ECOMORPHOLOGICAL ASSOCIATIONS OF FEEDING HABITS IN HYPERCARNIVORES

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ABSTRACT

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The classification scheme for Carnivora put forth by Van Valkenburgh (2007) is frequently used as a guideline for feeding ecology throughout the history of the Order. However, the categorization system used is too broad and may lead to species being classified into incorrect ecomorphs. Further, many ecomorphological studies rely on linear measurements, which fail to capture the full change in skull shape across species. We analyzed 7 hypercarnivorous species using geometric morphometric techniques to assess its effectiveness in conjunction with ecomorphological analyses, and partial least squares analysis to test the adequacy of Van Valkenburgh's classification system. We found a surprising amount of shape variation throughout the wolf-like hypercarnivores, with some species appearing more similar to those within the other categories. Morphological differences were also observed among the bone eating hyenids. Our analyses suggest that Van Valkenburgh's hypercarnivore classifications are in need of revision. We suggest a system that subdivides the wolf-like ecomorph into several, more distinct categories.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The Order Carnivora includes only 286 recognized species today (Eizirik *et al.* 2010), but its members have expanded to cover a vast array of ecological niches both in the past and the present. Carnivora is of particular interest because of its diversity in both form and function, with several common adaptive types appearing independently in more than one lineage. Van Valkenburgh (2007) attributed this repeated development of similar forms to two factors, the first being that there are a limited number of ways to partition the carnivore niche ecologically, and the second, that there have been no changes in the basic properties of muscle, skin, and bone throughout the history of Carnivora. If these two factors act as constraints, then evolution will lead to similar forms developing throughout time, because such forms would succeed in meeting similar functional demands, such as the need to break apart hard foods without damaging the feeding apparatus.

Many studies have focused on dentition and linear measurements of the jaw in order to compare species with respect to morphology and associated dietary habits. Recently, there has been increasing interest in gross morphological shape and its correlation with diet. While linear measurements and area estimates can provide useful information such as bite force and feeding gape (Christiansen and Adolfssen 2005, Christiansen and Wroe 2007, Wroe *et al.* 2005), studies of morphological shape as a whole provide a more complete picture of the associations among the various modules that make up the feeding apparatus. Goswami and Polly (2010) suggested that trait integration for cranial modules may limit the morphological variation possible for some traits. Thus, analyses using gross morphological shape can offer greater insight than simple, linear measurements into potential selective forces and constraints that might influence both the morphology and ecological niche of a species.

Ecomorphology.—

By looking at morphological characteristics and the ecological habits of the organisms that possess them, scientists can make inferences about the ecological relevance of different morphologies. Such inferences can informate about of the mechanical requirements associated with a particular diet (e.g., soft or hard foods), and of the evolutionary history of certain morphological traits associated with dietary habits (e.g., the degree of undulation in the banding pattern of tooth enamel seen in Hyaenidae and its relationship to bone eating behavior, as described by Ferretti (2007)). Raia (2004), for example, used geometric morphometrics to compare mandibular shape in 18 extant and 3 extinct species from the Order Carnivora. He found that mandibular shape correlates strongly with diet in large carnivores, although phylogeny accounted for the greatest portion of shape variation. Paleontological research makes wide use of ecomorphology by comparing morphological characteristics of living organisms with known ecological and dietary habits to extinct taxa in order to make ecological inferences about extinct species. In one such study, Werdelin and Solounias (1996) devised a categorization method for Hyaenidae in which they divided the various taxa among six ecomorph types based on morphological form and function, as well as expected dietary habits. Their categorization method has allowed scientists to trace the evolution of the bone breaking morphology seen in extant hyenas throughout the known history of the Family, and can be used as a starting point in identifying potential familial relationships among newly discovered species.

Such categorization methods can be informative at higher levels of taxonomy as well. A review by Van Valkenburgh (2007) summarized the array of ecomorphs seen among large

(>7kg), terrestrial members of the Order Carnivora in both extinct and extant taxa (Table 1). She described three major ecomorphs based on predatory method, dietary composition, and phylogenetic placement: hypocarnivores, in which the diet is >70% non-vertebrate foods; mesocarnivores, with a diet of 50-70% meat and the remainder non-vertebrate foods; and hypercarnivores, defined as having a diet of >70% vertebrate prey. Hypercarnivores were further divided into three generalized ecomorphs: cat-like (including sabertooth cats and those with conical canine teeth), wolf-like, and hyena-like. Van Valkenburgh noted that the generalized mesocarnivorous morphology was common in the early members of most families of Carnivora, and that this morphology provides the starting point for species to evolve towards or away from a diet focused on vertebrate food. The development of a feeding morphology specialized for a particular diet is often accompanied by a loss of features that are not relevant to that diet (e.g., the reduction in cheek teeth in the insectivorous Aardwolf), making it unlikely that a radically different specialization will develop in the descendents of such a species (Holliday and Steppan, 2004).

Species within a given ecomorph tend to have similar adaptations in dentition and skull shape. For instance, postcarnassial grinding dentition is greatly reduced or absent in all three hypercarnivorous forms, and cranial and jaw characteristics that increase the mechanical advantage of the jaw adductors (temporalis and masseter) are shared among hypercarnivorous ecomorphs. Differences among hypercarnivorous taxa are thought to reflect differences in prey acquisition (e.g., whether they chase and drag down their prey or pounce and deliver a killing bite) and dietary preferences (e.g., whether bone is a significant portion of the diet). The diversity of these ecomorphs within families, and the repeated evolution of similar forms across families, suggest that certain combinations of morphological characteristics are matched to particular ecological niches, and that species with a morphology that allows for adaptation to those niches may fill a vacant niche when such an opportunity arises.

Although it is clear that certain morphological characteristics are vital to the acquisition and processing of certain types of foods, the extent to which the skull as a whole varies in response to dietary composition is not well defined. The skull is made up of several parts that serve various functions (e.g., vision and the orbits, hearing and the auditory bullae), and their associated functional requirements and morphological constraints leads to a lack of developmental independence in those parts. Studies such as that by Sacco and Van Valkenburgh (2004) have developed indices of linear measurements that reflect dietary habits. However, each measurement only takes into account a small portion of the variation in shape seen across different dietary ecologies, and a particular morphological characteristic is not likely to be independent of those that are used in conjunction with it. Linear measurement techniques can also be time consuming, with only a fraction of the measurements taken resulting in significant association with dietary habits. Analysis of the overall differences in the shape of the feeding apparatus between species with different dietary habits is required for a more thorough understanding of the morphological characteristics associated with a given feeding ecology. Such studies are of great value in furthering our understanding of trait evolution and the ecology of extinct taxa.

Aims of this Research.—

In this study, I use geometric morphometrics to investigate the skull morphology of members of the hypercarnivorous ecomorphs described by Van Valkenburgh (2007). I focus specifically on 7 species, representing 4 extant families, to assess the variation seen in morphology of the cranium and jaw and examine their associations with dietary habits and hunting strategies. My primary goal is to identify correlations between skull shape, food acquisition, and diet, and to evaluate the adequacy of the classification system as it now stands. Van Valkenburgh's classification system is a useful tool in the determination of ecomorphological associations in extant and extinct members of Carnivora, but I believe the hypercarnivore sub-categories are too broad and in need of revision so that future ecomorphological studies can more easily and accurately classify ecological habits of extinct species. Two Block Partial Least Squares analysis is used to examine the relationship between skull morphology, visualized as relative warps that define the changes in the relative positions of pre-determined landmarks from one morphology to the other, and feeding ecology, defined using a categorical rating system that takes into account food acquisition and consumption habits. Phylogenetic relatedness is then assessed in order to determine the extent to which phylogeny might explain the observed patterns of morphological and ecological variation.

METHODS

Specimens.—

Craniums and mandibles of 419 individuals, representing 7 extant species and 4 families from the Order Carnivora were borrowed from the following museum collections: Michigan State University Museum (East Lansing, Michigan), University of Michigan Museum of Zoology (Ann Arbor, Michigan), Tel Aviv National Museum of Natural History (Tel Aviv, Israel), British Museum of Natural History (London, England), Field Museum of Natural History

(Chicago, Illinois), the National Museum of Kenya (Africa), and the Royal College of Surgeons (London, England). All specimens were adults, based on the presence of a fully erupted adult dentition. Some outliers (described below) were removed after preliminary analyses because the cranium or jaw showed signs of significant deformation due to disease, improper specimen preparation, or improper specimen care. Specimens included in analyses are listed in Appendix 1 along with their museum catalog number, sex, and the views that were used in geometric morphometric analyses.

Digitization.—

Skulls were photographed using a Fuji FinePix S5 Pro digital camera with a 70mm Sigma macro lens. Craniums were photographed in the ventral view with the palate parallel to the image plane, and in the lateral view with the anteroposterior axis parallel to the image plane. Intact mandibles were photographed in lateral view with the mid-sagittal axis parallel to the image plane. A scale was included in all photographs. Landmarks, visibly observable and biologically meaningful locations that are persistent across all taxa used in the study, were digitized onto images of the skulls in all three views to help define the shape of the specimens. Twenty-seven landmarks were selected from the ventral cranium for analysis of shape in that view (Figure 1, Appendix 2). Landmarks alone cannot fully capture the complexity of the dorsal curve of the lateral cranium or the mandibular ramus, so these were analyzed using a combination of landmarks and semi-landmarks. Fourteen landmarks and 32 semi-landmarks were selected from the lateral view (Figure 1, Appendix 2), and 11 landmarks and 75 semi-landmarks were chosen from the mandibular view (Figure 1, Appendix 2). Landmarks and semi-landmarks were digitized using tpsDig2.15 (Rohlf 2010). Semi-landmarks were obtained by applying the curve-tracing function and selecting “resample,” which results in even spacing between points.

Morphometric Analyses.—

Landmarks were superimposed using Generalized least squares (GLS) Procrustes Analysis, a procedure that removes variation in scale, position, and orientation (Zelditch *et al.* 2004). Bilaterally homologous landmarks in the ventral view were first reflected and averaged in order to reduce the error that such estimations may cause. Semi-landmarks require a specialized superimposition method because their spacing is biologically arbitrary. In this study, semi-landmarks were superimposed so as to minimize the Procrustes distance from the mean shape. Skull size was quantified using centroid size, which is defined as the square root of the summed square distances from each landmark to the geometric center of an object. Landmark superimposition was performed using Coordgen6f (Sheets 2009). Semi-landmarks were superimposed using Semiland6 (Sheets 2003). Reflection and averaging of bilaterally homologous landmarks was done in Sage (Marquez 2007). To identify outliers, principal components analyses were performed using PCAGen6 (Sheets 2001) with specimens grouped by species. Extreme outliers were re-examined and eliminated if it appeared that they were the result of significant damage caused by disease, injury, or specimen breakage.

Sexual Dimorphism.—

Species were measured individually for evidence of sexual dimorphism prior to all further analyses to determine whether males and females should be combined or treated separately in subsequent analyses. Sexual dimorphism in skull shape was examined in each species individually using Goodall's F test with 2,500 permutations for each of the 3 views. Cases of significant sexual dimorphism (p-value <0.05) were further analyzed using permutation tests on explained variance with centroid size as the covariate in order to determine the percentage of shape variation explained by differences in size, and the percentage explained by sex. A Bonferroni adjustment (which corrected the p-value for significance to p<0.002) was used to account for the multiple tests associated with each species. Goodall's F test was performed in Twogroup6h (Sheets 2003), and the permutation test on explained variance was performed in Manovaboard6 (Sheets 2006).

Ecological Index.—

Ecological factors associated with food acquisition and diet were identified for use in ecomorphological correlation assessment, and the hunting and feeding ecologies of the species were classified following a review of the literature (Table 2). Species were categorized based on the importance of meat and bone in their diet, the size of their hunting groups, and the methods typically used to kill their prey. A numerical index (Table 3) was created for each category for use in partial least squares analysis (see below). The value associated with each option within a category does not express any degree of significance or strength, but rather acts as a marker for grouping species with similar ecological behaviors together for use in partial least squares analysis. For the meat and bone categories, consumption was scored (1-3, or 1-4, respectively), such that higher values correspond to greater dietary importance. The hunting party category was scored (1-4) based on group size, with 1 representing solitary hunters and foragers, 2 species that infrequently form small groups based on food availability, 3 species that frequently hunt in small groups, and 4 representing obligate pack hunters. Killing strategy ranged from 1 to 5, with 1 representing species that primarily scavenge rather than hunt. Mid-range values (2 and 3) correspond with chasing strategies, with 2 involving knocking down the prey and 3 a biting or worrying strategy. Higher values (4 and 5) were associated with species that stalk their prey. Species rated as 4 perform a killing blow, while a species rated as a 5 kills by brute force or crushing. Table 4 summarizes the values assigned in each category for all species.

Preliminary Analysis and Ordination.—

Species were compared to one another in all 3 views using Goodall's F test with 2,500 permutations in Twogroup6h (Sheets 2003) to evaluate whether the differences in shape between them were significant. P-values <0.02 (following Bonferroni adjustment) for species comparisons could be indicative of significant shape differences and suggest that the species can be reliably distinguished from one another. Canonical variates analysis (CVA) was used (CVAGen6, Sheets 2003) to simplify the descriptions of differences between species. This method rescales the axes of the new coordinate system so as to maximize the ability to discriminate between groups (Zelditch *et al.* 2004). Bartlett's test for differences in the value of Wilk's lambda (Λ), which is the within-groups sum of squares divided by the total sum of squares, was used to determine how many CVs were effective at discriminating between species. An assignment test was performed in CVAGen6 in which the Mahalanobis' distance between group means was used to determine the probability that each specimen is indeed a member of the group to which it is assigned (Zelditch *et al.* 2004), and a jack-knife groupings test was performed to obtain the rate at which specimens were correctly classified. Visual representations of the morphological differences between groups described by CVs 1 and 2 were obtained in the form of CVA deformation grids. Skulls from each species were visually compared to identify additional features not found through the morphometric analyses that might be relevant to the ecological variables of interest. The percentage of variance explained by the CVs for species in each view were obtained using MorphoJ 1.02j (Klingenberg 2011).

