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MORPHOLOGICAL VARIATION IN A DUROPHAGOUS CARNIVORE,
THE SPOTTED HYENA, *CROCUTA CROCUTA*

By

Teresa Lynn McElhinny

A DISSERTATION

Submitted to
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ABSTRACT

MORPHOLOGICAL VARIATION IN A DUROPHAGOUS CARNIVORE, THE SPOTTED HYENA, *CROCUTA CROCUTA*

By

Teresa Lynn McElhinny

Spotted hyenas (*Crocuta crocuta*) are wide ranging African carnivores. Across their range, they display high levels of morphological variation and behavioral lability. In an effort to provide a more accurate description of the patterns of variation in this species, I examined several aspects of morphology in spotted hyenas, primarily in the skull. Dental attrition levels were high, as is expected of a durophagous carnivore, but loss of the bone-crushing teeth occurred at lower levels than that reported for wolves.

This species is often cited as exhibiting female-biased sexual size dimorphism, but empirical data have not supported this assertion. Using large samples of animals measured in the field, I observed slight but significant female-biased sexual size dimorphism. Further, power analyses indicated that large sample sizes are required to detect the phenomenon, but that the differences are maintained in animals bred in captivity and fed uniform diets. I observed no sexual dimorphism in skull size or shape, examined using geometric morphometric methods.

Using geometric a large sample of skulls from across the African continent, I examined patterns of variation in skull size and shape. *Crocuta* has long been held as an example of a species that conforms to Bergmann's rule.

However, spotted hyena skull centroid size, instead of increasing with distance from the equator, shows a pattern in which the smallest animals are clustered in eastern/northeastern Africa. Additionally, the relationship with temperature is opposite that predicted by Bergmann's rule; skull centroid size increases with increasing minimum temperature. Data presented here indicate that prey base affects body size distribution.

Allometric shape variation is highlighted by localized changes in structures that serve as origin or insertion points for head and neck muscles. Non-allometric shape variation exhibits a clinal pattern. Northeastern specimens are intermediate in shape between north-central and southern African specimens for all three views. Further work is needed to determine the functional significance of the geographic variation in shape.

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To Rosie

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GENERAL INTRODUCTION

Spotted hyenas (*Crocuta crocuta*), the most abundant large carnivores in Africa, are of interest not only for their influence on ecosystems and populations of prey species, but also for their morphological and behavioral plasticity. The species has a wide geographical range that encompasses much of sub-Saharan Africa and occupies a variety of different habitat types. Throughout their range, spotted hyenas exhibit considerable variation in behavior and morphology, with groups ranging in size from 8-80 animals, and adult body mass ranging from 40-80 kg. Exploring the underlying evolutionary processes that produce such variation is central to understanding evolution by speciation (Gould and Johnston, 1972; Endler, 1977).

There is considerable variation in body size and pelage characteristics in the spotted hyena, and many subspecies have been described historically (Meester et al., 1986). Although Matthews (1939b) found significant variation in pelage color and skull size, he was able to discern no clear geographical pattern to the variation. He concluded that the previously described subspecies were based merely on individual variation, and his monospecific description of the spotted hyena is the systematic convention followed today.

While Matthews noted no geographical regularity to the variation in spotted hyena size, other authors have described a geographical cline in body size, with the smallest forms at the equator, and size increasing to the north and the south (Kurten, 1957; Turner, 1984; Klein, 1986). These studies had a narrow geographical scope, and the authors focused almost entirely on surrogates for

body size, ignoring variation in skull shape. The observed size variation was attributed simply to variation in ambient temperature, disregarding other environmental variables as well and the influence of evolutionary history.

Spotted hyenas are durophagous carnivores; literally, *durus* (*L*) hard, *phago* (*Gr*) to eat. They will consume a kill in its entirety, save for the rumen contents and the bony bases of ungulate horns in larger species (Estes, 1991). This capability is facilitated by a robust skull and impressive dental battery, both of which are built to withstand large amounts of pressure from the action of the adductor muscles used to close the jaws. Despite being a streamlined machine built for processing bone, there is considerable variation in skull morphology.

In this dissertation, I focus primarily on morphological variation in the spotted hyena skull, using museum specimens. I present data on tooth loss and on supernumerary teeth. I examine three issues regarding size variation within this species, that between sexes, across the continent, and the effect that skull size has on shape. I assess shape variation across the continent in the context of past subspecies designations, and the Pleistocene refugium hypothesis, which has been proposed to explain mitochondrial DNA variation in this species.

I traveled to 13 museums in the United States, United Kingdom, Europe, and Kenya to examine over 600 *Crocuta crocuta* skulls. The privilege of studying such a large sample of any one species allows for direct observation of morphological variation, but evaluating patterns within such a large group of specimens presents a challenge. Geometric morphometrics, a group of methods for the multivariate statistical analysis of form based on landmark coordinates,

allows for easier interpretation of variation within large samples. These methods facilitate the analysis of patterns in size and shape variation that would be difficult to extract using traditional linear measurements. The thin plate spline interpolation method is used to create deformation grids that permit the visualization of shape change between groups or along gradients.

OVERVIEW OF CHAPTERS

The following chapters have been written as independent manuscripts, and are presented as such.

In Chapter One, I report on anomalies and levels of attrition that I observed in my studies of museum specimens. I found supernumerary teeth, some anomalous, or of developmental disturbance origin, and others that I determined to be atavistic. Being durophagous carnivores, spotted hyenas often break their teeth, but are able to survive the loss of one or more teeth. Tooth breakage and loss occur at higher rates in spotted hyenas compared to many other carnivores. Canines are the teeth that are broken most often, but they are rarely completely lost. The assertion that the teeth of spotted hyenas possess deficient safety factors, that the bone-crushing break frequently compared to other teeth and to other taxa is re-evaluated. As expected, dental attrition is significantly correlated with increasing age in this species. The predicted correlation between high level of competition and dental attrition is not realized, in fact the opposite relationship is demonstrated, but this may have been due to small sample size, and a difference in average age of the specimens.

The first step in any analysis of skull variation is to address potential sexual dimorphism. In Chapter Two, I address this question in spotted hyenas, using both skull and linear body measures. Perhaps influenced by the unique female-dominated social system, *Crocuta* was long assumed to be sexually dimorphic. In fact, spotted hyenas were described as a robust example of female-biased sexual size dimorphism in the definitive review paper on the subject (Ralls, 1976); however, reports of field measurements failed to reach a consensus. Some authors reported that females were larger than males, others failed to find a significant difference.

I investigate size differences in body measurements taken from wild animals, and shape and size differences using geometric morphometric analyses of the skull, between male and female spotted hyenas. Females are indeed larger than males in certain body dimensions, but skulls are sexually isometric in size and shape. The differences in body measurements are maintained in captive populations, and therefore are not the result of higher food quality afforded to the dominant females. The discord in the literature regarding sexual dimorphism in this species is likely due to the small sample sizes used in the reports. I use a resampling-based method to illustrate that the slight dimorphism in head-body length and chest girth require very large sample sizes to show a significant result, but that only a handful of animals is required for mass.

I examine another long-held hypothesis about spotted hyenas in Chapter Three- that they conform to Bergmann's rule. Bergmann's rule predicts that, within a species, larger bodied individuals are found at greater distances from the

equator, and thus at lower temperatures. Spotted hyenas were reported to 'obey' Bergmann's rule based on a correlation between latitude and the length of the first lower molar (Klein, 1986). It was suggested that the relationship between body size and temperature in this species was so tight, that *Crocuta* might be used as an indicator species for predicting paleotemperature in Eurasia (Klein and Scott, 1989).

Using ventral centroid size as a proxy for body size, I demonstrate that the pattern in body size variation is not a strictly linear relationship with latitude. Rather, the smallest individuals are found concentrated in eastern Africa, and larger animals span the equator outside of this area. This geographic pattern in body size is not related to temperature, but to the diversity of the prey available. Additionally, although the length of the first lower molar is significantly correlated with average minimum temperature, this relationship explains less than 20% of the variance in first lower molar length, not an ideal level for using the measure to predict paleotemperature.

Lastly, in Chapter Four I examine allometric shape variation in the skull, and shape variation across the continent. Shape variation that is the result of increasing size is related to muscle size and activity. There is also a cline of shape change from north-central Africa, through northeastern Africa, to the southern part of the continent that harkens back to the descriptions of subspecies past. This cline further supports the notion that spotted hyenas were affected by Pleistocene climate change, and movements were limited by inhospitable habitat.

CHAPTER ONE

ANOMALIES AND ATTRITION IN THE DENTITION OF SPOTTED HYENAS, *CROCUA CROCUA*

INTRODUCTION

Each family within the Class Mammalia can be characterized by its dental formula, the numbers of incisors, canines, premolars, and molars present in the permanent adult dentition. However, variations in dental formulae can and regularly do occur (Hall, 1940). Oligodonty, the absence of one or more teeth within an individual, may be due to congenital, pathological, or traumatic causes. With congenital oligodonty, the tooth in question never develops. Alternatively, a normally developed tooth can be lost as the result of disease or injury. Polyodonty is the development of supernumerary teeth, teeth in excess of the number specified in the species' dental formula. These departures from the norm are of interest because they can provide insight into systematics, tooth development, and genetic heritability of dental traits (D'Souza and Klein, 2007; Hall, 1984; Manville, 1963).

Many species within the Order Carnivora possess dentitions that are reduced in number from the ancestral Eutherian condition, and/or possess highly specialized morphology for processing animal foods. Deviations from the dental formula, in the form of lost or supernumerary teeth, within species that exhibit highly modified dental arcades are of particular interest because there is seemingly little room for error. Breakage, deletions, or duplications of teeth in a streamlined, highly specialized dental arcade might result in impaired function.

Reports of dental anomalies within the Order Carnivora are well represented in the literature. Variations in dental formulae have been described for most of the caniform families, including Canidae (Andersone and Ozolins, 2000; Buchalczyk et al., 1981; Gisburne and Feldhamer, 2005; Nentvichova and Andera, 2008; Paradiso, 1966; Szuma, 1999; Vila et al., 1993, Mustelidae (Wolsan, 1989; Wolsan, 1984; Hauer, 2002), Procyonidae (Hall, 1940), and Ursidae (Hall, 1940). However, fewer studies have investigated dental anomalies in the feliform carnivores, including true cats, hyenas, mongooses, and civets (but see (Manville, 1963). Within this group, the bone-cracking hyaenids, which includes three extant species (brown, striped, and spotted hyenas), are particularly intriguing due to their robust and highly specialized dentition designed to split open large bones.

The normal dental formula for the spotted hyena (*Crocuta crocuta*) is incisors 3/3 canines 1/1 premolars 4/3 molars 0-1/1 =32-34 (Figure 1.1); this formula is considerably reduced along the cheek tooth row from the ancestral carnivoran formula, I 3/3 C 1/1 P 4/4 M 3/3=44. Spotted hyenas do not deliver a 'killing bite' to suffocate their prey. Instead, a kill is made by biting the prey with the incisors and canines, and tearing off flesh, until the prey animal is no longer able to flee. The carnassial teeth (P^4/M_1) are then used to cut open the hide and sever connective tissue (Van Valkenburgh, 1996). Spotted hyenas are durophagous carnivores, able to consume the long bones of even very large prey. The robust upper and lower third premolars are used to break open large-diameter bones to obtain the nutritious marrow inside (Kruuk, 1972).

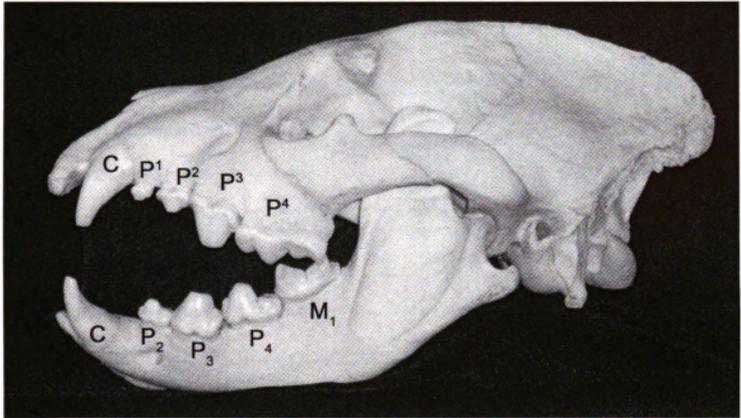


Figure 1.1. Normal dentition of *Crocuta crocuta*.

The aim of this chapter is to document the occurrences of tooth breakage, oligodonty, and polydonta in *Crocuta crocuta*. Spotted hyenas are known to exhibit high levels of tooth breakage relative to other carnivores, which Van Valkenburgh (1988, 2009) suggested is the result of high stresses placed on the teeth due to the durophagous diet. Vila et al. (1993) proposed that one could infer the importance of a tooth to an animal's survival by the rate of complete loss of the tooth and reossification (resorption) of the alveolus. That is, teeth that are less important are lost at higher rates than those that are essential to survival. Vila et al. (1993) found high levels of attrition in wolves at both upper and lower premolars 1-3, and concluded that while loss at these teeth may increase processing time of food, prey capture was likely not affected. In order to compare the findings of Vila et al. (1993) on oligodonty due to trauma and/or disease in

wolves (*Canis lupus*) with that in spotted hyenas, tooth fracture and complete loss separately were examined separately.

Complete tooth loss (oligodonty) due to pathological and/or traumatic causes can be separated from congenital oligodonty, in which the tooth never forms. As the total number of teeth is already reduced in the spotted hyena from the ancestral number, and the teeth are highly specialized for the species' durophagous diet (Van Valkenburgh, 1996), I expected congenital oligodonty to be low, as has been shown for felids (Hall, 1940).

Fenton et al. (1998) suggested that incidence of tooth damage may be associated with longer life spans in mammals. Indeed, Van Valkenburgh (1988; 2009) found a trend involving higher rates of damaged or missing teeth in older individuals. I estimated individual ages from tooth wear to examine the relationship between dental attrition and age in *Crocuta*. Van Valkenburgh (2009) hypothesized that the higher level of tooth fracture in Pleistocene carnivores than in recent carnivores was due to higher levels of intraspecific competition during the Pleistocene. I tested this hypothesis in *Crocuta* using specimens from eastern and southern Africa, which experience high and low intensities of feeding competition, respectively.

I classified instances of polydonta according to what is currently known about the etiology of supernumerary teeth.

METHODS

I examined 472 complete skulls (i.e. crania with mandibles), and an additional 11 mandibles (without crania) and 23 crania (without mandibles), from adult and subadult spotted hyenas (Table A.1) housed in 13 museums in the United States, Europe, and Kenya (Table A.2). These skulls were collected from across sub-Saharan Africa, although specimens from western Africa were few. Sex is excluded from descriptions and analyses, except where noted, because there is no evidence of sexual dimorphism in the dentition (Van Horn et al., 2003), and sex assignments of museum specimens are not consistently reliable due to monomorphism of the external genitalia. All statistical tests were performed in R (R Development Core Team, 2009).

Broken teeth and instances of oligodonty were identified from digital photographs of the ventral crania. Photographs of the occlusal view of the mandibles were not available, so fracture and oligodonty data are from crania only. Oligodonty was classified as being due to trauma and/or disease (hereafter referred to as pathological oligodonty), or due to congenital absence. Pathological loss of a tooth during the animal's lifetime can be identified by the resultant gap between the adjacent teeth, and the presence of porous, bony overgrowth of the alveolous (Figure 1.2); both of these traits are absent when oligodonty is due to congenital absence (Vila et al., 1993). Loss of a tooth post-mortem is indicated by an open alveolous. In order to utilize skulls with teeth that were lost post-mortem without skewing results, individual teeth were counted,

and the totals of fractured and lost teeth were compared to the total number of teeth counted (e.g. number I¹ broken/total number I¹ observed).

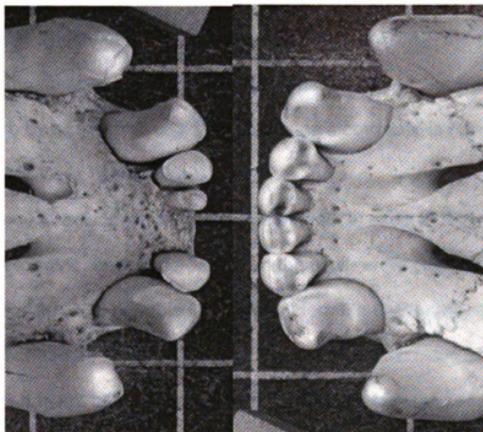


Figure 1.2. Alveolar overgrowth. A. Left first incisor missing. B. Normal dentition.

To examine the relationship between age and dental attrition, I aged 405 adult skulls (see Table A.1) using Van Horn et al.'s (2003) mixed-sex age estimation models (equations 2 and 3) for *Crocuta*, and regressed the number of fractured and lost teeth onto age for each specimen (least squares regression). As spotted hyenas are physiologically competent to breed at 24 months of age (Glickman et al., 1992), I included animals whose estimated ages were between 24 and 281 months.

In an attempt to assess the contribution of feeding competition to dental attrition, I compared skulls (n=108) from eastern Africa, where clan size is very

high (n=47 – 54) (Frank, 1986a; Hofer and East, 1993; Kruuk, 1972), to those in southern Africa (n=17), where clan size is much smaller (n=4 – 14) and feeding competition at kills is far less intense (Henschel, 1986; Mills, 1984; Tilson and Henschel, 1986; Trinkel et al., 2004; Whateley and Brooks, 1978) I performed ANCOVA on the number of teeth affected by fracture or loss (total of fracture + loss/individual) by geographic region, with age as a covariate in R version 2.8.1 (R Development Core Team, 2009).

Instances of polydonty, the presence of teeth in excess of those in the normal dental formula, were recorded when the skulls were photographed.

The peg-like M¹ is variable in the dental formula of *Crocuta*, and has been previously described as frequently absent (Lumsden, 1981; Miles and Grigson, 1990), but this has not been systematically studied. M¹ is often difficult to see in photographs of the ventral cranium as the tooth can be obscured by P⁴.

Therefore, presence or absence of M¹ was investigated with the skulls in hand. I used 74 specimens collected from a single population in what is now the Ngorongoro Conservation Area, Tanzania (see Table A.1). I considered the presence of an open alveolus with no bony overgrowth as evidence that the tooth was lost from the skull postmortem. As these specimens were dissected upon collection, sex assignments were reliable, and data on sex were included in this analysis. Age of the hyenas from which the skulls were collected was estimated using mixed-sex estimation models developed for this species (Van Horn et al., 2003), and age was tested as a factor in loss of M¹ using a Welch t-test for unequal variances in R.

Abnormal tooth rotation has been examined in other carnivores (Gisburne and Feldhamer, 2005; Szuma, 1999), but is not considered here because rotation of the cheek teeth is highly variable in this species. Former subspecies descriptions used rotation as a character (e.g. *Crocuta crocuta fortis*, Allen, 1924). This practice has been abandoned and these subspecies of *Crocuta* are now collapsed (Matthews, 1939b).

