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Functional morphology and convergent evolution in the skulls of diurnal raptors

By

Mackenzie Emma Kirchner-Smith

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Rauri C. K. Bowie, Chair

Professor Charles R. Marshall

Professor Jun Sunseri

Summer 2024

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Mackenzie Emma Kirchner-Smith

Abstract

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Professor Rauri C. K. Bowie, Chair

Researchers have sought to understand the link between the avian skull and dietary preferences for centuries by studying vision, brain size, beak shape, and the complex evolutionary relationship of the beak relative to the cranium. One group of birds of recurring interest to researchers are the raptors. The term 'raptor' colloquially encompasses three orders: Accipitriformes, Falconiformes, and Strigiformes. This study provides a comprehensive comparison of species among the diurnal raptors: Accipitriformes and Falconiformes, including the skulls of 150 species. It is one of the largest studies of the overall morphology of these two orders to date and lays the groundwork for further research into the diet, function, anatomy, taxonomy, and morphological diversity of living and extinct raptors. All three chapters rely on the use of 2D geometric morphometrics to draw conclusions about shape variation in the skulls of raptors.

In Chapter 1, I investigated the effect of the rhamphotheca on the shape of the bird beak in raptors by comparing the shape of the beak with and without a rhamphotheca in the same species. This chapter provides answers to the question of whether a combination of skulls with and without the rhamphotheca can be used in geometric morphometric analyses of skull shape. The rhamphotheca adds length and creates a sharper point in the beaks of raptors, but the extent to which the shape of the beak changes compared to the bone underneath had not been investigated. A geometric morphometric analysis of five different species of raptors from different orders and families found that the rhamphotheca does differ significantly from the shape of the underlying boney beak in every case. This has implications for the study of bird beaks when the rhamphotheca isn't available, as is often the case when looking at fossil birds. These results also resulted in the exclusion of rhamphotheca from the analyses of skulls in chapters two and three.

In Chapter 2, I explored the general morphology of the raptor skull using 2D landmarks of skulls from the Accipitriformes and Falconiformes. This chapter details the morphology of the raptor skull, what features scavenging members of each order have in common, and how scavengers and non-scavengers differ morphologically. Scavenging has a significant effect on the overall shape of the skull, driving the evolutionary difference

between the families and subfamilies of the Accipitriformes and Falconiformes. The results of this chapter strongly suggest the presence of a feeding guild structure within the accipitrid and cathartic vultures and point to the progressive evolution of 'vulture-like' traits in the Polyborinae subfamily of the Falconiformes.

In Chapter 3, I analyzed the scavenging members of each order in greater detail, to discuss and reevaluate the guild structures proposed by Kruuk (1967) and Hertel (1994). I also evaluate the inclusion of the caracaras into this guild structure, based on geographical distribution and known overlap with the vultures of the Accipitriformes. Chapter 3 also discusses the shape of the vulture skull through time by including fossil specimens from the La Brea and McKittrick tar pits. Using the knowledge about existing scavenger guild structures, I apply this knowledge to fossil and extinct species of raptors and scavengers of the Pleistocene. The statistical results from this study support the existence of the guild structures proposed by Hertel (1994), with only minor differences with respect to which species fit within each guild. The caracaras may comprise their own guild structure independent of cathartid and accipitrid vultures, but more observational data needs to be collected in order to draw firm conclusions.

Dedication

I dedicate this work to my family:

my parents, my loving husband Ky Statham, and my cat Simba.

*You were my inspiration and my foundation, and I will always be grateful to you all
for supporting me through everything it took to reach this point.*

Acknowledgements

There are countless people in my life I could thank for helping me reach this point, but I must extend my thanks especially to my family. Thank you to my parents for inspiring me to go this far at all – to my mom, Gretchen, for her encouragement and for fostering my love of biology and paleontology, and to my dad, Dennis, for fostering my love of art and always supporting me through every degree, every cross-country move, and every milestone. Thank you both for being there with me through everything.

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Table of Contents

Abstract.....	1
Dedication	i
Acknowledgements.....	ii
Table of Contents.....	iv
List of Tables	vi
List of Figures	vii
List of Appendices.....	viii
General Introduction	ix
Chapter 1	1
1.1 Introduction	1
1.2 Materials and Methods	3
1.2.1 Materials.....	3
1.2.2 Data collection.....	3
1.2.3 Analysis.....	4
1.3 Results	5
1.3.1 Traditional morphometrics	5
1.3.2 Geometric morphometrics	5
1.4 Discussion.....	6
1.5 Conclusions and Future Directions.....	8
1.6 Tables and Figures	10
Chapter 2.....	15
2.1 Introduction	15
2.2 Materials and Methods	18
2.2.1 Data analyses	19
2.3 Results	20
2.3.1 Combined orders analyses – skull shape	20
2.3.2 Combined orders analyses – cranium shape	21
2.3.3 Combined orders analyses – premaxillary shape.....	21
2.3.4 Accipitriformes analyses – skull shape.....	22
2.3.5 Accipitriformes analyses – cranium shape	23
2.3.6 Accipitriformes analyses – premaxillary shape.....	24
2.3.7 Falconiformes analyses – skull shape.....	24

2.3.8	Falconiformes analyses – skull shape.....	25
2.3.9	Falconiformes analyses – skull shape.....	25
2.4	Discussion.....	26
2.5	Conclusions and Future Directions.....	28
2.6	Tables and Figures	30
2.7	Supporting Documents.....	44
2.7.1	Supplementary Tables	44
2.7.2	Supplementary Figures	47
Chapter 3		52
3.1	Introduction	52
3.1.1	Vulture phylogenetic relationships.....	52
3.1.2	Vulture fossil record and geographic origins	53
3.1.3	Vulture feeding guilds.....	54
3.1.4	Scavenging in the Falconiformes	55
3.1.5	Scope of this study.....	55
3.2	Materials and Methods.....	56
3.2.1	Materials.....	56
3.2.2	Data collections	56
3.2.3	Data analyses and statistics.....	57
3.3	Results	58
3.3.1	Comparison of three families – whole skull	58
3.3.2	Comparison of three families – whole skull: modern	59
3.3.3	Comparison of three families – whole skull: fossil	60
3.3.4	Comparison of three families – cranium only	61
3.3.5	Comparison of three families – cranium only: modern	62
3.3.6	Comparison of three families – cranium only: fossil	62
3.3.7	Comparison of three families – premaxillary only	63
3.3.8	Comparison of three families – premaxillary only: modern.....	64
3.3.9	Comparison of three families – premaxillary only: fossil.....	64
3.3.10	Accipitridae and Cathartidae – whole skull.....	65
3.3.11	Accipitridae and Cathartidae – whole skull: modern.....	65
3.3.12	Accipitridae and Cathartidae – whole skull: fossil.....	66
3.3.13	Accipitridae and Cathartidae – cranium only	67
3.3.14	Accipitridae and Cathartidae – cranium only: modern	67

3.3.15 Accipitridae and Cathartidae – cranium only: fossil	68
3.3.16 Accipitridae and Cathartidae – premaxillary only.....	69
3.3.17 Accipitridae and Cathartidae – premaxillary only: modern	69
3.3.18 Accipitridae and Cathartidae – premaxillary only: fossil	70
3.3.19 Accipitridae and Cathartidae guilds – whole skull	71
3.3.20 Accipitridae and Cathartidae guilds – cranium only.....	72
3.3.21 Accipitridae and Cathartidae guilds – premaxillary only	72
3.3.22 Accipitridae and Cathartidae guilds with Polyborinae present.....	73
3.4 Discussion.....	74
3.5 Conclusions and Future Directions.....	77
3.6 Tables and Figures	78
General Conclusion	101
References	103
Appendices	117

List of Tables

Table 1.1: Distribution of skins and skeletons per species.....	10
Table 1.2: Table of values for the traditional measurements of the beak.....	11
Table 1.3: Table of results for ANOVA tests on beak shape PCAs.....	12
Table 2.1: Table of values for ANOVA tests on modern skull, cranium, and premaxillary shape PCAs	30
Table 2.2: Table of Tukey’s test adjusted p-values	32
Table S2.1: Table of values for ANOVA tests on modern only skull, cranium, and premaxillary shape PCAs.....	44
Table S2.2: Table of ANOVA p-values to assess the effect of fossils on the morphospace	46
Table 3.1: Known fossil vultures	78
Table 3.2: Guild descriptions and classifications	80
Table 3.3: Table of results for ANOVA tests on skull, cranium, and premaxillary shape PCAs	82
Table 3.4: Table of Tukey’s test adjusted p-values	86

List of Figures

Figure 1.1: Diagrams of measurements and landmarks placed on the beak	13
Figure 1.2: Backtransform PCA plots.....	14
Figure 2.1: Diagram of placement of landmarks and curves for shape analyses	37
Figure 2.2: Backtransform PCAs showing family distribution of all orders	38
Figure 2.3: Backtransform PCAs showing subfamily distribution of all orders	39
Figure 2.4: Backtransform PCAs showing scavenger distribution of all orders	40
Figure 2.5: Backtransform PCAs showing family distribution of Accipitriformes	41
Figure 2.6: Backtransform PCAs showing scavenger distribution of Accipitriformes .	42
Figure 2.7: Backtransform PCAs of Falconiformes	43
Figure S2.1: Backtransform PCAs showing family distribution of all orders without fossils	47
Figure S2.2: Backtransform PCAs showing subfamily distribution of all orders without fossils	48
Figure S2.3: Backtransform PCAs showing scavenger distribution of all orders without fossils	49
Figure S2.4: Backtransform PCAs showing family distribution of modern accipiters ...	50
Figure S2.5: Backtransform PCAs showing scavenger distribution of modern accipiters.....	51
Figure 3.1: Diagram of placement of landmarks and curves for shape analyses	89
Figure 3.2: Backtransform PCAs for the skull showing family distribution.....	90
Figure 3.3: Backtransform PCAs for the skull showing subfamily distribution.....	91
Figure 3.4: Backtransform PCAs for the cranium showing subfamily distribution	92
Figure 3.5: Backtransform PCAs for the premaxillary showing subfamily distribution	93
Figure 3.6: Backtransform PCAs for the skull showing subfamily distribution of Accipitriformes only	94
Figure 3.7: Backtransform PCAs for the cranium showing subfamily distribution of Accipitriformes only	95
Figure 3.8: Backtransform PCAs for the premaxillary showing subfamily distribution of Accipitriformes only	96
Figure 3.9: Backtransform PCAs for the skull showing guild map of Accipitriformes only.	97

Figure 3.10: Backtransform PCAs for the cranium showing guild map of Accipitriformes only	98
Figure 3.11: Backtransform PCAs for the premaxillary showing guild map of Accipitriformes only	99
Figure 3.12: Backtransform PCAs for the skull showing guild map of all species	100

List of Appendices

Appendix 1.1: Comprehensive list of specimens and their measurements	117
Appendix 2.1: Comprehensive list of landmarked specimens	122
Appendix 3.1: Comprehensive list of landmarked specimens	131

General Introduction

Avian skull anatomy and morphology has been studied for centuries. There are two primary approaches to studying the avian skull. The first and most typical approach has been to investigate one cranial structure at a time, or to limit analysis to very few taxa. Such analytical approaches have typically focused on small passerines, such as the Darwin's Finches (e.g. Mallarino et al., 2011) or Hawaiian honeycreepers (Tokita et al., 2017). Such approaches can be very informative for understanding how the skull functions and the feeding and life strategies of different species, especially if they represent an adaptive radiation. More broadly, the endocast of birds has been used to study the evolution of flight (Dominguez et al., 2004; Beyrand et al., 2019), the transition from non-avian dinosaurs to crown birds (Balanoff et al., 2013; 2016), and to make behavioral inferences (Early, 2019; Early et al., 2020). The 'whole skull' approach is sometimes considered problematic due to the debated extent of modularity of the avian skull. Some authors favor treating the cranium and beak as separate elements that are evolving independently of each other, whereas others argue that their development, and therefore evolutionary trajectory, are linked and as such all parts of the skull must be considered together to assess avian cranial evolution. Both morphological and molecular approaches have been used on large numbers of taxa to try to answer this question, often result in divergent conclusions being drawn (e.g. Felice & Goswami, 2017; Klingenberg & Marugán-Lobón, 2013). Felice and Goswami (2017) using a molecular approach found that the bird skull has many anatomical modules, and showed a mosaic of evolutionary rates in each module. In contrast, Klingenberg and Marugán-Lobón (2013) making use of a morphological approach, concluded that the face and braincase of the skull are evolutionarily integrated and not modular, i.e. their evolutionary rates are tightly linked with one another.

The second approach utilizes a large taxonomic range of species to address broad evolutionary or phylogenetic questions. These studies sample across all or most of avian diversity, making inferences from a few representative taxa of each avian order (e.g., Felice & Goswami, 2017; Hackett et al., 2008; Livezey, 1998; Prum et al., 2015). Many of these studies have even extended to theropod dinosaurs, the ancestors of extant birds, to investigate deeper divergence and pedomorphism (e.g. Bhullar et al., 2016, 2012, 2015b).

Skull morphology has been investigated in many different orders of birds, and particularly for raptors – species of the orders Accipitriformes, Falconiformes, and Strigiformes. The members of the Accipitriformes are a diverse and geographically widespread order of birds. This group comprises most of what is colloquially known as raptors, which are defined by their carnivorous diet, strongly curved bills and talons, and keen eyesight (Snyder & Snyder, 1991; Jones, Pierce, & Ward, 2007; McClure et al., 2019). As such, much research about these birds has focused on beak and talon

morphology, and on their ecology as it relates to prey choice and acquisition. The Accipitriformes also contains the two families of birds that are most well-known for being primarily carrion eaters, the clades known as 'Old World' (Gypaetinae, Aegypiinae) and 'New World' (Cathartidae) vultures. Vultures have a distinct morphology from the rest of the Accipitriformes that is associated with scavenging. These birds have long necks and long hooked beaks for reaching into large carcasses, with heads that are mostly or entirely devoid of feathers (Buechley & Sekercioglu, 2016). Additionally, they have lost some of the specialized features of the feet and talons, no longer needing them for prey capture (Buechley & Sekercioglu, 2016; M. O. Campbell, 2015).

The caracara falcons, of the subfamily Polyborinae, are a less well-known scavenging clade of birds. As they are part of the order Falconiformes, they represent an independent origin of the scavenger life history strategy. The caracaras have also evolved distinctive traits that separate them from the rest of the falcons, including longer heads that partially lack feathering, reduced beak and talon curvature, and a very large body size relative to most falcons (Morrison & Saggese, 2024). These large, opportunistic scavengers overlap geographically with many species of New World vultures in South and Central America, and the fossil record supports their existence during a species rich and diverse California Pleistocene (K. E. Campbell, 1979; Howard, 1932). Despite their characteristic morphological features, the caracaras have never been considered to be part of the vulture guild.

Geometric Morphometrics (GM) is the study of shape and compares the shape of groups of objects or organisms to each other. GM is performed as either a 2D (photograph) or a 3D (CT scan, surface scan, photogrammetry, etc.) analysis. Geometric morphometrics utilizes a technique called Procrustes superimposition. Procrustes superimposition removes aspects of size including rotation, scale, and translation from the specimens included in the analysis. The analysis then uses the coordinate data collected from all shapes in the analysis to create an average shape (Bookstein, 1996). This average lies at the centroid (0,0) of the PCA graph and becomes the basis of comparison for all other shapes in the analysis. The amount of variation in each specimen as compared to the average shape is calculated and represented on a graphical morphospace as Principal Components (PC). PCs are numbered based on the percentage of variation explained, starting at PC1 and decreasing in percentage from there. In the Principal Component morphospace, every point represents one specimen and is placed along the x-axis according to the amount of difference it shows from the centroid x-coordinate, and along the y-axis according to the amount of difference it shows from the centroid y-coordinate. Individual specimens that are close together on the PC morphospace are more similar in shape to each other than to individuals further away.

For my dissertation I investigated raptor skull morphology using geometric morphometrics. I made use of museum specimens to investigate the convergence of traits across lineages and made use of both extant species and fossils to investigate how

trait convergence has changed through time. My dissertation consists of three chapters: (1) The importance of the rhamphotheca and its relationship to beak shape in the morphometric analysis of bird ecomorphology; (2) assessing skull characters and modularity in the premaxillary and cranium of diurnal raptors and; (3) vulture feeding guilds from the late Pleistocene to the modern day. The first chapter assessed how much of an impact the keratinous rhamphotheca has on the overall shape of the beak in five species of raptors, establishing a groundwork for analyses performed in chapters two and three. The second chapter focused on members of the orders Accipitriformes and Falconiformes, drawing comparisons between the scavengers and non-scavengers of each order. The third chapter then paired down this dataset to focus on the scavengers alone, the accipitrid vultures, cathartid vultures, and caracara falcons, to reevaluate the guild structures proposed by Hertel (1994), Houston (1988), and Kruuk (1967).

Chapter 1

The importance of the rhamphotheca and its relationship to beak shape in the morphometric analysis of bird ecomorphology

1.1 Introduction

Studies of avian ecomorphology have long emphasized bill morphology and how it relates to diet, feeding mechanics, and behaviors. However, the study of the avian bill is often limited by the approach used to measure or otherwise analyze this element. The avian beak is composed of two parts – the bony premaxilla and the keratinous rhamphothecae, known as the rhinotheca on the premaxillary and gnathotheca on the mandible, a sheath of modified epidermis that is abundant in calcium phosphate and keratin (Cunningham et al., 2013; Genbrugge et al., 2012). This sheath covers and, in many cases, extends beyond the bony premaxilla (rhinotheca) and mandible (gnathotheca). A keratinous sheath on the premaxilla and mandible is not exclusively found in living birds also being present in turtles (Urano et al., 2018). While the rhamphothecae are rarely preserved in fossils due to the soft nature of keratin (Briggs, 2003), there is evidence that many extinct birds (Falk et al., 2019; Miller et al., 2020), some non-avian dinosaurs (Lautenschlager et al., 2013), and some pterosaurs (Fastnacht, 2001; Pinheiro et al., 2011) did possess rhamphothecae. The shape and composition of the rhamphotheca have been studied for a variety of reasons including diet and feeding behavior (Herrel et al., 2005; Mallarino et al., 2011; Navalón, Bright, Marugán-Lobón, et al., 2019), object manipulation (Matsui et al., 2016; Weir et al., 2002), display (Mayr, 2018), song modulation (Derryberry et al., 2012; Podos, 2001), thermoregulation (Friedman et al., 2017; Gardner et al., 2016; Ryeland et al., 2017; Tattersall et al., 2016), and as a bioindicator for pollutants in bird populations (de Medeiros Costa et al., 2021).

Birds collected and prepared as specimens are mostly preserved as either a round skin or a skeleton. Skins of bird specimens typically have an attached rhamphotheca, whereas most skeletal specimens have either lost the rhamphotheca in the preparation process or no longer have it attached to the bony premaxilla and mandible. The keratin sheath becomes soft when soaked in hydrogen peroxide, which is a common practice when cleaning prepared skeletons and can come loose. Studies that observe living birds, or use museum skins, will almost always take into account the shape of the rhamphotheca (e.g. Benham & Bowie, 2021; Cooney et al., 2017), while the majority of studies that use skeletal museum specimens use specimens that do not have a rhamphotheca, and usually exclude those that do for the sake of ease and consistency (Bright et al., 2016;

Felice et al., 2019; Navalón, Bright, Marugán-Lobón, et al., 2019; Olsen, 2017; Pecsics et al., 2019; Simonetta, 1960).

Geometric Morphometrics (GM) is the study of shape and compares the shape of groups of objects or organisms to each other. GM is performed as either a 2D (photograph) or a 3D (CT scan, surface scan, photogrammetry, etc.) analysis. When analyzing the shape of the beak using GM, whether the rhamphotheca is present or not may influence the resulting recorded shape of the morphology of a structure on a specimen, and if some specimens have the rhamphotheca present while others do not, it may skew the results. This is generally not an issue when performing a 3D analysis where the specimen has been CT scanned as the keratinous rhamphotheca has a lower density than bone and can be removed digitally during segmentation of the scanned specimen. For 3D surface scans and 2D data, the rhamphotheca must be considered part of the specimens' overall shape with no option for removal. But how accurately do studies that do not include the rhamphotheca reflect avian skull morphology, particularly in birds of prey where the tomial hook is an important adaptation for the tearing of food items? Studying only the bony portion of the beak runs the risk of concluding that beak morphology is more conserved than it may truly be when the morphology of the rhamphotheca is considered.

Several recent studies have investigated differences in the rhamphotheca versus bony beak shape. Urano et al. (2018) compared the curvatures of bony beak and rhinotheca in birds and turtles. Using CT scans, they landmarked the culминаl margin of the bony beak and rhinotheca to create a profile for each specimen. They found that the culминаl profiles for beak bone and rhinotheca differed in each species. Across birds, the rhinotheca was anywhere from 1.31 to 1.48 times longer than the beak, but their findings suggested that the curvature of the beak was not significantly different. Eliason et al. (2020) CT scanned the skulls of kingfishers and used geometric morphometrics to model the evolutionary covariation between the rhamphotheca and bone. Their study concluded that beak and rhamphotheca shape differed and urged caution, as in kingfishers the angle of the rhamphotheca is underestimated when using the bony beak shape as a proxy for beak angle. In both studies, differences were seen in the rhamphotheca and bony shape, but the variation within a single species was not addressed directly.

Bird beaks are functional structures, and a highly curved, hooked beak is one of the defining characteristics of the raptorial lifestyle. This reliance on a particular beak morphology for feeding and prey acquisition makes raptors ideal candidates for investigating the effect of the rhamphotheca on beak shape. This study aims to quantify the degree to which the rhamphotheca impacts the shape of the premaxilla in raptors. We collected 2D landmark data for a geometric morphometric analysis on several skeletonized museum specimens that do and do not have a rhamphotheca present and round-skin specimens with visible and complete rhamphotheca. Comparisons are drawn

among five raptor species across the Accipitriformes, Falconiformes, and Strigiformes. Several studies sought to determine the relationship between beak shape and diet in raptors, but these studies have overlooked the importance of including the rhamphotheca in the shape analysis (Guangdi et al., 2015; Bright et al., 2016; Felice & Goswami, 2018; Felice et al., 2019), or they have used skeletal specimens but have not specified if the skulls possessed a rhamphotheca or not (Pecsics et al., 2019). Significant changes in the shape of the premaxilla when the rhamphotheca is present will affect how researchers approach future studies of the avian skull, particularly when using skeletonized museum specimens to study and interpolate shape. This may also have implications for how we interpret avian food preference, feeding strategies, and convergence in the fossil record.

1.2 Materials and Methods

1.2.1 Materials

Materials for this project included 29 specimens of *Buteo jamaicensis* (red-wing hawk), 39 specimens of *Cathartes aura* (turkey vulture), 27 specimens of *Pandion haliaetus* (osprey), 30 specimens of *Falco mexicanus* (prairie falcon), and 43 specimens of *Bubo virginianus* (great horned owl) (Table 1.1 and Appendix 1.1). This provided at least one representation of the major raptor orders and one example of a related avian scavenger. Ontogenetic differences were not considered in this study, therefore only adult specimens were used for these analyses. A combination of cleaned skulls and skins were utilized in this study.

1.2.2 Data Collection

This study used traditional measurements taken with digital calipers and 2D Geometric Morphometrics (GM), which utilized digital landmarks on photographed specimens. Traditional measurements for the beak followed those taken by Hertel (1995) (Figure 1.1a). Premaxillary length, premaxillary width, premaxillary depth, and premaxillary chord measurements were taken by MK using a VINCA DCLA-0605 electronic digital caliper with +/- 0.03 mm accuracy. Specimens were photographed with a Nikon D3400 DSLR camera and AF-P Nikkor 18-55 mm lens on a 1.27 x 1.27 cm gridded mat. Specimens were photographed in the left lateral view when possible. For specimens that were damaged on the left side, a photograph of the right lateral view was taken and mirrored for landmarking. We also recorded data on sex for all specimens; however some specimens included in this analysis are unsexed.

Landmarking was performed in R using the package StereoMorph (Olsen & Westneat, 2015). The package allows the user to manually place landmarks onto photographs. Landmarks and curves were centered on capturing the culминаl and tomial curvatures of the bill. Two types of landmarks were used: Type I landmarks, which are defined as clearly homologous points of correspondence, and sliding or semi-landmarks,

which exist as equally spaced points along a curve of the specimen being analyzed (Bookstein, 1997; Mitteroecker & Gunz, 2009). StereoMorph also allows for the capture of scale for each specimen by the placement of two additional landmarks on a scale bar in the photo. The user provides a value to the distance between the two points on the scale bar, thereby giving scale to the specimen. Each photo received three landmarks, and every species, apart from *Falco mexicanus*, had 10 equally spaced semi-landmarks per curve, for a total of 20 sliding semi-landmarks per specimen (Figure 1.1b). *Falco mexicanus* received 10 semi-landmarks on the upper curve and 20 semi-landmarks on the tomial curve to account for the slightly more complex shape of the tomial tooth in these birds, totaling 30 semi-landmarks per specimen (Figure 1.1c). While this analysis focused on the rhinotheca, it will be referred to as the rhamphotheca for the remainder of the text.

1.2.3 Analysis

Each species included in this study was analyzed individually. This allowed the principal changes occurring to be centered on the beak shape and size, without the noise of taxonomic differences.

The landmark coordinate data extracted from the StereoMorph package was subjected to a Procrustes superimposition and Principal Components Analysis (PCA) using the geomorph package in R (Adams & Otárola-Castillo, 2013). Procrustes superimposition removes aspects of size including rotation, scale, and translation from the specimens included in the analysis. The analysis then uses the coordinate data collected from all shapes to create an average shape (Bookstein, 1996). This average lies at the centroid (0,0) of the PCA graph and becomes the basis of comparison for all other shapes included in the analysis. The amount of variation in each specimen as compared to the average shape is calculated and represented on a graphical morphospace as principal components (PC). PCs are numbered based on the percentage of variation explained, starting at PC1, and decreasing in percentage from there. In the Principal Component morphospace, every point represents one specimen and is placed along the x-axis according to the amount of difference it shows from the centroid x coordinate, and along the y-axis according to the amount of difference it shows from the centroid y coordinate. Individual specimens that are close together on the PC morphospace are more similar in shape to each other than to individuals further away.

We performed one-way analysis of variance (ANOVA) statistical tests and linear regressions for each species in the study. For the traditional measurements, each beak measurement was tested for its relationship to rhamphotheca presence. Similarly, for the geometric morphometric data, the PC1 and PC2 were compared against each dataset's rhamphotheca presence to test if either shape variable explains the variation in size or shape of the raptor beaks. R-squared values were multiplied by PC values to score

significance for each test variable. Principal component analysis, spline, and backtransform morphospace plots were produced using the R packages StereoMorph, geomorph, and ggplot (Wickham & Wickham, 2007). Backtransform morphospace plots were created for each species, following the R protocol developed by Olsen (2017). These plots provide a visual representation of the morphological changes happening on the x- and y-axes.

Raptors (Accipitriformes, Falconiformes, and Strigiformes) are known to generally exhibit a reversed sexual dimorphism in body size, where the females tend to be larger on average than the males (Amadon, 1975). While sex was recorded for each specimen, sex was not an even split of males and females among the rhamphotheca and non-rhamphotheca specimens, either due to sex being unidentified or collections lacking additional specimens. To isolate sex differences, we created subsets for species that consisted of the males and females – excluding specimens with unidentified sex – with the rhamphotheca and without the rhamphotheca. This resulted in two groups for each species. To test for adequate sample sizes, we ran power tests on each subset in R. The power tests returned a power value of 0.5567 or less in every group, indicating that a larger sample size would be needed to accurately reflect potential sex differences in the sizes and shapes of raptor beaks both with and without the rhamphotheca present.

1.3 Results

1.3.1 Traditional morphometrics

The mean values of the beak indices and their associated P-values, F-stats, df, and r-squared values are listed in Table 1.2 (for all measurements see Appendix 1.1). The ANOVA tests for rhamphotheca presence or absence indicated that height and chord measurements were significant across all species. The length measurement was significant for all species except *Buteo jamaicensis*. The width measurement was significant in *Pandion haliaetus*, *Bubo virginianus*, and *Buteo jamaicensis*. Traditional morphometric measurements of the beak were consistently larger on average in specimens with a rhamphotheca, indicating that the rhamphotheca adds significant size to the beak in three dimensions: length, chord, and height with commensurate differences in force available at the distal end.

1.3.2 Geometric morphometrics

Proportion of Variance (PoV), P-values, F-stats, df, and r-squared values for the geometric morphometric analyses are listed in Table 1.3. Values were calculated from ANOVA tests with rhamphotheca presence as the independent variable and PC1 or PC2 as the dependent variable. In each species analysis, a clear shape difference was observed between specimens that possess and lack a rhamphotheca, which can be visually discerned in the PCA backtransform morphospace plots (Figure 1.2). P-values

from the ANOVA tests were found to be significant for at least one of the PC axes of every species, supporting the presence or absence of the rhamphotheca as a primary factor of shape difference within the species of raptors studied.

Every species had significant P-values on PC1 when comparing rhamphotheca presence versus absence. The percentage of overall shape variation explained by the presence or absence of the rhamphotheca obtained from multiplying the principal component proportion of variance with the r-squared value ranged from 63.69% in *Pandion haliaetus* to 22.19% in *Bubo virginianus*. Every species except for *Pandion haliaetus* also had significant P-values on the PC2 axis, confirming that in most cases some amount of the beak shape variation is seen across both axes. Multiplying the PC2 proportion of variance (PoV) by the r-squared value for each of these datasets showed only a small amount of rhamphotheca shape variation was accounted for by the PC2 axis, ranging from as little as 1.43% in *Falco mexicanus* to as much as 9.73% in *Bubo virginianus* (Table 1.3). *Bubo virginianus* had the highest amount of shape variation attributed to principal component 2 (20%) of all the species analyzed, which is 5% higher than the next highest PC2 PoV (Table 1.3).

1.4 Discussion

Combining traditional and geometric morphometrics to analyze beak shape in raptors points to there being not only a distinct size difference between specimens when the rhamphotheca is present versus when it is not but also a significant shape difference. Traditional measurements indicated that a significant amount of length and height is added to the beak when the rhamphotheca is present. The rhamphotheca did not appear to add a significant amount of width to the beak in any of the species. The layer of keratin that the rhamphotheca is composed of tends to be relatively thin, which would not be expected to contribute much to the width of the beak. By comparison, the keratin extends well past the boney beak as the beak curves, adding significant length and height.

While the traditional measurements made clear that there is a size difference in rhamphotheca presence, Procrustes superimposition removes all aspects of size, leaving only shape information in the resulting principal components. The results of the geometric morphometric analyses indicated that in addition to the size increase, there is a significant change in the shape of the beak when the rhamphotheca is present in raptors. In addition to an overall lengthening of the beak, individuals with a rhamphotheca also tended to have a greater degree and depth of curvature. These two changes seem to be the primary shape change occurring across the x-axis as defined by PC1 in all species and PC2 in most species, as illustrated in the backtransform morphospace plots generated for each analysis (Figure 1.2). This was true across raptors of different orders, and even in *Cathartes aura*, despite this species being a scavenger that does not use its beak to hunt prey actively. Raptors likely benefit from this additional length and curvature in particular

due to the use of their beak for capture, dispatch, and consumption of prey (Errington, 1932).

Pandion haliaetus had the overall most apparent differentiation of rhamphotheca in the 2D morphospace (Figure 1.2A). Specimens with a rhamphotheca had a much more slender profile, greater beak curvature, and decreased posterior depth. Per the statistical analyses, *Bubo virginianus* showed more split variation across the x- and y-axes, though only small percentages of the shape variation are accounted for by PC2 (y-axis) in each of these species. *Buteo* specimens showed a similar trend to that seen in *Pandion*, but with all specimens tending towards a more slender profile regardless of rhamphotheca presence, and variation of curvature being less pronounced. In *Buteo*, the x-axis (PC1) defines the overall posterior depth of the beak, while variation in the amount of curvature is seen along the y-axis (PC2) (Figure 1.2B). Differing slightly from these trends, beak curvature was a major difference in specimens of *Cathartes aura*, appearing to influence both the x- and y-axis variation (Figure 1.2C). This results in a more diagonal skew across the plot, with rhamphotheca specimens tending to have greater beak depth overall in addition to greater curvature. Specimens of *Cathartes* without a rhamphotheca tended to have a deep posterior but come to a much more abrupt and slender point.

As for *Falco mexicanus*, the presence of a significant tomial tooth seems to play a prominent role in the shape change. There is a large amount of individual variation as to whether the tomial tooth is well-defined in the bone of the beak and the keratin of the rhamphotheca. Some individuals had a very sharply defined tomial tooth in the bone, while others did not, and the same trend was observed in the rhamphotheca. Tomial tooth presence overall did tend to be more pronounced in individuals with a rhamphotheca, while the variation was more widespread across the x-axis (PC1) in individuals that lacked a rhamphotheca (Figure 1.2D). The presence of the tomial tooth is a particular feature of members of the Falconiformes but is present to a degree in some members of the Accipitriformes as well. Further analysis of falcons and accipiters with a pronounced tomial tooth may give a clearer picture of the significance of this feature in raptor beak morphology.

Bubo specimens with a rhamphotheca tended to have a more robust beak profile along with greater beak curvature and depth. Specimens of *Bubo* without a rhamphotheca tended towards a more gracile shape, sometimes with great beak depth but lacking the deep curve and coming to more of a slender point (Figure 1.2E). Overall, *B. virginianus* statistically differed the most from the other species in having the least amount of shape variation being explained by the presence or absence of the rhamphotheca on any of the principal components. This indicates that there is some other factor influencing the shape of the beak in these owls besides rhamphotheca presence/absence. Owls may exhibit a greater degree of individual variation or sexual variation than members of other orders.

Avian raptors rely heavily on their beaks for prey acquisition and feeding, and the rhamphotheca plays an important role in the functionality of their beak in these tasks by adding size, length, and curvature. In nearly all species, the range of shape variation was higher in the bony beak, and lower in the rhamphotheca, as indicated by the amount of spread of specimens in the PCA morphospace. Bone therefore may be more prone to intraspecific variation, and the keratin sheath normalizes the shape within a species. This suggests that in raptors, the functional role of the beak is the driving mechanism behind the final shape of the keratinous beak, reducing intraspecific variation in beak shape that may be detrimental to beak function. Studies such as those done by Guangdi et al. (2015) and Bright et al. (2016) draw their conclusions from the skull morphology of skeletonized museum specimens, which only evaluated shape based on the bony beak and excluded the effect of the rhamphotheca. Pecsics et al. (2019) do not specify if they only used specimens with a rhamphotheca, only specimens without, or a combination of the two. Based on the results of the study presented here, the conclusions Guangdi et al. (2015), Bright et al. (2016), and Pecsics et al. (2019) drew about raptors and how the shape of the beak relates to raptor diet may benefit from a reevaluation that includes rhamphotheca shape.

But the rhamphotheca is present in all living birds, many of which possess modifications such as serrations or lamellae and can provide a variety of functions for birds beyond feeding. The rhamphotheca is also a continuously growing structure that is subject to wear and seasonal variation (Greenberg et al., 2013; Matthysen, 1989; Pomeroy, 1962). Due to the fluctuating nature of the rhamphotheca, it is worth considering that beak shape and degree of intraspecific variation may vary with age, sex, season, or use across different taxa. Some non-raptor avian taxa may not see the same degree of size or shape change in the beak and may not have as large of a discrepancy between bony beak and rhamphotheca shape as was seen in raptors.

1.5 Conclusions and Future Directions

Avian beak morphology and variation are extensively studied and used to make conclusions about feeding behavior and dietary preferences, but most studies choose to focus on only the bony beak or the rhamphotheca. This study used five species of different families of raptors to question this practice. Despite different phylogenetic origins for the taxa used in this analysis, there are recurring trends of beak size and shape change in raptors based on rhamphotheca presence. These findings agree with the conclusions of Urano et al. (2018) and Eliason et al. (2020), that the rhamphotheca does have noteworthy implications for the dietary and ecological conclusions in studies that exclude rhamphotheca from their analyses. It emphasizes the need to include the rhamphotheca in comparative dietary analyses to have truly meaningful results. Future analyses with a greater emphasis on sexual variation in the dataset will be necessary to investigate

whether sexual dimorphism has a significant effect on the size and shape of the beak in raptors. Additionally, the question remains as to whether or not this trend will be seen in non-raptor taxa, or how beak shape may change as a bird ages. Future work will look at the amount of variation in the beak in taxa outside of raptors and at birds through various ontogenetic stages to help address this question of size and shape variation in the bony beak and rhamphotheca.

1.6 Tables and Figures

Table 1.1. Distribution of skins and skeletons per species. Table showing the distribution of specimens for each species in the study. Most rhamphotheca shapes came from skins due to the lack of rhamphotheca presence in skeletonized specimens.

	Skins	Skeleton (rham)	Skeletons (no rham)	Total (rham)	Total (no rham)	Total Specimens
<i>Pandion haliaetus</i>	12	1	14	13	14	27
<i>Buteo jamaicensis</i>	6	9	14	15	14	29
<i>Cathartes aura</i>	11	9	19	20	19	39
<i>Falco mexicanus</i>	15	0	15	15	15	30
<i>Bubo virginianus</i>	15	7	20	22	20	42

Table 1.2. Table of values for the traditional measurements of the beak. Columns one and two are the average of the measurement of all specimens in that species. Remaining columns are the result of one-way analysis of variance (ANOVA) tests. In all tests, each measurement (width, height, length, cord) was used as the quantitative variable and rhamphotheca presence was used as the independent variable. P-values are considered significant at ≤ 0.05 and are marked with an asterisk (*).

<i>Pandion haliaetus</i>	Rham Average (mm)	No Rham Average (mm)	P-value	r-squared	F-statistic
Width	16.26	18.48	1.22E-04*	0.4893	22.08 (1, 21)
Height	27.40	16.00	3.93E-13*	0.9187	249.7 (1, 21)
Length	22.87	16.70	1.13E-09*	0.8273	106.4 (1, 21)
Chord	33.56	23.17	4.66E-12*	0.8972	193.1 (1, 21)
<i>Buteo jamaicensis</i>					
Width	14.30	15.65	0.044*	0.1101	4.464 (1, 27)
Height	23.48	17.35	1.62E-09*	0.7365	79.24 (1, 27)
Length	18.07	17.63	0.6601	-0.0295	0.1977 (1, 27)
Chord	26.29	20.85	5.34E-10*	0.7642	91.77 (1, 27)
<i>Cathartes aura</i>					
Width	14.23	13.87	0.1701	0.02458	1.957 (1, 37)
Height	21.20	15.33	1.14E-15*	0.8223	176.9 (1, 37)
Length	19.87	15.93	1.38E-07*	0.5196	42.09 (1, 37)
Chord	23.96	18.90	2.69E-15*	0.8139	167.2 (1, 37)
<i>Falco mexicanus</i>					
Width	14.38	14.49	0.8444	-0.03427	0.0392 (1, 28)
Height	18.77	12.92	7.83E-11*	0.7767	101.9 (1, 28)
Length	16.82	13.74	1.22E-04*	0.3943	19.88 (1, 28)
Chord	20.03	16.54	1.31E-06*	0.5574	37.52 (1, 28)
<i>Bubo virginianus</i>					
Width	17.55	14.92	3.07E-06*	0.4014	29.17 (1, 41)
Height	25.56	19.31	2.20E-16*	0.8402	221.8 (1, 41)
Length	20.18	17.75	5.24E-04*	0.2387	14.17 (1, 41)
Chord	27.74	20.95	9.18E-12*	0.6836	89.6 (1, 41)

Table 1.3. Table of results for ANOVA tests on beak shape PCAs. Table of values for the one-way analysis of variance (ANOVA) tests on geometric morphometric data, which included all specimens regardless of sex. In all tests, percentage of variance (PoV %) for the principal component was used as the quantitative variable and rhamphotheca presence (rham) or sex was used as the independent variable. P-values below 0.05 are marked with an asterisk (*) and R-squared values were only reported when the P-value was below 0.05. Percent variance is the r-squared value multiplied by the PoV.

<i>Pandion haliaetus</i>	PoV (%)	P-value	r-squared	F-statistic	% Variance
PC1	72.3	1.93E-13*	0.8846	200.3 (1, 25)	63.96
PC2	15.44	0.305	0.0037	1.097 (1, 25)	0.06
PC3	8.88	0.5264	-0.0231	0.4127 (1, 25)	-0.21
<i>Buteo jamaicensis</i>					
PC1	72.87	9.39E-07*	0.5809	39.81 (1, 27)	42.33
PC2	14.61	4.00E-04*	0.2413	9.904 (1, 27)	3.53
PC3	8.87	0.7579	-0.03332	0.09699 (1, 27)	-0.30
<i>Cathartes aura</i>					
PC1	74.76	1.59E-06*	0.4533	32.51 (1, 37)	33.89
PC2	13.14	1.34E-04*	0.3106	18.12 (1, 37)	4.08
PC3	6.57	0.1029	0.04513	2.796 (1, 37)	0.30
<i>Falco mexicanus</i>					
PC1	77.21	4.27E-07*	0.5907	42.86 (1, 28)	45.61
PC2	13.72	0.0477*	0.1019	4.289 (1, 28)	1.40
PC3	4.37	0.2644	0.01015	1.297 (1, 28)	0.04
<i>Bubo virginianus</i>					
PC1	67.95	3.78E-05*	0.3263	21.34 (1, 41)	22.17
PC2	19.84	8.11E-06*	0.3733	26.02 (1, 41)	7.41
PC3	6.79	0.261	0.261	1.299 (1, 41)	1.77

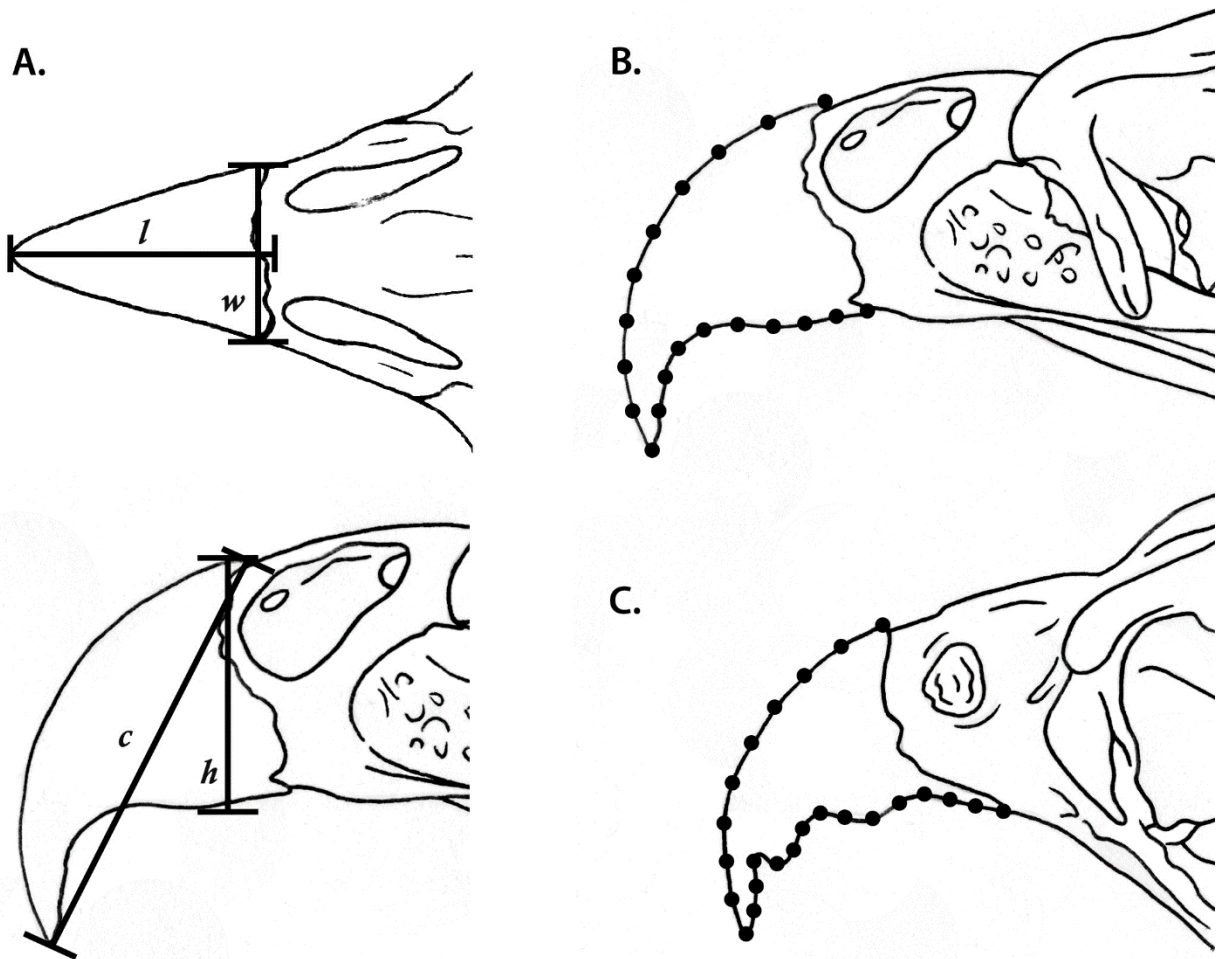


Figure 1.1. Diagrams of measurements and landmarks placed on the beak. Diagram of measurements taken (A) and semi-landmark placement on the culминаl and tomial margins (B, C). Traditional measurements consisted of premaxillary length (l), premaxillary width (w), premaxillary height (h), and premaxillary chord length (c). Every curve consisted of 10 evenly spaced semi-landmarks as illustrated in *Buteo* (B) except for the tomial margin of the *Falco* (C) specimens.

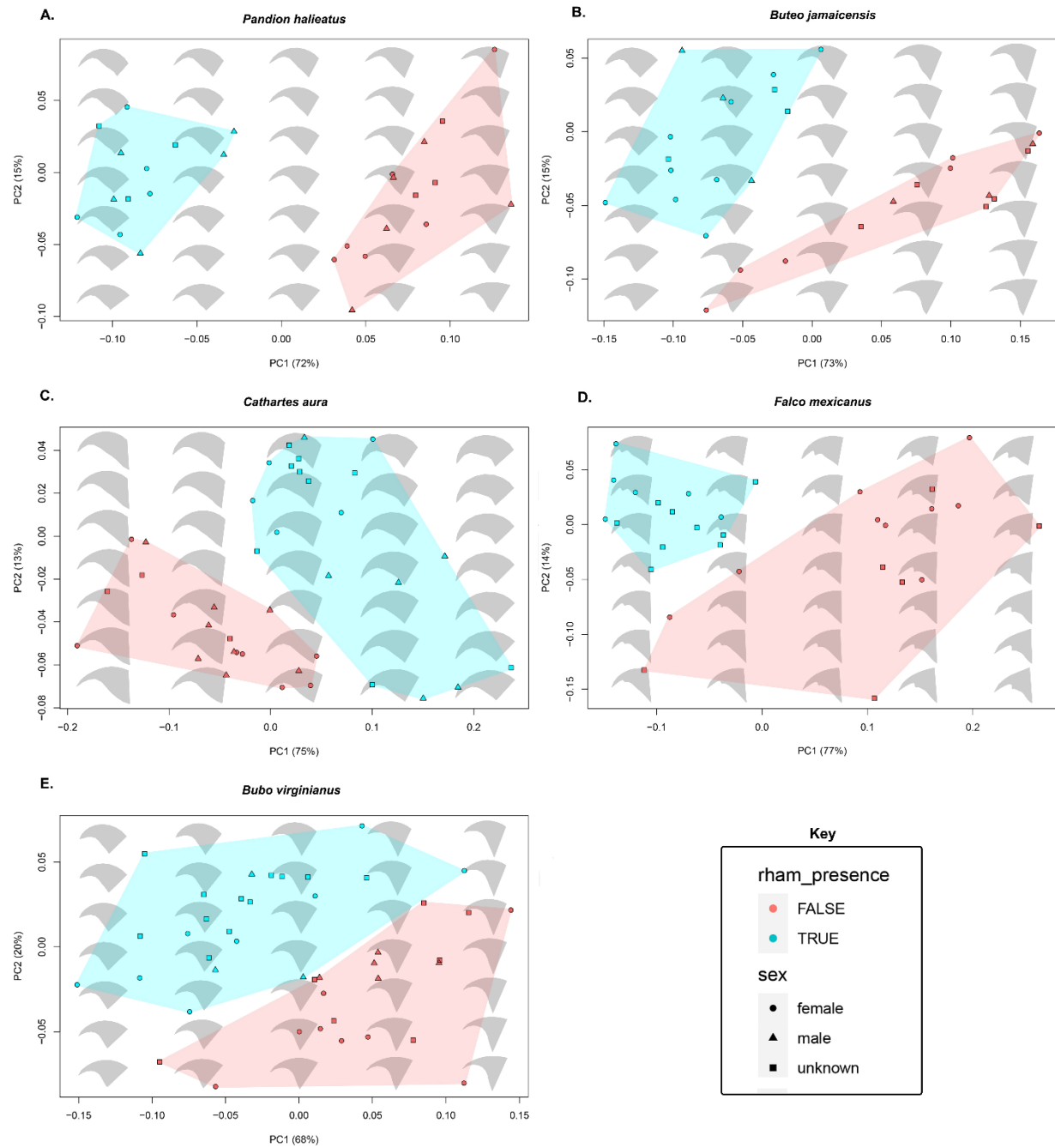


Figure 1.2. Backtransform PCA plots. Principal component backtransform morphospace plots for the five species included in this analysis.