Partial Least Squares.—

Two Block partial least squares (PLS) analysis was used to investigate the correlations between morphological features and ecological strategy, with each of the three views examined separately. In each PLS analysis, the first block consisted of the Procrustes coordinates for all individuals of all species in a given view. The second block contained the ecological index scores for all specimens, with all individuals within a species having the same index scores. Partial least squares predictor coefficients were obtained for the ecological index scores along with the RV coefficient, which is a multivariate analogue of the squared correlation coefficient, for the overall strength of association between the blocks. A permutation test was performed (10,000 iterations) to test the data against the null hypothesis of complete independence between the two blocks of data. Singular values and pairwise correlations were obtained for each PLS axis pair, along with the percent of covariance explained by each axis pair. Partial least squares analysis was performed in MorphoJ 1.02j (Klingenberg 2011).

Phylogenetic Signal.—

Similarities in shape among taxa due to phylogenetic relatedness can lead to errors in interpretation of morphometric data by obscuring the degree to which species have come to differ through evolutionary processes. A species is generally expected to be more similar in form and function to those more closely related to it than to those from a distantly related clade. Analyses were thus performed to measure the extent to which morphological differences among species are explained by phylogeny.

Phylogenetic trees for the 7 species of Carnivora were constructed following the phylogeny put forth by Eizirik *et al.* (2010) (Figure 2). Arbitrary branch length methods were used in place of estimated branch lengths due to uncertainty in the divergence times among some of the taxa. Four trees, differing only in branch length, were generated through pdtree (Modford *et al.*, 2010) in Mesquite for comparison of phylogenetic signal across various arbitrary branch length methods, with 1 tree each following the methods put forth by Grafen (1989), Nee (cited in Purvis 1995), and Pagel (1992). The fourth tree had all branch lengths set to 1.0. The trees were exported from Mesquite as separate NEXUS files for use in statistical analyses. A consensus tree was then generated from the 4 branch length method trees. The NEXUS files for the trees were created using Mesquite 2.74 (Maddison and Maddison, 2010).

The consensus tree was used to map the Procrustes coordinates of each view to the phylogeny in MorphoJ 1.02j (Klingenberg 2011). A permutation test (10,000 iterations) was performed against the null hypothesis of no phylogenetic signal. Views found to have a p-value <0.05 have significant evidence of phylogenetic signal in skull shape. All phylogenetic trees were imported into R 2.12.1 (R Development Core Team 2011) along with the matrix of ecological index ratings for statistical testing of phylogenetic signal in the ecological variables. Values for Blomberg's K (Blomberg 2003) were obtained through picante (Kembel *et al.* 2010) in R. Blomberg’s K is a measure of phylogenetic signal that compares the observed signal of a trait (i.e., ecological strategies) to an expected signal obtained under the Brownian motion model of trait evolution. A K value close to zero suggests random evolution or convergence, a value of 1 indicates some conservatism or phylogenetic signal, and values greater than 1 represent strong phylogenetic signal. The ecological traits were tested with each of the four phylogenetic trees and the consensus tree, and the K values obtained under each arbitrary branch length method were compared in order to determine the influence of phylogenetic signal on ecological strategy. P-values, representing the quantile for the observed phylogenetic independent contrast variance versus the null distribution, as described by Kembel (2010), were also obtained. Traits with a p-value <0.05 have non-random phylogenetic signal.

RESULTS

Sexual Dimorphism.—

The polar bear, African lion, and gray wolf each showed evidence of sexual dimorphism in shape for at least 1 view ($p<0.05$; Table 5). However, the gray wolf was the only species with significant sexual dimorphism ($p<0.002$, following Bonferroni adjustment for multiple tests). In the gray wolves, sex was responsible for only a small portion of the total variance (<2.5% in the mandible, <2% in the ventral view), with size accounting for the majority of the shape differences between the sexes. Because variation in size is removed through Generalized

Procrustes Analysis, male and female gray wolves were combined. In addition, specimens of unknown sex were added (where available) to species samples.

Species Differences.—

All species were significantly different from one another in shape for all views ($p<0.0004$), and all specimens were assigned to the correct species/view by the corresponding assignment test. The jack-knife groupings test correctly classified 100% of the specimens in the lateral and mandibular views, and nearly 99% in the ventral view. The percentages of variance explained by the CVs for each view are summarized in Table 6. In the lateral view, the first 2 CVs explain over 96% of the variance; these CVs are plotted against one another in Figure 3, along with their respective deformation grids. The first CV clearly separates African lions and polar bears (with high scores on CV1) from the remaining species. Morphological changes in transitioning from left to right along CV1 include marked reduction in concavity of the facial profile and reduction in the posterior margin of the sagittal crest. The jugal also expands slightly and moves to a more anterior position relative to the rest of the skull. The second CV in this view separates the 3 hyenas, which have a very prominent sagittal crest and expansive zygomatic region, from the other species, in which those regions are not as strongly emphasized. The hyenas also show a significant reduction in the size of the jugal within the zygomatic arch relative to the rest of the skull and in the area between the infraorbital and lacrimal foramen, along with an anteriorally-directed shift in the postorbital process.

In the mandibular view, the first 2 CVs explain almost 80% of the variance across species (Table 6). On CV1 of the corresponding plot (Figure 4), striped hyenas (low scores) and African lions (high scores) are at the extremes, with the remaining species falling near the middle of the axis. The associated deformation grid shows a dorsally directed shift in the ventral margin of the mandibular body from the middle of the tooth row to where the angular process joins the ramus, resulting in a more ventral placement of the angular process relative to the rest of the mandible. This shape change discriminates the striped hyena from the spotted and brown hyenas with the latter having a more ventrally placed angular process relative to the rest of the mandible. There is also an expansion of the dorsal ramus relative to the rest of the mandible, and a broadening of the condyloid and coronoid processes along CV1. On the second CV, the 3 caniforms (i.e., polar bear, gray wolf, African wild dog) form a tight cluster that is separated from the feliforms (i.e., hyenas, lions). Graphical representations of the changes along this CV axis show a reduction in the relative depths of the ramus and the mandibular body below the tooth row, and a marked widening of the mid-dorsal ramus in caniforms compared to feliforms. The tooth row expands anteroposteriorally behind the canine relative to the rest of the mandible.

The scale used for the ventral view plot is significantly smaller than that used for the other 2 views, showing that species differences dependent on our choice of landmarks in the ventral view do not discriminate the species from one another as strongly as those in the other views. The first 2 CVs explain nearly 75% of the variance across species (Table 6). The first CV separates species with a relatively rounded skull (low scores) from those with a more stream-lined ventral skull morphology (high scores, Figure 5). Shape change is marked by a slight medial compression in the tooth row, contraction of the palatine, and a narrowing and posterior displacement of the zygomatic arches. The area between the external auditory meatus is also shifted posteriorally and compressed medially relative to the rest of the skull. The second CV contrasts the hyenids (low scores) with the polar bear (high scores). Changes along this axis emphasize a narrowing of the zygomatic breadth, relative to the rest of the skull, in non-bone cracking species. The tooth row shows compression similar in direction and scale to that seen in CV1. The area between the external auditory meatus is medially compressed relative to the rest of the skull in the polar bear compared to the hyenids, but there is no posteriorally-directed shift as seen in CV1.

Partial Least Squares Analysis.—

Results from the PLS analyses are shown in Tables 7 and 8. A lack of independence between shape and the ecological variables is supported by the permutation tests for all 3 views (Table 7). The RV coefficient for each view is high and positive (0.66 for lateral, 0.73 for mandible, and 0.39 for ventral), signifying a strong degree of correlation between the Procrustes coordinates and the ecological index. The first 2 PLS axis pairs explain more than 94% of the total covariance between shape and ecology in every view, with the first alone explaining at least 86% of total variance. Loadings for the ecological variables (Table 8) on the first 2 PLS axis pairs are remarkably similar across views, with killing strategy and hunting party both highly positive and bone consumption having the only negative loading for PLS1. Partial least square axis pair 2 is characterized by a highly positive loading for hunting party, a moderately positive loading for bone consumption, and negative loadings for meat consumption and killing strategy.

The relationship between shape and the ecological variables represented by PLS1 is depicted for each view in Figures 6-8. Changes in morphology along the shape PLS1 axis (Figure 6) are associated with a shift from negative to positive ecological scores along the ecology PLS1 axis, where positive ecological scores are associated with an anterodorsal elevation of the rostrum, a reduction in the height of the sagittal crest region relative to the crown of the skull (with the exception of the nuchal crest, which shows dorsally-directed expansion), and dorsal and anteroposterior expansion of the jugal. The non-hyenids also show an anteroposterior expansion of the cranium posterior to the tooth row.

Shape change in the mandible (Figure 7) follows a nearly linear relationship with the ecological PLS scores. A higher score on the ecological PLS axis (i.e., species that consume little to no bone) is associated with an increase in mandibular depth anterior to and below the canine and in the angular process, and a reduction in the depth of the mandible below where the tooth row meets the ramus. The ramus/tooth row juncture expands dorsally relative to the rest of the mandible while the posterior margin of the ramus expands posteriorally, and the tooth row expands along the anteroposterior axis relative to the rest of the mandible.

The relationship between shape in the ventral view and the ecological variables for PLS1 is depicted in Figure 8. Shape change along PLS1 is similar to ventral CV2 for species, with a medially-directed narrowing of the maxilla, zygomatic arches, and the area between the external auditory meatus, and anteroposterior reduction in the maxilla relative to the rest of the skull. The premaxilla and the area between external auditory meatus expand slightly along the anteroposterior axis relative to the rest of the skull. Anteroposterior expansion from the palate to the back anterior edge of the foramen magnum is emphasized more strongly here than in ventral CV2.

Phylogenetic Signal.—

The p-values for the permutation tests of the hypothesis of no phylogenetic signal in shape are $p<0.0312$, $p<0.0082$, and $p<0.0011$ for the lateral, mandibular, and ventral views, respectively. Therefore, the null hypothesis is rejected for all 3 views, as all show significant evidence of phylogenetic signal in skull shape. The results of the phylogenetic signal analysis for the ecological variable are shown in Table 9. Bone eating has the lowest K, and the only value less than 1, indicating random or convergent evolution in the acquisition of bone consumption among the hypercarnivores. The K value for hunting group is very close to 1, indicating that evolution of hunting group follows Brownian motion and has some phylogenetic signal. The p-values are significant for killing method across all branch length methods, suggesting non-random phylogenetic signal for killing method. Meat consumption falls marginally short of being significant for all branch length estimations.

DISCUSSION

There is a high degree of morphological variation in the skulls of the hypercarnivorous members of Order Carnivora, both within and across families. The results suggest that refinement of the classification system put forth by Van Valkenburgh (2007) is needed to adequately capture the ecomorphological forms seen among extant species. Key features, such as the shape of the dorsal curvature of the cranium and the position of the angular process relative to the ventral margin of the mandible, may be useful in further subdividing and discriminating between the hypercarnivorous ecomorphs. Phylogenetic relatedness plays a significant role in the distribution of both morphological and ecological characteristics throughout Carnivora, but this does not depreciate the value of a more refined ecomorphological classification system.

Analysis of the mandible resulted in a clear separation of feliform (represented by the African lion and the 3 hyena species) and caniform species (the polar bear, gray wolf, and African wild dog), reflecting the deeper mandibular body and narrower dorsal ramus of members of the feliform lineage. These results compliment the findings of Raia (2004), who found that phylogeny accounted for the greatest portion of variation in mandible shape in a similar study. These differences in shape likely reflect differences in attachment, size, and configuration of the masseter and temporalis muscles, resulting in different areas of focused strain during mastication. Indeed, muscle usage and development has been shown to play a part in the development of bone morphology (Horowitz and Shapiro, 1955). Caniforms and feliforms may differ in the ways they dissipate the stresses associated with biting and food processing, as suggested in stress distribution analyses performed by Tseng and Binder (2010), in which finite element models showed significant differences in mandible strain between spotted hyenas and gray wolves. Identification of distinguishing skull characteristics, such as the relative size of muscle attachment sites and areas important in stress dissipation, is beneficial to paleontological studies, as it offers a starting point from which to make inferences about familial relationships among extinct taxa. Further, such characteristics can be used to identify possible instances of convergent evolution in morphological features.

The results suggest that the wolf-like ecomorph may contain a greater range of shape variability across its members than is true for the other 2 hypercarnivorous sub-categories, and a greater degree of shape variability than feliforms. The wide range of skull morphologies seen in the caniforms reflects the wide range of ecological traits observed across the group. In general, caniforms have a narrower and more elongated skull compared to feliforms, but the location on the skull where this manifests, and the degree to which this elongation occurs, varies across species. The gray wolf, with its anteriorally elongated tooth row and rolling brow curvature, represents the average caniform morphology, whereas the African wild dog shows comparatively less anterior expansion in the tooth row and a steeper inclination of the brow. The relatively long skull of the polar bear is achieved very differently, with most of the elongation centered behind the tooth row. Given these marked differences in skull morphology among caniforms, further refinement of the wolf-like ecomorph might be valuable to more adequately describe the diversity among living and extinct taxa. The wolf-like ecomorph might be best split into 3 sub-categories based on diet, with 1 group including species with meat-exclusive diets (e.g., the polar bear), another housing species with diets high in tough foods (e.g., the African wild dog and the giant panda), and the final group including those with more omnivorous tendencies (e.g., the gray wolf).

