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Annie P. McIntosh
DePaul University, anniemcintosh0@gmail.com

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Geometric Morphometric Analysis of the Pedal Claw of the Early Cretaceous Bird *Confuciusornis sanctus* (Confuciusornithidae) and Its Functional and Behavioral Implications

A Thesis Presented in

Partial Fulfillment of the

Requirements for the Degree of

Master of Science

August 2017

By

Annie P. McIntosh

Department of Biological Sciences

College of Science and Health

DePaul University

Chicago, Illinois

TABLE OF CONTENTS

Title Page.....i

Table of Contents.....ii

List of Figures.....iii

List of Tables.....vi

Acknowledgments.....vii

Abstract.....viii

Introduction.....1

Materials and Methods.....10

Results.....21

Discussion.....36

Conclusion.....43

References.....46

Appendix 1.....53

LIST OF FIGURES

Figure 1 Cladogram showing relationship of theropod dinosaurs and birds 2

Figure 2 Photograph of the *Confuciusornis sanctus* specimen and a close up of the right foot 5

Figure 3 Illustration of the skeleton of *Falco peregrinus* (peregrine falcon) indicating the right and left pedal digits I-IV 6

Figure 4 Right second pedal digit claw of extant *Falco columbarius* (merlin) in lateral view showing the positions of the geometric morphometric landmarks 12

Figure 5 Steps of a Procrustes superimposition 14

Figure 6 Illustration of a consensus shape and a deformation grid 15

Figure 7 Partial warps across principal components one and two 24

Figure 8 Line graph showing the distribution of specimens.....25
across principal components one and two with
specimens color-coded by order

Figure 9 Principal component analysis plot plotting principal.....26
component one against principal component two
with specimens grouped by order

Figure 10 Principal component analysis plot plotting principal.....27
component one against centroid size with specimens
grouped by order

Figure 11 Line graph showing the distribution of specimens.....28
across principal components one and two with
specimens color-coded by behavior (revised four
behavioral groups)

Figure 12 Principal component analysis plot plotting principal.....30
component one against principal component two
with specimens grouped by behavior (original 10
behavioral groups)

Figure 13 Principal component analysis plot plotting principal component one against centroid size with specimens grouped by behavior (original 10 behavioral groups).....31

Figure 14 Principal component analysis plot plotting principal component one against centroid size with specimens grouped by behavior (revised four behavioral groups).....32

Figure 15 Principal component analysis plot plotting principal component one against centroid size with specimens grouped by behavior (revised four behavioral groups) showing the relationship of *Confuciusornis sanctus* to the most morphologically similar extant specimens.....33

Figure 16 Principal component analysis plot plotting principal component one against principal component two with specimens grouped by behavior (revised four behavioral groups).....35

LIST OF TABLES

Table 1 Original 10 behavioral groups used in the analysis.....19
and their codes and descriptions

Table 2 Revised four behavioral groups used in the analysis.....20
and their codes and descriptions

Table 3 Percent explained for relative warps.....23

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Silhouettes for the cladogram (Fig. 1) are from **http://phylopic.org/** (except *Confuciusornis*) and are provided by Dori <dori@merr.info> (source photo) and Nevit Dilmen (Columbiformes), Jan Sevcik (photo), John E. McCormack, Michael G. Harvey, Brant C. Faircloth, Nicholas G. Crawford, Travis C. Glenn, Robb T. Brumfield, and T. Michael Keesey (Cathartiformes), Rebecca Groom (Charadriiformes), Scott Harmon (Allosauria, *Archaeopteryx*, Ceratosauria, Deinonychosauria, Ornithischia, Sauropodomorpha, and Tyrannosauroidea), Maija Karala (Anseriformes), Liftarn (Falconiformes), Matt Martyniuk [Oviraptorosauria and Palaeognathae (vectorized by T. Michael Keesey)], Ferran Sayol (Gruiformes), Michael Scroggie (Psittaciformes), L. Shyamal (Passeriformes), Steven Traver (Accipitriformes, Galliformes, Piciformes, Sphenisciformes, and Strigiformes), and Emily Willoughby (Coelophysoidea). The *Confuciusornis* silhouette is from **http://dinogoss.blogspot.com/** and is provided by Matt Martyniuk.

ABSTRACT

Confuciusornis sanctus (Hou et al., 1995) is an Early Cretaceous bird from the Liaoning Province of northeastern China. Much work has been published on this species, but some details of its habitat and behavior remain unclear. In this study, a geometric morphometric analysis of the ungual of the second pedal digit of *Confuciusornis sanctus* was performed to determine how its morphology compares to that of extant birds and which morphological variables best distinguish between taxonomic and behavioral groups. A total of 128 specimens was examined, comprising 104 extant bird species across 15 orders and *Confuciusornis sanctus*. Three fixed landmarks and 50 sliding semilandmarks were used to define shape. A principal component analysis gave two axes explaining over 73% of the variation in shape. Principal component one, which varies in the angle of claw curvature, explains 56% of the morphological variation whereas principal component two, which varies in claw thickness, explains 17.44%. Specimens are relatively evenly spread across principal component one. There is a large amount of overlap between specimen groups across principal component two. When principal component one is plotted against centroid size, specimen groups become more distinguishable. When specimens are grouped by order, groups show a large amount of overlap, indicating that taxonomic order is not strongly correlated with pedal claw morphology. Behavioral groups show much less overlap, indicating that differences in pedal claw morphology are more strongly correlated to behavior than ordinal-level taxonomic relationship. Additionally, claw curvature and claw size are the variables that

are most correlated with differences in behavior, whereas claw thickness is not an informative morphological variable.

The claw of *Confuciusornis sanctus* is morphologically similar to extant birds displaying arboreal behaviors. *C. sanctus* had the capability for short-term flight, and other aspects of the morphology of *C. sanctus* also support an arboreal lifestyle. The claw of *C. sanctus* also shows similarities to extant terrestrial birds. Other morphological characteristics suggest that it was not completely specialized for perching behavior, and it likely spent time on the ground as well as in the trees. Its claw morphology was dissimilar to that of extant birds of prey, indicating that it was unlikely that *C. sanctus* used its claws to seize prey. The pedal claw morphology of *C. sanctus* was most similar to that of *Passer griseus*, which inhabits woodland areas and feeds on seeds, grains, and small insects in trees and on the ground. It is likely that *C. sanctus* also fed on similar food sources. Its short, robust, toothless beak is ideal for a granivorous diet. However, it would have also been suited for piscivory. There is little direct evidence of its diet with the exception of a previously reported specimen preserving fish remains in the alimentary canal. This specimen combined with my study suggest that *C. sanctus* likely had an omnivorous diet, and elicits interesting questions about the evolution of the bird digestive system.

INTRODUCTION

Modern birds comprise about 10,000 known species and are the most diverse group of extant tetrapods (Gill, 2007). They are found all over the world and are characterized as bipedal, warm-blooded vertebrates that possess beaks and wings with feathers. Most species are known to have the capability to fly. Birds first evolved around 150 million years ago in the Late Jurassic from a group of dinosaurs known as Theropoda, the main carnivorous group of dinosaurs including the iconic *Tyrannosaurus rex*. Within Theropoda is the clade Avialae (Fig. 1) that includes modern birds and their earliest Mesozoic relatives, such as *Archaeopteryx* and *Confuciusornis* (Chatterjee, 2015).

Early bursts in the evolution of birds during the Early Cretaceous gave rise to basal avialans, pygostylians such as *Confuciusornis* (Fig. 1), enantiornithines, and the more derived ornithuromorphs (Chatterjee, 2015). Basal avialans such as *Jeholornis* retain the long bony tail of their theropod ancestors and were most likely arboreal climbers and stable gliders whereas in Pygostylia, loss of the long tail and development of pygostyle, an abbreviated bony tail in which the distal-most tail vertebrae fuse into a single element to support tail feathers, aided in the loss of stability and gain of maneuverability (Chatterjee, 2015). Enantiornithines have the more derived thorax of modern birds, with keels and elongated coracoids and modified glenoid fossae (Chatterjee, 2015). Radiation of modern birds began in the Early Paleogene period of the Cenozoic and by the Eocene period, most modern orders of nonpasserine birds had appeared, whereas passerines appeared in the Oligocene period (Chatterjee, 2015).