RESULTS

Breakage and Oligodonty

Tooth fracture was detected in 29.1 % (144/495) of individuals, with 3.28% (250/7634) of all teeth broken. Tooth fracture was most frequent at the canine, and least frequent at P⁴ (Table 1.1). I found no instances of congenital tooth loss, but 11.5% (57/495) of individuals showed evidence of pathological tooth loss (Table 1.2). All missing teeth were recognized by alveolar resorption and a gap in the tooth row where the missing tooth had been. Of the 104 pathologically missing teeth, nearly half were P¹. The least pathological loss was seen at P⁴.

The number of broken or missing teeth was positively correlated with age (Figure 1.3) ($r^2=0.267$, $F_{1,405}=148.8$, $p<2.2\times 10^{-16}$). There was a significant difference in dental attrition between eastern and southern Africa. East African skulls had a mean of 1.79 affected teeth, compared to 2.39 in southern Africa (ANCOVA: provenance: $F=7.22$, $p=0.045$, age $F=30.727$, $p=0.0001$). Calculated mean ages also differed between regions, 124.1 months in eastern Africa, and 144.3 in southern Africa.

Table 1.1. Upper tooth fracture in *Crocota crocuta*. I=incisors, C=canines, P=premolars.

	I ¹	I ²	I ³	C	P ¹	P ²	P ³	P ⁴	Total
Number of fractured teeth	12	25	61	71	29	17	29	6	250
Total number teeth examined	847	893	877	874	846	987	989	967	7280
Percentage of fractured teeth	1.42	2.8	6.96	8.12	3.33	1.72	2.93	0.62	3.43

Table 1.2. Pathological oligodonty in upper teeth of *Crocota crocuta*. I=incisors, C=canines, P=premolars.

	I ¹	I ²	I ³	C	P ¹	P ²	P ³	P ⁴	Total
Number of teeth lost	12	5	9	5	51	14	5	3	104
Total number teeth examined	847	893	877	874	846	987	989	967	7280
Percentage of teeth lost	1.42	0.56	1.03	0.57	6.03	1.42	0.51	0.31	1.43

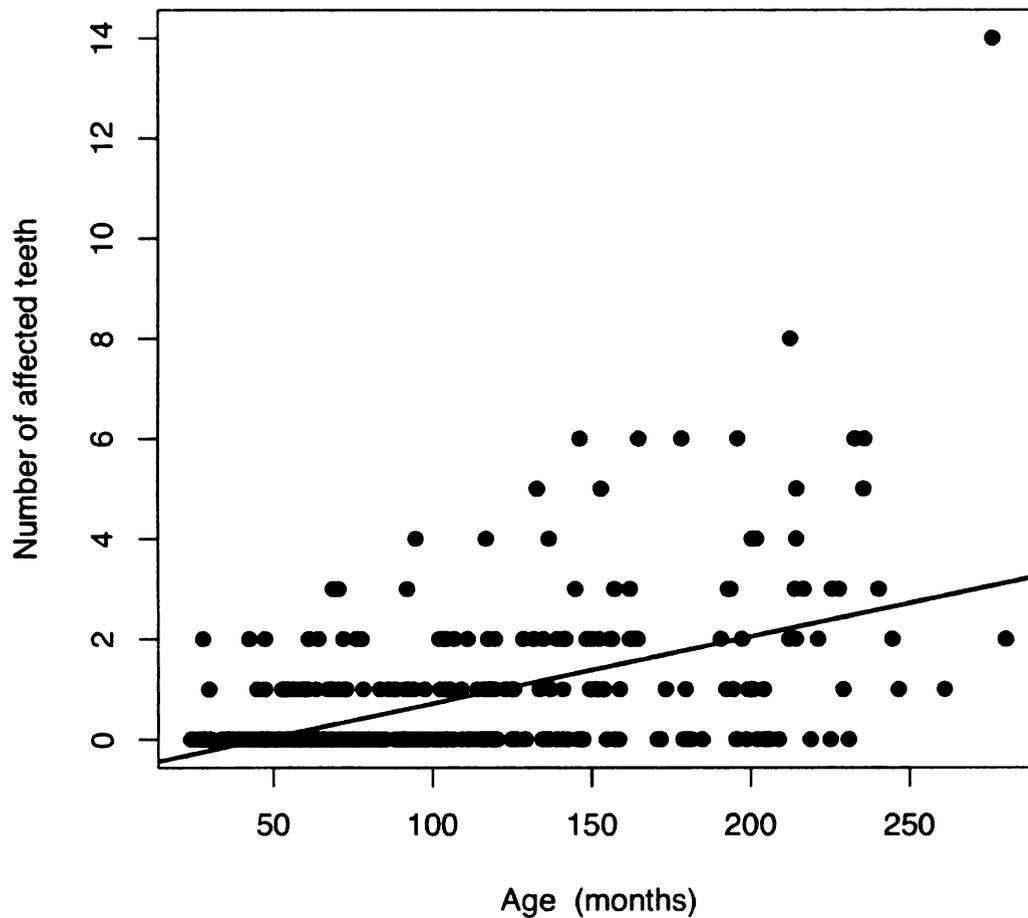


Figure 1.3. Scatterplot of the number of broken and missing teeth against age in months of spotted hyenas. Age was calculated as calculated by a mixed-sex model developed for this species by Van Horn et al. (2003). The line represents a least-square fitted linear regression ($r^2=0.267$, $F_{1,405}=148.8$, $p<2.2\times 10^{-16}$).

Polydonty

Supernumerary teeth were present in the cheek tooth rows of 11 of 472 (2.33%) complete skulls, plus one additional cranium without a mandible. I observed no polydonty of the upper or lower canines or incisors, and no instances of polydonty on both the upper and lower jaws of any single individual.

Anomalous P¹

Anomalous first upper premolars were present in 4 specimens: unilaterally in three specimens from Kenya (NMK-OM 2706 and 7761, and USNM 182082), and one on each side bilaterally in a skull from the Democratic Republic of Congo (AMH 52068) (Figure 1.4). In all cases, P¹ appeared to be abnormally large. On close inspection, a normal P¹ was seen to be fused to a supernumerary tooth sitting directly anterior, resulting in a bifid crown. The anterior tooth was smaller than P¹, and the extent of separation of the roots of the teeth was unclear. Without x-ray examination, it was impossible to determine whether the teeth shared a pulp chamber.

Supernumerary upper molar

A supernumerary tooth is present at the end of the tooth row in the left maxilla of a specimen from Chilongozi Game Reserve, Zambia (BM 65.537; Figure 1.5). A remnant alveolus of M¹ is present at the posterior edge of the palate. The supernumerary tooth appears to have three roots, and is situated lingual to P⁴, which was lost postmortem and is represented by its alveolus. The

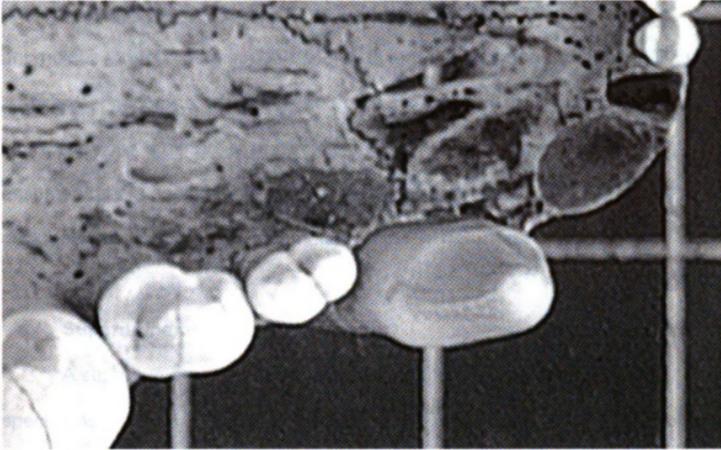


Figure 1.4. Anomalous P¹ (NMK-OM 2706).

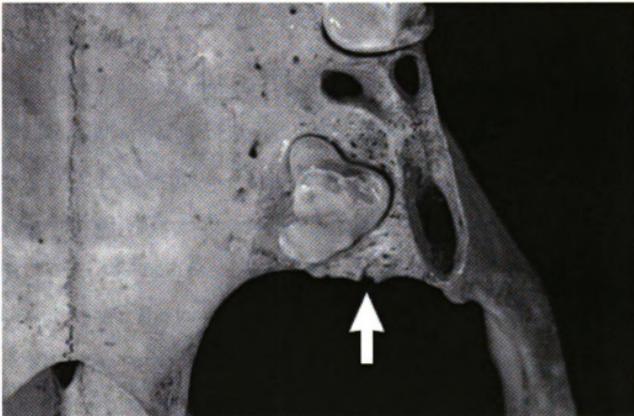


Figure 1.5. Supernumerary molar (BM 65.537). Remnant alveolus of M¹ is indicated by the arrow.

presence of the supernumerary tooth does not affect the position of P⁴. This anomalous tooth has the appearance of an antero-posteriorly contracted P⁴, with a parastyle, paracone, metastyle, and protocone (Figure 1.5). The paracone is worn, and although there is no mandible deposited with this specimen, it is assumed that M₁ would have slid between this supernumerary molar and P⁴ as it occluded with the paracone and metastyle of P⁴.

Supernumerary P₁

A supernumerary first lower premolar, or its alveolus, is present in 6 specimens (Table A.3). When present, the tooth was single-rooted, small, robust, and column-like, situated just anterior and lingual to P₂ (Figure 1.6).

Supernumerary 'P₃'

A supernumerary premolar is present in the left mandible of a specimen from the Masai Mara National Reserve, Kenya (MSU 36364), lingual to P₃ (Figure 1.7). Due to its position with reference to P₃, I refer to this tooth as supernumerary 'P₃'. The tooth has 2 roots, and is intermediate in size between P₂ and P₃. Like P₃, the tooth possesses a paracone and a metacone, and unlike P₂, it lacks a parastyle. The tooth is in the correct orientation with reference to the tooth row; that is, it is not a mirror image of P₃. P₃ is displaced labially and ventrally (Figure 1.7). The post-canine diastema is 0.3 mm, which is shorter than diastemata of other skulls collected in this geographic region (0.86 ± 0.03 , $n=32$). There is evidence that this anomalous premolar was present bilaterally during



Figure 1.6. Supernumerary P₁ (Cambridge 4065).

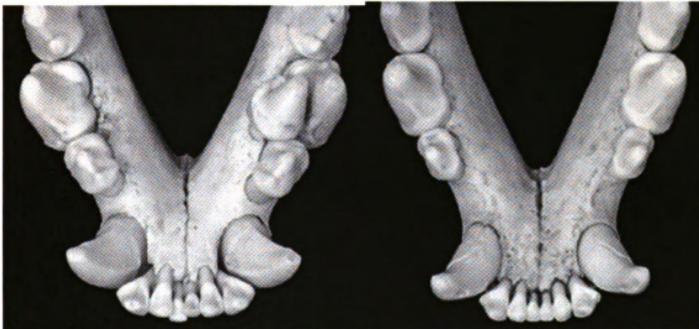


Figure 1.7. Supernumerary 'P₃'. A. Supernumerary tooth in left mandible. B. Normal dentition. Note the difference in post-canine diastema length (MSU 36364).

life, as there is alveolar overgrowth in the same position of the right mandible. P₃ displacement and a shortened diastema are also evident in the right mandible.

Supernumerary M₂

A left M₂ and a right M₂ alveolus are present posterior to M₁ in a skull from Kitanga, Kenya (USNM 161909), and a left M₂ is present in the mandible of a skull from the Balbal plains of Tanzania (BM 39.378). The teeth are very small and each appears to be singly-rooted, with a single, central, pointed cusp (Figure 1.8).

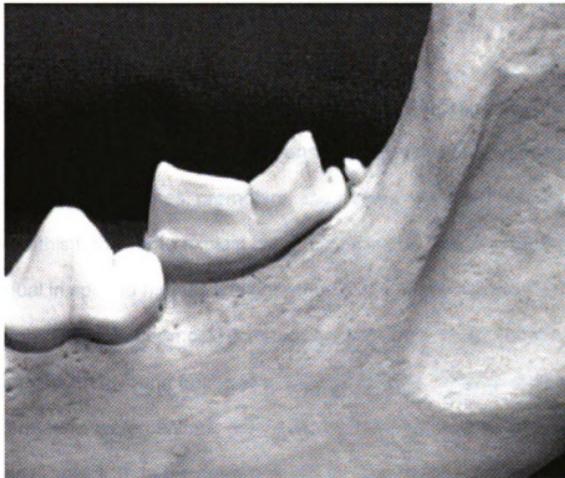


Figure 1.8. Supernumerary M₂ (USNM 161909).

M¹- the variant tooth

I examined the presence of the variable upper molar in a sample of reliably sexed *Crocuta* skulls from a single collection site in northeastern Tanzania. M¹ is present bilaterally in 59% (44/74), and on at least one side in 85% (63/74) specimens. There is no difference in mean age between hyenas that possessed at least one M¹, and those that did not (Welch t-test for unequal variances, $t=-0.6808$, $df=16.548$, $p=0.5054$). Skulls from 86% (37/43) of males, and 83% (26/31) of females possess M¹ on at least one side, indicating that there is no sex bias (Fisher's Exact test for small sample sizes, $p=0.7592$).

DISCUSSION

The perils of durophagy

Spotted hyenas regularly process and consume large pieces of bone from their prey. Van Valkenburgh (1996) demonstrated that spotted hyenas utilize all tooth types (incisors, canines, premolars, and molars) when processing bone, and invoked this behavior to explain her finding that the rate of tooth breakage per individual in spotted hyenas is higher than that of other carnivores (Van Valkenburgh, 1988). In her most recent study Van Valkenburgh (2009) reported that the specific teeth found fractured in spotted hyenas, in order of decreasing relative frequency, were canines, premolars other than P⁴, incisors, and the carnassials (Table 1.3). In the current study, the results for breakage of upper teeth were similar, except that I found relatively more broken incisors than premolars (Tables 1.1 and 1.3). Here, teeth that were completely lost, with

Table 1.3. Order of relative frequency of tooth fracture and/or loss in *Crocuta*, based on the number of broken teeth/number observed. I=incisors, C=canines, P=premolars other than P⁴.

Source of affected teeth	Order of relative frequency of affected teeth
Broken (Van Valkenburgh, 2009)	C=P>I>P ⁴ /M ₁
Broken (this study)	C>I>P>P ⁴
Lost (this study)	P>I>C>P ⁴
Broken + lost (this study)	C>P>I>P ⁴

resorbing or completely overgrown alveoli, in order of decreasing frequency, were premolars other than P⁴, incisors, the canine, and P⁴ (Table 1.3). The most striking difference between the fracture data (Van Valkenburgh, 2009; this study) and the resorption data is that, although canines are broken with the highest relative frequency in spotted hyenas (Table 1.3), the canines show very little alveolar overgrowth (Table 1.2). That is, canines are most frequently broken but rarely ever completely lost. This is probably because once the tip of a canine is broken the tooth is under less stress during prey capture, i.e. if the tooth is still in use, the bending stress of the broken tooth would be much lower, thus the tooth would no longer be under the intense pressure that would lead to further breakdown and eventual loss. Vila, et al. (1993) proposed that inferences could be made about the importance of a tooth to the survival of the animal based on the rate of alveolar resorption; teeth that are lost frequently could be considered to be less important. While there is little doubt that the canine is more important to prey capture than is P¹, the fact that the former is rarely completely lost, while

the latter is frequently so, probably has more to do with the size and placement of the tooth than the effect of the loss of these teeth on survival.

Comparative analyses of breakage and oligodonty

Most studies of tooth loss in carnivores pool congenital and pathological oligodonty. I found no congenital oligodonty in spotted hyenas. Keeping in mind that the present study only considers teeth in the cranium, the 11.5% oligodonty in *Crocuta* is still higher than that seen in *Vulpes vulpes* (2.8%, Szuma, 1999; 8.6%, Gisburne and Feldhamer, 2005), or *Canis lupus* (3.4%, Buchalczyk et al., 1981), but lower than that seen in *Urocyon cinereoargenteus* (19.8%, Gisburne and Feldhamer, 2005). A study that separated pathological from congenital oligodonty in gray wolves reported 12.4% pathological loss (Vila et al., 1993).

Van Valkenburgh (1988) found that wolves and spotted hyenas are similar in terms of the overall incidence of tooth fracture, which is elevated compared to other large carnivores. Comparison of complete tooth loss in these two species, both of which include bone in their diets, also reveals many similarities (Table 1.4). As in wolves (Vila et al., 1993) tooth loss in spotted hyenas is highest at the first premolar, and tends to decrease toward the carnassials. Both spotted hyenas and wolves show low rates of loss at the canine. Another parallel is in the loss pattern of the incisors. The relative frequency of loss is the same in both species: the highest rate of loss is seen in the first incisor, followed by the third and second incisors ($I^1 > I^3 > I^2$).

Table 1.4. Rates of complete tooth loss in the upper teeth of spotted hyenas and wolves (number lost/number observed, multiplied by 100).

	I ¹	I ²	I ³	C	P ¹	P ²	P ³	P ⁴	M ¹	M ²
Spotted hyenas (this study)	1.42	0.56	1.03	0.57	6.03	1.42	0.51	0.31	NA	NA
Wolves (Vila et al., 1993)	1.31	0.49	0.82	0	2.60	1.31	1.47	0.33	0.65	0.98

Van Valkenburgh (1988) suggested that the high fracture rate in spotted hyena premolars indicates inferior safety factors within these teeth relative to those in other predatory carnivores. A safety factor is the ratio of the breaking stress of a tooth to the estimated maximum stress expected in ordinary use. She concluded that the durophagous diet of *Crocuta* regularly places loads on the premolars that exceed the ability of these teeth to withstand breakage. However, because Van Valkenburgh (1988) grouped P¹⁻³ together, her premolar fracture count was undoubtedly strongly influenced by the high rate of breakage at P¹. Carnivore premolars are quite variable in size and shape (e.g., see Figure 1.1). Rather than lumping premolars into a single group, and comparing spotted hyena premolars to premolars in other carnivore species, a more appropriate comparison would be to compare the teeth responsible for processing bone among species. In the upper dentition of spotted hyenas, the teeth that perform the majority of the bone-cracking are P³, and to a lesser extent, the protocone of P⁴ (Ewer, 1954). Wolves do not crack bones, but rather crush them using the post-carnassial molars (Werdelin, 1989). Wolves show higher rates of loss in the bone-processing teeth (M¹⁻²) than do spotted hyenas (P³⁻⁴; see Table 1.4). That

is, although spotted hyenas do fracture and sometimes lose their bone-cracking premolars, this loss occurs at a lower rate than that among wolf teeth with the same function, indicating that the bone-cracking premolar teeth in spotted hyenas are indeed relatively resistant to attrition.

Effects of age and competition on dental attrition

Tooth fracture should correlate with the age of the animal (Fenton et al., 1998; Van Valkenburgh, 1988; Van Valkenburgh, 2009). A trend for increased tooth fracture with increased tooth wear has been described in several large carnivore species, indicating an association between age and tooth breakage (Van Valkenburgh, 2009). Here, I demonstrated a significant positive correlation of dental attrition with age (Figure 1.3).