One unexpected finding was the repeated grouping of the polar bear and the African lion with respect to skull shape in the lateral and mandibular views. The smoothing of the dorsal curvature and high degree of postorbital elongation of the cranium shared by both species are associated with stalking behavior, as killing strategy discriminated the polar bear and the African lion from all the other species. Both species also have meat-exclusive diets with little to no bone consumption. Thus, features important to the consumption of hard foods, such as the broad zygomatic arches and vaulted forehead exemplified by the spotted hyenas (see Tanner *et al.,* 2008), are absent in both polar bears and African lions. Given the similarities in killing strategy and diet between these species and the associated similarities in cranium shape, the polar bear fits better in the cat-like ecomorph (Van Valkenburgh, 2007) than in the wolf-like ecomorph.

Studies with additional hypercarnivorous caniforms would help determine whether the polar bear is unique and deserves to be re-classified as a cat-like ecomorph, or if a sub-categorization scheme as described above would be the better approach.

The classification of the African wild dog in the wolf-like ecomorph seems misleading, as this species shares morphological characteristics with both the gray wolf and hyenas. The African wild dog and gray wolf share an anteroposteriorally elongated jugal, dorsoposteriorally slanted orbitals, and a jugal-squamosal suture that extends to the tip of the jugal and forms the ventroposterior base of the orbit. This last characteristic may be unique to Canidae, as it was not seen in any of the other families. The African wild dog and hyenas share a dorsal expansion of the sagittal crest relative to the rest of the skull, a trait that is thought to be important for breaking bones, and nasals that do not extend as far posteriorally as in the other species. The African wild dog displays dorsoanterior inflation in the brow, resulting in a steep incline from the muzzle to the top of the cranium. A similar morphology is seen in the hyenas in association with a caudally elongated frontal sinus, which is thought to aid in stress dissipation during osteophagy (Tanner *et al.*, 2008). The maxilla and zygomatic arches are also broader laterally relative to the skull in the African wild dog and the hyenas than in the other species examined.

In contrast to the cranial similarities seen in the African wild dog and the hyenas, the mandible clearly discriminates the two groups, placing the African wild dog in close proximity to the gray wolf. The greater depth of the mandible and the dorsoventrally broader jugal seen in the hyenas, but not in the African wild dog, may suggest differences in the requirements and stresses associated with bone eating between the 2 groups. Reduction in the size of the jugal relative to the rest of the skull as seen in the hyenas, but not in the African wild dog, may be related to stress distribution during bone breaking in the hyenas, as the end of the jugal anterior to the jugal-squamosal suture was found to be a high stress point during biting in finite element analyses by Tanner *et al.* (2008). The similarities in form and function seen between the hyenas and the African wild dog, and also between the polar bear and African lion, are further evidence that the wolf-like ecomorph may require sub-categorization based on dietary habits.

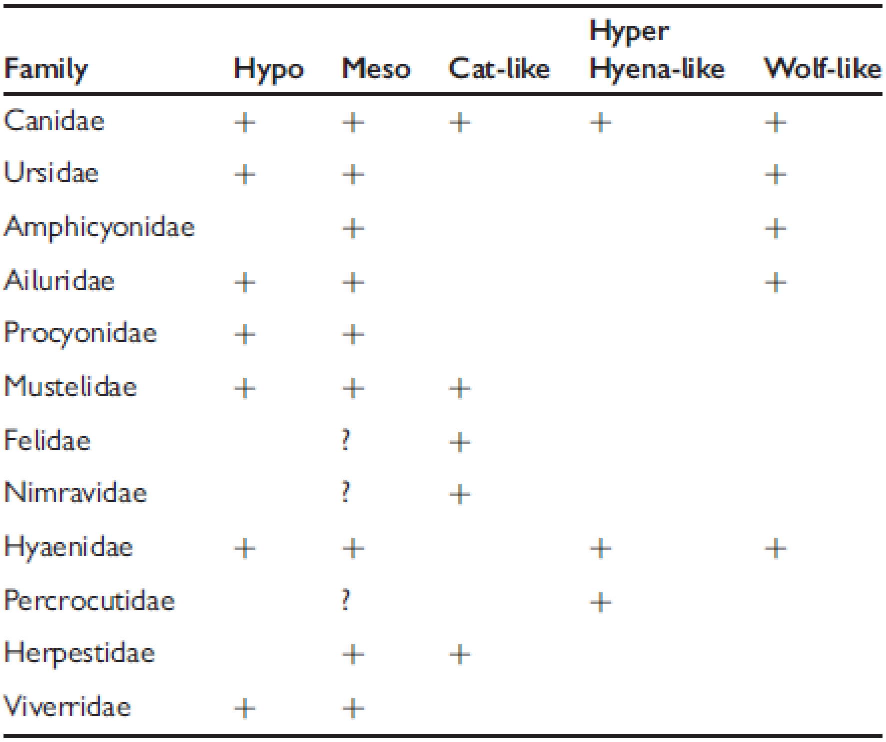
The hyenas are of special interest in that, despite close historical relatedness and ecological similarities, differences in shape discriminate them clearly from one another in all 3 cranial views. Brown and striped hyenas are often seen to be more extreme in shape than the spotted hyena when compared to the other species. This is particularly evident in the ventral view, where brown and striped hyenas differ from spotted hyenas in having anteroposterior expansion of the maxilla and dorsal expansion of the palatine relative to the rest of the skull, and a dorsally-directed reduction in size of the areas posterior to the postglenoid processes. The spotted hyena shows a greater dorsoanterior expansion in the sagittal crest, and a more developed nuchal crest. The jugal also shows a greater contraction relative to the rest of the skull in the spotted hyena than in the other hyenas. These differences in shape may reflect the different dietary habits of the hyenas. Spotted hyenas primarily hunt for food, whereas the majority of meat consumed by the other 2 hyenas is scavenged from carcasses left by other predators, drought, or disease. The scavenging hyenas also compliment their diets with a vast assortment of other foods when vertebrate prey is not available, resulting in a more omnivorous diet compared to spotted hyenas. In addition, differences may be related to the size of the bones being consumed. Spotted hyenas often take down prey considerably larger than themselves, while the other hyenas rely more on carcasses and the occasional small prey item. Kruuk (1975) stated that fecal samples from striped hyenas contain a relatively small amount of large prey items compared to that of spotted hyenas, suggesting differences in the sizes of the bones consumed by each species. Although the differences among the hyenas are not great enough to warrant refinement of the hyena-like ecomorph, they do show that spotted hyenas differ significantly in shape from the scavenging members of Hyaenidae.

Phylogeny was expected to play a significant role in the distribution of the ecological traits due to the way in which they were assigned (i.e. the distribution of traits such as scavenging and pack hunting). It was not surprising then that killing strategy, meat consumption, and hunting party all show a phylogenetic signal ($K>1$). Of these traits, only killing strategy was found to be statistically significant, possibly reflecting the small sample size (i.e., number of species). Evidence of a phylogenetic signal was also expected for skull morphology. Raia (2004) found that phylogeny accounts for a significant amount of shape variation in the carnivoran mandible. He attributed this to the fact that closely related species share a common ancestor and thus a common ancestral shape. While the shape of the cranium may be affected by more functional requirements than the mandible, similarities due to common ancestry will still be noticeable throughout Carnivora.

Identifying morphological characteristics shared by taxa with similar behavioral ecologies is an important step in furthering our ability to make inferences about the behaviors of both living and extinct species. Moreover, variation in the shape of the skull, and its dietary and ecological implications, are key to studies of carnivoran evolution. The ability to look at shape difference throughout the skull as a complete entity is vital to furthering our understanding of these differences, and will permit us to further study the interactions and associations among the morphological features that make up the feeding apparatus. Future ecomorphological analyses would benefit greatly from a broader usage of geometric morphometric techniques, as they offer the ability to visualize both small and sweeping changes in shape across the entire skull when used in conjunction with ecological assessments. Through our analyses, we were able to identify several morphological features that can be used to discriminate hypercarnivorous species from one another. While feature such as a greater steepness of the brow and a prominent sagittal crest (features thought to be associated with the bone eating behavior seen in the hyenids) have been described in the past, the differences in the relative shape of the jugal (seen and the position of the angular process relative to the ventral margin of the mandible have not been previously identified.

The results presented here suggest that the hypercarnivore classification system described by Van Valkenburgh (2007) may be in need of revision. While the system put forth by Van Valkenburgh has been a useful tool for ecomorphologists looking to assess the possible ecological behaviors of extinct species, our analyses show that the categorization method used may be too broad to accurately make such inferences. Our analyses show this to be especially true for the wolf-like ecomorph, which Van Valkenburgh describes as being not as extreme in skull and dental modifications as the other 2 ecomorphs. A classification scheme which subdivides the wolf-like ecomorph into several distinct categories would be better suited for use in future ecomorphological studies. A possible classification scheme would include a generalized wolf-like ecomorph, similar to the gray wolf, and a durophagious category with species like the African wild dog. If further analyses find that the polar bear is not unique in its similarities to the cat-like ecomorph, then a third category bridging the gap between the cat-like and wolf-like ecomorph may also be needed. A more encompassing analysis (e.g., more taxa, 3D visualization, greater ecological classification) would be beneficial to determining the extent to which such categories should be broken down, and what morphological features exemplify each category.

Table 1 - Chart from Van Valkenburgh 2007 showing the occurrence of ecomorphs throughout the evolution of the carnivoran families, with emphasis on terrestrial species larger than 7kg in mass. A "+" indicates that at least one species in the fossil record is known to have displayed a particular ecomorph. "?" indicates that the existence of a species with a particular ecomorph is unknown given the limited fossil record.



				Hyper	
Family	Hypo	Meso	Cat-like	Hyena-like	Wolf-like
Canidae	+	+	+	+	+
Ursidae	+	+			+
Amphicyonidae		+			+
Ailuridae	+	+			+
Procyonidae	+	+			
Mustelidae	+	+	+		
Felidae		?	+		
Nimravidae		?	+		
Hyaenidae	+	+		+	+
Percrocutidae		?		+	
Herpestidae		+	+		
Viverridae	+	+			

Table 2 – Descriptions of the common behavioral traits assigned to prey acquisition and consumption for each species used in the study following a literature review. Characteristics assigned to species are taken as common tendencies and do not reflect behaviors that occur infrequently.

Species	Meat	Bone	Hunting Party	Strategy	Sources
Spotted Hyena	Mostly	About 10%	Alone or small groups	Hunters and scavengers, prey is often large, large prey ripped open, small prey killed with bite to head/neck	MacNulty et al. 2007, Owen-Smith and Mills 2008, Van Valkenburgh 1996
Striped Hyena	As available, supplemented with other foods	Some	Forage and feed alone	Primarily scavenging, very little killing of prey and then only of small animals	Leakey *et al.* 1999, Wagner 2006
Brown Hyena	As available, supplemented with other foods	Some	Forage alone, sometimes gather at large carcasses and feed in turn	Primarily scavenging, very little killing of prey and then only of small animals	Mills 1982, Wiesel 2006
Polar Bear	Almost all	Little	Alone or in groups depending on food abundance	Wait and stalk, kill with brute force, no specific killing posture, large prey but frequently small compared to them	DeMaster and Stirling 1981, Sacco and Van Valkenburgh 2004
African Wild Dog	Mostly	About 10%	Pack	Stalk and chase, smaller prey are mobbed, larger prey slashed with teeth until shocked/exhausted, prey often eaten alive, prey are generally as big or bigger than them	Estes and Goddard 1967, MacNulty et al. 2007, Owen-Smith and Mills 2008, Van Valkenburgh 1996
Gray Wolf	Mostly	Smaller bones	Pack	Pursue and/or harass followed by multiple bites, mainly large prey	MacNulty *et al.* 2007, Mech 1974, Stahler *et al.* 2006
African Lion	Almost all	Smaller bones	Usually hunt in groups	opportunistic scavengers when possible (up to 40% of diet), most prey is large, stalk or pursue and pounce, killing bite and twist?	Haas *et al.* 2005, MacNulty et al. 2007, Owen-Smith and Mills 2008, Tsukahara 1993, Van Valkenburgh 1996

Table 3 – Index of ecological categories and the values assigned to them for use in partial least squares analysis. Values for ecomorph were ordered arbitrarily.

Value	Meat Consumption	Bone Consumption	Hunting Party	Killing Strategy
1	As available, omnivorous diet	Little to none	Solitary	Primarily scavenging
2	Most of diet	Smaller bones only, little portion of diet	Occasionally in groups (depending on food abundance)	Chase, knock down, tear apart
3	Nearly exclusive	easily-broken bones, significant part of diet	Alone or small groups	Chase, bite/exhaust, tear apart
4	---	Any that can be broken, considerable part of diet	Packs or large groups	Stalk and pounce, killing bite
5	---	---	---	Stalk, kill with brute force

Table 4 – Values assigned to each species following the ecological index in Table 3. Assignment of values was performed by comparing the descriptive summaries from Table 2 to the categories described in Table 3.