Chapter 2

Assessing skull characters and modularity in the premaxillary and cranium of diurnal raptors

2.1 Introduction

Skull morphology has been used for centuries to infer diet, taxonomy, homology, behavior, thermoregulation, and many other aspects of bird ecology and systematics (e.g. Bhullar et al., 2015; Bright et al., 2016; Cooney et al., 2017; Mallarino et al., 2011; Tokita et al., 2017). The importance of beak morphology is reflected in the use of descriptor terms for non-monophyletic assemblages of birds such as raptors for predatory birds that possess strongly curved beaks and large talons for dealing with live prey. The avian orders typically associated with the term raptor are the diurnal raptors, Accipitriformes (hawks, eagles, kites, vultures) and Falconiformes (falcons, falconettes, caracaras), and the nocturnal raptors, Strigiformes (owls).

The order Accipitriformes and its families include the greatest diversity of diurnal birds of prey, containing 266 species of eagles, hawks, kites, the secretarybird, osprey, and vultures (Gill et al., 2023). Originally diagnosed as an order in the early 1800's by Vieillot (1816), they were later combined with falcons and caracaras (E. Mayr, 1959; Starck, 1959). While the two groups are morphologically similar and both constitute primarily diurnal raptors, a 2008 study using molecular sequence data (Hackett et al., 2008) established that falcons are more closely related to parrots and songbirds (Passeriformes), a result that has been consistently supported using larger DNA sequence datasets (Prum et al., 2015; Stiller et al., 2024).

Accipitriformes contains four families: Accipitridae, Pandionidae, Sagittariidae, and Cathartidae (Gill et al., 2023), though some studies consider Cathartidae to be the sole family of their own order, Cathartiformes (del Hoyo et al., 2014; Hudson, 1948). For the purposes of this study, the Cathartidae are considered a family within the Accipitriformes in accordance with the current IOC World Bird List (Gill et al., 2023). The fossil record of the Accipitridae dates to the early Eocene, with fossils attributed to the family found in Belgium and France (Harrison & Walker, 1976; G. Mayr, 2022; G. Mayr & Smith, 2019; Walker & Dyke, 2006). The oldest fossils to show affinities consistent with the Cathartidae are from the middle (47.8-38 Ma) and late Eocene (38-33.9 Ma). The extinct teratornithids, some of the largest flighted predatory birds known to exist, were traditionally recognized as members of the Cathartidae due to the similarities in skull and hindlimb morphology (Brodkorb, 1964; L. Miller, 1910; L. H. Miller, 1909). They have since been designated as their own family, the Teratornithidae, and their fossil remains are found in the Pleistocene deposits of North and South America (K. E. Campbell & Tonni,

1981; Cenizo et al., 2021). As the placement of the Teratornithidae in a phylogenetic context is still debated (K. E. Campbell & Tonni, 1981), here we consider them to be independent of the other lineages investigated.

Although Falconiformes presently comprises a single family, the Falconidae, three subfamilies are recognized: Falconinae, Herpetotherinae, and Polyborinae (Fuchs et al., 2012). The Falconinae make up the majority of the Falconidae, with 44 species in three genera. The subfamily Polyborinae comprise the caracaras while the subfamily Herpetotherinae comprise the laughing falcon and seven species of forest falcons. There are nine species of caracaras, and they have generally larger body sizes with proportionately longer legs, faces and heads that are partially or completely bare of feathers, and also have a reduced beak and talon curvature relative to other falcons (Morrison & Saggese, 2024). Unlike the rest of the Falconiformes, caracaras are not considered fast-flying aerial predators, but tend to be slower moving opportunistic scavengers of food on the ground. The fossil record of falcons is fragmentary and poorly documented but appears to date back to at least the early Eocene (56-47.8 Ma), with the oldest fossils sharing characteristics with the Polyborinae (Cenizo et al., 2016; G. Mayr, 2022; Tambussi & Acosta Hospitaleche, 2007). Fragmentary fossil remains of the caracara *Polyborus prelutosus* also appear in the Pleistocene era La Brea tar pits (approximately 38,000 years ago) of California alongside many fossil vultures (Harris & Jefferson, 1985).

Raptors are known for their predatory characteristics: namely their sharp, highly curved talons and beaks, which allow them to capture, immobilize, and consume prey (Fowler et al., 2009). They are also well-known for having acute vision which assists them with finding and capturing prey (Potier, 2020; Potier et al., 2016, 2017). However, there do exist carrion eating specialists among the diversity of the Accipitriformes and Falconiformes, a life history that appears to have evolved at least four separate times: (1) Cathartidae, (2) Gypaetinae, (3) Aegypiinae, and (4) Falconidae (Buechley & Sekercioglu, 2016; Morrison & Saggese, 2024). These species, usually referred to as vultures, tend to have reduced talon and bill curvature compared to other raptors, as well as other morphological characters that align them with each other, such as a partially or completely featherless head (M. O. Campbell, 2015). While the act of facultative scavenging is not uncommon in the animal kingdom, obligate scavenging is rare. The 23 species of cathartid and accipitrid vultures alive today are the only extant obligate scavengers among land vertebrates (Zou et al., 2021), making them both highly important to their ecosystems as a primary source of disposal for decaying matter and a unique case study in what adaptations are required for this lifestyle in vertebrate animals (DeVault et al., 2003; Hill et al., 2018; Wilson & Wolkovich, 2011). Strigiformes, the owls, also have the specialized features of raptors and are not entirely devoid of instances of scavenging, but there is little evidence that they contain a lineage that specializes in consuming carrion.

More research and observations are needed to assess the extent of scavenging behavior in owls (Allen et al., 2019). Therefore, we do not consider owls further in this study.

Previous research that has investigated the morphological differences in the skulls of raptors focused primarily on the beak morphology, musculature, and vision of these birds as it pertains to their feeding mechanisms. Traditional measurements have been used to associate skull characteristics with different dietary preferences and then applied these inferences to fossils to postulate the diets of extinct raptor species (Hertel, 1995).

More recently morphological approaches that account for allometry when investigating shape, i.e. geometric morphometrics, have also been applied to raptor skulls to assess feeding ecology and skull modularity ((Bright et al., 2016; Çakar et al., 2024; Guangdi et al., 2015; Pecsics et al., 2019; Steinfield et al., 2023; Sun et al., 2018). Some studies using these methods have recovered a link between dietary preference and skull or beak shape (Çakar et al., 2024; Guangdi et al., 2015).

There is disagreement on whether the bird cranium and beak are treated as separate elements that are evolving independently of each other, or if their development and therefore evolutionary trajectory are linked. As such, all parts of the skull must be considered to assess avian cranial evolution. Both traditional measurement and molecular approaches have been used on large numbers of taxa to try to answer this question, with differing conclusions (e.g. Felice & Goswami, 2018; Klingenberg & Marugán-Lobón, 2013). Felice and Goswami (2018) used a phylogenetic approach and found that the bird skull has many anatomical modules, showing a mosaic of evolutionary rates in each module, while Klingenberg and Marugán-Lobón (2013) used a morphological approach, and concluded that the face and braincase of the skull are evolutionarily integrated and not modular. Still other studies have proposed that shape of raptor beaks is constrained by genetics and linked to allometry, arguing that the overall raptor skull is not modular, but rather that the brain case and premaxillary are strongly integrated and the evolution of their shape is due to factors other than diet (Bright et al., 2016; Sun et al., 2018).

This study aims to further quantify the differences in the skull morphology of raptors that led to primarily predatory versus primarily scavenger lifestyles, and to determine the extent to which the cranium, premaxillary, or integrated skull, are correlated with dietary preferences. It also investigates the likelihood of a putative feeding guild structure in falcons, considering the Polyborinae preference for scavenging and overlap in morphology with cathartid and accipitrid vultures. 2D geometric morphometric outline analyses are utilized to reinvestigate the overall morphology of the raptor skull, cranium, and premaxillary, providing detailed comparisons of 137 living and extinct species in the Accipitriformes, Falconiformes, and Cariamiformes. The only two living species of the order Cariamiformes, the predatory sister taxa to Falconiformes in the Australaves, are

also included in these analyses due to their morphological similarities to the secretarybird of the Accipitriformes (Gill et al., 2023).

2.2 Methods

The skulls of specimens from the orders Accipitriformes, Falconiformes, and Cariamiformes were photographed with a Nikon D3400 DSLR camera and AF-P Nikkor 18-55 mm lens in the lateral view. When possible, specimens were photographed in the left lateral view. For specimens damaged or missing bones on the left side, a photograph of the right lateral view was taken, and the photograph mirrored for landmarking.

For Accipitriformes the assembled dataset comprised 491 individuals representing all four families, 59 of 75 genera, and 101 of 266 species, including all living members of the families Cathartidae ($n = 7$), Pandionidae ($n = 1$), and Sagittariidae ($n = 2$). The dataset for Falconiformes comprised 119 individuals representing all 11 genera, and 32 of 60 species. Both living species for the Cariamiformes ($n = 2$) are included in the analyses. In total, there are 150 species included in this study – 135 extant and 15 extinct (Appendix S2.1). Between one and four specimens were photographed per species. Specimens with significant damage were not used in the analyses. In addition, specimens with a rhamphotheca present on the premaxilla were not included in this analysis. The rhamphotheca can cause significant changes to the shape of the premaxilla (see results of Chapter 1).

Landmark-based geometric morphometrics (GMM) were used to analyze differences in skull shape among raptorial birds using a 2D approach by placing landmarks onto photographs of the specimens. Three types of landmarks were used. (1) Type I landmarks, which are defined as clearly homologous points of correspondence among different taxa. (2) Type II landmarks which are tips, the highest or lowest points of curves, and other geometric boundaries; and (3) sliding or semi-landmarks, which exist as equally spaced points along a curve demarcated between two Type II landmarks (Bookstein, 1997; Mitteroecker & Gunz, 2009).

Landmarking was performed in R using the package StereoMorph (Olsen & Westneat, 2015). Curves and outlines composed of sliding semi-landmarks were used to capture the overall morphology of the skull. StereoMorph was also used to capture the scale for each specimen by the placement of two additional landmarks on a scale bar in the photo, which assists with accounting for allometry. Curves were drawn excluding the shape of the lacrimal and quadrate bone since many specimens were missing these two bones or they had become fragmented with preparation of the skull. Each skull received three landmarks that were used as the end points for all the curves, 85 evenly distributed semi-landmarks for the skull outline, 70 evenly distributed semi-landmarks for the cranial outline, and 60 evenly distributed semi-landmarks for the premaxillary outline (Figure 2.1).

In addition to analyzing all specimens in a single dataset, the data was also partitioned into eight subsets: The (1) premaxillary curves for all specimens; (2) the cranial curves for all specimens; (3) the full skull outlines for Accipitriformes, (4) the premaxillary outlines for Accipitriformes, (5) the cranial outlines for Accipitriformes, (6) the full skull outlines for Falconiformes, (7) premaxillary outlines for Falconiformes, and (8) the cranial outlines for Falconiformes. These subsets of data were used to address specific questions related to phylogenetic signal and modularity of the raptor skull, and to investigate the morphological relationships and differences within and between each phylogenetic order.

2.2.1 Data Analyses

The landmark coordinate data extracted from the StereoMorph package was subjected to a Procrustes superimposition and Principal Components Analysis (PCA) using the geomorph package in R (Adams & Otárola-Castillo, 2013). Procrustes superimposition removes aspects of size including rotation, scale, and translation from the specimens included in the analysis. The analysis then uses the coordinate data collected from all shapes in the analysis to create an average shape (Bookstein, 1996). This average lies at the centroid (0,0) of the PCA graph and becomes the basis of comparison for all other shapes in the analysis. The amount of variance in each specimen as compared to the average shape is calculated and represented on a graphical morphospace as Principal Components (PC). In the Principal Component morphospace, every point represents one specimen and is placed along the x-axis according to the amount of difference it shows from the centroid x-coordinate, and along the y-axis according to the amount of difference it shows from the centroid y-coordinate. Thus, individual specimens that are close together on the PC morphospace are more similar in shape to each other than to individuals further away.

A one-way ANOVA was used to compare the general differences between the families and subfamilies of raptors included in this study, and a two-way ANOVA was used to determine the effect that the presence of fossil specimens in the dataset had on the results of the PCA. The Tukey's test was used to determine where significant difference among the groups being compared resided. For the entire dataset an ANOVA and Tukey's test was performed at the level of order and family, as well as 'vulture/scavenger' which for this analysis was the cathartid and accipitrid vulture subfamilies Gypaetinae and Aegypiinae, and the Falconidae subfamily Polyborinae combined. The linear regression performed within the ANOVA provides an r-squared value, which when multiplied against the principal components relays the percentage of change occurring on that PC.

2.3 Results

2.3.1 Combined specimen analyses – skull shape

The x-axis is represented by PC1, which accounted for 49% of all shape change in the skull. PC1 generally represents a shift from a proportionately longer and narrower skull to a laterally shorter skull (Figure 2.2A). The y-axis is represented by PC2, which accounted for 12% of all shape changes in the skull. PC2 represents a shift from a skull proportionately shorter in height to overall taller, which is evident in both the cranium and the beak. PC2 also visualizes a slight shift from a less curved to a more curved premaxillary (beak). Families were found to be significantly different from each other on PC1, PC2, and PC3 ($p < 0.001$, Table 2.1), and the presence of fossils in the analysis did have a significant effect on the distribution of specimens in the morphospace, but only for the Accipitridae on PC1 and PC2 and Cathartidae on PC2 and PC3 (Table S2.1, Figure S2.1). More families differed significantly from each other on PC2 than on PC1 (Table 2.2). Accipitridae differed significantly on PC1 from Cariamidae, Falconidae, and Cathartidae, and Pandionidae differed significantly from Cariamidae and Cathartidae. Falconidae also differed from Cariamidae and Cathartidae, as well as Sagittariidae. The Teratornithidae did not have any significant differences from other families on PC1, but on PC2 it differed from all other families except Cathartidae (Table 2.2). On PC3 only the Cathartidae differed significantly from other families, and only from Falconidae and Cariamidae (Table 2.2).

Each species was also categorized as a scavenger or not, which in this analysis separated the cathartid and accipitrid vultures from the rest of the Accipitriformes and the Polyborinae from the rest of the Falconiformes (Figure 2.3A; Table 2.1). This designation was used to determine whether scavengers generally differed in the morphospace from non-scavengers, and a Tukey's test was used to break down which subsets of scavengers differed most. The general scavenger and non-scavenger morphospaces overlapped (Figure 2.3A), but each scavenger group (accipitrid vultures and Polyborinae) separated well from other lineages of their respective orders (Figure 2.4A). Scavengers were found to be significantly different from non-scavengers on PC1 ($p < 0.001$;) but not on PC2 or PC3 (Table 2.1) and fossils did have a significant effect on the distribution (Table S2.1). While the designation of scavenger did not have a significant p-value on PC2 or PC3, some individual scavenging groups did differ on those principal components. On PC1 the accipitrid vultures differed significantly from Accipitridae, Falconidae, Pandionidae, and Polyborinae (Table 2.2). Polyborinae also differed from Accipitridae, Cariamidae, and Falconidae, in addition to Cathartidae. Accipitrid vultures and Polyborinae differed from the same groups again on PC2, but each also differed from Teratornithidae. The only difference on PC3 was separation of the Accipitrid vultures from the Cathartidae (Table 2.2).

2.3.2 Combined specimen analyses – cranium shape

For cranial morphology, the differences among families was most significant in the height and relative length of the cranium. PC1 accounted for ~34% of the shape differences, whereas PC2 and PC3 accounted for 25% and 12% respectively. As in the skull shape PCA, the Falconidae and Cariamidae fell mostly within the Accipitriformes (Accipitridae, Cathartidae, and Pandionidae) morphospace (Figure 2.2B). At the family level, the p-value was significant for all three principal components (Table 2.1, Figure 2.2B). On PC1 fossils had a significant effect on the distribution of points in the morphospace for Accipitridae, and on PC2 they had an effect on Cathartidae (see Tables 2.2 and S2.1). A Tukey's test showed that on PC1, Falconidae differed significantly from Accipitridae, Cathartidae, and Cariamidae, but no other significant differences were observed (Table 2.2). On PC2, Falconidae differed from Cathartidae and Cariamidae, but no longer differed significantly from Accipitridae. In addition to Falconidae, Cathartidae was found to differ significantly from all other families in the Accipitriformes, the Accipitridae, Pandionidae, and Sagittariidae. Accipitridae also differed from the Cariamidae on PC2. On PC3, Falconidae and Accipitridae again differed significantly, and Sagittariidae differed from all other families except Accipitridae (Table 2.2).

The separation of scavenger and non-scavenger was also significant on all three PCs, the greatest difference in shape distribution continued to be in that of the Cathartidae (Figure 2.4B). Only on PC2 did fossils have a significant effect on the distribution of points in the morphospace (Table S2.2). Scavengers span the majority of the x- and y-axes of morphospace, whereas non-scavengers clustered near the positive end of the x-axis, exhibiting a proportionately shorter and taller skull on average (Figures 2.3B and 2.4B). When a Tukey's test was applied, it was found that on PC1 Accipitrid vultures differed significantly from all other groups except for Pandionidae, Sagittariidae, and Cariamidae, whereas Polyborinae only differed from the Accipitrid vultures, Cathartidae, and Teratornithidae (Table 2.2). Fewer groups differed significantly on PC2 and PC3. On PC2 the Accipitrid vultures differed from the Accipitridae, Falconidae, and Polyborinae, and the Polyborinae only differed from the Accipitrid vultures and Falconidae (Table 2.2). On PC3 the Accipitrid vultures and Polyborinae both differed significantly from Accipitridae and Sagittariidae (Table 2.2).

2.3.3 Combined specimen analyses – premaxillary shape

On PC1, which accounted for 45% of the shape explanation, the isolated premaxillary trended similarly to that of the cranium and skull, with much of the differences being in the relative length and height of the beak (Figure 2.2C). The premaxillary also exhibited varying lengths of bone at the site of articulation with the jugal. PC2 accounted for 21% of the shape variation primarily reflecting a change in height of the premaxillary but also a change in articular shape from longer thinner bone at the positive end of the y-

axis to shorter and thicker bone with a longer jugal articulation point at the negative end. The premaxillary of Accipitridae and Falconidae exhibited greater diversity of shape than they did in the cranium, whereas the opposite was true in the Cathartidae, which exhibited a much more restricted premaxillary shape than was seen in the cranium (Figure 2.2C). In the shape of the premaxillary, Cariamidae and Sagittariidae both fell mostly between the Cathartidae and Falconidae shape spaces.

Fossils had a significant effect on the shape spaces of Accipitridae and Falconidae on PC1, but no effect on PC2 or PC3 (Tables 2.1, 2.2, and S2.1). On PC1, Cathartidae differed the most from other families in shape. A Tukey's test found that Cathartidae differed significantly from Accipitridae, Cariamidae, Falconidae, Pandionidae, and Sagittariidae on PC1 (Table 2.2). Additionally, Accipitridae differed significantly from Falconidae and Cariamidae. On PC2, Cathartidae had fewer significant differences, but Cariamidae differed significantly from Accipitridae, Cathartidae, Falconidae, and Pandionidae (Table 2.2). Falconidae and Accipitridae also differed significantly from each other. In PC3 Cariamidae and Cathartidae both differed the most from other families (Table 2.2).

Unlike the complete skull and the cranium, the scavengers were significantly different from each other only on PC1 and PC2 when looking at the premaxillary (Figure 2.4; Table 2.1). The Falconidae and Polyborinae shape spaces cluster closely with the Accipitridae where beak shape is shorter and proportionately taller, whereas the vultures (both Cathartidae and the Accipitrid Gypaetinae/Aegypiinae) overlap only slightly with the non-vulture Accipitridae shape space (Figures 2.3C). The non-Polyborinae Falconidae and Polyborinae spaces, while both resting within the Accipitridae shape space, similarly only overlap with each other very slightly in the middle of morphospace. The Polyborinae shape space trends in the same direction as that of the vultures, i.e. towards proportionately longer and more slender beaks. When looking at scavengers and non-scavengers overall, the shape spaces each take up a similar amount of morphospace and overlap significantly in the middle of the PCA (Figure 2.4C). Overall, the addition of fossil specimens into the dataset did not significantly alter the distribution of shapes in the PCAs (see Table 2.1, Table S2.1, and Figures S2.1 – S2.3).

2.3.4 Accipitriformes analyses – skull shape

When restricting the analyses to the Accipitriformes, PC1 for the complete skull accounted for 45% of all shape variation in this group (Table 2.1). PC1 reflected changes in shape along the x-axis from a proportionately longer and narrower skull at the negative end of the axis to a skull that is more rounded in shape at the positive end of the axis (Figure 2.5A). PC2 accounted for 13% of the shape variation and emphasized the narrowing of the overall skull. Members of the Cathartidae fell closer to the negative ends

of the x- and y-axes where skull shapes are longer and narrower, while Sagittariidae and Pandionidae stayed within the Accipitridae space (Figure 2.5A).

At the family level, all three PCs had a significant p-value (<0.05 ; Table 2.1), and the presence of fossils had a significant effect on the shape space of the Accipitridae on all three of the PCs (Tables S2.2). A Tukey's test found that Cathartidae and Accipitridae differed significantly from each other on all three PCs (Table 2.2). Pandionidae and Sagittariidae differed from Cathartidae on PC1 and PC2, and Pandionidae differed from Accipitridae on PC2. Fossils had a significant effect on the shape space of the Accipitridae on all three PCs (Tables S2.1, S2.2). One specimen of Teratornithidae was included in this analysis, and it did not differ significantly from any other families on PC1, but on PC2 it differed significantly from all other families except for Cathartidae (Table 2.2).

When grouping the specimens by scavenger, the morphospace distribution did not change significantly (Figure 2.5A). Scavengers were found to be significantly different from non-scavengers on PC1 and PC2 (Table 2.1). The presence of fossils in the dataset had a significant effect on the non-scavengers on all PCs, and on the scavengers on PC2 (Figures 2.5A and S2.4A; Table S2.2). Teratornithidae did not significantly differ from either the accipitrid or cathartid vultures on any of the PCs (Table 2.2).

2.3.5 Accipitriformes analyses – cranium shape

Shape variation was broader in the PCA of the cranial shapes, especially in the Cathartidae (Figure 2.5B). The x-axis, represented by PC1 accounted for 38% of the overall shape variation, shifting from a more round to a less round overall shape along the negative to positive ends of the axis. PC2 accounted for 21% of the shape variation, with change along the y-axis representing a shift from a rounder to proportionately more narrow and elongated shape. While still trending closer to the narrower end of the morphospace, Cathartidae cranial shape spanned the entire y-axis and nearly the entire x-axis. Accipitridae shape space was slightly more restricted to the negative end of the x-axis. Pandionidae and Sagittariidae fell in the overlap between Accipitridae and Cathartidae (Figure 2.5B). One of two specimens of Teratornithidae fell out with the Cathartidae, while the other one just barely passed into the Accipitridae morphospace (Figure 2.5B).

A significant p-value was found for all PCs (Table 2.1). Fossils were found to have a significant effect on the shape space of the Accipitridae on PC1 and a significant effect on Cathartidae on PC2 and PC3 (Table S2.2). A Tukey's test found that Cathartidae and Accipitridae were significantly different from each other on both PC1 and PC2 (Table 2.2). Pandionidae and Sagittariidae were only significantly different from Cathartidae on PC1. Sagittariidae and Pandionidae also differed significantly from each other on PC3 only. Teratornithidae differed significantly from Accipitridae on PC1 and from Sagittariidae on PC3. Scavengers were significantly different from non-scavengers on all three PCs

(Figure 2.6B; Table 2.1) and fossils only influenced the shape of scavengers on PC1 and non-scavengers on PC2 (Table S2.2).

2.3.6 Accipitriformes analyses – premaxillary shape

Unlike for cranial shape, Accipitridae exhibited a greater diversity of shape in the premaxillary while the portion of morphospace occupied by the Cathartidae became more restricted (Figure 2.5C). The x-axis, accounting for 51% of the variation, showed a shift from a proportionately thinner to a thicker beak. PC2 on the y-axis, accounts for 19% of the variation and reflects a change in proportionate length and thinness of the premaxillary, and a shift from a long, thin point of articulation with the jugal to a very short one. Unlike in the cranium, the shape space of the Cathartidae premaxillary was restricted to the thinner, longer beak shapes with a moderately long jugal articulation.

All three PCs had significant p-values (< 0.001 ; Table 2.1). The presence of fossils had a significant effect on the shape space of Accipitridae on PC1 and PC3, and on the Cathartidae on PC3 (Table S2.2). A Tukey's test found that Cathartidae was significantly different in shape from both Accipitridae, Pandionidae, and Sagittariidae on PC1, but not from Teratornithidae (Table 2.2). Pandionidae was significantly different from both Cathartidae and Accipitridae on PC2 and on PC3 (Table 2.2). Pandionidae and Sagittariidae differed significantly from each other on PC2.

When shape spaces were grouped by scavenger versus non-scavenger for the premaxillary, there was a small amount of overlap for the two shape spaces in the middle of the PCA, where a few species of accipitrid vultures fell into both the scavenger and non-scavenger spaces. Scavengers were found to be significantly different from non-scavengers on PC1 and PC2 ($p > 0.001$), but not on PC3 (Table 2.2). The presence of fossil specimens had a significant effect on the shape space of the scavengers on PC1 and PC3, and on non-scavengers on PC3 and the overall morphospace (Table S2.2; Figures S2.5C & S2.6C).

2.3.7 Falconiformes analyses – skull shape

Falconiformes was analyzed as a separate group, though the order only consists of a single family. Therefore, the only analysis performed was the difference between members of the subfamily Polyborinae and all other members of the Falconidae family broken down by skull, cranium, and premaxillary shape (Figure 2.7). Tukey's tests were not performed because there are only two means to be compared to each other. Instead, significant differences were interpreted from the principal component analyses.

Shape changes along the x-axis, represented by PC1 account for 60% of the overall variation, and exhibited skulls that were proportionately taller and rounder in shape towards the negative end, and proportionately longer and thinner towards the positive of the axis (Figure 2.7A). PC2 accounted for 11% of the total shape variation, was changes

along this axis were more subtle, primarily reflecting a more pointed, prominent jugal articulation point. Polyborinae was found to be significantly different from the rest of the Falconidae on PC1 (Table 2.1). Only one complete fossil skull of a falcon was available for analysis, *Polyborus prelutosus*, and including it did not affect any of the shape spaces of this PCA.

2.3.8 Falconiformes analyses – cranium shape

When restricting the analysis to just cranial shape, the change in is subtle (Figure 2.7B). Most of the change in shape occurs along the x-axis, presented by PC1 which accounts for 50% of the overall shape variation. The shift in shape is primarily related to changes in the shape of the palatine bones. At the positive end of the x-axis, the palatine bones were not easily distinguishable from the rest of the skull, while at the negative end they protruded more prominently from the underside of the cranium. PC2 accounted for 16% of the overall variation in shape, reflecting a small shift in the proportionate length of the cranial shape along the y-axis. Although overlap was observed in the cranial shape the Polyborinae cranium was found to be significantly different in shape on PC1 and PC2 ($p < 0.001$), exhibiting a greater amount of palatine prominence and a proportionately slightly longer cranium length from the rest of the Falconidae. Four fossil crania of *Polyborus* were included in this analysis and their inclusion did not influence any of the shape spaces (Table S2.2).

2.3.9 Falconiformes analyses – premaxillary shape

The shape changes that occurred in the premaxillary of the falcons are more complex than that of the cranium (Figure 2.7C). PC1 accounted for 34% of the variation, three important changes in morphology occur. The ratio of the length to height of the overall beak shifts from a very stout but tall beak at the positive end to a longer and narrower beak at the negative end of the x-axis. There was also a decrease in the presence of the tomial tooth reflecting positive to negative values, and a longer, more prominent point of articulation between the premaxillary and the jugal. PC2 accounted for 26% of the shape variation, with the proportional height of the beak and the prominence of the tomial tooth increasing from positive to negative values on the y-axis. The robustness of the jugal articulation also increased from positive to negative, being much thinner at the negative end of the y-axis.

The shape of the Polyborinae premaxillary was found to be significantly different from other falcons on all three PCs (Table 2.1). The Polyborinae shape space primarily occupied the negative end of the x-axis and positive end of the y-axis, exhibiting a slenderer overall beak shape and jugal articulation, and generally lacked a tomial tooth. The rest of the Falconidae exhibited a proportionately shorter and thicker beak with a prominent tomial tooth. Ten fossil premaxillary of *Polyborus* and one fossil premaxillary

of *Falco rusticolus swarthi* were included in this analysis. The presence of fossils in this analysis did have a statistically significant effect on the shape space of the Polyborinae ($p < 0.05$), but not of the Falconidae (Table S2.2).

2.4 Discussion

The principal component morphospace for all extant specimens showed that the overall shape of the skull falls into three primary regions. The Accipitriformes exhibit considerable skull diversity, occupying most regions of the available morphospace. The Accipitriformes also displays a greater range of skull shape compared to the Falconiformes. This is especially true on the PC2 y-axis of the morphospace, with more than half of accipiter species residing in the region of morphospace with laterally longer skulls that are shorter in relative cranium height (Figure S2.1A). When broken down, the scavenging accipiters – subfamilies Gypaetinae and Aegypiinae and family Cathartidae – group together at one end of the x-axis, occupying the region of morphospace with the proportionately longest and thinnest skulls (Figure 2.2A).

Studies that have included falcons in their analyses have found that the two orders differ significantly in morphospace (Çakar et al., 2024). And while falcon skulls tended to have a proportionately taller skull with a shorter beak, resulting in a rounder or more oval skull shape, the Falconiformes and the Accipitriformes exhibited a significant amount of overlap in cranial shape (Figure 2.2B). The exception to this trend in the Falconiformes is the skull shape of the subfamily Polyborinae (Figure 2.7). These falcons exhibited a much longer and narrower skull shape, with almost no overlap in shape to the other falcon species (Figure 2.7A). This is consistent with the morphological trend seen in the vultures as they have evolved away from other accipitrids towards a longer and narrower beak and skull that accommodates a scavenging lifestyle (Figure 2.7A, C).

Approximately half of the entire cranial morphospace is represented by members of the Cathartidae. Intriguingly, when only examining the premaxillary, the Cathartidae premaxillary morphoshape is highly restricted to longer, thinner shapes. In contrast the shape of the Accipitridae premaxillary were very diverse, overlapping with all other groups and spanned almost the entire morphospace. When the Cathartidae, Gypaetinae and Aegypiinae were grouped together, and distinguished from the rest of the Accipitridae, it became clear that the scavenging species underlie the diversity of premaxillary shapes in the Accipitridae, and that the Gypaetinae and Aegypiinae are more like the Cathartidae than other members of the Accipitridae. The morphospace of the skull mirrored the morphospace of the premaxillary most closely, while cranial shape was more varied, meaning that premaxillary shape is likely the largest influencing factor in the overall skull shape while cranium shape is more conserved. This suggests that the skull may be more modular, with the premaxillary evolving with respect to outside forces such as diet while the cranium stays more conserved. This is in contrast with the results of Bright et al.

(2016) and Sun et al. (2018), which state that the beak and cranium are tightly integrated. Pecsics et al. (2019) also found that beak shape was related to feeding strategy, such as in species like the snail kite (*Rosthramus sociabilis*) which uses a thin and pointed beak to extract snails from their shells, supporting the idea that the beak has evolved independently from the skull.

As seen in the analyses performed with both Accipitriformes and Falconiformes combined, the scavenging and non-scavenging species were significantly different from each other (Figure 2.4). This was true in the complete skull, the isolated cranium, and the isolated premaxillary. This delineation, however, was most clear in the morphospace of the premaxillary (Figure 2.4C). The Cathartidae premaxillary shape space did not overlap with the morphospace of the Accipitridae, and the combined scavenger morphospace overlapped with the non-scavengers to a small extent through placement of the two species of Gypaetinae and three species of Aegypiinae in morphospace. The two Gypaetinae found in the region of overlap were *Gypohierax angolensis* and the extinct genus *Neophrontops*. However, only one out of nine specimens of *Neophrontops* and two of the three specimens of *G. angolensis* were in this overlap region, and all other specimens of these two species fell into the scavenger area of the morphospace. The Aegypiinae was more cut and dry - all six specimens of *Torgos*, *Trigonoceps*, and *Aegyptius* fell in the overlapping space between scavenger and non-scavenger. Apart from *Neophrontops*, all the species that fell into this overlap zone are large-bodied birds that tend to have more robust beaks and are more similar to the skulls and beaks of eagles.

While the subfamily Polyborinae did not overlap significantly with the accipitrid vultures, the shape of the skull and premaxillary trended away from the rest of the Falconidae in the same direction of the morphospace as the Cathartidae, Gypaetinae, and Aegypiinae did from the rest of the Accipitriformes (Figure 2.3A & C). While all analyses of the falcon skull shape (skull, cranium, and premaxillary) found the Polyborinae to be significantly different from the rest of the Falconidae, the shape of the premaxillary created the clearest delineation between the Polyborinae and the remainder of Falconidae. Polyborinae beaks were proportionately longer and thinner compared to the beaks of other falcons. Additionally, the Polyborinae premaxillary shape space is the only time fossils played a significant role in driving shape space, and fossil specimens of *Polyborus* were the only reason the Polyborinae and Falconidae shape spaces overlapped (Figure 2.7C). In all three analyses, the fossil specimens of *Polyborus* were among those that trended closer to the Falconidae space. Overall, the fossil Polyborinae tended to fall between the modern Polyborinae specimens and the rest of the falcons (Figure 2.7). This could indicate that the Polyborinae of today have evolved more of the specialized scavenger morphologies, like those seen in the Cathartidae, Gypaetinae, and Aegypiinae, since the Pleistocene.

While all the Polyborinae showed clear separation from the rest of the Falconidae, the species that was most disparate was that of *Caracara cheriway* (Figure 2.7). All extant individuals of *C. cheriway* fell at the negative end of the x-axis, while the fossil *C. cheriway* specimens tended to be closer to other falcons. The Polyborinae specimens closest to the Falconidae were the extinct *Caracara prelutosus*, meaning they had beaks that were less elongated and not as narrow compared to other caracara falcons. Falcons are active predators who differ from accipiters in their foraging methods in that they utilize their beak more than their talons for prey restraint, relying on the presence of the tomial tooth to grip and rend prey (Sustaita, 2008; Sustaita & Hertel, 2010). Many falcon species are also avivores, meaning they specialize in hunting other birds. But polyborid falcons have a reduced tomial tooth and are opportunistic in their hunting and foraging, with much less specialized diets (Del Hoyo et al., 1992). And while the Polyborinae do not share the extreme lengthening of the beak and skull that vultures have, overall, they resemble the Accipitriformes more than they do other falcon species.

2.5 Conclusions and Future Directions

Given the large number of species included (491 specimens, 38% of all Accipitriformes species and 53% of all Falconiformes species), this study provides a broader perspective on the overall morphological variation of the skull of the Accipitriformes and Falconiformes. Though the diets of these birds can vary significantly, the most significant changes occurring in the skull are strongly correlated with the difference between birds that actively hunt their prey and those that scavenge.

A primarily scavenger lifestyle has evolved a minimum of four times across the orders Accipitriformes and Falconiformes (Fuchs et al., 2015; Zou et al., 2021). These groups have each converged upon an optimal morphological configuration for scavenging, with the key features being an increase in beak length and narrowness, and to a lesser degree the narrowing and lengthening of the entire skull. When it comes to cranial shape, the Accipitriformes and Falconiformes differ significantly less from each other than when looking at the complete skull or the premaxillary. The scavenging Cathartidae exhibit the most variation in cranial shape, likely due to the overall skull lengthening occurring in their lineage. This differs from the findings of others who have suggested that the skull is too highly integrated to be driven by diet (Bright et al., 2016; Sun et al., 2018). Cranial shape is significantly less variable than the premaxillary shape, suggesting that the cranium is phylogenetically constrained to a higher degree than the shape of the premaxillary, which may respond more readily to selection imposed from the environment.

Notably, while there were significant differences between families in the analyses focused only on the Accipitriformes, the percent variance of PC1 explained by the designation of scavenger versus non-scavenger (24%; Table 2.2) was double the amount

explained by family alone (12%). Percent variance represents what percentage of the principal component is explained by each variable. In this case, family explained about a quarter of this variation, while scavenger designation explained over half. This means that, at least in the case of the Accipitriformes, whether a species is a scavenger or not appears to be more detectable in the shape of the skull than predicting the family it belongs to.

The findings of this study agree with those found by Steinfield et al. (2023), emphasizing that while diet may not be a driving factor in bird skull evolution, feeding ecology can be reliably assessed from skull morphology. Initial analyses also suggest that the presence of a guild structure as suggested by Hertel (1994) may exist within the vultures. The scavenger morphospace of the PCA showed that grouping within the scavengers was not strictly based on phylogenetic relatedness, but on morphological similarities across the Gypaetinae, Aegypiinae, and Cathartidae. Some members of the Cathartidae were much closer morphologically to those of the Gypaetinae and Aegypiinae than to other members of Cathartidae. These morphological features likely correspond to the individual feeding habits of those species, indicative of convergence in traits both within and across these groups. A closer look at the vultures on their own will need to be conducted to assess the trends of convergence and presence of a guild structure in the vultures. Whether or not the Polyborinae have their own guild structure or may fit within the guild structure of the Cathartidae vultures is still unclear. It seems likely that more field research observing the behavior of the Polyborinae while interacting with cathartid vultures around a carcass will need to be conducted to make these kinds of inferences.

2.6 Tables and Figures

Table 2.1. Table of values for ANOVA tests on modern skull, cranium, and premaxillary shape PCAs.

One-way ANOVA tests were performed on geometric morphometric data for each PCA performed. In all tests, percentage of variance (PoV %) for the principal component was used as the quantitative variable and while the independent variable changed depending on whether order, family, or scavenger status was being evaluated. P-values below 0.05 are marked with an asterisk (*). The percent variance determined specifically by the independent variable being examined (% Variance) is the r-squared value multiplied by the PoV.

Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	48.73	0.0000*	0.381	40.11 (6, 375)	18.57
	PC2	12.41	0.0000*	0.189	15.76 (6, 375)	2.34
	PC3	9.04	0.0006*	0.046	4.04 (6, 375)	0.41
Scavenger	PC1	48.73	0.0000*	0.401	256.00 (1, 380)	19.54
	PC2	12.41	0.3762	-0.001	0.78 (1, 380)	-0.01
	PC3	9.04	0.1262	0.004	2.35 (1, 380)	0.03
Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	33.92	0.0000*	0.533	82.85 (6, 425)	18.07
	PC2	24.55	0.0000*	0.196	18.55 (6, 425)	4.82
	PC3	12.18	0.0000*	0.081	7.36 (6, 425)	0.99
Scavenger	PC1	33.92	0.0000*	0.400	96.70 (1, 430)	13.56
	PC2	24.55	0.0000*	0.068	11.43 (1, 430)	1.66
	PC3	12.18	0.0001*	0.040	6.97 (1, 430)	0.49
Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	45.47	0.0000*	0.625	121.30 (6, 427)	28.42
	PC2	20.80	0.0000*	0.074	6.73 (6, 427)	1.53
	PC3	14.74	0.0000*	0.135	12.25 (6, 427)	1.99
Scavenger	PC1	45.47	0.0000*	0.468	381.40 (1, 432)	21.27
	PC2	20.80	0.0006*	0.025	12.03 (1, 432)	0.52
	PC3	14.74	0.6738	-0.002	0.18 (1, 432)	-0.03
Accipiter Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	45.20	0.0000*	0.279	27.23 (4, 267)	12.62
	PC2	13.35	0.0000*	0.197	17.60 (4, 267)	2.63
	PC3	11.52	0.0005*	0.058	5.19 (4, 267)	0.67
Scavenger	PC1	45.20	0.0000*	0.533	310.30 (1, 270)	24.09
	PC2	13.35	0.0000*	0.118	37.23 (1, 270)	1.57
	PC3	11.52	0.7914	-0.003	0.07 (1, 270)	-0.04

Accipiter Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	38.04	0.0000*	0.486	76.53 (4, 315)	18.50
	PC2	20.54	0.0003*	0.053	5.49 (4, 315)	1.09
	PC3	11.31	0.0191*	0.024	2.99 (4, 315)	0.28
Scavenger	PC1	38.04	0.0000*	0.386	201.1 (1, 318)	14.66
	PC2	20.54	0.0000*	0.119	43.92 (1, 318)	2.44
	PC3	11.31	0.0005*	0.034	12.27 (1, 318)	0.39
Accipiter Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	50.84	0.0000*	0.585	111.30 (4, 309)	29.74
	PC2	19.46	0.0017*	0.042	4.42 (4, 309)	0.82
	PC3	14.17	0.0000*	0.069	6.82 (4, 309)	0.98
Scavenger	PC1	50.84	0.0000*	0.674	648.80 (1, 312)	34.28
	PC2	19.46	0.0002*	0.039	13.79 (1, 312)	0.76
	PC3	14.17	0.4983	-0.002	0.46 (1, 312)	-0.02
Falcon Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Scavenger	PC1	59.77	0.0000*	0.677	217.10 (1, 102)	40.48
	PC2	11.21	0.2416	0.004	1.39 (1, 102)	0.04
	PC3	7.31	0.1458	0.011	2.15 (1, 102)	0.08
Falcon Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Scavenger	PC1	46.25	0.0000*	0.449	87.43 (1, 105)	20.77
	PC2	16.93	0.0441*	0.029	4.15 (1, 105)	0.49
	PC3	11.48	0.1351	0.135	2.27 (1, 105)	1.55
Falcon Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Scavenger	PC1	42.11	0.0000*	0.652	214.60 (1, 113)	27.46
	PC2	18.93	0.0000*	0.149	20.90 (1, 113)	2.81
	PC3	12.81	0.0313*	0.032	4.75 (1, 113)	0.41

Table 2.2. Table of Tukey's test adjusted p-values. Table summarizing the adjusted p-values produced by a Tukey's test applied to each PCA performed. The Tukey's test compared each variable to each other variable to determine if the two were significantly different from each other. P-values less than or equal to 0.05 are marked with an asterisk (*). The variable 'Old World' refers to the accipitrid vulture subfamilies of Gypaetinae and Aegypiinae.