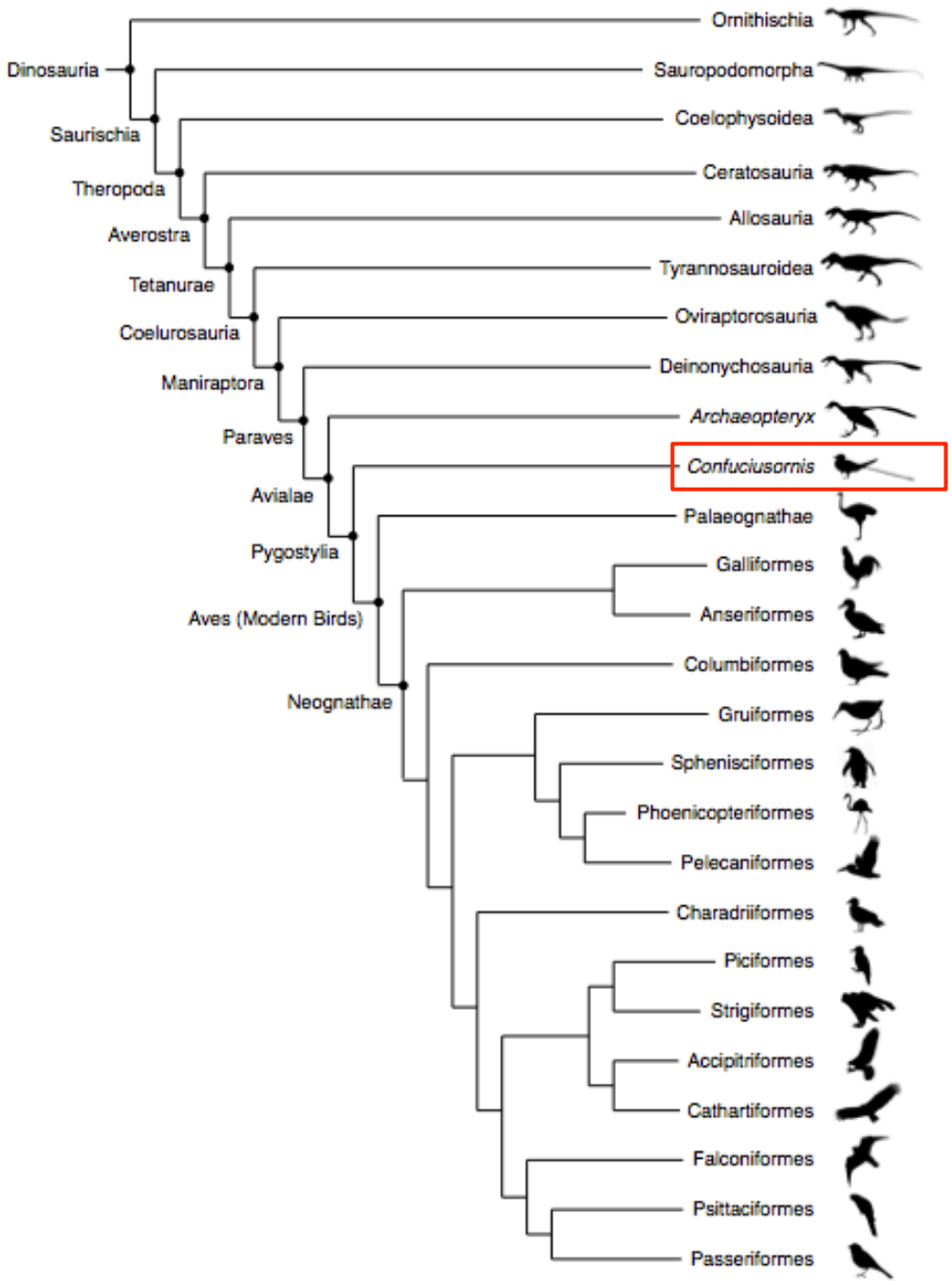


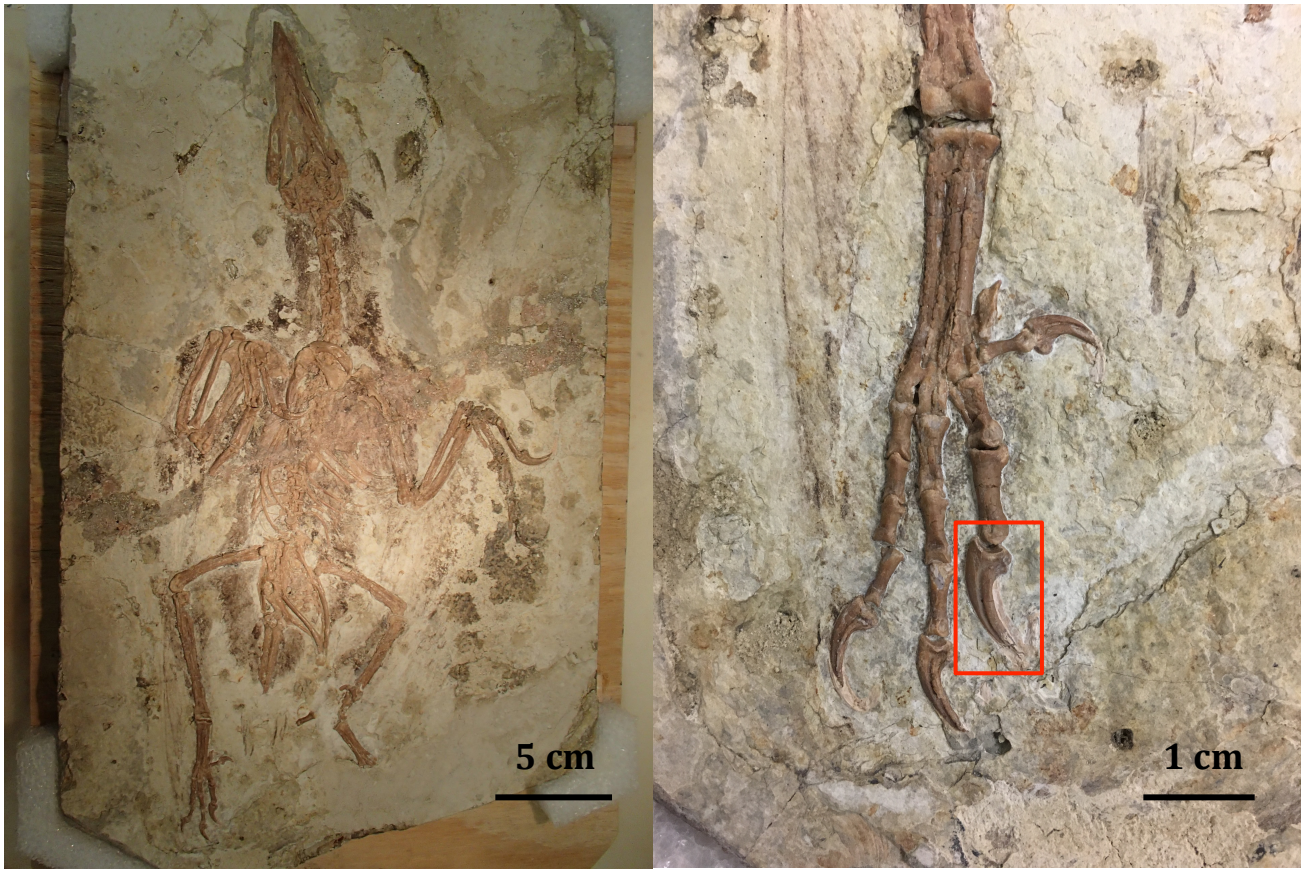
Figure 1. Cladogram showing relationship of theropod dinosaurs and birds. Phylogenetic classification follows that of Chatterjee (2015) for Avialae and Hendrickx et al. (2015) for all others. *Confuciusornis* is indicated by a red rectangle. Sources for silhouettes are given in Acknowledgments.

Confuciusornis sanctus (Hou et al., 1995) (Fig. 2A) is one of the geologically earliest known beaked birds belonging to the family Confuciusornithidae that lived about 125 million years ago in what is now the Liaoning Province in northeastern China (Xu and Norell, 2006). *Confuciusornis sanctus* is found in the Yixian and Jiufotang formations of the Early Cretaceous Jehol Group, a lacustrine Lagerstätte with a highly diverse biota, including many insects and plants such as ginkgoes, ferns, and early angiosperms (Zhou and Zhang, 2003). It is also rich in fossil vertebrates such as fishes, amphibians, mammals, turtles, squamates, pterosaurs, and dinosaurs, including many feathered theropods and one-third of all known Mesozoic bird species (Zhou and Zhang, 2003). The paleoenvironment of the Jehol Group is interpreted as a hot, humid landscape of forests and shallow lakes with periodic flooding and volcanic ash falls (Chatterjee, 2015).

Confuciusornis sanctus was crow-sized and likely a poorly maneuverable flier that lacked the ability for controlled slow flight. The anatomy of its shoulder girdles prevented sufficient elevation of the wing to power the downward stroke necessary for controlled flapping flight (Senter, 2006). However, despite lacking maneuverability during flight, it was likely an adept and stable glider (Chatterjee, 2015). Modified bones in the hands and the presence of feathers indicate that *C. sanctus* was capable of short-term flight (Zhou and Hou, 1998). The third digit of the foot is the longest, and the claw on that digit is also longer and more curved. This condition indicates that *C. sanctus* could extend and flex its toes, suggesting that it displayed grasping behavior (Hou, 1995). Additionally, fluorescent imaging has revealed that the morphology of the toe pads and scales on the foot were ideal for clinging to tree branches (Falk et al., 2016). However,

the specific nature of the arboreal behavior of *C. sanctus* is not entirely clear, where interpretations vary from *C. sanctus* climbing on vertical surfaces (Martin and Zhou, 1998; Zhang et al., 2009) to perching (Hembree, 1999). Additionally, details of the diet of *C. sanctus* are not agreed upon. Some workers interpret this species to be granivorous, consuming seeds and/or other plant matter (Hou et al., 1999; Zhou and Zhang, 2003). Whereas some suggested that *C. sanctus* was not predatory (e.g., Chiappe et al., 1999), others considered the fossil bird to have had a more carnivorous diet. Elzanowski (2002) hypothesized that confuciusornithids lacked the flight maneuverability needed to pursue mobile prey among trees and branches, but instead seized prey from the ground or water. Dalsätt et al. (2006) reported a specimen of *C. sanctus* containing disarticulated partial fish remains in the digestive system, suggesting that *C. sanctus* may have been at least partially piscivorous. Subsequently, Zinoviev (2009) suggested that confuciusornithids caught fish from the surface of the water.

Claw morphology (Fig. 3) has been used to assess possible functions and behaviors in both extinct and extant taxa. Fowler et al. (2009) used measurements such as angle of claw curvature and claw height to show that variation in claw size among pedal digits corresponds to predatory strategy in extant birds of prey. Feduccia (1993) used similar geometric measurements of the third pedal digit in extant birds to determine whether claw geometry can be used to distinguish among ground-dwelling birds, perching birds, and trunk-climbing birds. He also used claw geometry of both the manus



A **B**

Figure 2. Specimen of *Confuciusornis sanctus* (LH PV50). A) Photograph of entire specimen. B) Close-up photograph of right foot highlighting claw of digit II by red rectangle).

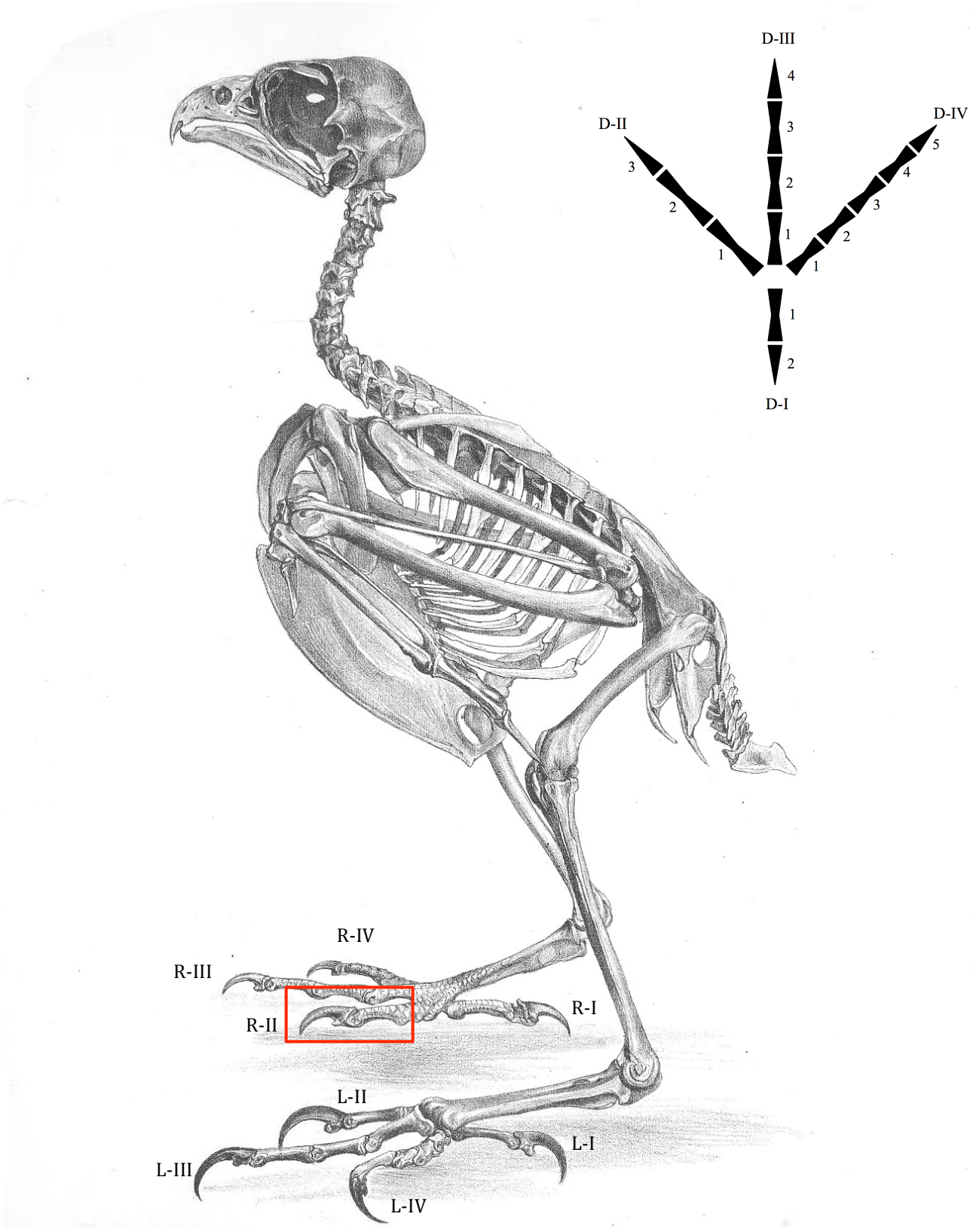

D-III
4
3
2
1
D-II
3
2
1
D-IV
5
4
3
2
1
1
2
D-I
R-IV
R-III
R-II
R-I
L-II
L-I
L-III
L-IV

Figure 3. Illustration of skeleton of *Falco peregrinus* (peregrine falcon) indicating right and left (labeled 'R' and 'L,' respectively) pedal digits I–IV (modified from Eyton, 1867, plate 3A). Digit used in this study (R-II) is indicated by a red rectangle. Inset shows a diagram of the right foot of *Confuciusornis*. Phalanges are numbered on each digit, with the terminal phalanx, or ungual, of each digit representing the claw.

and pes to assess the arboreal habits of *Archaeopteryx*. Feduccia (1993) found that ground-dwelling birds are easily distinguishable from arboreal birds, and that perching and trunk-climbing birds are mostly distinguishable from each other and that *Archaeopteryx* engaged in both perching and trunk-climbing behaviors.

In this study, I use an alternate claw-based approach to assess possible functions and behaviors in birds with the goal to assess the lifestyle of *Confuciusornis sanctus*. I examine pedal claw morphology of extant birds and relate patterns of variation in shape to the taxonomic order to which each species belongs, as well as to the behavioral niche occupied by the species, in order to establish whether phylogenetic relatedness or behavior affects claw morphology more strongly. I also analyze the relationships among different size and shape variables to discern which contribute most to the morphological variation among species. Additionally, I investigate different behavioral groupings to determine which behavior groups are most easily distinguishable from each other based on claw morphology. I then evaluate the morphology of the pedal claw of *C. sanctus* and its relationship to extant species to elucidate details of its habitat, behavior, and diet. I hypothesize that pedal claw morphology is affected more by the behavior of the bird than by its phylogenetic origin and will be more distinguishable based on behavioral niche than taxonomic order. The short, robust, toothless beak of *C. sanctus* is well suited for a granivorous diet (Zhou and Zhang, 2003), and poor maneuverability during flight (Chatterjee, 2015) would have made the pursuit of various food sources ideal. The robust beak would also have been well adapted to an omnivorous diet (Falk et al., 2016). The discovery of a *Confuciusornis* specimen with fish remains interpreted to be alimentary contents of the bird (Dalsätt et al., 2006) suggests a diet that was at least partially piscivorous. Aspects of the morphology of *Confuciusornis* indicate arboreal behavior, such as the flexibility of the toes (Hou, 1995) and the morphology of the soft tissue of the foot (Falk et al., 2016). Additionally, although not suited for long-term, controlled flight (e.g., Elzanowski, 2002; Senter, 2006; Chatterjee, 2015), *Confuciusornis* was capable of

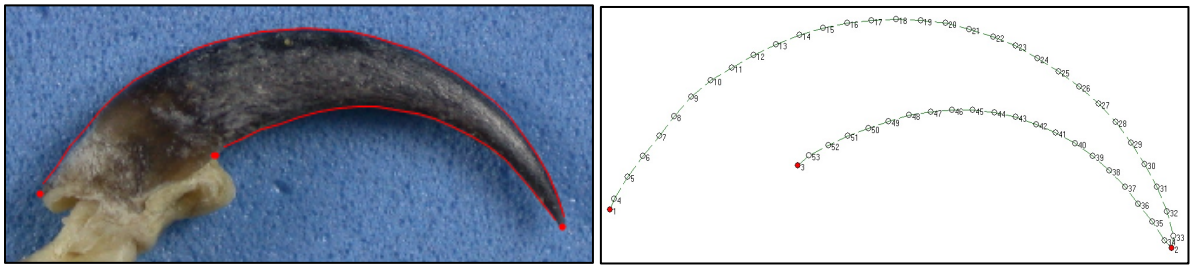
short-term flight and stable gliding (Chatterjee, 2015). I therefore hypothesize that the claw of *C. sanctus* will be most morphologically similar to extant birds that show arboreal behaviors.