Species	**Meat**	**Bone**	**Hunting Party**	**Strategy**
Spotted	2	4	3	2
Striped	1	3	1	1
Brown	1	3	1	1
Polar	3	1	2	5
Wild Dog	2	4	4	3
Wolf	2	2	4	3
Lion	3	2	4	4

Table 5 – Results from the Goodall's F test with permutation for signs of sexual dimorphism in shape, and the subsequent Mancova for shape with size as a covariate that were significant prior to Bonferroni adjustment (p<0.002).

Species – View	Goodall's p-value	Mancova p-value	% Variance explained by size	% Variance explained by sex	Total % variance explained
Polar Bear – Mandible	0.0116	0.0172	26.19	9.9548	36.1448
African Lion – Mandible	0.0352	0.0432	23.297	5.3505	28.6475
African Lion – Ventral	0.0476	0.6312	11.871	2.3934	14.2644
Gray Wolf – Mandible	0.0016	0.014	8.645	2.4659	11.109
Gray Wolf – Ventral	0.0004	0.0792	5.778	1.7393	7.5173

Table 6 – Canonical variates (CVs) obtained for all 3 views with the percent of variance explained by each CV and cumulative percentage of explained variance for that view.

View	CV	Eigenvalues	% Variance	Cumulative %
Lateral	1	1596.862879	90.155	90.155
	2	120.094379	6.78	96.935
	3	31.07215079	1.754	98.69
	4	12.56631796	0.709	99.399
	5	7.47116971	0.422	99.821
	6	3.17229624	0.179	100
Mandible	1	2269.458657	57.375	57.375
	2	862.7065408	21.81	79.186
	3	561.0455231	14.184	93.37
	4	160.1684887	4.049	97.419
	5	80.52965515	2.036	99.455
	6	21.55710116	0.545	100
Ventral	1	47.09877689	49.749	49.749
	2	23.77994285	25.118	74.867
	3	16.59380728	17.527	92.394
	4	4.51629731	4.77	97.165
	5	2.07546399	2.192	99.357
	6	0.60870517	0.643	100

Table 7 – Results from partial least squares analyses examining covariation between skull morphology and ecological variables (Table 4). The RV coefficient for a given view is inserted below the name of the corresponding view in the first column.

View	Variable	Singular Value	Independence Test P-value (permutation)	% Total Covariance	Correlation
Lateral	PLS1	0.08538319	<.0001	88.946	0.93636
RV	PLS2	0.02783738	<.0001	9.454	0.74652
0.6595	PLS3	0.0113086	<.0001	1.56	0.68632
	PLS4	0.00179605	<.0001	0.039	0.61973
Mandible	PLS1	0.0666852	<.0001	91.77	0.93929
RV	PLS2	0.01810571	<.0001	6.765	0.80229
0.7309	PLS3	0.00829509	<.0001	1.42	0.63083
	PLS4	0.00147778	<.0001	0.045	0.52652
Ventral	PLS1	0.06819104	<.0001	85.62	0.80991
RV	PLS2	0.02191763	<.0001	8.845	0.83781
0.3900	PLS3	0.01720183	<.0001	5.448	0.60626
	PLS4	0.00216774	<.0001	0.087	0.63211

Table 8 – Weighting coefficients assigned to each ecological variable for the first 2 pairs of partial least square axes for each of the 3 views following partial least squares analysis.

View	Variable	PLS1	PLS2
Lateral	**Meat**	0.34883278	-0.34819878
	Bone	-0.31468029	0.1965845
	Hunting Group	0.58584705	0.80563216
	Kill Strategy	0.66035993	-0.43711436
Mandible	**Meat**	0.36140411	-0.24619879
	Bone	-0.29723917	0.35997854
	Hunting Group	0.56258882	0.81376489
	Kill Strategy	0.6815642	-0.38417225
Ventral	**Meat**	0.27946663	-0.2647549
	Bone	-0.38624738	0.32677728
	Hunting Group	0.61971087	0.78340854
	Kill Strategy	0.62343388	-0.45759425

Table 9 – Blomberg's (2003) K statistic and the p-values for tests of phylogenetic independent contrast variance under each of the 4 branch length estimation methods tested for all ecological variables, and for the consensus tree obtained from the 4 single trees. 1 = all branch lengths set to 1.0, G = Grafen (1989), N = Nee (cited in Purvis 1995), and P = Pagel (1992). P-values <0.05 show signs of non-random phylogenetic signal.

Variable	K	PIC Variance p-value (1)	PIC Variance p-value (G)	PIC Variance p-value (N)	PIC Variance p-value (P)	PIC Variance p-value (Consensus)
Meat	1.495	0.0755	0.0605	0.0565	0.0555	0.057
Bone	0.695	0.584	0.5505	0.536	0.562	0.5475
Hunting group	1.055	0.096	0.0805	0.092	0.1005	0.0995
Killing Strategy	1.647	0.0365	0.037	0.028	0.028	0.0365

Figure 1 - - Lateral, mandibular, and ventral views of a *Crocuta crocuta* skull, showing locations of landmarks (red, numbered dots, see Table 2), and semi-landmarks (red, unnumbered triangles). For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

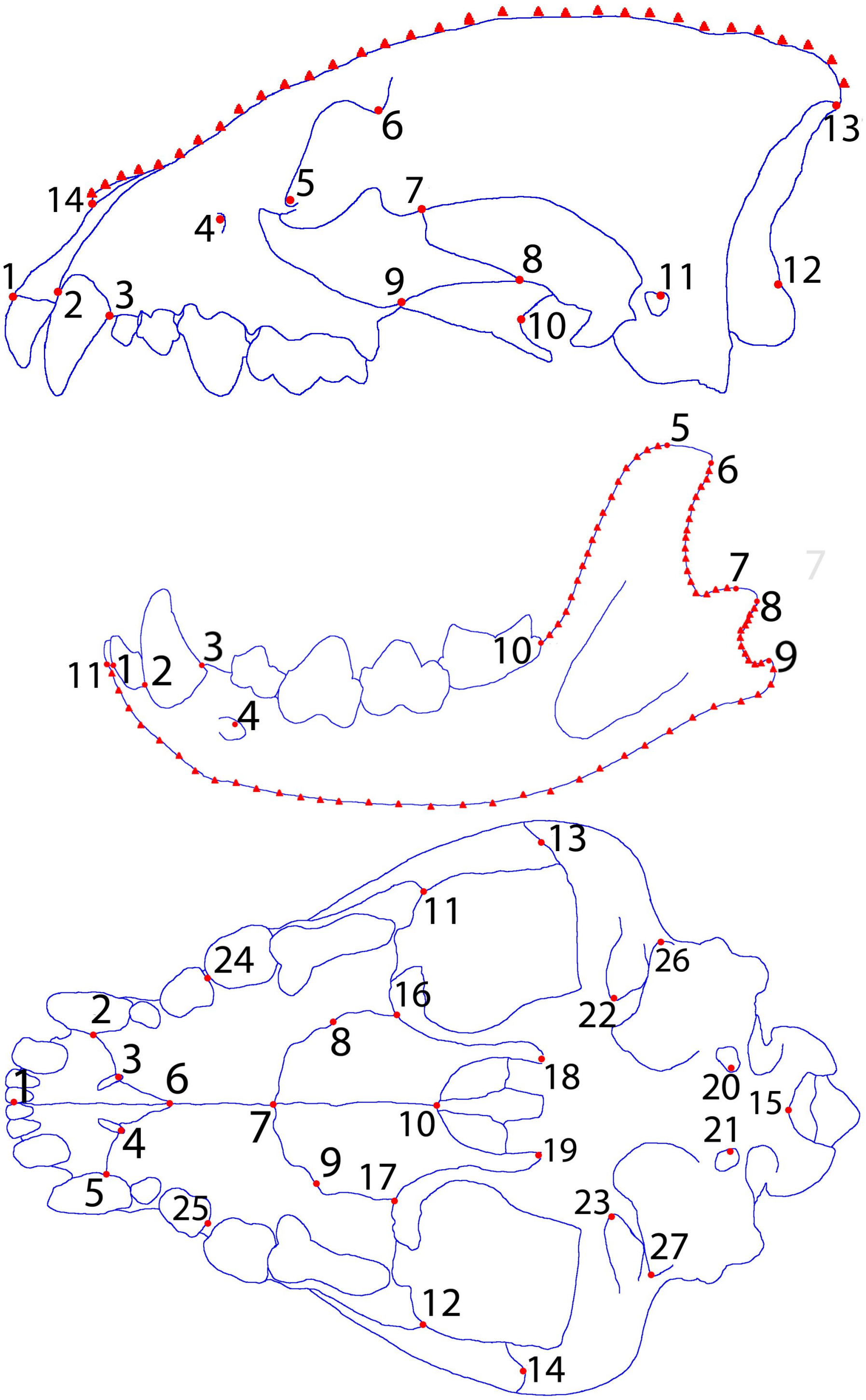


Figure 2 - Phylogenetic tree of the 7 Carnivora taxa included in this study. Relationships are based on Eizirik *et al.* 2010.

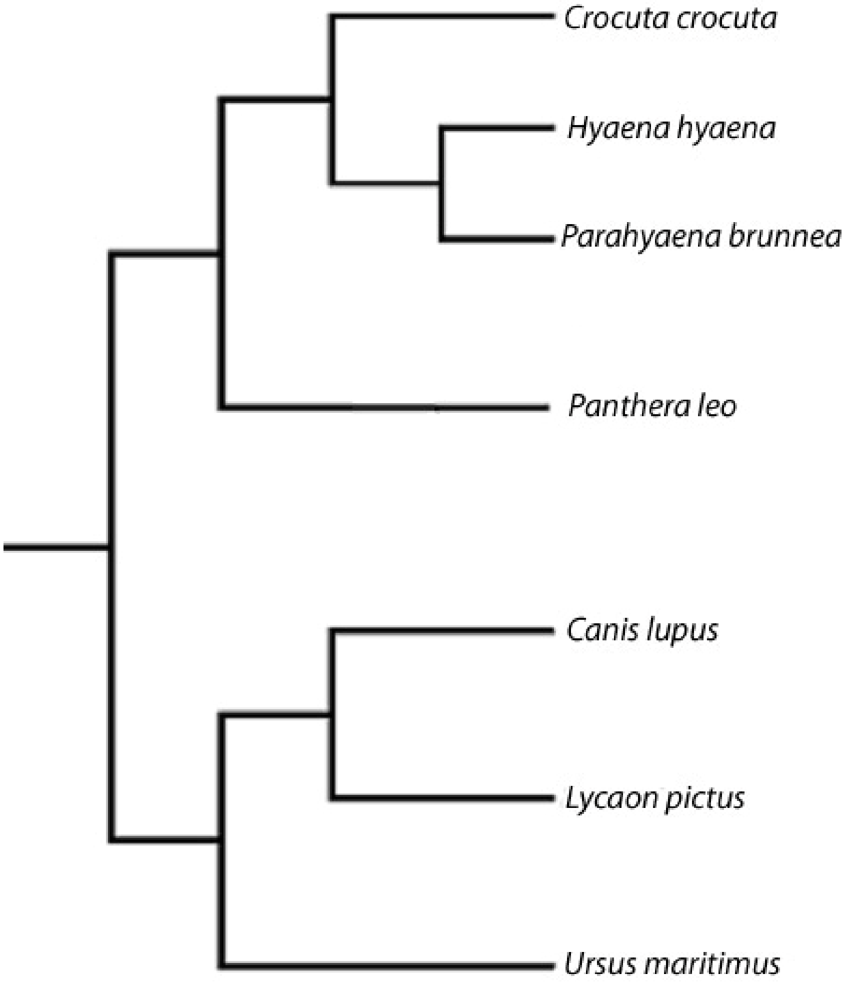


Figure 3 - Plot of lateral view CV1 vs. CV2 for species, with deformation grids depicting shape change along CV1 (bottom right) and CV2 (top left). The legend (bottom left) lists the symbol associated with each species.

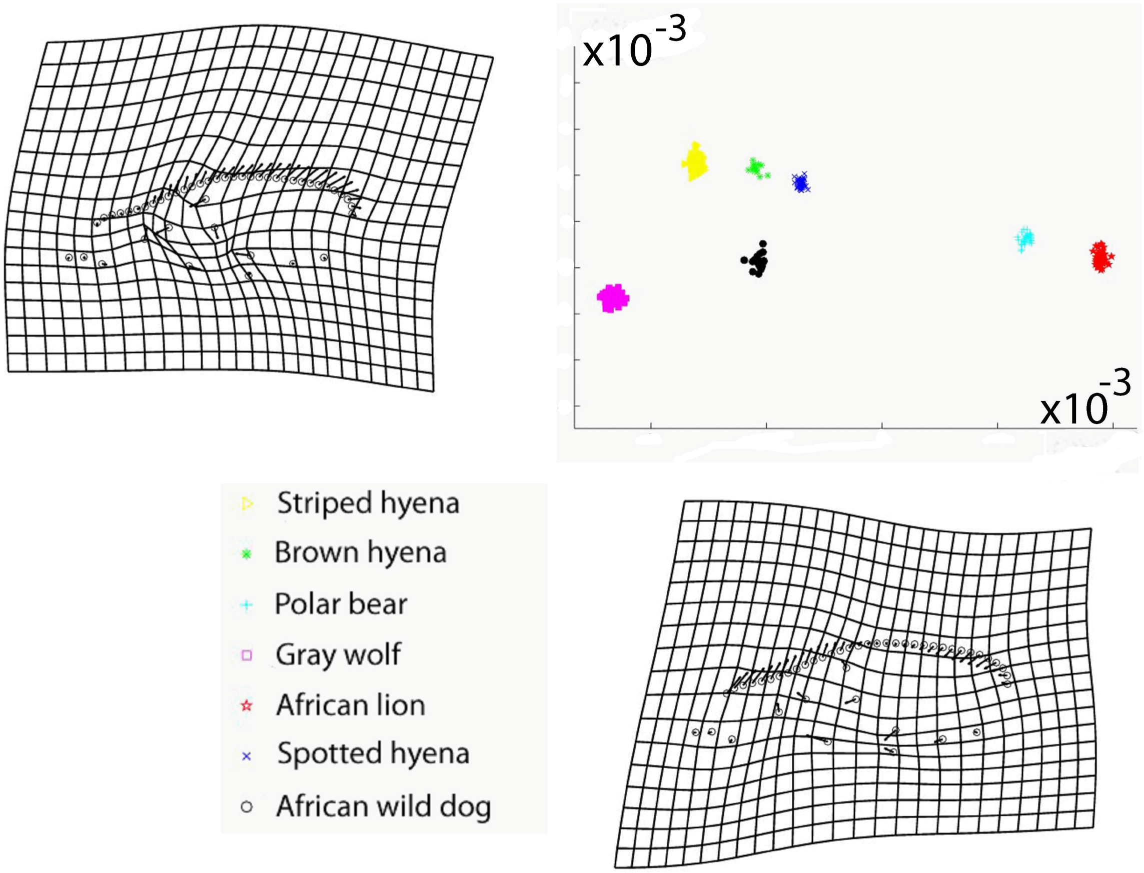


Figure 4 - Plot of mandibular view CV1 vs. CV2 for species, along with its deformation grids and legend as described in Figure 3.