All Specimens Skull Outline Tukey Test p-values						
Family	Modern and Fossil			Modern		
	PC1	PC2	PC3	PC1	PC2	PC3
Cariamidae - Accipitridae	0.0000*	1.0000	0.0867	0.0000*	0.4243	0.3794
Cathartidae - Accipitridae	0.0000*	0.0000*	0.1205	0.0000*	0.0013*	0.6065
Falconidae - Accipitridae	0.0000*	0.0000*	0.5949	0.0000*	0.0000*	0.0000*
Pandionidae - Accipitridae	0.9999	0.0392*	0.9434	0.9912	0.1356	0.4470
Sagittariidae - Accipitridae	0.4195	0.8708	0.8614	0.2659	0.9979	0.2316
Teratornithidae - Accipitridae	0.5164	0.0149*	0.8738	-	-	-
Cathartidae - Cariamidae	0.9162	0.5318	0.0073*	0.7257	0.9999	0.1434
Falconidae - Cariamidae	0.0000*	0.7934	0.2580	0.0000*	0.0153*	1.0000
Pandionidae - Cariamidae	0.0219*	0.3038	0.8832	0.0351*	0.0250*	1.0000
Sagittariidae - Cariamidae	0.8000	0.9520	0.9930	0.8117	0.6607	0.9932
Teratornithidae - Cariamidae	0.9999	0.0369*	1.0000	-	-	-
Falconidae - Cathartidae	0.0000*	0.0000*	0.0078*	0.0000*	0.0000*	0.0000*
Pandionidae - Cathartidae	0.0248*	0.0001*	0.4641	0.1138	0.0018*	0.1796
Sagittariidae - Cathartidae	0.9832	0.1069	0.4302	0.9987	0.5733	0.0928
Teratornithidae - Cathartidae	1.0000	0.1727	0.6354	-	-	-
Pandionidae - Falconidae	0.2194	0.6767	0.9973	0.1361	0.9093	0.9999
Sagittariidae - Falconidae	0.0067*	1.0000	0.9696	0.0048*	0.9849	0.9910
Teratornithidae - Falconidae	0.0816	0.0015*	0.9439	-	-	-
Sagittariidae - Pandionidae	0.7999	0.9743	0.9998	0.7627	0.8452	0.9886
Teratornithidae - Pandionidae	0.7031	0.0004*	0.9918	-	-	-
Teratornithidae - Sagittariidae	0.9968	0.0079*	0.9994	-	-	-
Scavengers	PC1	PC2	PC3	PC1	PC2	PC3
Old World - Accipitridae	0.0000	0.0013	0.6457	0.0000	0.0000	0.9993
Old World - Cariamidae	0.5248	0.9270	0.5177	0.4442	1.0000	0.4677
Old World - Cathartidae	0.9890	0.8622	0.0393	1.0000	1.0000	0.9910
Old World - Falconidae	0.0000	0.0086	1.0000	0.0000	0.0000	0.0014
Pandionidae - Old World	0.0028	0.0002	1.0000	0.0172	0.0003	0.5380
Sagittariidae - Old World	0.9975	0.2813	0.9975	0.9998	0.5099	0.2976
Teratornithidae - Old World	0.9999	0.0557	0.9888	-	-	-
Polyborinae - Old World	0.0000	0.0000	0.9322	0.0000	0.0000	0.0000
Polyborinae - Accipitridae	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000
Polyborinae - Cariamidae	0.0000	0.0018	0.1594	0.0001	0.0000	0.9901
Polyborinae - Cathartidae	0.0000	0.0000	0.6815	0.0000	0.0000	0.0000
Polyborinae - Falconidae	0.0000	0.0000	0.7674	0.9998	0.0000	0.2387
Polyborinae - Pandionidae	0.9987	0.9949	0.9808	0.9971	0.8478	0.9805
Sagittariidae - Polyborinae	0.6706	0.6268	0.9350	0.6900	0.1111	1.0000
Teratornithidae - Polyborinae	0.5218	0.0000	0.9397	-	-	-

All Specimens Cranium Outline Tukey Test p-values						
Family	Modern and Fossil			Modern		
	PC1	PC2	PC3	PC1	PC2	PC3
Cariamidae - Accipitridae	0.0349*	0.2987	0.1917	0.0846	0.0013*	0.1252
Cathartidae - Accipitridae	0.0000*	0.9509	0.0077*	0.7360	0.0000*	0.2031
Falconidae - Accipitridae	0.9713	0.0000*	0.0001*	0.0000*	0.8667	0.0001*
Pandionidae - Accipitridae	0.8530	0.9212	1.0000	0.8043	0.3125	0.9675
Sagittariidae - Accipitridae	0.9483	1.0000	0.0227*	1.0000	0.8002	0.0186
Teratornithidae - Accipitridae	0.0002*	0.9994	1.0000	-	-	-
Cathartidae - Cariamidae	0.0440*	0.5838	0.8842	0.3529	0.1663	0.6738
Falconidae - Cariamidae	0.1104	0.0000*	0.9714	0.0000	0.0048*	0.7980
Pandionidae - Cariamidae	0.9902	0.1677	0.9224	0.0682	0.8749	0.8858
Sagittariidae - Cariamidae	0.9925	0.8225	0.0006*	0.4734	0.7067	0.0007*
Teratornithidae - Cariamidae	0.5075	0.9994	0.9203	-	-	-
Falconidae - Cathartidae	0.0000*	0.0000*	0.9960	0.0000*	0.0000*	0.9876
Pandionidae - Cathartidae	0.0011*	0.7705	1.0000	0.5385	0.0054*	1.0000
Sagittariidae - Cathartidae	0.0073*	1.0000	0.0011*	0.9915	0.0044*	0.0024*
Teratornithidae - Cathartidae	1.0000	1.0000	0.9996	-	-	-
Pandionidae - Falconidae	0.9630	0.9907	0.9990	0.9430	0.4868	0.9997
Sagittariidae - Falconidae	0.9900	0.6346	0.0004*	0.5246	0.9077	0.0007*
Teratornithidae - Falconidae	0.0007*	0.3000	0.9969	-	-	-
Sagittariidae - Pandionidae	1.0000	0.9984	0.0942	0.9814	0.9988	0.0378*
Teratornithidae - Pandionidae	0.1215	0.9213	1.0000	-	-	-
Teratornithidae - Sagittariidae	0.1587	0.9997	0.4521	-	-	-
Scavengers	PC1	PC2	PC3	PC1	PC2	PC3
Old World - Accipitridae	0.0000	0.0108	0.0114	0.0029	0.0000	0.0001
Old World - Cariamidae	0.9867	0.9728	0.9315	0.8596	1.0000	0.9876
Old World - Cathartidae	0.0000	0.3886	0.9999	0.8431	0.8841	0.9122
Old World - Falconidae	0.0001	0.0000	0.9999	0.0000	0.0000	0.9880
Pandionidae - Old World	0.9999	0.1989	0.9994	0.2126	0.0000	0.9986
Sagittariidae - Old World	0.9999	0.9584	0.0007	0.9279	0.9911	0.0004
Teratornithidae - Old World	0.0436	1.0000	0.9972	-	-	-
Polyborinae - Old World	0.0410	0.0053	1.0000	0.0061	0.0082	0.9979
Polyborinae - Accipitridae	0.5773	0.9107	0.0202	0.9857	0.0121	0.0044
Polyborinae - Cariamidae	0.2491	0.0984	0.9429	0.0241	0.0329	0.9261
Polyborinae - Cathartidae	0.0000	0.4730	0.9998	0.2990	0.0000	0.9989
Polyborinae - Falconidae	0.9847	0.0000	1.0000	0.0000	0.5564	1.0000
Polyborinae - Pandionidae	0.9932	0.9897	0.9993	0.9954	0.8795	0.0012
Sagittariidae - Polyborinae	0.9984	1.0000	0.0007	1.0000	0.9982	1.0000
Teratornithidae - Polyborinae	0.0014	0.9816	0.9968	-	-	-

All Specimens Premaxillary Outline Tukey Test p-values						
Family	Modern and Fossil			Modern		
	PC1	PC2	PC3	PC1	PC2	PC3
Cariamidae - Accipitridae	0.0003	0.0238	0.0000	0.0001	0.1435	0.0000
Cathartidae - Accipitridae	0.0000	0.0076	0.0706	0.0000	0.0024	0.0000
Falconidae - Accipitridae	0.0000	0.0082	0.0009	0.0000	0.1447	0.0010
Pandionidae - Accipitridae	0.9281	0.1690	0.0144	0.9002	0.0726	0.0291
Sagittariidae - Accipitridae	0.8881	0.9441	1.0000	0.7685	0.9299	0.9999
Teratornithidae - Accipitridae	0.7371	0.9983	1.0000	-	-	-
Cathartidae - Cariamidae	0.0382	0.0006	0.0000	0.1794	0.0026	0.0000
Falconidae - Cariamidae	0.0000	0.0012	0.0001	0.0000	0.0288	0.0000
Pandionidae - Cariamidae	0.3512	0.0013	0.8623	0.1860	0.0034	0.3289
Sagittariidae - Cariamidae	0.5987	0.9093	0.0045	0.4638	0.9753	0.0005
Teratornithidae - Cariamidae	0.9996	0.9815	0.1420	-	-	-
Falconidae - Cathartidae	0.0000	0.9868	0.0000	0.0000	0.3114	0.0000
Pandionidae - Cathartidae	0.0000	0.8017	0.0010	0.0000	0.7969	0.0001
Sagittariidae - Cathartidae	0.0002	0.4766	0.9993	0.0009	0.2947	0.7846
Teratornithidae - Cathartidae	0.5078	0.9405	1.0000	-	-	-
Pandionidae - Falconidae	0.0820	0.6335	0.1918	0.0428	0.2769	0.3030
Sagittariidae - Falconidae	0.1064	0.6061	0.9414	0.0388	0.6936	0.8922
Teratornithidae - Falconidae	0.2159	0.9670	0.9920	-	-	-
Sagittariidae - Pandionidae	1.0000	0.1892	0.1933	0.9996	0.1174	0.2373
Teratornithidae - Pandionidae	0.9781	0.6823	0.5897	-	-	-
Teratornithidae - Sagittariidae	0.9925	1.0000	1.0000	-	-	-
Scavengers	PC1	PC2	PC3	PC1	PC2	PC3
Old World - Accipitridae	0.0000	0.2255	0.0065	0.0000	0.7307	0.0330
Old World - Cariamidae	1.0000	0.2039	0.0005	0.9990	0.4613	0.0000
Old World - Cathartidae	0.0000	0.0003	0.0001	0.0000	0.0007	0.0000
Old World - Falconidae	0.0000	0.0000	1.0000	0.0000	0.0000	0.9880
Pandionidae - Old World	0.0099	0.0324	0.3547	0.0062	0.0182	0.4651
Sagittariidae - Old World	0.1172	0.9999	0.9686	0.1374	0.9988	0.9613
Teratornithidae - Old World	0.9999	1.0000	0.9976	-	-	-
Polyborinae - Old World	0.0000	0.9931	1.0000	0.0000	0.0617	0.8117
Polyborinae - Accipitridae	0.1184	0.0066	0.0107	0.3639	0.0000	0.0000
Polyborinae - Cariamidae	0.0000	0.4317	0.0004	0.0000	0.9996	0.0004
Polyborinae - Cathartidae	0.0000	0.0000	0.0002	0.0000	0.0000	0.0000
Polyborinae - Falconidae	0.0000	0.0000	1.0000	0.0000	0.0000	0.1618
Polyborinae - Pandionidae	0.7580	0.0093	0.3118	0.7349	0.0001	0.8848
Sagittariidae - Polyborinae	0.6570	1.0000	0.9772	0.4813	0.9989	0.7003
Teratornithidae - Polyborinae	0.3826	1.0000	0.9983	-	-	-

Accipitriformes Skull Outline Tukey Test p-values						
Family	Modern and Fossil			Modern		
	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Accipitridae	0.0000	0.0000	0.0078	0.0000	0.0000	0.0014
Pandionidae - Accipitridae	0.9799	0.0016	1.0000	0.7037	0.0458	0.0470
Sagittariidae - Accipitridae	0.1671	0.2681	0.9213	0.0658	0.2791	0.9995
Teratornithidae - Accipitridae	0.2712	0.0381	0.0408	-	-	-
Pandionidae - Cathartidae	0.0200	0.0000	0.8011	0.1105	0.0000	0.0007
Sagittariidae - Cathartidae	0.9619	0.0021	0.4027	0.9966	0.0028	0.5941
Teratornithidae - Cathartidae	0.9985	0.3983	0.0080	-	-	-
Sagittariidae - Pandionidae	0.6053	0.9408	0.9526	0.5600	0.9973	0.4224
Teratornithidae - Pandionidae	0.5039	0.0004	0.0698	-	-	-
Teratornithidae - Sagittariidae	0.9746	0.0053	0.2539	-	-	-
Scavengers	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Accipitridae	0.0000	0.0000	0.0537	0.0000	0.0000	0.0001
Old World - Accipitridae	0.0000	0.1642	0.0374	0.0000	0.1980	0.0000
Old World - Cathartidae	0.9752	0.0223	0.0001	0.9993	0.0239	0.9944
Pandionidae - Cathartidae	0.0014	0.0000	0.8701	0.0425	0.0000	0.0005
Sagittariidae - Cathartidae	0.9538	0.0027	0.4805	0.9989	0.0041	0.6833
Teratornithidae - Cathartidae	0.9991	0.4824	0.0099	-	-	-
Pandionidae - Old World	0.0059	0.0002	0.9050	0.0603	0.0127	0.0003
Sagittariidae - Old World	0.9923	0.1113	1.0000	0.9998	0.1414	0.5801
Teratornithidae - Old World	0.9945	0.1341	0.1660	-	-	-

Accipitriformes Cranial Outline Tukey Test p-values						
Family	Modern and Fossil			Modern		
	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Accipitridae	0.0000	0.0003	0.9760	0.0000	0.0000	0.2717
Pandionidae - Accipitridae	0.7816	0.8401	0.3590	0.2939	0.9995	0.8666
Sagittariidae - Accipitridae	0.9365	0.8743	0.1698	0.6517	0.9802	0.0153
Teratornithidae - Accipitridae	0.0074	0.6812	0.3781	-	-	-
Pandionidae - Cathartidae	0.0082	0.2240	0.4709	0.1601	0.0725	0.9996
Sagittariidae - Cathartidae	0.0165	0.3265	0.1356	0.1295	0.0759	0.0036
Teratornithidae - Cathartidae	0.9999	0.9843	0.4543	-	-	-
Sagittariidae - Pandionidae	0.9998	1.0000	0.0318	0.9923	0.9962	0.0280
Teratornithidae - Pandionidae	0.2231	0.4474	0.9942	-	-	-
Teratornithidae - Sagittariidae	0.2106	0.4776	0.0407	-	-	-
Scavengers	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Accipitridae	0.0000	0.0000	0.6180	0.0000	0.0000	0.1678
Old World - Accipitridae	0.0002	0.0001	0.0004	0.0015	0.0000	0.0518
Old World - Cathartidae	0.0000	0.9996	0.0918	0.0000	0.7937	0.9944
Pandionidae - Cathartidae	0.0085	0.2574	0.5409	0.2049	0.0661	1.0000
Sagittariidae - Cathartidae	0.0177	0.3750	0.1588	0.1660	0.0696	0.0049
Teratornithidae - Cathartidae	1.0000	0.9941	0.5231	-	-	-
Pandionidae - Old World	1.0000	0.2218	0.9818	0.9796	0.2154	1.0000
Sagittariidae - Old World	0.9999	0.3320	0.0183	0.9999	0.1975	0.0028
Teratornithidae - Old World	0.1077	0.9974	0.9154	-	-	-

Accipitriformes Premaxillary Outline Tukey Test p-values						
Family	Modern and Fossil			Modern		
	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Accipitridae	0.0000	0.7731	0.0002	0.0000	0.7079	0.0000
Pandionidae - Accipitridae	0.5959	0.0021	0.0536	0.3423	0.0021	0.0320
Sagittariidae - Accipitridae	0.9085	0.8157	0.9999	0.8433	0.8915	0.9441
Teratornithidae - Accipitridae	0.6490	0.9122	0.9998	-	-	-
Pandionidae - Cathartidae	0.0001	0.0008	0.0012	0.0005	0.0010	0.0000
Sagittariidae - Cathartidae	0.0001	0.9388	0.7400	0.0003	0.9839	0.0595
Teratornithidae - Cathartidae	0.4167	0.9605	0.9906	-	-	-
Sagittariidae - Pandionidae	0.9983	0.0098	0.4485	0.9643	0.0195	0.5046
Teratornithidae - Pandionidae	0.9790	0.1044	0.6433	-	-	-
Teratornithidae - Sagittariidae	0.9443	0.9996	0.9995	-	-	-
Scavengers	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Accipitridae	0.0000	0.4061	0.0037	0.0000	0.4224	0.0000
Old World - Accipitridae	0.0000	0.0018	0.0183	0.0000	0.0009	0.0948
Old World - Cathartidae	0.0000	0.4624	0.0000	0.0000	0.4129	0.0000
Pandionidae - Cathartidae	0.0000	0.0009	0.0014	0.0000	0.0010	0.0000
Sagittariidae - Cathartidae	0.0000	0.9694	0.8179	0.0000	0.9959	0.0843
Teratornithidae - Cathartidae	0.1680	0.9823	0.9972	-	-	-
Pandionidae - Old World	0.1164	0.0001	0.4712	0.1895	0.0000	0.3132
Sagittariidae - Old World	0.0699	1.0000	0.9905	0.0514	0.9975	1.0000
Teratornithidae - Old World	0.9978	0.9995	0.9898	-	-	-

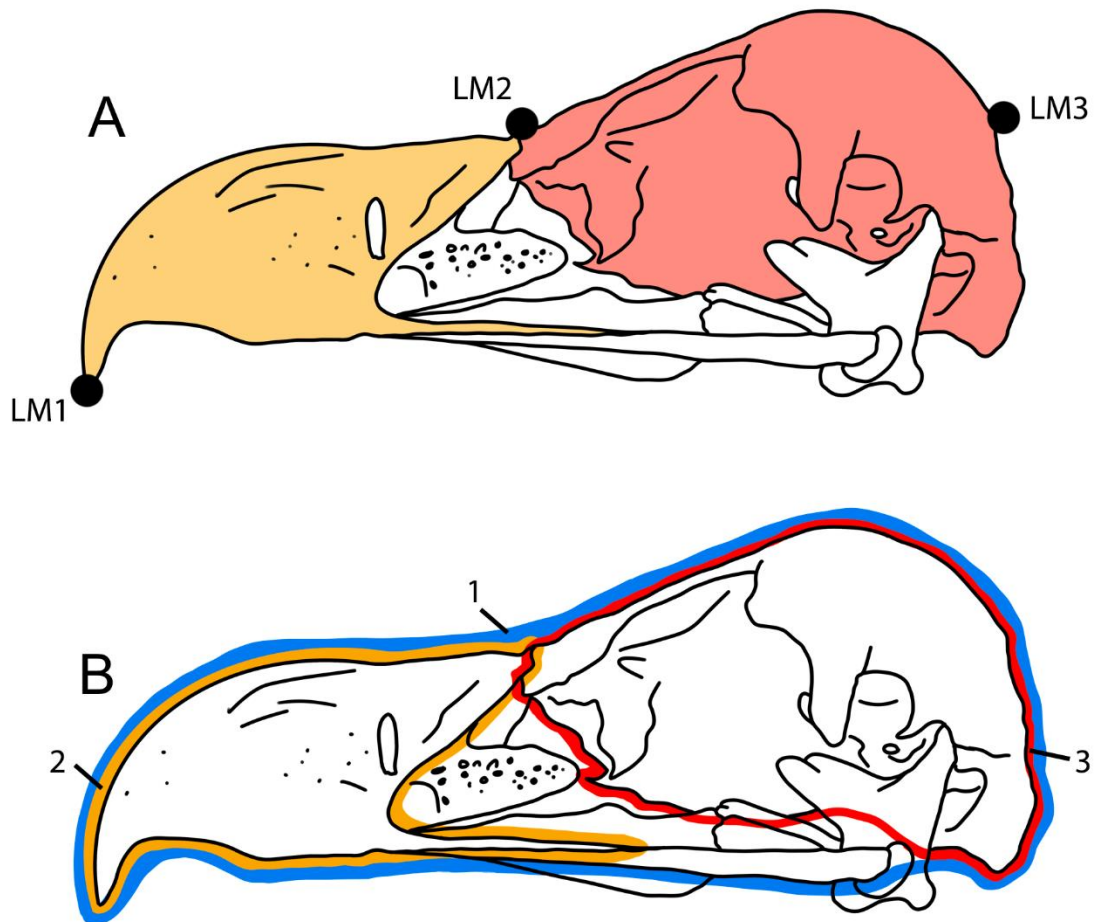


Figure 2.1. Diagram of placement of landmarks and curves for shape analysis. **A.** Drawing of a lappet-faced vulture (*Torgos tracheliotus*) skull highlighting the parts of the skull that were focused on for analysis. The premaxillary is highlighted in yellow and the cranium is highlighted in red. Landmarks LM1 (beak tip), LM2 (craniofacial hinge), and LM3 (occipital protuberance) were used as the end points for the curves creating the outlines. **B.** The same drawing showing the outline paths used to perform the geometric morphometric analyses: (1) blue outline following the shape of the full skull, (2) yellow outline following the shape of the premaxillary, and (3) red outline following the shape of the cranium.

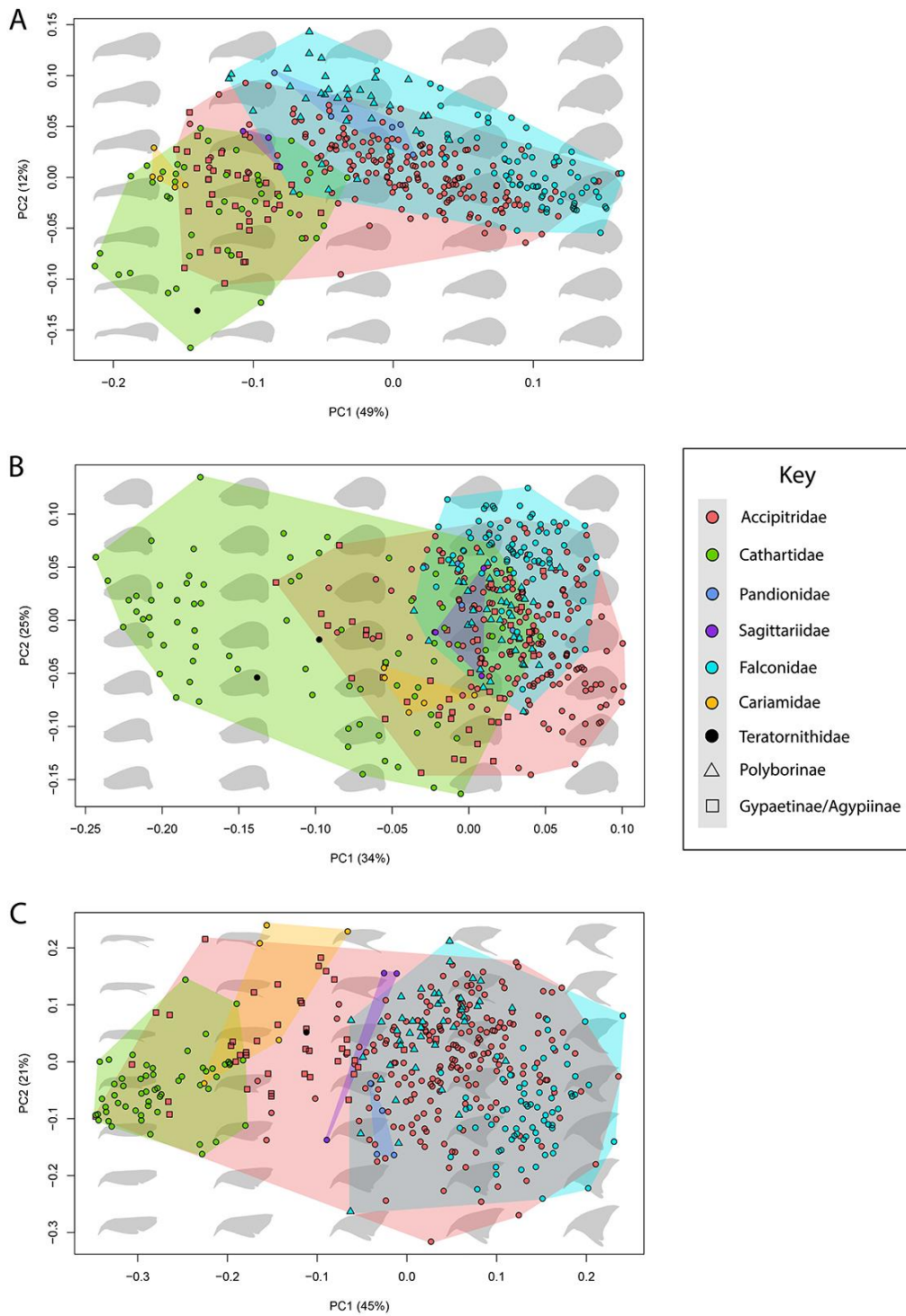


Figure 2.2. Backtransform PCAs showing family distribution of all orders. Three PCAs showing the shape distributions of the: (A) entire skulls, (B) crania, and (C) premaxillary of all species included in this analysis, with shape spaces mapped to the family level. A minimum of three specimens was required to create a polygon for each family, therefore the family Teratornithidae is only represented by points.

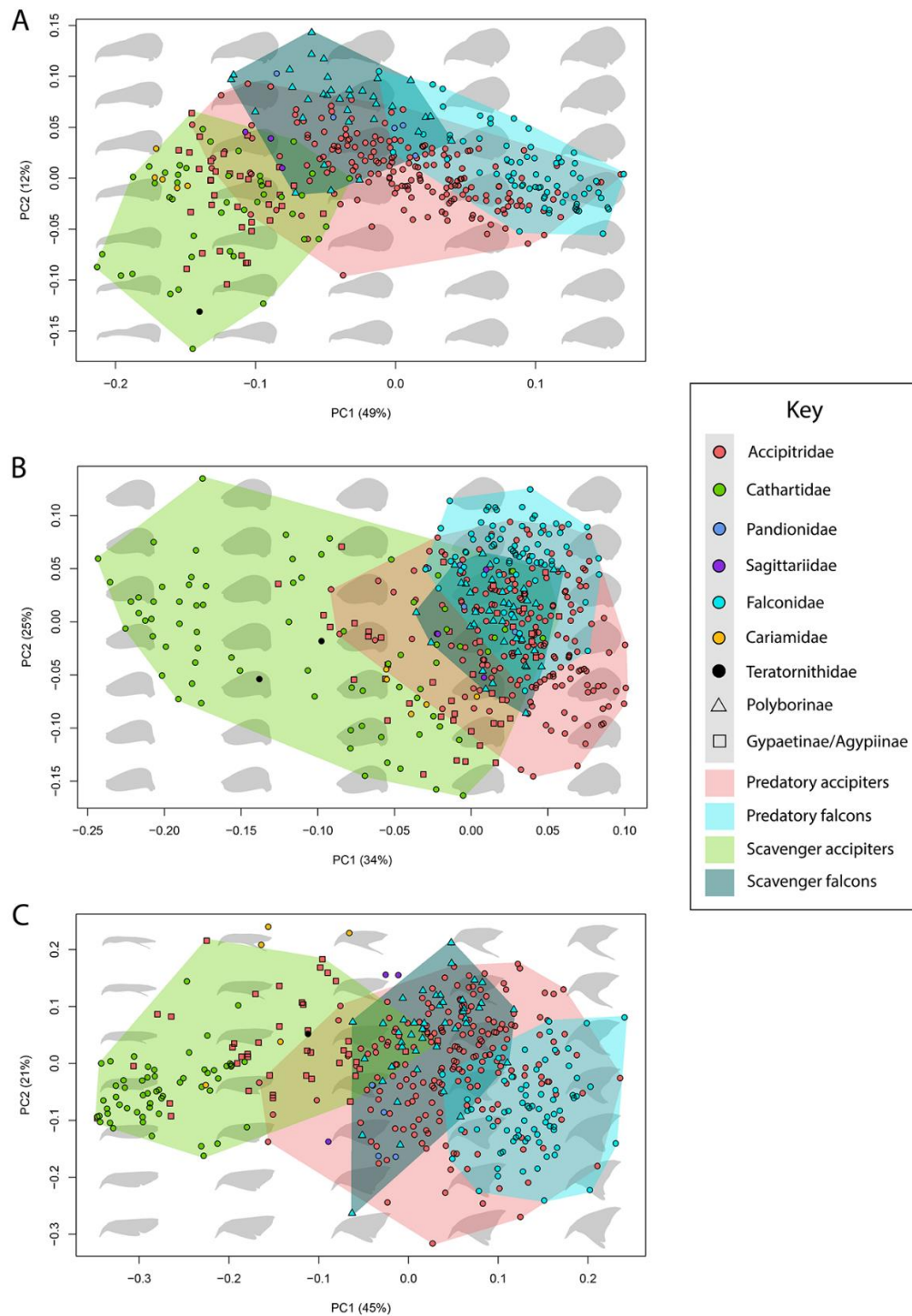


Figure 2.3. Backtransform PCAs showing subfamily distribution of all orders. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species included in this analysis, with shape spaces mapped to show the different spaces occupied by the scavenging versus the predatory members of each order. A minimum of three specimens was required to create a polygon for each family, therefore the family Teratornithidae is only represented by points.

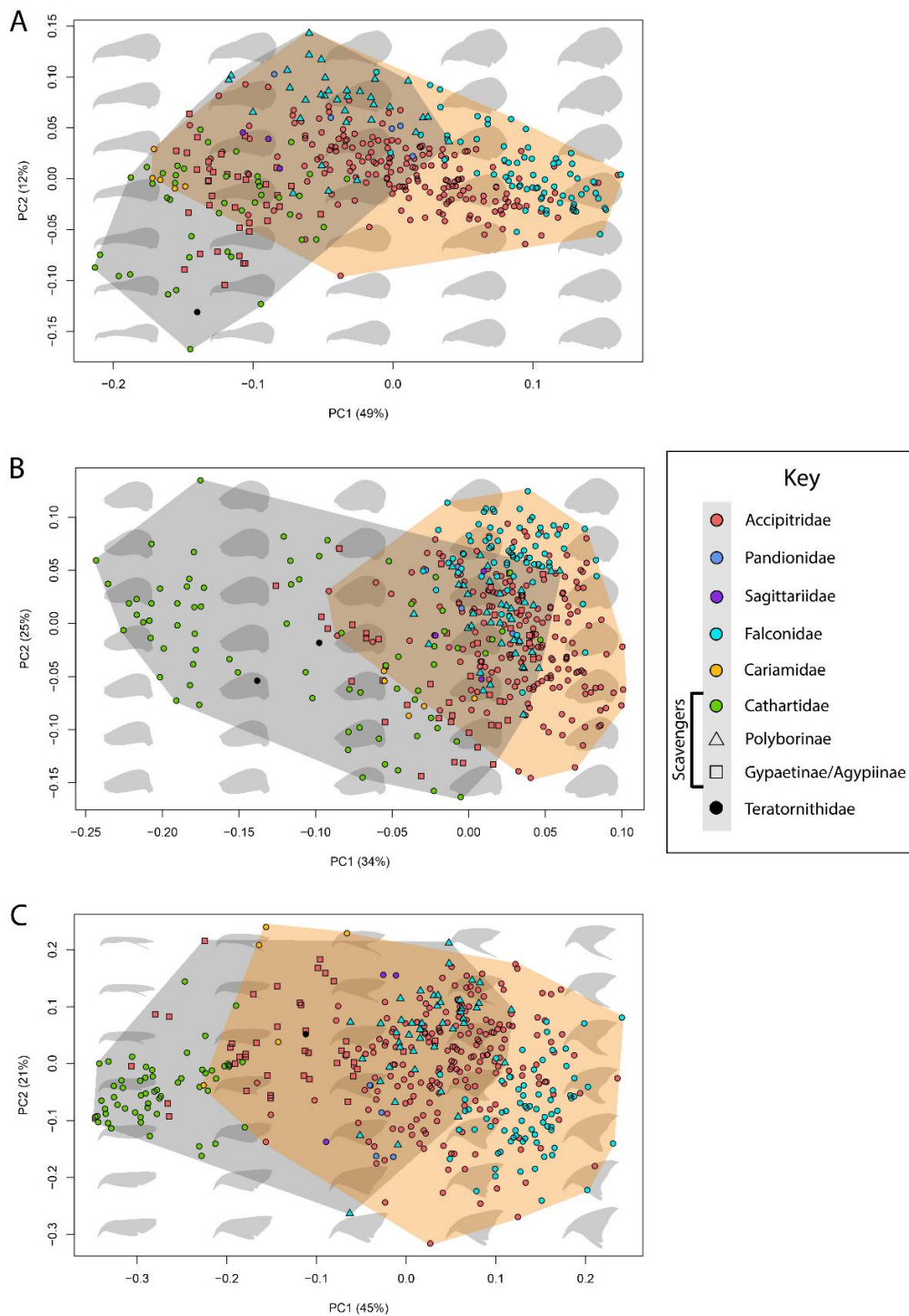


Figure 2.4. Backtransform PCAs showing scavenger distribution of all orders. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species included in this analysis, with shape spaces mapped to show the different spaces occupied by the scavenging (gray space) versus the predatory (orange space) species. A minimum of three specimens was required to create a polygon for each family, therefore the family Teratornithidae is only represented by points.

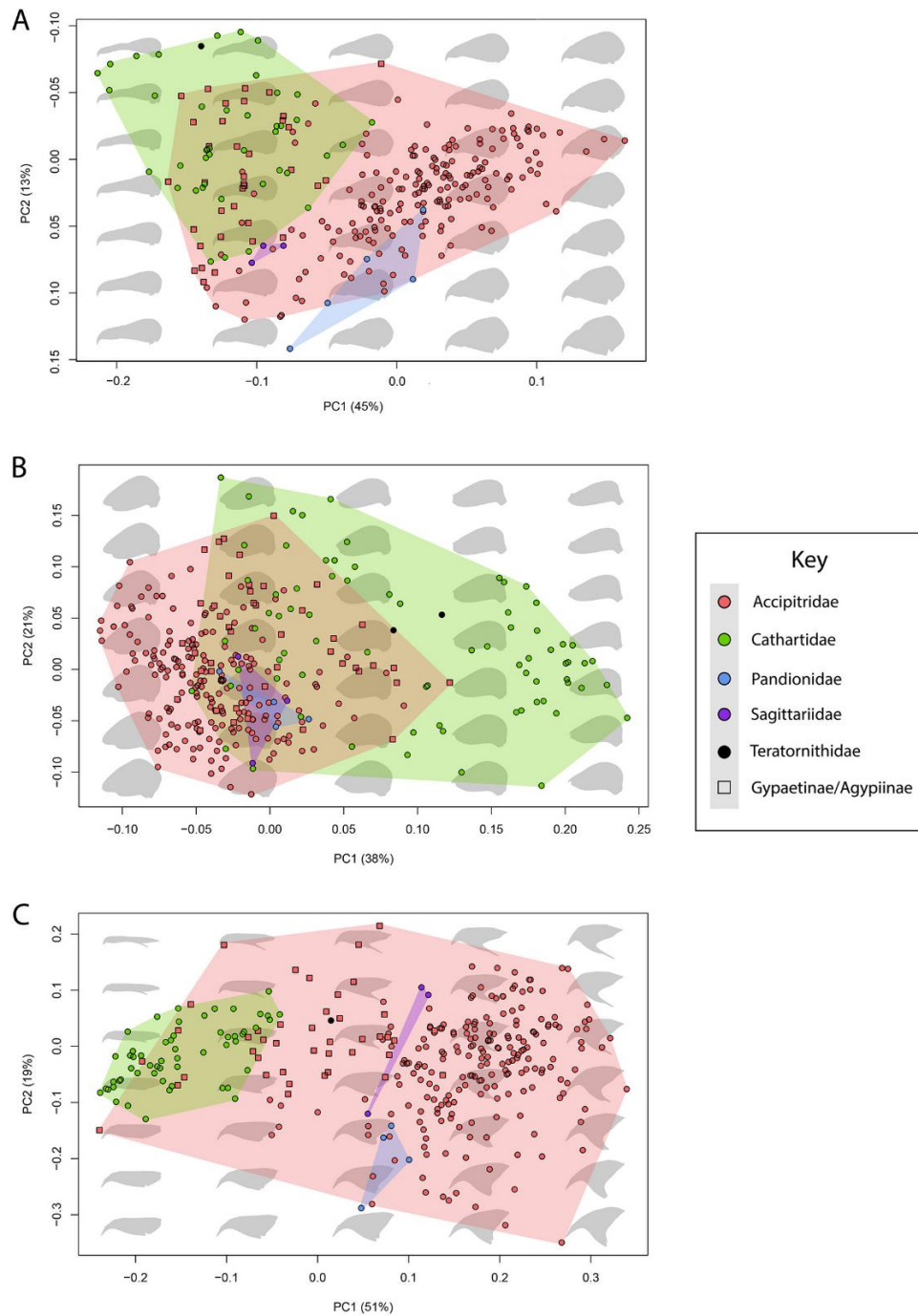


Figure 2.5. Backtransform PCAs showing family distribution of Accipitriformes. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all specimens of the order Accipitriformes, with shape spaces mapped to the family level. A minimum of three specimens was required to create a polygon for each family, therefore the family Teratornithidae is only represented by points.

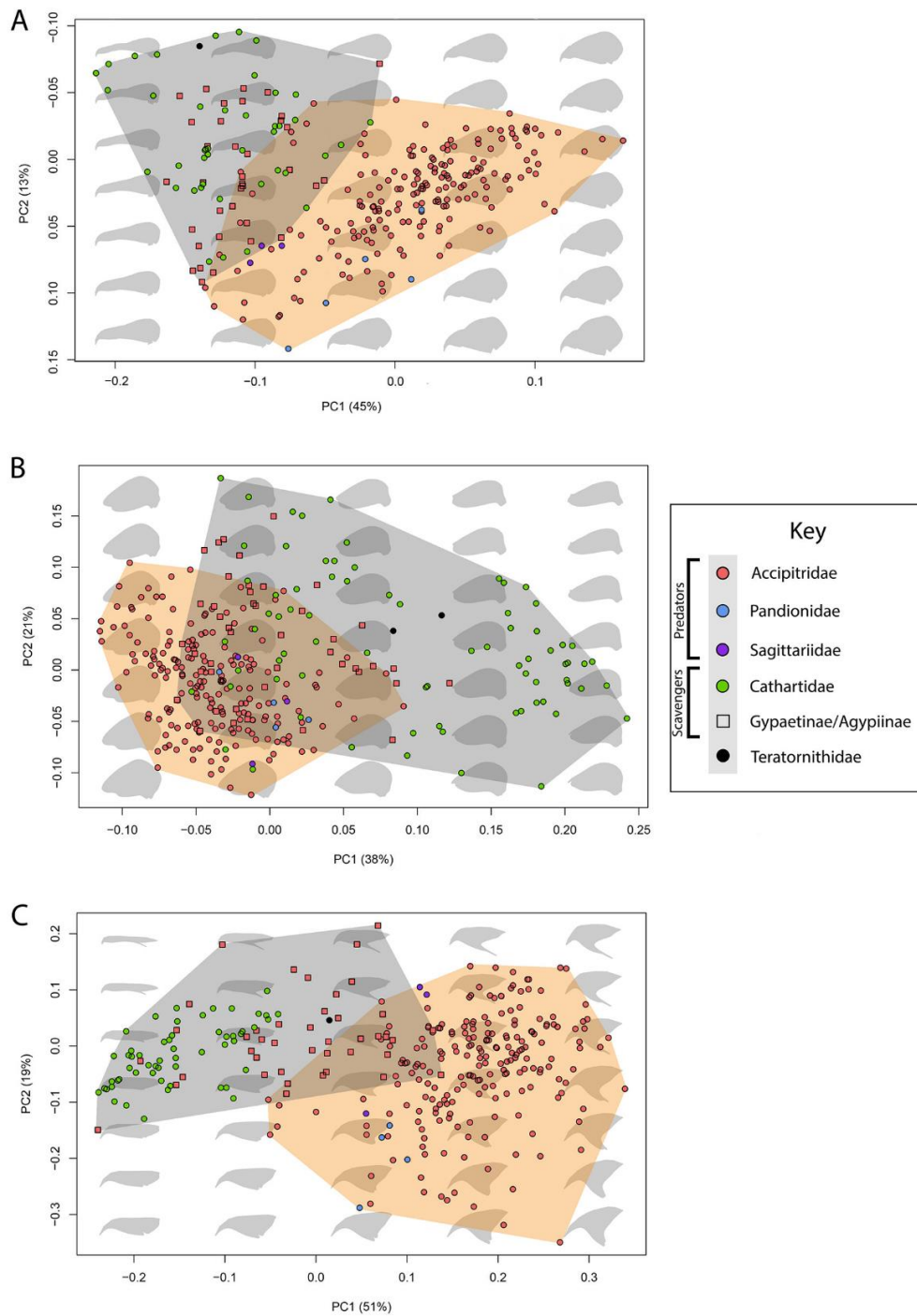


Figure 2.6. Backtransform PCAs showing scavenger distribution of Accipitriformes. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all specimens of the order Accipitriformes, with shape spaces mapped to show the different spaces occupied by the scavenging (gray space) versus the predatory (orange space) species. A minimum of three specimens was required to create a polygon for each family, therefore the family Teratornithidae is only represented by points.

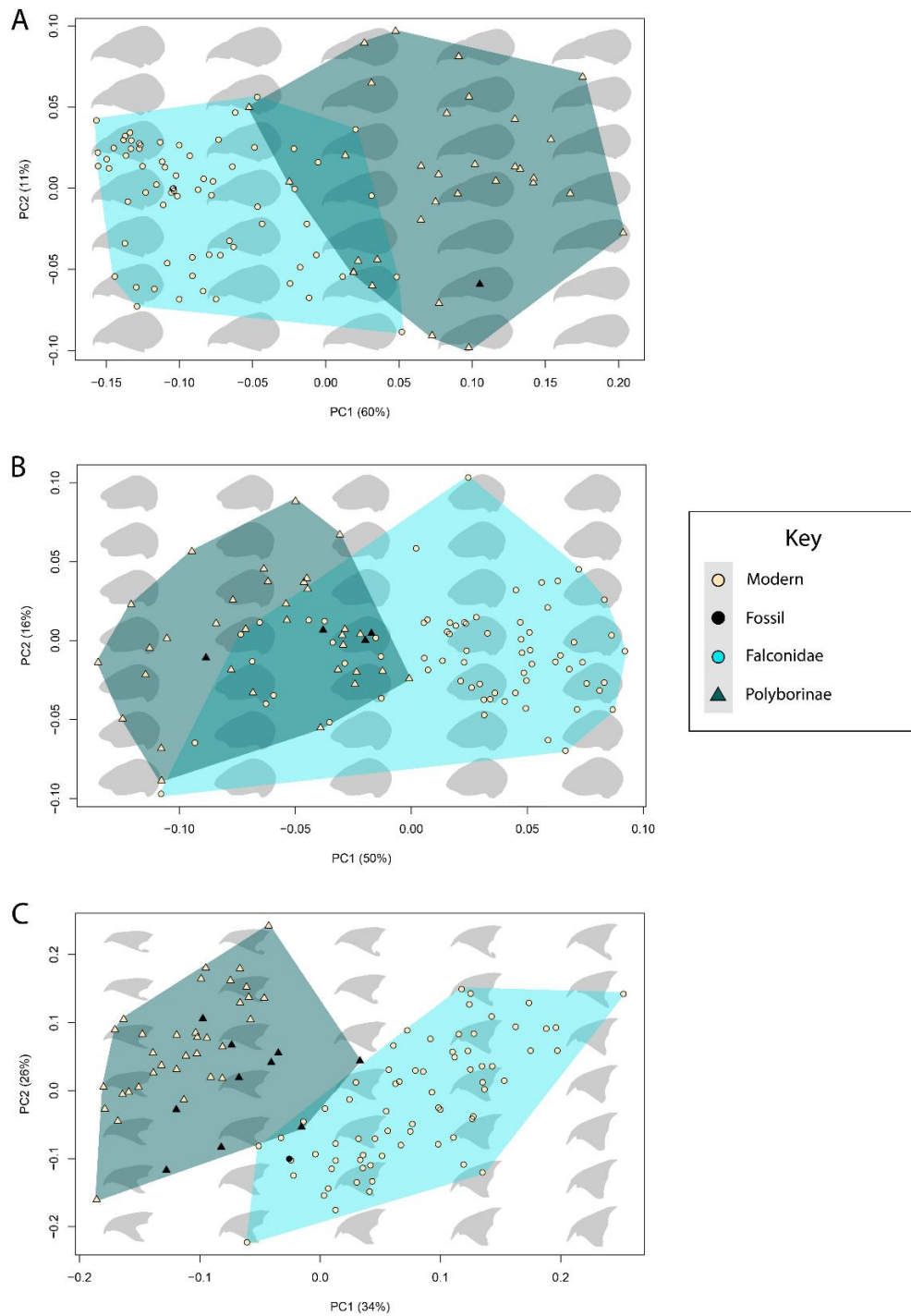


Figure 2.7. Backtransform PCAs of Falconiformes. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species of the order Falconiformes. The fossil specimens are colored black, with shape spaces mapped to show the different spaces occupied by the Polyborinae (dark blue) versus the remaining Falconidae (light blue) species.

2.7 Supporting Documents

2.7.1 Supplementary Tables

Table S2.1. Table of values for ANOVA tests on modern only skull, cranium, and premaxillary shape PCAs. In all tests, percentage of variance (PoV %) for the principal component was used as the quantitative variable and while the independent variable changed depending on whether order, family, or scavenger status was being evaluated. P-values below 0.05 are marked with an asterisk (*). The percent variance determined specifically by the independent variable being examined (% Variance) is the r-squared value multiplied by the PoV.

Modern Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	49.32	0.0000*	0.327	35.76 (5, 353)	16.12
	PC2	11.57	0.0000*	0.146	13.24 (5, 353)	1.69
	PC3	8.67	0.0000*	0.171	15.73 (5, 353)	1.48
Scavenger	PC1	49.32	0.0000*	0.376	216.20 (1, 357)	18.52
	PC2	11.57	0.5422	-0.002	0.37 (1, 357)	-0.02
	PC3	8.67	0.8167	-0.003	0.05 (1, 357)	-0.02
Modern Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	30.10	0.0000*	0.276	20.57 (7, 352)	8.31
	PC2	26.33	0.0000*	0.513	55.11 (7, 352)	13.52
	PC3	13.61	0.0000*	0.125	8.36 (7, 352)	1.71
Scavenger	PC1	30.10	0.0000*	0.065	25.80 (1, 358)	1.94
	PC2	26.33	0.0000*	0.297	152.70 (1, 358)	7.82
	PC3	13.61	0.0000*	0.045	17.73 (1, 358)	0.61
Modern Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	42.27	0.0000*	0.562	93.75 (5, 356)	23.77
	PC2	22.01	0.0000*	0.071	6.52 (5, 356)	1.56
	PC3	14.75	0.0000*	0.210	20.18 (5, 356)	3.10
Scavenger	PC1	42.27	0.0000*	0.448	293.30 (1, 360)	18.92
	PC2	22.01	0.0016*	0.025	10.12 (1, 360)	0.54
	PC3	14.75	0.8015	-0.003	0.06 (1, 360)	-0.04
Modern Accipiter Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	45.64	0.0000*	0.228	25.60 (3, 247)	10.40
	PC2	12.49	0.0000*	0.150	15.74 (3, 247)	1.88
	PC3	11.43	0.0001*	0.070	7.31 (3, 247)	0.80

Scavenger	PC1	45.64	0.0000*	0.471	223.4 (1, 249)	21.49
	PC2	12.49	0.0000*	0.112	32.66 (1, 249)	1.40
	PC3	11.43	0.0000*	0.144	43.14 (1, 249)	1.65
Modern Accipiter Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	32.89	0.0000*	0.315	39.41 (3, 248)	10.35
	PC2	25.46	0.0000*	0.144	15.04 (3, 248)	3.66
	PC3	12.81	0.0046*	0.005	4.45 (3, 248)	0.06
Scavenger	PC1	32.89	0.0000*	0.253	86.20 (1, 250)	8.33
	PC2	25.46	0.0000*	0.275	96.21 (1, 250)	7.00
	PC3	12.81	0.0009*	0.039	11.29 (1, 250)	0.50
Modern Accipiter Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	48.25	0.0000*	0.499	84.93 (3, 250)	24.06
	PC2	22.11	0.0021*	0.046	5.03 (3, 250)	1.01
	PC3	12.84	0.0000*	0.162	17.26 (3, 250)	2.08
Scavenger	PC1	48.25	0.0000*	0.666	504.30 (1, 252)	32.11
	PC2	22.11	0.0001*	0.052	144.94 (1, 252)	1.15
	PC3	12.84	0.0178*	0.018	5.69 (1, 252)	0.23

Table S2.2. Table of ANOVA p-values to assess the effect of fossils on the morphospace. Table of p-values for the two-way analysis of variance (ANOVA) tests on geometric morphometric data for each PCA performed. This test was performed on datasets that contained both modern and fossil specimens to assess whether families or groups were affected by the presence of fossils in the analysis. P-values below 0.05 are marked with an asterisk (*).

