Evaluating The Hominin Scavenging Niche Through Analysis of the Carcass-Processing Abilities of the Carnivore Guild

by

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Date: July 27, 2008

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Christine Wall

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of Biological
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ABSTRACT

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Abstract

Humans are more carnivorous than other hominoids. It has been hypothesized that, during the evolution of this increased carnivory, hominins transitioned through a scavenging niche made viable by certain carnivoran taxa (especially sabertooths) that may have lacked the morphology necessary to fully utilize all parts of carcasses (e.g., marrow), therefore leaving an open niche in the form of high-quality scavengable remains available for hominins. In this dissertation, I examine the postcanine dentition of modern carnivorans, using quantifications of occlusal radii-of-curvature and intercuspid notches, and study the correlation of this morphology with carcass-processing behavior. I use these correlations to deduce the carcass-processing capabilities of the Plio-Pleistocene carnivores of South Africa (a guild for which we have a good appreciation of taxonomic diversity, and that existed at an important time during the evolution of our lineage – possibly the time that we transitioned into that guild), and compare these results with those of previous studies that relied on more conventional morphological measures.

Both radius-of-curvature and intercuspid notch data do a good job of separating taxa by dietary category, revealing subtle patterns including possible differences in the carcass-processing abilities of fossil and modern members of some extant species. Other strong trends confirm that the "hunting-hyena," *Chasmaporthetes*, was probably a hypercarnivore, and not a durophage like its modern confamilial taxa. Somewhat surprisingly, results do not support the hypothesis that sabertooth felids were more hypercarnivorous than modern felids. Furthermore, though the sympatric hypercarnivorous taxa were more numerous, so too were the durophagous taxa, with one taxon, *Pachycrocuta*, probably exceeding the durophagous capabilities of modern durophages.

As such, this dissertation shows no evidence that members of the paleo-carnivore guild were capable of producing higher quality scavengable carcasses than are modern carnivorans, and thus, based on these analyses of fossil carnivorans, it does not appear that high-quality scavengable remains were more available in the Plio-Pleistocene than there are today. Therefore, though there is clear evidence from other sources that hominins did scavenge at least occasionally, this dissertation does not support the hypothesis that there was an open niche consisting of high-quality scavengable remains.

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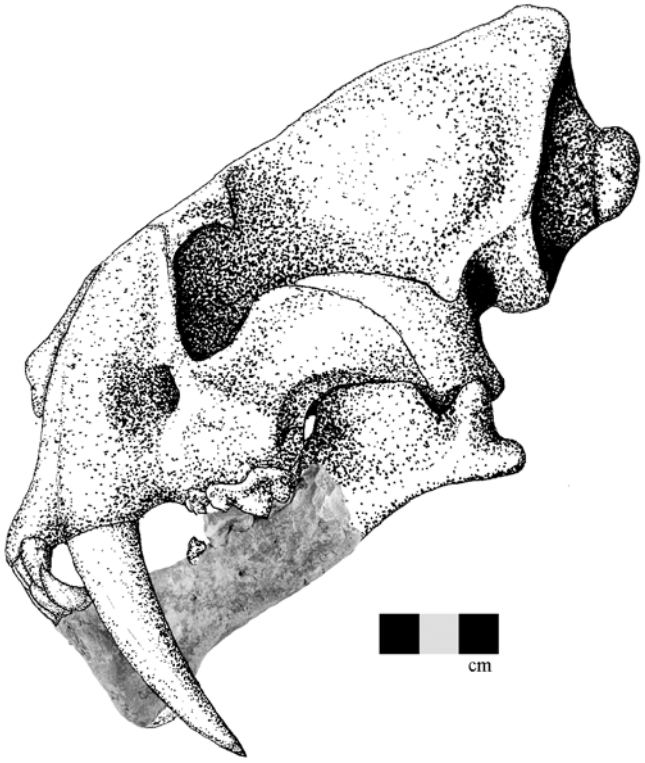

Figure 1: *Megantereon whitei*.

Cranial reconstruction with CD 5997 mandible from Coopers Cave, Gauteng South Africa

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Far from being a marginal strategy, scavenging may alone have provided a source of animal foods sufficiently abundant and regular to have had a major influence on hominid foraging strategies and on the course of human evolution in general.

Blumenschine 1989 pp. 345-346

CHAPTER 1: Introduction

Scavenging may have been an important part of the transition from a predominantly vegetarian diet to one of more substantial carnivory in early members of the genus *Homo* (Blumenschine 1986, 1987, 1995; Blumenschine *et al.* 1994; Bunn 1986; Bunn and Ezzo 1993; Bunn and Kroll 1986; Capaldo 1997; Dominguez-Rodrigo 1999; Lewis 1997; Lupo 1998; Marean 1989; Oliver 1994; Potts 1988; Selvaggio 1998; Shipman 1983, 1986, 1987; Speth 1989; Turner 1988). There is substantial zooarchaeological evidence to suggest that Plio-Pleistocene hominins extracted marrow from the long bones of mammals killed by large-bodied carnivores (see Blumenschine *et al.* 1994 and references therein), but the frequency of scavenging by hominins and the dietary importance thereof are extremely difficult to assess. One avenue for understanding the role of scavenging in human evolution is to illuminate the carcass-processing abilities of the carnivores that existed sympatrically with the hominins when they presumably made the transition to a diet that included more animal tissue, and thus to evaluate the nature and quality of scavengable resources available to hominins during this period.

An understanding of how early humans interacted with the carnivore guild is of great importance to the study of the evolution of human diets. As humans made the dietary transition to greater carnivory, their relationship with members of the carnivore guild would have changed from one of a prey species (Brain 1981) to one of a significant competitor. A period of scavenging seems to be a natural dietary and behavioral bridge between frugivory and hunting. Several studies have attempted to verify this dietary strategy through analyses of the ecology of sympatric carnivores (e.g., Blumenschine 1986, 1987; Marean 1989).

Most studies of hominin scavenging have focused on the fossil evidence for marrow extraction (e.g., Blumenschine *et al.* 1994), and few have examined the carcass-processing abilities of specific carnivores to deduce the viability of a scavenging niche. Those who have done so have focused primarily on the environmental (geographical and ecological) overlap between hominins and carnivorans[1] (Marean 1989) and their carcass transport and caching abilities (Lewis 1995, 1997; Marean and Ehrhardt 1995). Those studies that have examined the carcass-processing abilities of carnivorans (e.g., Van Valkenburgh 1989, 1996) have done so too coarsely to divide the extinct species into detailed categories of ability, and have not extended the work to the impact of carnivores on hominin evolution.

[1] Throughout this dissertation the term "carnivoran" is used in reference to a member of the order Carnivora. "Carnivore" refers to animals having a diet that includes vertebrate soft tissues. As such, crocodiles are carnivores but not carnivorans, and the insectivorous aardwolf (a member of Hyaenidae), is a carnivoran, but not a carnivore.

In this study, I will investigate the hominin scavenging niche through examination of the carcass-processing abilities of the postcanine dentition of the carnivorans that were sympatric with hominins during the Plio-Pleistocene. To do this, I will build on the results of previous studies by using dental morphology that will allow me to apply the findings to fossil taxa, and a sample of carnivores that includes greater taxonomic diversity in the key dietary categories.

Background

Understanding the nature of guilds of paleo-carnivorans is extremely important for understanding hominin evolution. At some point during the course of human evolution, hominins made the shift from being a prey item to being a significant predator, possibly passing through a scavenging niche (Leakey 1967; Speth 1989; Stiner 1994), with each stage implying very different relationships with the members of the carnivore guild. How, when, and hopefully why these major changes took place may be deduced from a close examination in the changing composition of the paleo-carnivore guild. Given the diversity of carnivore species found in Africa during the Plio-Pleistocene (Blumenschine 1987; Brain 1981; Selvaggio 1998; Selvaggio and Wilder 2001; Shipman 1983), perhaps interspecific competition within the group of carnivorans prevented any single species from dominating the carnivore guild, thus allowing our primarily frugivorous ancestors to expand into a very different role in the environment. This is a

hypothesis that has yet to be tested, though it may yield important information about a possible driving force in the evolution of our lineage.

How humans were able to move into higher trophic levels is an important question because carnivory has been argued to play an important role in the autocatalytic feedback loop that has been used to explain advances in human cognitive evolution (Flinn *et al.* 2005; Godfrey and Jacobs 1981). That is, meat consumption may have provided the calories and essential fatty acids necessary for increases in brain size, which may have led to increased cognitive abilities such as innovation, which may have led to more complex tools, which would have allowed more efficient hunting and processing of meat (Aiello and Wheeler 1995). While there is a dangerous potential for circularity in such arguments, it does seem clear that increased consumption of animal tissues (possibly through scavenging), use of stone tools, and expansion of brain volume all co-occur in the archeological and fossil record attributable to early *Homo* (Johanson and Edgar 1996). Interpreting the interrelations between these events is central to understanding the early evolution of our genus. This requires a better understanding of the nature of early human scavenging and of the carcass-processing abilities of the sympatric carnivores.

Much has been written about hominin scavenging (see Bunn 1986; Bunn and Ezzo 1993; Bunn and Kroll 1986; Dominguez-Rodrigo 1997; Shipman 1978, 1983, 1987, Selvaggio and Wilder 2001 and references therein). The involvement of certain species as primary predators has also been hypothesized, and chains of succession documented (Selvaggio 1998; Selvaggio and Wilder 2001). However, no analysis of the specific

nature of scavenged remains has been undertaken. They hypothesis that scavenging was a significant hominin activity and that scavenged remains represented an important food resource for evolving hominins rests on the assumption that there were abundant remains of sufficiently high quality to serve as a consistent and reliable source of calories and nutrients for early hominins. Numerous studies have hypothesized that certain extinct carnivores, namely the sabertooth felids, produced these high-quality scavengable remains because of the unique qualities of their feeding morphology that prevented carcass depeletion (e.g., Blumenschine 1987, 1995; Capaldo 1997; Ewer 1973; Marean 1987, 1989). Other studies (e.g., Lewis 1995; Marean and Ehrhardt 1995) have countered these conclusions on the grounds of uncertainty about the true carcass-processing abilities of these extinct species. Thus there is a clear need to further analyze what the carnivorans sympatric with ancient hominins were able to consume to determine where in the feeding succession hominins would have had to break in to obtain enough calories and essential fatty acids to make the scavenging niche viable.

Approach

This work focuses on the Plio-Pleistocene carnivoran guild of the Sterkfontein Valley (Gauteng Province, South Africa) and the geographically close (approximately 325 km North of Johannesburg; Sponheimer *et al.* 1999) fossil locality, Makapansgat. The Sterkfontein sites date from approximately 2.5 million years old (no fossils were

included in this study from the controversially dated oldest locality within the Sterkfontein cave, the "Silberberg Grotto," containing the remains of "Little Foot" STW 573) to about 1.5 million years old, though the dating of all South African fossil sites is still highly debated (Johanson and Edgar 1996). These qualifications aside, the Sterkfontein valley is well-suited for this study because it is geographically constricted, encompassing only 47,000 hectares, and very important for our understanding of human evolution: it is home to some of the earliest fossils of *Homo ergaster*, most of the fossils of *Australopithecus africanus*, and all of the fossils of *Paranthropus robustus*. Additionally, this region contains the first evidence of the controlled use of fire and direct evidence of carnivore predation on early hominins (Brain 1981). Furthermore, all of the fossil hominin material (with the exception of the earliest known remains of *A. africanus*) dates to the narrow time interval of the terminal Pliocene and early Pleistocene which saw substantial increases in hominin cranial capacity. For this reason it is an ideal place to study the hominin shift to significant carnivory. Carnivore fossils are also abundant, and include all species of carnivores presently found in the area as well as three genera of sabertooth cats (*Dinofelis*, *Homotherium* and *Megantereon*), two genera of extinct hyena (*Pachycrocuta* and *Chasmaporthetes*) and an extinct wolf-like dog (Brain 1981; Hartstone-Rose *et al.* no date-a; Hartstone-Rose *et al.* no date-b). The relatively abundant carnivoran fossils from Makapansgat (which, at approximately 3 million years old, is slightly older than the other sites included in this study; Sponheimer *et al.* 1999) are included to help boost the sample sizes of these species.

To understand the nature of the hominin shift toward increased carnivory, we must first appreciate carnivoran richness at the time, and the role of large carnivorans in the Plio-Pleistocene world. The most recent comprehensive analysis of the Plio-Pleistocene carnivores of Africa is that of Lewis (1995), who looked at the effect the large carnivores had on human evolution. Lewis laid a solid and invaluable foundation for the analysis of the Plio-Pleistocene carnivorans of Africa, but since 1995 there have been several important discoveries in South Africa that add to our understanding of the guild: the new site of Motsesti appears to be a lair of *Dinofelis*, one of the major predators of that time and place. If this is confirmed, it will be the first known faunal assemblage as yet diagnosed that was accumulated predominantly by an extinct African carnivoran. Also, a new, as yet undescribed species (possibly representing a new genus) of canid has been identified at two sites – Gladysvale and Cooper's Cave (Hartstone-Rose *et al.* no date-a; Hartstone-Rose *et al.* no date-b). Many other small discoveries – such as the recovery of new remains of the genus *Megantereon* from a site at which it was previously unrecorded (Hartstone-Rose *et al.* 2007) – underscore the need for a revision of all of the extinct taxa of the Sterkfontein Valley.

Van Valkenburgh (1989, 1996) made significant strides in understanding dental adaptations along a scale characterizing carnivore diets ranging from hypercarnivory[2] to durophagy (Figure 2). In one study (Van Valkenburgh 1989), the relative importance of

[2] The term "hypercarnivore" (sensu Holliday 2001; Holliday and Steppan 2004) refers to taxa that specialize in soft tissue (particularly flesh) consumption to the exclusion of tougher or harder tissues (such as bone).

bone, flesh and non-vertebrate foods was predicted from measures of the canine and post-canine dentition for 47 taxa of carnivorans. This paper shows many important trends in the relationship between dental design and diet. However, it generalizes the diets of the taxa into broad categories. For instance, all three species of hyaena are the sole representatives of the primarily bone-eating group, and all of the felids are lumped into the predominantly meat-eating group. The breadth of these groupings leads to two problems: 1) with all the hyenas in one group and all of the felids in another, phylogenetic effects may be significantly influencing the results. Furthermore, 2) it is difficult to extend these findings to the fossil taxa, because though they are easily grouped into their higher taxonomic units, even finer divisions must be made within clades to examine more detailed dietary differences. We know that this is possible from empirical observation. For instance, cheetahs are quickly displaced by other carnivores (Kruuk 1972; Schaller 1972), and are therefore presumably predominantly flesh-only eaters. Their displacers, often other felids like lion (*Panthera leo*) and leopard (*P. pardus*), are presumably further on the continuum toward durophages (Figure 2). And as such, they probably consume some tissues harder than flesh because, when they scavenge, they do not have access to the choicest parts that are already consumed by the primary predator. Even with primary access to a carcass, lions and leopards may consume some bony elements (such as vertebrae) that cheetahs would not (Brain 1981). In a more recent paper examining the teeth used to disassemble different parts of prey carcasses (Van Valkenburgh 1996), the finer details of these dietary derivations were

explored between a bone-crunching hyaenid (*Crocuta*), the hypercarnivorous hunting dog (*Lycaon*) and two felid taxa, the more hypercarnivorous cheetah (*Acinonyx*) and the more generalized carcass-consuming lion (*P. leo*). This study demonstrated morphological correlates of feeding behavior in the dentition of the carnivores studied, suggesting that extending this work across a broader comparative group, coupled with experimental work on tooth strength, will allow further extrapolation into the behavior of extinct taxa.

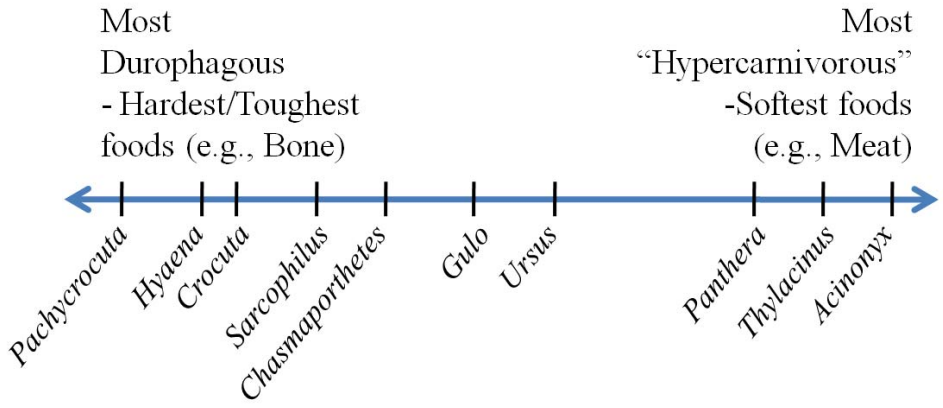

Figure 2: Schematic Durophage-Hypercarnivore Scale

Schematic morphospace scale that this dissertation will explore with hypothetical positions of taxa.

Variation in carcass consumption across carnivorans should be reflected in variation in dental anatomy. Indeed, qualitatively we recognize that the bone crushing hyaenids have extremely stout teeth relative to the blade-like teeth of felids. However, aside from simple shape variables (e.g., mesiodistal length relative to buccolingual width) of the teeth, the finer details of the dental biomechanics of the various carnivorans relative to their carcass exploitation have yet to be fully studied. Specifically,

quantification of the occlusal radii-of-curvature and intercuspid notches (both of these sets of variables will be described in chapter 3) as they correlate with specific diet and consumption abilities of different carnivorans of extant species should help us assess the diet and consumption abilities of their extinct relatives.

Specific Aims and Hypotheses

The goals of this study are to assess the dental adaptations of the various extant and extinct carnivores of the Sterkfontein Valley as they relate to their carcass-processing abilities and to assess the caloric and nutritional quality of the resources various carnivorans would have left behind after feeding on a carcass.

Multiple hypotheses relating tooth morphology to diet/carcass-processing behavior will be tested. The comparisons between extant taxa and their diet will take place both within and between families. (Choice of variables is explained in Chapter 3: Materials and Methods). (For all aims, the null-hypothesis, H_0 is: There is no difference in the focal variable when comparing hyper-carnivores and durophagous carnivorans.)

Aim 1 (Evaluated in Chapter 4):

To assess the total length of the premolar and carnassial row of teeth devoted to slicing as opposed to puncture/crushing in various species of carnivores.

There should be an inverse relationship between the total length of the slicing tooth (the carnassial) and the length of the dentary devoted to puncture/crushing (the premolars) in the post-canine tooth row, and these "puncturing teeth" will be stouter in more durophagous taxa.

H_{1a}: The carnassials will represent a higher proportion of the total length of the tooth row in flesh eaters relative to bone eaters.

H_{1b}: Durophagous taxa will have relatively wider premolars than hypercarnivorous species.

Aim 2 (Evaluated in Chapter 5):

To assess the relative acuity of the slicing crests of the various species of carnivores.

As there is a tradeoff between crest sharpness and crest strength (Lucas 2004), carnivores that specialize in eating flesh as opposed to durophagy should have more acutely angled slicing cusps (Figure 3).

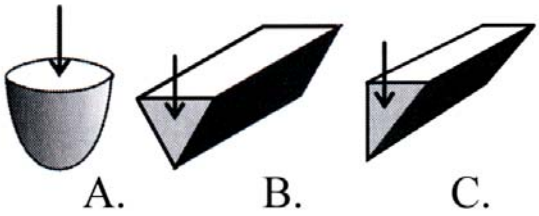

Figure 3: Geometric Simplification of Dental Morphology.

Arrows represent direction of force during mastication. Modified from Lucas 2004. Each of these forms is found in various carnivoran dentition with A. being a typical puncture/grinding cusp (occlusal surface can be modeled as a semisphere), B. being the crest shape typically found in the premolars of meat-eating specialists (crest cross-sectional angle can be modeled as the peak of an isosceles triangle), C. being the generalized shape of the carnassial crest (crest cross-sectional angle can be modeled as the acute angle of right triangle).

H_2: Species that consume a higher proportion of flesh in their diets will have sharper premolars and carnassial cusps as measured by radii-of-curvature.

Aim 3 (Evaluated in Chapter 6):

To assess the relative abundance of inter-cusp notches in various species of carnivores.

Typically, where two sharp crests coincide at a concavity (i.e., in a valley as opposed to a point), they form a notch or groove roughly perpendicular to the long axis of the tooth row (Figure 4). These notches may have various functions in flesh consumers. However, they may be a structurally vulnerable point (Lucas 2004), and thus represent the cost of this morphology for durophagous taxa. As such:

H_3: Flesh eaters will have more intercuspid notches than bone eaters.

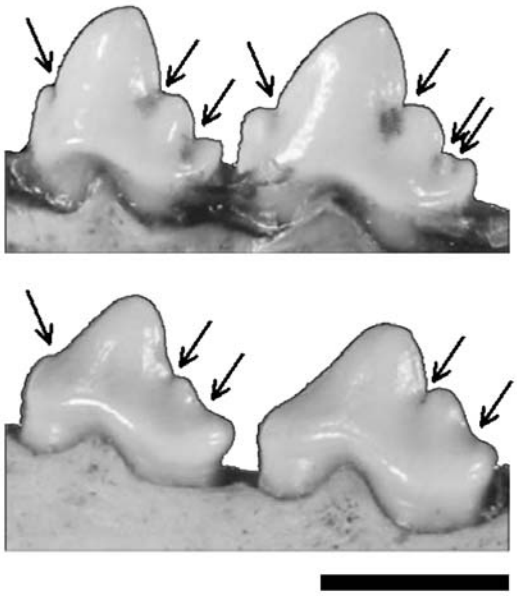

Figure 4: Intercuspid Notches.

Left P_2 and P_3 of *Lycaon pictus* USNM 470144 (top) and *Canis lupus* USNM 64960 (bottom). Mesial is to the left. Scale = 1 cm. Arrows indicate the inter-cusp notches.

Multiple hypotheses relating tooth morphology to several dietary descriptors will be tested. The comparisons between extant taxa and their diet will take place both within and between families. For an explanation of the variables and why these equations were selected, see Chapter 3.

The fossil carnivorans will be assessed relative to these extant patterns, once established.

More so than many other groups…, the carnivorans have retained a versatile dentition, with different teeth adapted for cutting meat, crushing bone, and grinding insects and fruits. This versatility has led to the evolution of divergent dental patterns and diets within the order, presumably largely as a result of competition for food.

Van Valkenburgh 1989; p. 410

CHAPTER 2: A Brief Introduction to Carnivoran Dentitions

During the course of human evolution our ancestors moved into the carnivore guild, possibly by transitioning through a scavenging niche, before settling into a position as the most lethal (though not the most carnivorous) predator in the world. Understanding the structure of the modern carnivore guild, and how niches are partitioned between its members, will help us understand where hominins may have been able to break into the paleo-carnivore guild.

The carnivores partition their dietary niches not only according to factors of prey size and environmental preferences, but, more important from the perspective of scavenging, they partition resources within individual carcasses. That is, competitive exclusion within modern carnivorans occurs, to a great extent, at the level of individual carcass elements, with some taxa (e.g., felids) specializing in the soft tissues (e.g., flesh) while other taxa (e.g., hyaenids) specialize in the harder or tougher (e.g., bone) elements (Ewer 1973). This is not to say that all carnivorans are so highly specialized that they ignore the elements targeted by other taxa (indeed some felids eat some hard or tough

elements, and hyaenids include large amounts of soft elements in their diets too), but evolution has led to the displacement of characters (some of which are studied in this dissertation) enabling greater feeding efficiency for particular carcass elements for particular carnivorans.

While this character displacement has led to anatomical adaptations in the post-crania (Lewis 1995, 1997; Turner and Antón 1997) and crania (Biknevicius and Van Valkenburgh 1996; Emerson and Radinsky 1980), the most important modifications that allow niche partitioning within a carcass are dental adaptations. That is, teeth are the anatomical elements that first process the food, and it is this anatomy that evolution has acted most dramatically on to equip carnivorans with differential carcass-processing abilities.

It is the variation in dental anatomy as it relates to carcass niche partitioning that is the focus of this dissertation. This chapter introduces the general form of carnivoran dentition to lay a foundation for understanding how different species have adapted this basic set of tools to most efficiently process their specific diets.

Carnivoran Dental Functional Regions

Biknevicius and Van Valkenburgh (1996: p. 396) describe the carnivoran dental arcade as being comprised of three regions, the "grasping incisors, penetrating canines and food-processing cheek teeth." Previously, Van Valkenburgh (1989: p. 410)

described “four functionally distinct areas,” grouping the 1) anterior teeth (canines and incisors) used for “display, defense, killing prey and dismembering carcasses,” the 2) premolars which serve as “piercers” in some species and “crushers” in others, the 3) “primary cutting tools,” the carnassials, and the 4) post-carnassial molars “devoted to grinding.” These descriptions are oversimplifications, and I offer here an alternative description.

The generalized carnivoran dental row (Figure 5) can be broken into five functional units: the incisors, canines, premolars, carnassials, and post-carnassial molars. Often these teeth are described metaphorically as the “tool kit” that enables its users to procure and process its food (e.g., Biknevicius and Van Valkenburgh 1996; Van Valkenburgh 2007). Though each of the functional regions is named for the teeth that constitute the majority of their function, they often contain other teeth. For instance, in saber-tooth felids (as well as some non-carnivoran sabertooths) the lower canine is functionally part of the “incisor region.” Likewise, the “post-carnassial” region, where it truly exists in certain taxa, invariably contains part (namely the talonid) of the lower carnassial. As such, it may seem tempting to name these regions according to their function; however, these functions are so variable across taxa that this solution would be even more confusing.

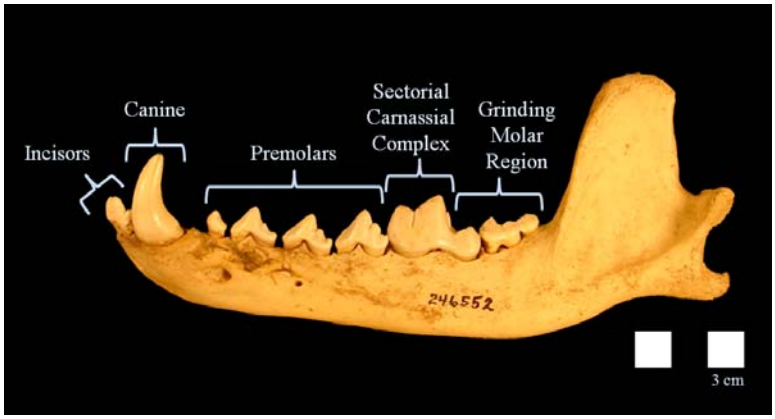

Figure 5: Relatively Generalized Carnivoran Lower Dentary.

Of the major groups of carnivorans, canids (e.g., Red Wolf, *Canis rufus*, above) have the most generalized carnivoran dentition with the standard grasping incisors (I_1-I_3), large canine (C_1), multi-use premolars (P_1-P_4), large sectorial carnassial region (on the M_1) and long grinding molar region (M_1 talonid – M_3). Note, in this lateral view it is clear how the lower "carnassial," M_1, is split between two functional regions. USMN 246552.

Grasping Incisor Functional Region

In most carnivorans, as is the case in canids, the incisors are relatively pointed, usually arranged in a procumbent semicircular arc (Figure 6), and are used for biting during hunting, stabilizing prey during killing, and nipping pieces of flesh off of carcasses during feeding (Marean 1989). As such, this anterior-most region can legitimately be considered the "grasping" region (Biknevicius and Van Valkenburgh 1996).

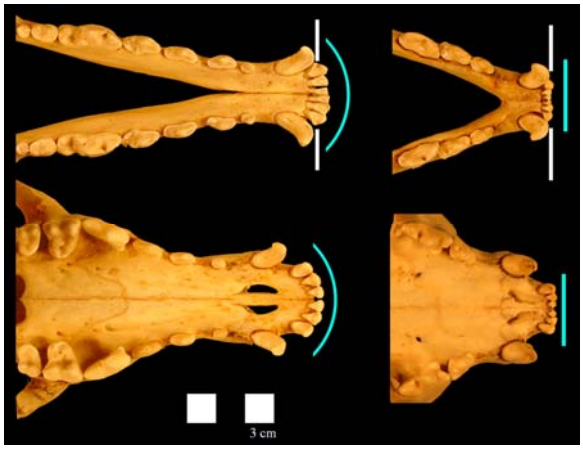

Figure 6: Incisor Functional Region

Mandibular (top) and maxillary (bottom) dental arcades of a typical canid (*Canis simensis*, left) and a typical felid (*Catopuma temminickii*, right). Note the curved canid and straight felid incisor arcades (blue lines) and the extent to which the canid incisors protrude in front of the anterior edge of the lower canines relative to the felid incisors which are essentially in line with the anterior edged of the lower canine (white lines).

While the region is comprised exclusively of the incisors in the generalized carnivoran dentition as seen in wolves, in other taxa the canines also contribute to this grasping function. For instance, bears probably use both their incisors and canines in a grasping manner for tearing flesh off of carcasses (Figure 7C). Indeed, as will be discussed later, it appears that bears use this anterior-most dental region as their primary flesh processing region (as opposed to almost all other carnivorans that use their carnassial region for this function), and they do so by using their enormous strength not to slice (as would other carnivorans with their carnassials) but to tear the flesh from the carcass (Van Valkenburgh, pers. comm.). Hyaenids also do some of this grasping and

tearing with both their mandibular and maxillary canines incorporated into the anterior-most dental functional region (Van Valkenburgh 1996, Figure 7B).

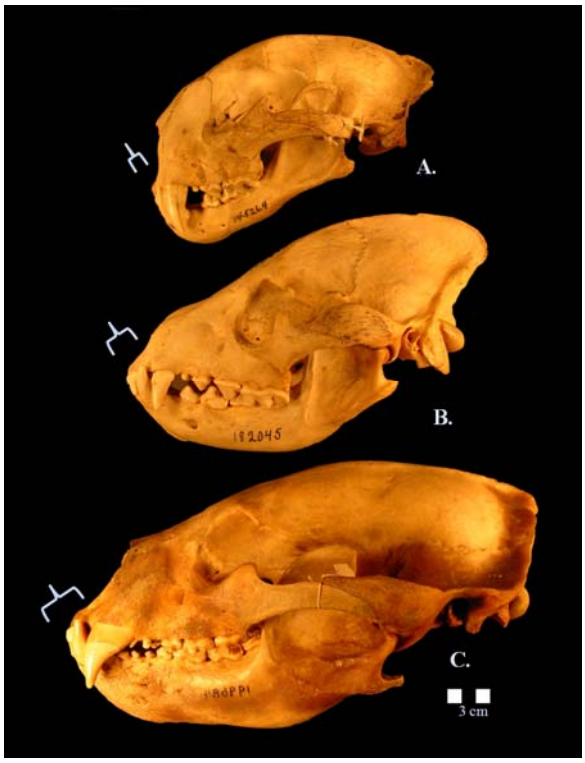

Figure 7: Cranial profiles displaying differential incisor procumbence.

Lateral views of the crania of A. *Puma concolor,* B. *Hyaena brunnea* and C. *Ursus thibetanus* showing increasing anterior dentition functional grasping region (brackets).

The incisors of extant felids are not arranged in a procumbent arcade, and do not function in this way (Figure 7A.). Modern felids (and primitive felids like *Pseudaelurus* as well) have small, mediolaterally-compressed incisors (with the exception of the lateral maxillary incisor which is relatively more robust and caniform) that are organized in a

straight dental row perpendicular to the long axis of the skull. The extant felid incisors do not need to be mediolaterally robust because they are buttressed from mediolateral force by the stout mandibular canines and lateral maxillary incisors, and functionally they may serve as a buttress for the canines during killing bites (Biknevicius *et al.* 1996). To a certain extent, modern felids use their anterior teeth (though, unlike canoids and hyaenids, they use mostly their canines) to grasp and tear flesh away from their prey, though their predominant tool used for defleshing is the carnassial region (Antón and Galobart 1999; Biknevicius and Van Valkenburgh 1996; Biknevicius *et al.* 1996; Emerson and Radinsky 1980; Schaller 1972; Turner and Antón 1997; Van Valkenburgh 1996). Other lineages of carnivorans have converged on this reduced grasping region as well. Notably, some (but not all) of the canoid mustelids have displayed this flat incisor profile including the three large taxa (*Enhydra, Gulo* and *Pteronura*) included in this study. Unlike all of the other cats, which, as described above lack this grasping function in their incisors, the sabertooth felids have a very well developed procumbent grasping incisor functional group (Figure 1 and Figure 8).

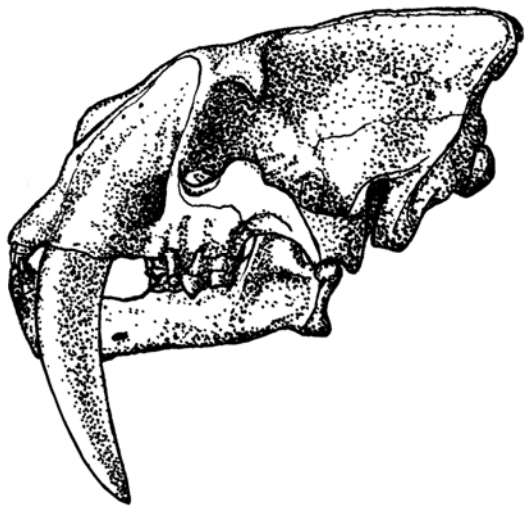

Figure 8: Sabertooth Skull Showing Procumbent Grasping Incisor Dental Arcade

***Smilodon californicus*. Note how the anterior dentition (upper and lower incisors and lower canines) protrude beyond the anterior edge of the "saber" tooth.**

Relative to extant felids, sabertooth felids and nimravids exhibit sharp, robust and procumbent incisors and procumbent incisiform mandibular canines, all of which are organized in an arched dental arcade (Emerson and Radinsky 1980; Marean 1987; Scott and Jepsen 1936; Turner and Antón 1997). As such, the anterior dental arcades of these sabertooth carnivores (especially the nimravids) are more comparable to those of modern canids than to those of felids (Biknevicius *et al.* 1996). This modification to the anterior dentition is most likely a reflection of changes necessitated by the defleshing technique employed by sabertooths (Emerson and Radinsky 1980). Their incisors (and mandibular canine) moved forward out of their location between the canines, became more robust

(presumably to prevent breakage because they were no longer functioning in concert with strong conical maxillary canines), and they reorganized into an arched array, like those of canids, for efficient grasping (Biknevicius *et al.* 1996).