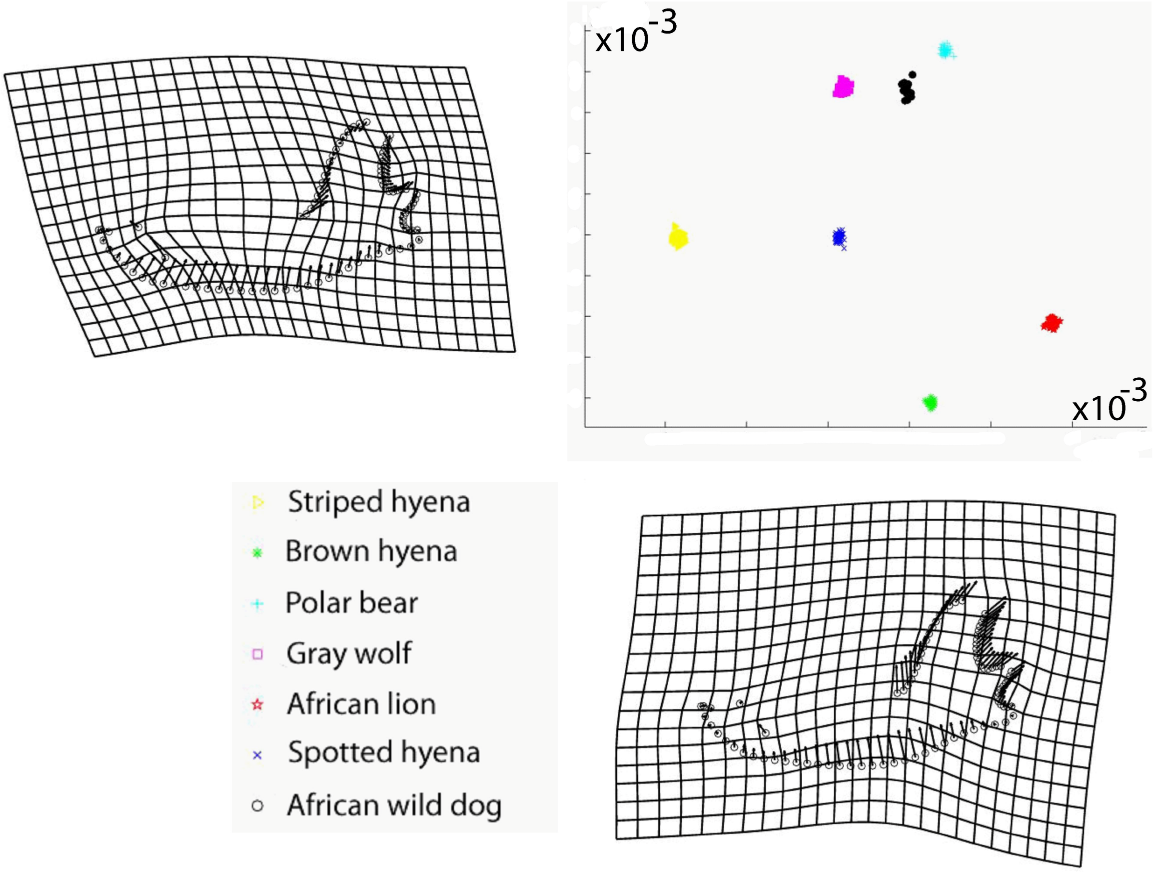


Figure 5 - Plot of ventral view CV1 vs. CV2 for species, along with its deformation grids and legend as described in Figure 3. Note the axis ranges are significantly less than that seen in the other 2 views.

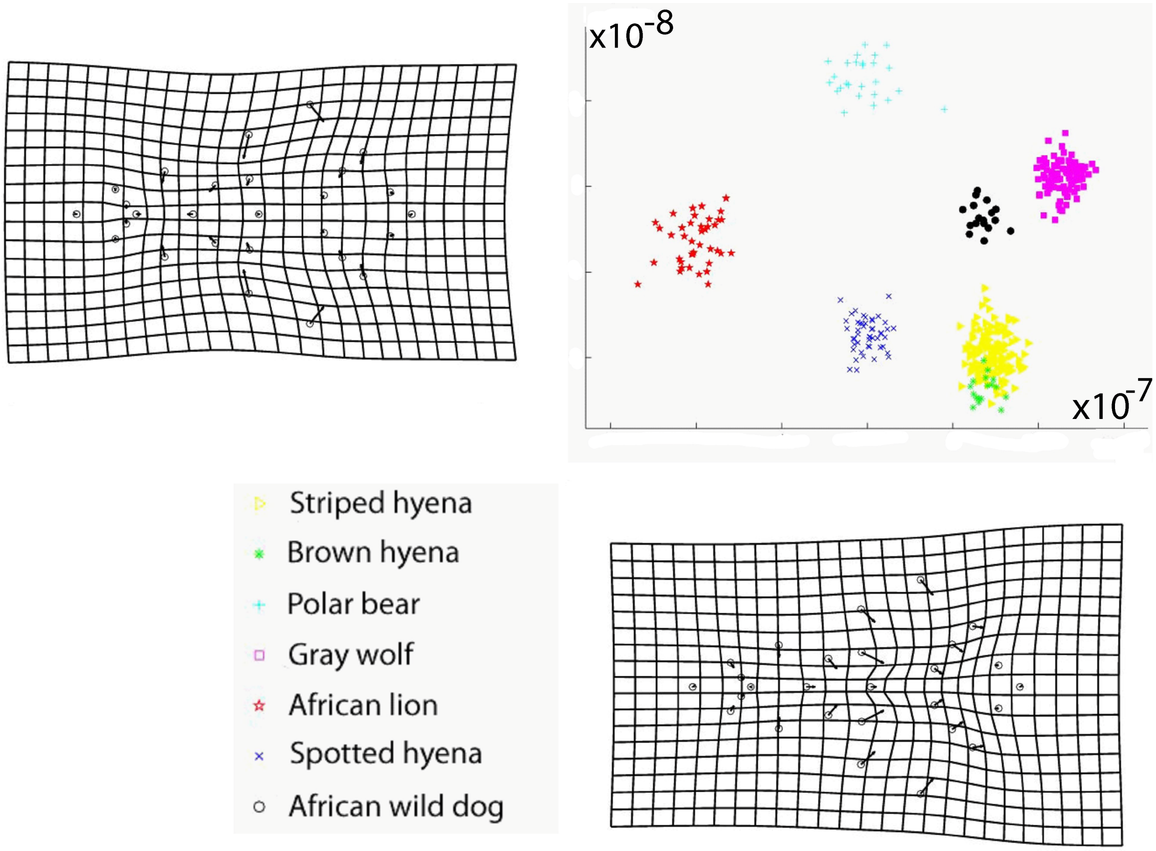


Figure 6 – Plot of partial least squares for shape axis 1 vs. ecology axis 1 for the lateral view. A plot of PLS1 vs. PLS2 for the ecological traits showing the directionality and relative strength of the trait coefficients is inserted to the right of the plot. Below the plot is a deformation grid showing the shape change associated with left to right movement along shape PLS1.

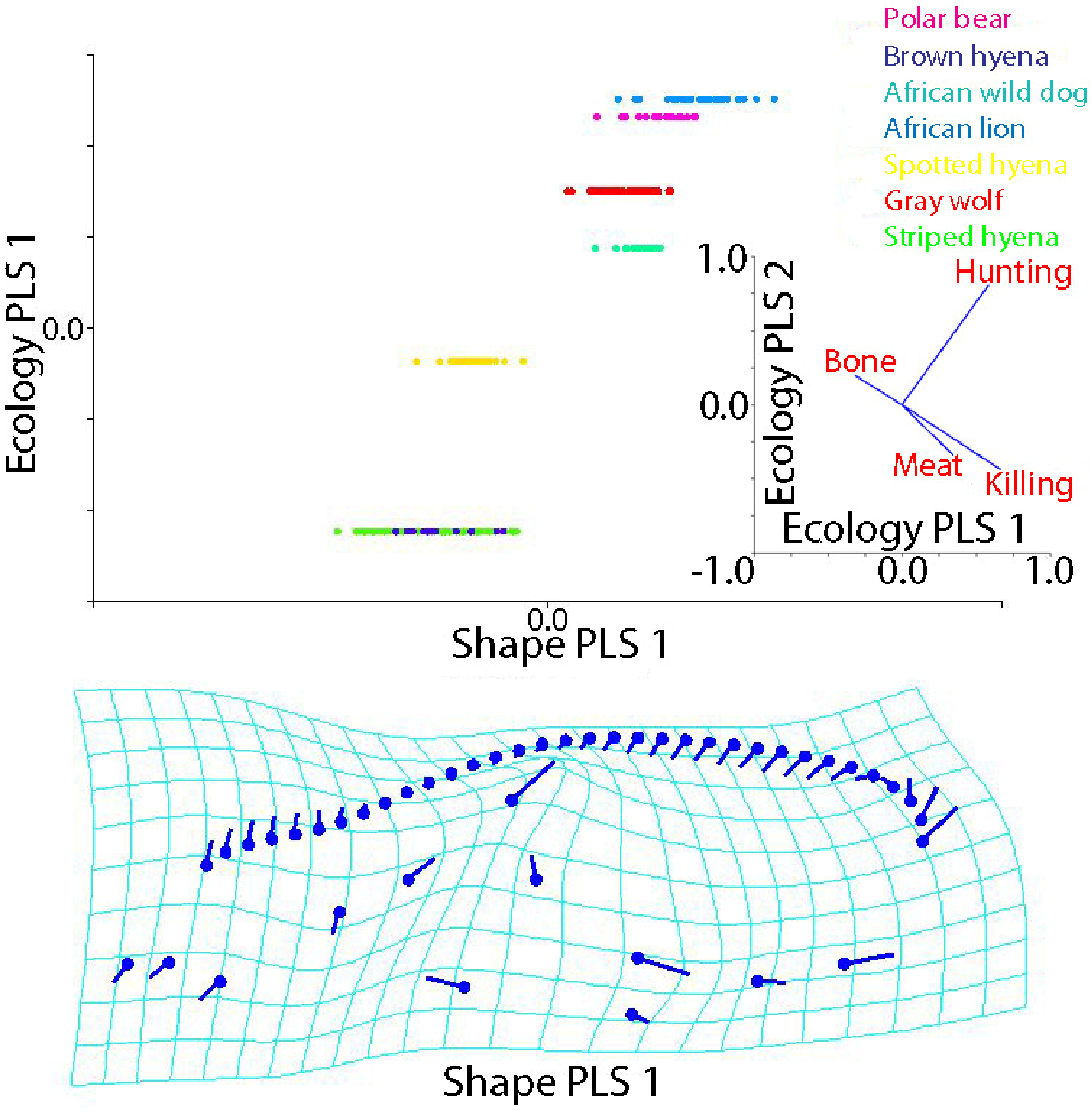


Figure 7 – Plot of partial least squares for shape axis 1 vs. ecology axis 1 for the mandibular view. See Figure 6 for further explanation.