MATERIALS AND METHODS

A total of 128 specimens was examined, consisting of 104 extant bird species and *Confuciusornis sanctus* (Appendix 1). All extant specimens used in this study are skeletal preparations of subadult or adult individuals with the exception of the three specimens of *Aramus guarauna* (Gruiformes), which are skin preparations. All are housed in the ornithological collection (Bird Division) of the Department of Zoology at the Field Museum of Natural History (FMNH) in Chicago, Illinois, U.S.A. The species used were chosen to represent a wide variety of bird groups from various geographic and environmental locations. Samples of each taxon were chosen randomly among those available in the collection, provided they were adult individuals and had an intact terminal phalanx on the right second pedal digit. All specimens were held still and photographed against a uniform background. Larger specimens (larger than approximately 1 cm) were photographed using a Nikon digital camera whereas smaller specimens (smaller than approximately 1 cm) were photographed using an AmScope microscope camera. The specimen of *C. sanctus* examined (Fig. 2) belongs to the vertebrate paleontology (VP) collection of the Long Hao Institute for Stratigraphic Paleontology (LH) in Hohhot, P.R. China and is on long-term loan at the University of Chicago in Chicago, Illinois, U.S.A. The adult bird is approximately 35 cm long and approximately 16.5 cm wide. It is a nearly complete adult specimen preserved on a single slab exposing its ventral view.

The second digit (Fig. 3) was chosen for the analysis due to the importance of the sickle-shaped claw on this digit in eumaniraptoran theropods, which are the closest

dinosaurian relatives of birds (Chatterjee, 2015). Only the right foot, which was chosen based on availability of skeletal elements in the collection, was measured on each specimen to maintain consistency (Fig. 3). The claws were oriented horizontally to photograph its right lateral side, with the proximal end (claw base) to the left and the distal end (claw tip) to the right (Fig. 4). Because the second right ungual of the *Confuciusornis* specimen was preserved in medial view (Fig. 1B), this photograph was reversed to provide the same orientation as the extant specimens. Because the silhouette does not change, this does not affect the overall shape of the claw. Based on the photographs, three landmarks and two curves were digitized using tpsDig2 (Rohlf, 2015a). The curves were oriented along the dorsal and plantar curves of the claw and were resampled to include 30 and 20 landmarks, respectively, equally spaced along the curve. The curve points were then converted to landmarks using tpsUtil (Rohlf, 2015c). The three original landmarks were designated as fixed landmarks, whereas the remaining 50 that were converted from the two curves were designated as sliding semi-landmarks using tpsUtil. Sliding semilandmarks are used to analyze homologous points along with curves or edges (Gunz and Mitteroecker, 2013). The semilandmarks are distributed along the curve in an equal number among the specimens of interest (Gunz and Mitteroecker, 2013). The semilandmarks are then equally spaced between two fixed landmarks (Gunz and Mitteroecker, 2013). Additionally, they are allowed to slide along the curve to optimize their spacing (Gunz and Mitteroecker, 2013). Two of the fixed landmarks were placed at the proximal end of the claw, and the third was placed at the distal end, with each of the two curves designated between two fixed landmarks (Fig. 4). A generalized



A **B**

Figure 4. Right second pedal digit claw of extant *Falco columbarius* (merlin; FMNH 467626) in lateral view. A) Three fixed landmarks (represented by red circles) and two curves (represented by red lines). Each curve is composed of equally spaced landmarks, which are not visible here, with 30 along dorsal curve and 20 along plantar curve. B) Three fixed landmarks (represented by red circles) and 50 sliding semilandmarks (represented by open circles outlined in black) created from landmarks associated with each curve.

Procrustes analysis of the specimens allowed for the specimens to be rotated, aligned, and scaled with each other so that their morphology could be compared (Fig. 5).

It should be noted that traditional morphometric studies use several quantitative morphological variables, such as length, width, and height, in multivariate statistical analyses to compare details of shape across different specimens. However, this type of analysis obscures some aspects of shape if undefined by any measurements. Geometric morphometric analyses eliminate some of the obfuscation caused by the inability to define certain measurements by comparing homologous morphological variables and outlines among specimens (Adams et al., 2004). Variables can be defined using coordinate-based landmarks that represent homologous structures in each specimen. Curves and edges can also be traced in each specimen, allowing unconventional shapes to be compared (Adams et al., 2004). The landmark configurations of the specimens then undergo a generalized Procrustes analysis (GPA), which superimposes the specimens, aligns the centroids, rotates each specimen to minimize the difference in orientation, and scales all specimens to a common unit size (Fig. 5). Centroid size (Csz) is calculated by taking the square root of the summed squared deviations of the coordinates from their centroid (the center of mass of a geometric object) (Mitteroecker and Gunz, 2009). The resulting Procrustes shape coordinates, or partial warps, which represent the shape of each specimen, can then be analyzed using statistical techniques such as principal component analysis (PCA) (Mitteroecker and Gunz, 2009; Fig. 6).

PCA is a multivariate statistical technique that allows the variation in a dataset to be emphasized through the conversion of dependent shape variables into new variables

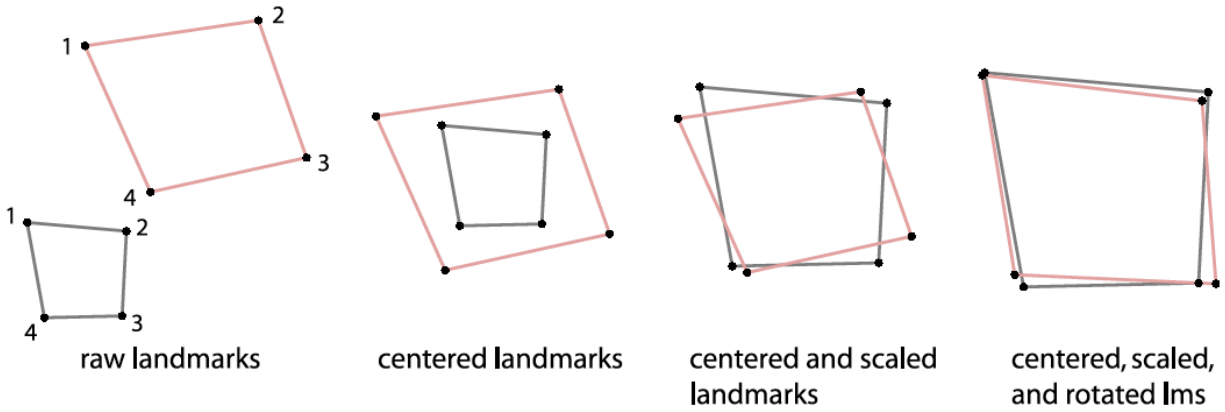


Figure 5. Steps of Procrustes superimposition: raw landmarks, landmarks centered through translation to common origin, landmarks scaled to common unit centroid size, and rotation of landmarks to minimize sum of squared Euclidean distances among homologous landmarks (taken from Mitteroecker and Gunz, 2009, fig. 3).

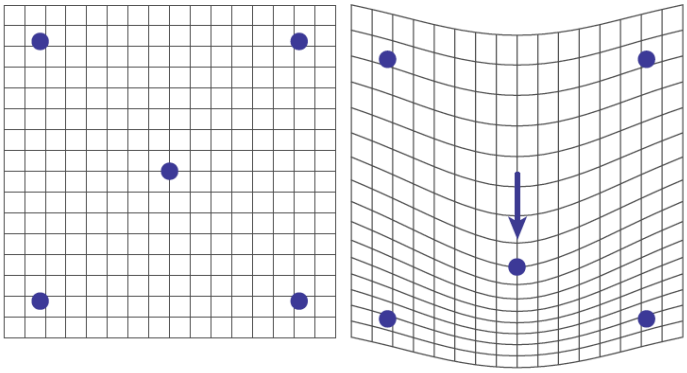


Figure 6. Consensus shape (left) and deformation grid (right) illustrate differences in shape between two specimens (taken from Mitteroecker and Gunz, 2009, fig. 4).

called principal components, or relative warp scores. The coordinate system of the original variables is redefined such that the first axis, principal component one (PC1), represents the axis of maximum variation among specimens, with each subsequent principal component (i.e., PC2, PC3, and so on) representing the next most variable axis in a direction orthogonal to each previous axis (Abdi and Williams, 2010). Differences in shape among landmark configurations can then be visualized as deformation grids created using a thin-plate spline (TPS) function in order to determine the characteristics of shape that are contributing to the variation among specimens (Mitteroecker and Gunz, 2009; Fig. 6).

I performed a PCA on all 128 specimens using tpsRelw (Rohlf, 2015b) to identify the axes of maximal variation in shape (i.e., principal components). Deformation grids were visualized to describe the consensus shape as well as differences in shape associated with PC1 and PC2. The resulting relative warp scores and centroid sizes (Csz) for each specimen were then analyzed using the paleontological statistics (PAST) software program (Hammer et al., 2001). It should be noted that whereas tpsRelw reports sliding semilandmarks as one variable, the PAST software does not recognize sliding semilandmarks and therefore treats them as individual variables rather than as just one variable (Rohlf and Corti, 2000). As a result PAST recognizes 102 principal components rather than 52 (Rohlf and Corti, 2000). PC1, PC2, and Csz were compared to determine which of these variables are most informative, and to which extant species *Confuciusornis sanctus* is most morphologically similar. Specifically, PC1 was plotted against both PC2 and Csz to determine whether PC2 or Csz was more effective in separating specimens across the PCA plot and therefore more important in differentiating

among specimens. The spread of specimens was visualized by grouping specimens by both taxonomic order and behavior to determine which is more important in differentiating among species. The patterns observed in the PCA plots were then analyzed to determine how the size and shape of the second pedal claw interact and relate to the function of the claw in the ecological role of the bird. Additionally, the effects of evolutionary relationship (i.e., the taxonomic order in which a bird belongs) and behavioral niche are compared to determine which plays a larger role in identifying the form and function in the pedal claw of extant birds.

The examined samples consisted of the following 16 taxonomic orders: Confuciusornithiformes (*Confuciusornis sanctus*; *n* = 1), Passeriformes (*n* = 45), Falconiformes (*n* = 4), Accipitriformes (*n* = 13), Cathartiformes (*n* = 2), Anseriformes (*n* = 8), Phoenicopteriformes (*n* = 1), Sphenisciformes (*n* = 2), Piciformes (*n* = 9), Pelecaniformes (*n* = 4), Strigiformes (*n* = 5), Psittaciformes (*n* = 6), Columbiformes (*n* = 4), Charadriiformes (*n* = 12), Gruiformes (*n* = 6), and Galliformes (*n* = 6) (Appendix 1). The specimens were then divided into the following 10 behavioral groups for the purpose of this study: unknown (*C. sanctus*; *n* = 1), aquatic (*n* = 14), aquatic/terrestrial (*n* = 19), terrestrial (*n* = 5), terrestrial/perching (*n* = 16), perching (*n* = 39), climbing (*n* = 4), manipulating (*n* = 6), predatory (*n* = 21), and scavenging (*n* = 3) (Table 1). Behavioral groups were determined based on information gathered from BirdLife International (2011) and the Cornell Lab of Ornithology (Powell, 2010). After the initial analysis, the number of behavioral groups was reduced to the following four groups: unknown (*C. sanctus*; *n* = 1), aquatic/terrestrial (*n* = 38), arboreal (*n* = 65), and predatory (*n* = 24) (Table 2).

The examination of whether pedal claw morphotypes can be effectively differentiated based on behavioral niche in extant birds would allow me to determine whether the claw morphology of an extinct bird can be used to infer the behavioral niche of that bird. The patterns of morphology and behavior found among the extant birds in this study were used to discuss the possible behavioral niche of *Confuciusornis sanctus* based on its claw morphology (Fig. 2B). These inferences were then discussed in relation to previously suggested hypotheses about *C. sanctus* and its behavior.

Table 1. Ten behavioral groups used in initial analysis as well as their analysis codes and descriptions (see Appendix 1 for the behavior code for each specimen).

Code	Behavior	Description
1	unknown	N/A (*Confuciusornis sanctus*)
2	aquatic	swimming, diving
3	aquatic/terrestrial	wading (shorebirds and seabirds)
4	terrestrial	completely terrestrial
5	terrestrial/perching	both terrestrial and arboreal behavior
6	perching	arboreal behavioral
7	climbing	climbing on vertical surfaces
8	manipulating	holding, manipulating, and pulling apart food
9	predatory	catching, killing, carrying, and holding prey
10	scavenging	carnivorous, with some degree of scavenging

Table 2. Four behavioral groups (reduced from initial 10 groups: Table 1) as well as their analysis codes and descriptions (see Appendix 1 for the behavior code for each specimen).

Code	Behavior	Description
1	unknown	N/A (*Confuciusornis sanctus*)
2	aquatic/terrestrial	aquatic and/or terrestrial behavior
3	arboreal	primarily perching and/or climbing
4	predatory	predators and scavengers

RESULTS

My PCA gave 102 principal components (Table 3). PC1 is a strong axis that explains 56.45% of the overall variation in shape among specimens. PC2 and PC3 explain 17.44% and 11.39% of variation in shape, respectively. The remaining principal components explain less than 10% of variation, with PC7 through PC102 each explaining less than 1% (Table 3).

