in the depth of the fovea ligamentosus capitus.

042. Facies articularis antitrochanterica: (0) indistinct, continuous with femoral shaft; (1) articular surface present; (2) prominent flange or overhang on to the posterior surface (Figure 3.04).

Figure 3.04. Character 042, facies articularis antitrochanteris **A**, character state 1 (LACM K3030 *Ciconia maltha*); **B**, character state 2 (LACM E9151 *Ardea herodias*). Anterior views. This character codes the relative amount of anterior projection of the facies articularis antitrochanteris, which contributes to the relative amount of articular surface of the foramen acetabulum. All elements scaled to equal mediolateral length proximally.

Comment—This character is similar to character 1975 of Livezey and Zusi (2006).

043. Impressiones iliotrochantericae strength: (0) absent; (1) faint impressions; (2) small mounds; (3) strong ridges; (4) strong mounds; (5) flattened surfaces (Figure 3.05).

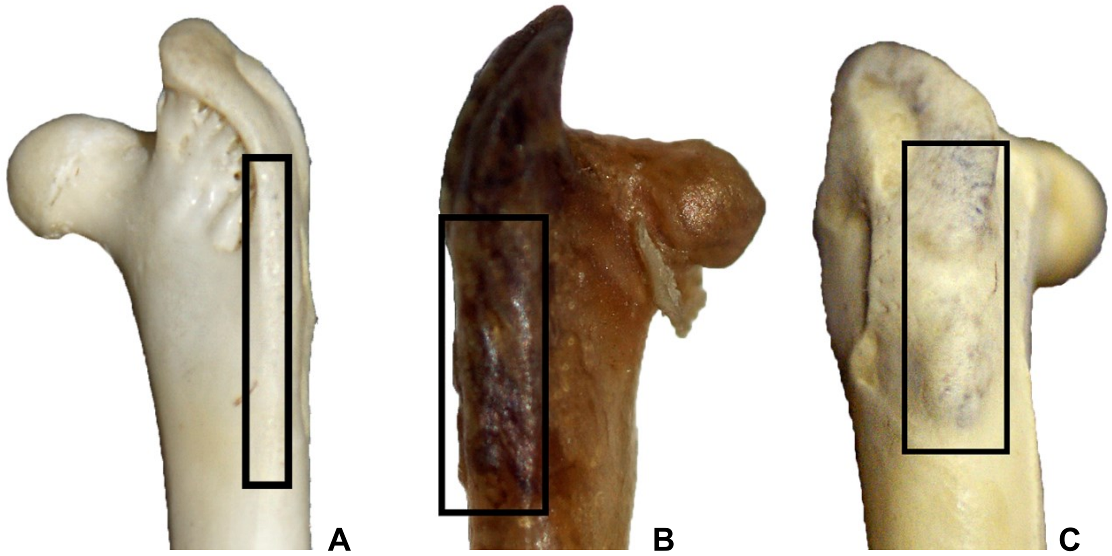

Figure 3.05. Character 043, impressiones iliotrochanteris **A**, character state 1 (RBCM 10157 *Lagopus muta*, anterior view); **B**, character state 3 (RBCM 18305 *Calidris alba*, anterior view); **C**, character state 4 (BCPM 10089 *Falco perigrinus*, anterolateral view). These character states are coded to capture the degree of rugosity of the impressiones iliotrochanteris, which were observed to vary from a flattened surface, to multiple rugosities, to rugosities concentrated in mound-like processes. Elements scales to approximately the same mediolateral proximal length.

Comment—Characters 043 and 044 are, in part, addressed by character 1979 of Livezey and Zusi (2006); however, the character states for character 1979 are absent or present. The present study includes character states that code not only the shape of the impressiones iliotrochantericae, but the number of impressions/mounds/ridges expressed.

044. Impressiones obturatoriae: (0) absent; (1) faint impression; (2) distinct ridges; (3) distinct projections or mounds (Figure 3.06).

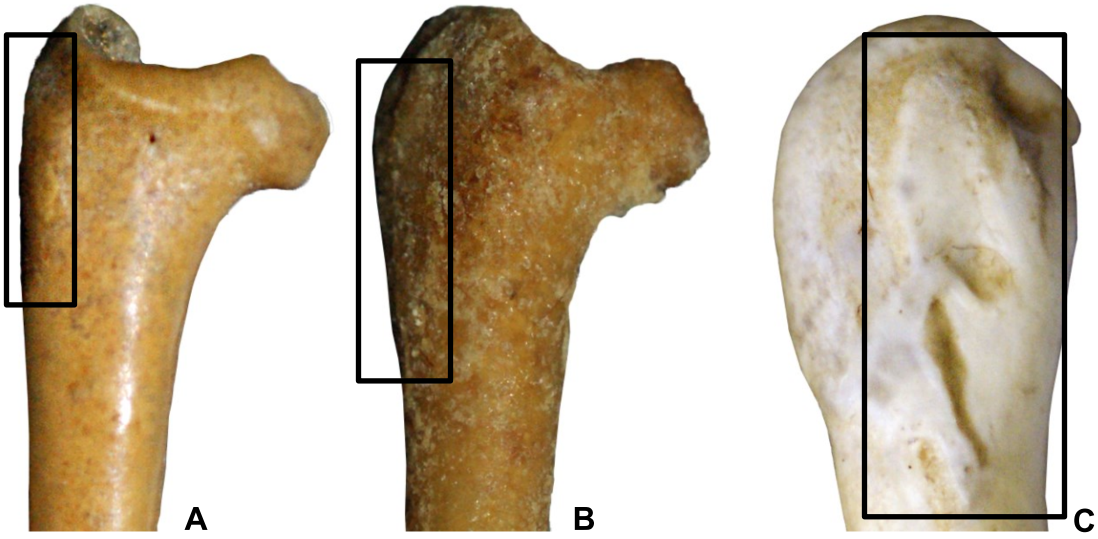

Figure 3.06. Character 044, iliotrochanteris obturatoraie **A**, character state 1 (RBCM no number *Limnodromus griseus*, anterior view); **B**, characters state 2 (BCPM 17777 *Tringa solitaria*, anterior view); **C**, character state 3 (RBCM 22363 *Buteo jamaicensis*, lateral view). The character states code the variation observed in the strength and rugosity of the iliotrochanteris obturatoraie. **A**, **B**, scaled to the same mediolateral length; **C**, enlarged to show the rugosity of the structure.

Comment—Character 1994 of Livezey and Zusi (2006) combine the recesses of the crista femoris and the impressiones obturatoriae in to an absence/presence character. Observations of study taxa show that there is a distinction between the impressiones obturatoriae, the distal expression of the crista trochanteris on the corpus femoris, and the recusses pneumaticum. Livezey and Zusi (2006) note, however, that there are several impressiones insertii (for mm. iliotrochantericus caudalis, iliotrochantericus cranialis, ischiofemoralis et iliofemoralis externus, impressiones ligamentosae, and obturatorius medialis) that can complicate the morphology.

045. Trochanter femoris: (0) absent, continuous with articular surface; (1) slight protuberance; (2) distinct protuberance; (3) distinct flange-like process; (4) tall flange; (5) asymmetrical flange only (Figure 3.07).

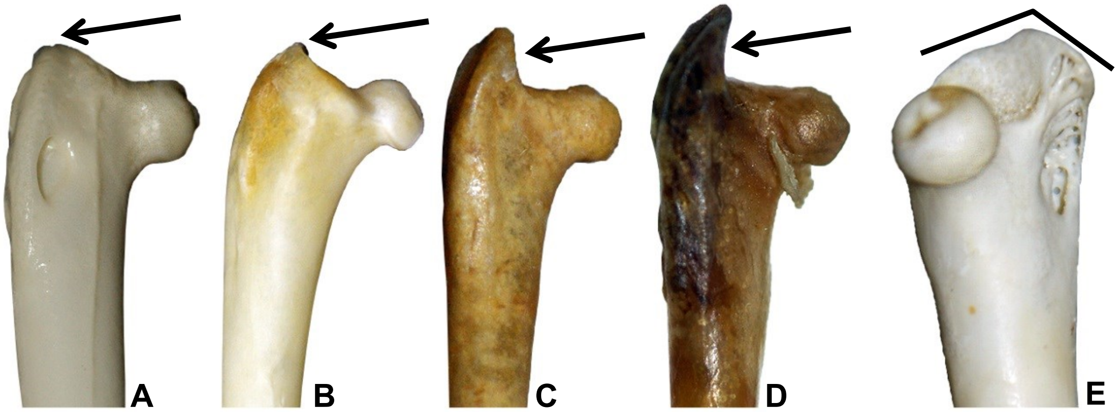

Figure 3.07. Character 045, trochanter femoris **A**, character state 0 (BCPM 12155 *Accipiter striatus*); **B**, character state 1 (BCPM 16186 *Bonasa umbellus*); **C**, character state 2 (BCPM 10175 *Calidris minutilla*); **D**, character state 3 (BCPM 10151 *Larus californicus*); **E**, character state 4 (RBCM 10157 *Lagopus muta*). All specimens scaled to the same size. **A**–**D**, anterior view; **E**, medial view. The trochanter femoris is the insertion point for several muscles, including the m. iliotrochantericus cranialis, m. iliotrochantericus caudalis, and m. iliotrochantericus medius, m. iliofemoralis externus and internus (Vanden Berge and Zweers, 1993).

Comment—Similar to character 1995 in Livesey and Zusi (2006).

046. Fossa trochanteris: (0) absent; (1) one shallow depression; (2) two shallow depressions (Figure 3.08).

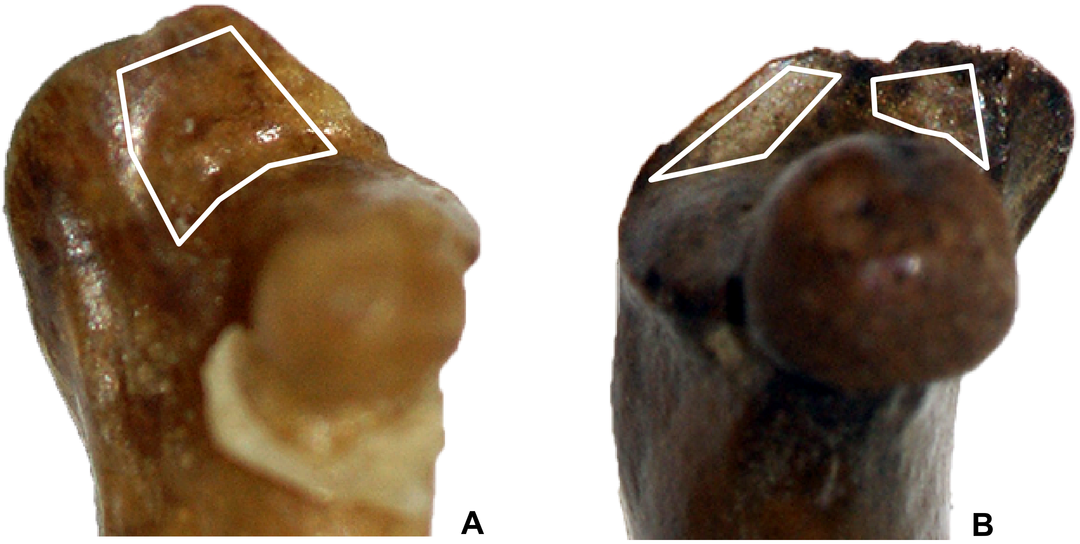

Figure 3.08. Character 046, fossa trochanteris **A**, character state 1 (RBCM 18305 *Calidris alba*, medial); **B**, character state 2 (LACM L182 *Callipepla californicus*, medial). Medial views. While subtle, specimens coded '2' for character 046 have a weak ridge bisecting the fossa trochanteris. This is different than the apparent second depression formed by the ridge of the crista trochanteris extending anteriorly and distally on the femoral shaft. Specimens scaled to approximately the same anteroposterior length.

Comment—This character is similar to character 1997 of Livezey and Zusi (2006).

047. Crista trochanteris: (0) absent; (1) slightly protruding from femoral shaft; (2) distinct yet flattened; (3) distinct with strong ridges; (4) recusses pneumaticum with flattened ridge; (5) deep recusses pneumaticum, strong ridge (Figure 3.09)

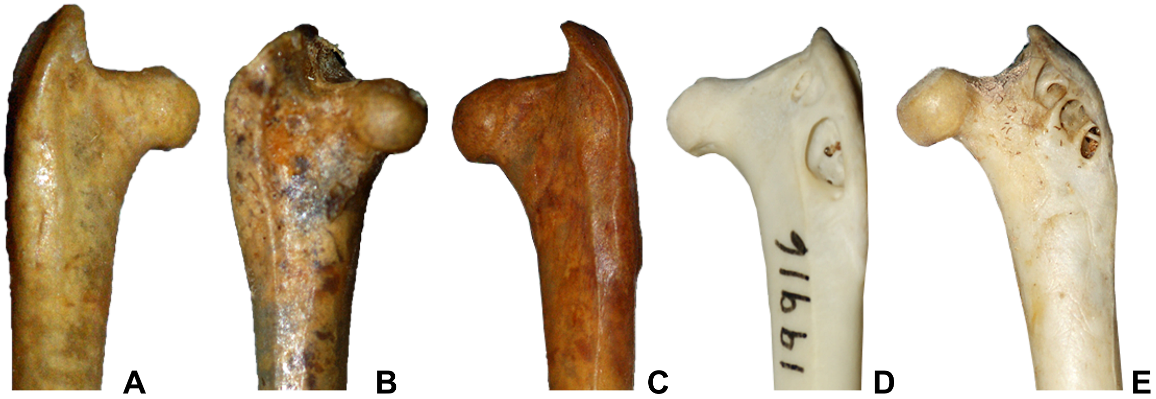

Figure 3.09. Character 047, crista trochanteris. **A**, character state 1 (BCPM 10175 *Calidris minutilla*); **B**, character state 2 (RBCM 23815 *Tringa flavipes*); **C**, character state 3 (BCPM 10151 *Larus californicus*); **D**, character state 4 (CVM 19916 *Buteo platypterus*), **E**, character state 5 (CVM 3149 *Falcipennis canadensis*). Anterior views. The crista trochanteris varies greatly in shape and its association with recusses pneumaticum. A-C show cristae conditions that do not exhibit recusses, while D-E are examples of recusses. In the study taxa, recusses pneumatica are associated with either a flattened or a sharp crista trochanteris, and are restricted to Falconiformes and Galliformes. All specimens scaled to approximately the same mediolateral length at the proximal end.

Comment—While part of this character (recusses pneumaticum) was coded in character 1994, character 047 of the present study addresses the morphology of the crista trochanteris with respect to its shape (flattened versus sharp crista) and association with recusses pneumaticum.

048. Facies cranialis: (0) not distinct, rounded; (1) slightly flattened; (2) strongly flattened; (3) distinct ridges (Figure 3.10).

Figure 3.10. Character 048, facies cranialis. **A**, character state 0 (CVM 14476 *Larus delawarensis*); **B**, character state 1 (CVM 14428 *Charadrius vociferus*). Anterior views. Specimens scaled to same proximodistal length. A rounded facies cranialis appears to be associated with a strong yet discontinuous linea intermuscularis cranialis. The flattened facies cranialis is associated with a well-developed m. femorotibialis.

Comment—Similar to character 2003 of Livezey and Zusi (2006).

049. Linea intermuscularis cranialis: (0) absent; (1) strongly developed; (2) weakly developed (Figure 3.11).

Figure 3.11. Character 049 linea intermuscularis cranialis of the femur. **A**, character state 0 (BCPM 10175 *Calidris minutilla*); **B**, character state 1 (BCPM 10151 *Larus californicus*). Anterior views. Specimens scaled to approximately the same proximodistal length.

Comment—Similar to character 2006 of Livezey and Zusi (2006).

050. Linea intermedialis cranialis: (0) weak or absent; (1) straight with femoral shaft; (1) curved medially (Figure 3.12).

Figure 3.12. Character 050, linea intermuscularis cranialis shape. **A**, character state 0 (BCPM 10175 *Calidris minutilla*); **B**, character state 1 (BCPM 22403 *Accipiter cooperii*); **C**, character state 2 (RBCM 10157 *Lagopus muta*). Anterior views. Specimens scaled to approximately the same proximodistal length.

Comment—Similar to character 2007 of Livezey and Zusi (2006).

051. Sulcus patellaris: (0) absent or indistinct; (1) shallow development; (2) strongly developed, deep.

Comment—Similar to character 2038 of Livezey and Zusi (2006). This character is likely uninformative in the present study, as all taxa in the present study have a strongly developed sulcus patellaris.

052. Epicondylus medialis: (0) indistinct; (1) weakly developed; (2) strongly developed (Figure 3.13).

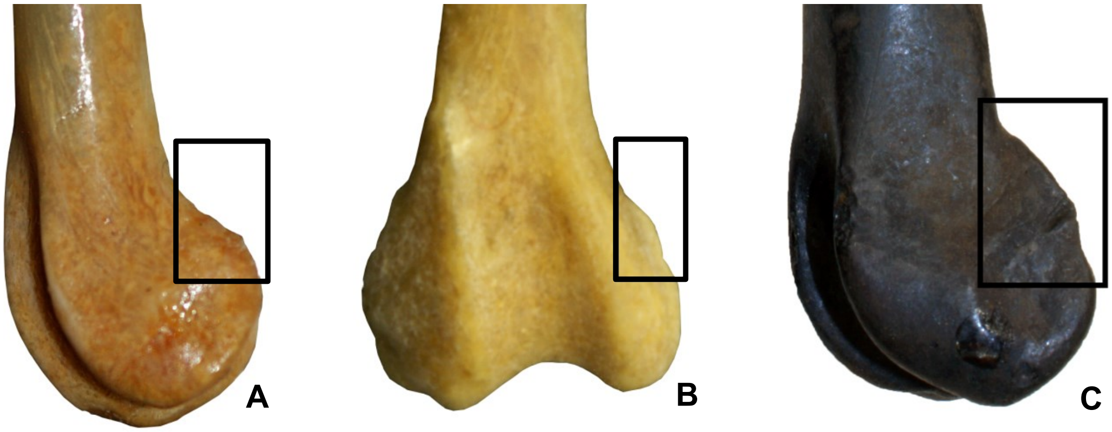

Figure 3.13. Character 052, epicondylus medialis of the distal femur. **A**, character state 0 (BCPM 12011 *Larus californicus*, medial view); **B**, character state 1 (CVM 14428 *Charadrius vociferus*, anterior view); **C**, character state 2 (LACM K3030 *Ciconia maltha*, medial view). Specimens scaled to approximately the same distal mediolateral length.

Comment—Similar to character 2030 of Livezey and Zusi (2006).

053. Epicondylus lateralis: (0) indistinct; (1) weakly developed; (2) strongly developed (Figure 3.14).

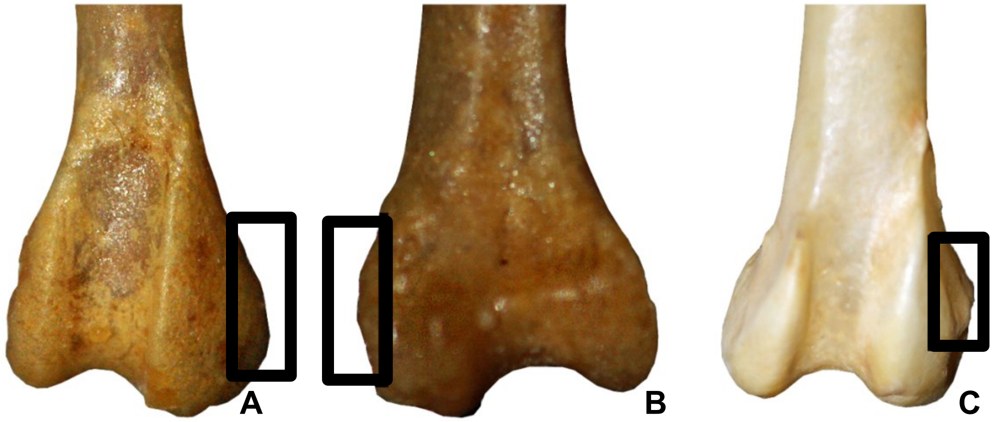

Figure 3.14. Character 053, epicondylus lateralis of the distal femur. **A**, character state 0 (BPM 23807 *Charadrius vociferus*); **B**, character state 1 (BCM 16984 *Tringa solitaria*); **C**, character state 2 (CVM 3151 *Falcipennis canadensis*). Anterior views. Specimens scaled to approximately the same mediolateral length.

Comment—Similar to character 2022 of Livezey and Zusi (2006) (Figure 3.14).

054. Crista supracondylaris medialis: (0) indistinct; (1) weakly developed; (2) strongly developed (Figure 3.15).

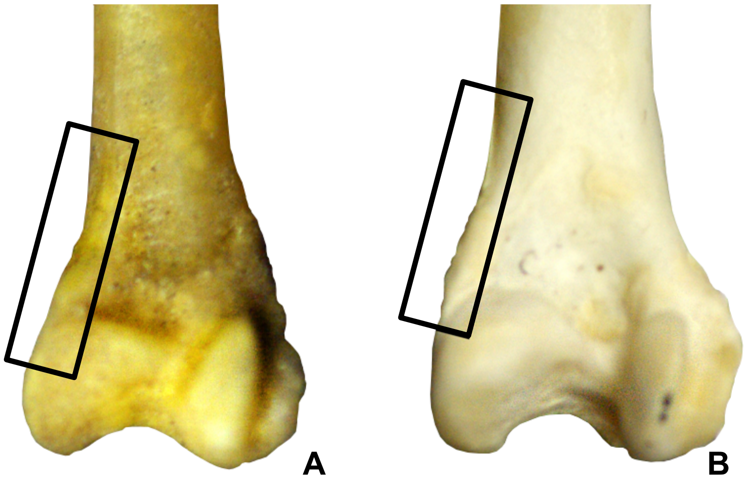

Figure 3.15. Character 054, crista supracondylaris medialis of the distal femur. **A**, character state 1 (BCPM 9943 *Tringa melanoleuca*); **B**, character state 1 (BCPM 10089 *Falco periginus*). Posterior views. Specimens scaled to approximately same distal mediolateral length.

Comment—Similar to character 2037 of Livezey and Zusi (2006).

055. Tuberculum m. gastrocnemius lateralis of the distal femur: (0) indistinct/absent; (1) weak mound; (2) strong mound; (3) distinct process, separate; (4) expressed on posterior surface (Figure 3.16).

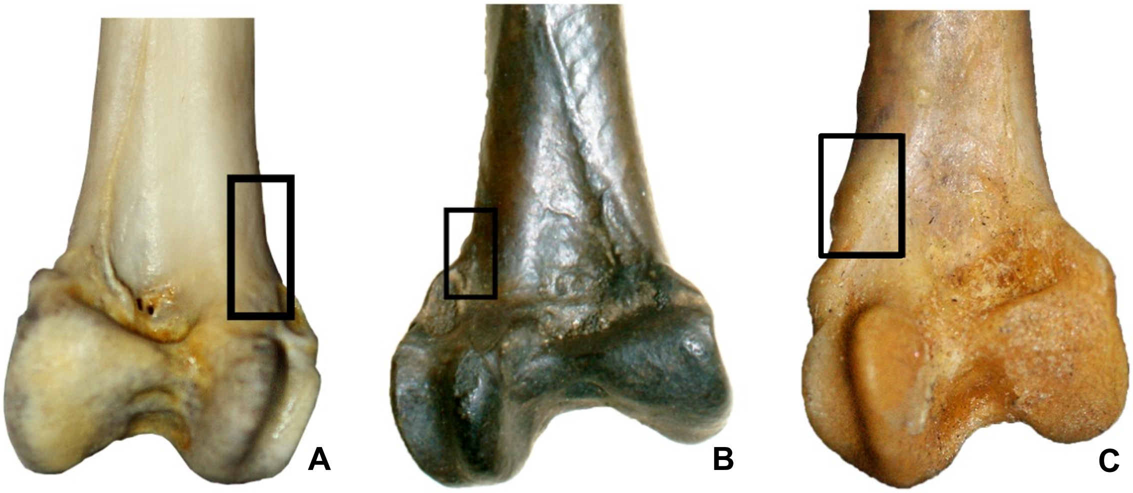

Figure 3.16. Character 055, tuberculum m. gastrocnemialis lateralis of the distal femur. **A**, character state 0 (RBCM 23589 *Lagopus lagopus*); **B**, character state 1 (LACM E5309 *Parapavo californicus*); **C**, character state 2 (BCPM 11285 *Larus californicus*). Posterior views. All specimens scaled to approximately the same distal mediolateral length.

Comment—Similar to character 2029 of Livezey and Zusi (2006), but with greater differentiation in the size of the tuberculum m. gastrocnemius lateralis. Livezey and Zusi (2006) note that there is very little variation in this character among Neornithes.

056. Impressiones ansae m. iliofibularis: (0) indistinct/absent; (1) shallow indent; (2) small pit; (3) large pit (Figure 3.17).

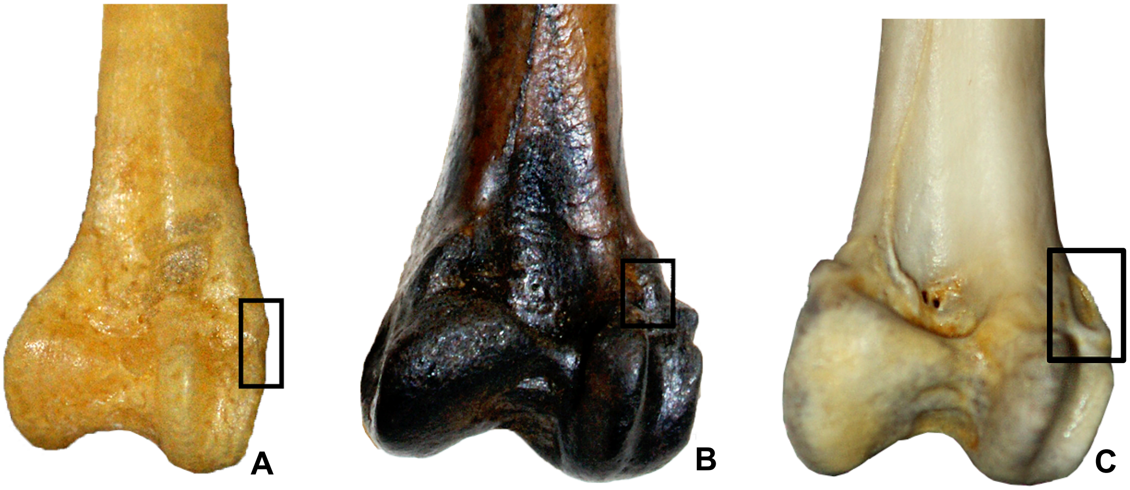

Figure 3.17. Character 056, impressio anasae m. iliofibularis of the distal femur. **A**, character state 1 (BCPM 15442 *Calidris minutilla*); **B**, character state 2 (LACM E9151 *Ardea herodias*); **C**, character state 3 (RBCM 23589 *Lagopus lagopus*). Posterior views. All specimens scaled to approximately the same distal mediolateral length.

Comment—Livezey and Zusi (2006) code this character as either absent or variably prominent for character 2050. Observation of taxa in the present study supports this variable expression, and the character is coded as a multistate character.

057. Trochlear fibularis: (0) absent; (1) weakly developed; (2) strongly developed (Figure 3.18).

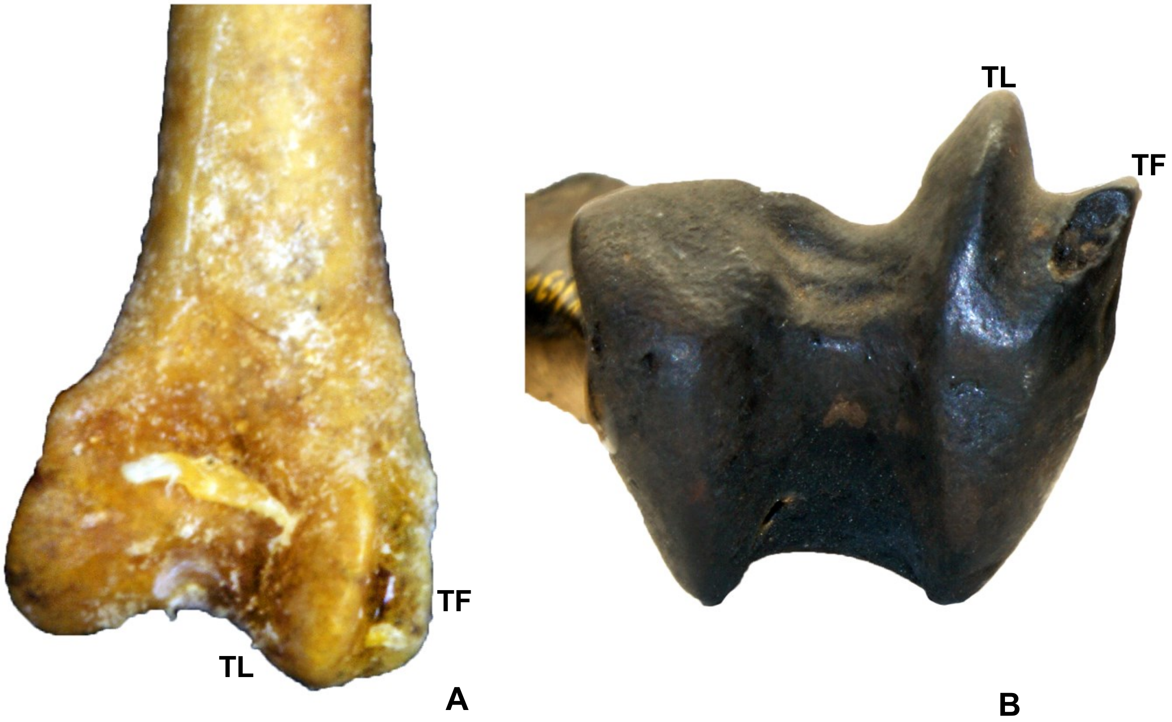

Figure 3.18. Character 057, trochlear fibularis of the distal femur. **A**, character state 1 (CVM 15407 *Limnodromus griseus,* posterior view) **B**, character state 2 (LACM F347 *Ciconia maltha*, distal view). The trochlear fibularis is associated with a well-developed fibular head, which is present in all taxa in the present study. There was very little variation observed within the study taxa in the strength of the trochlear fibularis. TF, trochlear fibularis; TL, trochlear lateralis.

Comment—Taxa examined for this study show a strong trochlea fibularis. This character can be difficult to code for fossil taxa or juvenile taxa where the distal end of the femur is less developed or less well preserved.

058. Crista tibiofibularis: (0) absent; (1) weak ridge; (2) strong ridge.

Comment—Character 2010 in Livezey and Zusi (2006) describes the crista fibularis as either subequal or distinctly proximal in terms of its proximodistal extent relative to the crista tibiofibularis. All specimens examined have a crista fibularis that is smaller proximodistally than the crista tibiofibularis.

059. Fovea tendineus m. tibialis cranialis: (0) absent; (1) weak, shallow; (2) strong cranialis; (3) strong and small; (4) strong and large (Figure 3.19).

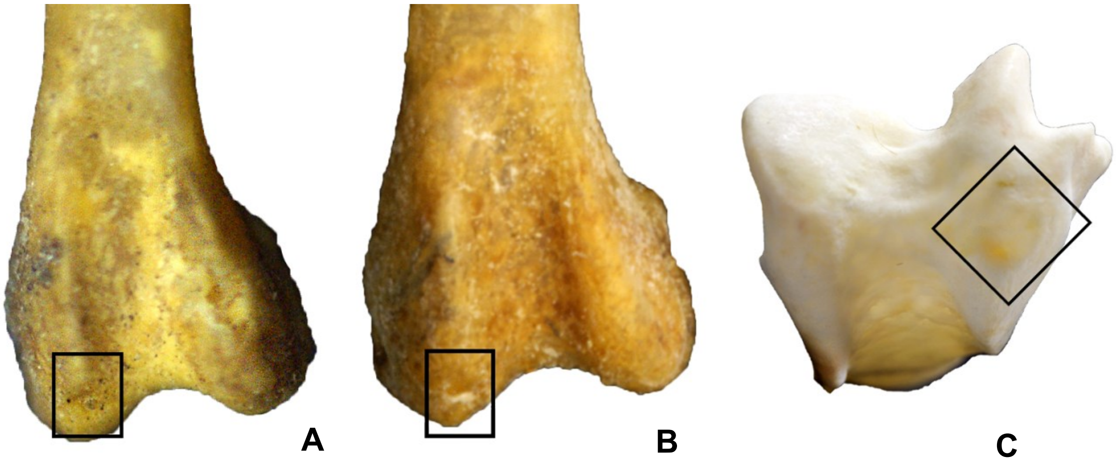

Figure 3.19. Character 059, fovea tendineus m. tibialis cranialis of the distal femur. **A**, character state 0 (BCPM 9943 *Tringa melanoleuca*, anterior view); **B**, character state 1 (CVM 15074 *Limnodromus griseus*, anterior view); **C**, character state 2 (RBCM 22530 *Buteo jamaicensis*, distal view). All specimens scaled to approximately the same mediolateral distal length.

Comment—Similar to character 2015 of Livezey and Zusi (2006).

060. Impressio ligamentosus collateralis lateralis: (0) absent; (1) weak; (2) strong (Figure 3.20).

Figure 3.20. Character 060, impressio ligamentosus collateralis lateralis of the distal femur. **A**, character state 1 (BCPM 9943 *Tringa melanoleuca*); **B**, character state 2 (LACM K5401 *Buteogallus daggetti*). Anterior views. Specimens scaled to approximately the same distal mediolateral length.

Comment—There is no similar character coded in Livezey and Zusi (2006), but the impressio ligamentosus collateral is lateralis has variable expression on the condylus lateralis of the femur.

061. Fossa poplitea: (0) small, shallow; (1) small, deep; (2) large, shallow; (3) large, deep (Figure 3.21).

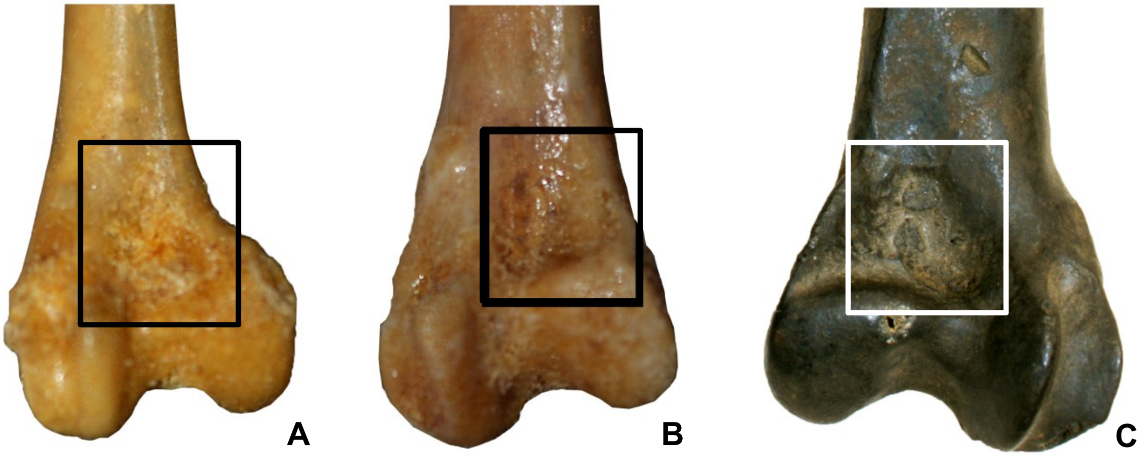

Figure 3.21. Character 061, fossa poplitea of the distal femur. **A**, character state 0 (CVM *Limosa fedoa*); **B**, character state 1 (BCPM 12053 *Larus californicus*); **C**, character state 2 (LACM K3030 *Ciconia maltha*). Posterior views. All specimens scaled to approximately the same distal mediolateral length.

Comment—Documented by Currie and Carpenter (2000) as being attributed to the fossa poplitea of non-avian dinosaurs.

062. Impressio ligamenti cruciati caudalis: (0) absent, indistinct; (1) shallow, small; (2) strong, deep (3.22).

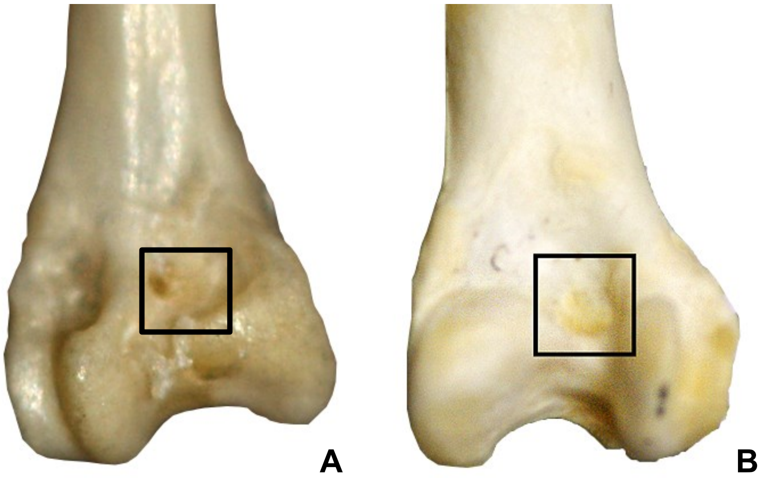

Figure 3.22. Character 062, impressio ligament cruciati caudalis of the distal femur. **A**, character state 1 (BCPM 10147 *Calidris pusilla*); **B**, character state 2 (BCPM 10089 *Falco perigrinus*). Posterior views. All specimens scaled to approximately the same distal mediolateral length.

Comment—Similar to character 2016 of Livezey and Zusi (2006) in that this feature is difficult to discern, but more character states were added to code the variation observed among the taxa in the present study.

063. Impressio ligamenti cruciati cranialis: (0) absent, indistinct; (1) weak depression, shallow; (2) shallow, well-defined borders; (3) deep, well-defined borders (Figure 3.23).

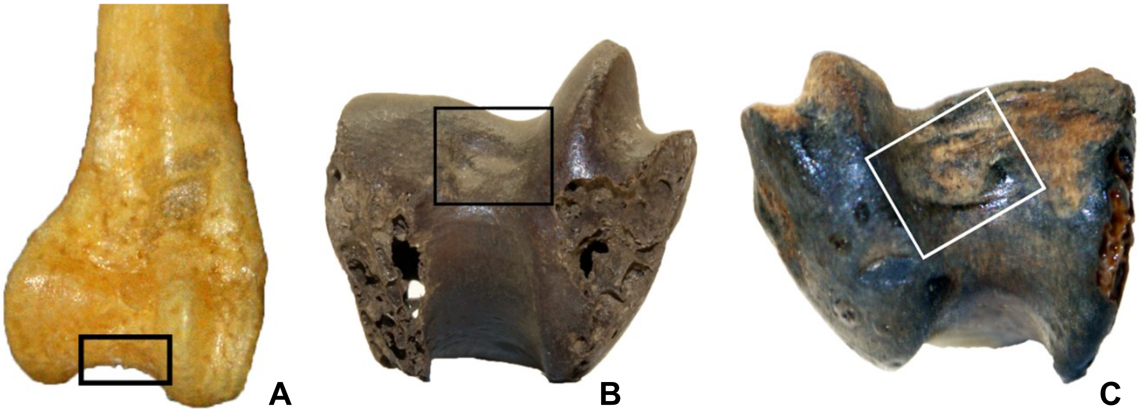

Figure 3.23. Character 063, impressio ligamenti cruciati cranialis of the distal femur. **A**, character state 1 (BCPM 15442 *Calidris minutilla*, posterior view); **B**, character state 2 (LACM F4636 *Grus pagei*, distal view); **C**, character state 3 (LACM L190 *Callipepla californicus*, distal view).

Comment—Livezey and Zusi (2006) note in character 2025 that the variation in the impressio ligamenti cruciati cranialis was intractable. The present analysis notes that, while there is variable expression in the depth of the structure and the strength of its boundaries, it is present as either shallow or deep, with generally well-defined borders.

064. Supratendineus: (0) absent; (1) thin connection; (2) thick connection (Figure 3.24).

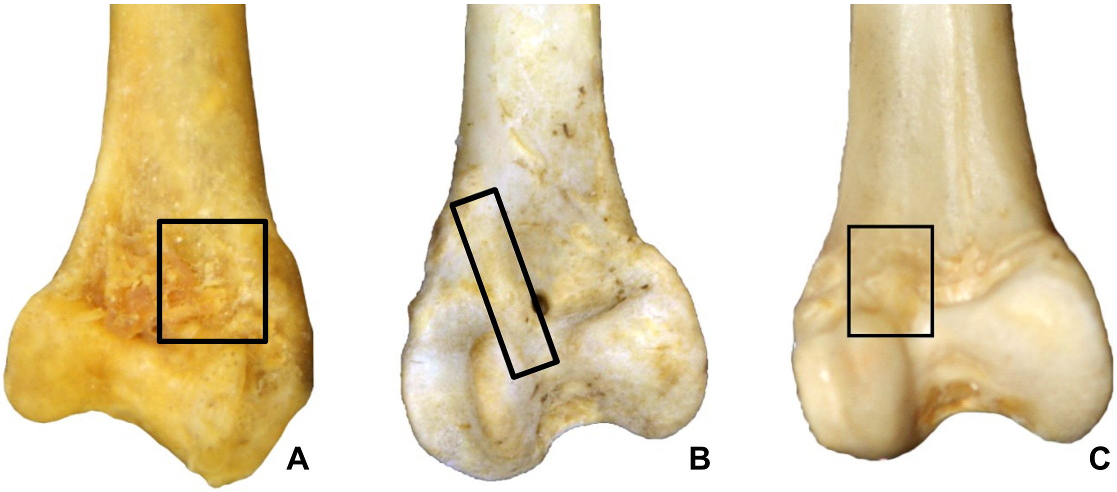

Figure 3.24. Character 064, supratendineus of the distal femur. **A**, character state 0 (CVM 14542 *Recurvirostra americana*); **B**, character state 1 (CVM 14476 *Larus delawarensis*); **C**, character state 2 (CVM 3149 *Falcipennis canadensis*). Posterior views. Specimens scaled to approximately the same distal mediolateral length.

Comment—The supratendineus for most of the study taxa that possessed it as a weakly developed thick, proximodistally oriented ridge that did not form a bridge over the fossa poplitea. The supratendineus was typically located after locating the impression ligamentum cruciate caudalis.

065. Femur bowing: (0) straight; (1) slight bowing; (2) strong bowing (Figure 3.25).

Figure 3.25. Character 065, bowing of the femur. **A** character state 0 (RBCM 23797 *Calidris pusilla*); **B**, character state 1 (CVM 3149 *Falcipennis canadensis*); **C**, character state 2 (CVM 14383 *Lagopus lagopus*). Posterior views. Specimens scaled to approximately the same proximodistal length.

066. Facies caudalis/planum suprapoplitea: (0) rounded; (1) slightly flattened; (2) strongly flattened (Figure 3.26).

Figure 3.26. Character 066, planum suprapoplitea of the femur. **A**, character state 0 (RBCM 23797 *Calidris pusilla*, posterior view); **B**, character state 1 (RBCM 10157 *Lagopus muta*, posterior view); **C**, character state 2 (LACM K5123 *Ardea herodias*, medial view). Specimens scaled to approximately the same proximodistal length.

Comment—Livezey and Zusi (2006) establish a new term (planum suprapoplitea) in character 2004 to describe the degree to which the facies caudalis is flattened with respect to the lineae intermuscularis caudalis.

067. Linea intermuscularis caudalis: (0) absent; (1) separated from crista supracondylaris medialis and single; (2) bifurcated and separate; (3) connected and single; (4) connected and bifurcated (Figure 3.27).

Figure 3.27. Character 067, linea intermuscularis caudalis of the femur. **A**, character state 0 (BCPM 9978 *Charadrius vociferus*); **B**, character state 1 (LACM K3030 *Ciconia maltha*); **C**, character state 2 (LACM E9151 *Ardea herodias*); **D**, character state 3 (LACM L182 *Callipepla californicus*). Posterior views. All specimens scaled to approximately the same proximal mediolateral length.

Comment—Livezey and Zusi (2006) do not code a similar character. In all examined (adult) specimens in the present study, the medial branch of the linea intermuscularis caudalis is variably continuous with the crista supracondylus medialis at its most distal demarcation. Livezey and Zusi (2006) note for character 2042 that assignment of some character states in the distal end of the femur was problematic due to the presence of several features (condylus medialis, crista supracondylaris medialis, facies insertii m. gastrocnemialis medialis).

068. Tuberculum m. gastrocnemialis medialis: (0) absent, indistinct; (1) directly above medial condyle; (2) on the surface of medial condyle (Figure 3.28).

Figure 3.28. Character 068, tuberculum m. gastrocnemialis medialis. **A**, character state 1 (BCPM 17157 *Pluvialis squatarola*); **B,** character state 2 (BCPM 12078 *Larus californicus*). Medial views. Specimens scaled to approximately equal proximodistal length.

Comment—Similar to character 2044 of Livezey and Zusi (2006).

069. Tibiofibularis crista: (0) absent; (1) simple; (2) jugum crista (Figure 3.29).

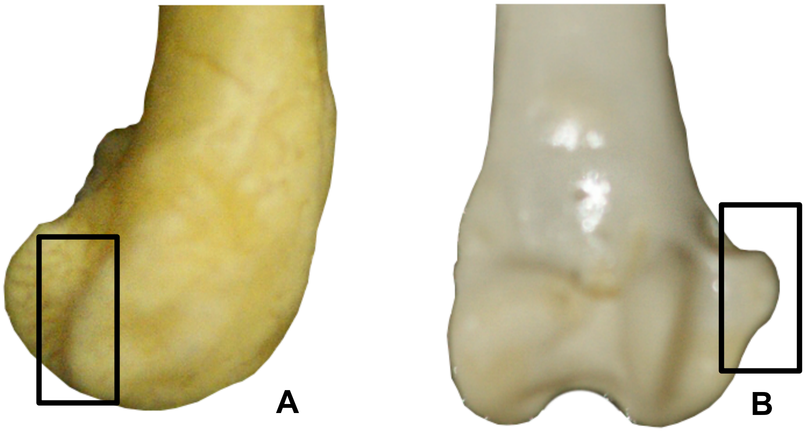

Figure 3.29. Character 069, tibiofibularis crista of the femur. **A**, character state 1 (BCPM 15491 *Charadrius vociferus*, lateral view); **B**, character state 2 (BCPM 12155 *Accipiter striatus*, posterior view). Specimens scaled to approximately the same distal mediolateral length.

Comment—Jugum crista was established as a new term in Livezey and Zusi (2006) for character 2084.

Tibiotarsus

070. Crista cnemialis cranialis: (0) level with area interarticularis; (1) slightly elevated above area interarticularius; (2) greatly elevated above area interarticularis; (3) greater than 10% length of tibiotarsus in length (Figure 3.30).

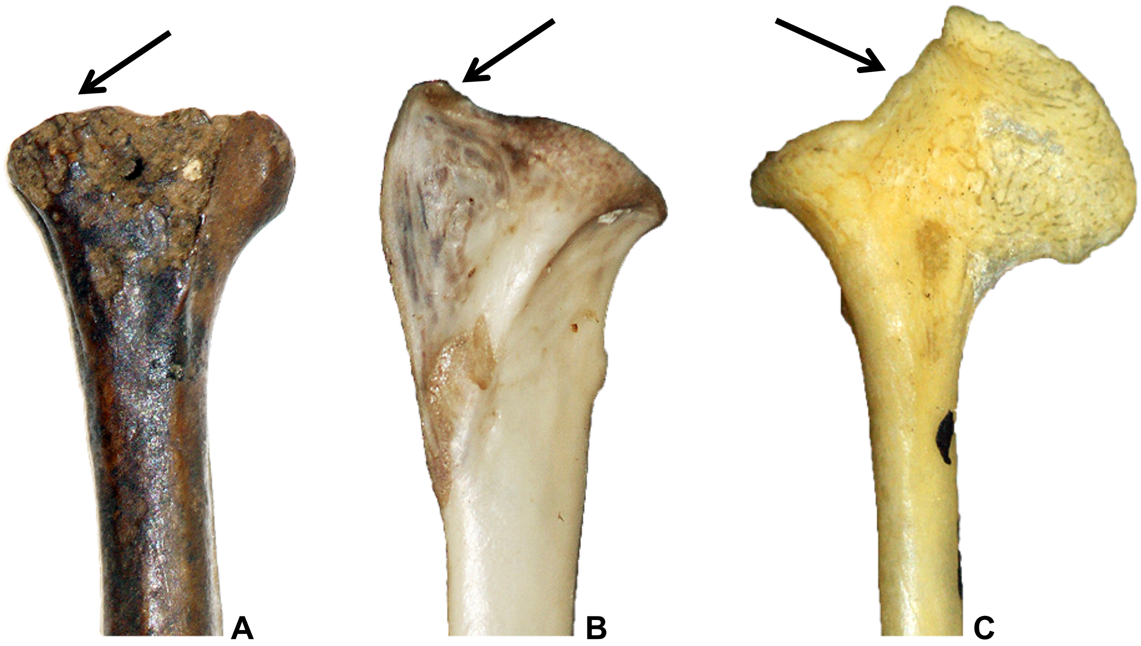

Figure 3.30. Character 070, crista cnemialis cranialis height of the proximal tibiotarsus. **A**, character state 0 (LACM F8433 *Callipepla californicus*); **B**, character state 1 (BCPM 22403 *Accipiter cooperii*); **C**, character state 2 (BCPM 15491 *Charadrius vociferus*). Medial views. Specimens scaled to approximately the same proximal anteroposterior length.

Comment—Except for the Galliformes, all of the taxa examined in this study have a distinct (if not large in some taxa) crista cnemialis cranials.

071. Crista cnemialis cranialis: (0) less than a 90° angle with crista cnemialis lateralis; (1) roughly equal to 90° with crista cnemialis lateralis; (2) greater than 90° with crista cnemialis lateralis (Figure 3.31).

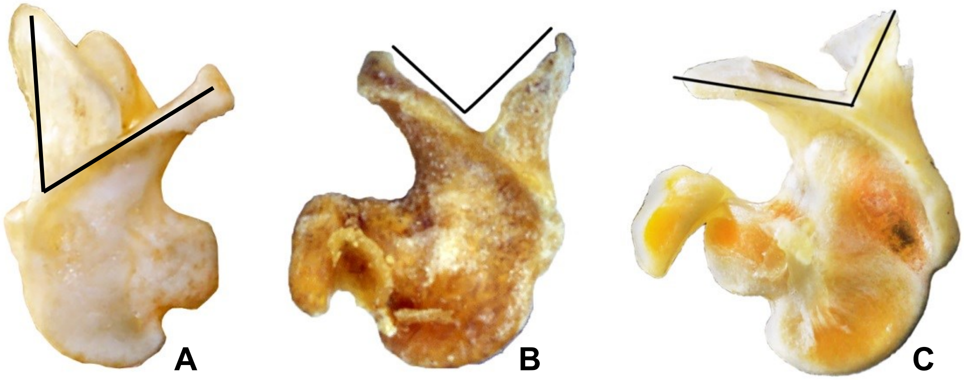

Figure 3.31. Character 071, crista cnemialis cranialis angle of the proximal tibiotarsus. **A**, character state 0 (BCPM 10147 *Calidris pusilla*); **B**, character state 1 (CVM 15077 *Limnodromus griseus*); **C**, character state 2 (BCPM 9978 *Charadrius vociferus*). Proximal views. All specimens scaled to approximately equal proximal mediolateral length.

Comment—Character 2080 of Livezey and Zusi (2006) code character states regarding the point of attachment of the crista cnemialis cranialis relative to that of the cnemialis lateralis. Livezey and Zusi (2006) do code character states for character 2075 for the crista cnemialis cranialis either oriented perpendicular or not to the crista cnemialis lateralis, but do not distinguish among the marginal inequalities. Character 2080 addresses how the crista cnemialis cranials connects with the crista cnemialis lateralis, which also affects the angle of attachment. The curvature of the crista cnemialis cranialis, which has a direct effect on the angle of attachment, is coded in character 2082 (Livezey and Zusi 2006).

072. Crista cnemialis cranialis: (0) triangular, anterior length decreases down tibiotarsal shaft; (1) rectangular; (2) triangular, anterior length greatest at mid crista length; (3) triangular, anterior length increases down tibiotarsal shaft; (4) thin, short projection (Figure 3.32).

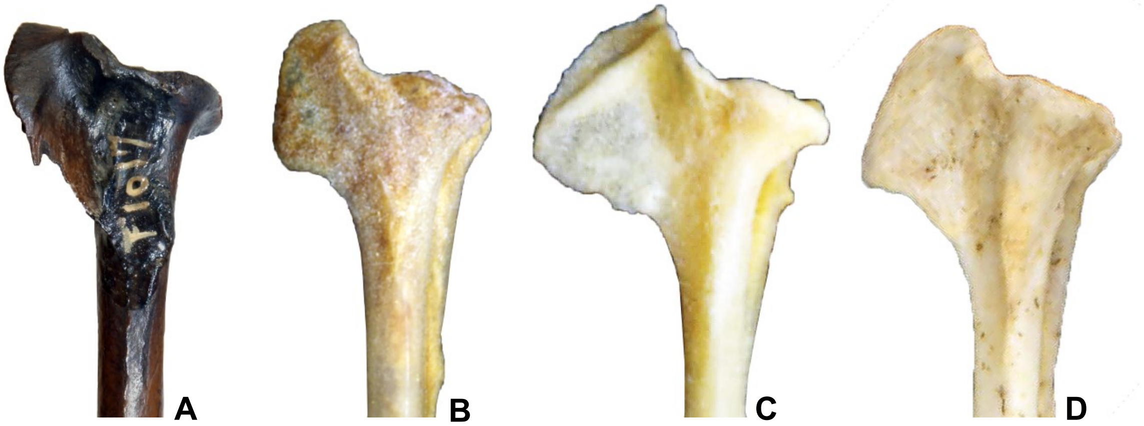

Figure 3.32. Character 072, crista cnemialis cranialis shape of the proximal tibiotarsus. **A**, character state 0 (LACM F1017 *Grus pagei*); **B**, character state 1 (CVM 15075 *Limnodromus griseus*); **C**, character state 2 (CVM 14428 *Charadrius vociferus*); **D**, character state 3 (CVM 14476 *Larus delawarensis*). Medial views. Specimens scaled to approximately equal in proximal anteroposterior length.

073. Crista cnemialis cranialis: (0) does not extend far down tibiotarsal shaft; (1) extends short distance down tibiotarsus shaft; (2) extends down the tibiotarsal shaft for at least half of the length of the tibiotarsus shaft (Figure 3.33).

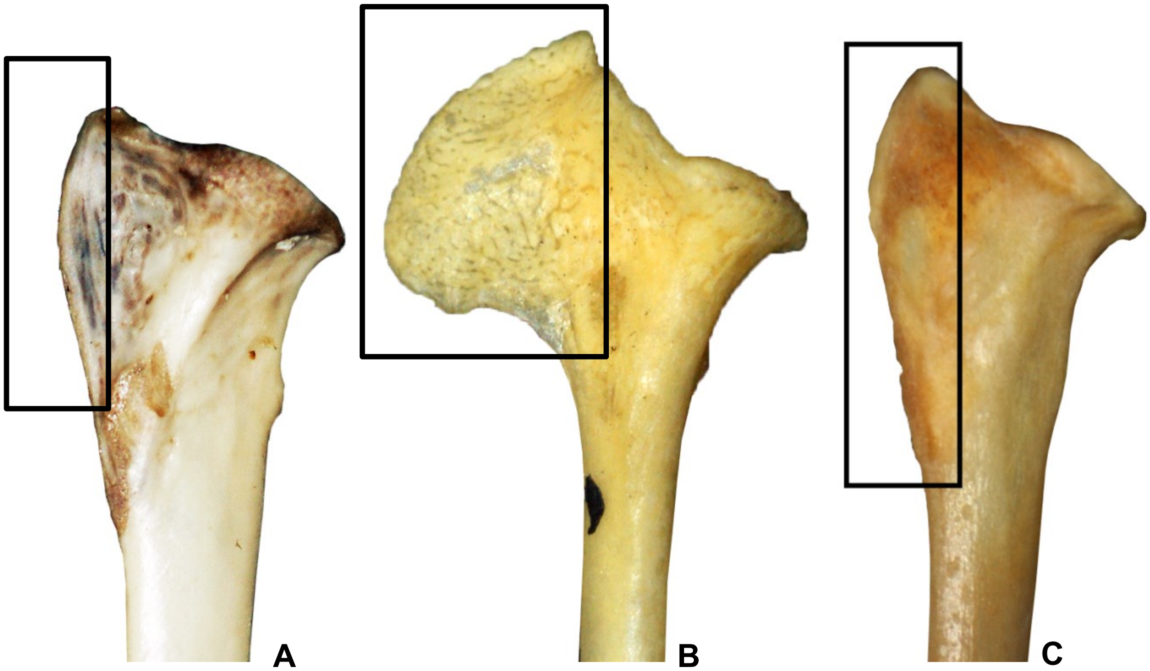

Figure 3.33: Character 073, crista cnemialis cranialis extension of the proximal tibiotarsus. **A**, character state 0 (BCPM 22403 *Accipiter cooperii*); **B**, character state 1 (BCPM 15491 *Charadrius vociferus*); **C**, character state 2 (RBCM 19916 *Buteo platypterus*). Medial views. Specimens scaled to approximately equal proximal anteroposterior length.

Comments—Characters 072 and 073 of this analysis are similar to character 2071 of Livezey and Zusi (2006).

074. Crista cnemialis lateralis: (0) not evident, very weak; (1) present and smaller than crista cnemialis cranialis; (2) present and equal in size to crista cnemialis cranialis; (3) present and larger than crista cnemialis cranialis (Figure 3.34).

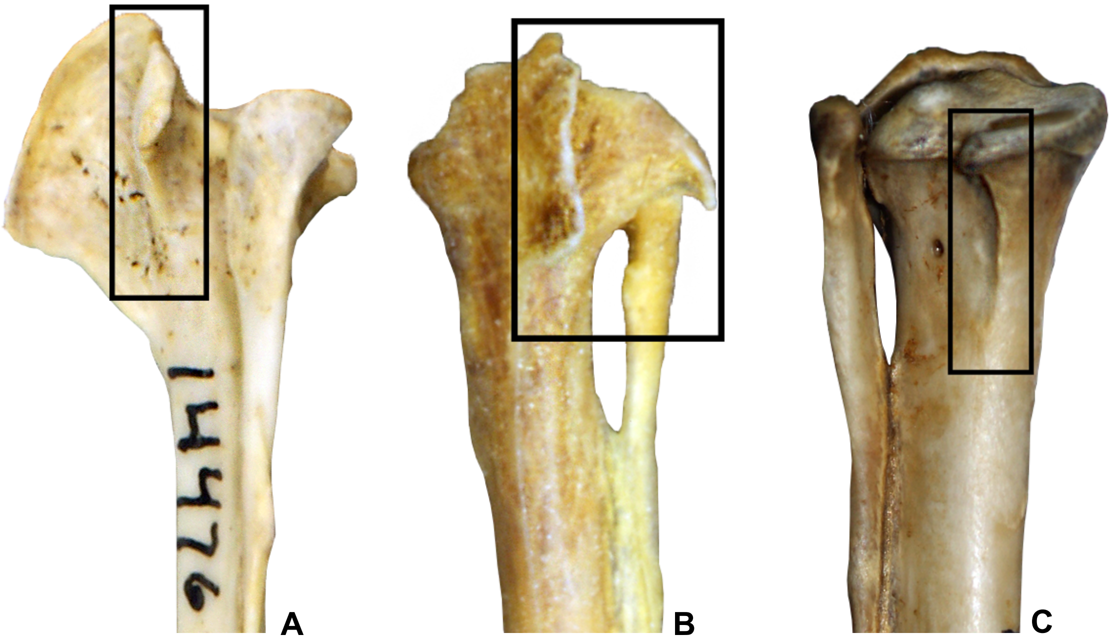

Figure 3.34. Character 074, crista cnemialis lateralis of the proximal tibiotarsus. **A**, character state 0 (CVM 14476 *Larus delawarensis*); **B**, character state 1 (CVM 15073 *Limnodromus griseus*); **C**, character state 2 (RBCM 22457 *Lagopus lagopus*). Anterior views. Specimens scaled to approximately equal in proximal mediolateral length.

Comment—Similar to character 2086 of Livezey and Zusi (2006), but addresses the orientation of the crista cnemialis lateralis (addressed in character 071 of this study) rather than the degree of development.

075. Area interarticularis: (0) weak, same level as facies interarticularis; (1) projects weakly above articular facies; (2) projects strongly above articular facies (Figure 3.35).

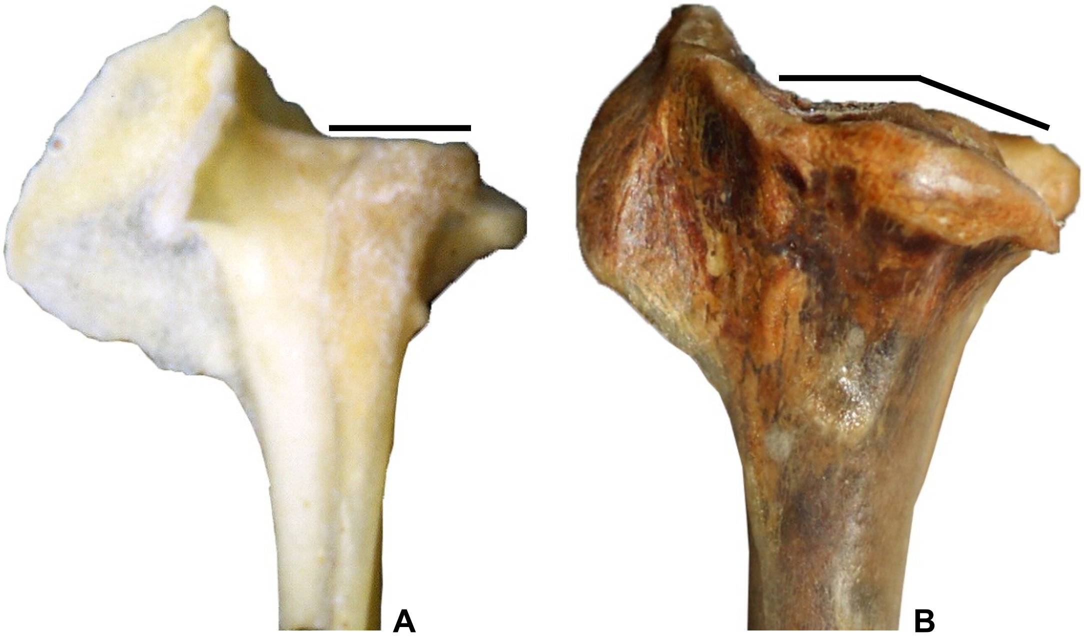

Figure 3.35. Character 075, area interarticularis of the proximal tibiotarsus. **A**, character state 0 (CVM 14428 *Charadrius vociferus*); **B**, character state 1 (CVM 14718 *Perdix perdix*). Lateral views. Specimens scaled to approximately equal proximal anteroposterior length.

Comment—The area interarticularis is described in character 2068 of Livezey and Zusi (2006) as obsolete (no distinction between the facies medialis and facies lateralis) or marked.

076. Facies articularis medialis: (0) same level/lower than facies articularis lateralis; (1) higher than facies articularis lateralis (Figure 3.36).

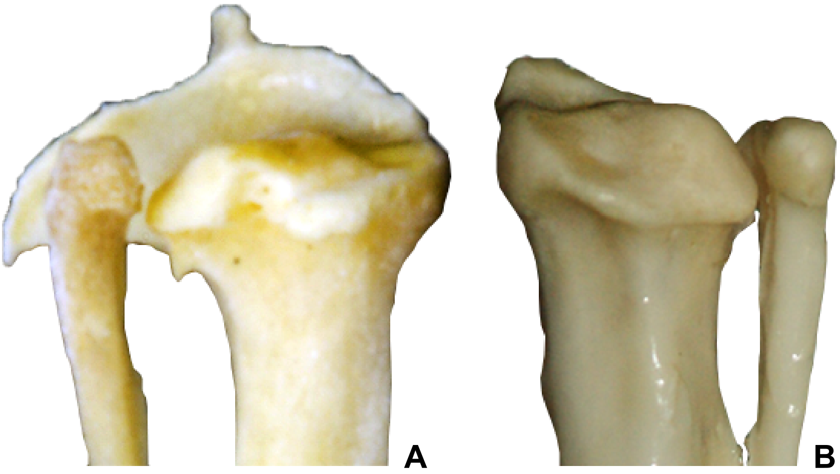

Figure 3.36. Character 076, facies articularis medialis of the proximal tibiotarsus. **A**, character state 0 (CVM 14428 *Charadrius vociferus*); **B**, character state 1 (BCPM 12155 *Accipiter striatus*). Posterior views. Specimens scaled to approximately equal proximal mediolateral size.

Comment—There are several characters (2060–2062, 2067, Livezey and Zusi 2006) that address the relative size and shape of the facies articularis medialis. In the sample taxa for this study, there was very little variation in the size, shape, and elevation relative to the facies articularis lateralis.

077. Incisura tibialis: (0) not visible; (1) shallow, almost continuous in line with crista cnemialis patellaris; (2) deeply excavated with visible groove (Figure 3.37).

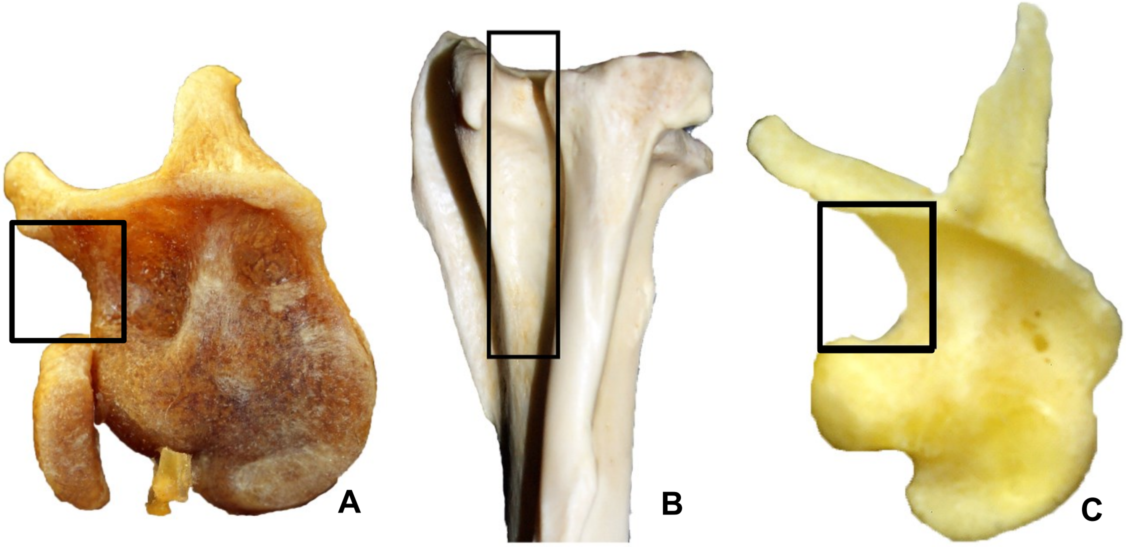

Figure 3.37. Character 077, incisura tibialis of the proximal tibiotarsus. **A**, character state 1 (CVM 3151 *Falcipennis canadensis*, anterior view); **B**, character state 2 (left, BCPM 22247 *Buteo regalis*, lateral view; right, CVM 14428 *Charadrius vociferus*, anterior view). Specimens scaled to approximately equal proximal mediolateral size.

Comment—The incisura tibialis is used as a delineating structure separating the crista cnemialis cranialis et lateralis (character 2093, Livezey and Zusi 2006). Its broadness (absent or present, in conjunction with other features, character 2104), and its length (character 2116) are also addressed (Livezey and Zusi 2006).

078. Facies articularis fibularis: (0) rounded; (1) flattened and smooth; (2) flattened and rugose; (3) fibular head fused with tibiotarsus; (4) concave and smooth.

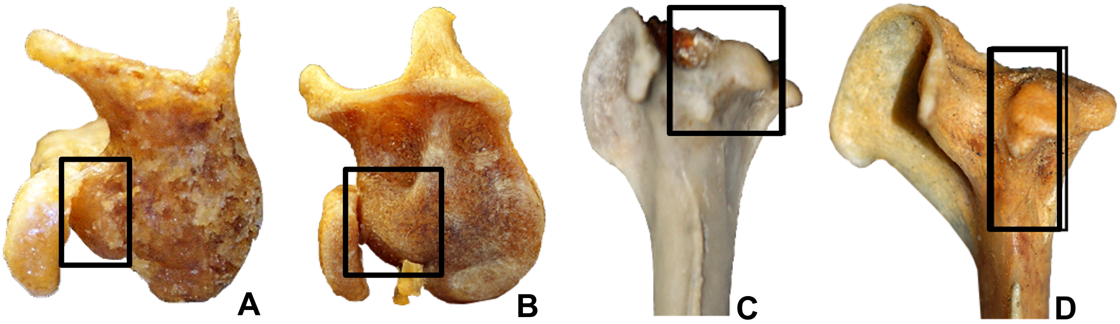

Figure 3.38. Character 078, facies articularus fibularis of the proximal tibiotarsus. **A**, character state 0 (RBCM 23178 *Tringa solitaria*, anterior view); **B**, character state 1 (CVM 3151 *Falcipennis canadensis*, anterior view); **C**, character state 2 (RBCM 10157 *Lagopus muta*, lateral view); **D**, character state 4 (BCPM 11285 *Larus californicus*, lateral view). Specimens scaled to approximately equal proximal mediolateral length.

Comment—Livezey and Zusi (2006) code the facies articularis fibularis as absent or present for character 2058. Examination of the sample taxa in the present study shows there is variation in the size, shape, and rugosity of the facies articularis fibularis, and the character states capture the observed variation.

079. Facies articularis lateralis: (0) weak, non-protruding and continuous with lateral surface of tibiotarsus shaft; (1) weakly protruding; (2) strongly protruding (Figure 3.39).

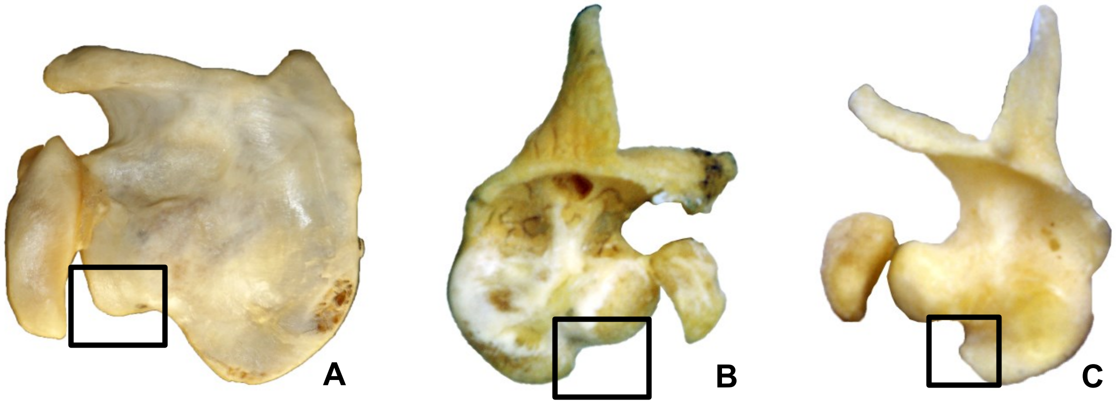

Figure 3.39. Character 079, facies articularis lateralis of the proximal tibiotarsus. **A**, character state 0 (CVM 10089 *Falco perigrinus*); **B**, character state 1 (CVM 14485 *Charadrius semipalmatus*); **C**, character state 2 (CVM 14428 *Charadrius vociferus*). Proximal views. Specimens scaled to approximately equal proximal mediolateral length.

Comment—See comments for character 078 for the crista cnemialis lateralis.

080. Tuberositas popliteus: (0) continuous with posterior edge of facies articularius; (1) weakly protruding; (2) strongly protruding (Figure 3.40).

081. Tuberositas popliteus: (0) ridge does not extend past proximal articular surface; (1) ridge extends less than one third (< 1/3) down the shaft of tibiotarsus; (2) ridge extends equal to or more than one third (> 1/3) down the shaft of tibiotarsus (Figure 3.40).

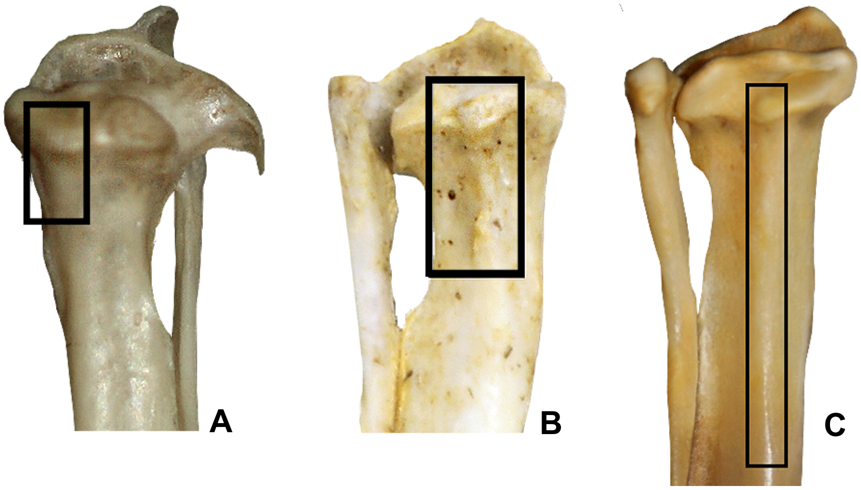

Figure 3.40. Character 081, tuberositas popliteus ridge of the proximal tibiotarsus. **A**, character state 0 (BCPM 10147 *Calidris pusilla*); **B**, character state 1 (CVM 14476 *Larus delawarensis*); **C**, character state 2 (RBCM 19916 *Buteo platypterus*). Posterior views. Specimens scaled to approximately equal proximal mediolateral length.

Comment—These characters were not coded in either Livezey and Zusi (2006) or Livezey (2010). Within the study taxa examined there is variation in the expression of the tuberositas popliteus. No discernable patterns were recognized in relation to the expression of the tuberositas popliteus *a priori*.

Unanalyzed character.

Crista patellaris: ridge (0) does not extend; (1) less than two-thirds (< 2/3) down the shaft of the tibiotarsus; (2) less than two-thirds (> 2/3) down the shaft of the tibiotarsus.

Comment—Livezey and Zusi (2006) comment in great detail on the past treatment and condition of the crista cnemialis cranialis, crista lateralis, and crista patellaris. In short, Livezey and Zusi found no support for claims that patellae fused with cnemial crests or extremitas proximalis tibiotarsi, or that the patellae have originated by fracturing of the cristae cnemialis (2006). Baumel and Witmer (1993) also noted that the crista patellaris is variable in Aves depending on the elevation of the crista cnemialis cranialis above the facies articularis medialis et lateralis and, in those taxa possessing a separate patella, there is a syndesmosis with the crista patellaris (Livezey and Zusi 2006). In the sample taxa analyzed in this study, no patellae were observed connected to the crista patellaris in any of the study taxa.

082. Ridge of crista cnemialis lateralis: (0) does not extend down the tibiotarsus shaft; (1) extends less than half (< ½) down the length of the tibiotarsus shaft; (2) extends more than half (> ½) down the length of the tibiotarsus shaft (Figure 3.41).

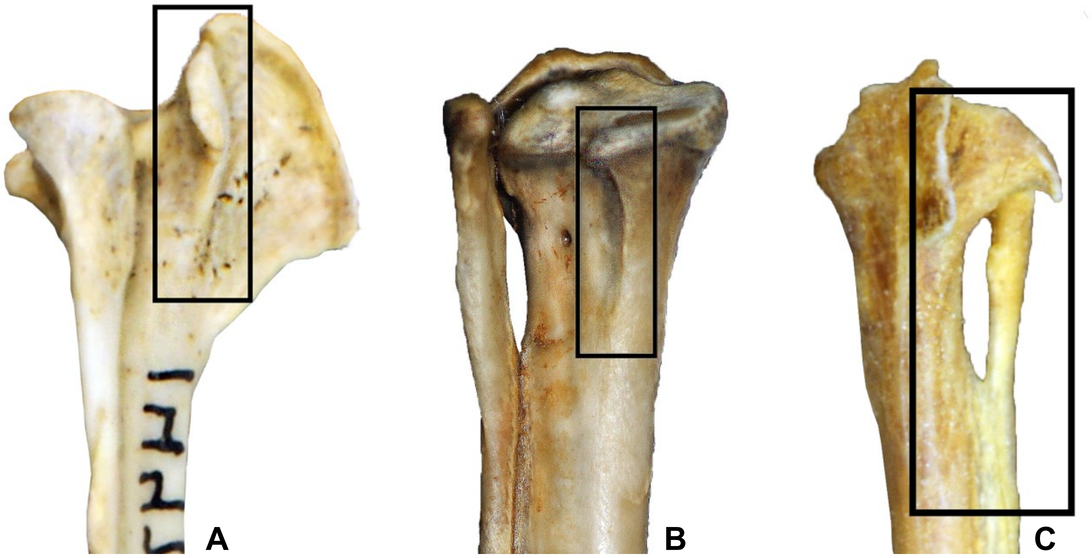

Figure 3.41. Character 082, crista cnemialis lateralis ridge extension of the proximal tibiotarsus. **A**, character state 0 (CVM 14476 *Larus delawarensis*, lateral view), **B**, character state 1 (RBM 22457 *Lagopus lagopus*, posterior view); **C**, character state 2 (CVM 15073 *Limnodromus griseus*, medial view). Specimens scaled to approximately equal proximal mediolateral length.

Comment—Similar to character 2099 of Livezey and Zusi (2006) which compared the comparative distal extent on the corpus tibiotarsus. The crista patellaris, in the sample taxa for the present study, does not appear as a distinct feature on the crista cnemialis lateralis, and does not extend down the shaft of the tibiotarsus.

083. Impressiones ligamentous collateralis medialis: (0) weak; (1) small prominence, rounded, not ridge-like; (2) strong, pronounced, ridge-like, elongate; (3) large, mound shaped; (4) large, flattened (Figure 3.42).

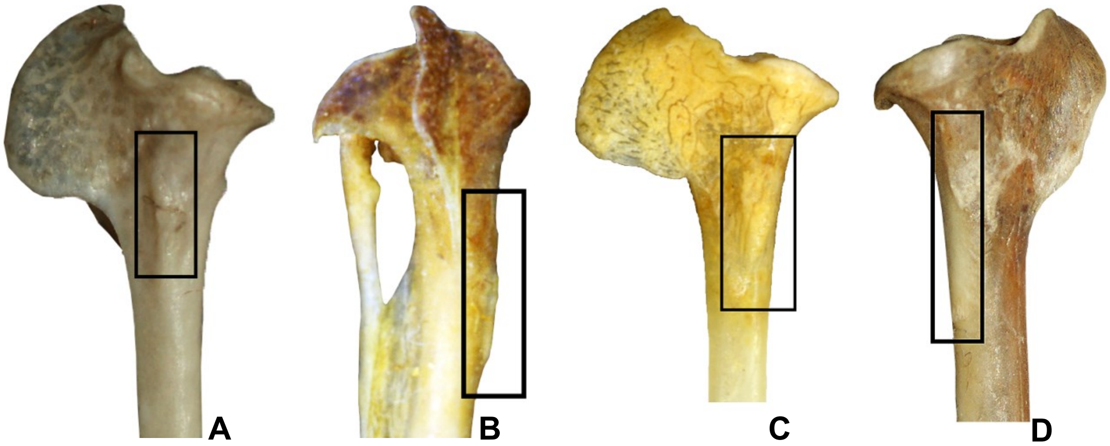

Figure 3.42. Character 083, impressiones ligamentosus collateralis medialis of the proximal tibiotarsus. **A**, character state 1 (BCPM 10147 *Calidris pusilla*, medial view); **B**, character state 2 (CVM 15078 *Limnodromus scolopaceus*, anterior view); **C**, character state 3 (CVM 14485 *Charadrius semipalmatus*, medial view); **D**, character state 4 (CVM 3149 *Falcipennis canadensis*, medial view). Specimens scaled to approximately equal proximal anteroposterior length.

Comment—Similar to character 2114 of Livezey and Zusi (2006).

084. Fossa flexoria: (0) continuous with posterolateral surface of the tibiotarsus; (1) weakly excavated, not extending; (2) weakly excavated, extends down half of the length of the tibiotarsus shaft; (3) strongly excavated, not extending; (4) strongly excavated, extends down half of the length of the tibiotarsus shaft; (5) flattened (Figure 3.43).

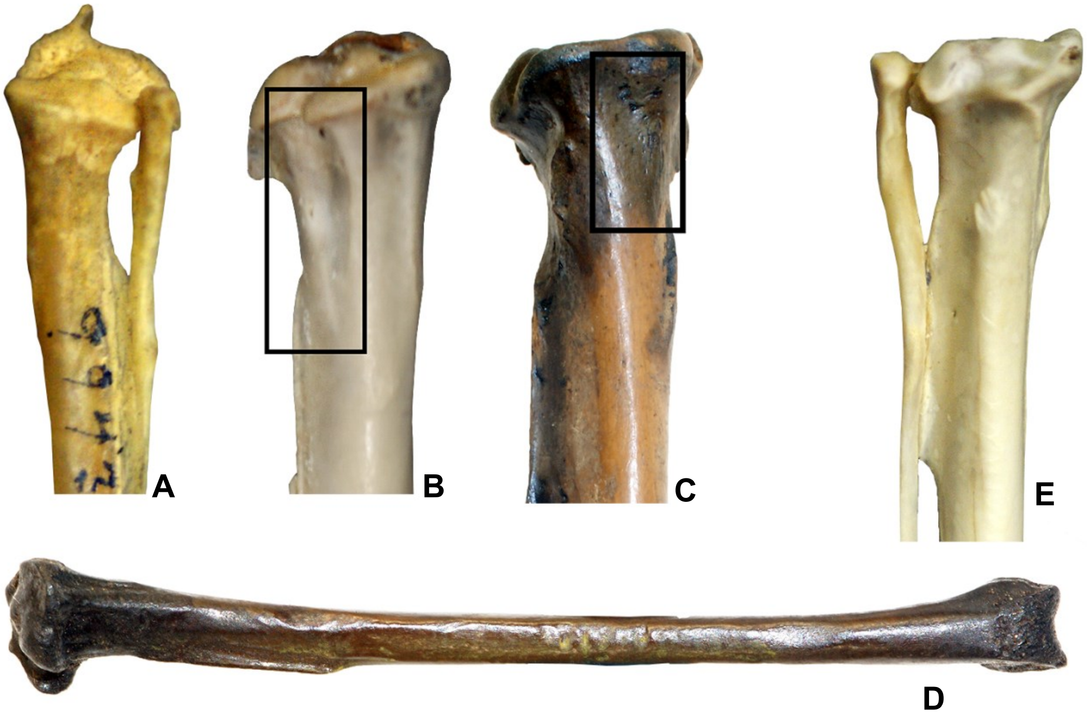

Figure 3.43. Character 084, fossa flexoria of the proximal tibiotarsus of the proximal tibiotarsus. **A**, character state 0 (BCPM 9943 *Tringa melanoleuca*); **B**, character state 1 (RBCM 10157 *Lagopus muta*); **C**, character state 3 (LACM B5750 *Grus americana*); **D**, character state 4 (LACM F8433 *Callipepla californicus*); **E**, character state 5 (BCPM 10089 *Falco perigrinus*). Posterior views. Specimens A–C, E scaled to approximately equal proximal mediolateral length.

Comment—Coded as character 2115 in Livezey and Zusi (2006) as absent or present. In the taxa examined in the present study, variation in the amount excavation and distal extension of the fossa flexoria was observed.

085. Crista fibularis: (0) continuous with lateral surface of the tibiotarsus shaft; (1) weak ridge or impression, not extensive; (2) weak, extends approximately one quarter (1/4) of the length of the tibiotarsus shaft; (3) strongly protruding rectangular flange, not extensive; (4) strong flange, one quarter (1/4) of the length of the tibiotarsus shaft; (5) complete fusion of crista fibularis and corpus fibularis (Figure 3.44).

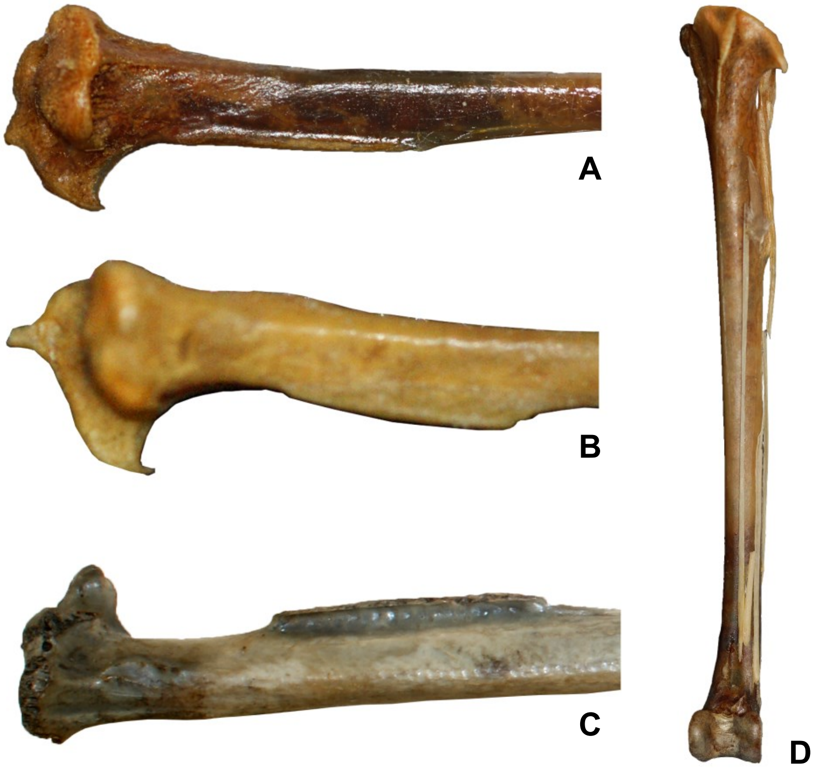

Figure 3.44. Character 085, crista fibularis of the proximal tibiotarsus. **A**, character state 0 (CVM 14572 *Perdix perdix*); **B**, character state 1 (BCPM 11606 *Tringa flavipes*); **C**, character state 2 (LACM K3133 *Grus pagei*); **D**, character state 3 (RBCM 23582 *Dendragapus obscurus*). Posterior views. A–C scaled to approximately equal proximal mediolateral length.

Comment—Characters 2121–2122 of Livezey and Zusi (2006) address the extent and the shape of the crista fibularis.