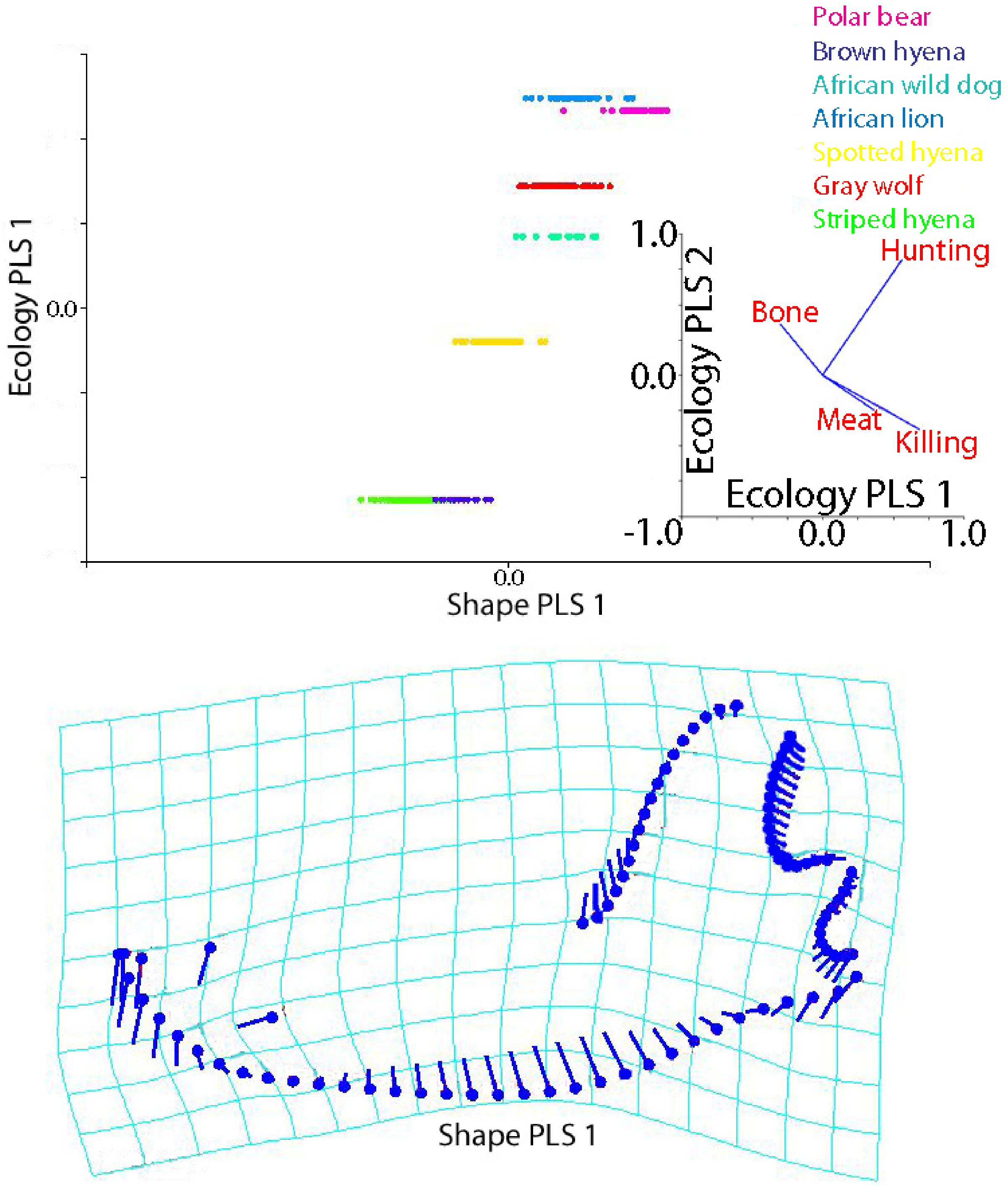
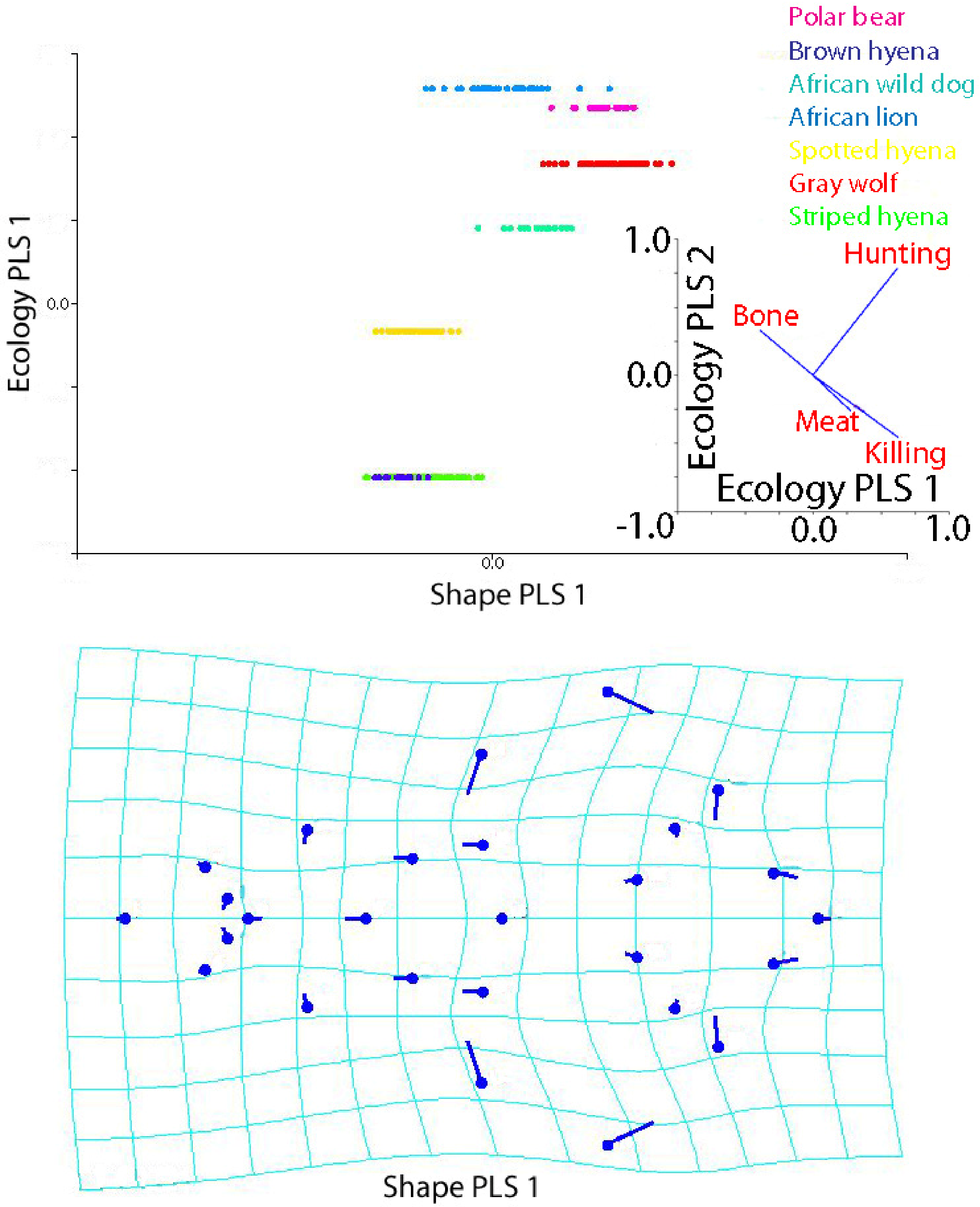


Figure 8 – Plot of partial least squares for shape axis 1 vs. ecology axis 1 for the ventral view. See Figure 6 for further explanation.



APPENDICES

APPENDIX A

List of included museum specimens

Table 10 - List of specimens used in this study. Abbreviations within the Museum column represent where the specimen is located. (MSU = Michigan State University, East Landing, MI, TAU = Tel Aviv University, London, England, BMNH = British Museum of Natural History London, England, FMNH = Field Museum of Natural History, Chicago IL, NMK = National Museums of Kenya, Africa, RCSOM = Royal College of Surgeons, London, England). Specimens whose sex could not be determined were marked "?" in the Sex column. Lateral, ventral, and mandible refer to the digitization views used. Those specimens marked "Y" were included in the corresponding view analyses, whereas that marked with a "-" were not.

Museum	Number	*Species*	Sex	Lateral	Ventral	Mandible
?	225 VGS	*Crocuta crocuta*	M	-	-	Y
?	486 ECO	*Crocuta crocuta*	F	-	-	Y
?	799 HUM	*Crocuta crocuta*	M	-	-	Y
?	897 BFT	*Crocuta crocuta*	M	-	-	Y
MSU	35852	*Crocuta crocuta*	M	Y	Y	Y
MSU	35853	*Crocuta crocuta*	M	Y	Y	Y
MSU	35854	*Crocuta crocuta*	M	Y	Y	Y
MSU	35855	*Crocuta crocuta*	M	Y	Y	Y
MSU	35856	*Crocuta crocuta*	F	Y	Y	Y
MSU	35857	*Crocuta crocuta*	?	Y	Y	Y
MSU	35858	*Crocuta crocuta*	?	Y	Y	Y
MSU	35859	*Crocuta crocuta*	F	Y	Y	Y
MSU	36008	*Crocuta crocuta*	F	Y	Y	Y
MSU	36009	*Crocuta crocuta*	?	Y	Y	Y
MSU	36011	*Crocuta crocuta*	F	Y	Y	Y
MSU	36074	*Crocuta crocuta*	F	Y	Y	Y
MSU	36077	*Crocuta crocuta*	F	Y	Y	Y
MSU	36078	*Crocuta crocuta*	M	Y	Y	Y
MSU	36079	*Crocuta crocuta*	M	Y	Y	Y
MSU	36080	*Crocuta crocuta*	F	Y	Y	Y
MSU	36081	*Crocuta crocuta*	F	Y	Y	Y
MSU	36082	*Crocuta crocuta*	F	Y	Y	Y
MSU	36083	*Crocuta crocuta*	F	Y	Y	Y
MSU	36084	*Crocuta crocuta*	M	Y	Y	Y
MSU	36094	*Crocuta crocuta*	F	Y	Y	Y
MSU	36156	*Crocuta crocuta*	F	Y	Y	Y
MSU	36160	*Crocuta crocuta*	F	Y	Y	Y
MSU	36161	*Crocuta crocuta*	?	Y	Y	Y
MSU	36162	*Crocuta crocuta*	M	Y	Y	Y
MSU	36163	*Crocuta crocuta*	M	Y	Y	Y

Table 10 (cont'd)

MSU	36164	*Crocuta crocuta*	?	Y	Y	Y
MSU	36165	*Crocuta crocuta*	F	Y	Y	Y
MSU	36167	*Crocuta crocuta*	?	Y	Y	Y
MSU	36168	*Crocuta crocuta*	M	Y	Y	Y
MSU	36550	*Crocuta crocuta*	F	Y	Y	Y
MSU	36551	*Crocuta crocuta*	F	Y	Y	Y
MSU	36552	*Crocuta crocuta*	F	Y	Y	Y
MSU	36553	*Crocuta crocuta*	F	Y	Y	Y
MSU	36556	*Crocuta crocuta*	F	Y	Y	Y
MSU	36558	*Crocuta crocuta*	F	Y	Y	Y
MSU	36566	*Crocuta crocuta*	?	Y	Y	Y
MSU	36567	*Crocuta crocuta*	F	Y	Y	Y
MSU	36568	*Crocuta crocuta*	?	Y	Y	Y
MSU	36569	*Crocuta crocuta*	F	Y	Y	Y
MSU	36570	*Crocuta crocuta*	F	Y	Y	Y
MSU	36571	*Crocuta crocuta*	F	Y	Y	Y
MSU	36576	*Crocuta crocuta*	?	Y	Y	Y
MSU	36580	*Crocuta crocuta*	?	Y	Y	Y
MSU	36581	*Crocuta crocuta*	F	Y	Y	Y
TAU	2208	*Crocuta crocuta*	?	Y	Y	-
TAU	8005	*Crocuta crocuta*	F	-	Y	-
TAU	7026	*Crocuta crocuta*	M	-	Y	-
BMNH	0.5.12.1	*Hyaena hyaena*	?	Y	Y	Y
BMNH	1096	*Hyaena hyaena*	F	-	Y	-
BMNH	1495	*Hyaena hyaena*	?	-	Y	-
BMNH	1937.10.30	*Hyaena hyaena*	F	-	Y	-
BMNH	1938.10.18.48	*Hyaena hyaena*	?	Y	Y	Y
BMNH	1990.389	*Hyaena hyaena*	?	Y	Y	Y
BMNH	20.10.27.1	*Hyaena hyaena*	M	-	Y	-
BMNH	20.10.27.2	*Hyaena hyaena*	F	-	Y	-
BMNH	23.1.1.78	*Hyaena hyaena*	M	Y	Y	Y
BMNH	23.1.1.79	*Hyaena hyaena*	F	Y	Y	Y
BMNH	23.1.1.80	*Hyaena hyaena*	F	Y	Y	Y
BMNH	23.3.4.9	*Hyaena hyaena*	M	-	Y	Y
BMNH	24.10.5.5	*Hyaena hyaena*	?	-	Y	-
BMNH	26.10.8.72	*Hyaena hyaena*	M	Y	Y	Y
BMNH	26.10.8.73	*Hyaena hyaena*	F	-	Y	-

Table 10 (cont’d)