The consensus shape for the specimens shows a moderate angle of curvature, moderate thickness, and a moderately sharp claw tip (Fig. 7). Shape deformation along PC1 occurs in the angle of claw curvature and the sharpness of the claw tip. The negative extreme of PC1 represents a low angle of claw curvature and a blunt claw tip, whereas the positive extreme represents a highly curved claw with a sharp tip. Along PC2, shape deformation occurs in the dorsoplantar thickness of the claw, with the negative extreme representing thick claws and the positive extreme representing thinner claws (Fig. 7).

When the specimens are grouped by taxonomic order, a large amount of overlap is seen among groups. There is a moderate amount of overlap across PC1, with specimens spread relatively equally across this axis (Figs. 8–10). Across PC2, the overlap is nearly complete, with the majority of specimens falling within a small range around the average. A few outliers fall far outside this range, which falsely gives the impression of large variation across this shape variable. This variable does not provide enough variation along its axis to clearly separate specimens into distinct morphological groups based on taxonomic order (Figs. 8, 9). When PC1 is plotted against Csz, the orders become more distinguishable from one another than when PC1 is plotted against PC2 (Fig. 10). PC1

and Csz provide the largest amount of variation and separation for visualizing the morphological variation among specimens. The large number of taxonomic orders and the lack of clear separation among groups, however, indicate that this grouping system does not adequately define claw shape.

The specimens were initially grouped into 10 behavioral groups, including *Confuciusornis sanctus*, labeled as 'Unknown' (Table 1). Across PC1, there is a moderate amount of overlap among groups (Figs. 11–13). Aquatic, aquatic/terrestrial, and terrestrial birds show a large amount of overlap with each other and are isolated from other behavioral groups at the negative extreme for PC1. The remaining seven groups show some overlap with each other. However, birds that are at least somewhat arboreal (terrestrial/perching, perching, and climbing) are concentrated nearer to the consensus shape, whereas carnivorous birds (predatory and predatory/scavenging) are concentrated nearer to the positive extreme (see Fig. 7). Manipulating birds overlap near the average and the positive extreme. With PC1 plotted against PC2 (Figs. 11, 12), it can be seen that PC2 does not provide enough variation for clearly visualizing distinctions among the 10 behavioral groups. When PC1 is plotted against Csz (Fig. 13), the behavioral groups become even more distinguishable from one another. Whereas aquatic, aquatic/terrestrial, and terrestrial birds again overlap with each other, the remaining seven behavioral groups become separated into two broad groups. One group comprises terrestrial/perching, perching, climbing, and manipulating birds, and another consists of predatory and predatory/scavenging birds, although terrestrial/perching and manipulating birds show some overlap with predatory and predatory/scavenging birds.

Table 3. Percent explained for relative warps. Principal components 32–102 each explained less than 0.01% of variation and are omitted from the table.

Principal Component	% Explained	Cumulative % Explained
1	56.45%	56.45%
2	17.44%	73.90%
3	11.39%	85.29%
4	7.24%	92.53%
5	2.84%	95.37%
6	1.53%	96.90%
7	0.92%	97.82%
8	0.75%	98.57%
9	0.33%	98.89%
10	0.28%	99.17%
11	0.20%	99.38%
12	0.14%	99.52%
13	0.09%	99.61%
14	0.06%	99.66%
15	0.05%	99.72%
16	0.04%	99.75%
17	0.03%	99.78%
18	0.02%	99.81%
19	0.02%	99.83%
20	0.02%	99.85%
21	0.02%	99.86%
22	0.01%	99.88%
23	0.01%	99.89%
24	0.01%	99.90%
25	0.01%	99.91%
26	0.01%	99.91%
27	0.01%	99.92%
28	0.01%	99.93%
29	0.01%	99.93%
30	0.01%	99.94%
31	0.01%	99.94%

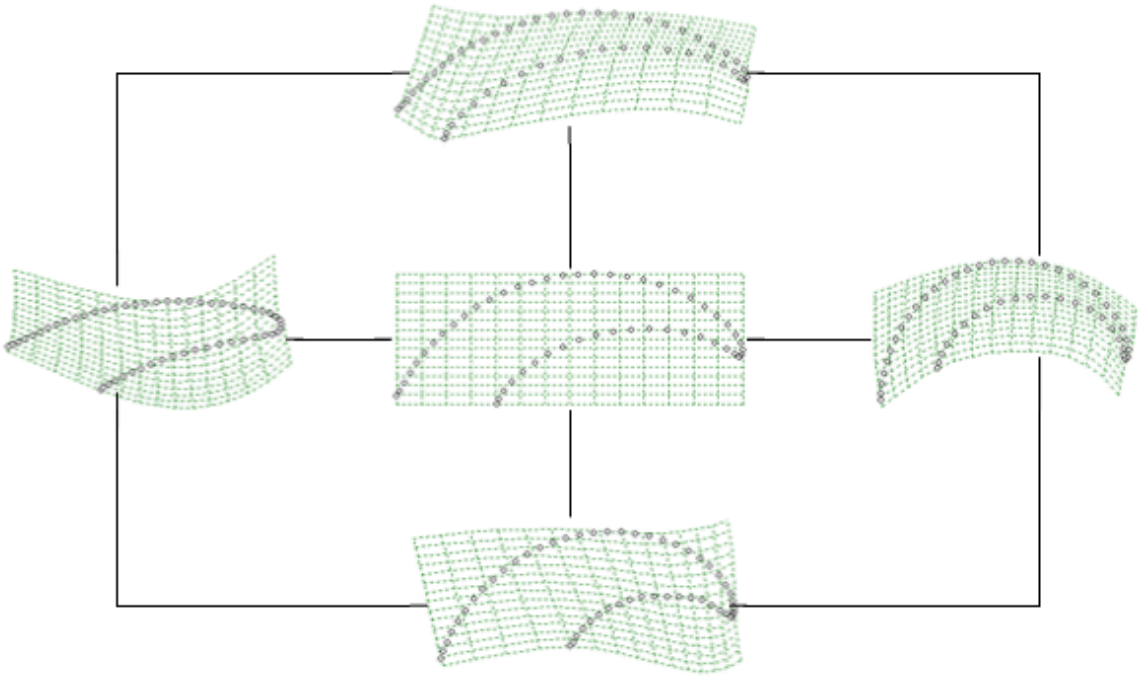


Figure 7. Partial warps across principal components one (PC1) and two (PC2). Consensus shape is shown in middle. PC1 varies along horizontal (x) axis and PC2 varies along vertical (y) axis.

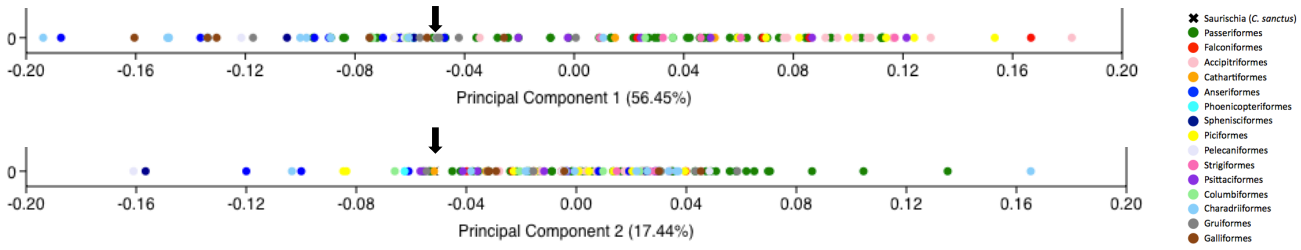


Figure 8. Line graphs (created using PAST) showing distribution of specimens color-coded by taxonomic order across principal component one (PC1) and principal component two (PC2). Because the overlap of specimens makes it difficult to see the location of *Confuciusornis sanctus*, its position along the graph is indicated by a black arrow.

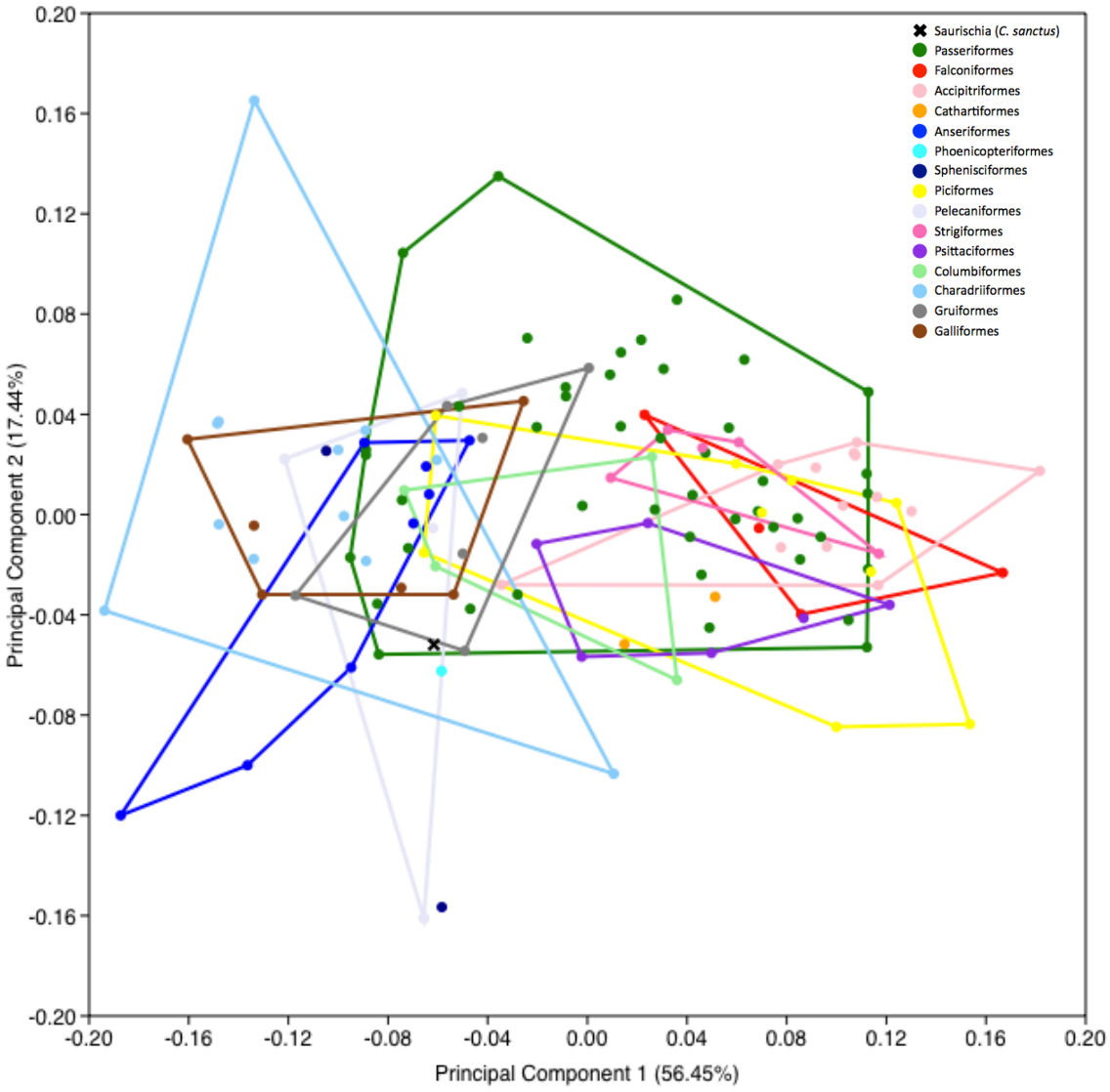


Figure 9. Principal components analysis (PCA) plot created using PAST. Principal component one (PC1) is plotted along x-axis and principal component two (PC2) is plotted along y-axis. Specimens are grouped by taxonomic order and convex hulls are drawn around each order except those with two or fewer specimens. *Confuciusornis sanctus* is indicated by black X-mark.