086. Facies cranialis: (0) rounded, continuous with tibiotarsus shaft; (1) flattened; (2) concave; (3) concave and continuous with sulcus extensorius; (4) facies contains prominent ridges (Figure 3.45).

Figure 3.45. Character 086, facies cranialis of the tibiotarsus. **A**, character state 0 (LACM F8433 *Callipepla californicus*); **B**, character state 1 (BCPM 12078 *Larus califormicus*); **C**, character state 2 (CVM 3149 *Falcipennis canadensis*); **D**, character state 3 (BCPM 10089 *Falco perigrinus*). Anterior views. Specimens scaled to approximately the same proximodistal length.

Comment—Similar to characters 2118 and 2120 of Livezey and Zusi (2006) which addresses (absent or present) the convexity of the facies cranialis corporis. Character 2120 also addresses the proximal segment of the sulcus extensorius, and whether it is included in the distal end of a flattened or concave facies cranialis.

087. Sulcus extensorius: (0) flat, shallow, wide; (1) concave and wide; (2) narrow and concave, forms tendinal groove; (3) wide and concave, forms tendinal groove (Figure 3.46).

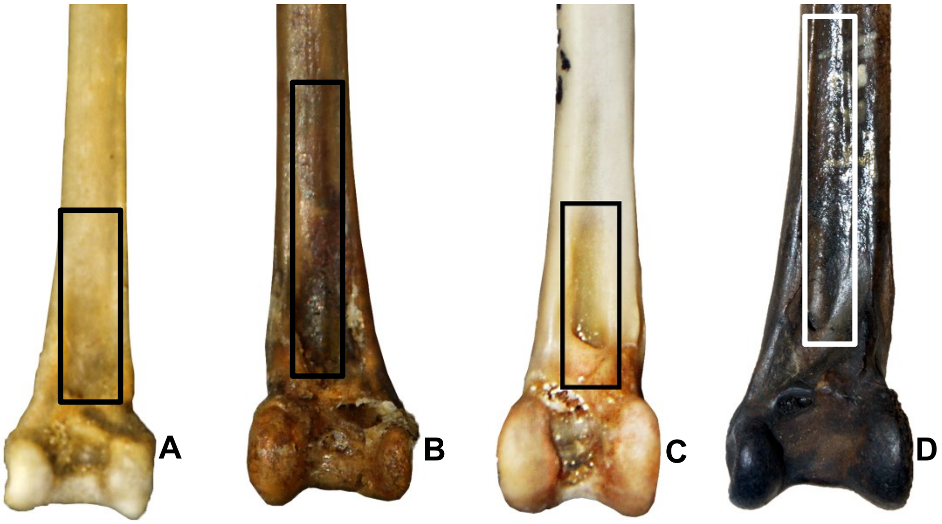

Figure 3.46. Character 087, sulcus extensorius of the distal tibiotarsus. **A**, character state 0 (CVM 14428 *Charadrius vociferus*); **B**, character 1 (RBCM 23178 *Tringa solitaria*); **C**, character state 2 (RBCM 10157 *Lagopus muta*); **D**, character state 3 (LACM J9744 *Buteogallus daggetti*). Anterior views. Specimens scaled to approximately the same distal mediolateral length.

Comment—Character 2134 of Livezey and Zusi (2006) describes character states for the sulcus extensorius as absent or obsolete or present, presenting a continuum of proximal extents, widths, and demarcations.

088. Pons supratendineus/supratendinal bridge: (0) absent; (1) solid, such as an ascending process; (2) horizontal bridge over canalis extensorius; (3) diagonal bridge over canalis extensorius; (4) vertical or near vertical bridge, medially displaced, over canalis extensorius.

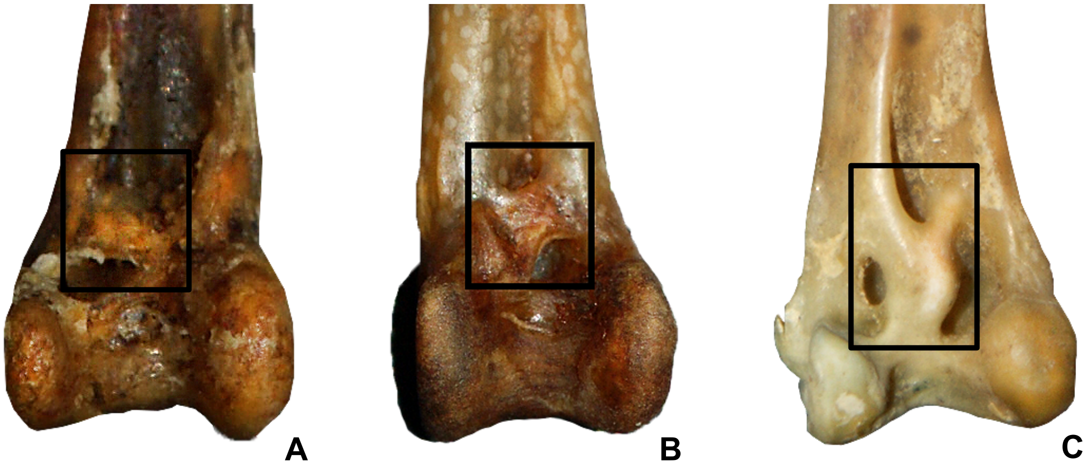

Figure 3.47. Character 088, pons supratendineus of the distal tibiotarsus. **A**, character state 2 (RBCM 23178 *Tringa solitaria*); **B**, character state 3 (CVM 14573 *Dendragapus obscurus*); **C**, character state 4 (BCPM 10788 *Falco mexicanus*). Anterior views. Specimens scaled to approximately the same distal mediolateral length.

Comment—Character 2176 of Livezey and Zusi (2006) addresses the presence/absence character state of the pons supratendineus, while character 2177 addresses its orientation over the sulcus extensorius.

089. Pons supratendineus: (0) ungrooved; (1) grooved; (2) attaches in middle of canalis extensorius, not over it; (3) possesses papilla for tibialis anticus (Figure 3.48).

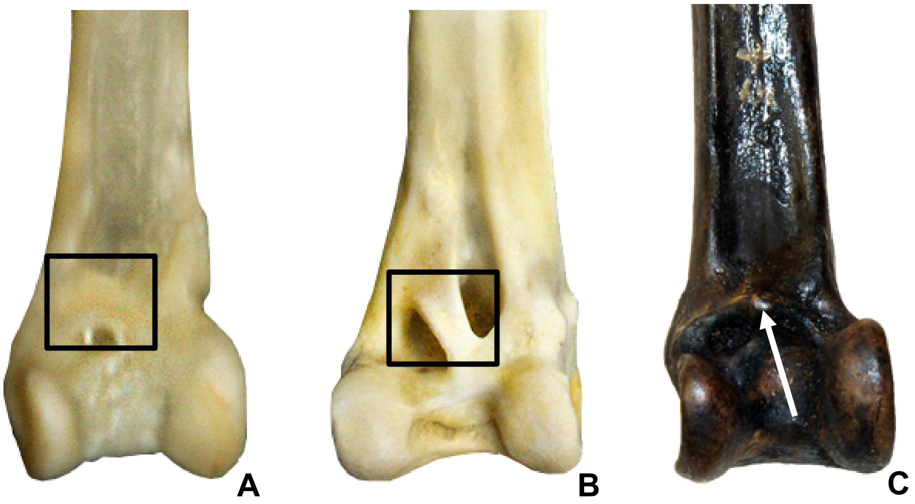

Figure 3.48. Character 089, pons supratendineus groove of the distal tibiotarsus. **A**, character state 0 (BCPM 15491 *Charadrius vociferus*); **B**, character state 1 (BCPM 22247 *Buteo regalis*); **C**, character state 2 (LACM T945 *Ciconia maltha*), with arrow indicating the papilla for the tibialis anticus. Anterior views. Specimens scaled to approximately equal distal mediolateral length.

Comment—Similar to characters 2178–2181 of Livezey and Zusi (2006); however, the papilla for tibialis anticus was not addressed in that study.

Osteologic characters of the distal condyles of the tibiotarsus were coded in characters 2208–2216 as the os tibiale (astragulus) and os fibulare (calcaneum) in Livezey and Zusi (2006). The study specimens are, with the exception of juvenile specimens of *Lagopus leucurus* and *Parapavo californicus*, adult specimens. The study specimens possess a completely ossified os tibiale et os fibulare, with complete ossification to the distal end of the tibiotarsus. Characters of

Livezey and Zusi (2006) include character states that address Crocodylomorpha, Ornithischia, non-avian theropods, and avian theropods. All specimens (again, with the exception of the specimens of juvenile birds) display an expanded and proximad orientation on the distal end of the tibiotarsus, which makes a variant of character 2210 of Livezey and Zusi (2006) uninformative to code. Characters 2211–2216 (Livezey and Zusi) are only observed in the development of early juvenile specimens, and would also be applicable to the study of non-avian Dinosauria.

090. Distal condyles: (0) in line with tibiotarsus shaft; (1) slight medial displacement; (2) strongly displaced medially (Figure 3.49).

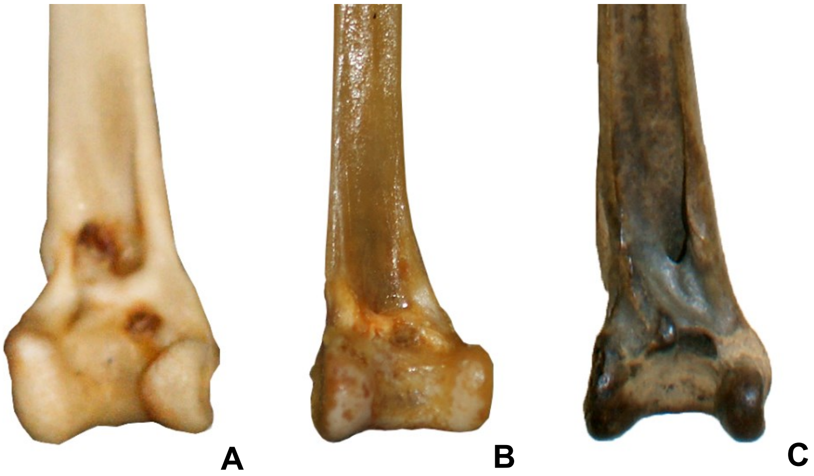

Figure 3.49. Character 090, distal condyle orientation of the distal tibiotarsus. **A**, character state 0 (BCPM 10760 *Charadrius vociferus*); **B**, character state 1 (BCPM 12052 *Larus californicus*); **C**, character state 2 (LACM K3133 *Grus pagei*). Anterior views. Specimens scaled to approximately equal distal mediolateral length.

Comment—While most of the study taxa possess a distal tibiotarsus with distal condyles with a slight medial displacement from the midline of the corpus tibiotarsus, there was interspecific variation expressed in this character.

091. Internal ligamental prominence: (0) no medial process; (1) small medial process, weak; (2) large, strongly projecting medial process (Figure 3.50).

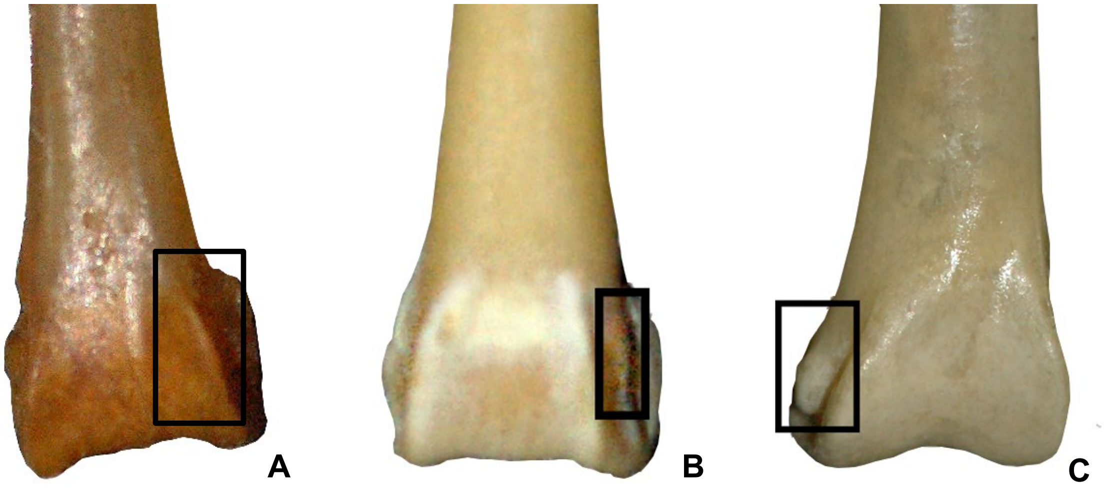

Figure 3.50. Character 091, internal ligamental prominence of the distal tibiotarsus. **A**, character state 0 (BCPM 23807 *Charadrius semipalmatus*); **B**, character state 1 (BCPM 11606 *Tringa flavipes*); **C**, character state 2 (BCPM 12155 *Accipiter striatus*). Posterior views. Specimens scaled to approximately the same distal mediolateral length.

092. Sulcus extensorius (most distal): (0) between medial and lateral condyles, most distal; (1) exits above but midline of the condyles; (2) exits directly above the medial condyle; (3) exits directly above the lateral condyle (Figure 3.51).

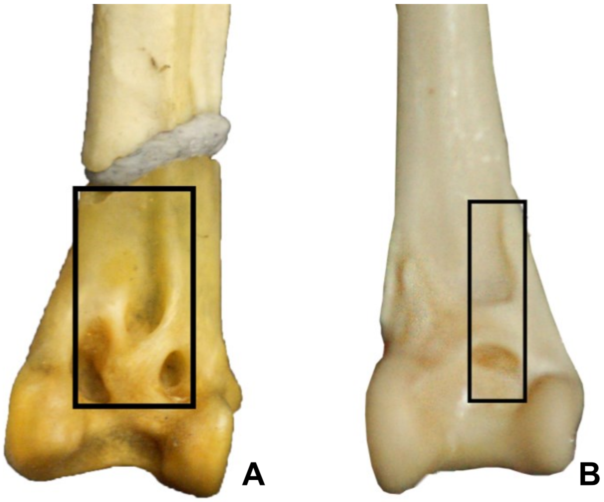

Figure 3.51. Character 092, sulcus extensorius of the distal tibiotarsus. **A**, character state 1 (BCPM 10089 *Falco perigrinus*); **B**, character state 2 (BCPM 10175 *Calidrius minutilla*). Anterior views. Specimens scaled to approximately the same distal mediolateral length.

Comment—Similar to character 2135 of Livezey and Zusi (2006).

093. Tuberculum retinacula m. fibularis: (0) absent, weakly expressed; (1) small projection; (2) elongate projection; (3) multiple ridges; (4) large rounded process (Figure 3.52).

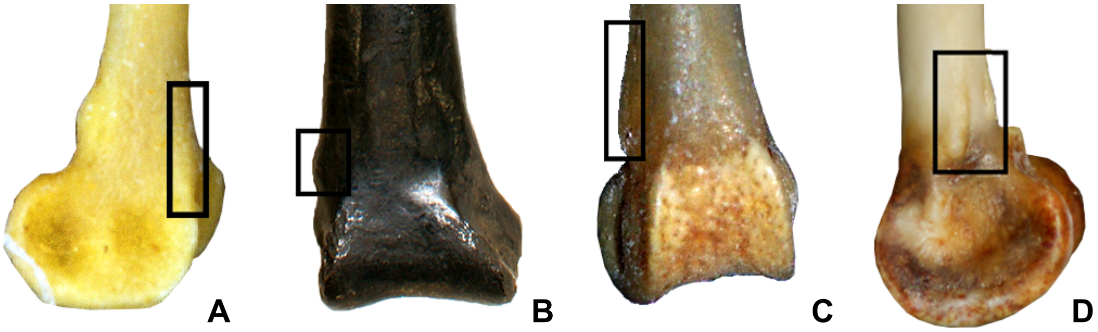

Figure 3.52. Character 093, tuberculum retinacula m. fibularis of the distal tibiotarsus. **A**, character state 0 (CVM 15047 *Limnodromus griseus*, lateral view), **B**, character state 1 (LACM J9744 *Buteogallus daggetti*, posterior view); **C**, character state 2 (BCPM 17451 *Charadrius semipalmatus*, posterior view); **D**, character state 3 (RBCM 23589 *Lagopus lagopus*, lateral view). Specimens scaled to approximately equal distal mediolateral length.

Comment—Similar to character 2138 of Livezey and Zusi (2006), but more character states are here recognized to encompass the variation observed on the study taxa.

094. Articulation of distal fibula to facies lateralis of corpus tibiotarsus: (0) absent; (1) weak expression, flattened area where spina fibula contacts tibial shaft; (2) flange-like projection.

Comment—Distal ossification of the distal most fibula to the corpus tibiotarsus, in some taxa (Falconiformes, Galliformes) is such that a small flange is developed on the facies lateralis of the corpus tibiotarsus.

095. Sulcus m. fibularis (where m. fibularis brevis tendon runs): (0) absent; (1) weak groove; (2) strong groove (Figure 3.53).

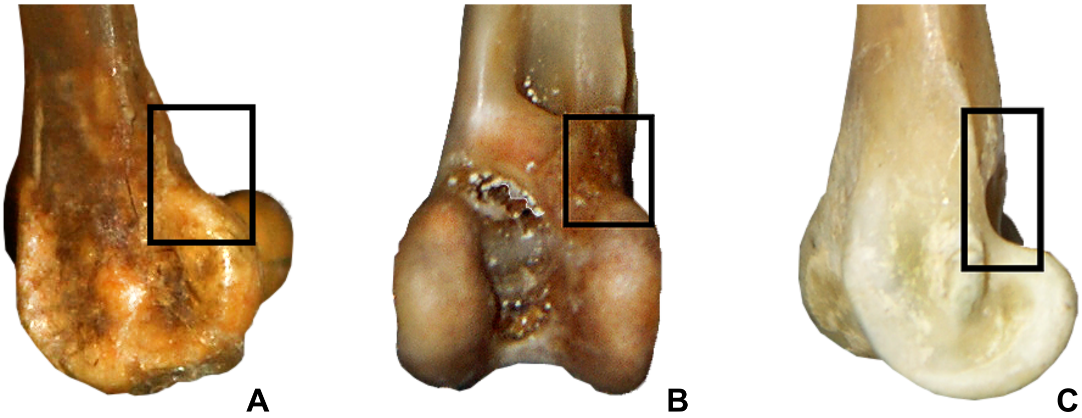

Figure 3.53. Character 095, sulcus m. fibularis of the distal tibiotarsus. **A**, character state 0 (RBCM 23797 *Calidris pusilla*, lateral view); **B**, character state 1 (RBCM 10157 *Lagopus muta*, anterior view); **C**, character state 2 (BCPM 10788 *Falco mexicanus*, lateral view). Specimens scaled to approximately equal distal mediolateral length.

Comment—Similar to character 2295 of Livezey and Zusi (2006).

096. Epicondylus medialis: (0) absent; (1) weak, non-curved; (2) weakly projecting, inward curve; (3) strong and long; (4) small ridge (Figure 3.54).

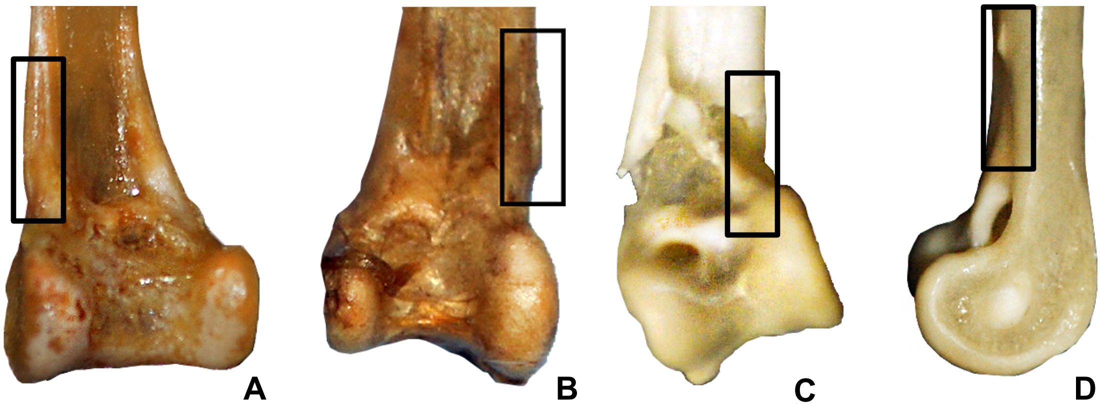

Figure 3.54. Character 096, epicondylus medialis of the distal tibiotarsus. **A**, character state 1 (BCPM 12052 *Larus californicus*, anterior view); **B**, character state 2 (BCPM 17450 *Tringa solitaria*, anterior view); **C**, character state 3 (BCPM 9978 *Charadrius vociferus*, anterior view, distal end broken and displaced); **D**, character state 4 (BCPM 12155 *Accipiter striatus*, medial view). Specimens scaled to approximately the same distal mediolateral length.

Comment—While similar to character 2153 of Livezey and Zusi (2006), the character is coded in that study as either absent or present. The coding of the present study uses character states that encompass the various intermediate morphologies observed on the study taxa.

097. Trochlear cartilage tibialis: (0) weakly developed; (1) equal to condyle height; (2) extends proximal to the condyles (Figure 3.55).

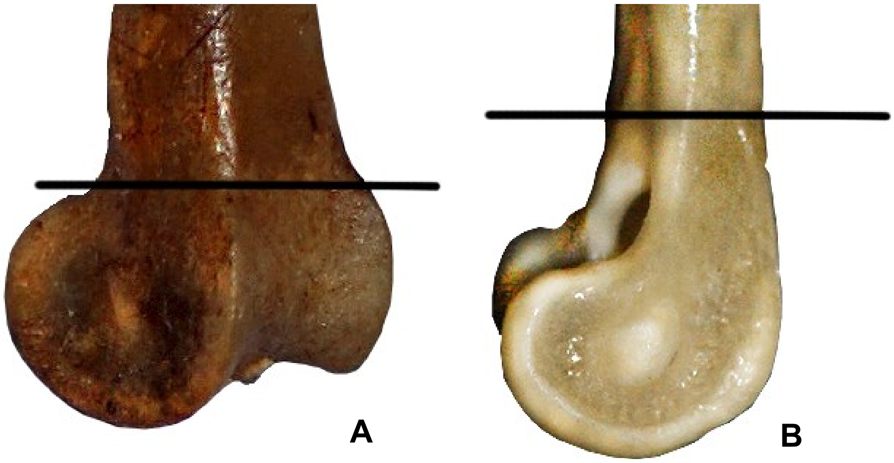

Figure 3.55. Character 097, trochlear cartilaginis tibialis height of the distal tibiotarsus. **A**, character state 1 BCPM 17450 *Tringa solitaria*, posterior view); **B**, character state 2 (BCPM 12155 *Accipiter striatus*, medial view).

098. Trochlear cartilaginis tibialis: (0) smooth; (1) small thin weak ridge; (2) strong secondary ridge; (3) accessory mounds or projections (Figure 3.56).

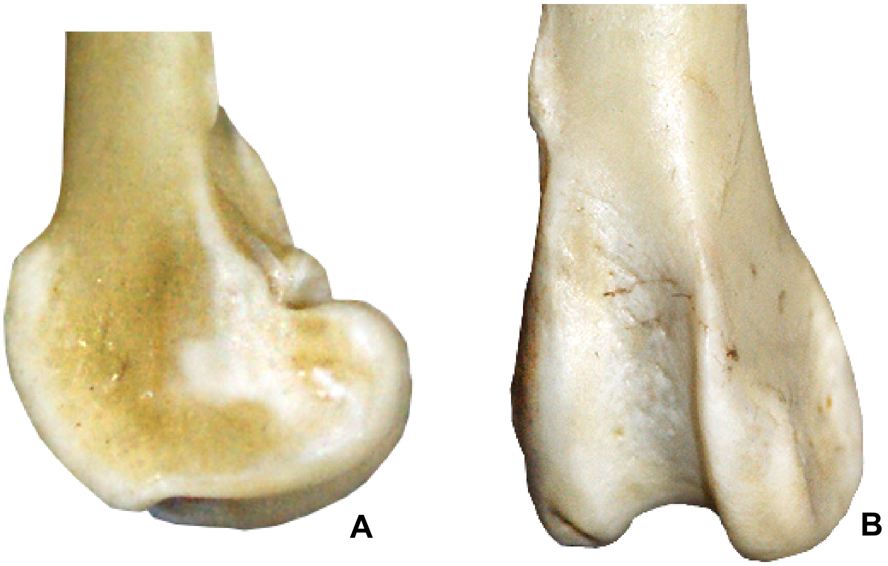

Figure 3.56. Character 098, trochlear cartilaginis tibialis strength of the distal tibiotarsus. **A**, character state 2 (BCPM 15491 *Charadrius vociferus*, medial view); **B**, character state 3 (BCPM 10089 *Falco perigrinus*, posterior view).

Comment—Similar to character of 2151 of Livezey and Zusi (2006).

099. Crista cnemialis lateralis: (0) small swelling; (1) flange-like extension; (2) distally-hooked projection (Figure 3.57).

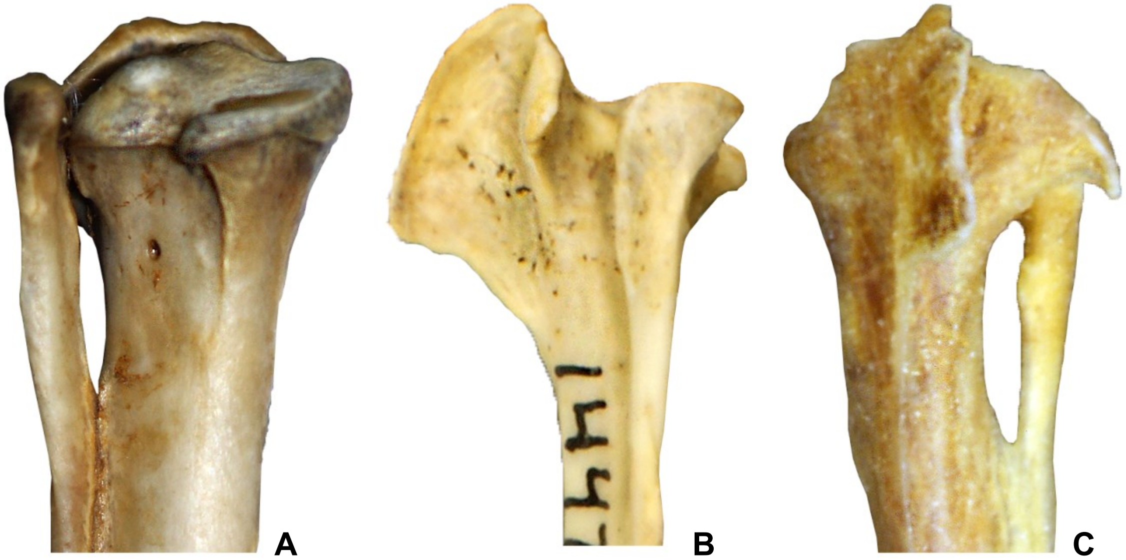

Figure 3.57. Character 099, crista cnemialis lateralis shape. **A**, character state 0 (RBCM 22457 *Lagopus lagopus*, anterior view); **B**, character state 1 (CVM 14476 *Larus delawarensis*, lateral view); **C**, character state 2 (CVM 15073 *Limnodromus griseus*, anterior view). Specimens scaled to approximately the same proximal mediolateral length.

Comments—Similar to character 1347 of Livezey and Zusi (2006).

Tarsometatarsus

100. Ementia intercotylaris: (0) absent; (1) present, does not exceed elevation of cotlyar borders; (2) present, extends slightly above cotlyar borders; (3) present, extends greatly above cotlyar borders; (4) slight rising, without distinct boundaries (Figure 3.58).

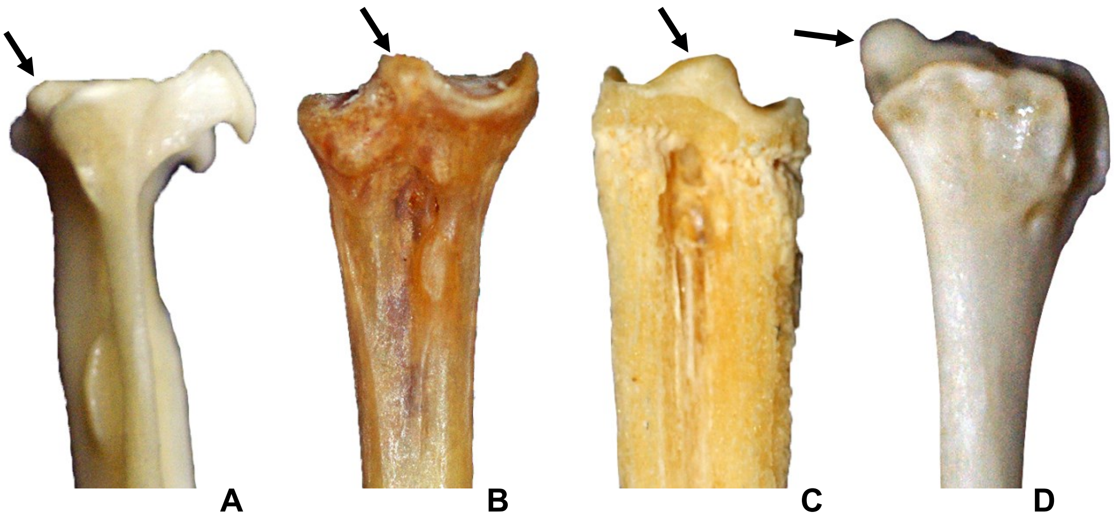

Figure 3.58. Character 100, ementia cotylaris (arrows) of the proximal tarsometatarus. **A**, character state 0 (BCPM 12155 *Accipiter striatus*, medial vew); **B**, character state 1 (BCPM 16186 *Bonasa umbellus*, anterior view); **C**, character state 2 (BCPM 11606 *Tringa flavipes*, anterior view); **D**, character state 3 (BCPM 10175 *Calidris minutilla*, lateral view). Specimens scaled to approximately the same proximal mediolateral length.

Comments—The size and shape of the ementia intercotylaris is used in the dichotomous key of Gilbert et al. (1996) in terms of whether the ementia intercotylaris (there called the intercotylar prominence) was indistinct. Livesey (2010) does not use the ementia intercotylaris in his analyses of Charadriiformes (or if it was used, it was referred to by unfamiliar nomenclature). The ossifications of the distal tarsals on to the proximal tarsometatarsus of Aves (referred to as the ossa tarsi distale in Livesey and Zusi 2006) are discussed in detail in Livesey and Zusi (2006), and one character (2254) codes the ementia intercotylaris as either absent or rudimentary, or present. The present analysis, based on observations of the variable morphology of the ementia intercotylaris in skeletal specimens and those depicted in Gilbert et al. (1996), differentiates the present code to capture the differing sizes of the ementia intercotylaris.

101. Area intercotlyaria: (0) poorly defined; (1) present but minute; (2) present and triangular; (3) present and rectangular, mediolaterally wide; (4) present and rectangular, proximodistally wide (Figure 3.59).

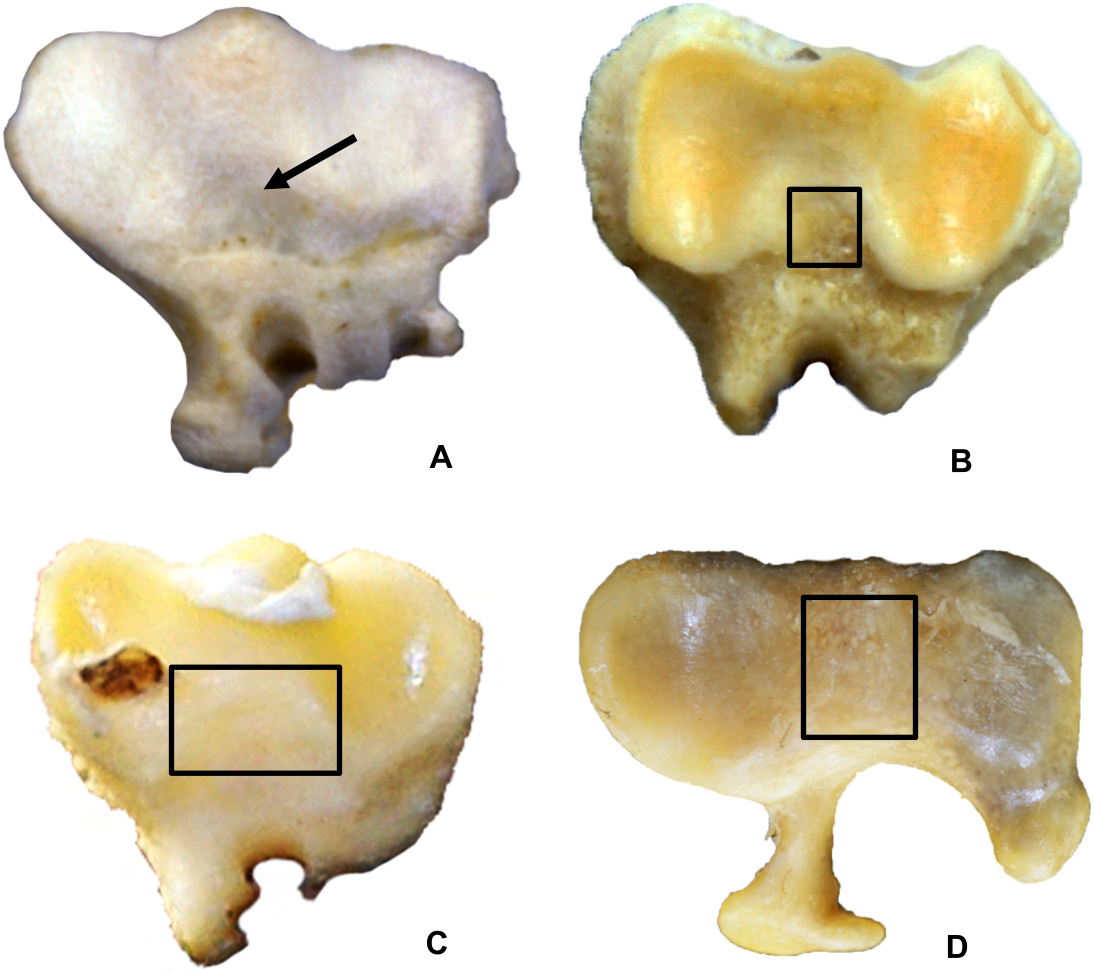

Figure 3.59. Character 101, area intercotylaria of the proximal tarsometatarus. **A**, character state 0 (CVM 14476 *Larus delawarensis*); **B**, character state 1 (CVM 14542 *Recurvirostra americana*); **C**, character state 3 (BCPM 10147 *Calidris pusilla*); **D**, character state 4 (BCPM 10089 *Falco perigrinus*). Proximal views. Specimens scaled to approximately the same mediolateral length.

Comments—The area intercotylaris is addressed in Livezey and Zusi (2006) and coded as absent or obsolete, present, moderately deep, subelliptical, or present, exceptionally deep. Observations of skeletal specimens of Charadriiformes in the present study reveals that there is more varation in the shape of the area intercotylaris than previously addressed, and this is reflected in the character states used in this analysis.

Campbell (1995) uses the shape and proportions of the cotlya medialis to differentiate *Grus pagei* from the similar sized (but slightly larger) *Grus canadensis*. Cotylare medialis et lateralis are not used in the analyses of Livezey (2010); however, characters 2245–2254 of Livezey and Zusi (2006) address the area intercotylaris and cotylares medialis et lateralis. Character 2252 of Livezey and Zusi (2006) codes the cotlyae medialis et lateralis as both cotylae concave, and cotyla lateralis convex. All specimens examined had both cotylae medialis et lateralis concave, so this character would have proved uninformative in the analyses of the sample taxa. Characters 2250–2251 and 2253 of Livezey and Zusi (2006), dealing with the asymmetry of the cotylar surface area and the rims (respectively), would also prove uninformative as all study taxa had a slightly larger cotyla medialis, asymmetry of the cotylar rims, and the cotyla medialis being higher than in cotyla lateralis.

102. Sulcus ligamentosus: (0) absent or poorly defined; (1) present but not mediolaterally continuous; (2) present, thin, mediolaterally continuous; (3) large, broad, and mediolaterally continuous; (4) small, only present medially or laterally; (5) present only on proximal surface of medial and lateral hypotarsal ridges (Figure 3.60).

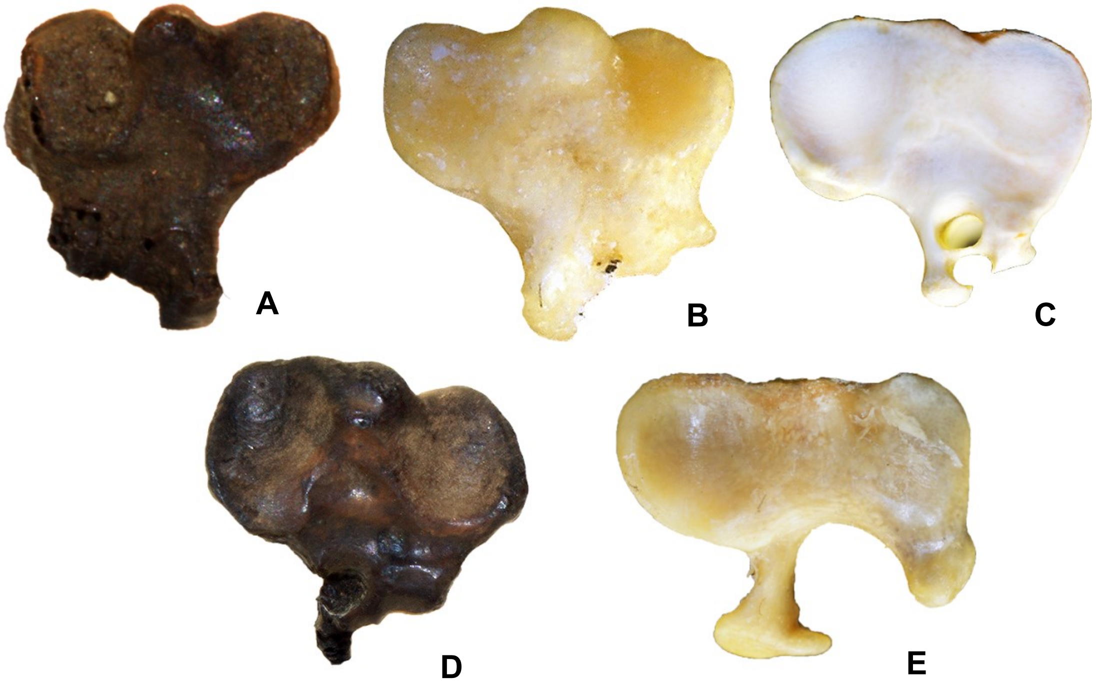

Figure 3.60. Character 102, sulcus ligamentosus of the proximal tarsometatarus. **A**, character state 1 (LACM K1125 *Pluvialis squatarola*); **B**, character state 2 (BCPM 9943 *Tringa melanoleuca*); **C**, character state 3 (CVM 13393 *Lagopus muta*); **D**, character state 4 (LACM E5075 *Parapavo californicus*); **E**, character state 5 (BCPM 10089 *Falco perigrinus*). Proximal views. Specimens scaled to approximately the same mediolateral length.

Comments—Livezey and Zusi (2006) recognize the character states of absent or obsolete, present [and] shallow, and present and deep for the sulcus ligamentosus. Livezey (2010) observed the character states of present, often unilateral and laterally descendent or absent. Observations made of skeletal specimens for present analysis reveals other character states for this character. For some examples, the sulcus ligamentosus for those specimens with a reduced/fused number of hypotarsal ridges (e.g. members of the Falconiformes) shows that the sulcus ligamentosus is only expressed on the proximal surface of the hypotarsal ridges and is not connected to the area intercotylaris. Also, there are differences in the anteroposterior length of the sulcus ligamentosus that can be expressed as thin and broad. Finally, the sulcus ligamentosus is not mediolaterally continuous in all specimens (e.g. *Ciconia maltha*). Character states for the sulcus ligamentosus were created to address this variable morphology to see if this variation contained systematic information.

103. Tuberculum m. fibularis brevis: (0) absent; (1) present but weakly developed; (2) strongly developed and small; (3) strongly developed and large, rounded; (4) hook-like; (5) distally expressed (Figure 3.61)

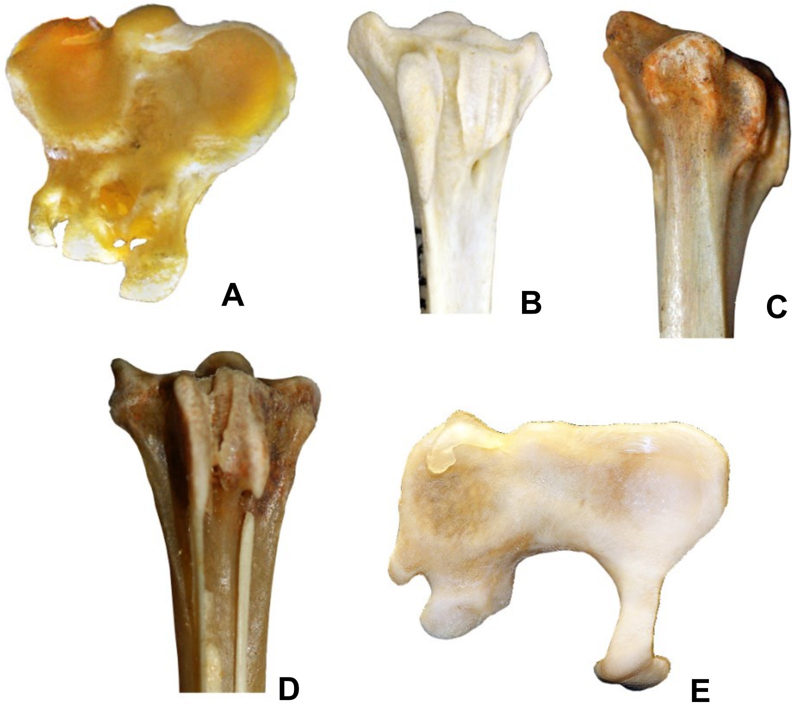

Figure 3.61. Character 103, tuberculum m. fibularis brevis of the proximal tarsometatarsus. **A**, character state 0 (BCPM 9943 *Tringa melanoleuca*, proximal view); **B**, character state 1 (CVM 14476 *Larus delawarensis*, posterior view); **C**, character state 2 (BCPM 11285 *Larus californicus*, lateral view); **D**, character state 3 (CVM 14123 *Bonasa umbellus*, posterior view); **E**, character state 4 (BCPM 2247 *Buteo regalis*, proximal view). Specimens scaled to approximately equal proximal mediolateral length.

Comments—Livezey and Zusi (2006) coded the tuberculum m. fibularis brevis as possessing the character states of absent or indistinct impression or tumulus, or a present, prominent processus. The present analysis recognizes a more varied morphology of the tuburculum m. fibularis brevis, from absent to weak, to large and hook-like.

104. Fossa parahypotarsalis lateralis: (0) continuous with lateral hypotarsal ridge; (1) weakly developed/shallow; (2) strongly developed/deep (Figure 3.62).

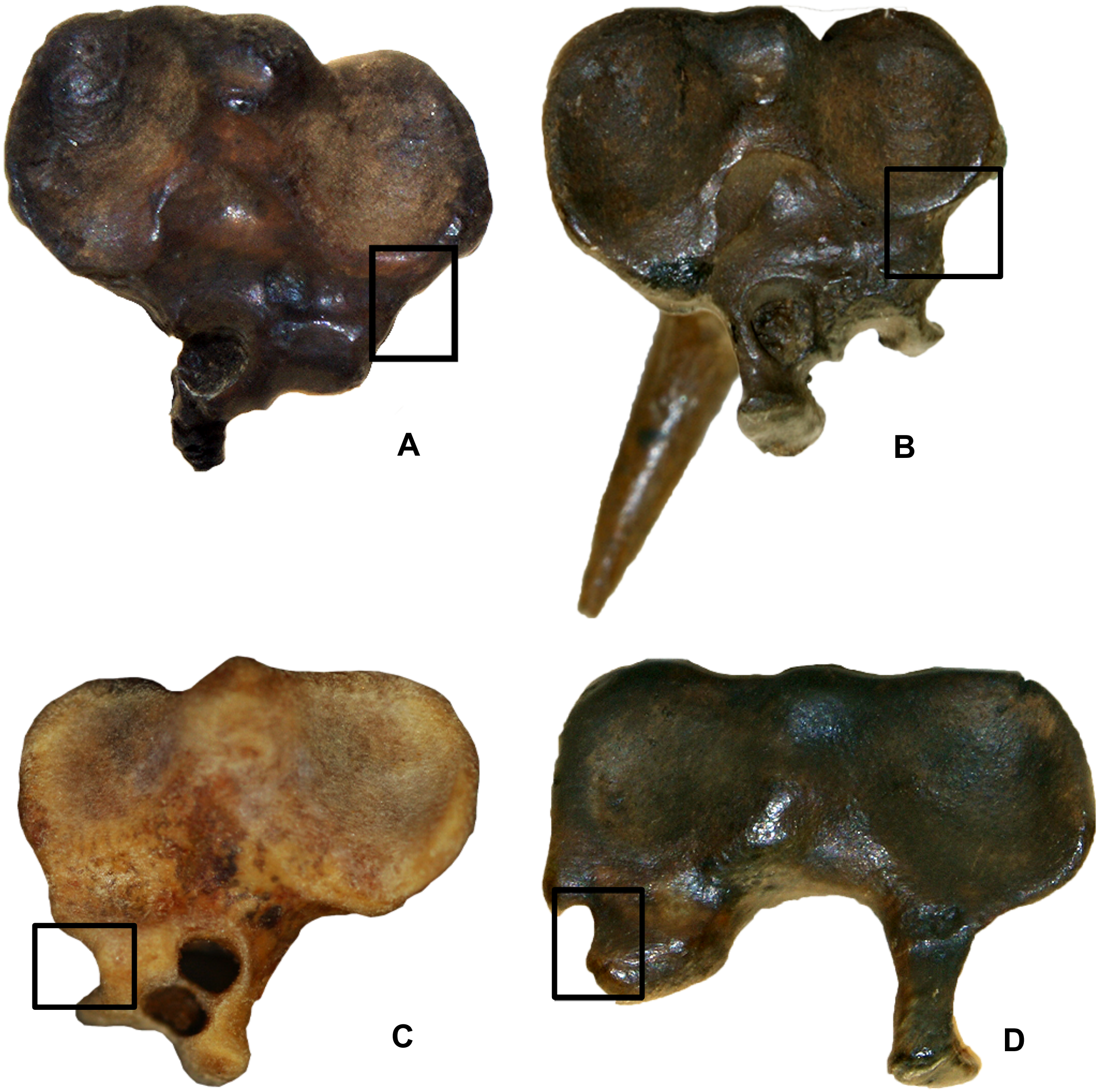

Figure 3.62. Character 104, fossa parahypotarsalis lateralis of the proximal tarsometatarsus. **A**, female *Paravapo californicus*, character state 0 (LACM E5075); **B**, male *Parapavo californicus*, character state 1 (LACM E5333); **C**, character state 2 (RBCM 23589 *Lagopus lagopus*); **D**, character state 3 (*Buteogallus daggetti*, LACM, unnumbered). Proximal views. Specimens scaled to approximately the same mediolateral length.

105. Fossa parahypotarsalis medialis: (0) continuous with medial hypotarsal ridge; (1) weakly developed/shallow; (2) strongly developed/deep (Figure 3.62).

Comments—Character states for fossae parahypotarsalis medialis et lateralis are similar to characters 2256–2258 of Livezey and Zusi (2006; see references within for other treatments of these characters).

106. Hypotarsal ridges: (0) absent; (1) only cristae medialis and lateralis present; (2) cristae intermediae hypotarsi present, up to four (Figure 3.63).

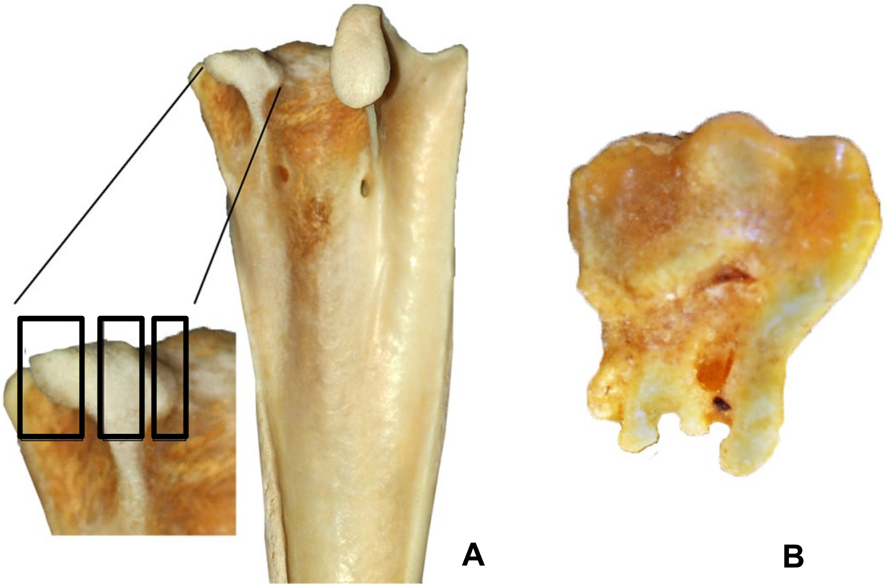

Figure 3.63. Character 106, hypotarsal ridges of the proximal tarsometatarsus. **A**, character state 1 (BCPM 22247 *Buteo regalis*, posterior view); **B**, character state 2 (BCPM 11285 *Larus californicus*, proximal view). Specimens scaled to approximately the same mediolateral length. The absence of the hypotarsal ridges is not due to ontogeny, as metatarsals from juvenile specimens lack hypotarsal ridges, as well as the cotlyar region of the proximal surface. The single lateral hypotarsal ridge in A appears to be a secondary fusion of the lateral and intermediate hypotarsal ridges.

Comments—There is a great deal of variation in describing and coding the hypotarsus for cladistics analyses. Strauch (1978) describe the canals formed in (some) Aves as tendinale passages 2–4, with passage 2 likely referring to the canalis tendinorum, passage 3 being the canalis tendinis insertii m flexor halluces longus, and passage 4 being the canalis tendinis insertii m. fibularis longus (Livezey 2010). Stauch's (1978) tendinal passage characters were reanalyzed (and discarded) by Mickevick and Patenti (1980), and analyzed again by Chu (1995). Hypotarsal ridges/canals form a substantial part of morphological phylogenetic analyses in Livezey (2010, characters 0409–0417), and Livezey and Zusi (2006, characters 2278–2286 for the hypotarsus proprius). See Livezey (2010) for a complete reference list of the treatment of the canales tendinale.

107. Hypotarsal ridges/canalis tendinalis: (0) no enclosed canals; (1) partially enclosed canals; (2) fully enclosed canals (Figure 3.64).

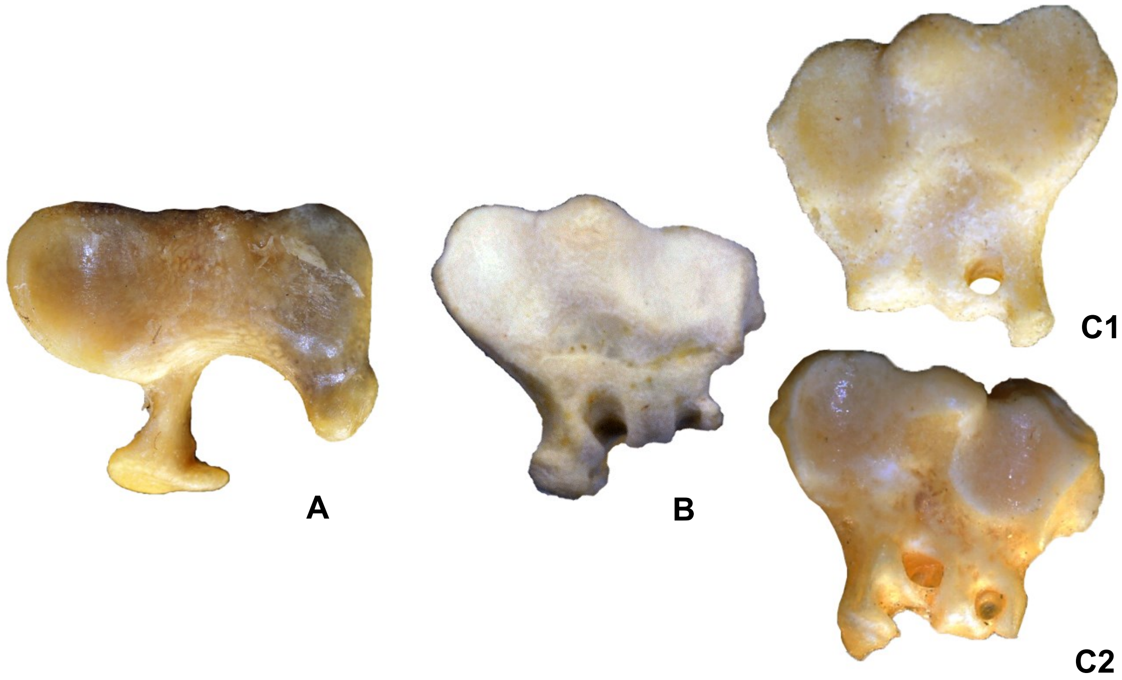

Figure 3.64. Character 107, canalis tendinalis of the proximal tarsometatarsus. **A**, character state 0 (BCPM 10089 *Falco perigrinus*); **B**, character state 1 (CVM 14476 *Larus delawarensis*), **C**, character state 2 (C1, *Tringa melanoleuca*; C2, BCPM 15491 *Charadrius vociferus*). Proximal views. Specimens scaled to approximately the same mediolateral length.

Comment—Refer to comments for character 106 for the hypotarsal ridges.

108. Hypotarsal ridges: (0) all equal in plantar length; (1) medial and lateral largest; (2) medial largest, lateral same as accessory; (3) lateral largest, medial same as accessory (Figure 3.65).

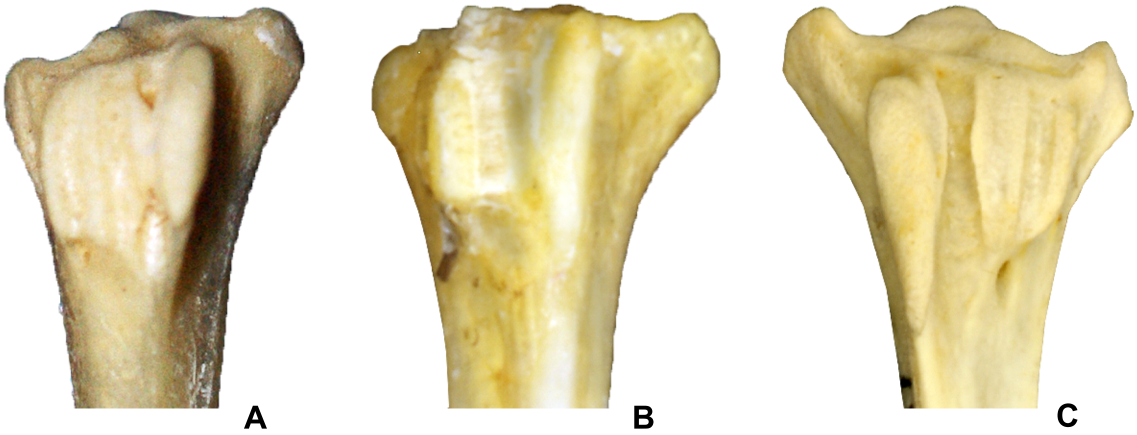

Figure 3.65. Character 108, hypotarsal ridge length of the proximal tarsometatarsus. **A**, character state 0 (BCPM 17451 *Charadrius semipalmatus*); **B**, character state 1 (RBCM 18305 *Calidris pusilla*); **C**, character state 2 (CVM 14476 *Larus delawarensis*). Posterior views. Specimens scaled to approximately the same mediolateral length.

Comment—Similar to character states encompassed by characters 2278–2286 in Livezey and Zusi (2006).

109. Hypotarsal ridges: medial hypotarsal ridge (0) straight; (1) ends inflated/enlarged; (2) inflated and laterally curled; (3) large, extends length of the metatarsal shaft of medial flexor crista (Figure 3.66).

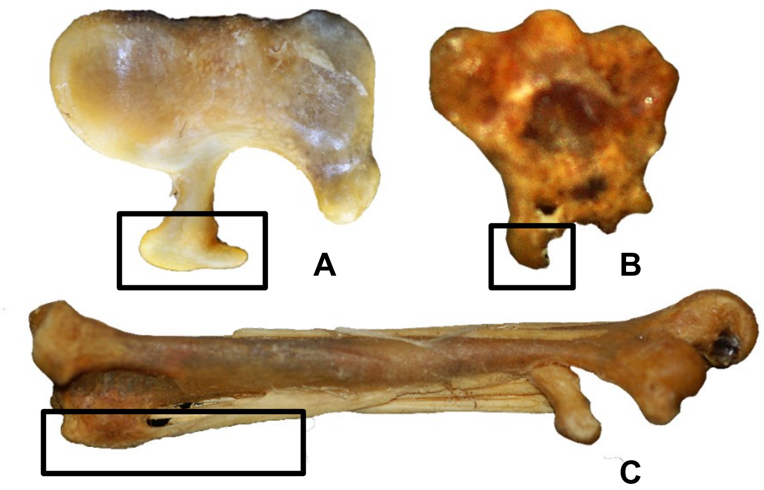

Figure 3.66. Character 109, medial hypotarsal ridge of the proximal tarsometatarsus. **A**, character state 1 (BCPM 10089 *Falco perigrinus*, proximal view), **B**, character state 2 (RBCM 23178 *Tringa solitaria*, proximal view); **C**, character state 3 (CVM 3149 *Falcipennis canadensis*, medial view). Specimens scaled to approximately the same mediolateral length.

Comment—Similar to characters 2276–2277 of Livezey and Zusi (2006). The present study includes character states that account for the lateral curl or lateral projection seen on the most posterior portion of the medial hypotarsal ridge, and distinguishes this lateral projection from the mediolateral flaring or expansion that was observed in some taxa.

110. Hypotarsal ridges: accessory hypotarsal ridges (0) absent; (1) attached to medial and medial intermediate hypotarsal ridge only; (2) on medial and lateral hypotarsal ridges; (3) on lateral hypotarsal ridge only; (4) same as for character state 1, and also attached to intermediate hypotarsal ridges (Figure 3.67).

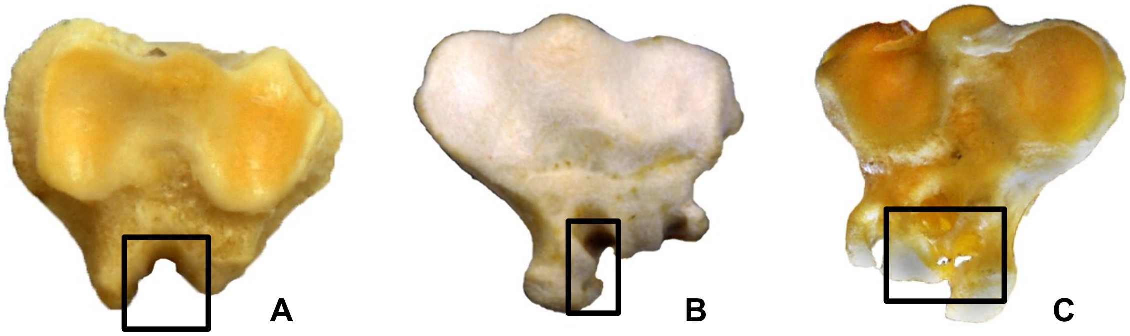

Figure 3.67. Character 110, accessory hypotarsal ridges of the proximal tarsometatarsus. **A**, character state 1 (CVM 14542 *Recurvirostra americana*); **B**, character state 2 (CVM 14476 *Larus delawarensis*); **C**, character state 3 (BCPM 9978 *Charadrius vociferus*). Proximal views. Specimens scaled to approximately the same mediolateral length.

Comment—This character is similar to character 2274–2275 of Livezey and Zusi (2006), who recognize the character states of absent or present and distinct for intermediate hypotarsal ridges. However, these character states do not address accessory ridges that encompass the canales tendinales of the hypotarsal ridges. Whereas these features are indirectly coded in characters 2278–2286 of Livezey and Zusi (2006), they would be difficult to recognize in incompletely preserved or prepared specimens, where damage to the delicate bone enclosing the canales tendinales is probable (and was observed in fossil specimens).

111. Hypotarsal ridges: lateral hypotarsal ridge (0) distinct and separate from intermediate hypotarsal ridges; (1) slight fusion with intermediate hypotarsal ridges anteriorly; (2) lateral and intermediate ridges extending from a single bony projection; (3) single and/or secondarily fused (Figure 3.68).

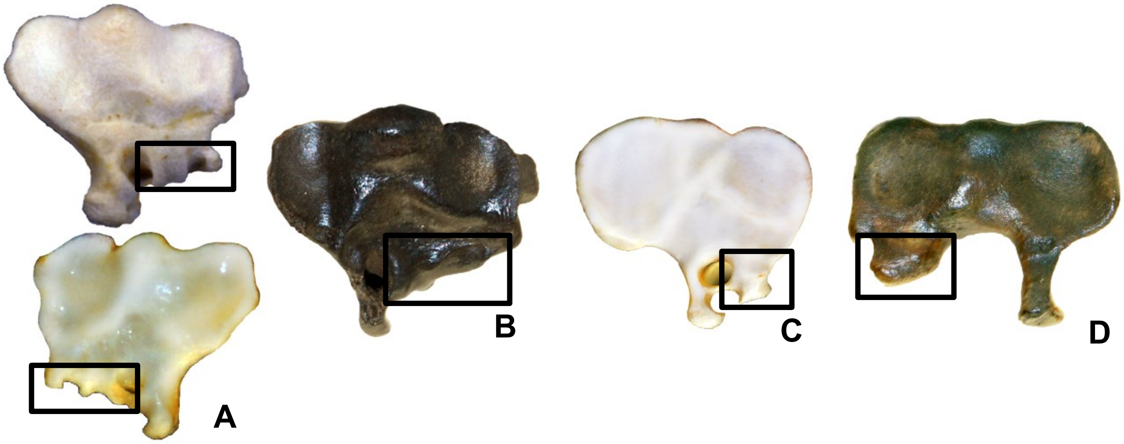

Figure 3.68. Character 111, lateral hypotarsal ridges of the proximal tarsometatarsus. **A**, character state 0 (CVM 14476 *Larus delawarensis*, top; BCPM 10175 *Calidris minutilla*, bottom); **B**, character state 1 (LACM F452 *Grus pagei*); **C**, character state 2 (CVM 13393 *Lagopus lagopus*); **D**, character state 3 (*Buteogallus daggetti*, LACM, unnumbered). Proximal views. Specimens scaled to approximately the same mediolateral length.

Comment—Part of the hypotarsus proprius of Livezey and Zusi (2006), this character is similar to character 2272 of that study; however, the nature of the attachment to the proximal tarsometatarsus was not elaborated on. Also, observations of the hypotarsal ridges of Ciconiiformes and Falconiformes reveal that the intermediate hypotarsal ridges are not absent, but are likely secondarily fused into a single, most lateral hypotarsal ridge. While this character was analyzed in an unordered state, there may be justification in future analyses to order these character states.

112. Impressiones ligamentum collateralis lateralis: (0) absent or poorly developed; (1) weakly developed; (2) strongly developed (Figure 3.69).

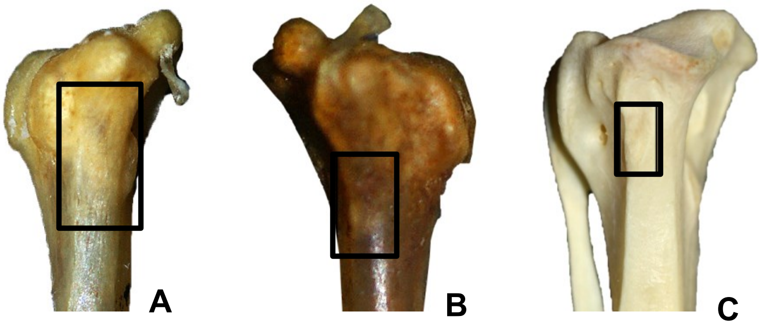

Figure 3.69. Character 112, impressiones ligamentum collateralis lateralis of the proximal tarsometatarsus. **A**, character state 0 (RBCM 18305 *Calidris alba*); **B**, character state 1 (RBCM 23797 *Calidris pusilla*); **C**, character state 3 (CVM 13393 *Lagopus muta*). Lateral views. Specimens scaled to approximately the same mediolateral length.

Comment—This character is similarly coded in Livezey and Zusi (2006), who made the differentiation between whether impressions ligamentum collateralis lateralis is expressed as a tuberosity or a fovea. In the present study it was not necessary to differentiate between a fovea or tuberosity, as this feature was weakly expressed.

113. Tuberositas m. tib. cranialis: (0) absent; (1) weakly developed; (2) strong and rounded; (3) strong and elongate; (4) rounded, not centered; (5) elongate, not centered; (6) surrounding foramen.

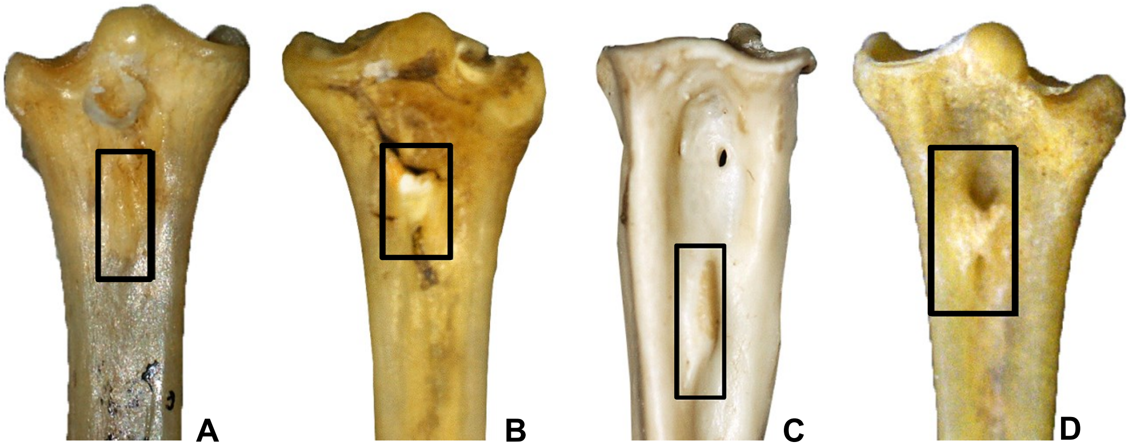

Figure 3.70. Character 113, tuberositas m. tibialis cranialis of the proximal tarsometatarsus. **A**, character state 1 (BCPM 18305 *Calidris alba*); **B**, character state 2 (CVM 11485 *Charadrius semipalmatus*); **C**, character state 3 (BCPM 22403 *Accipiter cooperii*); **D**, character state 4 (BCPM 9978 *Chardrius vociferus*). Anterior views. Specimens scaled to approximately the same mediolateral length.

Comment—The tuberositas (insertii) m. tibialis cranialis is coded by Livezey and Zusi (2006) as character 2260 as obsolete or small, subcircular, moderately elevated, or typically angling towards facies medialis corporis. It is also treated as part of the character states of character 2306 for the impressiones retinacula extensorii. The present study treats the tuberositas m. tibialis cranialis separate from the impressiones retinacula extensorii. The character states used in the present study describe the variation of morphologies observed in the study taxa.

114. Fossa infracotlyar dorsalis: (0) absent, continuous with metatarsal shaft; (1) weakly developed, shallow; (2) strongly developed, deep, no visible foramen; (3) strongly developed, deep, visible foramen (Figure 3.71).

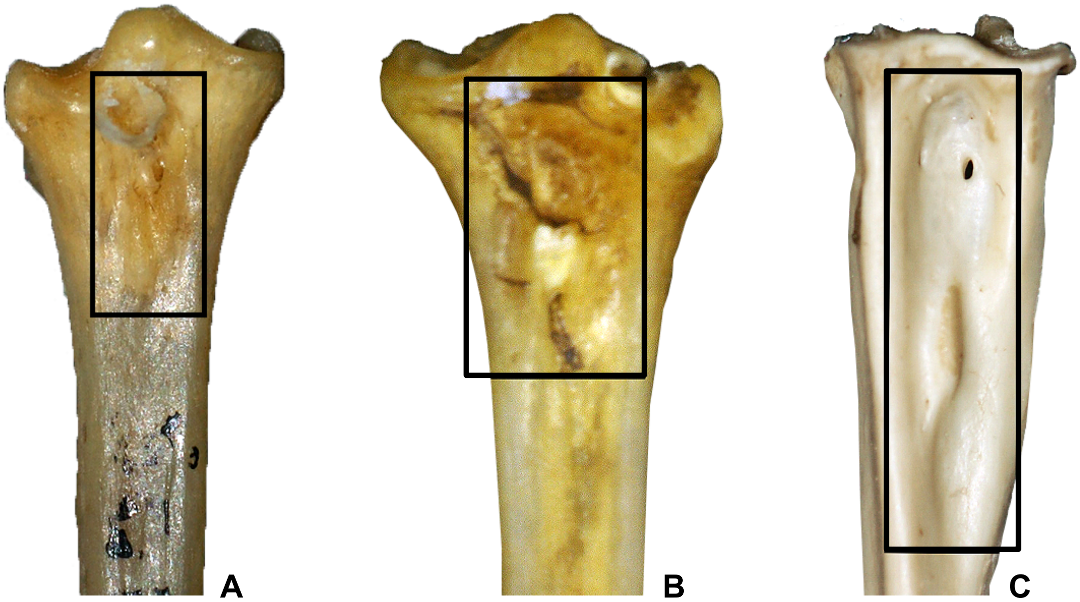

Figure 3.71. Character 114, fossa infracotlyar dorsalis of the proximal tarsometatarsus. **A**, character state 1 (BCPM 18305 *Calidris alba*); **B**, character state 2 (CVM 11485 *Charadrius semipalmatus*); **C**, character state 3 (BCPM 22403 *Accipiter cooperii*). Anterior views. Specimens scaled to approximately the same mediolateral length. Large tuberositas m. tibialis cranialis is typically associated with a large, deeply excavated fossa infracotlyar dorsalis.

Comment—Similar to character 2259 and 2265 of Livezey and Zusi (2006).

115. Impressiones retinaculi extensorii: (0) absent; (1) weakly developed or single; (2) strongly developed, multiple (Figure 3.72).

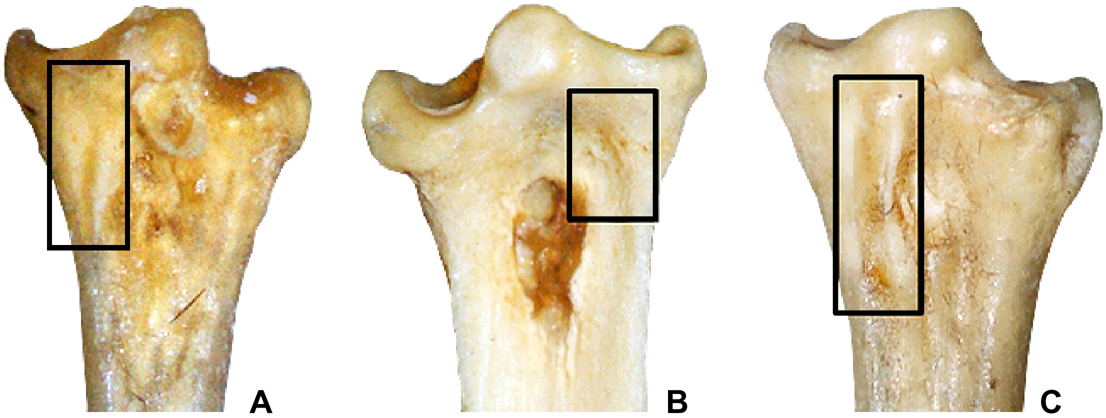

Figure 3.72. Character 115, impressiones retinacula extensorii of the proximal tarsometatarsus. **A**, character state 0 (BCPM 17434 *Calidris pusilla*); **B**, character state 1 (BCPM 10769 *Charadrius vociferus*, juvenile); **C**, character state 2 (BCPM 17451 *Charadrius semipalmatus*, adult). Anterior views. Specimens scaled to approximately the same mediolateral length. There is significant ontogenetic variation in the presence of the impressiones retinacula extensorii, seen in their absence in juveniles (B) and their strong presence in adults (C) of the same genus (*Charadrius*).

Comment—This character is coded by Livezey and Zusi (2006) in characters 2306 and 2307 to describe both the strength and the shape of the impressiones retinacula extensorii. This character does not include the tuberositas m. tibialis cranialis, as it is in character 2306 of Livezey and Zusi (2006).

116. Sulcus m. fibularis longi: (0) absent; (1) weak/shallow; (2) strongly developed (Figure 3.73).

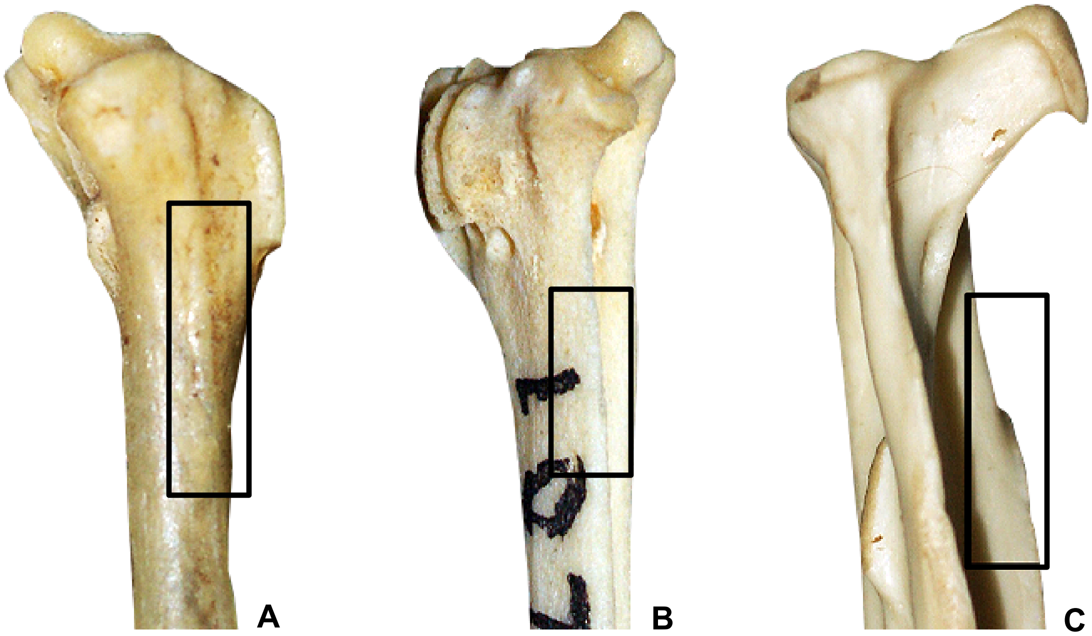

Figure 3.73. Character 116, sulcus m. fibularis longi of the proximal tarsometatarsus. **A**, character state 0 (BCPM 17451 *Charadrius semipalmatus*, lateral view); **B**, character state 1 (BCPM 10760 *Charadrius vociferus*, lateral view); **C**, character state 2 (RBCM 22366 *Buteo jamaicensis*, medial view). Specimens scaled to approximately equal proximal anteroposterior length.

Comment—This character is similar to character 2295 of Livezey and Zusi (2006).

117. Cristae plantares medialis et lateralis: (0) rounded, absent; (1) weak ridges; (2) strong ridges (Figure 3.74).

Figure 3.74. Character 117, cristae plantares medialis et lateralis of the tarsometatarsus. **A**, character state 0 (BCPM 10147 *Calidris pusilla*, posterior view); **B**, **C**, character state 1 (B, BCPM 10760 *Charadrius vociferus*, posterior view; C, CVM 14573 *Dendragapus obscurus*, posterior view); **D**, character state 2 (BCPM 220403 *Accipiter cooperii*, medial view). Specimens scaled to approximately equal proximodistal length.

Comment—Similar to character 2294 of Livezey and Zusi (2006).

118. Facies dorsalis: (0) continuous with metatarsal shaft; (1) weakly excavated; (2) strongly excavated; (3) strong shaft torsion, medially.

Comment—While partially encompassed by character 2289 in Livezey and Zusi (2006), the morphology of the facies dorsalis is directly influenced by the strength and length of the fossa infracotylar dorsalis and the sulcus extensorius. In some taxa, the facies dorsalis is anteroposteriorly compressed such that there is strong medial torsion in the corpus metatarsus.

119. Foramen vasculare distale: (0) absent; (1) close to intertrochlear notch; (2) separated from intertrochlear notch (Figure 3.75).

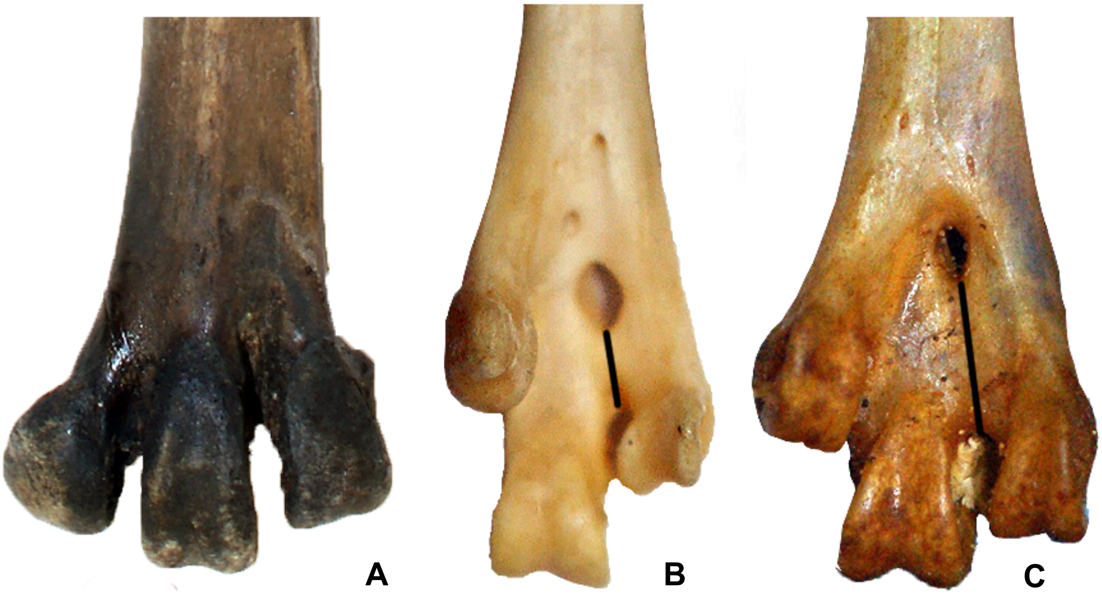

Figure 3.75. Character 119, foramen vasculare distale of the distal tarsometatarsus. **A**, character state 0 (LACM F496 *Ardea herodias*); **B**, character state 1 (RBCM 16247 *Calidris minutilla*); **C**, character state 2 (BCPM 10151 *Larus californicus*). Posterior views. Specimens scaled to approximately equal distal mediolateral length.

Comment—The relative position of the foramen vasculare distale is not addressed in Livezey (2010), but is described in character 2315 of Livezey and Zusi (2006).

120. Incisura intertrochlearis: (0) equal in length; (1) II-III smaller than III-IV; (2) II-III larger than III-IV (Figure 3.76).

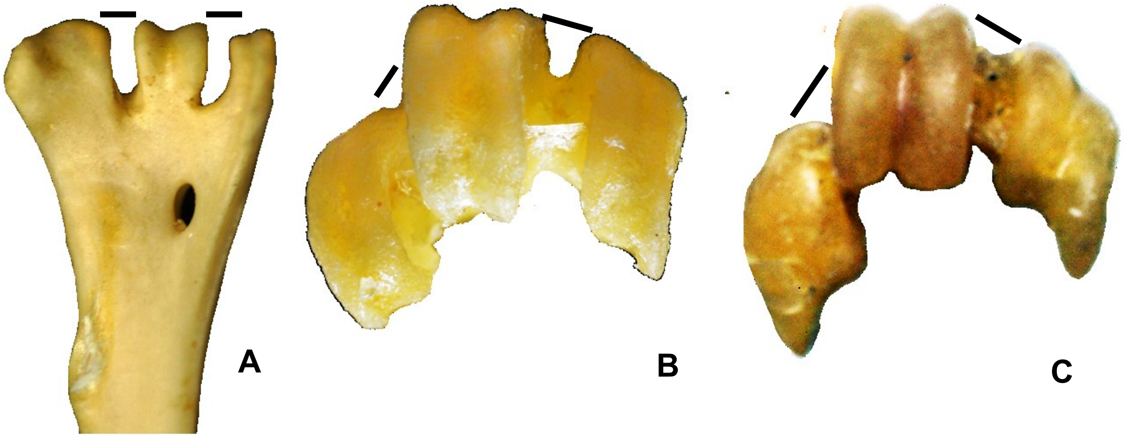

Figure 3.76. Character 120, incisura intertrochlearis widths of the distal tarsometatarsus. **A**, character state 0 (BCPM 9919 *Accipter cooperii*, posterior view); **B**, character state 1 (BCPM 23257 *Actitis macularius*, distal view); **C**, character state 2 (CVM 14428 *Charadrius vociferus*, distal view). Specimens scaled to approximately equal distal mediolateral length. Intertrochlear widths indicated by black lines.

Comment—Livezey and Zusi (2006) compare the size of the foramen vasculare distale to the incisura intertrochlearis III et IV.

121. Distal tarsometatarsus: metatarsus II (0) plantar displacement of distal end equal to that of MTIV; (1) slightly greater plantar displacement than MTIV; (2) much greater displacement than MTIV, extensor surface of MTII not past plantar surface of MTIV; (3) much greater displacement than MTIV, extensor surface level or past plantar surface of MTIV; (4) plantar displacement of MT IV greater than II (Figure 3.77).

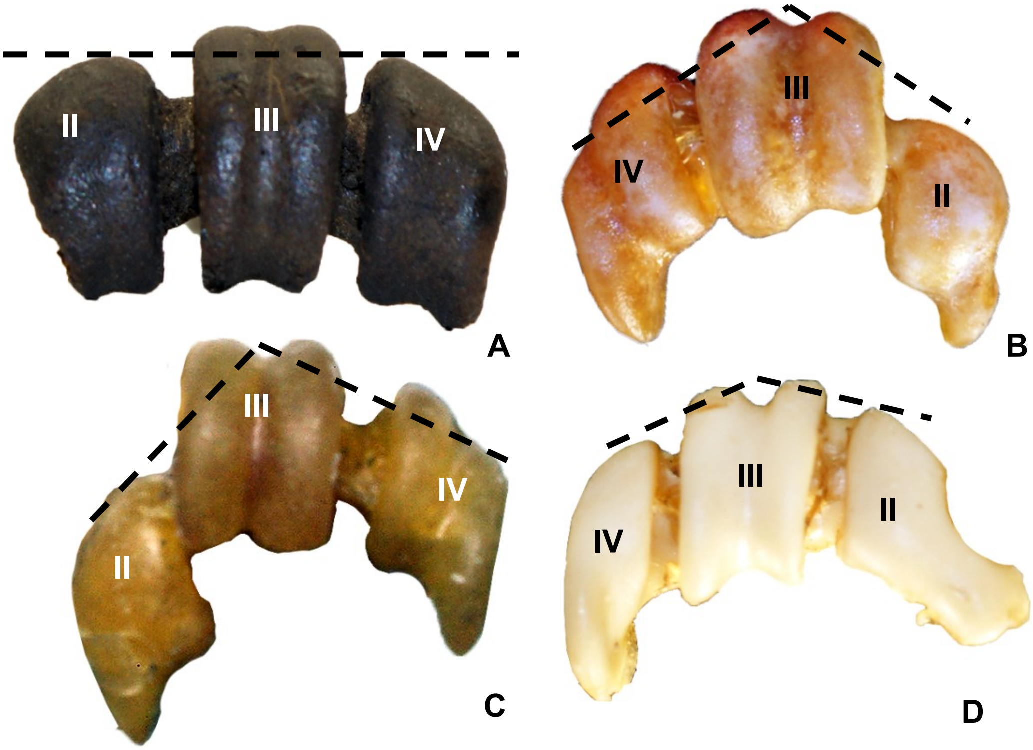

Figure 3.77. Character 121, plantar displacement of trochlear surface of distal metatarsal II. **A**, character state 0 (LACM G4896 *Ardea herodias*); **B**, character state 1 (CVM 2149 *Falcipennis canadensis*); **C**, character state 2 (CVM 14485 *Charadrius semipalmatus*); **D**, character state 4 (BCPM 22403 *Accipiter cooperii*). Distal views. Specimens scaled to approximately equal distal mediolateral length. Dashed lines indicate the degree of plantar displacement relative to the most anterior point of the trochlear groove of metatarsal III. Refer to the comments for detailed explanation of this character, and to Figure 4.02 in Chapter 4 on the relative plantar displacements in avian versus non-avian theropods.

Comment—This character is partially encompassed in several characters used by Livezey and Zusi (2006). Character 2344 (Livezey and Zusi, 2006) describes the relative position of the trochlea of metatarsal III to that of II and IV; character 2352 (Livezey and Zusi, 2006) describes the position of the trochlea medioplantaris of metatarsal II, with one of the character states referring to the torsion of the trochlea of metatarsal II; character 2358 (Livezey and Zusi, 2006) describes the mediolateral (there called lateromedial) splaying of the trochlea of metatarsals II–IV, with character state 2358(b) (Livezey and Zusi, 2006) similar to charater 22(2–3) of the present study, and 2358(d) (Livezey and Zusi, 2006) similar to 22(0) of the present study. While Livezey and Zusi (2006) describe the relative mediolateral splaying of metatarsals II–IV to be comparatively invariant and difficult to assess in repeatable fashion in Neornithes, they did state that the most informative component was the relative lateral displacement of trochlea metatarsi II and the medial displacement of trochlea metatarsi IV, and the mediolateral splay related to the mediolateral size of the intertrochlear notches (Livezey and Zusi 2006). This character was differentiated in Livezey (2010) in character 0436–0437, which specifically addresses the relative position of the trochlea of metatarsal II with relation to metatarsals III and IV.