In addition to the flesh grasping ability, it has been hypothesized that the procumbent incisors were used "for prey stabilization during killing bites" (Biknevicius *et al.* 1996; p. 510). This hypothesis does not make much sense given that the procumbent incisors could only be used for stabilization when in opposition, an action that could not have been achieved while opening the jaws to achieve the gape necessary for biting with enlarged canines. If they mean to imply that the mandibular incisors (and presumably the canine too) were used for stabilization in opposition of a maxillary canine bite (a proposition that will be discussed later), then it is unclear why the anterior dental arcade would need to be procumbent.

Though this state appears to have evolved in the felid and nimravid lineages of sabertooth carnivores, it is not seen in all sabertooth species: the incisors of the pre-carnivoran creodont *Machaeroides*, while still sharp and in an arched dental arcade, are slender with transversely flattened roots that appear to be adapted more for piercing than grasping/tearing (Gazin 1946), and no sabertooth deviates more from this aspect of the sabertooth suite of morphology than does the marsupial *Thylacosmilus*, which had no incisors at all. What makes this morphology all the more perplexing is that *Thylacosmilus* exhibits no other craniodental morphology that could be used to deflesh the carcasses of their prey (Emerson and Radinsky 1980; Turnbull 1978). The

postcranial morphology of *Thylacosmilus* also seems to be lacking any morphology that could be used to compensate (Argot 2002). Clearly, more work needs to be done to figure out how this sabertooth taxon defleshed its prey.

Canine Killing Functional Region

Carnivores use their canines for display and intraspecific aggression, uses seen in other lineages including cervids (e.g., Barrette 1977) and primates (e.g., Chamberlain *et al.* 1995). However, for most carnivorans, the canines are the primary tool used for killing (Akersten 1985; Anyonge 1996; Biknevicius and Van Valkenburgh 1996; Bryant 1990; Christiansen 2007a; Dayan *et al.* 1990; Feranec 2004; Gittleman and Van Valkenburgh 1997; Marean 1989; Simpson 1941).

So many studies have been done on carnivoran canine function that it would be nearly impossible to summarize them all, and completely superfluous as part of a study about carcass-processing and mastication as very few carnivores use their canines for that purpose (although bears may use them in defleshing carcasses: see below). This is probably not a strong selective pressure on canine morphology. With that said, some of the interesting work on canine function in carnivores and the use of canines for diagnosing behavior in extinct carnivores are worth discussing.

In many studies of canine function, canines have been modeled as cantilevered beams (Biknevicius and Van Valkenburgh 1996; Christiansen 2007a, b; Jones 1997;

Jones and Stoddart 1998; Radinsky 1981; Van Valkenburgh and Ruff 1987). That is, when carnivores plunge their canines into their prey to secure a killing bite (Ewer 1973; Leyhausen 1979), reaction forces place great bending moments on the tooth. Different carnivores use slightly different killing bites that subtly affect the way these forces are transmitted (e.g., whereas the typical felid neck bite makes their canines susceptible to great lateral shearing forces, the typical canid slashing bite places almost all of the force in the antero-posterior plane), and these force differences are reflected in the cross-sectional geometry of the teeth (Van Valkenburgh and Ruff 1987). Despite evolutionary trends to modify this tooth to resist forces, it is by far the most commonly broken tooth in large carnivorans (Van Valkenburgh 1988a).

Premolar Crushing or Slicing Functional Region

The premolar region of the carnivoran dental arcade may be the single most important region for the deduction of carcass-processing behavior. This is inferred from the fact that the premolars have been modified the most to accommodate dietary differences among the Carnivora. For instance, in hyaenids, the premolars do the bulk of the crushing (Werdelin and Solounias 1991), whereas in extant felids they are used more for slicing. Sabertooth felids reduced their premolars in size and sometimes number, suggesting that this highly adaptable tooth was not only unneeded for carcass processing,

but was actually interfering with other functional necessities, almost certainly relating to the large maxillary canine.

While the morphology of the carnivoran premolar is not as simple as that of the single cusped canine, it is still rather simple, consisting chiefly of a central cusp: the protocone on the maxillary premolars and the paraconid on the mandibular premolars. The simplest premolars (e.g., the first premolars in many canids) have only this single cusp. However, the central premolar cusp also usually is flanked by other distal and/or mesial cusps (Figure 5). Though some researchers have assigned these cusps specific names (e.g., protoconid), they are more often simply referred to as anterior (mesial) or posterior (distal) "accessory" cusps or cuspids (for upper and lower teeth respectively). The number of these cusps within lineages and even within some species is highly variable (Jernvall 2000). In most carnivoran species, these cusps form a roughly straight mesiodistal line. Sometimes they are rotated off of this axis. This usually occurs in species with highly compressed dental arcades and is perhaps the result of what can be termed "crowding."

Premolar morphology is the subject of much of the analyses and results in this dissertation, and will be returned to later.

Sectorial Carnassial Region

The carnassial complex, consisting of the parastyle and paracone of the upper fourth premolar and the paraconid and protoconid of the lower first molar (Figure 9), is the defining feature of the order Carnivora. All carnivorans evolved from an ancestor with this functional complex (Ewer 1973). It is generally considered the region of the dentition specialized for slicing flesh and little else (Ewer 1973; Lucas 1979; Marean 1989; Van Valkenburgh 1989), though we now recognize that carnivores often (though perhaps unintentionally), process harder foods with this region as well (Van Valkenburgh 1996). Matt Cartmill's dogs use if to slice carrots (Matt Cartmill pers. comm.), though this is not the likely evolutionary function.

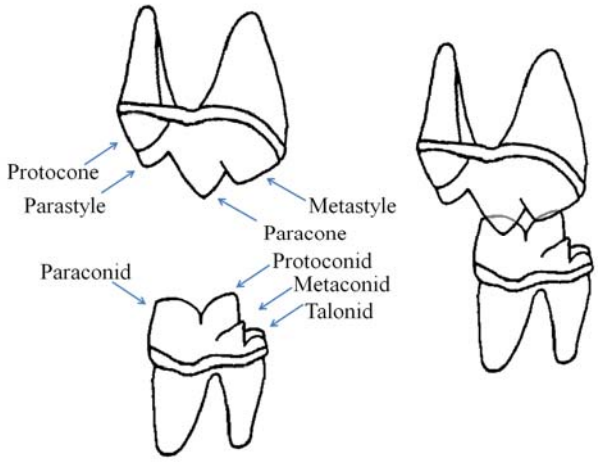

Figure 9: Upper and Lower Carnassial Teeth Labeled.

Right teeth, lingual view, mesial is to the left. Note the diamond formed by the paracone, metastyle, paraconid and protoconid as the carnassials move into occlusion (right). In some taxa (e.g., sabertooth felids, especially *Dinofelis*), the P^4 parastyle and paracone meet up with the paraconid and distal accessory cusp of the P_4 to form another carnassiiform diamond, as do the notches on the other premolars (the subject of Chapter 6). Modified from Marean 1989.

Other lineages (e.g., creodonts and dasyurids) have developed sectorial complexes with similar morphology on other teeth. However the diamond shaped carnassial complex, when relegated to the P^4 and M_1, is the diagnostic feature the order Carnivora (Ewer 1973). Some members of the carnivoran lineage (e.g., *Enhydra* and *Proteles*) have lost their functional sectorial carnassial complex however the carnassial complex is symplesiomorphic for the order.

During occlusion, the lingual surfaces of the two upper crests of the carnassial complex slide along the buccal surface of the lower carnassial to form a decreasing diamond shape (Figure 9, right). The crests of this diamond pattern slice through flesh, compressing it toward the center much as wire cutters compress ductile wire inward. If the carnassials did not have these v-shaped notches, the ductile flesh would spread out elastically and require more force to cut (Lucas 2004).

In most carnivorans the carnassial teeth (P^4 and M_1) contain more than the sectorial carnassial complex. Their distal regions belong functionally to a grinding molar region. This is especially obvious in the lower carnassial tooth in generalized carnivorans (e.g., canids; see Figure 5), in which the high-crowned sectorial trigonid functions as the lower part of the carnassial complex and the low-crowned talonid falls at the same crown height as the distal molars and functions along with them in a grinding complex.

Grinding Molar Functional Region

The most distal dental functional group is the grinding molar region. This region is especially important in the canoid carnivores, and is generally lost in the feloids. Indeed the feliform carnivores lack second and third molars and most of them have highly reduced, usually non-occlusal, M_1 talonids. Members of the Felidae have almost no talonid at all.

Being so close to the mandibular axis of rotation, this functional region has the advantage of good leverage for high bite force at the cost of wide gape. And as would be expected of this geometry, in carnivores that preserve this region, it is generally used for hard or tough object manipulation (Ewer 1973; Van Valkenburgh 1989). It is ironic that the most durophagous carnivorans, the hyaenids, completely lack this functional region (though their carnassials have larger talonids than felids, they are still too small to be used for post-carnassial durophagy) – a consequence of their phylogenetic origin in the non-durophagous side of the carnivoran family. With that said, the marsupial borhyaenids and creodont hyaenodonts, both durophagous lineages, converged on the hyaenid form of durophagy in which the premolars and not the distal molars are used for hard-object consumption. This probably reflects the more pressing functional need for large gape instead of maximum forceful leverage.

While this functional region is clearly important to understand the durophagous tendencies in canoid carnivores, because most of the carnivorans in the South African fossil record are feloid, it was generally excluded from this study.

Although it cannot be said with certainty, it seems likely that sabertooth kills of very large animals… would have been abandoned with considerable amounts of flesh (and within-bone contents) and provided more frequent flesh bonanzas for a series of scavengers than is observed in modem settings.

Blumenschine 1987 p. 393

CHAPTER 3: Materials and Methods

In this chapter I will outline the sample used in this study (with short descriptions of each family examined), and method used to choose species and specimens. I will then outline the variables used to evaluate the aims of this research with special focus on how species were categorized by diets and weights and the particular methods used to measure and score uncommon or novel variables (i.e., radii-of-curvature and intercuspid notch scores).

Fossil Sample

All of the large-bodied Plio-Pleistocene fossil carnivoran specimens curated at the Transvaal Museum, Pretoria, and the University of the Witwatersrand, Johannesburg that are represented by at least some postcanine dentition were studied. A total of 137 fossil

specimens were studied from all of the large-bodied carnivore fossil species found in Makapansgat and the Sterkfontein Valley representing extant and extinct taxa (Table 1).

Table 1: Fossil Taxa Studied

Lines delineate families; From top to bottom, Canidae, Felidae, Hyaenidae – the only large carnivorans in the Plio-Pleistocene South African fossil record.

Species	Total No. Studied (Molded and/or Measured)	Extant Species?
Canis atrox	1	No
Canis cf. mesomelas	24	Yes (if *C. mesomelas*)
Canis sp.	5	?
Canis sp. nov.	2	No
Nyctereutes terblanchei	1	No
Acinonyx jubatus	1	Yes
Dinofelis barlowi	4	No
Dinofelis piveteaui	1	No
Dinofelis sp.	6	No
Felid sp.	4	?
Felis "brickhilli"	2	No
Felis "issiodorensis"	1	No
Homotherium	1	No
Machairodus transvaalensis	1	No
Megantereon whitei	7	No
Panthera leo	4	Yes
Panthera pardus	20	Yes
Chasmaporthetes nitidula	23	No
Crocuta crocuta	9	Yes
Hyaena bellax	1	No
Hyaena makapania	5	No
Hyaenid sp.	7	?
Pachycrocuta brevirostris	3	No
Parahyaena brunnea	6	Yes

Extant Sample

To maintain the focus of this work on the African Plio-Pleistocene carnivore guild, three groups of extant species were included as a comparative sample that represent 1) relatively large-bodied (≥ the body mass of *Canis mesomelas*) African carnivorans, 2) non-African carnivorans that compare favorably to the African carnivorans in body size and diet, and 3) relatively large-bodied carnivorous marsupials to serve as a phylogenetic out-group with similar dietary functional constraints.

Introduction to Taxa in the Study

In this section I will briefly discuss the general characteristics of the families included within this study with special reference to the variables of greatest importance to this dissertation, namely size variability (important for the exploration of scaling), diet, and carcass-processing abilities.

All of the taxonomy for the extant species conforms to names recognized by Wilson and Reeder (2005) with only a few exceptions: The snow leopard, though often listed under its own monospecific genus *Uncia uncia* (e.g., Wilson and Reeder 2005) has been shown to be genetically nested within the genus *Panthera* (actually as the sister taxon to *P. tigris* at the exclusion of the clade consisting of the three African and Neotropical species; Johnson *et al.* 2006; O'Brien and Johnson 2005) and as such is included in that genus. Also, though some split the Malagasy carnivores into their own

family ("Eupleridae"; Wilson and Reeder 2005), in this dissertation they are referred to as members of the widespread civet family, the Viverridae. Though some group both the brown and striped hyena into the single genus *Hyaena*, and indeed both taxa are unified by their retention of the M^1, which *Crocuta* lacks, I believe that they are sufficiently distinct to warrant the use of *Parahyaena* for the brown hyena (sensu Werdelin and Solounias 1991). Also, some elevate the marsupial wolf, *Thylacinus* into its own monospecific family (the "Thylacinidae"; Wilson and Reeder 2005), though I follow others (e.g., Vaughan 1978) in lumping it into the Dasyuridae. The last taxonomic decision worth noting is the inclusion of the black-backed jackal, *C. mesomelas*, in the genus *Canis*. While this is the standard taxonomy for the genus (e.g., Nowak 2005; Wilson and Reeder 2005) it is becoming increasingly evident, based primarily on new molecular studies, that this genus is wildly paraphyletic (with the highly derived *Lycaon* nested within it; Lindblad-Toh *et al.* 2005; Zrzavy and Ricankova 2004), and in order to resolve some of this paraphyly, this taxon probably should be elevated to the monospecific genus *Lupulella* Hilzheimer, 1906 (Zrzavy and Ricankova 2004). However, as this is a subject of much current debate, I have followed the more historical taxonomy throughout this dissertation.

Felids

The cats are unique among the carnivorans in their body size diversity and dietary homogeneity. That is, felids range in size from approximately 1.5 kg in the rusty-spotted

and black-footed cats, *Felis rubinginosus* and *F. nigripes* respectively, to 306 kg in the Siberian tiger, *Panthera tigris altaica* (Nowak 2005), and yet all felids generally consume only vertebrate flesh. Some regularly incorporate small vertebrate bone, e.g., the fishing cat, *Prionailurus viverrinus* consumes its prey whole (Nowak 2005), and some large felid taxa (e.g., lions and tigers, *Panthera leo* and *P. tigris*, respectively) have been described as consuming bone on rare occasions, or, more commonly, eat parts of carcasses that have fleshy and bony components (lions, leopards, *P. pardus*, and less commonly for cheetahs, *Acinonyx jubatus*; Blumenschine 1987; Brain 1981; Marean 1989; Schaller 1967, 1972). However, even when consumed, bony parts are always a very small component of the felid diets (only about 10-15% in one study of large African cats: Van Valkenburgh 1996). The incorporation of hard or tough objects into the diet is much less common in felids than in any other lineage in this study.

This lack of dietary diversity in felids is problematic in this study. Ideally, each lineage included would span the dietary niches so that phylogenetic inertia could be parsed from functional morphological evolution – the main interest of this work. Furthermore, what little dietary diversity there is within the felids cannot be captured within this study – simply put, the few sources that quantify in some detail the diets of carnivores do so either too superficially (noting only general impressions) or for too few taxa (e.g., Van Valkenburgh was able to document, in detail, the carcass-processing behavior for only four taxa in her 1996 study). For this reason, all cats were relegated to the same hypercarnivorous dietary category during statistical analysis (see Material and

Methods). However, certain taxa (e.g., lions based on Van Valkenburgh 1996, jaguars, *Panthera onca*, Emmons 1989, leopards, *P. pardus*, Brain 1981) that are known to incorporate some hard objects in their diets will be discussed accordingly during the qualitative sections of the analyses and results.

The dietary homogeneity (and also the subtle dietary diversity) within the felids is reflected in their morphology (Figure 10); it is commonly recognized that extant cats are among the most (if not the single most) morphologically uniform families of carnivorans. Many morphological variables scale remarkably tightly across the entire body size range of the family (Hartstone-Rose and Perry 2007a, b).

Figure 10: Typical Felid Dentition

The mandibular tooth row of *Panthera tigris*. USNM 25328.

This morphological homogeneity exhibited by the extant Felidae does not extend to all of the extinct members of the family. The sabertooth cats (the Machairodontinae), display a suite of morphology remarkably different from that of living cats and all other living species.

Emerson and Radinsky (1980) begin the introduction to their analysis of the cranial morphology of sabertoothed mammals by noting that the enlarged, saber-like maxillary canine evolved independently in at least four lineages of carnivorous mammals – namely the felids, the basal feloid nimravids, the pre-carnivoran creodonts, and the marsupial borhyaenids (Figure 11).

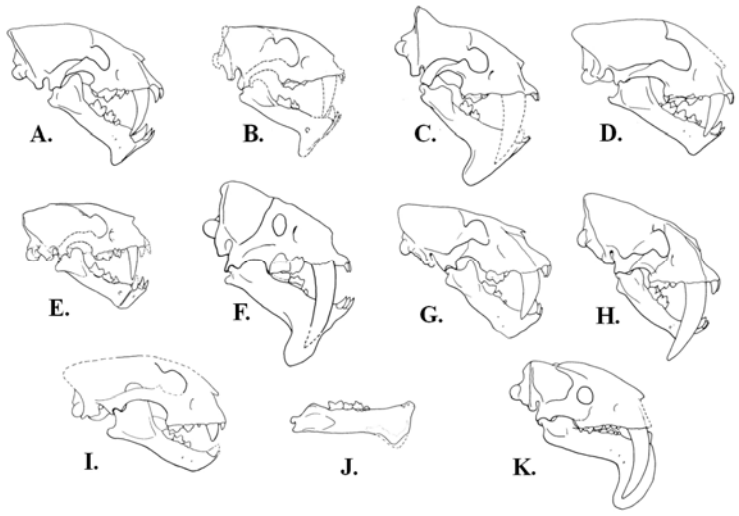

Figure 11: Skulls (and jaws) of various sabertooth taxa (and one non-sabertooth early felid).

A. *Hoplophoneus primaevus,* B. *Eusmilus olsontau,* C. *Eusmilus sicarius,* D. *Dinictis feline,* E. *Nanosmilus kurteni,* F. *Barbourofelis fricki,* G. *Homotherium nestianus,* H. *Smilodon californicus,* I. non-sabertooth early felid, *Pseudaelurus sinclairi* J. *Apataelurus kayi,* K. *Thylacosmilus atrox.* A-F are nimravids, G-I are felids, J is a creodont, and K is a marsupial. B and E modified from Martin 1992 and all others modified from Emerson and Radinsky 1980. Not to scale.

What Emerson and Radinsky fail to point out is that the elongation of the canines, in and of itself, is not particularly remarkable; it has occurred in many lineages that they do not discuss, including other carnivorous felids (e.g., the clouded leopard, *Neofelis*), non-felid carnivores (e.g., the extant walrus, *Odobenus*, and extinct cetacean *Odobenocetops*), non-carnivorous mammals (e.g., primates such as *Papio*, and several

cervids including *Muntiacus*), and many extant and extinct non-mammals with sabertooth-like teeth (e.g., *Tyrannosaurus*). While it is true that none of these species exhibit true saber teeth, there is so much diversity among recognized saber teeth that the morphology of the tooth itself could hardly be considered the defining factor in the designation "sabertooth." Some carnivorous dinosaur teeth could be argued to exhibit more saber-like morphology than the canines of some recognized sabertooth species such as *Dinofelis* or *Dinictus* (see discussion below about maxillary canine morphology). However, no one would seriously consider baboons or muntjacs to be "sabertooths." Furthermore, the term "sabertooth" is clearly not a phylogenetic term if we are to recognize the species discussed by Emerson and Radinsky (1980) and dozens of others as sabertooths. Rather, the term "sabertooth," as it is used in the literature, refers to animals possessing a consistent suite of morphological craniodental and postcranial features (Figure 12 and Table 1).

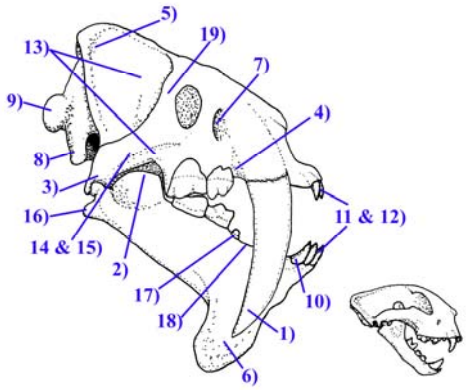

Figure 12: The sabertooth suite of craniodental morphological features.

The skull of the nimravid *Barbourofelis* (left) and extant *Felis* (right) for comparison. Skulls not to scale. Numbers correspond to those in Table 2. Note that although no single taxon exhibits the complete suite of sabertooth features *Barbourofelis* comes close.

Table 2: Sabertooth Morphology

Morphology found, to varying extents, in all four lineages of mammalian sabertooths and in all sabertooth felids. Numbers 1-19 (craniodental variables) correspond to morphology noted in Figure 12.

	Killing Morphology
1	Maxillary Canine Modification Elongation Mediolateral compression Anteroposterior elongation Serration
	Gape Modification
2	Reduced Coronoid Process
3	Inferoventrally Displaced Glenoid Fossa
4	Dorsal rotation of Splanchnocranium
5	Superodorsally Displaced Occiput
6	Chin Flange
7	Large Infraorbital Canal – for vibrissae to place bite
8	Enlarged Nuchal/Mastoid Muscle Attachments
9	Caudally Protruding Occiput
	Carcass-processing Morphology
10	Procumbent Anterior Dentition
11	Incisiform Mandibular Canine
12	Arched Anterior Dental Arcade and Robust Anterior Dentition
13	Vertically Oriented Temporalis and Masseter Muscles
14	Narrow Bizygomatic Breadth
15	Short Zygomatic Arches
16	Lateral Flaring Angular Processes
17	Posterior Displacement of Post-canine Dentition
18	Reduced Premolars and Post-canine Diastema
19	Post-Orbital Bar
	Hunting Morphology
20	Strong Forelimbs
21	Long Neck – for specific bite placement
22	Short Tail
23	Overall Sexual Dimorphism

Remarkable convergences (e.g. winged flight) occur throughout all levels of organismal life. This is not to discount the sabertooth convergence; truly it is one of the most remarkable examples. But what is more perplexing about sabertooths is not only the degree of their convergence, but also the fact that they were clearly very successful and yet no living example exists. That is, although we can document the extent to which they were alike, and hypothesize about the special behavior for which their highly specialized morphology was adapted, we can only hope to fully understand the role that they played in their environments.

Much scientific discourse has focused on the most dramatically modified sabertooth feature: the elongated maxillary canines. Almost all of the other craniodental autapomorphies (derived traits) exhibited by sabertooths can be considered functional corollaries necessitated by the elongation of the canines. For example, the reduced coronoid process and inferiorly oriented glenoid fossa reflect modifications that allow the increased gape necessary to wield the enlarged canines. Likewise, the diagnostic sabertooth chin flange probably evolved as support for the maxillary canines, as it is improbable that the canines evolved in relation to the already developed flange. Most of the characteristically sabertooth morphology is more pronounced in taxa with longer canines (Emerson and Radinsky 1980; Matthew 1910).

The identification of these traits as related to the sabertooth feeding adaptation, rather than traits indicative of phylogenetic relationship, has been important for the reconstruction of phylogenies and will still be important for future cladistic analyses.

Beyond these changes, it is likely that all of the modifications to the carcass-processing morphology were necessitated by the changes to the killing morphology. That is, the procumbent anterior dentition evolved to compensate for the loss of the primary felid carcass disarticulation approach, which relies on the use of stout canines and posterior dentition to tear at meat. The elongated upper canines of sabertooths would have been ineffective in this process and also probably would have interfered with the posterior teeth. Likewise, the changes necessitated by the enlargement of the gape were probably the driving force for the modifications to the masticatory apparatus.

The carcass-processing abilities of sabertooths have been discussed at length in the literature, especially in relation to their implications for hominin scavenging (Blumenschine 1988, 1995; Blumenschine and Madrigal 1993; Marean 1987, 1989; Shipman 1983; Speth 1989). While there is no clear agreement on the precise carcass-processing abilities of these enigmatic taxa, studies to explore these behaviors could yield important information about niches available during human evolution.

Several modern species of felids were found in the South African carnivore guild, including lions (*Panthera leo*), leopards (*P. pardus*), and rarely cheetahs (*Acinonyx jubatus*). Furthermore, these extant species coexisted in Plio-Pleistocene South Africa with at least three sabertooth felids, *Dinofelis, Megantereon,* and *Machairodus*.

Canids

In addition to the felids, the other highly speciose family of medium to large carnivorans is the Canidae. The living dogs are arguably the most dietarily diverse group of carnivorans, occupying important niches on all continents north of Antarctica. Though some members of the group are highly specialized, most dogs are dietary generalists (Nowak 2005), and most of the lineage maintains the primitive carnivoran set of dentition (Figure 5). The relatively large canids range from hypercarnivorous flesh eaters (e.g., *Canis lupus*) to mostly carnivorous though also including a small amount of non-vertebrate food in their diets (Van Valkenburgh 1988b; Van Valkenburgh and Gittleman 1989). Though dogs clearly have a propensity for gnawing bones and hide (as any dog owner can attest), these items are still very rare in their diets and all taxa fall in the two most dedicated flesh eating dietary categories (as will be elaborated upon in the following chapter).

In addition to their moderate dietary diversity (more than the felids, but less than some other carnivoran clades), canids exhibit great size range (though not as great as that found within the cats). They are important to consider in the context of this study because two modern species, the "painted dog," *Lycaon pictus*, and the black-backed jackal, *C. mesomelas* are key members of the modern African medium-large bodied carnivore guild. Furthermore, fossil specimens usually (though incorrectly) attributed to *C. mesomelas* are highly plentiful in the South African Plio-Pleistocene record. (These fossils are, among other morphological distinctions, more robust than extant jackals and

should be placed in their own species; Hartstone-Rose in prep.) In addition to this fossil dog, at least two other fossil *Lycaon*-sized taxa (*Canis atrox* and *Canis sp. nov.* Hartstone-Rose *et al.* no date-a; Hartstone-Rose *et al.* no date-b) and one primitive dog (usually put in the "raccoon-dog" genus *Nyctereutes*) were present in the Plio-Pleistocene Sterkfontein valley. The *Nyctereutes* and *Canis atrox* are so rare in the South African fossil record (the latter represented by only two teeth), that they will not figure very prominently in this work. The new species of dog has yet to be published, and, therefore, it too will be excluded from the majority of this work.

With that said, extant canids represent one of the best sources of body size and dietary variability within the carnivorans, and therefore, at least their extant members, figure prominently in this study.

Hyaenids

The fossil and extant members of the Hyaenidae represent the third important group of large carnivorans in both modern and Plio-Pleistocene Africa, and as such, feature prominently in this work. Unfortunately, for a study focusing on dietary diversity, especially over a wide range of body sizes, the extant carnivorous hyenas display neither. There are only three species of extant hyenas: the spotted hyena, *Crocuta crocuta*, the striped hyena, *Hyaena hyaena*, and the brown hyena, *Parahyaena brunnea*, all of which are similar in size (average body sizes of 63 kg, 40 kg, and 42.25 kg,

respectively) and all of which have similar diets with a large osteophagous component (Nowak 2005).

While the fourth extant member of the family, the aardwolf, *Proteles cristatus*, is smaller than the other hyenas (at 9-14 kg) it is nearly entirely insectivorous (Kingdon 1997; Nowak 2005), and, like many insectivorous animals, has very reduced dentition. As such, it is excluded from this study.

The dentition of extant hyaenids is more massive than those of other living carnivores, particularly in the premolars (Figure 13). These teeth, namely the P^3, P_3 and P_4, are the primary tools hyenas use to break into the long bones of large mammals (Kruuk 1972). However, they use other teeth in this task as well (Van Valkenburgh 1996), and all of their teeth are markedly stout.

Figure 13: Typical Hyaenid Dentition

The mandibular tooth row of *Parahyaena brunnea*. USNM 429178.

Like the felids, the hyaenids include extinct species with more diverse diets than those of the extant forms. That is, the Plio-Pleistocene hyenas from South Africa appear to have occupied a wider array of dietary niches than their extant relatives (Agusti and Anton 2002; Werdelin and Solounias 1991). In the Plio-Pleistocene South African fossil record, fossil members of all three extant genera of hyena are found along with representatives of two extinct genera that appear to extend the extant hyaenid dietary range in both directions: the highly robust and likely highly durophagous giant *Pachycrocuta brevirostris*, and the relatively gracile "hunting hyena," *Chasmaporthetes nitidula*. This latter species probably represents the least durophagous of the Plio-Pleistocene vertebrate-eating hyenas.

Pachycrocuta, on the other hand, while clearly remarkable in its morphology, is included only in the qualitative results of this dissertation. In all of the key variables (e.g., tooth length, width) all specimens of *Pachycrocuta* fall far beyond the range of even the largest extant carnivoran teeth. And since it is not possible to accurately predict any variable when known variables of the fossil taxon fall outside of the range of the independent variables of the comparative groups (Jungers ***et al.*** 1995), *Pachycrocuta* had to be excluded from all but the qualitative portions of this work. Furthermore, certain key pieces of morphology are simply unknown for *Pachycrocuta*. Every South African *Pachycrocuta* tooth is worn far beyond the limit necessary for estimation of dental radius-of-curvature (Chapter 5). In fact, no one has ever found unworn *Pachycrocuta* teeth (Revealing Hominid Origins Initiative's Carnivora Analytic Working Group,

Poitiers, France, May 2008). While all osteologically adult hyenas have at least moderately worn teeth (see Chapter 3), members of *Pachycrocuta* appear to have worn their teeth more extensively than even their extant relatives. Though their teeth cannot be incorporated into quantitative dietary analyses, it is obvious that *Pachycrocuta* was highly durophagous, and no one has ever suggested otherwise.

Mustelids

The weasel family, the Mustelidae, members of which are found on many continents, is another speciose group of carnivorans, though they are dietarily diverse and span a fairly wide range of body sizes – including the smallest of all carnivorans, the least weasel, *Mustela nivalis*, weighing as little as 0.025 kg (Nowak 2005). They are included, to a certain extent because 1) some relatively large members of the family are found in both modern and Plio-Pleistocene South Africa (namely the ratal, or honey badger, *Mellivora capensis*, and the cape clawless otter, *Aonyx capensis*), and 2) some lineages (e.g., the otters, the Lutrinae) display remarkable dietary diversity including relatively large bodied members that eat soft vertebrate flesh (e.g., the giant river otter, *Pteronura brasiliensis*) and hard brittle objects (e.g., the sea otter, *Enhydra lutris*).

The dentition of these canoid carnivorans is rather primitive (like other canoid carnivorans, they tend to have a fuller set of dentition than the feloids), but it is highly variable depending on the diet (Figure 14). For instance, the teeth of *Enhydra* are arguably more derived for durophagy than those of hyenas, having rounder cusps and

very thick enamel, a fact that has drawn attention to them as a possible model for human evolution (e.g., Kelley and Swanson 2008; Lucas *et al.* 2008; Schwartz 2000; Walker 1981).

Figure 14: Mustelid Dentition

The mandibular tooth row of *Mellivora capensis*. USNM 270224.

Ursids

The largest of all terrestrial carnivorans are the Ursidae, the bears. While they are not a very speciose group (represented by only eight extant species; Nowak 2005), those members are very dietarily diverse. While some species are among the most omnivorous of all carnivorans (e.g., the black bear, *Ursus americanus* and the brown or grizzly bear, *U. arctos*), some species are among the most specialized: during much of the year the diet of the polar bear, *U. maritimus*, consists almost solely of pinnipeds, while, on the other

end of the carnivoran dietary spectrum, the panda bear, *Ailuropoda melanoleuca*, has a diet consisting of little more than bamboo (Nowak 2005).

Because of this dietary diversity and their large body size (they are the only carnivores in the sample that overlap in body size with the largest felids), a few individuals of each of the eight species were included in the study. However, their dentition (Figure 15) is very different from those of the other large carnivorans in the study. Bear teeth are generally flatter and have larger grinding surfaces than those of other carnivorans, and seemingly lack any definable sectorial complex (see highlighted section in Figure 15). This is true even in *U. maritimus*, the most carnivorous of the bears, which evolved from a more omnivorous ancestor (McLellan and Reiner 1994). Simply put, when bears consume flesh, they do so in a manner unlike that of other carnivoran. Their dental morphology is therefore, in many ways, not comparable with those of the other species included in this study.

Figure 15: Typical Ursid Dentition

The mandibular tooth row of *Tremarctos ornatus*. USNM 170656. The bracket highlights the portion of the carnassial tooth (M_1) that corresponds to the mandibular part of the carnassial complex.

Viverrids

Like the mustelids, the civet family, the Viverridae, is another speciose group of medium-to-small, dietarily diverse carnivorans found on many continents. Unfortunately, there are few viverrids that fall at the high end of the body size range (i.e., within the size range that may help to inform human evolution). Only two viverrids weigh more than a few kilograms, and one of them (the "bear-cat," *Arctictis binturong*) is such a highly specialized frugivore that it had to be excluded on dietary grounds, in much the same way *Proteles* was. For these reasons, only one species, the Malagasy fossa, *Cryptoprocta ferox* is included in this study.

