



Systematic palaeontology (vertebrate palaeontology)

Using radii-of-curvature for the reconstruction of extinct South African carnivoran masticatory behavior

Adam Hartstone-Rose^{a,*}, Shaina Wahl^b

^a Department of Biology, Pennsylvania State University, Altoona 205 Hawthorn Building, 3000 Ivyside Park, Altoona, PA 16601, USA

^b Baltimore College of Dental Surgery, University of Maryland Dental School, 650 West Baltimore Street, Baltimore, MD 21201, USA

Received 1st September 2008; accepted after revision 29 September 2008

Written on invitation of the Editorial Board

Abstract

Paleoanthropologists have hypothesized that, during the evolution of increased carnivory in our lineage, hominins transitioned through a scavenging niche created by certain carnivoran taxa (especially sabertooths) that may have lacked the morphology necessary to utilize all parts of carcasses, thus leaving an open niche of high-quality scavengable remains. In this article, we examine the postcanine dentition of modern and fossil carnivorans using quantifications of occlusal radii-of-curvature (ROC) and correlate this morphology with feeding behavior to deduce the carcass-processing capabilities of the Plio-Pleistocene carnivores of South Africa. ROC data do a good job of separating taxa by dietary category, revealing possible differences in the carcass-processing abilities of fossil and modern members of some extant species, and confirming that *Chasmaporthetes* was probably a hypercarnivore and not a durophage like the modern hyenas. Contrary to previous hypotheses, sabertooth felids do not appear to have been more hypercarnivorous than modern felids based on these data. **To cite this article:** A. Hartstone-Rose, S. Wahl, C. R. Palevol 7 (2008). © 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Résumé

Utilisation des rayons de courbure pour reconstituer le mode de mastication des carnivores fossiles d'Afrique du Sud. Certains paléanthropologistes ont émis l'hypothèse que, pendant l'évolution de l'augmentation du régime carné dans notre lignée, les hominiens passèrent par la phase transitoire d'une niche écologique de type charognard, facilitée par certains taxons de carnivores (en particulier les félins à canines en lames de sabre) qui auraient pu être dépourvus de la morphologie nécessaire pour exploiter pleinement toutes les parties des carcasses (par exemple la moelle), laissant ainsi ouverte une niche favorable aux charognards et disponible pour les hominiens. Dans cet article, nous examinons la denture postcanine de carnivores actuels et fossiles en quantifiant le rayon de courbure occlusal en corrélant la morphologie au comportement alimentaire, pour en déduire les capacités d'utilisation des carcasses des carnivores pliopléistocènes d'Afrique du Sud. Les données sur les rayons de courbure constituent un bon outil pour séparer les taxons par catégories de régime alimentaire, révélant de possibles différences dans la capacité d'utiliser les carcasses chez les membres fossiles ou modernes de quelques espèces et de confirmer que *Chasmaporthetes* était probablement un hypercarnivore

* Corresponding author.

E-mail address: adam.hartstone-rose@psu.edu (A. Hartstone-Rose).

et non un animal durophage comme les hyènes actuelles. Contrairement aux hypothèses précédentes, les félins aux dents en lame de sabre n'apparaissent pas avoir été plus hypercarnivores que les félins modernes en se basant sur ces données. **Pour citer cet article** : A. Hartstone-Rose, S. Wahl, C. R. Palevol 7 (2008).

© 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Keywords: Hominin; Hominid; Scavenging niche; Sabertooth; *Chasmaporthetes*; Durophage; Hypercarnivore

Mots clés : Homininae ; Hominidae ; Niche de charognard ; *Chasmaporthetes* ; Durophage ; Hypercarnivore

1. Introduction

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 carnivorous 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 paper, we examine the postcanine dentition of modern carnivores, using quantifications of occlusal radii-of-curvature (ROC) and study the correlation of this morphology with carcass-processing behavior. We 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.

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

The large carnivore guild of Plio-Pleistocene South Africa was more speciose and, probably, more dietarily diverse than its contemporary equivalent. The guild contained representatives of all of the modern taxa as well as at least one species of extinct canid, three species of machairoid felids, and several species of extinct hyaenids, including the gracile *Chasmaporthetes* and the impressively robust *Pachycrocuta*. These taxa are of interest from functional (e.g., much has been written about the function of the sabertooth suite of morphology) and ecological perspectives. This set of carnivores is of particular interest to paleoanthropologists focused on evaluating the hypothesized hominin scavenging niche.

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* [1–4,6–10,22,23,25,29,31,34–39]. There is substantial zooarchaeological evidence to suggest that Plio-Pleistocene hominins extracted marrow from the long bones of mammals killed by large-bodied carnivores ([4] 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 [5] 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 [1,2,25].

Most studies of hominin scavenging have focused on the fossil evidence for marrow extraction [4], 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 [25] and their carcass transport and caching abilities [21,22,26]. Those studies that have examined the carcass-processing abilities of carnivorans [44,45] 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.

In this study, we investigate the carcass-processing abilities of the carnivorans that were sympatric with hominins during the Plio-Pleistocene with a specific focus on the ROC of the postcanine dentition.

2. 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 [40]) 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 the “Little Foot” STW 573 australopithecine) to about 1.5 million years old, though the dating of all South African fossil sites is still highly debated [17]. 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 [5]. 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

dog¹ [5]. 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; [40]) 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. One of the most recent comprehensive analyses of the Plio-Pleistocene carnivores of Africa is that of Lewis [21], 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 yet to have been incorporated into our understanding of the guild including the new site of Motsesti which 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 Cave². Many other small discoveries – such as the recovery of new remains of the genus *Megantereon* from a site at which it was previously unrecorded [14] – have underscored the need for a revision of many of the extinct taxa of the Sterkfontein Valley.