Character 0437 of Livezey (2010) is similar to the angle formed by the distal ends of metatarsals II and IV as measured by Falk et al. (2011); however, the focus of the their study was ecological, not phylogenetic. The relative plantar displacements of metatarsals II and IV in relation to metatarsal III was expanded on in Buckley et al. (2015) and McCrea et al. (2015). The relative displacement of metatarsal II–III and III–IV was demonstrated in Charadriidae, but not Scolopacidae, to be significantly different (Chapter 6; Buckley et al., 2015; McCrea et al., 2015). The plantar displacement of metatarsal II–III and III–IV is examined in more detail in Buckley et al. (2015), where a pattern is observed: in non-avian theropods and Coelurosauria there is neither strong plantar displacement nor medioplantar rotation of the distal ends of both metatarsals II and IV. The lack of plantar displacement and medioplantar rotation in metatarsals II and IV is secondarily absent in perching birds, and those non-perching birds that frequently stand on branches as part of their behavior.

122. Distal metatarsal II: trochlea (0) roughly equal in size; (1) lateral trochlear ridge slightly enlarged and rounded; (2) lateral trochlear ridge much larger, with medial ridge flange-like, but still trochlear in shape; (3) lateral trochlear ridge rounded and contributes to majority of metatarsophalangeal joint, small medial flange; (4) lateral trochlear ridge rounded and contributes to majority of metatarsophalangeal joint, large or long medial flange (Figure 3.78).

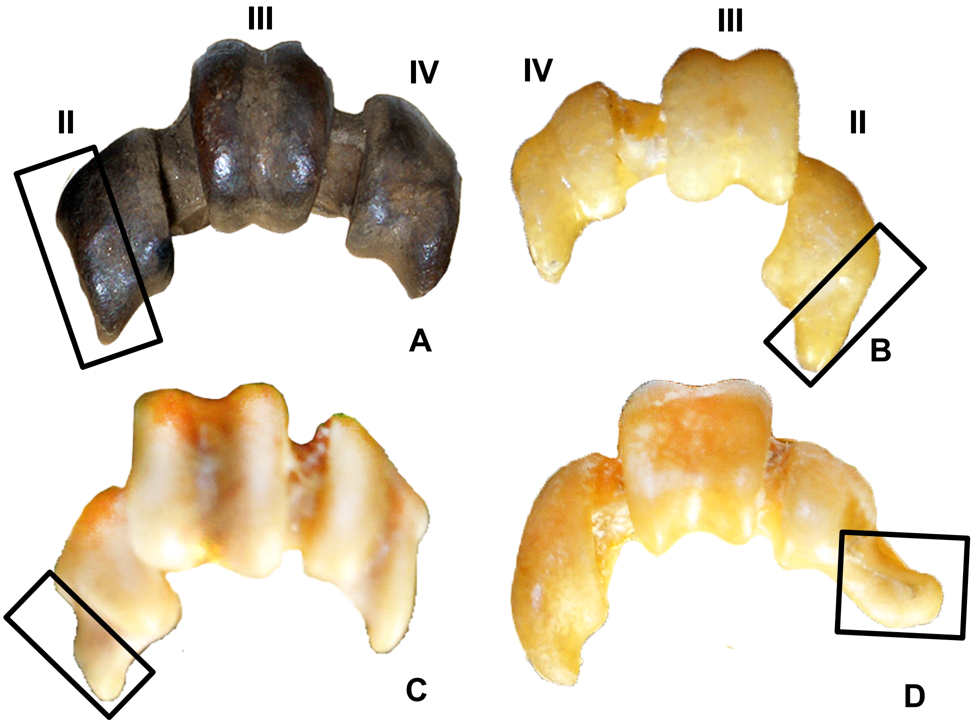

Figure 3.78. Character 122, distal metatarsal II, trochlear shape of the distal tarsometatarsus. **A**, character state 1 (LACM K3156 *Ciconia maltha*); **B**, character state 2 (RBCM 18305 *Calidris alba*); **C**, character state 3 (RBCM 10157 *Lagopus muta*); **D**, character state 4 (BCPM 10788 *Falco mexicanus*). Distal views. Specimens scaled to approximately equal distal mediolateral length. Small flange-like medial trochlea are a characteristic of (in this study) Galliformes (C), while medially elongate medial trochlear ridges are restricted (in this study) to Falconiformes (D).

Comment—A new term was proposed by Livezey and Zusi (2006) to describe the medioplantar extension of the medial trochlea of metatarsal II (processus medioplantaris), and is restricted to Falconiformes.

123. Metatarsal IV, distal: trochlea (0) roughly equal in size; (1) medial slightly larger; (2) medial much larger and rounded, lateral flange-like; (3) lateral larger (Figure 3.79).

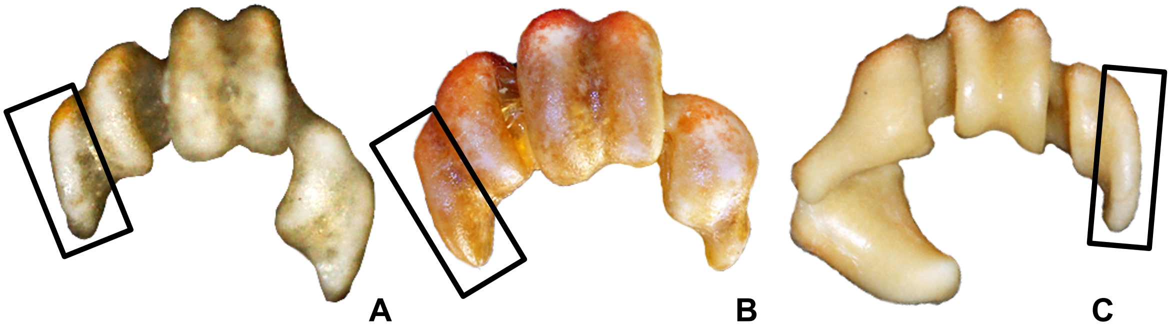

Figure 3.79. Character 123, metatarsal IV, trochlear sizes. **A**, character state 0 (BCPM 15442 *Calidris minutilla*); **B**, character state 1 (RBCM 10157 *Lagopus muta*); **C**, character state 2 (RBCM 19916 *Buteo platypterus*). Distal views. Specimens scaled to approximately equal distal mediolateral length. Equal lateral and medial trochlea in metatarsal IV (or lateral trochlea that are only slightly smaller than medial trochlea) is characteristic of Charadriiformes (A), while larger lateral trochlea is restricted (in this study) to Falconiformes (C).

124. Distal tarsometatarsus: MTII, III, and IV (0) III longest, II and IV roughly equal in length; (1) III longest, IV slightly longer than II; (2) II much shorter than IV; (3) all three distal metatarsals equal in length; (4) metatarsal IV shorter than II (Figure 3.80).

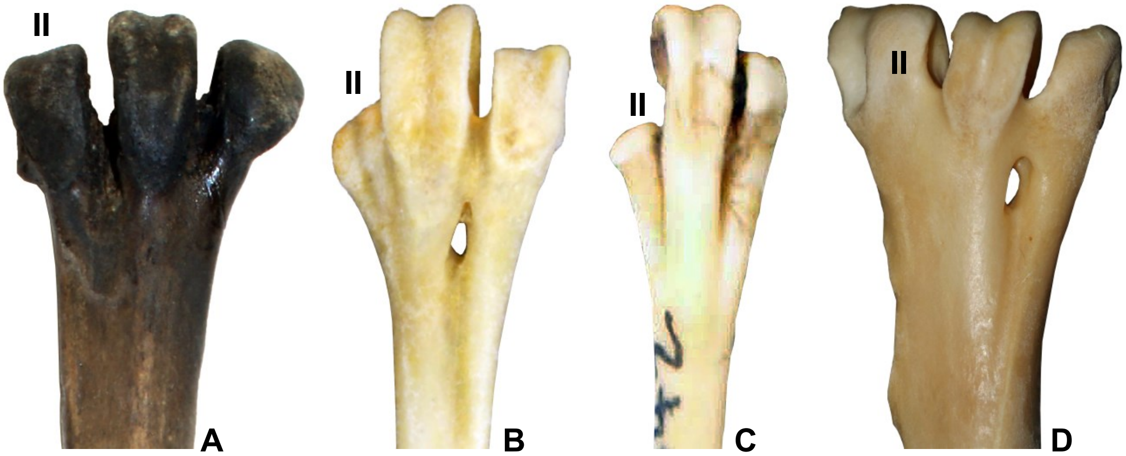

Figure 3.80. Character 124, relative plantar extension of tarsometatarsi. **A**, character state 1 (LACM G4896 *Ardea herodias*); **B**, character state 2 (CVM 14476 *Larus delwarensis*); **C**, character state 3 (CVM 14428 *Charadrius vociferus*); **D**, character state 4 (BCPM 22247 *Buteo regalis*). Anterior views. Specimens scaled to approximately equal distal mediolateral length. Charadriidae (C) display much shorter metatarsal II length, relative to metatarsal IV, than do Scolopacidae.

Comment—This character is similar to character 0438 of Livezey (2010; modified character 2361 of Livezey and Zusi 2006). Character state 25(1) is common (although not exclusive to) in Scolpacidae, 25(2) is common (although not exclusive to) in Charadriidae, and 25(4) is restricted to Falconiformes.

125. Foramen vasculare distale: (0) absent; (1) small and elongate; (2) small and rounded; (3) large and elongate; (4) large and rounded (Figure 3.81).

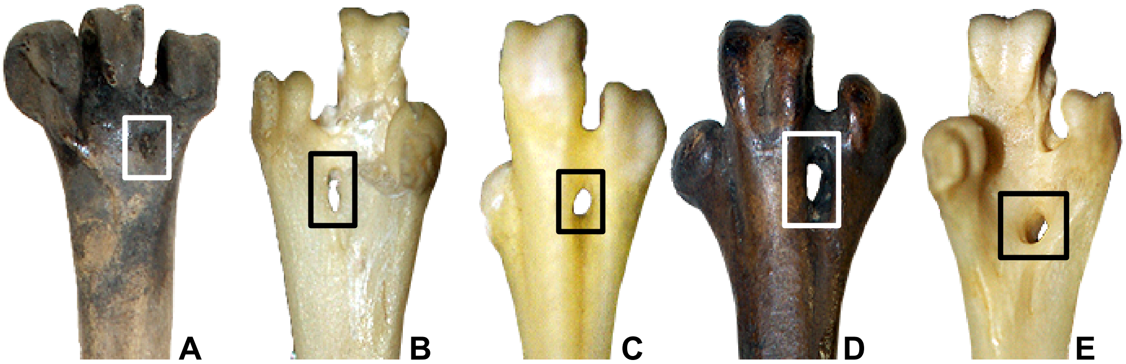

Figure 3.81. Character 125, foramen vasculare distale shape of the distal tarsometatarsus. **A**, character state 0 (LACM K3122 *Ardea herodias*); **B**, character state 1 (BCPM 10147 *Calidris pusilla*); **C**, character state 2 (BCPM 15491 *Charadrius vociferus*); **D**, character state 3 (LACM E5075 *Parapavo californicus*); **E**, character state 4 (BCPM 17157 *Pluvialis squatarola*). Anterior views. *Ardea herodias* has a shallow depression rather than a complete foramen (A). Foramen in Charadriidae (*Charadrius*, C; *Pluvialis*, E) are rounded, compared to the elongate foramen of Scolopacidae (B). Specimens scaled to approximately the same distal mediolateral length.

Comment—This character is similar to character 0426 of Livezey (2010) and character 2316 of Livezey and Zusi (2006).

126. Foramen vasculare distale: (0) no proximal groove; (1) weak proximal groove; (2) strong proximal groove (Figure 3.82).

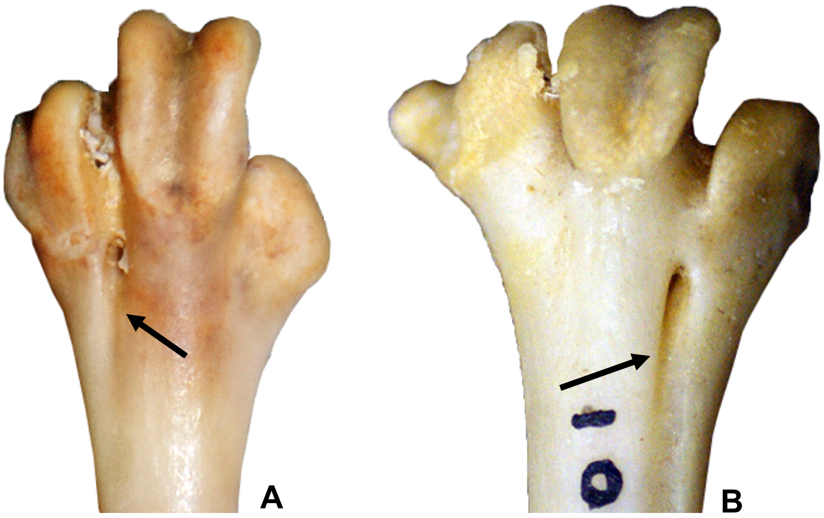

Figure 3.82. Character 126, foramen vasculare distale of the distal tarsometatarsus. **A**, character state 1 (RBCM 10157 *Lagopus muta*); **B**, character state 2 (BCPM 10089 *Falco perigrinus*). Anterior views. Specimens scaled to approximately equal in distal mediolateral length. Proximal groove of foramen vasculare distale indicated by arrows.

Comment—This character is similar to character 0427 of Livezey (2010).

127. Sulcus extensorius: (0) round; (1) flat; (2) shallow excavation; (3) deeply excavated (Figure 3.83).

Figure 3.83. Character 127, sulcus extensorius of the anterior tarsometatarsus. **A**, character state 1 (RBCM 23797 *Calidris pusilla*); **B**, character state 2 (BCPM 22247 *Buteo regalis*). Anterior views. Specimens scaled to approximately equal proximodistal length.

Comment—Similar to character 0422 of Livezey (2010), where the sulcus extensorius is excavated so that it extends the fossa infracotylaris dorsalis.

128. Tarsometatarsus shaft: (0) rounded; (1) square or rectangular; (2) triangular.

Figure 3.84. Character 128, tarsometatarsus shape. **A**, character state 0 (CVM 15072 *Limnodromus griseus*); **B**, character state 1 (RBCM 23582 *Dendragapus obscurus*); **C**, character state 2 (LACM D4486 *Amplibuteo woodwardi*). Lateral views. Specimens scaled to approximately equal in proximodistal length. Triangular cross section of the tarsometatarsal shaft is restricted in this study to Falconiformes.

Comment—Similar to character 0424 for the sulcus flexorius of Livezey and Zusi (2006) as (simplified) absent or present. However, the present analysis notes that there is more variation than absent or present for the concavity of the sulcus flexorius, the concavity of which can be greatly enhanced by the presence of well-developed cristae plantaris medialis et lateralis, and the corpus metatarsus is, in some taxa, compressed anteroposteriorly such that the corpus metatarsus is most thin at the center of mass. The development of the sulcus flexorius directly influences the shape of the tarsometatarsal shaft, and was not coded separately to avoid weighting the characters.

RESULTS

Description of Topology Using All Characters, All Taxa

The topology recovered by the strict consensus tree is uninformative. The majority rule consensus tree is slightly more informative, although a large polytomy is present (Figure 3.85). The support for the terminal nodes is weak, but above 50% (0.54–0.71). *Accipiter*, *Charadrius*, *Falco*, and *Grus* were recovered as monophyletic groups (Figure 3.85).

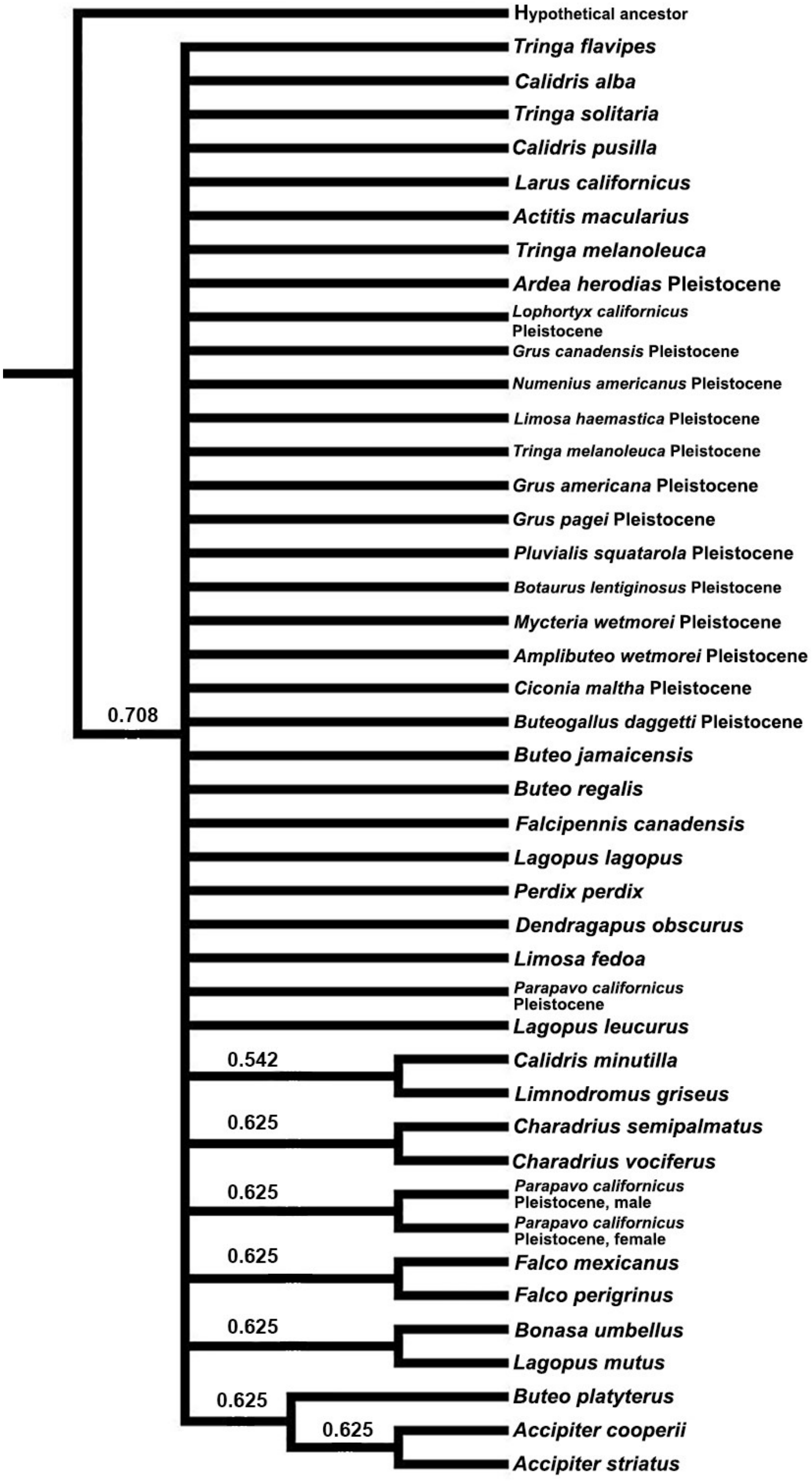
Hypothetical ancestor
Tringa flavipes
Calidris alba
Tringa solitaria
Calidris pusilla
Larus californicus
Actitis macularius
Tringa melanoleuca
Ardea herodias Pleistocene
Lophortyx californicus Pleistocene
Grus canadensis Pleistocene
Numenius americanus Pleistocene
Limosa haemastica Pleistocene
Tringa melanoleuca Pleistocene
Grus americana Pleistocene
Grus pagei Pleistocene
Pluvialis squatarola Pleistocene
Botaurus lentiginosus Pleistocene
Mycteria wetmorei Pleistocene
Amplibuteo wetmorei Pleistocene
Ciconia maltha Pleistocene
0.708
Buteogallus daggetti Pleistocene
Buteo jamaicensis
Buteo regalis
Falcipennis canadensis
Lagopus lagopus
Perdix perdix
Dendragapus obscurus
Limosa fedoa
Parapavo californicus Pleistocene
Lagopus leucurus
0.542
Calidris minutilla
Limnodromus griseus
0.625
Charadrius semipalmatus
Charadrius vociferus
0.625
Parapavo californicus Pleistocene, male
Parapavo californicus Pleistocene, female
0.625
Falco mexicanus
Falco perigrinus
0.625
Bonasa umbellus
Lagopus mutus
0.625
Buteo platyterus
0.625
Accipiter cooperii
Accipiter striatus

Figure 3.85. Majority-rule consensus tree (0.50 minimum frequency for node support) of 1000 shortest trees from a heuristic (swap and prune replacement) of characters coded for the humerus, femur, tibiotarsus, and tarsometatarsus of select taxa within Charadriiformes, Falconiformes, and Galliformes (see Study Taxa). Despite the relatively lower support for the deeper nodes, the terminal nodes show support (0.54–0.71). Not surprisingly, ontogenetic stage of the specimens is a large influence on character states. Genera *Accipiter*, *Charadrius*, *Falco*, and *Grus*, and form monophyletic groups (frequencies of 0.63). The fossil taxa representing Ciconiidae (*Ciconia maltha*, *Mycteria wetmorei*) do not form a monophyletic clade: as only data from the tarsometatarsus were available, it may not have been enough data to support a monophyletic group.

The coded characters were sparse in comparison to those of Livezey and Zusi (2006) and Livezey (2010), and no elements of the axial skeleton (skull, vertebral elements, sternum) clavicle, or pelvic elements were used in the analyses. This may have resulted in a topology that is poorly resolved. No monophyletic groups established by Sibley and Ahlquist (1990) were recovered. However, within the small sample of Neognathae, there are notable patterns in the topology of the majority-rule consensus.

Congruence Between Recovered Monophyletic Groups and Systematics

Charadriiformes

Charadriiformes was not recovered as a monophyletic group in this analysis. *Calidris* did not resolve within the polotomy (Fig. 3.85). Despite the gross morphological differences between *Calidris minutilla* (Least Sandpiper, a short-legged sandpiper) and *Limnodromus griseus* (Short-billed Dowitcher, a long-legged sandpiper), these two species form a monophyletic group. The *Calidris minutilla* + *Limnodromeus griseus* clade was supported by characters states of the humerus 24(1), 26(1), 31(3), the femur 46(1), 55(2), 65(0), 69(2), tibiotarsus 70(2), 74(2), 75(1), 80(1), 84(1), 85(1), 86(0), 88(2), 89(0), 91(1), 95(1), 99(2), tarsometatarsus 101(2), 103(2), 106(2, although this is character state is shared among all non-birds of prey), 107(2), 109(2), 110(1), 111(1), 115(2), 117(0), 122(2, although found in all Scolopacidae in this analysis), 123(2), 125(1), 126(2), 127(1). Character state 60(3) is unique to *Limnodromus griseus*.

Charadrius—The majority rule consensus tree recovered clade *Charadrius* with a frequency of 0.625. It was interesting to see that the fossil specimen of *Pluvialis squatarola* (Charadriidae, Pleistocene) did not form a clade with *Charadrius semipalmatus* and *Charadrius vociferus*(both extant specimens). However, the one character state that is unique to the polyphyletic Charadriidae (*Charadrius* + *Pluvialis*) is tarsometatarsus character 122(3), the medial trochlea ridge of metatarsal II is rounded and contributes to the majority of the trochlear surface, with the lateral trochlear ridge a small flange. Also, character state 121(2), the plantar displacement of the distal end of metatarsal II such that the extensor surface of MTII is level with (or more planter than) the plantar surface of MTIV, is unique to *Charadrius vociferus* and *Pluvialis squatarola* (Pleistocene). It is possible that the amount of missing data (tarsometatarus only) for *Pluvialis squatarola* accounts for its placement outside of *Charadrius*.

The *Charadrius* clade is supported (but not exclusively supported) by the following character states: 2(2, also with *Ardea herodias*), 18(3), 33(2), 43(5), 54(2), 59(3), 60(2), 63(1), 67(5), 72(3), 100(1, also shares with *Pluvialis*, most species of *Tringa*, and most grouse), 102(2, also with *Ardea herodias*, *Calidris alba*, *C. pusilla*), 121(2, also shared with *Pluvialis squatarola*), 122(3, also shared with *Pluvialis squatarola*), and 125(4, shared with traditional Falconiformes). There are character states *Charadrius* shares with *Pluvialis squatarola* to the exclusion of all other taxa examined. These are of the distal tarsometatarsus: 121(2), and 122(3). Other character states that are shared by Charadrius and Pluvialis, but also shared with some Scolopacidae examined are 100(2), 104(2), 107(1), 108(2), 109(2), 111(2), 123(2), 127(2). Despite all of the shared character states, a Charadriidae clade (*Charadrius*, *Pluvialis*) does not resolve in the majority rule consensus. The fossil specimen of *P. squatarola* examined was missing the proximal end, which may account for the lack of data available to more accurately resolve a Charadriidae clade.

Tringa—Species of *Tringa* did not form a monophyletic clade, but collapsed within the polotomy of the sample taxa. There are character states that are chared among all sampled species of Tringa; however, many of these character states are shared with other shorebirds. Character states 13(5, humerus), 25(5, humerus, but also shared with *Limnodromus*, *Limosa*), 32(2, humerus, but also shared with most other shorebirds), 60(1, femur, also shared with *Calidris*, grouse), 87(1, tibiotarsus, also in *Calidris*, *Charadrius*), 88(2, tibiotarsus, also in *Actitis*, *Calidris alba*, *Limosa*, *Numenius*), 93(2, tibiotarsus, also some shorebirds, *Falco*, and *Perdix*), 94(1, tibiotarsus, also in extant grouse and some birds of prey), 102(1, tarsometatarsus, in several shorebirds), 103(2, tarsometatarsus, also in many shorebirds and all extant grouse), 104(1, tarsometatarsus, also in many birds of prey), 118(1, tarsometatarsus, also in many shorebirds), and 125(1, tarsometatarsus, also shared with *Calidris*).

Although both one fossil and extant samples of *Tringa melanoleuca* were included in the analysis, the extant and fossil *T. melanoleuca* did not form a monophyletic clade. There are two reasons for this lack of resolution. One reason is that only tarsometatarsi were available for examination for the Pleistocene material, and any slight damage to the tarsometatarsi would increase the large amount of missing data already present in the dataset. The second reason is that there is a strong possibility the isolated fossil tarsometatarsi are not those of *T. melanoleuca*. Any character states that are present in both extant and fossil *T. melanoleuca* are also shared in other species of *Tringa* and other shorebirds. These character states are 100(2), 102(1), 104(1), 116(1), 118(1), 122(2), 124(1), and 125(1). An in-depth analysis of skeletal characters of species of extant Tringa will be required to resolve this issue.

Ciconiidae-Falconiformes

There was no support for a Ciconiidae-Falconiformes. However, there are character states that are shared by both Ciconiidae (*Ciconia*, *Mycteria*) and Falconiformes (*Accipiter*, *Amplibuteo*, *Buteo*, *Buteogallus*, *Falco*) to the exclusion of the other study taxa. Character states that support this grouping are of the femur 69(3, shared with *Ardea herodias*), and tarsometatarsus 106(1), 107(0), 111(3).

Ciconiidae separate themselves from Falconiformes by character states 43(3, femur, also seen in *Ardea herodias*), 64(2, femur, but also seen in *Buteogallus*, *Dendragapus*, *Falcipennis*, *Perdix*), 79(0, tibiotarsus), 84(4, tibiotarsus, although shared with *Buteogallus*), 85(1, tibiotarsus, also shared with the *Calidris minutilla-Limnodromus griseus* clade), 90(0, tibiotarsus, also shared with *Limnodromus*, *Lophortyx*, and *Numenius*), 97(3, tibiotarsus, also shared with *Falcipennis*, female *Parapavo*), 100(3, tarsometatarsus, shared with *Ardea*, *Grus*), and 101(4, tarsometatarsus, exclusive to *Ciconia*) Ciconiidae groups with *Falco* in character states 78(2, tibiotarsus), 119(2, tarsometatarsus), but exclude all other Falconiformes (Accipitridae: *Accipiter*, *Amplibuteo*, *Buteo*, *Buteogallus*). As there was limited material available for the Pleistocene storks, it is likely that missing data contributed to the lack of resolution of the Ciconiidae-Falconiformes clade.

***Accipiter*—**Species of *Accipiter* (*Accipiter cooperii*, *Accipiter striatus*) was recovered as a monophyletic group in the majority rule consensus tree as a sister group to *Buteo platypterus* (Fig. 3.86). Character states that support the *Accipiter* group exclusively are those of the humerus 4(1), 17(2, but also seen in grouse), 25(1, but also seen in female *Parapavo californicus*), 32(4, but also in *Falco*), 33(5), 34(3, also in *Falco*), and femur 55(3, but also seen in *Falco mexicanus*). Many other character states that support the *Accipiter* clade that are also seen in traditional Falconiformes and only appear in the birds of prey in this analysis (see Falconiformes). The *Accipiter* + *Buteo platypterus* group is supported (but not exclusive to the *Accipiter* + *Buteo platypterus* group) by character states of 5(3), 13(6, also in all *Buteo*), 30(1), 72(4, also in *Falco mexicanus*), and 92(3, but also seen in *Grus americanus* and *G. pagei*). Character states of the femur 43(4), tibiotarsus 77(2), 81(1), 82(0), 91(2), 93(3), 97(2), 98(0), and tarsometatarsus 114(3), 118(2), 125(4), 126(2), and 127(3) also support the *Accipiter* + *Buteo platypterus* group, but also appear in several grouse and shorebird taxa.

***Buteo*—**Species of *Buteo* did not form a monophyletic group. Character states that are shared among all species of *Buteo* are also shared in other specimens examined of Falconiformes. These include 87(2, tibiotarsus, also in *Dendragapus*, *Limnodromus*, *Perdix*), 88(4, tibiotarsus), 90(1, tibiotarsus, also in *Charadrius*, *Lophortyx*, *Parapavo*), 93(3, tibiotarsus), 95(1, tibiotarsus, also in shorebirds), 100(4, tarsometatarsus), 102(5, tarsometatarsus), 103(4, tarsometatarsus), 106(1, tarsometatarsus, also in storks), 107(0, tarsometatarsus, also in storks), 108(1, tarsometatarsus, some grouse, shorebirds, storks), 109(0, tarsometatarsus, also in shorebirds, storks), 110(0, tarsometatarsus, also in shorebirds, storks), 111(3, tarsometatarsus, also in storks), 114(3, tarsometatarsus, also in grouse), 117(3, tarsometatarsus), 118(2, tarsometatarsus, but also seen in *Ciconia*, *Grus*, grouse) 119(3, tarsometatarsus), 120(1, tarsometatarsus, shared with *Ciconia*), 121(4, tarsometatarsus), 122(4, tarsometatarsus), 123(4, tarsometatarsus), 124(4, tarsometatarsus), and 125(4, tarsometatarsus).

Falconiformes—Falconiformes is paraphyletic in this analysis, with character states that are unique to traditional Falconiformes. The Falconiformes-specific character states of are 67(4, femur), 88(4, tibiotarsus), 100(4, tarsometatarsus), 102(5, tarsometatarsus), 103(4, tarsometatarsus), 117(3, tarsometatarsia, except for *Falco perigrinus*), 121(4, tarsometatarsus), 122(4, tarsometatarsus), 123(4, tarsometatarsus), and 124(4, tarsometatarsus, except for *Amplibuteo*)

Falco—*Falco* (*Falco mexicanus*, *F. perigrinus*) is supported by several character states to the exclusion of all other taxa. These character states are 5(4, humerus), 12(4, humerus), 13(3, humerus), and 70(0, tibiotarsus). *Accipiter* (including *Accipiter* + *Buteo platypterus*) and *Falco* clades share several character states to the exclusion of other study taxa, including 31(2, humerus), 32(4, humerus), 34(3, humerus), and 99(1, tibiotarsus). However, *Accipiter* and *Falco* also share several character states that are present in extant and fossil Falconiformes in this study (see *Accipiter*, *Buteo*). The similarities between *Accipiter* and *Falco* may be related to convergence (Discussion).

Galliformes

Galliformes did not return a monophyletic group in the consensus tree, despite the morphological disparity between birds of prey, grouse, and shorebirds. There are several character states that are restricted within both fossil and extant Galliformes. The exception to these character states is seen in the juvenile specimens (*Lagopus leucurus*, *Parapavo californicus*), as these specimens either shared character states with the outgroup, or were equivocal for many characters. The Galliformes-only character states are 1(4, humerus), 4(1, humerus), 6(1, humerus), 20(5, humerus, although only in extant Galliformes), 31(1, humerus, although only in extant grouse and not in *Perdix*), 39(3, femur), 54(0, femur, restricted to extant Galliformes), 85(2, tibiotarsus), 102(3, tarsometatarsus), 109(3, tarsometatarsus, restricted to extant Galliformes, and also seen in *Falco mexicanus*), and 123(3, tarsometatarsus). Character 114 of the tarsometatarsus served to separate Galliformes into two groups. Character state 114(2) was possessed by only *Lagopus* (*L. lagopus*, *L. leucurus*, *L. mutus*) and juvenile, male, and female specimens of *Parapavo californicus*, whereas character state 114(3) is shared by *Bonasa*, *Dendragapus*, *Falcipennis*, and *Perdix*.

Within Galliformes, two monophyletic groups resolved: that of *Bonasa umbellus* and *Lagopus mutus*, and that of male and female *Parapavo californicus*. Although there are several character states that support the *Bonasa*-*L. mutus* and the *Parapavo* groupings, the majority of these states are also shared with the other Galliformes, birds of prey, or shorebirds in the analysis. The only character state that is exclusive to either of these groups is 91(0, tibiotarsus) for the *Bonasa*-*L. mutus* clade: all other character states that support *Bonasa*-*L. mutus* and/or *Parapavo* are shared with other taxa.

Lagopus—Species of *Lagopus* (*L. lagopus*, juvenile *L. leucurus*, *L. mutus*) did not resolve into a monophyletic group. Juvenile *Lagopus leucurus* possesses character states that are (for the most part) exclusive to that taxon, including 10(1 humerus), 12(2, humerus, shared with female *Parapavo californicus*), 19(1, humerus), 21(5, humerus), and 26(4, humerus). However, the only specimen available of *L. leucurus* was juvenile, and it is likely that these character states exclusive to *L. leucurus* are the result of ontogeny.

Tarsometatarsus-only cladistic analysis

Observing the patterns of shared character states in the cladistic analysis reveals that several character states that resolve traditional morphologic taxonomies are those of the tarsometatarsus. A tarsometatarsus-only cladistic analysis confirms this observation (Fig. 3.86). The resolution of the tarsometatarsus analysis is much stronger, with support for recovered nodes ranging between 0.63—0.99. Support for clades Accipitridae, Charadriidae, Ciconiidae, Gruidae, and Phasianidae is strong. Falconidae and Scolopacidae are not recovered. *Calidris* and *Tringa* were also not recovered, although *Calidris alba* and *C. minutilla* were recovered, but excluded *C. pusilla*.

Accipitridae were recovered a sister clade to Ciconiidae, which is consistent with previous morphology-based analyses. Character states supporting the Accipitridae-Ciconiidae clade are 106(1, also in *Falco*), 111(3, also in *Falco*), 117(2, but also in some Scolopacidae), and 126(3, also seen in *Falco*, *Grus*).

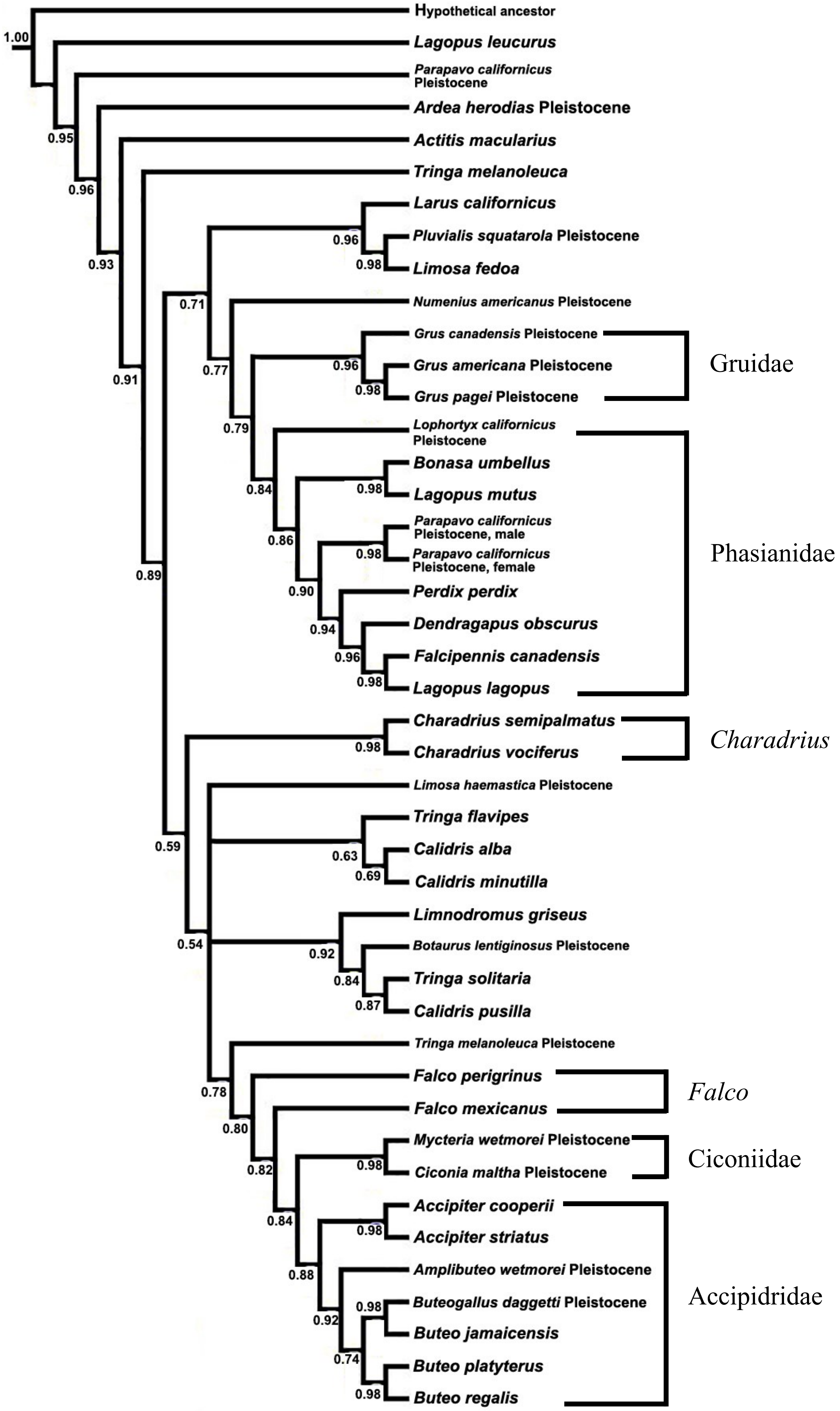
Hypothetical ancestor
Lagopus leucurus
Parapavo californicus Pleistocene
Ardea herodias Pleistocene
Actitis macularius
Tringa melanoleuca
Larus californicus
Pluvialis squatarola Pleistocene
Limosa fedoa
Numenius americanus Pleistocene
Grus canadensis Pleistocene
Grus americana Pleistocene
Grus pagei Pleistocene
Gruidae
Lophortyx californicus Pleistocene
Bonasa umbellus
Lagopus mutus
Parapavo californicus Pleistocene, male
Parapavo californicus Pleistocene, female
Perdix perdix
Dendragapus obscurus
Falcipennis canadensis
Lagopus lagopus
Phasianidae
Charadrius semipalmatus
Charadrius vociferus
Charadrius
Limosa haemastica Pleistocene
Tringa flavipes
Calidris alba
Calidris minutilla
Limnodromus griseus
Botaurus lentiginosus Pleistocene
Tringa solitaria
Calidris pusilla
Tringa melanoleuca Pleistocene
Falco perigrinus
Falco mexicanus
Falco
Mycteria wetmorei Pleistocene
Ciconia maltha Pleistocene
Ciconiidae
Accipiter cooperii
Accipiter striatus
Amplibuteo wetmorei Pleistocene
Buteogallus daggetti Pleistocene
Buteo jamaicensis
Buteo platyterus
Buteo regalis
Accipidridae
1.00
0.95
0.96
0.93
0.91
0.89
0.71
0.96
0.98
0.77
0.96
0.98
0.79
0.84
0.98
0.86
0.98
0.90
0.94
0.96
0.98
0.98
0.59
0.63
0.69
0.54
0.92
0.84
0.87
0.78
0.80
0.82
0.98
0.84
0.98
0.88
0.98
0.92
0.74
0.98

Figure 3.86. Majority rule consensus tree of 1000 most parsimonious trees recovered from a heuristic search (tree length: 274, consistency index: 0.310; retention index: 0.627) of the characters of the tarsometatarsus only for the study taxa. This analysis returns a more resolved topology, with Accipitridae, Charadriidae, Ciconiidae, Gruidae, and Phasianidae recovered. Scolopacidae remains unresolved.

DISCUSSION

Morphologic Convergence in Disparate Study Taxa

Convergence, Morphology versus Molecular Phylogenies: Ciconiiformes and Traditional Falconiformes—Ligon (1967) performed a comparison of skeletal elements of herons, storks, New World vultures, and (what were then considered) accipitrids (eagles, hawks, kites, Old World vultures). Ligon (1967) noted that without knowledge of the functional significance of the various osteological characters one cannot be certain of their relative importance in a study of phylogeny. Ligon (1967) also notes that that very few of the similarities between ciconiids and cathartids could be attributed to convergence, while convergence may be more probable among herons and storks, and vultures and accipitrids.

Ligon (1967) described characters of the humerus, femur, tibiotarsus, and tarsometatarsus that are similar between storks and vultures. One feature that is noted is the simplicity of the hypotarsus between Accipitridae (simple), Cathartidae (almost squared), and Ciconiidae (U-shaped). By simple, Ligon (1967) referred to the apparent lack of cristae intermediae hypotarsi in these three groups. Strigidae (owls) also possess a simple cristae hypotarsi (Baumel and Witmer, 1993). The cristae hypotarsi (medial surface of the crista hypotarsus medialis, lateral surface of the crista hypotarsus lateralis) form attachment sites for important flexor muscles of the foot. The fossa paraphypotarsalis medialis (on the medial surface of the crista hypotarsus medialis) is the attachment site for the m. flexor hallucis brevis. The canalis flexorius metatarsi extend from the distal end of the hypotarsus as a bundle of tendons of the flexor muscles of the digits. Having a simplified hypotarsus (cristae hypotarsali medialis et lateralis only) would allow for larger tendons of the flexor muscles of the digits, particularly digits I and II. Well-developed perching and gripping features in the feet of birds of prey (Accipitridae) and storks (Ciconiidae) are likely to have developed convergently: different behaviors resulting in similar morphologic adaptations. *Mycteria americana* (Wood Stork) roosts in trees over the water (Pearson et al., 1992) and engage in many display behaviors while perching, and also nests in trees (Coulter et al., 1999). *Accipiter* and *Falco* also spend time perching in trees when foraging, and nest in trees or cliffs.

Birds of prey have digits (digits I and II) that are specialized for a raptorial habitat. Digits I and II oppose one another and apply the most power to the handled and restrained prey (Einoder and Richardson, 2007; Fowler et al., 2009), and the talons of digits I and II are often the largest, and have large flexor tubercules (Mosto and Tambussi, 2013). Cristae hypotarsi medialis et lateralis are relatively shorter anteroposteriorly and wider mediolaterally. This would serve as strong attachment points for the m. flexor hallucis brevis and the tendon bundle of the flexor muscles. It is interesting to note that, while superficially the crista hypotarsalis lateralis appears to be a single structure, it displays features that suggest the remnants of being three separate cristae earlier in development that have secondarily merged and fused (Fig. 3.63). Interestingly, the lack of well-developed (even partially developed) cristae hypotarsi intermediae is also observed in *Tringa solitaria*. This is note-worthy because this member of Scolopacidae perches and nests in low coniferous and willow trees surrounding wetland habitats (pers. obs.), even though *T. solitaria* possesses neither a digit I (hallux) nor a distal tarsometarsus II–IV morphology consistent with those of perching birds. This suggests that there is strong convergence in the morphology of the hypotarsus among non-passerine birds which regularly perch, and that the simplified cristae hypotarsi of storks, vultures, birds of prey, and even some shorebirds is the result of convergence.

Morphological phylogenetic trees have consistently reproduced Accipitridae and Ciconiidae and as a monophyletic group, with *Falco* not forming a monophyletic group, but grouping with the Accipitridae-Ciconiidae clade. Analyses of Mayr and Clarke (2003, although the relationship of the classic birds of prey group is unresolved with respect to Ciconiiformes in a strict consensus tree) and Mayr (2005) support the Accipitridae + Falconidae clade, with Ciconiiformes as ancestral to traditional Falconiformes. In the morphological phylogenetic analysis on Neornithes performed by Livezey and Zusi (2006) that included both soft- and hard-tissue characters, Ciconiiformes resolved with Ardeiformes rather than with Accipitridae, while Falconidae and Accipitridae retained their group.

Molecular phylogenies support the interpretation that the similarities in the tarsometatarsus (and other skeletal elements detailed by Ligon, 1967) are due to convergence rather than shared common ancestry. Jarvis et al. (2014) demonstrate that traditional Falciformes (Accipitridae and Falconidae) paraphyletic, and that herons and ibises are more closely related to pelicans than to storks, and do not share a common ancestor with either Old or New World vultures.

Given the similar use of the pes in Accipitridae and Falconidae, there is strong convergence in other structures of the skeletal elements of hind limb, particularly those of the tarsometatarsus. These convergent morphologies appear as synapomorphies in the current analysis that serve to create paraphyletic groups; however, these clades are paraphyletic only with respect to molecular analyses. These character states include the simplified cristae hypotarsi, the reduced area intercotylaris and the placement of the sulcus ligamentosus on the proximal surfaces of the cristae hypotarsi medialis et lateralis, the distal end of metatarsus II extending relatively longer than that of metatarsal IV, and the large flange-like most medial trochlear ridge of metatarsal II.

Convergence Due to Hunting Strategies—Traditional Falconiformes, once including both accipitrids and falconids, is now considered to be paraphyletc, with Falconiformes more closely related to Psittaciformes than Accipitriformes (Jarvis et al., 2014). This is recovered in both the appendicular skeletal and tarsometatarsal consensus trees (Figs. 3.85—3.86). Any characters shared by Accipitridae and Falconidae are (from a molecular perspective) the result of convergence rather than shared common ancestry. *Accipiter* and *Falco* shared a few features that can best be described as convergence in morphology based on the behavior of the taxa in question. Species of *Accipiter* (*A. cooperii*, *A. striatus*) and *Falco* (*F. mexicanus*, *F. perigrinus*) have disparate habitats, with *F. mexicanus* occurring mostly in open habitat with food capture (mammals, lizards, and birds) occurring mostly on the ground (Steenhoff, 2013). *A. cooperii* occurs mostly in woodlands, hunts medium-sized birds and small mammals using a perch-and-scan method, and uses bursts of speed when hunting from perches (Odette et al., 2006). *A. striatus* occurs in most forest types, and takes birds and small mammals in the upper canopy that are both perched and (for birds) in the air (Bildstein and Meyer 2000). The habitat of *F.*

perigrinus is more varied, but it prefers cliff-nesting in open-air biomes (White et al., 2002). The prey of *F. perigrinus* consists of 77% – 99% birds (Sherrod, 1978), and most prey is taken on the wing (White et al. 2002). All four species are of disparate sizes in wing length (for adult females: *A. cooperii* wing length average = 256 mm, Odette et al., 2006 and references within; *A. striatus* average = 202 mm, Bildstein and Meyer, 2000 and references within; *F. mexicanus* average = 346 mm, Steenhof, 2013 and references within; *F. perigrinus* average = 325 – 357.6 mm among subspecies, White et al., 2002 and references within), but they can all be generally classified as small birds of prey.

Given the disparate habitats, sizes, and general hunting strategies among these four species of small birds of prey, there is one characteristic that all four share: the need for speed and accuracy in diving and ambush attacks. Not surprisingly, the character states that are shared by *Accipiter* and *Falco* and to the exclusion of large birds of prey (*Amplibuteo*, *Buteo*, *Buteogallus*) those of the distal humerus (characters 032, 034). The process flexorius is the attachment site of the tendinous head of the m. flexor carpi ulnaris (Baumel and Witmer, 1993). The m. flexor carpi ulnaris has two functions: flexion of the wrist, and movement and positioning of the flight feathers (Vanden Berge and Zweers, 1993), both actions that are important in quick maneuverability in varied terrain.

The epicondylus ventralis (or epicondylaris ulnaris) possesses a large, flange-like protuberance in *Accipiter* and *Falco*, and is the origin for the m. entepicondylo-ulnaris, which inserts on the posterior face of the ulna. Again, this is a muscle that is important in controlling ulna position and positions of flight feathers, which is crucial for maneuverability and speed. Conversely, the larger Accipitridae (*Amplibuteo*, *Buteo*, *Buteogallus*) do not rely so much on speed and maneuverability to capture prey as they do impact. For example, *Buteo jamaciencis*

(Red-tailed Hawk) is described as being poorly adapted to hunting in flight, and utilizes the perch-and-scan method for capturing prey on the ground (Preston and Beane, 2009). However, they are known to use *Accipiter*-like hunting strategies in dense forest (Lowe, 1978). Red-tailed hawks (Accipitridae) tend to select the largest prey items available, and will typically have legs extended when 3 m from the target (Preston and Beane, 2009). While the process flexorius and epicondylaris ulnaris are still well-developed in the sampled Accipitridae, the level of precision control of the ulna needed in the Falconidae hunting strategy may be related to the relatively larger development observed in these two structures.

Convergence versus common ancestry—Species of *Lagopus* did not form a monophyletic group, but did group within the extant Galliformes clade in the tarsometatarsus analysis. The species of Galliformes with which *Lagopus lagopus* and *L. muta* (excluding *L. leucurus*, as the only specimen analyzed was a juvenile and it grouped with other juvenile and hypothetical ancestral forms) group is consistent with some morphological, hybridization, and genetic studies. Subfamily Tetraorninae (*Bonasa*, *Dendragapus*. *Falcipennis*, *Lagopus*) was recovered as a monophyletic group; however, that is where the similarities between morphologic and molecular phylogenies end. Short (1967) proposed that, based on a comparison of natal plumage, adult coloration, and number of retrices, *Bonasa* was basal to a group that contains the *Dendragapus* + *Lagopus* group (*Dendragapus*, *Falcipennis*). Molecular analyses of Lucchini et al. (2011) produce a phylogenetic tree that removes *Falcipennis* from the *Dendragapu*s group, but still retains *Bonasa* as basal to *Falcipennis* + [*Dendragapus* + *Lagopus*] group.

Dendragapus and *Lagopus* form a monophyletic group in both the dendrogram of Short (1967) and molecular phylogeny of Lucchini et al. (2011). This was not reproduced in either of the present skeletal analyses. *Bonasa umbellus* and *Lagopus muta* form one group, while *Perdix*

perdix (Gray Partridge) formed a separate group with *Dendragapus obscurus* + [*Falcipennis canadensis* + *L. lagopus*].

There are skeletal characters present in *Lagopus lagopus* and *L. muta* and that are shared with extant Galliformes in the present study: absent to weakly developed fossa parahypotarsalis medialis, a deep fossa infracotylaris dorsalis that lacks visible foramen, weak impressiones ligamentosus collateralis medialis (shared with *Falcipennis canadensis*), diagonally oriented pons supratendinosus (shared with *Bonasa umbellus*), strong yet flattened impressiones iliotrochanericae (shares with *Bonasa umbellus*, *Callipepla californicus*, *Parapavo californicus*), asymmetrical trochanter femoris (also present in *Calidris alba*, *Tringa flavipes*), fossa trochanteris with two depressions (shared with *Callipepla californicus*, *Parapavo californicus*,), flattened crista trochanteris with recessus pneumaticae (shares with *Accipier*, *Perdix perdix*), small shallow fossa poplitea (shared with *Parapavo californicus* within Galliformes), strong crus ventrale (shared with *Parapavo californicus* within Galliformes), processus supracondylaris dorsalis expressed as a ridge with a small yet distinct protuberance, and a small processus flexorius. It is likely the limitations of this analysis (too few characters coded and/or too few species analyzed) resulted in the present recovered topology of Galliformes.

Morphology versus Molecular: Applications to Resolving Relationships of Fossil Taxa

This relatively limited (with respect to the soft- and hard-tissue morphologic phylogenetic analyses of Livezey and Zusi, 2006; 2007) skeletal phylogenetic analysis, created without prior reference to other skeletal analyses (e.g. Livezey and Zusi, 2006; 2007; Mayr 2003; 2005) demonstrates that some of the well-established higher-level phylogenies can be reproduced using skeletal characters of the appendicular limbs alone. Interestingly, from a paleontological perspective, these higher-level phylogenies are now considered "traditional" with the increased use of molecular phylogenies.

What are the implications, from a paleontological perspective, for Falonidae and Accipitridae appearing to share a node in a skeletal-only analysis when molecular analyses demonstrate that traditional Falconiformes is paraphyletic? On one hand, it is the lower taxonomic level groupings (familial, generic, specific) that provide the most accurate information with respect to consensus with molecular analyses. Species-groupings of *Accipiter, Charadrius. Falco,* and *Grus* have strong support in the majority-rule consensus tree at the generic level. Species of *Tringa* used in this study (*T. flavipes*, *T. melanoleuca*, *T. solitaria*) did not resolve as a monophyletic clade in either of the present skeletal analyses. Greater and Lesser yellowlegs not resolving as sister taxa is supported by the skeletal analysis of Chu (1995), and the molecular analyses of Gibson and Baker (2012); in fact, *Tringa* does not form a monophyletic group in these analyses. Despite the similarity in external morphology, there is consensus with both skeletal and molecular analyses that *Tringa* is parphyletic. Fossil (Pleistocene) tarsometatari of *T. melanoleuca* did not group with extant *Tringa*, although they do share several features with extant *Tringa* (non-continuous sulcus ligamentosus, weakly developed fossa hypotarsalis lateralis, strong and elongate tuberositas m. tibialis cranialis, medial trochlear ridge of metatarsal II rounded but still trochlear in shape).

Accipitridae (fossil and extant), Ciconiidae, and Phasianidae were also recovered. Conversely, *Calidris* does not form a monophyletic group. Monophyly of *Calidris* is not supported by molecular analysis of Gibson and Baker (2012): however, Gibson and Baker (2012) found that the monophyly of colloquial groupings of "sandpipers" (short-legged shorebirds) and "shanks" (long-legged shorebirds) was supported, along with the familial level grouping Scolopacidae, even if the generic-level groupings were not recovered.

The most pressing concern with the disparity between morphologic and molecular phylogenetic analyses is that the evolutionary relationships of fossil taxa may be erroneously inferred. However, which analysis is erroneous? Is one analysis more accurate than the other at determining the evolutionary relationships of the fossil organisms for which we are limited to hard-tissue data? Which analysis is better at determining how extant Aves relates to extinct Aves and Paraves?

While the morphology and molecular phylogenetic analyses have differing levels of congruence in how the lower level taxonomic groupings resolve, it is the relationships among the higher (familial and higher) taxonomic groupings that appear most sensitive to differences between morphologic and molecular data. The relationships among Accipitridae, Ciconiidae, Falconidae are a perfect example: the generic groupings are well-resolved at lower taxonomic levels in both morphologic and molecular analyses, while the ordinal and familial level relationships remain contentious.

Another troubling concern (in terms of the present analysis) is that, while this analysis recovered skeletal synapomorphies for familial and generic groupings, very few autapomorphies were recovered that would, for example, distinguish *Calidris alba* from all other sandpipers: a combination of autapomorphic characters is necessary for species-level resolution. The lack of resolution may be the result of too few characters used in this analysis. The lack of resolution may also be because there is not enough species-specific skeletal variation among similarly-sized species of *Calidris* that are unique to *Calidris*, and can differentiate among species of *Calidris*. *Calidris* may be an example of a biologic taxon that would not be identifiable at the generic level using appendicular skeletal elements. An analysis using multiple individual specimens of multiple species of *Calidris* as terminal taxa (as in Tschopp et al., 2015, for sauropods) may prove to be more informative.

It would be taxonomically reassuring to state with all certainty that there is (or is not) correlation between taxonomic organizations that are based on soft-tissue morphology, hard-tissue morphology, and molecular data. Future examinations including both more taxa and more skeletal characters, as well as treating multiple specimens of each taxon as terminal taxa, may improve the resolution of similar-sized taxa that share similar ecosystems.

CHAPTER 4

BIRDING BY FOOT: A CRITICAL LOOK AT THE SYNAPOMORPHY- AND PHENETIC-BASED APPROACHES TO TRACKMAKER IDENTIFICATION OF ENIGMATIC TRIDACTYL MESOZOIC TRACES.

INTRODUCTION

Vertebrate paleoichnology goes beyond simply the naming of shapes created by once living vertebrates: vertebrate ichnology uses trace fossils as an available source of data to determine the paleoecological makeup of vertebrate paleoecosystems. Part of this exercise in ichnological interpretation involves, invariably, proposing an identity for a vertebrate trackmaker to a certain taxonomic level (Carrano and Wilson, 2001). A classic example is the history of the *Chirotherium* trackmaker (Swinton, 1960), where several researchers proposed different taxa for these (at the time) enigmatic traces (including the amphibian with a cross-over gait depicted by Lyell, 1855). Soergel (1925) predicted the morphology of the *Chirotherium* trackmaker decades before an osteological specimen was discovered. This is the part of the ichnologic exercise that makes paleontologists (and reviewers of ichnology publications) who work with skeletal specimens wary: identities of skeletal specimens are made using skeletal synapomorphies, whereas trackmaker identifications are typically made using what has been previously described as phenetic correlation - the similarity between a track and the skeletal dimensions of the foot of the possible trackmaker (Carrano and Wilson, 2001; see also McCrea, 2001, and McCrea et al., 2001 for the discernment between thyreophoran and ceratopsian tracks; Farlow, 1992 for the discernment of sauropod trackmakers; Lockley et al., 2004; Li et al., 2007; Kim et al., 2008;

Cowen et al., 2010; Kim et al., 2012; Xing et al., 2013a; Lockley et al., 2014 for Dromaeosauridae trackmakers *Dromaeopodus*, *Dromaeosauripus*, *Velociraptorichnus*), and that of correlation with contemporaneous body fossils (Xing et al., 2013b).

Farlow et al. (2013) stated the best case of our ability to identify the makers of dinosaur tracks would be in which the shape of a footprint reflected the proportions of its maker's foot skeleton with perfect fidelity. This in turn leads us to inquire as to what features, and at what taxonomic level, we could use to tell foot skeletons apart. The synapomorphy-based correlation method, outlined in Olsen (1995) and expanded upon by Carrano and Wilson (2001) states that ichnotaxa can be assigned to biological taxa only if they have shared derived characters of those taxa. There are benefits to the synapomorphy-based correlation method: the greatest of all is that it provides an unambiguous identity to the proposed trackmaker. The synapomorphy-based method, of course, relies on using synapomorphies (derived character traits shared by two or more taxa within a monophyletic group) established during cladistic analyses, and, as acknowledged by Carrano and Wilson (2001), there are few synapomorphies established for the pedal elements of most dinosaurian taxa (see Using The Synapomorphy-Based Method of Trackmaker Attribution).

International Code of Zoological Nomenclature and Ichnotaxonomy

A word must be said about attributing an ichnologic taxon to a morphologic taxon. Ichnotaxonomy is a parataxonomy, a method of grouping the traces of organisms in to their least inclusive units that is used in parallel with traditional taxonomic systems. Ichnotaxonomy is regulated by the International Code of Zoological Nomenclature (ICZN). The following information is found in the International Code of Zoological Nomenclature, 4th Edition (2014).

Article 1.2.1 of the ICZN states “[t]he scientific names of extant or extinct animals include names based on domesticated animals, names based on fossils that are substitutions (replacements, impressions, moulds and casts) for the actual remains of animals, names based on the fossilized work of organisms (ichnotaxa), and names established for collective groups (specifically Articles 10.3, 13.3.2, 23.7, 42.2.1, 66.1, 67.14), as well as names proposed before 1931 based on the work of extant animals.” Article 10.3 of the ICZN states “[a] name proposed for a collective group is treated as a genus-group name [Art. 42.2.1]; a name proposed for an ichnotaxon is a family-group name, or genus-group name, or species-group name, according to the way in which it is first established (for names established for ichnotaxa for use at genus-group level, see Article 42.2.1)”. Although there is no cross-referencing in the ICZN as it pertains to establishing ichnogenera and ichnospecies, ichnotaxonomy is governed by the ICZN the same as for biological taxa. Also, ichnotaxa do not compete for priority with biological taxa, as stated by Article 23.7.3: “[a] name established for an ichnotaxon does not compete for priority with a name established for an animal (even for the animal that formed, or may have formed, the trace fossil).” This is why the ichnospecies *Tyrannosauripus pillmorei* (Lockley and Hunt, 1994) and the species *Tyrannosaurus rex* (the likely trackmaker) can coexist. Also, Article 72.5.1 states that eligible name-bearing types are an animal, or any part of an animal, or an example of the fossilized work of an animal, or of the work of an extant animal, if the name based on it was established before 1931. As such, there is no inherent conflict in employing ichnotaxonomy within the framework of the ICZN, nor is there any conflict with traces being produced by an osteologic specimen being named in a parataxonomic system.

The International Code of Zoological Nomenclature accepts the establishment of new taxa at the familial, generic, and specific levels using a variety of criteria: Article 13.1.1 states that new names published after 1930 must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon, and recommends that the authors should provide a clear summary of the characters that differentiate the new nominal taxon from related/similar taxa in languages used in the regions relevant to the taxa diagnosed (Recommendations 13A and 13B). This is the only specific criteria given for what characters can be used to differentiate among taxa. This criterion can be interpreted that the characteristics used to differentiate among taxa need only be useful within that particular field of study. Vertebrate paleontologists, but the nature of the preserved material, use the morphological species concept for establishing families, genera, and species. The morphologic characters used to differentiate among the identified groups are osteologic characters.

The primary goal of ichnotaxonomy is not to exactly mimic or correlate with biologic or morphologic taxonomy (Lockley and Harris, 2010). The approach that taxonomic designations be correlative is a worthwhile goal, but a strict application of this approach may not always be practical. Examination of the ilia of extant *Bufo* by Bever (2005a) showed that the ilial characters used in phylogenetic analyses of extinct *Bufo* were not unambiguously diagnostic for extant *Bufo*. In other words, the characters used to differentiate extinct species of *Bufo* could not be applied to extant species of *Bufo*. Conversely, applying the characters used to differentiate species of extant *Bufo* could not be applied to fossil *Bufo*, as many of the characters are those of features that do not preserve (amphibian skin color, breeding times, etc.). Bever (2005b) also demonstrated that dental characters in Pleistocene *Canis lepophagus* and extant *C. latrans* displayed such a large degree of variation as to be impractical for species-level identifications.

Bochenski (2008) addresses this issue, specifically with pairs of closely related species (grebes, crows, and turkeys). The best osteological characters used to differentiate between the species in each pair were effective for 66%—94% of specimens, although, when fully feathered the species within each pair were simple to differentiate (Bochenski, 2008). There were no osteological characters that were 100% effective in differeniating species that are identified using characters that do not fossilize (color, genetic differences, vocalizations, etc.). Also, it was found that characters other than those first used to name the taxon in question are required to attribute specimens to said taxa. This is a similar scenario faced when attributing an ichnotaxon to a fossil osteotaxon. While both categories of taxa are fossils, they preserve different aspects of the trackmaker's anatomy: the soft tissue of the trackmaker's phalanges, as well as the movement and behavior of the living trackmaker during the process of forming the trace, can mask or alter the appearance of the osteologic anatomy (and associated synapomorphies) of the trackmaker (Farlow et al., 2013). Given that osteologic synapomorphies are not likely to be consistently preserved in the form of traces, are osteologic synapomorphies required to attribute an ichnotaxon to an osteologic taxa?

The answer depends on the purpose of attributing a trace to a trackmaker. If the intent of attributing an ichnotaxon to an osteologic taxon is to informally (in the sense of the International Code of Zoological Nomenclature) propose a possible trackmaker, then characters that are recognized as synapomorphies for the proposed skeletal trackmaker are not technically necessary, although they would strengthen the attribution. Morphologic similarity, even with those morphologies not considered synapomorphies, is sufficient to propose a potential trackmaker. Also, if the ichnotaxon in question is being assigned to a taxonomic level that is not formally governed by the ICZN (taxonomic levels higher than the family level), there are no formal requirements for assigning taxa to those levels, and characters from multiple taxon recognition concepts may be employed. The same consideration should be given to those traces that are attributed to a family or lower taxonomic group: characters that are shared between the ichnotaxon and the proposed skeletal taxon, not limited to skeletal synapomorphies, can be employed to support the attribution. However, if the goal is to emend the diagnosis of a family or lower level taxon group to include ichnologic characters, Recommendations 13A and 13B to Article 13 state that at least one character should be used that is also used to differentiate the osteologic family in question. This character must be able to be preserved as an impression, or, given the potential of the lack or inconsistency of preservation of synapomorphic characters, that sufficient justification be provided in the emendation that can link a taxon named using one species concept so that the same taxon be recognized (or recovered with at least 66% consistency; Bochenski, 2008). An example of such an emendation that could occur involve the ichnotaxa *Dromaeopodus*, *Dromaeosauripus*, and *Velociraptorichnus*, for which the character of a reduced and redacted digit II (a synapomorphy for Paraves, Carrano and Wilson, 2001) is found on both the skeletal pedes and is consistently preserved in the aforementioned ichnotaxa as a reduced or absent digit II (Lockley et al., 2004; Li et al. 2007; Kim et al., 2008; Cowen et al., 2010; Mudroch et al., 2011; Kim et al., 2012; Xing et al., 2013a; Lockley et al., 2014).

Large Terrestrial/Wading Bird or Small Non-Avian Theropod?

Birds and non-avian theropods occupied the same paleoecosystems for at least 100 million years (Middle/Late Jurassic–Latest Cretaceous, Lockley and Harris, 2010). Both birds and non-avial theropods show diversity and disparity in size, and also the potential for overlap in size. As such, there is potential size overlap in the traces of avian and non-avian theropods.

Using the Synapomorphy-Based Method of Trackmaker Attribution—Applying the synapomorphy-based approach to track identification is not without its problems. There are two notes of caution that must be considered when applying a synapomorphy-based approach to trackmaker identification. One, tracks are not consistently preserved so as to reproduce the proportions of the trackmaker's foot with perfect fidelity. To be more specific, tracks made with fully fleshed-out pedes (epidermis, muscle, cartilage, etc.) by an animal in motion might not preserve the proportions of a skeletal trackmaker's foot with perfect fidelity. Two, the study of features related to the morphologies of dinosaur feet (and, following that the establishment of skeletal synapomorphies) is limited by the number of well-preserved feet (Farlow et al., 2013). Lucas (2007) notes that, for tracks attributed to Ceratopsidae, two of the characters used in the synapomorphy-based method do not by themselves distinguish ceratopsid tracks. This is applicable for small-bodied trackmakers as phalanges and unguals are small elements that are easily disrupted by erosional forces, although there are exceptions. *Coelophysis* is known to have *in situ*, well-preserved pedal phalanges (Rinehart et al., 2009). The pedal phalanges and metatarsi of many of the birds from China are intact, although these are Enantiornithes (for which pedal synapomorphies that could be potentially reflected in tracks were not described by Walker, 1981) and Confuciusornithidae (Chiappe et al., 1999, for which pedal synapomorphies are not detailed). This provides a challenge to the ichnologist when attempting to attribute a trace to a group that has a relatively poor skeletal fossil record: this applies directly to attributing avian trace fossils, mostly left by shore- and wading birds, to contemporaneous body fossils. More body fossils of shorebird analogs are being discovered (e.g. *Archaeornithura meemannae*, Wang et al., 2015), but their number is still too low to confidently attribute avian tracks to the avian trackmaker.

Carrano and Wilson (2001:578–581) detailed the synapomorphies that have the potential to be preserved in trace fossils of Dinosauria, including those synapomorphies that can be used to attribute traces to Theropoda, Coelurosauria, Maniraptora, Paraves, and Aves. However, only three synapomorphies were listed which can be utilized on a practical level in identifying trackmakers for the majority of functionally tridactyl tracks: clawed pedal unguals and mesaxonic pes for Theropoda; pedal print with a reduced digit II with lack of pedal ungual impression for Paraves; a reversed hallux print in a thin substrate for Aves. These are higher taxonomic levels: ordinal and familial level synapomorphies that have any chance of preserving in the ichnological record are those of resting traces (e.g. as reported in Milner et al., 2009), and these do not make up the majority of the ichnological record for mesaxionic, sharp-ungual traces for Theropoda.

The given synapomorphies also do not provide enough practical options for distinguishing between the traces of theropods and those of Aves. In other words, all Aves are Theropoda, but not all Theropoda are Aves. Given that all specimens of Aves are also Theropoda (Gauthier, 1986), all avian prints will share features with those of Theropoda, namely sharp pedal unguals, three weight-bearing digits, and a mesaxionic pedal structure. Regardless of the taxon in question, the functionally tridactyl foot structure is conservative within Theropoda. Due to morphologic convergence in size (Wright, 2004), footprints of small, non-avian theropods will share foot characteristics with large avians, such as slender digits and unguals (Wright, 2004). Also, phalangeal proportions carry a strong functional signal, and proportions of phalanges differ between arboreal and terrestrial avian species, showing that there is strong convergence in foot morphology (Farlow et al., 2013).

Most of the skeletal synapomorphies for Aves are from the elements of the skull, axial skeleton, and pectoral girdle and limbs: these are not skeletal elements that often come into contact with substrate (with the exception of feeding traces), and, in the event that these parts of the trackmaker's body did contact the ground, the soft-tissue covering the skeletal synapomorphies would be imprinted, not the synapomorphies themselves. It is not systematically inaccurate to identify the trace of a large, functionally bipedal avian as belonging to Theropoda; however, it is not the most taxonomically refined identification that is possible. If ichnologists limit themselves to those traits directly related to a skeletal synapomorphy, the identification of a trackmaker would be contingent on the preservation of the track being such that either the trackmaker squatting or tripping and falling in to the sediment (which have yet to be documented), or the pedal traces would have to be preserved in deep enough substrate that digit I is unambiguously impressed.

Using The Phenetic-Based Method Of Trackmaker Attribution—Lockley et al. (1992) establish phenetic-based criteria for recognition of traces as avian. These are: similarity of fossil tracks to those of modern birds; small size; slender digit impressions with indistinct differentiation of digital pads; wide divarication angles between digits II and IV of about 110° - 120° or more; a posteriorly-directed hallux (digit I); slender claws (unguals); distal curvature of lateral and medial claws away from the central axis of the foot. Other criteria also identified are behavioral: track density; associated fossils and feeding behavior; sedimentological evidence regarding track-bearing deposits. These are the criteria that many ichnologists have used to propose an avian identity for small theropod/large avian traces, with mixed results (see specifically the issues with *Magnoavipes* ichnosp., Lee, 1997; Lockley et al., 2001; Matsukawa et al., 2014; McCrea et al., 2014a; Buckley et al., in press, and individual points discussed subsequently). However, most of the problems encountered with using phenetic-based criteria arise when only one or two criteria have been relied upon, especially relating to the criterion of digit divarication (Lee, 1997), when applied to poorly preserved material or single specimens. A combination of the key criteria and further suggested criteria that will be discussed should be applied to well-preserved specimens with a significant sample of specimens.

APPROACHES

This aim of this paper is to attempt to correlate the phenetic- and synapomorphy-based methods for distinguishing between the traces of avians and those of small theropods, and to examine the practical application of the features used in both the phenetic- and synapomorphic-based approaches, particularly the utility in using each of the features as stand-alone identifiers for avian and non-avian theropod traces.

METHODS

Neoichnology Replicas

Neoichnology replicas were cast for trackways of large wading- and small shorebirds from the Peace Region of northeast British Columbia between 2009—2014. These birds were selected based on their similarity in the size ranges seen in Mesozoic tracks of wading- and shorebirds, and their ease of access during the study. All neoichnology replicas (designated as PRPRC NI) were made by pouring fiberglass-reinforced plaster of Paris (Hydrocal FGR-95) into the trackways. Therefore, all PRPRC NI trackways are infilled casts (as opposed to exact replicas of natural molds). Prior to trackway replication, track areas were observed and local avian fauna documented. Trackways collected were either those where the trackmaker was observed making the traces, or traces collected from where the trackmaker was observed leaving the track area.

Photogrammetry

A Hydrocal FGR-95 plaster cast of RTMP 1999.059.0001 housed at the PRPRC was digitized using photogrammetry. The 3D photogrammetry image is a compilation of 48 photographs, taken at an average elevation from subject of 0.3 m, with a Canon EOS 70D camera (Focal Length 18mm, resolution of 5472 x 3648; pixel size accuracy to 0.00417 mm). The model was rendered with Agisoft Photoscan Professional (v.1.0.4) with an error of 0.145 pixels. The 3D model was converted into a colour topographic profile image using CloudCompare (v.2.5.3).

Institutional Abbreviations

CVM, Cowan Vertebrate Museum, Beaty Biodiversity Museum, 2212 Main Mall, University of British Columbia, Vancouver, British Columbia, V6T 1Z4 Canada; **LACM**, Page Museum at the La Brea Tar Pits (Los Angeles County Museum), 5801 Wilshire Blvd., Los Angeles, California, 90036 USA; **MCZ,** Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, 02138 USA; **PRPRC,** Peace Region Palaeontology Research Centre, 255 Murray Drive, Tumbler Ridge, British Columbia, Canada; **TMP,** Royal Tyrrell Museum of Palaeontology, Hwy 838, Drumheller, Alberta, T0J 0Y0 Canada.

UTILITY OF PHENETIC- AND SYNAPOMORPHY-BASED CHARACTERS

Gestalt of Bird Tracks

Similarities to Traces of Extant Birds—Identifying a potential trackmaker as avian based on the bird-like attributes of a trace is, in essence, the basis of the phenetic-based method for attributing traces to an avian trackmaker. The overall similarities of fossil tracks to those of extant avians using several lines of observation, or the gestalt, of the tracks, is detailed in features two through nine. Feature ten, sedimentological evidence of Lockley et al. (1992), is encompassed in the discussion of the individual features as to how it assists (or hinders) the identification of an avian print.

Anatomical Features of Potential Trackmakers

Size (Lockley et al., 1992)—Size is often used in identifying the traces of avian trackmakers in the Mesozoic, but used in addition to other pes characteristics that have been associated with avian prints, such as the synapomorphic reversed hallux, or digit I (Carrano and Wilson, 2001). It comes as no surprise that size alone is not a strong character with which to diagnose an ichnotaxon: using size to distinguish the body fossils of coelurosaurs was shown to be problematic (Gauthier, 1986; Gauthier and Padian, 1989). Gauthier and Padian, (1989) make a point of discussing the disparate sizes within both extinct and extant Theropoda, and how using size as a diagnostic feature results in paraphyly.

The same argument can be made for the tracks produced by monophyletic trackmakers of disparate size. While ichnotaxonomy is a parataxonomy, and issues of paraphyly are less problematic for ichnology than for osteologic taxonomy, the knowledge that monophyletic groups can contain individual taxa of disparate sizes cannot be ignored when attributing a trace to a possible trackmaker. Given the range of sizes observed in Coelurosauria, and more specifically Aves, the attribution of tracks to an avian trackmaker should not be restricted to small size (as was once done for coelurosaurs). For example, there are no avian characteristics that can be ascribed to *Minisauripus* (Xing et al., 2010), although the small size is similar to those of small extant shorebirds. While size can be a potentially useful character in trackmaker identification, it is a character subject to the alternate interpretations of ontogeny and homoplasy (Carrano and Wilson, 2001; Farlow et al., 2013).

Lower Cretaceous deposits of Australia, China, and North America preserve traces that can be attributed to those made by large (> 9 cm in footprint length) avians (Martin et al., 2013; McCrea et al., 2014a; Xing et al., 2015). The traces from Australia are unambiguously avian as they have a distinct posteriorly oriented pedal digit I (Martin et al., 2013); however, the sediments in which the trackmaker impressed its foot were soft enough to leave sediment deformation traces, which may have allowed the pes to sink into the substrate deep enough for the impression of digit I. This was not the case for *Limiavipes* (McCrea and Sarjeant, 2001; McCrea et al., 2014a) and *Wupus* (Xing et al. 2015): to date, each print attributed to these ichnotaxa is functionally tridactyl with no trace of a hallux (see posteriorly-directed hallux for further interpretation).

Avian skeletal remains large enough to have produced tracks as large as *Limiavipes* and *Wupus* have been reported (*Patagopteryx* of Alvarenga and Bonaparte, 1992, and Chiappe, 1995; *Gargantuavis* of Buffetaut et al. 1995); howerver, the body fossils are not contemporaneous with the footprints. While it is unlikely that these specific osteotaxa were the trackmakers of

Limiavipes curriei, *Wupus agilis*, and the large avian traces of Australia, these skeletal specimens demonstrate that large avians, although their recorded occurrences are rare, were part of the Cretaceous paleoecosystem. Size alone should be used with extreme caution when discerning between the traces of large avians and small theropods, especially because trackmaker size will influence features (slender digits, sharp claws, trackway density) that are used in the phenetic based approach to attributing traces to an avian trackmaker (Wright, 2004).

Slender digit impressions (Lockley et al. 1992)—Slender pedal digits are a feature that is generally referred to as avian, and appearing often in avian ichnosystematic sections. However, digit slenderness can be an extramorphological feature produced by the consistency of the track-bearing surface at the time of pedal impression (McCrea et al., in press). Matsukawa et al., (2014) in their examination of the ichnogenus *Magnoavipes*, determined that one of the diagnostic features (digit slenderness) was likely an extramorphologic feature due to poor preservation: collapse and inflow of sediment into the digits of the freshly-made track would give digits the artificial appearance of slenderness. Examining the traces of extant shorebirds shows that one individual can leave traces of varying thickness due to variations in substrate consistency (Fig. 4.01). As substrate decreases in saturation and saturated mud content, avian digits increase in thickness and in the amount of detail that is preserved (Fig. 4.01).

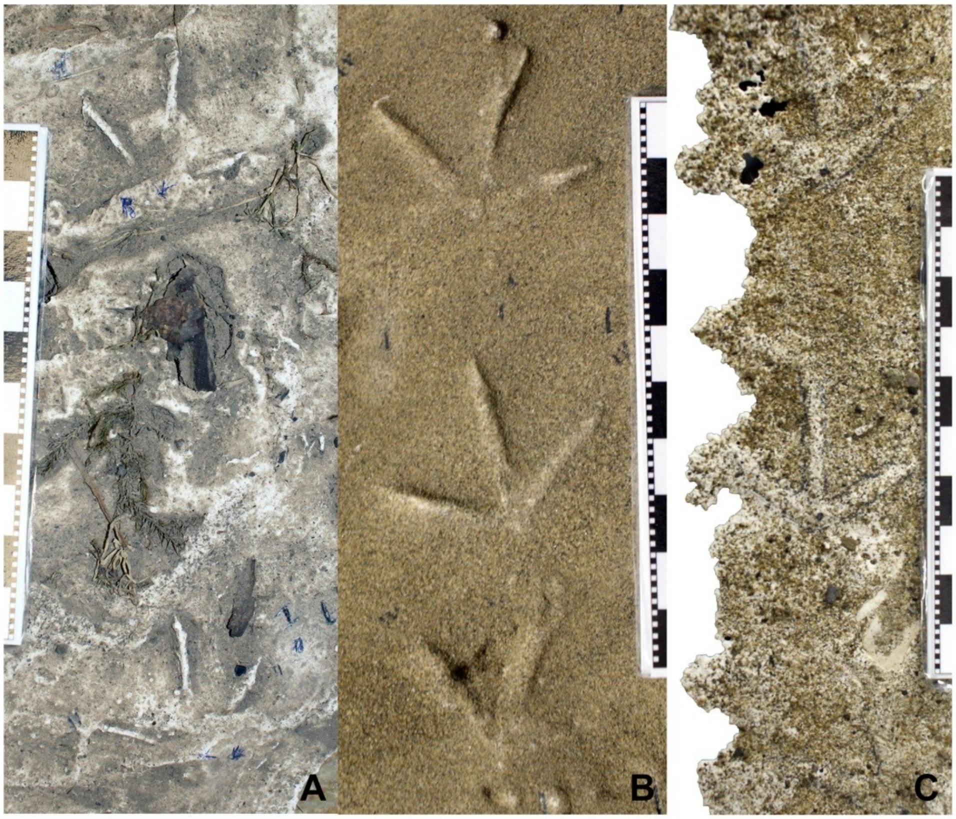

Figure 4.01. Three trackways of *Tringa solitaria* (Solitary Sandpiper) made in different substrates, demonstrating natural variation in the tracks of one species of trackmaker. **A,** PRPRC NI2011.002, made in firm mud with a high organic content and a penchant for thixotropy, track surface exposed; **B,** PRPRC NI2011.001, made in wet, firm medium- to fine-grained sand, track-surface exposed; **C,** PRPRC NI2009.003, made in coarse-grained sand mixed with small pebbles at the edge of a river, track surface partially submerged. While all tracks pictured have a characteristic "slender" digit, there is variation in digital width, from 1.8 mm (A, track 2, digit IV), 4.9 mm (C, track 2, digit II), to 5.5 mm (B, track 3, digit IV).

Digit thickness and size are also correlated: relative digit thickness, in general, increases with increased size of the trackmaker (Lockley et al., 2007), but there is considerable variation. Farlow et al. (2013) compared the pedes of extant and extinct ground-dwelling birds and found that birds of comparable size had variation in digital thickness: emu, cassowary, and moa have relatively wide digits, compared to *Emeus*, rhea, and *Pachyornis*, which have relatively narrow digits (Farlow et al., 2013, fig. 5.6).

Whereas digit width, or digit thickness, is not a commonly measured variable for avian ichnology (Chapter 5), there are Cretaceous ichnospecies described for which digit robustness, rather than slenderness, is an identifying character. *Morguornipes robusta* (Xing et al., 2011) and *Tataronipes chabuensis* (Lockley et al., 2012) and have relatively robust digits compared to other avian ichnotaxa from the Cretaceous. Given the high degree of variation in digit proportions, and that the digit thickness can be affected by substrate conditions, digit thickness should not be considered to the exclusion of condition of the track-bearing substrate or the natural variation within an ecological group (ecological bin of Bell and Chiappe, 2011), as foot (phalangeal) proportions display a strong functional signal (Farlow et al., 2013).

Wide divarication angles between digits II and IV of about 110°—120° or more (Lockley et al. 1992)—Of all of the phenetic characters (both in conjunction with and in the absence of a preserved digit I impression) divarication is most often used to distinguish the traces of avians from those of small theropods. A high angle (about 110°–120° or more) of divarication between digits II and IV has been used in many publications of Mesozoic avian traces.

In the absence of a preserved digit I, divarication appears to be the logical feature with which to distinguish between avian and non-avian theropods. Within Neognathes that are analogous to the shore- and wading birds of the Cretaceous, there is a wide range intraspecific variation of digit divarication within species, and even a wide range of variation of divarications within the trackway of one individual. One can argue that a way to utilize the high divarication angle is to use average divarication, but this is also problematic. In the traces of the *Ardea herodias* (Great Blue Heron, including those of landing traces) the average divarication between digits II–IV is 97.7° (PRPRC NI2014.001 and NI2014.002, 88°–110°, n = 10), traces of *Branta canadensis* (Canada Goose, PRPRC NI2009.009) is 82.6° (73°–95°, n = 15), of *Actitis macularius* (Spotted Sandpiper, PRPRC NI2009.001, NI2009.002, NI2010.002, and NI2011.002) is 106.1° (86°–133°, n = 34), Common Snipe (PRPRC NI2011.010, NI2013.001) is 110.4° (89°–135°, n = 14), and *Tringa solitara* (Solitary Sandpiper, PRPRC NI2012.001, NI2011.001, NI2011.002, and PRPRC NI2014.003) is 111° (90°–130°, n = 20). The average total divarication (another term often used for divarication between digits II and IV) for these extant avians is high; however, the range of divarications is also high. The total divarication in the footprints of extant ground birds can also be 90° or less (Farlow et al., 2000). A high angle of divarication between digits have been documented in the theropod ichnogenus *Magnoavipes* (Lockley et al., 2001; Matsukawa et al., 2014), and ichnospecies of which were erroneously attributed to an avian trackmaker due to over-interpretation of the single character of divarication (Lee, 1997; Fiorillo et al., 2011); Lockley et al. (2001) and Matsukawa et al. (2014) provide a strong case for the trackmaker belonging to Ornithomimidae based on size, digit proportions, and paleogeographic range of this theropod ichnotaxon.

The divarication values displayed in the final impression have the potential to be influenced by anatomy, behavior, and substrate consistency. In terms of anatomy, avians and arctometatarsalian theropods have a similar metatarsal structure, and both types of trackmakers have the potential to produce symmetrical footprints (Wright, 2004). The arrangement of the distal tarsometatarsi has been used as a coded character in analyses of Neornithes by Livezey (2010). Characters 0434, 0436–0439 in Livezey (2010) deal with the relative positions of the trochlea of the distal tarsometatarsi, the relative degrees of separation of the medial and lateral trochlea from that of metatarsal III, and the amount of torsion or rotation of the medial and lateral trochlea relative to that of metatarsal III. As these characters deal specifically with Neornithes, they in themselves do not offer synapomorphies that can be used to distinguish the prints of birds from those of non-avian theropods: however, there is potential for these characters to be applied to vertebrate ichnology.

The arrangement of the distal tarsometatarsus has been used to successfully place birds within ecotypes (Falk et al., 2011) and may even have a systematic signal within Charadriiformes at the familial level (Chapters 3, 6). A comparison of the trochlear arrangement of the distal tarsometatarsi of Theropoda, Coelurosauria, Paraves, and Aves shows that, as the tarsometatarsus changes from the theropod morphology to that of a bird, the torsion of the distal end of metatarsal II increases relative to the position of metatarsal III, and the relative size of the intertrochlear notches between metatarsals II–III and III–IV increase (Fig. 4.02).