Cryptoprocta has fairly primitive teeth for a feloid (Figure 16). Though little is known about its diet (they are highly elusive animals), they have been reported to

consume mammalian prey (e.g., lemurs) whole – including their bones (Britt *et al.* 2001; Goodman *et al.* 1997; Hawkins and Racey 2008), and are thus of interest in this study.

Figure 16: Viverrid Dentition

The mandibular tooth row of *Cryptoprocta ferox*. USNM 112841.

Marsupials

The last group of carnivores included in this study are the dasyurid marsupials *Sarcophilus harrisii*, the Tasmanian devil, and *Thylacinus cynocephalus*, the Tasmanian wolf or tiger.

Sarcophilus and *Thylacinus* are the two largest modern carnivorous marsupials. As can be seen from their carnassiform molars (Figure 17), they display remarkable dental convergence with the eutherian carnivorans. Although the thylacine has been extinct since 1936 (though many alleged sightings have been reported more recently; Rounsevell and Smith 1982), much is known about its feeding behavior and diet, which

could be described as that of a hypercarnivore (Le Souef and Burrell 1926). By contrast, the diet of *Sarcophilus*, approaches the durophagy of the hyaenids (Le Souef and Burrell 1926; Nowak 1999). The two marsupials therefore offer a valuable comparative check of the conclusions derived from eutherian carnivores with similar dietary specializations. While the inclusion of so few marsupial taxa (indeed these are the only two modern marsupials that are similar in body size to the generally larger eutherian sample) may bias the results, and the fundamental differences between marsupial and carnivoran dental anatomy may ultimately hinder comparisons, if patterns can be found that apply to both marsupial and eutherian dentition, than statements can be made about the morphology of carnivorous mammals – whereas, if marsupials were excluded from this research, than the study could hope to extrapolated the dietary behavior of only fossil carnivorans.

Figure 17: Dasyurids Dentition

The mandibular tooth row of *Sarcophilus harrisii* (USNM 238342, reversed, top) and *Thylacinus cynocephalus* (USNM 238474, bottom).

Other Carnivores

Other dietarily diverse lineages or species within the above described lineages were excluded because they are too small for consideration and thus consume their food differently. The other large bodied lineage of carnivorans, the pinnipeds, though somewhat dietarily diverse (some consume mostly fish, others consume mostly mollusks) were excluded because their teeth are so different from those of the carnivorans included in the study (see Jernvall 2000 for a discussion of pinniped dentition).

Specimen Selection

Extant specimens (Table 3) were selected from the collections of the American Museum of Natural History, New York, and the National Museum of Natural History (Smithsonian), Washington, DC. Specimens were selected based on the following criteria in descending order of importance: 1) dental quality (minimal wear), 2) maturity (dentally and osteologically adult specimens – see exception below), 3) sex (roughly equal numbers of males and females), 4) wild specimens (preferred over captive), 5) regional variation (attempts were made to include specimens from all parts of the natural range).

Table 3: Extant Specimens Studied.
Lines delineate families.

Species	Common Name	N Females	N Males
Canis lupus	Grey Wolf	3	4
Canis mesomelas	Black-Backed Jackal	2	3
Canis rufus	Red Wolf	9	9
Canis simensis	Ethiopian Wolf	2	2
Chrysocyon brachyurus	Maned Wolf	4	6
Cuon alpinus	Dhole	3	3
Lycaon pictus	African Hunting Dog or Painted Dog	3	8
Acinonyx jubatus	Cheetah	9	7
Caracal caracal	Caracal or African Lynx	2	2
Catopuma temmincki	Asiatic Golden Cat	6	2
Neofelis nebulosa	Clouded Leopard	10	7
Panthera leo	Lion	5	6
Panthera onca	Jaguar	6	8
Panthera pardus	Leopard	6	14
Panthera tigris	Tiger	4	6
Panthera uncia	Snow Leopard	6	6
Prionailurus viverrinus	Fishing Cat	1	2
Profelis aurata	African Golden Cat	0	3
Puma concolor	Mountain Lion, Cougar, Puma, or Catamount	10	4
Crocuta crocuta	Spotted Hyena	4	8
Hyaena hyaena	Striped Hyena	9	3
Parahyaena brunnea	Brown Hyena	6	3
Enhydra lutris	Sea Otter	1	1
Gulo gulo	Wolverine	4	5
Mellivora capensis	Ratel or Honey Badger	1	1
Pteronura brasiliensis	Giant Otter	0	2
Ailuropoda melanoleuca	Giant Panda or Panda Bear	1	2
Helarctos malayanus	Malaysian Sun Bear	1	1
Melursus ursinus	Sloth Bear	1	1
Tremarctos ornatus	Spectacled Bear	1	1
Ursus americanus	Black Bear	1	1
Ursus arctos	Brown or Grizzly Bear	1	2
Ursus maritimus	Polar Bear	1	1
Ursus thibetanus	Asiatic Black Bear	1	1
Cryptoprocta ferox	Fossa	3	2
Sarcophilus harrisii	Tasmanian Devil	4	5
Thylacinus cynocephalus	Thylacine, Tasmanian Wolf, or Tasmanian Tiger	9	6

Criterion 1 was obeyed for the majority of specimens. In some rare taxa, dentally worn specimens were included to increase sample size for the variables that are not affected by dental wear (i.e., all those other than crown Height, Radii-of-Curvature, shape derivatives thereof, and, to some extent, Notch Score). Likewise, in all cases except for hyenas, only dentally and osteologically mature specimens (criterion 2) were used. For the hyenas, most individuals included were dentally mature, but osteologically immature for the simple reason that all wild hyenas examined that had relatively unworn teeth were not fully osteologically adult (judging from unfused cranial sutures, and relatively smaller jaws and crania). In other words, all wild hyenas appear to wear their teeth substantially before they reach full size. Since tooth sharpness (as measured by various methods) is central to the current study, criterion 1 was prioritized over criterion 2, but this was a conflict only for this lineage. For all but two rare non-focal taxa, it was possible to obtain measurements of both males and females (criterion 3) though for some taxa, roughly equal sex balance could not be obtained without higher-priority criteria. In most cases enough wild specimens (criterion 4) were available for study, though, again, for some rare taxa, captive specimens were incorporated. Captive specimens were used only if they showed relatively little sign of the influence of their captivity. For example, captive specimens with excessive plaque, a common dental ailment of zoo animals, were excluded. Though regional variation is well represented within this sample from each species, again, rare species may be biased toward restricted regions by the curatorial sampling.

Variables

Since analyses of upper and lower carnivoran teeth have been shown to yield very similar results (Evans *et al.* 2007) for this project, all analyses are restricted to the lower dentition with data for two upper teeth per individual (i.e., canines and upper carnassial) recorded for scaling purposes. (Data from the upper dentition of fossil carnivorans were also collected for later analysis, but are not included in these results.)

Table 4: Variables

Lines delineate general variable categories (see text above) . * Upper and Lower Carnassials are P^4 and M_1 respectively in carnivorans. Since marsupials do not have true carnassials, the distal-most molars were measured instead for these variables.

Variable	Units	Source	Description
Specimen Number	Nominal	Museum Designated	Number unique to specimen.
Sex	Nominal	Museum Designated	Sex of specimen.
Location	Nominal	Museum Designated	Geographic locality recorded for specimen.
Species	Nominal	Museum Designated	Linnaean name attributed to specimen including sub-specific designation.
Species Group	Nominal	Reduced from Above	Reduced Linnaean name sorting out taxonomic uncertainty, grouping all subspecies into a single taxon, or all species into a single genus if specific designation is spurious.
Family	Nominal	Reduced from Above	Higher taxonomic level.
Diet	Nominal	From the Literature	See section below on assignment of this variable.
Weight	Kilograms	From the Literature	See section below on assignment of this variable.
Wear	Semi-continuous	Scored	On a scale of 0-10. See section below on assignment of this variable.
Tot Jaw Length	Millimeters	Measured	Condylion to infradentale.
Incisor row length	Millimeters	Measured	Mesial-most point on I_1 to distal-most point on I_3.
CP Diast	Millimeters	Measured	Diastema from distal-most point on C_1 to mesial-most point on mesial-most premolar.
Ant P/3 Height	Millimeters	Measured	Height of mandible in coronal plane anterior to P_3.
Ant P/3 Width	Millimeters	Measured	Width of mandible perpendicular to "Ant P/3 Height."
Sub M/1* Height	Millimeters	Measured	Height of mandible in coronal plane from carnassial* notch of M_1* to ventral mandibular border.
Sub M/1* Width	Millimeters	Measured	Width of mandible perpendicular to "Sub M/1* Height."
Ant P/3-Cond Length	Millimeters	Measured	Condylion to mesial edge of P_3
Carnassial*-Cond Length	Millimeters	Measured	Condylion to carnassial* notch
Condyle Height	Millimeters	Measured	Maximum measurement from angle to superior point on condyle
Coronoid process Height	Millimeters	Measured	Maximum measurement from angle to superior point on coronoid process
Symphysis Length	Millimeters	Measured	Maximum (roughly AP) length of mandibular symphysis
Symphysis Width	Millimeters	Measured	Perpendicular to "Symphysis Length"
PM Row	Millimeters	Measured	Mesial edge of mesial-most premolar to distal edge of distal-most molar.

Variable	Units	Source	Description
Upper Carnassial* Length, Total Width, Buccal Width, and Height	Millimeters	Measured	Maximum mesiodistal length and buccolingual width and crown height (measured from the lingual CEJ). "Buccal width" is maximum width excluding the protocone (which protrudes lingually off of the main carnassial blade: Figure 9).
(Tooth) Length, Width, Height and Perpendicular Height. For C^1, C_1, P_1, P_2, P_3, and P_4	Millimeters	Measured and Calculated from Measurements	Maximum mesiodistal length and buccolingual width and crown height (measured from the buccal CEJ). "Perpendicular crown height" calculated using Pythagorean theorem by using "Height" as the hypotenuse and ½ "Width" as the base of one half of the tooth modeled as an isosceles triangle (Figure 3B).
M_1* Total Length, Total Length (Cast), Width, Width (Cast), Height, Trigonid Length, Cusp Points Length, Ant. Crest Length, Post. Crest Length	Millimeters	Measured	Standard measurements (length, width and height) of the lower carnassial* tooth, with redundant measures of length and width of both real tooth and tooth cast (for use in calculation of error introduced by using measurements taken on molded and cast specimens), and special measurements of carnassial portion of tooth: mesiodistal length of trigonid (excluding talonid) as well as measures from the tip of the paraconid to the tip of the protoconid, the tip of the paraconid to the carnassial notch ("Ant. Crest") and the tip of the protoconid to the carnassial ("Post. Crest").
(Tooth) Shape. For C^1, P^4*, C_1, P_1, P_2, P_3, P_4, M_1* and M_1* trigonid	Unit Free	Calculated from Measurements	Length/width of teeth and M_1* trigonid length/ M_1* Width.
(Tooth) Angle. For P_1, P_2, P_3, P_4, and M_1*	Degrees and Radians	Calculated from Measurements	Calculated from tooth widths and heights modeling premolars as isosceles triangles (Figure 3B) and M_1* as a right triangle (Figure 3C).
M_1* Notch Angle	Degrees and Radians	Calculated from Measurements	Calculated using M_1* "Cusp Points Length," "Ant. Crest Length," "Post. Crest Length." Modeling notch as a scalene triangle.
(Tooth) Radius and Radius-of-Curvature (1/radius). For P_2, P_3, P_4, M_1* Ant and M_1* Post.	Millimeters	Measured	Abbreviated "ROC." See section below on measurement of this variable.
Relative (Tooth) Radius. For P_2, P_3, P_4, M_1* Ant and M_1* Post.	Unit Free	Calculated from Measurements	(Tooth) Radius/(Tooth) Width
(Tooth) Notch Scores. For, P_1, P_2, P_3 and P_4	Discontinuous	Scored	See section below on scoring of these variables.

Measurement and Scoring

Each variable was recorded, scored, calculated or measured by me with the exception of the radius-of-curvature data. These were measured by Shaina Wahl using the method I developed and under my supervision.

All variables were collected on the original specimens except for the radii-of-curvature (see specific methods section on that process), and premolar and carnassial measurements and (a set of measurements that, had they been done on original specimens, would have required much more time in museums). The premolars and molars of one hemi-mandible per specimen were molded using Regular Body President Jet (Coltene-Whaledent), and then cast using Smooth-Cast (Smooth-On). To ensure that the use of casts did not introduce extreme error, and to quantify the effect of this method versus utilization of only original material, two key variables, total carnassial length and total carnassial width,[1] were collected on both the original specimens and their casts. No significant differences (slopes of 1.005 and 0.991, and r^2 of 0.99 and 0.98 for length and width respectively) were found between the measurements (see Chapter Four).

Dietary Categorization

To make my results as compatible as possible with those of previous studies, dietary categorizations of the taxa in this study are based on those used by Van

[1] Since marsupials do not have true carnassials, the distal-most molar (the largest in the series) was used as a proxy for all carnassial variables for dasyurid specimens. From henceforth in this dissertation, all references to the "carnassial" and M_1 refer to, not the first molar in the marsupial specimens, but the last.

Valkenburgh (1988b, 1989). Her four dietary categories (identical in the two studies) classify all of the species she included into consumers of:

> 1. Meat: greater than 70% meat
> 2. Meat/bone: greater than 70% meat with the addition of large bones
> 3. Meat/nonvertebrate: 50-70% meat, with fruit and/or insects making up the balance
> 4. Nonvertebrate/meat: less than 50% meat, with fruit and/or insects predominating.
>
> Van Valkenburgh 1989 p. 415

The species are assigned to these categories on the basis of the 82 behavioral references listed in Van Valkenburgh 1989.

In general, I concur with Van Valkenburgh's dietary categorizations of the carnivoran taxa, with only a few exceptions. For example, she classifies polar bears (*Ursus maritimus*) as "Meat/Non-Vertebrate" eaters (Van Valkenburgh 1988b, 1989). This correctly classifies that taxon as the most carnivorous of the bear family – all others consume mostly or almost exclusively non-vertebrate foods (see references in Nowak 2005; Van Valkenburgh 1989). However, it places them in a less carnivorous category than most of the canids. Though there are many published accounts that confirm that polar bears are omnivorous, including those cited by Van Valkenburgh (Jonkel *et al.* 1976; Stirling *et al.* 1977) as well as other detailed accounts (e.g., Russell 1975), it is not clear that they eat more vegetation than wolves, *Canis lupus*, and bush dogs, *Speothos venaticus*, both of which are classified by Van Valkenburgh in the "Meat" only category. Furthermore, some taxa may be arguably included in the "Meat/Bone" category that have been excluded. For instance the difficult-to-categorize *C. lupus* is also known to consume nearly entire carcasses of animals as large as deer, bone and all (Mech *et al.*

1971), a fact that would place it on the most durophagous end of the scale (if the four categories are thought of as roughly falling along the scale in Figure 2), whereas Van Valkenburgh (1989) assigns them to the most hypercarnivorous of her categories. Subtleties like this are where subjectivity strongly affects results, as literature (e.g., Macdonald 2006) could be mounted to support multiple possible dietary categorizations of various carnivoran taxa.

With that said, in an effort to make this study compatible with previous publications, I have decided not to reclassify any of the taxa included in Van Valkenburgh's studies, but only to broaden some of her dietary categorizations to include taxa that she excluded (Table 5). In an effort to expand the taxonomic and dietary breadth of the species included in this study, I have expanded Van Valkenburgh's "Nonvertebrate/Meat" group to include carnivoran taxa that consume little or no meat (e.g., the bamboo specialist giant panda, *Ailuropoda*) and have renamed this group simply "Nonvertebrate" consumers, to reflect the majority of their diet. I have also renamed Van Valkenburgh's "Meat/Bone" group "Durophage" consumers, to reflect the hard-object feeding functional signal I am seeking in the morphology, and also to include the molluscivorous sea otter, *Enhydra*. In previous studies (Van Valkenburgh 1988b, 1989), the durophagous category included only members of the monophyletic group of hyaenids, thereby making it difficult to separate functional and phylogenetic signals. To remedy this situation, my "Durophage" category also includes the phylogenetically distant carnivoran *Enhydra* and the even more distantly related marsupial Tasmanian devil, *Sarcophilus*.

Table 5: Dietary Categorization.

See text for explanation of categories. Blank spaces in the Van Valkenburgh categorizations indicate taxa not included in her studies. Lines delineate families; From top to bottom, Canidae, Felidae, Hyaenidae, Mustelidae, Ursidae, Viverridae and Dasyuridae.

Species	Categorization from Van Valkenburgh 1988b, 1989; Van Valkenburgh and Gittleman 1989	Designation in this Study
Canis lupus	Meat	Meat
Canis mesomelas	Meat/Non-Vertebrate	Meat/Non-Vertebrate
Canis rufus		Meat
Canis simensis		Meat
Chrysocyon brachyurus	Meat/Non-Vertebrate	Meat/Non-Vertebrate
Cuon alpinus	Meat	Meat
Lycaon pictus	Meat	Meat
Acinonyx jubatus	Meat	Meat
Caracal caracal	Meat	Meat
Catopuma temmincki	Meat	Meat
Neofelis nebulosa	Meat	Meat
Panthera leo	Meat	Meat
Panthera onca	Meat	Meat
Panthera pardus	Meat	Meat
Panthera tigris	Meat	Meat
Panthera uncia	Meat	Meat
Prionailurus viverrinus	Meat	Meat
Profelis aurata	Meat	Meat
Puma concolor	Meat	Meat
Crocuta crocuta	Meat/Bone	Durophage
Hyaena hyaena	Meat/Bone	Durophage
Parahyaena brunnea	Meat/Bone	Durophage
Enhydra lutris		Durophage
Gulo gulo	Meat/Non-Vertebrate	Meat/Non-Vertebrate
Mellivora capensis	Meat/Non-Vertebrate	Meat/Non-Vertebrate
Pteronura brasiliensis		Meat/Non-Vertebrate
Ailuropoda melanoleuca		Non-Vertebrate
Helarctos malayanus		Non-Vertebrate
Melursus ursinus		Non-Vertebrate
Tremarctos ornatus	Non-Vertebrate/Meat	Non-Vertebrate
Ursus americanus	Non-Vertebrate/Meat	Non-Vertebrate
Ursus arctos	Non-Vertebrate/Meat	Non-Vertebrate
Ursus maritimus	Meat/Non-Vertebrate	Meat/Non-Vertebrate
Ursus thibetanus	Non-Vertebrate/Meat	Non-Vertebrate
Cryptoprocta ferox		Meat
Sarcophilus harrisii		Durophage
Thylacinus cynocephalus		Meat

Unfortunately greater expansion of dietary diversity within families was not possible – there are no truly durophagous felids or canids, nor any felids that consume significant quantities of non-vertebrate foods. That fact is itself significant: especially in Africa, the focal area of this study, these broad dietary categorizations reflect specialization at the family level – within families, there is relative homogeneity. Furthermore, the fossil taxa that have been theorized to have crossed over into another family's dietary niche (e.g., the possibly less durophagous, "hunting hyena," *Chasmaporthetes*) have not survived in that ecospace to the present day. The niche competition that led to the family level dietary specialization may be the cause of their extinction.

Classification of Body Mass

Body size is at the heart of many morphological analyses. Indeed it is often used in the denominator of "relative" variables in an effort to scale them (e.g., by Van Valkenburgh and Koepfli 1993). Unfortunately, this important variable is seldom recorded for each specimen in the major museum collections, and indeed none of the specimens included in this study were associated with their mass data. Their body masses can only be estimated on the basis of metrics derived from other specimens of their species. However, summarizing the mass of a taxon is a difficult task that is often done with too little consideration of the complexity of this variable (Glander *et al.* 2006). The task is made difficult by many factors including intraspecific variability. That is,

individuals within a species often vary more than comparing the means of those species interspecifically. For instance, mean body masses of wolves (*Canis lupus*) range from 18 to 80 kg (Nowak 2005).

Another factor that adds to the complexity of categorizing species by mass is sexual dimorphism. Significant sexual dimorphism of body mass is found in about half of the carnivoran taxa included in this study (Table 6). In general, males in all these families are substantially larger than conspecific females. The main exception to this rule is in the female-dominant hyaenids, where females are as large as males or, in the case of the spotted hyena *Crocuta*, slightly larger (Nowak 2005). This follows other well documented trends where the extent of dominance (or lack thereof) correlates with the extent of sexual dimorphism regardless of which sex is dominant (see Mittermeier *et al.* 2006; Moors 1980; Silk 2007 and references therein).

Table 6: Average Species Body Mass

In kilograms (Range). Carnivorans from Nowak 2005 and marsupials from Nowak 1999. For primary sources of these data, please see references therein. Weights are either the stated means, or the midpoint of the stated range. Lines delineate families; From top to bottom, Canidae, Felidae, Hyaenidae, Mustelidae, Ursidae, Viverridae and Dasyuridae.

Species	Non-Sexually Dimorphic	Females	Males
Canis lupus		37 (18-55)	40 (20-80)
Canis mesomelas		9.25 (6-12.5)	10.25 (7-13.5)
Canis rufus	30 (20-40)		
Canis simensis		13.1 (11-15.2)	16.1 (13.2-19)
Chrysocyon brachyurus	23 (20-26)		
Cuon alpinus		13.5 (10-17)	18 (15-21)
Lycaon pictus	26.5 (17-36)		
Acinonyx jubatus	46.5 (21-72)		
Caracal caracal	12.5 (6-19)		
Catopuma temmincki	11.5 (8-15)		
Neofelis nebulosa	19.5 (16-23		
Panthera leo		151 (120-182)	200 (150-250)
Panthera onca		75 (60-90)	105 (90-120)
Panthera pardus		57 (28-86)	63.5 (37-90)
Panthera tigris		133.5 (100-167)	243 (180-306)
Panthera uncia	50 (25-75)*	37.5 (35-40)*	50 (45-55)*
Prionailurus viverrinus	10.85 (7.7-14)		
Profelis aurata	10.65 (5.3-16)		
Puma concolor		48 (36-60)	85 (67-103)
Crocuta crocuta		66.3 (46.6-86)	59.7 (40-79.4)
Hyaena hyaena	40 (25-55)		
Parahyaena brunnea	42.25 (17-47.5)		
Enhydra lutris lutris		23.5 (15-32)	33.5 (22-45)
Gulo gulo		14.7 (7-22.4)	20.55 (9.1-32)
Mellivora capensis	10 (7-13)		
Pteronura brasiliensis		24 (22-26)	30 (26-34)
Ailuropoda	117.5 (75-160)		
Helarctos malayanus	46 (27-65)		
Melursus ursinus	100 (55-145)		
Tremarctos ornatus		61 (60-62)	140 (140)
Ursus americanus		116 (92-140)	192.5 (115-270)
Ursus arctos	181 (102-324)		
Ursus maritimus		225 (150-300)	460 (420-500)
Ursus thibetanus	110 (47-173)*	77.5 (65-90)*	80 (50-110)*
Cryptoprocta ferox	9.5 (7-12)		
Sarcophilus harrisii		6.1 (4.1-8.1)	8.65 (5.5-11.8)
Thylacinus cynocephalus	22.5 (15-30)		

*In these cases Nowak 2005 listed specific ranges *and* sex-specific ranges from multiple studies. In this dissertation, the sex specific mean was used.

Even when each taxon is separated according to sex, there is still a very wide size range in some of them. For example, though male wolves are generally larger than female wolves, adult male wolves vary in mass by a factor of four (Nowak 2005). Much of the size variation remaining after sexual dimorphism is controlled for is due to geographic range; taxa with the largest geographic ranges in my sample (e.g., wolves, and leopards, *P. pardus*) also have the largest variation in their morphology in general, and in their overall body size specifically. Certain biogeographic rules influence these trends, including Bergmann's Rule, which states that taxa that live in colder climates (higher elevations and latitudes) will have larger body masses (Blackburn *et al.* 1999). For instance, the warm-climate Mexican wolf (*Canis lupus baileyi*) weighs much less than its cold-adapted Canadian and Alaskan brethren (*Canis lupus occidentalis*) (Mech 1970). Many other factors contribute to the intraspecific variability of body size including seasonal body size fluctuations (Glander *et al.* 2006), variation in measurement and reporting, and variation in thoroughness of study (many of these taxa are insufficiently studied in the wild).

Ideally, the weight of each individual studied would be known. However, since this is not the case for the present sample, some other approach must be taken. If conspecific published weight ranges are used, it may be possible to distribute the known variation in weight to the measured individuals based on the variance they display in one morphological variable or some kind of geometric mean of multiple variables. (E.g., the animal with the shortest total jaw length would be assigned the minimum of the weight range of that taxon, the longest-jawed animal the heaviest weight, and the intermediate

individuals intermediate weights based on deviations from the mean.) However, this approach would involve many untenable assumptions. For instance, though weights of each species are probably normally distributed (at least within sexes), this cannot necessarily be assumed or determined from most of the published literature, which tends to give body size ranges separated by sex, at best. For the purposes of this study, average body sizes, calculated from the published body size ranges (for each sex, where sexual dimorphism is noted) summarized by Nowak (2005) are used. Nowak's recent edition, the latest on carnivorans in the *Walker's Mammals of the World* series is a respected secondary source, that offers several advantages for the current study: The authors and editors of the series apply consistent standards when extracting data from the literature, and include high-quality citations on each taxon. Furthermore, the weights included in Nowak (2005) correspond well to those published in other studies that included more extensive searches (e.g., Van Valkenburgh 1985, 1989). Where a mean weight is listed, it is used. However, Nowak (2005) mostly gives weight ranges, and in these cases the median point is used as the weight proxy. Wherever a sex specific mean or range is given, these means and medians are included in this study accordingly. The "Mammalian Species Accounts" (MSA) published by the American Society of Mammalogists, are also highly regarded and contain more detailed accounts than those found in Nowak (2005). However, some of the accounts are several decades out of date, and not every species included in this study has a published MSA. Nowak (2005) was used for it consistency across species and the fact that it was recently updated with the most current citations.

Scoring of Tooth Wear

Since this dissertation focuses on the geometry of the occlusal surfaces of the carcass-processing teeth, it is important to consider the effects of dental wear on occlusal functional morphology. Most anthropology, primatology and carnivore studies of dental geometry focus on the shape of unworn teeth. This convention probably has to do with the underlying assumption that evolution is acting on the geometry of unworn teeth, and not on their shape as they wear (Peter Lucas pers. comm.). This assumption is clearly false in many cases. For instance, unworn bovid teeth are not at all useful for the processing of vegetation; the enamel and dentine folds that are used for grinding tough foods are not exposed until the enamel tips are worn from their cheek teeth.

The adaptive value of wear is less obvious for carnivores. However, the fact remains that most mammals spend most of their reproductive lives feeding with worn dentition, and worn teeth are not necessarily less advantageous for processing their foods. Are the teeth of tough-object-feeding primates like orangutans (*Pongo*) or gelada baboons (*Theropithecus*) adapted for a similar enamel, dentine wear pattern as bovids for grinding their food? If so, why do we usually strive to study their teeth in an unworn state? Furthermore, as with the rodent incisor, a hard enamel edge backed by a soft dentine core can create a sharper sectorial cutting edge through wear. Does this ever occur in primates that use their tooth crests for slicing?

This sectorial dentine-enamel wear adaptation clearly functions in the carnassials of flesh-eating carnivorans; moderate wear exposes the dentine on the buccal surface of

the mandibular carnassial and the lingual surface of the upper carnassial, thus creating a perpetually self-sharpening scissor mechanism (Figure 18).

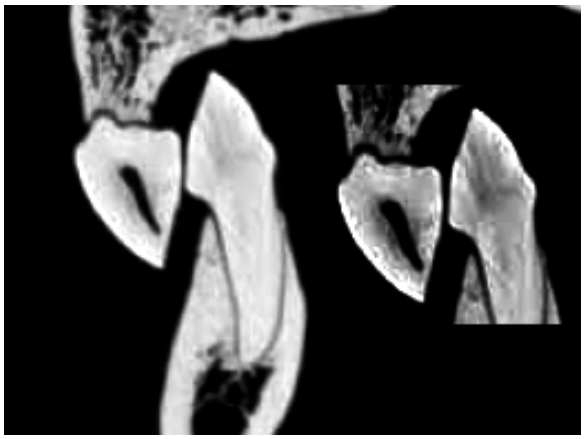

Figure 18: Carnassial Honing Mechanism

Coronal tomography section of spotted hyena (*Crocuta*) carnassials (left) and color adjusted (right) to highlight enamel caps (densest and therefore bright white) worn to reveal dentine (gray) contact surfaces. Buccal is to the left. Image modified from http://www.digimorph.org.

Though this type of honing can be found on other carnivoran postcanine teeth in some lineages (e.g., the P_4 in *Dinofelis* is incorporated into this honing complex and wears similarly), most of the other teeth wear apically in a way that makes them blunter, not sharper (Figure 19).

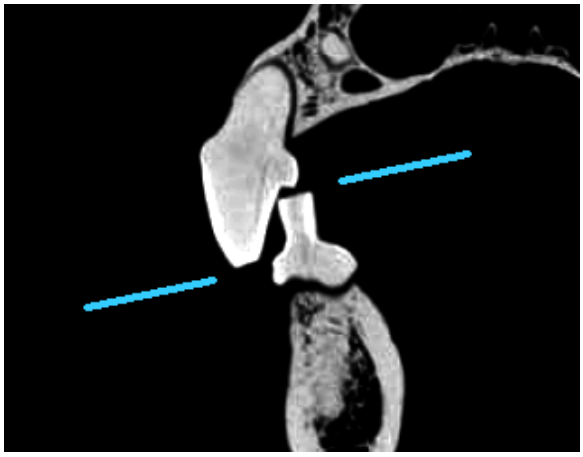

Figure 19: Wear Flattened Premolars

Coronal tomography section of the same spotted hyena (*Crocuta*) imaged in Figure 18. This section is rostral to the carnassial section and shows an upper and lower premolar displaying typical premolar apical wear (approximately in the plane denoted by the parallel lines). Buccal is to the left. Image modified from http://www.digimorph.org.

While this apical wear does not lead to much sharpening of the premolars (or canines, which also tend to wear in this way in carnivorans, though notably many primates wear their canines more like the carnassial honing mechanism), it could serve other adaptive biomechanical functions. For instance, flatter contact surfaces on teeth would serve to dissipate forces over a larger area, reducing the pressure for a given force placed on the tooth crown. This could serve to protect teeth of durophages from cracking. However, this reduction in occlusal pressure should lead to a proportional reduction in the localized pressure placed on the food object. Thus the specific adaptive significance of this type of wear is less clear.

What is clear is that most of the specimens included in this study have moderate wear. Specimens with highly worn postcanine teeth were excluded for almost all data and analyses. As discussed above, the exceptions to this rule are the hyenas; all

osteologically adult hyenas (i.e., those with fused cranial sutures, etc.) have fairly heavily worn teeth. Therefore, for the purpose of evaluating variables like jaw length, some worn specimens are included in the sample, though their teeth are excluded from analyses pertaining to occlusal shape. Likewise, hyena specimens with unworn teeth that are dentally adult (i.e., all teeth fully erupted) but osteological juveniles (i.e., unfused cranial sutures) are included for the purposes of occlusal analysis, but excluded for osteological metrics. The species averages for the three hyaenid species represent chimerical specimens that are both osteologically and dentally adult, a condition that does not exist in the wild. While this is clearly problematic for a number of reasons, for the purposes of the analyses included in this dissertation, this solution was deemed best.

So as to understand the influence of wear on the analyses in this study, and for the purposes of adding more objectivity to the decision to exclude specimens, all specimens were scored on a tooth-wear scale of 0-10. The following scores were assigned based on the following tooth-wear stages (Figure 20):

A score of 0 was assigned to a postcanine dental set displaying completely unworn premolars. Scores of 1-3 were recorded for varying degrees of minor to moderate wear on the central (paraconid) premolar cusp. 4 corresponds to major paraconid wear with no wear on the accessory cuspids, and 5 to teeth with minor wear on accessory cuspids. Scores 6-8 represent increasing levels of wear on all cusps, and a score of 9 was attributed to specimens with paraconids worn almost completely to the accessory cuspids. The score of 10 is relegated to teeth displaying paraconid wear so extreme that all of the intercuspid notches are obliterated.

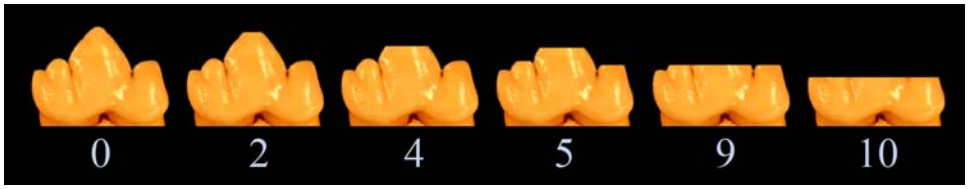

Figure 20: Schematic Depiction of Wear Stages

Depiction of wear stages modified from the same unworn lion (*Panthera leo*) P_4 (stage 0 is unmodified). Stages correspond to the state descriptions above with intermediaries falling between these states as would be expected.

The distribution of these wear states in the sample is analyzed in the following chapter. Suffice it to say here, nearly the entire sample falls within wear stages 1-4, and almost no specimens were included from wear stages 7-10.