Rates of tooth fracture may be associated with the level of feeding competition to which an animal is exposed. Higher rates of tooth fracture are seen in Pleistocene carnivores, where feeding competition was relatively high, than in their Recent counterparts where feeding competition is lower, even where tooth wear indicates that mean ages do not differ (Van Valkenburgh and Hertel, 1993; Van Valkenburgh, 2009). Here I found a relationship between attrition and competition level, but attrition was higher in southern Africa where feeding competition is lower, than in eastern Africa, opposite of expectations. Age may have affected this result, as the skulls from southern Africa were from older animals, on average. Although the sample size from southern Africa was too

small to test the hypothesis, it is possible that spotted hyenas live longer in areas of lower competition.

Historical significance of polydonty

Although Wozencraft (1989) cited the loss of P₁ as a synapomorphy uniting Felidae and Hyaenidae, the absences of P₁ and of M₂ are derived characters within the advanced bone-cracking hyaenids (Werdelin and Solounias, 1991) (Figure 1.9). During the evolution of the Hyaenidae, P₁ is lost independently in many lineages at the transition from the late Miocene, when hyaenids evolved from small insectivore/omnivores to carnivorous cursors (Werdelin and Solounias, 1990; Werdelin and Solounias, 1991; Werdelin and Solounias, 1996)). The loss of M₂ likely occurred more than once, and was often coupled with the loss of P₁ (Werdelin and Solounias, 1991).

Where P₁ occurs in extant *Crocuta* (Figure 1.6), it has similar dimensions and is in a similar position as seen in its sister taxon (*Adcrocuta exima*), and in other early bone-cracking hyaenid species (Figure 1.9). In contrast, M₂ as seen in modern *Crocuta* does not resemble the larger quadrituberculate M₂ seen in the transitional bone-cracking species of hyaenid (*Ikelohyaena abronia*, (Hendey, 1974); *Palinhyaena reperta*, (Werdelin, 1988); *Lyceeaena lycyaenoides*, (Qiu, 1987); *Belbus beaumonti*, (Solounias and de Beaumont, 1981)), the most recent hyaenids to possess the tooth (Figure 1.9). Therefore, M₂ in extant spotted hyenas offers a glimpse at a transitional form of M₂ during the evolutionary loss

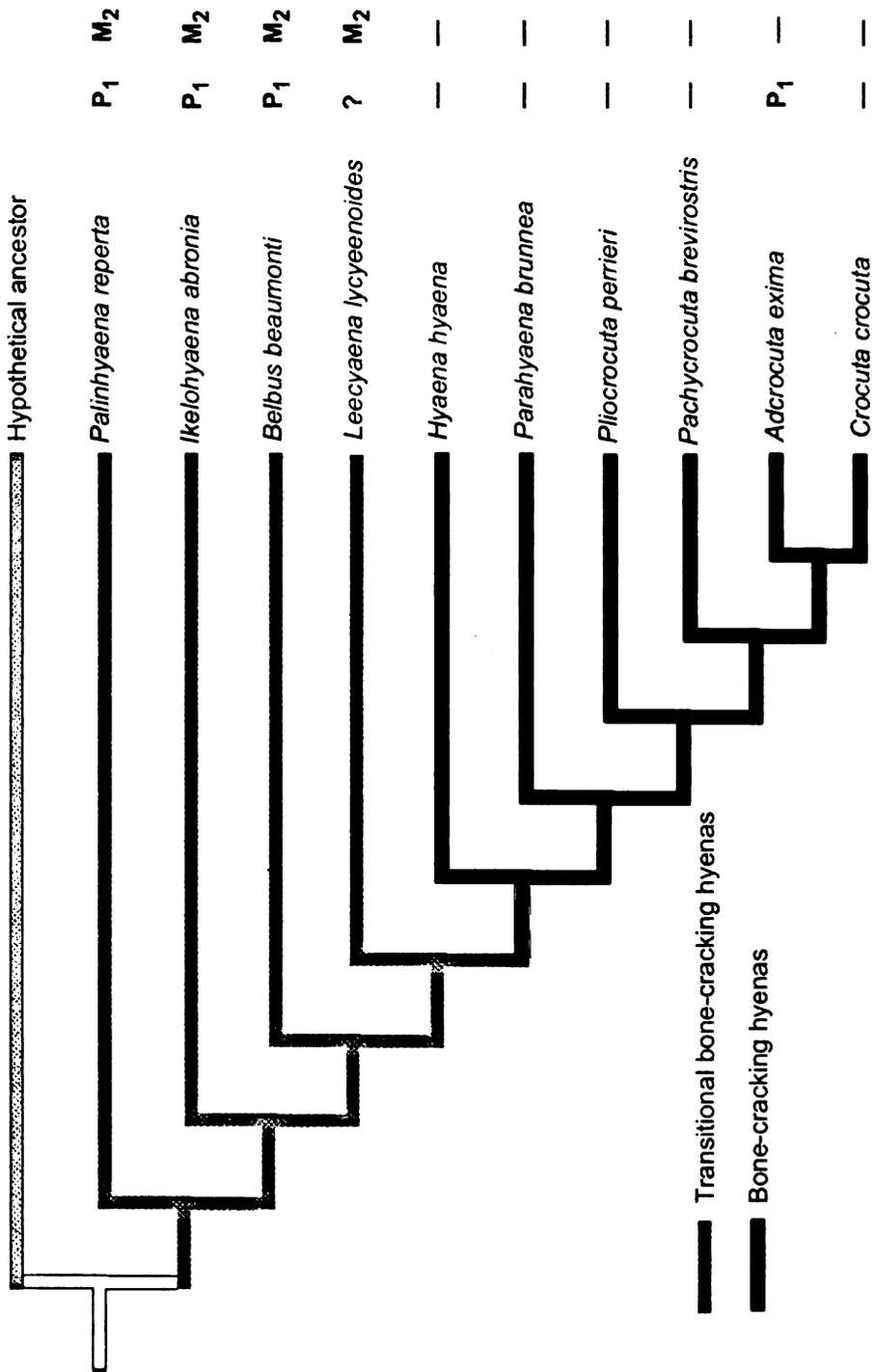


Figure 1.9. The presence of P₁ and M₂ in recent ancestors of *Crocuta*. Phylogeny after Werdelin and Solounias (1991).

of this tooth within the bone-cracking hyaenids, suggesting that a reduction in size over evolutionary time preceded complete loss (Figure 1.8).

Wolsan (1989) warned against classifying supernumerary teeth as atavisms or anomalies when they may just be polymorphisms within a range of morphological variation. Atavism is indicated by the apparent reappearance of a character that was absent in the animal's recent ancestors, but was present in all members of an ancestral population or taxon (Hall, 1984). As evolutionary reduction in tooth number in mammals begins at the level of the first premolar and the last molar, and moves inward toward the carnassials (Ziegler, 1971), supernumerary teeth at the anterior and posterior extremes of the cheek tooth row are more likely to be atavistic than supernumerary teeth within the tooth row. The argument that a supernumerary tooth be considered atavistic is further strengthened by the identification of a homologue in related fossil taxa, as seen for both P_1 and M_2 .

A supernumerary tooth that cannot be classified as a retained deciduous tooth, or as an atavistic tooth, may have resulted from developmental disturbance to the tooth bud. Partial splitting of a single bud, or gemination, can result in a tooth with a single root and pulp chamber, but two crowns. The tooth looks abnormally large, and the crowns may be completely split, or separated by a groove or notch (Langlais and Miller, 2002; Tannenbaum and Alling, 1963). Complete splitting of a single bud, or twinning, results in a supernumerary tooth that is the mirror image of the normal tooth (Tannenbaum and Alling, 1963). The four anomalous P^1 teeth described here appear to be the result of gemination

(Figure 1.4). Although it is unknown whether the two crowns share the same root and pulp chamber, they are separated by a groove in each case, resulting in what appears to be a single tooth that is larger than normal, but that probably does not seriously influence function.

The supernumerary 'P₃' (Figure 1.7) is also the result of developmental disturbance. The tooth has no homologue in the recent evolutionary history of the bone-cracking hyaenids, and is of similar size and shape as P₃. The supernumerary tooth is not a mirror image of the normal tooth, but this is not a requirement for gemination according to most authors (see Verstraete, 1985).

Taken together, the data presented in this chapter support the assertion that a durophagous diet is damaging to an animal's dentition, but these data also demonstrate that the teeth of hyenas are up to the challenge. Although the teeth of spotted hyenas are regularly subject to high forces, the teeth responsible for the majority of the bone-cracking action, P³⁻⁴, experience less attrition than the bone processing teeth in wolves. These data would be strengthened by work that models the forces exerted on the bone-cracking teeth, and the ability of the teeth to withstand those forces.

As there is little polydonty or oligodonty at the carnassials of carnivores, it has been suggested that these teeth are evolutionarily conserved e.g. (Gisburne and Feldhamer, 2005). The data presented here indicate that the bone-cracking P³ in spotted hyenas, with low levels of loss during life and zero observed polydonty, is also highly conserved.

CHAPTER TWO

SEXUAL DIMORPHISM IN THE SPOTTED HYENA (*CROCUTA CROCUTA*), A REASSESSMENT: ARE FEMALE SPOTTED HYENAS TRULY LARGER THAN MALES?

INTRODUCTION

Sexual dimorphism is defined as any difference between males and females of the same species, manifested as a physiological, behavioral, or morphological difference (Glucksman, 1974). Sexual dimorphism is widespread among mammals, where it is most commonly expressed as a sex difference in weapon or body size. In contrast to other vertebrate Classes, sexual dimorphism in mammals is typically male-biased, such that males are larger and/or have more robust weapons than conspecific females (Andersson, 1994). The reason for this male-biased pattern of dimorphism is well established, with sexual selection shaping and maintaining differences between the sexes (Darwin, 1871; Trivers, 1972). Specifically, in most mammalian species, males compete directly or indirectly with other males for mating access to females, and as a result, males have been favored that possess relatively large bodies or weapons. In conjunction with their larger size and superior armaments, males are socially dominant to females in most species of mammals, they have higher priority of access to food than females, and they are also often more pugnacious than females (Bouissou, 1983; Trivers, 1972).

There are only a few species of mammals in which females are socially dominant to males. We define female dominance as the ability of adult females to win against adult males in contests over resources, and to evoke submissive

behavior from males in dyadic contexts. Mammalian species in which females dominate males include two species of mole-rats (Clarke and Faulkes, 1997), several species of lemurs (Kappeler, 1993), and spotted hyenas (*Crocuta crocuta*) (Kruuk, 1972). In many of these cases, it is not clear whether social dominance by females is associated with a female-biased sexual dimorphism in body size (Brett, 1991; Kappeler, 1991). Here we explore this question in spotted hyenas.

Naturalists have historically experienced substantial difficulty distinguishing male from female spotted hyenas. Sexual dichromatism is absent, and the external genitalia of the female are so heavily “masculinized,” that spotted hyenas were long believed to be hermaphrodites (Glickman, 1995). The sexual dimorphism in the shape of the glans of the phallus, which allows sex determination in the field, was not described until 1990 (Frank et al., 1990). Although Matthews (Matthews, 1939a) unequivocally put the myth of the hermaphroditic hyena to rest with his detailed description of internal and external reproductive anatomy in both sexes, distinguishing between living male and female *Crocuta* nonetheless remains difficult. The literature contains conflicting reports regarding whether or not female-biased sexual size dimorphism occurs in this species, and estimates of the degree of sexual size dimorphism in *Crocuta* vary considerably for several characteristics, including head and body length, body mass, girth, skull condylobasal length, and zygomatic arch breadth (Table 2.1).

Table 2.1. Published accounts of sexual dimorphism, or lack thereof, in *Crocota crocuta*. BL= body length, CBL= skull condylobasal length, HBL= head-body length, SH= shoulder height, ZB= zygomatic breadth. van Jaarsveld (1988) n=30 total, but numbers of males and females were not reported. Matthews (1939b) did not perform statistical analyses, but did demonstrate that the median size of females was larger than that of males.

Females>Males	Females=Males	# males	# females	Locality	Reference
HBL	CBL, ZB	63	40	Tanzania	Matthews (1939b)
Mass***		12	8	Tanzania	Kruuk (1972)
BL*, CBL*, ZB***	Mass, SH	5	5	South Africa	Skinner (1976)
	Mass, HBL	13	12	South Africa	Whateley (1980)
Mass†		5	5	Kenya	Neaves et al. (1980)
Mass**, girth**	HBL	25	18	Kenya	Hamilton et al. (1986)
Mass*, girth*	SH	8	6	South Africa	Henschel (1986)
	HBL, SH			South Africa	van Jaarsveld et al. (1988)
Mass†, girth*	HBL	9	7	South Africa	Mills (1990)
	Mass, girth, HBL	5	9	Kenya	Sillero-Zubiri and Gottelli (1992b)

† $P < 0.001$, *** $P < 0.01$, ** $P < 0.02$, * $P \leq 0.05$

There are a number of possible explanations for the conflicting data summarized in Table 2.1. First, whether or not individuals are measured during the breeding season might contribute to variation in mass and girth in both males and females. However, *Crocuta* are aseasonal breeders (Kruuk, 1972; Lindeque and Skinner, 1982), so we can discount that possibility here. Second, the discrepancies may be due to small sample sizes and inadequate statistical power. In those studies reporting female-biased sexual size dimorphism in *Crocuta*, the difference between males and females was slight. The F/M ratio in raw body mass ranges from 1.09–1.20 (Hamilton et al., 1986; Kruuk, 1972; Mills, 1990; Neaves et al., 1980; Skinner, 1976; van Jaarsveld et al., 1988) compared to a mean F/M ratio of 0.62 for the most male-biased mammalian taxa (Weckerly, 1998). As the differences documented between male and female *Crocuta* have been slight, and sample sizes in most studies have been small (Table 2.1), larger sample sizes may be required to demonstrate significant differences between males and females in some measures. Third, age may play a role if subadult individuals are measured along with adults. Spotted hyenas exhibit a relatively slow postnatal growth rate, continuing to develop both cranially (Tanner et al., 2009) and postcranially (van Jaarsveld et al., 1988) after attainment of sexual maturity. Finally, the disparities may reflect geographic variation in the strength of sexual size dimorphism in this species. The studies included in Table 2.1 were undertaken over a range of about 30 degrees in latitude. When sexual dimorphism is present within other mammalian species, the magnitude of the sex differences can vary with geography (e.g., raccoons, (Ritke and Kennedy, 1993);

bobcats, (Dobson and Wigginton, 1996); *Mustela* spp, (Ralls and Harvey, 1985). Ralls (1976) suggested that geographic variation in the strength of sexual dimorphism among *Crocuta* might be substantial.

The conflicts apparent in earlier published accounts of dimorphism in *Crocuta* led Frank (1986a) to conclude “earlier assertions that the female is larger are not strictly correct” (p. 1524). Our aims here were twofold. The first was to use large samples of museum specimens to compare male and female spotted hyenas with respect to cranial size and shape, and use large samples of living individuals to compare males and females with respect to body mass and linear body size measures. Our second goal was to evaluate the effect of sample size on the detection of sexual dimorphism in this species.

METHODS

Skull Samples

Given the difficulties inherent in assigning sex to spotted hyenas, we were reluctant to trust the sex assignments of specimens housed in museum collections. Many *Crocuta* specimens at visited museums were catalogued without sex information, and several specimens in the Natural History Museum, London were labeled “both sex”. Here we used only two large and reliably sexed groups of specimens. The first, from the Natural History Museum, London, consisted of specimens collected by L. Harrison Matthews on the Ol Balbal plain in what is now the Ngorongoro Conservation Area (NCA), northeastern Tanzania (decimal latitude and longitude, -3.0, 35.467). Matthews (1939a) used dissection

to conduct a detailed study of the reproductive tracts of the same animals from which he collected the skulls measured here, so we are confident that his sex assignments were correct. For our analyses, we used 75 (44 adult males and 31 adult females) of the 103 specimens that Matthews collected, excluding specimens that were damaged or not adults (Table A.4). To be considered adult, a specimen had to have complete or nearly complete closure of the lambdoid and basilar sutures, and tooth wear such that the bilateral mean of the length of the occlusal surface of the third lower premolar was at least 5.0 mm. Age, as estimated to +/- 6 months based on tooth wear (Van Horn et al., 2003), did not differ significantly between the males and females in this sample ($t=-0.718$, $d.f.=73$, $P=0.4749$).

The second set of specimens was collected by KEH and colleagues in the Masai Mara National Reserve (MMNR) in southwestern Kenya (-1.417, 34.917); this set is housed in the collections of the Michigan State University Museum. This set includes 10 adult males and 22 adult females (Table A.4). These specimens were judged to be adult based on the same criteria morphological outlined above, and average age of the sexes did not differ significantly in this sample ($t=0.189$, $d.f.=30$, $P=0.8511$). We kept the NCA and MMNR samples separate throughout our analyses to avoid the potential confound of geographic variation in dimorphism.

Image capture and data acquisition

We used two-dimensional geometric morphometrics to evaluate sexual dimorphism in the spotted hyena skull. The use of geometric morphometrics to assess sexual dimorphism offers not only powerful methods for looking at size differences, but also allows evaluation of variation in shape (Hood, 2000; Leigh and Cheverud, 1991). Photographs of skulls were taken with a Fuji FinePix S1 Pro digital camera fitted with a Nikon AF Nikkor 28-80 mm lens. Images were saved directly to a laptop computer. A 1 cm scale was included in all photographs for all views. Three views were captured for each skull: ventral cranium, lateral cranium, and lateral mandible (Figure 2.1). Views of some NCA specimens were excluded from analysis because of damage that obscured one or more landmark locations (see Table A.5 for landmark locations, and Table A.4 for specimen list).

Landmarks, points presumed homologous across specimens, were selected so as to provide even coverage, and digitized using tpsDig 2.10 (Rohlf, 2005). Fusion of the sutures associated with the braincase is typically complete in adult *Crocuta* (Schweikher, 1930), particularly along the sagittal crest, and there are few structures that make for suitable homologous landmarks on the mandible. Therefore, semi-landmarks, points evenly spaced along curves beginning and ending at homologous landmarks, were used in the lateral cranium and mandible views to capture the overall shape of the specimen (Bookstein, 1997).