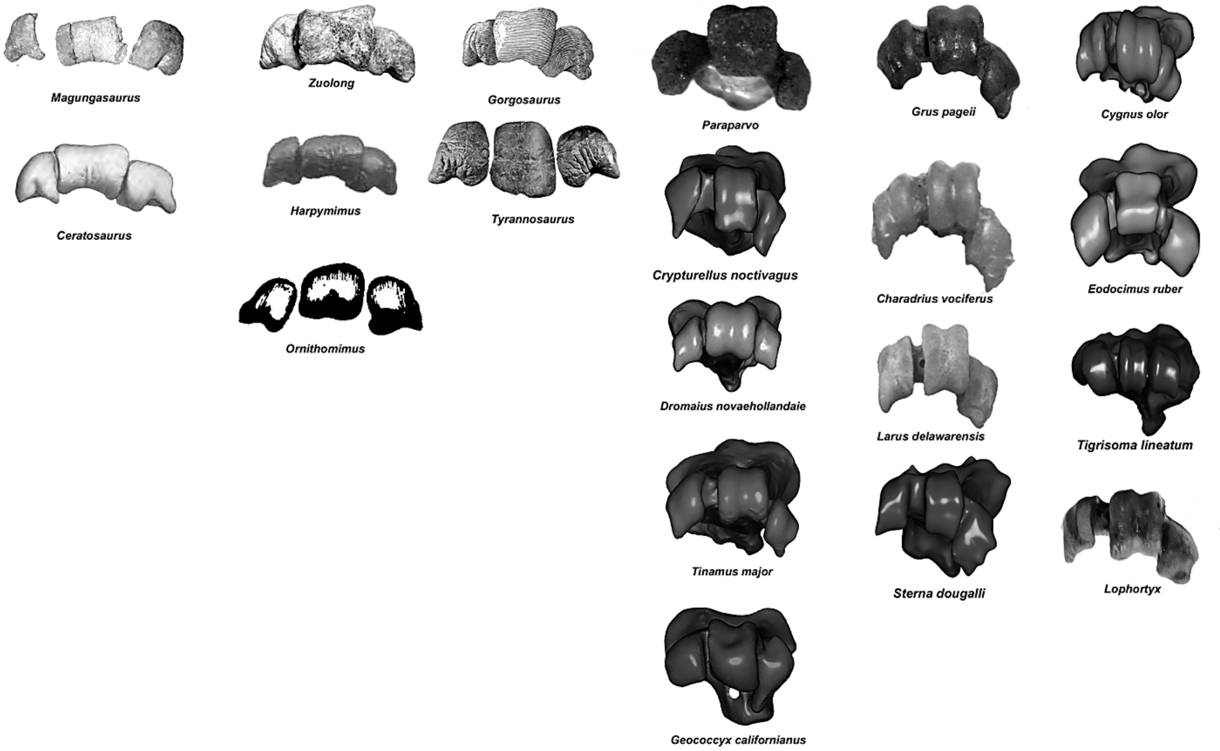

Figure 4.02. Comparison of plantar torsion of the trochlear ends of metatarsal II of Theropoda, Coelurosauria, and Aves (fossil and extant), presented so that metatarsal II is on the right side of the individual images, and are modified from the cited publications. There is a trend, from non-avian theropods *Majungosaurus* (Carrano, 2007) and *Ceratosaurus* (Gilmore, 1920), to arctometatarsalian coelurosaurs *Zuolong* (Choiniere et al., 2010), *Harpymimus* (Kobayashi and Barsbold, 2005), *Ornithomimus* (Marsh, 1890), *Gorgosaurus* (Lambe, 1917) and *Tyrannosaurus* (Brochu, 2003), and of fossil Aves *Callipepla* (= *Lophortyx*) (LACM L244), *Grus pageii* (LACM F452), *Gastornis* (Angst et al., 2013), *Paraparvo* (LACM E6793), and extant avians *Charadrius vociferus* (CVM 14428), *Cryturellus noctivagus* (MCZ 340276), *Cygnus olor* (MCZ 347051), *Dromaius novaehollandaie* (MCZ 1586),), *Eodocimus ruber* (MCZ 347446), *Geococcyx californianus* (MCZ 343239), *Larus delawarensis* (CVM 14476), *Sterna dougalli* (MCZ 337064), *Tigrisoma lineatum* (MCZ 343831), *Tinamus major* (MCZ 342774). Images

scaled to be size equivalent. The observed difference between non-avian theropods and birds in medial and lateral trochlear torsion is present in large animals: *Dromaius* still exhibits trochlear torsion, while *Harpymimus*, *Ornithomimus*, and *Zuolong* do not. In other words, the size, and likely weight, of the animal does have a strong enough effect to mask trochlear torsion. Colored images of 3D scans used with permission from aves3D.org and Harvard Museum of Comparative Zoology.

Posteriorly-directed hallux (digit I) (Carrano and Wilson, 2001)—The presence of an unambiguous posteriorly directed digit I (along with high angle of divarication between digits II and IV) is the most often used character in identifying a trace as being made by an avian trackmaker. This character is one of the synapomorphy characters listed by Carrano and Wilson (2001). This is a feature that is not only directly related to the osteologic anatomy of the trackmaker's foot, but is used in systematic analyses to identify skeletal specimens as avian.

There are issues surrounding the presence of a hallux as an unambiguous, synapomorphy-supported character to discern avian tracks from those of small theropods. Metatarsal I is described as articulating on the distal quarter of the medial or posteromedial portion of the body of metatarsal II in Avialae (Gauthier, 1986, and references within). Also, the presence of a hallux was found by Livezey and Zusi (2006, char. 2221) to be polymorphic within some extant taxa, including *Calidris*, in some instances being completely absent in taxa where a digit I is typically present.

Extant avians produce footprints that do not consistently preserve digit I, even when this digit is skeletally present. Digit I will also be variably preserved depending on which layer of the track-bearing sediment is preserved. In modeling footprint formation in guineafowl, digit I only preserved in the final-formed footprint in the surface layer of “sediment” (poppy seeds), as well as the layers at 1 cm and 2 cm depths (Falkingham and Gatesy, 2014, fig. 3). Variable preservation of digit I is also noted in the trackways of *Actitis macularius* (Spotted Sandpiper), *Gallinago delicate* (Wilson’s Snipe), and *Tringa solitaria* (Solitary Sandpiper) (Fig. 4.03). This pattern of an ephemeral digit I impression is also seen in the tracks of Mesozoic avians: *Koreanaornis* ichnosp. (Lockley et al., 2006) and *Pullornipes aureus* (Lockley et al., 2005) show prints where digit I is not consistently preserved. This is in contrast to *Aquatilavipes swiboldae* (Currie, 1981), *Koreanaornis dodsoni* and *Morguiornipes robusta* (Xing et al., 2011), and *Tatarornipes chabuensis* (Lockley et al., 2012), which consistently do not exhibit a digit I impression.

Figure 4.03. Shorebirds with incumbent foot structure and a skeletally present digit I which does not consistently impress. **A**, PRPRC NI2010.003, trackway of *Actitis macularius* (Spotted Sandpiper) walking in firm substrate (**A**, left) and saturated substrate (**A**, right). Left and right images taken from a continuous series of footprints made by one individual; **B**, PRPRC NI2013.001 (**B**, left) and PRPRC NI2011.010 (**B**, right), trackways of *Gallinago delicata* (Wilson's Snipe) preserved in firm substrate (**B**, left) and saturated substrate (**B**, right). The first print figured for PRPRC NI2013.001 is in close association with an isolated print of *Actitis macularius* (Spotted Sandpiper), giving it the appearance of possessing a digit I; **C**, PRPRC NI2014.003, *Tringa solitaria* (Solitary Sandpiper), with digit I not impressing on any of the footprints occurring on the specimen (including the Spotted Sandpiper tracks). Scale bar = 10cm.

Digit I typically impresses in birds where it is a weight-bearing digit, such as *Ardea herodius* (Great Blue Heron): this is also seen in the Mesozoic Ignotornidae (Kim et al., 2006), Jindongornipodidae (Lockley et al., 2006), and Shandongornipodidae (Lockley et al., 2007). However, many trackways of Ignotornidae feature footprints where digit I is inconsistently preserved within the same trackway, and some of the prints exhibit a tridactyl morphology (see *Goseongornipes markjonesi*, figs. 8–9 in Kim et al., 2012). Extant large-bodied wading avians with a robust digit I, such as Ardeidae, Cicioniidae, and Rallidae can also produce prints where the digit I trace is ambiguously preserved, even though it is stated that digit I tends to register: Elbroch and Marks (2001) figure a footprint from *Rallus limicola* (Virginia Rail) where digit I is ambiguously preserved (2001). Also, Elbroch and Marks (2001) figure the tracks of *Grus canadensis* (Sandhill Crane) where digit I is inconsistently impressed, and also state that the impression of digit I is dependent on substrate consistency.

The prints of extant *Grus* are important to note because, at a footprint length range of 9.5 cm - 12.1 cm and a walking stride range of 30.7 cm–53. 4 cm (Elbroch and Marks, 2001), they are similar in size to the prints of *Limiavipes curriei* (McCrea and Sarjeant, 2001; McCrea et al. 2014a). The latter is a tridactyl trace from the Early Cretaceous (Albian) with wide divarication and lacking digit I that is attributed to a large wading avian. It is possible that the trackmaker of *Limiavipes* possessed a similar digit I size and placement on the distal tarsometatarsus (or an incumbent foot structure) as seen in *G. canadensis* (Fig. 4.04). This does not preclude the presence of a Cretaceous large-bodied wading avian without a robust digit I or with an incumbent foot. This also does not preclude a large-bodied wading avian with a robust digit I from leaving traces that do not (or ambiguously) preserve digit I.

Figure 4.04. Distal tarsometatarsus of *Grus canadensis* (LACM G4882, Pleistocene), showing the attachment scar for metatarsal I (circled in red). Extant *Grus canadensis* produce footprints that are consistent in size with those of *Limiavipes curriei* (Early Cretaceous: Aptian-Albian), a trace attributed to a large wading avian (McCrea et al., 2014a), and also produce prints that variably preserve digit I (Elbroch and Marks 2001:135). A large wading avian trackmaker from the Cretaceous may have a distal tarsometatarsus and placement of the attachment of metatarsal I that is similar in structure to that of the trackmaker of *Limiavipes curriei*.

If a small coelurosaur steps into soft substrate, there is a possibility that digit I (more proximal on the shaft of metatarsal II than in Avialae but in a more posterior position than seen in non-coelurosaurs, Gauthier, 1986), could leave an impression in the trackway and make a bird-like footprint (McCrea et al., 2015), as demonstrated by Falkingham and Gatesy (2015). Also, a track in soft substrate that is deep enough to impress digit I has more chance of its morphology being altered by extramorphologic features, such as sediment collapse into digits creating the appearance of slender digits (Kuban, 1989; Farlow, et al., 2012, fig. 17; Matsukawa, et al., 2014; McCrea et al., 2015). Deep substrate has the potential to include an impression of the distal metatarsal shaft: in its posterior position relative to the digits, a metatarsal impression could resemble a poorly preserved digit I (the likelihood of this misidentification is decreased if the substrate is soft enough to preserve both digit I and the metatarsal bundle). Plantigrade postures in either a non-avian theropod or a bird (Paulson, 2005, fig. 24.3; Milán, 2006) also may preserve a metatarsus impression. An example is TMP 1999.059.0001, a specimen consisting of a bipedal trackway of two natural cast, seemingly tetradactyl prints (Fig. 4.05). When initially discovered, the long, posteriorly-directed impression on each of the two prints was interpreted as a weight-bearing hallux, similar to that seen in extant *Adrea herodias* (Great Blue Heron), as well as the prints being similar in size to prints of extant *Ardea herodias*, and also possessing a high digit divarication. However, the “hallux” of these prints is in fact a metatarsal impression (Fig. 4.05), with a smaller, more subtle hallux impression preserved on print 2 of the trackway. This trackway is currently under study.

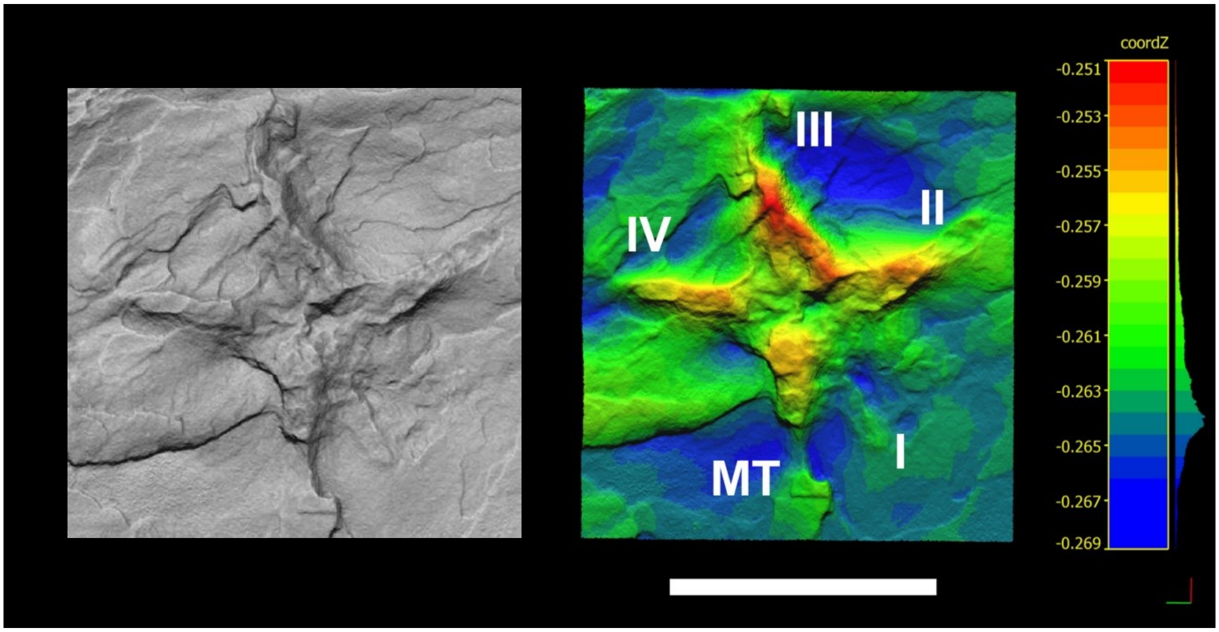

Figure 4.05. Greyscale image (left) and three-dimensional photogrammetric image of the second print in a natural cast trackway (right; TMP 1999.059.0001, McCrea et al., 2014a, fig. 73). On initial examination the long posteriorly-oriented impression could be mistaken for the impression of a weight-bearing hallux. On closer examination, a clear yet more subtle impression of digit I is present. Given the depth of the foot impressions, the stronger the posterior structure is, the more likely the impression is that of the distal metatarsus. Although there are only two prints in this trackway, the small digit I is not impressed in print 1 of the trackway. X-axis scale = 12.0 cm; Y-axis scale represents depth in meters.

The presence of a posteriorly-directed digit I in a trace is a useful feature that can allow ichnologists to use a synapomorphy-based character when proposing a trackmaker; however, given the anatomical and substrate variables that can affect the presence of digit I in a trace, the absence of a posteriorly directed digit I impression should not exclude the possibility of an avian trackmaker.

Slender claws (Lockley et al., 1992; Wright, 2004), and 7. Distal claw curvature away from the central axis of the foot (Lockley et al., 1992)—Claw (ungual) impressions, when included in the descriptions for avian ichnotaxa, are often described as sharp, narrow and/or acute (as in the emendation of *Aquatilavipes swiboldae* by McCrea and Sarjeant, 2001). Claw impressions within Theropoda vary from sharp to blunt, with smaller trackmakers having sharper, more slender claws (Wright, 2004). Both extant and extinct birds exhibit diverse claw shapes, and these shapes correlate with the lifestyles of the trackmakers. For example, confuciusornids are attributed to an arboreal lifestyle with a well-developed digit I and sharply curved pedal unguals (Hou et al., 1995), and the enantiornithines have been ascribed to a scansorial or raptorial arboreal habitat based on the long recurved pedal unguals (Li et al., 2014; Wang et al., 2014), although both basal pygostalians and enantiornithines fall within groups that overlap known extant ecological groups (terrestrial, aquatic, arboreal, wing-powered) of birds (Bell and Chiappe, 2011). No tracks have yet to be attributed to enantiornithine or confuciusornid birds; however, in extant birds with curved unguals similar to Enantiornithes and Confuciusornithidae, often only the most distal portion of the claw impresses, creating a space between the distal claw tip and the distal end of the digit (see Elbroch and Marks, 2001, for many figured examples). It is likely that the walking traces of confuciusornids and enantiornithines would leave similar looking traces to those of extant arboreal birds.

Claw impressions of traces attributed to Mesozoic avians closely resemble those traces of extant shore- and wading birds of Ardeidae, Charadriiformes, Cicioniidae, Galliformes, and Rallidae. These are birds that spend a great deal of time on the ground in environments that are conducive to footprint preservation. Claw impressions on these birds are short, sharp, triangular in shape, narrow relative to the width of the digit, and not separate from the most distal end of the digit. This last feature indicates a pedal phalanx (and keratinous sheath) that is not highly recurved (although see Senter, 2009, fig. 8 for images of the digit II ungual of *Grus canadensis* that is highly recurved), which is a similar to the pedal digits in many Theropoda, and those tracks attributed to small non-avian theropods, such as *Grallator* ichnosp. (Lockley and Harris, 2010, fig. 1). In contrast, traces attributed to large ground-dwelling birds such as *Dinornis* ichnosp. (Lockley et al., 2007; Lockley and Harris, 2010) and *Gastrornis* ichnosp. (Patterson and Lockley, 2004) have ungual impressions that range from triangular to rounded in shape, providing another example of how claw impression shape is variable with trackmaker size.

Some traces of shore- and wading birds, both extant and extinct, exhibit unguals with a slight curve away from the midline of the footprint. Currie (1981) describes that the medial and lateral digits of the holotype of *Aquatilavipes swiboldae* as curving so that the distal ends [of the digits] point away from the central axis of the foot, and this feature is figured for selected prints shown in fig. 2 of that study. This feature is apparent in several of the tracks of *Ignotornis mcconnelli* figured in Lockley et al. (2009), in traces figured in Kim et al. (2012), and is figured for the Eocene ichnospecies *Avipeda phoenix* (Sarjeant and Langston, 1994, fig. 10) but was not included in the emendation of that ichnospecies. The lateral and medial curvature of digits and unguals away from the midline of the footprint is not consistently preserved in monoichnospecific track specimens (see figures for Currie, 1981; Lockley et al., 2009; Kim et al., 2012 for examples). Tracks for which this character does not apply are palmate tracks of Anseriformes, the Cenozoic *Anatipeda* ichnosp. (Sarjeant and Langston, 1994), and the Mesozoic ichnotaxa *Hwangsanipes* ichnosp. and *Uhangrichnus* ichnosp. (Yang et al., 1995):

medial and lateral digits of palmate feet tend to curve towards the midline of the footprint. Also, the Cenozoic ichnotaxon *Avipeda thrinax* (Sarjeant and Reynolds, 2001, fig. 3) displays unguals on lateral digits that curve towards the midline of the footprint.

Medial and lateral digits with unguals that curve away from the midline of the footprint are not restricted to those tracks attributed to avian trackmakers: this characteristic can also be observed as inconsistently preserved in the prints of non-avian theropods. A slight lateral curvature to the unguals can be seen in both *Eubrontes* ichnosp. and *Grallator* ichnosp. traces figured in Olsen et al. (1998), as well as tyrannosaurid tracks (McCrea et al., 2014b). Ungual shape in tracks is likely convergent in large wading birds and small non-avian theropods due to the size and the (paleo)ecology of the trackmaker.

Behavioral Features of Trackmakers

Avian and maniraptoran theropods share behavioral characteristics, such as nesting (Norell et al., 1995; Varricchio et al., 1999) and brooding (Norell et al., 1995; Hopp and Orsen, 2004). While this behavior and others are not necessarily synapomorphic characters, when such behavior is preserved it adds valuable information about the trackmaker, regardless of its identity. However, there are behaviors that are more avian than others, or that are similar to the behavior of extant birds. The following two characters have been attributed to both the extant and fossil traces of avians, and have potential to support the avian identity of a trackmakers (Lockley and Harris, 2010).

Track Density (Lockley et al., 1992; Lockley and Harris, 2010)—Many Mesozoic and Cenozoic shorebird traces are characterized by a high track density of > 100 per m^2 (Lockley and Harris, 2010). This is seen in the Mesozoic tracksites of Korea, where track density has been reported at ~ 600 per m^2 (Kim et al., 2012). This high-density occurrence of traces in Mesozoic avian track assemblages such as those in Korea have been attributed to the concentration of trackmakers foraging along a shoreline (Kim et al., 2012). This flocking, high-density behavior is observed in extant shore and wading birds during high tides, whereas flocks tend to segregate into their preferred foraging zones once the tides recede (Elbroch and Marks, 2011).

Behavioral traces attributed to Mesozoic avians are not common, but what is available provides insight into the other types of non-locomotory behaviors that can be preserved. Gregarious behavior has been interpreted for *Ignotornis mcconnelli* (Lockley et al., 2009); however, this is not a behavioral interpretation that is restricted to avians (for examples see Currie, 1998 and McCrea et al., 2014b for tyrannosaurs; Myers and Fiorillo, 2009 for sauropods; Ostrom, 1972 and Li et al., 2007 for dromaeosaurs (Paraves); Matsukawa et al., 1997 for small tridactyl trackmakers), and should only be used to provide supporting information for trackmaker behavior, rather than a diagnosis of an avian trackmaker.

Associated fossils and feeding behavior (Lockley et al., 1992)—Feeding traces are also associated with fossilized avian traces. Lockley et al. (2009) interpret the shuffling and stop-start movement in the trackways as foot stirring foraging activity. Feeding traces also provides insight into both the skeletal anatomy and feeding behavior for avians for which skeletal material have not yet been found. The type trackway of *Ignotornis gajinensis* (Kim et al., 2012, fig. 5) also preserves what is described as a repeated association of arcuate, double-grooved impressions that are convergent in morphology to open-billed sweeping traces when extant spoonbills are foraging invertebrates (Swennen and Yu, 2005, fig. 2). The trackmaker of *Ignotornis gajinensis* can be interpreted to have possessed (and used) a keratinous bill with a distally broad and flattened tip, similar in morphology to that of extant spoonbills.

Bill sweeping is not the only feeding trace reported for fossil avian traces. Dabbling and pecking, such as that observed in the *Branta canadensis* (Canada Goose), have been documented in palmate Cenozoic (Eocene) traces of *Presbyorniformipes feduccii* (Yang et al., 1995), for which a keratinous bill with a rounded tip can be interpreted for the trackmaker. Structures interpreted as bill probe traces are associated with traces of *Koreanaornis* ichnosp. (Falk et al., 2010; Falk et al., 2014). Avian traces, both fossilized and extant, are often associated with invertebrate burrows. Falk et al. (2010) note that *Arenicolites* ichnosp., *Cochlichnus* ichnosp., and *Steinichnus* ichnosp.are associated with traces of *Koreanaornis* ichnosp., and the invertebrate tracemakers were likely the target of the *Koreanaornis* ichnosp. trackmaker foraging activities. The preserved morphology of bill probes, as with vertebrate footprints, is dependent on substrate consistency. A water saturated substrate may not accurately preserve the morphology of the bill (Fig. 4.06). Also, extant shorebirds will probe visible burrows, which may alter the morphology of the impression of the distal bill (Fig. 4.06).

Figure 4.06. Differences in bill probe morphology. **A**, bill probes showing impressions of the distal end of the upper and lower mandible of *Branta canadensis*, similar in morphology to foraging marks preserved with traces of *Presbyorniformes feduccii* (Yang et al., 1995), scale = 10 cm. **B**, bill probes of *Actitis macularius*, showing both the upper and lower mandible in wet, medium-fine wet sand, pen cap = 30 mm. **C**, *Actitis macularius* tracks leading up to a false burrow created using the end of a pencil. The pseudoburrow was created to observe how extant shorebirds may use the visible portions of invertebrate traces in their foraging behavior. Probing of the experimental pseudoburrow occurred (note the distortion on the upper left edge of the pseudoburrow), but the morphology of the distal end of the bill is not preserved, demonstrating that the presence of existing invertebrate traces may obscure or not preserve feeding traces. Scale (water damaged) in centimeters. **D**, bill probes associated with prints of *Tringa solitaria* (Solitary Sandpiper) on fine wet silty sand. The high water content distorts the morphology of some of the probes, making delineation between the upper and lower mandible indistinct. Scale = 10 cm.

The record of non-avian theropod feeding traces is relatively rare, and is dominated by tooth marks attributed to large theropods (Hone and Rauhut, 2010, and references within). Feeding behaviors that involve bill probing or sweeping suggest that thecodont dentition is either not present or not employed in the preserved foraging behavior, and also suggests partial edentulism and the presence of rhamphothecae. Edentulism is not an avian-specific character: edentulism is known in Oviraptorosauria (Osmólska et al., 2004), Ornithomimosauria (Norell et al., 2001; Ji et al., 2003), and Therizinosauria (Lautenschlager et al., 2013; Pu et al., 2013). However, no feeding traces that have been attributed to these maniraptoriformes to date. Keratinous structures are also documented in avian theropods (Schweitzer et al., 1997). Tooth loss occurred several times in Aviale (Xu et al., 2011), and the loss of enameled teeth may have occurred approximately 116 million years ago (Meredith et al., 2014). While foot-stirring, bill-sweeping, and bill probing are theoretically not restricted to Aves, their presence strongly suggests both anatomy and behavior that are both convergent with extant Aves and likely ancestral in Avialae.

Possible Avian Trait: High Footprint Length to Pace Length Ratio (FL:PL)

At a glance, traces of both extant and extinct small wading birds exhibit short pace lengths relative to footprint length. Footprint length to pace length ratio (FL:PL), is both morphological and behavioral. Traces of *Ignotornis mcconnelli* (Lockley et al., 2009**)** and *Ignotornis gajinensis* (Kim et al., 2012) are associated with feeding traces, and while feeding traces were not reported (or not observed) with the other traces of the Cretaceous, Cenozoic, and extant birds, the possibility that these avian trackmakers were engaging in foraging behavior should be considered. No feeding traces have been noted for *Columbosauripus* ichnosp., *Irenesauripus* ichnosp., *Irenichnites* ichnosp., or *Magnoavipes* ichnosp. The avian and non-avian theropod trackmakers with footprint lengths that overlap in size differ in this ratio, even though there is an overlap in range: traces of large extant and extinct wading avians (those within the size range of traces attributed to small non-avian theropods; FL < 20 cm) appear to have shorter paces in comparison with footprint size (a higher average FL:PL).

This is specifically seen in the ichnotaxon *Magnoavipes* ichnosp. The FL:PL ratio is the most similar to that of other (non-controversial) traces attributed to small and medium-sized theropod trackmakers than it is to large wading avians. Also, recent (Xing et al., 2015) multivariate statistical analyses comparing large avian traces from the Cretaceous and Cenozoic, and from extant birds with those traces attributed to small-, medium-, and large-sized non-avian theropods show that *Magnoavipes* ichnosp. groups with the traces of non-avian theropods to the exclusion of avian traces. This supports the interpretations of Lockley et al. (2001) and Matsukawa et al. (2014) of *Magnoavipes* ichnosp. as the trace of a theropod trackmaker attributed to Ornithomimidae. Given the many non-avian theropod characters of *Magnoavipes* ichnosp. (Lockley et al., 2001; Matsukawa et al., 2014), the natural variability in digit divarication, and the supporting multivariate analyses of Xing et al. (2015), there is little evidence to support *Magnoavipes* ichnosp. as the trace of a large avian: all of the recent analyses support *Magnoavipes* ichnosp. as the trace of a non-avian theropod.

Once footprint length in traces (attributed to large theropods) approach lengths > 20 cm (*Columbosauripus* ichnosp. and *Irenesauripus* ichnosp.), the FL:PL ratio approaches that of Cenozoic and extant birds (Fig. 4.07). The similarity in FL:PL between small and large avian traces and those of large non-avian theropods is likely due to allometric scaling. In Tyrannosauridae, tibiae, flibulae, metatarsals, and pedal phalanges III-1 and III-2 increase in size with negative allometry in relation to femur length (Currie, 2003). In other words, large theropods are not going to maintain the same limb proportions as those of small theropods, and may approach proportions that are closer to those of small and large wading avians (Buckley, in prep). As large non-avian theropod traces are not going to be misidentified as traces of avians, the FL:PL ratio can be used to aid in discerning between the traces of large avians and those of small non-avian theropods. This was seen in diagnosing *Wupus agilis* as the trace of a large wading avian, rather than that of a small non-avian theropod (Xing et al., 2015). Relatively low FL:PL ratios are documented in non-avian theropods, such as the slow-walking large theropod from Lark Quarry site in Queensland, Australia (Thulborn and Wade, 1979; 1984), turning theropods (Sampson and Currie, 1996; McCrea et al., 2014a), and trackways exhibiting ichnopathologies (McCrea et al., 2015, fig. 7), and these may approach the FL:PL ratios (although probably not the FL values) typical of avians. These examples demonstrate how behavior (other than the behavior of walking from Point A to Point B) can affect footprint features.

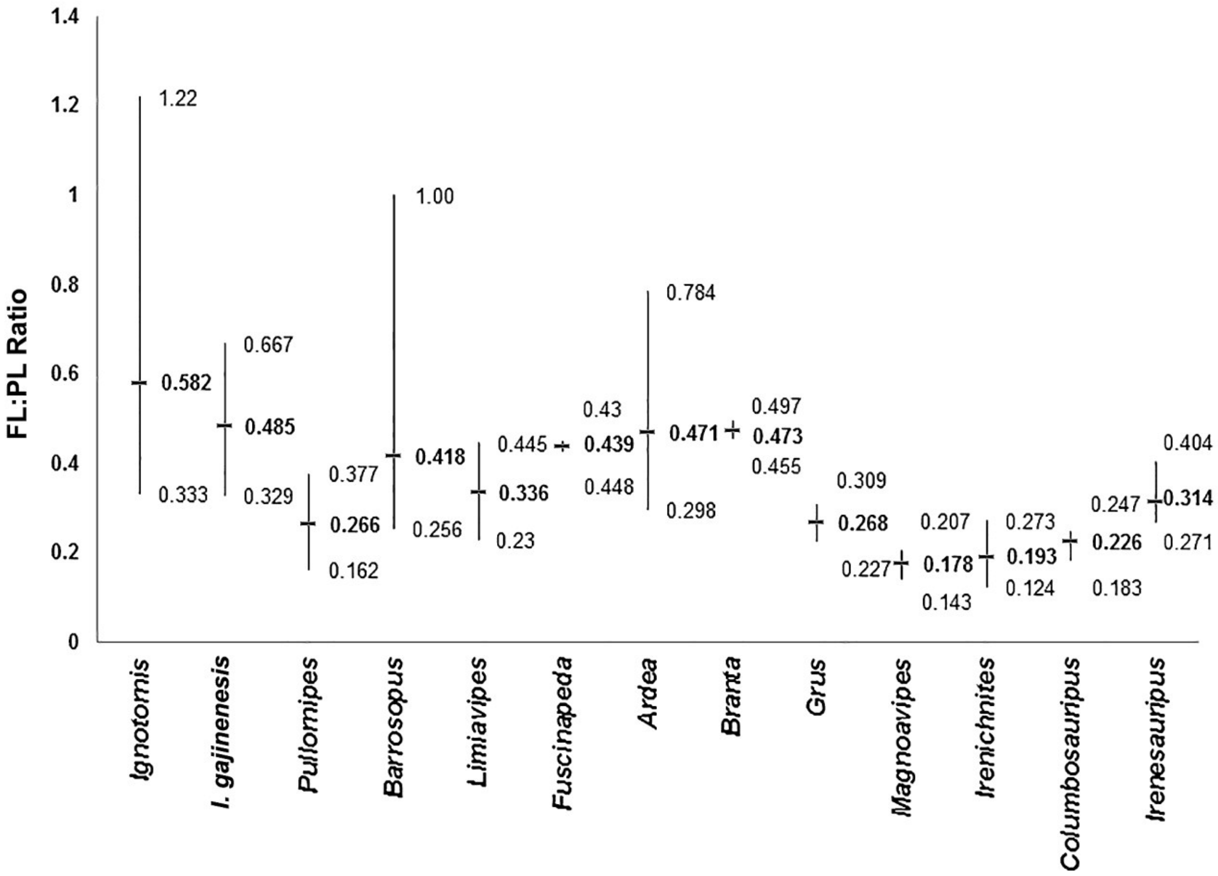

Figure 4.07: Plotted average, maximum, and minimum footprint length (FL) to pace length (PL) ratios for Cretaceous small avian traces (*Barrosopus slobodai*, Coria et al., 2002; *Ignotornis gajinensis* with an associated feeding trace, Kim et al., 2012; *Ignotornis mcconnelli*, Lockley et al., 2009; *Pullornipes aureus*, Lockley et al., 2005), Cretaceous large avian wading traces (*Limiavipes curriei*, McCrea and Sarjeant, 2001; McCrea et al., 2014a), Cenozoic large avian (*Fuscinapeda meunieri* and *Fuscinapeda texana*, Sarjeant and Langston, 1994), Extant large avians (*Ardea herodius*, PRPRC NI2014.001, NI2014.002; *Branta canadensis* PRPRC NI2014.004; *Grus canadensis*, Elbroch and Marks, 2001), *Magnoavipes* ichnosp., originally identified as avian by Lee (1997) and Fiorillo et al. (2011) but attributed to Ornithomimosauria by Lockley et al. (2001) and Matsukawa et al. (2014); the small theropod trace *Irenichnites* ichnosp., medium theropod trace *Columbosauropus* ichnosp., and the large theropod trace

Irenesauripus ichnosp. (McCrea, 2001). Data on graph show the low (bottom value), mean (middle value, bold), and high (upper) value for the FL:PL for each of the ichnotaxa presented. While there is overlap in range, tracks of birds and those attributed to birds have a larger FL:PL ratios than do tracks of non-avian theropods. Interestingly, tracks attributable to medium and large theropods approach FL:PL ratios of those traces of birds. See Xing et al. (2015) for more details of this analysis. This suggests that, even though there is a good track record for large theropod traces, they may provide misleading information when attempting to distinquish between the traces of small non-avian theropods and large birds.

DISCUSSION

Distinguishing Between the Traces of Large Avians and Small Non-Avian Theropods

Impressed Synapomorphies—The only character used in both the phenetic- and synapomorphy-based methods for assigning an avian trackmaker is the reversed hallux, or pedal digit I. When preserved, this is the most distinguishing character for assigning an avian identity to the trackmaker. However, preservation of digits, particularly of digit I (Figs. 4.03, 4.05), is variable for those avians with an incumbent foot structure, and even for those avians with a functional, weight-bearing digit I preservation can be affected by substrate consistency. A strict application of the synapomorphy-based method does not aid paleontologists in discerning between the tracks of large avians and those of small theropods if a) the substrate is not conducive to the preservation of a synapomorphic trait, b) the trait, while present, did not contact the substrate during locomotion of a sharply ungualed, mesaxionic trackmaker, or c) the preserved impression is misinterpreted as a synapomorphic character, which can be illustrated in numerous examples of fossil and extant avian tracks (Fig. 4.03). Conversely, caution is needed when using only one of the phenetic-based characters highlighted in Lockley et al. (1992), as many are convergent due to size and shared paleoecological niches. This requires that several lines of evidence be used to support the attribution to an avian trackmaker, rather than a single feature. Given that many of the synapomorphies attributed to Aves are not pedal, most of the skeletal synapomorphies used to discern Aves from non-avian Theropoda have little chance of preserving as ichnites.

Preservation versus Anatomy: Digit Slenderness—Trackmakers do not walk in sediments that accurately replicate the morphology of their pedes 100% of the time. In the case of avian trackmakers that spend time on the ground in environments conducive to footprint preservation, they are walking on substrates that are water saturated. The majority of footprints made by small shorebirds are either substantively altered by sediment deformation, or are erased from the track surface as the footprint collapses (pers. obs.). *Magnoavipes* ichnosp. is one example of a track type, originally attributed to a large avain trackmaker, in which the slenderness of the digits was an artefact of substrate collapse (Matsukawa et al, 2014). While digit slenderness is an ichnologic character fraught with preservational and interpretive peril, it cannot be dismissed from consideration when examining both avian and non-avian theropod traces.

The size of the trackmaker as it relates to digit thickness has been previously discussed in this chapter: larger avian trackmakers (e.g. *Dromaius*) have more robust digits than do relatively smaller avian trackmakers (e.g. *Ardea herodias*). Size may not be the only factor influencing digit thickness. Volant avians are not restricted to a ground-dwelling habitat. While shore- and wading birds may spend a considerable amount of their lives on the ground foraging and nesting (with the exception of *Tringa solitaria*, which nests in trees), these birds are not dependent on their pedes as their sole means of locomotion. Their digits, not being subject to constant ground-based activities, may not have had the selective pressures to become more robust. Also, a volant bird would also face selective pressures to possess lightweight feet in the form of weight reduction, whereas a flightless bird would not be subject to the same selective pressures.

One cannot discuss (relatively) large slender digits without addressing the *Magnoavipes* trackmaker. While the digits of the first described ichnospecies (*M. lowei*) were artificially slender, *M. caneeri* and *M. denaliensis* also possess slender digits. *Magnoavipes* possesses a footprint length that is comparable to similar-sized small- to medium-sized non-avian theropod trackmakers with more robust digits. One notable difference between the traces of *Magnoavipes* and those of similar-sized theropods is the pace length. *Magnoavipes*, attributed to an ornithomimid trackmaker (Matsukawa et al., 2014), has a relatively long pace length compared to footprint length. One interpretation of a relatively long pace length is a relatively higher trackmaker speed. Slender digits may be correlated with higher speeds: this is a relationship that will be examined in future studies.

The Gestalt Method of Discerning Avian Traces—The practical realities of morphologic and preservational variations in small tridactyl ichnites do not necessarily make trackmaker identification unlikely, improbable, or impractical. Although caution is needed in interpreting characters as avian using the phenetic-based method, multiple phenetic-based features provide practical guidelines for examining and identifying a potential trackmaker for small ($\leq$ 20 cm) tridactyl traces. While the identification of a trackmaker is not the ultimate goal for vertebrate ichnology (Lockley and Harris, 2010), vertebrate traces are oftentimes the only, or the most complete, record of vertebrates in regional paleoecosystems (McCrea et al., 2014a). Traces of extant shore- , wading-, and ground-dwelling (but not necessarily flightless) birds are convergent in foot forms, bill morphologies, and ecosystems with their Cretaceous analogs. Extant birds and their traces provide a wealth of information on variation in preservational (see Falkingham and Gatesy, 2014), ecological (Falk et al., 2011), and morphological (McCrea et al., 2015) features.

Feature 1 in Lockley et al.'s (1992) listed traits attributed to bird tracks, "similarity to those of extant birds", is an area that is open for future work. The gestalt of a trace (as used by Farlow et al., 2013) sounds highly qualitative, but may be quantitatively examined (Buckley et al., 2015; Xing et al., 2015). Features that are qualitatively avian can be examined to determine whether they are isolated to extant Aves, and these features (morphologic and behavioral) can also be examined for their presence in Cretaceous traces, such as footprint length to pace length ratio (FL:PL). Considering the gestalt of a trace requires that multiple characters be used to attribute a trace to an avian trackmaker: no one character should be used to the exclusion of all other characters (i.e. as has been done with digit divarication) when identifying avian traces.

The extant ichnological record provides an accessible and interactive natural laboratory in which to test hypotheses of discerning traces of large wading birds from those of small non-avian theropods, especially when those avian traces do not preserve the synapomorphic trait of a reversed digit I or that appear larger than the typical small shorebird traces due to anatomy, behavior, substrate consistency, or a combination of the aforementioned variables. Given that multiple variables can affect the final appearance of a footprint, and also given the variability in morphology exhibited in digit I of extant shore and wading birds, one should expect the lack of a synapomorphy supported feature, rather than its presence. However, it is likely that as traces are discovered that represent trackmakers close to the divergence of avians from theropods, the similarities in skeletal morphology between avian and non-avian theropods will make discerning the identity of the trackmaker difficult. That being said, the lack of a synapomorphy-based feature should not deter one from attempting to discern the identity of the trackmaker: as challenging and enigmatic as these traces may be to interpret, they provide data on a group of vertebrates that are poorly preserved as skeletal specimens, and provide insights into the diversity of Cretaceous avian theropods that are not available from skeletal data alone.

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CHAPTER 5: UTILITY OF MULTIVARIATE STATISTICAL ANALYSES IN AVIAN ICHNOLOGY

INTRODUCTION

Avian track types (or morphotypes) can be generally assigned to ecological niches using overall track size, and pace and stride data (i.e., long-legged wading birds vs. short-legged shorebirds). Other track features, such as the extent of interdigital webbing and the degree of rotation of individual tracks in a trackway, may also provide information that allows ichnologists to propose a well-supported modern analog for the Cretaceous avian trackmaker (i.e., *Uhrangichnus*, Figure 5.01). In recent years, many novel traces attributed to Mesozoic birds have been described, as well as higher order classifications, such as avian ichnofamilies (Lockley et al., 1992; 2006; Lockley and Harris, 2010; McCrea et al., 2014). Avian ichnotaxonomy exists to provide a means by which to both document and discuss discrete patterns in the variation of footprint shapes that are attributable to now extinct birds. Ichnotaxonomic groupings for traces identified as avian in origin have the potential to not only identify ecological partitions among extinct avians (Falk et al., 2011), but also to potentially describe the biologic diversity of known Mesozoic avians whose traces are preserved within the ecological niches of shorebird and wading bird.

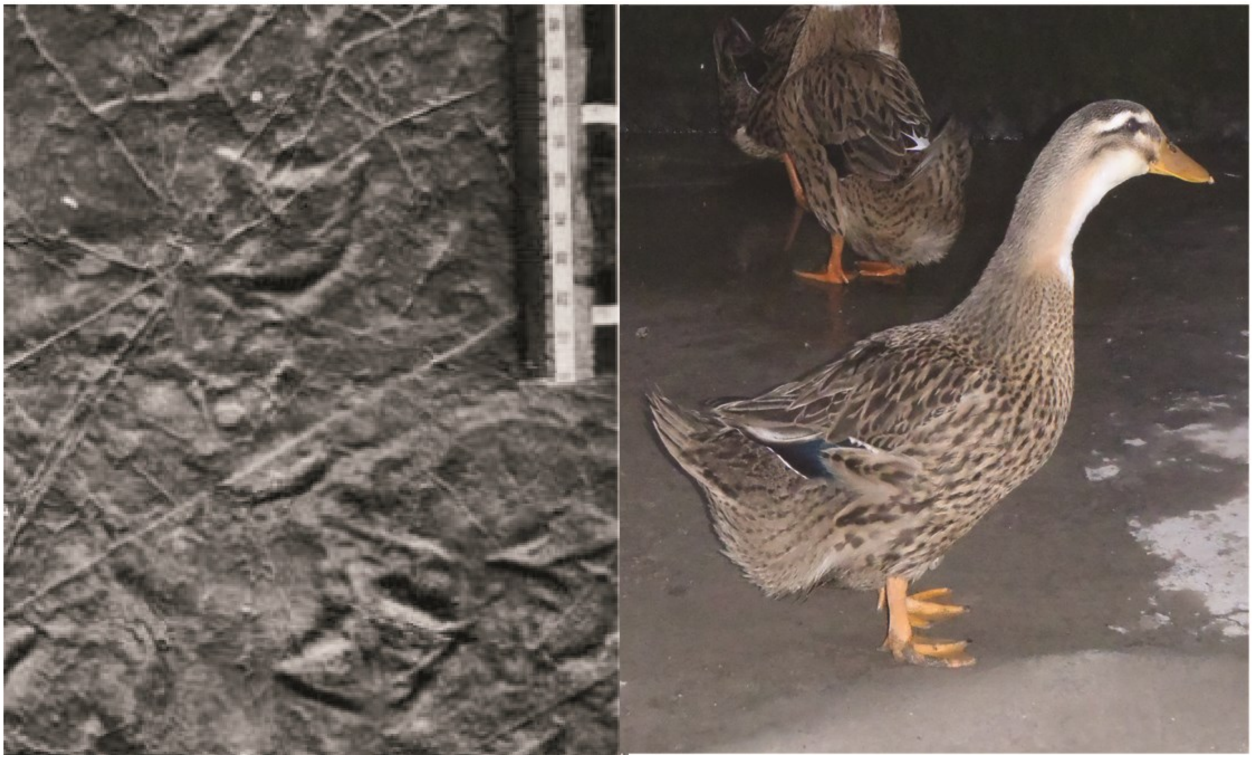

Figure 5.01. An example of an avian ichnotaxon (*Uhangrichnus chuni*, left) and an extant avian analog (right). Left, modified from Yang et al. (1995); right from author's personal photos.

Avian ichnites avoid many of the pitfalls ascribed to large vertebrate tracks due to their nature; avian trackmakers are typically too small and too light to produce substantive undertracks, or to produce many extramorphological features (metatarsal or "heel" drag marks, sediment displacement bulges, track margin collapse, etc.), although there are exceptions (features interpreted as toe drag marks in trackways of *Pullornipes aureus*, Lockley et al., 2006b; toe drags seen in *Ignotornis mcconnelli*, Lockley et al., 2009; potential for small-scale extramorphological features as proposed by guineafowl walking in artificial sediment, Falkingham and Gatesy, 2014). As such, qualitative (visual) differences among groups of avian ichnites are more likely to be anatomical features of the trackmaker rather than preservational in origin.

The study of avian ichnites, however, is not without challenges. First, the challenge of identifying the potential trackmaker of large bird versus small non-avian theropod for certain ichnotaxa remains despite many efforts to clarify the issue (Lockley et al., 2001; Wright, 2004; Fiorillo et al., 2011): this is not surprising given that Aves nest within the Theropoda. Wright (2004) observed many bird-like features in dinosaur tracks, and noted many of the issues distinguishing the tracks of bipedal, tridactyl dinosaurs and avians that may be subject to similar functional constraints in locomotion. However, theropod locomotion is more hip-driven (Gatsey, 1990; Farlow et al., 2000) than knee-driven, as it is in birds (Rubenson et al., 2007), but the extent to which these factors contribute to qualitative and/or quantitative ichnotaxonomic differences is unknown. While a high average total divarication (~ 110°) has been used to tentatively identify avian tracks (e.g., Lockley et al., 2001), using an average calculated from a large sample to determine the identity of one track has the potential to be misleading (see Chapter 4 for more details).

One ichnotaxon in particular is problematic in identifying the affinity of the trackmaker. The ichnogenus *Magnoavipes* (Figure 5.02) was first described by Lee (1997) as a trace attributable to a large avian from the Woodbine Formation (Cenomanian) based on the slender digits and wide total divarication. A reanalysis of the ichnogenus led Lockley et al. (2001) to attribute *Magnoavipes* to a theropod, rather than avian, trackmaker based on large size, lack of a hallux (as seen in extant large wading birds) and narrow trackway. However, Fiorillo et al. (2011) describe a new ichnospecies of *Magnoavipes* (*M. denaliensis*) and attribute it to an avian trackmaker based on the high total divarication. The strengths of the opposing diagnostic criteria (high total divarication vs. trackway characteristics) are tested in Chapters 4, 5, and 6.

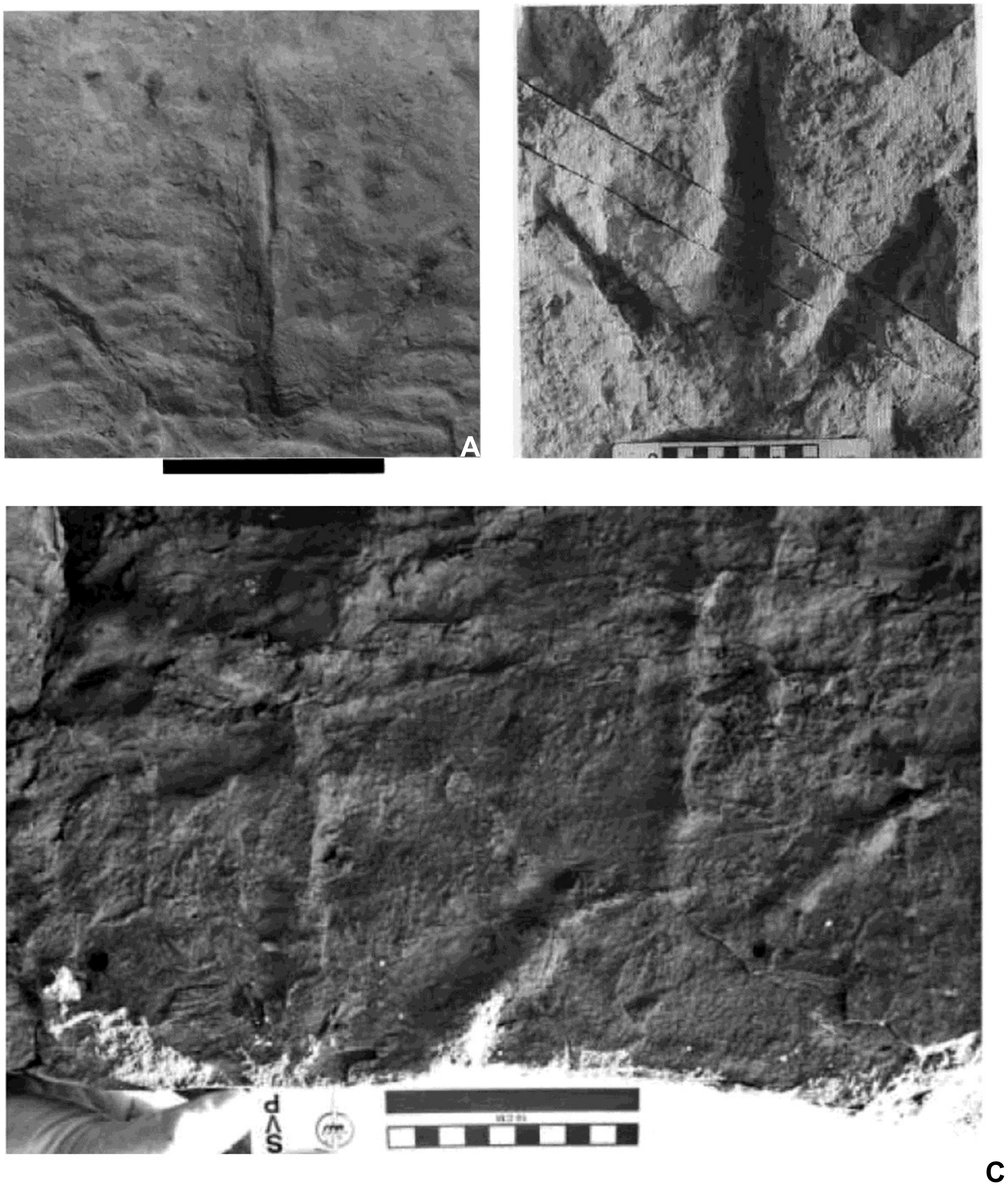

Figure 5.02. *Magnoavipes*. **A**, *Magnoavipes lowi* (Lee, 1997); **B**, *Magnoavipes caneeri* (Lockley et al., 2001); **C**, *Magnoavipes denaliensis* (Fiorillo et al., 2011). *Magnoavipes* demonstrates how determining track maker affinity can be difficult when an ichnite exhibits both avian (high total divarication) and theropod (narrow trackway, long pace and stride, low footprint rotation) traits. Scale = 10 cm.

Second, while bird tracks are generally immune to common extramorphologic features sometimes preserved in the tracks of much larger animals, they do exhibit variability in preservation of certain morphologic features, specifically of digit I (hallux) and of webbing. There are examples in the literature where, within an individual trackway, the hallux (i.e. *Goeseongornipes markjonesi*, Kim et al., 2012, fig. 9A) is inconsistent (see Chapter 4 for an in-depth treatment of this issue). The presence of semipalmate webbing (webbing restricted to the proximal part of the digits) may be difficult to detect due to sediment consistency and preservation, and over-reliance on modeling may lead to misinterpretation of webbing as sedimentological features (see Falkingham et al., 2009).

A Brief Review of Avian Ichnofamilies from the Mesozoic

There are seven ichnofamilies currently attributed to avian traces from the Mesozoic. Refer to the references cited within this section for more detailed information on the systematics of these ichnofamilies and the assignments of the ichnogenera therein.

Avipedidae—Avipedidae (Fig. 5.03) was originally described by Sarjeant and Langston (1994) as tridactyl prints with webbing that is limited to the most proximal part of the interdigital angles (Sarjeant and Langston, 1994). The type ichnogenus for Avipedidae is *Avipeda* (Vialov, 1965), whose original diagnosis and description was emended by Sarjeant and Langston (1994) to remove the wastebasket nature of both *Avipeda* and the ichnofamily (or morphofamily of Sarjeant and Langston, 1994) for which *Avipeda* is the type ichnogenus. Sarjeant and Langston also assign *Aquatilavipes swiboldae* (Currie, 1981) to Avipedidae. Cretaceous Avipedidae, to date, includes *A. swiboldae* (Currie, 1981), and *A. izumiensis* (Azuma et al., 2002).

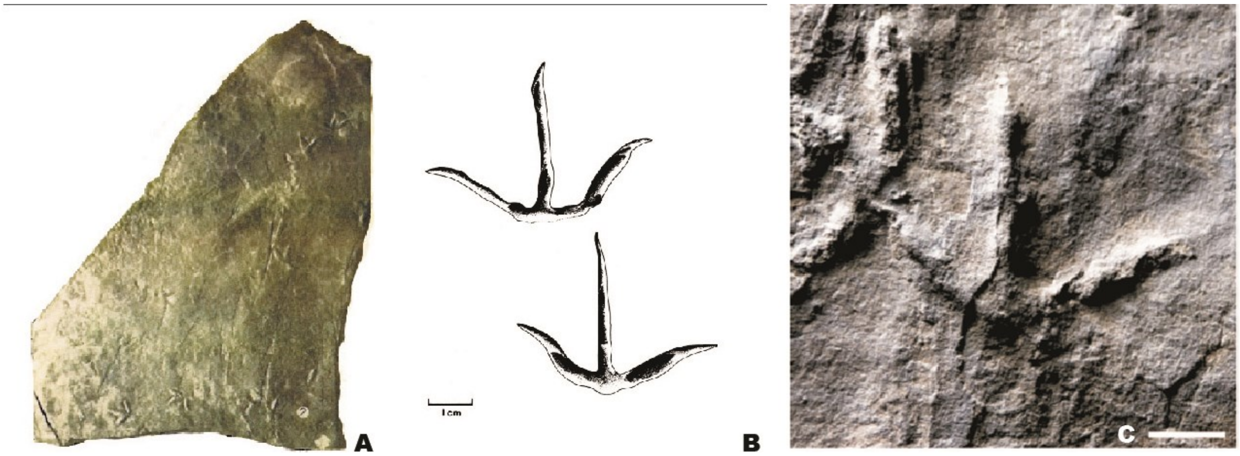

Figure 5.03. Avipedidae. **A**, *Avipeda* (modified from Vialov, 1965); **B**, *Aquatilavipes swiboldae*, scale = 1.0 cm (modified from Currie, 1981); **C**, *Aquatilavipes izumiensis* (modified from Azuma et al., 2002, scale = 1.0 cm).

Ignotornidae—The ichnofamily Ignotornidae was first erected by Lockley et al. (1992) and diagnosed as tetradactyl, slightly asymmetric bird tracks with variably preserved, posteriorly directed hallux impressions showing significant medial rotation towards trackway midline (Lockley et al., 1992). Originally, Ignotornidae included both *Jindongornipes kimi* and *Koreananoris hamanensis*, which were originally assigned to the ignotornids based on the presence of a well-defined, posteriorly-oriented hallux. However, as more tetradactyl bird tracks were discovered with halluces of varying lengths and orientations, Ignotornidae was revised (by the emendation to *Ignotornis* by Kim et al., 2006) to include only those ichnotaxa that possess a slight proximal webbing, and a prominent posterior-medially oriented hallux impression. Ignotornidae include *Goseongornipes markjonesi* (Lockley et al., 2006a) and *Hwangsanipes choughi* (Kim et al., 2006) (Fig. 5.04).

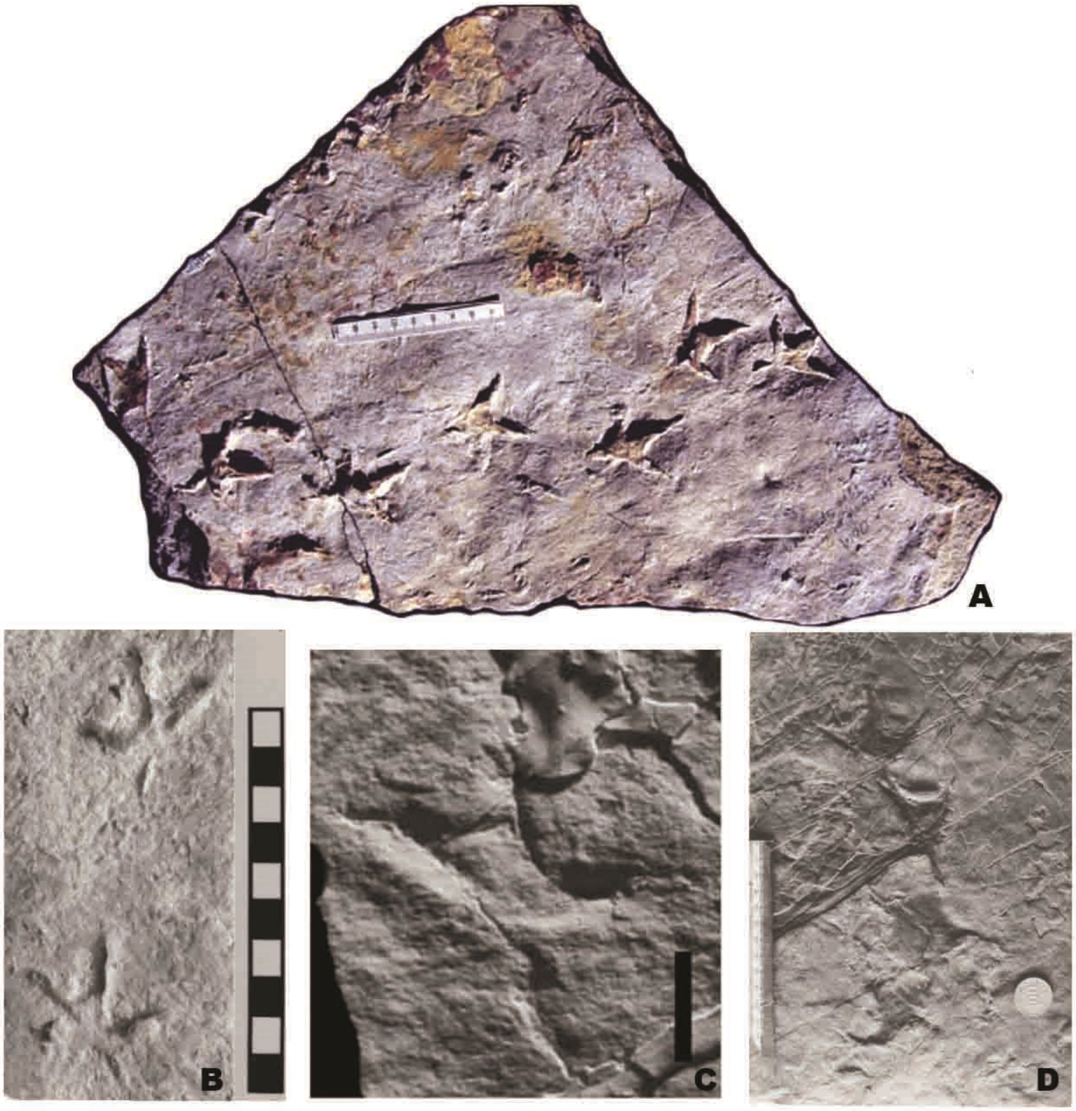

Figure 5.04. Ignotornidae. **A**, *Ignotornis mcconnelli*, holotype (Lockley et al., 2009); **B**, *Goseongornipes markjonesi* (Lockley et al., 2006a); **C**, *Ignotornis yangi* (Kim et al., 2006); **D**, *Hwangsanipes choughi* (Yang et al., 1995). Scale divisions in centimeters.

Koreanaornipodidae—Koreanaornipodidae (Fig. 5.05) was erected by Lockley et al. (2006a) to include all small, wide, sub-symmetric, functionally tridactyl tracks with slender digit impressions, and wide divarication between digits II and IV. Koreanornipodidae also possess a small occasionally present hallux posteromedially directed approximately 180° away from digit IV (Lockley et al., 2006a). This differs from the diagnosis of Avipedidae in that a hallux is not usually preserved in Avipedidae. Koreanaornipodidae includes not only the type ichnogenus *K. hamanensis*, but also *K. dodsoni* (Xing et al., 2011) and *Pullornipes aurea* (Lockley et al., 2006b).

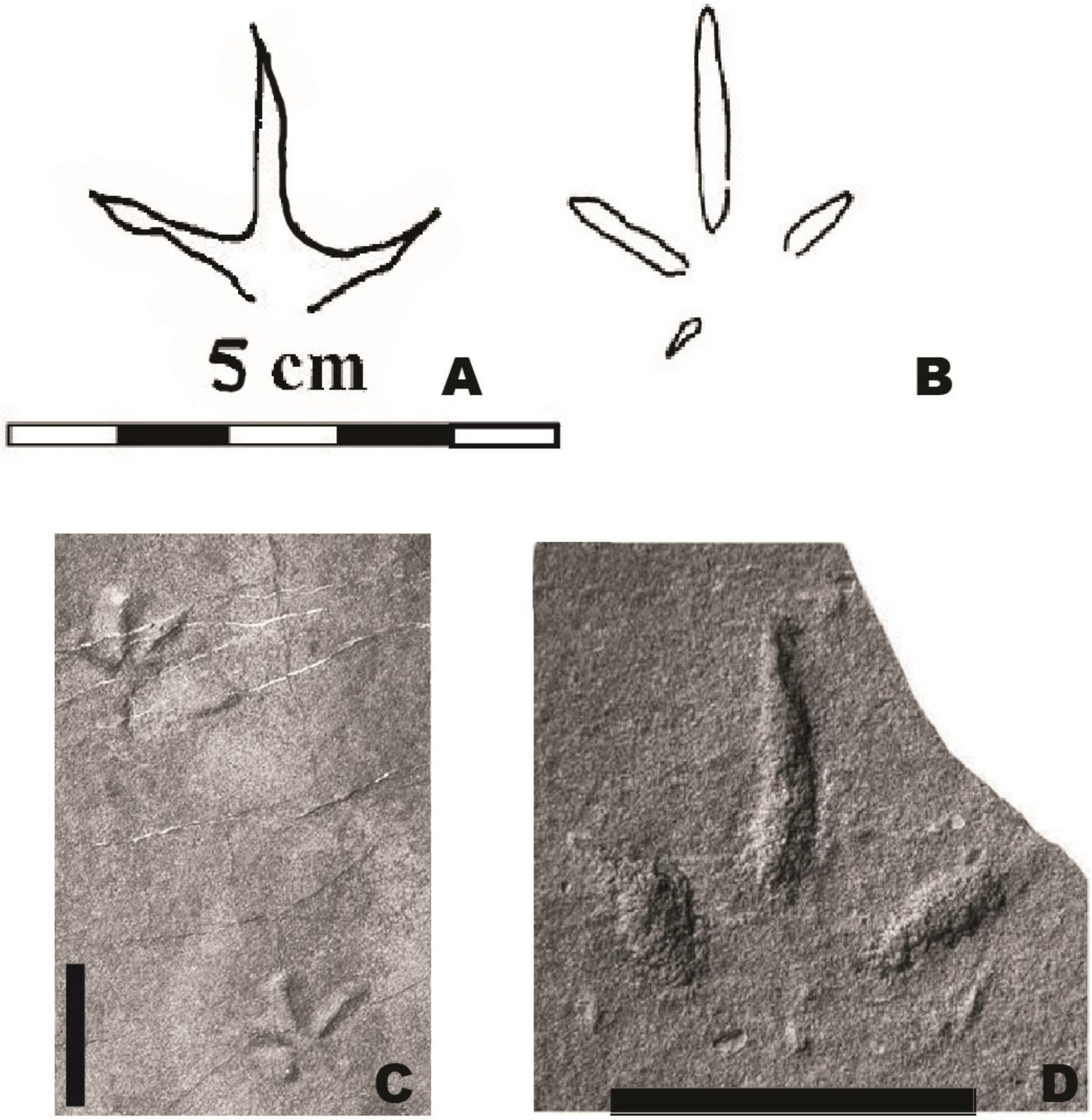

Figure 5.05. Koreanaornipodidae. **A**, **B**, *Koreanaornis hamanensis* (Kim, 1969); **C**, *Pullornipes aurea* (Lockley et al., 2006b); **D**, *Koreanaornis dodsoni* (Xing et al., 2011). Scale bar = 5.0 cm.

Jindongornipodidae—Jindongornipodidae (Fig. 5.06) was named by Lockley et al. (2006a) in their emendation of Ignotornidae. Jindongornipodidae is diagnosed by medium sized tetradactyl tracks with digit II shorter than digit IV, and a moderately long, posteriorly directed hallux (Lockley et al. 2006a). To date, Jindongornipodidae is a monoichnospecific ichnofamily, whose type ichnospecies is *J. kimi* (Lockley et al., 1992).

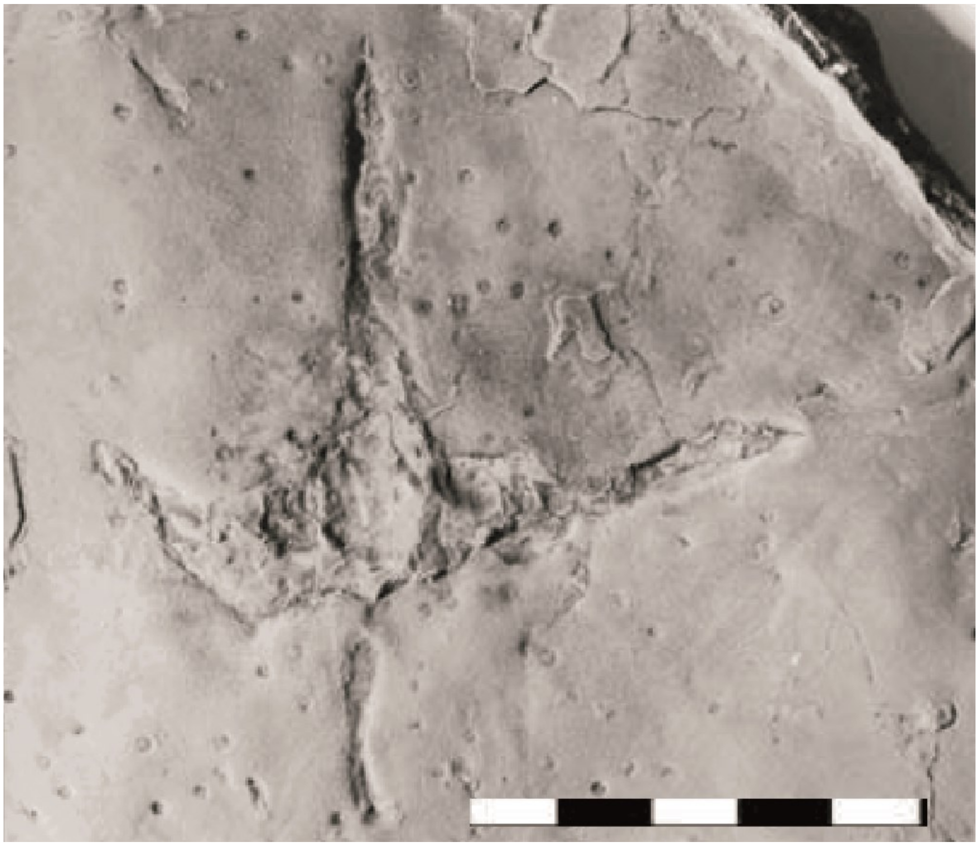

Figure 5.06. Jindongornipodidae. *Jindongornipes kimi* (Lockley et al., 2002). Scale = 5.0 cm.

Limiavipedidae—It has been known for some time (Lockley and Harris, 2010) that *Aquatilavipes curriei* (McCrea and Sarjeant, 2001) did not match the ichnomorphology of other ichnospecies of *Aquatilavipes* (*A. izumiensis, A. swiboldae*). *A. curriei* prints are attributed to large, long-legged avian track-maker with a functionally tridactyl pes tracks possessing no obvious webbing (McCrea and Sarjeant, 2001). Tracks attributed to Limiavipedidae also possess no hallux impressions, and have a pace and stride that is relatively short compared to similarly-sized theropod ichnotaxa, but longer when compared to other avian ichnotaxa. Tracks of the Limiavipedidae are also strongly rotated towards the midline of the trackway. McCrea et al. (2014) erected a novel ichnofamily, Limiavipedidae, for avian ichnotaxa that are attributed to those tracks previously described as *A. curriei*. Currently, there are two ichnogenera ascribed to Limiavipedidae (Fig. 5.07): *Limiavipes curriei* from the Early Cretaceous (Albian) of North America (McCrea and Sarjeant, 2001; McCrea et al., 2014), and *Wupus agilis* from the Early Cretaceous (Albian) of Chongqing, China (Xing et al., 2015; Chapter 6).

Figure 5.07. Limiavipedidae. A, B, *Wupus agilis*, modified from Xing et al. (2015), scale in centimeters; C, *Limiavipes curriei*, modified from McCrea et al. (2014), scale 10 cm.

Shandongornipodidae—Shandongornipodidae (Fig. 5.08) represents traces attributable to tetradactyl, paraxonic, zygodactyl avians (Lockley et al., 2007), and is currently represented by only one ichnospecies, *Shandongornipes muxiai* (Li et al., 2005).

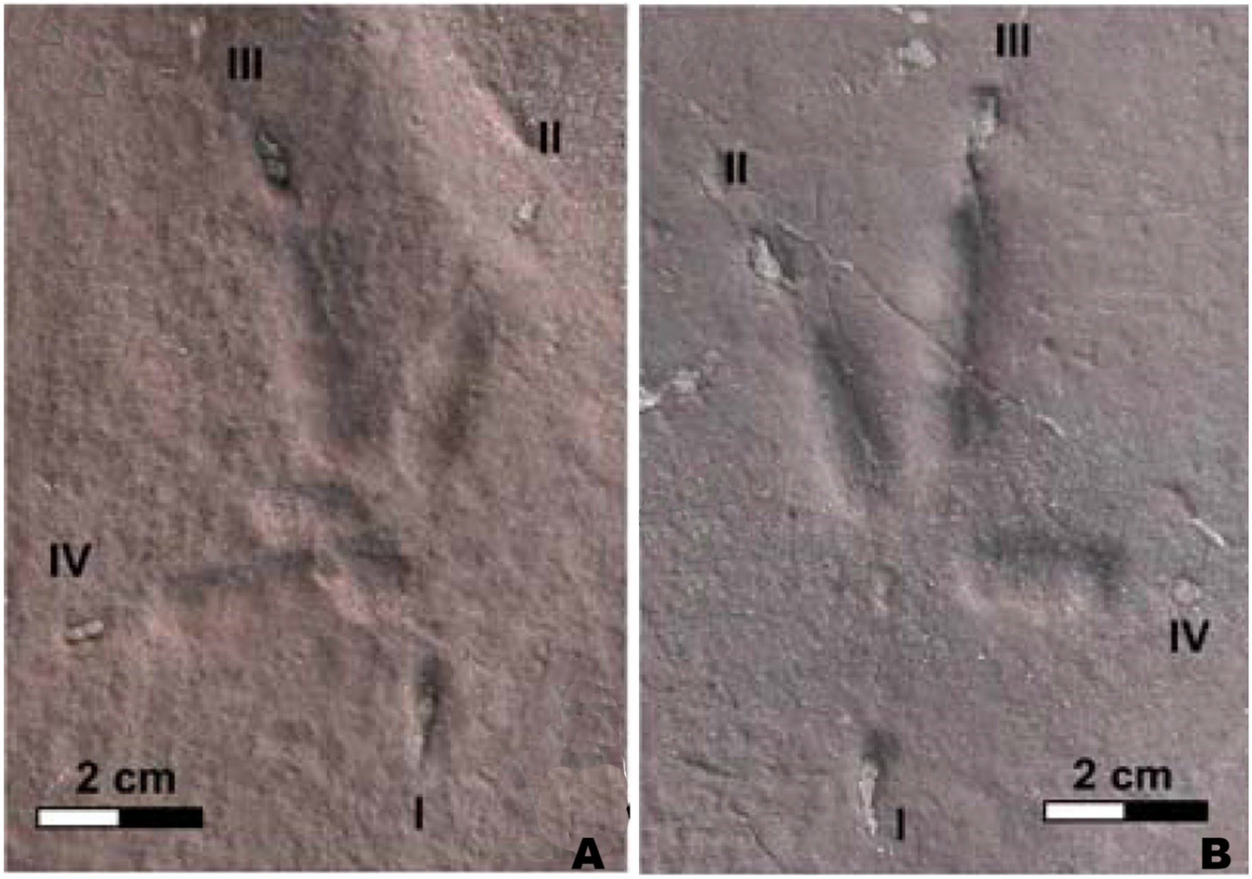

Figure 5.08. Shandongornipodidae. *Shandongornipes muxiai* (Lockley et al., 2007). Scale = 2.0 cm.

Rationale For Study—The goal of this study is to examine the current ichnotaxonomic assignments of bird tracks using multivariate statistical analyses for additional statistical support, and to examine data of both bird and small theropod tracks and trackways to test other morphologic criteria by which to distinguish between tracks of birds and small theropods. The working hypothesis to be tested is that footprint proportions, as expressed by ratios (Methods) will reveal significant differences between the tracks of theropods and birds.

METHODS

Data Used

The linear and angular data (Appendix 5.01) for 584 tracks was collected from ichnotaxonomic descriptions and data tables made available in the avian ichnology literature (see references and Appendix 5.01 for a complete list). Each data point in the graphical results of the analyses represents one footprint. The avian ichnotaxa examined in this study are listed in Table 5.01. The amount and types of data collected varied considerably: some data included only maximum values and averages for the ichnotaxa that were reported, whereas the data for all measured tracks were presented for other ichnotaxa (Appendix 5).

Aquatilavipes izumiensis	Fukui Prefecture, Japan	Azuma et al., 2002
Aquatilavipes swiboldae	Peace Region, British Columbia	Currie, 1981
Barrosopus slobodai	Neuquén, Argentina	Coria et al., 2002
Dongyangornipes siniensis	Zhejiang Province, China	Azuma et al., 2012
Goseongornipes markjonesi	Kosong County, South Korea	Lockley et al., 2006a
Gruipeda vegrandiunus^	Denali National Park, Alaska	Fiorillo et al., 2011
Hwangsanipes choughi	Hwangsan Basin, South Korea.	Yang et al., 1995
Ignotornis mcconnelli	Golden, Colorado	Mehl 1931; Lockley et al. 2009
Ignotornis yangi	Changseon and Sinsu Islands, South Korea	Kim et al., 2006
Ignotornis gajiensis	Gajin, Korea	Kim et al., 2012
Jindongornipes kimi	Kyeongsangnam Province, Korea	Lockley et al., 1992
Koreanaornis dodsoni	Xinjiang Uyghur Autonomous Region, China	Xing et al., 2011
Koreanaornis hamanensis	Gyeongsang Province, Korea.	Kim, 1969
Limiavipes curriei	Grande Cache, Alberta	McCrea and Sarjeant, 2001; McCrea et al., in press
*Magnoavipes caneeri**	Dinosaur Ridge, Colorado	Lockley et al., 2001
*Magnoavipes denaliensis**	Denali National Park, Alaska	Fiorillo et al., 2011
*Magnoavipes lowei**	Denton County, Texas	Lee 1997
Moguiornipes robusta	Wuerhe District, China	Xing et al., 2011
Pullornipes aureus	Laoning Province, China	Lockley et al., 2006b
Sarjeantopodus semipalmatus^	Niobrara County, Wyoming	Lockley et al., 2004
Shandongornipes muxiai	Shandong Province, China	Li et al., 2005; Lockley et al., 2007
Tatarornipes chabuensis	Chabu Area, Inner Mongolia	Lockley et al., 2012
Uhangrichnus chuni	Uhangri, China	Yang et al., 1995
Wupus agilis	Chongqing, China	Xing et al., 2015

Table 5.01: Avian ichnotaxa used in this study. Amended from Lockley and Harris (2010).

*Denotes ichnotaxa whose assignment to Aves is contentious: Lockley et al (2001) convincingly demonstrate that *Magnoavipes* is an ichnogenus attributed to theropods. ^ Denotes ichnotaxa for which there is too little data reported to be used in the multivariate statistical analyses.

Standardization of Data

Data also varied in the number of variables that were reported. Some ichnotaxa included only their lengths, widths, and total divarications, while other ichnotaxa were presented with more comprehensive data (Fig. 5.09). All data were converted to millimeters. Data were entered to fit into a standard table (Appendix 5). Data that were not available, either due to exclusion in the published data sets or due to incompleteness of the measured tracks, were entered as "?". The dataset is set up to accommodate tetradactyl tracks (digits I–IV), and for tridactyl tracks digit I was coded as 0.00 mm (rather than "?" for missing) to indicate the absence of that digit for the ichnotaxon in question. For ichnotaxa with trackways where digit I is inconsistently preserved, however, digit I was coded as "?" to indicate missing data. This allows for tridactyl and tetradactyl tracks to be analyzed together, and the structural presence (or absence) of digit I to be recognized in the total analysis. If digit I were coded as "?" for functionally tridactyl footprints, the multivariate program PAleontological STatistics (PAST) v. 2.17 would treat functionally tridactyl tracks as having missing data and use pair-wise substitution (Hammer et al., 2001) for the value digit I instead of recognizing that digit I was not present.

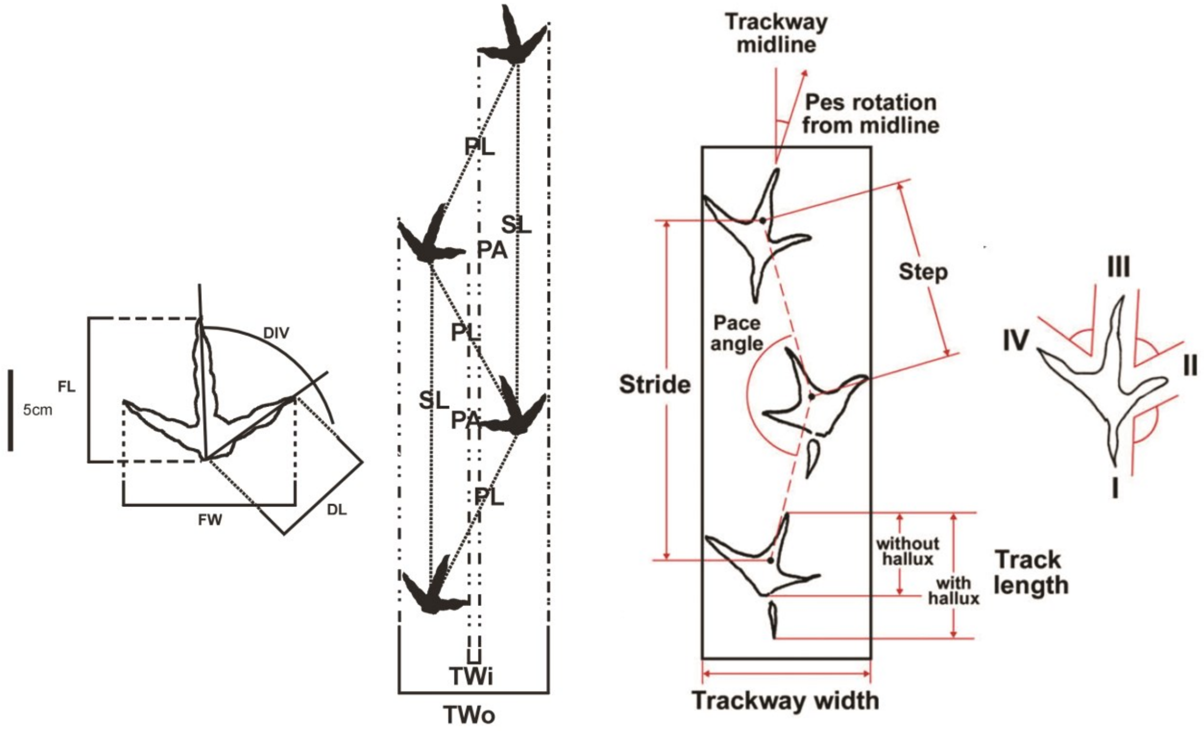

Figure 5.09. Measurements collected for avian ichnites. Left, complete data that is recommended to be collected (where possible) for both previously described and novel avian ichnotaxa; right, an example of thorough data collection in the reassessment of *Ignotornis mcconnelli* (Lockley et al., 2009). DIV, digit divarication; **DL**, digit length; **DW**, digit width; **FL**, footprint length without hallux; **FLwH**, footprint length with hallux; **FR**, footprint rotation towards trackway midline; **PA**, pace angulation; **PL**, pace length; **SL**, stride length; **TWi**, inner trackway width; **TWo**, outer trackway width.

Angular measurements:

- Divarication of digits I and II (DIV I–II): the angle formed between the distal points of digits I and II, with the footprint center as the origin of the angle;

- Divarication of digits II and III (DIV II–III): the angle formed between the distal points of digits II and III, with the footprint center as the origin of the angle;
- Divarication of digits III and IV (DIV III–IV): the angle formed between the distal points of digits III and IV, with the footprint center as the origin of the angle;
- Footprint rotation (FR): the angle at which the individual footprint is rotated towards (positive) or away (negative) from a straight line running through the center of the footprint that is parallel to the midline of the trackway;
- Pace angulation (PA): the angle formed by three consecutive footprints in a trackway, with the angle formed at the footprint center of the middle footprint of the consecutive sequence;
- Total divarication (DIVTOT): the angle formed between the distal points of digits II and IV, with the footprint center as the origin of the angle. DIVTOT is also known in the literature as DIV II–IV.

Linear measurements used in this study are:

- Digit lengths: the lengths of the individual digits (digit I length, DL-I; digit II length, DL-II; digit III length, DL-III; and digit IV length, DL-IV) as measured from either the footprint center or the entire preserved proximodistal length of the footprint, whichever is best preserved;
- Digit widths: the mediolateral widths of the individual digits (digit I width, DW-I; digit II width, DW-II; digit III width, DW-III; and digit IV width, DW-IV) as measured at the most proximal point of the free digit;

- Footprint center: not a linear measurement but a point of reference, as measured from straight lines drawn from the distal ends of digits II–IV to their proximal point of convergence;
- Footprint length (FL): the distance as measured from the caudal (posterior) margin of the metatarsal pad (or, lacking the preservation of the metatarsal pad, the caudal points of digits II and IV) to the most distal end of digit III. In some cases, the length of digit III is used as FL;
- Footprint length with hallux (FLwH): the distance as measured from the distal tip of digit III to the distal tip of digit I. If no hallux is present, FLwH is treated the same as FL;
- Footprint width (FW): the distance as measured from the most distal point of digit II to the most distal point of digit IV;
- Pace length (PL): the distance measured from a distinct point (usually footprint center) on one footprint to the next footprint in the sequence of the trackway (left footprint to right footprint, or right footprint to left footprint);
- Stride length (SL): the distance measured from a distinct point (usually footprint center) from left footprint to left footprint, or from right footprint to right footprint.

Ratios

Ratios are useful in comparing ichnologic data as they remove the size component from the analyses:

- Footprint length to footprint width ratio (FL/FW): the ratio obtained by dividing FL by FW. This value can also be described as the “splay” of the digits of a footprint. FL/FW is the only ratio that is consistently calculated in vertebrate ichnology.

Digit length ratios: the ratios of the different digit lengths provide the relative lengths of one digit as compared to the other digit in the ratio. Digit length ratios used in this analysis are:

- DLI/DLII: the ratio of digit I length and digit II length;
- DLI/DLIII: the ratio of digit I length and digit III length;
- DLI/DLIV: the ratio of digit I length and digit IV length;
- DLII/DLIII: the ratio of digit II length and digit III length;
- DLIV/DLIII: the ratio of digit III length and digit IV length.

Divarication ratios: the ratios of divarication data describe the percentage of splay on each lateral side of the footprint of the total divarication. Digit divarication ratios are:

- DIVII-III/DIVTOT: the percentage of divarication between digits II–III of the total divarication;
- DIVIII-IV/DIVTOT: the percentage of divarication between digits III–IV of the total divarication;
- DIVII-III/DIVIII-IV: the ratio of DIVII–III as compared to DIVIII–IV.

Statistical Analyses

Bivariate and multivariate analyses on the avian and theropod dataset were performed using PAleontological STatistics (PAST) version 2.17 (Hammer et al., 2001). Analyses performed were the t-test (bivariate), and principle component, discriminant, and canonical variate analyses (multivariate, Hammer and Harper, 2006).

Principal component analysis (PCA) is the two-dimensional projection of a multivariate projection of data to identify the components that account for the maximum amount of variance in the data (Hammer and Harper, 2006). It reveals the relative variation contributed to the data set by each measured variable, produces principal component ordinance plots that visually project three-dimensional plots of specimens in two dimensions, and may reveal discrete groupings among specimens. PCA ordinance plots are often displayed with variance vectors that show the relative amount of variation that each measured variable contributes to the overall variation in the data set (Hammer and Harper, 2006). The first principal component represents variation based on size (even in log-adjusted data) and the largest principal component in terms of percentage of total variance within the sample (Hammer and Harper, 2006). However, careful examination of the variance vectors is required to determine the exact nature of PC1: depending on the data, PC1 may not represent variation based on size. PCA was used to find the percentage of total variation (variance) that each measured variable, or combination of variables, contributed to the total variation in the data set. However, PCA is not statistics (Hammer and Harper, 2006), and the PCA results will only be dicussed if a more in-depth examination of variables is required to see why a priori groupings are not supported. PAST replaces missing data using pairwise substitution (Hammer et al., 2001). The strength in principle component analysis is not in determining the significance of the differences among qualitative groupings—principal component analysis is not statistics (Hammer and Harper, 2006)—but in revealing which variables contribute to distinguishing among ichnotaxonomic groups.

Discriminant analysis (DA) in PAST is a two-dimensional projection of multivariate data that maximizes separation between two *a priori* separated groups: in this case, the *a priori* groups are ichnotaxonomic assignments of Mesozoic bird tracks. This is a useful tool for testing hypotheses of morphologic similarity or difference between two groups. A 90% or greater separation between two groups is considered sufficient support for the presence of two taxonomically distinct morphotypes (Hammer and Harper, 2006). However, 100% is ideal (see Discussion). Canonical variate analysis (CVA) in PAST compares specimens *a priori* categorized in three or more groups using the same principles as discriminant analysis. The p_{same} between two *a priori* groups was determined using Hotelling's t^2 test (the multivariate version of the t-test, Hammer and Harper, 2006) to determine significance at $p \geq 0.05$.

Challenges and Assumptions of Performing Multivariate Statistical Analyses on Ichnologic Data

Limited data, small sample size, and unequal sample sizes—In the cases where only maximum values and averages were presented in ichnotaxonomic descriptions, those ichnotaxa provided limited data to the overall analysis. Sample sizes less than three will cause a multivariate analysis of a specimen to fail. Despite their limited contribution of variation data, *Dongyangornips sinensis*, *Jindongornipes kimi*, and *Magnoavipes denaliensis* were left in most of the analyses to determine where in morphospace these ichnotaxa were likely (but not conclusively) to group if more data were available. However, only sparse data (or the mean values of data) for *Gruipeda vegrandiunus* (Fiorillo et al., 2011) and *Sarjeantopodus semipalmatus* (Lockley et al., 2003) were provided with the ichnotaxonomic descriptions, and they were not included in the analyses.