Measurement of Radius-of-Curvature

Radii-of-curvature were measured using a technique similar to that used by Popowics and Fortelius (1997). As described above, the lower postcanine teeth of all specimens were molded using regular-body President Jet (Coltene Whaledent), a quick-setting product developed for the dental industry, and then cast using Smooth-Cast (Smooth-On), a fast-setting, low-viscosity, two-part resin. These casts were then sectioned at the apices of their cusps along the short axis of the tooth, roughly in the coronal plane. Each premolar was sectioned at the main cusp (paraconid) and the carnassial was sectioned at the anterior (paraconid) and posterior (protoconid) carnassial cusps (Figure 9) using a scroll saw (Craftsman). To minimize the influence of the kerf (the material removed by the saw), the blade was placed slightly to the anterior or

posterior of the dental midline, and the section face containing the actual midline was scanned. Once the cusps were cut, they were scanned (Figure 22) using a flatbed scanner (Hewlett-Packard).

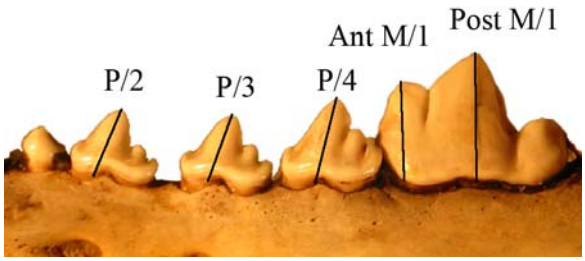

Figure 21: Approximate planes of dental sections for radius-of-curvature analysis

P_1 through M_1 of a Gray Wolf (*Canis lupus*). AMNH 5381.

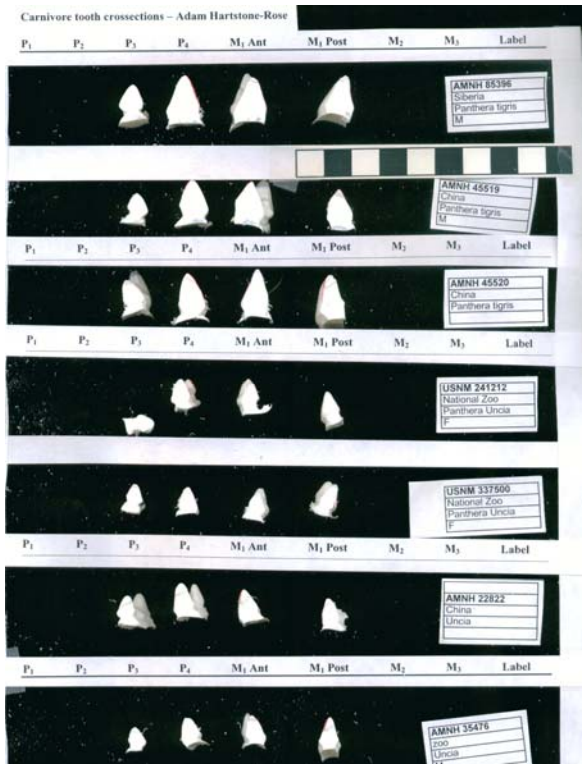

Figure 22: An example plate of dental cross-sectional scans

Single plate of postcanine tooth cross-sections for seven individual felids. Scale bar in centimeters.

The radius-of-curvature (1/r) of each target tooth was approximated in ImageJ (NIH; Figure 23) by fitting a circle to the point of the crown.

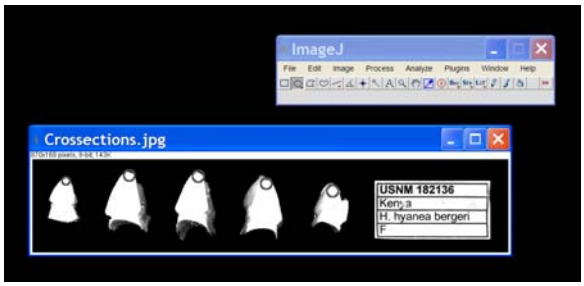

Figure 23: Radius Measurement in ImageJ

Postcanine tooth cross-sections for one individual (*H. hyaena* USNM 182136). Note: circles in this figure were enhanced for graphical purposes; actual ImageJ circles were fitted with more care, and are too thin to see well at this resolution.

The biggest challenge to this method is the approximation of radii for worn teeth. Ideally, if we imagine that the evolutionary pressure on this morphology is greatest on the unworn state, then only unworn teeth would be used for this purpose. However, as discussed above, this supposition about the evolutionary pressure is probably incorrect, and almost all adult carnivorans display at least moderate wear on their teeth. Thus, regardless of the ideal state of the sample, excluding all worn individuals from the study would exclude almost all individuals.

A method had to be devised to include the worn individuals. The method settled upon recognizes that, in cross-section, moderately worn teeth can be fitted with approximate radii as long as the occlusal curvature is not completely obliterated (Figure 24). Note that if the cross-sectional shape of these teeth were elliptical or parabolic, a

large number of progressively smaller circles could be fit within with nearly equal descriptive value. However, if we consider the cross-section of the tooth to be more of a pyramid topped with a semisphere, than only one circle would fit this ideal. Partially worn teeth (e.g., Figure 24 C) can be fit with a circle (e.g., Figure 24 D) as long as enough of the occlusal semisphere is present to indicate the curve of the inscribed circle. Specimens that were worn beyond this point (e.g., Figure 24 E) were excluded from these radii analyses.

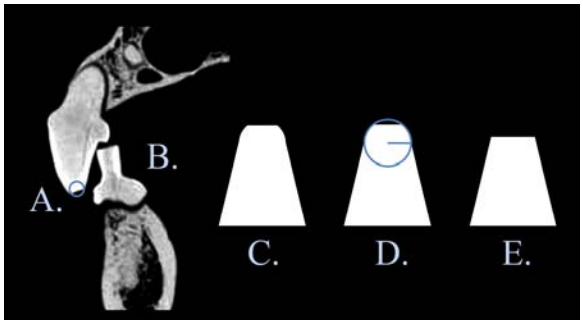

Figure 24: Measurment of Radii in Moderately Worn Teeth

Note that moderately worn teeth (e.g. A and schematic C) can have approximate circles fitted to the remnants of the occlusal curvature (D), but teeth that are worn beyond this curvature (e.g., B and schematic E) cannot.

Obviously there is some subjectivity involved in this data collection method, partially confounded by the annoying fact that biological specimens seldom exhibit perfect geometries. While greater reproducibility and accuracy could probably be achieved with the utilization of some sort of computer macro to fit the circles to the scanned cross-sections, this method was applied and its reliability was tested through multiple replications of a few individual teeth and deemed to be an accurate enough approximation to yield interesting data.

Scoring of Intercuspid Notches

The final variables that need to be described in greater detail are the premolar intercuspid notch scores (Figure 25).

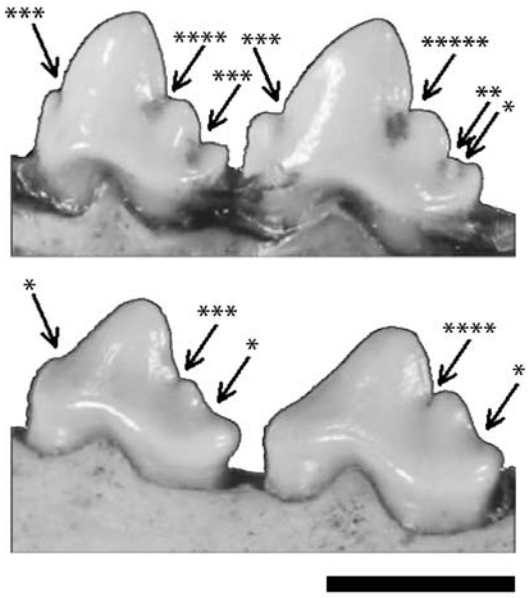

Figure 25: Intercuspid Notches.

Left P_2 and P_3 of *Lycaon pictus* USNM 470144 (top) and *Canis lupus* USNM 64960 (bottom). Mesial is to the left. Scale = 1 cm. Arrows indicate the inter-cusp notches and asterisks indicate notch score.

While it is customary to view teeth as sets of cusps, the carnivoran carnassial is better described as a set of shearing crests that meet in a notch. That is, from a functional perspective, the important elements in the sectorial component of a lower carnassial are not a pair of cuspids, but the crests and notch that span them. I hypothesize, in Aim 3 of this dissertation (evaluated in Chapter 6), that the same can be said of the configuration of the premolars in carnivorans. Qualitatively hypercarnivorous carnivoran premolars, 1)

have more accessory cuspids, and 2) sharper crests uniting in intercuspid notches when compared to more durophagous species.

To address this hypothesis from a more quantitative perspective, each intercuspid notch on each lower premolar was scored on a scale of 0-5 with "0" assigned to teeth with no intercuspid notches, "1" assigned to a barely present minor accessory cuspid, "2" assigned to a notch formed by the confluence of two dull (i.e., > ca. 45˚) crests, "3" assigned to a notch formed by one dull and one sharp (i.e., < ca. 45˚) crest, "4" assigned to a confluence of two sharp crests and "5" assigned to a "*carnassiform*" notch (see Figure 26 and its caption for an explanation of this term). The significance of this morphology and analyses thereof are the subject of chapter 6.

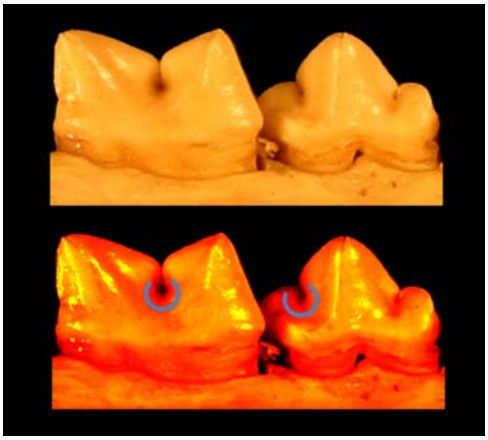

Figure 26: Carnassiifrom Notch

Lingual view of felid P_4 (right) and M_1, and color adjusted to highlight notch morphology (below). The mandibular carnassial notch in most carnivorans has a distinct keyhole pattern: as the two occlusal crests slope toward the middle, they nearly meet in sharp vertical notch and then, at their ventral terminus, expand in a semicircular loop (as highlighted in bottom set). This keyhole, or "*carnassiform*" notch can be found on the premolars of lineages tending toward hypercarnivory.

Evaluations

The following will be used to evaluate the aims of this dissertation and test the hypotheses outlined in the introduction:

Species and families that consume more flesh than bone, relative to the other species within their family and other families respectively, **will have**…

1) Longer carnassials (M_1, the dedicated slicing tooth) relative to their premolars. That is, they will have higher values for the following:

M_1 Total Length / (P_1 Length + P_2 Length + P_3 Length + P_4 Length) (1)

2) Longer trigonids (the slicing part of the carnassials) relative to overall carnassial length. That is, they will have higher values for the following:

M_1 Trigonid Length / M_1 Total Length (2)

3) Sharper dental angles. That is, they will have lower values for the following:

ArcTangent (Tooth [P_1, P_2, P_3, P_4 and M_1] Width / Tooth Height) (3)

4) Higher radii-of-curvature. That is, they will have higher values for the following:

Tooth (P_1, P_2, P_3, P_4 and M_1) Radius of Curvature (4)

5) Higher relative radii-of-curvature. That is, they will have higher values for the following:

Tooth (P_1, P_2, P_3, P_4 and M_1) Radius of Curvature / Tooth Width (5)

6) More intercuspid notches on their premolars. That is, they will have higher values for the following:

P_1 Notch Count + P_2 Notch Count + P_3 Notch Count + P_4 Notch Count (6.1)

P_3 Notch Count + P_4 Notch Count (6.2)

7 More extreme intercuspid notches on their premolars. That is, they will have higher values for the following:

Sum of Tooth (P_1, P_2, P_3, and P_4) Summed Notch Scores (7.1)

Sum of P_3Notch Scores + Sum of P_4 Notch Scores (7.2)

Statistical Comparisons

To compare the significance of differences between dietary categories for continuous variables I follow the methods outlined in Lin and Haseman (1978). They compared several commonly used nonparametric multiple comparison procedures and found one preferred method that first applies a Kruskal-Wallis test to the whole sample using a standard alpha of 0.05 and then a Wilcoxon test to compare each pair of samples with comparison-wise error rate. As such, with my four dietary categories, Kruskal-Wallis ChiSq p-values of less than 0.05 signify significant differences between the categories, and for each pair of dietary categories, Wilcoxon ChiSq p-values less than 0.00833 (or 0.05 divided by 6, the number of pairs) signify statistical differences between those pairs. This approach was found to have consistently greater power than the other common methods tested, even at small values for N (Lin and Haseman 1978).

Given the problems of prey capture, carcass consumption, and carcass retention, predaceous carnivorans must be equipped with appropriate tools for efficiently subduing prey and for rapidly ingesting large quantities of meat.

Biknevicius and Van Valkenburgh 1996; p. 396

CHAPTER 4: General Results

In this chapter I first explore basic statistics of my sample (e.g., comparisons of measurements from casts and original specimens, degrees of sexual dimorphism) and then results of standard dental measurements (especially those used by Van Valkenburgh) as they correlate with carcass-processing behavior.

Basic Sample Statistics

Before using the data to test the hypotheses relating to carcass-processing abilities, it is worth examining the effects of three possible sources of bias in my sample: the effects of 1) using casts for measurement, 2) sexual dimorphism, and 3) unequal amounts of wear within species.

Validity of Measurements Based on Cast Specimens

As discussed in the previous chapter, in an effort to minimize time spent in extant collections (and to maximize the number of individuals studied while in those collections), many of the focal measurements (namely those taken on the lower premolars and first molar) were taken on casts of the original specimens. The use of casts is widely

regarded as inferior, and rightly so; it introduces sources of error during both the molding and the casting processes due to the properties of the materials used, as most molding and casting materials are known to shrink. Furthermore, the inherent malleability of molds (almost all molds must yield to a certain extent to allow for the removal of specimens with undercut surfaces) introduces the possibility of plastic distortion during the casting process. However, modern molding and casting materials are much better than previous generations of materials, and accordingly the error introduced by casting is smaller.

The molding compound used in this study was developed for the dental industry, and as such it has several properties that help reduce the error it introduces: namely, it is very stiff (it does not require the traditional stiff "jacket" that many softer molding materials need for support) and captures very high detail (early generations of casts can even be used for the study of micro-wear). It has the added benefits of being easy to use, non-toxic (even for oral applications) and fast-setting – all of which alleviate the need for cumbersome techniques required for other molding materials, again reducing possible sources of error by allowing for highly consistent procedures. Likewise the casting material selected for this project is also very easy to use, fast-setting, and relatively stable, thus reducing error.

Though these materials are of high-quality, to confirm the validity of using casts for these measurements and to quantify the error introduced by this technique (as discussed in the previous chapter) duplicate measurements were taken from both original specimens and casts of the M_1 length and width. Reduced-major-axis comparison of these variables (Figure 27) shows, as expected, very tight correlations between cast and

original specimens with $r^2 > 0.99$ and 0.98 for length and width respectively, and neither of the slopes or intercepts are significantly different from 1 or 0 respectively. Thus, measurements taken from casts are considered adequate for the evaluation of the hypotheses.

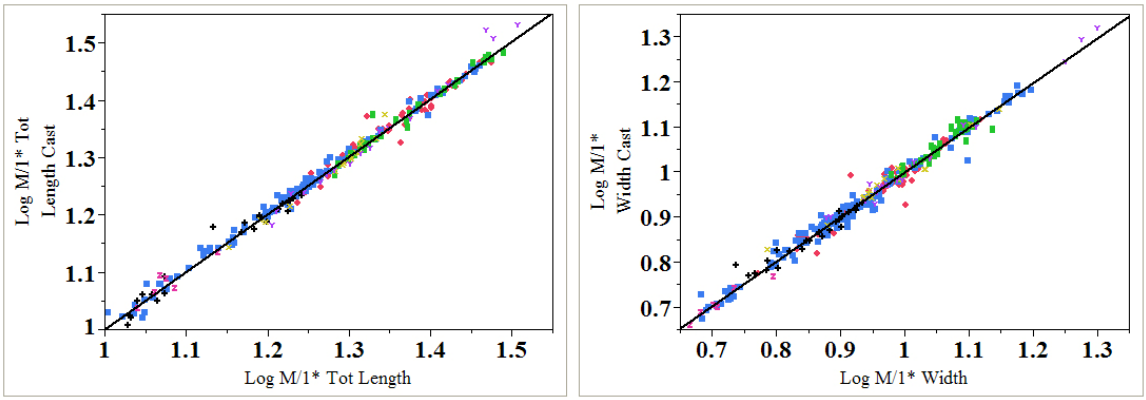

Figure 27: RMA Comparison Between Measurments of Original and Cast Specimens

M_1 Length (left; cast length = 1.00499*real length – 0.0045) and Width (right; cast length = 0.9907*real length + 0.00789). Symbols as described in Table 7.

Table 7: Marker Key For All Graphs

For focal families (i.e., canids, felids and hyaenids), Closed Markers = Modern Specimens, and Open Markers = Fossil Specimens.

Family	Marker	Color
Canidae	Circle	Red
Felidae	Square	Blue
Hyaenidae	Rectangle	Green
Mustelidae	X	Yellow
Ursidae	Y	Purple
Viverridae	Z	Pink
Dasyuridae	+	Black

Sexual Dimorphism

Before detailed interspecific statistics can be explored for each variable it is important to understand the intraspecific distribution and variability of that morphology, and the first place to do this is in an exploration of sexual dimorphism. The presence or absence of sexual dimorphism in each variable will dictate the appropriateness of lumping sexes for that variable, and will therefore have an effect on total sample size within each species.

Each variable (with the exception of those in Table 8) was studied for each species (with the exception of those in Table 9) for sexual dimorphism using a non-parametric Wilcoxon test (Table 10 and Table 11). The variables and taxa that were excluded, were excluded because of small sample sizes ($n < 3$) per sex per variable. These data tables (Table 10 and Table 11) treat each analysis of each variable for each species as independent tests. However, this approach leads to inflated type I error rates because all of the variables in each species constitute a family of variables. For this reason, a sequential Bonferroni correction (Rom 1990) was applied to the analysis, as discussed in the sections following the tables. For reasons discussed below, however, this analysis should be regarded as useful more for developing an impression of sexual dimorphism than as rigorous tests thereof.

Table 8: Variables Excluded from Sexual Dimorphism Comparisons.

Variables for which no species had an *n* > 3 for each sex.

Variables Excluded
Upper C Height
Upper C Height Perp.
Upper P4 Buc. Width
Upper P4 Height
C/1 Height
C/1 Height Perp.
Incisor row length
CP Diast.
Ant P3 Height
Ant P3 Width
Sub M1* Height
Sub M1 Width
Ant P3-Cond Length
Carnassial-Cond. Length
Condyle Height
Coronoid process Height
Symphysis Length
Symphysis Width

Table 9: Species Excluded from Sexual Dimorphism Comparisons.

Species with *n* < 3 for each sex.

Species Excluded
Canis mesomelas
Canis simensis
Caracal caracal
Catopuma temmincki
Prionailurus viverrinus
Profelis aurata
Enhydra lutris
Mellivora capensis
Pteronura brasiliensis
Ailuropoda melanoleuca
Helarctos malayanus
Melursus ursinus
Tremarctos ornatus
Ursus americanus
Ursus arctos
Ursus maritimus
Ursus thibetanus
Cryptoprocta ferox

Table 10: Sexual Dimorphism, Wilcoxon Test, for Canids, Hyaenids and *Gulo*.

Key: "*" = p < .05, "" = p < .01, "***" = p < .001, "/" = *n* too small to compare for this variable (*n* < 3 per sex), "NS" = not statistically sexually dimorphic, "." = taxon does not have this tooth.**

Species	*Canis lupus*	*Canis rufus*	*Chrysocyon sp.*	*Cuon alpinus*	*Lycaon pictus*	*Crocuta crocuta*	*Hyaena hyaena*	*Parahyaena brunnea*	*Gulo gulo*
Family	Canidae	Canidae	Canidae	Canidae	Canidae	Hyaenidae	Hyaenidae	Hyaenidae	Mustelidae
Total *n*	7	18	10	6	11	12	12	9	9
n Females	3	9	4	3	3	4	9	6	4
n Males	4	9	6	3	8	8	3	3	5
Tot Jaw Length	NS	NS	NS	NS	NS	NS	NS	/	NS
C1/ Length	NS	*	*	NS	NS	NS	NS	NS	NS
C1/ Width	NS	*	NS	NS	NS	NS	NS	NS	NS
P4/* Length	NS	NS	*	NS	NS	NS	NS	NS	NS
P4/* Total Width	NS	NS	*	NS	NS	NS	NS	NS	NS
C/1 Length	NS	*	*	NS	NS	NS	NS	NS	NS
C/1 Width	NS	*	*	NS	NS	NS	NS	NS	*
Wear	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/1 Length	NS	NS	NS	NS	NS	.	.	.	NS
P/1 Width	NS	NS	NS	NS	NS	.	.	.	NS
P/1 Height	/	NS	/	/	/	.	.	.	NS
P/1 Height Perp.	/	NS	/	/	/	.	.	.	NS
P/2 Length	NS	NS	NS	NS	NS	NS.	NS	NS	NS
P/2 Width	NS	NS	NS	*	NS	NS	NS	NS	NS
P/2 Height	NS	NS	/	/	/	NS	NS	NS	NS
P/2 Height Perp.	NS	NS	/	/	/	NS	NS	NS	NS
P/3 Length	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/3 Width	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/3 Height	NS	NS	/	/	/	NS	NS	NS	NS
P/3 Height Perp.	NS	NS	/	/	/	NS	NS	NS	NS

Species	*Canis lupus*	*Canis rufus*	*Chrysocyon sp.*	*Cuon alpinus*	*Lycaon pictus*	*Crocuta crocuta*	*Hyaena hyaena*	*Parahyaena brunnea*	*Gulo gulo*
P/4 Length	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/4 Width	NS	NS	NS	*	NS	NS	NS	NS	*
P/4 Height	NS	NS	NS	/	NS	NS	NS	NS	NS
P/4 Height Perp.	NS	NS	NS	/	NS	NS	NS	NS	NS
M/1* Tot Length Cast	NS	NS	NS	*	NS	NS	NS	NS	NS
M/1* Width Cast	NS	NS	NS	NS	NS	NS	NS	NS	*
M/1* Trigonid Length	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Cusp Points Length	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Ant Crest Length	NS	NS	NS	NS	NS	NS	*	NS	*
M/1* Post Crest Length	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Height	NS	NS	/	NS	NS	NS	NS	NS	NS
M/1* Tot Length	NS	NS	*	NS	NS	NS	NS	NS	NS
M/1* Width	NS	NS	*	NS	NS	NS	NS	*	*
P/1 Shape	NS	NS	NS	NS	*	.	NS	.	NS
P/2 Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/3 Shape	NS	NS	NS	NS	NS	NS	NS	*	NS
P/4 Shape	NS	NS	NS	NS	NS	NS	NS	*	NS
M/1* Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Trigonid Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Trigonid/Length	NS	NS	NS	NS	NS	NS	NS	NS	NS
Upper Canine Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS
Lower Canine Shape	NS	NS	NS	NS	NS	NS	NS	NS	*
Upper Carnassial Shape	NS	NS	NS	NS	NS	*	NS	NS	NS

Species	*Canis lupus*	*Canis rufus*	*Chrysocyon sp.*	*Cuon alpinus*	*Lycaon pictus*	*Crocuta crocuta*	*Hyaena hyaena*	*Parahyaena brunnea*	*Gulo gulo*
P/2 radius	NS	NS	NS	/	NS	NS	NS	NS	/
P/3 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/4 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1 ant radius	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1 post radius	NS	NS	NS	NS	NS	**	NS	NS	NS
Relative P/2 radius	NS	NS	NS	/	NS	NS	NS	NS	/
Relative P/3 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS
Relative P/4 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS
Relative M/1 ant radius	NS	NS	NS	NS	NS	NS	NS	NS	NS
Relative M/1 post radius	NS	NS	NS	NS	NS	*	NS	NS	NS
Carnassial Notch Degrees	NS	NS	/	NS	NS	NS	NS	NS	NS
P/1 Angle Degrees	NS	NS	/	/	NS	.	.	.	NS
P/2 Angle Degrees	*	NS	/	/	NS	NS	NS	NS	NS
P/3 Angle Degrees	NS	NS	/	/	NS	NS	NS	NS	NS
P/4 Angle Degrees	NS	NS	NS	/	NS	NS	NS	NS	NS
M/1* Angle Degrees	NS	NS	/	*	NS	NS	NS	NS	NS

Table 11: Sexual Dimorphism, Wilcoxon Test, for Felids and Dasyurids.

Key: "*" = p < .05, "" = p < .01, "***" = p < .001, "/" = *n* too small to compare for this variable (*n* < 3 per sex), "NS" = not statistically sexually dimorphic, "." = taxon does not have this tooth.**

Species	*Acinonyx jubatus*	*Neofelis nebulosa*	*Panthera onca*	*Panthera uncia*	*Panthera leo*	*Panthera tigris*	*Panthera pardus*	*Puma concolor*	*Sarcophilus*	*Thylacinus*
Family	Felidae	Felidae	Felidae	Felidae	Felidae	Felidae	Felidae	Felidae	Dasyuridae	Dasyuridae
Total *n*	16	17	14	12	11	10	20	19	9	15
n Females	9	10	6	6	5	4	6	9	4	9
n Males	7	7	8	6	6	6	14	10	5	6
Tot Jaw Length	**	*	**	*	*	-	***	**	NS	NS
C1/ Length	***	**	**	*	*	*	***	*	NS	*
C1/ Width	*	*	**	*	NS	*	***	*	NS	**
P4/* Length	NS	**	**	**	NS	NS	**	*	NS	NS
P4/* Total Width	**	**	**	**	NS	*	**	*	NS	NS
C/1 Length	**	**	**	**	*	*	***	NS	*	**
C/1 Width	**	**	**	NS	*	*	***	*	*	*
Wear	NS	NS	NS	NS	NS	NS	NS	NS	-	-
P/1 Length	.	.	.	.	.	.	.	.	.	-
P/1 Width	.	.	.	.	.	.	.	.	.	NS
P/1 Height	.	.	.	.	.	.	.	.	.	NS
P/1 Height Perp.	.	.	.	.	.	.	.	.	.	NS
P/2 Length	.	.	.	.	.	.	.	.	.	NS
P/2 Width	.	.	.	.	.	.	.	.	.	NS
P/2 Height	.	.	.	.	.	.	.	.	.	NS
P/2 Height Perp.	.	.	.	.	.	.	.	.	.	NS
P/3 Length	***	NS	*	*	NS	NS	***	NS	NS	NS
P/3 Width	**	*	**	*	NS	NS	**	*	NS	NS
P/3 Height	NS	NS	*	NS	NS	NS	*	NS	NS	NS
P/3 Height Perp.	NS	NS	*	NS	NS	NS	*	NS	NS	NS

Species	*Acinonyx jubatus*	*Neofelis nebulosa*	*Panthera onca*	*Panthera uncia*	*Panthera leo*	*Panthera tigris*	*Panthera pardus*	*Puma concolor*	*Sarcophilus*	*Thylacinus*
P/4 Length	**	**	**	*	NS	NS	**	*	NS	NS
P/4 Width	**	*	**	NS	NS	NS	**	*	NS	*
P/4 Height	**	*	**	NS	NS	*	**	NS	NS	NS
P/4 Height Perp.	**	*	**	NS	NS	*	**	NS	NS	NS
M/1* Tot Length Cast	**	**	**	**	NS	NS	**	*	*	NS
M/1* Width Cast	**	**	**	*	NS	NS	**	*	NS	NS
M/1* Trigonid Length	*	**	**	**	NS	NS	**	NS	NS	NS
M/1* Cusp Points Length	NS	NS	NS	**	NS	*	*	NS	NS	NS
M/1* Ant Crest Length	NS	NS	NS	NS	NS	NS	*	NS	NS	NS
M/1* Post Crest Length	NS	*	*	NS	NS	NS	*	NS	NS	NS
M/1* Height	NS	**	**	*	NS	NS	**	NS	NS	NS
M/1* Tot Length	**	**	**	**	NS	*	**	NS	NS	NS
M/1* Width	**	**	**	*	NS	NS	**	**	NS	NS
P/1 Shape	.	.	.	.	.	.	.	.	.	-
P/2 Shape	.	.	.	.	.	.	.	.	.	NS
P/3 Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/4 Shape	NS	NS	NS	*	NS	NS	*	NS	NS	NS
M/1* Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Trigonid Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1* Trigonid/Length	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
Upper Canine Shape	NS	NS	NS	NS	NS	NS	*	NS	NS	NS
Lower Canine Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
Upper Carnassial Shape	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Species	*Acinonyx jubatus*	*Neofelis nebulosa*	*Panthera onca*	*Panthera uncia*	*Panthera leo*	*Panthera tigris*	*Panthera pardus*	*Puma concolor*	*Sarcophilus*	*Thylacinus*
P/2 radius	.	.	.	.	.	.	.	.	.	NS
P/3 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/4 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1 ant radius	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
M/1 post radius	NS	NS	NS	NS	*	NS	NS	NS	NS	*
Relative P/2 radius	.	.	.	.	.	.	.	.	NS	NS
Relative P/3 radius	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Relative P/4 radius	*	NS	NS	NS	NS	NS	NS	NS	NS	NS
Relative M/1 ant radius	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Relative M/1 post radius	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
Carnassial Notch Degrees	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
P/1 Angle Degrees	.	.	.	.	.	.	.	.	.	-
P/2 Angle Degrees	.	.	.	.	.	.	.	.	.	-
P/3 Angle Degrees	NS	NS	NS	NS	NS	NS	NS	*	-	-
P/4 Angle Degrees	NS	NS	**	NS	NS	NS	NS	NS	-	-
M/1* Angle Degrees	NS	NS	NS	NS	*	NS	NS	NS	-	-

As discussed in the Variables and Species Selection sections in Materials and Methods, the underrepresented variables and species were included to expand the interspecific range of morphological and taxonomic variation; underrepresented variables were included to expand the overall descriptive morphology captured per species, while underrepresented taxa were included to expand the overall taxonomic breadth available for comparisons of the target taxa (namely large-bodied canids, felids and hyaenids). For these taxa/variables, specimens subjectively determined to be fairly representative of their species/sex (i.e., young but fully adult) were chosen. As they are only included as comparisons for the focal taxa/variables, taxonomic breadth was emphasized in these cases over intraspecific variability.

At these small sample sizes (the largest sample collected contains 20 individuals, with the largest sex-balanced sample containing 10 males and nine females), sexual dimorphism is hard to statistically exclude for the apparently less sexually dimorphic variables. That is, inclusion of a larger sample would almost certainly reveal greater sexual dimorphism for some of the apparently monomorphic taxa. Even in the present samples, a number of variables show significant sexual dimorphism for certain lineages. For instance, almost all of the linear measurements (as opposed to the angular, radial and shape derivatives) show significant sexual dimorphism in the felid sample (Table 11).

Within the cats, the African *Acinonyx jubatus*, and *Panthera pardus* and the latter's non-African congeners, *P. onca* and *P. uncia*, appear to be the most highly dimorphic for these variables, while their larger congeners *P. leo* and *P. tigris* appear to be less dimorphic. However, I suspect that this latter finding may be an artifact of the

relatively small sample sizes for these species (*n* = 5f, 6m and *n* = 4f, 6m respectively) as these taxa are widely regarded as being highly sexually dimorphic (Macdonald 1983, 2006; Nowak 2005). *Neofelis* appears to have moderate, though significant, sexual dimorphism. The well represented *Puma* (*n* second only, among the felids, to *P. pardus*) exhibits the least significant sexual dimorphism among the studied felid taxa.

After the felids, only the canids and marsupials (dasyurids) display statistically significant sexual dimorphism among the families studied. In fact, for these variables, only *Canis rufus* and *Chrysocyon* and the two marsupials display significant sexual dimorphism. Furthermore, the dimorphism is displayed only in the canine dimensions for the marsupials, and for the canines and upper carnassials for the two canids. (*Chrysocyon* also appears to display dimorphism in some of its lower carnassial measurements.) The other canids, including the African *Lycaon*, do not display significant sexual dimorphism.

The sole mustelid taxon with a sample size large enough for inclusion in the sexual dimorphism analysis, *Gulo*, displays some sexual dimorphism in its lower teeth, mostly in the width of its C_1, P_4 and M_1. The other variables are either not sexually dimorphic, or the sample size is too small to detect the dimorphism.

The hyaenids do not display much sexual dimorphism, and there are no obvious diagnosable patterns. Though the samples are skewed sexually (*Crocuta n* = 4f, 8m, *Hyaena n* = 9f, 3m and *Parahyaena n* = 6f, 3m), the total sample sizes are among the highest in the study, and (with the exception of *Parahyaena*) are within the sample-size-ranges of the canids and felids that displayed sexual dimorphism.

Very few of the derived shape and angle variables or radius-of-curvature variables show any levels of significant sexual dimorphism. However, it does appear that male *Crocuta* have smaller posterior carnassial crest radii (i.e., blunter crests) than females, both relative to their size (M_1 width) and absolutely. The same pattern is seen, to a certain extent, in *Panthera leo* and *Thylacinus*. These findings could be a purely statistical effect; when statistically examining this many relationships using these confidence intervals, a certain number of variables should display statistically significant results purely based on probability, despite not actually being functionally significant.

To correct for this type I error, the sexual dimorphism comparisons for each variable within taxa should be regarded as a family of variables, and then the alpha level should be adjusted accordingly (Rom 1990) by dividing the chosen family-wide alpha-level (of 0.05) by the total number of variables tested. Since I tested almost all of the variables I collected for sexual dimorphism, this denominator is as high as 59 (the maximum number of variables tested in some taxa) resulting in a minimum threshold of $p \leq 0.000847$, though this level is a bit higher for taxa that do not have values for all variables (such as the felids, which lack first and second premolars). At this level, only the eight tests denoted by the "***" in Table 11 (two for *Acinonyx jubatus* and six for *Panthera pardus*) are significant at the variable family-wide alpha level of 0.05. Various techniques could be used to expose more sexual dimorphism in my sample (for instance by simply narrowing my set of variables or lumping several in geometric means); however, the present sample of specimens is inappropriate for doing truly stringent analyses of sexual dimorphism. By trying to balance interspecific breadth, intraspecific

depth was sacrificed in ways that clearly compromise the extent to which much can be said with statistical justification about any intraspecific variation. With that said, these considerations of sexual dimorphism, while not very statistically powerful, can serve as a guide for making decisions about lumping data by species.