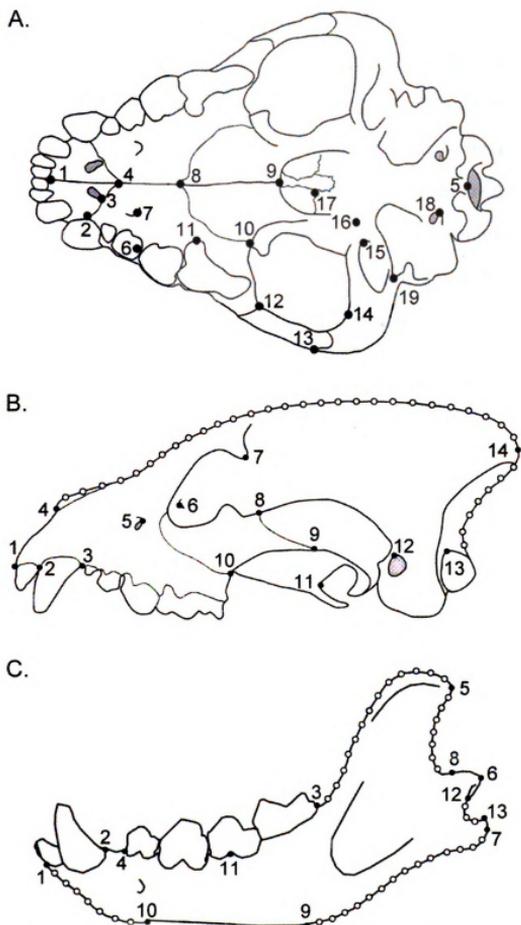


Figure 2.1. Landmarks (closed circles) and semi-landmarks (open circles) for A) ventral cranium, B) lateral cranium, and C) lateral mandible views. Numbers on landmarks correspond to descriptions in Table A.5

In the ventral view (Figure 2.1A), specimens were arranged such that the palate was parallel to the photographic plane. Landmarks were placed bilaterally and at the midline, but to avoid inflating degrees of freedom for subsequent analyses, the coordinates of bilaterally homologous landmarks were reflected across a baseline extending from landmark 1 to landmark 5 (Figure 2.1A) and averaged (BigFix, Sheets, 2001), yielding 19 total landmarks. In the lateral cranium view (Figure 2.1B), specimens were oriented such that the sagittal plane was parallel to the camera lens. Lateral crania were digitized with 14 landmarks and 35 semi-landmarks. In the lateral mandible view (Figure 2.1C), specimens were oriented such that the corpus of the mandible bone was parallel to the camera lens. Lateral mandibles were digitized with 13 landmarks and 44 semi-landmarks.

Analyses

Landmark and semi-landmark data were aligned with a Generalized Least-Squares Procrustes superimposition algorithm using CoordGen (Sheets, 2006) for the ventral cranium view, and SemiLand (Sheets, 2003a) for the lateral cranium and lateral mandible views. This removes data unrelated to shape, such as position, scale, and rotation (Rohlf and Slice, 1990; Zelditch et al., 2004). Procrustes distance was used to quantify the magnitude of sex differences in shape, which were tested using a resampling-based Goodall's *F*-test with 1600 bootstraps (Bookstein, 1996; Zelditch et al., 2004). Goodall's *F* tests were conducted using TwoGroup (Sheets, 2003c).

Our measure of skull size was centroid size, defined as the square root of the summed distances of the landmark points from the geometric center of the specimen. Differences between sexes in skull size were evaluated in R (R Development Core Team, 2009) using Student's-t tests.

Body measurements

We used three data sets to explore sex differences in body measures of spotted hyenas. The first consisted of matched head-body length measures from the 75 (44 male, 31 female) NCA specimens used in the analyses of skull size and shape. These data were collected from the catalogue and specimen tags at the Natural History Museum, London. The animals were measured by Matthews (Matthews, 1939b) post-mortem in the field to the nearest 0.5 in, which we converted to cm.

The second data set contained body measurements taken from wild **MMNR** animals anaesthetized during a longitudinal behavioral study conducted by KEH and colleagues. The data included measurements from 182 adults (75 **m**ales and 107 females) between the ages of 36 and 130 months, although **s**ample sizes for some measures are slightly smaller. The mean ages of males **a**nd females did not differ significantly in this sample ($t=0.63$, $d.f.=181$, $P=0.5319$).

Hyenas were anesthetized with Telazol (6.5 mg/kg; Fort Dodge Animal **H**ealth, Fort Dodge, IA) administered in a dart using a CO2-powered rifle (**T**elinject Inc., Agua Dulce, CA). Immobilizations were carried out according to

the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Gannon et al., 2007), with the approval of the Michigan State University Institutional Animal Use and Care Committee and the Kenyan Ministry of Education, Science, and Technology. Total body mass was measured for each darted hyena with a digital scale to within 0.1 kg. Linear body measures were taken with a cloth tape measure to within 0.1 cm, along one side of the body.

Thirty-one morphological measurements were routinely collected from darted hyenas, but to facilitate comparison of our data with those from previous studies, we focused on measures that were used most commonly by earlier workers. In addition to body mass, these included the following linear measurements: 1) head-body length: distance from the tip of the rhinarium to the base of the tail, measured along the sagittal midline and vertebral column; 2) neck circumference: circumference of the neck, measured midway between the shoulders and the head; 3) girth: circumference of the torso, measured immediately posterior to the forelegs, with the forelegs perpendicular to the body; 4) shoulder height: distance from the bottom of plantar pad of the forepaw to the cranial angle of the scapula, measured with foreleg extended perpendicular to the vertebral column; 5) head circumference: circumference of the head measured at the widest point of the zygomatic arches; 6) zygomatic to top of crest: distance from the widest point of the zygomatic arch dorsally to the sagittal crest, measured at a right angle to the sagittal plane; 7) zygomatic to back of

crest: distance from the widest point of the zygomatic arch postero-dorsally to the external occipital protuberance.

The third data set contained body measurements from captive spotted hyenas housed at the University of California, Berkeley Field Station for the Study of Behavior, Ecology, and Reproduction (UCB). These animals were all born in captivity, bred from animals collected in Narok District, Kenya, near the MMNR. Measurements were taken from 32 adults (19 males and 13 females) between the ages of 36 and 130 months. The mean ages of males and females did not differ significantly in this sample ($t = -0.51$, $d.f. = 30$, $P = 0.6124$). Each captive hyena was fed a uniform daily diet of 0.9-1.4 kg of Nebraska Brand standard feline diet (Central Nebraska Packing, Inc., North Platte, Nebraska, 69103). Animals were measured while immobilized with a combination of ketamine (maximum 10mg/kg; 100mg/ml), xylazine (1mg/kg; 100 mg/ml), and atropine (0.045 mg/kg; 15 mg/ml) administered via a dart (Telinject Inc., Agua Dulce, CA) using a blow-pipe (Addison Biological Laboratory, Inc., Fayette, MO). Total body mass, head-body length, and shoulder height were measured as described above. After all measurements were taken, xylazine sedation was reversed with yohimbine (0.075-0.12 mg/kg intravenously or intramuscularly; 2 mg/ml; Lloyd Incorporated, Shenandoah, IA).

Analyses

All analyses of body measures were performed in R on natural log-transformed values. Student's *t*-tests were performed on postcranial measures,

and *P*-values were corrected with a Bonferroni sequential step-down adjustment to control for use of multiple comparisons (Holm, 1979). Postcranial measures and body mass were analyzed together, separately from cranial measures.

We also conducted power analyses on head-body length, body mass, and girth of MMNR hyenas to determine the effect of sample size on detection of a significant sex difference in body size. These variables were selected because they are commonly presented in published accounts that address sexual size dimorphism (e.g., Hamilton et al., 1986; Mills, 1990; Sillero-Zubiri and Gottelli, 1992a). For each variable, we simulated power curves by calculating *t*-test *P*-values for successive sample sizes, created using the original measurement data, from *N*=5 males and 5 females until the simulated power was asymptotic. For each successive sample size (*N*), we created 500 independent, random sub-samples (with replacement) of the original data. For each value of *N*, power was calculated as the proportion of those 500 sub-samples with a significant difference between males and females at $\alpha=0.05$. We *a priori* selected 80% power as the minimum a test would need to consistently detect a significant difference. Our simulations estimate the minimum sample size needed to achieve 80% power. We calculated the mean and confidence intervals of the minimum sample size from 50 replications of the simulation described above, using the adjusted bootstrap percentile (BCa) method (Efron, 1987) from the “boot” library of the R program (Canty, 1998).

RESULTS

Skull Morphology

Males and females from our two populations of East African spotted hyenas (MMNR and NCA) did not differ significantly with respect to skull centroid size in the ventral, lateral cranium, or lateral mandible views, although females tended to be larger in both populations (Table 2.2). Furthermore, we found no significant sexual dimorphism in skull shape in ventral, lateral cranium, or lateral mandible views (Table 2.2).

Table 2.2. Sex differences in size and shape of spotted hyena skulls from two East African populations, Masai Mara National Reserve (MMNR) and Ngorongoro Conservation Area (NCA), based on a geometric morphometric analysis. Landmarks for these analyses are as in Figure 2.1. Skull size: mean centroid size ($\bar{x} \pm SE$) for males and females, and Student's-*t* results on centroid size. Skull shape: resampling-based Goodall's *F*-test results on Procrustes superimposition.

	View	Skull size					Skull shape	
		N	Sex	Mean centroid size	<i>t</i> _{d.f.}	<i>P</i>	<i>F</i>	<i>P</i>
MMNR	Lateral	10	M	648.7±7.9	0.93 ₃₀	0.36	0.72	0.70
		22	F	656.0±3.9				
	Ventral	10	M	295.5±3.0	0.83 ₃₀	0.41	1.04	0.37
		22	F	298.6±2.2				
	Mandible	10	M	631.5±7.3	1.19 ₃₀	0.24	0.68	0.65
		22	F	641.4±4.6				
NCA	Lateral	44	M	621.3±3.3	1.22 ₇₃	0.23	0.89	0.51
		31	F	627.6±4.1				
	Ventral	42	M	295.8±1.6	1.36 ₇₁	0.18	0.59	0.86
		31	F	299.6±1.9				
	Mandible	43	M	631.6±2.8	0.07 ₇₀	0.94	1.16	0.28
		29	F	631.3±3.9				

Table 2.3. Body mass and linear measures of living animals. Raw mean values for males and females ($\bar{x} \pm SE$), mass in kg, all other measures in cm. Student's *t*, with Holm sequential Bonferroni adjustment for multiple tests, on natural log-transformed variables.

	Males		Females				
	N	$\bar{x} \pm SE$	N	$\bar{x} \pm SE$	M/F*	<i>t</i> _{d.f.}	<i>P</i>
Body mass							
MMNR	65	51.7±6.4	87	58.4±6.3	0.96	6.51 ₁₅₀	4.35x10 ⁻⁹
Berkeley	19	49.0±1.3	13	55.6±2.0	0.96	2.89 ₃₀	0.0071
Head-body length							
NCA	44	118.5±0.9	31	123.1±1.0	0.96	3.33 ₇₃	0.0014
MMNR	75	124.7±14.4	107	127.3±12.3	0.98	3.0 ₁₈₀	0.0068
Berkeley	19	127.2±1.1	13	131.4±1.2	0.97	2.24 ₃₀	0.0193
Girth							
MMNR	74	80.5±9.4	106	83.7±8.1	0.96	4.10 ₁₇₈	0.0003
Neck circumference							
MMNR	74	48.6±5.7	104	50.4±5.0	0.96	3.81 ₁₇₆	0.0005
Shoulder height							
MMNR	74	77.9±9.1	106	78.2±7.6	1.00	0.66 ₁₇₈	0.5382
Berkeley	19	81.7±0.4	13	82.0±0.54	1.00	0.53 ₃₀	0.5996
MMNR Cranial							
Head circumference	75	50.9±5.9	104	52.4±5.1	0.97	4.47 ₁₇₇	4.16x10 ⁻⁵
Zygomatic to top crest	72	12.8±1.5	107	13.2±1.3	0.96	3.26 ₁₇₇	0.0027
Zygomatic to back crest	71	16.9±2.0	107	17.3±1.7	0.98	2.34 ₁₇₆	0.0202

*The ratio of the raw mean male value/ raw mean female value, which is indicative of the strength of sexual dimorphism for a particular measure. Note that for mass, to facilitate comparison with other measures, the ratio presented is that of the cube roots of the means (Ralls, 1976).

Linear measures

Females were larger than males for all seven of the body measurements taken in the field (Table 2.3). In both captive (UCB) and wild populations (MMNR), female spotted hyenas displayed significantly greater body mass. In captive animals and in wild populations from Kenya and Tanzania, the head-body length of females was significantly longer than that in males. Female spotted hyenas from MMNR had significantly greater neck circumference and chest girth than males (these measurements were not collected from either the Tanzanian specimens or captive animals). Neither captive animals nor those from MMNR showed any significant sex difference in height at shoulder (this measure was not collected from Tanzanian specimens). MMNR females were also significantly larger than males in head circumference, and the distances from the widest point of the zygomatic arch to both the top and to the back of the sagittal crest (Table 2.3). F/M ratio of dimorphism for significant linear measures ranged from 1.02 to 1.04. The only measurement for which we did not observe a significant sex difference was shoulder height.

Power analyses of body measures

The results of our power analyses indicate that the sample sizes required to demonstrate female-biased sexual size dimorphism ranges widely, depending upon the variable in question (Figure 2.2 A–C). Detection of a dimorphism in body mass requires a mean sample size of only 14.4 individuals for each sex (95% CI 14.06–14.66). Girth requires a larger sample size, with a mean of 38.9

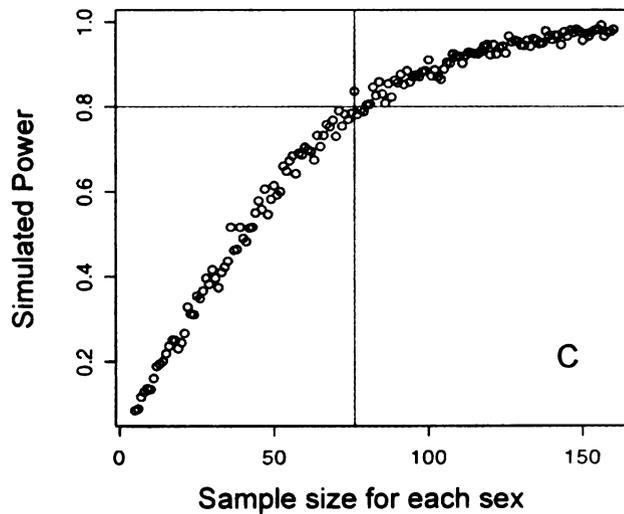
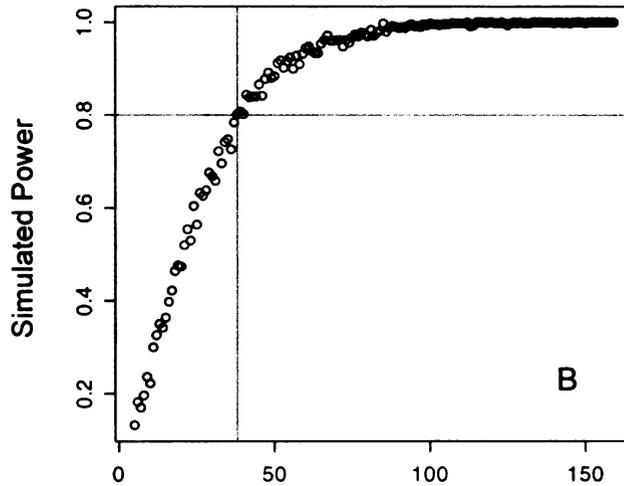
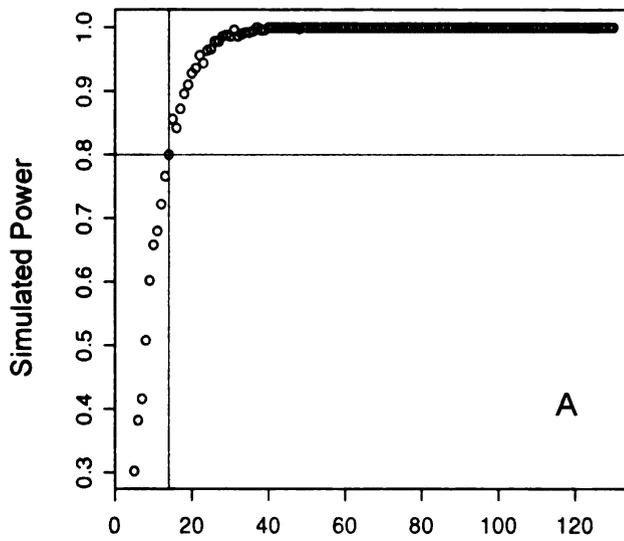


Figure 2.2. Power curves for A) mass, B) girth, and C) head-body length, generated by sampling t-test P-values for successively larger sub-sample sizes of measurement data. Simulated power is calculated as the proportion of samples with t-test p-values less than 0.05. The crossbars indicate the sample size needed for each sex to attain acceptable power (0.8).

individuals of each sex (95% CI 38.22–39.58). Head-body length, which was the characteristic showing the lowest level of dimorphism (Table 2.3), requires a mean sample containing 70.9 members of each sex (95% CI 69.88–71.92).

DISCUSSION

Although our geometric morphometric measurements revealed no sex differences in skull size or shape among adult spotted hyenas, female-biased sexual size dimorphism was nonetheless clearly apparent for body measurements among the animals in our sample. Using data from large numbers of adults in East Africa, we found that female spotted hyenas are approximately 11% heavier, 4% stouter, and 2–4% longer than males. Although females are not taller than males at the shoulder, overall females are huskier than their male counterparts (Table 2.3).

As female spotted hyenas are socially dominant to males, and can displace males from kills in nature, we might reason that males do not reach female size for the simple reason that they have inferior access to food. However, we demonstrated that these female-biased differences in body mass (12%) and head-body length (3%) are evident even among captive-bred animals fed a uniform diet, indicating that sex differences seen in free-living animals are not due to a higher food volume ingested or a higher quality diet afforded to the socially dominant females (see also Glickman et al., 1992).

That we found no sexual dimorphism in skull size or height at the shoulder was initially surprising, given the significant differences in other measurements.

However, it may be that males and females are skeletally isometric, but sex differences in head-body length and girth are explained by differences in muscle or fat mass. Despite finding no difference in skull size, we did observe a significant female bias in head measures from live animals, highlighting the mass of the temporalis and masseter muscles in living hyenas; this too supports the notion that female bias is caused by larger muscle and/or fat mass.

Here we were able to avoid all of the confounding factors that may have been responsible for conflicting results in earlier studies comparing male and female hyenas with respect to body size, including small sample sizes, geographic variation, or inclusion of subadult animals in samples. We could rule out these possibilities here by using large, age-matched samples from eastern Africa.

Our power analyses demonstrated that large sample sizes are required to achieve statistical significance in female-biased sexual size dimorphism in the spotted hyena. The mean total sample size required to elucidate sexual size dimorphism varied substantially among three morphological measures obtained from living hyenas (Figure 2.2 A–C). Of the previous studies of sexual size dimorphism in this species (Table 2.1), only one reached the required sample size for the variable measured (Hamilton et al., 1986), and demonstrated female-biased sexual size dimorphism for body mass. The results of the power analyses highlight the importance of adequate sample sizes required in to detect a dimorphism in taxa where differences are slight.

CHAPTER THREE

SIZE VARIATION IN A WIDE-RANGING CARNIVORE: DO SPOTTED HYENAS (*CROCUTA CROCUTA*) CONFORM TO BERGMANN'S RULE?