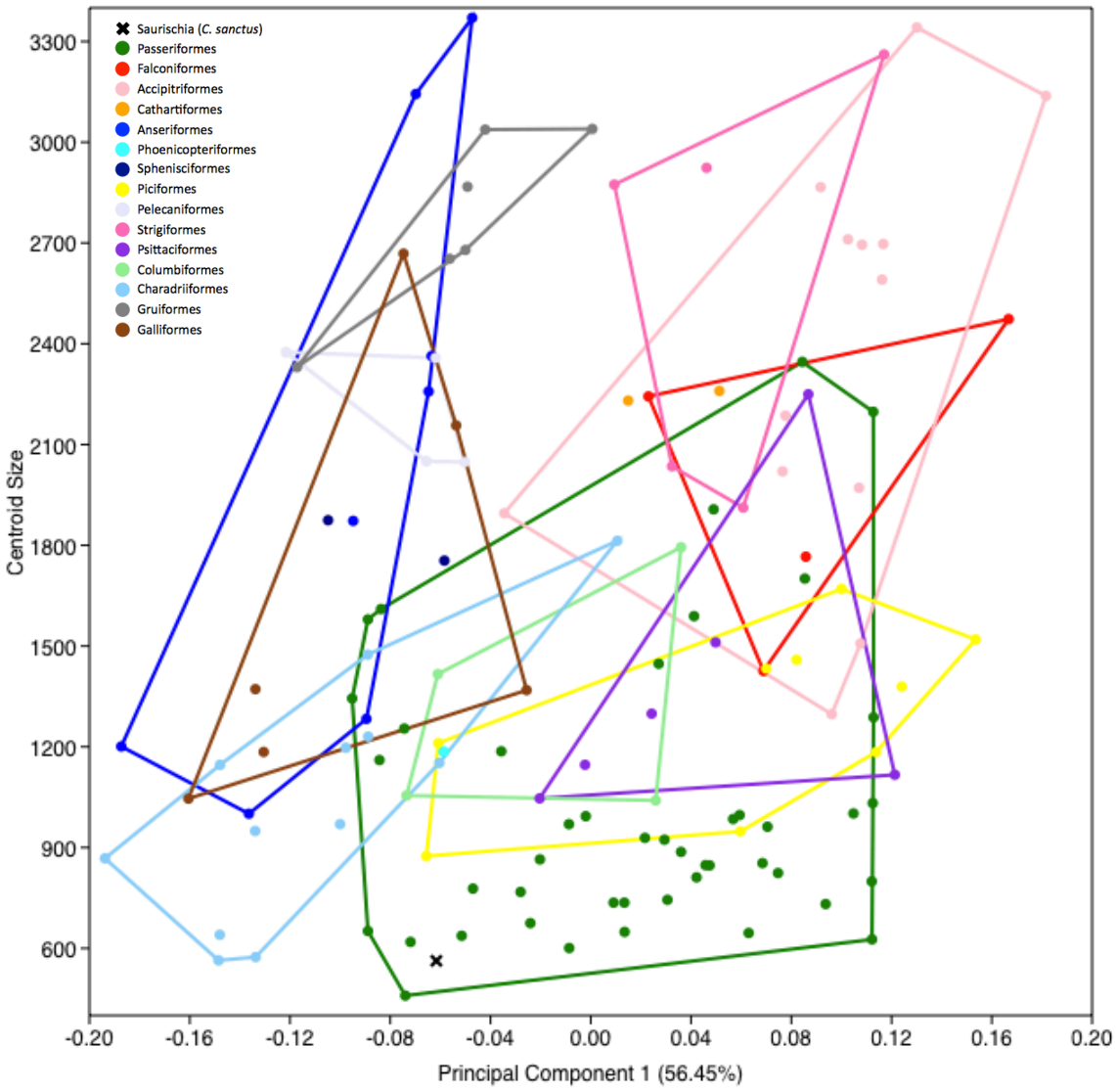


Figure 10. Principal components analysis (PCA) plot created using PAST. Principal component one (PC1) is plotted along x-axis and centroid size is plotted along y-axis. Specimens are grouped by taxonomic order and convex hulls are drawn around each order except those with two or fewer specimens. *Confuciusornis sanctus* is indicated by black X-mark.

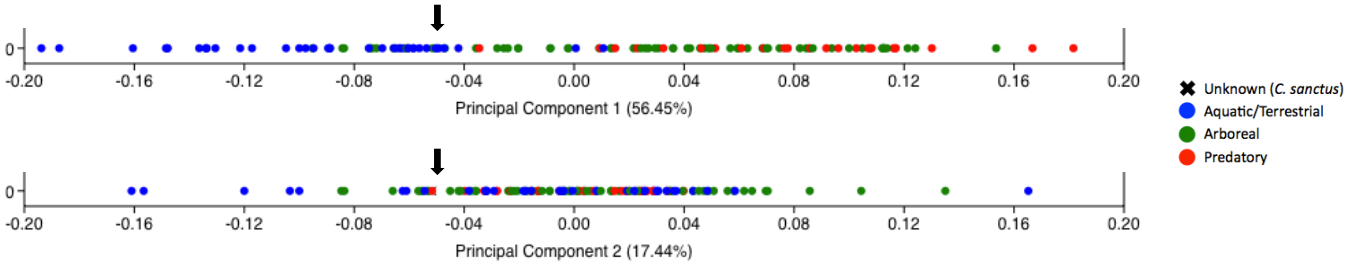


Figure 11. Line graphs (created using PAST) showing distribution of specimens color-coded by behavior (four behavioral groups reduced from 10; see text) across principal component one (PC1) and principal component two (PC2). Because the overlap of specimens makes it difficult to see the location of *Confuciusornis sanctus*, its position along the graph is indicated by a black arrow.

When the initial 10 behavioral groups are reduced to four (unknown, aquatic/terrestrial, arboreal, and predatory; Table 2) and PC1 is plotted against Csz (Fig. 14), the separation among these groups is found to be nearly complete, with limited overlap among groups. Aquatic/terrestrial birds have pedal claws that are less curved but that range in size from small to large. Arboreal birds have claws that are moderately curved to highly curved, and also range in size from moderate to small. Predatory birds tend to have highly curved claws and range in size from moderate to large.

Confuciusornis sanctus is located near the average for PC1, but lies slightly toward the negative extreme (Fig. 14). This represents a pedal claw that is moderately curved and slightly less curved than the consensus shape. It exhibits small size relative to the other samples in this study and is near the negative extreme for Csz. *Confuciusornis sanctus* falls well within the range of claw morphologies represented by arboreal birds. Conversely, the pedal claw of *C. sanctus* is very dissimilar from that of predatory birds. The claw morphology of *C. sanctus* is most similar to that of *Passer griseus* (northern grey-headed sparrow) and is also similar to that of *P. rutilans* (russet sparrow), *Seiurus aurocapilla* (ovenbird), and *Phylloscartes ventralis* (mottle-cheeked tyrannulet), all of which belong to Passeriformes (Fig. 15). It should be noted that I also plotted PC1 against PC2 based on the four behavioral groups (Fig. 16), and the position of *C. sanctus* along this variable falls within the range of size and shapes for both arboreal and terrestrial birds.

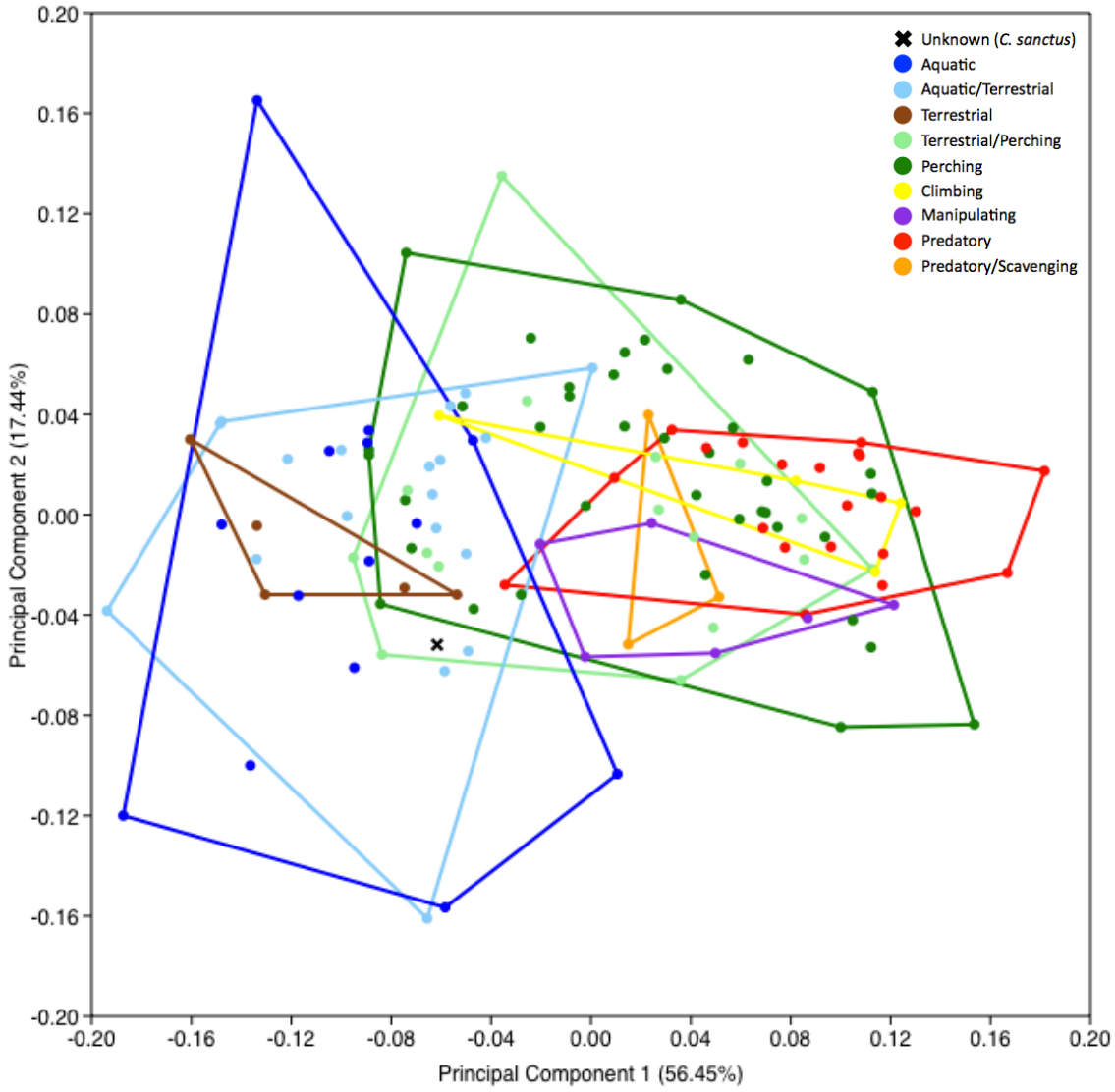


Figure 12. Principal components analysis (PCA) plot created using PAST. Principal component one (PC1) is plotted along x-axis and principal component two (PC2) is plotted along y-axis. Specimens are grouped by behavior (initial 10 behavioral groups) and convex hulls are drawn around each behavioral group. *Confuciusornis sanctus* is classified as 'Unknown' and is indicated by black X-mark.

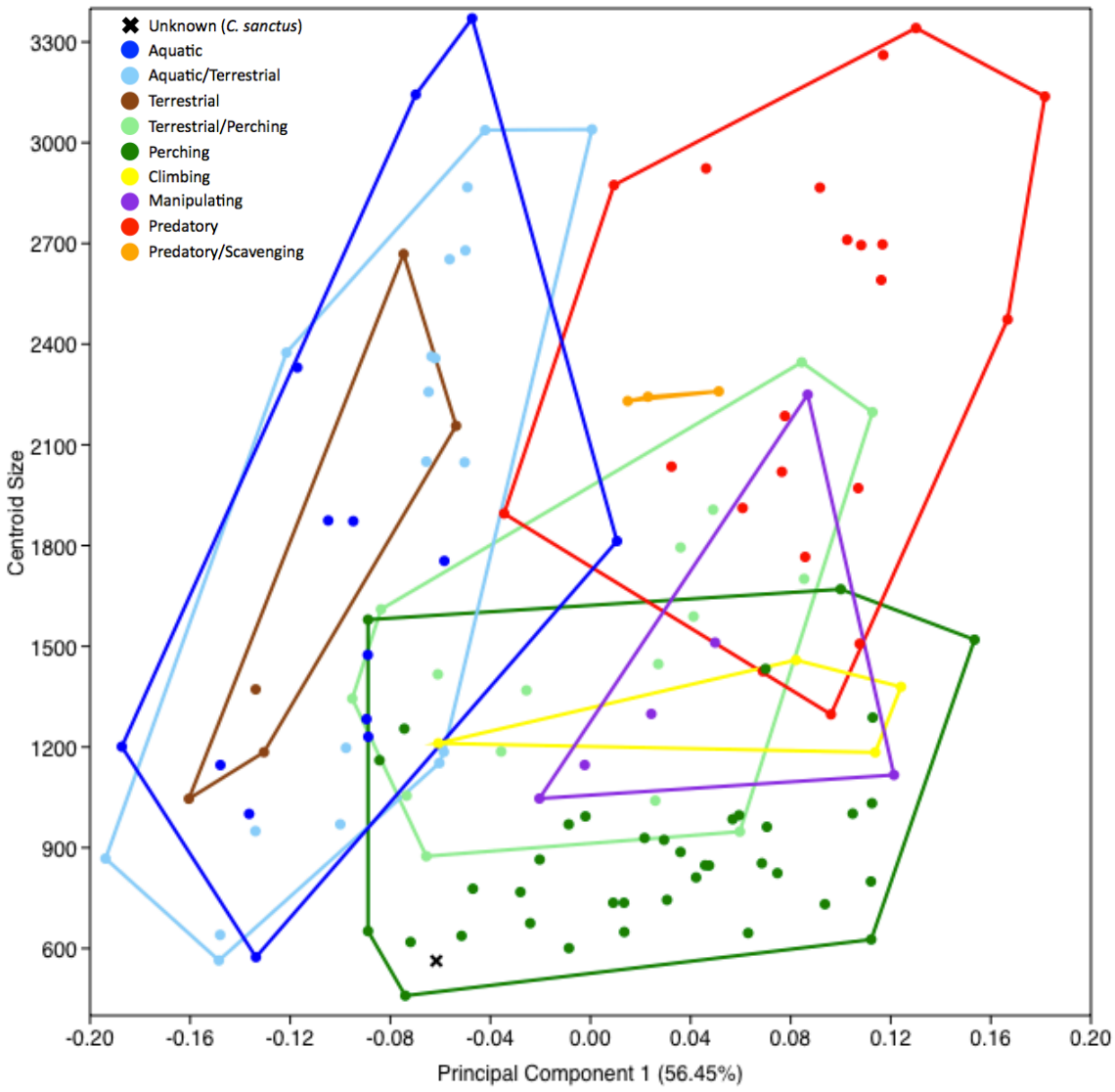


Figure 13. Principal components analysis (PCA) plot created using PAST. Principal component one (PC1) is plotted along x-axis and centroid size is plotted along y-axis. Specimens are grouped by behavior (initial 10 behavioral groups) and convex hulls are drawn around each behavioral group. *Confuciusornis sanctus* is classified as 'Unknown' and is indicated by black X-mark.