Complete Analyses				Cranium			Premaxillary		
Variables	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Accipitridae	0.0051*	0.0010*	0.3250	0.0002*	0.3697	0.4256	0.0130*	0.5216	0.1335
Cariamidae	-	-	-	-	-	-	-	-	-
Cathartidae	0.9873	0.0075*	0.0095*	0.8255	0.0388*	0.5308	0.8170	0.5518	0.0522
Falconidae	0.3355	0.8748	0.1830	0.2895	0.8247	0.8074	0.0273*	0.4646	0.3301
Pandionidae	-	-	-	-	-	-	-	-	-
Sagittariidae	-	-	-	-	-	-	-	-	-
Teratornithidae	-	-	-	-	-	-	-	-	-
Scavenger	0.0000*	0.3762	0.1262	0.1040	0.0062*	0.6629	0.7487	0.0391*	0.0472*
Non-Scavenger	0.0000*	0.0039*	0.0494*	0.0331*	0.0323*	0.0808	0.0005*	0.9211	0.0005*

Accipiter Analyses				Cranium			Premaxillary		
Variables	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Accipitridae	0.0007*	0.0554	0.0013*	0.0020*	0.1807	0.8705	0.0402*	0.5564	0.0630*
Cathartidae	0.9621	0.0096*	0.8195	0.9158	0.0382*	0.0074*	0.9872	0.8281	0.0469*
Pandionidae	-	-	-	-	-	-	-	-	-
Sagittariidae	-	-	-	-	-	-	-	-	-
Teratornithidae	-	-	-	-	-	-	-	-	-
Scavenger	0.7746	0.7745	0.0000*	0.0388*	0.1090	0.5546	0.0064*	0.2209	0.0016*
Non-Scavenger	0.0008*	0.0008*	0.0159*	0.3293	0.0141*	0.0777	0.8101	0.1602	0.0099*

Falcon Analyses				Cranium			Premaxillary		
Variables	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Scavenger	-	-	-	-	-	-	0.0360*	0.5002	0.3920
Non-Scavenger	0.6540	0.1280	0.9806	0.4270	0.9886	0.2980	0.2970	0.7688	0.4650

2.7.2 Supplementary Figures

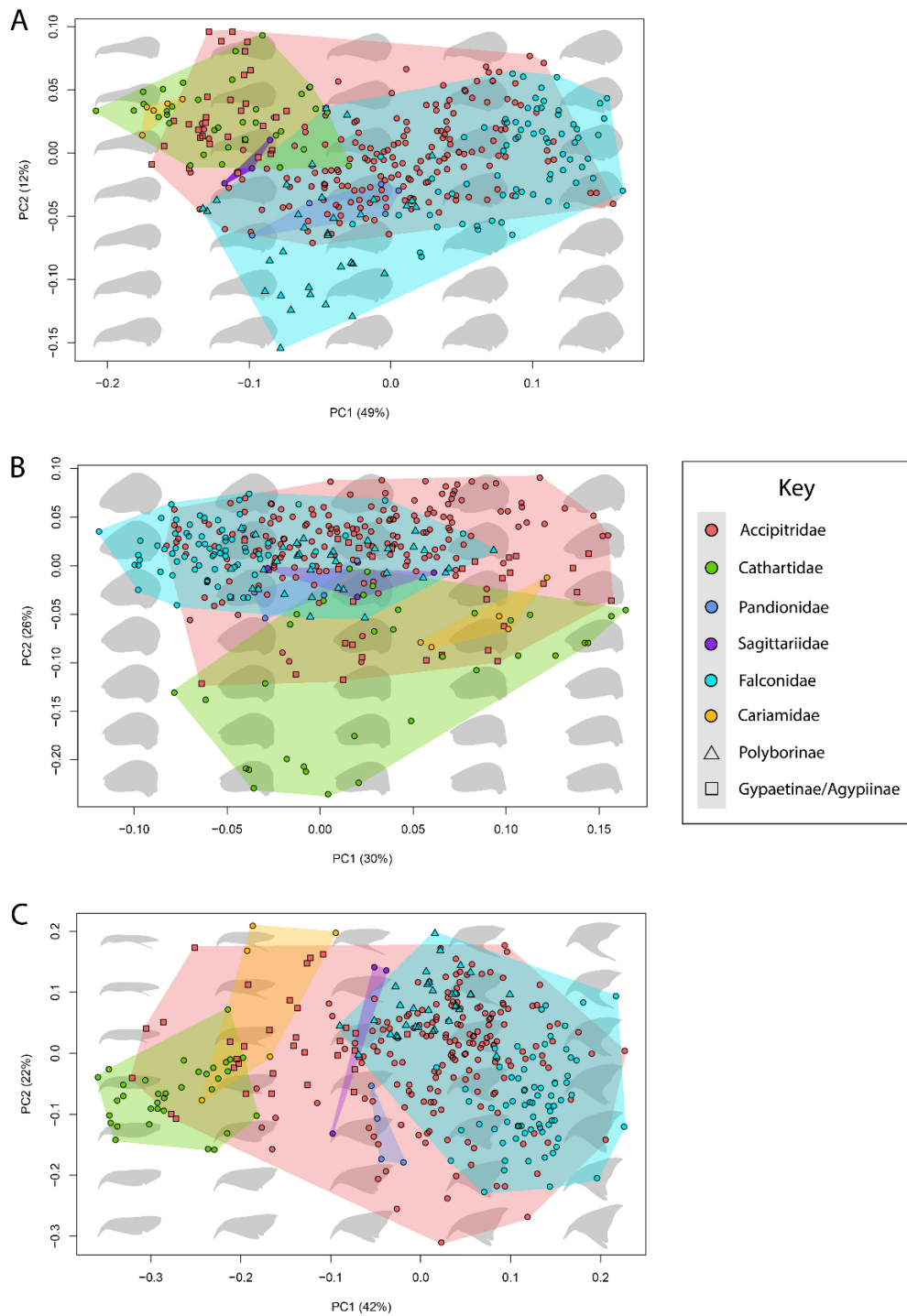


Figure S2.1. Backtransform PCAs showing family distribution of all orders without fossils. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species included in this analysis but excluding fossil samples, with shape spaces mapped to the family level.

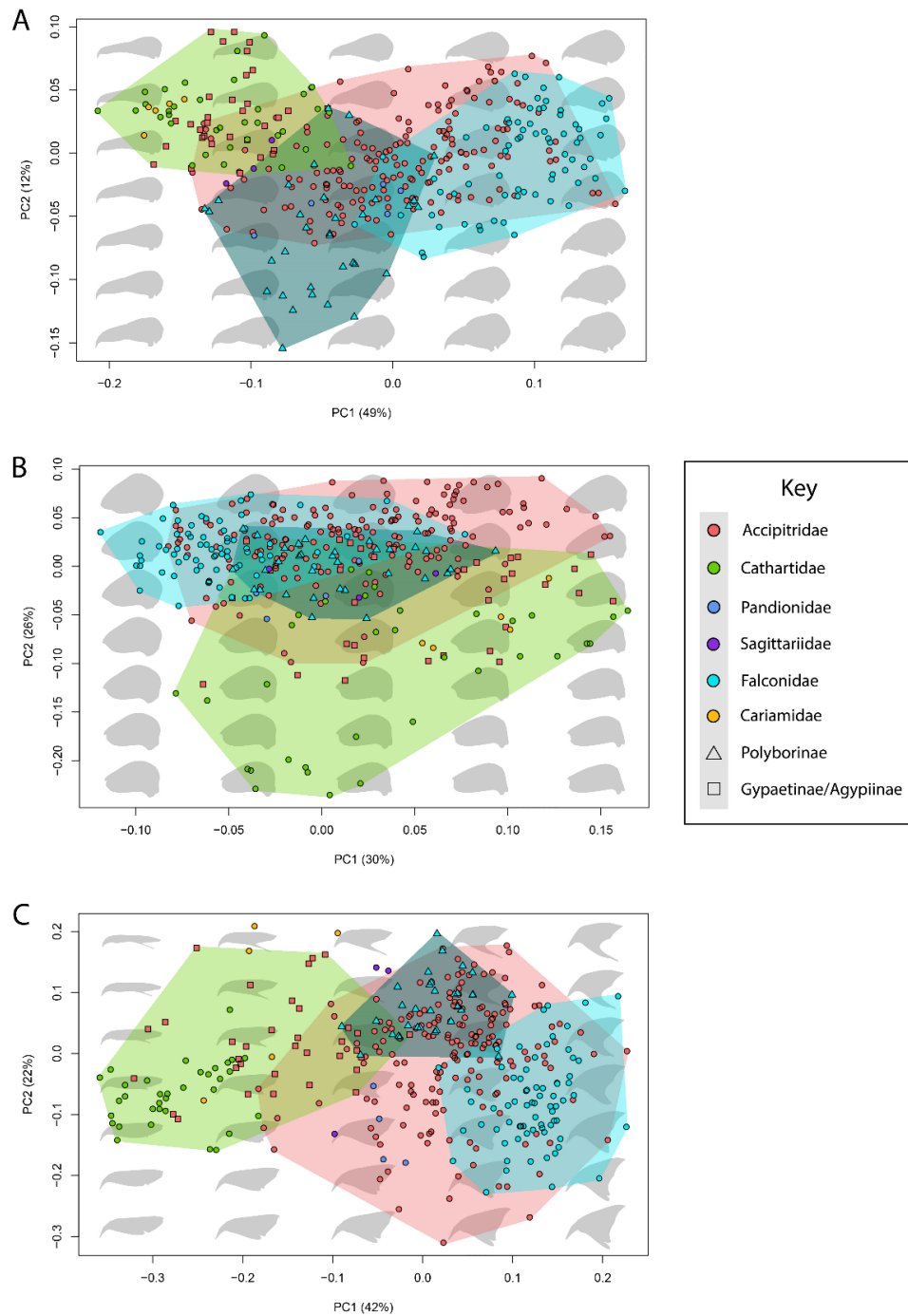


Figure S2.2. Backtransform PCAs showing subfamily distribution of all orders without fossils. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species included in this analysis but excluding fossil samples, with shape spaces mapped to show the different spaces occupied by the scavenging (green and dark blue shapes) versus the predatory (red and light blue) members of each order.

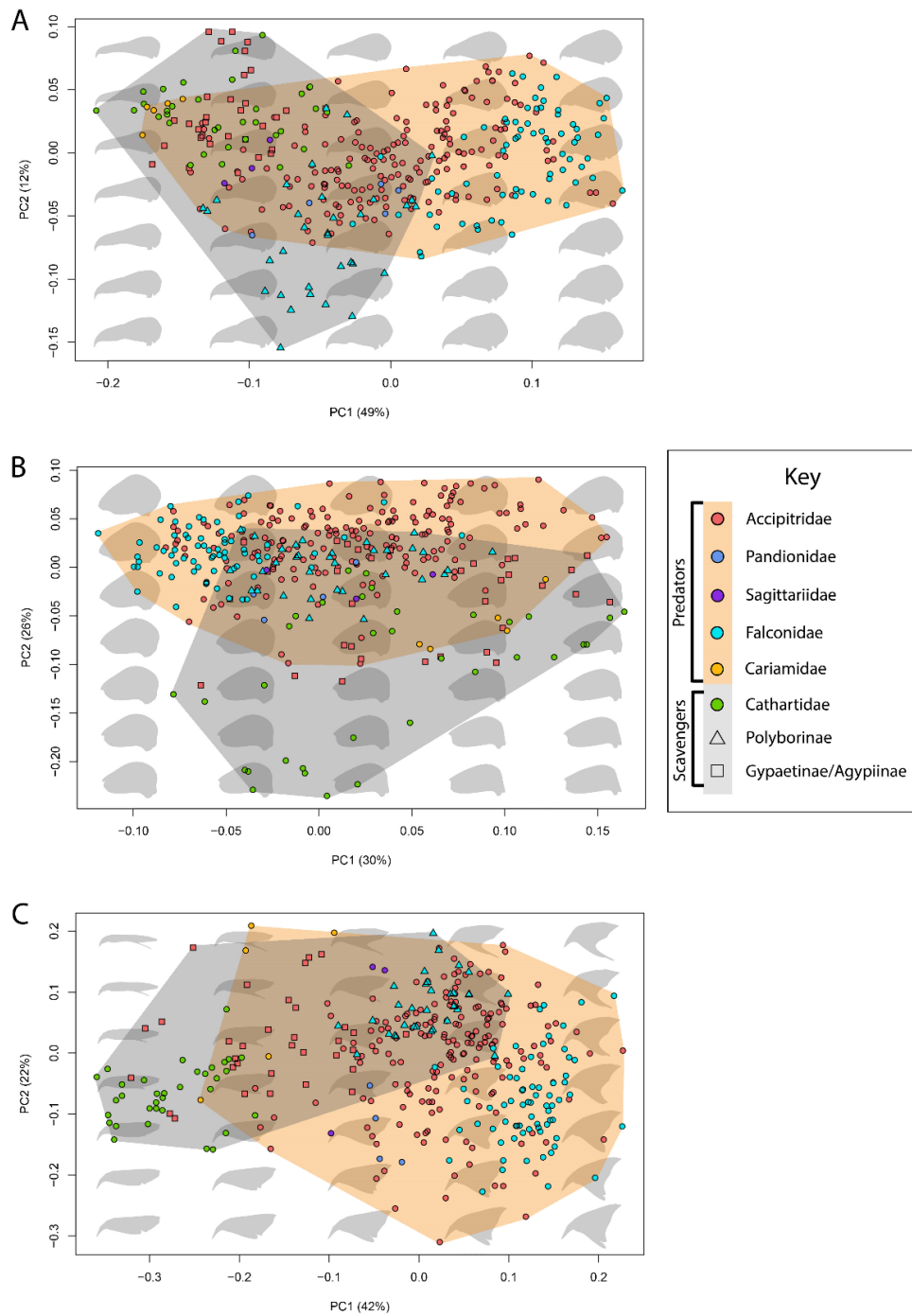


Figure S2.3. Backtransform PCAs showing scavenger distribution of all orders without fossils. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species included in this analysis but excluding fossil samples, with shape spaces mapped to show the different spaces occupied by the scavenging (gray space) versus the predatory (orange space) species.

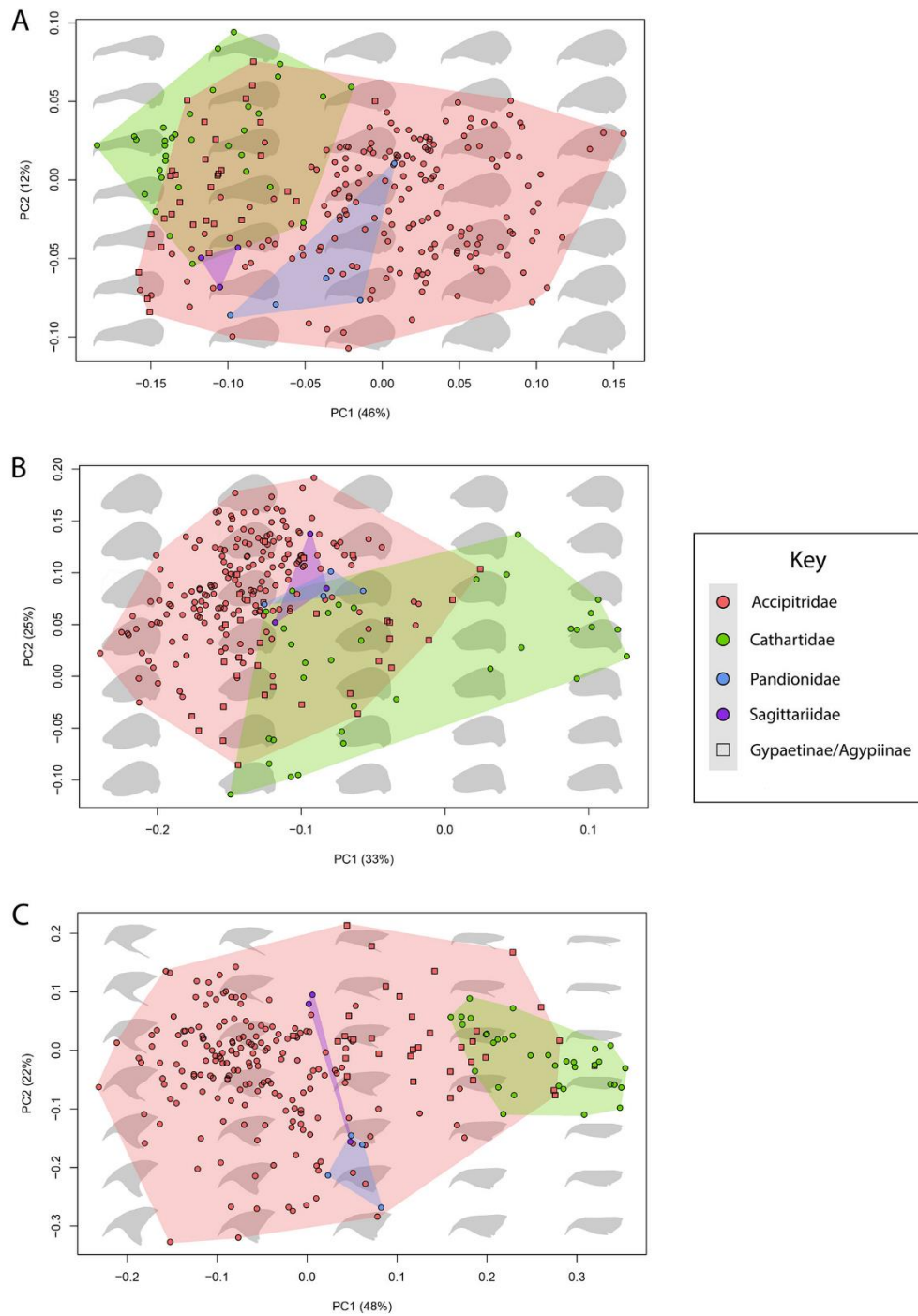


Figure S2.4. Backtransform PCAs showing family distribution of modern accipiters. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species of the order Accipitriformes excluding fossil specimens, with shape spaces mapped to the family level.

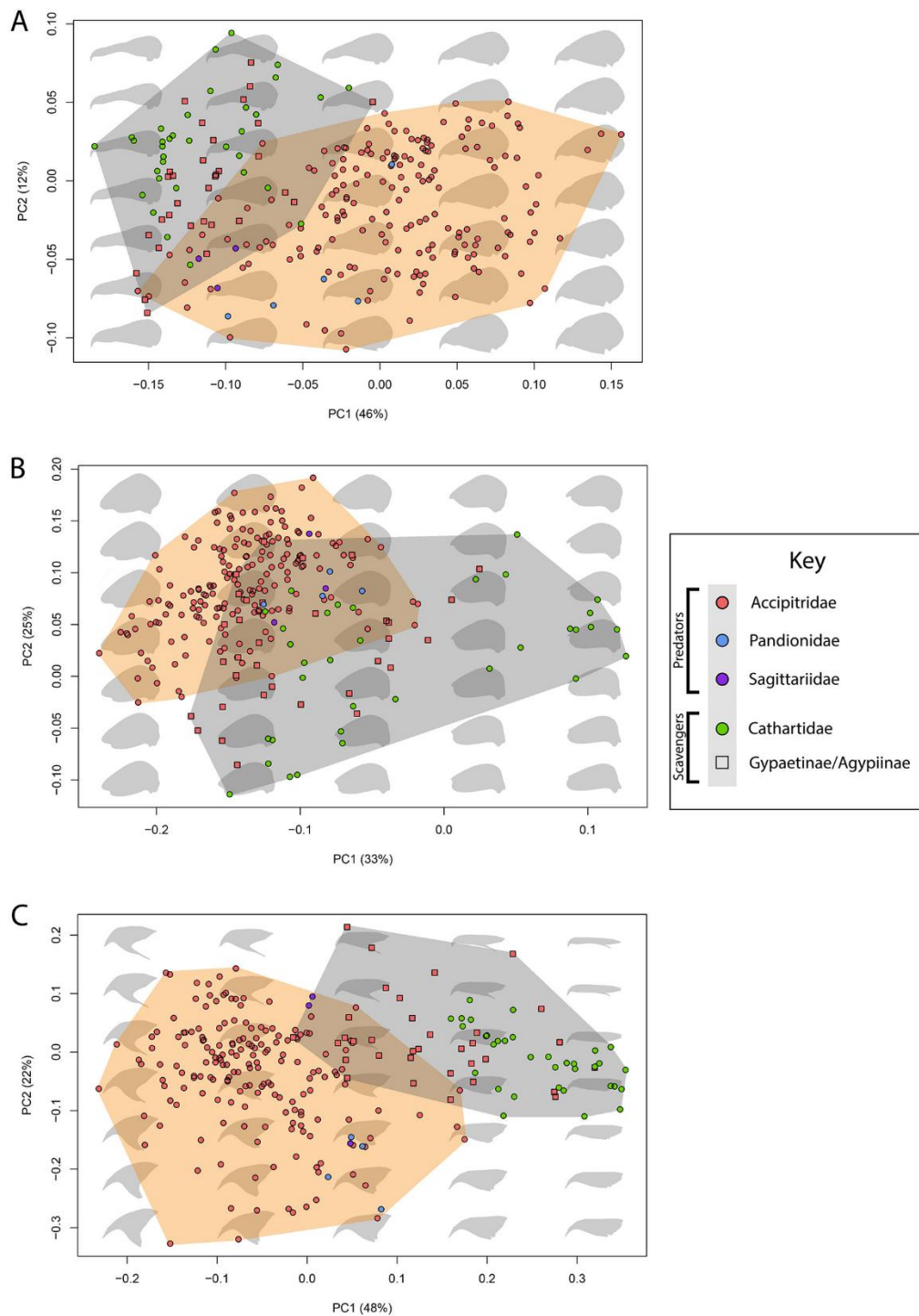


Figure S2.5. Backtransform PCAs showing scavenger distribution of modern accipiters. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillary (C) of all species of the order Accipitriformes excluding fossil specimens, with shape spaces mapped to show the different spaces occupied by the scavenging (gray space) versus the predatory (orange space) species.

Chapter 3

Vulture feeding guilds from the late Pleistocene to the modern day

3.1 Introduction

Scavenging, the consumption of organisms killed by causes other than direct predation, is a life strategy that provides an essential ecosystem service. Scavengers remove decaying organic material from the environment and help reduce instances of disease across the landscape (Ogada et al., 2012; Santangeli et al., 2019; Van Den Heever et al., 2021). While scavenging is common in carnivorous vertebrates, obligate scavengers are rare. The most well-known scavengers among vertebrates are vultures, which are represented by birds of prey in two families within the order Accipitriformes – Accipitridae (17 of 240 species) and Cathartidae (7 of 7 species).

Vultures are obligate scavengers with a fossil record dating back to the early Miocene (Feduccia, 1974; Howard, 1932; A. H. Miller & Compton, 1939; Stucchi et al., 2015; Zhang et al., 2012). Despite their common diets and characteristics, the ‘New World’ (Cathartidae) and ‘Old World’ (Accipitridae) vultures are not closely related (Hackett et al., 2008; Mindell et al., 2018; Stiller et al., 2024). Rather, these groups have converged on similar morphologies that allow for a scavenging lifestyle. Previous studies and observations have suggested that vultures have evolved guilds that consist of three primary feeding modes: rippers, gulpers, and scrappers, allowing the species to coexist while exploiting the same food source (Hertel, 1994; Houston, 2010; Kruuk, 1967). This work also postulates that similar feeding guilds have evolved independently in the two vulture lineages, Cathartidae and Accipitridae.

3.1.1 Vulture phylogenetic relationships

The Old World vultures have been split into two subfamilies, the Gypaetinae (*Gypaetus*, *Gypohierax*, and *Neophron*) and Aegypiinae (*Aegypius*, *Gyps*, *Necrosyrtes*, *Sarcogyps*, *Torgos*, and *Trigonoceps*), which are postulated to have independently evolved their primarily scavenger lifestyles (Lerner & Mindell, 2005). While both subfamilies are considered vultures, the Gypaetinae comprises two unique species with highly specialized diets. As opposed to scavenging meat from deceased animals, the Palm-nut Vulture (*Gypohierax angolensis*) specializes in eating fruit, whereas the Bearded Vulture (*Gypaetus barbatus*) extracts the marrow from bones of large mammals, which comprises between 85-90% of its diet (Ferguson-Lees and Christie, 2001). Cathartid vultures are morphologically and molecularly distinct from the accipitrid vultures (Wink, 1995), and some studies have recognized this distinction by designating a separate order, Cathartiformes (Mindell et al., 2018). However, most taxonomic

treatments have retained the Cathartidae as part of the order Accipitriformes, but noted that they are an old clade based on DNA dating, likely diverging from the rest of Accipitriformes in the late Paleocene approximately 62 million years ago (Prum et al., 2015; Stiller et al., 2024). We follow the IOC checklist and retain the Cathartidae within the Accipitriformes (Gill et al., 2023).

3.1.2 Vulture fossil record and geographic origin

Although the Cathartidae are often referred to as ‘New World’ or ‘Western Hemisphere’ vultures, as all living species are exclusively found in the Americas, the geographic origin of the Cathartidae is contested by their fossil record. The oldest fossil form of the Cathartidae is thought to be *Lithornis vulturinus*, named from a partial skeleton discovered in the late Paleocene deposits of Europe (Owen, 1841). However, the identity of this fossil has been interpreted differently throughout the years, shifting from the Old World Gypaetinae (Lambrecht, 1935; Lydekker, 1891) to the Cathartidae (Brodkorb, 1964). It has also been suggested to not be a vulture, but rather a member of the Palaeognathae in its own family, the Lithornithidae (Bourdon & Lindow, 2015; Grellet-Tinner & Dyke, 2005). Unfortunately, the identification of this fossil remains a mystery as it was destroyed in the World War II bombings of London (Grellet-Tinner & Dyke, 2005). The only accepted species of cathartid vulture that has been discovered in Europe is *Tapinopus ellioti* from the upper Eocene (~35-34 Ma) or possibly Oligocene (34-23.8 Ma) of France. The oldest accepted members of Cathartidae are *Phasmagyps patritus* and *Palaeogyps prodromus*, both of which were found in the Chadron Formation of Colorado and date back to the late Eocene (~35-34 Ma) (Wetmore, 1923). To date, 27 extinct species of cathartid vulture have been recognized, along with the seven living species (Alvarenga et al., 2008; Stucchi et al., 2015; Wink, 1995; Wink et al., 1995) (See Table 3.1 for a list of fossils).

In addition, there exists an extensive Pleistocene fossil record of birds of prey in the Rancho La Brea formation near Los Angeles, USA (Hertel, 1994). This record has unusually large numbers of carnivores and scavengers, due to the presence of megafauna that became trapped in the tar seeps, drawing scavengers in for an easy meal where they also became stuck (Akersten et al., 1983; Howard, 1962). This extremely well-preserved and sampled fossil record illustrates that there was a greater diversity of North American species of vultures in the Pleistocene than there are today (Emslie, 1988b). In California alone, there were three times as many species of vultures living concurrently in the Pleistocene as there are today (L. H. Miller, 1910). Fossil evidence suggests that vulture diversity was also previously higher in South America (Alvarenga et al., 2008).

The fossil record of accipitrid vultures, which are today distributed widely across Africa, Europe and Asia, also has an uncertain geographic origin. For example, the extinct genera *Palaeoborus* and *Neophrontops* are known from the Miocene, Pliocene, and

Pleistocene of North America (Cope, 1874; A. H. Miller & Compton, 1939; L. H. Miller, 1916; Wetmore, 1936) and the genus *Palaeohierax* from the lower Miocene of France (Brodkorb, 1964) suggesting accipitrid vultures were geographically more widespread than they are today. This makes it difficult to discern whether the ‘Old World’ vultures of the Accipitridae originated in the Afro-Eurasia region or in the Americas (Feduccia, 1974). Additionally, the Gypaetinae and Aegypiinae subfamilies may have different geographic origins from each other (Lerner & Mindell, 2005). There are even two extinct accipitrid vultures found at the La Brea tar pits, *Neophrontops americanus* that shares many affinities with the extant genus *Neophron*, and *Neogyps errans*, both of which are considered part of the subfamily Gypaetinae. Other genera of the Gypaetinae have been found in the late Miocene of Spain (Sánchez-Marco, 2022), and one species has been recovered from the Pleistocene of Australia (De Vis, 1905). Fossils of likely members of the Aegypiinae have also been found in Spain, China, France, and North America (see Table 3.1).

3.1.3 Vulture feeding guilds

Morphological characteristics associated with the scavenging lifestyle include a lack of feathers on the head, an elongated premaxillary relative to other birds of prey, and a reduction in the curvature of both the talons and the beak (M. O. Campbell, 2015). A classic study of ecomorphology by Kruuk (1967) described the feeding strategies and behaviors of vultures in East Africa. Kruuk’s (1967) work was observational where he noted that as many as six vulture species can be found feeding on a single carcass in some regions. Kruuk (1967) was the first to draw attention to differing skull morphologies among species of vultures directly competing for food and he used this to devise a classification of species into five feeding styles (see Table 3.2 for descriptions). Houston (1988) noted how the Turkey vulture (*Cathartes aura*), Black Vulture (*Coragyps atratus*), and King Vulture (*Sarcoramphus papa*) of the Cathartidae assemblage had distinct skull morphologies that appeared to correspond to their primary feeding strategy, and that they exhibited low interspecific aggression while sharing a carcass. Each of these papers described the interspecific interactions observed on and around a feeding site. Hertel (1994) then proposed a new guild structure for these species, drawing upon the works of Kruuk (1967) and Houston (1988), proposing three guilds: rippers, gulpers, and scrapers (Table 3.2). Hertel (1994) also investigate the skull morphology of fossil species to place them within his proposed guilds. Van Valkenburgh (1995) further expanded upon the concept of paleo guilds by looking at feeding guilds in extinct mammals and emphasized Hertel’s (1994) work as an example of guild structure that is repeated through time.

3.1.4 Scavenging in the Falconiformes

While vultures are the primary carrion eaters of the avian world and are often depicted as the classic example of the “scavenger” life history strategy, the Falconiformes has its own lineage of scavengers. Falcons fall within the colloquial term ‘raptors’ along with the Accipitriformes, sharing many of the same features such as highly recurved beaks and large talons (Fowler et al., 2009), but phylogenetically they are more closely related to parrots and passerines (Prum et al., 2015; Stiller et al., 2024). Like the accipiters, falcons are geographically widespread and found on every continent except Antarctica, but they are not as diverse, with only 11 genera and 60 species in a single family, the Falconidae (Gill et al., 2023). There are three subfamilies within the Falconidae: the Falconinae (falconets and true falcons), Herpetotherinae (forest falcons), and Polyborinae (caracaras). The earliest fossil remains of the Falconidae were found in Patagonia, *Badiostes patagonicus*, dating from the early Miocene (Ameghino, 1895). Interestingly, among fossil falcon species the vast majority have been referred to the subfamily Polyborinae, and particularly to the genera *Caracara* and *Polyborus* (M. P. Jones et al., 2007; Olson, 1982, 2008; Olson & Hilgartner, 1982; Steadman et al., 2007; Suárez & Olson, 2003, 2014; Wetmore, 1920).

The Polyborinae are another example of a branch of birds that have independently evolved a suite of carrion eating morphologies, including the reduction of head feathers and elongation of the beak (Dove & Banks, 1999; Potier, Bonadonna, Kelber, & Duriez, 2016). They are primarily found in Central America, South America, and Cuba, overlapping with as many as four species of New World vulture – the turkey vulture, black vulture, king vulture, and Andean condor (*Vultur gryphus*) – and have been known to compete with them (Wallace & Temple, 1987). One extinct species of caracara, *Polyborus prelutosus*, is also found in the Pleistocene La Brea tar pit deposits alongside other scavenging birds, which suggests the presence of these falcon-accipiter scavenging interactions at least as far back as 38,000 years ago (Howard, 1962). The feeding guild structure proposed for vultures by Hertel (1994) and extended by Van Valkenburgh (1995) has never been applied to the caracaras.

3.1.5 Scope of this study

The Accipitriformes is represented in this study by two families – the Accipitridae, subfamilies Gypaetinae and Aegypiinae, and the Cathartidae, which has been split into two primary clades following Johnson et al. (2016), the ‘vultures’ (*Cathartes* and *Coragyps*) and the ‘condors’ (*Sarcoramphus*, *Gymnogyps*, *Vultur*, and the extinct genus *Breagyps*) (Johnson et al., 2016). The Falconiformes and family Falconidae are only represented by the members of the subfamily Polyborinae in this study and will be referred to as the Polyborinae for the remainder of this chapter. The descriptions provided by Hertel (1994) did not always align with those of Kruuk (1967) or Houston (1988) (Table

2.2). Therefore, in this study the guild structures proposed by Kruuk (1967), Houston (1988), and Hertel (1994) were reevaluated using geometric morphometric techniques. The groups under consideration include the cathartid and accipitrid vultures, as well as the caracara falcons, which are often overlooked as a part of the scavenging dynamic. This study aims to quantify variation and modularity of the skulls of diurnal raptors by assessing their differences at the family level and between active predators and scavengers. This study also addresses the fossil vultures of the Pleistocene aged Rancho La Brea tar pits, and how avian scavenger diversity and dynamics have changed through time in California.

3.2 Materials and Methods

3.2.1 Materials

The skulls of specimens from the orders Accipitriformes and Falconiformes were photographed and evaluated. The focus centers on the scavenging members of these two orders, and includes the family Cathartidae, the subfamilies Gypaetinae, Aegypiinae, and the Polyborinae. A combination of recent and fossil material was included in this study. Fossil specimens came from the La Brea tar pits and the McKittrick tar pits, and all specimens were three-dimensionally preserved with little to no physical deformation. Despite a high level of preservation, the fossils were rarely complete skulls, often preserved as an isolated premaxillary or crania. Fourteen fossil skulls, 56 fossil crania, and 43 fossil premaxillaries were used in this study.

Between one and four specimens were included per species in the recent material. All living members of the Cathartidae and Aegypiinae, and all but one living member of each of the Gypaetinae and Polyborinae are represented by at least one specimen. Specimens with a rhamphotheca present on the premaxilla were not included in this analysis. The rhamphotheca can cause significant changes to the shape of the premaxilla, and specimens without a rhamphotheca are more common in museum skeletal collections. The rhamphotheca is also very rarely preserved in the fossil record, and none of the fossils used in this dataset included a rhamphotheca. Therefore, this study chose to exclude specimens with a rhamphotheca in the interest of consistency, but we note that some of the morphological relationships may differ in an analysis that includes the rhamphotheca (see chapter 1). A complete list of specimens included in this study can be found in Appendix 3.1.

3.2.2 Data collection

Specimens were photographed with a Nikon D3400 DSLR camera and AF-P Nikkor 18-55 mm lens in the lateral view. Specimens were photographed in the left lateral view whenever possible. For specimens damaged or missing bones on the left side, a

photograph of the right lateral view was taken, and the photograph mirrored for landmarking.

Landmark-based Geometric Morphometrics (GMM) is a two-dimensional (2D) or three-dimensional (3D) approach to quantitatively compare the morphology of objects and organisms. This study used a 2D approach, which includes placing landmarks onto the photographed specimens. Three types of landmarks were used on these specimens: Type I landmarks, which are defined as clearly homologous points of correspondence; Type II landmarks which are tips, the highest or lowest points of curves, and other geometric boundaries (Bookstein, 1997); and sliding or semi-landmarks, which exist as equally spaced points along a curve of the specimen being analyzed (Bookstein, 1997; Mitteroecker & Gunz, 2009).

Landmarking was performed in R using the package StereoMorph (Olsen & Westneat, 2015). The program allows the user to manually place landmarks onto photographs. StereoMorph also allows for the capture of scale for each specimen by the placement of two additional landmarks on a scale bar in the photo. The user provides a value to the distance between the two points, giving scale to the specimen. This later assists with accounting for allometry in the sample of specimens. The analysis focused on an outline of the lateral view of each specimen, composed of an upper skull curve ranging from the tip of the beak to the top of the occipital protuberance and a lower skull curve ranging from the occipital protuberance back to the tip of the beak. Each skull received a landmark at the start and end of the curves. Each specimen was outlined three times for three different analyses: an outline of the complete skull, an outline of the cranium, and an outline of the premaxillary. The upper skull curve consisted of 25 semilandmarks and the lower skull and premaxillary curves consisted of 60 semilandmarks. The upper cranium and premaxillary curves consisted of 20 landmarks and the lower cranium consisted of 50 landmarks. Placement of these curves is shown in Figure 3.1.

In addition to investigating the skull, cranium, and premaxillary shape individually, the data was separated into three data sets: (1) recent specimens, (2) fossils, and (3) all specimens combined. This was repeated for a subset of the data restricted to the accipitrid vultures. These subsets of data were used to address specific questions related to phylogenetic signal and modularity of the avian scavenger skull, and to investigate how the different parts of the skull align with the proposed guild structures.

3.2.3 Data analyses and statistics

The landmark coordinate data extracted from the StereoMorph package was subjected to a Procrustes superimposition and Principal Components Analysis (PCA) using the geomorph package in R (D. C. Adams & Otárola-Castillo, 2013). Procrustes superimposition removes aspects of size including rotation, scale, and translation from

the specimens included in the analysis. The analysis then uses the coordinate data collected from all shapes in the analysis to create an average shape (Bookstein, 1996). This average lies at the centroid (0,0) of the PCA graph and becomes the basis of comparison for all other shapes in the analysis. The amount of variance in each specimen as compared to the average shape is calculated and represented on a graphical morphospace as Principal Components (PC). In the Principal Component morphospace, every point represents one specimen and is placed along the x-axis according to the amount of difference it shows from the centroid x-coordinate, and along the y-axis according to the amount of difference it shows from the centroid y-coordinate. Individual specimens that are close together on the PC morphospace are more similar in shape to each other.

We performed one-way analysis of variance (ANOVA), two-way ANOVA, linear regression, and Tukey's tests for each data set in the study. PC1, PC2, and PC3 were compared against taxonomy (order when applicable, family, subfamily) to test whether phylogenetic relationships influence the shape of the skull, cranium, or beak. In the vulture only dataset, PC1, PC2, and PC3 were also tested against the guilds designated by Hertel (1994; Table 3.2). R-squared values were multiplied by PCA values to score significance for each test variable (Cooke & Terhune, 2015). The two-way ANOVA was used to determine whether the presence of fossils in the analysis of the combined dataset interacted with any of the other independent variables (order, family/subfamily, or guild) to affect the outcome of the PCA. Principal Component Analysis plots were produced using the R packages StereoMorph, geomorph, and ggplot (Wickham & Wickham, 2007). Backtransform morphospace plots were created for each species, following the R protocol developed by Olsen (2017). These plots provide a visual representation of the morphological changes happening on the x- and y-axes. Tukey's tests were used to focus on the largest value of difference between the two means of each independent variable. A Tukey's test (TukeyHSD) was run for the order and family variables of each dataset using the R package multcompView (Graves & Dorai-Raj, 2024).

3.3 Results

3.3.1 Comparison of three families – whole skull

In an analysis combining modern and fossil specimens the first three principal components accounted for 69% percent of the observed variation in the shape of the skull (PC1 = 37.56%, PC2 = 19.41%, PC3 = 12.17%) (Table 3.3). Plotting PC1 versus PC2, the primary change along the x-axis is a narrowing of the skull from left (negative values) to right (positive values) on the axis (Figure 3.2A). Positive values on the x-axis are also associated with a beak that is proportionately longer compared to the cranium, as well as a more pronounced hook on the tip of the beak. The y-axis also encompasses a narrowing of the skull; moving from the negative to the positive end of the axis, the beak becomes

longer and narrower with respect to the cranium. The y-axis also reflects a change in the angle of the beak relative to the cranium, shifting from a horizontally flat skull at the negative end of the axis to the beak being at approximately a 15-degree angle from the cranium at the positive end. Visually the Polyborinae (Falconidae) is well separated from the rest of the Accipitriformes (Accipitridae & Cathartidae), with only a small amount of overlap in morphospace towards the middle of the PCA (Figure 3.2A).

All three of the taxonomic groups— Polyborinae, Accipitridae, and Cathartidae – were found to have significantly different means from each other on PC1 (Table 3.3). On PC2 the Accipitridae differed significantly from the Cathartidae and Polyborinae, but the Cathartidae did not differ from the Polyborinae. On PC3 the Cathartidae differed significantly from the Polyborinae and Accipitridae, but the Accipitridae and Polyborinae did not differ from each other (Table 3.4). The very edge of the Cathartidae morphospace barely meets with the portion of morphospace occupied by Polyborinae towards the middle of the PCA (Figure 3.2A). Cathartidae shapes represent the positive half of the x-axis, with skulls that are longer and narrower overall than those of the Polyborinae. Unlike the Polyborinae, the skulls of cathartids trend towards the positive end of the y-axis, with cathartids possessing more of an angled beak than a beak in line with the cranium. The cathartids on the extreme positive end of the x-axis, have the narrowest skulls, and are primarily fossil specimens. When a two-way ANOVA was performed to compare the families and fossils, there was a significant interaction between the modern and fossil specimens of the Cathartidae on PC2 only ($p < 0.05$). This shows that the presence of the fossils in the data set contributes to the mean shape of the Cathartid skull.

For the Accipitridae, both subfamilies Gypaetinae and Aegypiinae, encompass the smallest polygon in PCA morphospace, falling between the Polyborinae and Cathartidae in shape, and consequently are closer in shape to the average of the entire dataset (Figure 3.3A). Statistically, most subfamilies had significantly different means from each other on PC1, with two exceptions (Table 3.4). The Gypaetinae did not differ significantly in shape from the Aegypiinae on any of the principal components and did not differ from the cathartid vulture clade on PC1 (Table 3.4). This can be seen on the PCA – the most significant overlap that occurs between the Accipitridae and Cathartidae in morphospace (Figure 3.2A). On PC2, only the Polyborinae and vulture clade differed significantly from both Gypaetinae and Aegypiinae, and on PC3 the vulture clade differed significantly from the Gypaetinae, Aegypiinae, and Polyborinae (Table 3.4; Figure 3.3A). Based on the two-way ANOVA, there is no significant interaction of the fossils with the subfamilies on any of the principal components (Table S3.2).

3.3.2 Comparison of three families – whole skull: modern

Family and subfamily had a significant effect on all three principal components in this dataset (Table 3.3; Figure 3.2B & 3.3B). The Tukey's test revealed that most

subfamilies differed significantly on PC1, with a few notable exceptions. Gypaetinae did not significantly differ from the Aegypiinae, the vulture clade, or the condor clade and vultures and condors did not differ significantly from each other on PC1 (Table 3.4). This result is similar to that of the analysis of the full dataset in that the two Accipitridae subfamilies did not differ significantly in skull shape and Gypaetinae was not significantly different from vultures. However, Gypaetinae did differ significantly from the condors (Table 3.4), indicating that the inclusion of fossils influenced the shape of morphospace occupied by the Cathartidae, particularly that of the condor clade. The Tukey's test for PC2 had far fewer significant differences. Here the only significant differences were that the Polyborinae and the vulture clade each differed significantly from Gypaetinae and Aegypiinae (Table 3.4). Finally, on PC3 the vulture clade differed significantly from Aegypiinae, Gypaetinae, and Polyborinae (Table 3.4).

3.3.3 Comparison of three families – whole skull: fossil

The dataset used for this analysis is smaller than the previous two datasets. Only one fossil specimen of the Polyborinae, four fossil specimens of the Gypaetinae, and nine fossil specimens of the Cathartidae had sufficiently complete skulls to be included in this dataset. All but one of the eight fossil species is extinct, and there were no fossil representatives of the subfamily Aegypiinae. Here, the percentage of shape explained by PC1 decreased by four percentage points, while the percentage of PC2 and PC3 each increased by five percentage points relative to the analysis of the combined scavenger dataset (Table 3.3). Despite the differing distribution of principal component percentage, there is a similar trend of shape change along the x- and y-axes to that observed from analysis of the full dataset (Figure 3.2C vs. 3.3C). The x-axis continues to represent the skull becoming overall slenderer, but the most slender skulls are now distributed towards the negative end of the x-axis instead of the positive end. The cranium also becomes proportionately smaller compared to the beak when moving from positive to negative on the x-axis. The y-axis has a similar shape change pattern to the analysis of the full dataset, with skulls going from a straighter shape to having a beak that is angled more downwards from the cranium. The y-axis has also flipped in this analysis, with more angled skulls now at the negative end of the axis. The biggest difference to the shape change observed on the y-axis is that the nature of the beak to cranium angle is more curved than in the previous two analyses.

The Polyborinae is only represented by a single specimen in this dataset and thus has significantly less influence on the predicted shapes in the morphospace than in the previous two analyses (Figure 3.3C). This is also likely why a one-way ANOVA and Tukey's test did not find any significant differences between the means of the two orders on any of the principal components. The condor clade occupied the greatest amount of space on the PCA, primarily at the negative end, covering half of the x-axis and the entire

range of the y-axis (Figure 3.3C). Contrary to the previous two principal component analyses, the four specimens of Gypaetinae were well separated from the Cathartidae clades on this PCA, occupying only the positive ends of the x- and y-axes (Figure 3.3C). The Gypaetinae showed less overall skull diversity, taking up less than half the amount of PCA morphospace as the condor and vulture clades. The single Polyborinae specimen, the extinct *Polyborus prelutosus*, sits at the positive end of the x-axis with the Gypaetinae specimens, but opposite them at the negative end of the y-axis.

Subfamily had a statistically significant effect on PC1 and on PC3, but not PC2 (Table 3.3). The subfamily Gypaetinae was determined by a Tukey's test to be significantly different from both the condor clade and the vulture clade, and the condor clade was found to be different from the Polyborinae on PC1 (Table 3.4). The only significant difference found by the Tukey's test on PC3 was between vultures and condors. This means that were PC2 to be replaced by PC3 as the y-axis, condors and vultures would likely be in slightly more distinct groups from each other (Table 3.4).

3.3.4 Comparison of three families – cranium only

The first three principal components made up 73% of the shape variation. PC1 represented by the x-axis, accounted for 40% of the shape variation, and represents a shift from a more narrow skull profile with pronounced occipital and paraoccipital processes on the negative end of the axis to a more bulbous shape at the positive end of the axis (Figure 3.4A). PC2 represented accounted for 22% of the overall shape change, where the cranium changes to a taller and proportionately rounder shape from the positive to the negative end of the y-axis, with an overall thinning of the occipital and paraoccipital processes. There are also more complex shape changes associated with the site of premaxillary articulation where the frontal bones of the cranium meet with the nasal bones to create a hinge (Bock, 1964; Zusi, 1993), a trait that is even more prominent in cathartid vultures (Fisher, 1944).

The condor clade trended towards a narrower, proportionately longer cranium shape, whereas the vulture clade tended to have a taller, more rounded cranium (Figure 3.4A). Accipitridae and Polyborinae fell within the Cathartidae space but were closer in shape to that of the vulture clade than the condor clade (Figure 3.4A). Only condors appeared to have significantly different skull shapes from all other subfamilies, which is supported by the Tukey's test results (Table 3.4). Gypaetinae and Aegypiinae occupy almost the same region of morphospace. Polyborinae overlaps with the vulture clade, Aegypiinae, and Gypaetinae. Polyborinae also occupies the least amount of morphospace on the PCA and on average has the shortest, roundest cranial shape of all the families and subfamilies included (Figure 3.4A).

Whether or not a specimen was a fossil did interact with the subfamily factor in some cases (Table 3.3). On PC1, Polyborinae and the condor clade shape spaces were

affected by fossils, on PC2, Polyborinae, Gypaetinae, and the condor clade were affected by fossils, and on PC3, only the condor clade was affected by fossils (Table S3.2). The Tukey's test showed that on PC1, the condor clade is significantly different from all other subfamilies (Table 3.4). On PC2, Polyborinae differed significantly from Aegypiinae, and both the condor and vulture clades (Table 3.4). On PC3, Aegypiinae differed significantly from all other subfamilies, and Polyborinae differed from the condor clade (Table 3.4).

3.3.5 Comparison of three families – cranium only: modern

The first three principal components of this analysis made up 73% percent of the shape variation in this dataset. PC1 accounted for 39% of the shape change, which is only 1% less than in the analysis of the full data set. Shape change along the x-axis is consistent with that of the complete cranium dataset, only reversed so that narrower crania are now at the positive end of the axis instead of the negative end (Figures 3.4A versus 3.4B). PC2 accounted for 23% of the shape change and is also consistent with that of the analysis of the full cranium dataset.

The condor clade is well-separated from the other subfamilies, with only one individual specimen of *Sarcoramphus papa* causing overlap (Figure 3.4B). The remaining four subfamilies overlap in morphospace with Gypaetinae occupying the negative end of the x-axis and the condor clade the right end of the axis. Without the presence of fossil specimens, Polyborinae occupies a greater proportion of morphospace than Gypaetinae. Aegypiinae and the vulture clade occupy almost the same shape space on the PCA, both extending only slightly past the average of the combined dataset. Aegypiinae tended to be more rounded whereas the vulture clade tended to be more elongate, a difference primarily seen on the y-axis.

For family and subfamily, a one-way ANOVA found significant differences on PC1, PC2, and PC3 (Table 3.3). A Tukey's test established that the condor clade differed significantly from all other subfamilies and the vulture clade differed from Gypaetinae on PC1 (Table 3.4). On PC2 the Polyborinae differed significantly from the vulture clade, the condor clade, and the Aegypiinae. Aegypiinae also differed from the vultures on PC2. On PC3 the Aegypiinae differed from the Polyborinae and both the Vulture and condor clades (Table 3.4).

3.3.6 Comparison of three families – cranium only: fossil

The first three principal components of this analysis accounted for 77% of all the shape variation in this dataset. PC1, on the x-axis, accounted for 42% of the shape change, which is 2% more than in the full dataset analysis and 3% more than in the modern specimen only analysis. As for the full data set shapes are shifting proportionately to longer and thinner crania with more pronounced occipital and paraoccipital processes (Figure 3.4C). PC2 accounts for 22% of the shape change on the y-axis, and again

exhibits a similar change in shape to that recovered with the full analysis with rounder crania now at the positive end of the y-axis (Figure 3.4C).