INTRODUCTION

Ecogeographical rules seek to describe biogeographic patterns of morphological variation within and among species. Among endotherms, rules have been proposed to explain geographic variation in body size (Bergmann, 1847; Foster, 1964), coloration (Gloger, 1833), and relative appendage size (Allen, 1877). The explanatory power of these rules has been debated in the past (e.g. (Geist, 1987)), but a recent resurgence of interest has been driven by the potential usefulness of these rules in predicting animal responses to global climate change (e.g. Meiri et al., 2009; Millien et al., 2006; Teplitsky et al., 2008). Of particular interest is Bergmann's rule, which predicts that, within genera, species with larger body sizes are found at higher latitudes, and at therefore cooler temperatures (Bergmann, 1847). Mayr (1954) and James (1970) revised the rule to address intraspecific body size clines that vary with temperature.

Early studies inquired whether or not certain species show a latitudinal cline in body size (e.g. Barnett, 1977; Brown and Lee, 1969). While some authors found Bergmann's rule a suitable construct to describe patterns of variation in body size, arguments arose regarding the physiological basis of body size increase in response to decreasing ambient temperature. Scholander (1955) pointed out that insulation from fur and vascular modulation were more effective means to control heat balance than changes in body size, and that the increases in body size observed were negligible in terms of physiological change. Geist

(1987) argued that in order for ambient temperature to be a valid driving force for evolution in body size, changes in body size would have to be nearly exponential to compensate for temperature changes.

Today, Bergmann's rule is regarded as an empirical generalization, and species that show a latitudinal size cline are thought to be responding to some environmental variable or set of variables for which latitude acts as a proxy. What exactly that variable or set of variables may be is open to interpretation. Many environmental variables are intercorrelated, and resolving their contributions and interactions can be challenging (Wigginton and Dobson, 1999). Most treatments of Bergmann's rule address two broad relationships: 1) a negative correlation of body size with temperature, measured as wet bulb temperature (James, 1970), temperature maxima (Yom-Tov and Geffen, 2006), or minima (Castro et al., 1992), and 2) a positive correlation with habitat productivity, measured as actual evapotranspiration (Rosenzweig, 1968), seasonality (Boyce, 1978), or duration of the annual productivity pulse (Geist, 1987).

Klein (1986) proposed that carnivores are more likely to 'obey' Bergmann's rule (defined as response to temperature) than herbivores, as carnivores are removed from direct reliance on herbaceous food supplies, which are affected by temperature variation. McNab (1971) postulated that prey availability may drive latitudinal body size clines among carnivores, and that this may involve not only distribution of prey, but competition with other sympatric carnivorous species. Meiri et al. (2007) found that variation in brown bear (*Ursus arctos*) body size correlates with salmon availability, indicating that spatial

distribution of prey affects body size in this species. Raia and Meiri (Raia and Meiri, 2006) also suggested that prey size might affect variation in carnivore body size.

Species with broad geographical ranges can be used to test the hypotheses that body size varies with latitude or specific ecological variables that might covary to some extent with latitude (e.g., Fuentes and Jaksic, 1979; Gay and Best, 1996; Kennedy and Lindsay, 1984; Sikes and Kennedy, 1992). The spotted hyena, *Crocuta crocuta*, is an excellent candidate for such analyses. Although now fragmented and contracted, the historical range of spotted hyenas extended across most of sub-Saharan Africa to the southern tip of the continent, a range of about 55 degrees in latitude (Kingdon, 1977). Reports of mean body size measures indicate that southern African specimens are larger than those from eastern Africa (Table 3.1). Kruuk (1972) also observed variation in body size, supporting the eastern Africa-southern Africa size dichotomy, and further noted that skull size was larger in specimens from Uganda than from Tanzania. Klein (1986) reported that extant *Crocuta* conform to Bergmann's rule south of the equator, and attributed the observed size cline to temperature-related variation.

Geographic variation in body size in *Crocuta* is also reported in the paleontological literature. Kurten (1956) compared size in extant (South Africa, Tanzania, Uganda, and Somalia) and fossil (Europe and Syria- late Pleistocene) spotted hyenas. He described a cline in size that increased with distance from the equator, both to the north and to the south, which he also attributed to

Bergmann's rule. Similarly, Baryshnikov (1999) invoked Bergmann's rule to explain a northerly increase in size among Pleistocene *Crocuta* of Russia.

Table 3.1. Geographical body size variation in spotted hyenas (*Crocuta crocuta*) (mean \pm standard error, where available).

Locality	Mass (kg)	Head-body length (cm)	Source
Aberdares National Park, Kenya	50.2 \pm 2.97 (N=14)	125.7 (N=14)	Sillero-Zubiri and Gottelli (1992b)
Masai Mara National Reserve, Kenya	51.6 (N=43)	126.1 \pm 4.70 (N=43)	Hamilton et al. (1986); Frank (1986b)
Hluhluwe and Umfolozi Game Reserves, Natal, South Africa	68.4 (N=23)	133.3 (N=25)	Whateley (1980)
Transvaal, South Africa	58.4 \pm 2.18 (N=9)	130.8 \pm 0.09 (N=9)	Skinner (1976)

Several authors have also found body size variation in fossil specimens from the same latitude, but deposited during different geologic time periods. *Crocuta* from glacial periods of Pleistocene Europe are significantly larger than animals found in interglacial sediments from similar latitudes (Klein and Scott, 1989; Kurten and Poulianos, 1977). A similar relationship between temperature and *Crocuta* body size is found in Holocene specimens from South Africa (Klein and Scott, 1989), and Pleistocene specimens from Russia (Baryshnikov, 1999). The variation in body size through geologic time is attributed to climate variation, such that larger body size in *Crocuta* is associated with colder ambient

temperatures (Baryshnikov, 1999; Klein and Scott, 1989; Kurten and Poulianos, 1977).

Observed body size variation in extant *Crocuta*, coupled with paleontological evidence, indicates that this species may indeed conform to Bergmann's rule. The paleontological data indicate that a latitudinal cline in body size within the species may correlate with a cline in ambient temperature. In fact, temperature and body size seem to be so tightly correlated, that Klein and Scott (1989) suggested that the size of fossil spotted hyenas could be used to predict paleotemperature. The purpose of this chapter is to document and describe the pattern of size variation in extant *Crocuta* on both sides of the equator, and examine the relationship between size variation and selected environmental variables. First I determine the relevance of centroid size, condylobasal length, and the length of the first lower molar as proxies for body size. I then evaluate the relationship of body size variation with that of latitude, longitude, minimum temperature, precipitation, and ungulate diversity. Finally, I re-evaluate the notion that spotted hyenas conform to Bergmann's rule.

METHODS

Body size data are often not recorded with large mammal specimens deposited in museums, so it is necessary to use a proxy measure to examine body size variation. Traditionally, the condylobasal length of the skull (CBL), the distance from the anterior edge of the premaxillae to the posterior facets of the occipital condyles, has been used to estimate body size. When skulls are

incomplete, as is often the case for fossils, the length of the first lower molar (M_1 length) is used. With the advent of geometric morphometric approaches to the study of skull morphology, authors have used centroid size (CS) as a proxy for body size (e.g., Cardini et al., 2007; Frost et al., 2003). Centroid size, the size metric used in geometric morphometrics, is the square root of the summed distances of the landmark points from the geometric center of the specimen.

To determine which metric would be the best proxy for body size in spotted hyenas, I measured CBL, M_1 length, and ventral cranial, lateral cranial, and lateral mandible CS for 338 adult spotted hyena skulls from museums in the US, Europe, and Kenya (sample sizes for some measures are lower due to incomplete or broken specimens, see Table A.6). Photographs were taken with a Fuji FinePix S1 Pro digital camera fitted with a Nikon AF Nikkor 28–80 mm lens. Images were saved directly to a laptop computer. A 1 cm scale was included in all photographs for all views. M_1 length and CBL were measured from digital photographs of the left lateral mandible and the ventral cranium, respectively, using TMorphGen (Sheets, 2002), which calculates traditional linear measurements with reference to the ruler in the photograph.

Three views were captured for each skull: ventral cranium, lateral cranium, and lateral mandible (Figure 3.1). CS was calculated for all three views. Landmarks were selected so as to provide even coverage (Table A.5), and digitized using tpsDig 2.10 (Rohlf, 2005). Fusion of the sutures associated with the braincase is complete in adult *Crocuta* (Schweikher, 1930), especially along the sagittal crest, and there are few structures that make for suitable homologous

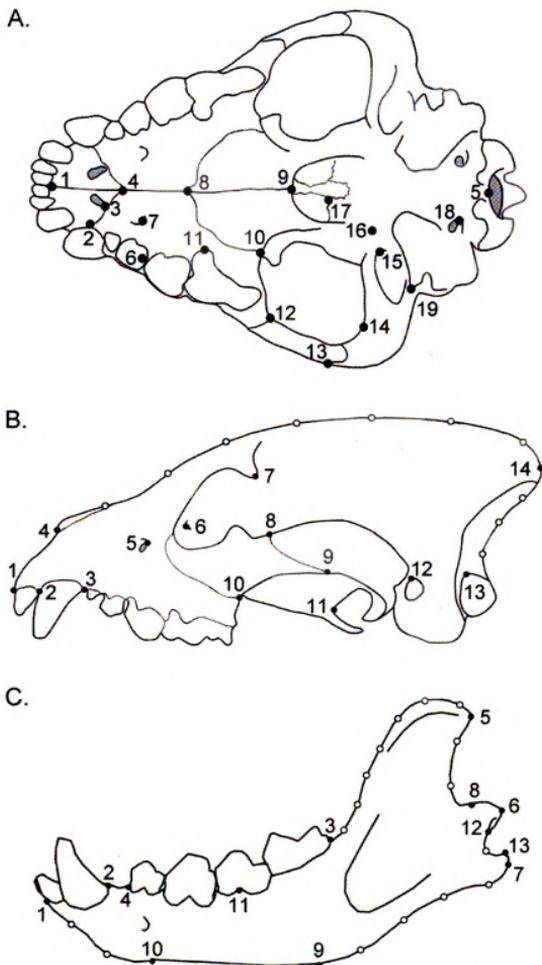


Figure 3.1. Landmarks (closed circles) and semi-landmarks (open circles) for ventral cranium (A), lateral cranium (B), and lateral mandible views (C). Numbers on landmarks correspond to descriptions in Table A.5

landmarks on the mandible. Therefore, semi-landmarks, points evenly spaced along curves beginning and ending at homologous landmarks, were used in the lateral cranium and mandible views to capture the overall shape of the specimen (Bookstein, 1997).

In cranium ventral view photographs, specimens were arranged so that the palate was parallel to the photographic plane. Landmarks were placed bilaterally and at the midline, but to avoid inflating degrees of freedom for subsequent analyses, the coordinates of bilaterally homologous landmarks were reflected and averaged across a baseline extending from landmark 1 to landmark 5 (Figure 3.1A), yielding 19 total landmarks (BigFix, Sheets, 2001).

In cranium lateral view photographs, the left side of the specimens was oriented such that the mid-sagittal plane was parallel to the photographic plane. If the left side of the specimen was not usable due to damage, the right side was photographed, and the photograph was digitally reflected. Lateral crania were digitized with 14 landmarks and 10 semi-landmarks (Figure 3.1B).

In mandible photographs, specimens were arranged so the left horizontal ramus was parallel to the photographic plane. As for the lateral cranium, if the left mandible was not usable due to damage, the right side was photographed, and the photograph was digitally reflected. Lateral mandibles were digitized with 13 landmarks and 16 semi-landmarks (Figure 3.1C).

Landmark and semi-landmark data were aligned with a Generalized Least-Squares Procrustes superimposition algorithm using CoordGen (Sheets,

2006) for the ventral cranium view, and SemiLand (Sheets, 2003a) for the lateral cranium and lateral mandible views. Both of these programs calculate CS.

To determine the appropriateness of M_1 length, CBL, and CS as proxy measures for body size in *Crocuta*, I examined pairwise correlations between these measures and head-body length in animals for which I had both the skull and body measurements that were taken while the animals were alive. Body measurements were taken during routine immobilization as part of a long-term behavioral study for 14 adult spotted hyenas (Table A.6) from the Masai Mara National Reserve in Kenya, and their skulls were deposited at the Michigan State University Museum post-mortem. Head-body length was used as the body size estimate because it is a more accurate metric of body size in this species than is body mass, which is highly variable due to variation in recent meal size (Kruuk, 1972).

Female-biased sexual size dimorphism is present in this species, but it is not evident in either the skull (Chapter 2 of this dissertation) or the dentition (Van Horn et al., 2003). Because of this, and the fact that sex assignments for many museum specimens of *Crocuta* are dubious due to the male-like genitalia of the females, sex is excluded from these analyses.

Geographical and environmental variables

Conventional latitude and longitude coordinates recorded for specimen collection sites were converted to decimal latitude and longitude using the Federal Communications Commission's online converter

(<http://www.fcc.gov/mb/audio/bickel/DDDMSS-decimal.html>). For specimens with place-name or landmark collection information, I determined the decimal latitude and longitude from the National Geospatial-Intelligence Agency's GEOnet Names Server (GNS, <http://earth-info.nga.mil/gns/html/index.html>). For specimens that had headings recorded (e.g. "80 mi N of Maun"), I took the decimal latitude and longitude from GNS, and calculated the coordinates given the heading with the Mammal Networked Information System (MANIS) Georeferencing Calculator (<http://manisnet.org/gci2.html>). Both decimal latitude and the absolute value of decimal latitude were used in analyses. Since the range of the spotted hyena straddles the equator, the absolute value of latitude, or distance from the equator, is a more appropriate measure than latitude in evaluating Bergmann's rule.

Georeferenced climate data for Africa were based on the Climatic Research Unit (CRU) TS 2.1 global climatic dataset, produced by the Climatic Research Unit of University of East Anglia. The CRU TS 2.1 Global Climate Dataset is comprised of 1224 monthly time-series of climate variables, for the period 1901-2002, covering the global land surface, excluding Antarctica, at 0.5 degrees resolution. I used a version of these data available from the Consortium for Spatial Information of the Consultative Group on International Agricultural Research (CGIAR-CSI), which has been reformatted for use in ArcGIS Grid format in decimal degrees using the World Geodetic System 1984 datum (WGS84) (Mitchell and Jones, 2005). This is the same system as was used for determining coordinates for the specimens. Annual means were calculated from

each monthly variable from 1901–1960, and a grand mean was calculated over the 60 years. Data from 1961 and later were not used. Climate values were assigned to specimens based on the 0.5 degree grid in which the specimen was located, by overlaying specimen locations on to the CGIAR-CSI grid file using ArcMap.

As the clinal relationship of body size with temperature predicted by Bergmann's rule has been related to extremes of temperature, especially extreme cold, I used mean minimum temperature as the ambient temperature variable. Exploratory analyses of other ambient temperature variables available through the Global Climate Dataset, daily mean temperature, and maximum temperature revealed high correlations with mean minimum temperature (mean temperature: $r=0.97$, $t=49.74$, $df=154$, $p<2.2\times 10^{-16}$; maximum temperature: $r=0.87$, $t=21.52$, $df=154$, $p<2.2\times 10^{-16}$).

In addition to temperature, studies of Bergmann's rule also traditionally examine water availability. Later studies have incorporated this variable into a measure of primary productivity, usually a combination of temperature and water availability (e.g. Le Houerou, 1984). However, since the effect of primary productivity would most likely be realized indirectly via the prey ingested by spotted hyenas, here I use a simpler measure of water availability, that of mean precipitation.

I chose the number of ungulate species present in an area (ungulate diversity) as a proxy for food availability. I used a distributional map of ungulate diversity for 89 species of ungulates ranging in body size from Kirk's dik-dik

(*Modoqua kirkii*) to the giraffe (*Giraffa camelopardalis*) (after Turpie and Crowe, 1994). The ungulate diversity cline map was digitized and georeferenced for use in ArcMAP based on the WGS84 datum (Figure 3.2). Ungulate diversity values were assigned to specimens according to the cline in which the specimen's collection locality was spatially contained, and were extracted using ArcMap's Spatial Analyst extension. Prey diversity varied from 0 to 35 in five-unit increments (Figure 3.2).

As latitude and longitude are not meaningful ecological variables, I did not use them in the multiple regression model; rather, I present correlations of both M_1 length and ventral CS with latitude and longitude. As the spotted hyena is suggested as an indicator species for predicting temperature (Klein and Scott, 1989), I also present correlations of both M_1 length and ventral CS with minimum temperature. I calculated Pearson's correlations in R (R Development Core Team, 2009). I used multiple regression in R to evaluate the effect of minimum temperature, precipitation, ungulate diversity, and the interaction between minimum temperature and precipitation on ventral CS.

RESULTS

CBL, ventral CS, and lateral CS all showed significant positive correlations with head-body length in 14 specimens from Kenya; M_1 length and mandible CS were positively correlated with head-body length, but not significantly so (Table 3.2). Ventral CS explained the most variation in head-body length, and was thus used in analyses to investigate the pattern of body size. Although CBL has long

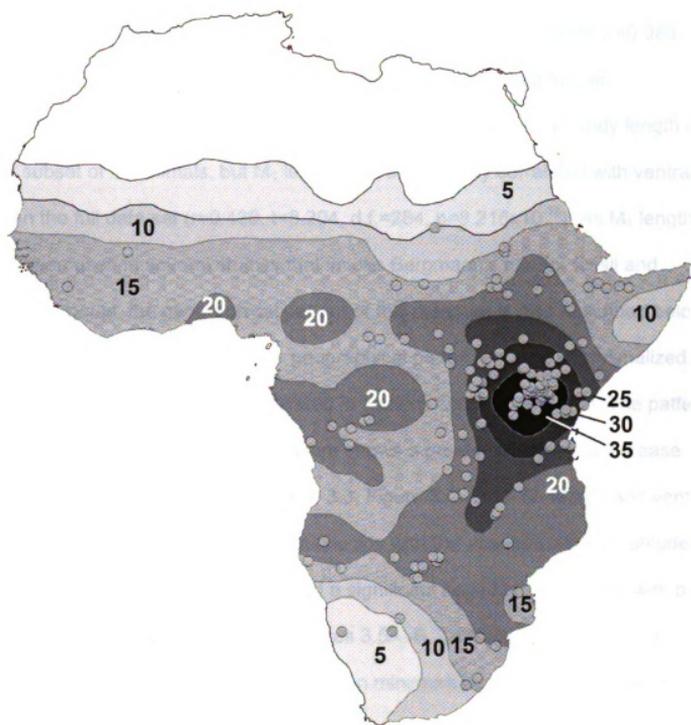


Figure 3.2. Map of the distribution of collection localities, overlaid on the scale for ungulate diversity. Dark areas with high numbers have the highest numbers of ungulate species.

been the traditional measure for analyses of body size in carnivores, this measure was highly correlated with ventral CS across all specimens ($r=0.983$, $t=91.882$, $d.f.=294$, $p<2.2\times 10^{-16}$), and therefore did not warrant further investigation. M_1 length was not significantly correlated with head-body length in this subset of 14 animals, but M_1 length was significantly correlated with ventral CS in the full data set ($r=0.438$, $t=8.204$, $d.f.=284$, $p=8.216\times 10^{-15}$). As M_1 length has been used in several studies that invoke Bergmann's rule for fossil and extant *Crocota*, the geographical pattern of this measure is also described below.