Assumption of consistency in data collection techniques—Unless specifically described in the methodology section of each published data source (i.e., Lockley et al., 2009;

Fig. 5.08), there is an assumption of a general standardized method for collecting both track and trackway data for the analyses herein.

The importance of size in multivariate statistical analyses of avian tracks—Given the large size range of the ichnotaxa in this study, analyses were conducted on $\log_{10}$-transformed data. However, there is justification for performing both non-transformed and $\log_{10}$-transformed data. Extant shorebirds reach adult size quickly, decreasing the likelihood that a significant difference in size between two ichnomorphotypes is ontogenetic. Although shorebird young are precocial and their young mature at a slower rate relative to birds with altricial young (Gill, 2007), the young of shorebirds reach maturity quickly: Young of *Charadrius vociferus* (Killdeer) leave the nest within 24 hours of hatching, and at day 17 the growth curve of chicks asymptotes (Bunni, 1959; Jackson and Jackson, 2001), and the young of *Actitis macularius* (Spotted Sandpiper) reach 82% of their adult wing-tip to wing-tip length at day 15 (Oring et al. 1997). In terms of hind limb development, long bones of the hind limb are roughly 30 to 35% of adult length at the time of hatching in *Larus californicus* (California Gull) and increase isometrically (along with foot surface area) with body mass (Carrier and Leon, 1990). Unless two different track size classes are documented within the separate ichnotaxon in question, it is parsimonious to assume that the trackmakers of each ichnotaxon are of adult- or approaching adult-size. Two avian ichnotaxa that exhibit a significant difference in size may reflect two separate trackmaking species. The quick attainment of adult body size by many extant shorebirds allows us to assume that, given their equal investment in both cursorial and aerial locomotory modes (Dial, 2003), shorebird hind limbs become functional shortly after hatching (Carrier and Leon, 1990) and foot lengths of shorebirds reach adult body sizes within days to weeks (Bunni, 1959; Carrier and Leon, 1990; Oring et al., 1997; Jackson and Jackson, 2001).

***A priori* groupings and contentious avian ichnotaxa**—One must proceed with caution when comparing data from ichnotaxa that have different potential trackmakers with a potential for large morphological similarities. Only specimens for which the affinity of the trackmaker is unambiguous should be used as the base data for multivariate statistical analysis, as many of the comparisons rely on accurate *a priori* ichnotaxonomic assignments, especially when testing the strength of ichnotaxonomic assignments. As such, ichnologic specimens from the Jurassic Period are not considered, as there is not enough data available to determine whether the trackmakers were true Avialae, non-avian theropods, or belonged to an intermediate branch of the theropod – avian phylogeny. See Chapter 6 for a case study in which using ichnotaxa with unambiguous trackmaker affinities was used to differentiate between the traces of large avian trackmakers and those of small non-avian theropods.

Ichnotaxa for which the trackmaker is of debatable affinity are also problematic in a multivariate statistical analysis. For example, the trackmaker for the ichnogenus *Magnoavipes* has been described by different authors as either avian (Lee, 1997; Fiorillo et al., 2011) or theropod (Lockley et al., 2001; Table 5.02). In cases such as this, the strength of the *a priori* assignment of either avian or theropod for the ichnotaxon in question may be tested in separately run analyses.

Total Divarication	**Number**	**Mean**	**Minimum**	**Maximum**
Theropod	26	87.8°	58°	120°
Semipalmate Avian	202	111°	58°	170°
Magnoavipes	23	93.4°	65°	118°

Table 5.02. Comparative total divarication data for Mesozoic tridactyl semipalmate avian footprints, the footprints of the ichnogenus *Magnoavipes*, and footprints of Early Cretaceous theropods. The data show that, while there are large differences among the mean total divarications of the three groups, the minimum and maximum value range has a great deal of overlap. This amount of variation between the total divarication of theropod and bird prints makes using the average total divarication value (or the total divarication of an isolated footprint) problematic.

Also, PAST version 2.17 does not offer more than 16 separate symbols for *a priori* categorization of specimens. This required that the ichnotaxa be *a priori* grouped by ichnogenera when analyzing all specimens. Specimens were coded as ichnospecies when in smaller analyses that involve fewer *a priori* groupings.

RESULTS

Support for Current Avian Ichnotaxonomic Assignments

Avian ichnofamilial assignments—Canonical variate analyses show that there is strong statistical support for all ichnofamilies analyzed (Hotelling's t^2: $p_{\text{same}} <<< 0.01$, Table 5.03). There is overlap in the graphical projection of the three-dimensional data onto a two-dimensional

XY graph (Fig. 5.10). The inclusion of *Limiavipes curriei* results in the data points of the much smaller ichnotaxa grouping on one side of the morphospace plot due to the larger overall footprint size and trackway dimensions of *L. curriei*, despite their significant differences within the smaller ichnotaxa. For example, *Dongyangornipes* is not significantly different from the Avipedidae (p_{same} = 0.900), Ignotornidae (p_{same} = 0.132), Koreanapodidae (p_{same} = 0.912), *Tatarornipes* (p_{same} = 0.373), and *Uhangichnus* (p_{same} = 0.635), despite the obvious visual differences between *Dongyangornipes* and the members of these ichnofamilies. Removing *L. curriei* from the ichnofamily analyses allows for a more accurate interpretation of the morphospace groupings among the remaining avian ichnotaxa. Canonical variate analyses with *L. curriei* removed still show strong statistical support for all analyzed ichnofamilies (Hotelling's t^2: $p_{\text{same}} <<< 0.01$, Fig. 5.10): however, *Barrosopus* (p_{same} = 0.112) and *Morguiornipes* (p_{same} = 0.187) are not significantly different from the Avipedidae in this specific analysis.

ICHNOFAMILY/TAXON	Ignotornidae	Koreanapodidiae	*Tatarornipes*	*Morguornipes*	*Uhangrichnus*	Limiavipedidae	Avipedidae	Shandongornipodidae	Jindongornipodidae	*Barrosopodus*	*Dongyangornipes*
Ignotornidae	0	7.88 × 10^{-84}	7.51 ×10^{-44}	6.26 × 10^{-09}	2.14 × 10^{-61}	9.67 × 10^{-96}	2.12 × 10^{-34}	6.32 × 10^{-32}	4.03 X 10^{-14}	1.16 X 10^{-12}	0.132
Koreanapodidiae	7.88 × 10^{-84}	0	6.25 × 10^{-36}	0.100	5.46 × 10^{-26}	5.66 × 10^{-60}	1.63 × 10^{-10}	1.38 × 10^{-24}	3.96 X 10^{-09}	3.39 X 10^{-05}	0.912
Tatarornipes	7.51 × 10^{-44}	6.25 × 10^{-36}	0	2.12 × 10^{-03}	1.06 × 10^{-15}	5.60 × 10^{-33}	1.46 × 10^{-09}	1.14 × 10^{-10}	6.68 X 10^{-05}	5.16 X 10^{-04}	0.373
Morguiornipes	6.26 × 10^{-09}	0.100	2.12 × 10^{-03}	0	1.19 × 10^{-03}	4.88 × 10^{-05}	0.148	Fail	Fail	Fail	Fail
Uhangrichnus	2.14 × 10^{-61}	5.46 × 10^{-26}	1.06 × 10^{-15}	1.19 × 10^{-03}	0	1.56 × 10^{-55}	7.89 × 10^{-03}	3.18 × 10^{-22}	1.26 X 10^{-09}	0.589	0.635
Limiavipedidae	9.67 × 10^{-96}	5.66 × 10^{-60}	5.60 × 10^{-33}	4.88 × 10^{-05}	1.56 × 10^{-55}	0	1.65 × 10^{-31}	2.17 × 10^{-13}	5.67 X 10^{-04}	3.40 X 10^{-15}	1.12 X 10^{-03}
Avipedidae	2.12 × 10^{-34}	1.63 × 10^{-10}	1.46 × 10^{-09}	0.148	7.89 × 10^{-03}	1.65 × 10^{-31}	0	5.20 × 10^{-09}	8.33 X 10^{-04}	0.323	0.900
Shandongornipodidae	6.32 × 10^{-32}	1.38 × 10^{-24}	1.14 × 10^{-10}	Fail	3.18 × 10^{-22}	2.17 × 10^{-13}	5.20 × 10^{-09}	0	Fail	Fail	Fail
Jindongornipodidae	4.03 × 10^{-14}	3.96 × 10^{-09}	6.68 × 10^{-05}	Fail	1.26 × 10^{-09}	5.67 × 10^{-04}	8.33 × 10^{-04}	Fail	0	Fail	Fail
Barrosopodus	1.16 × 10^{-12}	3.39 × 10^{-05}	5.16 × 10^{-04}	Fail	0.589	3.40 × 10^{-15}	0.323	Fail	Fail	0	Fail
Dongyangornipes	0.132	0.912	0.373	Fail	0.635	1.12 × 10^{-03}	0.900	Fail	Fail	Fail	0

Table 5.03: Canonical variate analysis results of log$_{10}$-transformed linear and unadjusted angle data (Appendix 5.01) of Mesozoic avian ichnotaxa a priori assigned to current ichnofamilies and those Mesozoic avian ichnotaxa currently unattributed to ichnofamilies. “Fail” indicates *a priori* groups for which too few data were available for statistical analysis.

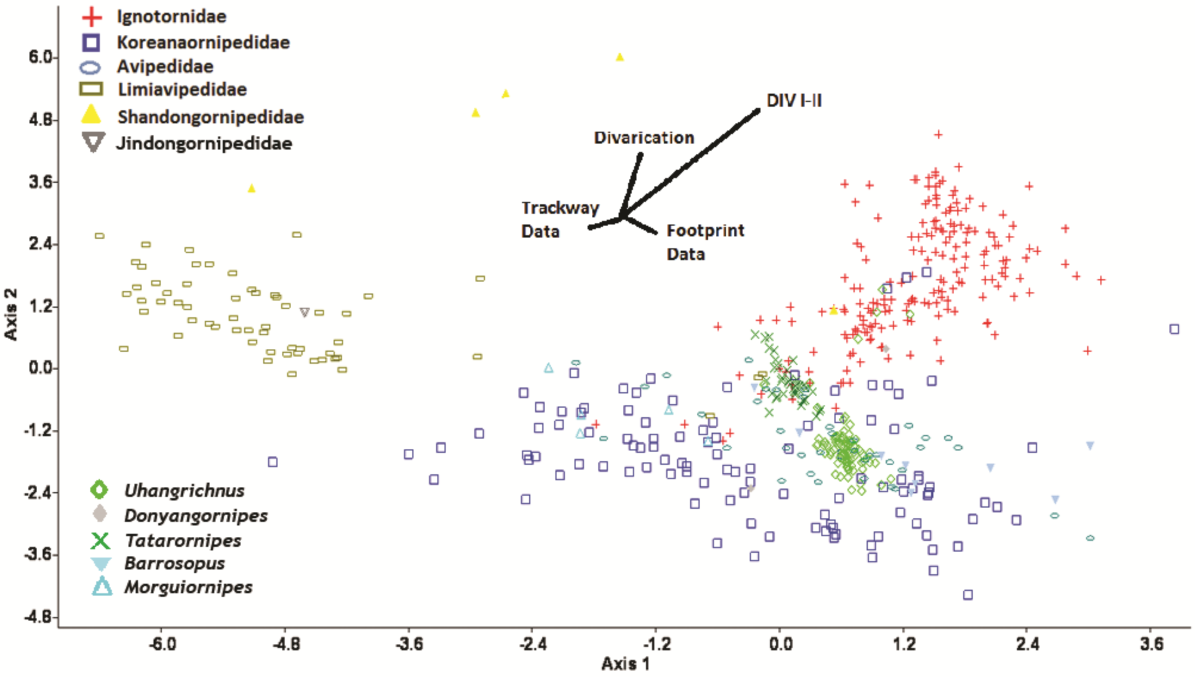

Figure 5.10. Canonical variate analysis plot of all Mesozoic avian ichnofamilies (except for *Gruipeda* and *Sarjeantopodus*, see Table 5.01). The inclusion of the Limiavipedidae (*Limiavipes curriei*), whose prints are much larger than the rest of the Mesozoic avian ichnotaxa, restricts the other ichnotaxa data points into one section of morphospace. All avian ichnogenera as categorized as ichnofamilies are shown to be significantly different from one another, despite their apparent overlap in morphospace (Table 5.03). Vectors show the relative amounts of variation each measured variable contributes to the total dataset.

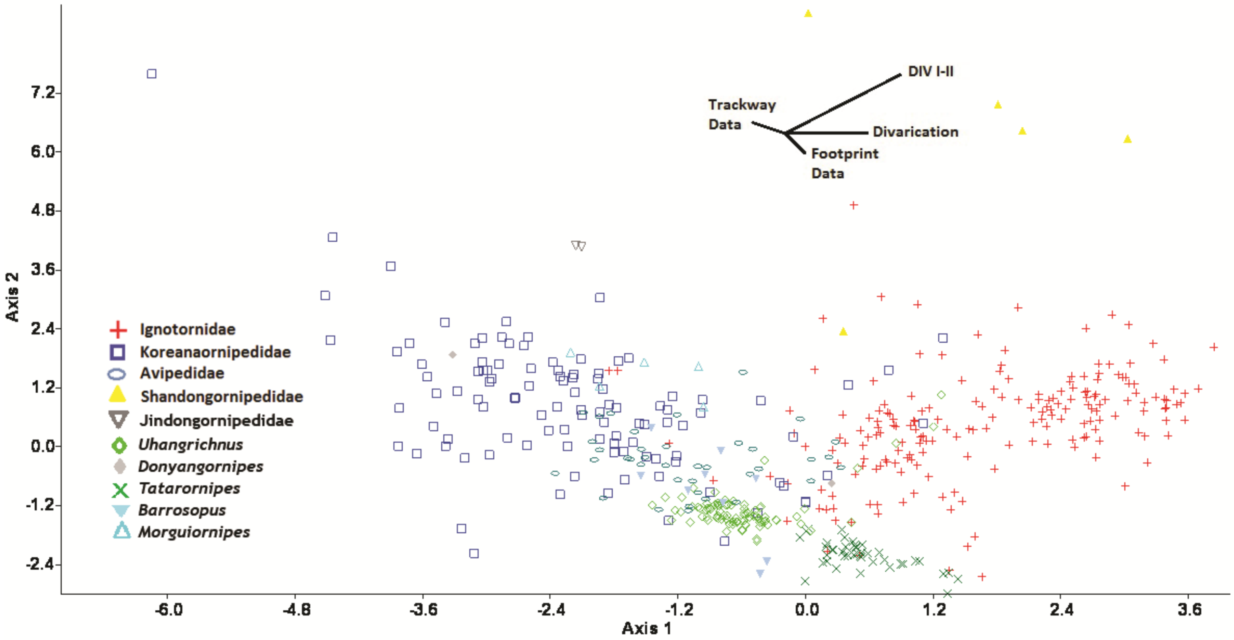

Figure 5.11. Canonical variate analysis plot of Mesozoic avian ichnofamilies excluding *Limiavipes curriei*. The removal of the much larger *L. curriei* allows for a more accurate analysis of the smaller avian ichnotaxa. There is a general grouping between tridactyl (left) and tetradatyl (right) avian prints. *Dongyangornipes sinensis* and *Shandongornipes muxiai* cluster discretely from the rest of the analyzed Mesozoic avian prints. **DIV**, digit divarication.

Tridactyl and Functionally Tridactyl Tracks

Avipedidae—Due to the close association of Avipedidae and Koreanaornipodidae, the results of the analyses for both ichnofamilies will be discussed together. The initial canonical variate analysis of all of the ichnotaxa currently assigned to Avipedidae (*Aquatilavipes izumiensis*, *A. swiboldae*) with the ichnotaxa assigned to Koreanaornipodidae and the unassigned ichnogenera reveals the same results as the analyses that included all avian ichnotaxa: the inclusion of *Limiavipes curriei* (McCrea et al., 2014) skews the results by forcing the ichnogenera with smaller overall footprint size into a concentrated area of morphospace.

The canonical variate analysis of the tridactyl tracks reveals interesting results. *Tatarornipes chabuensis* forms a discrete cluster in morphospace, save for one footprint of *Koreanaornis dodsoni* (Fig. 5.12): *T. chabuensis* has a larger footprint width and digit III length relative to the other ichnotaxa in the analysis. One of the diagnostic characteristics of *Tatarornipes chabuensis* is the robust width of the proximal digits (Lockley et al. 2012a). Digit width is not a variable that is often reported in avian tracks: one exception is Azuma et al. (2012), who report DW in their description of *Dongyangornipes sinensis*. Due to the large amount of missing data that digit width would have introduced to the analyses, DW was not included.

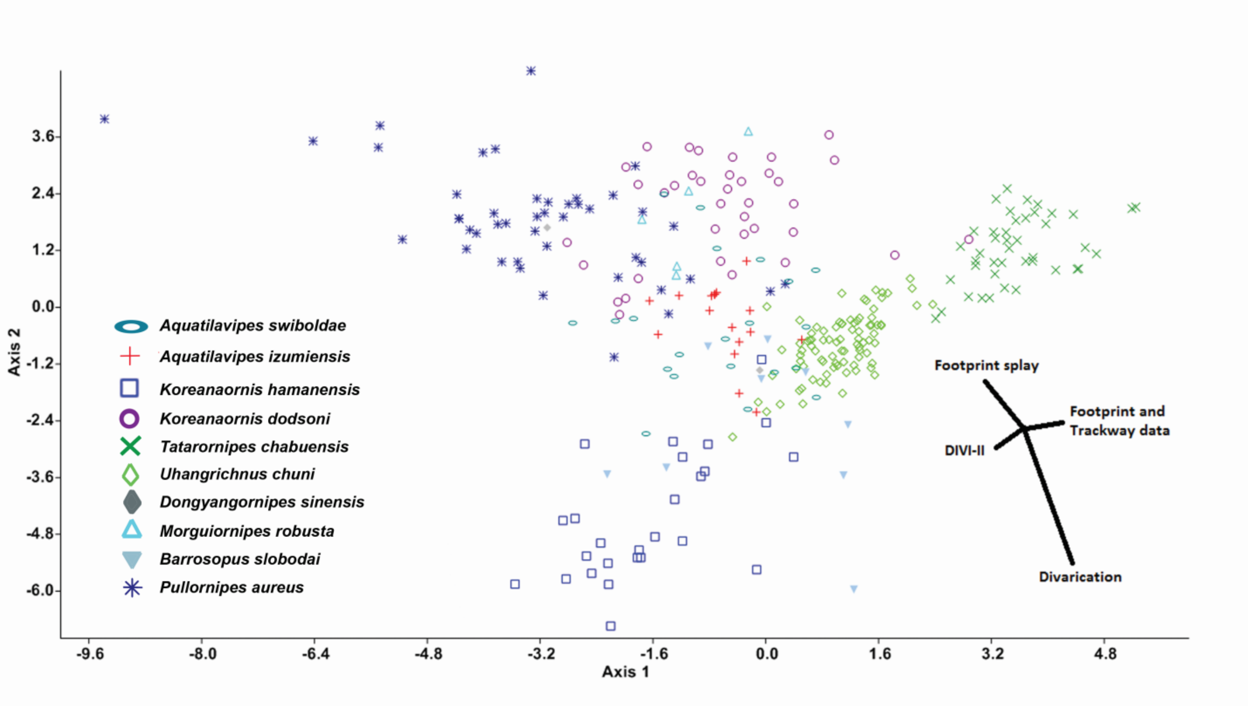

Figure 5.12. Canonical variate analysis plot of the ichnospecies of Avipedidae (*Aquatilavipes izumiensis*, *A. swiboldae*), the Koreanaornipodidae (*Koreanaornis dodsoni, K. hamanensis*, *Pullornipes aurea*) and those ichnotaxa not currently assigned to an ichnofamily (*Barrosopus, Dongyangornipes, Morguiornipes, Tatarornipes, Uhangrichnus*). Despite being assigned to the same ichnogenus, *K. dodsoni,* and *K. hamanensis* are significantly different and have 100% separation in morphospace. Due to the overall similarity in shape, there is a great deal of morphospace overlap between the avipedids and the koreanaornipedids. *Tatarornipes* forms a discrete cluster, suggesting that *Tatarornipes* does not belong within either the avipedids or the koreananornipedids.

Dongyangornipes siniensis and *Uhangrichnus chuni* are not significantly different (p_{same} = 0.282), which is not surprising given their overall visual similarities (see “Ichnotaxonomic revision of *Dongyangornipes sinensis*”). However, the small sample size of *D. siniensis* prints in the dataset may result in the non-significant differences seen both in the analysis of ichnofamilies (Figs. 5.10–5.11) and in the analysis of tridactyl prints only (Fig. 5.12). *Aquatilavipes izumiensis* and *A. swiboldae* show 100% overlap in morphospace despite a significant difference ($p_{\text{same}} = 9.87 \times 10^{-03}$), while *Koreanaornis dodsoni* and *K. hamanensis* show 100% separation and are significantly different ($p_{\text{same}} = 6.26 \times 10^{-19}$). However, *A. swiboldae* shows considerable overlap with *K. dodsoni*, *Morguiornipes*, and *Pullornipes*.

It is not unexpected that *Aquatilavipes* and *Koreanaornis* should occupy a similar morphospace: tracks of *Aquatilavipes* and *Koreananornis* are not significantly different in footprint length (FL, t-test: $p_{\text{same}} = 0.86$), or footprint splay (F/W ratio, t-test: $p_{\text{same}} = 0.56$). However, tracks of *Aquatilavipes* and *Koreanaornis* do differ significantly in their total digit divarication (DIVTOT, t-test: $p_{\text{same}} = 0.02$). Also, *Aquatilavipes* has not been reported with a preserved digit I (Currie, 1981; Azuma et al., 2002), whereas *Koreanaornis hamanensis* has been illustrated with a small, posteriomedially oriented hallux (Lockley et al., 1992; Figs. 5.04, 5.13). The combination of both qualitative and quantitiative differences between *Aquatilavipes* and *Koreanaornis* (small hallux and higher total divarication, respectively) are enough to justify their separation as discrete ichnomorphotaxa, and the high degree of morphospace overlap between these two ichnogenera can easily be explained by their similarities in footprint length and digit splay. Discriminant analyses on *Aquatilavipes* and *Koreananornis* reveals contradictory results. While the two groups are significantly different ($p_{\text{same}} = 9.80 \times 10^{-04}$), the percentage of individual prints correctly assigned to their *a priori* groups was only 72.3% (Fig. 5.13). In other words, while the mean values of *Aquatilavipes* and *Koreanaornis* prints are different, it takes a combination of both qualitative and quantitative data to accurately differentiate between individual prints of *Aquatilavipes* and *Koreanaornis*.

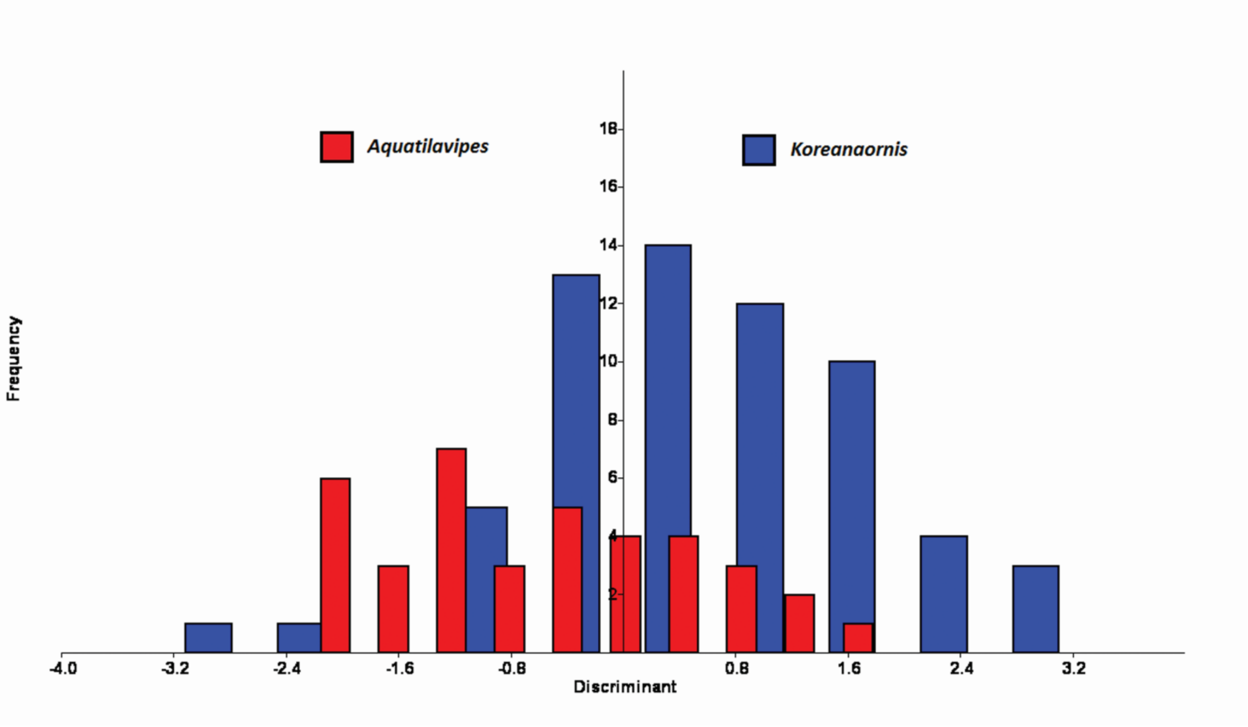

Figure 5.13. Discriminant analysis graphical results of a comparison between the ichnogenera *Aquatilavipes* (red) and *Koreanaornis* (blue). The similarity between the two ichnogenera makes the results of the discriminant analysis contradictory: the two groups are significantly different (p_{same} = 9.80 × 10-04), yet the percentage of individual prints correctly assigned to their *a priori* groups was only 72.3%.

Principal component analysis on only Avipedidae and Koreanapodidae also provides equivocal results. The first principal component (size, 27.5%) does not reveal much information, except to group the ichnotaxa by size, with *K. dodsoni* being larger (mean FL = 45.5 mm, N = 37) and *K. hamanensis* being smaller (mean FL = 26.3 mm, N = 24; Fig. 5.14). Principal components two (PC2, divarication/digit splay ratio) and three (PC3, digit I length/DIV III-IV ratio) do little to differentiate the ichnotaxa in morphospace (Figs. 5.14–5.15). It could be argued that Koreanaornipodidae do not form a natural group; however, it is the combination of qualitative (presence, ichnomorphology, orientation of the hallux) and quantitiative data that form Koreanaornipodidae. This is an example of how taxonomy by statistics can provide misleading or ambiguous results.

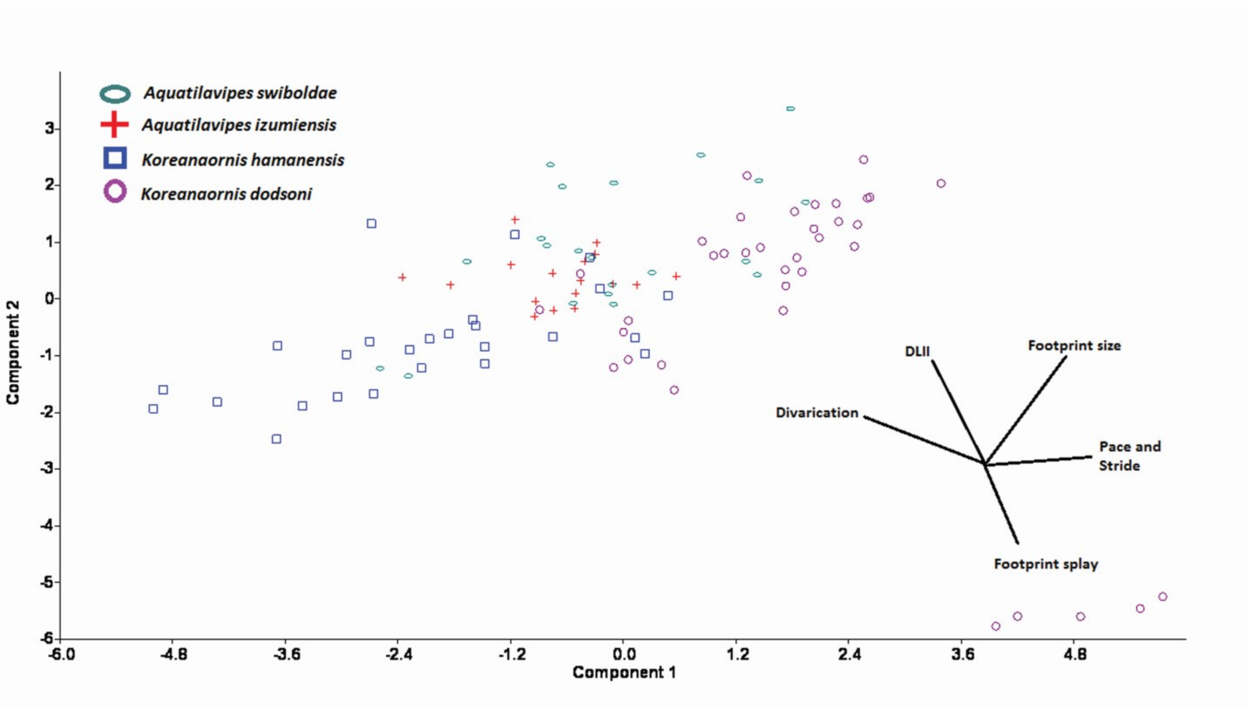

Figure 5.14. Principal component (PC) analysis graphical results of PC 1 (footprint size) and PC 2 (divarication/digit splay ratio) axes of ichnospecies of Avipedidae (*Aquatilavipes izumiensis*, *A. swiboldae*) and Koreanaornipodidae (*Koreanaornis dodsoni, K. hamanensis*, *Pullornipes aurea*), with ichnospecies unassigned to an ichnofamily.

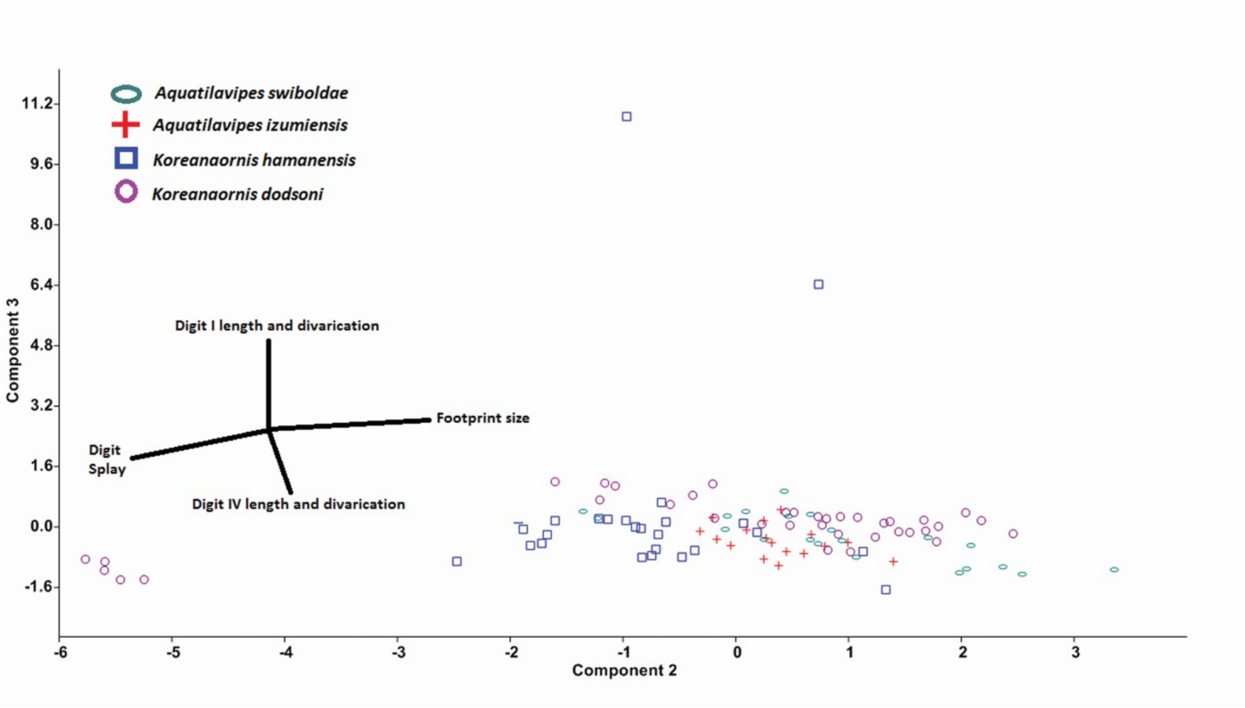

Figure 5.15. Principal component (PC) analysis graphical results of PC 2 (digit divarication – splay ratio) and PC 3 (digit I length/DIV III-IV ratio) axes of ichnospecies of Avipedidae (*Aquatilavipes izumiensis*, *A. swiboldae*) and Koreanaornipodidae (*Koreanaornis dodsoni, K. hamanensis*, *Pullornipes aurea*), with ichnospecies unassigned to an ichnofamily. *Pullornipes* has a relatively larger pace and stride.

Avipedidae shows considerable overlap with the Koreanaornipodidae along principal components one through three in a principal component analysis that includes all tridactyl ichnotaxa. There is a small separation seen between *A. izumiensis* and *A. swiboldae* along PC3 (PL and SL – digit lengths ratio): *A. izumiensis* has a slightly smaller mean footprint length (X = 37.7 mm) than *A. swiboldae* (X = 39.0 mm), although the difference is not significant (t-test: p_{same} = 0.69). There is also a slight, although not significant (t-test: p_{same} = 0.27), difference in total divarication between *A. izumiensis* (X = 120°, N = 17) and *A. swiboldae* (X = 114°, N = 20), which results in a separation along PC2 (digit splay – digit divarications ratio, Figs. 5.14 – 5.15).

Morguiornipes robusta is not shown to be significantly different from either both ichnospecies of *Aquatilavipes* (*A. izumiensis*, $p_{\text{same}} = 0.544$; *A. swiboldae*, $p_{\text{same}} = 0.744$). Discriminant analyses comparing *Aquatilavipes* to *M. robusta* shows that they are significantly different and have above 90% correct assignment to *a priori* categories (*A. izumiensis*: $p_{\text{same}} = 5.91 \times 10^{-03}$, 100%; *A. swiboldae*: $p_{\text{same}} = 0.024$, 90.1%).

Koreanaornipodidae—Canonical variate analysis on the ichnospecies within Koreanaornipodidae (*Koreanaornis dodsoni, K. hamanensis*, and *Pullornipes aurea*) and other tridactyl ichnospecies shows similar results to that of the canonical variate analysis results of the Avipedidae. There is no overlap between *K. dodsoni* and *K. hamanensis* (Fig. 5.16). *K. dodsoni* shows a small amount of morphospace overlap with *P. aurea* ($p_{\text{same}} = 3.11 \times 10^{-15}$), and there is no overlap of *K. hamanensis* with *P. aurea* ($p_{\text{same}} = 3.78 \times 10^{-22}$). *K. dodsoni* occupies almost the exact same morphospace as *Morguiornipes* ($p_{\text{same}} = 0.610$). While there is neither statistical nor morphospace support for the separation of *K. dodsoni* and *Morguiornipes*, they are visually distinct. In discriminant analyses, *Morguiornipes robusta* is not significantly different from *Koreanaornis dodsoni* ($p_{\text{same}} = 0.0569$), although 90.5% of prints were correctly identified (Fig. 5.16). Also, *Barrosopus* and *K. hamanensis* occupy a similar morphospace and are not significantly different ($p_{\text{same}} = 0.092$) (Figs. 5.12, 5.16) despite visual differences. (See Avipedidae for detailed results of the comparison between Avipedidae and Koreanaornipodidae.)

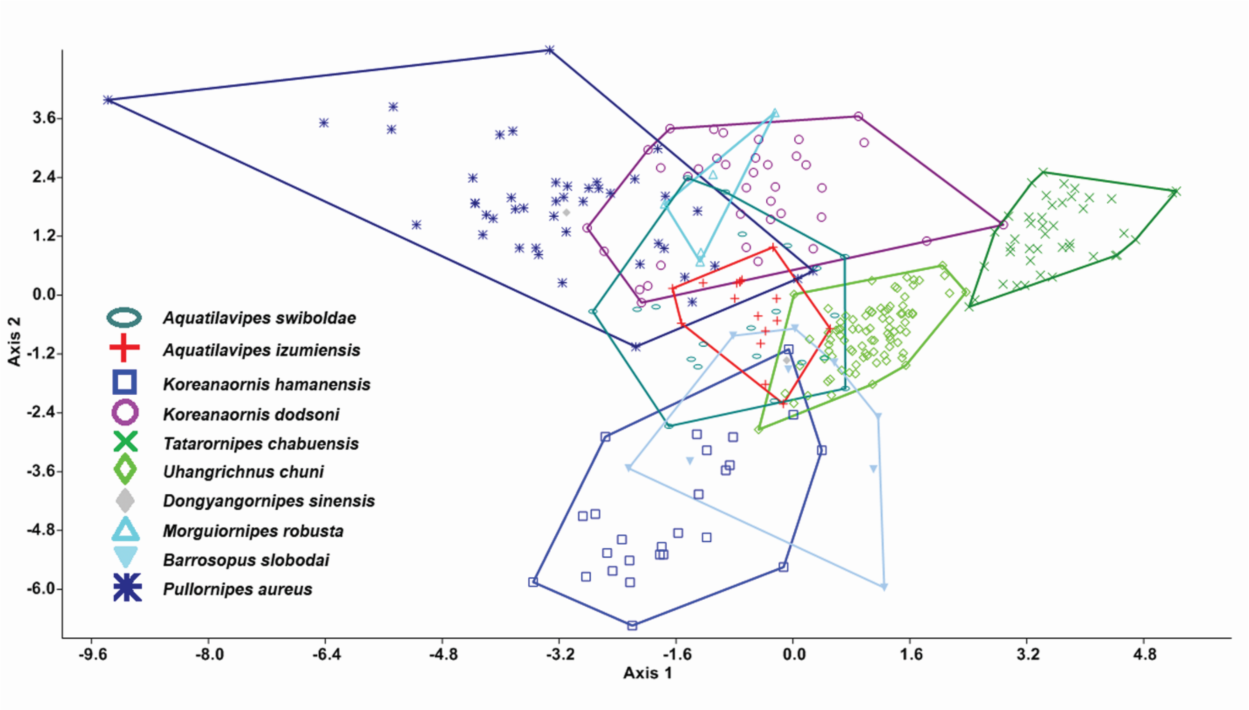

Figure 5.16. Canonical variate analysis of the ichnospecies within the Koreanaornipodidae against the unassigned ichnotaxa (*Barrosopus*, *Dongyangornipes*, *Morguiornipes*, *Tatarornipes*, *Uhangrichnus*). There is a considerable amount of overlap between *Koreanaornis dodsoni* and *Morguiornipes*.

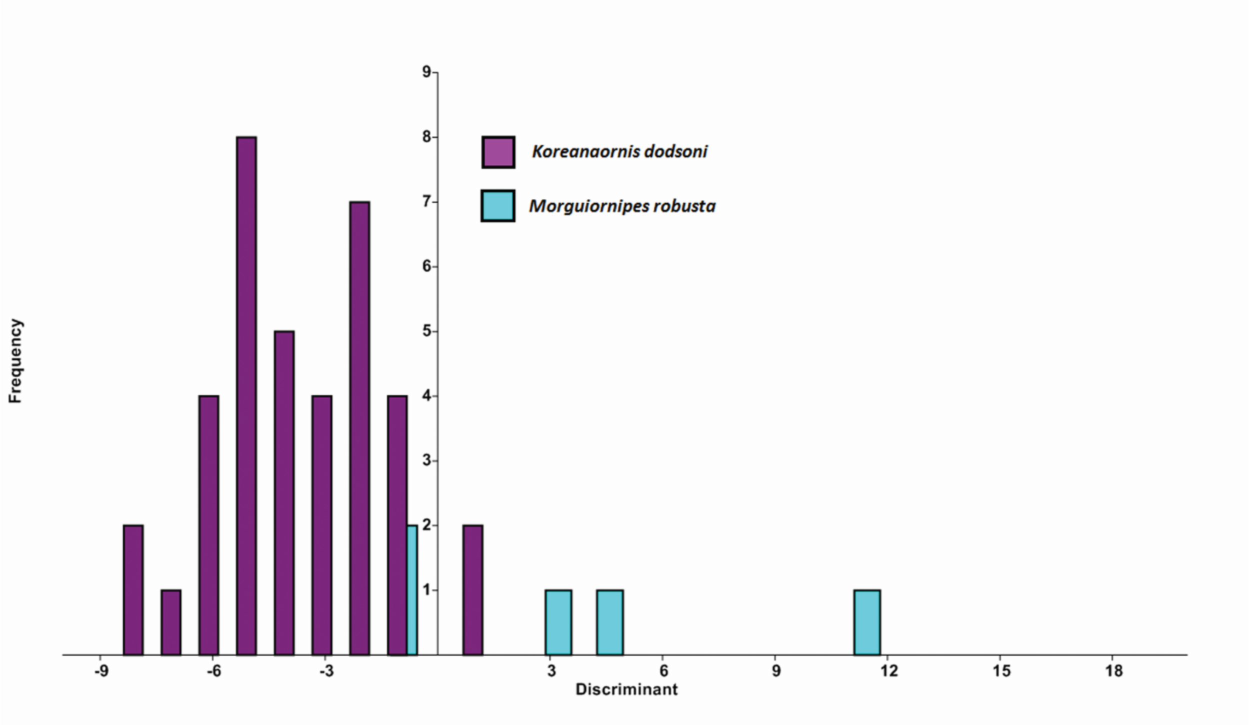

Figure 5.17. Discriminant analysis on *Koreanaornis dodsoni* and *Morguiornipes robusta*. Despite the large amount of overlap between the two ichnotaxa in Fig. 5.16 and that these two taxa are not significantly different ($p_{\text{same}} = 0.057$), discriminant analysis assigns 90.5% of the footprints correctly to their *a priori* determined groups.

Tetradactyl Avian Tracks

Ignotornidae—The individual ichnogenera within the Ignotornidae (*Goseongornipes*, *Hwangsanipes*, *Ignotornis*) occupy the same morphospace, although *Goseongornipes* and *Hwangsanipes* occupy the outer edges of the *Ignotornis* morphospace (Figs. 5.10, 5.18; Table 5.04). Canonical variate analysis of the ichnospecies within the ichnofamily Ignotornidae, analyzed with avian ichnotaxa currently not assigned to an ichnofamily reveals that, despite the strong statistical support for all of the individual ichnofamilies, there is a strong grouping in morphospace for *Goseongornipes markjonesi*, *Ignotornis mcconnelli*, and *I. yangi* (Fig. 5.18). However, *I. gajiensis* does not occupy a similar morphospace to that of *I. mcconnelli*, *I. yangi*, and *G. markjonesi* (and is significantly different from these ichnospecies) but occupies a similar morphospace for *Hwangsanipes* (Ignotornidae) and *Tatarornipes* (ichnofamily unassigned, Fig. 5.18). A principal component analysis performed on these ichnotaxa reveals that the main quantitative difference between the *Hwansanipes*-*I. gajiensis* group and the *Goseongornipes*-*Ignotornis* group is the size of digit I: the *Goseongornipes*-*Ignotornis* group has a longer digit I, as presented in the principal component analysis morphospace plot (Fig. 5.19).

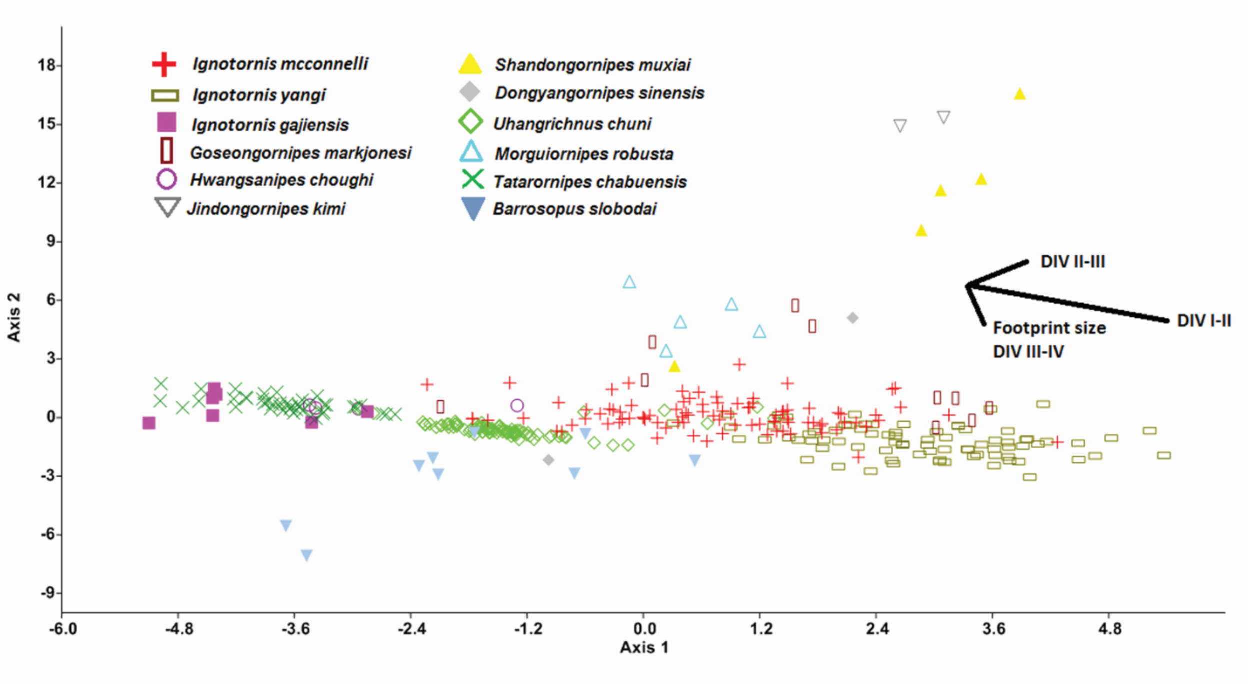

Figure 5.18. Canonical variate analysis of tetradactyl Mesozoic avian ichnites and the unassigned avian ichnotaxa (*Barrosopus*, *Dongyangornipes*, *Morguiornipes*, *Tatarornipes*, *Uhangrichnus*). *Jindongornipes kimi* and *Shandongornips muxiai* form discrete groups, while the ignotornids separate into the *Goseongornipes*-*I. mcconnelli*-*I. yangi*, and the *Hwangsanipes*-*I. gajiensis* groups.

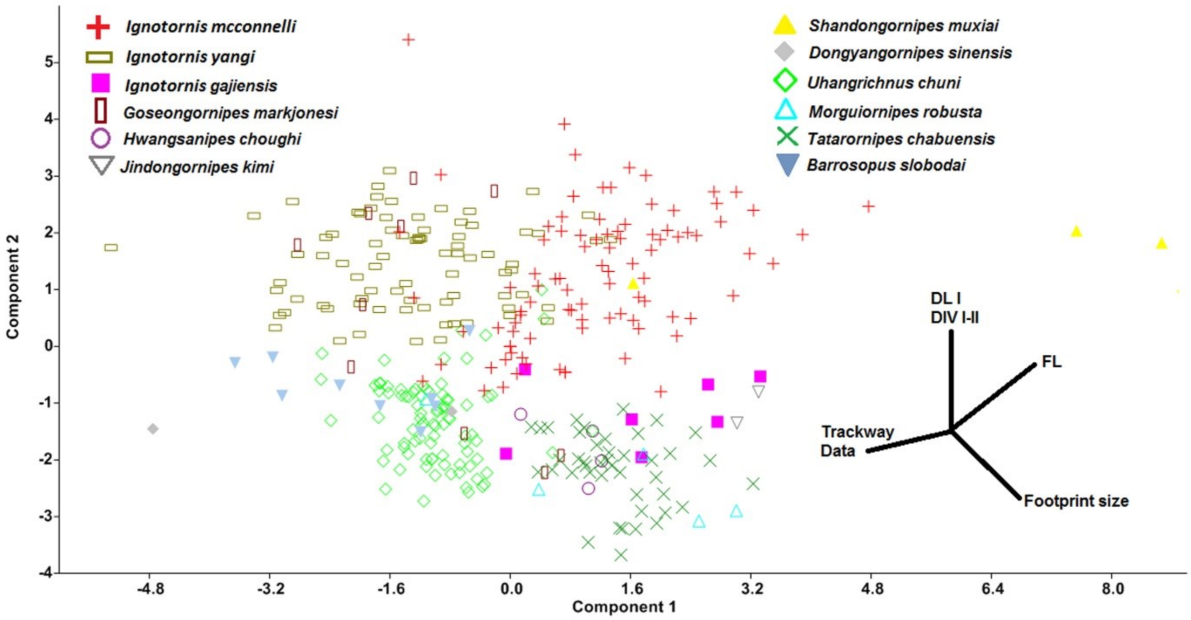

Figure 5.19. Principal component (PC) analysis graphical results of the tetradactyl Mesozoic avian ichnotaxa and the unassigned avian ichnotaxa. PC 1 represents data related to digit I, while PC 2 represents the footprint and trackway size data – divarication ratio. As in Fig. 5.18, *Ignotornis mcconnelli* and *Ignotornis yangi* cluster together. This grouping is due to similarities in divarications and footprint size, specifically having a relatively larger DIV I–II with a smaller foot and pace and stride. *Shandongornipes muxiai* forms a discrete cluster due to the relatively larger divarications between digit I–II and total divarication. **DIV**, digit divarication; **DL**, digit length.

Ichnotaxon	*Hwangsanipes*	*Uhangrichnus*	*Ignotornis yangi*	*Ignotornis gajiensis*	*Goseongornipes*	*Morguiornipes*	*Jindongornipes*	*Shandongornipes*	*Donyangornipes*	*Ignotornis mcconnelli*	*Barrosopus*	*Tatarornipes*
Hwangsanipes	0	7.18×10^{-03}	1.15×10^{-08}	Fail	Fail	Fail	Fail	Fail	Fail	1.60×10^{-05}	Fail	0.987
Uhangrichnus	7.18×10^{-03}	0	2.51×10^{-55}	1.11×10^{-17}	1.89×10^{-12}	6.82×10^{-14}	2.63×10^{-26}	5.74×10^{-30}	1.23×10^{-05}	1.84×10^{-51}	3.08×10^{-06}	1.97×10^{-34}
Ignotornis yangi	1.15×10^{-08}	2.51×10^{-55}	0	4.07×10^{-22}	1.64×10^{-13}	2.27×10^{-16}	3.01×10^{-24}	1.02×10^{-27}	5.00×10^{-06}	5.24×10^{-44}	3.17×10^{-17}	2.41×10^{-49}
Ignotornis gajiensis	Fail	1.11×10^{-17}	4.07×10^{-22}	0	Fail	Fail	Fail	Fail	Fail	6.08×10^{-18}	Fail	7.21×10^{-06}
Goseongornipes	Fail	1.89×10^{-12}	1.64×10^{-13}	Fail	0	Fail	Fail	Fail	Fail	2.31×10^{-15}	0.731	2.32×10^{-12}
Morguiornipes	Fail	6.82×10^{-14}	2.27×10^{-16}	Fail	Fail	0	Fail	Fail	Fail	4.07×10^{-17}	Fail	5.35×10^{-09}
Jindongornipes	Fail	2.63×10^{-26}	3.01×10^{-24}	Fail	Fail	Fail	0	Fail	Fail	3.70×10^{-27}	Fail	8.29×10^{-12}
Shandongornipes	Fail	5.74×10^{-30}	1.02×10^{-27}	Fail	Fail	Fail	Fail	0	Fail	2.30×10^{-29}	Fail	2.96×10^{-14}
Donyangornipes	Fail	1.23×10^{-05}	5.00×10^{-06}	Fail	Fail	Fail	Fail	Fail	0	2.51×10^{-07}	Fail	3.32×10^{-04}
Ignotornis mcconnelli	1.60×10^{-05}	1.84×10^{-51}	5.24×10^{-44}	6.08×10^{-18}	2.31×10^{-15}	4.07×10^{-17}	3.70×10^{-27}	2.30×10^{-29}	2.51×10^{-07}	0	7.48×10^{-18}	5.80×10^{-42}
Barrosopus	Fail	3.08×10^{-06}	3.17×10^{-17}	Fail	0.731	Fail	Fail	Fail	Fail	7.48×10^{-18}	0	5.44×10^{-10}
Tatarornipes	0.987	1.97×10^{-34}	2.41×10^{-49}	7.21×10^{-06}	2.32×10^{-12}	5.35×10^{-09}	8.29×10^{-12}	2.96×10^{-14}	3.32×10^{-04}	5.80×10^{-42}	5.44×10^{-10}	0

Table 5.04. Canonical variate analysis results of $\log_{10}$-transformed linear and unadjusted angle data (Appendix 5.01) of tetradactyl Mesozoic avian ichnotaxa *a priori* assigned to current ichnospecies and those Mesozoic avian ichnotaxa currently unattributed to ichnofamilies. “Fail” indicates *a priori* groups for which too few data were available for statistical analysis.

Given the morphologic similarity between *Ignotornis* and *Jindongornipes*, it was expected that the two ichogenera would occupy a similar morphospace: both ichnogenera have a well-defined digit I, digits II and IV have wide angles of divarication from digit III, and both have some indication of webbing between digits III and IV. One issue that affects the analysis of *Jindongornipes* is that there are only two data points available in the systematic description of *J. kimi*. However, based on the available data, the Ignotornidae and *Jindongornipes* are significantly different based on a discriminant analysis ($p_{\text{same}} = 2.97 \times 10^{-17}$). The Ignotornidae are smaller, have a longer digit I relative to footprint length (FL), and a higher digit divarication between digits I and II, whereas *Jindongornipes* has a relatively higher divarication between digits II and III (Figs. 5.18–5.19). The results of this analysis could be greatly altered by the inclusion of more data.

Jindongornipodidae—Jindongornipodidae is represented only by one ichnospecies, *Jindongornipes kimi*. Other than the observations made when compared to the Ignotornidae, the amount of footprint and trackway data available in the literature for these analyses (N = 2) caused many of the analyses to fail. However, with the data available, *J. kimi* does form a discrete group in the canonical variate analysis.

Shandongornipodidae—There is both strong qualitative and quantitative support for the ichnofamily Shandongornipodidae. *Shandongornipes muxiai* is the only described trackway of a zygodactyl trackmaker from the Mesozoic: the unique positioning and splay of the digits makes this ichnotaxon easily distinguishable from other described Mesozoic avian ichnotaxa. In canonical variate analysis, *S. muxiai* forms a discrete cluster in morphospace (Fig. 5.18, with the exception of one track that contained a large amount of missing data, which groups with *I. mcconnelli*). Principal component analysis reveals that *S. muxiai* is distinguished from the other tetradactyl avian ichnotaxa by the footprint length including the length of digit I along PC1 (footprint size – trackway dimensions ratio, Fig. 5.19). When size (PC1, 19.5% of total variation) is removed, *S. muxiai* groups with the tetradactyl ichnotaxa possessing a relatively large digit I and a high digit divarication DIV III-IV (PC2, 17.4% of total dataset variation, Fig. 5.20).

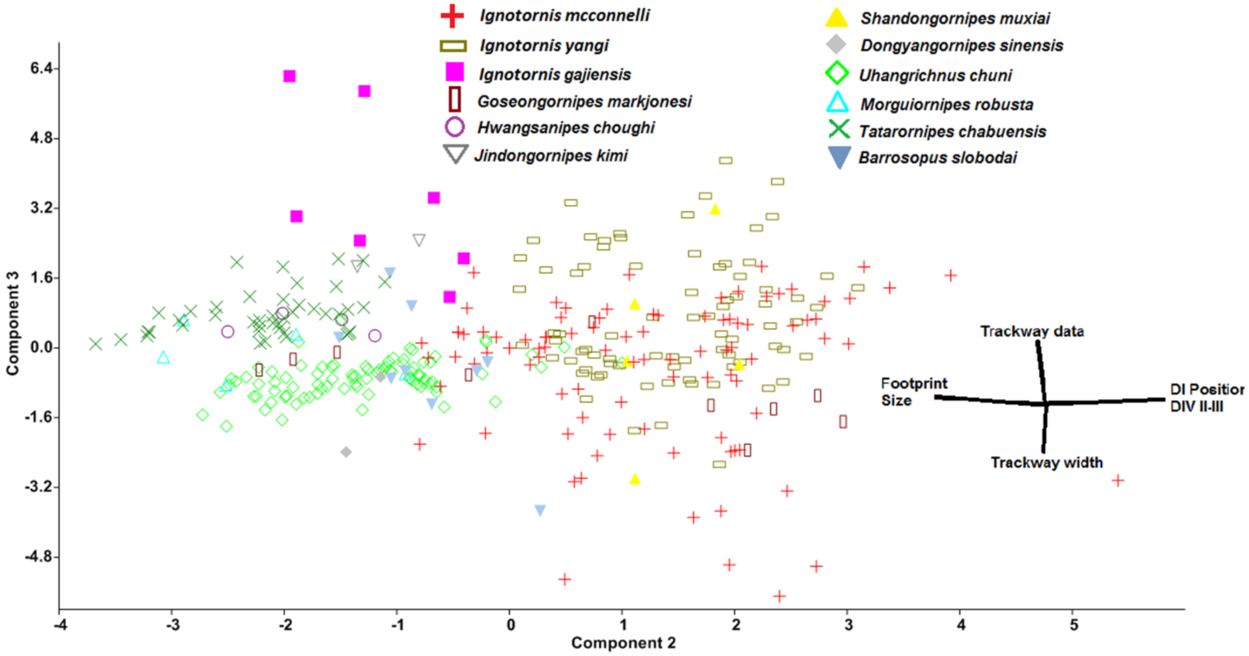

Figure 5.20: Principal component (PC) analysis graphical results of the tetradactyl Mesozoic avian ichnotaxa and the unassigned avian ichnotaxa with PC 1 (relative size of digit I) removed. The PC 2 axis represents digit I placement-footprint size ratio, and PC 3 represents trackway size-trackway width ratio. The groupings show more overlap, but as in Figs. 5.18–5.19 *Ignotornis mcconnelli* and *Ignotornis yangi* cluster together.

Avian Ichnospecies Currently Unassigned to Ichnofamilies

Barrosopus slobodai—Prior to the description of *Paxavipes babcockensis* (McCrea et al., 2015), *Barrosopus slobodai* was unassigned to any avian ichnofamily. Prints of *Barrosopus slobodai* are not significantly different from *Aquatilavipes izumiensis*, *A. swiboldae*, or *Koreanaornis hamanensis* (Fig. 5.12, Table 5.03). Discriminant analysis confirms the quantitative similarities of *B. slobodai* and *A. swiboldae* ($p_{\text{same}} = 0.831$, 76.7% correctly identified), *A. izumiensis* ($p_{\text{same}} = 0.403$, 73.1% correctly identified), and *K. hamanensis* ($p_{\text{same}} = 0.755$, 82.9% correctly identified). *Barrosopus slobobai* and *K. hamanensis* occupy a similar morphospace due to shared characteristics in overall footprint and trackway dimensions: they do not significantly differ in total divarication (t-test: $p_{\text{same}} = 0.50$), pace length (t-test: $p_{\text{same}} = 0.12$), or digit splay (FL/FW, t-test: $p_{\text{same}} = 0.087$).

Morguiornipes robusta—As described in the results of the Avipedidae and Koreanaornipedidae analyses, *Morguiornipes robusta* is not statistically different from *Aquatilavipes izumiensis*, *A. swiboldae*, and *Koreanaornis dodsoni*. Principal component analysis shows that *M. robusta* groups with the individual tracks of *A. swiboldae*, *Barrosopus slobodai*, *K. dodsoni, K. hamanensis* with similar digit lengths (Appendix 5.01). However, this grouping is due to similarity in variables: *Morguiornipes* is qualitatively distinct from *Aquatilavipes* and *Koreanaornis* in that it has much thicker (or wider) digits than the two aforementioned ichnogenera. The thicknesses of the digits are reminiscent of those observed in *Tatarornipes chabuensis*, but the digits of *M. robusta* do not taper sharply distally as the digits do in *T. chabuensis* (Fig. 5.21).

Tatarornipes chabuensis—In the analyses of tridactyl ichnotaxa, *Tatarornipes chabuensis* forms a discrete cluster from Avipedidae, Koreanaornipodidae, and the unassigned ichnospecies. The qualitative assignment to a discrete ichnospecies is justified statistically (p_{same}

<<<0.01). *Tatarornipes* is separated from the rest of the tridactyl ichnotaxa by its relatively large footprint width and digit III length (Figs. 5.11–5.12, 5.16). Because the current version of this manuscript has been submitted and reviewed, an addendum can be added to further clarify the ichnotaxonomic status of *Barrosopus* (McCrea et al., 2015).

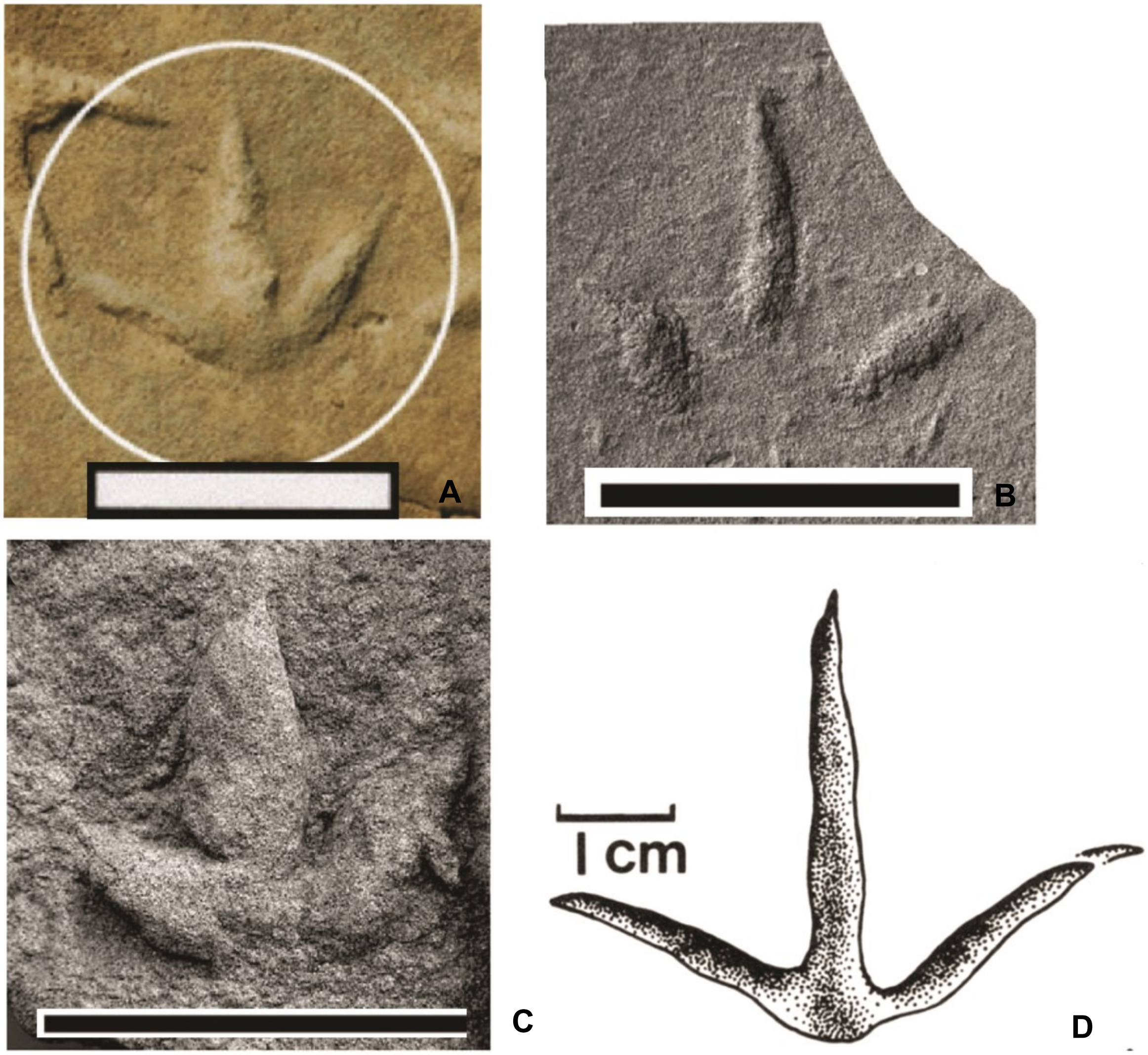

Figure 5.21. Functionally tridacyl Mesozoic avian footprints. **A**, *Tataronipes chaubensis* (Lockley et al., 2012); **B**, *Koreanaornis dodsoni* (Xing et al., 2011); **C**, *Morguiornipes robusta* (Xing et al., 2011); **D**, *Aquatilavipes swiboldae* (Currie, 1981). Despite their morphologic differences, these four ichnotaxa tend to group together in multivariate statistical analyses due to the similarity in their measured variables. Collecting the variable of digit width might cause these groups to separate in morphospace. Scale = 5.0 cm.

Large Avian Ichnites vs. Small Non-Avian Theropod Ichnites from the Cretaceous (*Magnoavipes*)

Magnoavipes is a contentious ichnogenus: the relatively large size, with footprint lengths approaching 200 mm or more (Appendix 5) is indicative of a small theropod trackmaker, while its high divarication (*M. caneeli* = 85.1°, *M. denaliensis* = 107°, *M. lowi* = 110°) suggests a trackmaker of avian affinity (Table 5.02). Divarication and trackway data were analyzed separately on Mesozoic avians, *Magnoavipes*, and Early Cretaceous theropods ($N_{\text{total}} = 59$, McCrea, 2000) to determine the diagnostic strength of total divarication and trackway data for distinguishing between bird and theropod ichnites.

First, using total divarication as a discriminatory tool between theropod and avian tracks holds when using t-tests of means: comparing the means of the total divarication of theropod (*Columbosauripus*, *Irenesauripus, Irenichnites*, and an unidentified small theropod; mean = 87.8°, N = 26) and tracks of semipalmate avians (*Aquatilavipes*, *Koreanaornis*, *Morguornipes, Tatarornipes*; mean = 111°, N = 202) does show a significant difference ($p_{\text{same}} = 5.40 \times 10^{-08}$). However, the range of data shows a considerable amount of overlap (Table 5.02). The total divarication of *Magnoavipes* is not significantly different than that of the theropod sample (t-test: $p_{\text{same}} = 0.245$), but the total divarication of *Magnoavipes* is significantly different than that of the semipalmate avians (t-test: $p_{\text{same}} = 7.23 \times 10^{-05}$).

Discriminant analyses on DIV II–III, DIV III–IV, and DIV TOT confirm the univariate statistical results. *Magnoavipes* is not significantly different than the sampled theropods ($p_{\text{same}} = 0.179$, 67.8% correctly identified). *Magnoavipes* is significantly different than the avian sample ($p_{\text{same}} = 1.37 \times 10^{-03}$, 71.3% correctly identified), and the theropod sample was significantly different than the avian sample ($p_{\text{same}} = 2.79 \times 10^{-04}$, 67.8% correctly identified). In all three discriminant analyses there was difficulty in correctly assigning each print to its *a priori* ichnotaxon. This is likely due to the large amount of variation in digit divarication of both birds and theropods: theropod tracks can reach total divarications of 120°, and bird tracks can exhibit total divarications as low as 60° (Table 5.02; Appendix 5). There is no one divarication value that clearly separates bird from theropod tracks. See Chapters 4 and 6 for more detailed analyses of the issue of divarication and trackmaker attribution.

Because of the great disparity in size between the tracks attributed to birds and those attributed to theropods and the ichnogenus *Magnoavipes*, the canonical variate analysis comparing these ichnotaxonomic groups was performed on $\log_{10}$-transformed linear data, and unaltered angle data. The results show that all three groups are significantly different; however, there is a great deal of overlap among the three groups (Fig. 5.22). Although the largest amount of relative variation occurs along the footprint data – trackway data axis, in morphospace there is little separation among the three ichnotaxonomic groups along this axis.

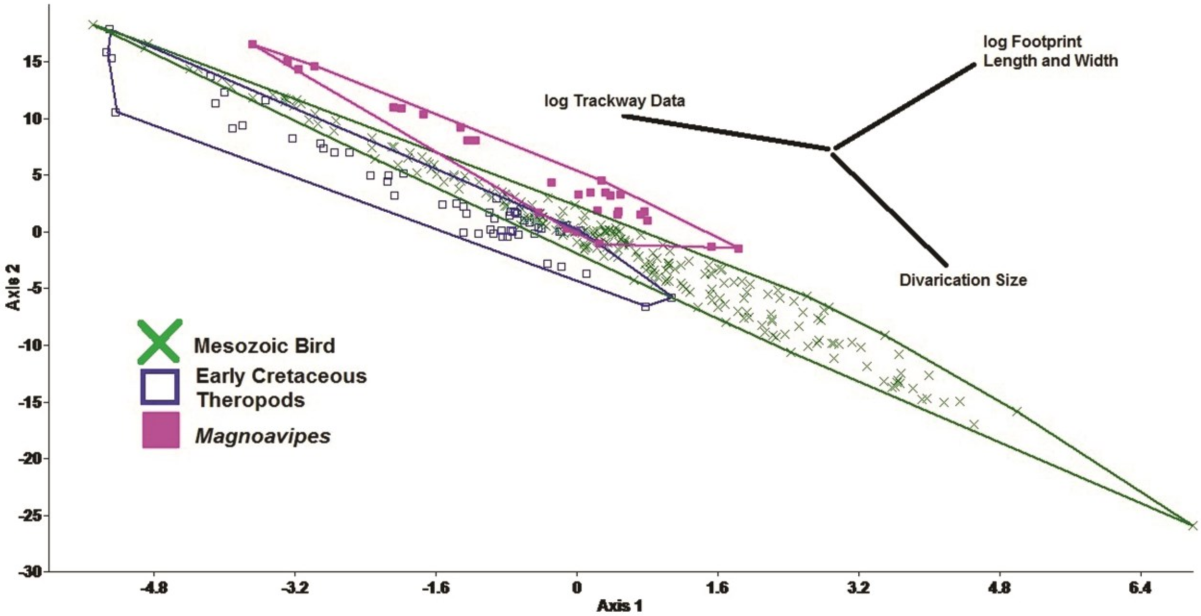

Figure 5.22. Canonical variate analysis on $\log_{10}$-transformed footprint and trackway data of *a priori* separated groups of *Magnoavipes*, Mesozoic tridactyl semipalmate avians, and Early Cretaceous theropods (*Columbosauripus, Irenesauripus*, *Irenichnites*, and one unidentified small theropod ichnite). There is a large amount of overlap among the three groups, and a slight separation of the *Magnoavipes* and theropod groups along the footprint size axis. Both *Magnoavipes* and the theropods occupy a close, but not overlapping, section of morphospace.

In order to determine whether footprint ratios could be used to discriminate between the tracks of birds (including *Limiavipes curriei*) and theropods (and to remove size as a factor in the analyses), the footprint ratios (see Materials and Methods) were analyzed using canonical variate analysis. While birds, *Magnoavipes*, and theropods were all significantly different from one another, they all occupy the same morphospace. The only indication of any ichnotaxonomic grouping was that tracks of *Magnoavipes* occupy almost the same morphospace as that occupied by tracks of the theropod sample (Fig. 5.23). It is evident that the footprint data alone (save for size) is not sufficient to separate the tracks of small non-avian theropods from those of birds in a multivariate analysis.

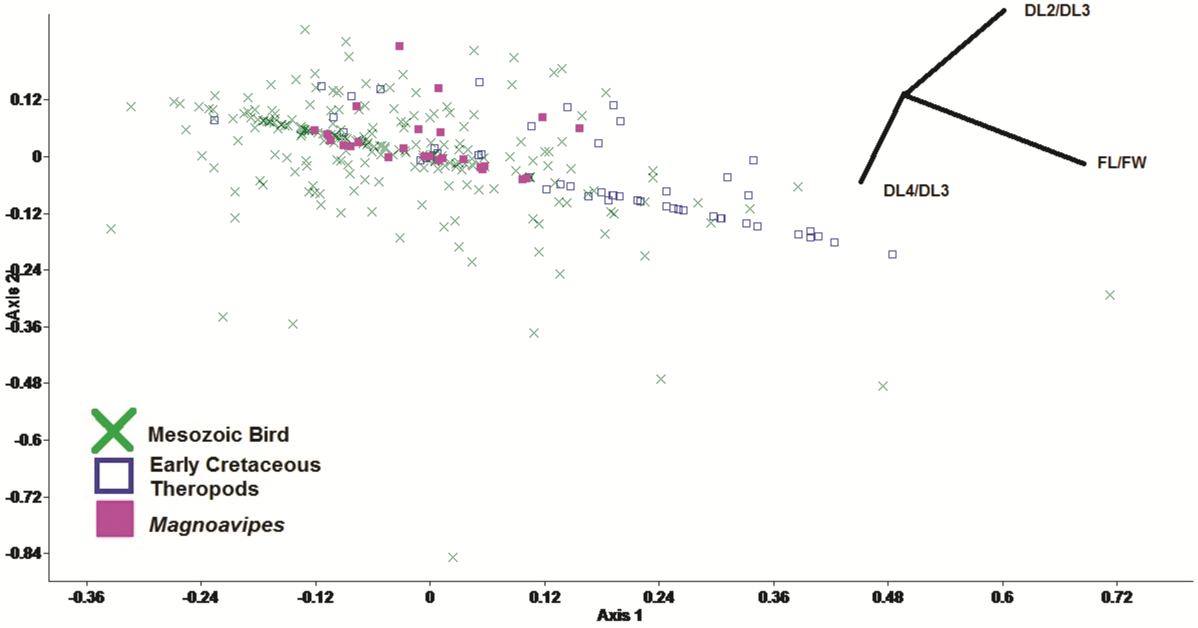

Figure 5.23. Canonical variate analysis on footprint measurement ratios (FL-FW, DL2/DL3, DL4/DL3) of *Magnoavipes*, Mesozoic tridactyl semipalmate avians, and Early Cretaceous theropods (*Columbosauripus, Irenesauripus*, *Irenichnites*, and one unidentified small theropod ichnite). The footprint ratios used in this analysis did not provide any for separating theropod ichnites from bird ichnites, but does show that theropods, because of the narrower splay on their digits, have a relatively larger FL/FW. All *a priori* groups are significantly different from one another.

Trackway data (pace and stride length, pace angulation, and footprint rotation) was analyzed using canonical variate analysis, and the results show that both theropods (p_{same} = 1.66

$\times 10^{-31}$) and *Magnoavipes* ($p_{\text{same}} = 1.94 \times 10^{-27}$) are significantly different from birds, while the prints of *Magnoavipes* are not significantly different from prints of theropods ($p_{\text{same}} = 0.987$). However, these differences are largely size-based, so the same analysis was run using $\log_{10}$-transformed pace and stride lengths. The results are similar: both theropods ($p_{\text{same}} = 9.84 \times 10^{-35}$) and *Magnoavipes* ($p_{\text{same}} = 7.27 \times 10^{-20}$, Fig. 5.24) are significantly different from the trackways of birds. These results are supported by the bivariate statistics: $\log_{10}$-pace lengths are significantly different between theropod and bird trackways ($p_{\text{same}} = 1.68 \times 10^{-6}$), and between bird trackways and the trackways of *Magnoavipes* ($p_{\text{same}} = 2.00 \times 10^{-03}$), while the difference between the $\log_{10}$-pace lengths of *Magnoavipes* and theropod trackways is significant at $p \geq 0.05$ but not at $p \geq 0.01$ ($p_{\text{same}} = 0.014$).

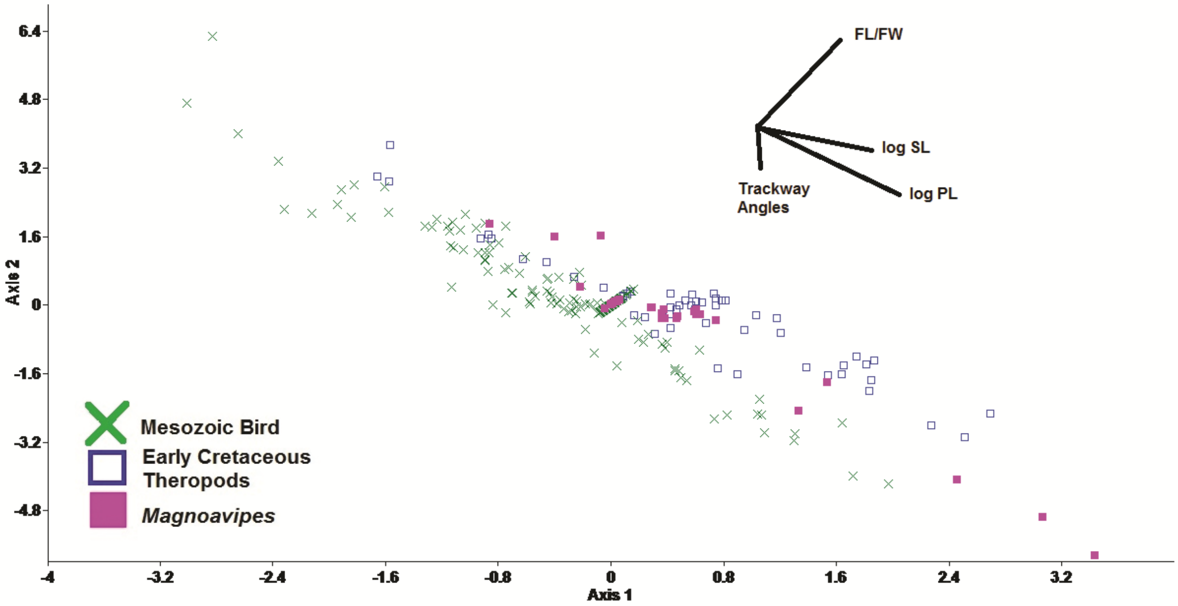

Figure 5.24. Canonical variate analysis on $\log_{10}$-tranformed pace (PL) and stride (SL) data, footprint rotation (FR), pace angulation (PA), and footprint length/footprint width ratios (FL/FW) of *Magnoavipes*, Mesozoic tridactyl semipalmate avians, and Early Cretaceous theropods (*Columbosauripus*, *Irenesauripus*, *Irenichnites*, and one unidentified small theropod ichnite). Birds have a relatively larger pace angulation and footprint rotation, while *Magnoavipes* and theropods have a relatively larger FL/FW. *Magnoavipes* and bird trackway data are significantly ($p_{\text{same}} = 2.00 \times 10^{-03}$), while *Magnoavipes* and theropod trackway data are significant at $p \geq 0.05$ but not at $p \geq 0.01$ ($p_{\text{same}} = 0.014$).

Ichnotaxonomic Revision of *Dongyangornipes sinensis*

Uhangrichnus chuni was established by Yang et al. (1995), and was the first described functionally tridactyl, palmate avian track. The description of *U. chuni* was emended by Lockley et al. (2012) based on the description by Lockley and Harris (2010) of a topotype specimen of *U.*

chuni with a short, postero-medially directed hallux. However, the emended diagnosis states that the web configuration is palmate (i.e., well-developed) and equally developed in hypicies between digits II and III and III and IV (Lockley et al. 2012). This is different than the webbing reported for *Dongyangornipes sinensis* by Azuma et al. (2013), who state that *Dongyangornipes* is similar to *U. chuni* in size and general morphology, *Dongyangornipes* differs in that the anterior margin of the web impression is connected from the apex of digit III to the apex of digits II and IV in *U. chuni*. Azuma et al. (2013) also state that web impressions between II and III are connected from the apex of digit II to the posterior third of digit III, and that the web impression between digits III and IV is linked from the apex of digit IV to the middle of digit III.

These differences in webbing are now considered to be more parsimoniously explained by preservational variation: it is not uncommon for webbed tracks of one trackmaker to present a variety of webbing conditions. Several of the tracks of *Uhangrichnus chuni* pictured in fig. 5 of Yang et al. (1995) display the webbing conditions (connected at the apices of digits II and IV, and connecting on the posterior third and middle of digit III, respectively; asymmetrical web impressions) described as unique to *Dongyangornipes sinensis*. Also, the tracks of *D. sinenesis* and *U. chuni* are similar in size: as noted by Azuma et al. (2013, the average (presumably) *D. sinensis* is footprint has a length of 3.64 cm and width of 3.96 cm. This falls within the size range reported for *U. chuni*, (FL: 3.30-4.62 cm, average 3.70 cm; FW: 3.8-5.4 cm, average 4.58 cm). The only quantitative difference between *D. sinensis* and *U. chuni* is that of footprint splay, as represented by total (II-IV) divarication and FL/FW. *U. chuni* has a wider splay (L/W: 0.81, total divarication 110°) than *D. sinensis* (L/W: 0.87, total divarication 100°); however, given the small reported sample size of *D. sinensis* compared to that of *U. chuni*, there are prints of *U. chuni* that also exhibit the same footprint splay seen in *D. sinensis*.

Given that the unique webbing characteristic of *Dongyangornipes* reported by Azuma et al. (2013) to separate *Dongyangornipes* from *Uhangrichnus* is also observed (if not reported) in the original description of *Uhangrichnus*, and that the sample size of *Dongyangornipes* is too small to preserve a sporadically preserved hallux, there is little to visually differentiate *Dongyangornipes* and *Uhangrichnus* and. *Dongyangornipes sinensis* is considered a subjective junior synonym of *Uhangrichnus chuni*.

SYSTEMATICS

Class Aves

Ichnofamily indet.

Uhangrichnus chuni (Yang et al., 1995; emend. Lockley et al., 2012)

Dongyangornipes sinensis Azuma et al., 2012

Referred material—Chun, 1990 p. 10a; "tracks of a bird with webbed feet" (Lockley et al., 1992, fig. 9); *Uhangrichnus chuni* (Yang et al., 1995, fig. 5); *Uhangrichnus chuni* (Yang et al., 1997, figs. 3–5); *Uhangrichnus chuni* (Lockley and Rainforth, 2002, figs. 17–12B); *Uhangrichnus chuni* (Kim et al., 2006, fig. 3D); *Uhangrichnus chuni* (Lockley, 2007, fig. 1D); *Uhangrichnus chuni* (Lockley and Matsukawa, 2009, fig. 15D); *Uhangrichnus* (Lockley and Harris, 2010, fig. 9C);

Emended diagnosis—Small, functionally tridactyl track of a web-footed bird with small, postero-medially directed hallux trace sporadically preserved. Web configuration palmate, with the posterior margins of the webbing ranging from equally developed between digits II and III and III and IV, to connecting at the middle to the posterior third of digit III. Footprint, excluding hallux, wider (w) than long (l), averaging 3.70 cm and 4.58 cm, respectively (l/w = 0.81), but footprint length with hallux slightly longer than wide (l/w = 1.1). Trackway narrow with short step and stride (7.8 and 15.7cm, respectively) and strong inward rotation (mean 20°) of digit III relative to trackway midline.

DISCUSSION

Qualitative Ichnotaxonomic Assignments of Avian Ichnotaxa Have Statistical Support

Multivariate statistical analyses are a useful tool in testing the qualitative ichntaxonomic assignments of avian ichnotaxa. These qualitative assignments, for the most part, are well-supported statistically. Although taxonomic assignments of ichnological specimens have received some criticism for being too subject to preservation and substrate consistency, the strong statistical support for the current avian ichnotaxa demonstrates that the assignment of vertebrate ichnotaxa is not random: the *qualitative* and simple quantitative differences observed in Mesozoic avian ichnotaxa have strong *quantitative* support.

Separating Tracks of Large Avians from Small Theropods

Save for size, there is a great deal of overlap in the track morphology data of small theropods and large avians. The multivariate statistical analyses support the assignment of the ichnogenus *Magnoavipes* to a theropod, rather than an avian, trackmaker by Lockley et al. (2001). The strongest support came from the trackway data: for all of the avian characteristics of the tracks of *Magnoavipes* (high total divarication, narrow digit widths, Lee, 1997), the data suggests that the trackmaker of *Magnoavipes* walked more like a theropod than a bird. The difference in pace angulation and footprint rotation between theropods and avians has long been observed: trackways attributed to theropods have higher angles in pace angulation (footprints placed closer to the midline of the trackway) and lower footprint rotation (footprints closer to parallel with the midline of the trackway) (Lockley et al., 2001).

Also, total divarication (DIV II–IV, as used in the original description of *Magnoavipes*, Lee 1997) is unreliable for separating bird tracks from theropod tracks, and there is a large amount of overlap in the range of total divarications exhibited by Mesozoic avian ichnites and those of Early Cretaceous theropod ichnites (Table 5.02). Also, digit divarication can vary considerably within a single trackway in both avians and theropods (Appendix 5). Determining the affinity of a trackmaker based largely on the average total divarication is arbitrary and ignores both extant avian track data and fossil data for tracks of both theropods and avians alike. Given that both extant and extinct shorebirds are/were capable of such extremes in digit divarication, ichnologists must accept that Mesozoic analogs to extant shorebirds were likely capable of similar extremes in digit divarication.

Trackway ratios, using the most common data collected for both avian and theropod tracks (footprint length, footprint width, digit lengths II, III, and IV; digit divarication) have the benefit of removing absolute size from the analyses but do not contain enough data to discriminate between avian and theropod tracks. Analyzed together, the number of measured footprint parameters outnumbers the trackway parameters, which may account for the lack of separation in morphospace between the traces of birds and those traces that are unequivocally identified as being those of non-avian theropods.

Multivariate Statistical Analyses are Not a Primary Tool for Ichnotaxonomic Assignment

Multivariate statistical analyses are a useful tool for testing previously established ichnotaxonomic assignments, and are also useful to test the quantitative support of the systematic assignment of future avian ichnotaxa. However, multivariate statistical analyses should not be used as the sole tool in either assigning an ichnite to an ichnotaxon, or as the sole means of identifying the potential trackmaker of one footprint. Statistics, whether they be bivariate or multivariate, are best in a supporting role in vertebrate ichnology rather than the primary source of interpretations.

Criticisms of using multivariate analyses as the sole means of identifying the trackmaker of an ichnite have been discussed in length by Thulborn (2013) in his analysis of the reinterpretation of the large tridactyl trackmaker in the famous Lark Quarry track site (Romilio and Salisbury, 2011). Many of these criticisms are valid: one cannot use a multivariate statistically determined cut-off value between two groups with *any* morphologic similarity to determine the accurate placement of single ichnites, or even single trackways (Thulborn, 2013). Statistically determined threshold values used to either assign previously unassigned ichnites to existing ichnotaxa, or to determine trackmaker affinity, are only as accurate as the degree of separation between the samples used to create the threshold value. The analyses are subject to the initial *a priori* assignments of the researchers. Any threshold value established between two groups with less than 100% separation will be inaccurate depending on the amount of morphologic overlap between the two groups: the more overlap, the greater the inaccuracy of the identification of the ichnite using the threshold. Although the multivariate data are a numeric representation of the ichnomorphological characters used to differentiate ichnotaxa, the measured data do not capture every aspect of the ichnomorphologic characters in question, nor does the measured data account for the large amount of variation in preservation of the ichnites (Chapter 4). In other words, a researcher should be able to see that Ichnotaxon A is different from Ichnotaxon B without the use of statistics, as morphologically distinct ichnotaxa may not be supported statistically (Figures 5.16; 5.21).