Van Valkenburgh [44,45] made significant strides in understanding dental adaptations along a scale characterizing carnivore diets ranging from hypercarnivory to durophagy (Fig. 1). (The term “hypercarnivore” – sensu [15,16] – refers to taxa that specialize in soft tissue – particularly flesh – consumption to the exclusion of tougher or harder tissues – such as bone.) In one study [44], the relative importance of bone, flesh and non vertebrate foods was predicted from measures of the canine and postcanine 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-

¹ A. Hartstone-Rose, L.R. Berger, S.E. Churchill, The Plio-Pleistocene Ancestor of Wild Dogs: *Canis sp. nov.* (in review).

² A. Hartstone-Rose, L.R. Berger, S.E. Churchill, The Plio-Pleistocene Ancestor of Wild Dogs: *Canis sp. nov.* (in review).

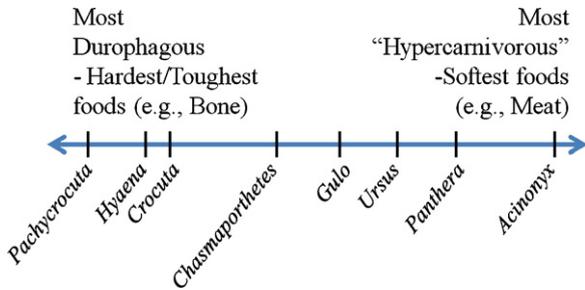


Fig. 1. Schematic Durophage-Hypercarnivore Scale.

Fig. 1. Échelle schématique Durophage-Hypercarnivore. Échelle schématique de morpho-espace avec la position hypothétique des taxons.

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 [20,33], 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 (Fig. 1). 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 [5]. In a more recent paper examining the teeth used to disassemble different parts of prey carcasses [45], 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 (*Panthera 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.

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 ROC 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.

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 study) and the crests and notches between them (the subject of other research along these lines; [13]).

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 [20]. However, beyond this ubiquitous subjective recognition of dental robusticity and several standard explorations of tooth dimensions using variables such as tooth width and length [44], 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 [19], and crown height [30], but according to one recent paper by some of the leading researchers in the field [12] quantification of the sharpness of teeth has only been carried out effectively once [30]. Popowics and Fortelius studied the sharpness of the occlusal surface created by occlusal wear on the carnassials.

In this paper, we attempt to expand on the classic approaches of correlations of diet and linear dental measures by incorporating ROC data in the exploration of the relationship between carnivoran dental adaptations and carcass-processing behavior.

3. Materials and methods

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

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.

Tableau 1

Taxons fossiles étudiés. Les lignes délimitent les familles. De haut en bas : Canidae, Felidae, Hyaenidae. Les seuls grands carnivores du Plio-Pléistocène d’Afrique du Sud.

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

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).

To maintain the focus of this work on the African Plio-Pleistocene carnivore guild, two groups of extant species were included as a comparative sample that represent: (1) relatively large-bodied (\geq the body mass of *Canis mesomelas*) African carnivorans; and (2) non-African carnivorans that compare favorably to the African carnivorans in body size and diet.

Extant specimens (Table 2) 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 speci-

mens – 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).

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, ROC, 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.

4. Dietary categorization

To make our 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 Valkenburgh [43,44]. 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;

Table 2

Extant specimens studied. Lines delineate families; from top to bottom, Canidae, Felidae, Hyaenidae, Mustelidae, Ursidae, Viverridae.

Tableau 2

Spécimens actuels étudiés. Les lignes délimitent les familles ; de haut en bas, Canidae, Felidae, Hyaenidae, Mustelidae, Ursidae, Viverridae.

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

4. nonvertebrate/meat: less than 50% meat, with fruit and/or insects predominating.

The species are assigned to these categories on the basis of the 82 behavioral references listed in [44]. In general, we 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 [43,44]. This correctly classifies that taxon as the most carnivorous of the bear family – all others consume mostly or almost exclusively non vertebrate foods [28,44]. 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 [18,41] as well as other detailed accounts [32], 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 from which they 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 [27], 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 Fig. 1), whereas Van Valkenburgh [44]

assigns them to the most hypercarnivorous of her categories. Subtleties like this are where subjectivity strongly affects results, as literature [24] 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, we 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 3). In an effort to expand the taxonomic and dietary breadth

of the species included in this study, we 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. We have also renamed Van Valkenburgh's "Meat/Bone" group "Durophage" consumers, to reflect the hard-object feeding functional signal we are seeking in the morphology, and also to include the molluscivorous sea otter, *Enhydra*. In previous studies [43,44], the durophagous

Table 3

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 as in table 2; from top to bottom, Canidae, Felidae, Hyaenidae, Mustelidae, Ursidae, Viverridae.

Tableau 3

Catégories de régime alimentaire. Voir le texte pour l'explication des catégories. Les espaces vierges dans la classification de Van Valkenburgh indiquent des taxons qui ne sont pas dans son étude. Les lignes délimitent les familles. De haut en bas, Canidae, Felidae, Hyaenidae, Mustelidae, Ursidae, Viverridae.