Ventral CS exhibits a clear geographical pattern that is easily visualized, with the smallest animals concentrated in eastern Africa (Figure 3.3). The pattern of M_1 length is similar, but this measure shows a greater tendency to increase with distance from the equator (Table 3.3, Figure 3.4). Both M_1 length and ventral CS exhibit a significant positive relationships with the absolute value of latitude and mean minimum temperature, and a significant negative relationship with both latitude and longitude (Table 3.3, Figures 3.5A–B, 3.6A–B, 3.7A–B, 3.8A–B).

Multiple regression of ventral CS on minimum temperature, precipitation, ungulate diversity, and the interaction between minimum temperature and precipitation was also highly significant, with all environmental variables tested making significant contributions to the model (Figures 3.8A–B, 3.9, 3.10). Ungulate diversity and the interaction between minimum temperature and precipitation made the most significant contributions to the model ($R^2=0.41$, $F_{4,319}=54.23$, $p<2.2\times 10^{-16}$, Table 3.4).

Table 3.2. Pearson's correlation coefficients describing the relationship between head-body length and various skull and tooth measures (d.f.=13). All measures were observed from free-living spotted hyenas in Kenya. M₁=first lower molar, CBL=condylobasal length, CS= centroid size.

Measure	r	t	p
M ₁ length	0.26	0.96	0.36
CBL	0.66	2.04	0.01
Ventral CS	0.68	3.32	0.01
Lateral CS	0.57	2.50	0.03
Mandible CS	0.49	3.16	0.06

Table 3.3. Pearson's correlation coefficients describing the relationships between first lower molar (M₁) length and ventral centroid (CS) and latitude, the absolute value of latitude ([latitude] i.e., distance from the equator), longitude, and minimum temperature.

	r	t _{d.f.}	p
M ₁ length			
[Latitude]	0.461	9.215 ₃₁₄	<2.2x10 ⁻¹⁶
Latitude	-0.223	-4.051 ₃₁₄	6.431x10 ⁻⁵
Longitude	-0.234	-4.265 ₃₁₄	2.646x10 ⁻⁵
Minimum temperature	0.168	3.020 ₃₁₄	0.003
Ventral CS			
[Latitude]	0.452	9.083 ₃₂₂	<2.2x10 ⁻¹⁶
Latitude	-0.225	-4.149 ₃₂₂	4.286x10 ⁻⁵
Longitude	-0.543	-11.602 ₃₂₂	<2.2x10 ⁻¹⁶
Minimum temperature	0.349	6.687 ₃₂₂	1.010x10 ⁻¹⁰

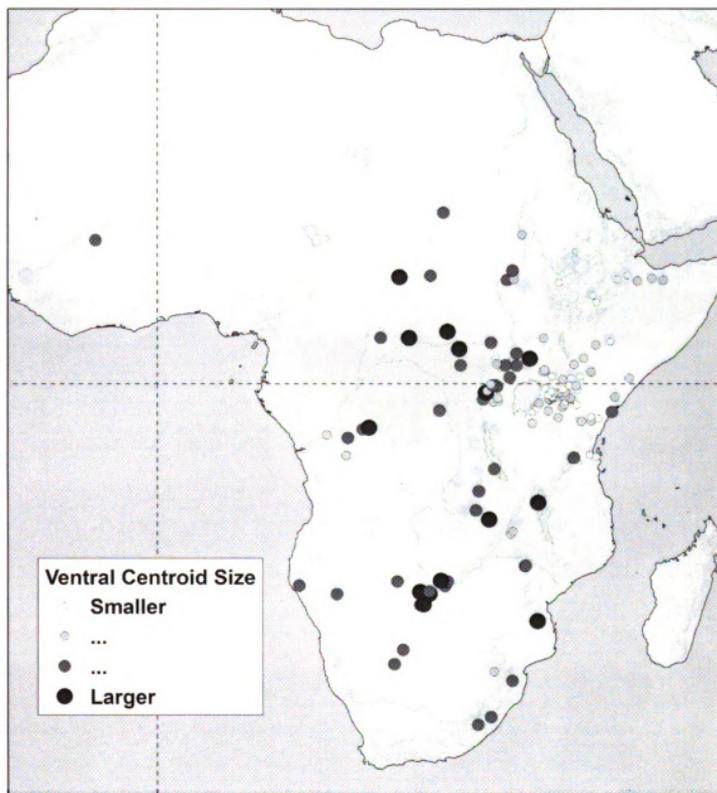


Figure 3.3. Geographic distribution of ventral centroid size. Small animals are indicated by light colored, small dots, and larger animals indicated by dark colored large dots. The Equator and Greenwich Meridian are indicated by dashed horizontal and vertical lines, respectively.

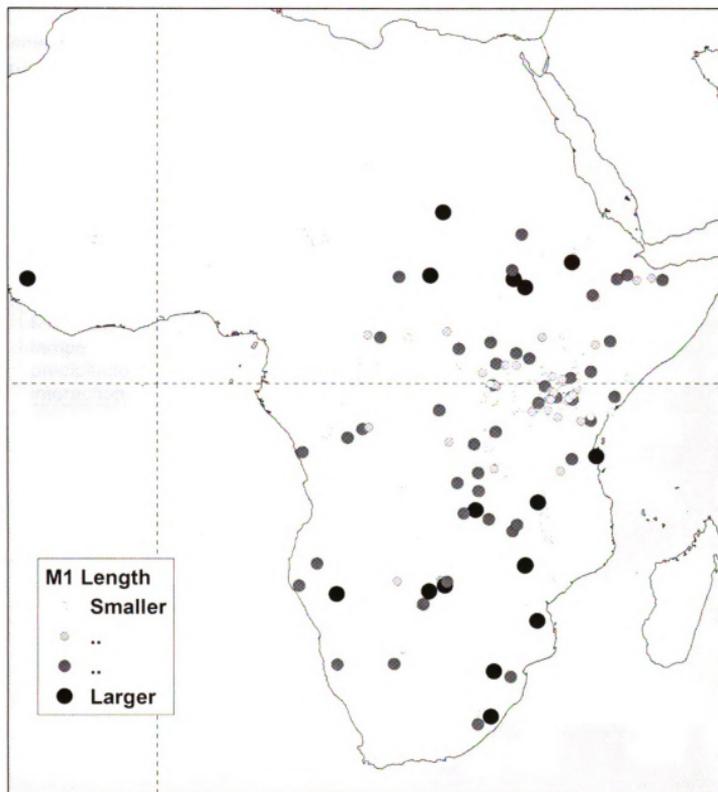


Figure 3.4. Geographic distribution of lower first molar length. Small teeth are indicated by light colored, small dots, and larger teeth indicated by dark colored large dots. The Equator and Greenwich Meridian are indicated by dashed horizontal and vertical lines, respectively.

Table 3.4. Multiple regression results of ventral centroid size against precipitation, minimum temperature, ungulate diversity, and the interaction of minimum temperature and precipitation.

	F/t	p
Model	54.23 _{4, 319}	< 2.2x10 ⁻¹⁶
Precipitation	-2.67	0.01
Minimum temperature	-2.32	0.02
Ungulate diversity	-9.84	< 2x10 ⁻¹⁶
Minimum temperature: precipitation interaction	3.49	0.001

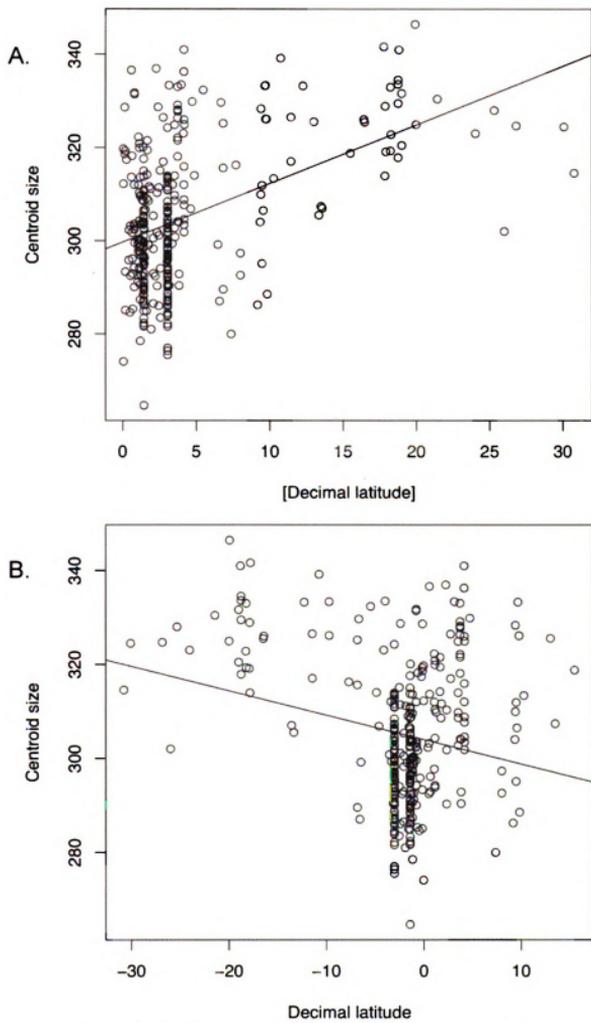
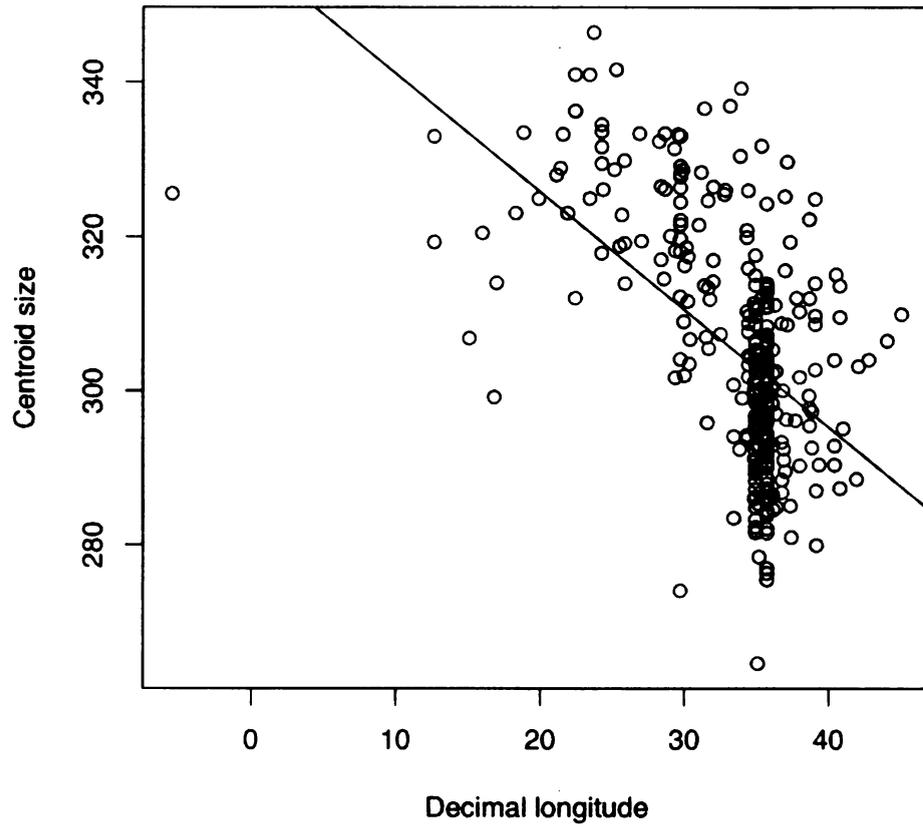


Figure 3.5. Scatterplots of A) centroid size and the absolute value of decimal latitude and B) centroid size and decimal latitude.

A.



B.

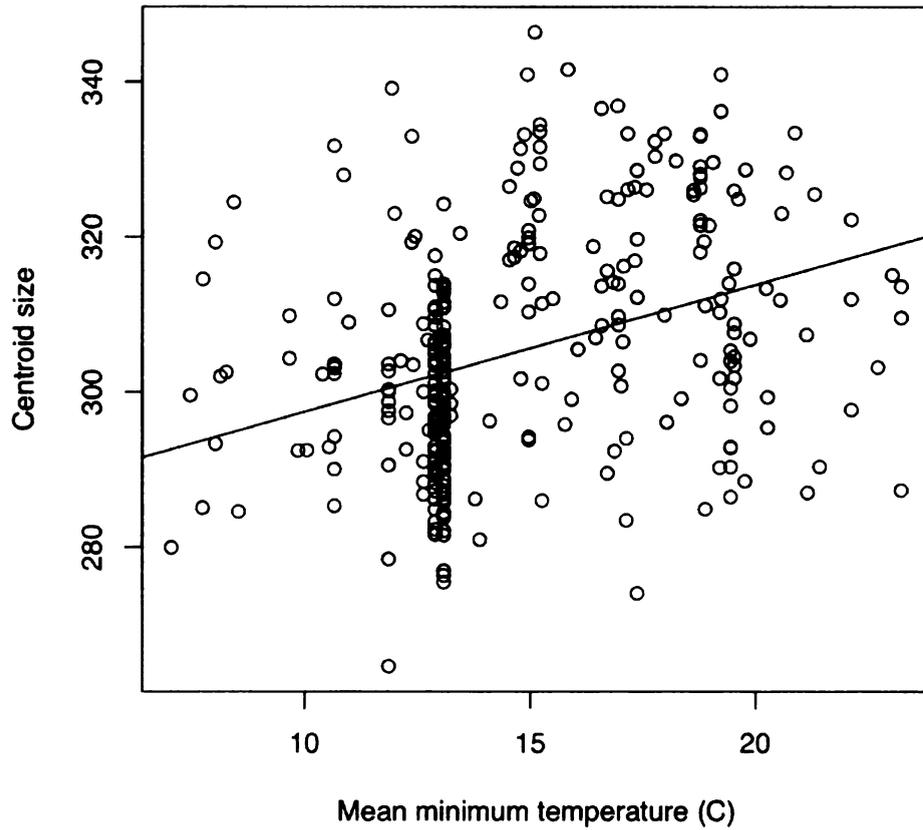


Figure 3.6. Scatterplots of A) centroid size and decimal longitude and B) centroid *size* and mean minimum temperature.

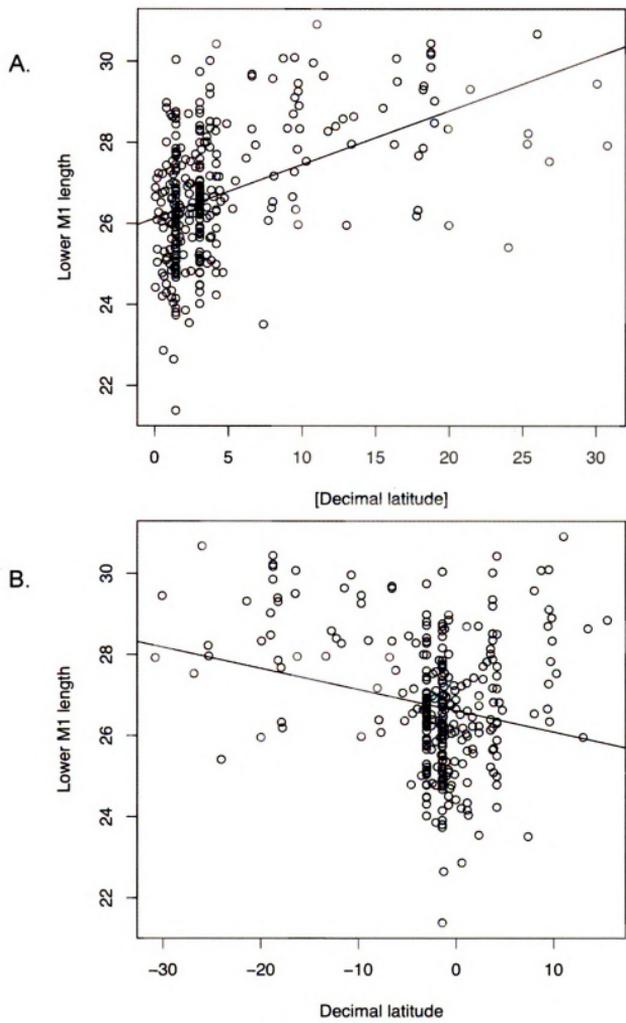


Figure 3.7. Scatterplots of A) centroid size and the absolute value of decimal latitude and B) lower M1 length and decimal latitude.

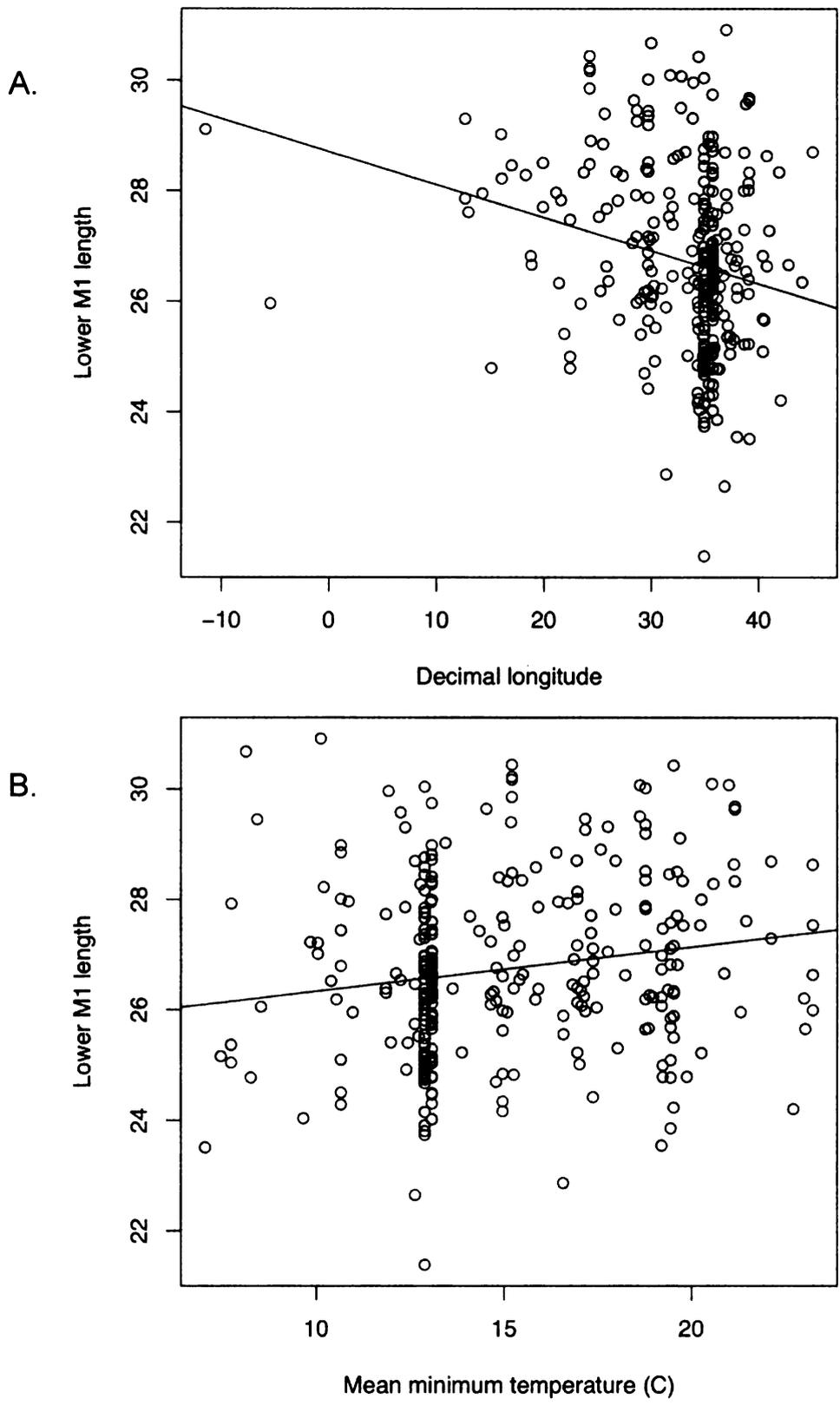


Figure 3.8. Scatterplots of A) lower M1 length and decimal longitude and B) lower M1 length and mean minimum temperature.