The Cathartidae continues to occupy most of the PCA morphospace (Figure 3.4C). Condors have the greatest diversity of cranial shape in the fossil subset of specimens. The only Accipitridae specimens in this fossil subset are those of the Gypaetinae. Gypaetinae and Polyborinae by comparison take up a tiny fraction of the PCA morphospace and are nested within the vulture and condor clade spaces, respectively (Figure 3.4C). Some condors trended towards a longer, narrower crania while others tended to be rounder. Most condors had more pronounced occipital and paraoccipital processes than other subfamilies. For subfamilies, the condor clade differed significantly from all other subfamilies on both PC1 and PC3, but no other subfamilies were found to differ significantly from each other (Table 3.4).

3.3.7 Comparison of three families – premaxillary only

The first three principal components of this analysis accounted for 85% of all the shape variation in this dataset. PC1 accounted for 43% of the shape variation alone. Changes across the x-axis included shifting from a more triangular premaxillary shape, with a less curved tip and wider proximal end, to a thinner beak that is more evenly sized along the length and has a more prominently hooked tip (Figure 3.5A). PC2 accounts for 27.5% of the shape change in this analysis, and changes across the y-axis are centered on the shape of the proximal end of the premaxillary. From the positive to the negative end of the axis, the point of articulation with the jugal becomes longer and more pointed. An increase in prominence of the hook at the tip of the beak can also be observed on the y-axis, thus, beaks with the longest and most curved tips are found at the negative end of the PCA, while those with much less of a hooked beak are found at the positive end of the PCA (Figure 3.5A).

The most amount of morphospace is occupied by the Polyborinae (Figure 3.5A), primarily towards the positive end of the x-axis and negative end of the y-axis. Unlike the cranium and skull overall, the Gypaetinae exhibits a greater range of shape variation in the premaxillary than the Aegypiinae, on both the x- and y-axes. The condor and vulture clades have overlap with each other and overlap to a greater degree with the Aegypiinae than the Gypaetinae (Figure 3.5A). A Tukey's test found all subfamilies differed significantly except for the Gypaetinae relative to the Aegypiinae and the Condors relative to the vultures on PC1 (Table 3.4). On PC2, only the Polyborinae differed from the Aegypiinae and vulture clade. Fossils did not have a multiplicative effect on subfamily in PC1 or PC2 but did on PC3 and influenced the condor clade on PC1 and on the Polyborinae on PC3 (Table S3.2).

3.3.8 Comparison of three families – premaxillary only: modern

The first three principal components of this analysis accounted for 84% of the shape variation in this dataset. PC1, represented by the x-axis, accounted for 50% of the shape variation alone, a full 10% higher than in analysis using the full data set (Table 3.3). Shape change along the x-axis is very similar to that seen in the previous analysis where fossils were included, but with fossils removed there was less extreme beak narrowing at the most negative end of the x-axis (Figure 3.5B). PC2 accounts for 22% of the variation and shape changes on the y-axis are consistent with those observed in analysis of the full data set (Figure 3.5B).

The Polyborinae drove shape change on the y-axis by having primarily shorter, wider, and more triangular beaks than the other subfamilies (Figure 3.5B). The biggest difference between the analysis of the full data set that included fossil specimens and this analysis restricted to modern specimens is that the range of shape change decreased for all groups except Aegypiinae (Figure 3.5B). There were significant differences between the subfamilies on PC1 and PC2, but not PC3 (Table 3.3). All subfamilies had significantly different means compared to each other on PC1 with only two exceptions – Gypaetinae and Aegypiinae, and the condor and vulture clades were each found to not differ significantly from each other. On PC2, vultures significantly differed from condors, and the Polyborinae differed significantly from the vultures, Gypaetinae, and Aegypiinae (Table 3.4).

3.3.9 Comparison of three families – premaxillary only: fossils

The first three principal components of this analysis accounted for 84% of the shape variation in this dataset (Table 3.3). PC1 accounted for 50% of the shape variation alone. Shape change on the x-axis was similar but flipped from negative to positive ends compared to analysis of the full dataset or that of only the modern specimens (Figure 3.5C). Overall, shape of the premaxillary narrowed from the negative to the positive end of the x-axis. PC2 accounts for 25% of the shape change. Changes in were similar to the results obtained with the full dataset but reversed on the y-axis from positive to negative. The shift in shape is from a less to more triangular shape and a lengthening of the point of articulation with the jugal going from the positive to negative end of the y-axis (Figure 3.5C).

The three families were well separated on the x-axis, with Polyborinae at the most negative end and Cathartidae at the most positive end (Figure 3.5C). Only PC1 exhibited a significant influence from any kind of phylogenetic signal, from family and subfamily (Table 3.4). Polyborinae and Accipitridae exhibited a wide range of shape change on the y-axis, while the vulture and condor clades were more limited in their y-axis shape variation (Figure 3.5C). A Tukey's test found that all subfamilies differed significantly

except for the vulture and condor clades to each other (Table 3.4). These two clades had significant overlap in the PCA morphospace (Figure 3.5C).

3.3.10 Accipitridae and Cathartidae – whole skull

The first three principal components of this analysis accounted for 70% of the shape variation in this dataset. PC1 accounted for 30% of the shape variation alone (Table 3.3). The shape change on PC1, from the negative end of the x-axis to the positive end, shifted from a beak that is slightly angled down and much thinner relative to the cranium, to a skull that is overall straighter with a beak that is thicker along the entire length (Figure 3.6A). The beak also tapers more quickly from the craniofacial hinge on the negative end of the x-axis. PC2 accounted for 25% of the shape variation. Overall, the skull and beak height are greater from the negative to the positive end of the y-axis, and the cranium has a rounder shape at the positive end of the y-axis (Figure 3.6A).

The condor clade space encompassed the entirety of the morphospace occupied by the vulture clade. However, skulls of members of the vulture clade are more constricted in shape than those of Condors, which tend to be moderately narrow along the length and slightly angled at the craniofacial hinge rather than straight (Figure 3.6A). The Gypaetinae also resides entirely within the Aegypiinae morphospace (Figure 3.6A). Members of the Gypaetinae have primarily thicker skulls with a very slight downward angle at the craniofacial hinge. Subfamilies were statistically different from each other on PC1 and PC2, but not on PC3, and fossils did not have a significant effect on the shape spaces of subfamilies on any principal components (Table S3.2). A Turkey's test found that Aegypiinae and Gypaetinae each differed significantly from the condor and vulture clades, but not from each other on PC1 (Table 3.4). Similarly, condors and vultures were not significantly different from each other on PC1, but they did differ on PC2. Condors also significantly differed from the Aegypiinae on PC2, but no other subfamily shape means differed significantly.

3.3.11 Accipitridae and Cathartidae – whole skull: modern

The first three principal components of this analysis accounted for 68% of all the shape variation in this dataset (Figure 3.6B). PC1 accounted for 37% of the shape variation alone, 7% higher than in the analysis of the full dataset. Shape change along the x-axis did not differ much from what was seen in the analysis of the full dataset, but the skull shape did not become as narrow towards the negative end of the x-axis as they did in the combined analysis. PC2 accounted for 20% of the shape variation, which is 5% less than the previous dataset. The y-axis shape range is also the same in this analysis as in the previous one (Figure 3.6B).

The Cathartidae (vulture and condor clades) morphospace was more confined to the negative end of the x-axis but covers most of the y-axis. Cathartidae skulls are overall

more angled and have proportionately narrower beaks (Figure 3.6B). Family was only significant for shape differentiation on PC1, and the same was true for subfamilies (Table 3.4). Aegypiinae occupies the same space as the general Accipitridae, as it did in the previous analysis, and Gypaetinae is still entirely within the Accipitridae/Aegypiinae morphospace (Figure 3.6B). Condor clade space is slightly different from the overall Cathartidae space in this analysis, as the vulture clade extends slightly outside of the condor clade space and sits much closer to the negative end of the x-axis (Figure 3.6B). Aegypiinae and Gypaetinae were each significantly different from the Condor and vulture clades, but not from each other. The vulture and condor clades also did not significantly differ from each other (Table 3.4).

3.3.12 Accipitridae and Cathartidae – whole skull: fossils

The first three principal components of this analysis make up 75% of all the shape variation in this dataset. PC1 accounted for 37% of the shape variation alone, 7% higher than in the previous analysis of vulture skulls (Table 3.3). Shape changes along the x-axis, dictated by PC1, were noticeably different from the previous two PCA morphospaces (Figure 3.6C). The change here was much more subtle reflecting a shift from a taller to shorter cranium proportionate to the beak. The beak also becomes slightly longer with respect to the cranium, but there is no longer an increase in angle at the craniofacial hinge. PC2 accounts for 23% of the shape variation, and beak angle relative to the cranium now shifts from more to less angled on the y-axis (Table 3.3; Figure 3.6). Specimens at the negative most corner of the PCA have the longest, thinnest, and most angled skulls. The occipital and paraoccipital processes also become more pronounced from positive to negative on the y-axis.

Cathartidae, mostly represented by condors, took up most of the shape space in this PCA, which was reversed from the other two datasets where Accipitridae was highly variable in skull shape (Figure 3.6C). Skull shape in the Accipitridae still had a lot of variability on the x-axis but almost none on the y-axis. Family had a statistically significant effect on the shape space on PC1 but not on PC2 or PC3 (Table 3.3). As in previous analyses discussed so far, all fossil members of the Accipitridae in this dataset were of the subfamily Gypaetinae, meaning they shared the same shape space. The condor clade took up most of the shape space in general, with one of the two vulture specimens within that space and the other sitting outside of it. Subfamily did not have a significant statistical effect on the shape space on any of the principal components (Table 3.4).

3.3.13 Accipitridae and Cathartidae – cranium only

The first three principal components of this analysis made up 72% of all the shape variation in this dataset. PC1, represented by the x-axis, accounted for 38% of the shape variation alone (Table 3.3). Cranial shape change was relatively subtle on PC1 across

the x-axis. The primary change seems to be a shift from a narrower distal end to a generally more uniform size from end to end in the lateral view of the cranium (Figure 3.7A). PC2 accounts for 22% of the shape variation, and the shape change from the negative to the positive end on the y-axis is more extreme than on the x-axis. Crania at the negative end of the y-axis are rounder overall and become more elongated with more complex structures at the site of articulation with the premaxillary and more pronounced occipital and paraoccipital processes towards the positive (Figure 3.7A). Unlike in the complete skull analyses, the Cathartidae were more variable in shape than the Accipitridae. Cathartidae spanned the entire x-axis and most of the y-axis, taking up nearly all the PCA morphospace (Figure 3.7A). The condor and vulture clades separated the Cathartidae shape space along the y-axis, with some overlap in the center of the PCA. Members of the condor clade primarily occupied the positive end of the y-axis and vultures the negative end. Both clades spanned the breadth of the x-axis in cranial variation. Aegypiinae mostly occupied the positive half of the x-axis and the negative half of the y-axis, with Gypaetinae falling primarily in the middle of that space, limited to an overall rounder cranial shape (Figure 3.7A).

Subfamily played a more significant role than family in the ANOVA tests and returned significant p-values on all three principal components (Table 3.3). Fossils did play a statically significant role in influencing the shape space of condors on all three principal components, and for Gypaetinae on PC2 only (Table S3.2). On PC1 a Tukey's test found that the vulture clade differed significantly in average shape from the condor clade and the Gypaetinae subfamily, but no other clades or subfamilies differed significantly (Table 3.4). In contrast, condors differed from all other clades and subfamilies on PC2 and Gypaetinae differed from all others on PC3. No other subfamilies or clades differed on PC2 or PC3 (Table 3.4).

3.3.14 Accipitridae and Cathartidae – cranium only: modern

The first three principal components of this analysis made up 74% of all the shape variation in this dataset. PC1 accounted for 44% of the shape variation alone, 6% higher than in the combined cranial dataset analysis (Table 3.3). Removing the fossils from the cranium dataset changed the shape differences occurring on the x- and y-axes. The shape change occurring on the x-axis is now a combination of what was seen on the x- and y-axes in the previous analysis, including the narrowing of the distal end of the cranium and the presence of more pronounced occipital and paraoccipital processes (Figure 3.7A vs. 3.7B). PC2 accounts for 21% of the overall shape variation, 1% lower than the previous analysis (Table 3.3). The change on the y-axis was similar to the previous analysis, with the cranium becoming overall more elongated from the negative to the positive end of the y-axis (Figure 3.7B). The amount of narrowing is less here than in the previous datasets that included fossils. The main change is that there is no

significant shift in the occipital or paraoccipital processes now, and changes to the point of articulation with the premaxillary are minimal.

All the members of the condor clade fell to the positive end of the x-axis in this analysis, with the exception of one specimen of *Sarcoramphus papa*, which instead falls within the vulture clade (Figure 3.7B). Likewise, the vulture clade clusters on the negative end of the PCA, except for one specimen of *Cathartes burrovianus*, which sits closer to the condor clade. Aegypiinae had the highest amount of variation between the two Accipitridae subfamilies, with Gypaetinae occupying the center of this space. Subfamily was found to play a significant role in shape distribution of the PCA morphospace on both PC1 and PC2 (Table 3.3). A Tukey's test found that condors significantly differed from all other subfamilies and clades, and vultures differed from the Aegypiinae, but not from the Gypaetinae on PC1 (Table 3.4). On PC2, the only statistically significant differences were between the Aegypiinae and both the condor and vulture clades (Table 3.4).

3.3.15 Accipitridae and Cathartidae – cranium only: fossils

The first three principal components of this analysis made up 77% of all the shape variation in this dataset. PC1, accounted for 42% of the shape variation alone, 4% higher than the combined dataset analysis and 2% lower than the modern dataset cranial analysis (Table 3.3; Figure 3.7C). The trend in the shape change along the x-axis was different from that of the previous two analyses. The cranium shape is longer with more distinct occipital and paraoccipital processes at the positive end on the x-axis and becomes rounder with fewer protruding features at the negative end. This is most like the y-axis in the previous two cranial analyses (Figure 3.7C vs. 3.7A & 3.7B). The y-axis, at 23% for PC2, displayed a more subtle change. There was some lengthening of the occipital and paraoccipital processes occurring from negative to positive values along the axis, and cranium height seemed to also decrease slightly in this direction (Figure 3.7C).

Despite the shifting of shape change on the axes, the overall shape distribution of the two families remains largely the same. Cathartidae continues to occupy the vast majority of PCA morphospace, with at least one specimen at the extreme ends of the x- and y-axes (Figure 3.7C). The main change is that less space is occupied at the negative end of the y-axis than in either of the two previous cranium analyses. Only a handful of specimens sit in this negative PC2 region, near the center of the x-axis. Accipitridae remains nested inside the shape space of the Cathartidae, primarily located at the negative end of the x-axis and towards the middle of the y-axis (Figure 3.7C). Family was not found to have a significant effect on any of the three principal components tested (Table 3.3).

The condor clade occupied most of the shape space of the PCA, with the vulture clade primarily in the same region as the Gypaetinae (Figure 3.7C). The vulture clade, like the Gypaetinae, took up less than a third of the PCA space occupied by the condors.

Subfamily had a statistically significant effect on the shape space on PC1 and PC3 (Table 3.3). A Tukey's test found that on both PC1 and PC3, condor shape average differed significantly from both the vultures and Gypaetinae (Table 3.4). No other differences were detected by the Tukey's test.

3.3.16 Accipitridae and Cathartidae – premaxillary only

The first three principal components of this analysis make up 80% of all the shape variation in this dataset. PC1 accounted for 38% of the shape variation alone (Table 3.3). Shape change for the premaxillary along the x-axis was primarily a shift from a stouter beak to a longer one (Figure 3.8A). The point of articulation with the jugal also shortened and became pronounced from the negative to positive end of the x-axis. PC2 accounted for 26% of the shape variation (Table 3.3). On the y-axis, the premaxillary becomes narrower from the negative to the positive end of the axis. The point of articulation with the cranium at the craniofacial hinge also becomes more pronounced from negative to positive on the y-axis, forming a deeper groove for articulation. Finally, the beak tip becomes slightly narrower along the y-axis (Figure 3.8A).

The subfamilies were found to be significantly different from each other on all three principal components (Table 3.4). Of the Accipitridae shape space, the Gypaetinae accounted for most of the range of variation in the family (Figure 3.8A). Gypaetinae spanned from the most positive to the most negative end of the x-axis. Aegyptiinae spanned far less of the x-axis than the Gypaetinae, but slightly more of the y-axis. The condor and vulture clade spaces each occupied a very similar range of shapes, located in the upper right quadrant of the PCA where the x- and y-axes were positive (Figure 3.8A). Both clades had on average a longer and thinner premaxillary than any of the Accipitridae. The main difference between the two clades of the Cathartidae was that the condors trended towards more robust beaks while vultures tended to have thinner and more slender beaks. Fossils interacted significantly with the condor clade on PC1 only (Table 3.3). On PC1, only one significant difference was found between subfamilies or clades after a Tukey's test - the condor clade against the subfamily Aegyptiinae (Table 3.4). On PC2, Condors and vultures differed significantly from every group except for each other. On PC3, Condors differed significantly from Gypaetinae and Aegyptiinae, but no other groups differed (Table 3.4).

3.3.17 Accipitridae and Cathartidae – premaxillary only: modern

The first three principal components of this analysis made up 80% of all the shape variation in this dataset. PC1 accounted for 39% of the shape variation (Table 3.3). The shape change occurring on the x-axis was the same as that seen in the previous analysis that included fossils (Figure 3.8B). PC2 accounted for 29% of the shape variation in this analysis (Table 3.3). The shape change remained consistent with that of the full dataset,

but the direction of the change flipped from positive to negative on the y-axis. Now the taller, more robust premaxillary shapes were found at the positive end of the y-axis and narrower shapes were found at the negative end (Figure 3.8B).

The condor and vulture clades occupied approximately the same shape space as in the previous premaxillary analysis. Subfamily distribution changed quite a lot when fossils were removed from the dataset (Figure 3.8B). The vulture clade and Aegypiinae subfamily stayed relatively similar to the previous full dataset analysis, but the condor clade and Gypaetinae spaces reduced significantly (Figure 3.8B vs 3.8A). Condors were now restricted to the positive end of the x-axis, exhibiting a much-reduced morphological range of long beaks that fell in the mid-range of robustness in the middle of the y-axis. Whereas Gypaetinae previously occupied the vast majority of the PCA morphospace, this subfamily now covered less than that of the vulture clade. Gypaetinae shape was restricted to the middle range of the y-axis and expanded across about two-thirds of the x-axis starting from the negative end. Three fossils, all in the extinct genus *Neophrontops*, extended extent of morphospace occupied by the Gypaetinae (Figures 3.8A vs. 3.8B). Subfamily was significant on all three of the principal components (Table 3.3). A Turkey's test found that on PC1, the condor clade differed significantly from all other clades and subfamilies, and on PC2 the vulture clade differed from all others. On PC 3, the Condors differed significantly from Gypaetinae and Aegypiinae, and vultures differed from Aegypiinae (Table 3.4).

3.3.18 Accipitridae and Cathartidae – premaxillary only: fossil

The first three principal components of this analysis encompassed 89% of all the shape variation in this dataset. PC1 accounted for 48% of the shape variation, 9% higher than in the modern only dataset and 10% higher than the complete dataset (Table 3.3). Shape change occurring along the x-axis changed from the previous two analyses (Figure 3.8C). The x-axis now only reflects a very small amount of overall narrowing while PC2, at 24% of the variation on the y-axis, continued to reflect a change from narrower overall to a more robust and thick premaxillary (Figure 3.8C). The jugal articulation also became longer from negative to positive of the y-axis (Figure 3.8C).

Despite the difference in the x-and y-axis shape change, the families and subfamilies had a very similar distribution on the PCA as seen in the analysis with only modern specimens (see Figures 3.8B and 3.8C). The Gypaetinae is the only subfamily to represent the Accipitridae in this fossil subset, and the eight specimens were widely distributed from each other in morphospace (Figure 3.8C). Condors had about the same amount of variability on the x-axis as Gypaetinae but were much more restricted to the negative end of the y-axis. The vulture clade was highly restricted in this analysis, overlapping with both the condor clade and the Gypaetinae (Figure 3.8C). Subfamily was found to have a significant effect on the shape distribution on PC1 and PC2 (Table 3.3).

A Tukey's test found that Gypaetinae was significantly different from the condor clade on both PC1 and PC2, and from the vulture clade as well on PC1 (Table 3.4).

3.3.19 Accipitridae and Cathartidae guilds – whole skull

When looking at the guild shape space of just accipitrid and cathartid vultures, there is significant overlap (Tables 3.3, 3.4). Vulture species identified as gulpers occupy the greatest amount of shape space on both the x- and y-axes (Figure 3.9A). Nearly all the specimens with proportionately thinner and more angled beaks in the gulper shape space are fossil condors. Rippers are in the upper right corner of the PCA, exhibiting the most robust skull shape. Specimens placed in the ripper guild by Hertel (1994) that are members of the condor clade – *Sarcoramphus papa* – tended to have more angled skulls than the Accipitridae ripper guild members (Table 3.2). Scrappers overlapped significantly with gulpers but tended to be restricted to overall thinner and more angled shapes (Figure 3.9A). Despite having overlapping spaces visually on the PCA, guild classification had a significant effect on the shape space of the skull on all three principal components (Table 3.3). Fossils only had a significant effect on the guild shape space on PC1 (Table S3.2). When a Tukey's test was performed, all the guilds differed from each other on PC1, and on both PC2 and PC3, gulpers differed from scrappers and rippers (Table 3.4).

Modern vultures still demonstrated a lot of overlap in guild classification (Figure 3.9B). The gulpers still occupy the largest area of the PCA, indicating the largest amount of variation for this feeding guild (Figure 3.9B). The ripper guild also seemed to occupy the same general shape space as it did in the dataset that had fossils included but extended a little more towards the negative end of the y-axis and overlapped with the gulper shape space to a greater degree. Scrappers were much more confined to the negative end of the x-axis in this dataset than in the previous one and overlapped with the gulpers less (Figure 3.9B). Guild classification influenced the shape on PC1 and on PC3. All three guilds had significantly different means from each other after a Tukey's test on PC1, and on PC3, gulpers were significantly different from rippers and scrappers, but rippers and scrappers did not significantly differ from each other (Table 3.4).

In just the fossil vultures, the gulpers most closely resembled the shape space occupied by the condors in earlier analyses (Figure 3.9C). Scrappers likewise extended the same amount of variation on the x-axis as the Gypaetinae morphospace but covered more of the y-axis than the Gypaetinae. In the fossil dataset of the present study, only *Neogyps* was identified as a member of the ripper guild by Hertel (1994), and this specimen fell just outside of the scrapper guild space at the positive end of the x- and y-axes (Figure 3.9C). Guild was not found to have a statically significant effect on any of the principal components, and the Tukey's test found no significant differences between the means of the three guilds in this fossil only subset (Table 3.4).

3.3.20 Accipitridae and Cathartidae guilds – cranium only

Guild classification had a significant influence on shape space distribution for the vulture cranium on PC2 and PC3 (Table 3.3). The gulper and scrapper shape spaces were largely reflective of the condor and vulture clade shape spaces, but with a little more overlap in the middle of the PCA (Figure 3.10A). The ripper shape space is primarily contained within the space occupied by the Accipitridae, within the scrapper space and overlaps with the . The rippers occupy a narrow portion of morphospace than the Accipitridae on the y-axis. Fossils had a significant effect on scrapper shape space on PC1 and PC2 and on gulper shape space on PC1. A Tukey's test found that the gulper guild was significantly different in mean shape to the scrappers and rippers on PC1 and that rippers were significantly different from guplers and scrappers on PC3 (Table 3.4).

Guild classification had a statistically significant effect on all three principal components when tested with just the modern specimens (Table 3.3). Species classified as guplers (Table 3.2) occupied the middle to positive range of the x-axis and spanned much of the y-axis as well, while scrappers primarily occupied the negative end of the x-axis. A single specimen of *Cathartes burrovianus*, the same specimen that dragged the vulture clade shape space into the condor clade range, now also brings the scrapper space into the guplers (see Figures 3.7B and 3.10B). Species classified as rippers occupied the negative half of the y-axis and the same range of the x-axis as the guplers (Figure 3.10B). A Tukey's test found that on PC1, the scrapper guild was significantly different from the gulper and ripper guilds (Table 3.4). On PC 2, the scrappers continued to be significantly different from the rippers, but not the guplers, while rippers and guplers now differed significantly on both PC2 and PC3 (Table 3.4).

When guild classification was taken into consideration for the fossil vulture crania, the gulper space was found to be the same as that of the condor clade shape space (Figure 3.10C), with condors (genera *Gymnogyps*, *Vultur*, and *Breagyps*) generally being classified as guplers (Table 3.2). The scrapper morphospace amounts to a combination of the Gypaetinae and vulture clade space, still primarily nested within the gulper shape space. The one specimen of *Neogyps errans* classified as a ripper sits on the inner boundary between the scrappers and guplers, and almost precisely at the origin of the PCA (Figure 3.10C). Like subfamily, guild was statistically significant on PC1 and PC3 (Table 3.3). A Tukey's test found guplers and scrappers to be significantly different from each other on PC1 and PC3 (Table 3.4).

3.3.21 Accipitridae and Cathartidae guilds – premaxillary only

When looking at the vulture premaxillary shapes, guild classification morphospace differed significantly from the taxonomic distribution. The scrapper and gulper spaces were each approximately twice the size of the ripper guild in the morphospace (Figure 3.11A). The shape space region of the guplers was very similar to that of the scrappers,

and the two overlapped significantly in the middle of the PCA. The gulper space extended more into the top left corner of the PCA, exhibiting a robust but longer beak with a pronounced and long jugal articulation. The scrapper space extended more into the opposite corner and exhibited almost no lengthening of the jugal articulation (Figure 3.11A). The rippers overlapped with both the other guild spaces, but to a less degree with the morphospace occupied by the scrappers. Rippers were restricted to the negative half of the y-axis but extended across most of the x-axis. Ripper beaks are proportionately thicker with a mostly extended jugal articulation point (Figure 3.11A). Guild was statistically significant on PC2 only and fossils had a multiplicative effect on all three of the guilds on PC2 (Table S3.2). A Turkey's test found a significant difference between scrappers and rippers on PC1 despite the lack of a significant p-value in the ANOVA test (Table 3.4). Rippers were significantly different from both gulpers and scrappers on PC2, but scrappers and gulpers did not differ significantly from each other (Table 3.4).

Looking at the modern vulture premaxillaries caused guild shape space to change significantly. Guilds were distinct along the y-axis with very little overlap, but all three spanned most of x-axis (Figure 3.11B). The rippers are at the positive most end of the y-axis and have the thickest, most robust beak shape. On the opposite end of the y-axis are the scrappers with the narrowest beaks, and gulpers sit in the middle. This is reflected in the statistics, as guild was only found to be statically significant after an ANOVA on PC2 (Table 3.3), and a Tukey's test determined that all three guilds had significantly different means (Table 3.4). But when guild classification is considered on the vulture premaxillary shape for fossils only, the distribution is less clear (Figure 3.11C). More like what was observed in the combined dataset, the gulpers overlap significantly with the scrappers, and sit lower on the y-axis than in the previous analysis with only modern specimens. The one specimen of *Neogyps errans*, the only example of a ripper in this fossil subset of data, still sits at the top of the y-axis where the premaxillaries are thickest. Guild classification was only significant on PC2, and a Tukey's test found that only Rippers were significantly different from both the other guilds in this instance (Table 3.4).

3.3.22 Accipitridae and Cathartidae guilds with Polyborinae present

When looking at guild classification that included the members of the Polyborinae, significant differences were found on PC1 and PC2, but not on PC3 (Figure 3.12A, Table 3.3). Of the three guilds, gulpers had the largest amount of shape variation. All the fossils and a handful of recent specimens of the scrapper and ripper guild classes overlapped into the gulper shape space. None of the specimens of unknown guild classification (Polyborinae) fell within the shape spaces of any of the guilds. However, two specimens strayed from the general region of other unknown guild cluster – *Polyborus megalopterus* and the extinct species *Polyborus prelutosus* (Figure 3.12A). Both specimens were notably further from other Polyborinae specimens, and *P. prelutosus* came much closer

to the scrapper shape space than any others. A Tukey's test revealed that when guild was compared against PC1, all three guilds – scrappers, gulpers, and rippers – were statistically different from each other (Table 3.4).

When looking at cranial shape distribution across all species, the gulpers and scrappers exhibited some overlap, while the ripper shape space resided entirely with that of the scrappers and partially extended into the gulpers (Figure 3.12B). Being that the specimens classified as an unknown guild are the Polyborinae, all but two fell within the space where scrappers, rippers, and gulpers all overlapped, like that seen in the subfamily distribution (compare to Figure 3.4A). Significant differences were present on all three principal components (Table 3.3). On PC1, gulpers were found to have a mean that was significantly different from both the rippers and scrappers (Table 3.4). Rippers and scrappers were not found to be significantly different. PC2 had the same result, but on PC3 the rippers were found to be significantly different in mean from all other groups.

The division of the PCA by guilds is clearest when looking at the combined premaxillary dataset (Figure 3.12C). As in looking at the subfamilies, the Polyborinae (unknown in Figure 3.12C) in this case occupy an equal amount of shape space on the PCA as the combined guilds. Scrappers and gulpers showed significant overlap on the PCA, while rippers occupied a slightly more distinct range of shapes that trended more towards being thick and robust. This was reflected in the statistical analyses, where a Tukey's test found that everything differed significantly except for the scrapper and gulper guilds from each other on PC1 (Table 3.4). On PC3 rippers were again statistically distinct from the gulpers and the scrappers (Table 3.4).

3.4 Discussion

Inspection of the combined accipitrid and falcon scavenger dataset indicates that the differences in skull shape are largely influenced by their phylogeny: falcons on average tend to have shorter, rounder skulls than accipiters. However, when the two main elements of the skull – the cranium and the premaxillary – are separated, it becomes clear that the differences between falcon and accipitrid scavengers is almost exclusively in the premaxillary.

In analyses that focused on the cranial shape, falcon shapes were consistently indistinguishable from those of all accipiter species apart from the condor clade. While vultures in general tend to have a longer skull compared to other accipiters, condors have evolved not only an elongated premaxillary but a significantly longer and narrower cranium. In the analyses of the cranium that included fossils, the condors had the widest range of variability in shape across the PCA morphospace. In the modern dataset, condors were entirely separate from the other subfamilies/clades in the morphospace except for one specimen of *Sarcoramphus papa*, which fell closer to the vultures and may be an outlier based on the shapes of three other *S. papa* individuals included in the

dataset. All other vulture subfamilies and clades tended to be more like each other, sharing a shorter, rounder cranium shape.

Fossils drive the positive end of the x-axis further to the extremes in the scavenger skull morphospace, and overall exhibit the most beak narrowness compared to members of the modern scavenger assemblage. Additionally, nearly all the upper region of the condor clade space was occupied by fossil specimens in the cranial analysis. The presence of a difference between fossils and non-fossils in the PCA, and the tendency for the fossils to be closer to the extreme end of the x-axis of scavenger skulls may mean that there is a trend towards less specialized diets in modern populations of scavenging birds. As the environment shifts and large carcasses became harder to find due to the decline in megafauna, both the taxonomic diversity and morphological specializations of avian scavengers may have dwindled.

While there was clear separation of groups based on phylogenetic components, in some analyses, guilds were a better predictor of shape differentiation among the scavengers based on the percent variance calculated from the PCA and ANOVA analyses (Table 3.3) and the results of the Tukey's tests (Table 3.4). The part of the skull that aligns most closely with guild structure is the premaxillary, and the guild classification scheme is supported by the ANOVA results when overall skull shape or premaxillary shape is considered as a proxy for it. Cranial shape is a much less reliable metric for determining what guild a species may fall into. The guilds with the least amount of separation on average were the gulpers and the scrappers. Both groups tended to have a narrower beak compared to that of the rippers, and often were not found to be statistically different from each other in mean shape. Hertel (1994) describes both gulpers and scrappers as being more likely to eat for what would be considered 'easier' parts of a carcass, in other words the scraps of meat and viscera around the body that require little to no tearing or the softer parts of the body that would also require significantly less effort to remove. In essence this would mean that the members of both the scrapper and gulper guilds would rely on the presence of the rippers to facilitate their ability to feed at the carcass, making them harder to distinguish from each other in a shared feeding situation. Mechanically the scrappers and the gulpers, which both have more narrow and slender beaks, are likely to have a similar capacity for tearing.

The Polyborinae have adaptations for a scavenging lifestyle, such as a lack of feathers on and around the face, and more elongated skulls than other falcons. Their range of shape variation, particularly in the premaxillary, is on par with the range of variation seen in the Cathartidae, Gypaetinae, and Aegypiinae. While they have not reached the same degree of skull elongation as that seen in the cathartid and accipitrid vultures, they trend away from other falcons in the same direction as vultures do from other accipitrids in PCA morphospace. The beaks of fossil Polyborinae species also appear to be more like the shape of the non-scavenging falcons than to those of their

direct decedents in the Polyborinae. These observations suggest that their evolutionary path is mirroring what has already occurred in the Accipitriformes, and the Polyborinae subfamily of the Falconiformes has continued to evolve skull shapes and beaks more suited to a scavenging lifestyle since the Pleistocene.

The result of this study partially supports the guilds proposed by Hertel (1994) in the overall shape of the skull and the shape of the premaxillary, but not in the shape of the cranium. Support for the guilds proposed by Hertel are not as clear when fossils species are included in the analyses (Table 3.4). This shows that when overall skull shape or just premaxillary shape are considered, they are good proxies for determining the feeding guild of living and extinct species of vultures when comparing within the Cathartidae and Accipitridae. Based on these results, two species of accipitrid vulture can confidently be assigned to guilds: the modern *Gyps tenuirostris* can be assigned to the gulper guild among other species of *Gyps*, and the fossil vulture *Neophrontops ricardoensis* can be assigned to the scrapper guild. Without observational data to assess the interactions of different species of caracara falcon on carcasses, it is difficult to assess how these species may fit into the existing guild structures proposed by Hertel (1994).

Two recent studies, one that looked at the 3D shape of the raptor skull (accipitrids and cathartids, plus one species of falcon) using geometric morphometrics (Steinfeld et al., 2023), and one that looked at skull and body length using traditional measurements (Linde-Medina et al., 2021), agree with the results of this study, finding that the guild structures proposed by Hertel (1994) were generally consistent with the results of the principal component analyses. Even when other, non-scavenger species were included in the dataset, guilds still grouped together in a statistically significant manner (Steinfeld et al., 2023). Steinfeld et al. (2023) did reclassify two species that were included in both analyses – *Gypohierax angolensis* and *Gypaetus barbatus*. These two species were classified by Hertel (1994) as gulpers, and their study found that both species were predicted to be scrappers. These two species are difficult to classify, as they have more specialized diets than other vultures. *Gypohierax angolensis*, the palm-nut vulture, consumes the fruits of palms for up to 60% of their diet (Van Zyl, 2006). *Gypaetus barbatus*, the bearded vulture, eats bones and bone marrow for up to 90% of their diet (Houston & Copsey, 1994). In this study, *Gypohierax angolensis* and *Gypaetus barbatus* skull shape overlapped spatially with the gulpers and the rippers, but not with the scrappers (Figure 3.9B). But when looking at the premaxillary shape only, both species overlapped with gulpers and scrappers, but not rippers (Figure 3.11B). Therefore, the present study best supports the gulper classification for both species but recognizes that other anatomical features may need to be considered when assigning a species to a guild.

3.5 Conclusions and Future Directions

Due to use of the same food source, vultures have evolved distinct skull morphologies that seem to correspond with their primary mode of feeding (Hertel, 1994, 1995; Houston, 2010; Kruuk, 1967; Van Valkenburgh, 1995, 2007). The diversity of species at a carcass has been recorded and their corresponding feeding methods described (Houston, 2010; Kruuk, 1967). The Cathartidae, Gypaetinae, Aegypiinae, and Polyborinae independently evolved this scavenging morphology, as well as the distinct skull features associated with their designated feeding guild. These scavenger features, such as an elongated premaxillary, reduced beak curvature, and increased skull height and narrowness are present in all four groups to varying degrees.

The Polyborinae species cannot easily be subdivided into guilds by skull shape alone, but the presence of a guild structure within the subfamily is possible. The Polyborinae are not considered to be obligate scavengers, but rather are opportunistic omnivores with scavenging tendencies. A clear guild structure for the Polyborinae would require further observation of their feeding behaviors around carcasses and their interactions with other scavenging birds, including the cathartid vultures with which they are known to overlap. That the Polyborinae often occupy their own region of the PCA morphospace, sometimes taking up the same amount of space as the Accipitridae and Cathartidae, which suggests that these scavenging falcons may possess their own guild structure that is like that of the accipitrid vultures, or that they may not fit into any of the guilds proposed by previous researchers because they are still evolving towards an optimal morphology for scavenging.

3.6 Tables and Figures

Table 3.1. Known fossil vultures. Table of the known fossil species for the family Cathartidae and subfamilies Aegypiinae, Gypaetinae, and Polyborinae.

Family: Cathartidae			
Name	Reference	Locality	Age
† <i>Aizengyps toomeyea</i>	Emslie (1998)	North America	Pleistocene
† <i>Breagyps clarki</i>	Miller (1910)	North America	Pleistocene
† <i>Cathartes fossilis</i>	Moreno and Mercerat (1891)	Argentina	Pleistocene
† <i>Coragyps occidentalis</i>	Miller (1909)	North America	Pleistocene
† <i>Coragyps seductus</i>	Suárez (2020)	Cuba	late Pleistocene
† <i>Coragyps shastensis</i>	Miller (1911)	North America	Pleistocene
† <i>Dryornis hatcheri</i>	Degrange (2021)	Argentina	early Miocene
† <i>Dryornis pampaenus</i>	Moreno and Mercerat (1891)	Argentina	early Pliocene
† <i>Gigantoheirax tchei</i>	Suárez (2020)	Cuba	late Pleistocene
† <i>Gigantoheirax suarezi</i>	Arredondo and Arredondo (2002)	Cuba	late Quaternary
† <i>Gymnogyps amplus</i>	Miller (1911)	North America	Pleistocene
† <i>Gymnogyps howardae</i>	Campbell (1979)	Peru	Pleistocene
† <i>Gymnogyps kofordi</i>	Emslie (1988a)	North America	middle Pleistocene
† <i>Gymnogyps varonai</i>	Arredondo (1971)	Cuba	late Pleistocene
† <i>Kuntur cardenasi</i>	Stucchi et al. (2015)	Peru	late Miocene
† <i>Palaeogyps prodromus</i>	Wetmore (1927)	North America	late Eocene
† <i>Pampagyps imperator</i>	Agnolín et al. (2017)	Argentina	Pleistocene/Holocene
† <i>Perugyps diazi</i>	Stucchi and Emslie (2005)	Peru	middle Miocene - early Pleistocene
† <i>Phasmagyps patritus</i>	Wetmore (1927)	North America	late Eocene
† <i>Pliogyps charon</i>	Becker (1986)	North America	middle/late Miocene
† <i>Pliogyps fischeri</i>	Tordoff (1959)	North America	middle Pliocene - late Pleistocene
† <i>Sarcoramphus fischeri</i>	Campbell (1979)	Peru	Pleistocene
† <i>Sarcoramphus kernensis</i>	Miller (1931)	North America	middle Pliocene
† <i>Sarcoramphus fossilis</i>	Moreno and Mercerat (1891)	Argentina	Pleistocene/Holocene
† <i>Sarcoramphus patruus</i>	Lönnberg (1903)	Bolivia	Pleistocene
† <i>Tapinopus ellioti</i>	Milne-Edwards (1891)	France	upper Eocene - middle Oligocene
† <i>Vultur messii</i>	Degrange et al. (2023)	Argentina	Late Miocene
Family: Accipitridae			
Subfamily: Gypaetinae			
Name	Reference	Locality	Age
† <i>Anchigyps voorhiesi</i>	Zhang and Feduccia (2012)	North America	middle/late Miocene
† <i>Arikarornis macdonaldi</i>	Howard (1966)	North America	early Miocene
† <i>Cryptogyps lacertosus</i>	de Vis (1905)	Australia	Pliocene/Pleistocene
† <i>Gypaetus georgii</i>	Sánchez-Marco (2022)	Spain	late Miocene
† <i>Neophron lolis</i>	Sánchez-Marco (2022)	Spain	late Miocene
† <i>Neophrontops americanus</i>	Miller (1916)	North America	early Miocene - late Pleistocene
† <i>Neophrontops dakotensis</i>	Compton (1935)	North America	lower/middle Pliocene
† <i>Neophrontops ricardoensis</i>	Rich (1980)	North America	middle Miocene

† <i>Neophrontops slaughteri</i>	Feduccia (1974)	North America	upper Pliocene
† <i>Neophrontops vallecitoensis</i>	Howard (1963)	North America	middle Pleistocene
† <i>Neophrontops vetustus</i>	Wetmore (1943)	North America	middle Miocene
Subfamily: Aegyptiinae			
† <i>Aegyptius prepyrenaicus</i>	Hernández (2001)	Spain	late Pleistocene
† <i>Aegyptius jinniushanensis</i>	Zhang et al. (2012)	China	middle Pleistocene
† <i>Gansugyps linxiaensis</i>	Zhang et al. (2010)	China	late Miocene
† <i>Gyps melitensis</i>	Hou (1984)	China	early Miocene
† <i>Mioaegyptius gui</i>	Brodkorb (1964)	Monaco, Austria, France	middle/late Pleistocene
† <i>Neogyps errans</i>	Miller (1916)	North America	middle Miocene
† <i>Palaeohorus howardae</i>	Wetmore (1936)	North America	middle Miocene
† <i>Palaeohorus rosatus</i>	Miller and Compton (1939)	North America	lower Miocene
† <i>Palaeohorus umbrosus</i>	Cope (1874)	North America	lower Pliocene
† <i>Palaeoheirax gervaisii</i>	Brodkorb (1964)	France	lower Miocene
Family: Falconidae			
Subfamily: Polyborinae			
Name	Reference	Locality	Age
† <i>Caracara creightoni</i>	Brodkorb (1959)	Cuba, the Bahamas	late Pleistocene
† <i>Caracara latebrosus</i>	Wetmore (1920)	Puerto Rico	late Pleistocene
† <i>Caracara major</i>	Jones et al. (2013)	Uruguay	late Pleistocene
† <i>Caracara prelutosus</i>	Howard (1938)	North America	late Pleistocene
† <i>Caracara seymouri</i>	Suárez and Olson (2014)	Peru	late Pleistocene
† <i>Caracara tellustris</i>	Olson (2008)	Jamaica	Quaternary
† <i>Milvago alexandri</i>	Olson (1976)	Hispaniola	Pleistocene
† <i>Milvago brodkorbi</i>	Campbell (1979)	Peru	Pleistocene
† <i>Milvago carbo</i>	Suárez and Olson (2003)	Cuba	late Pleistocene/early Holocene
† <i>Milvago diazfrancoi</i>	Suárez (2020)	Cuba	late Pleistocene
† <i>Phalcoboenus napieri</i>	Adams and Woods (2016)	Falkland Island	middle Holocene

† indicates extinct species

Table 3.2. Guild descriptions and classifications. Tables describing the guilds as they were defined by Kruuk (1967), Houston (1988), and Hertel (1994), and how the species they analyzed in each of their papers were classified.

Guild Descriptions		
Kruuk (1967)	1	Pulling out soft insides/fleshy parts
	2	Tearing strips off large bones/skin
	3	Eating large pieces scattered around the carcass
	4	Pecking minute bits off the ground around the carcass
	5	Pecking minute bits off the bones around the carcass
Houston (1988)	1	Pecking at small scraps on the ground
	2	Pecking at small scraps on the carcass
	3	Pecking out small muscle tissue and viscera
	4	Tearing off tendons from bone
	5	Tearing off pieces of skin
Hertel (1994)	Ripper	Tearing at tough skin/hide of carcass
	Gulper	Taking softer viscera/muscle from already opened carcasses
	Scraper	Picking up smaller scraps on and around the carcass

Guild Classifications				
Species	Kruuk (1967)	Houston (1988)	Hertel (1994)	This study
<i>Cathartes aura</i>	-	4, ~3, ~2, ~1	Scraper	Scraper, Gulper
<i>Coragyps atratus</i>	-	3, ~2, ~1	Scraper	Scraper
<i>Sarcophaga papa</i>	-	5, 4, ~3, ~2, ~1	Ripper	Ripper
<i>Cathartes burrovianus</i>	-	4, ~3, ~2, ~1	Scraper	Scraper, Gulper
<i>Torgos tracheliotus</i>	2, ~3	-	Ripper	Ripper
<i>Trigonoceps occipitalis</i>	2, 3, ~1	-	Ripper	Ripper
<i>Gyps ruppellii</i>	1, ~2	-	Gulper	Gulper
<i>Gyps fulvus</i>	1, ~2	-	Gulper	Gulper
<i>Necrosyrtes monachus</i>	4, ~5	-	Scraper	Scraper
<i>Neophron percnopterus</i>	4, 5	-	Scraper	Scraper, Gulper
<i>Aegypius monachus</i>	-	-	Ripper	Ripper
<i>Cathartes melambrotus</i>	-	-	Scraper	Scraper, Gulper
<i>Gymnogyps californianus</i>	-	-	Gulper	Gulper
<i>Gypaetus barbatus</i>	-	-	Gulper	Gulper
<i>Gypohierax angolensis</i>	-	-	Gulper	Gulper
<i>Gyps africanus</i>	-	-	Gulper	Gulper
<i>Gyps bengalensis</i>	-	-	Gulper	Gulper
<i>Gyps coprotheres</i>	-	-	Gulper	Gulper

<i>Gyps himilayensis</i>	-	-	Gulper	Gulper
<i>Gyps indicus</i>	-	-	Gulper	Ripper, Gulper
* <i>Gyps tenurostris</i>	-	-	*(Gulper)	Gulper
<i>Vultur gryphus</i>	-	-	Gulper	Scraper, Gulper
<i>Sarcogyps calvus</i>	-	-	Ripper	Ripper
† <i>Breagyps clarki</i>	-	-	Gulper	Scraper, Gulper
† <i>Gymnogyps amplus</i>	-	-	Gulper	Scraper, Gulper
† <i>Coragyps occidentalis</i>	-	-	Scraper	Scraper
† <i>Neogyps errans</i>	-	-	Ripper	Ripper
† <i>Neophrontops americanus</i>	-	-	Scraper	Scraper, Gulper
† <i>Neophrontops ricardoensis</i>	-	-	-	Scraper

† indicates extinct species **Gyps tenurostris* was formerly considered a subspecies of *Gyps indicus*, prior to Hertel's classifications

Table 3.3. Table of results for ANOVA tests on skull, cranium, and premaxillary shape PCAs. The one-way analysis of variance (ANOVA) test was applied to the geometric morphometric data for each PCA performed. In all tests, percentage of variance (PoV %) for the principal component was used as the quantitative variable and while the independent variable changed depending on whether family, scavenger status, or guild was being evaluated. P-values less than or equal to 0.05 are marked with an asterisk (*). The percent variance determined specifically by the independent variable being examined (% Variance) is the r-squared value multiplied by the PoV.