Recommendations for Future Data Collection and Data Reporting

Multivariate statistical analyses are only as accurate as the data used within the analyses. The analyses herein would have been greatly improved had data been reported for all of the track and trackway variables. This is not referring to the missing data that is inherent in so many vertebrate ichnology datasets: data cannot be reported for prints that are incompletely preserved. Data should, however, be collected for all footprint and trackway variables that can be measured, even if they do not immediately aid in the systematic classification of the ichnite in question. Depending on the nature of the avian ichnites, all data variables may not be available to collect. For example, *Aquatilavipes swiboldae* (Currie, 1981) and *Uhangrichnus chuni* (Yang et al., 1995) were described from specimens where individual trackways were difficult to discern, making the accurate collection of trackway data unfeasible. However, where feasible, thorough footprint and trackway data should be both collected and reported.

Re-examinations of avian ichnotaxa for which the original descriptions did not supply a large amount of data (either due to the original paucity of specimens at the time of description or lack of publishing the originally collected data), such as the re-examination of *Ignotornis mcconnelli* by Lockley et al. (2009), are extremely important to the study of avian ichnotaxonomy. As more specimens of existing avian ichnotaxa are recovered, such re-examinations of existing avian ichnotaxa will be beneficial for further resolving avian diversity in the Mesozoic.

CONCLUSIONS

This will not be the final statistical review of Mesozoic avian ichnotaxonomy. As more specimens of existing avian ichnotaxa are recovered, and as novel avian ichnotaxa are erected, the results will undoubtedly be refined. The analyses herein do reveal useful information in demonstrating that the valid Mesozoic avian ichnotaxa have strong statistical support. These analyses also demonstrate that ichnotaxa erected using qualitative observations on size, shape, and basic statistical data are not arbitrarily named shapes. Ichnotaxonomy is a discipline that will continue to draw heavily on qualitative information, and thus far qualitative information has proven reliable. However, with the development of new data collection technologies, useful quantitative data can be used to support the qualitative observations.

To aid in the future quantitative analyses of vertebrate ichnites, the following recommendations are offered:

1. A reanalysis of the existing avian ichnotaxa, in the manner of Lockley et al. (2009), is needed to amend the previously published datasets;
2. It is necessary to collect and publish as many track and trackway variables as is feasible for each specimen. It is not enough to merely report averages of novel ichnotaxa; all data should be made available for more accurate comparisons and future statistical analyses;

3. As potentially useful as multivariate statistical analyses are, the utility of such analyses in resolving contentious ichnotaxonomic assignments or providing information to support a novel ichnotaxonomic assignment will only be as accurate as the input data.

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CHAPTER 6

THESIS-RELATED CONTRIBUTIONS: THE CORRELATION BETWEEN OSTEOLOGICAL DATA AND ICHNOLOGICAL INTERPRETATIONS IN AVIAN AND NON-AVIAN THEROPOD DINOSAURS

INTRODUCTION

Trace fossils provide the only record of birds from the Early Cretaceous in many parts of the world. Detailed comparative ichnolomorphology comparisons and multivariate statistical analyses on both previously described and novel avian ichnotaxa provide additional information on the presence and the potential diversity of birds from the Early Cretaceous. Reanalyses of previous studies and new reports show that known avian diversity, as inferred from the diversity of avian traces, is greater than was previously reported. The two studies in this chapter serve to illustrate the potential for the information that is available through the study of avian traces. First, a reanalysis was completed on the ichnotaxon *Wupus agilis*, previously thought to be an ichnotaxon of a small theropod (Xing et al. 2007). A detailed look at the ichnomorphology of *W. agilis* reveals many similarities to the traces of large Cretaceous, Cenozoic, and extant avians. Also, the reassignment of *W. agilis* to Aves is tested using multivariate statistical analyses to determine if there is a significant difference between footprints identified as those of large avian and those of small non-avian theropods, and in which category (avian or non-avian theropod) Limiavipedidae is identified.

Documented differences between footprints and trackways of avian and non-avian theropods (Chapter 4, also see Buckley et al., 2015; Chapter 6, also see Xing et al., 2014) demonstrate that there are strong anatomical influences to footprint shape. Examination of distal tarsometatarsal morphology within Charadriiformes, Galliformes, and Falconiformes shows that trochlear torsion of the distal tarsometatarii has the potential to influence footprint morphology.

CASE STUDY DISCERNING TRACKS OF A LARGE AVIAN FROM THOSE OF A SMALL NON-AVIAN THEROPOD: *WUPUS AGILIS* (EARLY CRETACEOUS: APTIAN-ALBIAN)

Institutional Abbreviations

QJGM, Exhibition Hall of Qijiang County Bureau of Land and Resources, Chongqing, China; **PRPRC**, Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

METHODS

Footprint and Trackway Data Collection

One hundred and eighty-three prints of *Wupus agilis* (Figs. 6.01–6.02) were re-examined at the Lotus Stockade and Tracksite in Chongqing, China in November 2012 (Appendix 6). Measurements were collected directly from the *in situ* prints. To avoid introducing assumptive errors in the data, prints that were not part of a discernible trackway were not identified as either left or right, and lateral digits in relation to digit III were measured as left digit (LD) and right digit (RD); however, where it was clear from the morphology of the track which digits were digit II (DII) and digit IV (DIV), those labels were used (Fig. 6.03). A 1 m by 1 m grid was established along magnetic north-south and east-west lines on the track surface, and the tracks were traced on to a single sheet of acetate (Fig. 6.04). Individual prints were numbered according to the grid square they occupied (e.g. the second print found in grid A5 is labeled A5-2; Appendix 6). No permits were required in order to conduct this research.

Figure 6.01. *Wupus agilis* (A, B) and *Limiavipes curriei* (C). **A,** Print A6-1 (see Table S1 for footprint labels) of *W. agilis*. **B,** Print A6-2 of *W. agilis*. **C,** Replica of holotype RTMP 1998.089.0011 of *Limiavipes curriei* deposited at the PRPRC (McCrea et al., 2014). Scales in centimeters (Xing et al., 2014).

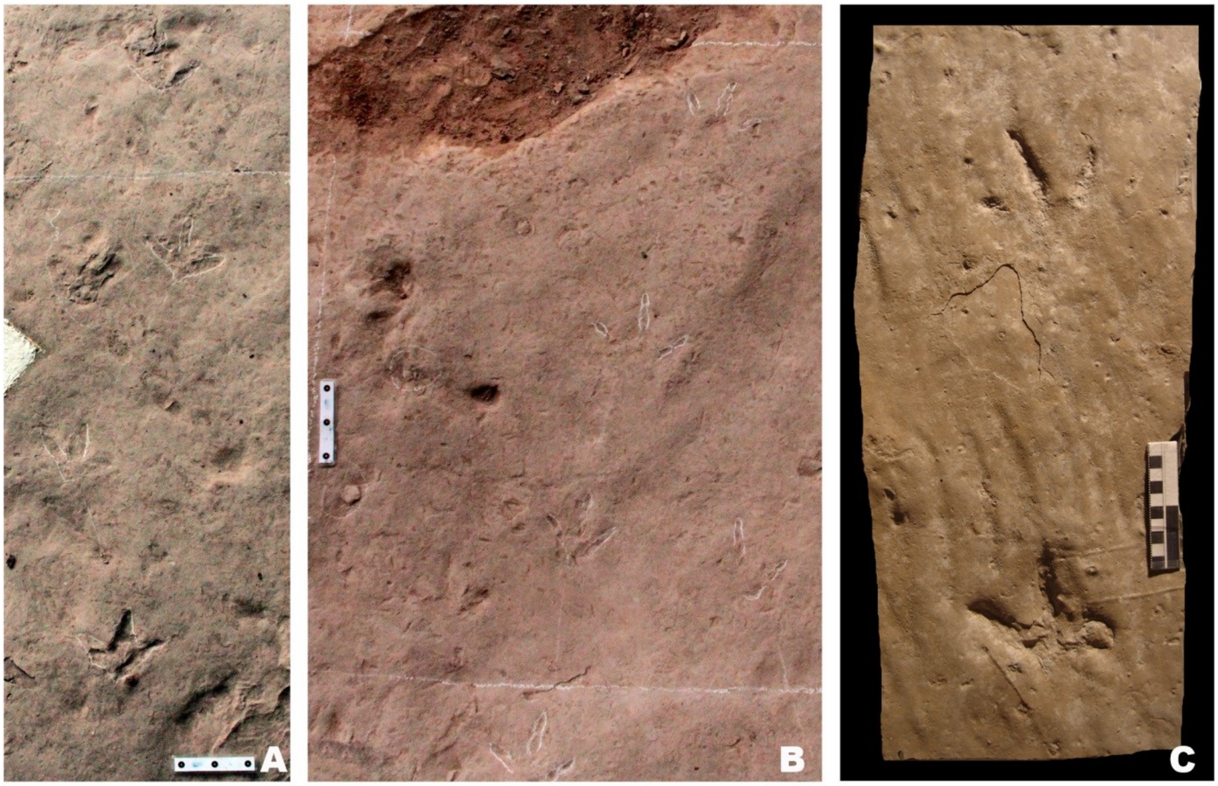

Figure 6.02. Two trackway segments (A-B) of *Wupus agilis* from the Lotus Stockade Tracksite. Note the short pace and stride relative to footprint length. **C,** PRPRC 2005.07.002, trackway of *Limiavipes curriei* (modified from McCrea et al., 2014). Scale = 10 cm (Xing et al., 2014).

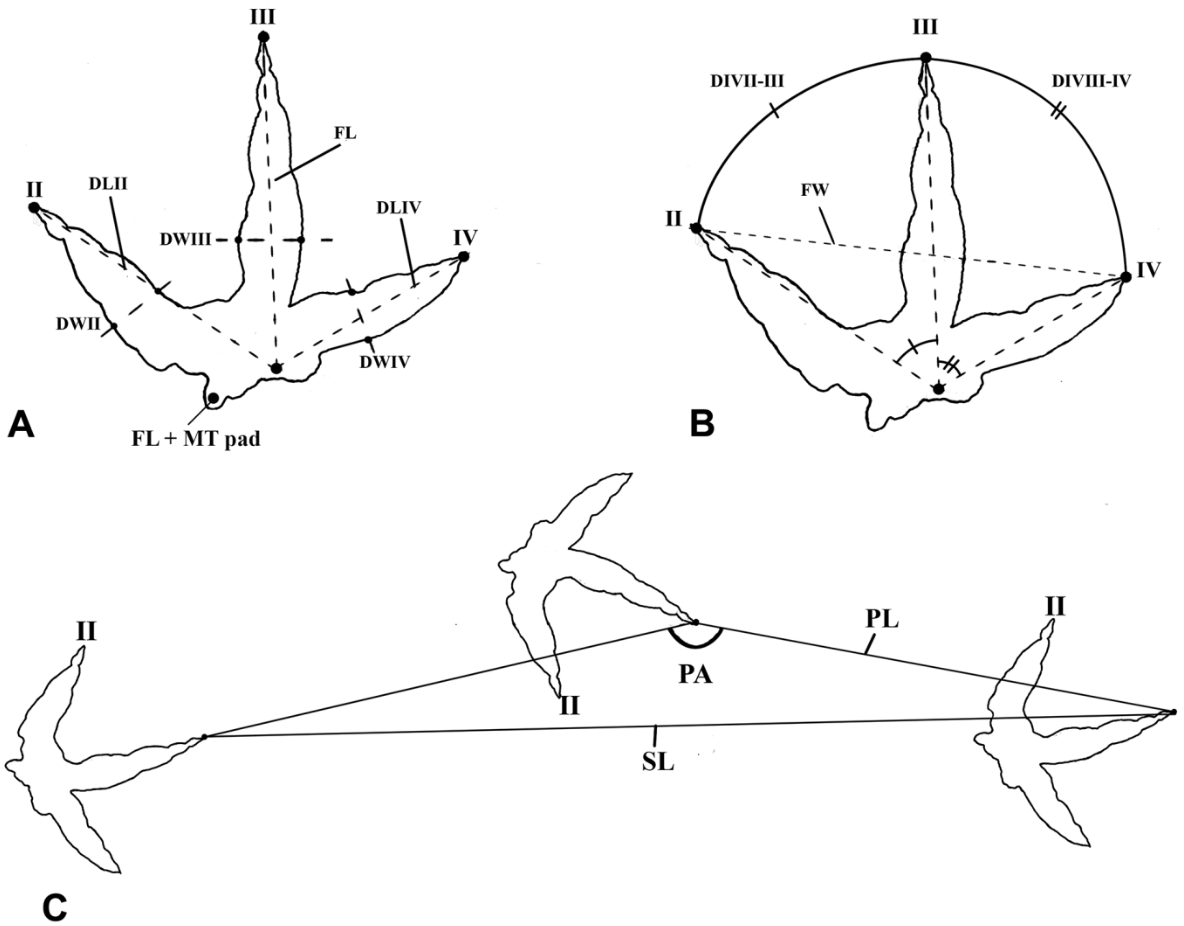

Figure 6.03. Diagrammatic representation of linear and angle measurements collected directly from individual prints (A,B) and trackways (C) of *Wupus agilis* (Tables S1-S2). **A**, Footprint measurements: **II**, digit II; **III**, digit III; **IV**, digit IV; **FL**, footprint length; **DLII**, digit II length; **DLIV**, digit IV length; **DWII**; digit II width; **DWIII**, digit III width; **DWIV**, digit IV width. **B**, **DIVII–III**, digit divarication II–III; **DIVIII–IV**, digit divarication III–IV; **FW**, footprint width; **C**, Trackway measurements: **PL**, pace; **PA**, pace angulation; **SL**, stride. DIVTOT (not shown), total divarication, summed from measurements of DIVII–III and DIVIII–IV (modified from Xing et al., 2014).

Statistical Analyses

Bivariate and multivariate analyses were performed on linear (FL, FW, DLII, DLIV, PL, SL,) and angular (DIVTOT, PA) data using PAleontological STatistics (PAST) version 3.0 (Hammer et al., 2001). Digit maximum width (DW) data were also collected (Appendix 6), but were not used in the analyses as this metric was usually notcollected or reported in previous analyses and including this metric in the multivariate analyses would introduce a large amount of missing data. Other data that were collected (Appendix 6) but were not used in the analyses were digit III length, and divarication angles between digits II–III and III–IV (DIVII–III; DIVIII–IV). This was done to compensate for the disparities in data collection and reporting for past studies of avian footprints. Digit III length is sometimes used as a proxy for footprint length, and using both footprint length and digit III length would result in one metric being included twice in the analyses. In some reports of fossil avian traces the authors do not (or cannot with certainty) identify left and right footprints: this makes identifying digits II and IV and in many instances divarication angles of digits II–III and digits III–IV are not reported. As the *Wupus agilis* and *Limiavipes curriei* samples are not reported with halluces, footprint length with hallux (FLwH) was also not used in the analyses. Data were $\log_{10}$-transformed and means were removed (Farlow et al., 2013) prior to analysis to reduce the effects of absolute size on the results. Analyses performed were the t-test (bivariate), discriminant, and canonical variate. Discriminant analysis (DA) projects a multivariate data set down to two dimensions in a way that maximizes separation between *a priori* separated groups: in this case, the *a priori* groups are ichnotaxonomic groups of footprints attributed to avian or theropod track-makers. The p_{same} between two *a priori* groups was determined using Hotelling's t^2 test, the multivariate version of the t-test (Hammer et al., 2001; Hammer and Harper, 2006) to determine significance at $p \geq 0.05$.

RESULTS

Ichnotaxonomic reassignment of *Wupus agilis* to an avian ichnofamily

Wupus agilis was originally attributed by Xing et al. (2007) to a theropod track-maker based on the characters of coelurosaur prints of Thulborn (1990): foot length usually does not exceed 20 cm, maximum foot length is usually larger than maximum width, and the divarication angle between digits II and III is approximately the same as that between digits III and IV. In the specific case of *Wupus*, the mean footprint length is 7.89 cm, and the mean footprint length to footprint width ratio (FL/FW) is 0.89, demonstrating that the footprint width exceeds footprint length. *Wupus* is morphologically similar to *Limiavipes curriei* (McCrea et al., 2014), emended from *Aquatilavipes curriei* (McCrea and Sarjeant, 2001); Figures 6.01C, 6.02C), from the Grande Cache Member of the Gates Formation (Early Cretaceous: Albian). The morphologic similarity between *Limiavipes curriei* and *Wupus agilis* was noted (McCrea et al., 2014), prompting a reanalysis of the attribution of *Wupus* as a non-avian theropod trace, and a reassignment of *Wupus* to the avian ichnofamily Limiavipedidae (McCrea et al., 2014).

Differentiating between a large avian and a small non-avian theropod track-maker

Given the general morphological similarities between the tracks attributed to large birds and those of small theropods (bipedal, functionally tridactyl, tapering or sharp claws), criteria are required to distinguish the tracks of large avians from those of small theropods. Lockley et al. (1992) list the criteria used to distinguish fossil avian tracks (Chapter 4). In contrast, ichnites attributed to theropod track-makers possess unequal lengths of digits II and IV, with digit IV being longer than digit II, an average total divarication between lateral digits of 90° or less, the theropod "notch", or indent, in the posterior margin of the print in the region of the metatarsophanageal pad posterior to digit II, and unguals of digits II and III curve medially, while the ungual of digit IV curves laterally (Wright, 2004).

As the dimensions of *Limiavipes curriei* and *Wupus agilis* overlap with those of small theropods (Tables 6.01–6.04), this requires that *Wupus agilis* be compared to traces of similarly-shaped (tridactyl, no hallux) small- medium-, and large-sized theropods, as well as those traces of large Mesozoic, Cenozoic and extant avians. To determine whether the traces of both *Limiavipes curriei and Wupus agilis* share more affinities with large avians than with traces of small theropods, the linear and angular data of Limiavipedidae were compared to those of small- (*Irenichnites gracilis*, McCrea, 2000), medium- (*Columbosauripus ungulates, Magnoavipes caneeri*, *Magnoavipes denaliensis*, *Magnoavipes lowei*; Lee, 1997; McCrea, 2000; Lockley et al., 2001; Fiorillo et al., 2011), and large-sized (*Irenesauripus mcclearni*, McCrea, 2000) theropod trackways from the Cretaceous of North America, and to traces attributed to large avians from the Mesozoic (*Archaeornithopus* ichnosp., Fuentes Vidarte, 1996; *Sarjeantopes* ichnosp., Lockley et al., 2004) and Cenozoic. Cenozoic avian ichnotaxa included were *Anatipeda* ichnosp. (Panin and Avram, 1962; Sarjeant and Langston, 1994; Sarjeant and Reynolds, 2001), *Ardeipeda* ichnosp. (Panin and Avram, 1962; Sarjeant and Langston, 1994), *Culcipeda* ichnosp. (Sarjeant and Reynolds, 2001), *Fuscinapeda* ichnosp. (Panin and Avram, 1962; Sarjeant and Langston, 1994), *Gruipeda* ichnosp. (Panin and Avram, 1962; Sarjeant and Langston, 1994), *Leptoptilostipus* ichnosp. (Payros et al., 2000), *Ornothotarnocia* ichnosp. (Kordos, 1985; Sarjeant and Reynolds, 2001), and *Pavoformipes* ichnosp. (Lockley and Delago, 2007). These avian ichnites have footprint lengths that fall within the ranges of *Limiavipes curriei* and *Wupus* *agilis*. Also included in the analyses are data from the traces of the large, extant wading avians *Ardea herodias* (PRPRC NI2014.001, PRPRC NI2014.002) and juvenile *Branta canadensis* (PRPRC NI2014.004) from northeast British Columbia, Canada.

Total divarication/footprint splay and determination of theropod versus bird tracks

High divarication has been used to differentiate between traces of large avians and those of small theropods (Lee, 1997; Lockley et al., 2001; Fiorillo et al. 2011). A total divarication of less than 90° is reported to be a feature in theropod prints (Wright, 2004), whereas a total divarication of greater than 100° has been used as an avian trace character (Lockley et al, 1992). In extant shorebirds, for example, total divarication (the divarication between digit II and digit IV) within a single trackway can range from 75.5°–116.5°, and have an average total divarication of 96.1° (PRPRC NI2011.003 , *Tringa solitaria*, Solitary Sandpiper). In a large wading bird, *Ardea herodias*, comparable in size to Limiavipedidae, total divarication ranges from 88°–110° with an average total divarication of 97.7° (Table 6.03). Conversely, the small-, medium- and large-sized theropod traces range in total divarication from 65°–120°, with an average total divarication of 72° for tracks attributed to small theropods (*Irenichnites* ichnosp.), 81° and 93° for tracks attributed to medium-sized theropods (*Columbosauripus* ichnosp. and *Magnoavipes* ichnosp., respectively), and 73° for tracks attributed to large-sized theropods (*Irenesauripus* ichnosp.; Table 6.03). Relying on total divarication alone would result in the tracks of large avians, such as traces of Cenozoic *Anatipeda* ichnosp. and *Gruipeda* ichnosp. from the Cenozoic, and traces of extant *Ardea herodias* and *Branta canadensis*, being classified as those of non-avian theropods if these traces were to be discovered in Mesozoic sediments, as these traces have an average total divarication of less than 100°. In general, total divarication of greater than 100°

is a characteristic that can be used to differentiate between small theropod and large bird traces from the Cretaceous only when those divarications are preserved, and this is demonstratively unrealistic based on the ranges of total divarication of the traces of both Cenozoic and extant avians. Average total divarication alone is a potentially misleading feature due to the large degree of overlap between the tracks of large avian and small theropod track-makers.

Track-maker	**Ichnotaxon**	**mean FL (mm)**	**minimum FL (mm)**	**maximum FL (mm)**	**Standard error, N**
Limiavipedidae	*Limiavipes*	78.9	63	101	1.2, 55
	Wupus	102	70	137	1, 160
Theropod	*Columbosauripus*	249.6	220	280	5.1, 13
	Irenesauripus	461.3	380	495	10.1, 13
	Irenichnites	164.1	135	190	4.7, 11
	Magnoavipes	196.8	170	230	3.1, 25
Mesozoic bird	*Archaeornithipes*	120	75	166	26.3, 3
Cenozoic bird	*Anatipeda*	65.5	58	73	2.7, 5
	Culcipeda	91.3	61	105	10.3, 4
	Fuscinapeda	98	96	100	2, 2
	Gruipeda	124	75	172	49, 2
	Leptoptilostipus	94.0	80	115	2.8, 12
Extant bird	*Ardea herodias*	120	115	123	0.9, 8
	Branta canadensis	103	98	108	2, 4

Table 6.01. Comparison of footprint lengths (mm) of *Limiavipes curriei* to *Wupus agilis* (Limiavipedidae), and to Cretaceous theropod traces *Irenichnites gracilis* (small), *Columbosauripus ungulates* and *Magnoavipes* (*M. caneeri*, *M. denaliensis, M. lowei*) (medium), *Irenesauripus mcclearni* (large), and traces of large Mesozoic, Cenozoic, and extant avians. If using size alone as a diagnostic criterion to distinguish small theropod traces from those of large avians, *Irenichnites* ichnosp. falls within a similar size class of trackmaker as those of *Gruipeda ichnosp.*, *Limiavipes curriei*, *Wupus agilis*, and the tracks of *Ardea* (extant).

Track-maker	**Ichnotaxon**	**mean FL/FW**	**min FL/FW**	**max FL/FW**	**Standard error, N**
Limiavipedidae	*Limiavipes*	0.76	0.59	0.94	0.01, 53
	Wupus	0.89	0.59	1.32	0.01, 144
Theropod	*Columbosauripus*	1.1	0.9	1.4	0.04, 12
	Irenesauripus	1.2	1.0	1.4	0.04, 12
	Irenichnites	1.2	1.1	1.3	0.02, 11
	Magnoavipes	0.87	0.74	1.0	0.02, 24
Mesozoic bird	*Archaeornithipes*	1.0	0.99	1.0	0.01, 3
Cenozoic bird	*Anatipeda*	0.92	0.84	1.04	0.04, 5
	Culcipeda	0.90	0.74	0.91	0.04, 4
	Fuscinapeda	1.17	1.16	1.17	0, 2
	Gruipeda	1.01	0.96	1.07	0.06, 2
	Leptoptilostipus	0.95	0.89	1.02	0.01, 12
Extant bird	*Ardea herodias*	0.89	0.59	1.32	0.01, 144
	Branta canadensis	0.76	0.59	0.94	0.01, 53

Table 6.02. Comparing footprint length to footprint width ratio (FL/FW) of *Limiavipes curriei* to the *Wupus agilis* (Limiavipedidae), and to the Cretaceous small- (*Irenichnites gracilis*), medium- (*Columbosauripus ungulates Magnoavipes caneeri*, *M. denaliensis, M. lowei*), and large-sized (*Irenesauripus mcclearni*large), theropod traces, and traces of large Mesozoic, Cenozoic, and extant avians. There is considerable overlap in FL/FW values between theropod and avian traces, making FL/FW an unreliable metric when used alone to distinguish between large avian and small theropod footprints.

Track-maker	**Ichnotaxon**	**mean DIVTOT (°)**	**minimum DIVTOT(°)**	**maximum DIVTOT(°)**	**Error, N**
Limiavipedidae	*Limiavipes*	125	107	150	2.0, 24
	Wupus	97.5	67	132	1.2, 147
Theropod	*Columbosauripus*	80.8	65	89	4.4, 5
	Irenesauripus	73.3	70	78	2.4, 4
	Irenichnites	72	65	83	5.6, 3
	Magnoavipes	93.4	65	118	3.4, 23
Mesozoic bird	*Archaeornithipes*	113	70	150	23, 3
Cenozoic bird	*Anatipeda*	92.4	84	98	3.4, 5
	Culcipeda	129	117	133	4, 4
	Fuscinapeda	105	105	105	0, 2
	Gruipeda	96.5	72	121	24.5, 2
	Leptoptilostipus	?	?	?	?, 12
Extant bird	*Ardea herodias*	97.7	88	110	2.6, 9
	Branta canadensis	92.5	90	95	1.0, 4

Table 6.03. Comparison of total divarication values (DIVTOT, also known as divarication between digits II–IV) values comparing *Limiavipes curriei* to *Wupus agilis* to (Limiavipedidae), and Cretaceous small- (*Irenichnites* ichnosp.) medium- (*Columbosauripus* ichnosp., *Magnoavipes* ichnosp.) and large-sized (*Irenesauripus* ichnosp.) theropod ichnotaxa, and the traces of Mesozoic, Cenozoic and extant avians. While traces of large birds do overlap in some aspects of morphology with similarly-sized theropod traces, the mean total divarication of *Wupus agilis* is more similar to that of a large bird than that of a small theropod. While *Limiavipes curriei* is close in morphology to *Wupus agilis*, they are different enough in both size (Table 6.01) and total divarication to be considered distinct ichnotaxa.

Footprint Length to Pace Length Ratio (FL/PL)

The pace in avian trackways is, on observation, relatively shorter than that seen in similarly-sized theropod traces. In Lockley et al.'s (2001) interpretation of *Magnoavipes* ichnosp. as having been made by a theropod (rather than avian) track-maker, they note that the relatively long pace and low footprint rotation of *Magnoavipes* ichnosp., despite the high total divarication (which can also be observed in the traces of ornithopod affinity), are more characteristic of theropod track-makers. To determine quantitatively if the pace in a bird trackway is relatively shorter than that of a theropod, the footprint length/pace length ratio (FL/PL) was calculated for those ichnotaxa for which the data were available (Table 6.04). The footprint length to pace length ratios (FL/PL) of *Limiavipes curriei* (0.34) and *Wupus agilis* (0.38) are on average larger when compared to the same ratios from small-sized (*Irenichnites* ichnosp., 0.19), medium-sized (*Columbosauripus* ichnosp., 0.23; *Magnoavipes* ichnosp., 0.18), and large-sized (*Irenesauripus* ichnosp., 0.31) theropod trackways from the Cretaceous of North America, although there is overlap in the range between the smallest and the largest ratio values (Table 6.04). The traces of *Limiavipes curriei* and *Wupus agilis* are closer in FL/PL to those of Cenozoic and extant avians: traces of *Fuscinapeda* ichnosp. display the largest FL/PL ratio (0.44), while the FL/PL ratio of *Ardea herodias* is 0.30 and *Branta canadensis* is 0.47.

Track-maker	**ichnotaxon**	**mean FL/PL**	**minimum FL/PL**	**maximum FL/PL**	**Number (N)**
Limiavipedidae	*Limiavipes*	0.34	0.23	0.45	42
	Wupus	0.38	0.22	0.66	17
Theropod	*Columbosauripus*	0.23	0.18	0.25	10
	Irenesauripus	0.31	0.27	0.40	12
	Irenichnites	0.19	0.12	0.27	9
	Magnoavipes	0.18	0.14	0.21	17
Cenozoic bird	*Fuscinapeda*	0.44	0.43	0.45	2
Extant bird	*Ardea herodias*	0.47	0.30	0.78	5
	Branta canadensis	0.47	0.46	0.50	3

Table 6.04. Comparing the footprint length (FL) to pace length (PL) ratios (FL/PL) of *Limiavipes curriei* to *Wupus agilis* (Limiavipedidae), and to small- (*Irenichnites* ichnosp.) medium- (*Columbosauripus* ichnosp., *Magnoavipes* ichnosp.) and large-sized (*Irenesauripus* ichnosp.) theropod ichnotaxa, and traces of large Cenozoic, and extant avians. *Limiavipes curriei* and *Wupus agilis* have a larger FL/PL than do small theropod traces of comparable size and those of medium-sized theropods. *Columbosauripus* ichnosp. has the largest mean FL/PL of the analyzed theropod traces. The FL/PL of *Limiavipes curriei* and *Wupus agilis* have the most overlap with the FL/PL of avian traces. This indicates that, relative to the length of the trackmaker's foot, the trackmakers of both *Limiavipes curriei* and *Wupus agilis* are either taking relatively shorter steps than similarly-sized theropods, or have relatively shorter legs than do similarly-sized theropods.

This metric indicates that, relative to the length of the trackmaker's foot, the track-makers of Limiavipedidae and large wading birds are either taking relatively shorter steps than theropods with similarly-sized pedes (due to either behavioral or biomechanical reasons), or have relatively shorter legs than do similarly-sized theropods. Both traces of *Limiavipes curriei* and *Wupus* *agilis* are preserved on fine-grained sandstone without any of the extramorphologic features (e.g. digit collapse, such as observed in *Magnoavipes* ichnosp. (slide marks, etc., Matsukawa et al., 2014) or trackway features (e.g. high inward footprint rotation) that would indicate atypical or hampered movement. This indicates that shortened steps are not artifacts of the original substrate composition.

Interpretation of the morphology and bivariate data of the traces of *Limiavipes curriei* and *Wupus agilis* (Figures 6.01–6.02) indicates that the Limiavipedidae share more characteristics with Cenozoic and extant avian track-makers than they do small- and medium-sized theropod track-makers, supporting the attribution of the Limiavipedidae to an avian track-maker.

Multivariate Statistical Analyses

Discriminant analysis on Limiavipedidae (*Limiavipes curriei*, *Wupus agilis*), small- (*Irenichnites* ichnosp.), medium- (*Columbosauripus* ichnosp., *Magnoavipes* ichnosp.), and large-sized (*Irenesauripus* ichnosp.) theropod ichnotaxa, Mesozoic (*Archaeornithipes* ichnosp., *Sarjeantopes* ichnosp.) and Cenozoic (*Anatipeda* ichnosp., *Culcipeda* ichnosp., *Fuscinapeda* ichnosp., *Gruipeda* ichnosp., *Leptoptilostipus* ichnosp.) avian ichnotaxa, and data collected from the tracks of extant large avians (*Ardea herodias*, juvenile *Branta canadensis*) indicate that Limiavipedidae share a morphospace with the tracks of both Cenozoic and extant avians, but does not share morphospace with the theropod ichnites (Figure 6.04, Tables 6.05–6.06). There are distinct avian and theropod morphospace groups ($p_{\text{same}} = 1.35 \times 10^{-84}$, 97.6% correctly identified). None of the footprints of Limiavipedidae were mistakenly classified as belonging to the theropod group, whereas the analysis misclassified 48 tracks of Limiavipedidae as belonging to several Cenozoic avian ichnotaxa (12 *Ardea herodias*, 11 Anseriformes, ten *Culcipeda* ichnosp., 11 *Gruipeda* ichnosp., seven *Leptoptilostipus* ichnosp., , with four prints identified as "bird", Table 6.06). Also, seven theropod prints (one of *Irenesauripus* ichnosp., six of *Magnoavipes* ichnosp.) were misclassified as belonging to Limiavipedidae, and are tracks that contain a large amount of missing data save for footprint length, and they could not be accurately placed by the analysis.

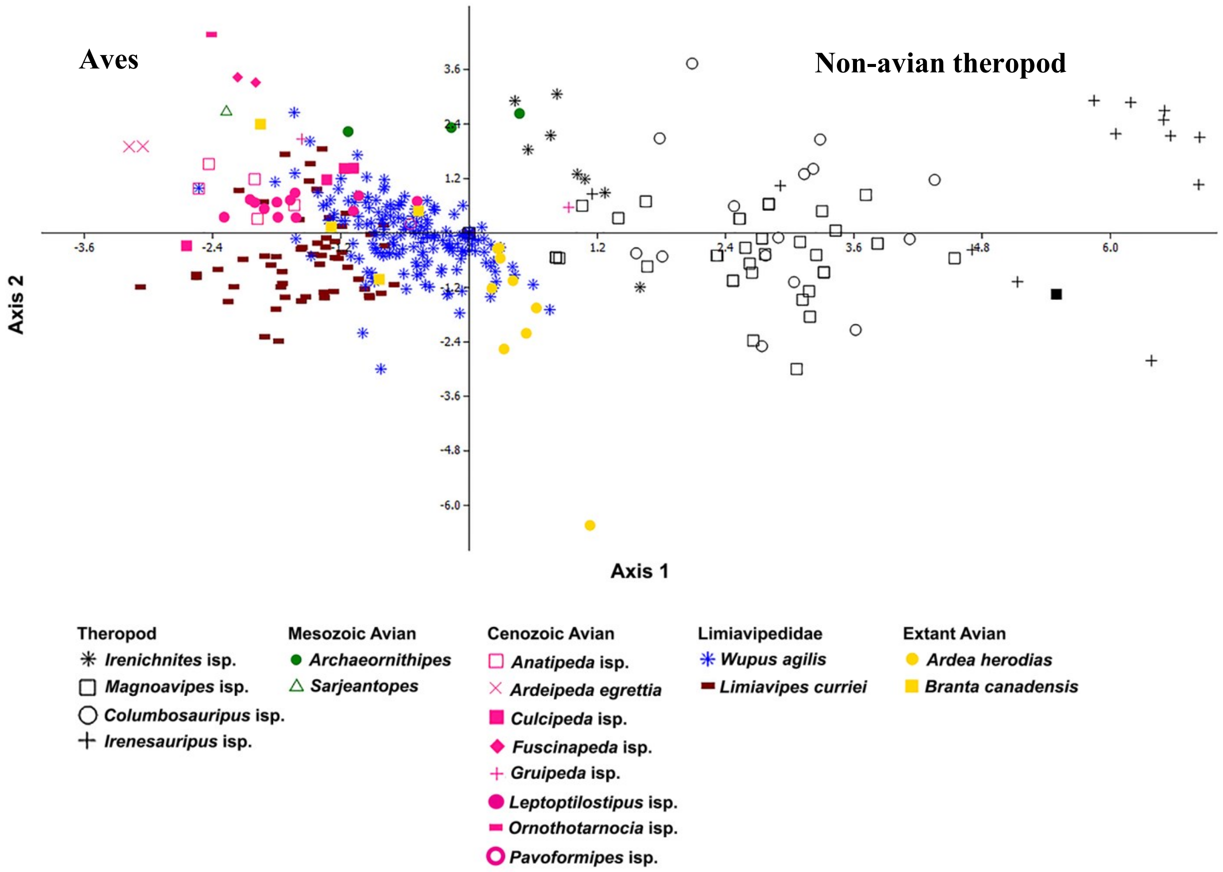

Figure 6.04. Discriminant analysis morphospace plot comparing Limiavipedidae (*Limiavipes* and *Wupus*) to prints of small- and medium-sized theropods and large wading birds. Discriminant analysis scatterplot comparing $\log_{10}$-transformed and mean removed linear data (footprint length, FL; footprint width, FW; digit II length, DLII; digit IV length, DLIV; pace length, PL; stride length, SL) and mean removed angular data (total divarication, DIVTOT; pace angulation, PA) of Limiavipedidae (*Limiavipes curriei*, dark brown; *Wupus agilis*, dark blue) to ichnotaxa of Cretaceous theropods (black), Mesozoic avians (green), Cenozoic avians (pink), and traces of extant avians (orange). The scatterplot shows that Limiavipedidae, as well as the Cenozoic avian ichnotaxa and ichnites from extant avians, do not share morphospace with Cretaceous theropod tracks. Axis 1 is interpreted as the size–total divarication axis; as size and

pace angulation increase (as the size of the trackmaker increases and as the trackway narrows), total divarication decreases. This is consistent with the observations of theropods having a smaller total divarication, as well as a larger size and narrower trackway. Theropods group positively along Axis 1, while birds, with their smaller size and higher total divarication, and more "toed-in" footprints, group negatively along Axis 1. Axis 2 is interpreted as the relationship between FW and the lengths of the lateral digits to FL, PL, and SL; footprints with longer lateral digits (DII, DIV) are relatively shorter in length, and are found in trackways with shorter PL and SL. Avian prints are interpreted to have subequal lateral digits and a higher L/W ratio, and the discriminant analysis correlates with the interpretation that avian prints belong to trackways with a relatively shorter pace length (Tables 6.04–6.05).

Multivariate analysis of variance (MANOVA) was conducted on Limiavipedidae with the small-, medium-, and large-sized theropod ichnotaxa, the Cenozoic avian ichnotaxa, and prints from extant large avians with footprints similar in size to traces of Limiavipedidae. The ichnites with which Limiavipedidae were mistaken in the confusion matrix indicate that Limiavipedidae is significantly different from the theropod ichnites ($p_{\text{same}} = 4.47 \times 10^{-27}$) and is also significantly different (although to a lesser degree) from Anseriformes ($p_{\text{same}} = 7.39 \times 10^{-04}$), extant *Ardea* (heron; $p_{\text{same}} = 5.58 \times 10^{-04}$), *Culcipeda* ichnosp. ($p_{\text{same}} = 6.61 \times 10^{-05}$), *Fuscinapeda* ichnosp. ($p_{\text{same}} = 0.04$), and *Leptoptilostipus* ichnosp. ($p_{\text{same}} = 9.03 \times 10^{-16}$). Limiavipedidae were not significantly different from the ichnites *Ardeipeda* ichnosp. ($p_{\text{same}} = 0.36$) or *Gruipeda* ichnosp. ($p_{\text{same}} = 0.36$). Multivariate statistical analyses comparing *Wupus* and *Limiavipes* to small- and medium-sized theropod ichnites, and to large avian ichnites from the Mesozoic, Cenozoic, and from extant avians reveals, 1) the similarity between *Limiavipes* and *Wupus*, providing additional support for the assignment of *Wupus* to Limiavipedidae, and 2) that the traces assigned to Limiavipedidae are more similar to those traces of large avians than they are to traces of small- and medium-sized theropods, and supports the attribution of Limiavipedidae to a large avian track-maker.

Variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10
FL	0.092	0.023	-0.001	0.010	-0.028	-0.026	0.023	-0.017	-0.017	$2.07 \times {}^{-238}$
FW	0.077	-0.012	-0.025	-0.003	-0.004	-0.001	0.001	0.030	0.015	$-3.09 \times {}^{-238}$
L/W	0.026	0.077	0.020	0.008	-0.045	0.011	0.058	-0.058	0.033	$8.98 \times {}^{-237}$
DLII	0.034	-0.047	-0.053	0.035	-0.021	-0.002	0.053	-0.020	-0.002	$-1.81 \times {}^{-237}$
DLIV	0.034	-0.051	-0.018	0.054	-0.016	-0.006	0.057	-0.010	0.006	$-1.63 \times {}^{-237}$
DIVTOT	0.082	0.051	-0.030	0.077	0.010	0.058	-0.062	-0.040	0.013	$6.33 \times {}^{-237}$
PL	0.062	0.013	0.004	-0.010	0.094	0.018	-0.005	-0.086	0.012	$1.38 \times {}^{-236}$
SL	-2.03	2.38	-3.67	1.13	7.32	-8.46	-0.874	6.87	0.620	$7.97 \times {}^{-235}$
PA	0.684	-0.208	-0.169	0.211	-0.324	-2.26	-2.42	-2.16	2.61	$2.95 \times {}^{-235}$

Table 6.05. Variable loadings for discriminant analysis comparing $\log_{10}$-transformed and mean removed linear data (footprint length, FL; footprint width, FW; digit II length, DLII; digit IV length, DLIV; pace length, PL; stride length, SL) and mean removed angular data (total divarication, DIVTOT; pace angulation, PA) of Limiavipedidae (*Limiavipes curriei*, *Wupus agilis*) to small- (*Irenichnites* ichnosp.) medium- (*Columbosauripus* ichnosp., *Magnoavipes* ichnosp.) and large-sized (*Irenesauripus* ichnosp.) theropod ichnotaxa, and Mesozoic (*Archaeornithipes* ichnosp., *Sarjeantopus* ichnosp.) and Cenozoic (*Culcipeda* ichnosp., *Fuscinapeda* ichnosp., *Gruipeda* ichnosp., *Leptoptilostipus* ichnosp., *Pavoformipes* ichnosp.) avian ichnotaxa, and data collected from the tracks of extant large avians (*Ardea herodias*, juvenile *Branta canadensis*). Axes 1 and 2 are the axes along which maximal separation of the grouped data occur. Axis 1 is interpreted as the effect of size on the variation present in the dataset; however, as size and pace angulation increase (as the size of the trackmaker increases and as the trackway narrows), total divarication decreases. This is consistent with the observations of theropods having a smaller total divarication, as well as a larger size and narrower trackway.

		Predicted Group											
	A priori groups	Theropod	Limiavipedidae	*Archaeornithipes*	*Leptoptilostipus*	*Gruipeda*	Anseriform	*Culcipeda*	*Ardeipeda*	*Fuscinapeda*	*Ardea herodias*	Bird	Total
Given Group	Theropod	61	7	1	0	8	0	0	0	0	3	0	80
	Limiavipedidae	0	188	1	7	11	11	10	0	0	12	3	243
	Archaeornithipes	0	0	1	0	0	1	0	0	0	0	1	3
	Leptoptilostipus	0	2	0	10	0	0	0	0	0	0	0	12
	Gruipeda	0	1	0	0	0	1	0	0	0	0	0	2
	Anseriform	0	0	0	0	0	7	0	1	0	1	0	9
	Culcipeda	0	0	0	0	0	0	4	0	0	0	0	4
	Ardeipeda	0	0	0	0	0	0	0	2	0	0	0	2
	Fuscinapeda	0	0	0	0	0	0	0	0	2	0	0	2
	Ardea herodias	0	2	0	0	0	0	0	0	0	7	0	9
	Bird	0	1	0	0	0	0	1	0	0	0	1	3
	Total	61	201	3	17	19	20	15	3	2	23	5	369

Table 6.06. Confusion matrix of discriminant analysis comparing $\log_{10}$-transformed and mean removed linear data (footprint length; footprint width; digit II length; digit IV length; pace length, PL; stride length, SL) and mean removed angular data (total divarication; pace angulation) of Limiavipedidae (*Limiavipes curriei*, *Wupus agilis*) to small- (*Irenichnites* ichnosp.), medium- (*Columbosauripus* ichnosp., *Magnoavipes* ichnosp.), and large-sized (*Irenesauripus* ichnosp.) theropod ichnotaxa, Mesozoic (*Archaeornithipes* ichnosp., *Sarjeantopes* ichnosp.) and Cenozoic (*Culcipeda* ichnosp., *Fuscinapeda* ichnosp., *Gruipeda* ichnosp., *Leptoptilostipus* ichnosp., *Ornothotarnocia* ichnosp., *Pavoformipes* ichnosp.) avian ichnotaxa, and data collected from the tracks of extant large avians (*Ardea herodias*, juvenile *Branta canadensis*). No individual footprints of Limiavipedidae were identified as theropod ichnites in the predicted groupings, while 48 prints of Limiavipedidae were misidentified as the avian ichnotaxa *Culcipeda* ichnosp., *Gruipeda*

ichnosp., *Leptoptilostipus* ichnosp., and “bird” (*Ornothotarnocia* ichnosp., *Pavoformipes* ichnosp., *Sarjeantopes* ichnosp.,), and the tracks of extant *Ardea herodias* and those of both extant and fossil Anseriformes.

Retention of *Limiavipes* and *Wupus* as separate ichnotaxa— The original assignment by Xing et al. (2007) of *Wupus agilis* as the trace of a small theropod is not accurate given detailed comparisons of traces of *Wupus agilis* to those ichnotaxa of large birds and small theropods. *Wupus agilis* closely conforms to the diagnosis for Limiavipedidae (McCrea et al., 2014). Well-preserved digits II–IV terminate distally in short, acuminate claws (Figure 6.01A,B), a feature that is identified as avian by Lockley et al. (1992). While the ungual of digit II in Dromaeosauridae is sharp, footprints attributed to Dromaeosauridae (Paraves) do not have an impressed digit II (Carrano and Wilson, 2001).

Comparison of *Wupus agilis* with *Limiavipes curriei* indicates that while there are many similarities, there are enough morphologic differences to retain *Limiavipes* ichnogen. and *Wupus* ichnogen. as distinct ichnotaxa. *Limiavipes curriei* has an average footprint length (FL) of 7.9 cm (6.3 cm – 10.1 cm), while *Wupus agilis* is larger, with an average FL of 10.3 cm (7.0 cm – 17.0 cm). In well-preserved prints of *Wupus agilis* the proximal margin of the pes is asymmetrically bi-lobed, displaying a short, postero-medially protuberance that may correlate with the metatarsal pad for an unimpressed hallux; however, no halluces were identified in 187 documented prints. The prints of *Wupus agilis* possess an average FL/footprint width (FW) of 0.9 (0.6 – 1.3), while those of *Limiavipes curriei* display a larger splay and possess a FL/FW of 0.75 (0.6 – 0.9) (Tables 6.01–6.02). The average total divarication (II-IV) of *Wupus agilis* is 96.9° (67° – 132°), which is smaller than the average total divarication of *Limiavipes curriei* (123°). In four trackways, the average P and S lengths of are 38.7 cm (23 cm – 63 cm) and 75.9 cm (48.5 cm – 113.5 cm), respectively, and a FL to PL ratio of 0.3 (0.2 – 0.6) (Table 6.03; Figure 6.02). This is similar to *Limiavipes curriei*, where average pace and stride lengths are 23.9 cm (18 cm – 31.5 cm) and 46.5 cm (36.5 cm – 60.0 cm), and a FL/PL of 0.3 (0.2 – 0.4). *Wupus* *agilis* represents a larger track-maker in both footprint length and leg length with more narrowly-splayed pedes than those of *Limiavipes curriei* (Tables 6.03–6.04).

DISCUSSION

Ichnomorphology, multivariate statistical analyses, and interpretations of total divarication, footprint splay, FL/PL support that *Wupus agilis* is the most similar to *Limiavipes curriei* and can confidently be assigned to the ichnofamily Limiavipedidae. Multivariate statistical analyses of *Limiavipes curriei* and *Wupus agilis* with tracks of Cretaceous small- (*Irenichnites* ichnosp.), medium- (*Columbosauripus* ichnosp., *Magnoavipes* ichnosp.), and large-sized (*Irenesauripus* ichnosp.) theropods, and with large avian traces from the Cenozoic and those of extant birds, demonstrate that Limiavipedidae is distinct from similarly-sized small- and medium-sized traces attributable to theropods. Limiavipedidae occupies a similar morphospace to traces of the Cenozoic avian ichnotaxa *Culcipeda*, ichnosp., *Fuscinapeda* ichnosp., *Gruipeda* ichnosp., and *Leptoptilostipus* ichnosp., Ichnomorphology, multivariate statistical analyses, and interpretations of total divarication, footprint splay, FL/PL support the attribution of *Limiavipes curriei* and *Wupus agilis* to large, wading avian track-makers.

Distinguishing Between the Tracks of Small Non-Avian Theropods versus Large Birds in the Cretaceous

Similarities in pes morphology between Cretaceous small- and medium-sized theropods and large wading birds can lead to multiple interpretations with respect to the potential track-maker. While it would be convenient if there were a single track or trackway feature exclusive to either small theropods or to large birds that is consistently preserved, nature is rarely so unambiguously dichotomous. Interpreting footprints requires addressing a high degree of natural variation in metrics inherent in the preserved movements of living animals. There are a number of different metrics that must be considered when attempting to make a distinction between the tracks of avians and those of small theropod. There are many bird-like features in theropod dinosaur footprints, and many of the issues in distinguishing the tracks of bipedal tridactyl dinosaurs from those of avians may be due to similar functional constraints in locomotion (Wright, 2004; although see Gatesy, 1990 and Farlow et al., 2000 for differences between avian and theropod locomotor constraints).

In short, there is no one feature that can be used to distinguish the print of a small theropod from that of a large wading bird 100% of the time; this particularly holds true when attempting to identify an isolated footprint or even a single trackway, as there can be a large amount of variability in digit splay and preservation of accurate digit lengths. Rather, a combination of features (size, divarication, digit splay, and footprint length to pace length ratio) should be used to distinguish between traces of small theropods and those of large wading avians.

Size alone does not a small theropod trace make—Comparisons of data (Tables 6.01–6.04) demonstrate that there is considerable overlap in the documented sizes of the avian prints of *Limiavipes curriei* and *Wupus agilis*, as well as prints of Cenozoic avians, with those prints attributed the small theropod trace *Irenichnites* ichnosp. (McCrea, 2000). If size were the sole criterion for distinguishing the tracks of theropods from those of birds, *Limiavipes curriei* and *Wupus agilis*, as well as traces of large Cenozoic avians, would erroneously be identified as belonging to a small theropod track-maker if found in Mesozoic strata. Once the linear data

(Appendix 6) are $\log_{10}$-transformed and the mean values of each variable removed, no print from Limiavipedidae shared the same morphospace as the theropod prints (although one avian print, *Gruipeda maxima*, did occupy the same morphospace as did the prints of small theropods), and no prints from Limiavipedidae were misidentified by the discriminant analysis as belonging to theropods. The seven prints of theropods (one of *Irenesauripus* ichnosp. and six of *Magnoavipes* ichnosp.) that were misidentified as belonging to Limiavipedidae were those prints that contain large amounts of missing data.

There is no definite delineation in total divarication between the tracks of small theropods and those of large birds—The digits of small theropods are reported to be, in general, less splayed than those of similarly-sized birds (total divarication of 90° or less), but total divarication cannot be used as the sole diagnostic feature, as it is highly variable in Cretaceous small- and medium-sized theropods, and in both Cretaceous and extant avians (Matsukawa et al., 2014; Table 6.03). For example, the cut-off value of 100° total divarication for *Magnoavipes denalisensis* is used to attribute these traces to those of a large avian (Fiorillo et al., 2011); however, this was based on misinterpretations of work by Lee (1997) of *Magnoavipes* ichnosp. traces as avian (rather than theropod) based on comparisons to only average total divarication (rather than examining the range of total divarications) of Cretaceous avian prints (Lockley et al., 2001; McCrea et al., 2014). Also, it was determined by Lockley et al. (2001) and Matsukawa et al. (2014) that many of the diagnostic features of the type trackway of *Magnoavipes lowei* are preservational artifacts due to both the substrate consistency and extramorphologic features (Lockley et al., 2001; Matsukawa et al., 2014). Based on long pace and stride compared to footprint length, high pace angulation, and low footprint rotation, the likely track-makers for *Magnoavipes* ichnosp. is Ornithomimidae (Ornithomimipodidae)

(Lockley et al., 2001; Matsukawa et al., 2014). Assigning *Magnoavipes* ichnosp. to Ornithomimidae (Ornithomimipodidae) is supported by the analyses herein. Trackways of *Magnoavipes* ichnosp. display the relatively low FL/PL ratio (0.18) of other trackways of theropods, and all specimens (save those with large amounts of missing data) fall within the theropod morphospace (Figure 6.07). Also, both *Magnoavipes* ichnosp. and the theropod morphospace group are significantly different from avian ichnotaxa and the avian morphospace group (Figure 6.07, Buckley et al., in press). It is only when looking at the maxima of total divarications (Table 6.03) is it obvious that traces of large avians have a consistently higher total divarication than do traces of small- and medium-sized theropods, as these values compare favorably with Wright's (2004) observation that the total divarication of theropod footprints is below 90°.

Footprint splay alone does not differentiate the tracks of large avians from those of small theropods—In this analysis, footprint splay (FL/FW) is also not sufficient to differentiate the traces of large avians from those of small theropods, although it has previously been used by McCrea and Sarjeant (2001, fig. 31.13) to differentiate the large avian trace, *Limiavipes curriei*, from several dinosaurian ichnotaxa. While, in general, theropod traces have footprint lengths that exceed footprint widths (FL/FW > 1.00), at the time of the study (McCrea and Sarjeant, 2001), there was little overlap in both size and morphology between theropod and avian traces preserved at that site, making their identification unambiguous. Furthermore, data from Cenozoic avian ichnotaxa provides new information on patterns of footprint splay of large avians tracks. Data (Table 6.03) indicate that the mean FL/FW is similar for both small theropod and large avian traces.

The difference in the average footprint length to pace length ratio between tracks of large birds and those of small theropods—It is only when the ratio of footprint length to pace length is examined (Table 6.04) that the trackways attributed to theropod track-makers display a consistently longer pace compared to footprint length than to those trackways attributed to similarly-sized avians. Pace (or step) lengths may be subjected to biomechanical controls. For example, a large wading avian may have a leg length that is relatively similar to that of a small theropod, but biomechanical differences in locomotion (Farlow et al., 2000) may constrain a large wading bird to taking shorter steps than its theropod counterpart. However, shortened steps may have a behavioral component. Avian traces that are associated with feeding traces have relatively shorter pace lengths than the same traces not associated with feeding traces (*Ignotornis mcconnelli*, Lockley et al., 2009; *Ignotornis gaijiensis*, Kim et al., 2012). Feeding traces do not consistently preserve, and much of the shore- and wading bird behavior exhibited by Cretaceous avian traces might be related to feeding activities. *Wupus agilis*, based on an examination of ichnomorphology, total divarication, footprint splay, FL/PL, and in discriminant analyses, is the most similar to *Limiavipes curriei*, and can confidently be assigned to the ichnofamily Limiavipedidae. Both *Limiavipes* and *Wupus agilis* can be attributed to large, wading avian track-makers.

Avian Diversity during the Early Cretaceous

The revised avian referral for *Wupus agilis* indicates the presence of at least one paleo-ecotype of large wading bird with a functionally tridactyl, (inferred) unwebbed, pes in the Early Cretaceous of China. The track-maker for *Wupus agilis* is distinct from the track-maker of *Limiavipes curriei* from western North America in being a larger bird based on a larger foot (larger footprint length), and, in part on its interpretation of having longer legs (larger pace). *Wupus agilis* lacks hallux impressions and thus can be inferred to be distinct from, and have had a different lifestyle, than the wading birds that made similarly-sized traces with extant heron-like halluces from the Lower Cretaceous (Albian) Eumeralla Formation at Dinosaur Cove, southern Australia (Martin et al., 2013). Thus, it can be concluded that there were at least three distinct morphotypes of large wading birds present during the Early Cretaceous for which skeletal material has not yet been recovered. Assuming that these birds were capable of sustained powered flight, they were probably capable of global distribution throughout Gondwana and Laurasia, similar to extant egrets and herons (Family Ardeidae, Gruidae) that are found in Asia, Australia, and North America.

The results of this study show that *Wupus agilis* is most similar in ichnomorphology to *Limiavipes curriei* and can be reassigned to the ichnofamily Limiavipedidae, and that multivariate statistical analyses indicate Limiavipedidae are significantly different from theropod ichnotaxa, and share ichnomorphologic traits with Cretaceous, Cenozoic, and extant avian ichnites. The results demonstrate that large wading birds had a global distribution in the Early Cretaceous, and that it is possible to differentiate between the traces of large wading birds and those of small theropods by using multiple lines of evidence. Future studies that collect and report complete datasets on Mesozoic, Cenozoic, and extant avian ichnites, and ichnites attributed to small theropods, rather than reporting data for the type material and average values only, will aid greatly in discerning improved criteria for differentiating between avian and theropod ichnites, and improve the paleofaunal data these ichnites provide.

CONGRUENCE BETWEEN OSTEOMORPHOLOGY AND ICHNOMORPHOLOGY IN AVIAN TRACES

The Mesozoic Avian Ichnofossil Record

The record of fossil avian tracks and the number of avian ichnotaxa has increased considerably in the past few years, particularly in Asia (Matsukawa et al., 2006; Lockley and Harris, 2010: Lockley et al., 2012). There are now a number of described avian ichnotaxa from Mesozoic and Cenozoic deposits worldwide (Chapter 5). Where trackways exist, these can be generally divided in to morphotypes of long-legged and short-legged ichnotaxa, each of which can be further sub-divided into categories based on numbers of digits, divarication between digit traces and the presence or absence of webbing. Presence or absence of webbing is influenced by substrate, and as such should not be considered as a consistent diagnostic character. However, when webbing is preserved, it is useful, such as in the palmate ichnotaxa *Presbyornithiformipes* and *Uhangrichnus* and, where clear web traces have been consistently well documented (Lockley and Harris, 2010). Likewise, the semi-palmate condition of some ichnotaxa such as *Sarjeantopodus* (Lockley et al., 2004) is highly diagnostic (contra Falkingham et al., 2009) and cannot be dismissed as unusual extramorphological preservation. It is likely that the lack of familiarity with the preservation of the webbing of extant shorebirds in the field leads some researchers to dismiss webbing as a potential diagnostic tool.

Paxavipedidae and digit divarication

During the description and analysis of *Paxavipes babcockensis* (McCrea et al., 2015), it was apparent that *Paxavipes* is most qualitatively similar in ichnomorphology to *Barrosopus* *slobodai* (Coria et al., 2002). This similarity lies in the seemingly larger divarication between digits II–III than III–IV, a condition that is not generally observed in the traces of extinct Mesozoic shorebirds. Nearly all tridactyl semipalmate avian ichnotaxa described to date either have nearly equal divarications between digits II–III and III–IV, or have higher divarications between digits III–IV and lower divarications between digits II and III. The consistently larger digit divarication II–III than III–IV documented in *Barrosopus slobodai* and *Paxavipes babcockensis* was described as a diagnostic character for Paxavipedidae (McCrea et al., 2015). Because this particular divarication condition is consistent among all footprints of *Paxavipes babcockensis*, this feature is likely due to the morphology and relative position of distal metatarsals II, III, and IV, rather than an artifact of sediment-digit interaction. The mediolateral width of the intertrochlear notches between the distal ends of metatarsals II–III and III–IV (incisurae intertrochlearis medialis et lateralis, Baumel and Witmer, 1993), and the degree of plantar displacement of the distal ends of metatarsals II and IV from the sagittal plane of the tarsometatarsus, should influence digit divarication. Examining the ichnomorphology of Paxavipedidae allows a comparison between this Cretaceous ichnofamily to the prints of extant shorebirds, and allows examination of the distal tarsometatarsii of extant shorebirds with a similar footprint to those of Paxavipedidae. Prints of *Paxavipes* prints are remarkably similar to those produced by extant members of Charadriiformes, particularly those of the modern Killdeer (*Charadrius vociferus*) (Elbroch and Marks, 2001). Is there a difference in the morphology of the distal tarsometatari in extant shorebirds that make prints similar to Paxavipedidae, compared to those extant shorebirds that make more "typical" footprints?

First, the footprints of extant plovers (Charadriidae) were compared to the footprints of extant sandpipers (Scolopaciidae). Second, the distal tarsometatarsi of extant specimens of

Charadriidae and Scolopaciidae were examined to determine if there are any anatomical differences that may account for differences in digit splay.

METHODS

Ichnological Data

Extant shorebirds provide modern analogs to investigate a possible osteological explanation for digit divarication in fossil avian footprints. However, unless there are observable differences between the tracks of extant shorebirds, it is fruitless to hypothesize on osteological causes of digit divarication conditions for extant shorebirds. The field guide to modern bird tracks and traces by Elbroch and Marks (2001) includes line drawings of the tracks of several species of modern shorebird. Using the same techniques to measure digit divarication used to document fossil avian footprints, digit divarications were measured from the line images of tracks of plovers (Charadriidae) and sandpipers (Scolopaciidae), and the data were statistically analyzed using t-test (Elbrock and Marks, 2001; Table 6.09).

Osteology Specimens and Data

Trochlear torsion angles were collected from extant and fossil specimens of Charadiidae (*Charadrius*, *Pluvialis*), gulls (*Larus*), traditional Falconiformes (*Accipiter*, *Buteo*, *Falco*), Phasianidae (*Bonasa*, *Callipepla*, *Dendragapus*, *Falcipennis*, *Lagopus*, *Parapavo*), large wading birds (*Ardea*, *Ciconia*, *Grus*), and Scolopacidae (*Actitis*, *Calidris*, *Tringa*). Trochlear torsion angles were measured using Adobe Photoshop CS2014 from digital photographs taken with a

Sony α350 SLR 12.1 megapixel digital camera. Images were edited and angles were measured using Adobe Photoshop CS2014. Intertrochlear angles of were measured from the long axes of the intertrochlear grooves of distal metatarsals II and IV, each measured from the intertrochlear groove of metatarsal III, as viewed from the distal end of the tarsometatarsus. Plantar angles were measured from the extensor end of the intertrochlear grooves of distal metatarsals II and IV as viewed from the distal the tarsometatarsus, and each angle for metatarsals II and IV were measured from the extensor end of the intertrochlear groove of metatarsal III. Discriminant analyses were performed using Palaeontological Statistics version 3.04 (see Methods in Chapters 4–5 for descriptions of multivariate statistical analyses).

RESULTS

Ichnomorphology and Osteology

Statistical analyses on the digit splay data collected from footprint images of plovers and sandpipers reveals a significant difference in digit divarications II–III for the tracks of plovers (Charadriidae), but not for sandpipers (Scolopaciidae) (Table 6.07). Although a small sample, it is sufficient to justify examining the hypothesized osteological cause for differences in digit divarication (Methods).

Taxon	**DIV II-III**	**DIV III-IV**
Charadriidae		
Charadrius melodus	71	71
Charadrius semipalmatus	62	62
Charadrius vociferus, trackway 1	72	51
Charadrius vociferus, trackway 2	76	50
Pluvialis squatarola	72	52
$p_{\text{same}} = 0.027$		
Scolopaciidae		
Actitis macularius	59	46
Arenaria interpres	49	51
Calidris alba	65	45
Calidris alpina, trackway 1	43	47
Calidris alpina, trackway 2	57	58
Calidris minutilla	58	51
Tringa flavipes	56	63
$p_{\text{same}} = 0.361$		

Table 6.07. Digit divarications measured from line drawings of individual tracks figured in Elbroch and Marks (2001) to test the observation that plovers (Charadriidae) have a significantly larger DIV II–III compared to DIV III–IV than do sandpipers (Scolopaciidae). Although the sample size is small, it does show that plover tracks have a significantly larger DIV II–III than DIV III–IV, whereas in sandpipers the DIV II–III and DIV III–IV are not significantly different. “Killdeer trackway 1” refers to the left trackway figured in Elbroch and Marks (2001: p.110), and “Killdeer trackway 2” refers to the right trackway figured in Elbroch and Marks (2001: p.110); “Dunlin trackway 1” refers to the left footprint figured in Elbroch and Marks (2001: p.109), while “Dunlin trackway 2” refers to the right prints figured in Elbroch and Marks (2001: p.109).

Osteology of the Distal Tarsometatarsus—Examination of osteology specimens of the tarsometatarsi of species of extant shorebirds with a semipalmate foot morphology reveal two ways in which the distal ends of metatarsals II and IV are deflected from the midline of the tarsometatarsus (long axis of metatarsal III, Fig. 6.05; also see Falk et al., 2011), and how this deflection may potentially contribute to digit divarication in avian footprints. One form is the angle difference (herein referred to as the intertrochlear angle) between the trochlear groove of metatarsal II and IV, and the trochlear groove of metatarsal III (Fig. 6.05). This angle captures both the mediolateral length of the intertrochlear notch and the degree of latero- and medioplanter rotation of the distal ends of metatarsals II and IV, respectively. The second form is the medio- and lateroventral displacement angle (hereon referred to as the plantar angle) from the distal ends of metatarsal III of the trochlear ends of metatarsals II and IV, respectively (Figs. 6.05–6.06). Relatively large intertrochlear and plantar angles are hypothesized to result in a large digit divarication for the digits in question.

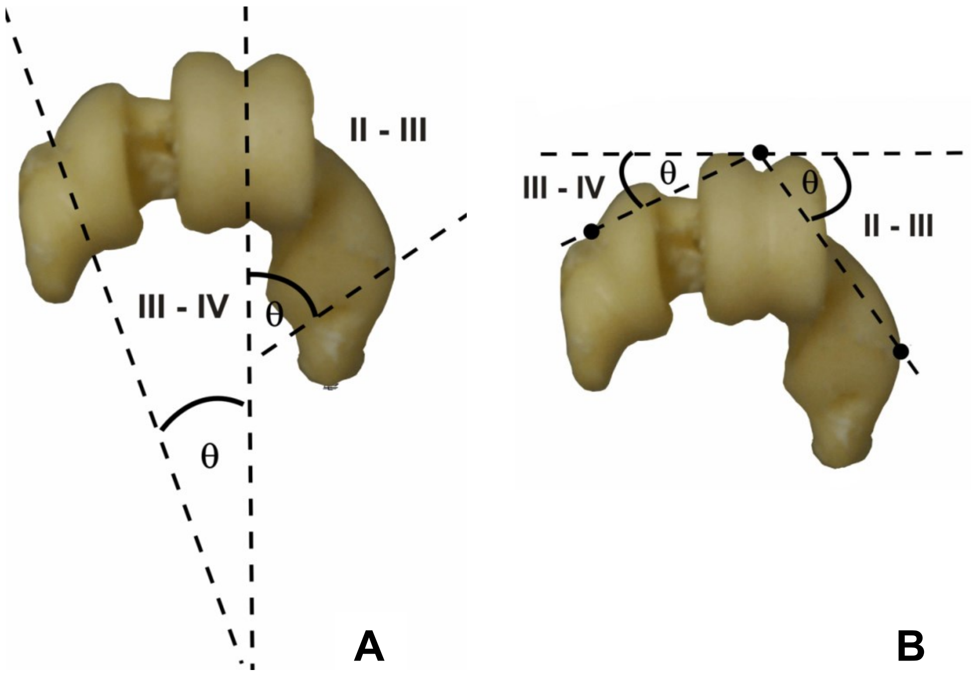

Figure 6.05. Schematic showing measurements taken for intertrochlear angle (A) and plantar angle (B), both of which contribute to the orientation of attached pedal phalanges of the digits during foot registration. The measurements are based on the trochlear grooves of the metatarsals, which will provide not only a consistent and obvious landmark, but also provide the natural "midpoint" of the digit, as there is natural variation in the degree to which pedal phalanges can move mediolaterally.

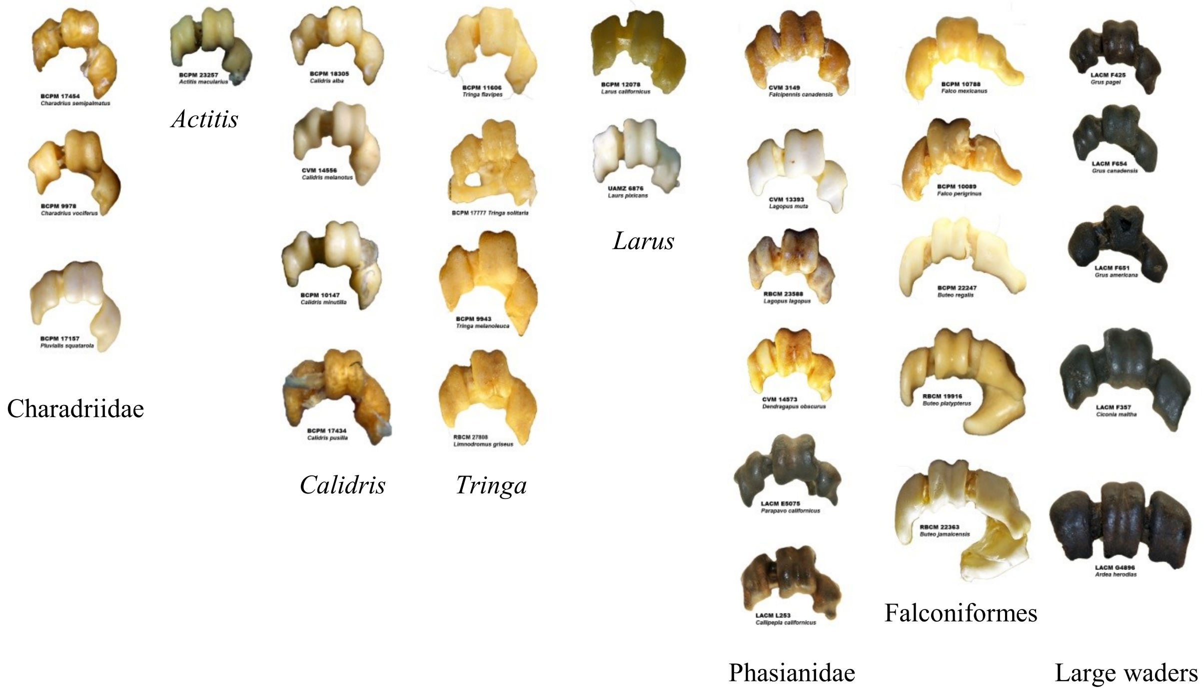

Figure 6.06. Representative distal tarsometatari of Charadiidae (*Charadrius*, *Pluvialis*), gulls (*Larus*), traditional Falconiformes (*Accipiter*, *Buteo*, *Falco*), large wading birds (*Ardea*, *Ciconia*, *Grus*), Phasianidae (*Bonasa*, *Callipepla*, *Dendragapus*, *Falcipennis*, *Lagopus*, *Parapavo*), and Scolopacidae (*Actitis*, *Calidris*, *Tringa*). Measurements from the distal tarsometatarsi were collected as per Figure 6.05. Refer to Appendix 6 for specimens and data used. See also Figure 4.02 in Chapter 4 for a comparison of Aves to non-avian Theropoda.

Discriminant Analyses Results of Distal Tarsometatarsus Data

Discriminant analysis on all data (shorebirds, large waders, gulls, gamebirds, birds of prey) shows that taxa separate based on ecology: birds of prey and *Larus* separate from small shorebirds, large wading birds, and phasianids (Fig. 6.07).

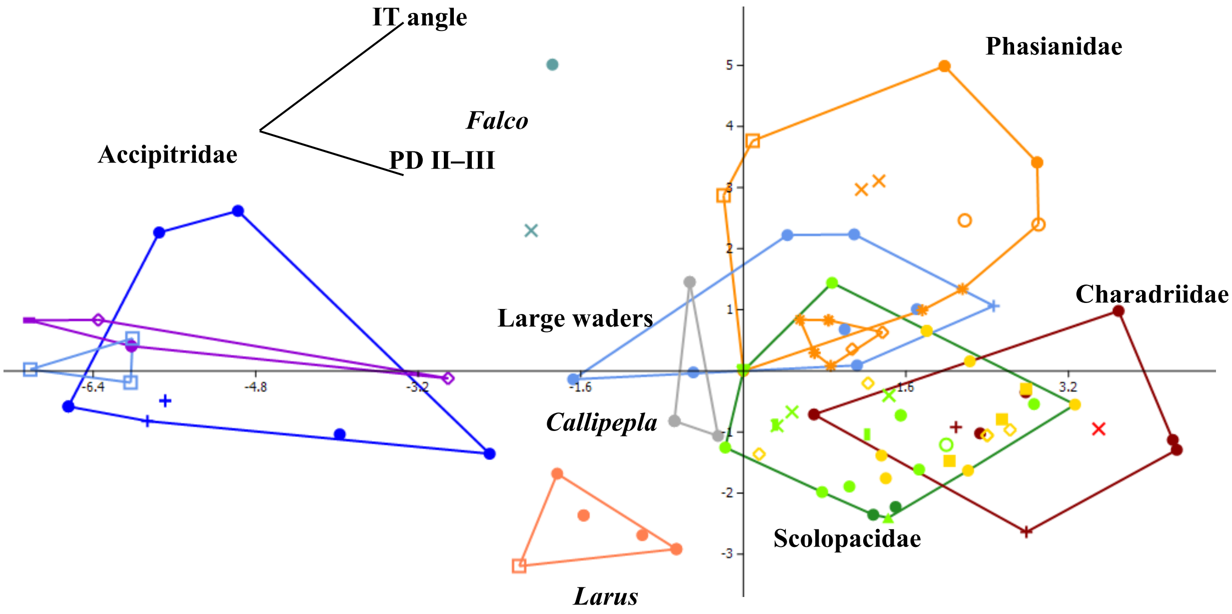

Figure 6.07. Discriminant analysis plot of birds of prey (*Accipiter*, *Buteo*, *Falco*), large wading birds (*Ardea*, *Ciconia*, *Grus*), Charadriidae (*Charadrius*, *Pluvialis*), gamebirds (*Bonasa*, *Callipepla*, *Dendragapus*, *Falcipennis*, *Lagopus*, *Parapavo*), gulls (*Larus*), and Scolopacidae (*Actitis*, *Calidris*, *Tringa*). Taxa are separated by the size of both the intertrochlear notch splay (IT angle) and plantar rotation (PD) (Tables 6.08–6.09). The lack of plantar rotation and intertrochlear notch splay in traditional Falconiformes has the effect of "pushing" the taxa with larger intertrochlear notch size and greater plantar rotation, particularly of the trochlear surface of distal metatarsal II, to the right of the plot.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**	**Axis 6**	**Axis 7**	**Axis 8**	**Axis 9**	**Axis 10**
PDII-III	3.68	-2.30	0.747	0.563	5.34×10^{-242}	4.15×10^{-313}	0	-0.515	3.51	-1.37
PDIII-IV	0.768	1.75	2.61	-2.44	6.84×10^{-242}	3.57×10^{-313}	0	-5.42	-3.09	-4.31
ITII-III	3.50	1.69	-3.44	-2.75	5.98×10^{-242}	5.08×10^{-313}	0	1.11	4.42	4.91
ITIII-IV	1.00	2.85	1.81	1.22	5.23×10^{-242}	6.27×10^{-313}	0	11.1	2.55	9.15

Table 6.08. Discriminant loadings for tarsometatarsus torsion of all analyzed specimens of taxa in Figure 6.06. See Appendix 6 for taxa and data used.

	Accipitrid	*Ardea*	*Buteo*	*Callipepla*	Charadriid	Falconid	*Grus*	*Larus*	*Parapavo*	Phasianid	Scolopacid
Accipitrid		0.93	0.98	0.49	0.03	0.93	0.58	0.14	0.41	0.17	0.01
Ardea	0.93		0.91	0.90	0.39	fail	0.99	0.54	0.92	0.95	0.20
Buteo	0.98	0.91		0.45	0.05	1.0	0.44	0.18	0.33	0.16	0.01
Callipepla	0.49	0.90	0.45		1.0	0.57	1.0	0.87	1.0	1.0	0.73
Charadriid	0.03	0.39	0.05	1.0		0.17	1.0	1.0	0.60	0.09	0.75
Falconid	0.93	fail	1.0	0.57	0.17		0.43	0.33	0.50	0.35	0.04
Grus	0.58	0.99	0.44	1.0	1.0	0.43		0.81	1.0	1	1.0
Larus	0.14	0.54	0.18	0.87	1.0	0.33	0.81		1.0	0.30	1.0
Parapavo	0.41	0.92	0.33	1.0	0.60	0.50	1.0	1.0		0.70	0.77
Phasianid	0.17	0.95	0.16	1.0	0.09	0.35	1.0	0.30	0.70		0.02
Scolopacid	0.01	0.20	0.01	0.73	0.75	0.04	1.0	1.0	0.77	0.02	

Table 6.09. Hotelling's t^2 values of family level groupings analyzed in Figure 6.06 (Appendix 6).

To examine whether convergence in foot morphology masks the taxonomic classification of birds of similar ecomorphotypes (ecological groupings of Falk et al. 2011), birds of prey, and herons and storks, *Ardea* and *Ciconia*, were removed from the analysis (herons and storks were initially included, but their relatively smaller intertrochlear notches and plantar displacement caused the analyses to react the same as including birds of prey in the initial analysis, Table 6.10–6.11, Fig. 6.08). *Larus* does not overlap with any of the Charadriiformes. Small phasianids are separated from shorebirds along the III–IV size axis: phasianids have a larger III–IV splay than Charadriiformes. Scolopacidae and Charadriidae do overlap, but are separated along the II–III size axis, with Charadriidae possessing a relatively larger metatarsal II trochlear torsion than similarly-sized Scolopacidae.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**
PDII-III	-1.32	2.89	1.40	-1.57	2.13×10^{-251}
PDIII-IV	1.39	1.24	1.37	3.45	3.05×10^{-251}
ITII-III	3.02	3.68	-3.70	-0.17	3.66×10^{-251}
ITIII-IV	2.63	-0.11	2.66	0.22	2.34×10^{-251}

Table 6.10. Discriminant loadings of Charadriidae (*Charadrius*, *Pluvialis*), *Grus*, *Larus*, Phasianidae (*Bonasa*, *Callipepla*, *Dendragapus*, *Falcipennis*, *Lagopus, Parapavo*), and Scolopacidae (*Actitis*, *Calidris*, *Tringa*). . Charadriidae, while displaying a large amount of overlap with Scolopacidae, separate from the scolopacids by a relatively larger plantar displacement of the trochlea of distal metatarsal II. *Larus*, a genus with palmate digits, forms a distinct group from other Charadriiformes and from Galliformes.

	Callipepla	**Charadriidae**	***Grus***	***Larus***	***Parapavo***	**Phasianidae**	**Scolopacidae**
Callipepla		0	0.94	0	0.32	0	0
Charadriidae	0		0	0.02	0	0	7.9×10^{-04}
Grus	0.94	0		0	0.02	0	0
Larus	0	0.02	0		0	0	1.0
Parapavo	0.32	0	0.02	0		0	0
Phasianidae	0	0	0	0	0		0
Scolopacidae	0	7.9×10^{-04}	0	1.0	0	0	

Table 6.11. Hotelling's t^2 of Charadriidae (*Charadrius*, *Pluvialis*), *Grus*, *Larus*, Phasianidae (*Bonasa*, *Callipepla*, *Dendragapus*, *Falcipennis*, *Lagopus*, *Parapavo*), and Scolopacidae (*Actitis*, *Calidris*, *Tringa*).

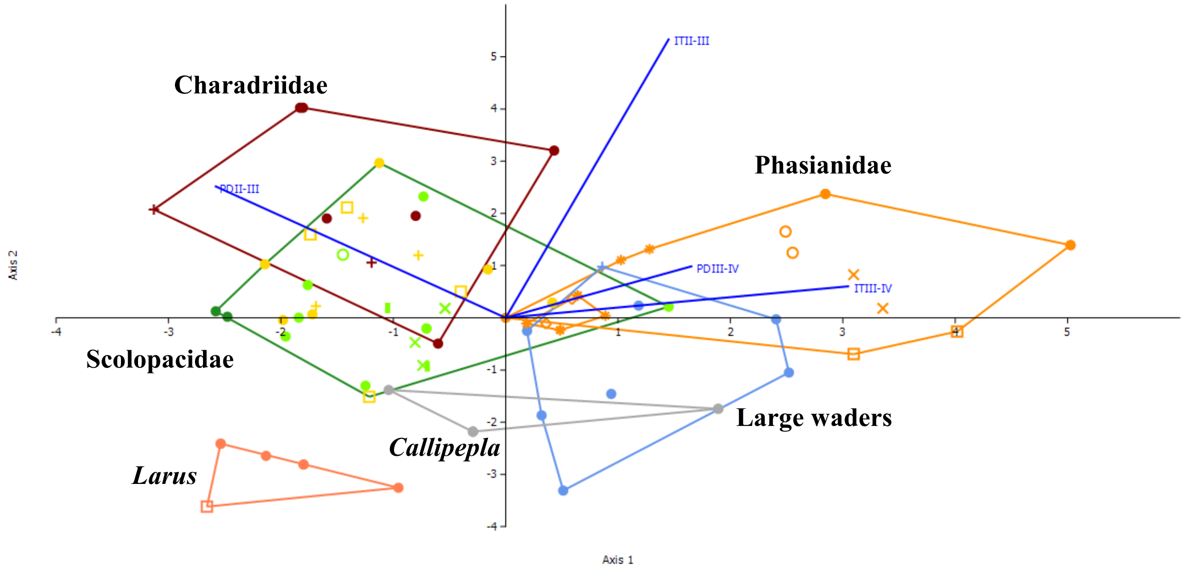

Figure 6.08. Discriminant graph of Charadriidae (*Charadrius*, *Pluvialis*), *Grus*, *Larus* Phasianidae (*Bonasa*, *Callipepla*, *Dendragapus*, *Falcipennis*, *Lagopus*, *Parapavo*), and Scolopacidae (*Actitis*, *Calidris*, *Tringa*). *Larus*, a palmate charadriiform, forms a discrete group from other Charadriiformes, large wading birds, and gamebirds. Although there is overlap between Charadriidae and Scolopacidae, Charadriidae separates from Scolopacidae by a relatively greater displacement of the distal end metatarsal II from the long-axis of the tarsometatarsus. See shorebird-only analysis in Table 6.12.

	Actitis	***Caladris***	***Charadrius***	***Tringa***
Actitis		**0.192**	**0.295**	**0.307**
Calidris	**0.192**		**0.014**	**4.80×10^{-04}**
Charadrius	**0.295**	**0.014**		**0.023**
Tringa	**0.307**	**4.80×10^{-04}**	**0.023**	

Table 6.12. Hotelling's t^2 values comparing *Charadrius* (Charadriidae) to *Actitis*, *Calidris*, and *Tringa* (Scolopacidae). *Charadrius* is significantly different from all scolopacids with the exception of *Actitis*.

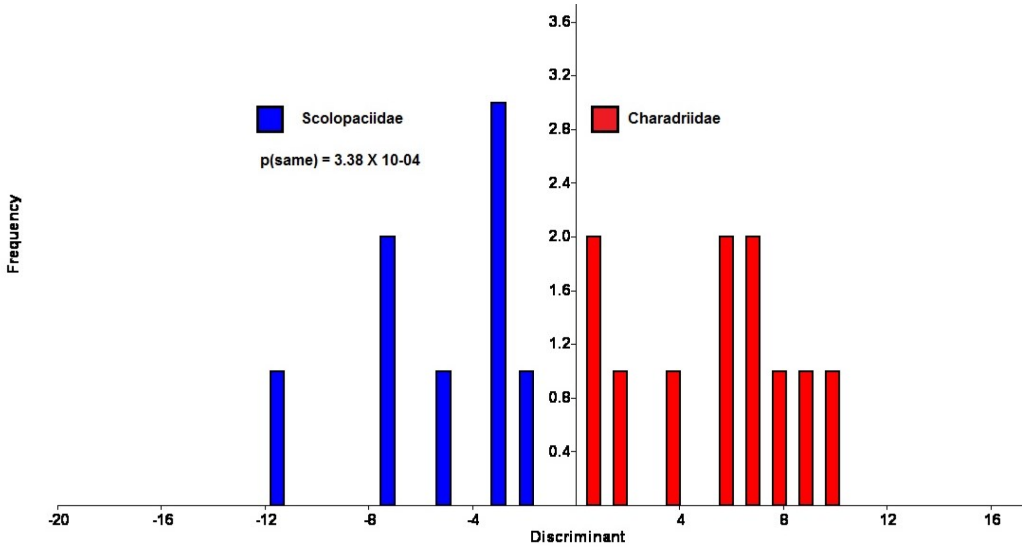

Figure 6.09. Discriminant analysis graphical results comparing intertrochlear angle (IT) and plantar displacement angle (PD) data collected on the distal tarsometatarsii of extant Charadriidae (*Charadrius vociferus*, *Charadrius semipalmatus*) and Scolopacidae (*Actitis macularia*, *Calidris alba*, *Calidris melanotos*). Charadriidae and Scolopaciidae are significantly different ($p_{\text{same}} = 3.38 \times 10^{-04}$), and there was 100% correct identification of each specimen to its *a priori* grouping of either Charadriidae or Scolopaciidae. The arrangement of the distal tarsometatarsus appears to correlate the larger digit divarication II–III seen in the measured Charadriidae as compared to the measured Scolopaciidae.