Species	Categorization from [23,34,38]	Designation in this study
<i>Canis lupus</i>	Meat	Meat
<i>Canis mesomelas</i>	Meat/Non-Vertebrate	Meat/Non-Vertebrate
<i>Canis rufus</i>		Meat
<i>Canis simensis</i>		Meat
<i>Chrysocyon brachyurus</i>	Meat/Non-Vertebrate	Meat/Non-Vertebrate
<i>Cuon alpinus</i>	Meat	Meat
<i>Lycaon pictus</i>	Meat	Meat
<i>Acinonyx jubatus</i>	Meat	Meat
<i>Caracal caracal</i>	Meat	Meat
<i>Catopuma temmincki</i>	Meat	Meat
<i>Neofelis nebulosa</i>	Meat	Meat
<i>Panthera leo</i>	Meat	Meat
<i>Panthera onca</i>	Meat	Meat
<i>Panthera pardus</i>	Meat	Meat
<i>Panthera tigris</i>	Meat	Meat
<i>Panthera uncia</i>	Meat	Meat
<i>Prionailurus viverrinus</i>	Meat	Meat
<i>Profelis aurata</i>	Meat	Meat
<i>Puma concolor</i>	Meat	Meat
<i>Crocota crocuta</i>	Meat/Bone	Durophage
<i>Hyaena hyaena</i>	Meat/Bone	Durophage
<i>Parahyaena brunnea</i>	Meat/Bone	Durophage
<i>Enhydra lutris</i>		Durophage
<i>Gulo gulo</i>	Meat/Non-Vertebrate	Meat/Non-Vertebrate
<i>Mellivora capensis</i>	Meat/Non-Vertebrate	Meat/Non-Vertebrate
<i>Pteronura brasiliensis</i>		Meat/Non-Vertebrate
<i>Ailuropoda melanoleuca</i>		Non-Vertebrate
<i>Helarctos malayanus</i>		Non-Vertebrate
<i>Melursus ursinus</i>		Non-Vertebrate
<i>Tremarctos ornatus</i>	Non-Vertebrate/Meat	Non-Vertebrate
<i>Ursus americanus</i>	Non-Vertebrate/Meat	Non-Vertebrate
<i>Ursus arctos</i>	Non-Vertebrate/Meat	Non-Vertebrate
<i>Ursus maritimus</i>	Meat/Non-Vertebrate	Meat/Non-Vertebrate
<i>Ursus thibetanus</i>	Non-Vertebrate/Meat	Non-Vertebrate
<i>Cryptoprocta ferox</i>		Meat

category included only members of the monophyletic group of hyaenids, thereby making it difficult to separate functional and phylogenetic signals, and while there is no other carnivoran that specializes in osteophagy to the extent that the hyaenids do, we included the phylogenetically distant carnivoran *Enhydra* in this study so that the “Durophage” category is no longer monophyletic.

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.

5. Measurement of ROC

ROC were measured using a technique similar to that used by Popowics and Fortelius [30]. 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 (Fig. 2) using a scroll saw (Craftsman). To minimize the influence of the kerf (the material removed by the saw), the blade was

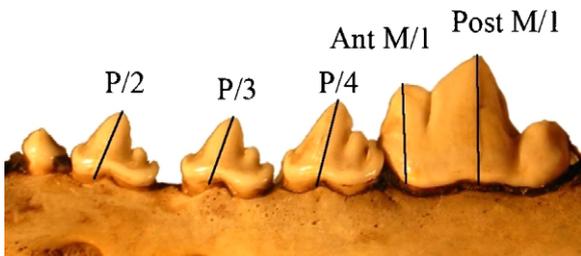


Fig. 2. Approximate planes of dental sections for ROC analysis P₁ through M₁ of a Gray Wolf (*Canis lupus*). AMNH 5381.

Fig. 2. Plans approximatifs des sections dentaires pour l’analyse des rayons de courbure.

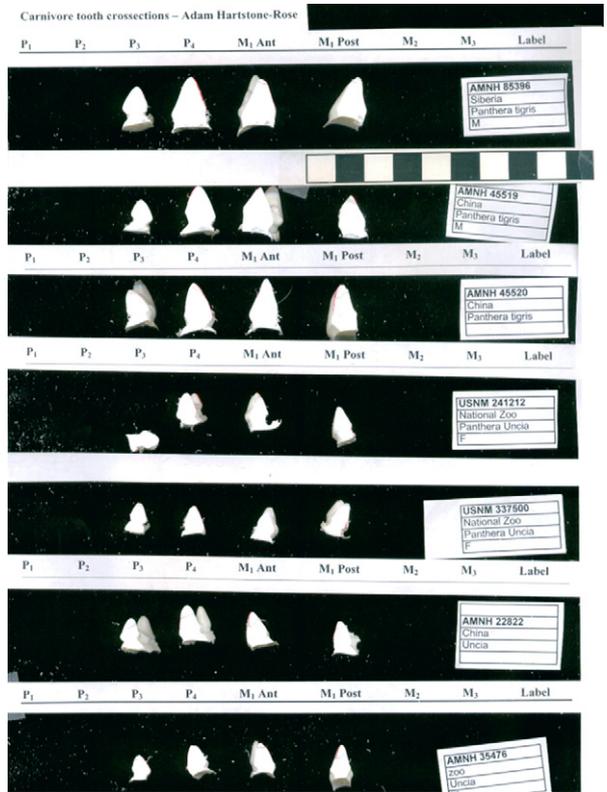


Fig. 3. An example plate of dental cross-sectional scans. Single plate of postcanine tooth cross-sections for seven individual felids. Scale bar in centimeters.

Fig. 3. Exemple d’une planche de sections transversales dentaires par scanner. Planche unique de sections dentaires transversales pour sept individus de félins. Barre d’échelle en centimètres.

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 (Fig. 3) using a flatbed scanner (Lexmark).

The ROC (1/r) of each target tooth was approximated in ImageJ (NIH; Fig. 4) by fitting a circle to the point of the crown.