Scavenger Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	37.56	0.0000*	0.768	185.90 (2, 110)	28.83
	PC2	19.41	0.0000*	0.184	13.59 (2, 110)	3.56
	PC3	12.17	0.0001*	0.146	10.56 (2, 110)	1.78
Subfamilies/Clades	PC1	37.56	0.0000*	0.788	105.30 (4, 108)	29.61
	PC2	19.41	0.0000*	0.195	7.77 (4, 108)	3.78
	PC3	12.17	0.0003*	0.148	5.87 (4, 108)	1.80
Guild	PC1	37.56	0.0000*	0.790	141.3 (3, 109)	29.66
	PC2	19.41	0.0000*	0.185	9.457 (3, 109)	3.59
	PC3	12.17	0.1084	0.028	5.87 (4, 108)	0.34
Modern Scavenger Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	37.85	0.0000*	0.824	230.40 (2, 96)	31.19
	PC2	21.04	0.0000*	0.224	15.18 (2, 96)	4.72
	PC3	12.77	0.0001*	0.153	9.88 (2, 96)	1.96
Subfamilies/Clades	PC1	37.85	0.0000*	0.822	114.00 (4, 94)	31.11
	PC2	21.04	0.0000*	0.221	7.94 (4, 94)	4.65
	PC3	12.77	0.0007*	0.149	5.27 (4, 94)	1.90
Fossil Scavenger Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	33.65	0.0004*	0.709	16.86 (2, 11)	23.87
	PC2	23.62	0.1052	0.215	2.78 (2, 11)	5.08
	PC3	16.80	0.3099	0.045	1.31 (2, 11)	0.76
Subfamilies/Clades	PC1	33.65	0.0020*	0.684	10.39 (3, 10)	23.03
	PC2	23.62	0.2186	0.149	1.76 (3, 10)	3.51
	PC3	16.80	0.0293*	0.451	4.56 (3, 10)	7.58
Scavenger Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	39.97	0.0000*	0.251	26.77 (2, 152)	10.02
	PC2	22.03	0.0000*	0.156	15.27 (2, 152)	3.44
	PC3	10.75	0.0001*	0.107	10.18 (2, 152)	1.14
Subfamilies/Clades	PC1	39.97	0.0000*	0.588	55.87 (4, 150)	23.49
	PC2	22.03	0.0000*	0.157	8.19 (4, 150)	3.47
	PC3	10.75	0.0000*	0.135	7.01 (4, 150)	1.45
Guild	PC1	39.97	0.0000*	0.376	31.96 (3, 151)	15.04
	PC2	22.03	0.0000*	0.219	15.42 (3, 151)	4.83
	PC3	10.75	0.0000*	0.206	14.28 (3, 151)	2.21
Modern Scavenger Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Order	PC1	45.47	0.0000*	0.093	18.65 (2, 97)	4.23
	PC2	20.80	0.0000*	0.039	18.61 (2, 97)	0.81
	PC3	14.74	0.0000*	0.089	17.93 (2, 97)	1.31
Families	PC1	45.47	0.0000*	0.625	68.82 (4, 95)	28.42
	PC2	20.80	0.0000*	0.074	10.74 (4, 95)	1.53
	PC3	14.74	0.0000*	0.135	12.08 (4, 95)	1.99

Fossil Scavenger Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Order	PC1	42.27	0.1348	0.180	2.083 (2, 52)	7.60
	PC2	22.01	0.6855	0.014	0.3803 (2, 52)	0.31
	PC3	14.75	0.0218*	0.110	4.122 (2, 52)	1.63
Families	PC1	42.27	0.0003*	0.562	7.48 (3, 51)	23.77
	PC2	22.01	0.1466	0.071	1.869 (3, 51)	1.56
	PC3	14.75	0.0001*	0.210	9.099 (3, 51)	3.10
Scavenger Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	42.62	0.0000*	0.792	273.4 (2, 141)	33.76
	PC2	27.51	0.0016*	0.074	6.75 (2, 141)	2.05
	PC3	13.81	0.9421	-0.013	0.0597 (2, 141)	-0.18
Subfamilies/Clades	PC1	42.62	0.0000*	0.799	142.7 (4, 139)	34.03
	PC2	27.51	0.0002*	0.119	5.846 (4, 139)	3.28
	PC3	13.81	0.4345	-0.001	0.9529 (4, 139)	-0.02
Guild	PC1	42.62	0.0000*	0.678	101.3 (3, 140)	28.90
	PC2	27.51	0.0029*	0.076	4.904 (3, 140)	2.08
	PC3	13.81	0.0000*	0.136	8.491 (3, 140)	1.88
Modern Scavenger Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	49.47	0.0000*	0.791	190.5 (2, 98)	39.14
	PC2	22.06	0.0011*	0.112	7.286 (2, 98)	2.46
	PC3	11.51	0.3898	-0.001	0.9512 (2, 98)	-0.01
Subfamilies/Clades	PC1	49.47	0.0000*	0.806	105 (4, 96)	39.88
	PC2	22.06	0.0000*	0.210	7.648 (4, 96)	4.63
	PC3	11.51	0.1556	0.027	1.703 (4, 96)	0.31
Fossil Scavenger Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Families	PC1	48.25	0.0000*	0.847	116.9 (2, 40)	40.85
	PC2	24.94	0.3347	0.006	1.125 (2, 40)	0.15
	PC3	15.07	0.3856	-0.001	0.9759 (2, 40)	-0.02
Subfamilies/Clades	PC1	48.25	0.0000*	0.844	76.43 (3, 39)	40.70
	PC2	24.94	0.5373	-0.019	0.7353 (3, 39)	-0.48
	PC3	15.07	0.3808	0.004	1.05 (3, 39)	0.06
Vulture Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	29.65	0.0000*	0.487	25.65 (3, 75)	14.43
	PC2	25.04	0.0015*	0.152	5.669 (3, 75)	3.81
	PC3	14.52	0.2466	0.016	1.41 (3, 75)	0.23
Guild	PC1	29.65	0.0000*	0.388	25.68 (2, 76)	11.49
	PC2	25.04	0.0001*	0.199	10.66 (2, 76)	4.97
	PC3	14.52	0.0008*	0.148	7.791 (2, 76)	2.15
Modern Vulture Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	36.59	0.0000*	0.517	24.2 (3, 62)	18.92
	PC2	20.25	0.7040	-0.025	0.4705 (3, 62)	-0.51
	PC3	11.42	0.6255	-0.019	0.5875 (3, 62)	-0.22
Guild	PC1	36.59	0.0000*	0.520	36.25 (2, 63)	19.04
	PC2	20.25	0.1258	0.031	2.142 (2, 63)	0.63
	PC3	11.42	0.0001*	0.228	10.59 (2, 63)	2.60

Fossil Vulture Skull Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	34.93	0.0609	0.314	3.75 (2, 10)	10.98
	PC2	23.21	0.1682	0.160	2.141 (2, 10)	3.71
	PC3	16.83	0.1939	0.136	1.942 (2, 10)	2.28
Guild	PC1	34.93	0.1698	0.158	2.128 (2, 10)	5.53
	PC2	23.21	0.1674	0.161	2.148 (2, 10)	3.73
	PC3	16.83	0.1875	0.141	1.988 (2, 10)	2.38
Vulture Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	38.45	0.0073*	0.075	4.207 (3, 115)	2.90
	PC2	22.02	0.0000*	0.589	57.28 (3, 115)	12.96
	PC3	10.85	0.0002*	0.133	7.014 (3, 115)	1.44
Guild	PC1	38.45	0.1777	0.013	1.754 (2, 116)	0.48
	PC2	22.02	0.0000*	0.489	57.42 (2, 116)	10.76
	PC3	10.85	0.0003*	0.117	8.803 (2, 116)	1.27
Modern Vulture Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	44.37	0.0000*	0.204	38.26 (3, 63)	9.06
	PC2	20.86	0.0006*	0.204	6.648 (3, 63)	4.26
	PC3	8.88	0.1126	0.047	2.074 (3, 63)	0.41
Guild	PC1	44.37	0.0000*	0.294	14.72 (2, 64)	13.03
	PC2	20.86	0.0051*	0.126	5.749 (2, 64)	2.62
	PC3	8.88	0.0016*	0.160	7.134 (2, 64)	1.42
Fossil Vulture Cranial Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	41.90	0.0001*	0.290	11.44 (2, 49)	12.17
	PC2	23.11	0.1108	0.049	2.302 (2, 49)	1.12
	PC3	11.96	0.0002*	0.264	10.16 (2, 49)	3.16
Guild	PC1	41.90	0.0001*	0.296	11.71 (2, 49)	12.39
	PC2	23.11	0.1841	0.029	1.752 (2, 49)	0.66
	PC3	11.96	0.0002*	0.267	10.31 (2, 49)	3.20
Vulture Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	37.68	0.0004*	0.150	6.703 (3, 94)	5.65
	PC2	26.14	0.0000*	0.393	21.89 (3, 94)	10.26
	PC3	16.24	0.0009*	0.133	5.961 (3, 94)	2.16
Guild	PC1	37.68	0.0552	0.039	2.987 (2, 95)	1.48
	PC2	26.14	0.1078	0.412	35.03 (2, 95)	10.78
	PC3	16.24	0.1078	0.026	2.281 (2, 95)	0.42
Modern Vulture Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	39.07	0.0000*	0.384	14.92 (3, 64)	15.01
	PC2	28.75	0.0000*	0.386	15.05 (3, 64)	11.10
	PC3	12.10	0.0000*	0.302	10.64 (3, 64)	3.65
Guild	PC1	39.07	0.6997	-0.020	0.3591 (2, 65)	-0.76
	PC2	28.75	0.0000*	0.751	102.1 (2, 65)	21.59
	PC3	12.10	0.1303	0.032	2.103 (2, 65)	0.39

Fossil Vulture Premaxillary Outline PCA	Principle Component	PoV (%)	P-value	r-squared	F-statistic	% Variance
Subfamilies/Clades	PC1	47.93	0.0363*	0.160	3.758 (2, 27)	7.66
	PC2	23.68	0.0081*	0.249	5.794 (2, 27)	5.88
	PC3	17.18	0.1295	0.077	2.207 (2, 27)	1.32
Guild	PC1	47.93	0.1088	0.089	2.411 (2, 27)	4.25
	PC2	23.68	0.0062*	0.263	6.173 (2, 27)	6.23
	PC3	17.18	0.5692	-0.030	0.5755 (2, 27)	-0.52

Table 3.4. Table of Tukey's test adjusted p-values. Table summarizing the adjusted p-values produced by a Tukey's test applied to each PCA performed. The Tukey's test compared each variable to each other to determine if the two variables were significantly different from each other. P-values less than or equal to 0.05 are marked with an asterisk (*).

Scavenger Skull Outline Tukey Test p-values									
Family	Modern and Fossil			Modern			Fossil		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Polyborinae	0.00*	0.88	0.01*	0.00*	0.99	0.02*	0.02*	0.31	0.31
Accipitridae - Polyborinae	0.00*	0.00*	0.51	0.00*	0.00*	0.21	0.99	0.11	0.30
Accipitridae - Cathartidae	0.00*	0.00*	0.00*	0.00*	0.00*	0.00*	0.00*	0.34	0.98
Subfamily/Clade	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Condor - Aegypiinae	0.00*	0.07	0.14	0.00	0.06	0.08	-	-	-
Gypaetinae - Aegypiinae	0.44	1.00	0.94	0.96	0.99	1.00	-	-	-
Polyborinae - Aegypiinae	0.00*	0.00*	0.97	0.00*	0.00*	0.47	-	-	-
Vulture - Aegypiinae	0.03*	0.00*	0.00*	0.00*	0.00*	0.00*	-	-	-
Gypaetinae - Condor	0.01*	0.12	0.06	0.08	0.12	0.42	0.00*	0.49	0.93
Polyborinae - Condor	0.00*	0.97	0.33	0.00*	0.96	0.68	0.05*	0.53	0.12
Vulture - Condor	0.02*	0.34	0.69	0.97	0.76	0.77	0.98	0.98	0.05*
Polyborinae - Gypaetinae	0.00*	0.02*	0.68	0.00*	0.01*	0.91	1.00	0.20	0.23
Vulture - Gypaetinae	0.95	0.00*	0.00*	0.17	0.01*	0.05*	0.03*	0.89	0.15
Vulture - Polyborinae	0.00*	0.62	0.01*	0.00	0.96	0.03*	0.13	0.49	1.00
Guild	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Ripper - Gulper	0.00*	0.50	0.93	-	-	-	-	-	-
Scraper - Gulper	0.06	0.00*	0.34	-	-	-	-	-	-
Scraper - Ripper	0.00*	0.00*	0.25	-	-	-	-	-	-

Scavenger Cranial Outline Tukey Test p-values									
Family	Modern and Fossil			Modern			Fossil		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Polyborinae	0.00*	0.00*	0.01*	0.00*	0.00*	0.71	0.19	0.99	0.04*
Accipitridae - Polyborinae	0.69	0.01*	0.00*	0.98	0.00*	0.00*	0.70	0.90	0.46
Accipitridae - Cathartidae	0.00*	0.10	0.10	0.00*	0.04*	0.00*	0.45	0.66	0.24
Subfamily/Clade	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Condor - Aegypiinae	0.00*	0.27	0.09	0.00*	0.96	0.03*	-	-	-
Gypaetinae - Aegypiinae	0.99	1.00	0.10	0.06	0.99	0.18	-	-	-
Polyborinae - Aegypiinae	0.75	0.03*	0.00*	0.95	0.02*	0.00*	-	-	-
Vulture - Aegypiinae	1.00	0.97	0.02*	1.00	0.02*	0.00*	-	-	-
Gypaetinae - Condor	0.00*	0.21	0.99	0.00*	1.00	1.00	0.03*	0.66	0.00*
Polyborinae - Condor	0.00*	0.00*	0.02*	0.00*	0.01*	0.26	0.03*	0.95	0.00*
Vulture - Condor	0.00*	0.60	0.91	0.00*	0.23	0.20	0.00*	0.11	0.00*
Polyborinae - Gypaetinae	0.98	0.16	0.27	0.15	0.07	0.35	0.87	1.00	0.69
Vulture - Gypaetinae	1.00	0.89	1.00	0.05*	0.37	0.28	0.94	0.84	1.00
Vulture - Polyborinae	0.84	0.00*	0.22	0.89	0.00*	1.00	0.98	0.83	0.57
Guild	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Ripper - Gulper	0.00*	0.02*	0.00*	-	-	-	-	-	-
Scraper - Gulper	0.00*	0.00*	0.61	-	-	-	-	-	-
Scraper - Ripper	0.86	0.94	0.00*	-	-	-	-	-	-

Scavenger Cranial Outline Tukey Test p-values									
Family	Modern and Fossil			Modern			Fossil		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Cathartidae - Polyborinae	0.00*	0.00*	0.98	0.00*	0.01*	0.37	0.00*	0.30	0.68
Accipitridae - Polyborinae	0.00*	0.00*	0.99	0.00*	0.00*	0.63	0.00*	0.63	0.35
Accipitridae - Cathartidae	0.00*	0.99	0.94	0.00*	0.96	0.90	0.00*	0.92	0.72
Subfamily/Clade	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Condor - Aegypiinae	0.00*	0.38	1.00	0.00*	0.23	0.93	-	-	-
Gypaetinae - Aegypiinae	0.33	0.99	0.63	1.00	0.77	0.49	-	-	-
Polyborinae - Aegypiinae	0.00*	0.02*	0.98	0.00*	0.03*	0.59	-	-	-
Vulture - Aegypiinae	0.00*	0.77	0.84	0.00*	0.35	0.90	-	-	-
Gypaetinae - Condor	0.00*	0.76	0.47	0.00*	0.07	0.24	0.00*	0.98	0.66
Polyborinae - Condor	0.00*	0.81	0.90	0.00*	1.00	0.27	0.00*	0.51	0.99
Vulture - Condor	0.43	0.03*	0.68	0.02*	0.00*	0.57	0.97	1.00	0.70
Polyborinae - Gypaetinae	0.00*	0.17	0.85	0.00*	0.02*	0.96	0.00*	0.80	0.51
Vulture - Gypaetinae	0.00*	0.59	0.99	0.00*	1.00	0.88	0.00*	0.99	1.00
Vulture - Polyborinae	0.00*	0.00*	0.98	0.00*	0.00*	0.99	0.00*	0.69	0.55
Guild	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Ripper - Gulper	0.01*	0.50	0.00*	-	-	-	-	-	-
Scraper - Gulper	0.59	0.81	0.30	-	-	-	-	-	-
Scraper - Ripper	0.00*	0.19	0.00*	-	-	-	-	-	-

Vulture Skull Outline Tukey Test p-values									
Subfamily/Clade	Modern and Fossil			Modern			Fossil		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Condor - Aegypiinae	0.00*	0.02*	0.98	0.00*	0.81	1.00	-	-	-
Gypaetinae - Aegypiinae	0.99	0.27	0.62	0.99	0.99	0.62	-	-	-
Vulture - Aegypiinae	0.00*	0.90	0.77	0.00*	0.99	0.97	-	-	-
Gypaetinae - Condor	0.00*	0.88	0.84	0.00*	0.97	0.63	0.07	0.21	0.24
Vulture - Condor	0.48	0.00*	0.55	0.20	0.66	0.96	0.98	0.35	0.39
Vulture - Gypaetinae	0.00*	0.10	0.21	0.00*	0.96	0.82	0.15	1.00	1.00
Guild	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Ripper - Gulper	0.00*	0.00*	0.01*	0.01*	0.12	0.00*	0.19	0.50	0.71
Scraper - Gulper	0.00*	0.00*	0.00*	0.00*	0.43	0.03*	0.49	0.18	0.17
Scraper - Ripper	0.00*	0.43	0.88	0.00*	0.60	0.06	0.46	0.99	0.96

Vulture Cranial Outline Tukey Test p-values									
Subfamily/Clade	Modern and Fossil			Modern			Fossil		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Condor - Aegypiinae	1.00	0.00*	0.95	0.00*	0.00*	1.00	-	-	-
Gypaetinae - Aegypiinae	0.99	0.92	0.00*	0.91	0.91	0.56	-	-	-
Vulture - Aegypiinae	0.07	0.99	0.98	0.01*	0.00*	0.40	-	-	-
Gypaetinae - Condor	0.99	0.00*	0.00*	0.00*	0.17	0.52	0.00*	0.69	0.00*
Vulture - Condor	0.01*	0.00*	0.73	0.00*	0.99	0.67	0.00*	0.09	0.00*
Vulture - Gypaetinae	0.03*	0.77	0.01*	0.30	0.19	0.09	0.92	0.56	1.00
Guild	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Ripper - Gulper	0.99	0.00*	0.01*	0.25	0.00*	0.00*	0.00*	0.16	0.00*

Scraper - Gulper	0.21	0.00*	0.25	0.00*	0.65	0.06	0.82	0.94	0.71
Scraper - Ripper	0.38	0.96	0.00*	0.01*	0.03*	0.20	0.75	0.98	0.89

Vulture Premaxillary Outline Tukey Test p-values									
	Modern and Fossil			Modern			Fossil		
Subfamily/Clade	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Condor - Aegypiinae	0.00*	0.00*	0.00*	0.00*	0.58	0.00*	-	-	-
Gypaetinae - Aegypiinae	0.37	0.82	1.00	1.00	0.16	0.83	-	-	-
Vulture - Aegypiinae	0.06	0.00*	0.58	0.70	0.00*	0.00*	-	-	-
Gypaetinae - Condor	0.12	0.00*	0.01*	0.00*	0.77	0.02*	0.03*	0.01*	0.48
Vulture - Condor	0.22	0.11	0.06	0.00*	0.00*	0.50	0.84	0.99	0.46
Vulture - Gypaetinae	0.94	0.00*	0.67	0.81	0.05*	0.19	0.16	0.02*	0.11
Guild	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Ripper - Gulper	0.16	0.00*	0.42	0.68	0.00*	0.13	0.22	0.01*	0.59
Scraper - Gulper	0.71	0.06	0.50	0.89	0.00*	0.35	0.23	0.43	0.98
Scraper - Ripper	0.04*	0.00*	0.09	0.90	0.00*	0.73	0.52	0.01*	0.54

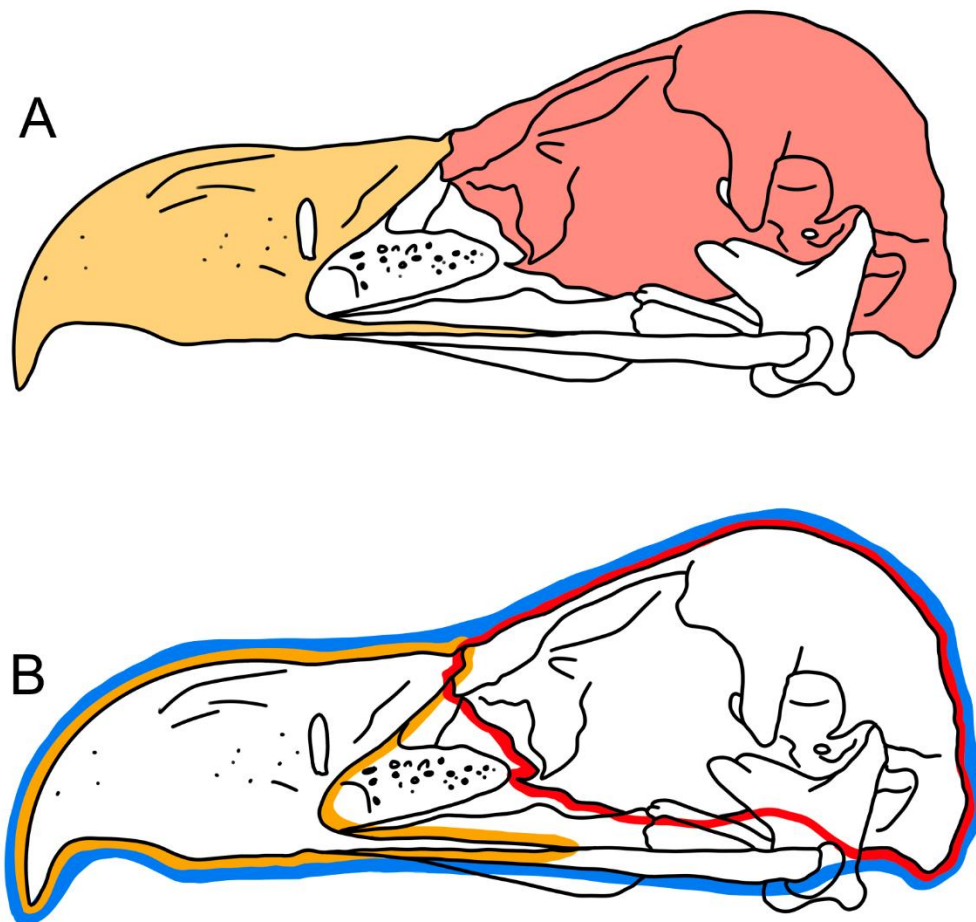


Figure 3.1. Diagram of placement of landmarks and curves for shape analyses. A. Drawing of a lappet-faced vulture (*Torgos tracheliotus*) skull highlighting the parts of the skull that were focused on for analysis. The premaxillary is highlighted in yellow and the cranium is highlighted in red. B. The same drawing, now showing the outline paths used to perform the geometric morphometric analyses, with the yellow outline following the shape of the premaxillary, the red outline following the shape of the cranium, and the blue outline following the shape of the full skull.

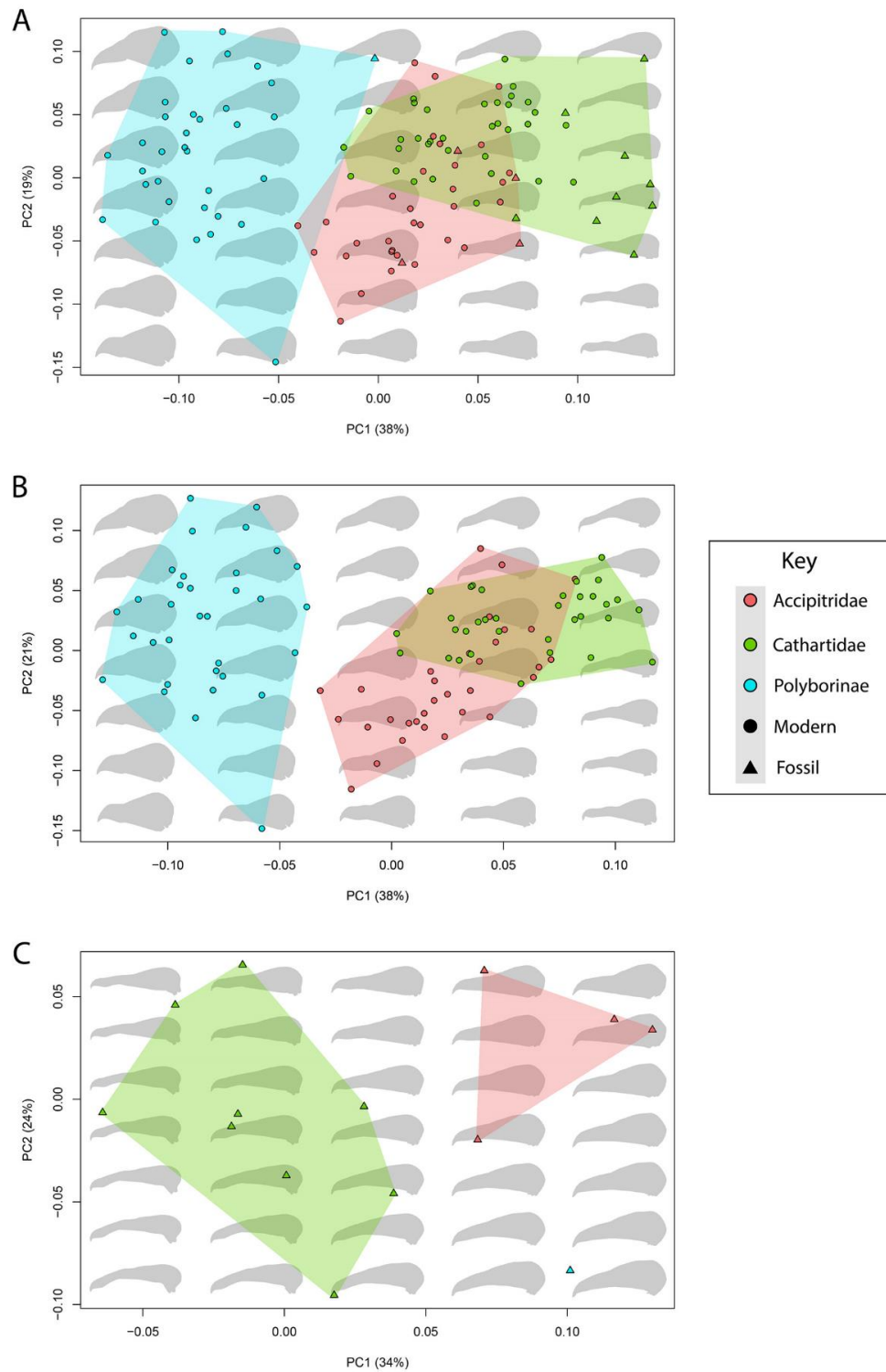


Figure 3.2. Backtransform PCAs for the skull showing family distribution. Three PCAs showing the shape distributions of the skulls of all scavengers (A), only modern scavengers (B), and only fossil scavengers (C), and their distributions by family.

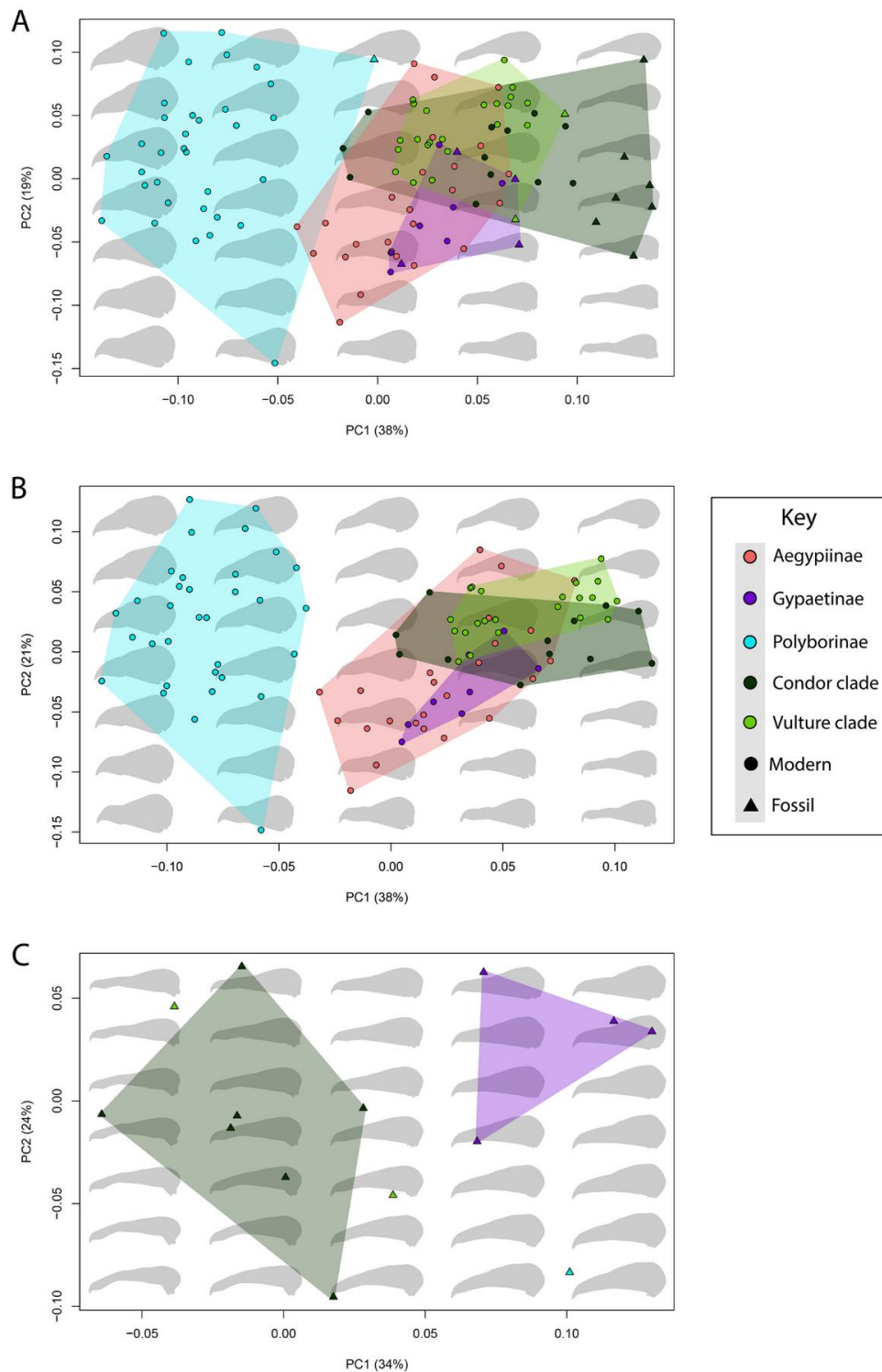


Figure 3.3. Backtransform PCAs for the skull showing subfamily distribution. Three PCAs showing the shape distributions of the skulls of all scavengers (A), only modern scavengers (B), and only fossil scavengers (C), and their distributions by subfamily.

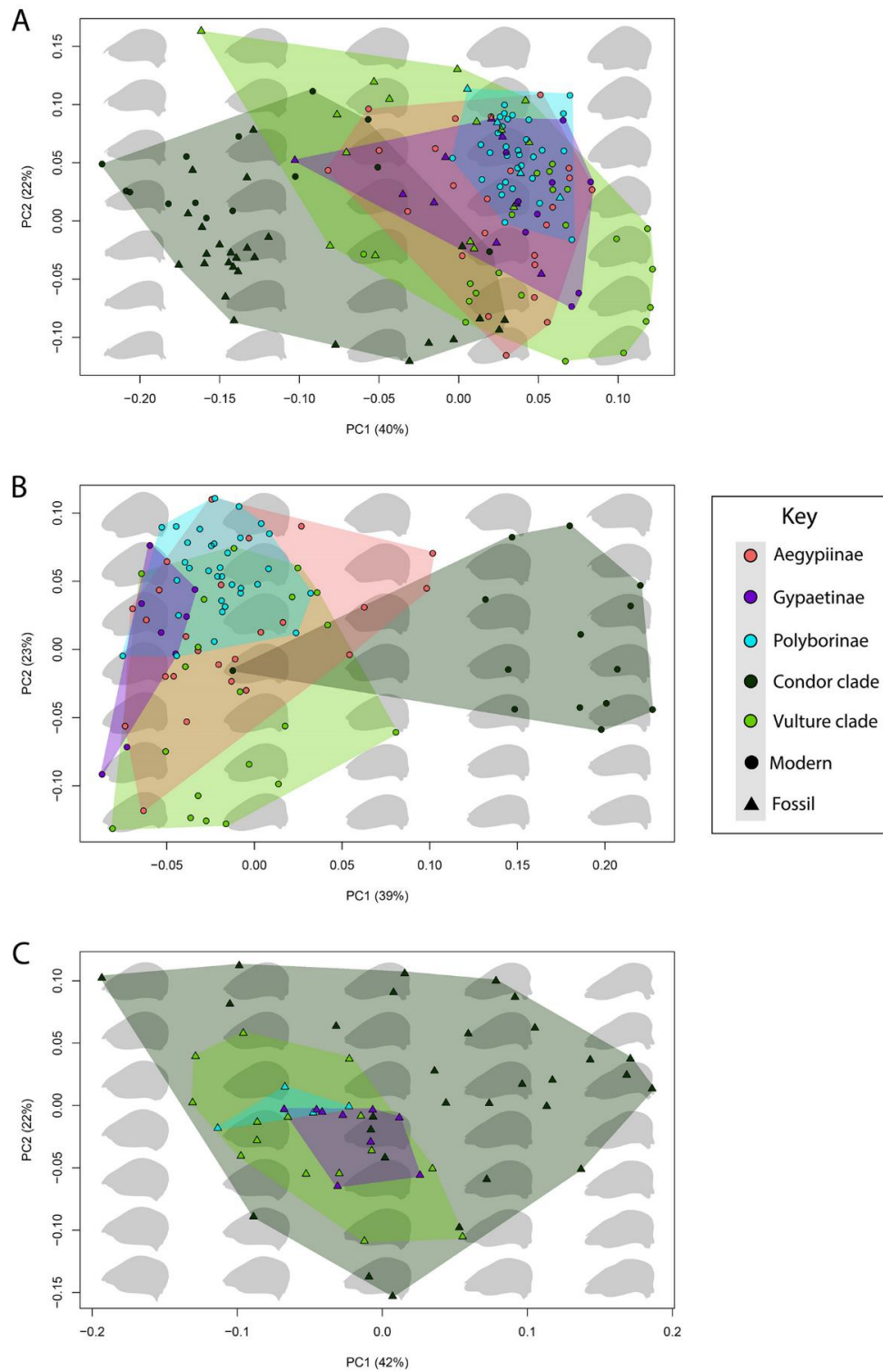


Figure 3.4. Backtransform PCAs for the cranium showing subfamily distribution. Three PCAs showing the shape distributions of the crania of all scavengers (A), only modern scavengers (B), and only fossil scavengers (C), and their distributions by subfamily.

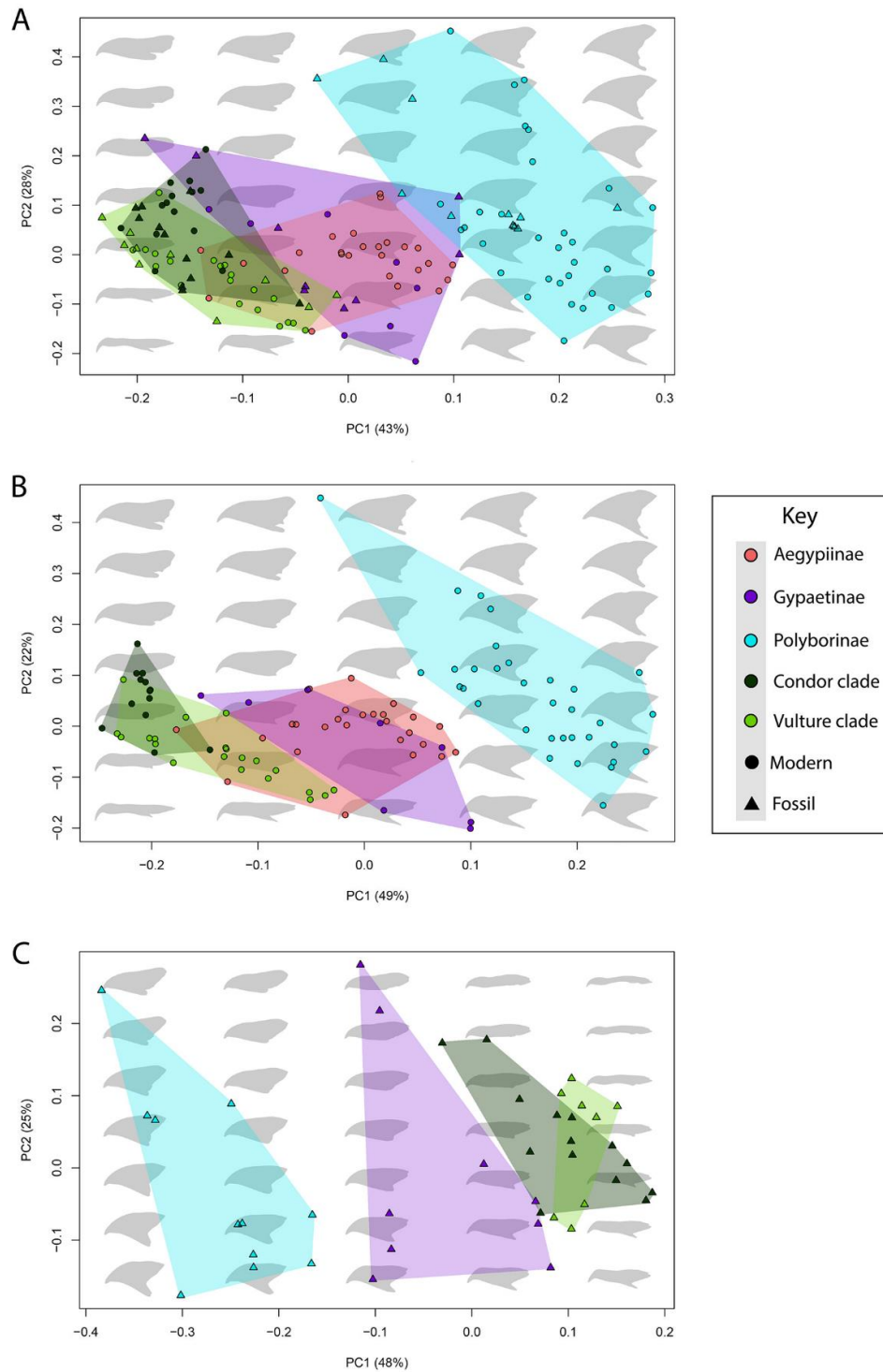


Figure 3.5. Backtransform PCAs for the premaxillary showing subfamily distribution. Three PCAs showing the shape distributions of the premaxillaries of all scavengers (A), only modern scavengers (B), and only fossil scavengers (C), and their distributions by subfamily.

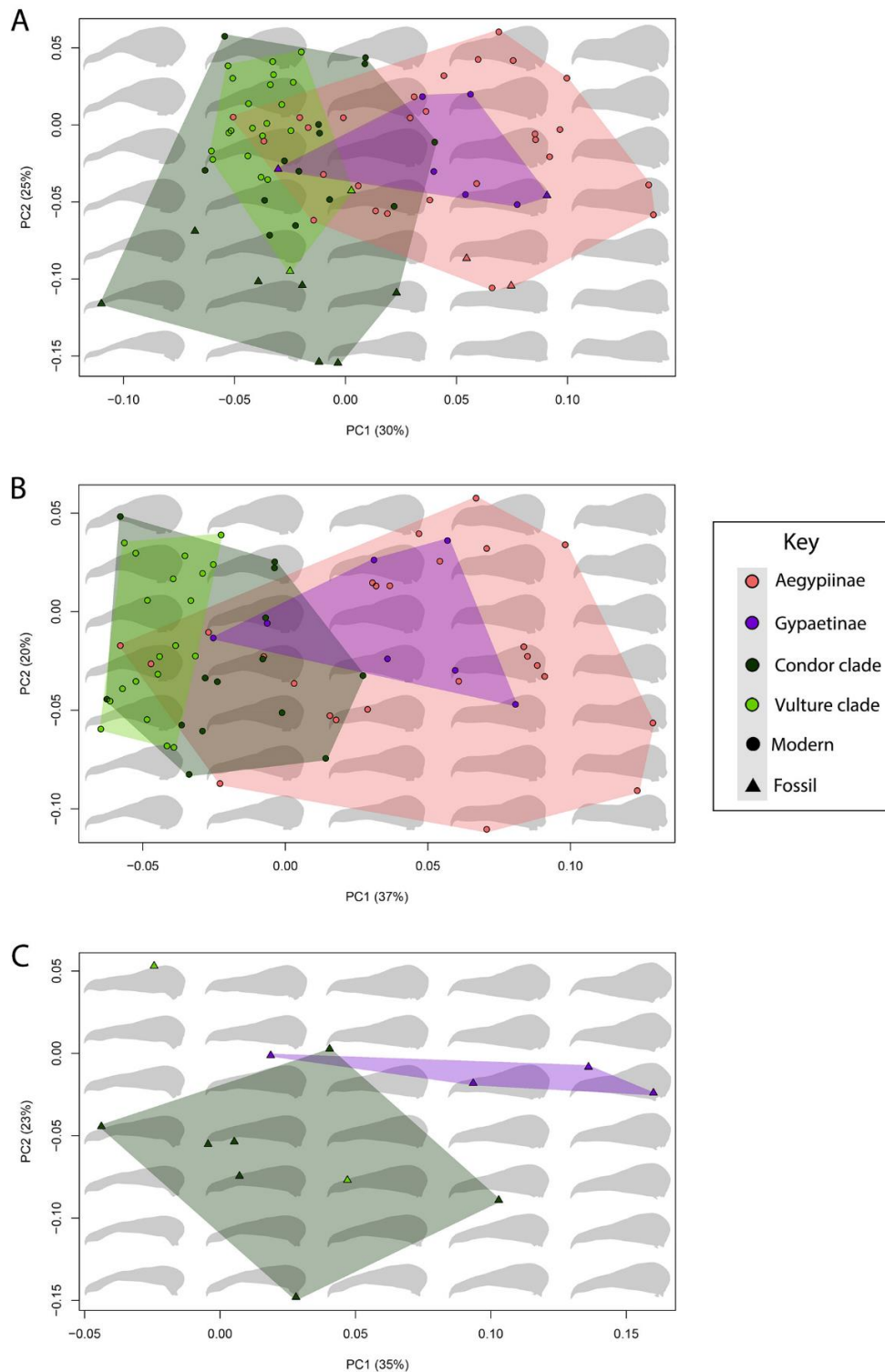


Figure 3.6. Backtransform PCAs for the skull showing subfamily distribution of Accipitriformes only. Three PCAs showing the shape distributions of the skulls of all the Accipitriformes (A), only the modern Accipitriformes (B), and only the fossil Accipitriformes (C) and their distributions by subfamily.

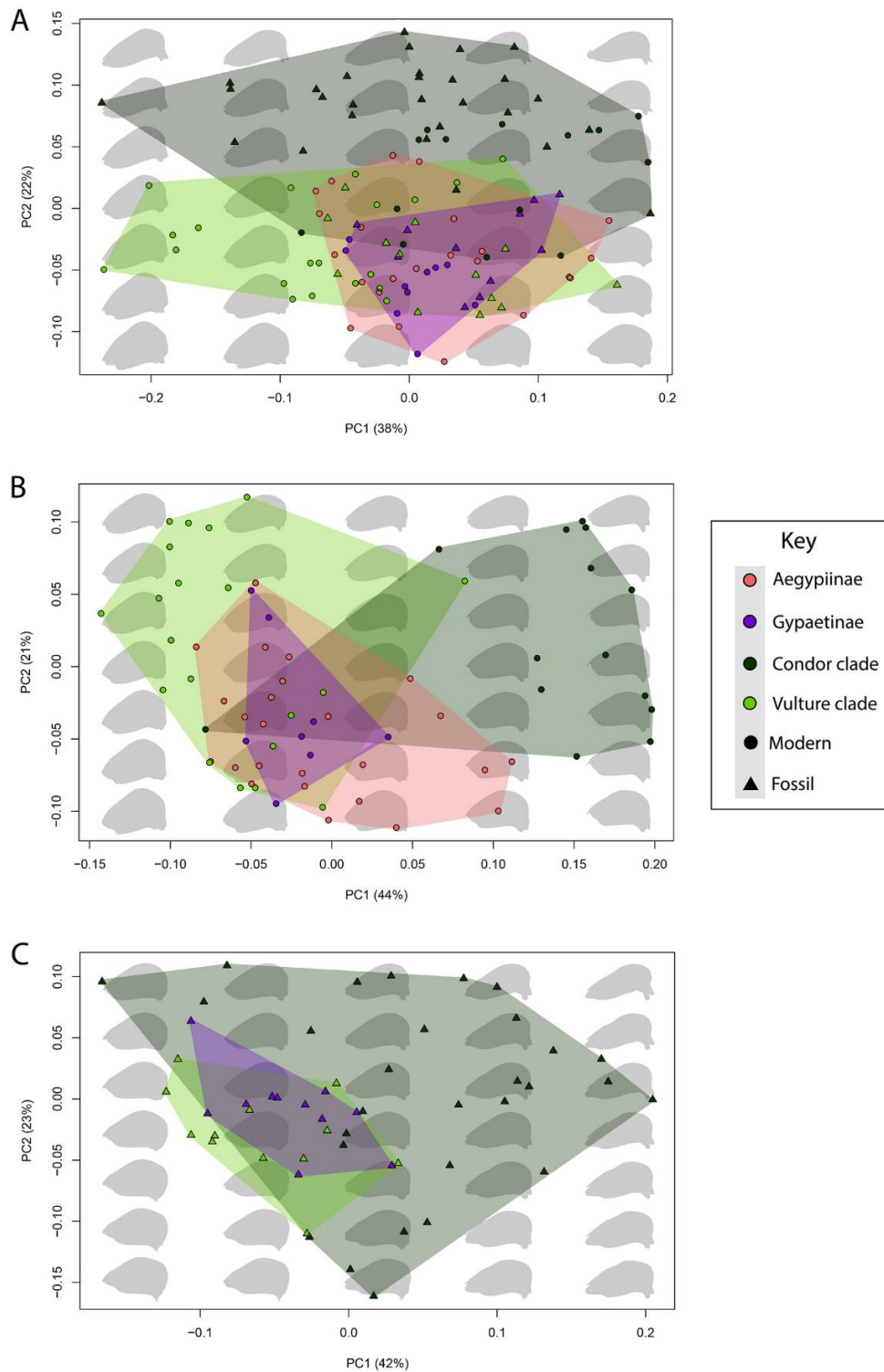


Figure 3.7. Backtransform PCAs for the cranium showing subfamily distribution of Accipitriformes only. Three PCAs showing the shape distributions of the crania of all the Accipitriformes (A), only the modern Accipitriformes (B), and only the fossil Accipitriformes (C) and their distributions by subfamily.