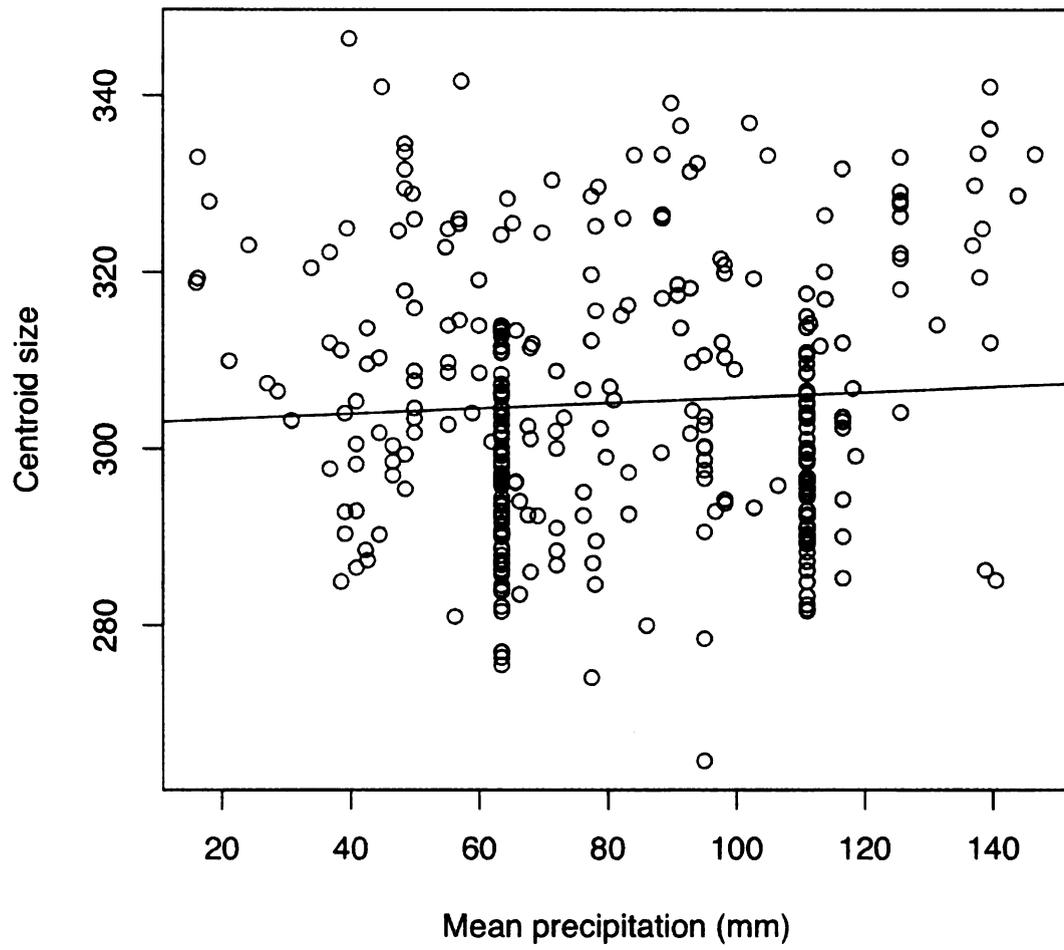


Figure 3.9. Scatterplot of centroid size and mean precipitation.

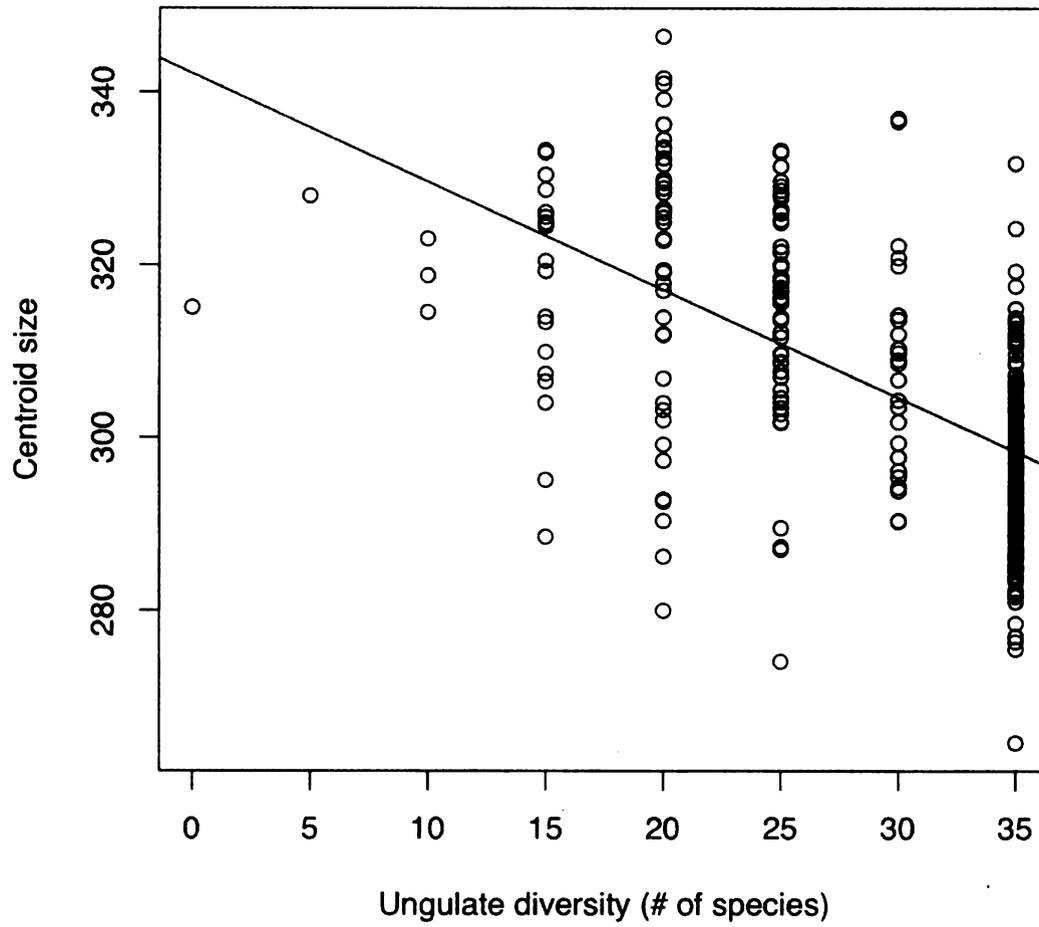


Figure 3.10. Scatterplot of centroid size and ungulate diversity.

DISCUSSION

The traditional interpretation of Bergmann's rule is that, within a species, a decrease in ambient temperature drives an increase in body size with increasing latitude. That is, animals get larger in the cold. Based on the work of Klein (1986, Klein and Scott, 1989), spotted hyenas have long been considered an example of a carnivore species that 'obeys' Bergmann's rule. As with Klein's work with M_1 length, I have shown here that there is indeed a correlation between ventral CS and latitude; spotted hyenas tend to get larger with increasing latitude (Figure 3.5A–B). Thus, at first blush, it would seem that spotted hyenas do obey Bergmann's rule, using latitude as a proxy for temperature. There are, however, two caveats to this conclusion.

The first is that the correlation between size and latitude is not based on a cline of increasing size from the equator, as predicted by Bergmann's rule. The significance of this relationship is driven by the cluster of the smallest animals east of 33°E longitude between 5°S and 10°N latitude, and this belies the true geographical pattern of body size (Figure 3.2). In fact, longitude actually explains more body size variation than latitude in this species ($r=-0.54$ vs. $r=0.45$ for [latitude], Table 3.3 Figure 3.6A), but we would certainly not conclude that there is a longitudinal cline in body size. Simply stating that spotted hyenas conform to Bergmann's rule based on the correlation of size with latitude is a misrepresentation of the actual geographical pattern.

The second caveat is that while the relationship with latitude is relatively strong ($r=0.45$ for [latitude]), the relationship with temperature is less so ($r=0.35$),

and it is in the opposite direction from that predicted by Bergmann's rule. That is, in spotted hyenas, animals tend to get smaller in the cold (Table 3.3 and Figure 3.6B). Thus, the complex geographical pattern in body size variation in the spotted hyena, based on the proxy of ventral CS, is not best described by invoking Bergmann's rule.

CBL and M_1 length are often used as proxy measures for body size in mammals. M_1 length is used when complete specimens are unavailable, and is particularly useful for fossil studies. Here, I have shown that ventral CS is a more appropriate proxy for head-body length for spotted hyenas than either CBL or M_1 length (Table 3.2), and CS should therefore be used when available.

Based on extant and fossil data, it was suggested that the variation in spotted hyena M_1 length was driven by temperature (Klein, 1986; Klein and Scott, 1989). In the current study, M_1 length shows similar patterns to those seen in ventral CS (Figures 3.7A–B, 3.8A–B) and is indeed significantly correlated with average temperature, but the relationship is weakly positive (Figure 3.8B). Again, this runs counter to the predicted relationship with temperature based on Bergmann's rule; some of the largest spotted hyenas hail from the warmest climates. Based on these data from extant spotted hyenas, it would be imprudent to use *Crocuta* as an indicator of paleotemperature. Dayan, et al (1991) urged caution when using dental data to infer paleoclimate, suggesting that competition may be a stronger force than climate on evolution of the dental arcade. That indeed may be the case here.

Meiri et al. (2007) proposed that some aspect of prey base drives conformation to Bergmann's rule in carnivores. In spotted hyenas, ungulate diversity was highly significant among environmental variables examined, such that smaller animals were found in areas of higher prey diversity (Figure 3.10). Why are larger spotted hyenas found in hot areas with low prey diversity? The most ecological information is available for populations in eastern and southern Africa. On average, animals in the southern part of the continent have much larger home ranges and lower prey density than their conspecifics in eastern Africa. Larger home ranges and lower prey density would mean travelling farther to defend the territory and to find food. McNab (1963) found a positive association between territory size and body mass in mammals. Thus, it would seem that body size variation in this species has more to do with socioecological factors.

Over 15 years after Geist (1987) deemed Bergmann's rule invalid, citing spurious correlations between body size and temperature, Meiri, et al. (2003) pronounced the rule sound based on meta-analysis of previously published tests of the rule, including the data from spotted hyenas (Klein, 1986). However, if meta-analyses such as these are based on spurious correlations, then the results of these analyses may themselves be misleading. Bergmann's rule was a useful construct for describing patterns of variation early in the 20th century, but today, ecological data beyond latitude are available. A more direct path is to describe patterns of variation within species, and test hypotheses posed to

explain those patterns, rather than try to fit the data to an outdated empirical generalization.

CHAPTER FOUR

ALLOMETRIC AND GEOGRAPHICAL VARIATION IN SKULL SHAPE IN THE SPOTTED HYENA (*CROCUTA CROCUTA*)

INTRODUCTION

For more than a century, studies of geographical variation within and between taxa have sought to advance our understanding of the mechanisms of evolution. As Gould and Johnston (1972) stated in their review article on the subject, "the foundation of most evolutionary theory rests upon inferences drawn from geographic variation or upon the verification of predictions made about it" (p. 457). Exploring the underlying evolutionary processes that produce morphological and behavioral variation within species is central to understanding evolution by speciation (Endler, 1977; Gould and Johnston, 1972).

Geographical variation in size is relatively easy to study, but because it is multivariate, shape presents more of a challenge. Traditional studies of shape using linear morphological measures are difficult to interpret because the description of shape is up to the investigator. Also, evaluating shape independently of size is difficult for classical morphologists, as linear shape measurements are confounded by size. Newer approaches, such as geometric morphometrics, permit assessment of shape independent of size and shape, use powerful multivariate statistical methods to test for shape variation, and illustrate shape change as a deformation grid. These methods have proven particularly useful for quantifying geographical variation in skull shape, especially with respect to phylogeography (e.g., Cardini and Elton, 2009; D'Anatro and Lessa, 2006; Frost et al., 2003).

For a number of reasons, the spotted hyena (*Crocuta crocuta*) is an excellent subject for a study that addresses phenotypic variation with geography. The species has a wide geographical range that encompasses much of sub-Saharan Africa, and includes a variety of different habitat types (Kingdon, 1977). The behavioral ecology of the species is well-studied (e.g., Hofer and East, 1995; Holekamp and Smale, 1991; Kruuk, 1972), although most workers have focused on animals inhabiting the eastern and southern parts of the species' range. Spotted hyenas are remarkably successful predators, and throughout their range they exhibit considerable variation in behavior, with groups ranging in size from 5–90 animals (Kruuk, 1972; Mills, 1990).

Because of the wide range of variation in body size (40–86 kg, (Kingdon, 1977) and pelage coloration, many forms of extant *Crocuta* were described and given scientific names, resulting in a long list of subspecies containing many likely synonyms. Between the years 1777 and 1924, no fewer than 21 spotted hyena subspecies were described in the literature (Meester et al., 1986). Most of these taxa seemed to have been established on the basis of pelage characteristics (e.g. Heller, 1910), although some researchers also considered differences in body size, and/or skull morphology. Among the skull characteristics used to distinguish taxa were size, shape of the posterior edge of the palate, degree of inflation of the auditory bullae, shape of the silhouette of the braincase, and breadth of the palate and of the skull overall (Allen, 1924; Cabrera, 1911; Matschie, 1900). In a re-evaluation of the many subspecific descriptions, Allen

Table 4.1. Former proposed subspecies of *Crocuta crocuta* (Allen, 1924).

Subspecies	Locality	Synonymous taxa
<i>Crocuta crocuta crocuta</i> Erxleben	South Africa	<i>Hyaena maculata</i> Thunberg <i>Hyaena rufa</i> Desmarest <i>Hyaena capensis</i> Desmarest <i>Hyaena encrita</i> Smith <i>Hyaena wissmanni</i> Matschie <i>Hyaena gariepensis</i> Matschie
<i>C. c. fisi</i> Heller	Northern Kenya	
<i>C. c. fortis</i> Allen	Democratic Republic of the Congo	
<i>C. c. germinans</i> Matschie	Tanzania, southern Kenya, Malawi	<i>Crocotta kibonotensis</i> Lönnberg <i>Crocotta panganensis</i> Lönnberg <i>Crocuta nzoyae</i> Cabrera <i>Crocuta nysae</i> Cabrera
<i>C. c. habessynica</i> Blainville	Ethiopia, Somalia, Uganda	<i>Hyaena (Crocuta) leontiewi</i> Satunin <i>Crocuta rufopicta</i> Cabrera <i>Crocuta thomasi</i> Cabrera
<i>C. c. theirryi</i> Matschie	Togo, Cameroon	<i>Hyaena togoensis</i> Matschie <i>Hyaena noltei</i> Matschie

(1924). revised the taxonomy of the species to contain six subspecies based on morphological variation and geographical locality (Table 4.1), but he noted that additional study was needed of the species across its range. Allen (1924) suggested restricting the subspecies of *Crocuta* to *Crocuta crocuta crocuta* in South Africa, *C.c. fortis* in the Democratic Republic of the Congo, *C.c. theirryi* in western Africa, *C.c. germinans* in Malawi, Tanzania, and southern Kenya, *C.c. fisi* in northern Kenya, and *C.c. habessynica* in Uganda, Ethiopia and Somalia. Matthews (1939b) later set out to systematically quantify morphological variation within the species, by documenting variation in pelage color, body size, and skull characters in the approximately 170 specimens of spotted hyenas then at the Natural History Museum, London. He observed considerable variation in this

sample, but was not able to discern a clear geographical pattern, and concluded that the previously described subspecies were invalid. His monospecific designation of extant *Crocuta crocuta* is the systematic convention still followed today (e.g., Wozencraft, 2005).

Recent molecular studies have attempted to clarify the evolutionary history of spotted hyenas and other African carnivores. A 2005 study of the spotted hyena (Rohland et al., 2005) revealed significant geographical structuring of cytochrome b sequences, with southern and northern clades that overlap at the equator. A southern/eastern distribution, with varying levels of admixture, is also seen among African wild dogs (Girman et al., 2001), lions (Dubach et al., 2005), and cheetahs (Freeman et al., 2001). The extent to which morphological variation corresponds to these phylogeographical patterns is unknown.

In this chapter, I assess the contribution of skull size to variation in skull shape in the spotted hyena, and examine the shape change associated with size. I determine the extent to which geographical variables explain the pattern of shape variation. I re-evaluate earlier taxonomic work on the species in light of the pattern of shape variation revealed with geometric morphometric methods. Finally, I evaluate the Pleistocene refugia hypothesis as a means to describe the current pattern in shape variation.

METHODS

Skull samples

I examined 385 skulls of adult *Crocuta crocuta* with associated locality data housed in 13 museums in the United States, Europe, and Kenya (Tables A.2 and A.7). To be considered as an adult in this study, a specimen had to have complete or nearly complete closure of the lambdoid and basilar sutures, and tooth wear such that the bilateral mean of the length of the occlusal surface of the third lower premolar (P_3) was at least 5.0 mm. P_3 is a large tooth, dominated by a robust, central, cone-shaped cusp. The length of the occlusal surface of P_3 is commonly used as a variable in equations for estimating the age of individual adults of this species (Van Horn et al., 2003). Using equation 3 from Van Horn et al. (2003) a P_3 occlusal surface length of 5.0 mm results in an estimated age of 38.37 months, which is over one year beyond the age of reproductive maturity (Glickman et al., 1992). In a recent study, Tanner et al. (2009) demonstrated that skull maturation is complete by 35 months of age, suggesting that the above guidelines for classifying a skull as fully adult are conservative. As we found no significant sexual dimorphism in skull centroid size or in skull shape in *Crocuta* (Chapter 2 of this dissertation), sexes were pooled for these analyses.