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, 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

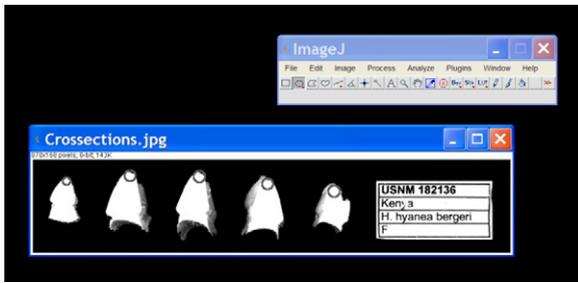


Fig. 4. Radius measurement in ImageJ. Postcanine tooth cross-sections for one individual (*H. hyaena* USNM 182136). Note: circles in this figure were enhanced for graphical purposes; actual ImageJ circles were fitted with more care, and are too thin to be seen well at this resolution.

Fig. 4. Mesure du rayon en imageJ. Sections transverses de dents postcanines d'un individu (*H. hyaena* USNM 182136). Notez que les cercles dans cette figure ont été renforcés; ces cercles ont été suivis soigneusement mais sont trop fins pour être bien visibles à cette résolution.

approximate radii as long as the occlusal curvature is not completely obliterated (Fig. 5). 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 (Fig. 5C) can be fit with a circle (Fig. 5D) 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 (Fig. 5 E) were excluded from these radii analyses.

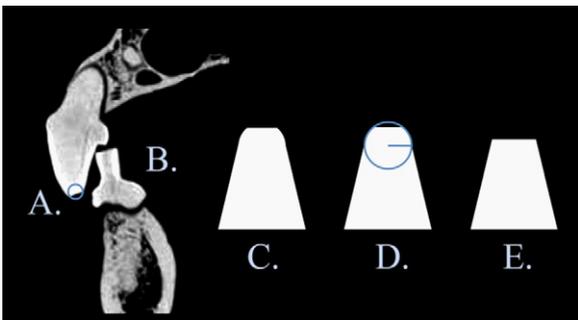


Fig. 5. Measurement of radii in moderately worn teeth. Note that moderately worn teeth (e.g. A and schematic C) can have approximate circles fitted to the remnants of the occlusal curvature (D), but teeth that are worn beyond this curvature (e.g., B and schematic E) cannot. Fig. 5. Mesures de rayons dans des dents modérément usées. Notez que les dents modérément usées (par exemple A et schéma de C) peuvent avoir des cercles approximatifs correspondant aux restes de la courbure occlusale (D), ce qui n'est pas le cas de celles usées au-dessous de cette courbure (par exemple B et le schéma E).

Obviously, there is some subjectivity involved in this data collection method, partially confounded by the fact that biological specimens seldom exhibit perfect geometries. While greater reproducibility and accuracy could probably be achieved with the utilization of a 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.

6. The scaling of ROC

Before the ROC 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. The problem is that the actual body size is not known for each of the specimens in our study. Instead, regression lines are fitted to data on radii relative to various body-size proxies. In this study, we include four of the most commonly used body-size proxies to evaluate these scaling effects: 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 and relative to tooth width, and the four body size proxies. Reduced-major-axis lines were fitted to the entire samples (excluding fossils) 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.

For a detailed discussion of the effects of scaling in this sample see [13]. In short, 152 lines of regression were studied including all individuals (both raw and relative radii for the total sample and for each of the three focal lineages. Sixty of the derived slopes (or 39.5%) are statistically different from isometry, and more than half of the allometry in the sample (55%) is found in the relative radii data. The trends suggest that large carnivores tend to 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.

The felids show almost as many significant allometric trends (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. 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, the scaling of radii was also studied using only (sex pooled) species averages. 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.

7. Carcass-processing correlates of ROC

While valuable information about the function of ROC can be gathered from examination of how these variables scale across body sizes, the real importance of a study of ROC in the context of evaluating the hominin scavenging niche, is in an examination of how these variables correlate with the carcass-processing behavior of modern carnivorans. When the ROC for all of the extant carnivorans are compared (Fig. 6), several trends emerge; the overarching revelation is that the ROC 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

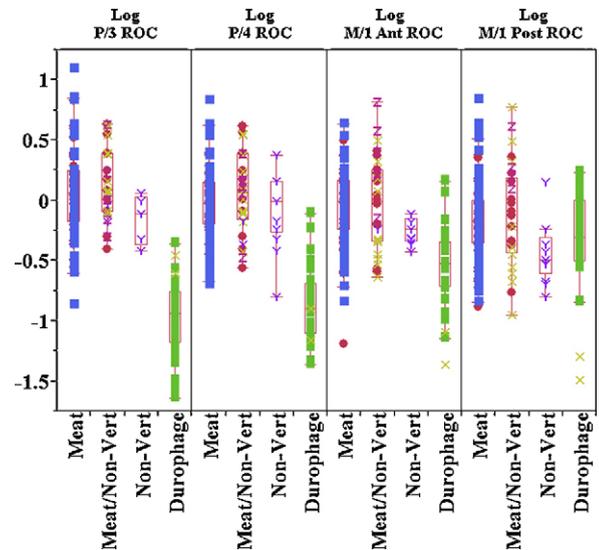


Fig. 6. Radii-of-curvature by dietary category. In Log mm with box plots for (from left to right) P_3 , P_4 , M_1 Paraconid (Ant) and Protoconid (Post). Extant specimens only. First and second premolars were excluded from analysis to maximize specific diversity within the samples. Symbols are as follows: Canidae = red circle, Felidae = blue square, Hyaenidae = green rectangle, Mustelidae = yellow X, Ursidae = purple Y, and Viverridae = pink Z.