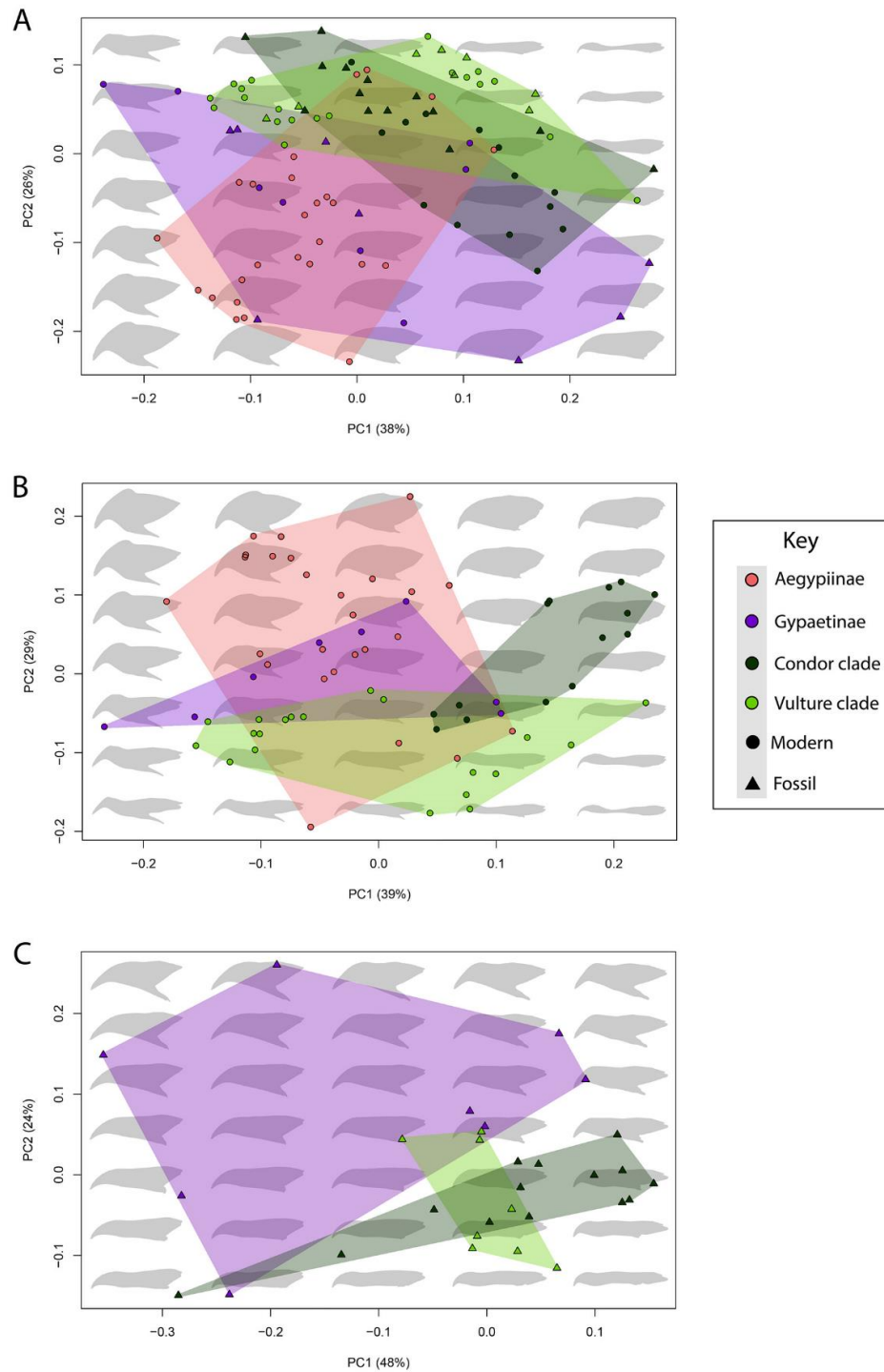


Figure 3.8. Backtransform PCAs for the premaxillary showing subfamily distribution of Accipitriformes only. Three PCAs showing the shape distributions of the premaxillaries of all the Accipitriformes (A), only the modern Accipitriformes (B), and only the fossil Accipitriformes (C) and their distributions by subfamily.

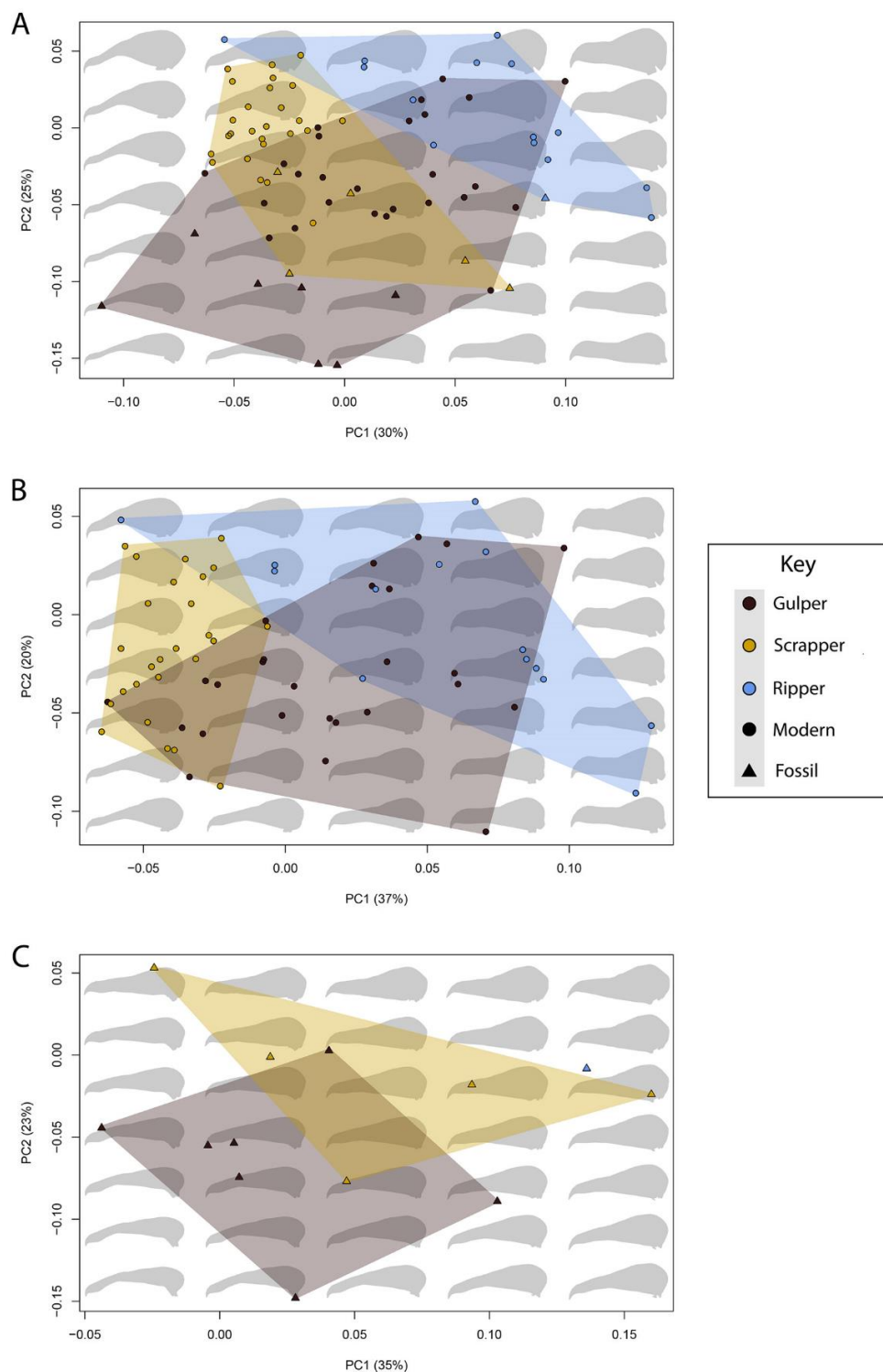


Figure 3.9. Backtransform PCAs for the skull showing guild map of Accipitriformes only. Three PCAs showing the shape distributions of the skull of all the Accipitriformes (A), only the modern Accipitriformes (B), and only the fossil Accipitriformes (C) and their distributions by guild designation (Hertel 1994).

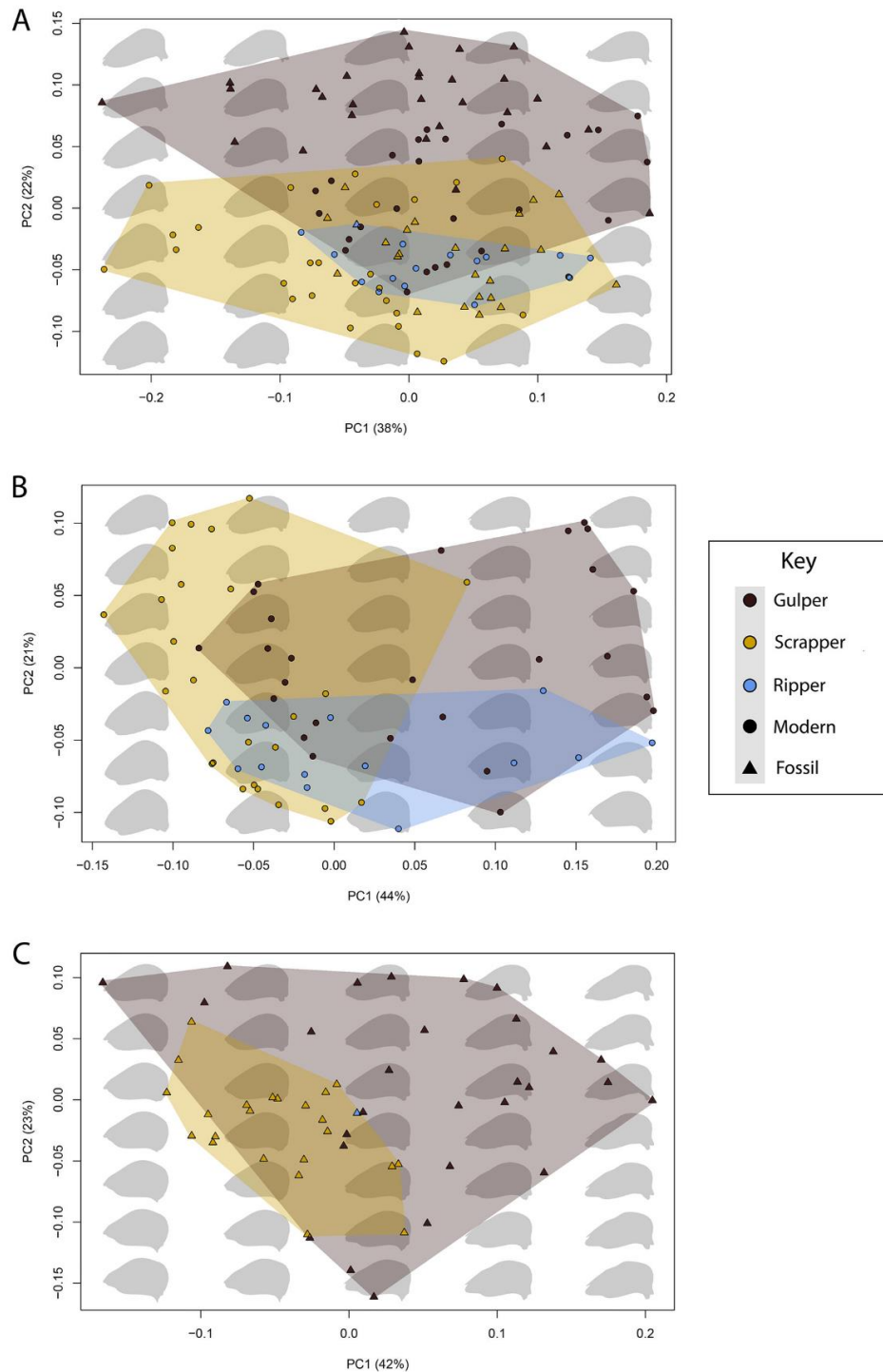


Figure 3.10. Backtransform PCAs for the cranium showing subfamily distribution of Accipitriformes only. Three PCAs showing the shape distributions of the crania of all the Accipitriformes (A), only the modern Accipitriformes (B), and only the fossil Accipitriformes (C) and their distributions by guild designation (Hertel 1994).

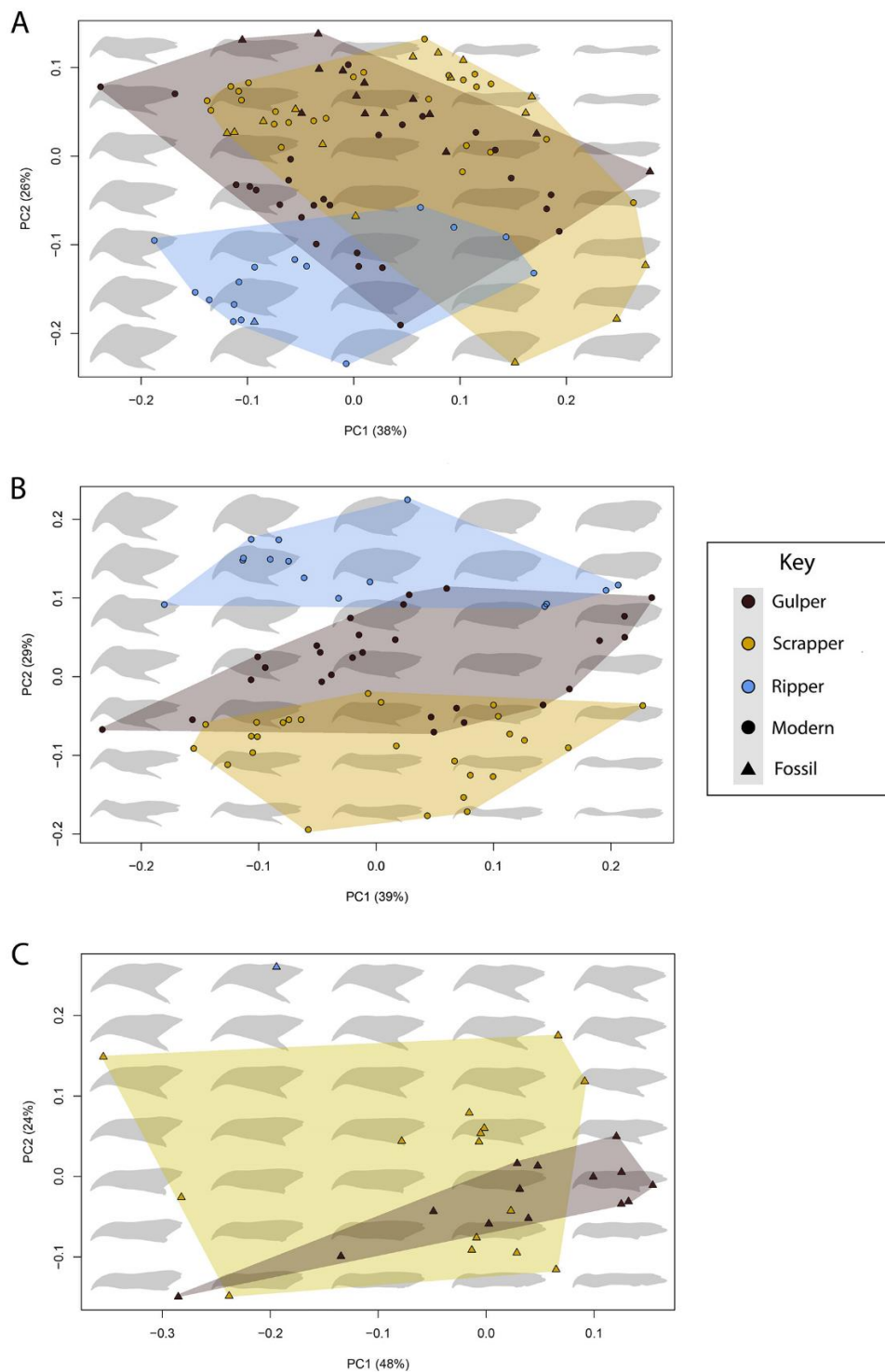


Figure 3.11. Backtransform PCAs for the premaxillary showing guild map of Accipitriformes only. Three PCAs showing the shape distributions of the premaxillaries of all the Accipitriformes (A), only the modern Accipitriformes (B), and only the fossil Accipitriformes (C) and their distributions by guild designation (Hertel 1994).

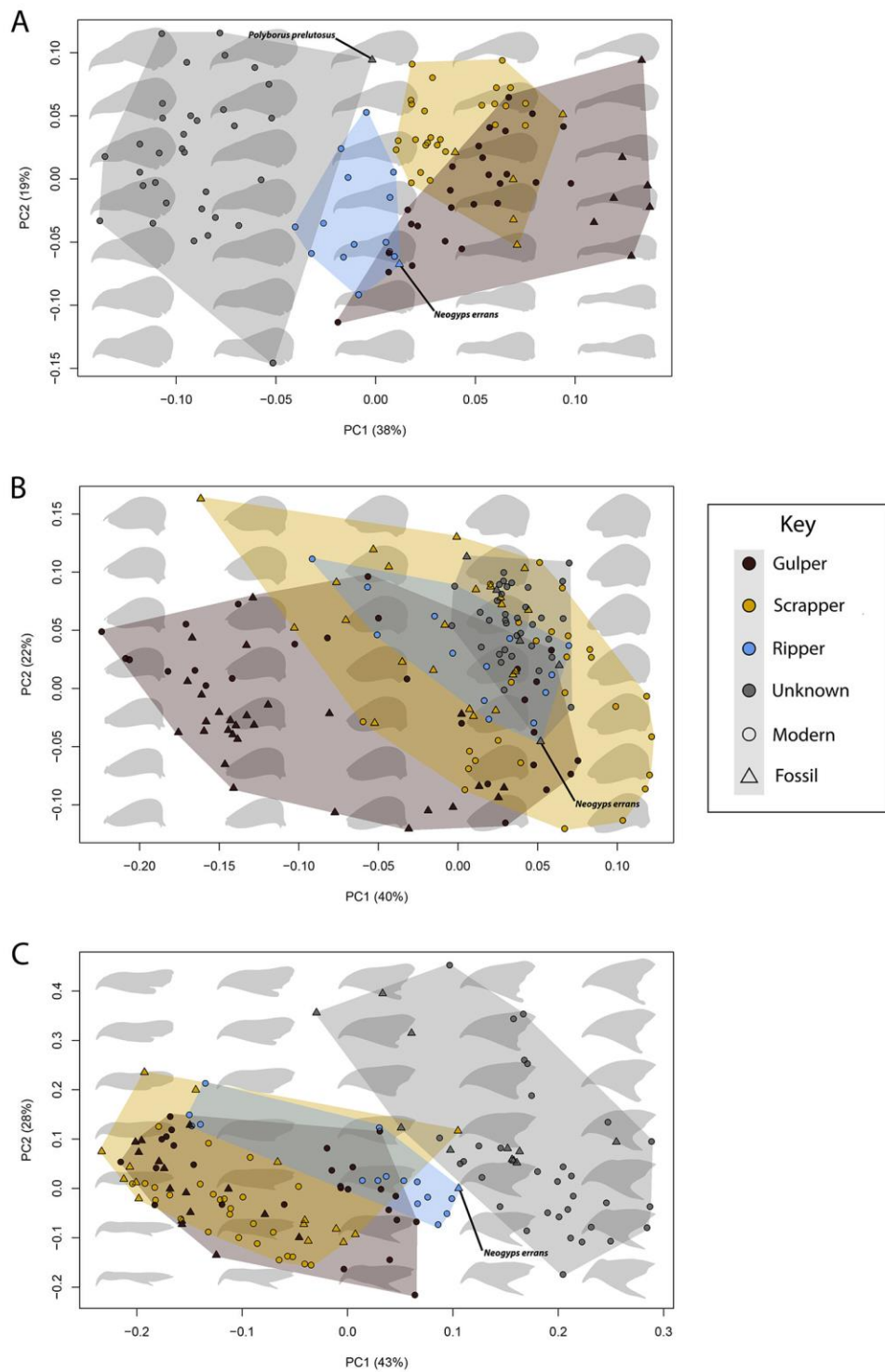


Figure 3.12. Backtransform PCAs for the skull showing guild map of all species. Three PCAs showing the shape distributions of the skulls (A), crania (B), and premaxillaries (C) of all specimens and their distributions by guild designation (Hertel 1994). Specimens of unknown guild classification are comprised of the Polyborinae subfamily.

General Conclusions

In this study I explored the topic of raptor skull morphology in greater depth than had been previously attempted. Modern and fossil skulls, crania, and premaxillary were subjected to geometric morphometric shape analyses and compared across three chapters.

In Chapter 1, I used geometric morphometrics to examine the beaks of bird with a rhamphotheca and without one. Avian beak morphology and variation are extensively studied and used to make conclusions about feeding behavior and dietary preferences, but most studies choose to focus on either the bony beak or the rhamphotheca. This study used five species of different families of raptors to question this practice. Despite different phylogenetic origins for the taxa used in these analyses, there are recurring trends of beak size and shape change in raptors based on rhamphotheca presence. These findings agreed with the conclusions of Urano et al. (2018) and Eliason et al. (2020), that the rhamphotheca does have noteworthy implications for the dietary and ecological conclusions in studies that exclude the rhamphotheca from their analyses. It emphasizes the need to include the rhamphotheca in comparative dietary analyses if the results are to lead to accurate inference about diet, and to look at this variation on a broader phylogenetic spectrum.

In Chapter 2, I used the skulls of 150 species of living and extinct diurnal raptors to investigate the differences between the skulls of active predators and scavengers. This chapter also addressed avian skull modularity, or the extent to which the beak is evolving independently of the cranium. The scavenger morphospace of the PCA showed that grouping within the scavengers was not strictly based on phylogenetic relatedness, but on morphological similarities across the Gypaetinae, Aegypiinae, and Cathartidae. While the Polyborinae did not group directly with the accipitrid and cathartid vultures, they exhibited morphological changes that make them distinctly different from other falcons in a way that mimics the evolutionary path vultures have taken from the rest of the Accipitriformes. As for skull modularity, cranial shape was shown to be significantly less variable than premaxillary shape, suggesting that the cranium is phylogenetically constrained to a higher degree than the premaxillary, which may respond more readily to selection imposed from the environment, such as diet.

In Chapter 3, I refined the data sets from Chapter 2 to focus on only the scavenging species and assess previously proposed guild structures and classifications. A primarily scavenger lifestyle has evolved a minimum of four times across the orders Accipitriformes and Falconiformes, with the Cathartidae, Gypaetinae, Aegypiinae, and Polyborinae independently evolving this specialized morphology, as well as the distinct skull features associated with their designated feeding guilds. This analysis generally supported the

guilds proposed by Hertel (1994), but the groups were not without overlap on the PCA morphospace, especially for the gulper and scrapper guilds. The caracaras cannot easily be subdivided into guilds by skull shape alone, but the presence of a guild structure within the subfamily is possible. It may be that they do not readily fit into any of the guilds proposed by previous researchers because they are still evolving towards an optimal morphology for scavenging as vultures already have.

Each of these chapters provided the groundwork for future research, including studies that explore the relationship of the keratinous rhamphotheca to the functional morphology of the beak in raptors and beyond (Chapter 1), a more integrated approach to what modularity in the avian skull may look like when other factors are considered (Chapter 2), and more observational field work to look at the feeding behaviors of the caracara falcons and their interactions with other avian scavengers to establish a more integrated guild structure and explore how these guilds may be changing (Chapter 3).

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Appendices

Appendix 1.1. Measured and landmarked specimens. Skeletal preparations lacked a rhamphotheca unless marked with an asterisk (*) and all skins possessed a rhamphotheca. Abbreviations used in this table are as follows: University of California Museum of Vertebrate Zoology, **MVZ**; Smithsonian National Museum of Natural History, **NMNH**; University of Washington Burke Museum of Natural History and Culture, **UWBM**.

Specimen Number	Specific Epithet	Preparation	Sex	Rham Width (mm)	Rham Height (mm)	Rham Length (mm)	Rham Chord (mm)
MVZ 123919	<i>Pandion haliaetus</i>	skin	female	14.97	30.45	23.03	35.23
UWBM 19946	<i>Pandion haliaetus</i>	skeleton*	unknown	-	-	-	-
MVZ 45847	<i>Pandion haliaetus</i>	skin	unknown	16.51	29.19	24.62	35.16
MVZ 47824	<i>Pandion haliaetus</i>	skeleton	unknown	18.88	15.25	16.35	21.83
MVZ 49450	<i>Pandion haliaetus</i>	skeleton	male	18.01	15.49	17.03	22.39
MVZ 49451	<i>Pandion haliaetus</i>	skeleton	female	20.56	16.68	16.96	24.46
MVZ 49452	<i>Pandion haliaetus</i>	skeleton	female	18.51	16.81	16.82	25.01
MVZ 72442	<i>Pandion haliaetus</i>	skin	unknown	17.42	26.90	23.85	35.07
UWBM 73955	<i>Pandion haliaetus</i>	skeleton	unknown	-	-	-	-
MVZ 85556	<i>Pandion haliaetus</i>	skeleton	female	17.96	17.53	17.32	25.75
MVZ 123920	<i>Pandion haliaetus</i>	skin	male	15.62	29.15	20.46	34.25
MVZ 127237	<i>Pandion haliaetus</i>	skin	unknown	17.70	23.99	21.88	31.92
MVZ 127238	<i>Pandion haliaetus</i>	skin	female	17.10	28.60	20.93	32.90
MVZ 144744	<i>Pandion haliaetus</i>	skin	female	16.01	27.02	24.10	35.36
MVZ 144745	<i>Pandion haliaetus</i>	skin	male	14.99	24.43	24.46	31.81
MVZ 144748	<i>Pandion haliaetus</i>	skin	female	14.98	27.17	22.76	33.62
MVZ 144749	<i>Pandion haliaetus</i>	skin	female	18.43	29.77	26.42	36.17
MVZ 151714	<i>Pandion haliaetus</i>	skeleton	female	17.00	14.61	17.37	21.72
MVZ 151715	<i>Pandion haliaetus</i>	skeleton	male	19.59	15.44	17.37	23.00
MVZ 151716	<i>Pandion haliaetus</i>	skeleton	female	17.62	15.14	16.28	21.89
MVZ 151717	<i>Pandion haliaetus</i>	skeleton	female	17.58	16.02	15.24	21.97
MVZ 154336	<i>Pandion haliaetus</i>	skin	male	16.26	24.58	20.74	30.16
MVZ 155825	<i>Pandion haliaetus</i>	skin	unknown	15.11	27.59	21.14	31.10
MVZ 164585	<i>Pandion haliaetus</i>	skeleton	unknown	18.01	15.19	16.09	21.73
MVZ 175991	<i>Pandion haliaetus</i>	skeleton	male	19.59	17.83	16.86	25.17
USNM 610343	<i>Pandion haliaetus</i>	skeleton	unknown	-	-	-	-
USNM 623392	<i>Pandion haliaetus</i>	skeleton	unknown	-	-	-	-
MVZ 144663	<i>Buteo jamaicensis</i>	skin	male	14.93	23.79	18.55	26.61
MVZ 23242	<i>Buteo jamaicensis</i>	skeleton	male	16.95	15.94	22.92	20.70
MVZ 27614	<i>Buteo jamaicensis</i>	skeleton	unknown	17.70	15.66	22.02	20.56
MVZ 49528	<i>Buteo jamaicensis</i>	skeleton	male	17.65	16.00	18.66	18.65
MVZ 49601	<i>Buteo jamaicensis</i>	skeleton	female	16.43	18.11	18.29	21.19
MVZ 51734	<i>Buteo jamaicensis</i>	skin	female	18.12	23.18	20.81	26.16
MVZ 51735	<i>Buteo jamaicensis</i>	skin	female	15.12	26.11	21.19	29.05

MVZ 53268	<i>Buteo jamaicensis</i>	skin	unknown	15.91	24.65	20.06	28.14
MVZ 64605	<i>Buteo jamaicensis</i>	skeleton	male	14.46	17.86	16.08	20.98
MVZ 66668	<i>Buteo jamaicensis</i>	skeleton	male	13.83	17.03	16.23	19.51
MVZ 66669	<i>Buteo jamaicensis</i>	skeleton	female	13.93	16.50	16.64	20.97
MVZ 68290	<i>Buteo jamaicensis</i>	skeleton*	unknown	10.93	20.76	13.09	22.56
MVZ 88317	<i>Buteo jamaicensis</i>	skin	male	16.05	26.67	20.28	26.98
MVZ 163686	<i>Buteo jamaicensis</i>	skeleton*	unknown	12.96	17.75	18.44	25.47
MVZ 170858	<i>Buteo jamaicensis</i>	skeleton	unknown	15.46	17.89	17.40	22.52
MVZ 179955	<i>Buteo jamaicensis</i>	skeleton	female	17.79	18.44	15.70	22.34
MVZ 179957	<i>Buteo jamaicensis</i>	skeleton*	female	13.68	23.50	16.70	26.20
MVZ 180153	<i>Buteo jamaicensis</i>	skeleton*	female	15.03	25.23	18.26	27.43
MVZ 180155	<i>Buteo jamaicensis</i>	skeleton*	female	13.25	22.86	16.95	25.81
MVZ 180162	<i>Buteo jamaicensis</i>	skeleton	male	15.84	16.41	17.13	19.02
MVZ 184003	<i>Buteo jamaicensis</i>	skeleton*	female	14.44	22.68	17.52	26.51
MVZ 184010	<i>Buteo jamaicensis</i>	skeleton*	female	13.78	25.19	17.87	27.84
MVZ 184012	<i>Buteo jamaicensis</i>	skeleton	female	16.87	18.31	17.08	22.93
MVZ 184013	<i>Buteo jamaicensis</i>	skeleton	female	14.99	19.69	17.42	20.52
MVZ 184014	<i>Buteo jamaicensis</i>	skeleton*	unknown	14.27	17.91	17.36	20.50
MVZ 189772	<i>Buteo jamaicensis</i>	skeleton*	female	11.91	23.21	16.65	24.49
MVZ 190543	<i>Buteo jamaicensis</i>	skeleton	male	12.73	21.88	15.43	24.39
MVZ 190708	<i>Buteo jamaicensis</i>	skin	female	12.96	18.74	14.93	22.84
MVZ 192381	<i>Buteo jamaicensis</i>	skin	female	15.60	24.81	19.22	26.72
MVZ 12687	<i>Cathartes aura</i>	skin	female	14.60	20.52	20.20	23.04
MVZ 5258	<i>Cathartes aura</i>	skin	male	13.60	14.58	16.82	19.96
MVZ 7561	<i>Cathartes aura</i>	skeleton	unknown	14.85	15.23	15.05	18.60
MVZ 7562	<i>Cathartes aura</i>	skeleton	unknown	13.25	21.22	17.67	22.77
MVZ 7844	<i>Cathartes aura</i>	skeleton*	unknown	13.51	22.30	20.38	25.65
MVZ 12713	<i>Cathartes aura</i>	skeleton*	female	13.52	15.04	16.32	18.79
MVZ 19782	<i>Cathartes aura</i>	skeleton	male	15.64	21.27	20.97	23.68
MVZ 24531	<i>Cathartes aura</i>	skeleton	female	14.65	14.47	17.21	17.88
MVZ 25539	<i>Cathartes aura</i>	skin	female	14.73	21.88	20.11	25.57
MVZ 46911	<i>Cathartes aura</i>	skin	female	14.66	22.65	19.18	25.17
MVZ 48416	<i>Cathartes aura</i>	skeleton	female	13.34	15.91	15.99	19.78
MVZ 61810	<i>Cathartes aura</i>	skin	male	13.76	22.73	21.31	26.11
MVZ 62781	<i>Cathartes aura</i>	skeleton	unknown	14.44	16.02	15.50	18.93
MVZ 63474	<i>Cathartes aura</i>	skeleton	male	14.32	14.29	15.64	17.76
MVZ 63475	<i>Cathartes aura</i>	skeleton	female	14.57	15.56	14.80	19.27
MVZ 65107	<i>Cathartes aura</i>	skeleton	unknown	12.83	13.63	15.86	18.95
MVZ 65173	<i>Cathartes aura</i>	skeleton	unknown	14.05	15.87	14.46	18.73
MVZ 65174	<i>Cathartes aura</i>	skeleton	female	14.01	15.35	15.91	18.60
MVZ 74187	<i>Cathartes aura</i>	skin	female	13.85	22.13	21.87	24.61
MVZ 99629	<i>Cathartes aura</i>	skin	male	14.61	22.45	21.87	24.61
MVZ 129623	<i>Cathartes aura</i>	skin	female	14.29	20.21	20.72	22.90
MVZ 142415	<i>Cathartes aura</i>	skin	male	14.09	21.84	23.18	24.00

MVZ 144612	<i>Cathartes aura</i>	skin	male	15.17	22.15	22.68	25.78
MVZ 151676	<i>Cathartes aura</i>	skeleton	male	14.50	15.06	15.79	17.83
MVZ 151677	<i>Cathartes aura</i>	skeleton	female	14.41	14.22	16.26	18.81
MVZ 151678	<i>Cathartes aura</i>	skeleton	female	13.38	14.18	16.06	18.24
MVZ 166158	<i>Cathartes aura</i>	skeleton	unknown	13.39	17.22	14.82	19.88
MVZ 166169	<i>Cathartes aura</i>	skeleton*	unknown	14.30	21.24	16.82	24.34
MVZ 175990	<i>Cathartes aura</i>	skeleton*	unknown	15.04	21.39	18.52	24.28
MVZ 179934	<i>Cathartes aura</i>	skeleton	female	13.60	15.44	15.82	19.56
MVZ 179935	<i>Cathartes aura</i>	skeleton*	male	13.47	15.32	14.09	19.73
MVZ 179936	<i>Cathartes aura</i>	skeleton*	male	14.46	21.15	17.71	23.33
MVZ 179938	<i>Cathartes aura</i>	skeleton	unknown	12.5	18.47	19.55	21.04
MVZ 180653	<i>Cathartes aura</i>	skin	male	14.21	21.50	17.84	23.43
MVZ 184116	<i>Cathartes aura</i>	skeleton	male	12.02	15.49	14.29	17.62
MVZ 189660	<i>Cathartes aura</i>	skeleton*	unknown	14.63	21.43	23.70	24.72
MVZ 189661	<i>Cathartes aura</i>	skeleton*	unknown	12.32	20.31	18.01	22.59
MVZ 189662	<i>Cathartes aura</i>	skeleton	unknown	15.57	15.20	16.50	18.93
MVZ 189663	<i>Cathartes aura</i>	skeleton*	unknown	14.08	20.31	20.62	22.97
MVZ 144757	<i>Falco mexicanus</i>	skin	female	13.36	20.60	20.02	22.01
MVZ 768	<i>Falco mexicanus</i>	skin	male	12.78	18.06	16.85	19.62
MVZ 9316	<i>Falco mexicanus</i>	skin	male	14.51	17.24	16.30	18.15
MVZ 24928	<i>Falco mexicanus</i>	skin	male	13.97	16.44	16.44	17.73
MVZ 41228	<i>Falco mexicanus</i>	skeleton	female	14.00	12.12	13.65	16.32
MVZ 43430	<i>Falco mexicanus</i>	skin	female	12.88	20.31	15.12	21.26
MVZ 47944	<i>Falco mexicanus</i>	skin	male	14.03	18.19	13.50	18.59
MVZ 53637	<i>Falco mexicanus</i>	skin	female	17.92	20.84	19.67	22.41
MVZ 53638	<i>Falco mexicanus</i>	skin	male	14.92	17.92	13.98	19.33
MVZ 54317	<i>Falco mexicanus</i>	skeleton	female	14.36	12.60	15.38	17.19
MVZ 54539	<i>Falco mexicanus</i>	skin	female	14.94	20.30	16.90	21.49
MVZ 57320	<i>Falco mexicanus</i>	skin	male	13.62	16.73	17.71	18.47
MVZ 68692	<i>Falco mexicanus</i>	skeleton	male	14.92	12.07	12.61	15.41
MVZ 68693	<i>Falco mexicanus</i>	skeleton	female	14.56	14.09	13.65	17.28
MVZ 68694	<i>Falco mexicanus</i>	skeleton	male	13.37	10.92	11.75	15.40
MVZ 79002	<i>Falco mexicanus</i>	skeleton	male	14.51	12.19	10.78	14.86
MVZ 79003	<i>Falco mexicanus</i>	skeleton	male	14.86	10.61	13.80	14.48
MVZ 79030	<i>Falco mexicanus</i>	skeleton	male	12.91	11.58	13.32	15.46
MVZ 84719	<i>Falco mexicanus</i>	skeleton	female	13.87	14.74	13.46	17.46
MVZ 144761	<i>Falco mexicanus</i>	skin	male	14.14	18.76	18.39	19.71
MVZ 144762	<i>Falco mexicanus</i>	skin	female	13.62	20.80	19.81	22.30
MVZ 144763	<i>Falco mexicanus</i>	skin	male	14.83	17.22	16.36	18.71
MVZ 151719	<i>Falco mexicanus</i>	skeleton	male	10.80	11.69	11.89	15.01
MVZ 151720	<i>Falco mexicanus</i>	skeleton	female	15.99	13.19	14.49	18.16
MVZ 180452	<i>Falco mexicanus</i>	skin	female	15.68	21.10	17.37	22.32
MVZ 183062	<i>Falco mexicanus</i>	skeleton	female	15.69	15.13	14.45	16.52
MVZ 185324	<i>Falco mexicanus</i>	skeleton	female	14.34	14.07	16.01	18.48

MVZ 187789	<i>Falco mexicanus</i>	skeleton	female	18.12	14.46	17.17	18.54
MVZ 189499	<i>Falco mexicanus</i>	skeleton	female	15.00	14.32	13.65	17.46
MVZ 192260	<i>Falco mexicanus</i>	skin	male	14.54	17.07	13.89	18.38
MVZ 5940	<i>Bubo virginianus</i>	skin	female	18.69	27.78	21.08	30.46
MVZ 7936	<i>Bubo virginianus</i>	skin	male	18.66	22.37	18.86	25.45
MVZ 17040	<i>Bubo virginianus</i>	skeleton	female	17.27	20.05	17.87	21.70
MVZ 26175	<i>Bubo virginianus</i>	skeleton	unknown	14.85	17.41	16.63	19.62
MVZ 28985	<i>Bubo virginianus</i>	skeleton	unknown	15.37	20.96	15.99	23.32
MVZ 31268	<i>Bubo virginianus</i>	skin	female	20.03	24.03	17.63	29.43
MVZ 32353	<i>Bubo virginianus</i>	skin	female	18.51	25.44	22.14	27.96
MVZ 40426	<i>Bubo virginianus</i>	skeleton	unknown	12.08	18.97	14.28	21.15
MVZ 45341	<i>Bubo virginianus</i>	skin	male	18.65	24.95	17.14	27.32
MVZ 53650	<i>Bubo virginianus</i>	skeleton	unknown	17.40	19.53	16.00	20.04
MVZ 56443	<i>Bubo virginianus</i>	skin	male	15.68	23.38	19.39	26.57
MVZ 59111	<i>Bubo virginianus</i>	skin	male	18.90	24.88	19.78	26.99
MVZ 66530	<i>Bubo virginianus</i>	skin	female	20.93	27.65	23.98	29.20
MVZ 66700	<i>Bubo virginianus</i>	skeleton	female	15.09	16.91	17.91	10.00
MVZ 66701	<i>Bubo virginianus</i>	skeleton	male	15.95	18.41	17.84	18.99
MVZ 67980	<i>Bubo virginianus</i>	skin	male	17.54	25.88	20.56	28.02
MVZ 68054	<i>Bubo virginianus</i>	skin	male	16.94	25.25	19.88	27.72
MVZ 79387	<i>Bubo virginianus</i>	skeleton	male	13.95	18.85	19.46	24.05
MVZ 87455	<i>Bubo virginianus</i>	skin	male	17.66	25.53	17.05	27.43
MVZ 87456	<i>Bubo virginianus</i>	skin	female	16.25	25.97	19.81	27.91
MVZ 91788	<i>Bubo virginianus</i>	skin	male	17.24	24.12	24.40	28.34
MVZ 93665	<i>Bubo virginianus</i>	skin	female	19.43	26.75	21.18	27.89
MVZ 145454	<i>Bubo virginianus</i>	skin	male	17.06	24.97	21.56	26.38
MVZ 151860	<i>Bubo virginianus</i>	skeleton*	male	17.06	26.16	20.21	27.88
MVZ 151862	<i>Bubo virginianus</i>	skeleton	male	15.61	19.49	20.34	23.26
MVZ 151865	<i>Bubo virginianus</i>	skeleton	female	11.15	19.43	12.54	21.54
MVZ 151866	<i>Bubo virginianus</i>	skeleton	female	17.14	20.94	17.94	22.12
MVZ 151868	<i>Bubo virginianus</i>	skeleton	male	14.59	18.11	17.16	18.71
MVZ 162348	<i>Bubo virginianus</i>	skeleton*	female	17.17	27.51	19.44	29.88
MVZ 176053	<i>Bubo virginianus</i>	skeleton*	unknown	16.49	27.70	19.67	28.12
MVZ 176054	<i>Bubo virginianus</i>	skeleton*	unknown	15.09	24.23	19.15	26.09
MVZ 180468	<i>Bubo virginianus</i>	skeleton*	male	15.67	26.13	20.17	26.93
MVZ 182833	<i>Bubo virginianus</i>	skin	male	17.35	26.40	21.12	29.04
MVZ 184099	<i>Bubo virginianus</i>	skeleton	female	13.92	19.25	17.54	21.26
MVZ 184100	<i>Bubo virginianus</i>	skeleton	female	16.05	20.42	18.97	21.48
MVZ 184101	<i>Bubo virginianus</i>	skeleton	male	16.45	20.07	19.24	22.07
MVZ 185328	<i>Bubo virginianus</i>	skeleton	unknown	15.10	20.63	21.00	23.38
MVZ 186062	<i>Bubo virginianus</i>	skeleton*	unknown	15.74	23.67	18.68	25.23
MVZ 189460	<i>Bubo virginianus</i>	skeleton	female	13.81	19.56	23.20	23.32
MVZ 189490	<i>Bubo virginianus</i>	skeleton	male	12.12	17.90	14.99	19.92
MVZ 189785	<i>Bubo virginianus</i>	skeleton	female	15.68	21.06	18.54	23.54

MVZ 192172	<i>Bubo virginianus</i>	skeleton*	female	16.97	27.22	21.29	-
MVZ 192385	<i>Bubo virginianus</i>	skeleton	male	14.81	18.16	17.49	19.48

Appendix 2.1. Comprehensive list of landmarked specimens. Abbreviations used in this table are as follows: British Museum of Natural History, **BMNH**; Natural History Museum of Los Angeles County, **NHMLA**; University of California Museum of Vertebrate Zoology, **MVZ**; Natural History Museum, **NHMK**; University of California Museum of Paleontology, **UCMP**; Smithsonian National Museum of Natural History, **NMNH**; University of Washington Burke Museum of Natural History and Culture, **UWBM**.