BMNH	27.2.14.27	*Hyaena hyaena*	?	Y	Y	Y
BMNH	31.1.2.10	*Hyaena hyaena*	?	Y	Y	Y
BMNH	34.11.28.10	*Hyaena hyaena*	F	Y	Y	Y
BMNH	34.11.28.11	*Hyaena hyaena*	M	Y	Y	Y
BMNH	34.11.28.12	*Hyaena hyaena*	M	Y	Y	Y
BMNH	34.11.28.13	*Hyaena hyaena*	M	Y	Y	Y
BMNH	34.11.28.16	*Hyaena hyaena*	M	Y	Y	Y
BMNH	34.11.28.18	*Hyaena hyaena*	F	Y	Y	Y
BMNH	34.11.28.3	*Hyaena hyaena*	M	-	Y	-
BMNH	34.11.28.4	*Hyaena hyaena*	F	-	Y	-
BMNH	34.11.28.5	*Hyaena hyaena*	M	-	Y	Y
BMNH	34.11.28.6	*Hyaena hyaena*	F	-	Y	Y
BMNH	34.11.28.8	*Hyaena hyaena*	M	-	Y	-
BMNH	34.8.4.7	*Hyaena hyaena*	M	Y	Y	Y
BMNH	35.1.1.1	*Hyaena hyaena*	?	-	Y	-
BMNH	35.1.1.2	*Hyaena hyaena*	?	-	Y	-
BMNH	38.8.4.6	*Hyaena hyaena*	?	-	Y	-
BMNH	39.439	*Hyaena hyaena*	M	-	Y	Y
BMNH	39.44	*Hyaena hyaena*	F	Y	Y	Y
BMNH	44.2.28	*Hyaena hyaena*	?	Y	Y	Y
BMNH	47.36	*Hyaena hyaena*	F	Y	Y	Y
BMNH	5.5.28.2	*Hyaena hyaena*	?	Y	Y	Y
BMNH	51.8.25.1	*Hyaena hyaena*	?	Y	Y	Y
BMNH	52.1483	*Hyaena hyaena*	F	Y	Y	Y
BMNH	56.5.6.50	*Hyaena hyaena*	?	Y	Y	Y
BMNH	58.209	*Hyaena hyaena*	?	Y	Y	Y
BMNH	58.6.24.125	*Hyaena hyaena*	?	Y	Y	Y
BMNH	6.5.4.3	*Hyaena hyaena*	M	Y	Y	Y
BMNH	8.7.24.12	*Hyaena hyaena*	?	Y	Y	Y
BMNH	85.6.13.1	*Hyaena hyaena*	?	Y	Y	Y
BMNH	85.8.1.50	*Hyaena hyaena*	M	-	Y	-
BMNH	92.2.8.2	*Hyaena hyaena*	M	Y	Y	Y
BMNH	HhNo#1	*Hyaena hyaena*	?	Y	Y	Y
BMNH	HhNo#2	*Hyaena hyaena*	?	-	Y	-
BMNH	15.3.6.18	*Hyaena hyaena*	M	-	-	Y
BMNH	1938.6.28.4	*Hyaena hyaena*	?	-	-	Y
BMNH	2.11.22.5	*Hyaena hyaena*	M	Y	-	Y

Table 10 (cont'd)

BMNH	2.11.4.2	*Hyaena hyaena*	?	Y	-	Y
BMNH	24.10.321	*Hyaena hyaena*	?	Y	-	-
BMNH	24.10-5.6	*Hyaena hyaena*	?	-	-	Y
BMNH	34.8.4.6	*Hyaena hyaena*	M	Y	-	Y
BMNH	93.12.1.1.	*Hyaena hyaena*	?	-	-	Y
FMNH	103991	*Hyaena hyaena*	M	Y	Y	Y
FMNH	107342	*Hyaena hyaena*	?	Y	Y	Y
FMNH	140215	*Hyaena hyaena*	?	Y	Y	Y
FMNH	140216	*Hyaena hyaena*	F	Y	Y	Y
FMNH	140218	*Hyaena hyaena*	F	Y	Y	Y
FMNH	140219	*Hyaena hyaena*	?	Y	Y	Y
FMNH	140220	*Hyaena hyaena*	?	Y	Y	Y
FMNH	103992	*Hyaena hyaena*	M	Y	Y	-
MSU	11143	*Hyaena hyaena*	?	Y	Y	-
MSU	13003	*Hyaena hyaena*	?	Y	Y	Y
MSU	36395	*Hyaena hyaena*	M	Y	Y	Y
NMK	3474	*Hyaena hyaena*	M	Y	Y	Y
NMK	4628	*Hyaena hyaena*	?	Y	Y	Y
NMK	8297	*Hyaena hyaena*	?	Y	Y	-
NMK	6297	*Hyaena hyaena*	?	-	-	Y
RCSOM	137.21	*Hyaena hyaena*	?	Y	Y	-
RCSOM	137.3	*Hyaena hyaena*	?	Y	Y	-
RCSOM	137.31	*Hyaena hyaena*	?	-	Y	Y
RCSOM	137.33	*Hyaena hyaena*	?	Y	Y	Y
RCSOM	144.44	*Hyaena hyaena*	?	-	-	Y
TAU	10236	*Hyaena hyaena*	F	Y	Y	Y
TAU	10616	*Hyaena hyaena*	F	Y	Y	Y
TAU	10617	*Hyaena hyaena*	M	Y	Y	-
TAU	10683	*Hyaena hyaena*	M	Y	Y	Y
TAU	11099	*Hyaena hyaena*	M	Y	Y	Y
TAU	11130	*Hyaena hyaena*	F	Y	Y	Y
TAU	11248	*Hyaena hyaena*	F	Y	Y	Y
TAU	11249	*Hyaena hyaena*	M	Y	Y	Y
TAU	11515	*Hyaena hyaena*	M	Y	Y	Y
TAU	11533	*Hyaena hyaena*	?	Y	Y	Y
TAU	11687	*Hyaena hyaena*	M	Y	Y	Y
TAU	11821	*Hyaena hyaena*	F	Y	Y	Y

Table 10 (cont'd)

TAU	11846	*Hyaena hyaena*	F	Y	Y	Y
TAU	11945	*Hyaena hyaena*	M	Y	Y	Y
TAU	12128	*Hyaena hyaena*	?	Y	Y	Y
TAU	2019	*Hyaena hyaena*	F	Y	Y	Y
TAU	22	*Hyaena hyaena*	M	Y	Y	Y
TAU	2484	*Hyaena hyaena*	M	Y	Y	Y
TAU	2536	*Hyaena hyaena*	F	Y	Y	Y
TAU	2714	*Hyaena hyaena*	M	Y	Y	-
TAU	276	*Hyaena hyaena*	M	Y	Y	Y
TAU	2814	*Hyaena hyaena*	?	Y	Y	Y
TAU	3201	*Hyaena hyaena*	M	Y	Y	Y
TAU	3316	*Hyaena hyaena*	F	Y	Y	Y
TAU	3597	*Hyaena hyaena*	F	Y	Y	Y
TAU	4035	*Hyaena hyaena*	M	Y	Y	Y
TAU	4376	*Hyaena hyaena*	F	Y	Y	Y
TAU	4746	*Hyaena hyaena*	F	Y	Y	Y
TAU	5106	*Hyaena hyaena*	M	Y	Y	Y
TAU	5127	*Hyaena hyaena*	F	Y	Y	Y
TAU	5379	*Hyaena hyaena*	F	Y	Y	Y
TAU	594	*Hyaena hyaena*	F	Y	Y	Y
TAU	6140	*Hyaena hyaena*	F	Y	Y	Y
TAU	6202	*Hyaena hyaena*	M	Y	Y	Y
TAU	6444	*Hyaena hyaena*	F	Y	Y	Y
TAU	6510	*Hyaena hyaena*	M	Y	Y	Y
TAU	6640	*Hyaena hyaena*	?	Y	Y	Y
TAU	6677	*Hyaena hyaena*	F	Y	Y	Y
TAU	6804	*Hyaena hyaena*	M	Y	Y	Y
TAU	6895	*Hyaena hyaena*	M	Y	Y	Y
TAU	7	*Hyaena hyaena*	M	Y	Y	Y
TAU	7119	*Hyaena hyaena*	F	Y	Y	Y
TAU	7216	*Hyaena hyaena*	M	Y	Y	Y
TAU	7217	*Hyaena hyaena*	?	Y	Y	Y
TAU	7238	*Hyaena hyaena*	F	Y	Y	Y
TAU	7256	*Hyaena hyaena*	M	Y	Y	Y
TAU	7335	*Hyaena hyaena*	F	Y	Y	-
TAU	7336	*Hyaena hyaena*	F	Y	Y	Y
TAU	7455	*Hyaena hyaena*	M	Y	Y	Y

Table 10 (cont'd)

TAU	7480	*Hyaena hyaena*	F	Y	Y	Y
TAU	7502	*Hyaena hyaena*	F	Y	Y	Y
TAU	7618	*Hyaena hyaena*	?	Y	Y	Y
TAU	7644	*Hyaena hyaena*	F	Y	Y	Y
TAU	7672	*Hyaena hyaena*	F	Y	Y	Y
TAU	7737	*Hyaena hyaena*	M	Y	Y	Y
TAU	7813	*Hyaena hyaena*	?	Y	Y	Y
TAU	7839	*Hyaena hyaena*	F	Y	Y	Y
TAU	7898	*Hyaena hyaena*	?	Y	Y	Y
TAU	7962	*Hyaena hyaena*	M	Y	Y	Y
TAU	8294	*Hyaena hyaena*	F	Y	Y	Y
TAU	8295	*Hyaena hyaena*	M	Y	Y	Y
TAU	8666	*Hyaena hyaena*	M	Y	Y	Y
TAU	9010	*Hyaena hyaena*	M	Y	Y	Y
TAU	9160	*Hyaena hyaena*	M	Y	Y	Y
TAU	9418	*Hyaena hyaena*	M	Y	Y	Y
TAU	9423	*Hyaena hyaena*	M	Y	Y	Y
TAU	9739	*Hyaena hyaena*	F	Y	Y	Y
TAU	9743	*Hyaena hyaena*	F	-	Y	-
TAU	9811	*Hyaena hyaena*	M	Y	Y	Y
TAU	9930	*Hyaena hyaena*	F	Y	Y	Y
TAU	8037	*Hyaena hyaena*	M	-	-	Y
TAU	9715	*Hyaena hyaena*	M	-	-	Y
BMNH	79.1631	*Parahyaena brunnea*	?	-	-	Y
BMNH	26.12.7.330	*Parahyaena brunnea*	F	-	Y	-
BMNH	26.12.7.331	*Parahyaena brunnea*	?	Y	Y	Y
BMNH	26.12.7.332	*Parahyaena brunnea*	?	Y	Y	Y
BMNH	26.12.7.333	*Parahyaena brunnea*	?	-	Y	Y
BMNH	35.9.1.284	*Parahyaena brunnea*	?	Y	Y	Y
BMNH	35.9.1.285	*Parahyaena brunnea*	F	Y	Y	Y
BMNH	35.9.1.286	*Parahyaena brunnea*	?	-	Y	-
BMNH	35.9.1.287	*Parahyaena brunnea*	M	Y	Y	Y
BMNH	35.9.1.288	*Parahyaena brunnea*	F	Y	Y	Y
BMNH	46.7.2.7	*Parahyaena brunnea*	?	Y	Y	-
BMNH	53.3.11.1	*Parahyaena brunnea*	?	-	-	Y
BMNH	66.5.2.1	*Parahyaena brunnea*	?	Y	Y	Y
FMNH	34585	*Parahyaena brunnea*	F	Y	Y	Y

Table 10 (cont'd)

FMNH	34586	*Parahyaena brunnea*	F	Y	Y	Y
MSU	33836	*Parahyaena brunnea*	M	Y	Y	-
NMNH	296134	*Parahyaena brunnea*	F	-	Y	-
NMNH	429178	*Parahyaena brunnea*	F	Y	Y	Y
MSU	3949	*Panthera leo*	M	Y	Y	Y
MSU	4251	*Panthera leo*	M	Y	Y	Y
MSU	4851	*Panthera leo*	M	Y	Y	Y
MSU	11240	*Panthera leo*	M	Y	Y	Y
MSU	11241	*Panthera leo*	M	Y	Y	Y
MSU	11242	*Panthera leo*	M	Y	Y	Y
MSU	11674	*Panthera leo*	M	Y	Y	Y
MSU	11675	*Panthera leo*	M	Y	Y	Y
MSU	12236	*Panthera leo*	M	Y	Y	Y
MSU	12392	*Panthera leo*	M	Y	Y	Y
MSU	16791	*Panthera leo*	M	Y	Y	Y
MSU	20127	*Panthera leo*	M	-	Y	-
MSU	20954	*Panthera leo*	M	Y	Y	Y
MSU	21884	*Panthera leo*	M	Y	Y	Y
MSU	24411	*Panthera leo*	M	Y	Y	Y
MSU	29954	*Panthera leo*	M	Y	Y	-
MSU	29988	*Panthera leo*	M	Y	Y	Y
MSU	28292	*Panthera leo*	M	Y	-	-
RCSOM	114.2	*Panthera leo*	M	-	Y	-
TAU	21	*Panthera leo*	M	Y	Y	Y
TAU	2552	*Panthera leo*	M	Y	Y	-
TAU	2810	*Panthera leo*	M	-	Y	Y
TAU	6614	*Panthera leo*	M	Y	Y	Y
TAU	7308	*Panthera leo*	M	Y	Y	Y
TAU	7638	*Panthera leo*	M	Y	Y	Y
BMNH	31.1.2.3	*Panthera leo*	F	Y	Y	Y
BMNH	31.1.3.2	*Panthera leo*	F	Y	Y	Y
BMNH	35.3.14.3	*Panthera leo*	F	Y	Y	Y
BMNH	43.64	*Panthera leo*	F	Y	-	Y
MSU	14954	*Panthera leo*	F	Y	Y	Y
MSU	20126	*Panthera leo*	F	Y	Y	Y
MSU	24405	*Panthera leo*	F	Y	Y	Y
MSU	36073	*Panthera leo*	F	Y	Y	Y

Table 10 (cont'd)