Distribution of Wear Patterns

Though one of the criteria for selecting specimens was dental quality (i.e., minimal wear) – indeed this was the first selection criterion – not all specimens fall into the minimal wear range. This is especially true for the hyaenids, which, as discussed previously, tend to wear their teeth very heavily, and for the rarer species (such as *Cuon*) because the scarcity of representatives curtailed selection of ideal specimens. Before more detailed examination of occlusal geometry is undertaken (e.g., the subjects of the following two chapters), it is helpful to understand the nature of the unequal distributions of wear patterns both between the fossil and modern sample (if fossils are more worn, in general, then this could skew further results) and between modern specimens.

To examine these trends, wear scores (described in the previous chapter) were converted to ranks and then compared using a one-way ANOVA (as described in Conover and Iman 1981) between the best represented (i.e., those included in the sexual dimorphism comparisons in Table 9) modern carnivorans (Figure 28) and between all modern specimens and all fossils. As expected, the ANOVA comparing the modern taxa (Figure 28) reveals significant differences for wear ranks within the sample ($p < 0.0001$).

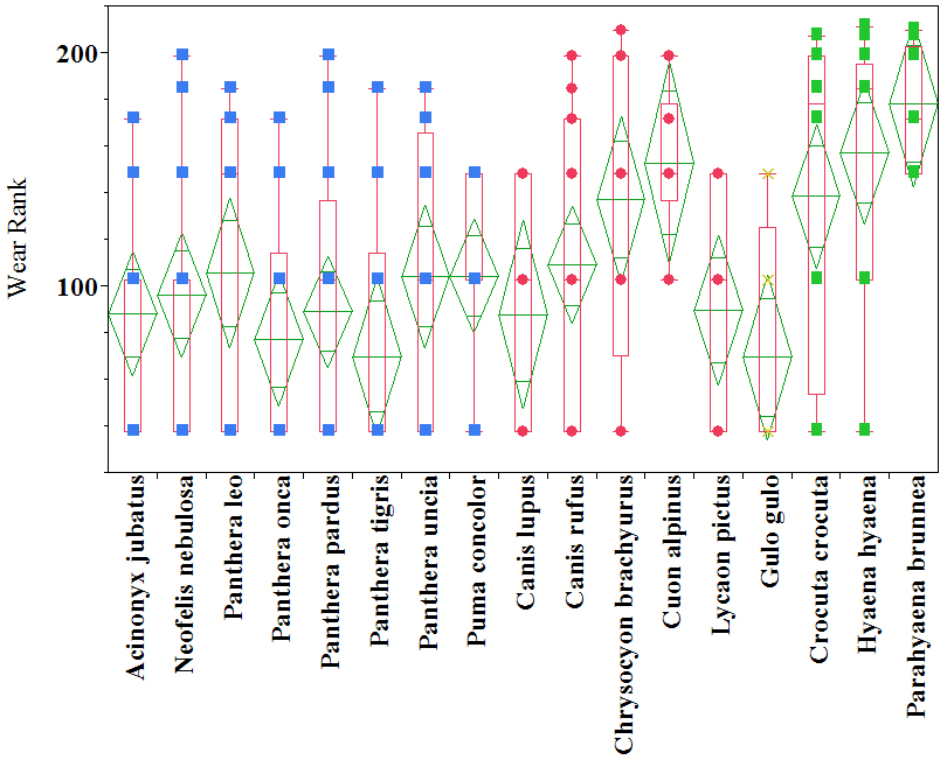

Figure 28: Comparison of Wear Ranks for Modern Taxa

Wear ranks of 211 modern specimens from the 17 best represented carnivorans with box plots (red) and ANOVA diamonds (green). Symbols as described in Table 7.

The variation within the sample shows that the three hyaena species, along with the two rarest canids included in this subset (*Chrysocyon* and *Cuon*) have higher average wear ranks than the other canids and all of the felids. Using an all-pairs Tukey-Kramer test (alpha = 0.05), these differences are, more or less confirmed (Figure 29). In fact, this test reveals three statistically separable groups: One group ("A" in Figure 29) contains the taxa with the most worn teeth and excludes most of the felids, *Lycaon* and *Gulo*; the next group ("B" in Figure 29) excludes the taxon with the most worn teeth (*Parahyaena*) and the three taxa with the least worn teeth (*Panthera onca, P. tigris,* and *Gulo*); and the

last group ("C" in Figure 29) separates the taxa with the most worn teeth (the two hyaenids *Parahyaena* and *Hyaena*) from all of the others.

Parahyaena brunnea	A
Hyaena hyaena	A B
Cuon alpinus	A B C
Crocuta crocuta	A B C
Chrysocyon brachyurus	A B C
Canis rufus	A B C
Panthera leo	A B C
Puma concolor	A B C
Panthera uncia	A B C
Neofelis nebulosa	B C
Lycaon pictus	B C
Panthera pardus	B C
Acinonyx jubatus	B C
Canis lupus	A B C
Panthera onca	C
Panthera tigris	C
Gulo gulo	C

Figure 29: Tukey-Kramer Wear Rank Groupings

Taxa not connected by the same letter are statistically different from each other based on their wear rankings.

(Using the Lin and Haseman (1978) test (i.e., using a comparison-wise error rate of $p < 0.0029$) reveals identical results, with the same species being statistically differentiable, suggesting that either method is useful in these approaches, though the Tukey-Kramer approach yields a graphical result (i.e., Figure 29) in JMP 7.0 that can aid in data interpretation.)

Given that almost all hyenas have relatively heavily worn teeth, it is not surprising that the two samples most distinguishably biased toward heavier wear are hyaenids,

Parahyaena and *Hyaena*. However, the fact that the wear rankings of the third hyaena, *Crocuta*, are indistinguishable from the least worn taxa is somewhat surprising. The reason that the *Crocuta* sample is not biased is because there are many more specimens of that taxon than the other two hyaenids in the collections studied. Specifically, while there are only a total of 12 *Parahyaena* individuals in both the AMNH and USNM combined, there are 140 *Crocuta* specimens. As such, it was possible to choose less worn *Crocuta* specimens, whereas nearly every *Parahyaena* specimen had to be included for maximal sample sizes. Though there are more *Hyaena* specimens than *Parahyaena* specimens in the two collections (33 combined), yielding a slightly larger and less worn sample included in this study, these specimens are not in very good condition (e.g., chipped teeth), and as such there was not enough flexibility to choose the optimal specimens.

The opposite trend is responsible for the surprisingly unworn *Gulo* sample. Given their greater durophagy, *Gulo* would be expected to have more worn teeth than those of the felids and canids. However, they fall with the least worn samples according to the Tukey-Kramer test. Just as the small sample of *Parahyaena* and *Hyaena* contributed to a bias toward heavier worn samples, the relatively large museum sample of *Gulo* (169 specimens in the AMNH and USNM) allowed for greater freedom in specimen selection, and therefore a less worn sample.

As would be expected based on the results of the Tukey-Kramer test, comparing the wear distributions of the dietary groups first using a Kruskal-Wallis test and then pair-wise Wilcoxon comparisons (as recommended in Lin and Haseman 1978) also yields

significant differences between the durophage and non-durophage groups. None of the other dietary pairings can be statistically differentiated.

The modern and fossil specimens were also compared based on wear ranks using a Wilcoxon test, and though the fossils appear to be slightly biased toward more wear (due to the fact that all fossil carnivorans were incorporated into the study regardless of wear score whereas modern specimens were selected to minimize wear when possible), this bias is not statistically significant ($p = 0.0751$).

Comparison With Van Valkenburgh's Findings

Citing the results of an earlier study eventually published in 1989, Van Valkenburgh (1988b; p. 156) states that "two of the indices, relative premolar size and relative blade length (RPS, RBL) ..., were able to clearly separate the extant Carnivora into four dietary groups on bivariate and multivariate plots." The 1989 paper notes that RPS (which she defines as the width of the largest premolar divided by the cube root of body weight) separates her "meat" group from her "meat/bone" group, her "meat/bone" group from both her "meat" and "meat/nonvertebrate" groups, her "meat/nonvertebrate" group from both her "meat/bone" and "nonvertebrate/meat" groups, and her "nonvertebrate/meat" group from her "meat/nonvertebrate" group. In other words, for this variable her least durophagous group can be distinguished only from her most durophagous group. The 1989 paper shows that RBL (which she defines as the M_1 trigonid divided by the M_1 total length) separates her sample into two groups: the "meat"

and “meat/bone” groups with high RBL and the two groups including “nonvertebrate” as a defining dietary component with small RBL. These separations are based on, two-tailed Student’s t tests (alpha = 0.05). Before applying these same (or similar) variables to my sample, it is worth considering what these indices reveal about the morphology.

The first of her key indices, RPS, essentially captures the fact that hyenas, the only members of her “meat/bone” group, have wider premolars relative to body size than any species in her sample, though they cannot be distinguished from the sample dominated by frugivores (which have large teeth adapted for grinding), and that her “meat” group has narrow premolars relative to body size, though they cannot be distinguished from the non-hyaenid sample. The second of her key indices, RBL, clearly separates the groups essentially by phylogeny. That is, 87% of the combined taxa in her “meat” and “meat/bone” groups are feloids, the carnivorans that have drastically reduced their talonids and post carnassial molars, and 83% of the combined vertebrate-consuming taxa are canoids, carnivorans known for emphasizing their post-carnassial dentition (Biknevicius and Van Valkenburgh 1996). Thus, though this index may reveal true dietary adaptation, it probably does so at a much higher taxonomic level (the suborder), and in this respect probably separates diets according to an *n* of one for each of the two lineages – a conclusion that would drastically reduce the significance of this finding.

Van Valkenburgh’s Key Indices Applied to This Sample

Using Van Valkenburgh’s two key indices reveals very similar results for her sample and this one. As in Van Valkenburgh (1989), when comparing species averages

my durophage group can be statistically differentiated (Wilcoxon ChiSq p-values less than 0.00833) from both the meat and meat/non-vertebrate groups using a relative premolar index (Figure 30). (Van Valkenburgh uses the width of the largest premolar for her RPS index, noting that the P_3 in hyenas is wider than the P_4, and as such uses it along with the P_4 of all other taxa for her index. However, given that P_3 and P_4 widths are highly correlated in my sample [r = 0.8611], I decided to consistently use P_4 width for this index.)

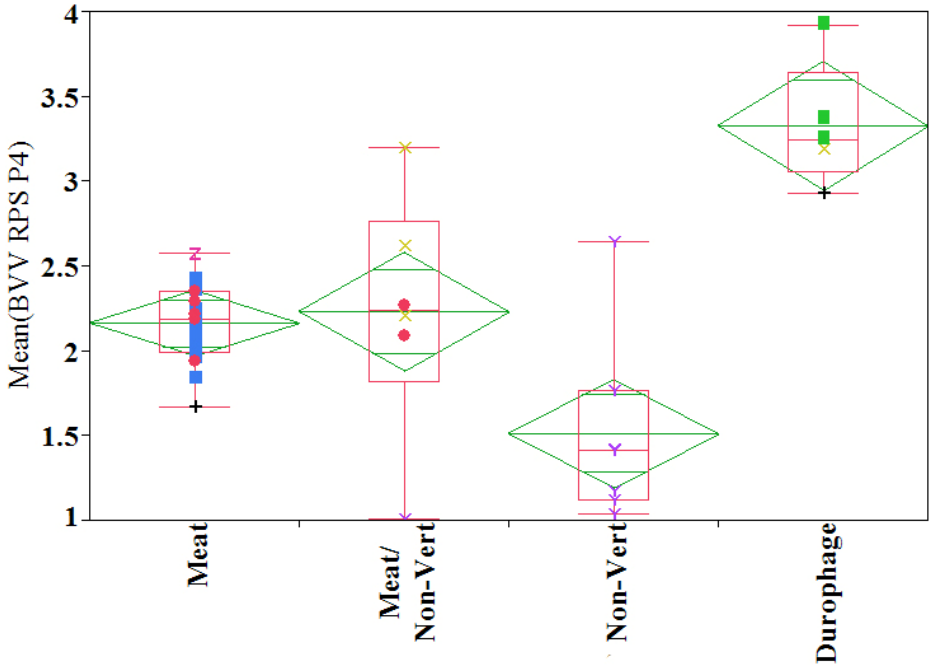

Figure 30: Relative Premolar Size

Species Averages with box plots and ANOVA diamonds. Symbols as described in Table 7.

The main difference in my findings for this index is that the "non-vertebrate" group is the most distant group from the durophages in my analysis, though it was not

statistically separable in her 1989 study. Unlike Van Valkenburgh's sample, which included some small taxa like raccoons (*Procyon lotor*) in the non-vertebrate group, taxa excluded from my study because they are too small or too derived (e.g., she also included in this group *Arctictis*, excluded from my sample for reasons discussed in the previous chapter), my sample for this dietary category is dominated by the ursids, a clade of species that have small teeth relative to their body size (the denominator in her index). Thus, my non-vertebrate group falls on the lowest end of this index and is statistically distinct from both the durophage and meat groups, but not from the meat/non-vertebrate group (which has a broad morphological range in this ratio). As is the case in her 1989 study, the other two groups in my sample, consisting predominantly of the cats and dogs, are indistinguishable in this index.

Likewise, my analysis of relative blade length (Figure 31) also statistically separates the dietary groups according to the anatomy that defines the carnassials of the phylogenetic groupings: feloid and canoid. As in the Van Valkenburgh sample, my meat-specialist group is dominated by felid species, and my durophage sample by hyaenids – both feloid families have minimized the post-carnassial grinding surfaces and therefore fall high on this index and are statistically indistinguishable. As in the Van Valkenburgh sample, the other two dietary categories are dominated by canoid taxa known to have fairly long talonid grinding surfaces and are also statistically indistinguishable. When the fossils (not in the figure) are included in this analysis (something that could not be done using Van Valkenburgh's RPS index, which relies on body mass in the denominator, which I did not want to estimate for the fossil taxa), they

fall within the ranges of their confamilials. In other words, even for the fossil taxa, this variable reveals much more about phylogenetic affinity than about carcass-processing behavior.

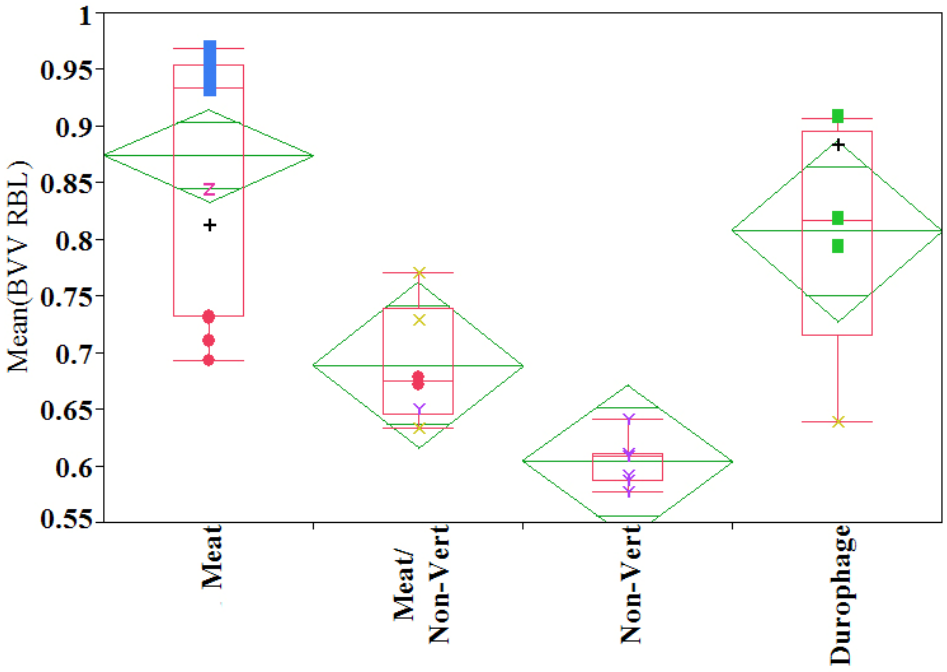

Figure 31: Relative Blade Length

Species Averages with box plots and ANOVA diamonds. Symbols as described in Table 7.

In Van Valkenburgh's papers, only the dietary categories are delineated graphically, without differentiation of the families within those categories. The influence of phylogeny is lumped in with the scatter of the dietary categories. When taxonomic information is included within these dietary categories, as in my univariate analyses, it becomes clear that Van Valkenburgh's RBL index is heavily influenced by phylogeny. Note that the canids (red circles) bring the mean of the meat-group RBL score down

toward that of the meat/non-vertebrate group. Indeed, if the feloid taxa within this group were not numerous enough to drag the mean higher on the index, the groups would probably not be statistically distinguishable.

Though she does not include a figure of her two key indices as a bivariate plot (it is worth noting that the 1989 paper does have several confusing plots with these as two of three axes along with log blade width), fitting my sample to these variables yields interesting results (Figure 32). Namely, though the axes conform to the descriptions above (i.e., the x-axis, RBL, mainly separates the feloids from the canoids, and the y-axis, RPS, separates the wide premolar hyaenids and the large bodied ursids from all the other taxa), this bivariate view allows for interpretation of more subtle variation within the sample that may be indicative of adaptation for carcass-processing behavior.

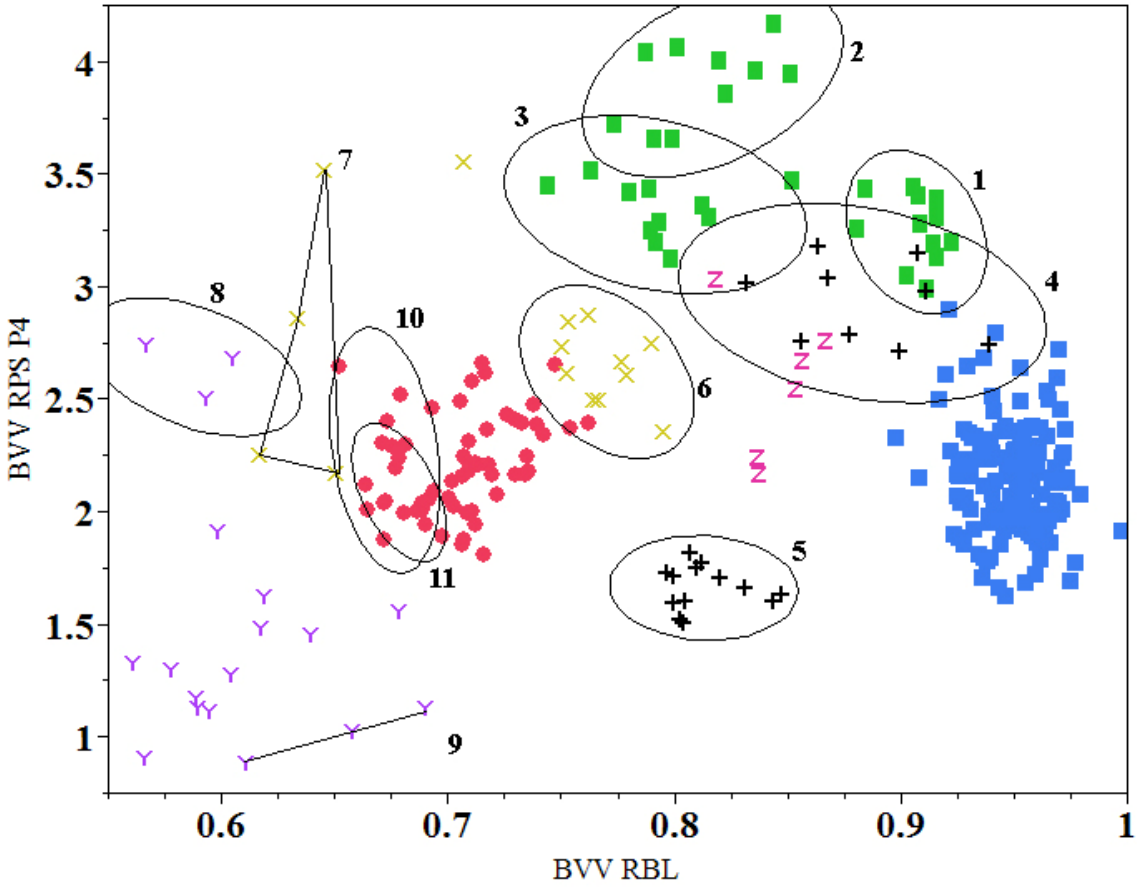

Figure 32: Bivariate Plot of Van Valkenburgh Indices

0.95 density ellipses, connecting lines and their associated numeric labels are for graphical purposes and are explained in the text. Symbols as described in Table 7.

For example, among the hyaenids, only *Crocuta* (ellipse 1) has lost it M^1, and, correspondingly, it has reduced its talonid. It has moved in the direction of the felids (blue squares) on the x-axis, away from *Parahyaena* (ellipse 2) and *Hyaena* (ellipse 3). These two taxa segregate on the y-axis, indicating that *Parahyaena* has wider premolars relative to its body mass, perhaps evidence of more advanced durophagous adaptation. Likewise, the marsupials *Sarcophilus* (ellipse 4) and *Thylacinus* (ellipse 5) segregate on the y-axis as would be expected according to their dietary categorizations, with the

former falling closer to the durophagous hyaenids, and the latter falling lower on the axis, with premolars relatively as narrow as the narrowest of felid premolars.

The same pattern is seen in the two otter species (7), with the durophagous *Enhydra* representing the two higher points in this grouping, and the more hypercarnivorous *Pteronura* falling lower on the axis. Interestingly the bears follow a similar pattern; though the panda (*Ailuropoda*) is not classified as a durophage – it does not eat hard and brittle items like bones and shells (as the "durophagous" hyaenids, *Sarcophilus*, and *Enhydra* do), but it eats very tough bamboo – and on this figure it falls at the high end of the bear sample on the y-axis (ellipse 8), suggesting that in this premolar measure hard object feeding requires the same adaptation as tough object feeding. This bear pattern is highlighted by the position of the most hypercarnivorous of the bears (*Ursus maritimus*) toward the bottom of the morphospace (9).

Interestingly, two groups do appear to split the morphospace along the x-axis, the mustelids, with *Gulo* (ellipse 6) displaying relatively longer carnassial blades than the confamilial lutrines, and the canids which, despite their relatively tight grouping display some morphological separation: the two least hypercarnivorous taxa, *Chrysocyon brachyurus* (ellipse 10) and *Canis mesomelas* (ellipse 11) fall toward the left of the other canids. Thus they display larger talonids and therefore can be said to be less specialized in the sectorial morphology of their carnassial.

Analyses of Other Linear Variables

As described in the previous chapter, before examining how radii-of-curvature and notch scores correlate with carcass-processing behaviors, it is worth examining how well premolar and carnassial length ratios may do the same job. In the first chapters of this dissertation, I hypothesized that species that consume a higher proportion of flesh in their diets will have cumulatively longer slicing crest lengths, by incorporating slicing crests onto the premolars, than bone eaters; that the carnassials will represent a higher proportion of the total length of the tooth row in flesh eaters relative to bone eaters; and that the robusticity (stoutness) of puncture cusps will be directly proportional to bone consumption or bone crushing across species.

The first of these Aim 1 hypotheses is subjectively true: more hypercarnivorous taxa do have more sectorial premolars than more durophagous taxa that have more puncture-type premolars. For instance, the most hypercarnivorous canid, *Lycaon*, has higher crowned premolars with more acutely angled mesial and distal margins than any of its confamilials. The same pattern is clear between carnivoran families as well with felids, for instance, having more sectorial premolars than hyaenids. To a certain extent, this hypothesis is addressed quantitatively in the results chapter (Chapter 6) assessing intercuspid notch score.

The other two Aim 1 hypotheses lend themselves to evaluation using standard linear measurements. Namely H_{1b} can be assessed using the relative length of the carnassial (carnassial length divided by the sum of the carnassial and all premolar lengths), and H_{1c} can be evaluated using premolar shapes (e.g., P_4 length/P_4 width).

Patterning in the relative length of the carnassial (Figure 33) fits the hypothesis that hypercarnivores emphasize the length of their carnassial (the slicing tooth) over the lengths of their premolars (generally the puncture or crushing teeth). As expected, this ratio separates the four dietary categories (Kruskal-Wallis $p < 0.0001$), with members of the durophage group having relatively shorter carnassials than the members of the meat specialist group (Wilcoxon ChiSq $p < 0.0001$). For this ratio, though their ranges overlap with the meat consuming category, the means of the two non-vertebrate consuming dietary groups (the only statistically indistinguishable dietary pair for this ratio) have significantly relatively longer carnassials than the other two dietary groups. As discussed above, this is probably an effect of phylogeny due to the elongated talonids of the canoid taxa that dominate these dietary categories.

It is worth noting that the two marsupial taxa included in this sample show the opposite pattern than that shown by the eutherians. Namely, the durophagous *Sarcophilus* has relatively short premolars, whereas the hypercarnivorous *Thylacinus* has long ones. This is probably highly influenced by the biomechanical adaptations displayed by these two taxa – namely, *Sarcophilus* has very short jaws (mean of 102.1 ± 8.7 mm, $n = 9$) and therefore more premolar crowding while *Thylacinus* has long jaws (mean of 179.4 ± 19.8 mm, $n = 12$) reflecting possible adaptations for strength (i.e., better leverage) in the durophagous former and for gape (i.e., longer jaws and more linear excursion) in the latter. This pattern is seen in other lineages (e.g., lemurs; Perry and Hartstone-Rose no date).

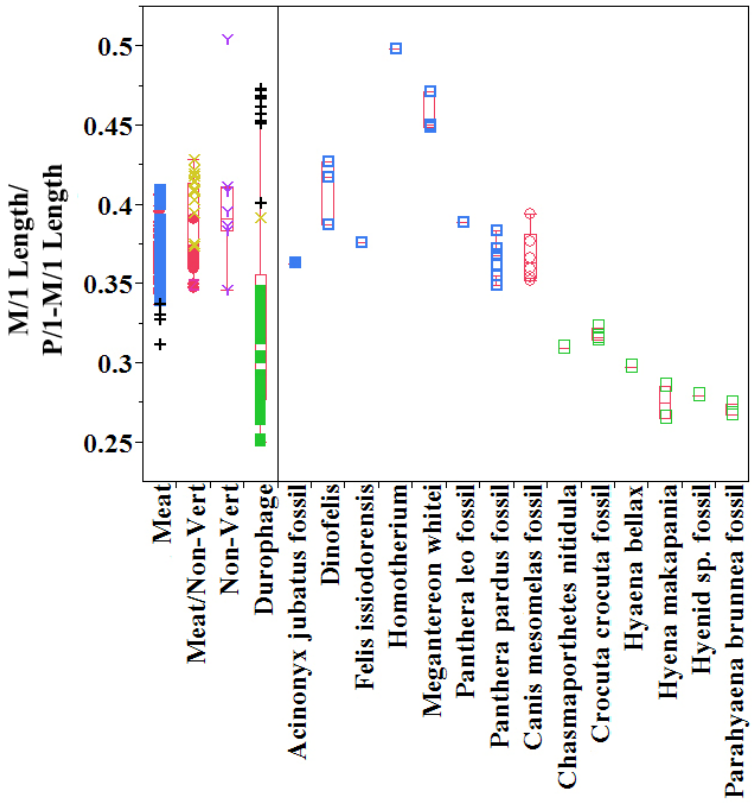

Figure 33: Percent of Premolar-Carnassial Row Dedicated to Carnassial

Carnassial Length divided by sum of all premolar lengths and carnassial length. Modern specimens lumped by dietary category (four groups on left), with fossils (on right). In order to include taxa that lack certain premolars (e.g., felids lack both the P_1 and P_2), lengths of "0" were entered into the equation for these teeth. Symbols as described in Table 7.

When assessing relative carnassial length in fossil specimens, a few interesting patterns emerge. As expected, all of the fossil hyaenids fall within the range of the modern hyaenid sample, just as the fossil members of the extant felids and canids fall with their living representatives. However, the three sabertooth felid taxa for which this ratio can be assessed all fall above the range of the extant felids. This finding adds quantitative support to the commonly recognized phenomenon that sabertooths deemphasize their premolars relative to their highly sectorial carnassials, probably in an

effort to increase the postcanine diastema to accommodate the anteroposteriorly elongated upper canine (Emerson and Radinsky 1980; Hartstone-Rose *et al.* 2007; Palmqvist *et al.* 2007). As such, if we just consider the feloid carnivorans and regard this as a variable describing the durophage-hypercarnivore scale (e.g., Figure 2), then, as hypothesized, this variable places sabertooths as more hypercarnivorous than their extant confamilials.

The P_4 shape ratio (length/width) also clearly separates the means of the dietary categories (Kruskal-Wallis $p < 0.0001$) in a similar way to relative carnassial length (Figure 34) with members of the durophage group having relatively squarer (i.e., more equal width and length) teeth than the members of the meat specialist group (Wilcoxon ChiSq $p < 0.0001$). However, unlike the carnassial-premolar ratio results, there is a clear trend through the four dietary categories with the intermediate dietary categories falling between the two extreme categories as expected. This trend is supported statistically with the meat/non-vertebrate consuming group having statistically squarer premolars than the meat group, and the durophage group having statistically squarer premolars than the meat/non-vertebrate group. However, as was the case for the carnassial-premolar ratio, the two intermediate dietary categories are statistically indistinguishable (though only barely so with a Wilcoxon ChiSq p-value of 0.030, slightly above the comparison-wise error rate of 0.00833), and for this variable, the durophage group is statistically indistinguishable from the non-vertebrate specialist group.

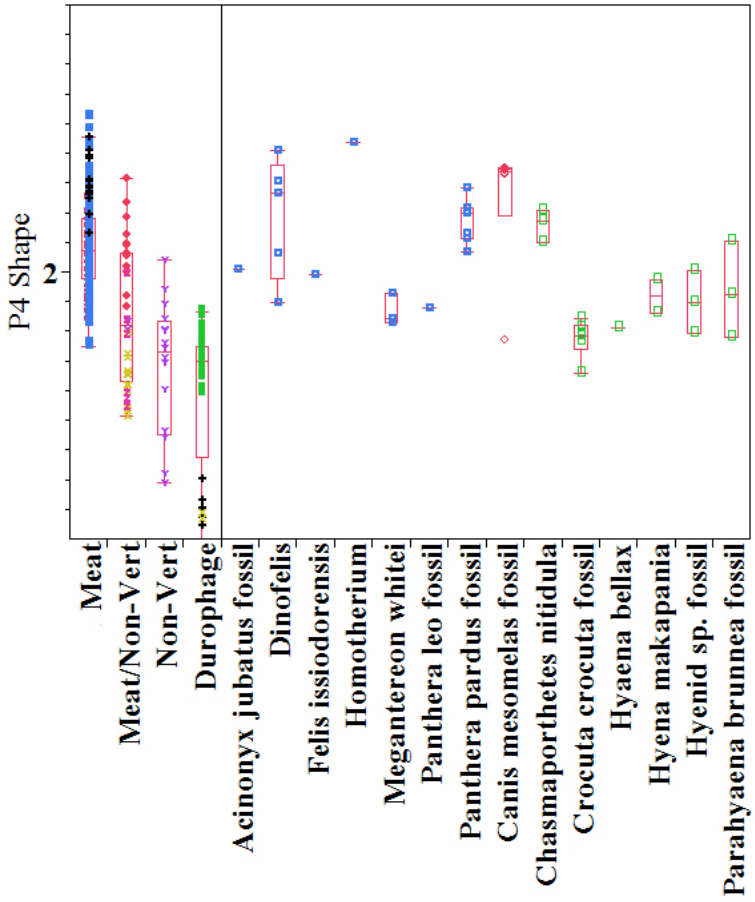

Figure 34: Fourth Premolar Shape

Fourth premolar length divided by width. Modern specimens lumped by dietary category (four groups on left), with fossils (on right). Symbols as described in Table 7.

Upon a more detailed examination of this variable a couple of interesting trends emerge. Unlike what was seen for the carnassial-premolar ratio, the marsupials follow the eutherian trend. That is, *Sarcophilus* overlaps with the durophagous *Enhydra*, and has relatively wider premolars than the durophagous hyaenids, and *Thylacinus* falls within the high end of the hypercarnivorous dietary category. (However, excluding the dasyurids does not affect the significance results.) Also unlike what was found with relative carnassial length, the sabertooths do not fall further along the durophage-

hypercarnivore scale for premolar shape than their confamilial modern felids, but are nested within the modern range.

The most interesting finding for this variable is the position of *Chasmaporthetes*. Namely, as expected, the "hunting hyena" falls closer to the hypercarnivores than it does to its confamilial durophage relatives, and is within the top 50% of the meat specialist range. This is the first linear variable, or ratio thereof, that reflects this hypothesized dietary categorization. The other fossil hyaenids are statistically indistinguishable from the modern hyenas for this variable.

Analyzing the shape of the third premolar (not figured) yields very similar results to those seen for the fourth premolar. The only interesting differences between the result of the two premolar shape comparisons are 1) though *Chasmaporthetes* still has relatively narrow P_3 shapes (slightly higher than most other hyaenids), the difference is no longer statistically significant, and 2) for reasons that are not all together clear, extant jackals (*Canis mesomelas*) have statistically significantly squarer third premolars than their fossil conspecifics. This may be evidence that, as discussed in the previous chapter, the fossils assigned to this species are in fact a different (and probably undescribed) taxon, though why they would appear more hypercarnivorous in this tooth (and not statistically so in their P_4 shape) is unclear.