Fig. 6. Rayons de courbure par catégories de régimes alimentaires. Distribution des boîtes en Log mm pour (de gauche à droite) P_3 , P_4 , paraconide et protoconide de M_1 . La première et la deuxième prémolaires sont exclues des analyses, dans le but d'augmenter la taille de l'échantillon. Symboles comme suit : Canidae = cercle rouge, Felidae = carré bleu, Hyaenidae = rectangle vert, Mustelidae = X jaune, Ursidae = Y violet et Viverridae = Z rose.

significant (using a comparison-wise alpha of 0.0125 and nonparametric Wilcoxon tests of each pair of categories) 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 ROC 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.

The other overarching interesting revelation that the quantification of ROC 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

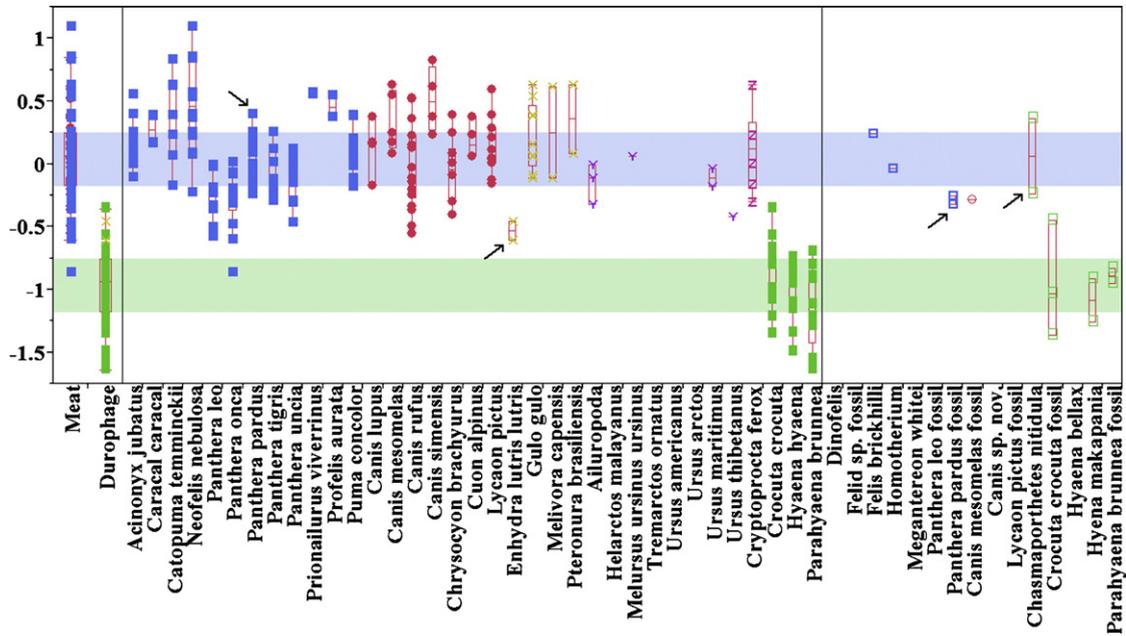


Fig. 7. P_3 radius-of-curvature. In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens. Arrows highlight *Enhydra*, *Chasmaporthetes*, and fossil and modern *Panthera pardus*, and are discussed in text. Green (lower) and blue (upper) bands delineate 50th percentile of Durophage and Meat groups respectively. Symbols same as in Fig. 6. Extant and extinct taxa are represented by solid and open symbols respectively.

Fig. 7. Rayon de courbure de P_3 . Comme pour la Fig. 6, de gauche à droite : les deux catégories de régime alimentaire, les plus divergentes chez les carnivores fossiles ou modernes. Les flèches indiquent *Enhydra*, *Chasmaporthetes*, et des *Panthera pardus* fossiles et modernes, et sont discutées dans le texte. Les bandes vertes (inférieures) et bleues (supérieures) délimitent les pourcentages de 50 % de durophages et de mangeurs de viande respectivement. Les symboles sont ceux de la Fig. 6. Les taxons actuels ou éteints sont représentés par des symboles pleins ou vides respectivement.

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 (Figs. 7–10).

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 [42,45], 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.

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 (*Crocota 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 $P/3$ ROC, suggesting that lions are capable of more hard-object feeding. Their new-world congener, the jaguar (*P. onca*), a known hard-object feeder [11], 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* (Fig. 7–10, marked by an arrow in Fig. 7, 8 and 10) consistently has very blunt teeth. What is most interesting about their ROC 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. How-