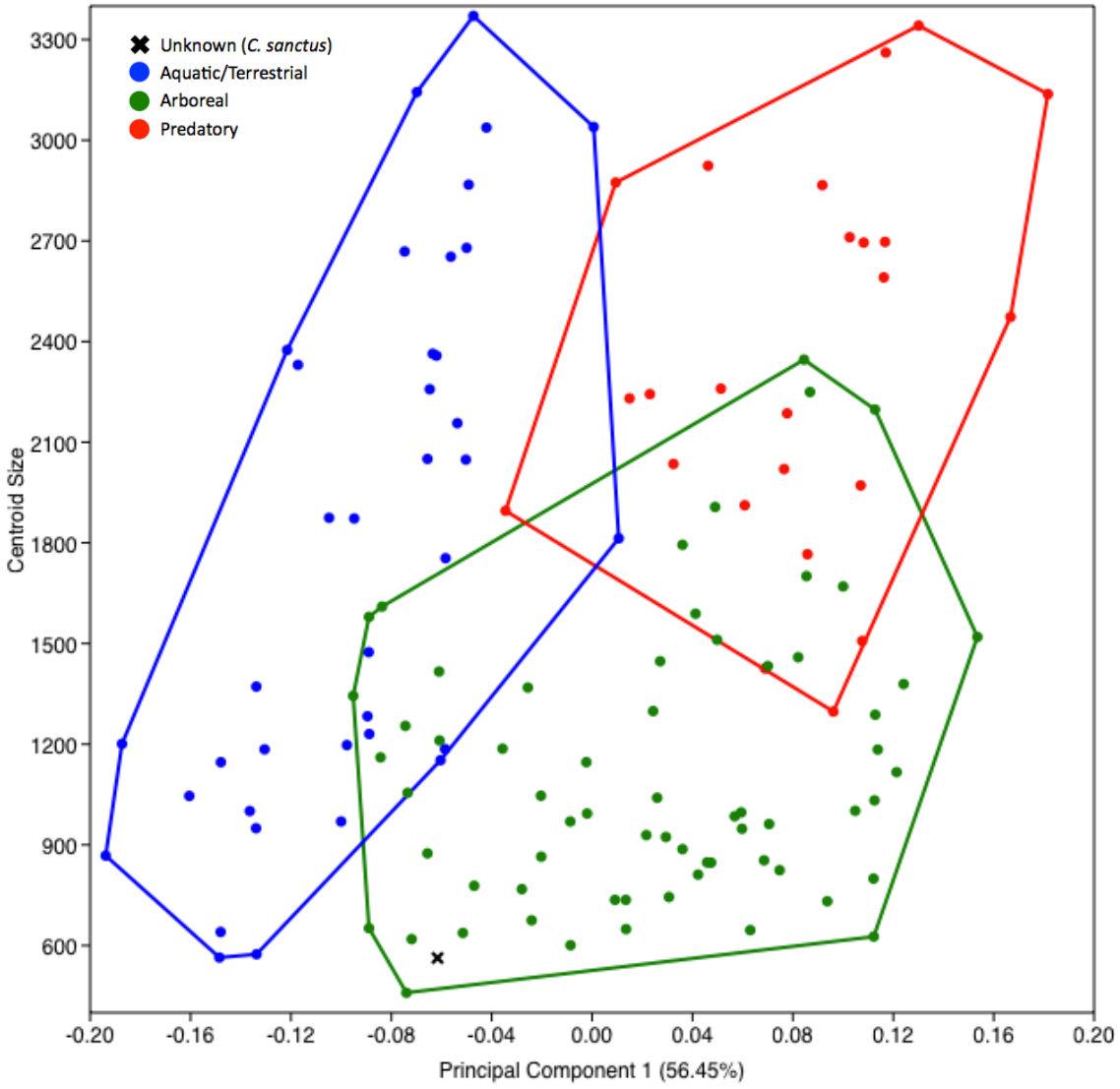
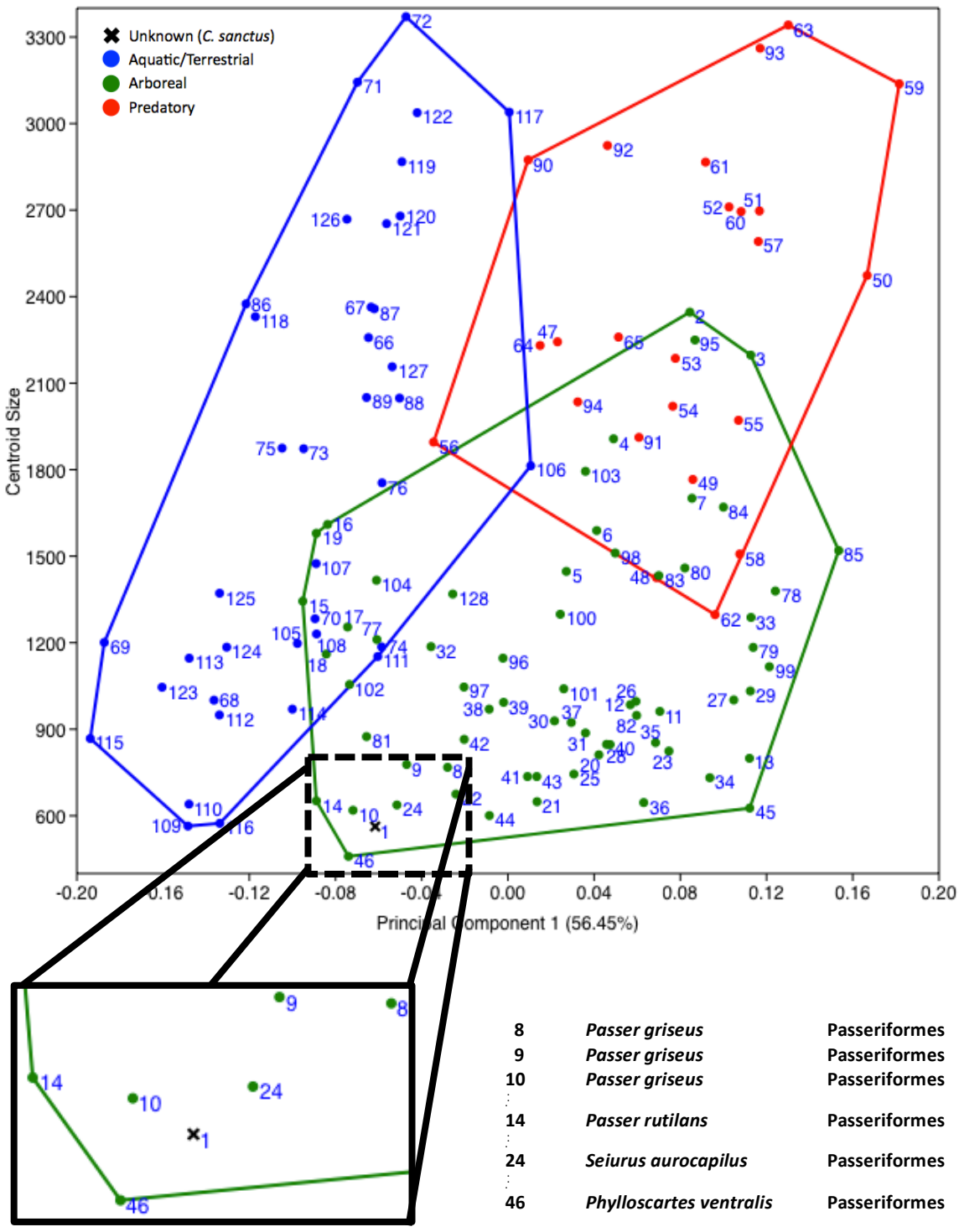


Figure 14. Principal components analysis (PCA) plot created using PAST. Principal component one (PC1) is plotted along x-axis and centroid size is plotted along y-axis. Specimens are grouped by behavior (four behavioral groups reduced from 10; cf. Fig. 13) and convex hulls are drawn around each behavioral group. *Confuciusornis sanctus* is classified as 'Unknown' and is indicated by black X-mark.



8	*Passer griseus*	Passeriformes
9	*Passer griseus*	Passeriformes
10	*Passer griseus*	Passeriformes
⋮		
14	*Passer rutilans*	Passeriformes
⋮		
24	*Seiurus aurocapilus*	Passeriformes
⋮		
46	*Phylloscartes ventralis*	Passeriformes

Figure 15. Principal components analysis (PCA) plot zoomed in to show position of plot for *Confuciusornis sanctus* (X-mark) relative to most morphologically similar extant taxa and specimens in this study (for complete list of specimens and taxa examined, see Appendix 1).

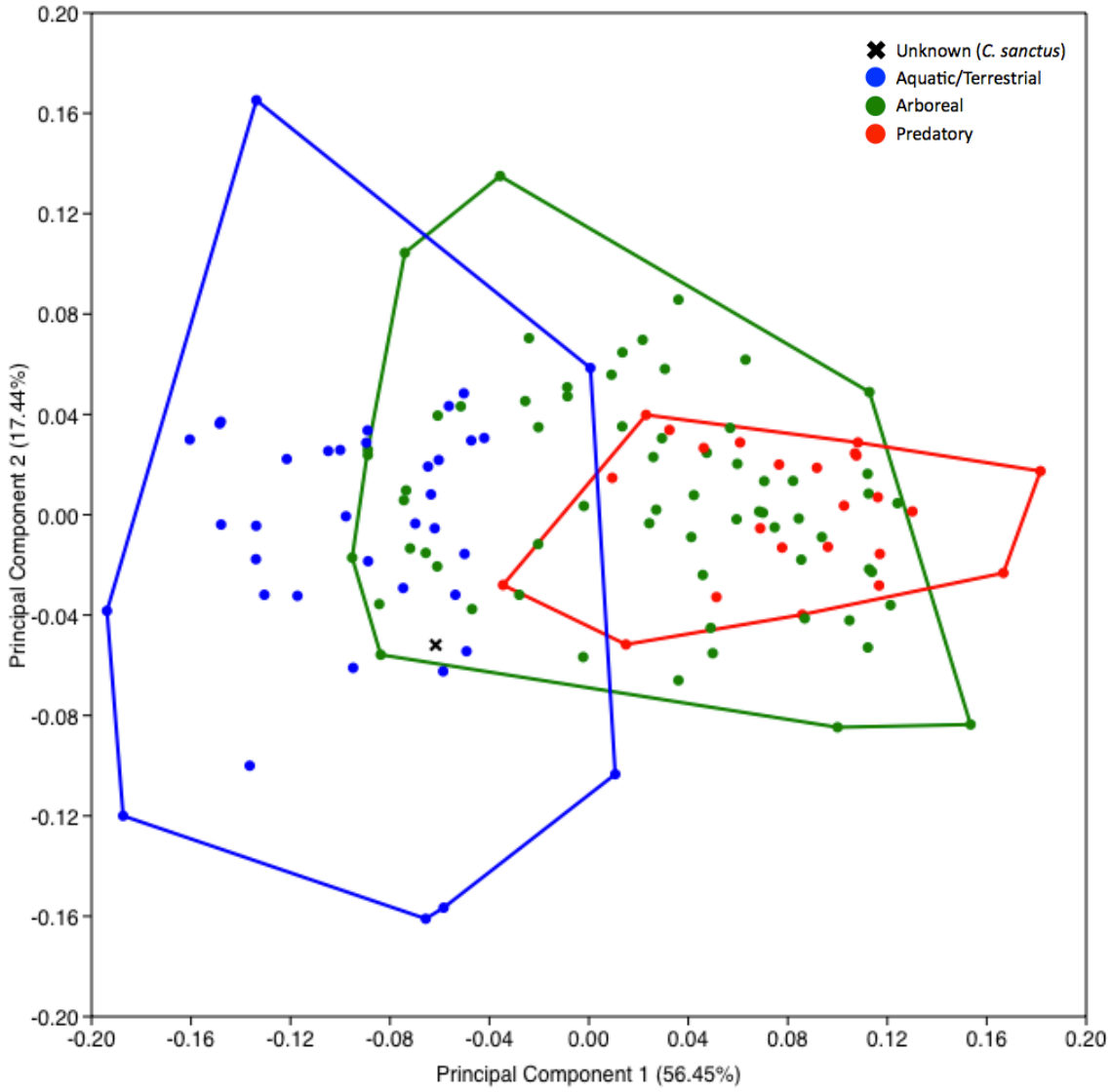


Figure 16. Principal components analysis (PCA) plot created using PAST. Principal component one (PC1) is plotted along x-axis and principal component two (PC2) is plotted along y-axis. Specimens are grouped by behavior (four behavioral groups reduced from 10; cf. Fig. 13) and convex hulls are drawn around each behavioral group. *Confuciusornis sanctus* is classified as 'Unknown' and is indicated by black X-mark.