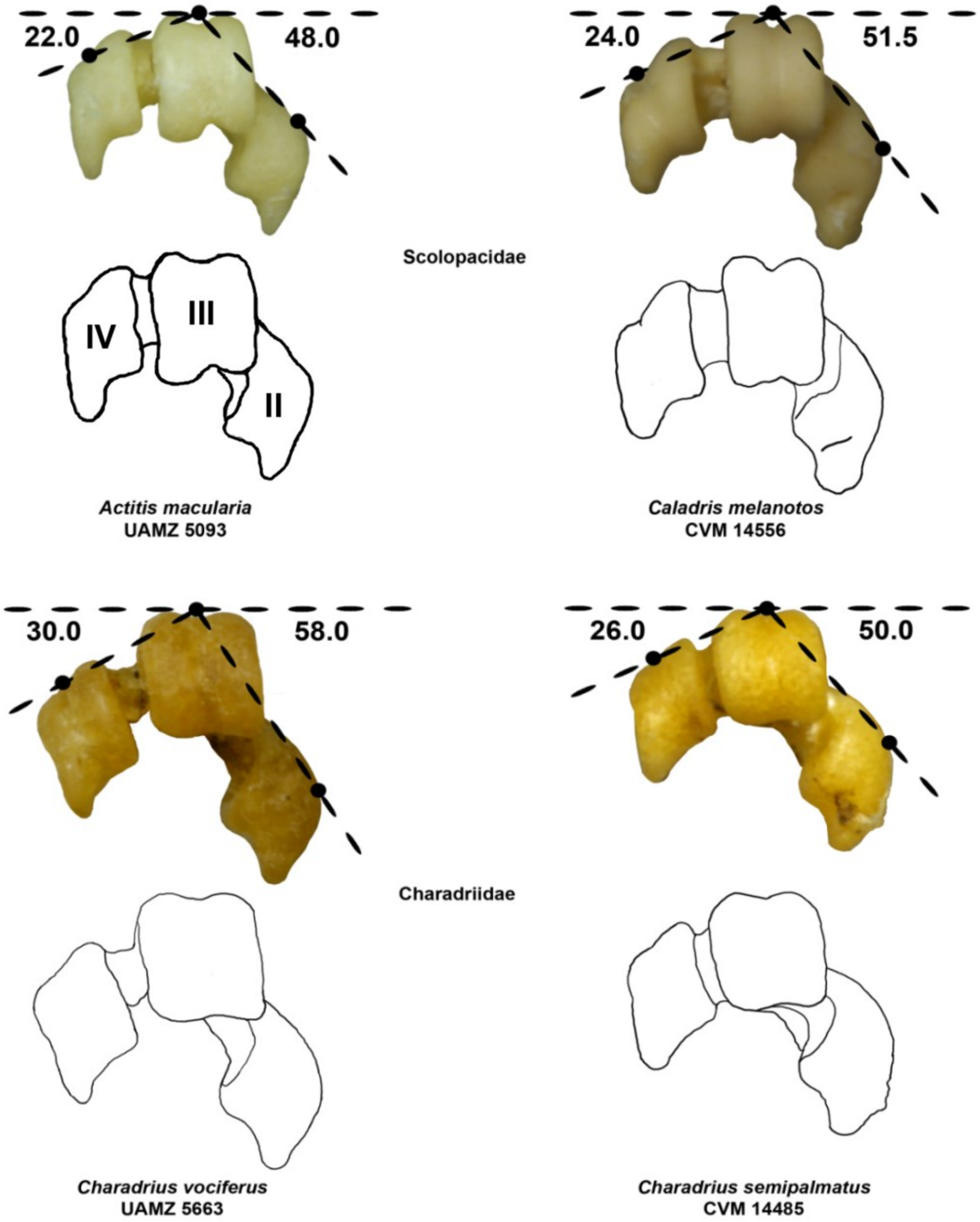

Figure 6.10. Trochlear torsion in Scolopacidae (top) and Charadriidae (bottom). Although of similar habitats, Charadriidae have a significantly greater trochlear torsion than Scolopacidae. This is a character that was demonstrated to be a useful in phylogenetic analyses (Chapter 3).

DISCUSSION AND CONCLUSIONS

Osteology and Footprint Morphology

Although the sample size for Chapter 6 is small, there is an indication that some ichnological features, such as digit divarication, are the direct result of osteologic characteristics (see Falk et al., 2011 for ecomorphologic groupings.) Furthermore, the osteologic characters (i.e. intertrochlear angle and intertrochlear notch size) that result in ichnological differences may correlate to systematic differences. Intertrochlear angle II–III is much larger compared to intertrochlear angle III–IV in the specimens of Charadriidae (plovers) than in Scolopacidae (sandpipers). When considering the potential trackmakers for *Paxavipes babcockensis* (McCrea et al., 2015), the footprint shape of *Paxavipes* is similar to that of extant charadriids. While the results do not suggest that the track-makers of *Paxavipes babcockensis* were Early Cretaceous charadriids (Baker et al., 2007 show through multigene Bayesian analysis that Charadriidae diverged during the Late Cretaceous), the results suggest that the morphology of the distal tarsometatarsus of the Early Cretaceous shorebird track-maker of *Paxavipes babcockensis* can be predicted to be similar to that seen in extant plovers.

Distal Tarsometatarsal Morphology and Synapomorphy-Based Identification of Avian and Non-Avian Theropod Footprints

There is potential to establish a new synapomorphy-based character to aid in the differentiation of avian from non-avian theropod footprints. Chapter 4 details the plantar displacement of the medial (II) and lateral (IV) metatarsals from the midline of the tarsometarsus. While Aves displays a greater plantar displacement and rotation of the distal ends of metatarsals II and IV towards the midline of the tarsometatarsus, there is a great deal of convergence in size in the distal metatarsal morphology of large avians (i.e. *Dromaius*) and that of non-avian theropods. However, even in the distal metatarsals of large avians, whereas there is little plantar displacement of the lateral metatarsals, there is still greater trochlear torsion towards the midline of the tarometatarsus.

The Aves-only analyses conducted in this chapter also shows that the distal tarsometatarsi of birds that spend much time on the ground (shorebirds, wading birds, gamebirds) are also subject to ecological convergence. However, ecological convergence does not mask systematic signals separating several groups: Charadriidae and Scolopacidae overlap but are significantly different in trochlear torsion data (Fig. 6.10). *Tringa solitaria*, a shorebird that utilizes trees for display and nesting, does not group separately from other species of *Tringa* or from other Scolopacidae. Conversely, larger wading birds, such as storks, that utilize trees for roosting, have a distal tarsometatarsus that exhibits little trochlear torsion, similar to that of birds of prey. Given the correlation between the greater trochlear torsion of metatarsal II in Charadriidae and the greater digit II–III than digit III–IV divarication seen in the footprints of Charadriidae, there is potential for trochlear torsion to be used as a synapomorphy-based character to distinguish among footprints of Aves. There is also potential, with more analyses, to incorporate relative differences in digit divarication as a synapomorphy-based character to distinguish avian footprints from those of non-avian theropod footprints. Together with the footprint/pace length ratio that separates trackways of large avians from those of small non-avian theropods, there are systematically useful characters of the hindlimbs and the pes that, to date, have been under-utilized and under-examined. These initial results on the correlation of pedal osteology, ichnology, and systematics in extant shorebirds and their implications for Cretaceous avian ichnotaxonomy will be the basis for my postgraduate work.

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CHAPTER 7

CONCLUSION

Correlation Between Biological and Morphological Species Concepts

Morphologic Convergence and Evolutionary History—There is little debate that morphologic convergence has a large effect on classifications of both extant and extinct avians. The best example is the continued debate regarding the classification of the traditional Falconiformes (*Accipiter*, *Buteo*, *Falco*), and its relationship with Ciconiiformes (morphologic). Morphologic analyses place Ciconiiformes with Accipitridae, whereas molecular analyses (Jarvis et al., 2015) show a paraphyly of traditional Falconiformes, with *Falco* closer to Psittaciformes than Accipitridae. The example of Falconiformes demonstrates an issue with correlating species recognition concepts in terms of determining the evolutionary relationships of the species in question: morphology, such as the apparent absence of intermediate hypotarsal ridges, with only cristae hypotarsali medialis et lateralis present in the species of both traditional Falconiformes and Ciconiiformes examined herein, and recovered by many morphologic phylogenetic analyses (Ligon, 1967; Mayr 2005) may support an evolutionary relationship (even in unweighted, unordered character states) that is contradicted by molecular studies of the same taxa (*Falco* closest to Psittaciformes; Jarvis et al., 2014).

As demonstrated in the cladistics analysis herein, morphologic phylogenetic analyses of a restricted sample of vertebrate fauna (in this case, birds) reproduces evolutionary hypotheses that are contradictory to results of previous, larger, morphologicstudies, and also contradictory to the classifications of the study taxa using soft-tissue morphology (coloration, vocalization, behavior, etc.): *Calidris* was not recovered as a monophyletic group, and the fossil (Pleistocene) tarsometatarsi of *Tringa melanoleuca* did not group with exant *T. melanoleuca*.

The approach of Silcox (2012) is the most practical for researchers working with fossil material: it is not practical to apply a biological species concept based on soft-tissue data to a morphological species concept that utilizes hard-tissue data. One cannot simply assume that osteological species groupings correlate 100% to those species-level groupings that are biology-based (Benton and Pearson, 2001): morphologic species groupings will not perfectly reflect the biologic diversity of a paleoecosystem. However, the lack of congruence between the morphologic and molecular phylogenies does become problematic in determining the most accurate hypotheses for evolutionary relationships. In the cladistic analyses herein, the shallow nodes had strong support, while the support for the deeper nodes was weak. In other words, the most "recent" morphologic divergences of genus- and species-level groupings may correlate with biologic/molecular systematics, but the evolutionary relationships of the higher level taxonomic groupings remain unclear.

Ecological Convergence—There is a degree to which morphologic convergence can mask the evolutionary history of the genetic heritage of study organisms. However, working with fossil organisms (and their traces) that have extant relatives can provide vertebrate paleontologists with valuable and abundant data on the effects of morphologic convergence due to shared ecological niches. Fossil Aves have extant representatives that frequent similar ecological niches similar to those of their fossil relatives. Extant Aves (specifically small shorebirds, large wading birds, and gamebirds) and the environments in which they are found serve as a "living laboratory" where vertebrate paleontologists and vertebrate ichnologists can test hypotheses of environmental (and preservational) influences on the recovery of accurate paleocommunity reconstructions.

Vertebrate ichnology, a parataxonomy classifying the behavioral traces of organisms, focuses on specific elements of vertebrate anatomy (distal appendicular elements) that frequently come into contact with the environment. One would expect that these elements, the phalanges and tarsometatarsi, should be heavily modified by convergence, and that the modification of the morphology of the pes due to convergence would remove the possibility of accurately documenting the avian (paleo)fauna of a study area. This was seen in the topology of the cladogram constructed from tarsometatari data, where the morphology of the hypotarsal ridges resulted in the monophyletic group of Accipitridae and Ciconiidae, repeating the results of previous cladistic analyses on avian skeletons (Mayr and Clarke, 2003). However, one must be cautious in becoming overly reliant on the assumption that convergence masks biologic or morphologic diversity: this assumption results in avoiding investigation of characters that can improve our understanding of vertebrate diversity as preserved in ichnofossils. A detailed examination of foot morphology in extant shorebirds (Buckley et al., 2015, Chapters 2, 4) demonstrates that there are character states of the trochlea of the distal tarsometatarsi that correspond with the family-level groupings of Accipitridae, Charadriidae, and Phasianidae (Chapter 3). The degree of plantar rotation and displacement of the trochlea of the medial (II) and lateral (IV) metatarsals and its ability to differentiate among Accipitridae, Charadriidae, and Phasianidae is also shown to be significant. For example, the relatively greater plantar displacement of the distal end of metatarsal II in extant plovers compared to extant scolopacids is a morphology that correlates with the familial level taxonomy within Charadriiformes (Chapter 6). Also, there are potential character states of the distal tarsometatarsus, specifically the plantar rotation and displacement of the trochlea of the medial (II) and lateral (IV) metatarsals that may prove to be an avian synapomorphy. This potential synapomorphy could be used as another synapomorphy-based feature used to separate avian traces from those of similarly sized non-avian theropods (Chapters 4, 6).

Testing the hypothesis that *Wupus agilis* may be the trace of a large wading avian, rather than the trace of a small non-avian theropod, revealed that a suite of ichnology characters, particularly the relative footprint length:pace length ratio, can be used to differentiate avian from non-avian theropod traces in the absence of impressed avian synapomorphies. Improved identification of large avian traces aids in recognizing the presence of large avian trackmaking taxa from localities where corresponding skeletal material is currently not known (Chapters 5–6). Within extinct and extant Aves, there are observed differences in digit splay and arrangement that have a strong correlation with the skeletal morphology of the trackmaker's foot, specifically the morphology and relative positioning of the trochlea of the distal tarsometatarsus. Charadriidae possess footprints with a significantly higher digit II–III angle than a digit III–IV angle (Charadriidae), as well as a significantly greater plantar displacement of the trochlea of metatarsal II than seen in Scolopacidae. In shorebirds with no significant difference in digit splay (Scolopacidae) the planter displacement of the metararsal II trochlea is smaller than in Charadriidae. This observation can also be extended to the Mesozoic avian ichnological record: we can hypothesize that the morphology of the distal tarsometatarus of the trackmakers of *Paxavipes* and *Barrosopus*, which also possess a significantly higher digit II–III angle than a digit III–IV angle, is similar to the condition observed in Charadriidae (Chapter 6).

Skeletal differences between the pes of biologic family-level groupings of extant shorebirds correlates with what would be interpreted as ichnogeneric- or ichnospecific-level differences in vertebrate ichnotaxonomy were these traces to be found in the fossil record. As the most complete record for Mesozoic avians in North America and other parts of Laurasia is from trace fossils, and it will only serve to improve understanding of the paleobiodiversity of Mesozoic avians and their relatives if the ichnological record examined in detail, and if possible congruences between ichnomorphology and osteomorphology are examined. Future work will focus on determining if the ichnogeneric diversity observed in the traces of Mesozoic avian trace fossils can serve as a proxy for hypothesizing the familial-level diversity of proposed trackmakers, prior to the discovery of their body fossils. While this and many other studies have demonstrated the evolutionary history of morphologic characters may not correlate with the evolutionary history of the genetic framework, it is possible to increase the correlation between morphologic-based taxonomy and ichnotaxonomy for extinct Aves. This will involve the continued study of the morphology of the pes of extant Aves and their resultant traces.

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APPENDICES

Appendix for Chapter 3: Appendix 3, Character Matrix.

Character	1	2	3	4	5	6
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	2	2	3	5	2	2
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	2	2	1	4	2	1
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	2	5	2	3	3	2
Actitis macularia	2	2	2	4	2	2
Calidris pusilla	2	2	2	5	2	2
Calidris alba	1	2	2	6	2	1
Calidris minutilla	2	2	2	4	1	1
Tringa flavipes	2	2	2	5	2	1
Tringa melanoleuca	2	2	2	5	1	3
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	2	2	2	2	1	3
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	2	4	1	2	2	2
Charadrius vociferus	2	4	1	2	2	2
Ardea herodias Pleist	2	4	3	3	3	2
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	?	?	?	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	5	2	1	1	3	3
Accipiter striatus	5	1	1	1	3	3
Falco mexicanus	5	3	2	2	4	3
Falco perigrinus	5	3	2	2	4	3
Buteo platypterus	5	3	2	2	3	3
Buteo jamaicensis	5	1	2	2	3	3
Buteo regalis	5	?	?	?	3	3
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	4	3	3	2	3	1
Callipepla californicus Pleist	?	?	?	?	?	?
Bonasa umbellus	4	3	3	1	2	1
Falcipennis canadensis	4	3	3	1	2	1
Perdix perdix	4	3	3	1	2	1
Dendragapus obscurus	4	3	3	1	2	1
Parapavo californicus PleistJ	4	?	?	?	?	?
Lagopus lagopus	4	3	3	1	2	1
Lagopus mutus	4	3	3	1	2	1
Lagopus leucurus J	?	1	4	?	1	0

Character	7	8	9	10	11	12
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	1	1	1	3	0	3
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	2	2	0	2	0	3
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	1	2	1	4	0	3
Actitis macularia	1	0	1	3	0	2
Calidris pusilla	3	0	1	3	0	3
Calidris alba	3	0	1	3	0	3
Calidris minutilla	3	1	1	3	0	3
Tringa flavipes	3	0	1	3	1	3
Tringa melanoleuca	1	1	1	3	0	3
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	3	1	1	3	1	3
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	1	0	1	3	0	3
Charadrius vociferus	2	1	1	3	0	3
Ardea herodias Pleist	2	2	2	2	0	2
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	?	?	?	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	1	2	1	2	0	2
Accipiter striatus	1	3	1	2	0	2
Falco mexicanus	2	1	1	2	0	4
Falco perigrinus	2	1	1	2	0	4
Buteo platypterus	1	0	1	2	0	3
Buteo jamaicensis	1	1	1	2	0	2
Buteo regalis	1	?	1	2	0	3
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	2	2	1	3	0	1
Callipepla californicus Pleist	?	?	?	?	?	?
Bonasa umbellus	1	0	1	3	0	2
Falcipennis canadensis	2	3	1	3	0	2
Perdix perdix	2	1	1	3	0	2
Dendragapus obscurus	2	1	1	3	0	2
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	3	1	3	0	2
Lagopus mutus	2	0	1	3	0	2
Lagopus leucurus J	0	0	0	1	0	1

Character	13	14	15	16	17	18
Hypothetical ancestor	0	1	0	0	2	2
Limnodromus griseus	4	2	0	1	3	1
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	1	3	2	1	2	2
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	5	2	2	2	1	1
Actitis macularia	4	2	0	1	2	3
Calidris pusilla	4	2	0	1	2	1
Calidris alba	4	0	1	1	1	1
Calidris minutilla	4	0	0	0	1	1
Tringa flavipes	5	2	2	1	2	1
Tringa melanoleuca	5	3	1	1	3	1
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	5	1	1	2	2	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	4	2	0	1	3	3
Charadrius vociferus	4	2	0	1	3	3
Ardea herodias Pleist	1	1	1	2	3	3
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	?	?	?	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	6	3	2	2	2	2
Accipiter striatus	6	3	2	2	2	1
Falco mexicanus	3	3	2	2	1	0
Falco perigrinus	3	2	2	2	2	2
Buteo platypterus	6	3	2	2	4	3
Buteo jamaicensis	6	2	2	2	2	2
Buteo regalis	6	?	2	2	?	?
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	5	2	2	2	2	2
Callipepla californicus Pleist	?	?	?	?	?	?
Bonasa umbellus	2	2	2	3	1	1
Falcipennis canadensis	2	3	2	3	2	2
Perdix perdix	2	3	2	3	2	2
Dendragapus obscurus	2	3	2	3	2	2
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	3	2	2	2	2
Lagopus mutus	2	2	2	2	1	1
Lagopus leucurus J	0	0	2	2	2	2

Character	19	20	21	22	23	24
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	3	1	0	0	0	1
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	4	0	0	0	0	3
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	3	0	0	0	1	3
Actitis macularia	3	0	0	0	0	1
Calidris pusilla	3	2	0	0	0	1
Calidris alba	3	2	0	0	0	1
Calidris minutilla	3	1	0	0	0	1
Tringa flavipes	3	1	0	0	0	2
Tringa melanoleuca	3	0	0	0	0	1
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	3	1	0	0	0	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	3	2	0	0	0	1
Charadrius vociferus	3	1	0	0	0	1
Ardea herodias Pleist	4	0	0	?	0	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	?	?	?	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	4	1	0	0	1	1
Accipiter striatus	4	1	0	0	1	1
Falco mexicanus	4	1	0	0	1	5
Falco perigrinus	4	1	0	0	1	5
Buteo platypterus	4	1	0	0	1	5
Buteo jamaicensis	4	1	0	1	1	5
Buteo regalis	4	1	0	0	1	5
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	3	3	1	0	0	5
Callipepla californicus Pleist	?	?	?	?	?	?
Bonasa umbellus	3	0	0	0	0	2
Falcipennis canadensis	3	5	0	0	0	2
Perdix perdix	3	1	0	0	0	2
Dendragapus obscurus	3	5	0	0	0	2
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	3	5	0	0	0	2
Lagopus mutus	3	5	0	0	0	2
Lagopus leucurus J	1	0	5	0	0	0

Character	25	26	27	28	29	30
Hypothetical ancestor	0	0	0	0	0	1
Limnodromus griseus	5	1	2	0	0	1
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	5	1	2	0	0	1
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	4	2	2	0	1	1
Actitis macularia	4	2	2	0	0	1
Calidris pusilla	4	1	1	0	0	2
Calidris alba	4	1	1	0	0	1
Calidris minutilla	4	1	2	0	0	1
Tringa flavipes	5	2	2	0	0	1
Tringa melanoleuca	5	2	1	0	0	2
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	5	1	2	0	0	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	4	2	2	0	0	1
Charadrius vociferus	4	2	2	0	0	1
Ardea herodias Pleist	?	?	?	?	?	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	?	?	?	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	1	1	3	0	2	1
Accipiter striatus	1	1	3	0	2	1
Falco mexicanus	2	3	3	0	2	1
Falco perigrinus	3	3	3	0	2	1
Buteo platypterus	3	2	3	0	1	1
Buteo jamaicensis	3	3	3	0	1	1
Buteo regalis	3	3	3	0	1	?
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	1	0	1	0	1	1
Callipepla californicus Pleist	?	?	?	?	?	?
Bonasa umbellus	3	1	2	1	1	2
Falcipennis canadensis	3	1	2	1	2	1
Perdix perdix	3	2	2	0	1	1
Dendragapus obscurus	3	1	2	0	0	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	1	2	0	0	1
Lagopus mutus	2	1	2	0	0	1
Lagopus leucurus J	0	4	?	?	?	?

Character	31	32	33	34	35	36
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	3	3	3	2	0	2
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	1	2	3	2	0	2
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	3	2	4	2	0	2
Actitis macularia	3	2	3	2	0	2
Calidris pusilla	3	1	1	2	0	2
Calidris alba	3	1	3	2	0	2
Calidris minutilla	3	1	0	2	0	2
Tringa flavipes	3	2	3	2	0	2
Tringa melanoleuca	3	2	3	2	0	2
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	3	2	2	2	0	2
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	3	2	2	2	0	2
Charadrius vociferus	3	2	2	2	0	2
Ardea herodias Pleist	?	?	?	?	?	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	?	?	?	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	2	4	5	3	0	1
Accipiter striatus	1	4	5	3	0	1
Falco mexicanus	2	4	7	3	0	2
Falco perigrinus	2	4	7	3	0	2
Buteo platypterus	3	3	6	2	0	2
Buteo jamaicensis	3	3	7	2	0	2
Buteo regalis	3	3	7	1	0	2
Parapavo californicus PleistM	?	?	?	1	?	?
Parapavo californicus PleistF	1	1	1	1	1	1
Callipepla californicus Pleist	?	?	?	?	?	?
Bonasa umbellus	1	2	2	2	1	0
Falcipennis canadensis	1	5	2	1	1	1
Perdix perdix	0	3	6	2	1	0
Dendragapus obscurus	1	3	6	2	1	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	1	3	6	1	1	0
Lagopus mutus	1	3	6	1	1	0
Lagopus leucurus J	?	?	?	?	?	1

Character	37	38	39	40	41	42
Hypothetical ancestor	?	0	0	0	0	0
Limnodromus griseus	2	0	2	1	2	2
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	0	1	2	2	1	1
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	2	?	2	0	2	1
Actitis macularia	?	?	2	1	1	2
Calidris pusilla	0	0	2	0	1	2
Calidris alba	?	0	2	0	0	2
Calidris minutilla	?	0	2	0	0	1
Tringa flavipes	?	0	2	1	0	1
Tringa melanoleuca	2	0	2	1	1	2
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	?	0	2	1	0	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	?	0	2	1	1	2
Charadrius vociferus	1	0	2	1	2	2
Ardea herodias Pleist	?	?	2	1	2	2
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	?	?	2	1	2	1
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	?	?	2	1	2	1
Accipiter striatus	0	0	2	1	2	1
Falco mexicanus	?	?	2	0	2	1
Falco perigrinus	1	2	2	0	1	2
Buteo platypterus	2	1	2	1	2	2
Buteo jamaicensis	0	2	2	1	2	1
Buteo regalis	?	?	2	1	?	?
Parapavo californicus PleistM	?	?	3	1	1	2
Parapavo californicus PleistF	1	2	3	1	1	1
Callipepla californicus Pleist	?	?	3	2	1	2
Bonasa umbellus	2	1	3	2	2	2
Falcipennis canadensis	1	1	3	2	2	2
Perdix perdix	1	2	3	2	2	2
Dendragapus obscurus	1	2	3	2	2	2
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	1	1	3	2	2	2
Lagopus mutus	?	?	3	2	2	2
Lagopus leucurus J	0	?	?	?	?	?

Character	43	44	45	46	47	48
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	1	3	3	1	1	0
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	2	3	3	1	3	1
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	4	2	3	2	2	0
Actitis macularia	4	3	2	1	3	0
Calidris pusilla	1	1	5	1	1	0
Calidris alba	1	3	4	1	2	0
Calidris minutilla	1	2	3	1	2	0
Tringa flavipes	1	3	4	1	2	1
Tringa melanoleuca	1	1	3	1	2	0
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	1	1	3	?	1	0
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	5	3	3	2	2	0
Charadrius vociferus	5	3	5	1	2	0
Ardea herodias Pleist	3	3	1	0	3	0
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	?	?	?	?	?	?
Grus pagei Pleist	?	?	?	?	?	?
Ciconia maltha Pleist	3	2	2	1	4	0
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	4	3	1	1	4	0
Accipiter striatus	4	3	0	0	4	0
Falco mexicanus	4	3	1	1	5	0
Falco perigrinus	4	3	1	1	5	0
Buteo platypterus	4	3	2	1	5	0
Buteo jamaicensis	4	3	2	1	5	1
Buteo regalis	5	3	2	?	5	?
Parapavo californicus PleistM	5	3	5	2	2	0
Parapavo californicus PleistF	5	3	5	2	2	0
Callipepla californicus Pleist	5	3	5	2	3	0
Bonasa umbellus	5	2	5	1	5	0
Falcipennis canadensis	4	2	3	1	5	0
Perdix perdix	4	2	5	1	4	1
Dendragapus obscurus	4	2	5	1	5	0
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	5	2	4	2	4	0
Lagopus mutus	5	2	4	2	4	0
Lagopus leucurus J	?	?	?	?	?	?

Character	49	50	51	52	53	54
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	1	1	2	1	2	1
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	0	0	2	2	2	0
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	1	1	2	1	1	1
Actitis macularia	0	0	2	1	?	2
Calidris pusilla	0	0	2	1	2	1
Calidris alba	0	0	2	1	2	1
Calidris minutilla	0	0	2	1	2	1
Tringa flavipes	0	0	2	1	1	1
Tringa melanoleuca	1	?	2	1	1	2
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	0	0	2	1	1	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	0	0	2	0	1	2
Charadrius vociferus	1	1	2	2	2	2
Ardea herodias Pleist	1	1	2	2	2	2
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	1	1	2	2	2	2
Grus pagei Pleist	?	?	2	2	2	2
Ciconia maltha Pleist	1	1	2	2	2	2
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	2	2	2	1
Accipiter cooperii	1	1	2	2	1	2
Accipiter striatus	1	1	2	2	1	2
Falco mexicanus	1	1	2	2	2	2
Falco perigrinus	1	1	2	2	2	2
Buteo platypterus	1	1	2	2	1	2
Buteo jamaicensis	1	1	2	2	2	2
Buteo regalis	?	1	?	?	?	?
Parapavo californicus PleistM	1	1	2	1	2	2
Parapavo californicus PleistF	1	1	2	1	2	1
Callipepla californicus Pleist	1	1	2	2	2	1
Bonasa umbellus	1	1	2	1	1	0
Falcipennis canadensis	1	1	2	1	2	0
Perdix perdix	1	1	2	2	2	0
Dendragapus obscurus	1	1	2	1	2	0
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	1	1	2	1	1	0
Lagopus mutus	1	1	2	0	2	0
Lagopus leucurus J	?	?	?	?	?	?

Character	55	56	57	58	59	60
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	2	1	2	2	1	3
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	1	1	2	2	1	2
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	2	1	2	2	3	2
Actitis macularia	0	1	?	?	?	?
Calidris pusilla	1	0	2	2	1	1
Calidris alba	1	1	2	2	1	1
Calidris minutilla	2	1	2	2	1	1
Tringa flavipes	2	0	2	2	1	1
Tringa melanoleuca	2	1	2	2	3	1
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	2	1	2	2	1	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	1	1	2	2	3	2
Charadrius vociferus	2	1	2	2	3	2
Ardea herodias Pleist	1	2	2	2	4	2
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	0	3	2	2	3	2
Grus pagei Pleist	0	0	2	2	?	?
Ciconia maltha Pleist	2	3	2	2	1	2
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	0	3	2	2	3	2
Accipiter cooperii	3	3	2	2	2	2
Accipiter striatus	3	2	2	2	3	1
Falco mexicanus	3	3	2	2	2	2
Falco perigrinus	1	2	2	2	3	2
Buteo platypterus	4	1	2	2	3	2
Buteo jamaicensis	1	2	2	2	1	1
Buteo regalis	?	?	?	?	?	?
Parapavo californicus PleistM	1	3	2	2	1	1
Parapavo californicus PleistF	1	1	2	2	1	1
Callipepla californicus Pleist	0	3	1	2	3	1
Bonasa umbellus	2	1	2	2	3	1
Falcipennis canadensis	1	3	2	1	1	1
Perdix perdix	0	1	1	1	1	1
Dendragapus obscurus	1	2	2	2	1	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	1	3	2	2	4	2
Lagopus mutus	2	1	2	2	1	1
Lagopus leucurus J	?	?	?	?	?	?

Character	61	62	63	64	65	66
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	0	2	2	0	0	0
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	2	2	2	0	0	0
Numenius americanus Pleist	?	?	?	?	?	?
Larus californicus	3	1	2	0	0	0
Actitis macularia	0	?	?	?	0	0
Calidris pusilla	0	0	0	0	0	0
Calidris alba	0	1	0	0	0	0
Calidris minutilla	0	0	1	0	0	0
Tringa flavipes	0	0	2	?	0	0
Tringa melanoleuca	1	1	1	0	0	0
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	0	0	1	?	0	0
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	2	1	1	0	0	0
Charadrius vociferus	1	2	1	0	0	0
Ardea herodias Pleist	3	0	3	0	0	0
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	0	1	1	0	0	0
Grus pagei Pleist	0	1	2	0	0	0
Ciconia maltha Pleist	1	1	2	2	0	0
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	0	1	2	2	?	?
Accipiter cooperii	1	2	2	0	1	0
Accipiter striatus	1	1	2	0	1	?
Falco mexicanus	3	1	2	0	1	0
Falco perigrinus	1	2	2	0	1	0
Buteo platypterus	2	2	3	0	1	?
Buteo jamaicensis	0	1	2	0	1	1
Buteo regalis	?	?	?	?	?	?
Parapavo californicus PleistM	0	1	2	0	1	0
Parapavo californicus PleistF	2	0	1	0	1	0
Callipepla californicus Pleist	0	0	3	0	0	1
Bonasa umbellus	2	1	2	0	1	?
Falcipennis canadensis	2	2	3	2	1	1
Perdix perdix	1	2	2	2	2	2
Dendragapus obscurus	2	2	3	2	1	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	0	2	3	1	2	1
Lagopus mutus	0	1	1	0	0	1
Lagopus leucurus J	?	?	?	?	?	?

Character	67	68	69	70	71	72
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	0	1	2	2	0	3
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	5	0	1	2	1	1
Numenius americanus Pleist	?	?	?	2	1	2
Larus californicus	2	1	2	1	1	3
Actitis macularia	2	?	?	1	1	3
Calidris pusilla	2	?	?	2	1	2
Calidris alba	2	?	1	2	1	2
Calidris minutilla	2	2	2	2	?	?
Tringa flavipes	1	?	?	2	1	2
Tringa melanoleuca	0	?	?	2	1	2
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	1	?	?	1	1	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	5	?	?	2	0	3
Charadrius vociferus	5	1	1	2	0	3
Ardea herodias Pleist	5	1	1	?	0	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	2	1	1	1	1	1
Grus pagei Pleist	2	1	1	2	0	0
Ciconia maltha Pleist	2	1	2	1	1	2
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	1	2	?	?	?
Accipiter cooperii	4	1	?	0	1	4
Accipiter striatus	4	?	?	1	1	4
Falco mexicanus	4	1	2	0	2	4
Falco perigrinus	4	2	1	0	1	1
Buteo platypterus	4	?	?	1	0	4
Buteo jamaicensis	4	1	2	1	1	2
Buteo regalis	4	?	?	1	?	?
Parapavo californicus PleistM	5	2	1	?	?	?
Parapavo californicus PleistF	5	1	1	?	2	2
Callipepla californicus Pleist	2	1	1	1	1	0
Bonasa umbellus	5	?	?	1	0	2
Falcipennis canadensis	5	2	1	1	1	0
Perdix perdix	5	1	1	2	1	1
Dendragapus obscurus	2	0	1	1	1	2
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	0	1	1	1	2
Lagopus mutus	2	?	?	1	1	1
Lagopus leucurus J	?	?	?	?	?	?

Character	73	74	75	76	77	78
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	0	2	1	1	2	0
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	3	1	1	1	0	1
Numenius americanus Pleist	0	1	2	0	2	0
Larus californicus	0	1	1	1	2	1
Actitis macularia	0	1	1	1	2	0
Calidris pusilla	0	2	1	1	2	1
Calidris alba	0	1	2	0	2	0
Calidris minutilla	?	2	1	?	?	?
Tringa flavipes	0	2	1	0	2	0
Tringa melanoleuca	1	1	2	0	1	0
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	0	1	0	0	2	0
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	0	1	2	1	2	0
Charadrius vociferus	0	1	2	1	2	0
Ardea herodias Pleist	?	?	?	?	?	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	0	2	2	0	1	0
Grus pagei Pleist	0	1	1	0	2	0
Ciconia maltha Pleist	1	2	2	0	0	2
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	?	?	?	?
Accipiter cooperii	0	1	1	0	2	1
Accipiter striatus	0	2	1	1	2	1
Falco mexicanus	0	3	2	1	2	2
Falco perigrinus	0	3	1	0	0	2
Buteo platypterus	1	2	2	1	2	?
Buteo jamaicensis	0	1	1	0	0	1
Buteo regalis	?	3	1	?	?	?
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	1	1	1	0	0	1
Callipepla californicus Pleist	2	2	2	0	1	2
Bonasa umbellus	0	2	2	1	2	1
Falcipennis canadensis	2	1	2	0	0	0
Perdix perdix	3	1	2	1	0	2
Dendragapus obscurus	1	1	2	2	1	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	1	2	1	1	1
Lagopus mutus	0	2	2	1	1	1
Lagopus leucurus J	?	?	?	?	?	?

Character	79	80	81	82	83	84
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	1	1	1	1	2	1
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	1	1	0	0	2	1
Numenius americanus Pleist	1	1	2	0	2	1
Larus californicus	2	2	1	0	2	1
Actitis macularia	2	0	0	0	2	0
Calidris pusilla	1	2	0	0	2	1
Calidris alba	1	1	0	0	1	1
Calidris minutilla	?	1	?	?	?	1
Tringa flavipes	1	1	1	0	2	1
Tringa melanoleuca	1	2	1	0	2	1
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	1	2	0	0	2	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	2	1	0	0	2	1
Charadrius vociferus	2	1	0	0	2	1
Ardea herodias Pleist	?	?	?	?	?	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	2	2	1	1	2	3
Grus pagei Pleist	2	2	1	0	2	3
Ciconia maltha Pleist	0	2	?	1	1	4
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	?	?	2	?	4	4
Accipiter cooperii	2	2	1	0	4	5
Accipiter striatus	2	2	1	0	4	5
Falco mexicanus	2	1	2	1	1	5
Falco perigrinus	2	1	2	0	4	5
Buteo platypterus	?	1	1	0	4	5
Buteo jamaicensis	2	2	2	2	4	5
Buteo regalis	2	1	2	1	4	5
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	1	1	1	0	0	3
Callipepla californicus Pleist	1	1	2	0	2	3
Bonasa umbellus	1	1	1	0	1	1
Falcipennis canadensis	1	1	1	1	0	1
Perdix perdix	1	2	1	2	1	1
Dendragapus obscurus	1	2	1	0	1	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	1	1	1	0	0	1
Lagopus mutus	2	1	1	0	0	1
Lagopus leucurus J	?	?	?	?	?	?

Character	85	86	87	88	89	90
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	1	0	2	2	0	0
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	3	0	1	2	0	1
Numenius americanus Pleist	3	1	3	2	0	0
Larus californicus	3	1	3	3	1	1
Actitis macularia	3	0	1	2	1	1
Calidris pusilla	3	0	1	3	0	1
Calidris alba	3	0	1	2	0	1
Calidris minutilla	1	?	1	2	0	1
Tringa flavipes	3	1	1	2	0	1
Tringa melanoleuca	3	1	1	2	1	1
Tringa melanoleuca Pleist	?	?	?	?	?	?
Tringa solitaria	3	1	1	2	0	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	3	0	1	3	0	1
Charadrius vociferus	3	0	1	3	0	1
Ardea herodias Pleist	?	?	?	?	?	?
Grus canadensis Pleist	?	?	?	?	?	?
Grus americana Pleist	4	1	?	?	3	2
Grus pagei Pleist	4	1	3	2	3	2
Ciconia maltha Pleist	1	3	3	2	3	0
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	?	?	?	?	?	?
Buteogallus daggetti Pleist	4	3	2	2	3	1
Accipiter cooperii	4	3	2	4	1	1
Accipiter striatus	4	3	2	4	1	1
Falco mexicanus	4	4	3	4	3	1
Falco perigrinus	4	4	3	4	3	1
Buteo platypterus	4	3	2	4	0	1
Buteo jamaicensis	4	3	2	4	1	1
Buteo regalis	?	3	2	4	1	1
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	2	2	3	2	3	1
Callipepla californicus Pleist	2	1	3	2	3	0
Bonasa umbellus	2	1	3	3	0	1
Falcipennis canadensis	2	3	1	2	0	1
Perdix perdix	2	4	2	2	1	1
Dendragapus obscurus	2	3	2	2	1	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	1	3	3	0	1
Lagopus mutus	2	1	3	3	0	1
Lagopus leucurus J	?	?	?	?	?	?

Character	91	92	93	94	95	96
Hypothetical ancestor	0	0	0	0	0	2
Limnodromus griseus	1	1	2	0	1	2
Limosa haemastica Pleist	?	?	?	?	?	2
Limosa fedoa	1	0	1	2	0	?
Numenius americanus Pleist	?	?	1	?	?	2
Larus californicus	1	1	2	1	0	4
Actitis macularia	2	2	1	0	1	3
Calidris pusilla	1	0	2	1	1	2
Calidris alba	1	1	1	0	1	?
Calidris minutilla	1	?	2	?	1	1
Tringa flavipes	1	2	2	1	2	2
Tringa melanoleuca	2	2	2	1	2	0
Tringa melanoleuca Pleist	?	?	?	?	?	2
Tringa solitaria	1	1	2	1	1	1
Pluvialis squatarola Pleist	?	?	?	?	?	?
Charadrius semipalmatus	1	1	2	0	2	0
Charadrius vociferus	1	2	2	0	2	2
Ardea herodias Pleist	?	?	?	?	?	0
Grus canadensis Pleist	?	?	?	?	?	2
Grus americana Pleist	1	3	?	?	1	?
Grus pagei Pleist	1	3	3	?	2	0
Ciconia maltha Pleist	2	2	1	1	2	?
Botaurus lentiginosus Pleist	?	?	?	?	?	?
Mycteria wetmorei Pleist	?	?	?	?	?	3
Amplibuteo woodwardi Pleist	?	?	?	?	?	3
Buteogallus daggetti Pleist	2	2	3	1	1	1
Accipiter cooperii	2	3	3	1	1	?
Accipiter striatus	2	3	3	2	0	?
Falco mexicanus	1	2	2	2	2	?
Falco perigrinus	1	1	2	2	2	2
Buteo platypterus	2	3	3	2	1	?
Buteo jamaicensis	2	1	3	2	1	1
Buteo regalis	1	?	3	2	1	1
Parapavo californicus PleistM	?	?	?	?	?	?
Parapavo californicus PleistF	2	0	3	2	0	?
Callipepla californicus Pleist	1	0	1	0	1	0
Bonasa umbellus	0	1	3	1	2	1
Falcipennis canadensis	1	1	3	1	2	1
Perdix perdix	1	1	2	1	2	2
Dendragapus obscurus	1	1	3	1	2	1
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	1	1	3	1	2	2
Lagopus mutus	0	2	3	1	2	2
Lagopus leucurus J	?	?	?	?	?	?

Character	97	98	99	100	101	102
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	1	0	2	2	2	1
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	2	2	2	2	2	1
Numenius americanus Pleist	1	1	2	2	?	?
Larus californicus	1	1	2	1	2	2
Actitis macularia	1	0	?	2	?	?
Calidris pusilla	1	0	2	2	2	1
Calidris alba	1	1	2	2	2	2
Calidris minutilla	?	?	2	1	2	2
Tringa flavipes	1	1	2	2	1	1
Tringa melanoleuca	1	0	2	2	3	1
Tringa melanoleuca Pleist	?	?	?	2	2	1
Tringa solitaria	2	1	2	1	2	1
Pluvialis squatarola Pleist	?	?	?	2	2	1
Charadrius semipalmatus	2	0	2	2	2	2
Charadrius vociferus	1	1	2	2	3	2
Ardea herodias Pleist	?	?	?	3	3	2
Grus canadensis Pleist	?	?	?	3	2	1
Grus americana Pleist	1	2	2	3	2	3
Grus pagei Pleist	1	2	2	3	2	3
Ciconia maltha Pleist	3	1	2	3	4	4
Botaurus lentiginosus Pleist	?	?	?	2	3	3
Mycteria wetmorei Pleist	?	?	?	3	2	4
Amplibuteo woodwardi Pleist	?	?	?	4	1	5
Buteogallus daggetti Pleist	4	1	?	4	2	5
Accipiter cooperii	2	0	1	4	2	5
Accipiter striatus	2	0	1	4	2	5
Falco mexicanus	1	0	1	4	2	5
Falco perigrinus	0	1	2	4	2	5
Buteo platypterus	2	0	1	?	?	?
Buteo jamaicensis	0	1	2	4	1	5
Buteo regalis	?	?	2	4	1	5
Parapavo californicus PleistM	?	?	?	2	2	3
Parapavo californicus PleistF	3	1	2	2	2	3
Callipepla californicus Pleist	0	0	2	2	2	3
Bonasa umbellus	1	0	2	2	2	3
Falcipennis canadensis	3	1	2	2	3	3
Perdix perdix	0	2	2	2	2	3
Dendragapus obscurus	0	1	2	2	3	3
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	0	0	2	2	3	3
Lagopus mutus	1	0	1	1	1	3
Lagopus leucurus J	?	?	?	?	?	?

Character	103	104	105	106	107	108
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	2	1	0	2	2	0
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	1	2	2	2	1	2
Numenius americanus Pleist	?	?	1	?	?	?
Larus californicus	1	2	2	2	2	2
Actitis macularia	2	2	1	2	1	2
Calidris pusilla	1	1	1	2	0	1
Calidris alba	0	2	2	2	1	2
Calidris minutilla	2	2	2	2	2	2
Tringa flavipes	2	1	2	2	1	2
Tringa melanoleuca	2	1	1	2	2	1
Tringa melanoleuca Pleist	1	1	0	2	1	2
Tringa solitaria	2	1	2	2	0	1
Pluvialis squatarola Pleist	1	2	2	2	1	2
Charadrius semipalmatus	2	2	0	2	1	2
Charadrius vociferus	2	2	2	2	1	2
Ardea herodias Pleist	2	2	1	2	2	2
Grus canadensis Pleist	2	0	1	2	2	2
Grus americana Pleist	2	0	1	2	2	1
Grus pagei Pleist	2	0	0	2	2	2
Ciconia maltha Pleist	3	1	1	1	0	1
Botaurus lentiginosus Pleist	2	1	0	2	2	2
Mycteria wetmorei Pleist	3	1	2	1	0	2
Amplibuteo woodwardi Pleist	1	1	1	1	0	1
Buteogallus daggetti Pleist	4	1	1	1	0	1
Accipiter cooperii	4	1	0	1	0	0
Accipiter striatus	4	1	1	1	0	0
Falco mexicanus	1	0	0	1	0	0
Falco perigrinus	1	0	2	1	0	1
Buteo platypterus	?	?	0	1	0	?
Buteo jamaicensis	4	0	1	1	0	1
Buteo regalis	4	2	0	1	0	1
Parapavo californicus PleistM	1	2	0	2	2	2
Parapavo californicus PleistF	1	2	1	2	2	2
Callipepla californicus Pleist	3	2	0	2	2	1
Bonasa umbellus	2	2	2	2	2	1
Falcipennis canadensis	2	2	2	2	2	2
Perdix perdix	2	2	2	2	2	2
Dendragapus obscurus	2	2	2	2	2	2
Parapavo californicus PleistJ	?	?	?	?	?	?
Lagopus lagopus	2	2	1	2	2	2
Lagopus mutus	2	2	0	2	2	2
Lagopus leucurus J	?	?	?	?	?	?

Character	109	110	111	112	113	114
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	2	1	1	1	1	2
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	2	0	2	1	2	3
Numenius americanus Pleist	?	?	?	?	2	3
Larus californicus	2	1	2	1	3	3
Actitis macularia	2	1	2	1	1	2
Calidris pusilla	2	1	1	0	1	1
Calidris alba	2	1	2	1	3	2
Calidris minutilla	2	1	1	0	2	1
Tringa flavipes	2	1	1	0	3	2
Tringa melanoleuca	2	4	2	0	2	2
Tringa melanoleuca Pleist	1	0	1	2	3	3
Tringa solitaria	2	1	1	0	2	2
Pluvialis squatarola Pleist	2	0	2	2	6	1
Charadrius semipalmatus	2	1	2	0	2	2
Charadrius vociferus	2	0	2	0	0	3
Ardea herodias Pleist	1	1	0	2	1	2
Grus canadensis Pleist	2	2	2	2	3	3
Grus americana Pleist	2	1	2	2	3	3
Grus pagei Pleist	2	1	2	2	3	2
Ciconia maltha Pleist	1	0	3	2	6	3
Botaurus lentiginosus Pleist	2	4	1	2	6	2
Mycteria wetmorei Pleist	1	0	3	2	6	3
Amplibuteo woodwardi Pleist	1	0	3	2	5	3
Buteogallus daggetti Pleist	1	0	3	2	5	3
Accipiter cooperii	2	0	3	2	3	3
Accipiter striatus	2	0	3	1	3	3
Falco mexicanus	3	0	3	2	2	3
Falco perigrinus	1	0	3	2	1	3
Buteo platypterus	?	0	3	?	5	3
Buteo jamaicensis	1	0	3	2	4	3
Buteo regalis	1	0	3	2	5	3
Parapavo californicus PleistM	3	1	2	2	3	2
Parapavo californicus PleistF	3	1	2	2	3	2
Callipepla californicus Pleist	2	4	2	2	3	3
Bonasa umbellus	3	4	2	2	4	3
Falcipennis canadensis	3	4	2	2	1	3
Perdix perdix	3	4	2	2	4	3
Dendragapus obscurus	3	4	2	2	4	3
Parapavo californicus PleistJ	?	?	?	0	0	2
Lagopus lagopus	3	4	2	2	1	2
Lagopus mutus	3	4	2	2	5	2
Lagopus leucurus J	?	?	?	?	?	2

Character	115	116	117	118	119	120
Hypothetical ancestor	0	0	0	0	0	0
Limnodromus griseus	2	2	0	1	1	2
Limosa haemastica Pleist	?	?	?	?	?	?
Limosa fedoa	1	1	1	0	2	1
Numenius americanus Pleist	2	2	0	0	2	2
Larus californicus	0	1	0	2	2	2
Actitis macularia	2	1	0	1	1	2
Calidris pusilla	2	0	0	1	1	2
Calidris alba	2	0	0	0	0	2
Calidris minutilla	2	1	0	0	0	2
Tringa flavipes	2	1	1	1	0	2
Tringa melanoleuca	1	1	0	1	1	2
Tringa melanoleuca Pleist	2	1	1	1	2	2
Tringa solitaria	2	2	1	1	1	2
Pluvialis squatarola Pleist	1	2	2	2	2	2
Charadrius semipalmatus	2	1	1	1	1	2
Charadrius vociferus	2	1	1	1	1	2
Ardea herodias Pleist	2	1	1	0	2	0
Grus canadensis Pleist	2	2	2	2	2	2
Grus americana Pleist	2	2	2	1	2	2
Grus pagei Pleist	2	2	2	1	2	2
Ciconia maltha Pleist	2	2	2	2	2	1
Botaurus lentiginosus Pleist	2	2	1	2	1	1
Mycteria wetmorei Pleist	2	?	?	?	?	?
Amplibuteo woodwardi Pleist	2	2	3	2	3	2
Buteogallus daggetti Pleist	1	2	3	2	3	2
Accipiter cooperii	2	2	3	2	3	2
Accipiter striatus	2	1	3	2	3	2
Falco mexicanus	0	2	3	2	2	2
Falco perigrinus	1	2	1	1	2	2
Buteo platypterus	?	1	3	2	3	2
Buteo jamaicensis	1	2	3	2	3	2
Buteo regalis	2	2	3	?	3	1
Parapavo californicus PleistM	2	2	1	1	1	2
Parapavo californicus PleistF	2	2	1	0	1	2
Callipepla californicus Pleist	2	2	2	2	0	1
Bonasa umbellus	2	1	1	2	0	2
Falcipennis canadensis	1	2	2	2	1	2
Perdix perdix	2	2	1	1	1	2
Dendragapus obscurus	2	2	1	1	1	2
Parapavo californicus PleistJ	1	?	0	0	1	0
Lagopus lagopus	1	2	1	1	1	2
Lagopus mutus	2	1	1	2	0	2
Lagopus leucurus J	?	?	0	0	1	0

Character	121	122	123	124	125	126	127
Hypothetical ancestor	0	0	0	0	0	0	0
Limnodromus griseus	1	2	2	2	1	2	1
Limosa haemastica Pleist	?	?	?	?	?	?	?
Limosa fedoa	1	2	2	1	3	1	2
Numenius americanus Pleist	1	1	2	1	3	2	3
Larus californicus	1	1	2	2	2	0	2
Actitis macularia	1	2	1	1	2	1	2
Calidris pusilla	1	2	0	1	1	2	2
Calidris alba	1	2	2	0	1	2	0
Calidris minutilla	1	2	2	1	1	2	1
Tringa flavipes	1	2	2	2	1	2	1
Tringa melanoleuca	1	2	1	1	1	1	2
Tringa melanoleuca Pleist	1	2	2	1	1	2	2
Tringa solitaria	1	2	0	1	1	2	2
Pluvialis squatarola Pleist	2	3	2	0	3	1	2
Charadrius semipalmatus	1	3	2	2	4	1	2
Charadrius vociferus	2	3	2	2	4	1	2
Ardea herodias Pleist	0	0	1	1	1	0	1
Grus canadensis Pleist	1	2	1	1	3	1	3
Grus americana Pleist	1	2	1	1	3	1	3
Grus pagei Pleist	1	1	1	1	3	1	3
Ciconia maltha Pleist	1	1	1	0	2	2	3
Botaurus lentiginosus Pleist	1	0	0	3	2	2	2
Mycteria wetmorei Pleist	?	?	?	?	?	?	?
Amplibuteo woodwardi Pleist	1	4	4	3	4	1	3
Buteogallus daggetti Pleist	4	4	4	4	4	2	1
Accipiter cooperii	4	4	4	4	4	2	3
Accipiter striatus	4	4	4	4	4	2	3
Falco mexicanus	4	4	4	4	2	2	3
Falco perigrinus	4	4	4	4	1	1	3
Buteo platypterus	4	4	4	4	4	2	3
Buteo jamaicensis	4	4	4	4	4	1	1
Buteo regalis	4	4	4	4	4	2	3
Parapavo californicus PleistM	1	1	3	1	4	1	2
Parapavo californicus PleistF	1	1	3	1	4	1	2
Callipepla californicus Pleist	1	2	3	1	3	0	1
Bonasa umbellus	1	2	3	2	2	1	1
Falcipennis canadensis	1	1	3	1	2	2	1
Perdix perdix	1	2	3	1	2	2	2
Dendragapus obscurus	1	1	3	1	2	2	1
Parapavo californicus PleistJ	1	1	3	1	0	0	0
Lagopus lagopus	1	1	3	1	2	2	1
Lagopus mutus	1	2	3	2	2	1	1
Lagopus leucurus J	1	1	0	0	0	0	1

Appendix for Chapter 5: Appendix A5.01, Footprint Data for Multivariate Analyses of Mesozoic Avian Ichnotaxa

Data—Data used in multivariate analyses of Mesozoic avian ichnotaxa. Data were compiled from references cited within the table. All data were standardized to fit the table presented here. Missing data are indicated by "?". Data that are not present due to morphology (i.e., no digit I) are indicated by "0". All linear measurements are in millimeters. All angle measurements are in degrees. All data are unadjusted. **DIV**, digit divarication; **DIVTOT**, digit divarication II-IV; **DL**, digit length; **DW**, digit width; **FL**, footprint length; **FLwH**, footprint length including hallux; **FR**, footprint rotation; **FW**, footprint width; **L/W**, footprint length to footprint width ratio; **P**, pace length; **PA**, pace angulation; **TW**, trackway width; **I**, digit I; **II**, digit II; **III**, digit III; **IV**, digit IV; **(H)**, holotype; (**P)**, paratype; (**T)**, topotype.

Institutional Abbreviations—CU, University of Colorado Denver, Dinosaur Tracks Museum; **DMNH**, Denver Museum of Natural History, Denver, Colorado; **FPDM**, Fukui Prefectural Dinosaur Museum, Japan; **KNUE**, Korea National University of Education, Cheongwon, Chungbuk, Korea; **KPE**, Kyungpook National University, Earth Science Education Department, Taegu, South Korea; **LRH**, Qingdao Institute of Marine Geology; **MGCM**, Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; **UCM**; University of Colorado Museum of Natural History at Boulder, Colorado; **ZMNH**, Zhejiang Natural History Museum, Zheijiang, China.

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Aquatilavipes izumiensis	Avipedidae	FPDM-V43.1	37.9	37.9	47	0.80	0	18	29.6	23.2	0	?	?	?	Azuma et al., 2002
		FPDM-V43.2	43.8	43.8	36	1.22	0	12	35.1	22.5	0	?	?	?	
		FPDM-V43.3	37.2	37.2	47	0.80	0	19	31.5	22.6	0	?	?	?	
		FPDM-V43.4	39	39	45	0.86	0	18	30.6	24.6	0	?	?	?	
		FPDM-V43.5	40.8	40.8	47	0.86	0	20	33.8	23.5	0	?	?	?	
		FPDM-V43.6	34.3	34.3	50	0.69	0	20	28.9	24.2	0	?	?	?	
		FPDM-V43.7	35.3	35.3	42	0.84	0	16	29.7	22.9	0	?	?	?	
		FPDM-V43.8	33.4	33.4	44	0.76	0	16	27.7	22.5	0	?	?	?	
		FPDM-V43.9	39.2	39.2	36	1.08	0	16	27.9	18.7	0	?	?	?	
		FPDM-V43.10	43.7	43.7	41	1.07	0	16	32.7	22.8	0	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Aquatilavipes izumiensis	Avipedidae	FPDM-V43.12	31.9	31.9	46	0.70	0	16	26.7	21.9	0	?	?	?	Azuma et al., 2002
		FPDM-V43.13	40.5	40.5	49	0.83	0	20	31.3	24.2	0	?	?	?	
		FPDM-V43.14	36.5	36.5	45	0.82	0	18	28.9	21.9	0	?	?	?	
		FPDM-V43.15	34	34	40	0.85	0	18	27.2	23	0	?	?	?	
		FPDM-V44.B1	40.5	40.5	52	0.79	0	20	30.8	22.6	0	?	?	?	
		FPDM-V44.B2	34.3	34.3	47	0.74	0	20	27.8	24.2	0	?	?	?	
Aquatilavipes swiboldae	Avipedidae	TMP 98.89.21-A	47	47	55	0.85	0	34	47	32	0	?	?	?	Currie, 1981; McCrea and Sarjeant, 2001
		TMP 98.89.21-B	44	44	57	0.77	0	42	44	38	0	?	?	?	
		TMP 98.89.21-C	42	42	33	1.27	0	32	42	30	0	?	?	?	
		TMP 98.89.21-D	32	32	37	0.86	0	25	32	27	0	?	?	?	
		TMP 98.89.21-E	31	31	43	0.72	0	23	31	24	0	?	?	?	
		TMP 98.89.21-F	35	35	35	1.00	0	26	35	26	0	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				References
							I	II	III	IV	I	II	III	IV	
Aquatilavipes swiboldae	Avipedidae	TMP 98.89.20-B	45	45	63	0.71	0	34	45	38	0	?	?	?	Currie, 1981; McCrea and Sarjeant, 2001
		TMP 98.89.20-C	33	33	45	0.73	0	24	33	33	0	?	?	?	
		TMP 98.89.20-D	?	?	49	?	0	28	?	28	0	?	?	?	
		TMP 98.89.20-E	25	25	31	0.81	0	19	25	20	0	?	?	?	
		TMP 98.89.20-F	?	?	40	?	0	?	?	?	0	?	?	?	
		TMP 98.89.20-G	?	?	?	?	0	40	?	?	0	?	?	?	
		TMP 90.30.1-A	40	40	55	0.73	0	33	40	27	0	?	?	?	
		TMP 90.30.1-B	37	37	57	0.65	0	26	37	35	0	?	?	?	
		TMP 90.30.1-C	41	41	55	0.75	0	29	41	32	0	?	?	?	
		TMP 79.23.3-	38	38	47	0.81	0	22	34	24	0	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				References
							I	II	III	IV	I	II	III	IV	
Hwangsanipes choughi	Ignotornidae	KPE50101-A38	50	?	?	?	?	?	50	?	?	?	?	?	Yang et al., 1995
		KPE50101-A39	?	?	61	?	?	?	?	?	?	?	?	?	
		KPE50101-A40	48	?	66	0.73	?	?	48	?	?	?	?	?	
		KPE50101-A41	48	?	62	0.77	?	?	48	?	?	?	?	?	
Ignotornis mcconnelli	Ignotornidae	Average	40	?	50	?	11	40	?	?	?	?	?	?	Lockley et al., 2009
		(H)-UCM17614-1.1	39	59	51	0.76	20	?	39	?	?	?	?	?	
		(H)-UCM17614-1.2	40	57	50	0.80	17	?	40	?	?	?	?	?	
		(H)-UCM17614-1.3	37	51	52	0.71	14	?	37	?	?	?	?	?	
		(H)-UCM17614-1.4	40	56	47	0.85	16	?	40	?	?	?	?	?	
		(H)-UCM17614-1.5	40	53	49	0.82	13	?	40	?	?	?	?	?	
		(H)-UCM17614-1.6	?	?	46	?	?	?	?	?	?	?	?	?	
		(P1)-UCM98120-2.1	45	63	52	0.87	18	?	45	?	?	?	?	?	
		(P1)-UCM98120-2.2	45	66	52	0.87	21	?	45	?	?	?	?	?	
		(P1)-UCM98120-2.3	44	64	52	0.85	20	?	44	?	?	?	?	?	
		(P1)-UCM98120-3.1	41	54	46	0.89	13	?	41	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Ignotornis mcconnelli	Ignotornidae	(P1)-UCM98120-3.2	44	59	43	1.02	15	?	44	?	?	?	?	?	Lockley et al., 2009
		(P1)-UCM98120-3.3	42	53	46	0.91	11	?	42	?	?	?	?	?	
		(P1)-UCM98120-3.4	44	56	44	1.00	12	?	44	?	?	?	?	?	
		(P1)-UCM98120-3.5	?	?	44	?	?	?	?	?	?	?	?	?	
		(P1)-UCM98120-4.1	44	61	46	0.96	17	?	44	?	?	?	?	?	
		(P1)-UCM98120-4.2	42	61	42	1.00	19	?	42	?	?	?	?	?	
		(P1)-UCM98120-4.3	41	56	41	1.00	15	?	41	?	?	?	?	?	
		(P1)-UCM98120-5.1	34	52	57	0.60	18	?	34	?	?	?	?	?	
		(P1)-UCM98120-5.2	?	?	51	?	?	?	?	?	?	?	?	?	
		(P1)-UCM98120-5.3	37	53	55	0.67	16	?	37	?	?	?	?	?	
		(P1)-UCM98120-5.4	37	53	51	0.73	16	?	37	?	?	?	?	?	
		(P2)-UCM98121-6.1	39	53	50	0.78	14	?	39	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Ignotornis mcconnelli	Ignotornidae	(P2)-UCM98121-6.2	39	49	50	0.78	10	?	39	?	?	?	?	?	Lockley et al., 2009
		(P2)-UCM98121-6.3	?	?	52	?	?	?	?	?	?	?	?	?	
		(P2)-UCM98121-7	42	54	5	8.40	12	?	42	?	?	?	?	?	
		(P2)-UCM98121-8	40	51	46	0.87	11	?	40	?	?	?	?	?	
		(P2)-UCM98121-9	?	?	?	?	?	?	?	?	?	?	?	?	
		(P3)-UCM98122-10	?	54	51	?	?	?	?	?	?	?	?	?	
		(P3)-UCM98122-11	40	52	52	0.77	12	?	40	?	?	?	?	?	
		(P3)-UCM98122-12	35	?	?	?	?	?	35	?	?	?	?	?	
		(P3)-UCM98122-13.1	35	?	45	0.78	?	?	35	?	?	?	?	?	
		(P3)-UCM98122-13.2	39	53	50	0.78	14	?	39	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis mcconnelli	Ignotornidae	(P3)-UCM98122-13.3	35	51	45	0.78	16	?	35	?	?	?	?	?	Lockley et al., 2009
		(P3)-UCM98122-14	?	?	52	?	?	?	?	?	?	?	?	?	
		(P3)-UCM98122-15	38	?	45	0.84	?	?	38	?	?	?	?	?	
		(T)-CU203.28-G1.1	35	?	44	0.80	?	?	35	?	?	?	?	?	
		(T)-CU203.28-G1.2	43	?	40	1.08	?	?	43	?	?	?	?	?	
		(T)-CU203.28-G1.3	40	?	49	0.82	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G2.1	?	?	?	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G3.1	40	?	50	0.80	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G4.1	45	?	50	0.90	?	?	45	?	?	?	?	?	
		(T)-CU203.28-G4.2	44	55	50	0.88	11	?	44	?	?	?	?	?	
		(T)-CU203.28-G4.3	50	60	49	1.02	10	?	50	?	?	?	?	?	
		(T)-CU203.28-G5.1	44	60	51	0.86	16	?	44	?	?	?	?	?	
		(T)-CU203.28-G5.2	44	53	53	0.83	9	?	44	?	?	?	?	?	
		(T)-CU203.28-G5.3	42	50	53	0.79	8	?	42	?	?	?	?	?	
		(T)-CU203.28-G6.1	40	54	40	1.00	14	?	40	?	?	?	?	?	
		(T)-CU203.28-G6.2	41	50	39	1.05	9	?	41	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G6.3	38	50	39	0.97	12	?	38	?	?	?	?	?	Lockley et al., 2009
		(T)-CU203.28-G6.4	41	49	37	1.11	8	?	41	?	?	?	?	?	
		(T)-CU203.28-G6.5	40	51	40	1.00	11	?	40	?	?	?	?	?	
		(T)-CU203.28-G6.6	39	49	40	0.98	10	?	39	?	?	?	?	?	
		(T)-CU203.28-G6.7	40	?	40	1.00	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G6.8	47	55	?	?	8	?	47	?	?	?	?	?	
		(T)-CU203.28-G7.1	?	?	?	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G7.2	43	57	45	0.96	14	?	43	?	?	?	?	?	
		(T)-CU203.28-G7.3	42	58	45	0.93	16	?	42	?	?	?	?	?	
		(T)-CU203.28-G8.1	40	?	47	0.85	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G8.2	40	?	?	?	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G8.3	43	?	45	0.96	?	?	43	?	?	?	?	?	
		(T)-CU203.28-G9.1	42	?	45	0.93	?	?	42	?	?	?	?	?	
		(T)-CU203.28-G9.2	39	?	?	?	?	?	39	?	?	?	?	?	
		(T)-CU203.28-G9.3	39	?	?	?	?	?	39	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G9.4	41	51	46	0.89	10	?	41	?	?	?	?	?	Lockley et al., 2009
		(T)-CU203.28-G9.5	48	59	47	1.02	11	?	48	?	?	?	?	?	
		(T)-CU203.28-G9.6	40	52	48	0.83	12	?	40	?	?	?	?	?	
		(T)-CU203.28-G10.1	31	46	37	0.84	15	?	31	?	?	?	?	?	
		(T)-CU203.28-G10.2	35	?	30	1.17	?	?	35	?	?	?	?	?	
		(T)-CU203.28-G10.3	?	?	?	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G11.1	45	62	50	0.90	17	?	45	?	?	?	?	?	
		(T)-CU203.28-G11.2	45	?	50	0.90	?	?	45	?	?	?	?	?	
		(T)-CU203.28-G11.3	35	?	45	0.78	?	?	35	?	?	?	?	?	
		(T)-CU203.28-G12.1	40	70	51	0.78	30	?	40	?	?	?	?	?	
		(T)-CU203.28-G12.2	45	?	50	0.90	?	?	45	?	?	?	?	?	
		(T)-CU203.28-G12.3	40	50	49	0.82	10	?	40	?	?	?	?	?	
		(T)-CU203.28-G13.1	45	60	41	1.10	15	?	45	?	?	?	?	?	
		(T)-CU203.28-G13.2	30	46	40	0.75	16	?	30	?	?	?	?	?	
		(T)-CU203.28-G13.3	?	45	36	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G14	44	61	49	0.90	17	?	44	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G15.1	?	53	?	?	?	?	?	?	?	?	?	?	Lockley et al., 2009
		(T)-CU203.28-G15.2	42	57	?	?	15	?	42	?	?	?	?	?	
		(T)-CU203.28-G16	45	?	?	?	?	?	45	?	?	?	?	?	
		(T)-CU203.28-G17.1	40	?	48	0.83	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G17.2	40	?	52	0.77	?	?	40	?	?	?	?	?	
		(T)-CU203.28-G17.3	46	?	53	0.87	?	?	46	?	?	?	?	?	
		(T)-CU203.28-G18.1	39	52	58	0.67	13	?	39	?	?	?	?	?	
		(T)-CU203.28-G18.2	44	59	54	0.81	15	?	44	?	?	?	?	?	
		(T)-CU203.28-G18.3	43	67	57	0.75	24	?	43	?	?	?	?	?	
		(T)-CU203.28-G18.4	44	52	55	0.80	8	?	44	?	?	?	?	?	
		(T)-CU203.28-G18.5	44	58	54	0.81	14	?	44	?	?	?	?	?	
		(T)-CU203.28-G18.6	45	58	56	0.80	13	?	45	?	?	?	?	?	
		(T)-CU203.28-G18.7	38	53	51	0.75	15	?	38	?	?	?	?	?	
		(T)-CU203.28-G18.8	42	61	52	0.81	19	?	42	?	?	?	?	?	
		Average	40	?	50	?	11	40	?	?	?	?	?	?	
Ignotornis yangi	Ignotornidae	KNUE040417-T1-01	34	56	51	0.67	16	28	34	33	?	?	?	?	Kim et al., 2006
		KNUE040417-T1-02	34	?	?	?	26	?	34	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis yangi	Ignotornidae	KNUE040417-T1-03	35	55	48	0.73	10	22	35	32	?	?	?	?	Kim et al., 2006
		KNUE040417-T1-04	34	56	46	0.74	18	24	34	30	?	?	?	?	
		KNUE040417-T1-05	33	55	47	0.70	12	23	33	30	?	?	?	?	
		KNUE040417-T1-06	32	52	46	0.70	11	22	32	30	?	?	?	?	
		KNUE040417-T1-07	33	58	48	0.69	13	23	33	31	?	?	?	?	
		KNUE040417-T1-08	35	59	48	0.73	19	26	35	29	?	?	?	?	
		KNUE040417-T2-09	37	58	49	0.76	17	24	37	32	?	?	?	?	
		KNUE040417-T2-10	35	?	45	0.78	?	23	35	30	?	?	?	?	
		KNUE040417-T2-11	36	54	51	0.71	17	23	36	31	?	?	?	?	
		KNUE040417-T2-12	36	60	47	0.77	15	24	36	30	?	?	?	?	
		KNUE040417-T2-13	28	?	38	0.74	?	22	28	22	?	?	?	?	
		KNUE040417-T2-14	29	?	38	0.76	?	23	29	20	?	?	?	?	
		KNUE040417-T2-15	29	?	40	0.73	?	24	29	25	?	?	?	?	
		KNUE040417-T2-16	31	?	40	0.78	?	24	31	23	?	?	?	?	
		KNUE040417-T2-17	28	?	40	0.70	?	22	28	25	?	?	?	?	
		KNUE040417-T3-18	31	38	43	0.72	10	23	31	28	?	?	?	?	
		KNUE040417-T3-19	34	44	45	0.76	4	25	34	28	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis yangi	Ignotornidae	KNUE040417-T3-20	34	47	47	0.72	8	25	34	32	?	?	?	?	Kim et al., 2006
		KNUE040417-T3-21	34	?	45	0.76	?	26	34	29	?	?	?	?	
		KNUE040417-T3-22	35	45	48	0.73	13	27	35	27	?	?	?	?	
		KNUE040417-T3-23	34	?	45	0.76	?	26	34	30	?	?	?	?	
		KNUE040417-T3-24	35	?	45	0.78	?	23	35	32	?	?	?	?	
		KNUE040417-T3-25	32	?	42	0.76	?	27	32	20	?	?	?	?	
		KNUE040417-T3-26	31	?	43	0.72	?	25	31	26	?	?	?	?	
		KNUE040417-T3-27	30	?	41	0.73	?	25	30	22	?	?	?	?	
		KNUE040417-T3-28	31	?	42	0.74	?	22	31	27	?	?	?	?	
		KNUE040417-T3-29	31	48	43	0.72	8	24	31	30	?	?	?	?	
		KNUE040417-T4-30	35	45	46	0.76	9	22	35	30	?	?	?	?	
		KNUE040417-T4-31	32	?	47	0.68	?	25	32	32	?	?	?	?	
		KNUE040417-T4-32	35	56	47	0.74	15	26	35	28	?	?	?	?	
		KNUE040417-T4-33	35	?	45	0.78	?	23	35	30	?	?	?	?	
		KNUE040417-T4-34	?	63	45	?	16	24	?	28	?	?	?	?	
		KNUE040417-T5-35	35	48	47	0.74	13	23	35	33	?	?	?	?	
		KNUE040417-T5-36	30	48	47	0.64	13	20	30	30	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**References**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis yangi	Ignotornidae	KNUE040417-T5-37	35	55	46	0.76	12	21	35	29	?	?	?	?	Kim et al., 2006
		KNUE040417-T5-38	32	?	44	0.73	?	22	32	30	?	?	?	?	
		KNUE040417-T5-39	33	63	47	0.70	16	23	33	34	?	?	?	?	
		KNUE040417-T5-40	?	?	?	?	13	?	?	?	?	?	?	?	
		KNUE040417-T5-41	30	48	41	0.73	13	22	30	23	?	?	?	?	
		KNUE040417-T5-42	35	62	45	0.78	18	22	35	31	?	?	?	?	
		KNUE040417-T5-43	30	48	45	0.67	9	23	30	25	?	?	?	?	
		KNUE040417-T6-44	35	45	47	0.74	8	25	35	29	?	?	?	?	
		KNUE040417-T6-45	35	?	46	0.76	?	23	35	30	?	?	?	?	
		KNUE040417-T6-46	32	48	45	0.71	15	25	32	25	?	?	?	?	
		KNUE040417-T6-47	36	?	47	0.77	?	30	36	27	?	?	?	?	
		KNUE040417-T7-48	30	?	41	0.73	?	27	30	28	?	?	?	?	
		KNUE040417-T7-49	31	47	42	0.74	5	23	31	27	?	?	?	?	
		KNUE040417-T7-50	32	?	41	0.78	?	25	32	22	?	?	?	?	
		KNUE040417-T7-51	30	48	42	0.71	6	22	30	30	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**References**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis yangi	Ignotornidae	KNUE040417-T7-53	30	47	42	0.71	10	23	30	25	?	?	?	?	Kim et al., 2006
		KNUE040417-T8-55	34	53	47	0.72	12	26	34	29	?	?	?	?	
		KNUE040417-T8-56	30	?	43	0.70	?	20	30	27	?	?	?	?	
		KNUE040417-T8-57	33	46	47	0.70	6	22	33	30	?	?	?	?	
		KNUE040417-T8-58	34	?	45	0.76	?	25	34	23	?	?	?	?	
		KNUE040417-T8-59	34	?	45	0.76	?	23	34	30	?	?	?	?	
		KNUE040417-T8-60	30	52	41	0.73	8	26	30	30	?	?	?	?	
		KNUE040417-T8-61	35	46	45	0.78	12	?	35	?	?	?	?	?	
		KNUE040417-T8-62	33	?	45	0.73	?	23	33	30	?	?	?	?	
		KNUE040417-T9-63	35	?	47	0.74	?	22	35	30	?	?	?	?	
		KNUE040417-T9-64	29	46	44	0.66	7	24	29	28	?	?	?	?	
		KNUE040417-T9-65	33	62	48	0.69	9	23	33	30	?	?	?	?	
		KNUE040417-T9-66	32	48	45	0.71	12	23	32	27	?	?	?	?	
		KNUE040417-T10-67	31	?	44	0.70	?	25	31	25	?	?	?	?	
		KNUE040417-T10-68	30	?	?	?	?	?	30	24	?	?	?	?	
		KNUE040417-T10-69	33	51	48	0.69	8	23	33	33	?	?	?	?	
		KNUE040417-T10-70	31	?	42	0.74	?	25	31	23	?	?	?	?	
		KNUE040417-T10-71	32	?	43	0.74	?	26	32	25	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Length**				**Digit Width**				**References**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Ignotornis yangi	Ignotornidae	KNUE040417-T10-72	31	?	43	0.72	?	27	31	25	?	?	?	?	Kim et al., 2006
		KNUE040417-T11-73	30	?	43	0.70	?	26	30	26	?	?	?	?	
		KNUE040417-T11-74	31	43	40	0.78	8	23	31	29	?	?	?	?	
		KNUE040417-75	35	?	48	0.73	?	25	35	30	?	?	?	?	
		KNUE040417-76	33	47	47	0.70	8	23	33	30	?	?	?	?	
		KNUE040417-77	35	?	47	0.74	?	24	35	34	?	?	?	?	
		KNUE040417-78	33	?	48	0.69	?	22	33	32	?	?	?	?	
		KNUE040417-79	30	48	40	0.75	12	23	30	27	?	?	?	?	
		KNUE040417-80	27	?	38	0.71	?	18	27	25	?	?	?	?	
Ignotornis gajinensis	Ignotornidae	KNUE081001-1	63	?	53	1.19	?	?	63	?	?	?	?	?	Kim et al., 2012
		KNUE081001-2	43	?	54	0.80	?	?	43	?	?	?	?	?	
		KNUE081001-3	58	?	51	1.14	?	?	58	?	?	?	?	?	
		KNUE081001-4	48	?	53	0.91	?	?	48	?	?	?	?	?	
		KNUE081001-5	63	?	53	1.19	?	?	63	?	?	?	?	?	
		KNUE081001-6	68	?	55	1.24	?	?	68	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Length				Digit Width				References
							I	II	III	IV	I	II	III	IV	
Ignotornis gajinensis	Ignotornidae	KNUE081001-7	64	?	58	1.10	?	?	64	?	?	?	?	?	Kim et al., 2012
Goseongornipes markjonesi	Ignotornidae	KPE50005	30.6	46	43	0.71	15	?	30.6	?	?	?	?	?	Lockley et al., 2006a
		KPE5005.041	26	38	37	0.70	12	?	26	?	?	?	?	?	
		KPE5005.042	27	36	36	0.75	9	?	27	?	?	?	?	?	
		KPE5005.043	26	35	33	0.79	9	?	26	?	?	?	?	?	
		KPE5005.044	27	38	38	0.71	11	?	27	?	?	?	?	?	
Goseongornipes isp.	Ignotornidae	MGCM.H23a	44	44	56	0.79	?	24	35	28	?	?	?	?	Xing et al., 2011
		MGCM.H23b	38	38	58	0.66	?	23	38	39	?	?	?	?	
		MGCM.H23c	43	43	60	0.72	?	31	32	29	?	?	?	?	
		MGCM.H23d	38	38	55	0.69	?	24	32	22	?	?	?	?	
		MGCM.H23e	38	38	48	0.79	?	24	27	23	?	?	?	?	
Koreanaornis hamanensis	Koreanaornipodidae	KoHaAverage	?	?	25	?	?	?	?	?	?	?	?	?	Lockley et al., 1992
		KoHaAverage	?	?	44	?	?	?	?	?	?	?	?	?	
Koreanaornis hamanensis	Koreanaornipodidae	ZMNH-M5010 Average	26	?	36	0.72	?	?	?	?	?	?	?	?	Azuma et al., 2012
		ZMNH-M8774 Average(4)	33	49	27	1.22	8	18	23	19	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Length**				**Digit Width**				**References**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Koreanaornis hamanensis	Koreanaornipodidae	ZMNH-M8774 Average (5)	35	54	34	1.03	19	?	35	?	?	?	?	?	Azuma et al., 2012
		ZMNH-M8772 Average	24	?	34	0.71	?	?	24	?	?	?	?	?	
Koreanaornis hamanensis	Koreanaornipodidae	KoHa-T1-L1	22.6	?	30	0.75	?	?	22.6	?	?	?	?	?	Kim et al., 2012
		KoHa-T1-R1	24.5	?	39	0.63	?	?	24.5	?	?	?	?	?	
		KoHa-T1-L2	26.4	?	37	0.71	?	?	26.4	?	?	?	?	?	
		KoHa-T1-R2	34.7	?	38	0.92	?	?	34.7	?	?	?	?	?	
		KoHa-T1-L3	26.4	?	38	0.70	?	?	26.4	?	?	?	?	?	
		KoHa-T1-R3	22.6	?	38	0.60	?	?	22.6	?	?	?	?	?	
		KoHa-T1-L4	18.9	?	33	0.57	?	?	18.9	?	?	?	?	?	
		KoHa-T2-L1	38	?	38	1.00	?	?	38	?	?	?	?	?	
		KoHa-T2-R1	27.2	?	38	0.71	?	?	27.2	?	?	?	?	?	
		KoHa-T2-L2	27.2	?	35	0.77	?	?	27.2	?	?	?	?	?	
		KoHa-T2-R2	32.6	?	41	0.80	?	?	32.6	?	?	?	?	?	
		KoHa-T3-L1	20.4	?	30	0.69	?	?	20.4	?	?	?	?	?	
		KoHa-T3-R1	20.4	?	26	0.80	?	?	20.4	?	?	?	?	?	
		KoHa-T3-L2	20.4	?	31	0.67	?	?	20.4	?	?	?	?	?	
		KoHa-T3-R2	20.4	?	31	0.67	?	?	20.4	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Koreanaornis hamanensis	Koreanaornipodidae	KoHa-T4-R1	28.5	?	33	0.86	?	?	28.5	?	?	?	?	?	Kim et al., 2012
		KoHa-T4-L1	29.1	?	32	0.89	?	?	29.1	?	?	?	?	?	
		KoHa-T4-R2	25.1	?	34	0.73	?	?	25.1	?	?	?	?	?	
		KoHa-T4-L2	25.1	?	34	0.75	?	?	25.1	?	?	?	?	?	
		KoHa-T4-R3	22.8	?	34	0.67	?	?	22.8	?	?	?	?	?	
Koreanornis dodsoni	Koreanaornipodidae	MGCM.H10a	42	42	63	0.67	0	13	36	30	?	?	?	?	Xing et al., 2011
		MGCM.H10b	40	40	53	0.75	0	15	29	12	?	?	?	?	
		MGCM.H11a	30	30	37	0.81	0	22	27	25	?	?	?	?	
		MGCM.H111a	59	59	55	1.07	0	26	41	31	?	?	?	?	
		MGCM.H111b	52	52	52	1.00	0	31	40	30	?	?	?	?	
		MGCM.H111c	52	52	53	0.98	0	28	40	33	?	?	?	?	
		MGCM.H11c	34	34	32	1.06	0	17	26	25	?	?	?	?	
		MGCM.H11d	35	35	34	1.03	0	21	27	22	?	?	?	?	
		MGCM.H11e	35	35	38	0.92	0	20	32	19	?	?	?	?	
		MGCM.H12	32	32	32	1.00	0	23	30	23	?	?	?	?	
		MGCM.H14(H)	44	44	47	0.94	0	23	37	24	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Koreanornis dodsoni	Koreanaornipodidae	MGCM.H 15a	45	45	50	0.90	0	24	38	28	?	?	?	?	Xing et al., 2011
		MGCM.H 15b	47	47	38	1.24	0	19	32	22	?	?	?	?	
		MGCM.H 15c	42	42	55	0.76	0	28	32	37	?	?	?	?	
		MGCM.H 15d	51	51	49	1.04	0	30	45	39	?	?	?	?	
		MGCM.H 15e	42	42	52	0.81	0	24	32	33	?	?	?	?	
		MGCM.H 16a	63	63	55	1.15	0	23	49	29	?	?	?	?	
		MGCM.H 16b	48	48	55	0.87	0	29	41	31	?	?	?	?	
		MGCM.H 16c	42	42	57	0.74	0	21	35	31	?	?	?	?	
		MGCM.H 16d	45	45	54	0.83	0	18	31	24	?	?	?	?	
		MGCM.H 17	45	45	54	0.83	0	20	42	26	?	?	?	?	
		MGCM.H 18a	43	43	46	0.93	0	26	38	29	?	?	?	?	
		MGCM.H 18b	34	34	40	0.85	0	22	27	21	?	?	?	?	
		MGCM.H 19a	44	44	54	0.81	0	21	37	30	?	?	?	?	
		MGCM.H 19b	49	49	50	0.98	0	21	41	32	?	?	?	?	
		MGCM.H 19c	44	44	50	0.88	0	22	34	20	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Koreanornis dodsoni	Koreanaornipodidae	MGCM.H19d	34	34	39	0.87	0	21	28	24	?	?	?	?	Xing et al., 2011
		MGCM.H19e	45	45	48	0.94	0	23	39	25	?	?	?	?	
		MGCM.H20a	52	52	68	0.76	0	30	43	39	?	?	?	?	
		MGCM.H20b	54	54	56	0.96	0	22	40	28	?	?	?	?	
		MGCM.H20c	46	46	59	0.78	0	31	41	31	?	?	?	?	
		MGCM.H20d	61	61	60	1.02	0	28	46	29	?	?	?	?	
		MGCM.H20e	46	46	61	0.75	0	29	36	36	?	?	?	?	
		MGCM.H20f	55	55	65	0.85	0	30	48	36	?	?	?	?	
		MGCM.H20g	51	51	64	0.80	0	28	42	38	?	?	?	?	
		MGCM.H20h	45	45	54	0.83	0	30	39	31	?	?	?	?	
		MGCM.H20i	56	56	54	1.04	0	28	41	19	?	?	?	?	
Jindongornipes kimi	Jindongornipedidae	KPE50006	80	80	65	1.23	?	?	80	?	?	?	?	?	Lockley et al., 1992
		KPE50006	80	80	75	1.07	?	?	80	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Shandongornipes muxiai	Shandongornipodidae	LRH-dz66	87	87	45	1.93	15	40	46	40	?	?	?	?	Li et al., 2005; Lockley et al., 2007
		LRH-dz67(H)	61	90	64	0.95	14	30	46	44	?	?	?	?	
		LRH-dz68(P)	54	88	57	0.95	13	30	45	40	?	?	?	?	
		LRH-dz69	?	?	?	?	15	?	?	?	?	?	?	?	
		LRH-dz70	60	82	67	0.90	14	40	45	41	?	?	?	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A01	33	33	47	0.70	?	15	19	23	?	?	?	?	Lockley et al., 2006b
		CU 212.21/22-A02	39	39	43	0.91	?	19	23	21	?	?	?	?	
		CU 212.21/22-A03	46	46	48	0.96	?	21	24	23	?	?	?	?	
		CU 212.21/22-A04	40	40	47	0.85	?	31	25	24	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A05	?	?	47	?	?	20	?	23	?	?	?	?	Lockley et al. 2006b
		CU 212.21/22-A06	42	42	44	0.95	?	23	25	22	?	?	?	?	
		CU 212.21/22-A07	47	47	44	1.07	?	20	20	23	?	?	?	?	
		CU 212.21/22-A08	39	39	40	0.98	?	18	12	25	?	?	?	?	
		CU 212.21/22-A12	41	41	42	0.98	?	16	28	23	?	?	?	?	
		CU 212.21/22-A13	?	?	?	?	?	?	?	20	?	?	?	?	
		CU 212.21/22-A14	39	39	33	1.18	?	16	23	21	?	?	?	?	
		CU 212.21/22-A15	44	44	44	1.00	?	20	33	30	?	?	?	?	
		CU 212.21/22-A27	?	?	47	?	?	13	25	29	?	?	?	?	
		CU 212.21/22-A28	40	40	?	?	?	25	25	?	?	?	?	?	
		CU 212.21/22-A29	45	45	?	?	?	22	26	25	?	?	?	?	
		CU 212.21/22-A30	37	37	35	1.06	?	23	26	25	?	?	?	?	
		CU 212.21/22-A31	47	47	42	1.12	?	14	26	23	?	?	?	?	
		CU 212.21/22-A32	43	43	35	1.23	?	24	28	25	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A33	45	45	49	0.92	?	23	27	25	?	?	?	?	Lockley et al. 2006b
		CU 212.21/22-A34	37	37	45	0.82	?	25	23	19	?	?	?	?	
		CU 212.21/22-A35	39	39	46	0.85	?	19	22	25	?	?	?	?	
		CU 212.21/22-A36	?	?	45	?	?	20	24	22	?	?	?	?	
		CU 212.21/22-A37	40	40	51	0.78	?	20	18	24	?	?	?	?	
		CU 212.21/22-A38	36	36	51	0.71	?	20	21	24	?	?	?	?	
		CU 212.21/22-A39	?	?	38	?	?	16	19	15	?	?	?	?	
		CU 212.21/22-A40	38	38	41	0.93	?	21	22	16	?	?	?	?	
		CU 212.21/22-A41	44	44	45	0.98	?	18	20	25	?	?	?	?	
		CU 212.21/22-A42	41	41	44	0.93	?	31	31	23	?	?	?	?	
		CU 212.21/22-A43	44	44	49	0.90	?	19	22	26	?	?	?	?	
		CU 212.21/22-A44	46	46	47	0.98	?	22	26	20	?	?	?	?	
		CU 212.21/22-A45	43	43	48	0.90	?	24	26	24	?	?	?	?	
Limiavipes curriei	Limiavipedidae	aa1R	77	77	112	0.69	0	?	?	?	?	?	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014.
		aa2L	85	85	115	0.74	0	?	?	?	?	?	?	?	
		aa3R	80	80	105	0.76	0	?	?	?	?	?	?	?	
		aa4L	65	65	110	0.59	0	?	?	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Limiavipes curriei	Limiavipedidae	aa5R	70	70	95	0.74	0	?	?	?	?	?	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014.
		aa6L	65	65	105	0.62	0	55	65	62	?	?	?	?	
		aa7R	68	68	95	0.72	0	?	?	?	?	?	?	?	
		aa8L	72	72	87	0.83	0	?	?	?	?	?	?	?	
		cd1R	70	70	101	0.69	0	60	70	55	?	?	?	?	
		cd2L	68	68	107	0.64	0	?	?	?	?	?	?	?	
		cd3R	76	76	95	0.80	0	?	?	?	?	?	?	?	
		cd4L	67	67	108	0.62	0	?	?	?	?	?	?	?	
		A1L	90	90	110	0.82	0	77	90	68	?	?	?	?	
		A2R	80	80	108	0.74	0	?	?	?	?	?	?	?	
		B1R	64	64	94	0.68	0	52	64	56	?	?	?	?	
		B2L	73	73	94	0.78	0	?	?	?	?	?	?	?	
		B3R	72	72	77	0.94	0	?	?	?	?	?	?	?	
		B4L	70	70	86	0.81	0	?	?	?	?	?	?	?	
		F1L	95	95	107	0.89	0	?	?	?	?	?	?	?	
		F2R	85	85	100	0.85	0	?	?	?	?	?	?	?	
		F3L	90	90	110	0.82	0	71	90	67	?	?	?	?	
		F4R	87	87	115	0.76	0	?	?	?	?	?	?	?	
		GF1L	78	78	99	0.79	0	?	?	?	?	?	?	?	
		GF2R	81	81	100	0.81	0	?	?	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Limiavipes curriei	Limiavipedidae	GF4R	75	75	104	0.72	0	58	75	55	?	?	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014.
		GF5L	80	80	96	0.83	0	?	?	?	?	?	?	?	
		GF6R	82	82	110	0.75	0	?	?	?	?	?	?	?	
		FG1L	70	70	103	0.68	0	?	?	?	?	?	?	?	
		FG2R	75	75	103	0.73	0	68	75	65	?	?	?	?	
		FG3L	72	72	102	0.71	0	?	?	?	?	?	?	?	
		FG4R	74	74	?	?	0	?	?	?	?	?	?	?	
		FG5L	74	74	106	0.70	0	?	?	?	?	?	?	?	
		FG6R	72	72	?	?	0	?	?	?	?	?	?	?	
		FG7L	76	76	?	?	0	?	?	?	?	?	?	?	
		H1L	63	63	?	?	0	?	?	?	?	?	?	?	
		H2R	75	75	?	?	0	?	?	?	?	?	?	?	
		H3L	70	70	115	0.61	0	60	70	65	?	?	?	?	
		H4R	80	80	?	?	0	?	?	?	?	?	?	?	
		PARA1R	90	90	120	0.75	0	73	90	67	?	?	?	?	
		PARA2L	83	83	126	0.66	0	79	83	60	?	?	?	?	
		PARA3R	95	95	110	0.86	0	55	95	62	?	?	?	?	
		PARA4L	101	101	116	0.87	0	62	101	71	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Limiavipes curriei	Limiavipedidae	PARA5R	89	89	116	0.77	0	68	89	67	?	?	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014.
		PARA6L	88	88	119	0.74	0	65	88	74	?	?	?	?	
		PARA7R	88	88	117	0.75	0	68	88	69	?	?	?	?	
		PARA8L	?	?	?	?	?	?	?	?	?	?	?	?	
		PARA9R	80	80	123	0.65	0	67	80	69	?	?	?	?	
		PARA10L	89	89	?	?	0	?	89	60	?	?	?	?	
		PARB1R	85	85	107	0.79	0	54	85	60	?	?	?	?	
		PARB2L	?	?	?	?	?	?	?	?	?	?	?	?	
		PARB3R	83	83	108	0.77	0	60	83	69	?	?	?	?	
		PARB4L	82	82	99	0.83	0	55	82	63	?	?	?	?	
		PARB5R	85	85	111	0.77	0	61	85	66	?	?	?	?	
		PARB6L	?	?	?	?	?	?	?	?	?	?	?	?	
		PARB7R	88	88	95	0.93	0	56	88	64	?	?	?	?	
		PARB8L	80	80	110	0.73	0	71	80	67	?	?	?	?	
		PARB9R	88	88	116	0.76	0	71	80	67	?	?	?	?	
Barrosopus slobodai	?	PVPH-SB-415-17C-86	?	?	?	?	0	?	?	?	0	?	?	?	Coria et al. 2002
		PVPH-SB-415-17C-87	29	29	35	0.83	0	21	29	29.7	0	5.6	6.8	5	
		PVPH-SB-415-17C-88	29	29	31	0.94	0	26	29	28	0	5	5.6	5	
		PVPH-SB-415-17C-89	34.5	34.5	37	0.93	0	20	34.5	26.8	0	6.6	6.7	6	
		PVPH-SB-415-17C-90	30	30	?	?	0	?	?	?	0	?	?	?	