The Functional units of a tooth…
are the occluding edges or blade tips….
Descriptions of mammalian tooth morphology have only qualitatively referred to the sharpness of the blade tip and the actual sharpness of the edges of mammalian teeth remains unknown.

Popowics and Fortelius 1997; p. 73

CHAPTER 5: Radius-of-Curvature

As discussed in the previous chapter, much can be learned about a carnivore's carcass-processing abilities from basic linear measurements of their teeth. Indeed most studies similar to this one, with the goal of reconstructing dietary behavior of extinct taxa, have relied solely on these type of measurements. However, animals do not process food at the cementoenamel junction, the standard location of the measures of tooth crown length and width, and therefore it is worth considering the relationship between diet and the actual functional components of teeth: the cusp points (the subject of this chapter) and the crests and notches between them (the subject of the next chapter).

No one would dispute the fact that relative to most other carnivorans, hyenas have stout teeth. Indeed this morphology has been correlated with their ability to thoroughly consume nearly every part of a carcass (e.g., Kruuk 1972). However, beyond this ubiquitous subjective recognition of dental robusticity and several standard explorations of tooth dimensions using variables such as tooth width and length (e.g., Van Valkenburgh and Gittleman 1989), no one has thoroughly quantified the geometry of

carnivoran teeth. The standard reliance on tooth width and length as dietary indicators has been augmented by other variables, such as crest length (e.g., Kay 1975), and crown height (e.g., Popowics and Fortelius 1997), but according to one recent paper by some of the leading researchers in the field (Evans *et al.* 2005) quantification of the sharpness of teeth has only been carried out effectively once (in Popowics and Fortelius 1997). Popowics and Fortelius studied the sharpness of the occlusal surface created by occlusal wear on the carnassials.

In this chapter, I attempt to expand on the classic approaches of correlations of diet and linear dental measures (like those explored in the previous chapter) by incorporating radii-of-curvature (ROC) data in the exploration of the relationship between carnivoran dental adaptations and carcass-processing behavior.

The Scaling of Radius-of-Curvature

Before the radii-of-curvature of the postcanine teeth are used to extrapolate the carcass-processing abilities of the fossil carnivores of the South Africa, it is important to understand how occlusal radii scale with body size (Table 12 and Table 13). The problem is that the actual body size is not known for each of the specimens in my study. Instead, regression lines are fitted to data on radii relative to various body-size proxies. Though my data include many suitable and commonly used body-size proxies (including measurements on upper and lower canines and carnassials, various mandibular measurements, etc.), I have decided to consider four of the most commonly used: Jaw

Length, M_1 Length, C_1 Length, and average species Body Weight (split by sex for dimorphic taxa). Sets of regressions were made that included all individuals, and species averages, and all plots are log/log bivariate comparisons of radii, both raw (Table 12) and relative to tooth width (Table 13), and the four body size proxies. Figure 35 is a reduced-major-axis regression of Log P_3 radius regressed on Log C_1 Length including all specimens in the sample. For this analysis of scaling, in an effort to use the most directly measured variable, the log-transformed radii were used instead of their reciprocal "radii-of-curvature." Reduced-major-axis lines were fitted to the entire samples (excluding fossils and marsupials) and to the three target families (felids, canids and hyaenids), and allometry was scored according to whether the resulting slopes fall outside the 95% confidence interval for isometry.

Table 12: Scaling of Occlusal Radii

Log/Log Reduced Major Axis Regressions including all fossil and modern carnivorans ("All Specimens") and species averages excluding fossil taxa ("Species Averages") with equations representing all carnivoran specimens studied (i.e., all lineages studied excluding the marsupials) with individual analyses of the three focal families (canids, felids and hyaenids). Radii (i.e., not ROC, or 1/radius) regressed on four standard body weight proxies: Species average body weight (split sex where dimorphic), lower canine length, mandible length, and lower carnassial length. Allometry of "0" = isometry (RMA slope inside the 95% confidence interval at alpha= 0.05), "+" = positive allometry (RMA slope above the 95% confidence interval at alpha= 0.05), "-" = negative allometry (RMA slope below the 95% confidence interval at alpha= 0.05), "/" = group excluded from regression because it lacks that tooth, or enough members to justify regression.

		All Specimens				Species Averages			
Y-axis (Variable Logged)	**X-axis (Variable Logged)**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**
P_2 Radius	**Jaw Length**								
	- All Carnivorans	1	2.17	0.55	+	1	1.41	0.71	0
	- Canids	1	1.78	0.39	0	1	0.98	0.75	0
	- Felids	/	/			/	/		
	- Hyaenids	1	5.18	0.63	+	/	/		
	M_1 Length	1				1			
	- All Carnivorans	1	2.36	0.26	0	1	1.54	0.53	0
	- Canids	1	1.79	0.31	0	1	0.95	0.59	0
	- Felids	/	/			/	/		
	- Hyaenids	1	-2	-0.25	0	/	/		
	Average Body Weight								
	- All Carnivorans	1	1.69	0.53	+	1	0.56	0.69	0
	- Canids	1	0.69	0.33	0	1	0.34	0.69	-
	- Felids	/	/			/	/		
	- Hyaenids	1	-1.54	-0.42	-	/	/		
	C_1 Length								
	- All Carnivorans	1	1.91	0.67	+	1	1.67	0.80	+
	- Canids	1	1.45	0.38	0	1	0.82	0.66	0
	- Felids	/	/			/	/		
	- Hyaenids	1	3.60	0.23	0	/	/		

		All Specimens				Species Averages			
Y-axis (Variable Logged)	**X-axis (Variable Logged)**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**
P_3 Radius	**Jaw Length**								
	- All Carnivorans	1	1.69	0.53	+	1	1.30	0.61	0
	- Canids	1	1.83	0.31	0	1	1.22	0.58	0
	- Felids	1	1.27	0.64	+	1	0.95	0.83	0
	- Hyaenids	1	3.98	0.58	+	/	/		
	M_1 Length								
	- All Carnivorans	1	1.89	0.45	+	1	1.44	0.58	0
	- Canids	1	1.97	0.32	0	1	1.18	0.72	0
	- Felids	1	1.36	0.63	+	1	1.04	0.88	0
	- Hyaenids	1	-2.35	-0.22	0	/	/		
	Average Body Weight								
	- All Carnivorans	1	0.59	0.39	-	1	0.44	0.52	-
	- Canids	1	0.78	0.37	0	1	0.43	0.72	0
	- Felids	1	0.41	0.64	-	1	0.31	0.88	-
	- Hyaenids	1	-1.44	-0.29	0	/	/		
	C_1 Length								
	- All Carnivorans	1	1.6	0.51	+	1	1.20	0.64	0
	- Canids	1	1.65	0.30	0	1	1.02	0.69	0
	- Felids	1	0.97	0.62	0	1	0.78	0.83	0
	- Hyaenids	1	-3.66	-0.02	0	/	/		
P_4 Radius	**Jaw Length**								
	- All Carnivorans	1	1.38	0.52	+	1	1.14	0.58	0
	- Canids	1	1.50	0.50	0	1	1.22	0.68	0
	- Felids	1	1.13	0.67	0	1	0.84	0.92	0
	- Hyaenids	1	4.57	0.70	+	/	/		
	M_1 Length								
	- All Carnivorans	1	1.57	0.46	+	1	1.27	0.49	0
	- Canids	1	1.53	0.45	0	1	1.18	0.64	0
	- Felids	1	1.28	0.68	+	1	0.92	0.95	0
	- Hyaenids	1	-1.89	-0.10	0	/	/		

		All Specimens				Species Averages			
Y-axis (Variable Logged)	**X-axis (Variable Logged)**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**
P_4 Radius (ctd.)	**Average Body Weight**								
	- All Carnivorans	1	0.47	0.4	-	1	0.36	0.50	-
	- Canids	1	0.63	0.46	0	1	0.43	0.70	0
	- Felids	1	0.35	0.62	-	1	0.27	0.93	-
	- Hyaenids	1	-1.5	-0.28	0	/	/		
	C_1 Length								
	- All Carnivorans	1	1.56	0.55	+	1	0.97	0.65	0
	- Canids	1	1.33	0.45	0	1	1.02	0.66	0
	- Felids	1	0.90	0.66	0	1	0.69	0.91	-
	- Hyaenids	1	3.50	0.22	0	/	/		
Ant M_1 Radius	**Jaw Length**								
	- All Carnivorans	1	1.13	0.47	0	1	0.81	0.72	0
	- Canids	1	2.17	0.30	0	1	1.34	0.68	0
	- Felids	1	0.96	0.62	0	1	0.63	0.95	-
	- Hyaenids	1	3.64	0.06	0	/	/		
	M_1 Length								
	- All Carnivorans	1	1.30	0.49	+	1	0.91	0.70	0
	- Canids	1	2.09	0.29	0	1	1.30	0.73	0
	- Felids	1	1.15	0.57	0	1	0.69	0.93	-
	- Hyaenids	1	2.04	0.27	0	/	/		
	Average Body Weight								
	- All Carnivorans	1	0.40	0.47	-	1	0.26	0.70	-
	- Canids	1	0.84	0.34	0	1	0.47	0.70	0
	- Felids	1	0.31	0.66	-	1	0.20	0.97	-
	- Hyaenids	1	1.37	0.27	0	/	/		
	C_1 Length								
	- All Carnivorans	1	1.06	0.51	0	1	0.72	0.71	0
	- Canids	1	1.78	0.33	0	1	1.12	0.77	0
	- Felids	1	0.80	0.59	0	1	0.52	0.91	-
	- Hyaenids	1	3.01	0.08	0	/	/		

		All Specimens				Species Averages			
Y-axis (Variable Logged)	**X-axis (Variable Logged)**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**	**Expected Slope**	**RMA Slope**	**R**	**Allometry**
Post M_1 Radius	**Jaw Length**								
	- All Carnivorans	1	1.15	0.40	0	1	0.87	0.72	0
	- Canids	1	1.76	0.33	0	1	1.01	0.78	0
	- Felids	1	1.10	0.52	0	1	0.67	0.94	-
	- Hyaenids	1	3.73	0.25	0	/	/		
	M_1 Length								
	- All Carnivorans	1	1.23	0.37	0	1	0.93	0.60	0
	- Canids	1	1.70	0.52	+	1	0.98	0.95	0
	- Felids	1	1.19	0.44	0	1	0.73	0.91	0
	- Hyaenids	1	-2.03	-0.26	0	/	/		
	Average Body Weight								
	- All Carnivorans	1	0.38	0.48	-	1	0.28	0.78	-
	- Canids	1	0.69	0.42	0	1	0.35	0.91	-
	- Felids	1	0.34	0.67	-	1	0.22	0.95	-
	- Hyaenids	1	-1.29	-0.38	-	/	/		
	C_1 Length								
	- All Carnivorans	1	1.02	0.40	0	1	0.76	0.69	0
	- Canids	1	1.45	0.41	0	1	0.84	0.95	0
	- Felids	1	0.86	0.49	0	1	0.55	0.89	-
	- Hyaenids	1	3.01	0.25	0	/	/		

Table 13: Scaling of Relative Occlusal Radii

Same as Table 12 except for dimensionless ratios radii/tooth width. Since the magnitude of the slope of regression of a dimensionless variable has no meaning, only the sign of the correlation coefficient is included (if statistically different than isometry) in the "Allometry" column.

		All Specimens		Species Averages	
Y-axis (Variable Logged)	X-axis (Variable Logged)	Expected Slope	Allometry	Expected Slope	Allometry
Rel P_2 Radius	**Jaw Length**				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	/	/	/	/
	- Hyaenids	0	0	/	/
	M_1 Length				
	- All Carnivorans	0	-	0	0
	- Canids	0	-	0	0
	- Felids	/	/	/	/
	- Hyaenids	0	-	/	/
	Average Body Weight				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	/	/	/	/
	- Hyaenids	0	-	/	/
	C_1 Length	0		0	
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	/	/	/	/
	- Hyaenids	0	0	/	/
Rel P_3 Radius	**Jaw Length**				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	0	0	0	0
	- Hyaenids	0	0	/	/
	M_1 Length				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	0	0	0	0
	- Hyaenids	0	-	/	/
	Average Body Weight				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	0	0	0
	- Hyaenids	0	-	/	/
	C_1 Length				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	0	0	0	0
	- Hyaenids	0	0	/	/

		All Specimens		Species Averages	
Y-axis (Variable Logged)	**X-axis (Variable Logged)**	**Expected Slope**	**Allometry**	**Expected Slope**	**Allometry**
Rel P_4 Radius	**Jaw Length**				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	+	/	/
	M_1 Length				
	- All Carnivorans	0	0	0	0
	- Canids	0	-	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	0	/	/
	Average Body Weight				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	-	/	/
	C_1 Length				
	- All Carnivorans	0	0	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	0	/	/
Rel Ant M_1 Radius	**Jaw Length**				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	0	/	/
	M_1 Length				
	- All Carnivorans	0	-	0	-
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	0	/	/
	Average Body Weight				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	0	/	/
	C_1 Length				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	-Hyaenids	0	0	/	/

		All Specimens		Species Averages	
Y-axis (Variable Logged)	**X-axis (Variable Logged)**	**Expected Slope**	**Allometry**	**Expected Slope**	**Allometry**
Rel Post M_1 Radius	**Jaw Length**				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	0	/	/
	M_1 Length				
	- All Carnivorans	0	-	0	-
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	-	/	/
	Average Body Weight				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	- Hyaenids	0	-	/	/
	C_1 Length				
	- All Carnivorans	0	-	0	0
	- Canids	0	0	0	0
	- Felids	0	-	0	-
	-Hyaenids	0	0	/	/

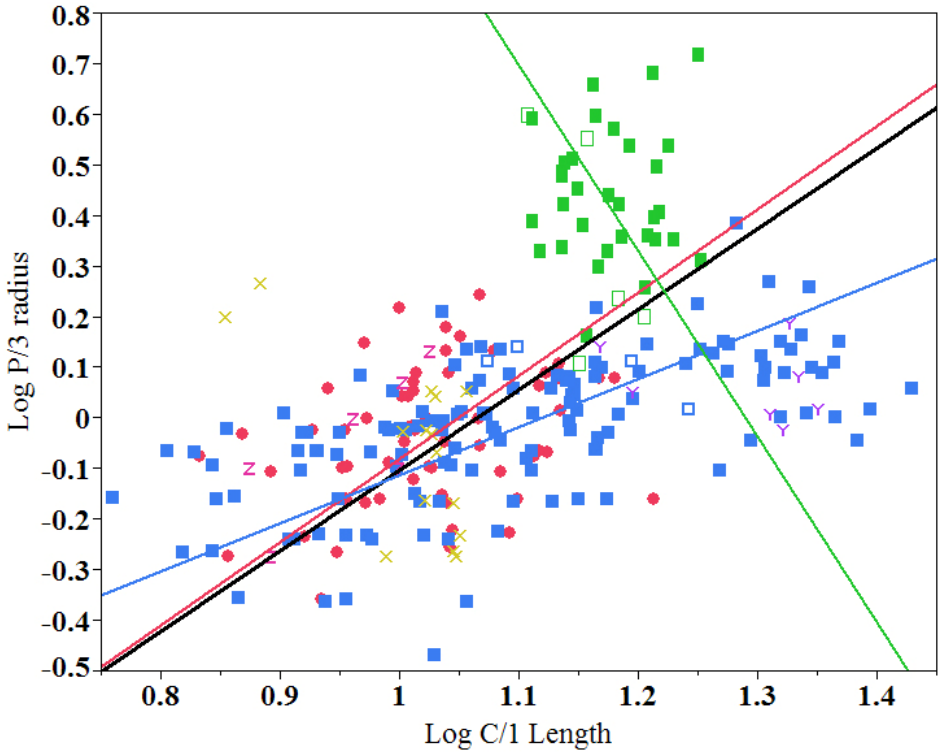

Figure 35: RMA log/log regression of P/3 Radius on C/1 Length – all specimens.

Fossils are included for graphical purposes but were excluded from regression calculations. Black, red, blue and green lines are RMA regression lines for all carnivorans, canids, felids and hyaenids respectively. Symbols as described in Table 7.

Regressions including all individuals (rather than only examining species averages) were studied because for some lineages (e.g., hyenas) and dietary categories (e.g., durophages, nearly synonymous with "hyenas" though also including among the Carnivora, *Enhydra*) contain too few taxa to yield meaningful results. With that said, regressions including all individuals are obviously biased by inequality in sampling, though, again, other biases occur in the species-average regressions because some lineages contain more species, and these lineages were more widely sampled.

There appear to be scaling patterns both in the raw data (beyond the simple recognition that larger taxa have larger radii) and the relative data. Overall, of the 152 lines of regression studied including all individuals (both raw and relative radii for the total sample and for each of the three focal lineages; Table 12), 60 of the derived slopes (or 39.5%) are statistically different from isometry. Of these, 18 (11.8%) are positively allometric and 42 (27.6%) are negatively allometric. More than half of the allometry in the sample (55%) is found in the relative radii data. In other words, carnivorans tend to have narrow teeth for their body size.

Examining these trends further, most of the positively allometric variables (16 of the 18) are the raw premolar radii and most of the negatively allometric variables (32 of 42) are the relative radii. This suggests that larger carnivores have relatively blunter premolars than smaller animals, though their teeth are also relatively wider (the denominator used to calculate the relative radius). In other words, though larger carnivores have blunter teeth than expected for their body-size proxies, they are sharper than expected relative to the overall width of their teeth.

Twenty-five of the significantly allometric trends (41.7%) – ten positive and 15 negative – correspond to the regressions of all carnivorans. The felids show almost as many significant allometric trends (three positive and 16 negative, or 31.7% of the allometry in the sample). These findings suggest that sample size is having an effect in the significance of these findings: the most significant allometry is found in the regression encompassing the total sample, and the second most numerous allometric trends are found in the largest subset of the total sample. Contrary to this, the hyaenids

display more numerous allometric trends than the canids (13 and three variables respectively) though fewer total individuals were included in the study (87 and 98) respectively. Furthermore, the magnitude of allometry was much higher in the hyaenids, with several variables deviating by more than three times the expected slope, and one (P_2 radius regressed on jaw length) having a slope 5.18 times higher than expected ($H_0 = 1$). While hyaenids are anomalous in many aspects of their dental anatomy, this finding is probably a statistical anomaly: all of the individuals in this sample are representatives of the three extant durophagous species, a set of taxa representing a very narrow size range – much narrower than that encompassed by the canid and felid samples in this study. (As noted in the third chapter, the only relatively small bodied hyaenid, the aardwolf, *Proteles cristatus*, 9-14 kg [Nowak 2005], was excluded from the study because it is a highly derived insectivore, with extremely reduced and vestigial postcanine dentition.) Thus, the x-axis for this lineage is very constrained, and this sample is biased by intraspecific effects introduced by the necessary reliance on the small number of species.

To address all intraspecific effects in this whole sample approach, a brief examination of the scaling of these variables using species averages is warranted. As such, the scaling of radii was also studied using only (sex pooled) species averages. These data are also presented in Table 12 with an example of the same RMA regression variables as presented in Figure 35 for all specimens, here restricted to species averages (Figure 36). Though the fossil taxa were included in the "all specimens" regressions, their small sample sizes did not have a strong effect on the slopes of the regressions. However, though the fossil taxa in the whole study are represented by relatively few

intraspecific samples (i.e., many more modern *Crocuta* than fossil *Chasmaporthetes* are included in the whole study), in these "species average" regressions, the inclusion of their taxonomic diversity would have a very large effect on the slopes of the lines. As such, they were excluded from these "species average" analyses.

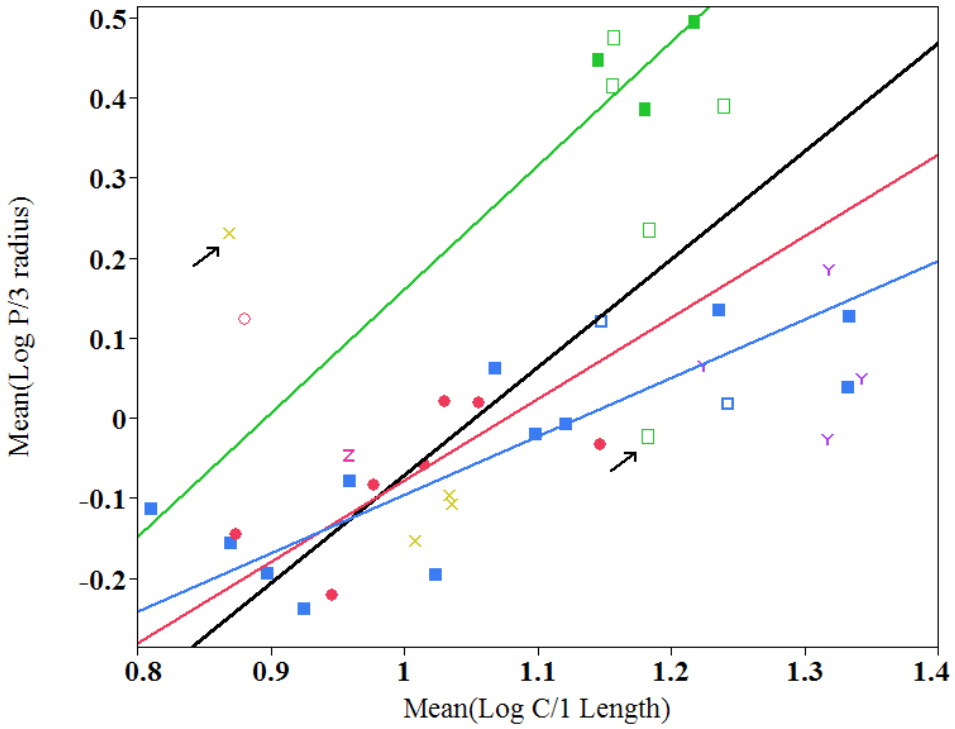

Figure 36: RMA log/log regression of P/3 Radius on C/1 Length – species averages.

Note the relatively high position of *Enhydra* (top arrow) and the relatively low position of *Chasmaporthetes* (bottom arrow). These will be discussed later in this chapter. Calculations and lines same as Figure 35. Regression line is shown for hyaenids for graphical purposes, but is excluded from Table 12 because of the small intrafamilial sample size. Symbols as described in Table 7.

As expected, the results are very similar to the "all specimens" analyses. (By design, care was taken to balance the numbers of taxa and specimens within families and dietary categories wherever possible.) However, also as expected, the reduced number of

data points also reduces the number of significant results – only 20.4% of the total number of species average regressions (down from 39.5% in the all specimen regressions) are significantly different from isometry. However, the reduction of data also yielded, in most cases, higher coefficients of correlation for most of the comparisons. All but one of the non-isometric regressions using species averages are negatively allometric.

Carcass-Processing Correlates of Radius-of-Curvature

While valuable information about the function of radii-of-curvature can be gathered from examination of how these variables scale across body sizes, the real importance of a study of radii-of-curvature in the context of this dissertation is, of course, an examination of how these variables correlate with the carcass-processing behavior of modern carnivorans. When the radii-of-curvature (ROC) for all of the extant carnivorans are compared (Figure 37) several trends emerge. (The marsupials were excluded from this analysis because of their peculiar results as can be seen the subsequent figures and the discussion following them.) The overarching revelation is that the radius-of-curvature accurately quantifies the subjective impression that durophage premolars are very blunt (have low ROC), and all of the other carnivorans studied are much more similar to each other in their dental morphology. This result is significant (using a comparison-wise alpha of 0.0125) for all dietary categories paired with the durophages

except for the carnassial protoconid ROC comparison of the durophages and non-vertebrate specialists. Furthermore, the other three dietary categories are statistically indistinguishable with the exceptions of the meat/non-vertebrate and non-vertebrate dietary categories (which are statistically distinct in the carnassial protoconid ROC comparison), and the meat and non-vertebrate dietary groups which are statistically separable in both carnassial radii. In other words, all four of these radii-of-curvature separate the durophage specialists from the meat specialists, and do a fairly good job separating the intermediary dietary categories from the durophage consumers as well.

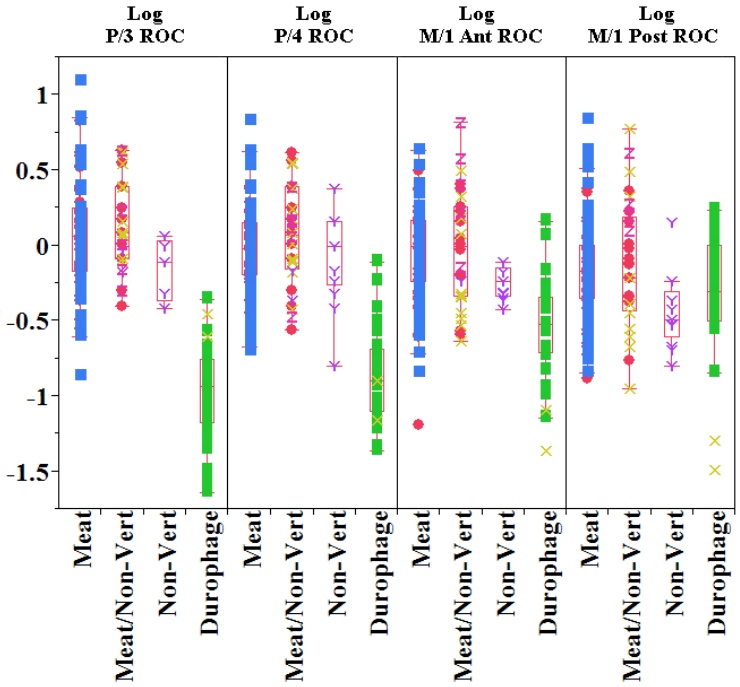

Figure 37: Radii-of-Curvature By Dietary Category

In Log mm with box plots for (from left to right) P_3, P_4, M_1 Paraconid (Ant) and Protoconid (Post). Symbols as described in Table 7. Extant specimens only. Excluding marsupials for reasons discussed in the text. First and second premolars were excluded from analysis to maximize specific diversity within the samples.

The other overarching interesting revelation that the quantification of radius-of-curvature exposes is that the radii of more mesial teeth correlate more tightly with carcass-processing ability. That is, durophage specialists are separated further from non-durophage consumers in the third premolars than in their fourth, and in their fourth than in their anterior carnassial, and in their anterior carnassial than in the posterior carnassial cusp. This can be seen by the increasing proximity of the green and blue bands in the sequence of figures on the following pages.

This phenomenon makes sense in the context of the differential use of the teeth: hyenas use their premolars for crunching bone, but, like other carnivores, they use their carnassials for slicing flesh. Though they sometimes violate this pattern and use their carnassials for rare durophagy (Van Valkenburgh 1985, 1996), this is probably accidental. Even so, this occasional mistake could account for the fact that the anterior cusps of the carnassials are more rounded than their posterior cusps – it is probably more likely, that if hard objects are brought into carnassial occlusion accidentally, they will more often come into contact with the anterior cusp (the cusp closer to the target premolars) than the posterior cusp.

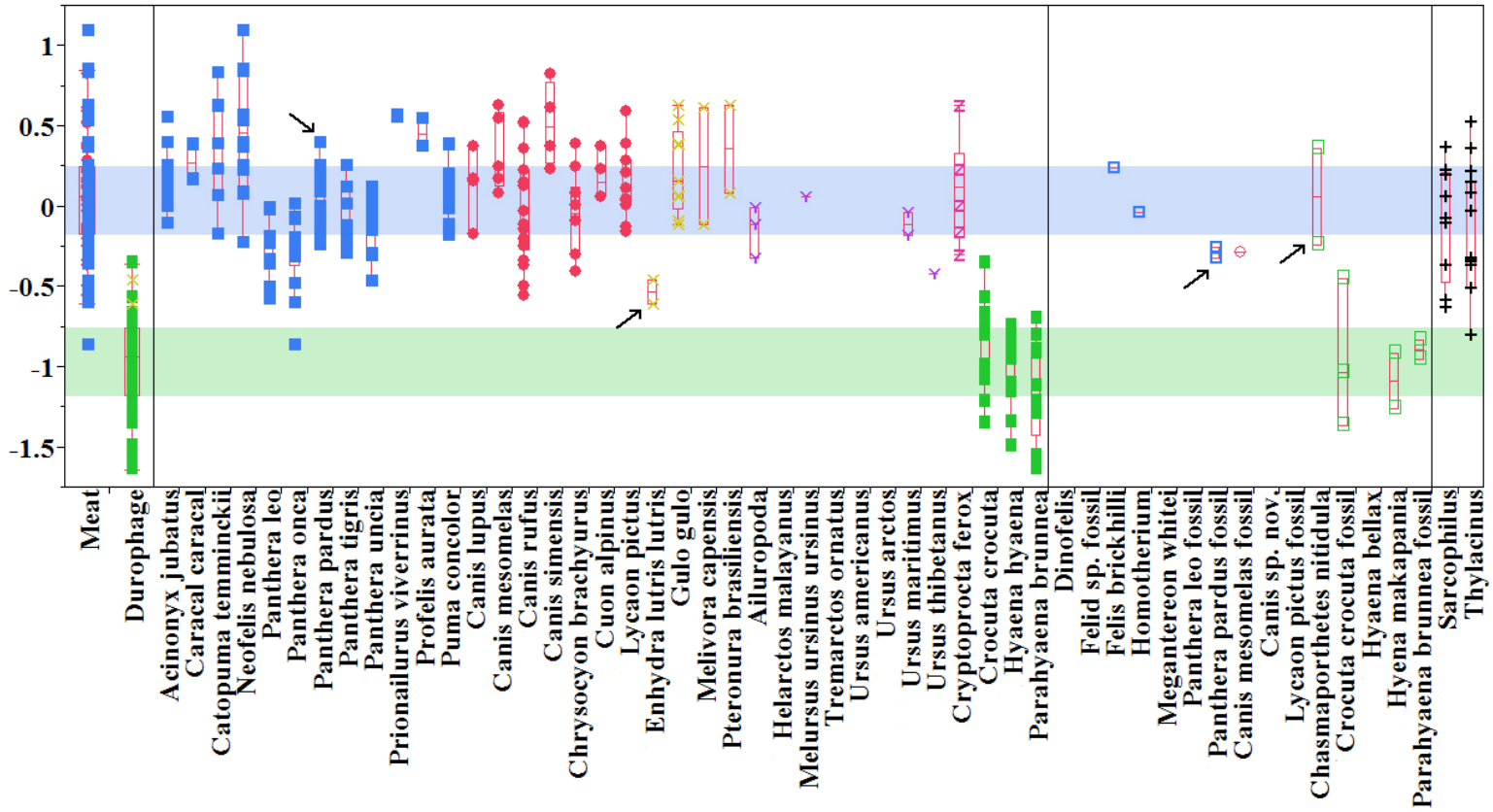

Figure 38: P_3 Radius-of-Curvature

In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens and marsupials. Arrows highlight *Enhydra*, *Chasmaporthetes*, and fossil and modern *Panthera pardus*, and are discussed in text. Green and blue bands delineate 50th percentile of Durophage and Meat groups respectively. Symbols as described in Table 7.

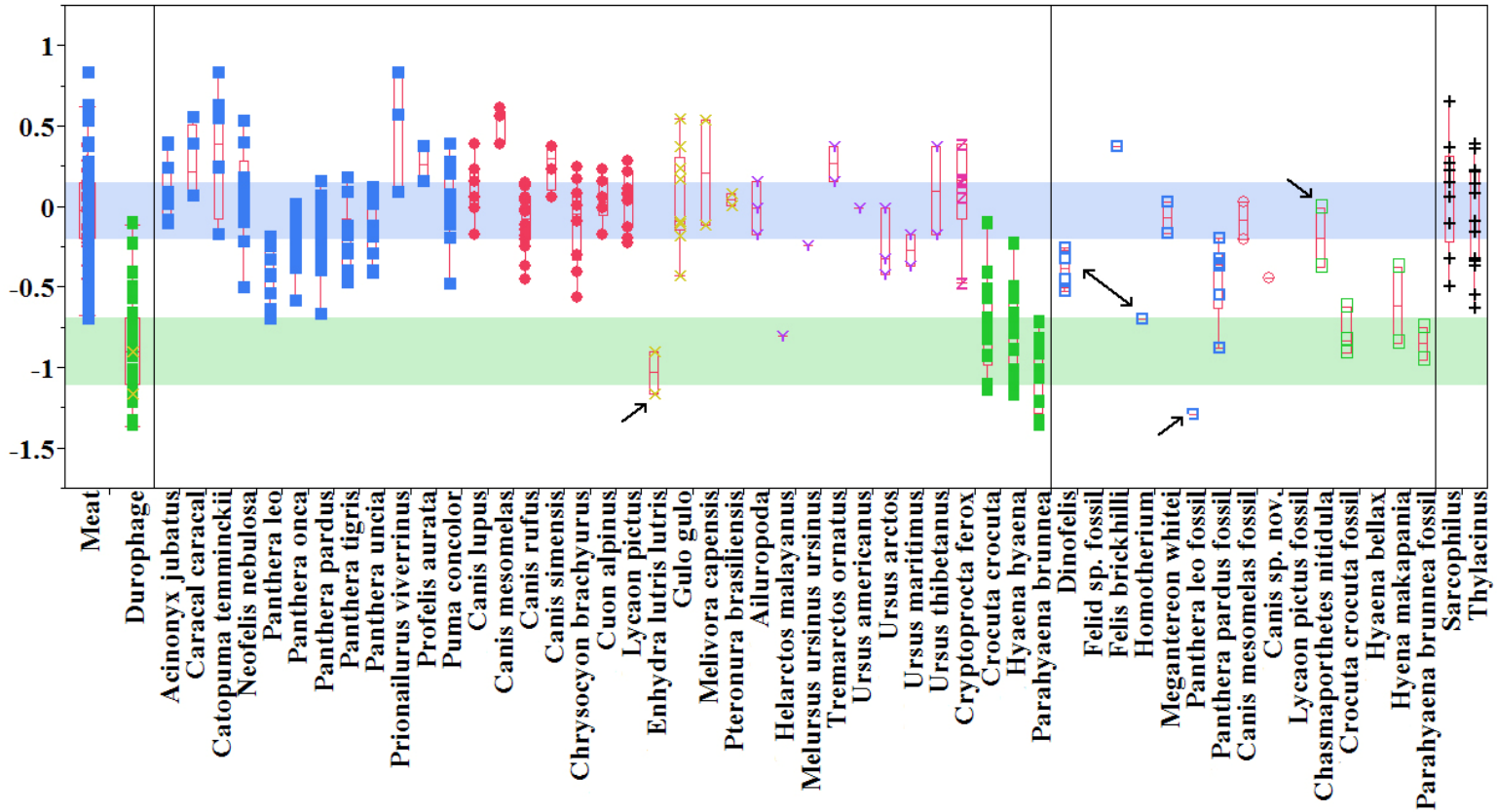

Figure 39: P_4 Radius-of-Curvature

In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens and marsupials. Arrows highlight *Enhydra*, *Chasmaporthetes*, *Dinofelis*, *Homotherium* and fossil *Panthera leo*, and are discussed in text. Green and blue bands delineate 50th percentile of Durophage and Meat groups respectively. Symbols as described in Table 7.