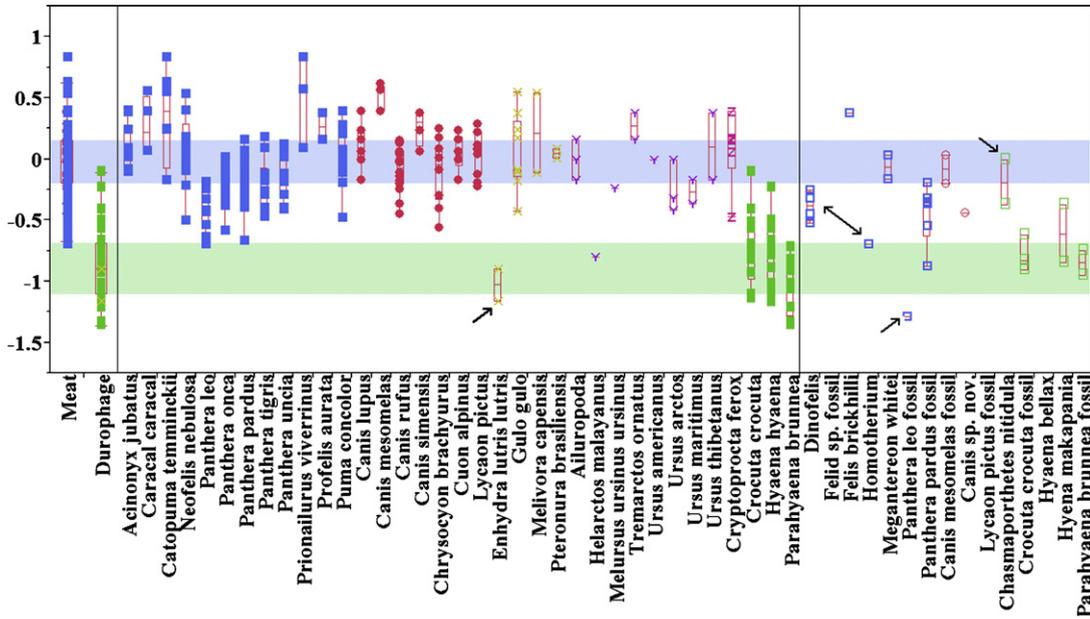


Fig. 8. P₄ radius-of-curvature. In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens. Arrows highlight *Enhydra*, *Chasmaporthetes*, *Dinofelis*, *Homotherium* and fossil *Panthera leo*, and are discussed in text. Symbols and bands same as in Fig. 7. Extant and extinct taxa are represented by solid and open symbols respectively.

Fig. 8. Rayons de courbure de P₄. Comme pour les Fig. 6 et 7, les boîtes correspondent de gauche à droite aux deux catégories de régime alimentaire, les plus divergentes pour les carnivores modernes ou fossiles. Les flèches indiquent *Enhydra*, *Chasmaporthetes*, *Dinofelis*, *Homotherium* et *Panthera leo* fossile et sont discutées dans le texte. Les symboles et bandes sont ceux de la Fig. 7. Les taxons actuels ou éteints sont représentés par des symboles pleins ou vides respectivement.

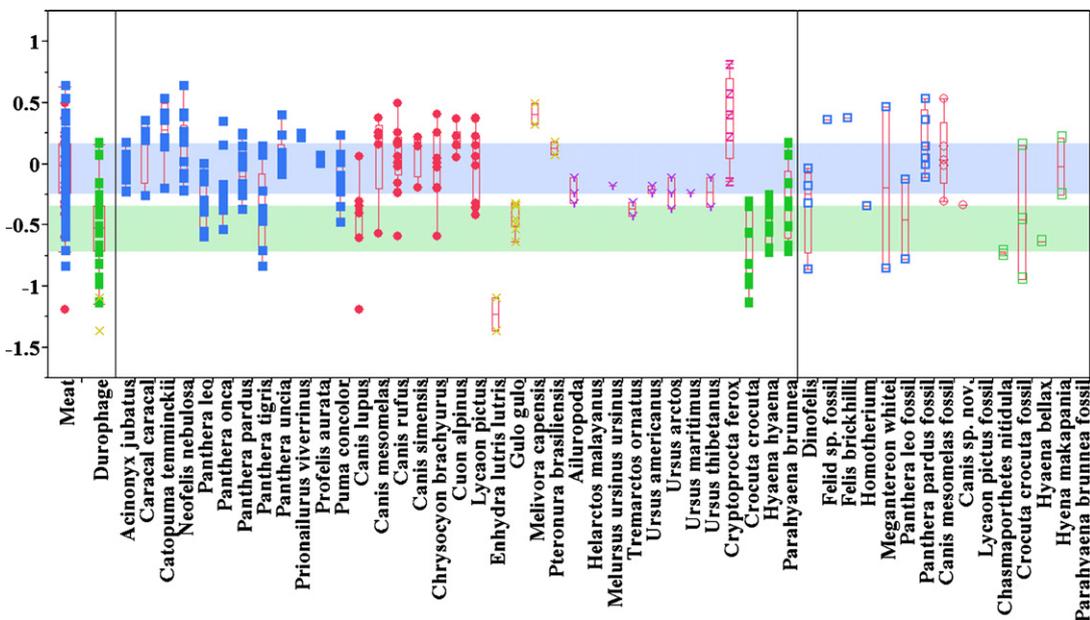


Fig. 9. M₁ anterior radius-of-curvature. In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens. Symbols and bands same as in Fig. 7. Extant and extinct taxa are represented by solid and open symbols respectively.

Fig. 9. Rayons de courbure antérieurs (protoconide) de M₁. Comme pour les Fig. 6–8, les boîtes correspondent de gauche à droite aux deux catégories de régime alimentaire, les plus divergentes pour les carnivores modernes ou fossiles. Les symboles et bandes sont ceux de la Fig. 7. Les taxons actuels ou éteints sont représentés par des symboles pleins ou vides respectivement.