DISCUSSION

My PCA gives 102 axes of variation with a strong PC1 (i.e., variation in the angle of curvature of the claw and the sharpness of the tip of the claw), explaining over half of the variation in pedal claw morphology among specimens. Specimens are relatively evenly spread across PC1, indicating that this shape variable provides sufficient variation and spread to differentiate among specimens and specimen groups (Fig. 11). On the other hand, specimens show much less spread across PC2 (i.e., variation in dorsoplantar thickness of the claw). The majority of specimens fall in the middle of PC2, but the presence of a few outliers at both extremes creates the illusion of more variability across that principal component (Fig. 11). Because of the lack of true variation, and the low percentage of variability explained by it, PC2 is not considered as reliable a shape variable as PC1 for differentiating among specimens, and therefore predicting behavior from pedal claw morphology.

When specimens are grouped by taxonomic order, groups show a large amount of overlap, making it difficult to distinguish among them (Figs. 9, 10). This condition indicates that ordinal-level taxonomy is not a reliable predictor of pedal claw morphology, and vice versa. There are, however, a few examples of taxonomic order and behavior being correlated such that certain orders would in fact indicate certain claw shapes. This observation reflects the relationship between taxonomic classification and homologous behaviors, as organisms tend to be similar to those to which they are most closely related. For example, birds of prey are represented by the orders Falconiformes, Accipitriformes, Cathartiformes, and Strigiformes.

The specimens were grouped by behavior initially into 10 behavioral categories including *Confuciusornis sanctus* as 'unknown.' My results (Figs. 12, 13) show that there are three major behavioral groups on the basis of pedal claw morphology: (1) a group comprising aquatic, aquatic/terrestrial, and terrestrial birds with pedal claws that are less curved and highly variable in size; (2) that comprising predatory and predatory/scavenging birds with generally large, highly curved pedal claws; and (3) that comprising terrestrial/perching, perching, climbing, and manipulating birds with claws that are generally small (except corvids [crows and their allies] and psittaciforms [parrots and their allies] with variable claw curvatures, from less curved to more highly curved. These three major groups form the basis to infer the behavior of *C. sanctus* (Fig. 14, 15).

The second pedal claw of *Confuciusornis sanctus* (Fig. 2) is very small compared to that of almost all other examined taxa in this study (Fig. 14; Appendix 1). It is moderately curved, only slightly less curved than the consensus shape (cf. Fig. 7). The claw of *C. sanctus* falls within the range of shapes and sizes for extant birds displaying some type of arboreal behavior, such as perching and tree trunk climbing (Fig. 14). Other aspects of the morphology of *C. sanctus* also support an arboreal lifestyle. The third pedal digit is the longest, and the claw on that digit is also the longest and most curved, suggesting that *C. sanctus* was capable of flexing and extending the claws on its feet, and therefore was suited for life in the trees (Hou, 1995). Falk et al. (2016) found through laser fluorescent imaging that *Confuciusornis* possessed toe pads that are similar to modern arboreal perching birds (large, fleshy phalangeal pads and reduced or absent interphalangeal pads). Additionally, Falk et al. (2016) found that the ventral side of the foot of *Confuciusornis* contained only reticulate scales, which are more flexible than

scutate scales and would have helped the bird to grasp and cling to tree trunks and branches. These facts indicate that *C. sanctus* likely spent time among trees and branches.

The claw of *Confuciusornis sanctus* also shows similarities to birds displaying terrestrial behaviors. The moderate curvature of the claw falls within the range of claw curvatures of terrestrial birds (Figs. 11, 14). In most modern birds, digit I (the hallux) is retroverted to oppose the other digits, which aids in grasping and perching (Middleton, 2001). In modern perching passerines, the hallux is as long as or longer than digit II, whereas in *C. sanctus* digit II is approximately twice the length of the hallux (Chiappe et al., 1999). This indicates that this digit was not completely specialized for perching behavior. Additionally, the proximal phalanx of digit III is the longest in *C. sanctus*, whereas in extant birds whose feet are specialized for grasping, intermediate phalanx 3 is longer than the proximal phalanx. The relative proportions of the phalanges of digit III in *C. sanctus* fall between those for extant birds that are predominantly arboreal and those that are predominantly terrestrial (Chiappe et al., 1999). It is therefore probable that whereas *C. sanctus* likely displayed arboreal behavior, it also spent some of its time on the ground. Although PC2 is not considered as reliably predictive of behavior, it should be noted that the position of *C. sanctus* along PC2 also shows morphological similarity with extant arboreal and terrestrial birds, providing further support for a partly terrestrial, partly arboreal lifestyle.

The claw of *Confuciusornis sanctus* is very dissimilar to extant predatory birds that seize and kill prey with its claws. The claw of *C. sanctus* has a lower angle of curvature than any of the samples of predatory birds included in this study, and is also much smaller than that of predatory birds (Fig. 14). Additionally, *C. sanctus* did not

possess teeth, or the sharp, hooked beak common in modern predatory birds, that would have allowed it to tear prey into smaller pieces, and did not have much maneuverability while flying (e.g., Zhou and Hou, 1998; Senter, 2006; Chatterjee, 2015). It is therefore highly unlikely that *C. sanctus* used its claws to catch its prey.

The claw of *Confuciusornis sanctus* is morphologically very similar to that of *Passer griseus* (northern grey-headed sparrow) (Fig. 15). *Passer griseus* occurs in a variety of habitats, including scrub plains, open savannahs, and deciduous woodland areas as well as both arid and humid environments (Clement, 1993). It roosts in bushes, shrubs, and trees, and feeds in vegetation and on the ground on cereal grains, grass seeds, and fruit, supplemented with occasional insects, especially termites and flying ants. It will also eat human food scraps in towns and villages (Clement, 1993). The Early Cretaceous Jehol Biota containing *C. sanctus* includes a wide variety of plants, including bryophytes, lycopsids, ferns, and sphenopsids, as well as seed-bearing plants such as bennettitaleans, czekanowkialeans, ginkgoaleans, gnetaleans, and a possible crown group angiosperm (*Archaefructus*) (Zhou and Zhang, 2003). It also comprises a diverse invertebrate fauna, including insects, spiders, crustaceans, bivalves, and gastropods, as well as a variety of fishes and small tetrapods (Zhou and Zhang, 2003). Reconstructions of the Jehol paleoecosystem suggest a forested environment surrounding numerous shallow lakes. Additionally, the morphology of the primary and secondary feathers of *Confuciusornis*, the presence of a small but extensive keel, and other features suggest the capability of flight (Falk et al., 2016). Therefore, *C. sanctus* may have fed on the ground and in trees and brush in wooded areas.

The presence of feathers and modified forelimb bones suggest that *Confuciusornis sanctus* was capable of short-term flight (Zhou and Hou, 1998). However, the position of the scapula and the orientation of the glenoid prevent sufficient elevation of the wing to produce the downward stroke necessary to power flapping flight (Senter, 2006). It was more likely a proficient glider, sacrificing maneuverability for stability (Chatterjee, 2015), and therefore would not have been able to pursue prey in flight among trees. The partly arboreal lifestyle of *C. sanctus*, along with its poor flying ability, indicates a probable shift from the ancestral obligatory carnivorous diet of theropods to include flightless insects and seeds or other plant matter. The reduction or loss of teeth in birds has been interpreted as being correlated with the evolution of seed-eating behavior (e.g., Zhou and Zheng, 2003; Zheng et al., 2011), and the short, robust, toothless beak of *C. sanctus* is interpreted to be well adapted for a granivorous diet (Zhou and Zhang, 2003).

The results of my study seem to conflict with the report of a specimen of *Confuciusornis* found with fish remains in the alimentary canal (Dalsätt et al., 2006). Dalsätt et al. (2006) document a specimen of *C. sanctus* preserving fish (cf. *Jinanichthys*) remains comprising approximately seven to nine disarticulated vertebrae and several ribs forming a 6-mm spherical cluster in the alimentary canal near the seventh and eighth cervical vertebrae of *Confuciusornis*. Although this specimen constitutes the first and only known case of direct evidence showing the bird's diet out of over 1,000 known specimens of *C. sanctus* (O'Connor and Zhou, 2015), it supports claims that the species practiced carnivory (e.g., Elzanowski, 2002; Dalsätt et al., 2006; Zinoviev, 2009). Therefore, *C. sanctus* would have been well suited for piscivory as well as granivory, and

it is likely that it had an omnivorous diet similar to that of a modern crow (Dalsätt et al., 2006).

Dalsätt et al.'s (2006) study combined with my study that suggests *Confuciusornis* probably had an omnivorous diet lends new insights into the evolution of the digestive system in birds. Dalsätt et al. (2006) interpreted the fish remains in *Confuciusornis sanctus* as not being contents of the proventriculus or gizzard because of their cranial position. They also interpreted the fragmentary, disarticulated condition of the remains to suggest that they were not contents being temporarily stored in the crop. These observations led Dalsätt et al. (2006) to conclude that the fish remains comprise a pellet that was about to be regurgitated (Dalsätt et al., 2006). Regurgitation of pellets containing indigestible food remains such as animal bones is common among modern seabirds and birds of prey (e.g., Bugoni and Vooren, 2004; Van Strien et al., 2015), and modern passerines have also been known to regurgitate pellets containing indigestible insect parts, the husks of grains and seeds, and the stones of small fruits (e.g., Tucker, 1944). Additionally, Wang et al. (2016) report a specimen of a new enantiornithine preserved with an orally regurgitated gastric pellet containing unarticulated fish remains. It is therefore possible that the fish remains found with *C. sanctus* do represent a pellet to be regurgitated.

Dalsätt et al. (2006) discounted the fish remains as crop contents due to their fragmented nature and the lack of maceration occurring in the crop. However, macerated fish remains have been reported in the crop of *Yanornis* (Zheng et al., 2014). In living birds, highly developed and enlarged crops are associated with seed-eating birds, whereas piscivorous birds possess a much smaller and simpler crop (Gill, 2007). The close ventral

association of the fish remains with the cervical vertebrae of *Confuciusornis sanctus* (Dalsätt et al., 2006) indicate that if they represent crop contents rather than materials to be regurgitated, the crop likely developed as a simple enlargement of a portion of the esophagus. O'Connor et al. (2015) hypothesized that the crop evolved in response to the decrease in body size during the dinosaur-avian transition (see also Turner et al., 2007), as well as in response to the energetic demands of flight (i.e., to be lightweight and efficient) (Gill, 2007). Regardless, previous studies as well as my study that suggest *C. sanctus* was well suited for granivory and piscivory are significant because they also provide bearing to the evolution of the digestive system in birds, for example, casting doubt on the idea that the crop evolved as an adaptation to seed eating in birds (e.g., Gill, 2007; Zheng et al., 2011).

CONCLUSION

This study demonstrates that evolutionary relationship (i.e., taxonomic order) is not correlated enough with differences in pedal claw morphology to demonstrate that claw shape can be used to infer phylogenetic relationship. However, the morphology of the second pedal claw in extant birds is correlated with behaviors related to locomotion, habitat, and feeding. Because of this correlation, it is reasonable to use the shape of this specific claw to assess possible behaviors of extinct bird species. The morphological variables of the second pedal claw of extant birds that show the most variability among specimens are the angle of claw curvature and the sharpness of the claw tip. Claw size is also important in differentiating among specimens. Birds showing aquatic/terrestrial, arboreal, and predatory (i.e., capturing prey with its claws) behaviors can be distinguished from one another based on these claw shape and size variables. It is therefore reasonable to analyze these variables in specimens of extinct birds in order to determine which of these behavioral category or categories they most likely belonged to, which can help elucidate details of the diet and habitat of bird taxa for which this information is undetermined.

The second pedal claw of *Confuciusornis sanctus* is small and moderately curved, and falls within the range of shapes and size for extant arboreal birds. Other aspects of the pedal morphology of *C. sanctus*, as well as its capability for short-term flight, also support an arboreal lifestyle, indicating that it spent at least some of its time among trees and branches. However, it was likely not completely adapted for perching, and aspects of its morphology, including the moderate angle of pedal claw curvature, indicate that it

probably spent time on the ground as well. The claw of *C. sanctus* was dissimilar to extant birds of prey, being much smaller and having a lower angle of curvature. Additionally, *C. sanctus* was likely not a strong flier and lacked the sharp, hooked beak of modern birds of prey (Perrins, 2003). It is therefore highly unlikely that *C. sanctus* captured and killed prey with its claws. The pedal claw morphology of *C. sanctus* is most similar to that of *Passer griseus*, which inhabits woodland areas and feeds on seeds, grains, and small invertebrates such as ants and termites in the trees and on the ground. It is likely that *C. sanctus* similarly fed on these types of food sources in trees or on the ground.

Confuciusornis sanctus was capable of short-term flight, but its morphology suggests that it would not have been capable of long-term powered flight. It likely lacked maneuverability and was instead a stable glider. Therefore, it would not have been able to pursue prey among trees and branches, indicating a likely shift from an ancestral carnivorous diet to one that included seeds and insects. The short, robust, toothless beak of *C. sanctus* is ideal for a granivorous diet, and would have also been well adapted for piscivory. Additionally, a specimen of *C. sanctus* found with fish remains preserved in the alimentary canal suggest that it fed on fish at least occasionally (Dalsätt et al., 2006). Environmental and taphonomic data indicate that it is likely that *C. sanctus* spent its time perching in trees near lakes and fed in the trees, on the ground, and from the surface of the water.