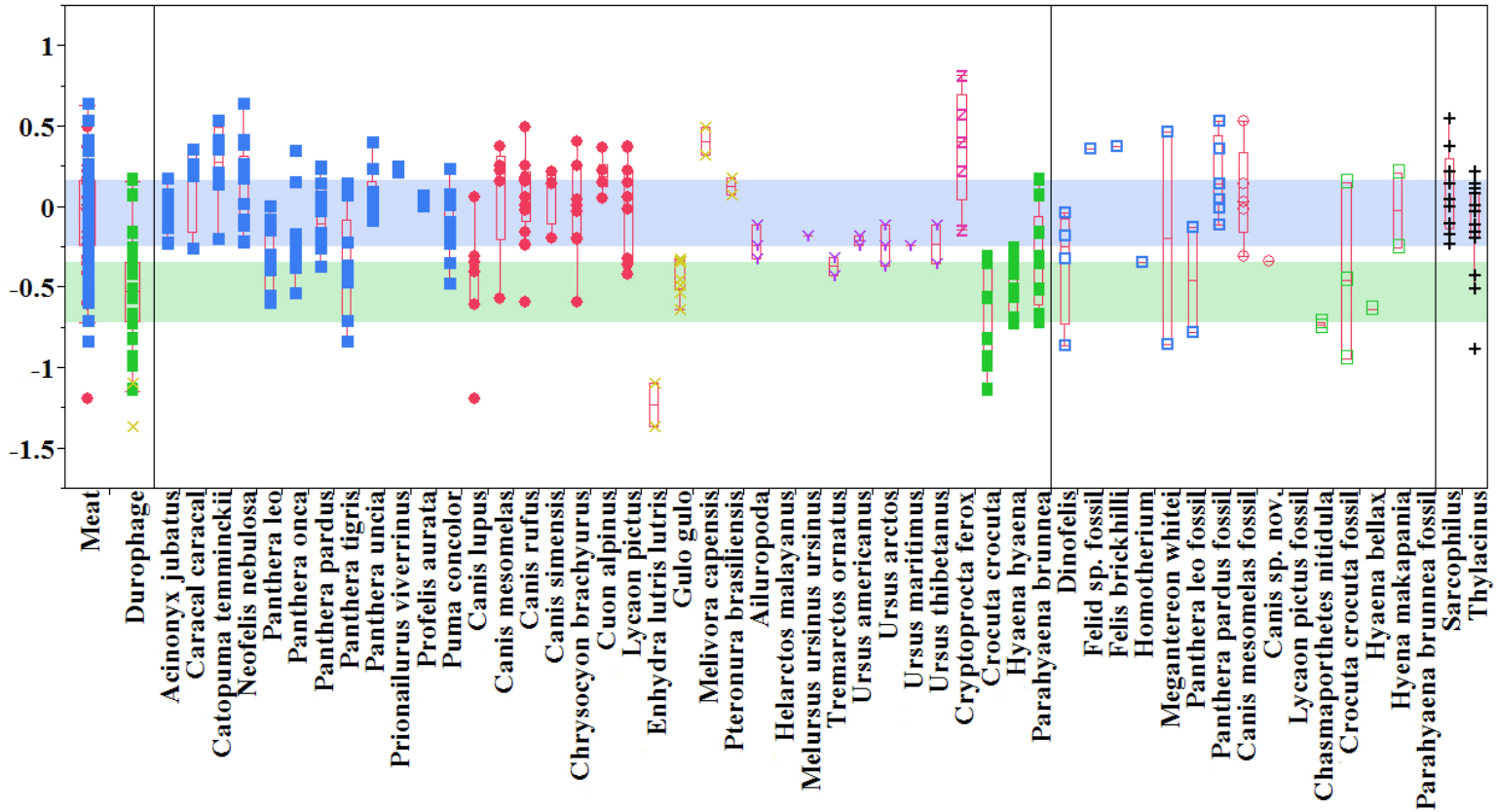

Figure 40: M_1 Anterior Radius-of-Curvature

In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens and marsupials. Green and blue bands delineate 50th percentile of Durophage and Meat groups respectively. Symbols as described in Table 7.

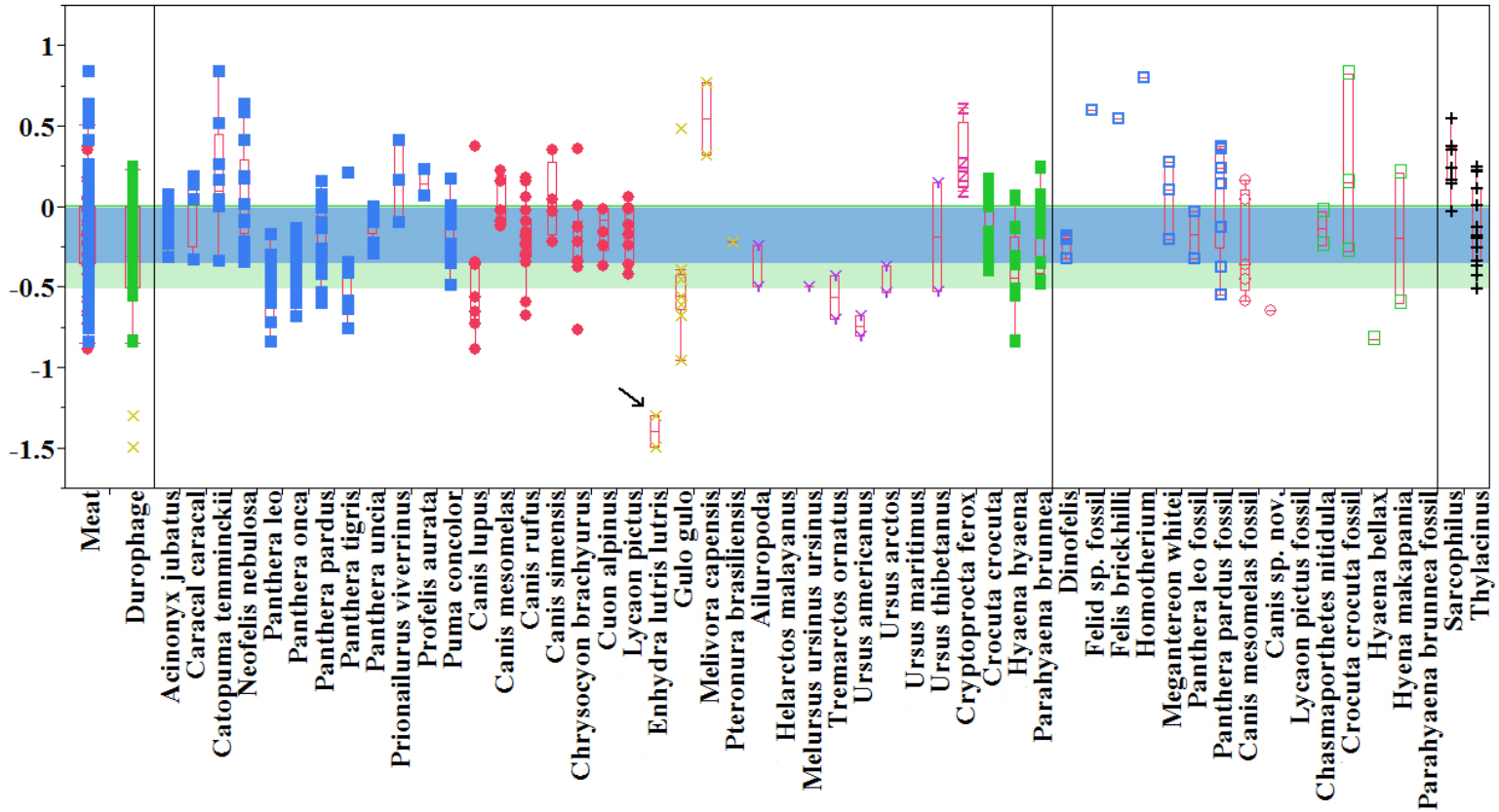

Figure 41: M_1 Posterior Radius

In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens and marsupials. Arrow highlights *Enhydra*, and is discussed in text. Green and blue bands delineate 50th percentile of Durophage and Meat groups respectively. Symbols as described in Table 7.

Though the significant differentiation of durophages from other dietary groups and the decreasing differentiation further back on the tooth row are the strongest and most obvious broad trends, these data capture other interesting and more subtle signals. For instance, the largest species of modern hyena (*Crocuta crocuta*) has significantly sharper premolars (including P_2, not shown) than its extant relative *Parahyaena brunnea*. These taxa are sympatric across much of their ranges and this occlusal anatomy could reflect subtle niche partitioning. Likewise, the similarly sized lions and tigers (*Panthera leo* and *P. tigris* respectively) have significantly different P/3 radii-of-curvature, suggesting that lions are capable of more hard-object feeding. Their new-world congener, the jaguar (*P. onca*), a known hard-object feeder (Emmons 1989), though being much smaller than them in body mass, also has statistically larger third premolar radii (and therefore lower ROC) than tigers.

Another obvious trend among the extant taxa is that *Enhydra* (marked by an arrow in Figures 36 and 38-40) consistently has very blunt teeth. What is most interesting about their radii-of-curvature is that, unlike the durophagous hyenas, the durophagous sea otters maintain the very blunt ROC all the way through their carnassials as well. This is probably a phylogenetic phenomenon as *Enhydra* is a member of the canoid clade, which, unlike the hyaenids (and their fellow feloids) is known to use its molars for hard-object feeding. However, this trend is not seen in the canids in the sample, which maintain a sectorial carnassial and use the postcarnassial molars for crushing (Van Valkenburgh 1996). This incorporation of the carnassial into the crushing

function is evidence that *Enhydra* is even more specialized for durophagy than are the hyaenids.

The last pattern seen in the extant species worth mentioning is that demonstrated by the marsupials. Simply put, they do not follow the carnivoran pattern for ROC – the durophagous *Sarcophilus* does not have blunter teeth than the hypercarnivorous *Thylacinus*. In fact, it has sharper teeth, on average, and statistically so for the M_1 protoconid radius. While trends like this can be influenced by differences in the size of pairs (ROC is derived from linear radius measurements that are not size-corrected), even when a scaled correction of ROC is applied (e.g., various divisions of radius by tooth width, or other body mass proxies), if anything, *Thylacinus* has blunter teeth than *Sarcophilus*, though in most cases they are statistically indistinguishable. It is not clear why this durophagous taxon has not converged on this aspect of carnivoran dental geometry when it has modified its masticatory apparatus in other ways that are very reminiscent of hard-object feeding eutherians (e.g., very broad teeth as discussed in the previous chapter). Suffice it to say, in terms of the radii-of-curvature of the postcanine dentition, as it relates to carcass-processing ability, marsupials and eutherians appear to be very different. While an exploration of this phenomenon with broader taxonomic diversity would be interesting, it will be hard to overcome the fact that these are the only medium or large carnivorous marsupial taxa, and this morphology is very different in small (generally high crested) carnivores that incorporate insects as a large component of their diet.

Other expected patterns, for instance subtle dietary differences within families (e.g., the more hypercarnivorous *Ursus maritimus*, or less hypercarnivorous *Canis mesomelas* or *Chrysocyon* within the bears and dogs respectively) were not obvious in these examinations of ROC or any other analyses (e.g., those that took body size into account; not shown) of dental occlusal radii, though the pattern within the mustelids may hint at one. Therefore, many of the clear differences within this morphology are seen at the family level, and greater sample sizes would be needed to tease out more subtle variation within the extant lineages.

ROC Implications for Deducing Carcass-Processing Behavior of Fossil Carnivorans

The inclusion of the fossil taxa is where the picture becomes truly interesting. For instance, though almost all of the fossil hyena specimens (*Hyaena bellax, H. makapania* and fossil members of extant *H. brunnea, Crocuta* and *Parahyaena*) fall neatly within the premolar ROC ranges of modern hyenas, the "hunting hyena," *Chasmaporthetes* (marked by arrows in Figure 38 and Figure 39), falls squarely within the "meat-eating" category. This confirms the hypothesis that this taxon was a hypercarnivorous member of the durophagous lineage, and that the other fossil members of the lineage had carcass-processing abilities similar to their modern relatives. Thus, *Chasmaporthetes* falls within its supposed functional group and not within its phylogenetic group. In its occlusal morphology, function has dominated over phylogeny.

The other important revelation is that, in several cases, the fossil members of extant taxa are more dentally robust than their living relatives. Specifically, the

premolars of fossil leopards, *Panthera pardus*, are statistically blunter (have lower ROC) than are those of their modern conspecifics. Likewise, though the fossil samples are too small to statistically differentiate, the premolars of fossil lions, *P. leo*, and jackals, *C. mesomelas*, also appear blunter than the modern members of their species. This could suggest that these taxa were forced into less desirable dietary niches due to the more speciose carnivore guild of which they were a part. This hypothesis has been used to explain greater incidence of tooth breakage in other species-rich fossil carnivore guilds (e.g., Van Valkenburgh and Hertel 1993).

These findings might be taken as evidence that the fossil members of modern taxa were being forced into more durophagous niches because the hypercarnivorous niches were occupied by the several species of sabertooths. While this may be broadly true (see chapter 7), it cannot be supported by this morphology in particular because a couple of the sabertooth taxa (namely *Dinofelis* and *Homotherium*; arrows in Figure 39) actually have rather blunt teeth, contrary to the hypothesis that their teeth should exhibit the hypercarnivorous sectorial pattern. With that said, some sabertooths (e.g., *Megantereon*) do display a large ROC, as expected, and none of the sabertooth sample sizes are large enough to make any statistically strong conclusions.

Wild dogs are expected to crunch bones primarily with their postcarnassial molars and avoid damage to their cutting blades. The probable function of their premolars is unclear.

Van Valkenburgh 1996 p. 242

CHAPTER 6: Intercuspid Notches

Premolars have long been recognized as functioning as tools for crushing (Kruuk 1972) or puncturing (Biknevicius and Van Valkenburgh 1996) in carnivorans in which these teeth are broad, stout, and conical (e.g., hyenas and most dogs). However, many carnivorans (e.g., cats and hunting dogs) have high crowned, sectorial premolars with geometries not well suited for crushing and puncturing, and these species have generally been ignored in the discussion of premolar function, or described as having premolars so mysteriously shaped as to be maladaptive for the general function normally performed by premolars (Van Valkenburgh 1996). These studies miss the fact that in many carnivorans, the premolars have been modified into sharp, sectorial geometries, with deep intercuspid notches, and some of these premolars are so sectorial and notched that they may even function as accessory carnassials.

In this chapter, I test the hypothesis that the number and magnitude of the intercuspid notches correlates with carcass-processing abilities, with taxa that have more heavily notched teeth specializing in hypercarnivory and species with less notched teeth specializing in greater durophagy.

As described in chapter 3, each intercuspid notch of each mandibular premolar of each specimen was scored from 0-5 with "0" assigned to teeth with no intercuspid notches, "1" assigned to a barely present minor accessory cuspid, "2" assigned to a notch formed by the confluence of two dull (i.e., > ca. 45˚) crests, "3" assigned to a notch formed by one dull and one sharp (i.e., < ca. 45˚) crests, "4" assigned to a confluence of two sharp crests and "5" assigned to a "*carnassiform*" notch (Figure 26 and its caption for an explanation of this term). The result is two types of data: information about the number of intercuspid notches on each premolar (the same as the total number of accessory cuspids) and the magnitude of those notches. Before analysis, the notch scores were converted to ranks.

Data were analyzed with several levels of pooling: from analysis of single notches to summation of notch magnitudes through multiple teeth. The following are results of analyses of third and fourth premolar notches. As was the case with the ROC analyses (from the previous chapter), analyses were relegated to these teeth so that the maximum number of taxa could be included in all analyses given that many of the taxa (e.g., felids) lack first and or second premolars.

Intercuspid Notch Correlation With Carcass-Processing Behavior

Many intercuspid notch counts, scores and sums thereof could be tested for correlation with carcass-processing abilities, but in this chapter I will focus on six: the score of the main notch (explained below), the number of notches, and the sum of all of

the notch scores on the fourth premolar as well as those same three variables summed for both the third and fourth premolar. The fourth premolar was chosen as the focal tooth because it has the most variation in notch number and scores (i.e., this tooth displays the maximum range of 0-4 notches, each with scores from 0-5, with a sum total observed score of 0-15). The third premolar was added to this because it has the next most variation. The "main notch," or first (anterior-most) distal notch, is the notch found between the paraconid and the anterior-most distal accessory cuspid (Figure 42). This intercuspid notch consistently has the highest score in each individual with the maximum inter-individual score range (0-5), and is thus the optimal choice for analysis if only a single intercuspid notch score is desired.

Figure 42: Definition of "Main Notch"

The "main" or first distal notch , is that found between the paraconid and first distal accessory cuspid, here shown on the fourth premolar of a red wolf, *Canis rufus*, USMN 246552.

Marsupials were excluded from these analyses for two reasons: 1) their intercuspid notches have slightly different forms than those found in the eutherian

carnivores, and as such I am not convinced that applying the same scoring scale to them truly reflects the same ontogenetic and evolutionary trends that I believe I am seeing in the carnivorans. Furthermore, 2) as was seen in the similarity between the two taxa in terms of their radii-of-curvature, both dasyurids display very similar intercuspid notch numbers and scores (both relatively low; e.g., Figure 17) and as such, their inclusion in the intercuspid notch comparisons would serve only to bring the hypercarnivore and durophage dietary categories closer together, thus diluting the carnivoran-only signal. As was the case with the radii-of-curvature data, the intercuspid notch data would seem to argue that something very different is going on with the carcass-processing morphology of carnivorous eutherians and marsupials.

While combining intercuspid notch variables is statistically questionable for the reasons discussed above, all of the six groupings yield very similar results, but as predicted, those with more variation (i.e., those with combined data) yield more subtle patterns (Figure 43). Specifically, in all six dietary comparisons, the hypercarnivorous group is statistically different from the durophagous group, with the former being, as predicted, "notchier" (i.e., having more notches and higher scoring notches) than the latter. Unlike what was seen in the results of the ROC analyses, the two more omnivorous dietary categories are morphologically closer to the durophagous than to the hypercarnivorous group, and in fact, have statistically less extreme (i.e., less "notchy") intercuspid notches for all six comparisons except for notch number (the comparison second from the left in Figure 43). In none of these six comparisons can these two intermediate dietary categories be statistically separated from each other.

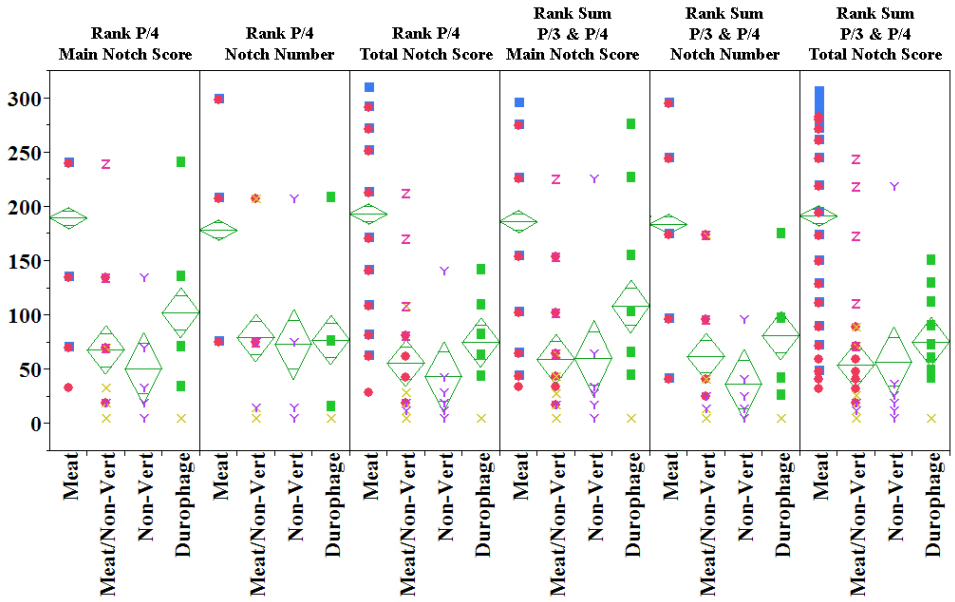

Figure 43: Intercuspid Notch Correlates of Carcass-Processing Behavior

Ranked intercuspid notch data by dietary category with mean diamonds. Ranked data from left to right: P_4 first distal accessory cuspid score, number of notches on the P_4, sum of all P_4 notch scores, and the same three with data summed for both the P_3 and P_4. Symbols as described in Table 7.

The reason that the two non-vertebrate consuming dietary categories fall below the mean notch ranks of the durophage group is obvious when these variables are examined on a species-by-species basis (e.g., figures below). Simply put, as was the case with Van Valkenburgh's relative blade-length ratio (discussed in chapter 4), notch score variables contain a phylogenetic signal: feloid taxa consistently have more notches and higher notch scores than canoid taxa, and as was seen in the Van Valkenburgh results, the two most extreme dietary categories are dominated by members of the former while the intermediate categories are dominated by members of the latter. However, unlike Van Valkenburgh's RBL ratio, though these variables are influenced by phylogeny, the stronger signal appears to be functional.

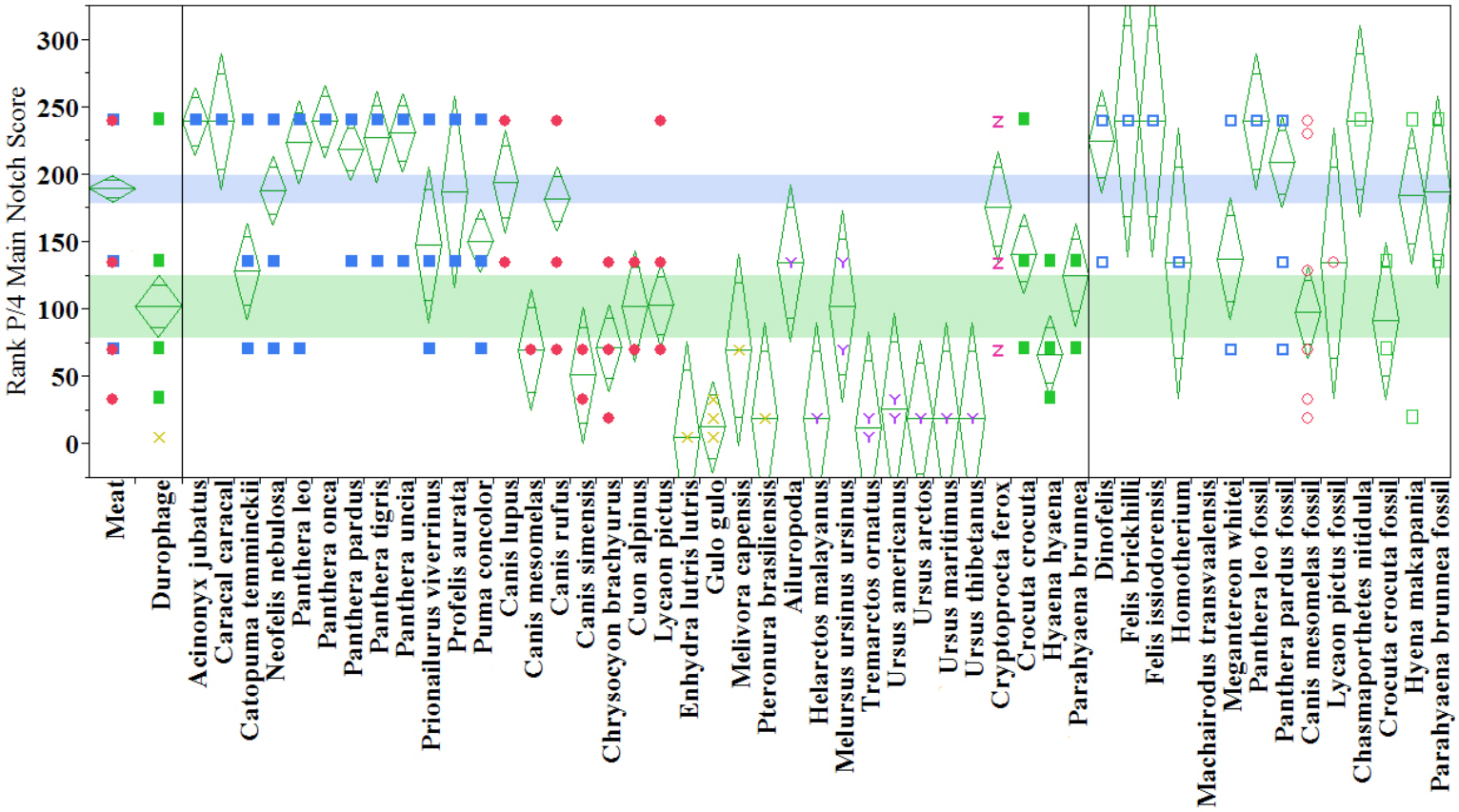

Figure 44: Rank of the P_4 First Distal Accessory Cuspid Scores

Ranked intercuspid notch data with Mean Diamonds. Boxes from left to right: two most divergent dietary categories, modern carnivorans, and fossil specimens. Green and blue bands delineate 95% mean confidence interval of Durophage and Meat groups respectively. Symbols as described in Table 7.

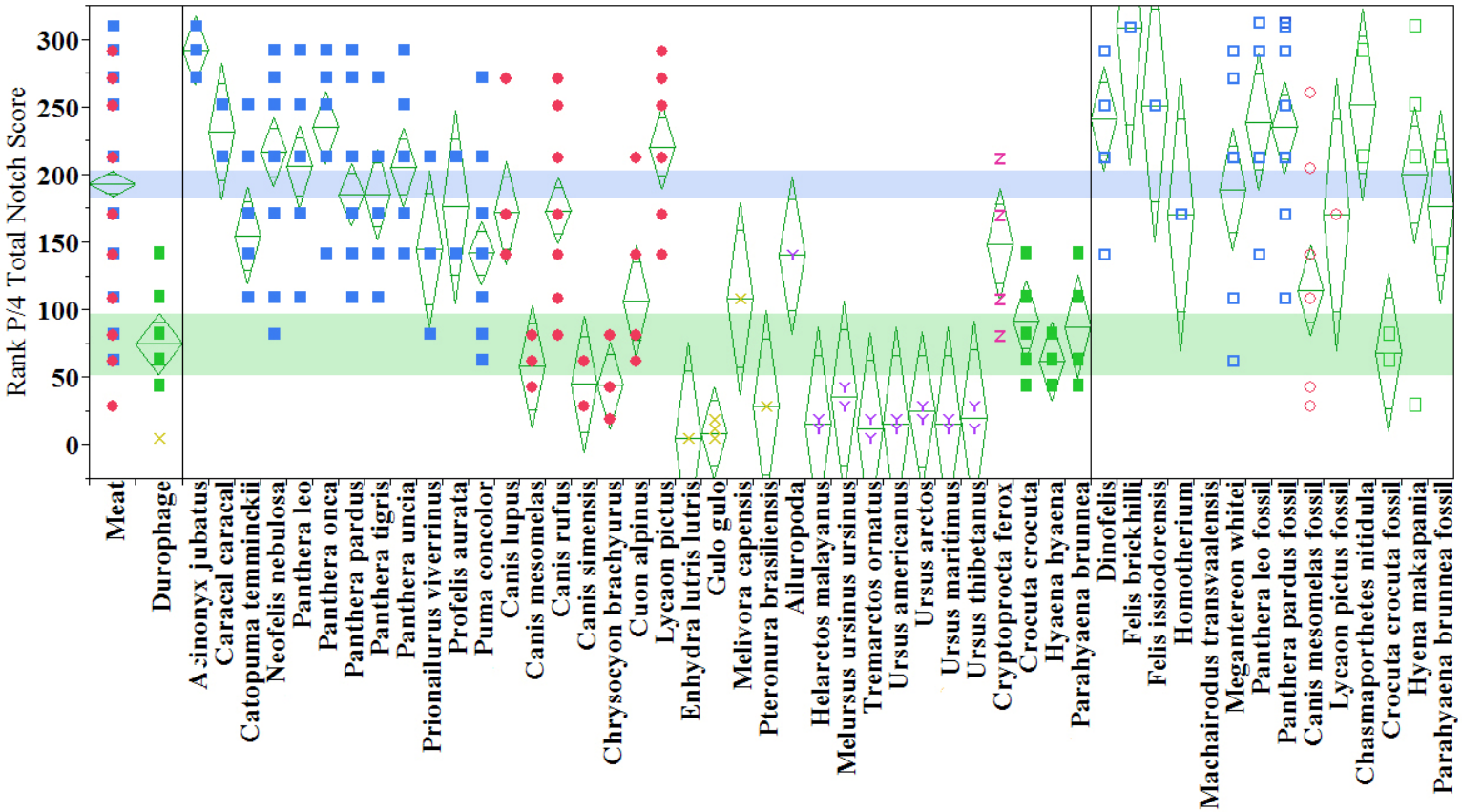

Figure 45: Rank of the Sum of P_4 Intercuspid Notch Scores

Ranked intercuspid notch data with Mean Diamonds. Boxes from left to right: two most divergent dietary categories, modern carnivorans, and fossil specimens. Green and blue bands delineate 95% mean confidence interval of Durophage and Meat groups respectively. Symbols as described in Table 7.

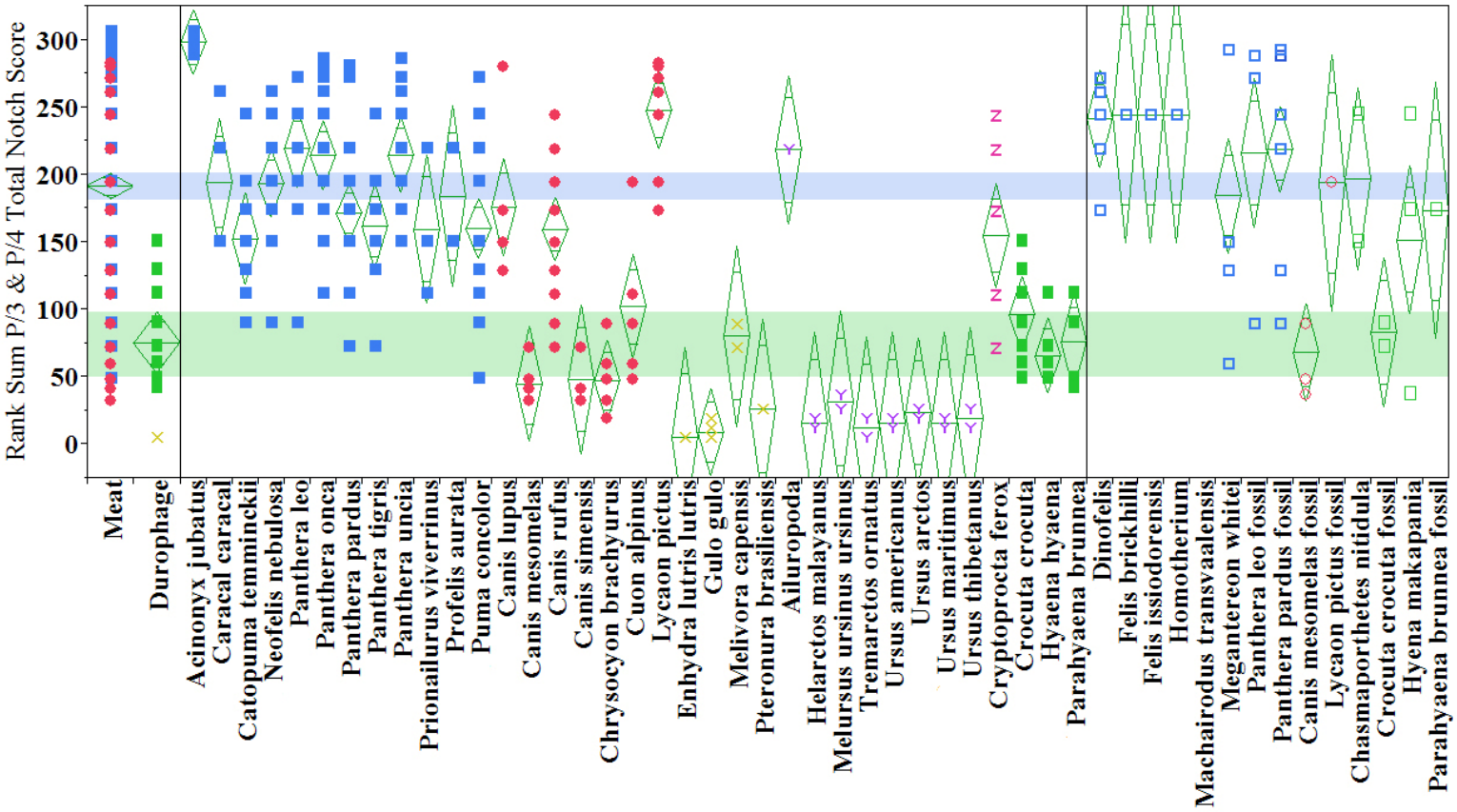

Figure 46: Rank of the Sum of P_3 and P_4 Intercuspid Notch Scores

Ranked intercuspid notch data with Mean Diamonds. Boxes from left to right: two most divergent dietary categories, modern carnivorans, and fossil specimens. Green and blue bands delineate 95% mean confidence interval of Durophage and Meat groups respectively. Symbols as described in Table 7.