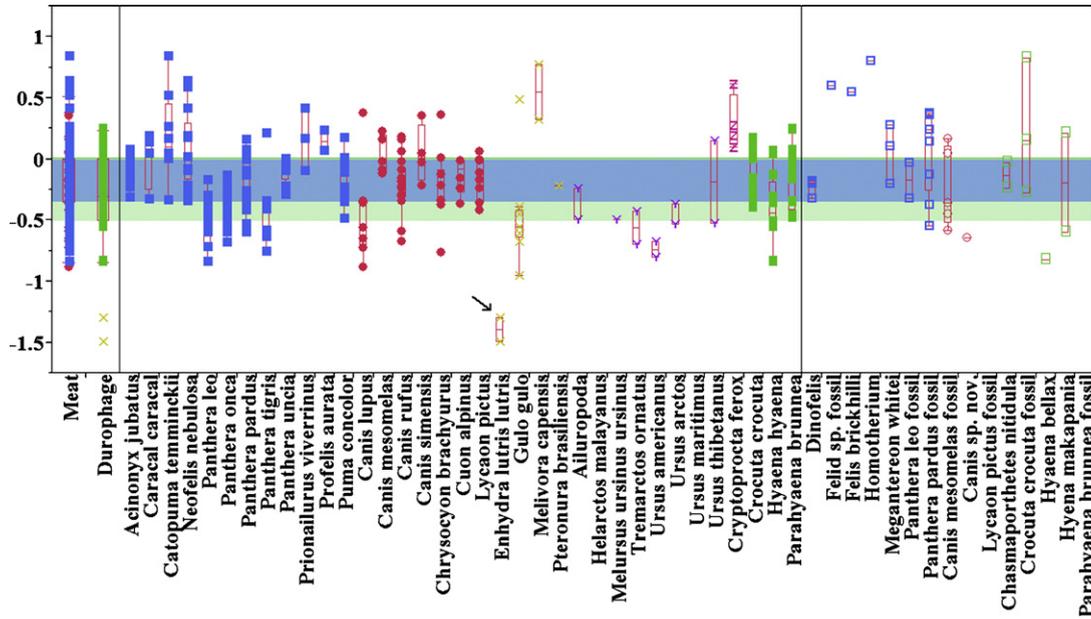


Fig. 10. M_1 posterior radius. In Log mm with box plots. Boxes from left to right: two most divergent dietary categories, modern carnivorans, fossil specimens. Arrow highlights *Enhydra*, and is discussed in text. Symbols and bands same as in Fig. 7, though here the bands overlap. Extant and extinct taxa are represented by solid and open symbols respectively.

Fig. 10. Rayons postérieurs (paraconide) de M_1 . Comme pour les Fig. 6–9. Les boîtes correspondent de gauche à droite aux deux catégories de régime alimentaire les plus divergentes pour les carnivores modernes ou fossiles. La flèche indique *Enhydra* et est discutée dans le texte. Les symboles sont ceux de la Fig. 7, excepté que les bandes se chevauchent. Les taxons actuels ou éteints sont représentés par des symboles pleins ou vides respectivement.

ever, this trend is not seen in the canids in the sample, which maintain a sectorial carnassial and use the postcarnassial molars for crushing [45]. This incorporation of the carnassial into the crushing function is evidence that *Enhydra* is even more specialized for durophagy than are the hyaenids.

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.

8. 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 Figs. 7 and 8), 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 [46].

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, it cannot be supported by this morphology in particular because a couple of the sabertooth taxa (namely *Dinofelis* and *Homotherium*; arrows in Fig. 6) 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.

Acknowledgements

We would like to thank Louis de Bonis for inviting us to give this talk, produce this manuscript and his wonderful coordination of both the conference and the resulting publication. We would also like to thank Steven Churchill and Christine Wall for their helpful advice in this research, and all of the members of the RHOI Carnivora working group (particularly Lars Werdelin and Margaret Lewis) for their advice and encouragement with this project. It has been an honor to participate in this conversation.