Genus	Species	Sex	Institution	ID	Element	Fossil	Scavenger
<i>Accipiter</i>	<i>bicolor</i>	M	MVZ	120712	skull	No	No
<i>Accipiter</i>	<i>cirrhocephalus</i>	M	UWBM	62799	skull	No	No
<i>Accipiter</i>	<i>cirrhocephalus</i>	M	UWBM	62860	skull	No	No
<i>Accipiter</i>	<i>cirrhocephalus</i>	M	UWBM	62903	skull	No	No
<i>Accipiter</i>	<i>cooperii</i>	M	MVZ	183983	skull	No	No
<i>Accipiter</i>	<i>gentilis</i>	M	MVZ	77815	skull	No	No
<i>Accipiter</i>	<i>gentilis</i>	F	MVZ	151682	skull	No	No
<i>Accipiter</i>	<i>gularis</i>	M	UWBM	59708	skull	No	No
<i>Accipiter</i>	<i>gularis</i>	M	UWBM	59884	skull	No	No
<i>Accipiter</i>	<i>nisus</i>	M	MVZ	140784	skull	No	No
<i>Accipiter</i>	<i>nisus</i>	M	MVZ	140785	skull	No	No
<i>Accipiter</i>	<i>nisus</i>	M	MVZ	140786	skull	No	No
<i>Accipiter</i>	<i>nisus</i>	M	MVZ	140787	skull	No	No
<i>Accipiter</i>	<i>novaehollandiae</i>	F	UWBM	63170	skull	No	No
<i>Accipiter</i>	<i>striatus</i>	F	MVZ	64626	skull	No	No
<i>Accipiter</i>	<i>striatus</i>	F	MVZ	177775	skull	No	No
<i>Accipiter</i>	<i>striatus</i>	F	MVZ	179318	skull	No	No
<i>Accipiter</i>	<i>virgatus</i>	F	UWBM	54182	skull	No	No
<i>Aegypius</i>	<i>monachus</i>	U	BMNH	UnN	skull	No	Yes
<i>Aegypius</i>	<i>monachus</i>	F	NMNH	428040	skull	No	Yes
<i>Aegypius</i>	<i>monachus</i>	U	NMNH	614152	skull	No	Yes
<i>Aquila</i>	<i>audax</i>	F	MVZ	143342	skull	No	No
<i>Aquila</i>	<i>audax</i>	U	MVZ	154316	skull	No	No
<i>Aquila</i>	<i>audax</i>	F	MVZ	155855	skull	No	No
<i>Aquila</i>	<i>audax</i>	U	MVZ	156031	skull	No	No
<i>Aquila</i>	<i>chrysaetos</i>	U	NHMLA	D165	crania	Yes	No
<i>Aquila</i>	<i>chrysaetos</i>	U	NHMLA	D6636	premaxillary	Yes	No
<i>Aquila</i>	<i>chrysaetos</i>	U	MVZ	115931	skull	No	No
<i>Aquila</i>	<i>chrysaetos</i>	F	MVZ	120362	skull	No	No
<i>Aquila</i>	<i>chrysaetos</i>	F	MVZ	151703	skull	No	No
<i>Aquila</i>	<i>chrysaetos</i>	U	UCMP	299794	crania	Yes	No
<i>Aquila</i>	<i>rapax</i>	F	NHMLA	88915	skull	No	No
<i>Aquila</i>	Unknown species	U	NHMLA	R12167	skull	Yes	No
<i>Aviceda</i>	<i>leuphotes</i>	F	UWBM	76131	skull	No	No
<i>Aviceda</i>	<i>subcristata</i>	F	MVZ	149271	skull	No	No
<i>Aviceda</i>	<i>subcristata</i>	F	NMNH	558306	skull	No	No
<i>Aviceda</i>	<i>subcristata</i>	F	UWBM	58695	skull	No	No
† <i>Breagyps</i>	† <i>clarki</i>	U	NHMLA	B3148	crania	Yes	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	NHMLA	J9071	premaxillary	Yes	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	NHMLA	UnN	skull	Yes	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	UCMP	28074	crania	Yes	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	UCMP	28077	crania	Yes	Yes
<i>Busarellus</i>	<i>nigricollis</i>	M	MVZ	85550	skull	No	No
<i>Busarellus</i>	<i>nigricollis</i>	M	NMNH	345773	skull	No	No
<i>Busarellus</i>	<i>nigricollis</i>	F	NMNH	431130	skull	No	No
<i>Busarellus</i>	<i>nigricollis</i>	U	NMNH	500622	skull	No	No
<i>Butastur</i>	<i>indicus</i>	F	MVZ	150967	skull	No	No
<i>Butastur</i>	<i>indicus</i>	U	NMNH	223986	skull	No	No
<i>Butastur</i>	<i>indicus</i>	F	NMNH	611765	skull	No	No

<i>Buteo</i>	<i>borealis</i>	U	UCMP	264323	skull	Yes	No
<i>Buteo</i>	<i>buteo</i>	U	MVZ	60219	skull	No	No
<i>Buteo</i>	<i>buteo</i>	M	MVZ	135141	skull	No	No
<i>Buteo</i>	<i>buteo</i>	U	MVZ	166159	skull	No	No
<i>Buteo</i>	<i>galapagoensis</i>	U	MVZ	134061	skull	No	No
<i>Buteo</i>	<i>galapagoensis</i>	U	MVZ	134080	skull	No	No
<i>Buteo</i>	<i>galapagoensis</i>	F	MVZ	140936	skull	No	No
<i>Buteo</i>	<i>galapagoensis</i>	M	MVZ	140937	skull	No	No
<i>Buteo</i>	<i>jamaicensis</i>	M	MVZ	66668	skull	No	No
<i>Buteo</i>	<i>jamaicensis</i>	F	MVZ	66669	skull	No	No
<i>Buteo</i>	<i>jamaicensis</i>	M	MVZ	180162	skull	No	No
<i>Buteo</i>	<i>jamaicensis</i>	F	MVZ	184013	skull	No	No
<i>Buteo</i>	<i>japonicus</i>	F	MVZ	135038	skull	No	No
<i>Buteo</i>	<i>japonicus</i>	F	MVZ	137504	skull	No	No
<i>Buteo</i>	<i>japonicus</i>	M	MVZ	149441	skull	No	No
<i>Buteo</i>	<i>japonicus</i>	M	MVZ	150925	skull	No	No
<i>Buteo</i>	<i>lagopus</i>	U	MVZ	7579	skull	No	No
<i>Buteo</i>	<i>lagopus</i>	U	MVZ	7580	skull	No	No
<i>Buteo</i>	<i>lagopus</i>	U	MVZ	7581	skull	No	No
<i>Buteo</i>	<i>lagopus</i>	F	MVZ	75116	skull	No	No
<i>Buteo</i>	<i>lineatus</i>	F	MVZ	179323	skull	No	No
<i>Buteo</i>	<i>lineatus</i>	M	MVZ	179324	skull	No	No
<i>Buteo</i>	<i>lineatus</i>	F	MVZ	183991	skull	No	No
<i>Buteo</i>	<i>nitidus</i>	F	NHMLA	86872	skull	No	No
<i>Buteo</i>	<i>plagiatusi</i>	M	MVZ	74854	skull	No	No
<i>Buteo</i>	<i>plagiatusi</i>	M	MVZ	78684	skull	No	No
<i>Buteo</i>	<i>plagiatusi</i>	M	MVZ	85539	skull	No	No
<i>Buteo</i>	<i>platypterus</i>	U	NHMLA	122432	skull	No	No
<i>Buteo</i>	<i>platypterus</i>	F	MVZ	125738	skull	No	No
<i>Buteo</i>	<i>regalis</i>	F	MVZ	84650	skull	No	No
<i>Buteo</i>	<i>sanctijohannis</i>	F	NHMLA	101392	skull	No	No
<i>Buteo</i>	<i>sanctijohannis</i>	M	NHMLA	112989	skull	No	No
<i>Buteo</i>	<i>solitarius</i>	F	UWBM	65841	skull	No	No
<i>Buteo</i>	<i>swainsoni</i>	U	NHMLA	J8712	premaxillary	Yes	No
<i>Buteo</i>	<i>swainsoni</i>	U	NHMLA	J8712	skull	Yes	No
<i>Buteo</i>	<i>swainsoni</i>	F	MVZ	68832	skull	No	No
<i>Buteo</i>	<i>swainsoni</i>	U	UCMP	264229	premaxillary	Yes	No
<i>Buteo</i>	<i>swainsoni</i>	U	UCMP	264230	premaxillary	Yes	No
<i>Buteo</i>	Unknown species	F	NHMLA	110094	skull	No	No
<i>Buteo</i>	Unknown species	U	NHMLA	110103	skull	No	No
<i>Buteo</i>	Unknown species	F	NHMLA	110104	skull	No	No
<i>Buteo</i>	Unknown species	U	UCMP	264246	crania	Yes	No
<i>Buteogallus</i>	<i>anthracinus</i>	M	MVZ	85545	skull	No	No
<i>Buteogallus</i>	<i>anthracinus</i>	M	MVZ	85547	skull	No	No
<i>Buteogallus</i>	<i>meridionalis</i>	M	MVZ	94066	skull	No	No
<i>Buteogallus</i>	<i>urubitinga</i>	F	MVZ	85542	skull	No	No
<i>Caracara</i>	<i>cheriway</i>	M	MVZ	74750	skull	No	Yes
<i>Caracara</i>	<i>cheriway</i>	F	MVZ	74855	skull	No	Yes
<i>Caracara</i>	<i>cheriway</i>	F	MVZ	85563	skull	No	Yes
<i>Caracara</i>	<i>cheriway</i>	M	MVZ	94070	skull	No	Yes
<i>Caracara</i>	<i>cheriway</i>	F	MVZ	120713	skull	No	Yes
<i>Caracara</i>	<i>cheriway</i>	M	MVZ	151718	skull	No	Yes
<i>Caracara</i>	<i>plancus</i>	M	UWBM	90170	skull	No	Yes
<i>Caracara</i>	<i>plancus</i>	F	UWBM	90171	skull	No	Yes
<i>Cariama</i>	<i>cristata</i>	U	MVZ	135153	skull	No	No
<i>Cariama</i>	<i>cristata</i>	F	MVZ	178928	skull	No	No
<i>Cariama</i>	<i>cristata</i>	U	NMNH	321574	skull	No	No

<i>Cariama</i>	<i>cristata</i>	M	NMNH	631175	skull	No	No
<i>Cathartes</i>	<i>aura</i>	M	MVZ	63474	skull	No	Yes
<i>Cathartes</i>	<i>aura</i>	F	MVZ	63475	skull	No	Yes
<i>Cathartes</i>	<i>aura</i>	F	MVZ	151678	skull	No	Yes
<i>Cathartes</i>	<i>aura</i>	F	MVZ	179934	skull	No	Yes
<i>Cathartes</i>	<i>aura</i>	U	MVZ	179938	skull	No	Yes
<i>Cathartes</i>	<i>aura</i>	U	UCMP	299110	skull	Yes	Yes
<i>Cathartes</i>	<i>burrovianus</i>	M	NMNH	622341	skull	No	Yes
<i>Cathartes</i>	<i>burrovianus</i>	M	NMNH	623071	skull	No	Yes
<i>Cathartes</i>	<i>burrovianus</i>	F	NMNH	632359	skull	No	Yes
<i>Cathartes</i>	<i>burrovianus</i>	F	NMNH	632364	skull	No	Yes
<i>Cathartes</i>	<i>melambrotus</i>	F	NMNH	559319	skull	No	Yes
<i>Cathartes</i>	<i>melambrotus</i>	F	NMNH	621939	skull	No	Yes
<i>Cathartes</i>	<i>melambrotus</i>	M	NMNH	637139	skull	No	Yes
<i>Cathartes</i>	Unknown species	U	UCMP	299097	premaxillary	Yes	Yes
<i>Cathartes</i>	Unknown species	U	UCMP	299107	crania	Yes	Yes
<i>Chondrohierax</i>	<i>uncinatus</i>	F	NMNH	611557	skull	No	No
<i>Chunga</i>	<i>burmeisteri</i>	F	NHMLA	88970	skull	No	No
<i>Circaetus</i>	<i>cinereus</i>	M	NMNH	430776	skull	No	No
<i>Circaetus</i>	<i>gallicus</i>	F	NMNH	430827	skull	No	No
<i>Circus</i>	<i>aeruginosus</i>	M	UWBM	56450	skull	No	No
<i>Circus</i>	<i>aeruginosus</i>	M	UWBM	56456	skull	No	No
<i>Circus</i>	<i>approximans</i>	M	UWBM	60455	skull	No	No
<i>Circus</i>	<i>approximans</i>	F	UWBM	78153	skull	No	No
<i>Circus</i>	<i>hudsonius</i>	M	MVZ	65111	skull	No	No
<i>Circus</i>	<i>hudsonius</i>	M	MVZ	65115	skull	No	No
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	66913	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	M	MVZ	78681	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	M	MVZ	79208	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	F	MVZ	79209	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	M	MVZ	79210	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	151679	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	175989	skull	No	Yes
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	180366	skull	No	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7017	crania	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7088	crania	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7895	crania	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7980	crania	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	UnN	skull	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	UCMP	10409	crania	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	UCMP	28086	crania	Yes	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	UCMP	299593	crania	Yes	Yes
<i>Coragyps</i>	Unknown species	U	NHMLA	E531	premaxillary	Yes	Yes
<i>Coragyps</i>	Unknown species	U	NHMLA	UnN	premaxillary	Yes	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299098	premaxillary	Yes	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299099	premaxillary	Yes	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299105	crania	Yes	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299108	premaxillary	Yes	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299157	crania	Yes	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299158	crania	Yes	Yes
<i>Daptrius</i>	<i>americanus</i>	M	NMNH	621388	skull	No	Yes
<i>Daptrius</i>	<i>americanus</i>	M	NMNH	621943	skull	No	Yes
<i>Daptrius</i>	<i>americanus</i>	F	NMNH	632410	skull	No	Yes
<i>Daptrius</i>	<i>ater</i>	F	NMNH	226167	skull	No	Yes
<i>Daptrius</i>	<i>ater</i>	M	NMNH	345776	skull	No	Yes
<i>Daptrius</i>	<i>ater</i>	F	NMNH	345777	skull	No	Yes
<i>Elanoides</i>	<i>forficatus</i>	M	MVZ	120956	skull	No	No

<i>Elanoides</i>	<i>forficatus</i>	F	MVZ	141724	skull	No	No
<i>Elanoides</i>	<i>forficatus</i>	F	MVZ	141725	skull	No	No
<i>Elanus</i>	<i>axillaris</i>	F	UWBM	62878	skull	No	No
<i>Elanus</i>	<i>leucurus</i>	U	MVZ	79327	skull	No	No
<i>Elanus</i>	<i>leucurus</i>	F	MVZ	124707	skull	No	No
<i>Elanus</i>	<i>leucurus</i>	U	MVZ	161438	skull	No	No
<i>Falco</i>	<i>berigora</i>	F	MVZ	143347	skull	No	No
<i>Falco</i>	<i>berigora</i>	F	MVZ	143348	skull	No	No
<i>Falco</i>	<i>berigora</i>	M	MVZ	143350	skull	No	No
<i>Falco</i>	<i>berigora</i>	M	MVZ	143351	skull	No	No
<i>Falco</i>	<i>biarmicus</i>	U	NMNH	620138	skull	No	No
<i>Falco</i>	<i>cenchroides</i>	M	MVZ	138014	skull	No	No
<i>Falco</i>	<i>cenchroides</i>	F	MVZ	143345	skull	No	No
<i>Falco</i>	<i>cenchroides</i>	F	NMNH	620193	skull	No	No
<i>Falco</i>	<i>cenchroides</i>	F	NMNH	620194	skull	No	No
<i>Falco</i>	<i>cherrug</i>	F	NMNH	500262	skull	No	No
<i>Falco</i>	<i>cherrug</i>	M	NMNH	500263	skull	No	No
<i>Falco</i>	<i>columbarius</i>	F	MVZ	15631	skull	No	No
<i>Falco</i>	<i>columbarius</i>	U	MVZ	79023	skull	No	No
<i>Falco</i>	<i>columbarius</i>	F	MVZ	134742	skull	No	No
<i>Falco</i>	<i>femoralis</i>	M	MVZ	125173	skull	No	No
<i>Falco</i>	<i>femoralis</i>	M	NMNH	614586	skull	No	No
<i>Falco</i>	<i>femoralis</i>	F	NMNH	622320	skull	No	No
<i>Falco</i>	<i>femoralis</i>	F	NMNH	630186	skull	No	No
<i>Falco</i>	<i>mexicanus</i>	M	MVZ	79002	skull	No	No
<i>Falco</i>	<i>mexicanus</i>	M	MVZ	79003	skull	No	No
<i>Falco</i>	<i>mexicanus</i>	F	MVZ	84719	skull	No	No
<i>Falco</i>	<i>mexicanus</i>	M	MVZ	151719	skull	No	No
<i>Falco</i>	<i>moluccensis</i>	F	NMNH	558272	skull	No	No
<i>Falco</i>	<i>moluccensis</i>	M	NMNH	560786	skull	No	No
<i>Falco</i>	<i>naumanni</i>	F	NMNH	603407	skull	No	No
<i>Falco</i>	<i>naumanni</i>	F	NMNH	603408	skull	No	No
<i>Falco</i>	<i>naumanni</i>	F	UWBM	60035	skull	No	No
<i>Falco</i>	<i>peregrinus</i>	U	MVZ	7563	skull	No	No
<i>Falco</i>	<i>peregrinus</i>	M	MVZ	77260	skull	No	No
<i>Falco</i>	<i>peregrinus</i>	U	MVZ	89963	skull	No	No
<i>Falco</i>	<i>peregrinus</i>	U	MVZ	135039	skull	No	No
<i>Falco</i>	<i>ruficularis</i>	M	MVZ	85564	skull	No	No
<i>Falco</i>	<i>ruficularis</i>	U	NMNH	289804	skull	No	No
<i>Falco</i>	<i>ruficularis</i>	F	NMNH	556276	skull	No	No
<i>Falco</i>	<i>ruficularis</i>	F	NMNH	612263	skull	No	No
<i>Falco</i>	<i>rusticolus</i>	F	MVZ	134736	skull	No	No
<i>Falco</i>	<i>rusticolus</i>	F	MVZ	134737	skull	No	No
<i>Falco</i>	<i>rusticolus</i>	F	MVZ	137248	skull	No	No
<i>Falco</i>	<i>rusticolus</i>	F	MVZ	141174	skull	No	No
<i>Falco</i>	<i>sparverius</i>	M	MVZ	79291	skull	No	No
<i>Falco</i>	<i>sparverius</i>	M	MVZ	184016	skull	No	No
<i>Falco</i>	<i>sparverius</i>	F	MVZ	184035	skull	No	No
<i>Falco</i>	<i>subbuteo</i>	F	NMNH	431432	skull	No	No
<i>Falco</i>	<i>subbuteo</i>	M	NMNH	603410	skull	No	No
<i>Falco</i>	<i>subbuteo</i>	F	NMNH	621279	skull	No	No
<i>Falco</i>	<i>swarhi</i>	U	UCMP	30953	premaxillary	Yes	No
<i>Falco</i>	<i>tinnunculus</i>	U	MVZ	115933	skull	No	No
<i>Falco</i>	<i>tinnunculus</i>	F	MVZ	149442	skull	No	No
<i>Falco</i>	<i>tinnunculus</i>	M	MVZ	150926	skull	No	No
<i>Falco</i>	<i>tinnunculus</i>	F	MVZ	152912	skull	No	No
<i>Falco</i>	<i>vespertinus</i>	U	NMNH	289434	skull	No	No

<i>Falco</i>	<i>vespertinus</i>	M	NMNH	621208	skull	No	No
<i>Falco</i>	<i>vespertinus</i>	F	NMNH	642634	skull	No	No
<i>Falco</i>	<i>vespertinus</i>	F	UWBM	56486	skull	No	No
<i>Gampsonyx</i>	<i>swainsonii</i>	F	NMNH	345789	skull	No	No
<i>Gampsonyx</i>	<i>swainsonii</i>	F	NMNH	622231	skull	No	No
<i>Gampsonyx</i>	<i>swainsonii</i>	F	NMNH	623084	skull	No	No
<i>Gampsonyx</i>	<i>swainsonii</i>	M	NMNH	623110	skull	No	No
<i>Geranoaetus</i>	<i>melanoleucus</i>	U	NMNH	318388	skull	No	No
<i>Geranoaetus</i>	<i>melanoleucus</i>	M	NMNH	319429	skull	No	No
<i>Geranoaetus</i>	<i>melanoleucus</i>	F	NMNH	429821	skull	No	No
<i>Geranoaetus</i>	<i>polyosoma</i>	M	MVZ	125169	skull	No	No
<i>Geranospiza</i>	<i>caerulescens</i>	M	MVZ	74747	skull	No	No
<i>Geranospiza</i>	<i>caerulescens</i>	M	MVZ	78685	skull	No	No
<i>Geranospiza</i>	<i>caerulescens</i>	F	MVZ	85555	skull	No	No
<i>Geranospiza</i>	<i>caerulescens</i>	F	MVZ	94068	skull	No	No
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	B1869	premaxillary	Yes	Yes
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	B1968	premaxillary	Yes	Yes
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	B2050	crania	Yes	Yes
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	B2050	skull	Yes	Yes
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	B8010	crania	Yes	Yes
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	F3245	crania	Yes	Yes
<i>Gymnogyps</i>	<i>†amplus</i>	U	NHMLA	UnN	skull	Yes	Yes
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	23459	skull	No	Yes
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	74888	skull	No	Yes
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	131373	skull	No	Yes
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	151086	skull	No	Yes
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	151087	skull	No	Yes
<i>Gymnogyps</i>	Unknown species	U	MVZ	133377	skull	Yes	Yes
<i>Gymnogyps</i>	Unknown species	U	UCMP	12103	skull	Yes	Yes
<i>Gymnogyps</i>	Unknown species	U	UCMP	22983	skull	Yes	Yes
<i>Gymnogyps</i>	Unknown species	U	UCMP	299082	skull	Yes	Yes
<i>Gypaetus</i>	<i>barbatus</i>	U	NMNH	17834	skull	No	Yes
<i>Gypaetus</i>	<i>barbatus</i>	U	NMNH	19383	skull	No	Yes
<i>Gypaetus</i>	<i>barbatus</i>	F	NMNH	345684	skull	No	Yes
<i>Gypohierax</i>	<i>angolensis</i>	U	NMNH	18892	skull	No	Yes
<i>Gypohierax</i>	<i>angolensis</i>	U	NMNH	224820	skull	No	Yes
<i>Gypohierax</i>	<i>angolensis</i>	F	NMNH	291078	skull	No	Yes
<i>Gyps</i>	<i>africanus</i>	M	NMNH	430014	skull	No	Yes
<i>Gyps</i>	<i>africanus</i>	M	NMNH	430016	skull	No	Yes
<i>Gyps</i>	<i>africanus</i>	F	NMNH	431403	skull	No	Yes
<i>Gyps</i>	<i>africanus</i>	F	NMNH	431591	skull	No	Yes
<i>Gyps</i>	<i>bengolensis</i>	U	NHMLA	116946	skull	No	Yes
<i>Gyps</i>	<i>coprotheres</i>	U	NMNH	561314	skull	No	Yes
<i>Gyps</i>	<i>fulvus</i>	F	NMNH	227051	skull	No	Yes
<i>Gyps</i>	<i>himilayensis</i>	M	NMNH	19534	skull	No	Yes
<i>Gyps</i>	<i>indicus</i>	U	NHMLA	86840	skull	No	Yes
<i>Gyps</i>	<i>ruppellii</i>	U	NMNH	430178	skull	No	Yes
<i>Gyps</i>	<i>tenuirostris</i>	U	BMNH	Unk	premaxillary	No	Yes
<i>Haliaeetus</i>	<i>leucocephalus</i>	U	NHMLA	K3123	skull	Yes	No
<i>Haliaeetus</i>	<i>leucocephalus</i>	F	MVZ	8326	skull	No	No
<i>Haliaeetus</i>	<i>leucocephalus</i>	M	MVZ	131005	skull	No	No
<i>Haliaeetus</i>	<i>leucocephalus</i>	U	MVZ	136146	skull	No	No
<i>Haliaeetus</i>	<i>leucocephalus</i>	U	MVZ	159643	skull	No	No
<i>Haliaeetus</i>	<i>leucogaster</i>	F	MVZ	137898	skull	No	No
<i>Haliastur</i>	<i>indus</i>	F	NMNH	347774	skull	No	No
<i>Haliastur</i>	<i>indus</i>	M	NMNH	430052	skull	No	No
<i>Haliastur</i>	<i>indus</i>	M	NMNH	556983	skull	No	No

<i>Haliastur</i>	<i>indus</i>	F	NMNH	556984	skull	No	No
<i>Haliastur</i>	<i>indus</i>	M	UWBM	58751	skull	No	No
<i>Haliastur</i>	<i>indus</i>	M	UWBM	83495	skull	No	No
<i>Haliastur</i>	<i>indus</i>	F	UWBM	117124	skull	No	No
<i>Haliastur</i>	<i>sphenurus</i>	F	MVZ	143339	skull	No	No
<i>Haliastur</i>	<i>sphenurus</i>	F	MVZ	143340	skull	No	No
<i>Harpagus</i>	<i>bidentatus</i>	F	MVZ	158073	skull	No	No
<i>Harpagus</i>	<i>bidentatus</i>	F	NMNH	559320	skull	No	No
<i>Harpagus</i>	<i>bidentatus</i>	F	NMNH	612259	skull	No	No
<i>Harpagus</i>	<i>bidentatus</i>	F	NMNH	632282	skull	No	No
<i>Harpia</i>	<i>harpyja</i>	U	NHMLA	104437	skull	No	No
<i>Harpia</i>	<i>harpyja</i>	U	NMNH	11108	skull	No	No
<i>Harpia</i>	<i>harpyja</i>	F	NMNH	429223	skull	No	No
<i>Harpia</i>	<i>harpyja</i>	F	NMNH	429721	skull	No	No
<i>Harpyhaliaetus</i>	<i>solitarius</i>	F	NHMLA	110091	skull	No	No
<i>Herpetotheres</i>	<i>cachinnans</i>	M	MVZ	85557	skull	No	No
<i>Herpetotheres</i>	<i>cachinnans</i>	F	NMNH	227379	skull	No	No
<i>Herpetotheres</i>	<i>cachinnans</i>	M	NMNH	346714	skull	No	No
<i>Hieraetus</i>	<i>morphnoides</i>	F	MVZ	143341	skull	No	No
<i>Hypomorphnus</i>	<i>fragilis</i>	U	NHMLA	UnN	skull	Yes	No
<i>Ictinia</i>	<i>mississippiensis</i>	M	MVZ	60938	skull	No	No
<i>Ictinia</i>	<i>mississippiensis</i>	M	MVZ	135172	skull	No	No
<i>Kaupifalco</i>	<i>monogrammicus</i>	M	NMNH	322456	skull	No	No
<i>Kaupifalco</i>	<i>monogrammicus</i>	F	NMNH	430682	skull	No	No
<i>Leptodon</i>	<i>cayanensis</i>	M	NMNH	613953	skull	No	No
<i>Leptodon</i>	<i>cayanensis</i>	M	NMNH	632286	skull	No	No
<i>Leucopternis</i>	<i>melanops</i>	M	MVZ	154276	skull	No	No
<i>Leucopternis</i>	<i>melanops</i>	F	NMNH	432181	skull	No	No
<i>Leucopternis</i>	<i>melanops</i>	F	NMNH	621194	skull	No	No
<i>Lophaetus</i>	<i>occipitalis</i>	M	NMNH	291451	skull	No	No
<i>Lophaetus</i>	<i>occipitalis</i>	M	NMNH	431672	skull	No	No
<i>Machaerhamphus</i>	<i>alcinus</i>	U	NMNH	559816	skull	No	No
<i>Micrastur</i>	<i>ruficollis</i>	M	NMNH	621387	skull	No	No
<i>Micrastur</i>	<i>semitorquatus</i>	M	MVZ	85561	skull	No	No
<i>Micrastur</i>	<i>semitorquatus</i>	M	NMNH	289773	skull	No	No
<i>Microhierax</i>	<i>caerulescens</i>	M	NMNH	492193	skull	No	No
<i>Microhierax</i>	<i>caerulescens</i>	F	NMNH	499825	skull	No	No
<i>Microhierax</i>	<i>erythronys</i>	F	NMNH	613009	skull	No	No
<i>Microhierax</i>	<i>erythronys</i>	F	NMNH	613010	skull	No	No
<i>Microhierax</i>	<i>erythronys</i>	M	NMNH	613695	skull	No	No
<i>Milvago</i>	<i>chimachima</i>	F	MVZ	94071	skull	No	Yes
<i>Milvago</i>	<i>chimachima</i>	F	MVZ	137560	skull	No	Yes
<i>Milvago</i>	<i>chimachima</i>	F	MVZ	137561	skull	No	Yes
<i>Milvago</i>	<i>chimachima</i>	F	NMNH	622211	skull	No	Yes
<i>Milvago</i>	<i>chimango</i>	F	NMNH	635742	skull	No	Yes
<i>Milvago</i>	<i>chimango</i>	M	NMNH	635870	skull	No	Yes
<i>Milvago</i>	<i>chimango</i>	F	NMNH	635931	skull	No	Yes
<i>Milvus</i>	<i>migrans</i>	M	MVZ	123134	skull	No	No
<i>Milvus</i>	<i>migrans</i>	F	MVZ	135035	skull	No	No
<i>Milvus</i>	<i>migrans</i>	F	MVZ	135037	skull	No	No
<i>Milvus</i>	<i>milvus</i>	U	NHMUK	S2020121	skull	No	No
† <i>Morphnus</i>	† <i>woodwardi</i>	U	NHMLA	UnN	skull	Yes	No
<i>Necrosyrtes</i>	<i>monachus</i>	U	NMNH	18894	skull	No	Yes
<i>Necrosyrtes</i>	<i>monachus</i>	F	NMNH	291441	skull	No	Yes
<i>Necrosyrtes</i>	<i>monachus</i>	F	NMNH	291442	skull	No	Yes
<i>Necrosyrtes</i>	<i>monachus</i>	U	NMNH	620645	skull	No	Yes
† <i>Neogyps</i>	† <i>terrans</i>	U	NHMLA	J9063	skull	Yes	Yes

<i>Neophron</i>	<i>percnopterus</i>	U	MVZ	179210	skull	No	Yes
<i>Neophron</i>	<i>percnopterus</i>	U	NMNH	17835	skull	No	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	D7752	skull	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	D887	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	F1966	premaxillary	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	UnkN	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	UnN	skull	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28060	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28079	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28081	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28082	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28085	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	241575	premaxillary	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	271575	premaxillary	Yes	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	299162	crania	Yes	Yes
† <i>Neophrontops</i>	† <i>ricardoensis</i>	U	UCMP	77702	skull	Yes	Yes
† <i>Neophrontops</i>	Unknown species	U	UCMP	28084	crania	Yes	Yes
<i>Pandion</i>	<i>haliaetus</i>	F	MVZ	85556	skull	No	No
<i>Pandion</i>	<i>haliaetus</i>	U	MVZ	175991	skull	No	No
<i>Pandion</i>	<i>haliaetus</i>	M	NMNH	610343	skull	No	No
<i>Pandion</i>	<i>haliaetus</i>	F	NMNH	632392	skull	No	No
<i>Pandion</i>	<i>haliaetus</i>	M	UWBM	73955	skull	No	No
<i>Parabuteo</i>	<i>unicinctus</i>	U	MVZ	74748	skull	No	No
<i>Parabuteo</i>	<i>unicinctus</i>	F	MVZ	74749	skull	No	No
<i>Parabuteo</i>	<i>unicinctus</i>	M	MVZ	116399	skull	No	No
<i>Parabuteo</i>	<i>unicinctus</i>	U	MVZ	124876	skull	No	No
<i>Pernis</i>	<i>ptilorhynchus</i>	F	NMNH	343984	skull	No	No
<i>Phalcoboenus</i>	<i>australis</i>	F	NMNH	490890	skull	No	Yes
<i>Phalcoboenus</i>	<i>australis</i>	F	NMNH	490979	skull	No	Yes
<i>Phalcoboenus</i>	<i>carunculatus</i>	F	NMNH	614838	skull	No	Yes
<i>Phalcoboenus</i>	<i>chimango</i>	U	NMNH	1817	skull	No	Yes
<i>Phalcoboenus</i>	<i>megalopterus</i>	M	MVZ	125171	skull	No	Yes
<i>Phalcoboenus</i>	<i>megalopterus</i>	U	NMNH	500273	skull	No	Yes
<i>Pithecophaga</i>	<i>jefferyi</i>	F	MVZ	134059	skull	No	No
<i>Pithecophaga</i>	<i>jefferyi</i>	U	MVZ	136481	skull	No	No
<i>Pithecophaga</i>	<i>jefferyi</i>	M	NMNH	499879	skull	No	No
<i>Polemaetus</i>	<i>bellicosus</i>	M	NMNH	430533	skull	No	No
<i>Polihierax</i>	<i>semitorquatus</i>	F	NMNH	322394	skull	No	No
<i>Polihierax</i>	<i>semitorquatus</i>	F	NMNH	344678	skull	No	No
<i>Polihierax</i>	<i>semitorquatus</i>	M	NMNH	642502	skull	No	No
<i>Polyborus</i>	<i>auduboni</i>	M	NHMLA	86915	skull	No	Yes
<i>Polyborus</i>	<i>megalopterus</i>	U	NHMLA	89954	skull	No	Yes
<i>Polyborus</i>	<i>plancus</i>	M	NMNH	227375	skull	No	Yes
<i>Polyborus</i>	<i>plancus</i>	F	NMNH	490931	skull	No	Yes
<i>Polyborus</i>	<i>plancus</i>	F	NMNH	614584	skull	No	Yes
<i>Polyborus</i>	<i>plancus</i>	M	NMNH	635720	skull	No	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	E2004	premaxillary	Yes	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	E4317	crania	Yes	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	F3159	premaxillary	Yes	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	K6028	premaxillary	Yes	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	UnN	skull	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	200102	crania	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	271547	premaxillary	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	271548	premaxillary	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299092	premaxillary	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299093	premaxillary	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299094	premaxillary	Yes	Yes

<i>Polyborus</i>	Unknown species	U	UCMP	299095	premaxillary	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299096	premaxillary	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299101	crania	Yes	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299101	crania	Yes	Yes
<i>Polyboides</i>	<i>typus</i>	F	NMNH	291787	skull	No	No
<i>Polyboides</i>	<i>typus</i>	F	NMNH	292399	skull	No	No
<i>Polyboides</i>	<i>typus</i>	M	NMNH	430435	skull	No	No
<i>Rostrhamus</i>	<i>sociabilis</i>	M	NMNH	553612	skull	No	No
<i>Rostrhamus</i>	<i>sociabilis</i>	F	NMNH	553613	skull	No	No
<i>Rostrhamus</i>	<i>sociabilis</i>	F	NMNH	631108	skull	No	No
<i>Rostrhamus</i>	<i>sociabilis</i>	M	NMNH	631216	skull	No	No
<i>Rupornis</i>	<i>magnirostris</i>	F	MVZ	85535	skull	No	No
<i>Rupornis</i>	<i>magnirostris</i>	M	MVZ	85537	skull	No	No
<i>Sagittarius</i>	<i>serpentarius</i>	F	MVZ	133559	skull	No	No
<i>Sagittarius</i>	<i>serpentarius</i>	F	NMNH	490786	skull	No	No
<i>Sagittarius</i>	<i>serpentarius</i>	F	UWBM	42963	skull	No	No
<i>Sarcogyps</i>	<i>calvus</i>	U	BMNH	S2013221	skull	No	Yes
<i>Sarcoramphus</i>	<i>papa</i>	U	MVZ	85524	skull	No	Yes
<i>Sarcoramphus</i>	<i>papa</i>	M	MVZ	85526	skull	No	Yes
<i>Sarcoramphus</i>	<i>papa</i>	M	MVZ	123768	skull	No	Yes
<i>Sarcoramphus</i>	<i>papa</i>	F	NMNH	320860	skull	No	Yes
<i>Spilornis</i>	<i>cheela</i>	U	NMNH	19474	skull	No	No
<i>Spilornis</i>	<i>cheela</i>	M	NMNH	343985	skull	No	No
<i>Spilornis</i>	<i>cheela</i>	U	UWBM	83642	skull	No	No
<i>Spizaetus</i>	<i>grinnelli</i>	U	NHMLA	UnN	skull	Yes	No
<i>Spizaetus</i>	<i>nipalensis</i>	U	NHMLA	114857	skull	No	No
<i>Spizaetus</i>	<i>ornatus</i>	F	MVZ	85551	skull	No	No
<i>Spizaetus</i>	<i>ornatus</i>	M	MVZ	85554	skull	No	No
<i>Spizaetus</i>	<i>tyrannus</i>	F	NHMLA	101724	skull	No	No
<i>Spizastur</i>	<i>malanoleucus</i>	U	NMNH	321507	skull	No	No
<i>Spiziapteryx</i>	<i>circumcinctus</i>	M	NMNH	227499	skull	No	No
<i>Spiziapteryx</i>	<i>circumcinctus</i>	M	NMNH	319444	skull	No	No
<i>Spiziapteryx</i>	<i>circumcinctus</i>	M	NMNH	319445	skull	No	No
<i>Stephanoaetus</i>	<i>coronatus</i>	F	MVZ	140190	skull	No	No
<i>Terathopius</i>	<i>ecaudatus</i>	M	NMNH	431431	skull	No	No
<i>Teratornis</i>	<i>merriami</i>	U	NHMLA	B1381	skull	Yes	No
<i>Terothopius</i>	<i>ecaudatus</i>	F	NMNH	289742	skull	No	No
<i>Terothopius</i>	<i>ecaudatus</i>	F	NMNH	319919	skull	No	No
<i>Terothopius</i>	<i>ecaudatus</i>	M	NMNH	634509	skull	No	No
<i>Torgos</i>	<i>tracheliotus</i>	U	MVZ	128911	skull	No	Yes
<i>Torgos</i>	<i>tracheliotus</i>	U	NHMLA	S19521172	skull	No	Yes
<i>Torgos</i>	<i>tracheliotus</i>	M	NMNH	320977	skull	No	Yes
<i>Torgos</i>	<i>tracheliotus</i>	F	NMNH	321827	skull	No	Yes
<i>Trigonoceps</i>	<i>occipitalis</i>	F	NMNH	320859	skull	No	Yes
<i>Trigonoceps</i>	<i>occipitalis</i>	U	NMNH	347358	skull	No	Yes
<i>Urotriochis</i>	<i>macrourus</i>	M	NMNH	292398	skull	No	No
<i>Vultur</i>	<i>gryphus</i>	U	NHMLA	90276	skull	No	Yes
<i>Vultur</i>	<i>gryphus</i>	U	MVZ	120364	skull	No	Yes
<i>Vultur</i>	<i>gryphus</i>	F	NMNH	346631	skull	No	Yes
<i>Vultur</i>	<i>gryphus</i>	F	NMNH	429839	skull	No	Yes
<i>Vultur</i>	<i>gryphus</i>	U	NMNH	500988	skull	No	Yes
Unknown genus	Unknown species	U	NHMLA	B1402	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	B1605	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	B1866	premaxillary	Yes	No
Unknown genus	Unknown species	U	NHMLA	B1957	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	B4774	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	B4915	crania	Yes	Yes

Unknown genus	Unknown species	U	NHMLA	B5415	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	B6410	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	B6888	crania	Yes	Yes
Unknown genus	Unknown species	U	NHMLA	F1859	premaxillary	Yes	No
Unknown genus	Unknown species	U	NHMLA	F3234	skull	Yes	No
Unknown genus	Unknown species	U	UCMP	28059	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	28063	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	28067	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	28069	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	28076	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	262342	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	262344	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	262345	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	262346	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	262348	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	262350	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	264415	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	267270	crania	Yes	No
Unknown genus	Unknown species	U	UCMP	267311	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	267312	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	267590	crania	Yes	No
Unknown genus	Unknown species	U	UCMP	271574	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299082	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	299085	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299089	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299091	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299100	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	299109	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299145	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	299148	crania	Yes	No
Unknown genus	Unknown species	U	UCMP	299155	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	299156	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	299159	crania	Yes	Yes
Unknown genus	Unknown species	U	UCMP	299594	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299595	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299596	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299597	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299598	premaxillary	Yes	No
Unknown genus	Unknown species	U	UCMP	299797	crania	Yes	No
Unknown genus	Unknown species	U	UCMP	I	premaxillary	Yes	Yes
Unknown genus	Unknown species	U	UCMP	II	premaxillary	Yes	Yes

† indicates extinct species

Appendix 3.1. Comprehensive list of landmarked specimens. Abbreviations used in this table are as follows: British Museum of Natural History, **BMNH**; Natural History Museum of Los Angeles County, **NHMLA**; University of California Museum of Vertebrate Zoology, **MVZ**; Natural History Museum, **NHMUK**; University of California Museum of Paleontology, **UCMP**; Smithsonian National Museum of Natural History, **NMNH**; University of Washington Burke Museum of Natural History and Culture, **UWBM**.

Genus	Species	Sex	Institution	ID	Element	Fossil
<i>Aegypius</i>	<i>monachus</i>	U	BMNH	UnN	skull	No
<i>Aegypius</i>	<i>monachus</i>	F	NMNH	428040	skull	No
<i>Aegypius</i>	<i>monachus</i>	U	NMNH	614152	skull	No
† <i>Breagyps</i>	† <i>clarki</i>	U	NHMLA	B3148	crania	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	NHMLA	J9071	premaxillary	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	NHMLA	UnN	skull	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	UCMP	28074	crania	Yes
† <i>Breagyps</i>	† <i>clarki</i>	U	UCMP	28077	crania	Yes
<i>Caracara</i>	<i>cheriway</i>	M	MVZ	74750	skull	No
<i>Caracara</i>	<i>cheriway</i>	F	MVZ	74855	skull	No
<i>Caracara</i>	<i>cheriway</i>	F	MVZ	85563	skull	No
<i>Caracara</i>	<i>cheriway</i>	M	MVZ	94070	skull	No
<i>Caracara</i>	<i>cheriway</i>	F	MVZ	120713	skull	No
<i>Caracara</i>	<i>cheriway</i>	M	MVZ	151718	skull	No
<i>Caracara</i>	<i>plancus</i>	M	UWBM	90170	skull	No
<i>Caracara</i>	<i>plancus</i>	F	UWBM	90171	skull	No
<i>Cathartes</i>	<i>aura</i>	M	MVZ	63474	skull	No
<i>Cathartes</i>	<i>aura</i>	F	MVZ	63475	skull	No
<i>Cathartes</i>	<i>aura</i>	F	MVZ	151678	skull	No
<i>Cathartes</i>	<i>aura</i>	F	MVZ	179934	skull	No
<i>Cathartes</i>	<i>aura</i>	U	MVZ	179938	skull	No
<i>Cathartes</i>	<i>aura</i>	U	UCMP	299110	skull	Yes
<i>Cathartes</i>	<i>burrovianus</i>	M	NMNH	622341	skull	No
<i>Cathartes</i>	<i>burrovianus</i>	M	NMNH	623071	skull	No
<i>Cathartes</i>	<i>burrovianus</i>	F	NMNH	632359	skull	No
<i>Cathartes</i>	<i>burrovianus</i>	F	NMNH	632364	skull	No
<i>Cathartes</i>	<i>melambrotus</i>	F	NMNH	559319	skull	No
<i>Cathartes</i>	<i>melambrotus</i>	F	NMNH	621939	skull	No
<i>Cathartes</i>	<i>melambrotus</i>	M	NMNH	637139	skull	No
<i>Cathartes</i>	Unknown species	U	UCMP	299097	premaxillary	Yes
<i>Cathartes</i>	Unknown species	U	UCMP	299107	crania	Yes
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	66913	skull	No
<i>Coragyps</i>	<i>atratus</i>	M	MVZ	78681	skull	No
<i>Coragyps</i>	<i>atratus</i>	M	MVZ	79208	skull	No
<i>Coragyps</i>	<i>atratus</i>	F	MVZ	79209	skull	No
<i>Coragyps</i>	<i>atratus</i>	M	MVZ	79210	skull	No
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	151679	skull	No
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	175989	skull	No
<i>Coragyps</i>	<i>atratus</i>	U	MVZ	180366	skull	No
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7017	crania	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7088	crania	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7895	crania	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	D7980	crania	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	NHMLA	UnN	skull	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	UCMP	10409	crania	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	UCMP	28086	crania	Yes
<i>Coragyps</i>	† <i>occidentalis</i>	U	UCMP	299593	crania	Yes
<i>Coragyps</i>	Unknown species	U	NHMLA	E531	premaxillary	Yes
<i>Coragyps</i>	Unknown species	U	NHMLA	UnN	premaxillary	Yes

<i>Coragyps</i>	Unknown species	U	UCMP	299098	premaxillary	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299099	premaxillary	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299105	crania	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299108	premaxillary	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299157	crania	Yes
<i>Coragyps</i>	Unknown species	U	UCMP	299158	crania	Yes
<i>Daptrius</i>	<i>americanus</i>	M	NMNH	621388	skull	No
<i>Daptrius</i>	<i>americanus</i>	M	NMNH	621943	skull	No
<i>Daptrius</i>	<i>americanus</i>	F	NMNH	632410	skull	No
<i>Daptrius</i>	<i>ater</i>	F	NMNH	226167	skull	No
<i>Daptrius</i>	<i>ater</i>	M	NMNH	345776	skull	No
<i>Daptrius</i>	<i>ater</i>	F	NMNH	345777	skull	No
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	B1869	premaxillary	Yes
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	B1968	premaxillary	Yes
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	B2050	crania	Yes
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	B2050	skull	Yes
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	B8010	crania	Yes
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	F3245	crania	Yes
<i>Gymnogyps</i>	† <i>amplus</i>	U	NHMLA	UnN	skull	Yes
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	23459	skull	No
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	74888	skull	No
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	131373	skull	No
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	151086	skull	No
<i>Gymnogyps</i>	<i>californianus</i>	U	MVZ	151087	skull	No
<i>Gymnogyps</i>	Unknown species	U	MVZ	133377	skull	Yes
<i>Gymnogyps</i>	Unknown species	U	UCMP	12103	skull	Yes
<i>Gymnogyps</i>	Unknown species	U	UCMP	22983	skull	Yes
<i>Gymnogyps</i>	Unknown species	U	UCMP	299082	skull	Yes
<i>Gypaetus</i>	<i>barbatus</i>	U	NMNH	17834	skull	No
<i>Gypaetus</i>	<i>barbatus</i>	U	NMNH	19383	skull	No
<i>Gypaetus</i>	<i>barbatus</i>	F	NMNH	345684	skull	No
<i>Gypohierax</i>	<i>angolensis</i>	U	NMNH	18892	skull	No
<i>Gypohierax</i>	<i>angolensis</i>	U	NMNH	224820	skull	No
<i>Gypohierax</i>	<i>angolensis</i>	F	NMNH	291078	skull	No
<i>Gyps</i>	<i>africanus</i>	M	NMNH	430014	skull	No
<i>Gyps</i>	<i>africanus</i>	M	NMNH	430016	skull	No
<i>Gyps</i>	<i>africanus</i>	F	NMNH	431403	skull	No
<i>Gyps</i>	<i>africanus</i>	F	NMNH	431591	skull	No
<i>Gyps</i>	<i>bengolensis</i>	U	NHMLA	116946	skull	No
<i>Gyps</i>	<i>coprotheres</i>	U	NMNH	561314	skull	No
<i>Gyps</i>	<i>fulvus</i>	F	NMNH	227051	skull	No
<i>Gyps</i>	<i>himilayensis</i>	M	NMNH	19534	skull	No
<i>Gyps</i>	<i>indicus</i>	U	NHMLA	86840	skull	No
<i>Gyps</i>	<i>rupPELLII</i>	U	NMNH	430178	skull	No
<i>Gyps</i>	<i>tenuirostris</i>	U	BMNH	Unk	premaxillary	No
<i>Milvago</i>	<i>chimachima</i>	F	MVZ	94071	skull	No
<i>Milvago</i>	<i>chimachima</i>	F	MVZ	137560	skull	No
<i>Milvago</i>	<i>chimachima</i>	F	MVZ	137561	skull	No
<i>Milvago</i>	<i>chimachima</i>	F	NMNH	622211	skull	No
<i>Milvago</i>	<i>chimango</i>	F	NMNH	635742	skull	No
<i>Milvago</i>	<i>chimango</i>	M	NMNH	635870	skull	No
<i>Milvago</i>	<i>chimango</i>	F	NMNH	635931	skull	No
<i>Necrosyrtes</i>	<i>monachus</i>	U	NMNH	18894	skull	No
<i>Necrosyrtes</i>	<i>monachus</i>	F	NMNH	291441	skull	No
<i>Necrosyrtes</i>	<i>monachus</i>	F	NMNH	291442	skull	No
<i>Necrosyrtes</i>	<i>monachus</i>	U	NMNH	620645	skull	No
† <i>Neogyps</i>	† <i>errans</i>	U	NHMLA	J9063	skull	Yes

<i>Neophron</i>	<i>percnopterus</i>	U	MVZ	179210	skull	No
<i>Neophron</i>	<i>percnopterus</i>	U	NMNH	17835	skull	No
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	D7752	skull	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	D887	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	F1966	premaxillary	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	UnkN	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	NHMLA	UnN	skull	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28060	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28079	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28081	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28082	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28085	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	241575	premaxillary	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	271575	premaxillary	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	299162	crania	Yes
† <i>Neophrontops</i>	† <i>americanus</i>	U	UCMP	28084	crania	Yes
† <i>Neophrontops</i>	† <i>ricardoensis</i>	U	UCMP	77702	skull	Yes
<i>Phalcoboenus</i>	<i>australis</i>	F	NMNH	490890	skull	No
<i>Phalcoboenus</i>	<i>australis</i>	F	NMNH	490979	skull	No
<i>Phalcoboenus</i>	<i>carunculatus</i>	F	NMNH	614838	skull	No
<i>Phalcoboenus</i>	<i>chimango</i>	U	NMNH	1817	skull	No
<i>Phalcoboenus</i>	<i>megalopterus</i>	M	MVZ	125171	skull	No
<i>Phalcoboenus</i>	<i>megalopterus</i>	U	NMNH	500273	skull	No
<i>Polyborus</i>	<i>auduboni</i>	M	NHMLA	86915	skull	No
<i>Polyborus</i>	<i>megalopterus</i>	U	NHMLA	89954	skull	No
<i>Polyborus</i>	<i>plancus</i>	M	NMNH	227375	skull	No
<i>Polyborus</i>	<i>plancus</i>	F	NMNH	490931	skull	No
<i>Polyborus</i>	<i>plancus</i>	F	NMNH	614584	skull	No
<i>Polyborus</i>	<i>plancus</i>	M	NMNH	635720	skull	No
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	E2004	premaxillary	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	E4317	crania	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	F3159	premaxillary	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	K6028	premaxillary	Yes
<i>Polyborus</i>	† <i>prelutosus</i>	U	NHMLA	UnN	skull	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	200102	crania	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	271547	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	271548	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299092	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299093	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299094	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299095	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299096	premaxillary	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299101	crania	Yes
<i>Polyborus</i>	Unknown species	U	UCMP	299101	crania	Yes
<i>Sarcogyps</i>	<i>calvus</i>	U	BMNH	S2013221	skull	No
<i>Sarcoramphus</i>	<i>papa</i>	U	MVZ	85524	skull	No
<i>Sarcoramphus</i>	<i>papa</i>	M	MVZ	85526	skull	No
<i>Sarcoramphus</i>	<i>papa</i>	M	MVZ	123768	skull	No
<i>Sarcoramphus</i>	<i>papa</i>	F	NMNH	320860	skull	No
<i>Torgos</i>	<i>tracheliotus</i>	U	MVZ	128911	skull	No
<i>Torgos</i>	<i>tracheliotus</i>	U	NHMUK	S19521172	skull	No
<i>Torgos</i>	<i>tracheliotus</i>	M	NMNH	320977	skull	No
<i>Torgos</i>	<i>tracheliotus</i>	F	NMNH	321827	skull	No
<i>Trigonoceps</i>	<i>occipitalis</i>	F	NMNH	320859	skull	No
<i>Trigonoceps</i>	<i>occipitalis</i>	U	NMNH	347358	skull	No
<i>Vultur</i>	<i>gryphus</i>	U	NHMLA	90276	skull	No
<i>Vultur</i>	<i>gryphus</i>	U	MVZ	120364	skull	No

<i>Vultur</i>	<i>gryphus</i>	F	NMNH	346631	skull	No
<i>Vultur</i>	<i>gryphus</i>	F	NMNH	429839	skull	No
<i>Vultur</i>	<i>gryphus</i>	U	NMNH	500988	skull	No
Unknown genus	Unknown species	U	NHMLA	B1402	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B1605	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B1957	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B4774	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B4915	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B5415	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B6410	crania	Yes
Unknown genus	Unknown species	U	NHMLA	B6888	crania	Yes
Unknown genus	Unknown species	U	UCMP	28059	crania	Yes
Unknown genus	Unknown species	U	UCMP	28063	crania	Yes
Unknown genus	Unknown species	U	UCMP	28067	crania	Yes
Unknown genus	Unknown species	U	UCMP	28069	crania	Yes
Unknown genus	Unknown species	U	UCMP	28076	crania	Yes
Unknown genus	Unknown species	U	UCMP	299082	crania	Yes
Unknown genus	Unknown species	U	UCMP	299100	crania	Yes
Unknown genus	Unknown species	U	UCMP	299145	crania	Yes
Unknown genus	Unknown species	U	UCMP	299155	crania	Yes
Unknown genus	Unknown species	U	UCMP	299156	crania	Yes
Unknown genus	Unknown species	U	UCMP	299159	crania	Yes
Unknown genus	Unknown species	U	UCMP	I	premaxillary	Yes
Unknown genus	Unknown species	U	UCMP	II	premaxillary	Yes

† indicates extinct species