RCSOM	114.91	*Panthera leo*	F	-	Y	-
TAU	1932	*Panthera leo*	F	Y	Y	Y
TAU	2553	*Panthera leo*	F	Y	Y	Y
TAU	3916	*Panthera leo*	F	Y	Y	Y
BMNH	14.4.12.190	*Panthera leo*	?	-	Y	Y
BMNH	36.3.14.24	*Panthera leo*	?	-	Y	-
?	K5482	*Panthera leo*	?	-	Y	-
MSU	KayNo#	*Panthera leo*	?	Y	Y	Y
MSU	8046	*Panthera leo*	?	Y	Y	Y
NMK	2523	*Panthera leo*	?	-	Y	-
NMK	4940	*Panthera leo*	?	Y	Y	-
NMK	4948	*Panthera leo*	?	Y	Y	-
TAU	No#	*Panthera leo*	?	-	Y	Y
BMNH	58.213	*Panthera leo*	?	Y	-	Y
BMNH	58.226	*Panthera leo*	?	Y	-	Y
BMNH	75.139	*Panthera leo*	?	Y	-	Y
BMNH	67.4.12.188	*Panthera leo*	?	-	-	Y
NMK	2632	*Lycaon pictus*	F	Y	-	Y
NMK	2636	*Lycaon pictus*	?	Y	Y	-
NMK	2639	*Lycaon pictus*	F	Y	Y	Y
NMK	2640	*Lycaon pictus*	F	Y	-	Y
NMK	2643	*Lycaon pictus*	?	Y	Y	Y
NMK	3404	*Lycaon pictus*	?	Y	Y	-
NMK	7425	*Lycaon pictus*	M	Y	Y	Y
NMK	7436	*Lycaon pictus*	?	-	Y	Y
NMK	7439	*Lycaon pictus*	?	Y	Y	Y
NMK	7516	*Lycaon pictus*	M	Y	Y	Y
NMK	7889	*Lycaon pictus*	?	Y	Y	Y
TAU	4003	*Lycaon pictus*	M	Y	Y	Y
TAU	4005	*Lycaon pictus*	M	Y	Y	Y
TAU	4006	*Lycaon pictus*	F	Y	Y	Y
TAU	4451	*Lycaon pictus*	F	Y	Y	Y
TAU	4767	*Lycaon pictus*	M	Y	Y	Y
TAU	5235	*Lycaon pictus*	M	-	Y	-
TAU	5437	*Lycaon pictus*	M	Y	Y	Y
TAU	5575	*Lycaon pictus*	F	Y	Y	Y
TAU	7025	*Lycaon pictus*	F	Y	Y	Y

Table 10 (cont'd)

MSU	11673	*Ursus maritimus*	M	Y	Y	Y
MSU	20963	*Ursus maritimus*	M	Y	Y	Y
MSU	22148	*Ursus maritimus*	M	Y	Y	Y
MSU	27987	*Ursus maritimus*	M	Y	Y	Y
MSU	36573	*Ursus maritimus*	M	Y	Y	Y
MSU	3696	*Ursus maritimus*	M	Y	Y	Y
MSU	4686	*Ursus maritimus*	M	Y	Y	Y
MSU	9322	*Ursus maritimus*	M	Y	Y	-
MSU	9323	*Ursus maritimus*	M	Y	Y	Y
MSU	9324	*Ursus maritimus*	M	-	Y	Y
MSU	9326	*Ursus maritimus*	M	Y	Y	Y
MSU	9327	*Ursus maritimus*	M	Y	Y	Y
MSU	9328	*Ursus maritimus*	M	Y	Y	Y
MSU	9330	*Ursus maritimus*	M	Y	Y	Y
MSU	9332	*Ursus maritimus*	M	Y	Y	Y
MSU	9335	*Ursus maritimus*	M	Y	Y	Y
MSU	12760	*Ursus maritimus*	F	Y	Y	-
MSU	2132	*Ursus maritimus*	F	Y	Y	-
MSU	23998	*Ursus maritimus*	F	Y	Y	Y
MSU	24317	*Ursus maritimus*	F	Y	Y	Y
MSU	24432	*Ursus maritimus*	F	Y	Y	Y
MSU	9325	*Ursus maritimus*	F	Y	Y	Y
MSU	9329	*Ursus maritimus*	F	Y	Y	Y
MSU	9333	*Ursus maritimus*	F	Y	Y	Y
MSU	9334	*Ursus maritimus*	F	Y	Y	-
MSU	16588	*Ursus maritimus*	?	Y	Y	Y
MSU	27845	*Ursus maritimus*	?	Y	Y	Y
MSU	33107	*Ursus maritimus*	?	Y	Y	Y
MSU	9312	*Ursus maritimus*	M	Y	Y	Y
MSU	9331	*Ursus maritimus*	?	Y	Y	Y
?	DSCF0320	*Ursus maritimus*	?	Y	-	-
MSU	10596	*Canis lupus*	M	Y	Y	Y
MSU	10663	*Canis lupus*	M	Y	Y	Y
MSU	24321	*Canis lupus*	M	Y	Y	Y
MSU	35868	*Canis lupus*	M	Y	Y	Y
MSU	35884	*Canis lupus*	M	Y	Y	Y
MSU	36213	*Canis lupus*	F	Y	Y	Y

Table 10 (cont'd)

MSU	36243	*Canis lupus*	M	Y	Y	Y
MSU	36248	*Canis lupus*	F	Y	Y	-
MSU	36251	*Canis lupus*	F	Y	Y	Y
MSU	36385	*Canis lupus*	F	Y	Y	Y
MSU	36387	*Canis lupus*	M	Y	Y	Y
MSU	36393	*Canis lupus*	F	Y	Y	Y
MSU	36394	*Canis lupus*	F	Y	Y	Y
MSU	36418	*Canis lupus*	F	Y	Y	Y
MSU	36420	*Canis lupus*	M	Y	Y	Y
MSU	36421	*Canis lupus*	F	Y	Y	Y
MSU	36422	*Canis lupus*	M	Y	Y	Y
MSU	36423	*Canis lupus*	F	Y	Y	Y
MSU	36424	*Canis lupus*	F	Y	Y	Y
MSU	36427	*Canis lupus*	F	Y	Y	Y
MSU	36428	*Canis lupus*	F	Y	Y	-
MSU	36430	*Canis lupus*	F	Y	Y	Y
MSU	36433	*Canis lupus*	M	Y	Y	Y
MSU	36442	*Canis lupus*	F	Y	Y	Y
MSU	36445	*Canis lupus*	F	Y	Y	Y
MSU	36446	*Canis lupus*	M	Y	Y	Y
MSU	36447	*Canis lupus*	M	Y	Y	Y
MSU	36448	*Canis lupus*	M	Y	Y	Y
MSU	36449	*Canis lupus*	F	-	Y	Y
MSU	36450	*Canis lupus*	F	Y	Y	Y
MSU	36451	*Canis lupus*	M	Y	Y	-
MSU	36452	*Canis lupus*	M	Y	Y	Y
MSU	36453	*Canis lupus*	M	-	Y	Y
MSU	36515	*Canis lupus*	F	Y	Y	Y
MSU	36516	*Canis lupus*	M	Y	Y	Y
MSU	36518	*Canis lupus*	M	Y	Y	Y
MSU	36519	*Canis lupus*	M	Y	Y	Y
MSU	36520	*Canis lupus*	M	Y	Y	Y
MSU	36521	*Canis lupus*	F	Y	Y	Y
MSU	36522	*Canis lupus*	M	Y	Y	Y
MSU	36523	*Canis lupus*	M	Y	Y	Y
MSU	36524	*Canis lupus*	M	Y	Y	Y
MSU	36527	*Canis lupus*	F	Y	Y	Y

Table 10 (cont'd)

MSU	36531	*Canis lupus*	F	Y	Y	-
MSU	36533	*Canis lupus*	F	Y	Y	Y
MSU	36534	*Canis lupus*	M	Y	Y	Y
MSU	36535	*Canis lupus*	M	Y	Y	Y
MSU	36536	*Canis lupus*	F	Y	Y	Y
MSU	36538	*Canis lupus*	M	Y	Y	Y
MSU	36539	*Canis lupus*	M	Y	Y	Y
MSU	36541	*Canis lupus*	M	Y	Y	Y
MSU	36542	*Canis lupus*	F	Y	Y	Y
MSU	37149	*Canis lupus*	F	Y	Y	Y
MSU	37150	*Canis lupus*	M	-	Y	Y
MSU	37151	*Canis lupus*	M	-	Y	Y
MSU	37152	*Canis lupus*	M	Y	Y	Y
MSU	37153	*Canis lupus*	M	Y	Y	Y
MSU	37154	*Canis lupus*	M	Y	Y	Y
MSU	37155	*Canis lupus*	F	Y	Y	Y
MSU	37156	*Canis lupus*	M	Y	Y	Y
MSU	37157	*Canis lupus*	M	Y	Y	-
MSU	37158	*Canis lupus*	F	Y	Y	Y
MSU	37159	*Canis lupus*	M	Y	Y	Y
MSU	37160	*Canis lupus*	M	Y	Y	Y
MSU	37161	*Canis lupus*	M	Y	Y	Y
MSU	37162	*Canis lupus*	M	Y	Y	Y
MSU	37163	*Canis lupus*	M	Y	Y	Y
MSU	37164	*Canis lupus*	F	Y	Y	Y
MSU	37165	*Canis lupus*	M	Y	Y	Y
MSU	37166	*Canis lupus*	M	Y	Y	Y
MSU	37167	*Canis lupus*	F	Y	Y	Y
MSU	37168	*Canis lupus*	M	Y	Y	Y
MSU	37169	*Canis lupus*	M	Y	Y	Y
MSU	37170	*Canis lupus*	F	Y	Y	Y
MSU	37171	*Canis lupus*	F	Y	Y	Y
MSU	37172	*Canis lupus*	M	Y	Y	Y
MSU	37173	*Canis lupus*	F	Y	Y	Y
MSU	37174	*Canis lupus*	M	Y	Y	Y
MSU	37175	*Canis lupus*	M	Y	Y	Y
MSU	37176	*Canis lupus*	F	-	Y	Y

Table 10 (cont'd)

MSU	37177	*Canis lupus*	F	Y	Y	Y
MSU	37178	*Canis lupus*	F	Y	Y	Y
MSU	37179	*Canis lupus*	F	Y	Y	Y
MSU	37180	*Canis lupus*	M	Y	Y	Y
MSU	37181	*Canis lupus*	F	Y	Y	Y
MSU	37182	*Canis lupus*	M	Y	Y	Y
MSU	37183	*Canis lupus*	F	Y	Y	Y
MSU	37184	*Canis lupus*	M	-	Y	Y
MSU	37185	*Canis lupus*	F	Y	Y	Y
MSU	37186	*Canis lupus*	F	Y	Y	Y
MSU	37187	*Canis lupus*	F	Y	Y	Y
MSU	37188	*Canis lupus*	F	Y	Y	Y
MSU	37189	*Canis lupus*	M	Y	Y	Y
MSU	37190	*Canis lupus*	F	Y	Y	Y
MSU	37191	*Canis lupus*	M	-	Y	Y
MSU	37192	*Canis lupus*	F	Y	Y	Y
MSU	37193	*Canis lupus*	M	-	Y	Y
MSU	37195	*Canis lupus*	F	-	Y	Y
MSU	9670	*Canis lupus*	M	Y	Y	Y

APPENDIX B

Locations of landmarks and semi-landmarks

Table 11 - Locations of landmarks and semi-landmarks for each of the three views.

Lateral Landmarks	
1	Anterior point of I3
2	Anterior point of canine
3	Posterior point of canine
4	Anterior point of the infraorbital foramen
5	Upper-most point of the lacrimal foramen
6	Tip of the post-orbital process
7	Dorsal edge of the jugal-squamosal suture
8	Ventral edge of the jugal-squamosal suture
9	Ventral tip of the jugal
10	Anterior-most point along the curve of the pterygoid
11	Upper-most point on the external auditory meatus
12	Upper-most point on the occipital condyle
13	Posterior-most point on the nuchal crest
14	Anterior-most point on the nasal-premaxilla suture
15, 16	10mm scale
17-48	Semi-landmarks evenly space from 14 to 13
Mandible Landmarks	
1	Anterior point of the I3-dentary boundary
2	Anterior point of the canine-dentary boundary
3	Posterior point of the canine-dentary boundary
4	Upper edge of the mental foramen
5	Dorsal apex of the curve on the coronoid process
6	Posterior-most point of the coronoid process
7	Anterior edge of the mandibular condyle
8	Posterior-most point of the mandibular condyle
9	Dorsal tip of the articular process
10	Posterior point of the tooth row
11	Anterior point of the I1-dentary boundary
12, 13	10mm scale
14-45	Semi-landmarks evenly spaced from 11 to 9
46-56	Semi-landmarks evenly spaced from 9 to 8
57-72	Semi-landmarks evenly spaced from 7 to 6
73-88	Semi-landmarks evenly spaced from 5 to 10

Table 11 (cont'd)

Ventral Landmarks	
1	Juncture between incisors on the premaxilla
2, 5	Intersection of premaxilla-maxilla suture and the medial edge of the canine
3, 4	Posterior point of the incisive foramen
6	Posterior point of the premaxilla-maxilla suture on the palate
7	Maxilla-palatine midline suture
8, 9	Medial curvature of the suture between the maxilla and the palate
10	Posterior-most edge of midline suture between the right and left palatine
11, 12	Medial edge of the maxilla-jugal suture
13, 14	Posterior-most edge along the jugal-squamosal suture
15	Anterior point on the foramen magnum
16, 17	Maxilla-palatine suture at the posterior edge of the palate
18, 19	Posterior tip of pterygoid
20, 21	Center of jugular foramen
22, 23	Medial edge of the glenoid process
24, 25	Posterior edge of P2
26, 27	Anterior edge of the external auditory meatus
28, 29	10mm scale

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