References

- [1] R.J. Blumenshine, Carcass consumption sequences and the archaeological distinction of scavenging and hunting, *J. Hum. Evol.* 15 (1986) 639–659.
- [2] R.J. Blumenshine, Characteristics of an Early hominid scavenging niche, *Curr. Anthropol.* 28 (1987) 383–407.
- [3] R.J. Blumenshine, Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at Flk Zinjanthropus, Olduvai Gorge, Tanzania, *J. Hum. Evol.* 29 (1995) 21–51.
- [4] R.J. Blumenshine, J.A. Cavallo, S.D. Capaldo, Competition for carcasses and early hominid behavioral ecology – a case-study and conceptual-framework, *J. Hum. Evol.* 27 (1994) 197–213.
- [5] C.K. Brain, *The Hunters or the Hunted?* Univ. Chicago Press, Chicago, 1981, 376 p.
- [6] H.T. Bunn, Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya *J. Hum. Evol.* 15 (1986) 673–690.
- [7] H.T. Bunn, E.M. Kroll, Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania, *Curr. Anthropol.* 27 (1986) 431–452.
- [8] H.T. Bunn, J.A. Ezzo, Hunting and scavenging by Plio-Pleistocene hominids – nutritional constraints, Archaeological Patterns, and Behavioral Implications, *J. Archaeol. Sci.* 20 (1993) 365–398.
- [9] S.D. Capaldo, Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania *J. Hum. Evol.* 33 (1997) 555–597.
- [10] M. Dominguez-Rodrigo, Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns, *Paleogeogr. Paleoclimatol. Paleocool.* 149 (1999) 373–388.
- [11] L.H. Emmons, Jaguar Predation on Chelonians, *J. Herpetol.* 23 (1989) 311–314.
- [12] A. Evans, J. Hunter, M. Fortelius, G.D. Sanson, The scaling of tooth sharpness in mammals, *Ann. Zool. Fenn.* 42 (2005) 603–613.
- [13] A. Hartstone-Rose, Evaluating the hominin scavenging niche through analysis of the carcass-processing abilities of the carnivore guild, *Biological Anthropology and Anatomy*, Duke University, Durham, 2008, 190 p.
- [14] A. Hartstone-Rose, D.J. de Ruiter, L.R. Berger, S.E. Churchill, A Saber-Tooth Felid from Coopers Cave (Gauteng, South Africa) and its Implications for *Megantereon* (Felidae, Machairodontinae) Taxonomy, *Palaeontol. Afr.* 44 (2007) 99–108.
- [15] J.A. Holliday, Evolution of hypercarnivory: The effect of specialization on character change, *Amer. Zool.* 41 (2001) 1474–1477.
- [16] J.A. Holliday, S.J. Stepan, Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity, *Paleobiol.* 30 (2004) 108–128.
- [17] D. Johanson, B. Edgar, *From Lucy to Language*, Simon & Schuster, New York, 1996, 272 p.
- [18] C. Jonkel, P. Smith, I. Stirling, G.B. Kolenosky, The present status of the polar bear in the James Bay and Belcher Islands area, *Occas. Pap. Can. Wildl. Serv.* 26 (1976) 1–42.
- [19] R.F. Kay, The functional adaptation of primate molar teeth, *Am. J. Phys. Anthropol.* 43 (1975) 195–215.
- [20] H. Kruuk, *The Spotted Hyena. A study of predation and social behavior*, University of Chicago Press, Chicago, 1972, 336 p.
- [21] M.E. Lewis, Plio-Pleistocene Carnivore Guilds: Implications for Hominid Paleocology, State University of New York at Stony Brook, New York, 1995, 567 p.
- [22] M.E. Lewis, Carnivore paleoguilds of Africa: implications for hominid food procurement strategies, *J. Hum. Evol.* 32 (1997) 257–288.
- [23] K.D. Lupo, Experimentally derived extraction rates for marrow: Implications for body part exploitation strategies of Plio-Pleistocene hominid scavengers, *J. Archaeol. Sci.* 25 (1998) 657–675.
- [24] D.W. Macdonald, *The encyclopedia of mammals*, New edit, Facts on File Inc, New York, 2006, 936 p.
- [25] C.W. Marean, Sabertooth cats and their relevance for early hominid diet and evolution, *J. Hum. Evol.* 18 (1989) 559–582.
- [26] C.W. Marean, C.L. Ehrhardt, Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den, *J. Hum. Evol.* 29 (1995) 515–547.
- [27] L.D. Mech, L.D.J. Frenzel, R.R. Ream, J.W. Winship, Movements, behavior, and ecology of timber wolves in Northeastern Minnesota, *U S Forest Serv. Res. Pap. NC 52* (1971) 1–35.
- [28] R.M. Nowak, *Walker's Carnivores of the World*, Johns Hopkins University Press, Baltimore, 2005, 328 p.

- [29] J.S. Oliver, Estimates of hominid and carnivore involvement in the Flk *Zinjanthropus* fossil assemblage – Some socioecological implications, *J. Hum. Evol.* 27 (1994) 267–294.
- [30] T.E. Popowics, M. Fortelius, On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals, *Ann. Zool. Fenn.* 34 (1997) 73–88.
- [31] R. Potts, On an early hominid scavenging niche, *Curr. Anthropol.* 29 (1988) 153–155.
- [32] R.H. Russell, Food-habits of polar bears of James Bay and South-west Hudson Bay in summer and autumn, *Arctic* 28 (1975) 117–129.
- [33] G. Schaller, *The Serengeti Lion*, University of Chicago Press, Chicago, 1972, 480 p.
- [34] M.M. Selvaggio, Evidence for a three-stage sequence of hominid and carnivore involvement with long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania, *J. Archaeol. Sci.* 25 (1998) 191–202.
- [35] P. Shipman, Early hominid lifestyle: hunting and gathering or foraging and scavenging? *Am. J. Phys. Anthropol.* 60 (1983) 253–253.
- [36] P. Shipman, Studies of hominid faunal interactions at Olduvai Gorge, *J. Hum. Evol.* 15 (1986) 691–706.
- [37] P. Shipman, Hunting for evidence of Pliopleistocene hominid scavengers – Response, *Am. Anthropol.* 89 (1987) 715–717.
- [38] J.D. Speth, Early hominid hunting and scavenging: the role of meat as an energy source, *J. Hum. Evol.* 18 (1989) 329–343.
- [39] A. Turner, Relative scavenging opportunities for East and South African Plio-Pleistocene hominids, *J. Archaeol. Sci.* 15 (1988) 327–347.
- [40] M. Sponheimer, K.E. Reed, J. Lee-Thorp, Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality, *J. Hum. Evol.* 36 (1999) 705–718.
- [41] I. Stirling, C. Jonkel, P. Smith, R. Robertson, D. Cross, The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay, *Occas. Pap. Can. Wildl. Serv.* 33 (1977) 1–64.
- [42] B. Van Valkenburgh, Locomotor diversity within past and present guilds of large predatory mammals, *Paleobiol.* 11 (1985) 406–428.
- [43] B. Van Valkenburgh, Trophic diversity in past and present guilds of large predatory mammals, *Paleobiol.* 14 (1988) 155–173.
- [44] B. Van Valkenburgh, Carnivore dental adaptations and diet: a study of trophic diversity within guilds, in: J.L. Gittleman (Ed.), *Carnivore Behavior, Ecology, and Evolution*, Chapman & Hall, London, 1989, pp. 410–435.
- [45] B. Van Valkenburgh, Feeding behavior in free-ranging, large African carnivores, *J. Mammal.* 77 (1996) 240–254.
- [46] B. Van Valkenburgh, F. Hertel, Tough times at La-Brea – tooth breakage in large carnivores of the Late Pleistocene, *Science* 261 (1993) 456–459.