Ichnotaxon	**Ichno-family**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Barrosopus slobodai	?	PVPH-SB-415-17C-91	40	40	40	1.00	0	?	?	?	0	?	?	?	Coria et al. 2002
		PVPH-SB-415-17C-92	30	30	36	0.83	0	?	?	?	0	?	?	?	
		PVPH-SB-415-17C-93	35.5	35.5	44	0.81	0	?	?	?	0	?	?	?	
		PVPH-SB-415-17C-94	28	28	38	0.75	0	?	?	?	0	?	?	?	
Dongyangornipes sinensis	?	ZMNH-M8774 Average	34.8	?	40	?	0	?	34.8	?	?	?	?	?	Azuma et al. 2013
		ZMNH-M8774 Holotype	36.4	36.4	40	0.92	0	17	22.8	21.3	?	3.7	6.4	4	
Moguiornipes robusta	?	MGCM.H25a	45	45	50	0.90	0	25	33	33	?	?	?	?	Xing et al. 2011
		MGCM.H25b	46	46	60	0.77	0	36	38	32	?	?	?	?	
		MGCM.H25c	49	49	?	?	0	34	43	?	?	?	?	?	
		MGCM.H25d	58	58	63	0.92	0	32	43	?	?	?	?	?	
		MGCM.H27a	40	40	?	?	0	?	30	26	?	?	?	?	
Tatarornipes chabuensis	?	1-CU 214	50	50	54	0.93	0	?	50	?	?	?	?	?	Lockley et al. 2012
		2-CU 214.184	48	48	56	0.86	0	?	48	?	?	?	?	?	
		3-CU 214.185	45	45	60	0.75	0	?	45	?	?	?	?	?	
		4-CU 214.184	46	46	62	0.74	0	?	46	?	?	?	?	?	
		5-CU 214.187	58	58	62	0.94	0	?	58	?	?	?	?	?	

Ichnotaxon	Ichno-family	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Tatarornipes chabuensis	?	6-CU 214.187	50	50	60	0.83	0	?	50	?	?	?	?	?	Lockley et al. 2012
		7-CU 214.188	50	50	64	0.78	0	?	50	?	?	?	?	?	
		8-CU 214.186	50	50	54	0.93	0	?	50	?	?	?	?	?	
		9-CU 214.184	58	58	54	1.07	0	?	58	?	?	?	?	?	
		10-CU 214.189	64	64	72	0.89	0	?	64	?	?	?	?	?	
		11-CU 214.14	60	60	53	1.13	0	?	60	?	?	?	?	?	
		12-CU 214.14	56	56	60	0.93	0	?	56	?	?	?	?	?	
		13-CU 214.11	51	51	57	0.89	0	?	51	?	?	?	?	?	
		14-CU 214.12	47	47	63	0.75	0	?	47	?	?	?	?	?	
		15-CU 214.10	52	52	64	0.81	0	?	52	?	?	?	?	?	
		16-CU 214.9	45	45	57	0.79	0	?	45	?	?	?	?	?	
		17-CU 214.6	58	58	71	0.82	0	?	58	?	?	?	?	?	
		18-CU 214.7	42	42	60	0.70	0	?	42	?	?	?	?	?	
		19-CU 214.8	56	56	71	0.79	0	?	56	?	?	?	?	?	
		20-CU 214.8	47	47	52	0.90	0	?	47	?	?	?	?	?	

Ichnotaxon	Ichno-family	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Tatarornipes chabuensis	?	1-CU 214.3	52	52	55	0.95	0	?	52	?	?	?	?	?	Lockley et al. 2012
		2-CU 214.3	45	45	51	0.88	0	?	45	?	?	?	?	?	
		3-CU 214.3	44	44	53	0.83	0	?	44	?	?	?	?	?	
		4-CU 214.5	46	46	62	0.74	0	?	46	?	?	?	?	?	
		5-CU 214.5	50	50	57	0.88	0	?	50	?	?	?	?	?	
		6-CU 214.18	56	56	80	0.70	0	?	56	?	?	?	?	?	
		7-CU 214.18	48	48	72	0.67	0	?	48	?	?	?	?	?	
		8-CU 214.160	50	50	72	0.69	0	?	50	?	?	?	?	?	
		9-CU 214.19	53	53	70	0.76	0	?	53	?	?	?	?	?	
		10-CU 214.19	43	43	62	0.69	0	?	43	?	?	?	?	?	
		11-CU 214.148	52	52	65	0.80	0	?	52	?	?	?	?	?	
		12-CU 214.149	55	55	57	0.96	0	?	55	?	?	?	?	?	
		13-CU 214.150	54	54	60	0.90	0	?	54	?	?	?	?	?	
		14-CU 214.151	54	54	57	0.95	0	?	54	?	?	?	?	?	
		15-CU 214.152	49	49	61	0.80	0	?	49	?	?	?	?	?	
		16-CU 214.152	54	54	70	0.77	0	?	54	?	?	?	?	?	

Ichnotaxon	**Ichno-family**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Tatarornipes chabuensis	?	17-CU 214.153	47	47	60	0.78	0	?	47	?	?	?	?	?	Lockley et al. 2012
		18-CU 214.155	54	54	60	0.90	0	?	54	?	?	?	?	?	
		19-CU 214.155	48	48	60	0.80	0	?	48	?	?	?	?	?	
		20:214.156	55	55	55	1.00	0	?	55	?	?	?	?	?	
		21-CU 214.154	46	46	64	0.72	0	?	46	?	?	?	?	?	
		22-CU 214.154	47	47	67	0.70	0	?	47	?	?	?	?	?	
		23-CU 214.154	52	52	64	0.81	0	?	52	?	?	?	?	?	
Uhangrichnus chuni	?	KPE50101-A01	35	35	39	0.90	?	?	35	?	?	?	?	?	Yang et al. 1995
		KPE50101-A02	35	35	47	0.74	?	?	35	?	?	?	?	?	
		KPE50101-A03	34.6	34.6	42	0.82	?	?	34.6	?	?	?	?	?	
		KPE50101-A04	33	33	?	?	?	?	33	?	?	?	?	?	
		KPE50101-A05	41.6	41.6	52	0.80	?	?	41.6	?	?	?	?	?	
		KPE50101-A06	42.2	42.2	?	?	?	?	42.2	?	?	?	?	?	
		KPE50101-A07	38	38	46	0.83	?	?	38	?	?	?	?	?	
		KPE50101-A08	36.3	36.3	49	0.75	?	?	36.3	?	?	?	?	?	

Ichnotaxon	Ichno-family	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Uhangrichnus chuni	?	KPE50101-A09	32.5	32.5	46	0.71	?	?	32.5	?	?	?	?	?	Yang et al. 1995
		KPE50101-A10	40.3	40.3	46	0.88	?	?	40.3	?	?	?	?	?	
		KPE50101-A11	37.8	37.8	49	0.78	?	?	37.8	?	?	?	?	?	
		KPE50101-A12	37.6	37.6	42	0.90	?	?	37.6	?	?	?	?	?	
		KPE50101-A13	39.3	39.3	49	0.80	?	?	39.3	?	?	?	?	?	
		KPE50101-A14	36.1	36.1	45	0.80	?	?	36.1	?	?	?	?	?	
		KPE50101-A15	37	37	44	0.84	?	?	37	?	?	?	?	?	
		KPE50101-A16	37	37	40	0.93	?	?	37	?	?	?	?	?	
		KPE50101-A17	37	37	40	0.93	?	?	37	?	?	?	?	?	
		KPE50101-A18	35	35	50	0.70	?	?	35	?	?	?	?	?	
		KPE50101-A19	36	36	40	0.90	?	?	36	?	?	?	?	?	
		KPE50101-A20	37.9	37.9	45	0.85	?	?	37.9	?	?	?	?	?	
		KPE50101-A22	36.1	36.1	44	0.82	?	?	36.1	?	?	?	?	?	
		KPE50101-A24	38.5	38.5	45	0.86	?	?	38.5	?	?	?	?	?	
		KPE50101-A25	37.4	37.4	42	0.89	?	?	37.4	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Uhangrichnus chuni	?	KPE50101-A26	39.2	39.2	48	0.82	?	?	39.2	?	?	?	?	?	Yang et al. 1995
		KPE50101-A27	40.2	40.2	47	0.86	?	?	40.2	?	?	?	?	?	
		KPE50101-A28	35.3	35.3	41	0.86	?	?	35.3	?	?	?	?	?	
		KPE50101-A29	50	50	?	?	?	?	50	?	?	?	?	?	
		KPE50101-A30	37	37	?	?	?	?	37	?	?	?	?	?	
		KPE50101-A31	37.3	37.3	45	0.83	?	?	37.3	?	?	?	?	?	
		KPE50101-A32	36.5	36.5	43	0.85	?	?	36.5	?	?	?	?	?	
		KPE50101-A33	37	37	?	?	?	?	37	?	?	?	?	?	
		KPE50101-A34	36.9	36.9	45	0.82	?	?	36.9	?	?	?	?	?	
		KPE50101-A34	36.9	36.9	45	0.82	?	?	36.9	?	?	?	?	?	
		KPE50101-A36	37	37	47	0.79	?	?	37	?	?	?	?	?	
		KPE50101-A37	37.9	37.9	?	?	?	?	37.9	?	?	?	?	?	
		KPE50101-A42	37.1	37.1	51	0.73	?	?	37.1	?	?	?	?	?	
		KPE50101-A43	33	33	46	0.72	?	?	33	?	?	?	?	?	
		KPE50101-A44	40.5	40.5	46	0.88	?	?	40.5	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Uhangrichnus chuni	?	KPE50101-A45	37	37	48	0.78	?	?	37	?	?	?	?	?	Yang et al. 1995
		KPE50101-A46	39	39	49	0.79	?	?	39	?	?	?	?	?	
		KPE50101-A47	40	40	48	0.83	?	?	40	?	?	?	?	?	
		KPE50101-A48	34	34	38	0.89	?	?	34	?	?	?	?	?	
		KPE50101-A49	36.9	36.9	43	0.86	?	?	36.9	?	?	?	?	?	
		KPE50101-A50	33	33	44	0.75	?	?	33	?	?	?	?	?	
		KPE50101-A51	38	38	?	?	?	?	38	?	?	?	?	?	
		KPE50101-A52	33.8	33.8	43	0.79	?	?	33.8	?	?	?	?	?	
		KPE50101-A54	41.7	41.7	?	?	?	?	41.7	?	?	?	?	?	
		KPE50101-A55	34.1	34.1	40	0.85	?	?	34.1	?	?	?	?	?	
		KPE50101-A56	30	30	38	0.79	?	?	30	?	?	?	?	?	
		KPE50101-A57	32.5	32.5	42	0.78	?	?	32.5	?	?	?	?	?	
		KPE50101-A58	29.7	29.7	42	0.71	?	?	29.7	?	?	?	?	?	
		KPE50101-A59	42	42	47	0.89	?	?	42	?	?	?	?	?	
		KPE50101-A60	37	37	48	0.77	?	?	37	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Uhangrichnus chuni	?	KPE50101-B01	37	37	49	0.76	?	?	37	?	?	?	?	?	Yang et al. 1995
		KPE50101-B02	34.2	34.2	?	?	?	?	34.2	?	?	?	?	?	
		KPE50101-B03	39.6	39.6	53	0.74	?	?	39.6	?	?	?	?	?	
		KPE50101-B04	36	36	43	0.84	?	?	36	?	?	?	?	?	
		KPE50101-B05	37.3	37.3	48	0.78	?	?	37.3	?	?	?	?	?	
		KPE50101-B06	41.3	41.3	48	0.87	?	?	41.3	?	?	?	?	?	
		KPE50101-B07	40	40	47	0.85	?	?	40	?	?	?	?	?	
		KPE50101-B08	36.2	36.2	46	0.78	?	?	36.2	?	?	?	?	?	
		KPE50101-B09	40.7	40.7	43	0.95	?	?	40.7	?	?	?	?	?	
		KPE50101-B10	39.4	39.4	42	0.93	?	?	39.4	?	?	?	?	?	
		KPE50101-B11	37.1	37.1	48	0.77	?	?	37.1	?	?	?	?	?	
		KPE50101-B12	37	37	45	0.82	?	?	37	?	?	?	?	?	
		KPE50101-B13	32.8	32.8	?	?	?	?	32.8	?	?	?	?	?	
		KPE50101-B14	40.9	40.9	48	0.85	?	?	40.9	?	?	?	?	?	
		KPE50101-B15	37	37	45	0.82	?	?	37	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Uhangrichnus chuni	?	KPE50101-B16	35.8	35.8	49	0.72	?	?	35.8	?	?	?	?	?	Yang et al. 1995
		KPE50101-B17	38	38	42	0.90	?	?	38	?	?	?	?	?	
		KPE50101-B18	?	?	46	?	?	?	?	?	?	?	?	?	
		KPE50101-B19	35.1	35.1	?	?	?	?	35.1	?	?	?	?	?	
		KPE50101-B20	39	39	47	0.82	?	?	39	?	?	?	?	?	
		KPE50101-C01	35.6	35.6	49	0.73	?	?	35.6	?	?	?	?	?	
		KPE50101-C02	33.7	33.7	?	?	?	?	33.7	?	?	?	?	?	
		KPE50101-C03	37	37	45	0.82	?	?	37	?	?	?	?	?	
		KPE50101-C04	46.2	46.2	50	0.92	?	?	46.2	?	?	?	?	?	
		KPE50101-C05	35	35	52	0.68	?	?	35	?	?	?	?	?	
		KPE50101-C06	36	36	52	0.70	?	?	36	?	?	?	?	?	
		KPE50101-C07	35	35	52	0.67	?	?	35	?	?	?	?	?	
		KPE50101-C08	35.1	35.1	45	0.78	?	?	35.1	?	?	?	?	?	
		KPE50101-C09	34	34	?	?	?	?	34	?	?	?	?	?	
		KPE50101-C10	37	37	48	0.77	?	?	37	?	?	?	?	?	
Uhangrichnus topotype	?	KPE50101-T1	36	?	?	?	?	?	36	?	?	?	?	?	Lockley et al. 2012

Ichnotaxon	Ichnofamily	Track #	FL	FLwH	FW	L/W	Digit Lengths				Digit Widths				Reference
							I	II	III	IV	I	II	III	IV	
Uhangrichnus topotype	?	KPE50101-T2	35	?	43	0.81	?	?	35	?	?	?	?	?	Lockley et al. 2012
		KPE50101-T4	40	49	48	0.83	9	?	40	?	?	?	?	?	
		KPE50101-T3	38	51	45	0.84	13	?	38	?	?	?	?	?	
Magnoavipes lowei	Theropod	DMNH918.1	210	210	250	0.84	0	175	210	180	?	?	?	?	Lee 1997
		DMNH918.2	190	190	250	0.76	0	160	190	160	?	?	?	?	
		DMNH918.3	210	210	250	0.84	0	167	210	145	?	?	?	?	
		DMNH918.4	210	210	240	0.88	0	155	210	160	?	?	?	?	
		DMNH918.5	200	200	270	0.74	0	198	200	160	?	?	?	?	
		DMNH918.6	210	210	240	0.88	0	160	210	180	?	?	?	?	
Magnoavipes caneeri	Theropod	CU MWC200-1.1	?	?	?	?	0	?	?	?	?	?	?	?	Lockley et al. 2001
		CU MWC200-1.2	200	200	250	0.80	0	?	200	?	?	?	?	?	
		CU MWC200-1.3	?	?	?	?	?	?	?	?	?	?	?	?	
		CU MWC200-1.4	?	?	?	?	0	?	?	?	?	?	?	?	
		CU MWC200-1.5	210	210	260	0.81	0	?	210	?	?	?	?	?	
		CU MWC200-1.6	?	?	?	?	0	?	?	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Magnoavipes caneeri	Theropod	CU MWC200-1.7	210	210	260	0.81	0	?	210	?	?	?	?	?	Lockley et al. 2001
		CU MWC200-1.8	230	230	270	0.85	0	?	230	?	?	?	?	?	
		CU MWC200-1.9	?	?	?	?	0	?	?	?	?	?	?	?	
		CU MWC200-1.10	220	220	240	0.92	0	?	220	?	?	?	?	?	
		CU MWC200-2.01	210	210	210	1.00	0	?	210	?	?	?	?	?	
		CU MWC200-2.02	180	180	210	0.86	0	?	180	?	?	?	?	?	
		CU MWC200-2.03	180	180	200	0.90	0	?	180	?	?	?	?	?	
		CU MWC200-2.04	180	180	?	?	0	?	180	?	?	?	?	?	
		CU MWC200-3.01	190	190	200	0.95	0	?	190	?	?	?	?	?	
		CU MWC200-3.02	180	180	190	0.95	0	?	180	?	?	?	?	?	
		CU MWC200-3.03	190	190	190	1.00	0	?	190	?	?	?	?	?	
		CU MWC200-3.04	170	170	180	0.94	0	?	170	?	?	?	?	?	
		CU MWC200-4.01	?	?	?	?	0	?	?	?	?	?	?	?	
		CU MWC200-4.02	200	200	260	0.77	0	?	200	?	?	?	?	?	
		CU MWC200-4.03	180	180	240	0.75	0	?	180	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**FL**	**FLwH**	**FW**	**L/W**	**Digit Lengths**				**Digit Widths**				**Reference**
							I	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**	
Magnoavipes caneeri	Theropod	CU MWC200-5.01	180	180	200	0.90	0	?	180	?	?	?	?	?	Lockley et al. 2001
		CU MWC200-5.02	180	180	230	0.78	0	?	180	?	?	?	?	?	
Magnoavipes denaliensis	Theropod	Smallest	195	195	200	0.98	0	150	195	130	?	?	?	?	Fiorillo et al. 2011
		Largest	205	205	200	1.03	0	150	205	130	?	?	?	?	

Appendix 5.02: Divarication and Trackway Data for Multivariate Analyses of Mesozoic Avian Ichnotaxa— Data used in multivariate analyses of Mesozoic avian ichnotaxa. Data were compiled from references cited within the table. All data were standardized to fit the table presented here. Missing data are indicated by "?". Data that are not present due to morphology (i.e., no digit I) are indicated by "0". All linear measurements are in millimeters. All angle measurements are in degrees. All data are unadjusted. **DIV**, digit divarication; **DIVTOT**, digit divarication II-IV; **DL**, digit length; **DW**, digit width; **FL**, footprint length; **FLwH**, footprint length including hallux; **FR**, footprint rotation; **FW**, footprint width; **L/W**, footprint length to footprint width ratio; **P**, pace length; **PA**, pace angulation; **TW**, trackway width; **I**, digit I; **II**, digit II; **III**, digit III; **IV**, digit IV; **(H)**, holotype; (**P)**, paratype; (**T)**, topotype.

Institutional Abbreviations: CU, University of Colorado Denver, Dinosaur Tracks Museum; **DMNH**, Denver Museum of Natural History, Denver, Colorado; **FPDM**, Fukui Prefectural Dinosaur Museum, Japan; **KNUE**, Korea National University of Education, Cheongwon, Chungbuk, Korea; **KPE**, Kyungpook National University, Earth Science Education Department, Taegu, South Korea; **LRH**, Qingdao Institute of Marine Geology; **MGCM**, Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; **UCM**; University of Colorado Museum of Natural History at Boulder, Colorado; **ZMNH**, Zhejiang Natural History Museum, Zheijiang, China.

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Aquatilavipes izumiensis	Avipedidae	FPDM-V43.1	0	48	68.5	117	?	?	?	?	?	Azuma et al. 2002
		FPDM-V43.2	0	48	60	108	?	?	?	?	?	
		FPDM-V43.3	0	45	80.5	126	?	?	?	?	?	
		FPDM-V43.4	0	45	65	110	?	?	?	?	?	
		FPDM-V43.5	0	56	66	122	?	?	?	?	?	
		FPDM-V43.6	0	65	66.5	131	?	?	?	?	?	
		FPDM-V43.7	0	44	77	121	?	?	?	?	?	
		FPDM-V43.8	0	62	80	142	?	?	?	?	?	
		FPDM-V43.9	0	47	62	109	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Aquatilavipes izumiensis	Avipedidae	FPDM-V43.10	0	55	40	95	?	?	?	?	?	Azuma et al. 2002
		FPDM-V43.11	0	46	69.5	115	?	?	?	?	?	
		FPDM-V43.12	0	71	80.5	152	?	?	?	?	?	
		FPDM-V43.13	0	54	68	122	?	?	?	?	?	
		FPDM-V43.14	0	52	57.5	109	?	?	?	?	?	
		FPDM-V43.15	0	49	62	111	?	?	?	?	?	
		FPDM-V44.B1	0	71	75	146	?	?	?	?	?	
		FPDM-V44.B2	0	42	65.5	108	?	?	?	?	?	
Aquatilavipes swiboldae	Avipedidae	TMP 98.89.21-A	0	46	62	108	?	?	?	?	?	Currie 1981; McCrea and Sarjeant 2001
		TMP 98.89.21-B	0	42	48	90	?	?	?	?	?	
		TMP 98.89.21-C	0	37	34	71	?	?	?	?	?	
		TMP 98.89.21-D	0	55	43	98	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Aquatilavipes swiboldae	Avipedidae	TMP 98.89.21-E	0	77	53	130	?	?	?	?	?	Currie 1981; McCrea and Sarjeant 2001
		TMP 98.89.21-F	0	47	48	95	?	?	?	?	?	
		TMP 98.89.20-A	0	58	68	126	?	?	?	?	?	
		TMP 98.89.20-B	0	61	71	132	?	?	?	?	?	
		TMP 98.89.20-C	0	53	52	105	?	?	?	?	?	
		TMP 98.89.20-D	0	68	66	134	?	?	?	?	?	
		TMP 98.89.20-E	0	53	52	105	?	?	?	?	?	
		TMP 98.89.20-F	0	?	?	?	?	?	?	?	?	
		TMP 98.89.20-G	0	61	62	123	?	?	?	?	?	
		TMP 90.30.1-A	0	75	73	148	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Aquatilavipes swiboldae	Avipedidae	TMP 90.30.1-B	0	84	61	145	?	?	?	?	?	Currie 1981; McCrea and Sarjeant 2001
		TMP 90.30.1-C	0	64	74	138	?	?	?	?	?	
		TMP 79.23.3-	0	48	70	118	?	?	?	?	?	
Hwangsanipes choughi	Ignotornidae	KP50101-A38	?	60	?	?	?	?	?	?	?	Yang et al. 1995
		KP50101-A39	?	?	?	?	?	?	?	?	?	
		KP50101-A40	?	57	59	116	?	?	?	?	?	
		KP50101-A41	?	51	55	106	?	?	?	?	?	
Ignotornis mcconnelli	Ignotornidae	Average	?	?	?	90	?	?	?	?	?	Lockley et al. 2009
		(H)-UCM17614-1.1	85	62	63	125	?	?	?	18	?	
		(H)-UCM17614-1.2	115	60	65	125	72	?	143	18	70	
		(H)-UCM17614-1.3	95	60	63	123	73	140	150	21	70	
		(H)-UCM17614-1.4	120	50	55	105	80	147	118	17	84	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis mcconnelli	Ignotornidae	(H)-UCM17614-1.5	90	60	65	125	60	121	120	5	76	Lockley et al. 2009
		(H)-UCM17614-1.6	100	57	50	107	49	94	?	15	?	
		(P1)-UCM98120-2.1	90	60	46	106	?	?	?	40	?	
		(P1)-UCM98120-2.2	95	57	50	107	87	?	?	25	?	
		(P1)-UCM98120-2.3	90	60	50	110	84	168	160	25	56	
		(P1)-UCM98120-3.1	95	80	60	140	?	?	?	15	?	
		(P1)-UCM98120-3.2	115	80	60	140	103	?	152	5	?	
		(P1)-UCM98120-3.3	90	80	55	135	100	197	160	8	60	
		(P1)-UCM98120-3.4	105	82	52	134	85	183	158	8	60	
		(P1)-UCM98120-3.5	110	67	53	120	87	169	?	10	60	
		(P1)-UCM98120-4.1	120	60	60	120	?	?	?	18	?	
		(P1)-UCM98120-4.2	100	52	68	120	98	?	140	0	67	
		(P1)-UCM98120-4.3	100	70	65	135	70	158	?	15	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Ignotornis mcconnelli	Ignotornidae	(P1)-UCM98120-5.1	65	90	72	162	?	?	?	18	?	Lockley et al. 2009
		(P1)-UCM98120-5.2	80	?	?	?	74	?	135	?	80	
		(P1)-UCM98120-5.3	80	80	65	145	86	146	135	11	85	
		(P1)-UCM98120-5.4	90	72	63	135	86	155	?	11	?	
		(P2)-UCM98121-6.1	95	60	50	110	?	?	?	-16	?	
		(P2)-UCM98121-6.2	70	50	75	125	62	?	128	38	75	
		(P2)-UCM98121-6.3	110	75	55	130	48	97	?	?	?	
		(P2)-UCM98121-7	85	60	65	125	?	?	?	?	?	
		(P2)-UCM98121-8	90	80	75	155	?	?	?	?	?	
		(P2)-UCM98121-9	?	?	?	?	?	?	?	?	?	
		(P3)-UCM98122-10	92	73	73	146	?	?	?	?	?	
		(P3)-UCM98122-11	?	80	60	140	?	?	?	?	?	
		(P3)-UCM98122-12	?	75	55	130	?	?	?	?	?	
		(P3)-UCM98122-13.1	?	37	68	105	?	?	?	16	?	
		(P3)-UCM98122-13.2	90	64	51	115	49	?	65	10	81	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Ignotornis mcconnelli	Ignotornidae	(P3)-UCM98122-13.3	122	65	47	112	42	49	?	6	?	Lockley et al. 2009
		(P3)-UCM98122-14	105	70	55	125	?	?	?	?	?	
		(P3)-UCM98122-15	?	65	55	120	?	?	?	?	?	
		(T)-CU203.28-G1.1	?	65	105	170	?	?	?	10	?	
		(T)-CU203.28-G1.2	?	?	87	?	85	?	150	28	59	
		(T)-CU203.28-G1.3	?	57	60	117	73	152	?	30	?	
		(T)-CU203.28-G2.1	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G3.1	?	48	62	110	?	?	?	?	?	
		(T)-CU203.28-G4.1	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G4.2	107	63	65	128	72	?	138	25	70	
		(T)-CU203.28-G4.3	80	75	75	150	60	123	?	25	?	
		(T)-CU203.28-G5.1	95	80	53	133	?	?	?	10	?	
		(T)-CU203.28-G5.2	?	50	77	127	75	?	148	30	68	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G5.3	100	62	58	120	70	138	?	24	?	Lockley et al. 2009
		(T)-CU203.28-G6.1	112	68	57	125	?	?	?	42	?	
		(T)-CU203.28-G6.2	112	43	62	105	65	?	155	34	50	
		(T)-CU203.28-G6.3	128	35	60	95	60	120	155	23	49	
		(T)-CU203.28-G6.4	92	57	47	104	57	116	167	33	41	
		(T)-CU203.28-G6.5	130	45	70	115	62	114	50	20	75	
		(T)-CU203.28-G6.6	100	62	58	120	32	53	?	10	70	
		(T)-CU203.28-G6.7	?	?	?	?	63	65	70	34	55	
		(T)-CU203.28-G6.8	?	?	?	?	78	142	?	5	?	
		(T)-CU203.28-G7.1	?	?	50	?	?	?	?	18	?	
		(T)-CU203.28-G7.2	63	77	55	132	90	?	120	19	76	
		(T)-CU203.28-G7.3	93	62	56	118	70	142	?	-11	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G8.1	?	71	71	142	?	?	?	12	?	Lockley et al. 2009
		(T)-CU203.28-G8.2	?	?	57	?	95	?	170	30	52	
		(T)-CU203.28-G8.3	?	45	70	115	82	170	?	37	?	
		(T)-CU203.28-G9.1	?	50	63	113	?	?	?	12	?	
		(T)-CU203.28-G9.2	?	?	60	?	90	?	158	20	59	
		(T)-CU203.28-G9.3	?	?	57	?	85	170	161	25	56	
		(T)-CU203.28-G9.4	133	65	45	110	78	162	144	10	66	
		(T)-CU203.28-G9.5	92	58	42	100	74	147	?	14	?	
		(T)-CU203.28-G9.6	95	80	45	125	?	?	?	12	?	
		(T)-CU203.28-G10.1	100	52	64	116	?	?	?	35	?	
		(T)-CU203.28-G10.2	?	?	?	?	105	?	162	10	50	
		(T)-CU203.28-G10.3	?	?	?	?	120	225	?	28	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G11.1	?	?	?	?	?	?	?	32	?	Lockley et al. 2009
		(T)-CU203.28-G11.2	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G11.3	?	?	?	?	?	?	?	24	?	
		(T)-CU203.28-G12.1	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G12.2	103	60	75	135	97	?	172	?	52	
		(T)-CU203.28-G12.3	?	?	?	?	99	195	?	?	?	
		(T)-CU203.28-G13.1	110	46	50	96	71	?	116	?	72	
		(T)-CU203.28-G13.2	?	?	?	?	65	120	101	?	70	
		(T)-CU203.28-G13.3	?	?	?	?	52	90	?	?	?	
		(T)-CU203.28-G14	110	55	67	122	?	?	?	?	?	
		(T)-CU203.28-G15.1	?	?	?	?	?	?	?	?	?	
		(T)-CU203.28-G15.2	?	?	?	?	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis mcconnelli	Ignotornidae	(T)-CU203.28-G16	?	?	?	?	?	?	?	?	?	Lockley et al. 2009
		(T)-CU203.28-G17.1	?	60	70	130	?	?	?	9	?	
		(T)-CU203.28-G17.2	?	?	?	?	85	?	90	23	96	
		(T)-CU203.28-G17.3	?	55	55	110	52	97	?	20	?	
		(T)-CU203.28-G18.1	78	70	70	140	?	?	?	35	?	
		(T)-CU203.28-G18.2	78	70	58	128	57	?	80	0	90	
		(T)-CU203.28-G18.3	85	68	56	124	72	85	92	-15	103	
		(T)-CU203.28-G18.4	?	65	61	126	65	98	135	0	82	
		(T)-CU203.28-G18.5	94	60	58	118	80	131	89	0	107	
		(T)-CU203.28-G18.6	90	85	61	146	94	120	139	15	75	
		(T)-CU203.28-G18.7	95	58	67	125	66	150	97	12	87	
		(T)-CU203.28-G18.8	90	68	56	124	56	93	?	13	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Ignotornis mcconnelli	Ignotornidae	Average	?	?	?	115	?	?	?	?	?	Lockley et al. 2009
Ignotornis yangi	Ignotornidae	KNUE040417-T1-01	83	63	59	122	?	?	?	?	?	Kim et al. 2006
		KNUE040417-T1-02	?	60	?	?	127	?	?	?	?	
		KNUE040417-T1-03	97	60	59	119	117	238	149	?	29	
		KNUE040417-T1-04	90	66	56	122	122	230	142	?	32	
		KNUE040417-T1-05	93	60	60	120	101	219	142	?	37	
		KNUE040417-T1-06	82	61	59	120	102	200	145	?	31	
		KNUE040417-T1-07	92	58	60	118	98	172	118	?	50	
		KNUE040417-T1-08	76	72	54	126	?	?	?	?	?	
		KNUE040417-T2-09	80	52	77	129	112	?	?	?	?	
		KNUE040417-T2-10	?	67	65	132	107	217	163	?	17	
		KNUE040417-T2-11	80	53	75	128	104	214	180	?	4	
		KNUE040417-T2-12	112	62	60	122	115	213	161	?	19	
		KNUE040417-T2-13	?	70	60	130	119	232	180	?	6	
		KNUE040417-T2-14	?	67	60	127	75	180	137	?	34	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Ignotornis yangi	Ignotornidae	KNUE040417-T2-15	?	65	68	133	93	150	125	?	36	Kim et al. 2006
		KNUE040417-T2-16	?	60	65	125	75	155	135	?	25	
		KNUE040417-T2-17	?	65	60	125	92	152	130	?	25	
		KNUE040417-T3-18	50	56	66	122	?	?	?	?	?	
		KNUE040417-T3-19	92	57	63	120	47	?	?	?	?	
		KNUE040417-T3-20	65	55	73	128	77	94	102	?	36	
		KNUE040417-T3-21	?	53	62	115	85	157	150	?	22	
		KNUE040417-T3-22	73	68	57	125	109	193	172	?	8	
		KNUE040417-T3-23	?	60	57	117	94	200	170	?	7	
		KNUE040417-T3-24	?	55	67	122	110	185	132	?	43	
		KNUE040417-T3-25	?	60	58	118	125	230	155	?	24	
		KNUE040417-T3-26	?	55	65	120	85	183	120	?	51	
		KNUE040417-T3-27	?	61	70	131	?	?	?	?	?	
		KNUE040417-T3-28	?	60	55	115	91	?	?	?	?	
		KNUE040417-T3-29	77	55	50	105	98	187	173	?	3	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Ignotornis yangi	Ignotornidae	KNUE040417-T4-30	90	59	60	119	?	?	?	?	?	Kim et al. 2006
		KNUE040417-T4-31	?	60	58	118	106	?	?	?	?	
		KNUE040417-T4-32	85	56	64	120	124	210	133	?	40	
		KNUE040417-T4-33	?	63	52	115	106	220	151	?	30	
		KNUE040417-T4-34	85	76	54	130	115	220	168	?	13	
		KNUE040417-T5-35	80	55	62	117	?	?	?	?	?	
		KNUE040417-T5-36	79	76	61	137	142	?	?	?	?	
		KNUE040417-T5-37	87	56	79	135	138	270	150	?	37	
		KNUE040417-T5-38	?	59	60	119	79	205	140	?	35	
		KNUE040417-T5-39	120	62	59	121	98	165	145	?	27	
		KNUE040417-T5-40	?	?	?	?	95	165	120	?	48	
		KNUE040417-T5-41	52	68	60	128	64	156	167	?	9	
		KNUE040417-T5-42	100	50	64	114	113	175	159	?	15	
		KNUE040417-T5-43	85	55	75	130	97	193	132	?	42	
		KNUE040417-T6-44	78	62	58	120	?	?	?	?	?	
		KNUE040417-T6-45	?	70	56	126	74	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis yangi	Ignotornidae	KNUE040417-T6-46	78	66	73	139	115	182	148	?	25	Kim et al. 2006
		KNUE040417-T6-47	?	70	55	125	81	184	138	?	33	
		KNUE040417-T7-48	?	63	55	118	?	?	?	?	?	
		KNUE040417-T7-49	95	57	68	125	90	?	?	?	?	
		KNUE040417-T7-50	?	58	66	124	55	136	137	?	27	
		KNUE040417-T7-51	113	55	68	123	93	142	147	?	19	
		KNUE040417-T7-52	90	59	70	129	93	176	155	?	19	
		KNUE040417-T7-53	79	57	63	120	94	176	148	?	25	
		KNUE040417-T8-54	?	68	63	131	?	?	?	?	?	
		KNUE040417-T8-55	90	45	77	122	120	?	?	?	?	
		KNUE040417-T8-56	?	70	54	124	130	243	150	?	32	
		KNUE040417-T8-57	110	47	60	107	99	234	180	?	13	
		KNUE040417-T8-58	?	68	56	124	126	225	175	?	12	
		KNUE040417-T8-59	?	56	59	115	100	223	164	?	14	
		KNUE040417-T8-60	110	64	56	120	111	203	150	?	23	
		KNUE040417-T8-61	92	62	67	129	104	215	150	?	28	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis yangi	Ignotornidae	KNUE040417-T8-62	?	68	59	127	127	225	157	?	23	Kim et al. 2006
		KNUE040417-T9-63	?	55	65	120	?	?	?	?	?	
		KNUE040417-T9-64	60	64	62	126	96	?	?	?	?	
		KNUE040417-T9-65	91	52	69	121	103	195	156	?	20	
		KNUE040417-T9-66	88	63	63	126	94	190	151	?	24	
		KNUE040417-T10-67	?	60	65	125	?	?	?	?	?	
		KNUE040417-T10-68	?	?	65	?	100	?	?	?	?	
		KNUE040417-T10-69	90	55	68	123	110	204	115	?	23	
		KNUE040417-T10-70	?	61	59	120	122	225	156	?	25	
		KNUE040417-T10-71	?	58	68	126	130	240	148	?	33	
		KNUE040417-T10-72	?	69	54	123	119	245	164	?	19	
		KNUE040417-T11-73	?	60	60	120	?	?	?	?	?	
		KNUE040417-T11-74	92	68	58	126	75	?	?	?	?	
		KNUE040417-75	56	64	?	120	?	?	?	?	?	
		KNUE040417-76	73	51	90	124	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Ignotornis yangi	Ignotornidae	KNUE040417-77	72	50	?	122	?	?	?	?	?	Kim et al. 2006
		KNUE040417-78	74	51	?	125	?	?	?	?	?	
		KNUE040417-79	52	68	85	120	?	?	?	?	?	
		KNUE040417-80	70	60	?	130	?	?	?	?	?	
Ignotornis gajinensis	Ignotornidae	KNUE081001-1	?	70	60	130	106	?	?	?	?	Kim et al. 2012
		KNUE081001-2	?	73	67	140	104	207	160	?	72	
		KNUE081001-3	?	80	60	140	87	173	130	?	92	
		KNUE081001-4	?	?	?	?	140	226	172	?	63	
		KNUE081001-5	?	75	70	145	104	226	145	?	58	
		KNUE081001-6	?	70	60	130	207	311	165	?	58	
		KNUE081001-7	?	75	65	140	144	342	155	?	?	
Goseongornipes markjonesi	Ignotornidae	KPE50005	?	71	65.1	137	64	129	150	8.9	?	Lockley et al. 2006a
		KPE5005.041	?	70	55	125	67	133	170	15	?	
		KPE5005.042	?	72	54	126	71	128	130	28	?	
		KPE5005.043	?	61	59	120	74	142	174	22	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Goseongornipes markjonesi	Ignotornidae	KPE5005.044	?	75	63	138	60	111	166	16	?	Lockley et al. 2006a
Goseongornipes isp.	Ignotornidae	MGCM.H23a	?	45	70	115	?	?	?	?	?	Xing et al. 2011
		MGCM.H23b	?	53	48	101	?	?	?	?	?	
		MGCM.H23c	?	52	57	109	?	?	140	?	?	
		MGCM.H23d	?	67	85	152	?	?	?	?	?	
		MGCM.H23e	?	63	59	122	?	?	?	?	?	
Koreanaornis hamanensis	Koreanaornipodidae	KoHaAverage	?	?	?	105	?	?	?	?	?	Lockley et al. 1992
	Koreanaornipodidae	KoHaAverage	?	?	?	125	?	?	?	?	?	
Koreanaornis hamanensis	Koreanaornipodidae	ZMNH-M5010 Average	?	?	?	128	127	251	171	?	?	Azuma et al. 2012
	Koreanaornipodidae	ZMNH-M8774 Average(4)	92	34	41	74	?	?	?	?	?	
	Koreanaornipodidae	ZMNH-M8774 Average(5)	22	?	?	138	?	?	?	?	?	
	Koreanaornipodidae	ZMNH-M8772 Average	?	?	?	118	?	?	?	?	?	
Koreanaornis hamanensis	Koreanaornipodidae	KoHa-T1-L1	?	50	75	125	?	?	?	?	?	Kim et al. 2012
	Koreanaornipodidae	KoHa-T1-R1	?	65	70	135	82.9	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Koreanaornis hamanensis	Koreanaornipodidae	KoHa-T1-L2	?	?	?	?	56.55	139.5	160	?	52.78	Kim et al. 2012
		KoHa-T1-R2	?	80	90	170	84.83	156.5	145	?	60.32	
		KoHa-T1-L3	?	50	80	130	77.29	165.9	177	?	45.24	
		KoHa-T1-R3	?	70	80	150	71.63	147	177	?	43.36	
		KoHa-T1-L4	?	40	85	125	82.94	152.7	160	?	52.78	
		KoHa-T2-L1	?	68	74	142	?	?	?	?	?	
		KoHa-T2-R1	?	75	60	135	130.3	?	?	?	?	
		KoHa-T2-L2	?	65	50	115	86.88	211.8	146	?	65.16	
		KoHa-T2-R2	?	65	45	110	114	200.9	180	?	38.01	
		KoHa-T3-L1	?	70	50	120	?	?	?	?	?	
		KoHa-T3-R1	?	70	60	130	45.9	?	?	?	?	
		KoHa-T3-L2	?	70	50	120	51	91.8	145	?	43.35	
		KoHa-T3-R2	?	70	60	130	76.5	122.4	145	?	51	
		KoHa-T4-R1	?	50	60	110	?	?	?	?	?	
		KoHa-T4-L1	?	50	60	110	62.7	?	?	?	?	
		KoHa-T4-R2	?	60	60	120	79.8	142.5	180	?	34.2	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Koreanaornis hamanensis	Koreanaornipodidae	KoHa-T4-L2	?	55	60	115	51.3	142.5	170	?	45.6	Kim et al. 2012
		KoHa-T4-R3	?	50	65	115	76.95	142.5	167	?	45.6	
Koreanornis dodsoni	Koreanaornipodidae	MGCM.H10a	?	48	54	102	?	?	?	?	?	Xing et al. 2011
		MGCM.H10b	?	49	55	104	?	?	?	?	?	
		MGCM.H11a	?	36	36	72	?	?	?	?	?	
		MGCM.H111a	?	41	47	88	?	?	?	?	?	
		MGCM.H111b	?	48	40	88	?	?	?	?	?	
		MGCM.H111c	?	36	44	80	?	?	?	?	?	
		MGCM.H11c	?	32	26	58	?	?	?	?	?	
		MGCM.H11d	?	32	31	63	?	?	?	?	?	
		MGCM.H11e	?	39	41	80	?	?	?	?	?	
		MGCM.H12	?	34	34	68	?	?	?	?	?	
		MGCM.H14(H)	?	40	51	91	?	?	?	?	?	
		MGCM.H15a	?	34	44	78	?	?	?	?	?	
		MGCM.H15b	?	30	32	62	?	?	?	?	?	
		MGCM.H15c	?	41	34	75	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
		MGCM.H15d	?	45	46	91	?	?	?	?	?	
		MGCM.H15e	?	34	42	76	?	?	?	?	?	
		MGCM.H16a	?	38	38	76	?	?	?	?	?	
		MGCM.H16b	?	43	50	93	?	?	?	?	?	
		MGCM.H16c	?	47	62	109	?	?	?	?	?	
		MGCM.H16d	?	53	43	96	?	?	?	?	?	
		MGCM.H17	?	51	50	101	?	?	?	?	?	
Koreanornis dodsoni	Koreanaornipodidae	MGCM.H18a	?	32	43	75	?	?	?	?	?	Xing et al. 2011
		MGCM.H18b	?	53	51	104	?	?	?	?	?	
		MGCM.H19a	?	42	51	93	?	?	?	?	?	
		MGCM.H19b	?	36	39	75	?	?	?	?	?	
		MGCM.H19c	?	56	44	100	?	?	?	?	?	
		MGCM.H19d	?	45	37	82	?	?	?	?	?	
		MGCM.H19e	?	57	46	103	?	?	?	?	?	
		MGCM.H20a	?	46	49	95	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Koreanornis dodsoni	Koreanaornipodidae	MGCM.H20b	?	57	47	104	?	?	?	?	?	Xing et al. 2011
		MGCM.H20c	?	40	37	77	?	?	?	?	?	
		MGCM.H20d	?	46	52	98	?	?	?	?	?	
		MGCM.H20e	?	44	43	87	?	?	?	?	?	
		MGCM.H20f	?	45	55	100	?	?	?	?	?	
		MGCM.H20g	?	43	46	89	?	?	?	?	?	
		MGCM.H20h	?	40	36	76	?	?	?	?	?	
		MGCM.H20i	?	50	55	105	?	?	?	?	?	
Jindongornipes kimi	Jindongornipedidae	KPE50006	?	?	?	125	?	?	140	?	?	Lockey et al. 1992
		KPE50006	?	?	?	150	?	?	140	?	?	
Shandongornipes muxiai	Shandongornipodidae	LRH-dz66	?	118	24	142	?	?	?	?	?	Li et al. 2005; Lockley et al. 2007
		LRH-dz67(H)	?	91	37	128	41	?	?	?	?	
		LRH-dz68(P)	?	100	35	135	46	86	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Shandongornipes muxiai	Shandongornipodidae	LRH-dz69	?	?	?	?	44	90	?	?	?	Li et al. 2005; Lockley et al. 2007
		LRH-dz70	?	92	38	130	45	88	?	?	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A01	?	82	50	132	?	?	?	2	?	Lockley et al. 2006b
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A02	?	49	56	105	151	?	?	10	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A03	?	45	42	87	177	327	?	25	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A04	?	39	80	119	148	325	?	15	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A05	?	?	?	?	?	?	?	?	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A06	?	44	75	119	?	315	?	20	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A07	?	50	51	101	163	?	?	2	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A08	?	60	50	110	127	288	?	?	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A12	?	40	40	80	?	?	?	1	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A13	?	?	?	?	?	?	?	?	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A14	?	36	52	88	?	280	?	10	?	
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A15	?	39	55	94	155	?	?	7	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A27	?	53	63	116	?	?	?	9	?	Lockley et al. 2006b
		CU 212.21/22-A28	?	28	?	?	152	?	?	?	?	
		CU 212.21/22-A29	?	49	?	?	220	352	?	?	?	
		CU 212.21/22-A30	?	42	62	104	147	347	?	11	?	
		CU 212.21/22-A31	?	61	56	117	177	320	?	1	?	
		CU 212.21/22-A32	?	48	55	103	166	340	?	?	?	
		CU 212.21/22-A33	?	77	64	141	170	335	?	1	?	
		CU 212.21/22-A34	?	56	84	140	150	320	?	2	?	
		CU 212.21/22-A35	?	53	70	123	172	322	?	?	?	
		CU 212.21/22-A36	?	51	68	119	142	313	?	?	?	
		CU 212.21/22-A37	?	70	56	126	182	323	?	5	?	
		CU 212.21/22-A38	?	64	61	125	112	299	?	?	?	
		CU 212.21/22-A39	?	74	67	141	184	300	?	2	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Pullornipes aureus	Koreanornipodidae	CU 212.21/22-A40	?	50	50	100	130	314	?	2	?	Lockley et al. 2006b
		CU 212.21/22-A41	?	40	59	99	170	298	?	5	?	
		CU 212.21/22-A42	?	50	64	114	128	295	?	1	?	
		CU 212.21/22-A43	?	53	85	138	162	288	?	12	?	
		CU 212.21/22-A44	?	90	42	132	122	286	?	10	?	
		CU 212.21/22-A45	?	49	90	139	136	260	?	15	?	
Limiavipes curriei	Limiavipedidae	aa1R	0	?	?	?	?	?	?	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014
		aa2L	0	?	?	?	240	?	150	?	?	
		aa3R	0	?	?	?	219	445	153	?	?	
		aa4L	0	?	?	?	248	450	157	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Limiavipes curriei	Limiavipedidae	aa5R	0	?	?	?	230	462	158	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014
		aa6L	0	68	54	112	235	455	159	?	?	
		aa7R	0	?	?	?	252	479	151	?	?	
		aa8L	0	?	?	?	240	473	?	?	?	
		cd1R	0	50	70	120	?	?	?	?	?	
		cd2L	0	?	?	?	220	?	135	?	?	
		cd3R	0	?	?	?	180	365	150	?	?	
		cd4L	0	?	?	?	235	405	?	?	?	
		A1L	0	50	60	110	230	?	?	?	?	
		A2R	0	?	?	?	?	?	?	?	?	
		AqCu-B1R	0	72	63	135	?	?	?	?	?	
		AqCu-B2L	0	?	?	?	261	?	163	?	?	
		AqCu-B3R	0	?	?	?	261	514	178	?	?	
		AqCu-B4L	0	?	?	?	254	514	?	?	?	
		AqCu-F1L	0	?	?	?	?	?	?	?	?	
		AqCu-F2R	0	?	?	?	220	?	140	?	?	
		AqCu-F3L	0	55	69	124	210	410	132	?	?	
		AqCu-F4R	0	?	?	?	250	420	?	?	?	
		AqCu-GF1L	0	?	?	?	?	?	?	?	?	
		AqCu-GF2R	0	?	?	?	218	?	127	?	?	
		AqCu-GF3L	0	?	?	?	225	396	144	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Limiavipes curriei	Limiavipedidae	AqCu-GF4R	0	67	65	132	220	423	149	?	?	McCrea and Sarjeant 2001; McCrea et al. 2014
		AqCu-GF5L	0	?	?	?	225	432	153	?	?	
		AqCu-GF6R	0	?	?	?	229	442	?	?	?	
		AqCu-FG1L	0	?	?	?	?	?	?	?	?	
		AqCu-FG2R	0	60	65	125	230	?	165	?	?	
		AqCu-FG3L	0	?	?	?	235	460	140	?	?	
		AqCu-FG4R	0	?	?	?	190	390	147	?	?	
		AqCu-FG5L	0	?	?	?	270	430	151	?	?	
		AqCu-FG6R	0	?	?	?	225	480	151	?	?	
		AqCu-FG7L	0	?	?	?	315	530	?	?	?	
		AqCu-H1L	0	?	?	?	?	?	?	?	?	
		AqCu-H2R	0	?	?	?	300	?	166	?	?	
		AqCu-H2R	0	?	?	?	300	?	166	?	?	
		AqCu-H3L	0	62	59	131	305	600	172	?	?	
		AqCu-H4R	0	?	?	?	260	570	?	?	?	
		AqCu-PARA1R	0	50	69	119	?	?	?	30	?	
		AqCu-PARA2L	0	52	82	134	208	?	156	-4	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Limiavipes curriei	Limiavipedidae	AqCu-PARA3R	0	63	74	137	273	476	156	22	?	McCrea and Sarjeant 2001; McCrea et al. 2014
		AqCu-PARA4L	0	58	68	126	227	489	159	35	?	
		AqCu-PARA5R	0	54	70	124	215	433	163	14	?	
		AqCu-PARA6L	0	61	58	119	215	?	?	23	?	
		AqCu-PARA7R	0	58	61	119	221	452	?	25	?	
		AqCu-PARA8L	0	?	?	?	?	?	?	19	?	
		AqCu-PARA9R	0	61	67	128	?	?	?	?	?	
		AqCu-PARA10L	0	55	76	131	234	?	?	41	?	
		AqCu-PARB1R	0	71	79	150	?	?	?	?	?	
		AqCu-PARB2L	0	?	?	?	?	?	?	?	?	
		AqCu-PARB3R	0	58	55	113	?	510	?	30	?	
		AqCu-PARB4L	0	61	53	114	248	?	?	16	?	
		AqCu-PARB5R	0	64	55	119	237	476	158	24	?	
		AqCu-PARB6L	0	?	?	?	?	?	?	-30	?	
		AqCu-PARB7R	0	50	57	107	?	525	?	16	?	
		AqCu-PARB8L	0	44	52	96	298	?	?	0	?	
		AqCu-PARB9R	0	84	53	137	214	510	173	27	?	
Barrosopus slobodai	?	PVPH-SB-415-17C-86	0	?	?	120	120	230	?	?	?	Coria et al. 2002
		PVPH-SB-415-17C-87	0	63	52	115	110	210	?	9	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Barrosopus slobodai	?	PVPH-SB-415-17C-88	0	66	54	120	100	235	?	19	?	Coria et al. 2002
		PVPH-SB-415-17C-89	0	68	42	110	135	225	155	6	?	
		PVPH-SB-415-17C-90	0	?	?	?	90	165	?	?	?	
		PVPH-SB-415-17C-91	0	?	?	100	110	185	?	?	?	
		PVPH-SB-415-17C-92	0	?	?	140	30	135	?	?	?	
		PVPH-SB-415-17C-93	0	?	?	120	?	?	?	?	?	
		PVPH-SB-415-17C-94	0	?	?	120	?	?	?	?	?	
Dongyangornipes sinensis	?	DoSi-Average	?	?	?	98	?	?	?	?	?	Azuma et al. 2013
		DoSi-Holotype	?	44	44	89	?	?	?	?	?	
Moguiornipes robusta	?	MGCM.H25a	?	48	42	90	?	?	?	?	?	Xing et al. 2011
		MGCM.H25b	?	54	39	93	?	?	?	?	?	
		MGCM.H25c	?	50	?	?	?	?	?	?	?	
		MGCM.H25d	?	57	42	99	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Moguiornipes robusta	?	MGCM.H27a	?	?	50	?	?	?	?	?	?	Xing et al. 2011
Tatarornipes chabuensis	?	1-CU 214	?	?	?	119	?	?	?	?	?	Lockley et al. 2012
		2-CU 214.184	?	?	?	105	?	?	?	?	?	
		3-CU 214.185	?	?	?	106	?	?	?	?	?	
		4-CU 214.184	?	?	?	125	?	?	?	?	?	
		5-CU 214.187	?	41	61	102	?	?	?	?	?	
		6-CU 214.187	?	?	?	108	?	?	?	?	?	
		7-CU 214.188	?	55	65	120	?	?	?	?	?	
		8-CU 214.186	?	?	?	105	?	?	?	?	?	
		9-CU 214.184	?	48	52	100	?	?	?	?	?	
		10-CU 214.189	?	?	?	118	?	?	?	?	?	
		11-CU 214.14	?	?	?	87	?	?	?	?	?	
		12-CU 214.14	?	?	?	97	?	?	?	?	?	
		13-CU 214.11	?	56	54	110	?	?	?	?	?	
		14-CU 214.12	?	?	?	107	?	?	?	?	?	
		15-CU 214.10	?	44	53	97	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Tatarornipes chabuensis	?	16-CU 214.9	?	?	?	98	?	?	?	?	?	Lockley et al. 2012
		17-CU 214.6	?	61	72	133	?	?	?	?	?	
		18-CU 214.7	?	?	?	122	?	?	?	?	?	
		19-CU 214.8	?	55	83	138	?	?	?	?	?	
		20-CU 214.8	?	61	53	105	?	?	?	?	?	
		1-CU 214.3	?	?	?	112	?	?	?	?	?	
		2-CU 214.3	?	?	?	118	?	?	?	?	?	
		3-CU 214.3	?	?	?	118	?	?	?	?	?	
		4-CU 214.5	?	?	?	101	?	?	?	?	?	
		5-CU 214.5	?	?	?	109	?	?	?	?	?	
		6-CU 214.18	?	65	59	124	?	?	?	?	?	
		7-CU 214.18	?	68	66	134	?	?	?	?	?	
		8-CU 214.160	?	?	?	135	?	?	?	?	?	
		9-CU 214.19	?	?	?	111	?	?	?	?	?	
		10-CU 214.19	?	?	?	98	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Tatarornipes chabuensis	?	11-CU 214.148	?	53	54	107	?	?	?	?	?	Lockley et al. 2012
		12-CU 214.149	?	40	56	81	?	?	?	?	?	
		13-CU 214.150	?	40	56	98	?	?	?	?	?	
		14-CU 214.151	?	46	48	94	?	?	?	?	?	
		15-CU 214.152	?	?	?	102	?	?	?	?	?	
		16-CU 214.152	?	?	?	126	?	?	?	?	?	
		17-CU 214.153	?	59	68	127	?	?	?	?	?	
		18-CU 214.155	?	?	?	115	?	?	?	?	?	
		19-CU 214.155	?	?	?	102	?	?	?	?	?	
		20:214.156	?	?	?	82	?	?	?	?	?	
		21-CU 214.154	?	?	?	129	?	?	?	?	?	
		22-CU 214.154	?	?	?	122	?	?	?	?	?	
		23-CU 214.154	?	32	63	95	?	?	?	?	?	
Uhangrichnus chuni	?	KPE50101-A01	?	45	50	95	?	?	?	?	?	Yang et al. 1995
		KPE50101-A02	?	54	55	109	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Uhangrichnus chuni	?	KPE50101-A03	?	?	?	?	?	?	?	?	?	Yang et al. 1995
		KPE50101-A04	?	52	60	112	?	?	?	?	?	
		KPE50101-A05	?	45	59	104	?	?	?	?	?	
		KPE50101-A06	?	42	56	98	?	?	?	?	?	
		KPE50101-A07	?	49	54	103	?	?	?	?	?	
		KPE50101-A08	?	58	59	117	?	?	?	?	?	
		KPE50101-A09	?	?	?	?	?	?	?	?	?	
		KPE50101-A10	?	51	52	103	?	?	?	?	?	
		KPE50101-A11	?	55	61	116	?	?	?	?	?	
		KPE50101-A12	?	46	51	97	?	?	?	?	?	
		KPE50101-A13	?	52	60	112	?	?	?	?	?	
		KPE50101-A14	?	46	60	106	?	?	?	?	?	
		KPE50101-A15	?	48	52	100	?	?	?	?	?	
		KPE50101-A16	?	45	55	100	?	?	?	?	?	
		KPE50101-A17	?	?	?	?	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Uhangrichnus chuni	?	KPE50101-A18	?	52	55	107	?	?	?	?	?	Yang et al. 1995
		KPE50101-A19	?	?	?	?	?	?	?	?	?	
		KPE50101-A20	?	54	58	112	?	?	?	?	?	
		KPE50101-A22	?	46	58	104	?	?	?	?	?	
		KPE50101-A24	?	47	53	100	?	?	?	?	?	
		KPE50101-A25	?	54	56	110	?	?	?	?	?	
		KPE50101-A26	?	48	54	102	?	?	?	?	?	
		KPE50101-A27	?	52	60	112	?	?	?	?	?	
		KPE50101-A28	?	40	48	88	?	?	?	?	?	
		KPE50101-A29	?	60	?	?	?	?	?	?	?	
		KPE50101-A30	?	55	62	117	?	?	?	?	?	
		KPE50101-A31	?	58	59	117	?	?	?	?	?	
		KPE50101-A32	?	54	56	110	?	?	?	?	?	
		KPE50101-A33	?	60	60	120	?	?	?	?	?	
		KPE50101-A34	?	50	50	100	?	?	?	?	?	
		KPE50101-A34	?	50	50	100	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Uhangrichnus chuni	?	KPE50101-A36	?	50	57	107	?	?	?	?	?	Yang et al. 1995
		KPE50101-A37	?	56	66	122	?	?	?	?	?	
		KPE50101-A42	?	57	63	120	?	?	?	?	?	
		KPE50101-A43	?	56	66	122	?	?	?	?	?	
		KPE50101-A44	?	61	62	123	?	?	?	?	?	
		KPE50101-A45	?	60	66	126	?	?	?	?	?	
		KPE50101-A46	?	47	53	100	?	?	?	?	?	
		KPE50101-A47	?	53	57	110	?	?	?	?	?	
		KPE50101-A48	?	58	60	118	?	?	?	?	?	
		KPE50101-A49	?	55	65	120	?	?	?	?	?	
		KPE50101-A50	?	63	65	128	?	?	?	?	?	
		KPE50101-A51	?	67	67	134	?	?	?	?	?	
		KPE50101-A52	?	58	62	120	?	?	?	?	?	
		KPE50101-A54	?	42	63	105	?	?	?	?	?	
		KPE50101-A55	?	56	64	120	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Uhangrichnus chuni	?	KPE50101-A56	?	61	63	124	?	?	?	?	?	Yang et al. 1995
		KPE50101-A57	?	42	68	110	?	?	?	?	?	
		KPE50101-A58	?	57	61	118	?	?	?	?	?	
		KPE50101-A59	?	42	68	110	?	?	?	?	?	
		KPE50101-A60	?	57	61	118	?	?	?	?	?	
		KPE50101-B01	?	47	50	97	?	?	?	?	?	
		KPE50101-B02	?	?	?	?	?	?	?	?	?	
		KPE50101-B03	?	48	52	100	?	?	?	?	?	
		KPE50101-B04	?	43	53	96	?	?	?	?	?	
		KPE50101-B05	?	57	58	115	?	?	?	?	?	
		KPE50101-B06	?	46	51	97	?	?	?	?	?	
		KPE50101-B07	?	45	48	93	?	?	?	?	?	
		KPE50101-B08	?	53	61	114	?	?	?	?	?	
		KPE50101-B09	?	54	66	120	?	?	?	?	?	
		KPE50101-B10	?	46	50	96	?	?	?	?	?	

Ichnotaxon	Ichnofamily	Track #	Divarication				PL	SL	PA	FR	TW	Reference
			I-II	II-III	III-IV	TOT						
Uhangrichnus chuni	?	KPE50101-B11	?	51	59	110	?	?	?	?	?	Yang et al. 1995
		KPE50101-B12	?	42	45	87	?	?	?	?	?	
		KPE50101-B13	?	?	?	?	?	?	?	?	?	
		KPE50101-B14	?	41	56	97	?	?	?	?	?	
		KPE50101-B15	?	48	60	108	?	?	?	?	?	
		KPE50101-B16	?	54	63	117	?	?	?	?	?	
		KPE50101-B17	?	58	62	120	?	?	?	?	?	
		KPE50101-B18	?	?	?	?	?	?	?	?	?	
		KPE50101-B19	?	42	63	105	?	?	?	?	?	
		KPE50101-B20	?	53	55	108	?	?	?	?	?	
		KPE50101-C01	?	59	66	125	?	?	?	?	?	
		KPE50101-C02	?	?	?	?	?	?	?	?	?	
		KPE50101-C03	?	51	68	119	?	?	?	?	?	
		KPE50101-C04	?	54	57	111	?	?	?	?	?	
		KPE50101-C05	?	61	63	124	?	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Uhangrichnus chuni	?	KPE50101-C06	?	66	69	135	?	?	?	?	?	Yang et al. 1995
		KPE50101-C07	?	55	58	113	?	?	?	?	?	
		KPE50101-C08	?	59	61	120	?	?	?	?	?	
		KPE50101-C09	?	?	?	?	?	?	?	?	?	
		KPE50101-C10	?	53	60	113	?	?	?	?	?	
Uhangrichnus topotype	?	KPE50101-T1	?	?	?	?	?	?	?	?	?	Lockley et al. 2012
		KPE50101-T2	?	?	?	?	77	?	?	30	?	
		KPE50101-T4	?	?	?	?	81	159	?	18	?	
		KPE50101-T3	?	?	?	?	77	155	?	12	?	
Magnoavipes lowei	Theropod	DMNH918.1	?	53	47	100	?	?	?	10	?	Lee 1997
		DMNH918.2	?	64	54	118	1070	?	?	28	?	
		DMNH918.3	?	60	50	110	1080	2170	1680	14	?	
		DMNH918.4	?	62	48	110	1040	2080	1630	35	?	
		DMNH918.5	?	62	47	109	980	2000	1780	25	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Magnoavipes lowei	Theropod	DMNH918.6	?	58	54	112	1100	2080	1700	40	?	Lee 1997
Magnoavipes caneeri	Theropod	CU MWC200-1.1	?	?	?	?	?	?	?	0	?	Lockley et al. 2001
		CU MWC200-1.2	?	40	60	100	1400	?	?	0	?	
		CU MWC200-1.3	?	?	?	?	?	2800	?	?	?	
		CU MWC200-1.4	?	?	?	?	?	?	?	?	?	
		CU MWC200-1.5	?	35	52	87	1370	2780	?	?	?	
		CU MWC200-1.6	?	?	41	?	1400	2830	?	0	?	
		CU MWC200-1.7	?	37	43	80	1420	?	?	?	?	
		CU MWC200-1.8	?	51	50	101	1380	?	?	?	?	
		CU MWC200-1.9	?	?	?	?	?	2680	?	?	?	
		CU MWC200-1.10	?	45	40	85	?	?	?	?	?	
		CU MWC200-2.01	?	35	45	80	?	?	?	?	?	
		CU MWC200-2.02	?	35	60	95	1000	?	?	?	?	

Ichnotaxon	**Ichnofamily**	**Track #**	**Divarication**				**PL**	**SL**	**PA**	**FR**	**TW**	**Reference**
			I-II	**II-III**	**III-IV**	**TOT**						
Magnoavipes caneeri	Theropod	CU MWC200-2.03	?	48	57	105	1050	2050	?	?	?	Lockley et al. 2001
		CU MWC200-2.04	?	?	50	?	990	2040	?	?	?	
		CU MWC200-3.01	?	32	37	69	?	?	?	?	?	
		CU MWC200-3.02	?	32	33	65	930	?	?	?	?	
		CU MWC200-3.03	?	32	37	69	920	1840	?	?	?	
		CU MWC200-3.04	?	34	37	71	930	1840	?	?	?	
		CU MWC200-4.01	?	?	?	?	?	?	?	?	?	
		CU MWC200-4.02	?	?	?	?	1170	?	?	?	?	
		CU MWC200-4.03	?	40	40	80	1130	?	?	?	?	
		CU MWC200-5.01	?	42	45	87	?	?	?	?	?	
		CU MWC200-5.02	?	43	60	103	?	?	?	?	?	
Magnoavipes denaliensis	Theropod	Smallest	?	?	?	97	?	?	?	?	?	Fiorillo et al. 2011
		Largest	?	?	?	116	?	?	?	?	?	

Appendix for Chapter 6

Appendix A6.01: Linear and angular data of footprints of *Wupus agilis* (Early Cretaceous) from the Lotus Tracksite, Chongqing, China—Linear and angular data collected from the *Wupus agilis* tracks at the Lotus Tracksite. Track # corresponds to individual tracks within the one meter X one meter grid system established on the track surface for the purposes of data collection. For example, C11 refers to grid square C11, and T refers to track, and the number refers to the order in which the footprint was documented within grid square C11. FL, footprint length; FLwPad, footprint length including proximal morphological features of the "heel;" FW, footprint width; L/W, footprint length:footprint width ratio; L, left; III, digit III; R, right; TOT, total divarication. See Figure 3 in text for schematic of footprint measurements.

Track #	**FL (mm)**	**FLwPad (mm)**	**FW (mm)**	**L/W**	**Digit lengths (mm)**			**Digit widths (mm)**			**Divarication (degrees)**		
					L	**III**	**R**	**L**	**III**	**R**	**L-III**	**III-R**	**TOT**
aa07-T01	91	91	97	0.94	75	91	64	?	14	14	45	40	85
aa08-T01	90	90	105	0.86	77	90	62	13	17	18	48	32	80
aa08-T02	120	120	117	1.03	85	120	83	?	17	17	47	47	94
aa10-T01	100	100	113	0.88	71	100	65	10	15	15	51	70	121
aa10-T02	80	80	?	?	59	80	?	?	11	?	60	?	?
A06-T01	99	99	117	0.85	80	99	67	10	10	14	53	54	107
A06-T02	116	116	150	0.77	101	116	78	10	13	13	51	60	111
A06-T03	81	81	100	0.81	63	81	65	9	9	7	62	50	112
A06-T04	110	110	130	0.85	90	110	80	15	21	20	50	50	100
A06-T05	100	100	131	0.76	85	100	70	15	15	?	54	63	117
A07-T01	108	108	92	1.17	81	108	75	?	9	15	32	38	70
A07-T02	107	107	124	0.86	96	107	80	20	25	17	44	40	84
A07-T03	110	110	124	0.89	80	110	74	?	14	12	43	55	98
A07-T04	90	90	122	0.74	81	90	78	12	?	18	46	51	97
A07-T05	?	?	?	?	?	?	?	?	?	?	?	?	?
A07-T06	92	92	128	0.72	85	92	90	?	15	10	48	46	94
A07-T07	94	94	113	0.83	73	94	61	?	15	?	58	53	111
A07-T08	90	90	110	0.82	81	90	60	8	11	12	51	31	82
A07-T09	82	82	95	0.86	61	82	60	9	15	14	45	59	104
A08-T01	?	?	100	?	80	?	62	12	10	15	54	44	98
A08-T02	97	97	113	0.86	70	97	70	17	15	16	46	48	94
A08-T03	100	100	125	0.8	85	100	80	15	20	10	53	31	84
A08-T04	?	?	?	?	?	?	?	?	?	?	?	?	?
A08-T05	100	100	114	0.88	80	100	70	?	15	?	43	39	82
A08-T06	115	115	123	0.93	97	115	73	20	20	15	50	45	95
A08-T07	105	105	115	0.91	80	105	80	13	15	16	48	47	95
A08-T08	94	94	106	0.89	73	94	75	10	15	17	55	37	92
A08-T09	95	95	112	0.85	78	95	70	?	16	15	47	34	81
A08-T10	112	112	145	0.77	80	112	90	19	15	?	53	59	112
A08-T11	?	?	?	?	?	?	?	?	?	?	?	?	?

A09-T01	108	108	135	0.80	85	108	90	?	16	?	56	59	115
A09-T02	90	90	130	0.69	?	90	?	?	?	?	?	?	?
A09-T03	85	85	105	0.81	67	85	75	14	17	18	45	55	100
A09-T04	110	110	115	0.96	85	110	66	20	18	23	46	55	101
A10-T01	137	137	110	1.25	110	137	107	12	15	?	35	?	?
A10-T02	116	116	?	?	?	116	83	?	10	15	?	49	?
A10-T03	101	101	132	0.77	79	101	80	13	20	17	63	59	122
A11-T01	94	94	116	0.81	72	94	68	15	16	10	60	55	115
B05-T01	89	89	113	0.79	74	89	62	11	14	19	45	62	107
B06-T01	100	100	100	1.00	64	100	70	10	15	12	42	48	90
B06-T02	87	87	105	0.83	70	87	70	10	15	11	48	45	93
B07-T01	95	95	87	1.09	75	95	55	13	14	14	42	33	75
B07-T02	94	94	100	0.94	65	94	65	17	15	19	49	46	95
B07-T03	95	95	97	0.98	77	95	74	22	15	11	35	40	75
B07-T04	93	93	90	1.03	62	93	62	14	17	11	42	45	87
B07-T05	?	?	?	?	?	?	?	?	?	?	?	?	?
B07-T06	77	77	?	?	?	77	62	?	14	15	?	64	?
B07-T07	115	115	134	0.86	88	115	95	?	16	15	51	46	97
B07-T08	112	112	108	1.04	88	112	82	13	16	19	44	34	78
B07-T09	118	118	150	0.79	100	118	84	16	16	11	45	60	105
B07-T10	?	?	?	?	?	?	?	?	?	?	?	?	?
B07-T11	102	102	120	0.85	75	102	71	15	14	16	52	53	105
B07-T12	102	102	117	0.87	73	102	73	?	?	12	51	55	106
B07-T13i	105	105	?	?	?	105	?	?	19	15	?	45	?
B07-T14	72	72	98	0.73	70	72	59	1	16	17	48	47	95
B07-T15	110	110	115	0.96	85	110	64	14	16	13	41	49	90
B07-T16	87	87	130	0.67	77	87	65	?	10	11	55	62	117
B07-T17	90	90	100	0.90	84	90	74	9	16	12	36	43	79
B08-T01	85	85	103	0.83	80	85	70	17	15	20	44	46	90
B08-T02	95	95	90	1.06	80	95	83	?	?	?	39	31	70
B08-T03	103	103	134	0.77	85	103	75	25	20	22	52	68	120
B08-T04	100	100	114	0.88	77	100	73	14	25	15	51	49	100
B08-T05	100	115	105	0.95	68	100	72	10	10	12	40	45	85
B08-T06	?	?	?	?	?	?	55	15	20	14	45	40	85
B08-T07	?	?	?	?	?	?	?	?	?	?	?	?	?
B09-T01	100	100	112	0.89	87	100	78	19	10	16	45	48	93
B09-T02	?	?	?	?	?	?	?	?	?	?	?	?	?
B09-T03	106	106	118	0.90	82	106	83	12	10	13	41	41	82
B09-T04	92	92	108	0.85	75	92	64	10	12	16	47	34	81
B09-T05	109	109	108	1.01	82	109	69	10	16	12	42	45	87
B09-T06	112	112	113	0.99	86	112	72	13	15	?	37	55	92
B09-T07	120	120	132	0.91	95	120	92	16	18	?	45	45	90

B09-T08	126	126	143	0.88	122	126	81	?	20	12	40	49	89
B09-T09	?	?	125	?	?	?	?	?	16	14	51	66	117
B09-T10	?	?	?	?	?	?	?	?	?	?	?	?	?
B09-T11	115	115	132	0.87	86	115	85	20	17	?	52	56	108
B09-T12	92	92	115	0.80	71	92	69	15	16	15	56	60	116
B10-T01	98	98	115	0.85	70	98	79	18	17	27	52	65	117
B10-T02	92	92	105	0.88	71	92	71	12	11	12	48	45	93
B10-T03	112	112	?	?	?	11.2	75	?	10	10	53	?	?
B10-T04	88	88	104	0.85	61	88	58	10	10	9	65	59	124
B10-T05	110	110	145	0.76	98	110	85	?	?	?	50	67	117
B10-T07	102	102	123	0.83	85	102	84	14	14	?	43	55	98
B10-T08	120	120	145	0.83	105	120	84	10	13	10	49	54	103
B11-T01	94	94	102	0.92	67	94	70	16	14	20	49	49	98
C04-T01	100	100	?	?	?	100	70	?	10	10	?	85	?
C05-T01	115	115	121	0.95	80	115	71	10	12	22	46	52	98
C05-T02	94	94	107	0.88	78	94	67	12	10	15	44	46	90
C05-T03	?	?	?	?	?	?	?	?	?	?	?	?	?
C06-T01	97	97	110	0.88	81	97	80	12	14	15	38	42	80
C06-T02	108	108	152	0.71	97	108	82	15	15	10	58	65	123
C06-T03	90	90	90	1.00	77	90	87	12	10	15	37	30	67
C06-T04	?	?	?	?	?	?	?	?	?	?	?	61	?
C06-T05	92	92	110	0.84	75	92	85	14	17	15	42	50	92
C06-T06m	100	100	118	0.85	80	100	77	17	23	17	45	36	81
C07-T01	70	70	93	0.75	62	70	59	10	9	10	50	53	103
C07-T02	125	125	120	1.04	105	125	85	?	15	14	44	41	85
C07-T03	100	100	?	?	?	100	80	?	15	23	?	45	?
C07-T04	113	113	125	0.90	92	113	83	18	17	15	45	47	92
C07-T05	84	84	?	?	?	84	65	?	10	10	37	?	?
C07-T06	88	88	97	0.91	60	88	62	18	13	16	50	52	102
C07-T07	78	78	105	0.74	65	78	59	15	?	15	65	50	115
C07-T08	80	80	108	0.74	75	80	75	15	15	10	47	49	96
C07-T09	105	120	137	0.77	95	105	75	12	15	20	50	68	118
C07-T10	105	105	114	0.92	85	105	70	15	15	?	50	55	105
C07-T11	105	120	137	0.77	93	105	72	15	17	17	48	65	113
C07-T12m	95	107	135	0.70	80	95	85	20	20	17	50	50	100
C07-T13	120	120	135	0.89	82	120	87	20	20	?	50	50	100
C07-T14	103	103	107	0.96	77	103	70	15	15	17	49	41	90
C07-T15	115	115	115	1.00	75	115	85	?	17	20	48	36	84
C08-T02	?	?	?	?	?	?	?	?	?	?	?	?	?
C08-T03	122	122	140	0.87	94	122	96	?	16	?	45	48	93
C08-T04	124	124	150	0.83	103	124	106	15	?	?	38	49	87
C08-T05	114	114	102	1.12	80	114	72	12	12	13	40	42	82

C08-T06	120	120	120	1	97	120	86	17	16	21	40	40	80
C08-T07	70	70	118	0.59	65	70	66	12	13	16	70	47	117
C08-T08	110	110	90	1.22	65	110	86	11	11	15	35	36	71
C08-T09	109	109	92	1.18	82	109	72	13	14	14	34	41	75
C08-T10	134	134	130	1.03	116	134	106	?	?	?	34	41	75
C09-T01	100	100	108	0.93	81	100	78	10	12	15	45	46	91
C09-T02	80	80	104	0.771	59	80	64	18	17	20	57	72	129
C09-T03	83	83	118	0.70	65	83	69	?	?	?	59	73	132
C09-T04	95	95	120	0.79	63	95	77	17	20	20	57	61	118
C09-T05	78	78	108	0.72	77	78	73	12	15	19	52	43	95
C09-T06	117	117	155	0.75	95	117	84	23	10	25	53	71	124
C09-T07	103	103	125	0.82	75	103	75	?	?	?	58	65	123
C09-T08	102	102	128	0.80	92	102	75	15	20	20	52	49	101
C09-T09	?	?	?	?	?	?	?	?	?	?	?	?	?
C09-T10	118	118	130	0.91	75	118	85	?	?	?	57	63	120
C10-T01	89	89	120	0.74	76	89	70	15	10	10	54	69	123
C10-T02	82	82	115	0.71	78	82	60	?	12	15	55	67	122
C10-T03	95	95	130	0.73	81	95	80	10	10	11	55	65	120
C10-T04	96	96	122	0.79	72	96	72	13	13	15	60	63	123
C11-T01	105	105	120	0.88	75	105	85	12	15	14	52	43	95
C11-T02	87	87	94	0.93	55	87	55	14	10	11	60	60	120
D05-T01	98	98	132	0.74	90	98	80	15	15	14	59	51	110
D05-T02	95	95	97	0.98	68	95	68	10	14	10	47	47	94
D06-T01	107	107	125	0.86	84	107	100	?	19	16	44	43	87
D06-T02	96	96	100	0.96	86	96	74	11	20	10	49	45	94
D06-T04	83	83	?	?	?	83	67	?	13	14	51	?	?
D06-T05	96	96	102	0.94	74	96	72	10	12	14	45	40	85
D06-T06	97	97	107	0.91	82	97	70	20	17	17	37	53	90
D06-T07	116	116	115	1.01	87	116	79	12	16	16	41	49	90
D06-T08	125	125	122	1.02	102	125	88	22	11	18	39	38	77
D06-T09	108	108	88	1.23	60	108	77	20	17	20	27	49	76
D06-T10	103	103	98	1.05	72	103	76	12	13	18	39	39	78
D07-T01	114	114	127	0.90	84	114	72	18	15	16	48	58	106
D07-T02	?	?	?	?	?	?	?	?	?	?	?	?	?
D07-T03	108	108	118	0.92	90	108	90	21	22	19	51	57	108
D07-T04	122	122	?	?	?	122	90	?	16	16	?	42	?
D07-T05	?	?	?	?	?	?	?	?	?	?	?	?	?
D07-T06	?	?	?	?	?	?	?	?	?	?	?	37	?
D08-T02	111	111	125	0.89	85	111	90	13	15	21	37	42	79
D08-T03	98	108	117	0.84	90	98	86	33	15	19	42	42	84
D08-T04	95	95	130	0.73	87	95	80	16	16	15	42	68	110
D08-T05	114	130	?	?	?	114	82	?	13	29	?	55	?

D08-T06	108	108	82	1.32	67	108	61	10	14	11	43	38	81
D09-T01	115	115	140	0.82	97	115	97	27	33	19	51	47	98
D09-T02i	116	116	?	?	?	116	77	?	16	14	?	43	?
D09-T03	103	103	123	0.84	90	103	83	15	20	25	41	49	90
D09-T05	125	133	137	0.91	90	125	84	21	15	23	50	54	104
D10-T01	92	92	?	?	75	92	?	13	17	?	69	?	?
D10-T02	100	100	113	0.88	69	100	80	15	15	16	52	50	102
D10-T03	118	118	129	0.91	97	118	90	26	29	26	41	65	106
D10-T04	105	105	119	0.88	86	105	86	17	20	22	43	65	108
D10-T05	89	110	122	0.73	75	89	80	23	20	20	48	54	102
D10-T06	?	?	?	?	?	?	?	?	17	12	?	49	?
D10-T07	?	?	?	?	?	?	?	?	?	?	?	?	?
D10-T08	?	?	?	?	?	?	?	?	?	?	?	?	?
D10-T09	111	111	?	?	?	111	80		13	18	?	48	?
E04-T01	111	111	150	0.74	82	111	89	27	23	27	75	54	129
E05-T01	98	98	107	0.92	78	98	72	10	15	20	45	47	92
E05-T02	83	83	97	0.86	62	83	59	11	10	15	57	48	105
E05-T03	97	97	100	0.97	81	97	70	?	15	15	40	43	83
E05-T04	?	?	97	?	72	?	62	14	17	12	47	46	93
E06-T01	102	102	117	0.87	90	102	89	?	?	?	36	41	77
E06-T02	?	?	90	?	?	?	?	?	?	10	45	35	80
E06-T03	96	96	93	1.03	79	96	61	?	17	12	42	39	81
E07-T01	98	98	?	?	82	98	?	11	16	?	43	?	?
E07-T02	?	?	?	?	?	?	?	?	?	?	?	?	?
E09-T01	105	105	117	0.90	92	105	74	?	17	20	45	47	92
E09-T02	115	115	136	0.85	93	115	82	24	21	?	49	51	100
E09-T03	124	124	146	0.85	96	124	100	24	17	17	50	44	94
E09-T04	?	?	?	?	?	?	?	?	?	?	?	?	?
E09-T05	122	122	134	0.91	95	122	87	19	23	17	46	46	92
E10-T01	100	100	?	?	88	100	?	18	15	?	48	?	?

Appendix A6.02: Linear and angular data of trackways of *Wupus agilis* (Early Cretaceous) from the Lotus Tracksite, Chongqing, China—Linear and angular data collected from the *Wupus agilis* tracks at the Lotus Tracksite. Track # corresponds to individual tracks within the one meter X one meter grid system established on the track surface for the purposes of data collection. For example, C11 refers to grid square C11, and T refers to track, and the number refers to the order in which the footprint was documented within grid square C11. PL, pace length; SL, stride length; FL, footprint length; PA, pace angulation; FR, footprint rotation; TW, trackway width.

Trackway number	Grid	Footprint #	Series in trackway	PL (mm)	SL (mm)	FL (mm)	PL (mm)	PL/FL
I	D10	T09	1	?	?	111	58.5	0.527027
I	C10	T01	2	58.5	?	89	58.5	0.657303
I	C10	T04	3	54.5	113.5	96	54.5	0.567708
I	B10	T02	4	31.5	86	92	31.5	0.342391
I	B10	T05	5	30	61	110	30	0.272727
I	B10	T07	6	39.5	67.5	102	39.5	0.387255
II	E09	T02	1	?	?	115	33.5	0.291304
II	D09	T01	2	33.5	?	115	33.5	0.291304
II	D09	T03	3	31	62.5	103	31	0.300971
II	D09	T05	4	38.5	65	125	38.5	0.308
II	C09	T10	5	35	70.5	118	35	0.29661
II	C09	T05	6	44.5	79	78	44.5	0.570513
II	C09	T08	7	34.5	76.5	102	34.5	0.338235
III	E08	?	1	?	?	?	63	?
III	D08	T02	2	63	?	111	63	0.567568
III	D08	T04	3	48.5	110.5	95	48.5	0.510526
III	C08	T03	4	47.5	96.5	122	47.5	0.389344
III	C08	T10	5	50	97.5	134	50	0.373134
IV	E06	T04	1	?	?	115	25.5	0.221739
IV	E06	T02	2	25.5	?	?	25.5	?
IV	D06	T02	3	23	48.5	96	23	0.239583
IV	D06	T05	4	31	54	96	31	0.322917
IV	D06	T06	5	32	63	97	32	0.329897
IV	D06	T07	6	27	57.5	116	27	0.232759
IV	C06	T01	7	34	60.5	97	34	0.350515
IV	C06	T?	8	?	?	?	?	?
IV	C06	T06	9	?	62	100	?	?