The preceding three graphs (a subset of those summarized in Figure 43) are representative of all of the comparisons of notch data and dietary categorizations, with the first being the least pooled data, the score of the first distal P_4 notch (Figure 44), the next, pooling scores from all of the notches on the P_4 (Figure 45), and the last being data pooled from all the notches on both P_3 and P_4 (Figure 46). The general patterns between the three of them are very similar: among the modern specimens the felids and feloid viverrid (*Cryptoprocta*) are higher-ranked than the canids, which are ranked about the same as the hyaenids, and all of the canoid ursids (except for *Ailuropoda*) and mustelids are ranked lowest.

The patterns in the three comparisons among the fossil specimens are also very similar: again, the fossil felids are relatively highly ranked in all three. However, though the fossil members of *Crocuta* fall close to the range of the modern hyaenids, the fossil members of the other two extant durophagous hyena genera (*Hyaena* and *Parahyaena*) have mean ranks much higher than their modern congeners. These differences are not statistically significant due to the very low sample sizes of the fossil specimens, but the result is still surprising given that in all previous analyses (e.g., those in chapters 4 and 5), all of the fossil hyenas (except *Chasmaporthetes*) have closely resembled the extant hyenas. As with the ROC analyses (in the previous chapter), for these variables, the hypothetically hypercarnivorous *Chasmaporthetes*, groups with the modern hypercarnivores and not the modern durophagous confamilial hyenas – though, again, the sample sizes for these variables are too small to statistically support this finding.

Though the broad patterns conform to expectations and support the conclusions found in previous analyses, what makes these notch variables so intriguing and useful for determination of carcass-processing abilities is their ability to differentiate subtle variation between taxa within families. That is, whereas the analyses of ROC data could not be used to separate confamilial modern taxa with any consistency, notch numbers, scores and sums thereof can. Indeed, as can be seen in both of the graphs with greater variation of data (and, therefore, arguably greater precision; Figure 45 and Figure 46), the more hypercarnivorous *Acinonyx* falls higher in the ranked data than its confamilial but more durophagous relatives in *Panthera*. Likewise, in these same figures, the most hypercarnivorous canid *Lycaon* has the highest rank within its family, followed by the two fairly hypercarnivorous wolves (*Canis lupus*, and *C. rufus*) and then the relatively hypercarnivorous *Cuon*. All of these fall within the "meat" specialist dietary category to the exclusion of *C. mesomelas* and *Chrysocyon*, both of which fall low on these notch scales. It is also note worthy that the rare *C. simensis* (a taxon for which there are few dietary/carcass-processing behavior data available) also falls at the low end of these scales, suggesting that perhaps it might well be reclassified in the second dietary category.

Among the fossil canids, the single *Lycaon* specimen falls high in the rankings for its intercuspid notch variables, as it should, and the fossil *C. mesomelas* fall relatively low. However, for some notch variables, fossil members of this latter taxon rank statistically higher on average than their modern conspecifics, suggesting the opposite dietary shift (toward more hypercarnivory) than the ROC data (of the last chapter)

suggested. In other words, though fossil *C. mesomelas* had blunter teeth than modern members of the same species, they also had (by some measures) more numerous and extreme intercuspid notches – a mixed signal that will be discussed in the final chapter.

Likewise, fossil members of *P. pardus* have statistically more intercuspid notches (though, unlike *C. mesomelas*, not higher-magnitude notches) than their modern conspecifics. Again, this contradicts the dietary signal found in the radius-of-curvature data. The same contradictory pattern is found in fossil and modern *P. leo*, though the means are closer together than in *P. pardus*, and the sample of fossil *P. leo* is too small to statistically support it. It is not at all apparent why the signal based on the occlusal surface would contradict that based on the intercuspid notches. With that said, the teeth of fossil lions and leopards do appear more robust (durophagous) than their modern conspecifics, despite the fact that they have more numerous intercuspid notches.

Though not as pertinent to the analysis of fossil African carnivorans, the ursid pattern is intriguing. Namely, the position of *Ailuropoda*, high in the rankings relative to its very low confamilials, suggests that, from a functional perspective, intercuspid notches are more important in differentiating dietary behavior among bears than are radius-of-curvature data. Furthermore, this variable highlights the different geometries necessary for consuming tough foods (numerous and extreme notches, presumably for cutting through fibers) versus hard foods (few if any notches of low magnitude). The same pattern was seen with the ROC data (pandas grouping with hypercarnivores), though it was less evident because the other bears also grouped with high ROC taxa. What this suggests is that in terms of ROC all the bears maintain fairly sharp teeth, but

the bears that specialize in grinding (i.e., all those other than *Ailuropoda*, which presumably slices through fibers) reduce their notches.

In sum, the apparent precision with which intercuspid notch data are able to tease out subtle intrafamilial dietary patterns makes these variables very intriguing. Furthermore, these analyses suggest dietary patterns among the fossil taxa that slightly contradict both assumptions and the findings of previous analyses. However, more data would bolster the statistical strength with which the carcass-processing behavior of these fossil taxa could be assessed and possibly resolve some of the potentially anomalous findings for which small sample sizes curtail statistically justifiable interpretations. With that said, because of its power to consistently parse subtle variation within families, intercuspid notch data has enormous potential, especially in combination with other variables (as will be discussed in the final chapter), for the interpretation of fossil carcass-processing behavior.

An understanding of a possible scavenging niche for early hominids must articulate knowledge gained from actualistic research with detailed reconstructions of extinct carnivore paleoecology….
Dental anatomy suggest[s] that sabertooths and modern felids were ecologically distinct….
Sabertooth… morphology indicates extreme flesh specialization and lack of bone-crushing ability.

Marean 1989; p. 559

CHAPTER 7: Discussion, Further Directions and Conclusions

What can we say about the carcass-processing behaviors of Plio-Pleistocene carnivorans based on the geometry of their postcanine dentition? And what does this knowledge about the fossil carnivores tell us about their influence on human evolution? Frustratingly, through we now have a much better understanding of carnivoran paleoecology, more work needs to be done to refine this view before strong conclusions can be reached about the carnivoran influence on the evolution of our lineage.

In this final chapter I review the results of the two distinctive methods employed in this research (analysis of radii-of-curvature and intercuspid notches) in the context of the standard approaches to the same questions, then I conclude by outlining future directions of exploration that would take us closer to a full synthesis of the role of paleo-carnivores in our evolution.

The Difficulties Associated With the Inclusion of Marsupial Carnivores

Marsupial carnivores were included in parts of this study in the hope that broad patterns of morphological convergence for carnivory could be detected. Frustratingly, the inclusion of marsupials was problematic for two main reasons: 1) marsupial teeth are very different from eutherian teeth in subtle ways. For example, the intercuspid notches are of sufficiently different from than those found in carnivorans that I was not comfortable lumping them into the broader sample. 2) While a broad sample of marsupials representing similar ecological niches and body sizes as those found in the carnivoran sample probably would have been very informative about the convergent evolution of form in the range of carnivore adaptation, that sample of historically recent marsupials simply does not exist. Though the extant *Sarcophilus* and the recently extinct *Thylacinus* apparently represent different ends of the durophagy-hypercarnivory spectrum, these are the only two recent marsupial taxa that fall within the target body size range (and only at the low end of it). It is not possible to make a robust statement about an evolutionary pattern based on the inclusion of only two taxa.

A possible solution to this problem would be the inclusion of extinct carnivorous marsupials like the borhyaenids (a group of large-bodied carnivores that included some apparently highly durophagous members), *Thylacoleo* (the "marsupial lion" – a large carnivore that evolved from the kangaroo lineage, the diprotodonts) and *Thylacosmilus* (the highly derived sabertooth marsupial). An examination of the morphological similarity between these large and ecologically diverse taxa and the carnivorans would be fascinating. However, including extinct forms in the comparative group would be

problematic because their diets would have to be predicted from independent variables – a task that may have yielded very interesting results, but would have lead to a very different dissertation.

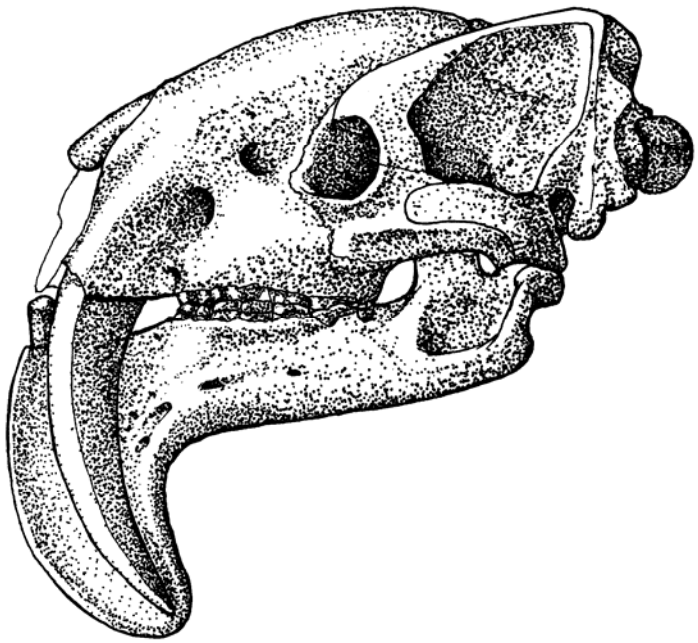

Figure 47: ***Thylacoleo atrox***

Redrawn from Riggs 1934.

While the successful inclusion of marsupial carnivores would have allowed extrapolation of the diets of carnivorous mammals in general, it is not necessary for the extrapolation of the diets of carnivorans in particular. In other words, though understanding the dental adaptations of marsupials would have deepened the results about the morphology of mammalian carnivores, it is not necessary to include them in a study focused on the deduction of the dietary behavior of extinct carnivorans.

Ultimately, this dissertation focuses solely on three extinct carnivoran lineages, the canids, felids, and hyaenids of Plio-Pleistocene South Africa. To deduce their dietary behavior, it is necessary to have an understanding of the morphology and diets of their extant confamilials, and a broader understanding of the other extant large members of their order buttresses these results. This study succeeds in these comparisons despite the difficulty of including a non-carnivoran comparative group.

The Carcass-Processing Behaviors of Plio-Pleistocene Carnivorans

Traditional linear measurements and ratios thereof can reveal extremely useful information about carnivoran carcass-processing behavior. For instance, two key indices, relative premolar size and relative blade length (Van Valkenburgh 1988b, 1989) do indeed separate the two most extreme dietary categories (meat specialists from durophages). However, both indices have limited ability to inform discussion about fossil carnivorans. For example, the premolar index (Figure 30) standardizes the width of the largest premolar by the cube root of body mass (Van Valkenburgh 1988b); to apply this index to fossil taxa requires estimation of body mass, a difficult task confounded by a limited fossil record which often leads to reliance on masticatory anatomy (usually carnassial lengths, canine dimensions and/or jaw lengths) for mass calculation, which adds another layer of uncertainty in that it incorporates non-independent variables into these equations. Even when body mass estimates are based on postcranial remains (e.g., Lewis 1995), these remains are so scarce that these estimates cannot address intraspecific

variability in this highly variable intraspecific variable. Accordingly, traditional indices have suffered from potentially great and unmeasurable sources of error.

Another key index, relative blade length (Figure 31), compares the length of the trigonid to that of the entire lower carnassial, and separates the two intermediate from the two extreme dietary categories. As discussed in chapter four, this index reflects phylogeny and not function – separating the two intermediate dietary categories dominated by the inclusion of canoid taxa with long talonids from the two extreme dietary categories dominated by short-talonid feloid taxa. Even if this ratio proves valid for separating taxa along dietary lines, it would address adaptations along a slicing/grinding scale (i.e., the ratio of the trigonid to talonid reflects the amount of the carnassial devoted to the sectorial portion of the tooth versus that devoted to the grinding portion), and not the slicing to crushing/puncturing scale that reveals more about carcass-processing behavior as it pertains to the possible hominin scavenging niche. In other words, from the perspective of scavenging, it is important to understand adaptations from slicing to crushing and puncturing that will reveal information about bone crunching and marrow extraction, not information about grinding that reveals incorporation of non-vertebrate foods.

Other ratios of simple linear measurements (e.g., percent of premolar-carnassial row devoted to carnassial length and fourth premolar shape; Figure 33 and Figure 34 respectively) get us closer to this dietary signal (especially in their easier applicability to the fossil record), but they do not do as good a job as analyses of radii-of-curvature and intercuspid notches do at picking up subtle inter- and intrafamilial dietary patterns. And

while the fourth premolar shape statistically assigns *Chasmaporthetes* to its hypothesized dietary group (with the meat specialists) and not its confamilial durophages, the more innovative methods (described in Chapters Five and Six) also pick up this pattern as well as more subtle signals missed by the analyses of the simple linear data.

Both radii-of-curvature and intercuspid-notch score data (the subjects of Chapters Five and Six respectively) separate taxa according to their dietary categories. The radii data are particularly good (and much better than the linear data are) at differentiating the most extreme hard-object feeders from the meat specialists, separating taxa like the durophagous *Enhydra*, and the apparently hypercarnivorous *Chasmaporthetes* more securely within the range of their dietary categories than their phylogenetic groups than any of the linear data do. Curiously, the radii measurements suggest that the fossil members of some extant taxa (specifically *Panthera pardus*, *P. leo* and *Canis mesomelas*) appear to have significantly blunter teeth than their modern relatives. While more data (namely, a wider sample size of all fossil taxa, examination of different variables to confirm these findings and further analysis of the proper classification of the *C. cf. mesomelas* fossils) would be useful to confirm this apparent trend, the implications of this pattern for the composition of the carnivore guild, and its possible effect on human evolution are interesting and will be discussed below.

Likewise, the intercuspid notch data also do a good job separating the taxa according to dietary category. In fact, they appear to do a better job of detecting the subtle interfamilial trends that the standard linear dimensions and radii-of-curvature seem to miss. That is, although these data also confirm the placement of extreme taxa (e.g.,

Enhydra and *Chasmaporthetes* as described above), they also separate the most hypercarnivorous taxa within the extant felids and canids (i.e., *Acinonyx* and *Lycaon* respectively) from their confamilials. These variables also group the tough-object feeding *Ailuropoda* with the hypercarnivores and not with the durophagous hyaenids or the even less notched confamilial ursids. Unlike any of the linear or radius data, the intercuspid notch data really highlight the difference between hard-object and tough-object feeding adaptations – a trend worthy of exploration in further directions with the inclusion of other taxa (discussed below). Curiously, the notch data suggest that fossil members of *Hyaena* and *Parahyaena* were less durophagous than their modern congeners. Furthermore, contrary to the results of the radius-of-curvature analyses, the intercuspid notch data seems to suggest that fossil *Panthera leo* and *P. pardus* were, if at all different, more hypercarnivorous than their modern conspecifics. With that said, the patterns seen in the fossil intercuspid notch data are not as clear as those seen in the radius data (e.g., there is greater variation about the means), and as with the radius data, more specimens and different variable analyses should be sought to confirm these results.

While the patterns seen in the radius and intercuspid notch data are informative on their own, in combination the dietary patterns are even clearer (Figure 48). In this bivariate view, the most hypercarnivorous canids cluster with the felids, as do *Ailuropoda* and *Chasmaporthetes*, *Acinonyx*, *Ailuropoda*, and *Lycaon* are clearly higher on the notch scale than the rest of their confamilials, and *Chasmaporthetes* and *Enhydra* are further along the ROC scale toward the hypercarnivores and durophages respectively than the other members of their families.

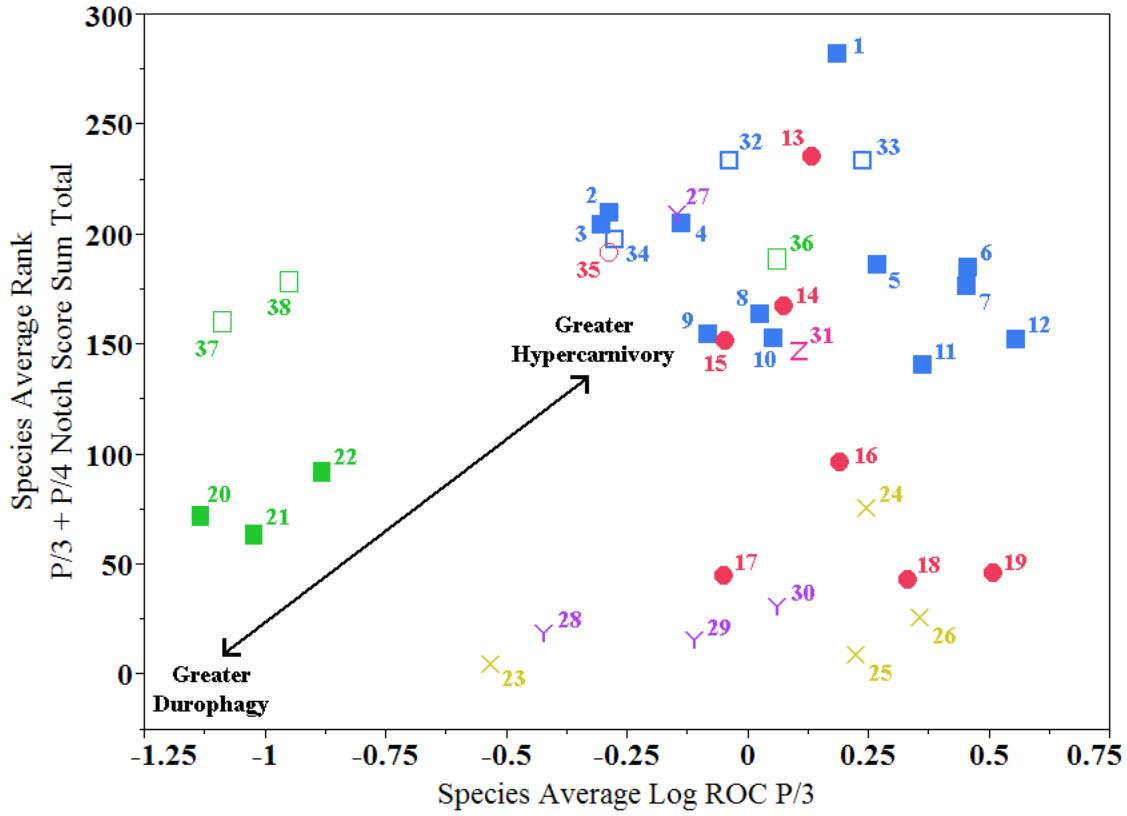

Figure 48: Bivariate of Intercuspid Notch and Radius-of-Curvature

Species Average log P_3 Radius-of-Curvature by Ranked intercuspid notch data. Symbols as described in Table 7. 1-31 are modern specimens, and 32- 38 are fossils. 1 = *Acinonyx*, 2 = *Panthera leo*, 3 = *P. onca*, 4 = *P. uncia*, 5 = *Caracal*, 6 = *Neofelis*, 7 = *Profelis*, 8 = *Panthera pardus*, 9 = *P. tigris*, 10 = *Puma*, 11 = *Catopuma*, 12 = *Prionailurus*, 13 = *Lycaon*, 14 = *Canis lupus*, 15 = *C. rufus*, 16 = *Cuon*, 17 = *Chrysocyon*, 18 = *Canis mesomelas*, 19 = *C. simensis*, 20 = *Parahyaena*, 21 = *Hyaena hyaena*, 22 = *Crocuta*, 23 = *Enhydra*, 24 = Mellivora, 25 = *Gulo*, 26 = *Pteronura*, 27 = *Ailuropoda*, 28 = *Ursus thibetanus*, 29 = *U. maritimus*, 30 = *Melursus*, 31 = *Cryptoprocta*, 32 = *Homotherium*, 33 = *Felis brickhilli*, 34 = Fossil *Panthera pardus*, 35 = Fossil *Canis mesomelas*, 36 = *Chasmaporthetes*, 37 = *Hyaena makapania*, 38 = Fossil *Crocuta*. Taxa included in this study but not listed on this figure lack data for one or both of these axes. Other similar bivariate plots (of notch data regressed on ROC data) yield very similar results. In general, from left to right and from bottom to top represents the durophagy to hypercarnivory scale.

Arguably the most surprising finding among all of the radius-of-curvature and intercuspid notch data is that, in general, the sabertooth taxa included in this study

(*Dinofelis*, *Homotherium*, *Machairodus* and *Megantereon*) do not appear to be more hypercarnivorous than modern felids. This could well be an artifact of the exceedingly small sample sizes of these taxa. However, as rare as they are, the few individuals available for study do not stand out as having postcanine dental adaptations of either their occlusal radii or intercuspid notches that would suggest hypercarnivory. Simply put, their premolars are fairly blunt and have a moderate number of intercuspid notches of moderate magnitude.

While this morphology would have had a functional effect (these teeth are less sectorial than modern felid teeth) and would seem to argue against the long-held belief that sabertooths were more hypercarnivorous than other felids, this result is probably confounded by another sabertooth trend: the reduction of the postcanine dentition in general and the premolars in particular (Emerson and Radinsky 1980; Hartstone-Rose *et al.* 2007; Palmqvist *et al.* 2007). Low premolar cusps subjectively appear to have reduced radius-of-curvature, and small teeth, reduced in the mesiodistal plane, also seem to have fewer and less extreme intercuspid notches. Thus, I believe, in general, that the reduction of the sabertooth premolars (which resulted from some biomechanical need to accommodate the maxillary canine through an elongation of the diastema and reduction of teeth that would encroach on this functional space) reduced the premolar sectorial function seen in other hypercarnivores. However, they display no dental morphology, in any region, that would suggest any durophagy despite research that suggest an ability to manipulate bones (Marean and Ehrhardt 1995). As such, sabertooths may have been (indeed I believe they probably were) hypercarnivores, as indicated by other pieces of

morphology (e.g., the elongated upper carnassial blades with reduced protocones; Marean 1989) utilizing other pieces of morphology (e.g., the procumbent anterior dentition described in chapter two) to process carcasses, but among these variables they do not appear to have been more hypercarnivorous than any of the extant hypercarnivores.

What the Carcass-Processing Behaviors of Plio-Pleistocene Carnivorans Tells Us About Human Evolution

The analyses in this dissertation explore the postcanine dental morphospace occupied by the members of the Plio-Pleistocene South African carnivore guild in an effort to evaluate the viability of a hominin scavenging niche. The foundation of this work is the longstanding belief that certain taxa, sabertooth felids in particular, created high-quality scavengable remains (i.e., with soft tissue still available, especially in the form of marrow) that would have been available for hominins (Blumenschine 1986, 1987, 1995; Blumenschine *et al.* 1994; Leakey 1967; Marean 1987, 1989; Shipman 1978, 1983, 1987; Shipman and Rose 1983; Speth 1989). This hypothesis rests on the assumption that sabertooths were incapable of processing carcasses as thoroughly as modern carnivores. It also rests on another unstated, and, in my opinion essential, assumption: if sabertooths were indeed incapable of fully processing carcasses, those remains would be easily available to hominins. In other words, for the hominin scavenging niche to be viable the carnivore guild would have to be expanded in the

hypercarnivore (i.e., non-durophagous) side of the guild, *and* no durophagous carnivores would exhaust those new resources.

This dissertation attempts to explore the first of these assumptions: Were there more medium-large bodied hypercarnivorous taxa in the paleo-carnivore guild that could have produced scavengable resources? The answer, based on the two focal sets of data explored in this research (the radius-of-curvature data discussed in chapter five and the intercuspid notch data discussed in chapter six) is an ambiguous "no." That is, although the hypercarnivorous taxa were more numerous in that space and time (all of the modern hypercarnivores lived in Plio-Pleistocene South Africa, and they were joined by the sabertooths and the apparently hypercarnivorous hyaenid, *Chasmaporthetes*), these taxa do not appear to have been, on the whole, more hypercarnivorous than the members of the modern guild. In other words, none of the fossil taxa had teeth that were sharper or contained more numerous or extreme intercuspid notches than any of the modern carnivorans. In fact, it appears that the non-sabertooth *Panthera leo* and *P. pardus* had more durophagous dentition than their modern relatives, though the intercuspid notch data may contradict this conclusion. Furthermore, the paleo-carnivore guild contained more specialized durophages, including *Pachycrocuta*, a hyena that appears to have been more durophagous (sporting huge, broad premolars with flat occlusal surfaces) than any modern carnivoran.

Thus, though there were more species of hypercarnivores, the data presented in this work strongly suggests that none exceeded the level of hypercarnivory seen in the modern guild, and some of the ancient members of extant hypercarnivores may have been

more durophagous than their modern conspecifics. Couple this with taxonomic expansion of the durophagous end of the carnivore guild, including the inclusion of a taxon that appears to have exceed the modern durophage capabilities, and it does not appear (based on taxonomic richness and morphospace occupied) that there was a broad scavenging niche with higher-quality scavengable remains available to hominins.

The fact remains that hominins did scavenge within-bone resources from the remains of carnivore kills (Blumenschine 1986, 1988). The question is the extent of these resources in the environment, a piece of information necessary to evaluate the evolutionary importance of these resources for hominin evolution. That is, though we know that hominins did access carcasses left by hypercarnivores, in order for this to have been an evolutionarily significant source of nutrition, these resources would probably have had to have been fairly plentiful in the environment. To assess this, it is important to go beyond the understanding of the abilities of individual carnivoran taxa, a study that evaluates the richness of occupied niches, to a an evaluation of the ratios of the niches filled by the paleo-carnivores. In other words, before the viability of the hominin scavenging niche can be fully assessed, we must consider the effect of taxonomic diversity in the guild. That is, though it appears, based on the number of species and their carcass-processing morphology, that the guild did not produce more scavengable remains than would a sample of modern carnivorans, if the hypercarnivorous animals outnumbered the durophagous taxa in such a way that more scavengable remains were produced than the less numerous durophagous carnivorans could exhaust, then there may

have been room for a hominin scavenger to enter the guild. However, it is likely that the population of durophagous carnivorans would expand to fill this niche.

The assessment of taxonomic diversity within the carnivore guild was outside the scope of this dissertation that sought to establish some key variables that correlate with the carcass-processing morphospace occupied by each taxon. There are many ways to try to evaluate this diversity (e.g., a deeper understanding of taphonomy and what modern accumulations of bone indicate about modern carnivoran diversity), however the scarcity of these specimens would probably hamper this type of research.

This is just one of many further directions into which this research could be expanded. Other areas include an evaluation of how the material properties of teeth influence their carcass-processing behavior, a deeper understanding of the function of certain dental geometries (e.g., the *carnassiform* notch) from an experimental perspective, revision to the taxonomy of certain fossils (specifically, new canid remains and a reevaluation of the *Canis cf. mesomelas* fossil) with specific emphasis on their masticatory morphology, and analyses of other non-dental masticatory anatomy (namely the soft tissue anatomy and osteological correlates thereof) that may reveal information about the carcass-processing abilities of the fossil carnivorans.

Deeper examinations of carnivoran dental morphology may tell us other information pertinent to hominin evolution. For instance, it is intriguing that the intercuspid notch data appears to reveal a signal for hard-object versus tough-object feeding (as exemplified by the position of the only tough-object feeder included in this study, *Ailuropoda*). Given that some enigmatic members of our lineage (namely the

paranthropines) have cranial adaptations that are indicative of both hard- and tough-object feeding, results of carnivoran studies may weigh in on this anatomy. To do so, more tough-object feeding carnivorans would have to be examined. As a first step in this direction, I have begun work on the procyonids, a canoid lineage excluded from this study because of the small size of all of its members that exhibits a very wide dietary diversity including general omnivores (e.g., *Procyon lotor*), and a highly specialized frugivore (*Potos flavus*), crab eater (*Procyon cancrivorous*) and a tough-object eater (*Ailurus fulgens*). In short, though these small carnivorans are, in most ways, very morphologically different from hominins, members of this single family encompass the entire hominin dietary spectrum.

Conclusions

Examining radii-of-curvature and intercuspid notches appears to reveal more about the diets of carnivorans than do standard linear variables. Using these variables, hypercarnivores can clearly be separated from durophagous taxa, and subtle dietary differences within families can also be deduced. For instance, hypercarnivores like *Acinonyx* and *Lycaon* are clearly more hypercarnivorous (based on their intercuspid notches) than are their confamilial taxa. Although these methods (as opposed to most traditional linear measurements) confirm that *Chasmaporthetes* is indeed more hypercarnivorous than its confamilial durophagous relatives, contrary to popular belief, the sabertooth felids do not appear more hypercarnivorous. Furthermore, some of the

fossil members of extant taxa display different morphology from their modern relatives, a trend worthy of further exploration.

In short, it does not appear that the members of the paleo-carnivore guild would have produced more scavengable remains than those produced by modern carnivorans; though there were more taxa that were hypercarnivorous, those taxa were not more hypercarnivorous than their modern relatives, and they were balanced by a greater number of durophagous taxa, including one taxon that may have been more durophagous than any member of the modern guild. Though a deeper understanding of the ratios of hypercarnivores to durophages in Plio-Pleistocene Africa may support the viability of the hypothetical hominin scavenging niche, this research, based on the carcass-processing abilities of the paleo-carnivorans, does not support the hypothesis that there were more high-quality scavengable remains available for Plio-Pleistocene hominins.

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Biography

Born May 8, 1981, New York, NY.

Education

Duke University, Trinity College, Durham, NC (August 1999 – May 2003) B.A.
Magna Cum Laude with Departmental Distinction, May 2003
Majors: 1) Biological Anthropology & Anatomy, and 2) English; **Minor**: Cultural Anthropology; **Certificate**: Primatology

Published Manuscripts

Hartstone-Rose A, DeRuiter D, Berger L, and Churchill S. 2007. A saber-tooth from Coopers Cave (Gauteng, South Africa) and its implications for *Megantereon* (Felidae, Machairodontinae) taxonomy. *Paleontologica Africana*. **44**:99-108.

Hartstone-Rose A, Wahl, S and Churchill S. in press. Using Radii-of-Curvature for the Reconstruction of Extinct South African Carnivoran Masticatory Behavior. In L de Bonis (ed.), Proceedings of the Revealing Hominid Origins Initiative (Analytical Carnivora Working Group). Poitiers, France.

Churchill SE, Berger LR, **Hartstone-Rose A**., and Zondo BH. in press. Body size in African Middle Pleistocene Homo. In SC Reynolds and CG Menter (eds.), Proceedings of the African Genesis Conference. Johannesburg: University of the Witwatersrand Press.

Published Abstracts

Hartstone-Rose A, and Perry JMG. 2008. The scaling of behaviorally significant gape: gape, fiber length, and skull dimensions in strepsirrhines.

Perry JMG, and **Hartstone-Rose A.** 2008. Chewing muscle size and diet in Eocene adapines.

Hartstone-Rose A, and Perry JMG. 2007. Masticatory anatomy of felids: stretch, strength and osteological correlates of muscle architecture. Proceedings of the 8th International Congress of Vertebrate Morphology; Abstract 50.

Hartstone-Rose A, and Perry JMG. 2007. Comparative anatomy of the felid masticatory system. Federation of American Societies for Experimental Biology. **21** (5): A85-A85.

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Perry JMG, and **Hartstone-Rose A.** 2007. Preferred bite size: a behaviorally-significant

measure of gape in strepsirrhine primates. Proceedings of the 8th International Congress of Vertebrate Morphologists. Abstract 95.

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Perry JMG, and **Hartstone-Rose A.** 2007. Do lemurs bite off more than they can chew? *American Journal of Physical Anthropology.* Suppl. **44**: 187.

Accepted Scholarships

2005-present **National Science Foundation Graduate Research Fellow** – full graduate tuition and a stipend of $30,000 per year for three years

2003-2007 **James Buchanan Duke Scholar**, Duke University **–** $4,000 stipend per year for four years

2003-2005 **Duke University Graduate Study Stipend** – full graduate tuition, health insurance, and a stipend of $16,000 per year for five years

Grants, Honors and Awards

2008-2009 **Bass Named Instructorship Award**, Duke University **–** $18,980 salary and fellowship to design and teach "Our First Homes: Hominin Paleoecology" in Fall 2008 (award not accepted)

2008 **Distinguished Leadership and Service Award- Expanding the Boundaries of Learning**, one of Duke's most prestigious awards, recognizing those whose influence and achievements have made a significant impact on education at Duke and beyond.

2008 **William J Griffith University Service Award- Outstanding Contributions to the Durham and Local Community**, Nominee, one of Duke's most prestigious awards, recognizing those whose influence and achievements have made a significant impact on the local community.

2007 **Graduate Student Mentorship Grant**, Duke University **–** $1,000 grant

2007 **Sigma Xi Mini Grant –** $500 grant

2007 **Graduate Student Mentorship Grant**, Duke University **–** $1,000 grant

2007 **Dean's Award for Excellence in Mentoring**, Duke University**,** award for outstanding mentorship of undergraduate scholars and a $1,500 honorarium

2006 **Elected Sigma Xi National Honor Society, Associate Member**

2006 **Duke Lemur Center Director's Fund** – $350 grant

2006 **Graduate Award for International Research**, Duke University – $3,000 grant

2006 **Aleane Webb Dissertation Research Fellowship**, Duke University – $250 grant

2005 **Graduate Student Mentorship Grant**, Duke University **–** $1,000 grant

2005 **Vertical Integration Grant**, Duke University – $4,000 grant

2004 **Elected Member Phi Beta Kappa Honor Society**

2004 **National Science Foundation Graduate Research Fellowship Honorable Mention**