The specimen preserving fish remains in the alimentary canal (Dalsätt et al., 2006) combined with my study as well as others suggesting an omnivorous diet for the geologically earliest beaked birds elicits interesting questions about the evolution of the

modern bird digestive system. It is possible that *C. sanctus* regurgitated pellets, similar to modern seabirds, perching birds, and birds of prey. However, if the fish remains represent crop contents, it sheds doubt on the hypothesis that the crop evolved as an adaptation to seed eating. The fact that *C. sanctus* likely lived a partly arboreal lifestyle and consumed fish as well as seeds and insects supports the alternative hypothesis that the crop evolved in response to the decrease in body size during the dinosaur-avian transition as a way to be able to cache enough food to sustain the energetic demands of flight while still maintaining a lightweight body (O'Connor et al., 2015; Turner et al., 2007).

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APPENDICES

Appendix 1. List of species examined in this study, along with the sample numbers (Sample #) by which they are identified in the statistical analyses, their initial behavioral group code (see Table 1), their behavioral groups code after the number of behavioral groups was reduced (see Table 2), their orders, their size, and their museum catalogue numbers (Catalogue #). Behavioral groups were assigned based on information from Powell, 2010, and del Hoyo et al., 2017. Size measurements for weight (g) and length (cm) were taken from Powell, 2010, and del Hoyo et al., 2017. Where a range of sizes was given, the average of the minimum and maximum was used. Measurements are given once per species and are rounded to the nearest tenth. The length measurement for *Confuciusornis sanctus* is taken from the specimen used in this study. The fossil specimen of *Confuciusornis sanctus* (Fig. 2) is catalogued at the Long Hao Institute for Stratigraphic Paleontology (LH PV) and all extant specimens are catalogued at the Field Museum of Natural History (FMNH).

Sample #	Initial Behavior Group Code	Reduced Behavior Group Code	Species	Order	Length (cm)	Weight (g)	Catalogue #
1	1	1	*Confuciusornis sanctus*	Confuciusornithiformes	35	—	LH PV50
2	5	3	*Corvus corax*	Passeriformes	62.5	1,157	FMNH 348327
3	5	3	*Corvus corax*	Passeriformes			FMNH 480449
4	5	3	*Corvus corax*	Passeriformes			FMNH 467688
5	5	3	*Corvus brachyrhynchos*	Passeriformes	46.5	468	FMNH 452169
6	5	3	*Corvus brachyrhynchos*	Passeriformes			FMNH 437427
7	5	3	*Corvus brachyrhynchos*	Passeriformes			FMNH 436229
8	6	3	*Passer griseus*	Passeriformes	14.5	30.5	FMNH 313269
9	6	3	*Passer griseus*	Passeriformes			FMNH 385367

10	6	3	*Passer griseus*	Passeriformes			FMNH 390181
11	6	3	*Passer domesticus*	Passeriformes	16	28.5	FMNH 483681
12	6	3	*Passer domesticus*	Passeriformes			FMNH 483683
13	6	3	*Passer rutilans*	Passeriformes	14.5	20.3	FMNH 347965
14	6	3	*Passer rutilans*	Passeriformes			FMNH 347967
15	5	3	*Grallina cyanoleuca*	Passeriformes	27.5	79.2	FMNH 106484
16	5	3	*Cracticus tibicen*	Passeriformes	40	286.5	FMNH 104244
17	6	3	*Chlamydera maculata*	Passeriformes	29	137.5	FMNH 106328
18	6	3	*Chlamydera maculata*	Passeriformes			FMNH 106379
19	6	3	*Epimachus fastuosus*	Passeriformes	82.5	239	FMNH 104467
20	6	3	*Spinus tristis*	Passeriformes	12	15.5	FMNH 363526
21	6	3	*Hypargos niveoguttatus*	Passeriformes	12.5	14.7	FMNH 290938
22	6	3	*Lonchura striata*	Passeriformes	11.5	11.3	FMNH 486017
23	6	3	*Vireo olivaceus*	Passeriformes	12.5	19	FMNH 484514
24	6	3	*Seiurus aurocapilus*	Passeriformes	12.5	22	FMNH 289474
25	6	3	*Geothlypis trichas*	Passeriformes	12	9.5	FMNH 367059
26	6	3	*Cardinalis cardinalis*	Passeriformes	22	45	FMNH 334730
27	6	3	*Spindalis zena*	Passeriformes	15	26	FMNH 331113
28	6	3	*Tangara velia*	Passeriformes	13	21	FMNH 319820
29	6	3	*Diuca diuca*	Passeriformes	17	36	FMNH 314883
30	6	3	*Spizella arborea*	Passeriformes	14	20.5	FMNH 467409
31	6	3	*Junco hyemalis*	Passeriformes	15	24	FMNH 340167
32	5	3	*Plectrophenax nivalis*	Passeriformes	15	38.5	FMNH 428967
33	6	3	*Sitta castanea*	Passeriformes	12.5	12	FMNH 347926
34	6	3	*Dicaeum nigrilore*	Passeriformes	9.8	11	FMNH 357596
35	6	3	*Lophozosterops goodfellowi*	Passeriformes	13.3	20	FMNH 364243
36	6	3	*Regulus ignicapillus*	Passeriformes	9	6	FMNH 363913
37	6	3	*Rhinomylas goodfellowi*	Passeriformes	18	31.7	FMNH 357503
38	6	3	*Hylocichla mustelina*	Passeriformes	20	45	FMNH 349310
39	6	3	*Turdus abyssinicus*	Passeriformes	22	72.5	FMNH 355652
40	6	3	*Alcippe atriceps*	Passeriformes	13	16.5	FMNH 355728
41	6	3	*Troglodytes aedon*	Passeriformes	12	11	FMNH 382309
42	6	3	*Mimus polyglottos*	Passeriformes	23.5	51.5	FMNH 428664
43	6	3	*Hirundo rustica*	Passeriformes	15	18.5	FMNH 376946
44	6	3	*Phylloscartes chapmani*	Passeriformes	12	8	FMNH 319383
45	6	3	*Phylloscartes orbitalis*	Passeriformes	11.5	8	FMNH 315957
46	6	3	*Phylloscartes ventralis*	Passeriformes	12	9	FMNH 323150
47	10	4	*Phalcobaenus megalopterus*	Falconiformes	51.5	795	FMNH 316427
48	9	4	*Falco sparvarius*	Falconiformes	26.5	122.5	FMNH 390970
49	9	4	*Falco columbarius*	Falconiformes	27	200	FMNH 467626
50	9	4	*Falco peregrinus*	Falconiformes	42.5	1065	FMNH 475251

51	9	4	*Buteo jamaicensis*	Accipitriformes	55	1075	FMNH 317256
52	9	4	*Buteo lagopus*	Accipitriformes	49.5	1057.5	FMNH 451961
53	9	4	*Buteo lineatus*	Accipitriformes	52	630	FMNH 342419
54	9	4	*Circus cyaneus*	Accipitriformes	48	525	FMNH 472540
55	9	4	*Circus cyaneus*	Accipitriformes			FMNH 475216
56	9	4	*Melierax gabar*	Accipitriformes	32	165	FMNH 368787
57	9	4	*Accipiter francesii*	Accipitriformes	31.5	144.5	FMNH 345603
58	9	4	*Accipiter striatus*	Accipitriformes	29	152.5	FMNH 342380
59	9	4	*Accipiter gentilis*	Accipitriformes	58.5	997.5	FMNH 398934
60	9	4	*Accipiter gentilis*	Accipitriformes			FMNH 348186
61	9	4	*Accipiter gentilis*	Accipitriformes			FMNH 314494
62	9	4	*Ictinia mississippiensis*	Accipitriformes	35.5	277.5	FMNH 486733
63	9	4	*Pandion haliaetus*	Accipitriformes	56	1700	FMNH 475181
64	10	4	*Cathartes aura*	Cathartiformes	72.5	2000	FMNH 452158
65	10	4	*Cathartes aura*	Cathartiformes			FMNH 458848
66	3	2	*Anhima cornuta*	Anseriformes	87	3075	FMNH 10563
67	3	2	*Chauna chavaria*	Anseriformes	83.5	3900	FMNH 10454
68	2	2	*Anas cyanoptera*	Anseriformes	39.5	390	FMNH 33017
69	2	2	*Anas clypeata*	Anseriformes	47.5	610	FMNH 43623
70	2	2	*Aix sponsa*	Anseriformes	50.5	658	FMNH 46617
71	2	2	*Cygnus buccinator*	Anseriformes	148	10200	FMNH 45447
72	2	2	*Cygnus olor*	Anseriformes	139.5	9900	FMNH 46619
73	2	2	*Anser caerulescens*	Anseriformes	76	2450	FMNH 35698
74	3	2	*Phoenicopterus chilensis*	Phoenicopteriformes	105	2300	FMNH 312924
75	2	2	*Pygoscelis papua*	Sphenisciformes	78.5	6500	FMNH 314863
76	2	2	*Spheniscus humboldti*	Sphenisciformes	67.5	4350	FMNH 347600
77	7	3	*Colaptes auratus*	Piciformes	29.5	135	FMNH 45877
78	7	3	*Sphyrapicus varius*	Piciformes	20	49	FMNH 482070
79	7	3	*Melanerpes erythrocephalus*	Piciformes	21	73.5	FMNH 31455
80	7	3	*Melanerpes erythrocephalus*	Piciformes			FMNH 45061
81	5	3	*Malacoptila semicincta*	Piciformes	18.5	44	FMNH 32101
82	5	3	*Malacoptila semicincta*	Piciformes			FMNH 32103
83	6	3	*Pteroglossus azara*	Piciformes	40.5	150	FMNH 32108
84	6	3	*Aulacorhynchus derbianus*	Piciformes	37	201.5	FMNH 31543
85	6	3	*Ramphastos sulfuratus*	Piciformes	48.5	412.5	FMNH 37672
86	3	2	*Ardea herodias*	Pelecaniformes	117	2300	FMNH 44348
87	3	2	*Nycticorax nycticorax*	Pelecaniformes	62	870.5	FMNH 452160
88	3	2	*Egretta caerulea*	Pelecaniformes	65	354	FMNH 33001
89	3	2	*Pelecanus occidentalis*	Pelecaniformes	118.5	3500	FMNH 43266
90	9	4	*Strix nebulosa*	Strigiformes	72.5	1200	FMNH 449048
91	9	4	*Asio otus*	Strigiformes	37.5	327.5	FMNH 475273

92	9	4	*Bubo virginianus*	Strigiformes	54.5	1705	FMNH 330017
93	9	4	*Bubo scandiacus*	Strigiformes	61.5	2275	FMNH 314849
94	9	4	*Tyto alba*	Strigiformes	36	550	FMNH 458830
95	8	3	*Amazona farinosa*	Psittaciformes	40.5	650.5	FMNH 36478
96	8	3	*Poicephalus meyeri*	Psittaciformes	23	132.5	FMNH 36309
97	8	3	*Psittacula krameri*	Psittaciformes	40	119	FMNH 312300
98	8	3	*Cacatua sulphurea*	Psittaciformes	33	350	FMNH 39072
99	8	3	*Nymphicus hollandicus*	Psittaciformes	31	90	FMNH 31511
100	8	3	*Nymphicus hollandicus*	Psittaciformes			FMNH 342670
101	5	3	*Zenaida macroura*	Columbiformes	34	128	FMNH 34263
102	5	3	*Zenaida macroura*	Columbiformes			FMNH 34767
103	5	3	*Columba livia*	Columbiformes	33	322.5	FMNH 47731
104	5	3	*Columba livia*	Columbiformes			FMNH 47954
105	3	2	*Thalasseus maximus*	Charadriiformes	47.5	400	FMNH 39694
106	2	2	*Fratercula arctica*	Charadriiformes	31	460	FMNH 39099
107	2	2	*Larus delawarensis*	Charadriiformes	48.5	500	FMNH 462160
108	2	2	*Leucophaeus atricilla*	Charadriiformes	42.5	287	FMNH 28991
109	3	2	*Charadrius semipalmatus*	Charadriiformes	18	47	FMNH 10504
110	3	2	*Charadrius semipalmatus*	Charadriiformes			FMNH 342530
111	3	2	*Pluvialis squatarola*	Charadriiformes	29	280	FMNH 364600
112	3	2	*Pluvialis dominica*	Charadriiformes	26	158	FMNH 31399
113	2	2	*Recurvirostra americana*	Charadriiformes	45	312.5	FMNH 36415
114	3	2	*Tringa flavipes*	Charadriiformes	24	80.5	FMNH 4645
115	3	2	*Tringa flavipes*	Charadriiformes			FMNH 290820
116	2	2	*Phalaropus fulicaria*	Charadriiformes	21	57	FMNH 36472
117	3	2	*Porphyrio martinica*	Gruiformes	36.5	248	FMNH 38916
118	2	2	*Fulica americana*	Gruiformes	41	650	FMNH 48246
119	3	2	*Grus canadensis*	Gruiformes	120	4150	FMNH 49045
120	3	2	*Aramus guarauna*	Gruiformes	68.5	1100	FMNH 43806
121	3	2	*Aramus guarauna*	Gruiformes			FMNH 16132
122	3	2	*Aramus guarauna*	Gruiformes			FMNH 38574
123	4	2	*Gallus gallus*	Galliformes	71.5	1061	FMNH 10537
124	4	2	*Lophura leucomelanos*	Galliformes	68.5	972.5	FMNH 104136
125	4	2	*Phasianus colchicus*	Galliformes	60	1750	FMNH 31451
126	4	2	*Meleagris gallopavo*	Galliformes	112.5	6650	FMNH 34249
127	4	2	*Meleagris gallopavo*	Galliformes			FMNH 45225
128	5	3	*Ortalis motmot*	Galliformes	48.5	482.5	FMNH 315150