Where available, latitude and longitude were recorded from the collection information at the museum; in each case, I converted the conventional coordinates to decimal latitude and longitude using the Federal Communications Commission's online converter (<http://www.fcc.gov/mb/audio/bicke/DDMMSS-decimal.html>). For specimens with place-name or landmark collection

information, I determined the decimal latitude and longitude from the National Geospatial-Intelligence Agency's GEOnet Names Server (GNS, <http://earth-info.nga.mil/gns/html/index.html>). For specimens that had headings recorded (e.g. "80 mi N of Maun"), I took the decimal latitude and longitude from GNS, and calculated the coordinates given the heading with the Mammal Networked Information System (MANIS) Georeferencing Calculator (<http://manisnet.org/gci2.html>). Some specimens were excluded from the analysis of one or more views due to damage (see Table A.7).

Data collection

Photographs were taken with a Fuji FinePix S1 Pro digital camera fitted with a Nikon AF Nikkor 28-80 mm lens. Images were saved directly to a laptop computer. A 1 cm scale was included in all photographs for all views. Three views were captured: ventral cranium, lateral cranium, and lateral mandible (Figure 4.1).

Landmarks were digitized at suture intersections and other presumed homologous points using tpsDig 2.10 (Rohlf, 2006). Fusion of the sutures associated with the braincase is mostly complete in adult *Crocuta* (Schweikher, 1930), especially along the sagittal crest, and there are few points that make suitable homologous landmarks on the mandible. Therefore, semi-landmarks, points evenly spaced along curves beginning and ending at homologous landmarks, were used in the lateral cranium and mandible views to capture the

overall shape of the specimen (see Table A.5 for a list and description of landmarks).

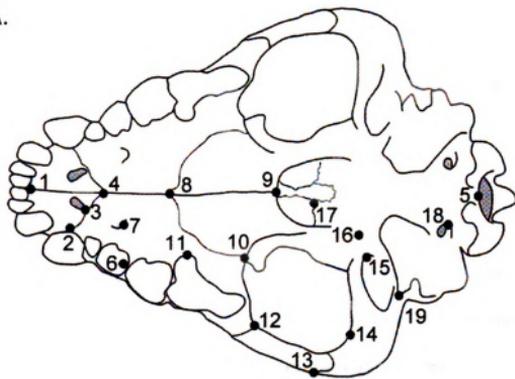
In cranium ventral view photographs, specimens were arranged so that the palate was parallel to the photographic plane. Landmarks were placed bilaterally and at the midline, but to avoid inflating degrees of freedom for subsequent analyses, the coordinates of bilaterally homologous landmarks were reflected and averaged, yielding 19 total landmarks (BigFix, Sheets, 2001, Figure 4.1A).

In cranium lateral view photographs, the left side of each specimen was oriented such that the mid-sagittal plane was parallel to the photographic plane. If the left side of the specimen was not usable due to damage, the right side was photographed, and the photograph was digitally reflected. Lateral crania were digitized with 14 landmarks and 10 semi-landmarks (Figure 4.1B).

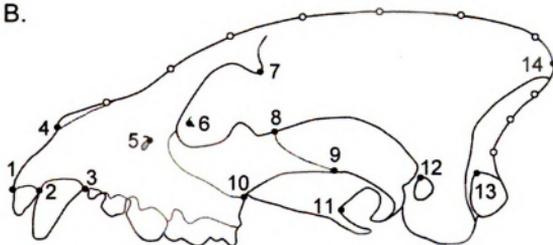
In mandible photographs, specimens were arranged so the left horizontal ramus was parallel to the photographic plane. As for the lateral cranium, if the left mandible was not usable due to damage, the right side was photographed, and the photograph was digitally reflected. Lateral mandibles were digitized with 13 landmarks and 16 semi-landmarks (Figure 4.1C).

Landmark and semi-landmark data were aligned using a Generalized Least-Squares Procrustes superimposition algorithm (GPA). This removes data unrelated to shape, such as position, scale, and rotation (Rohlf and Slice, 1990; Zelditch et al., 2004). Superimposition was performed with CoordGen (Sheets, 2006) for the ventral view, and SemiLand (Sheets, 2003a) for the lateral and

A.



B.



C.

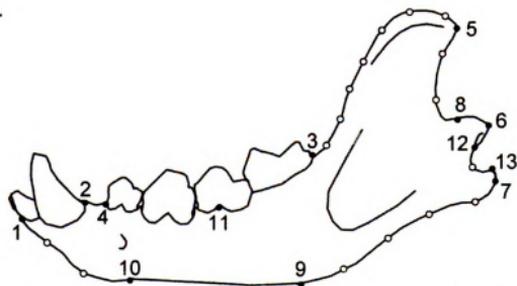


Figure 4.1. Landmarks (closed circles) and semi-landmarks (open circles) for ventral cranium A), lateral cranium B), and lateral mandible views C). Numbers on landmarks correspond to descriptions in Table A.5.

mandible views. Procrustes distances were used as shape variables in the statistical tests described below, and the differences were visualized with deformation grids generated using the thin-plate spline algorithm.

Data analysis

Allometry

While GPA separates shape from geometric scale, shape variation that is correlated with size (i.e. allometric shape variation) remains. Skull size varies geographically in *Crocota*, with the smallest skulls found in eastern Africa (Chapter Three of this dissertation). To examine the influence of size on shape, for each view, I performed a linear regression of shape on log centroid size to illustrate the changes in shape from small to large skulls (Regress6n, Sheets, 2008).

I then standardized the data for size, using Standard6 (Sheets, 2003b), which regresses shape on $\ln(\text{centroid size})$ and calculates residuals. These standardized data, which allow for analysis on shape independent of allometric variation, were used for all subsequent analyses. In addition, in an effort to clean up the geographical signal by removing localized individual variation, I took means of shape data for specimens having identical locality data, resulting in 157 total localities.

Geographical shape variation

I explored the contribution of drift, or isolation by distance, to non-allometric shape variation by performing Mantel tests on Procrustes and geographical distance matrices (Mantel, 1967). The Mantel test is a permutation test of the correlation between two matrices. Pairwise Procrustes distance matrices were generated for each view in CoordGen6h (Sheets, 2006), and a distance matrix of latitude and longitude was generated in R. Mantel tests for each view were performed in R 2.8.1 (R Development Core Team, 2009), using the mantel.rtest platform with 1000 permutations.

To further examine the relationship between shape and geography, I tested for covariation between shape and geographical variables with two-block partial least squares (PLS) analysis (Rohlf and Corti, 2000). PLS models the covariation between two sets of variables. PLS uses singular value decomposition (SVD) to create a pair of singular axes, one for each block of data, which maximizes the covariance between the blocks. The first block of data contained the geometric shape variables. The second block of data contained normalized latitude and longitude. Permutation tests were used to determine whether the covariance between the blocks was greater than that expected by chance (PLSMaker, Sheets, 2004; $n=1000$ permutations). I then regressed the standardized shape data for each skull view onto the first singular axis of the PLS analyses to determine how much variation the covariation between shape and geography explains, and regressed shape onto the dominant geographical variable to visualize the shape change with deformation grids.

Using the individual singular axis scores from the first shape vector from the PLS analysis, I calculated a pairwise Euclidean distance matrix. I used this distance matrix to perform an unweighted pair-group method with arithmetic mean (UPGMA) cluster analysis in R using the h.clust platform, and inspected the output for groups. I evaluated identified groups with canonical variate analysis (CVA), using CVAGen6o (Sheets, 2007) and illustrated shape between each pair of groups using TwoGroup6h (Sheets, 2003c). The robustness of the groups described by UPGMA was evaluated with a jack-knife reassignment test that randomly removed 10% of the sample and recalculated the canonical function, reassigning specimens to groups (Sheets, 2007). The rate of correctly classified specimens over 500 trials is reported.

RESULTS

Allometric shape variation

Centroid size of the spotted hyena skull is a significant predictor of skull shape in all views examined (ventral cranium: $F_{34,11526} = 8.70$, $p < 0.01$; lateral cranium: $F_{44,14872} = 18.61$, $p < 0.01$; lateral mandible: $F_{54,19224} = 12.85$, $p < 0.01$), but size explains only a small proportion of the variation in shape (Table 4.2). The shape changes that accompany increasing size are depicted by vectors on landmarks, and associated deformation grids (Figures 4.2–4.4). Shape change from small to large skulls in the ventral cranial view is dominated by a relative lengthening of the anterior basicranial region, and a broadening of the palate. The streamlining seen through the zygomatic arches is a function of changes

primarily along the jugal bone. In smaller skulls, the zygomatic arch bows outward at the jugal, whereas in the larger skulls, the lateral edge of this bone is flattened. The postglenoid process also lengthens medially (Figure 4.2). In the lateral view, shape change is dominated by a relative heightening of the cranial vault. This change is most noticeable just posterior to the orbit and along the anterior braincase. The zygomatic arch becomes broader dorso-ventrally, as shown by the ventral displacement of the lower zygomatic landmark (landmark 9). The posterior sagittal and upper nuchal crests are ventrally displaced, and the incisor is rotated downward (Figure 4.3). In the mandible, changes in shape are primarily observed in the coronoid process, the angular process, and the horizontal ramus. In the coronoid process, there is an increase in relative breadth, and a posterior displacement of the apex. The angular process is decreased in length and is ventrally displaced. Additionally, there is a dorso-ventral expansion of the horizontal ramus, particularly ventral to P₄ and M₁. A relative increase in length of the anterior horizontal ramus is indicated by an increase in post-canine diastema size, and posterior displacement of the incisors and the end of the mandibular symphysis (Figure 4.4).

Table 4.2. Results of regression of shape variables (partial warp +uniform component scores) on natural log centroid size.

View	Goodall's F _{df1, df2}	% variation explained	p-value
Ventral	8.70 _{34, 11526}	2.5	<0.01
Lateral	18.61 _{44, 14872}	5.22	<0.01
Mandible	12.85 _{54, 19224}	3.48	<0.01

Geographical shape variation

Mantel tests on geographic distance and size-adjusted Procrustes distance data were significant for all views (ventral: $r=0.183$, $p=0.001$; lateral: $r=0.183$, $p=0.003$; mandible: $r=0.107$, $p=0.018$), indicating that drift does have an effect on skull shape. That is, skulls collected geographically close to one another are more similar in shape to one another than to skulls collected farther away.

Additionally, a PLS analysis of shape variables revealed significantly greater covariance with latitude and longitude than would be expected by chance for all three skull views (Table 4.3). The first singular axis was significant for all three views, with the loadings for this axis almost completely dominated by latitude (Table 4.3). Taken together, these results indicate a structuring of shape variance along a latitudinal gradient. Regression of shape on the first singular axis for geography indicates that this covariation accounts for a modest portion of the overall variation in shape (Table 4.4).

Table 4.3. Summary of results for PLS analysis of shape with geographical variables.

View	Axis	Cov explained	p-value	Correlation	Latitude loading	Longitude loading
Ventral	SA1	98.52	0.00	0.503	0.996	0.094
Lateral	SA1	98.36	0.02	0.495	0.991	0.134
Mandible	SA1	91.68	0.03	0.318	0.992	0.132

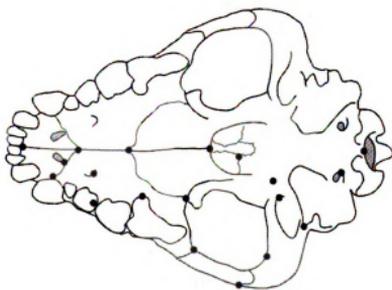
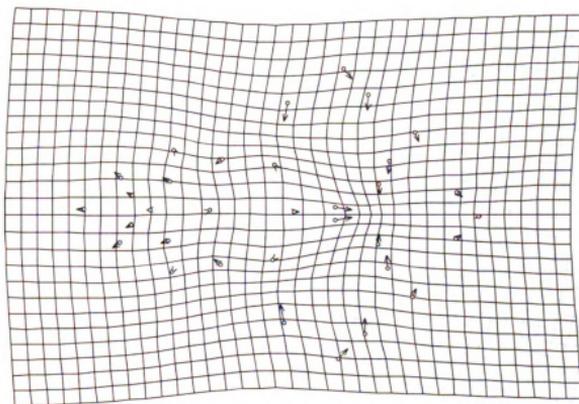


Figure 4.2. Deformation grid showing allometric changes from a linear regression of shape on $\log(\text{centroid size})$ in the ventral view. The landmarks have been back-reflected, and the deformation exaggerated 2.5 times for ease of interpretation. Vectors on landmarks in the deformation grid show the direction and magnitude of change from the smallest to the largest specimens.

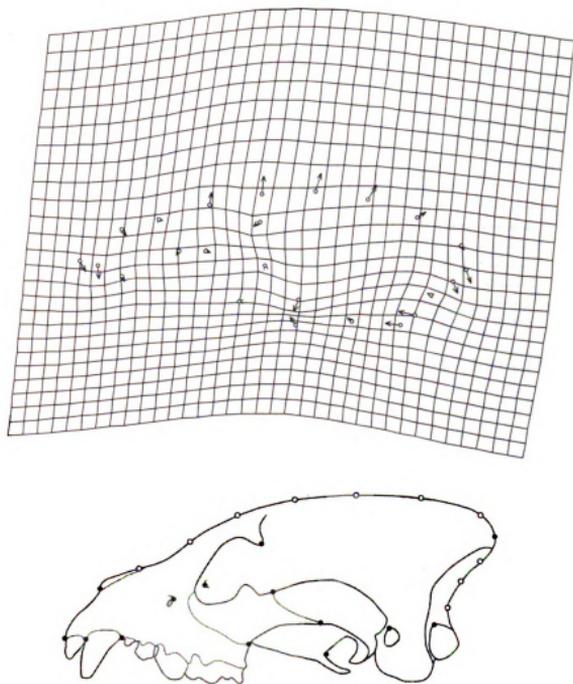


Figure 4.3. Deformation grid showing allometric changes from a linear regression of shape on $\log(\text{centroid size})$ in the lateral view. The landmarks have been back-reflected, and the deformation exaggerated 2.5 times for ease of interpretation. Vectors on landmarks in the deformation grid show the direction and magnitude of change from the smallest to the largest specimens.

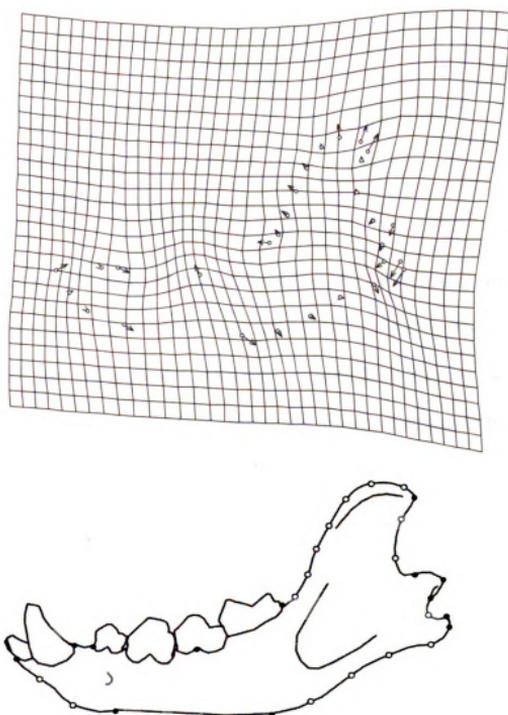


Figure 4.4. Deformation grid showing allometric changes from a linear regression of shape on $\log(\text{centroid size})$ in the mandible view. The landmarks have been back-reflected, and the deformation exaggerated 2.5 times for ease of interpretation. Vectors on landmarks in the deformation grid show the direction and magnitude of change from the smallest to the largest specimens.

Table 4.4. Results of regression of standardized shape variables on the first singular axis for geography of the 2-block partial least squares analyses.

View	Goodall's $F_{df1, df2}$	% variation explained	p value
Ventral	25.74 _{34,4420}	16.53	<0.01
Lateral	14.65 _{44,5632}	10.27	<0.01
Mandible	35.45 _{48,6576}	20.56	<0.01

Three major groups were identified from the UPGMA cluster analysis on the first singular axis for shape for all three skull views. The dendrogram for the ventral view is depicted in Figure 4.5, and the patterns for the other two views were similar. Plotted on a map of Africa, the three groups overlap at the equator (Figure 4.6). For each view of the skull, the area north of the equator is dominated by two groups, group 1 to the east, and group 3 to the west, whereas the area south of the equator is dominated by group 2 (coded specimens for the ventral view are mapped in Figure 4.6). For each skull view, CVA analysis found one significant canonical variate separating the three groups (ventral cranium: $\lambda=0.11$, $X^2=247.97$, $df=68$, $p<2.22 \times 10^{-16}$; lateral cranium: $\lambda=0.05$, $X^2=296.05$, $df=88$, $p<2.22 \times 10^{-16}$; lateral mandible: $\lambda=0.06$, $X^2=295.12$, $df=108$, $p<2.22 \times 10^{-16}$). When a jack-knifing procedure was applied to the canonical function, 87.5% of ventral, 83.8% of lateral, and 79.3% of mandible individual samples were correctly classified. For all three skull views, groups 1–3 represent a cline of shape change such that group 1 was situated between groups 2 and 3 when canonical variates 1 and 2 were plotted (Figure 4.7A–C).

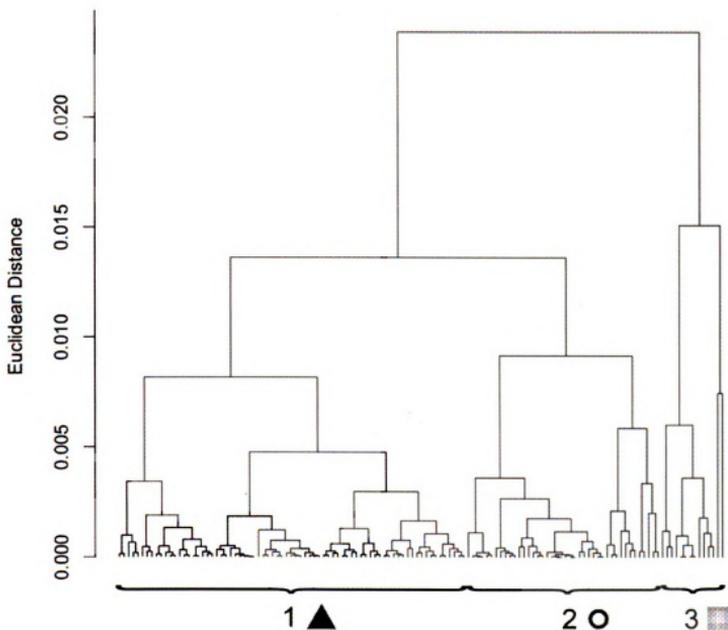


Figure 4.5. Dendrogram produced by a UPGMA cluster analysis based on a pairwise Euclidean distance matrix of the first singular axis for shape from the 2B-PLS analysis of the ventral view. The symbols correspond to those used for groups 1 – 3 in Figures 4.9 – 4.10.

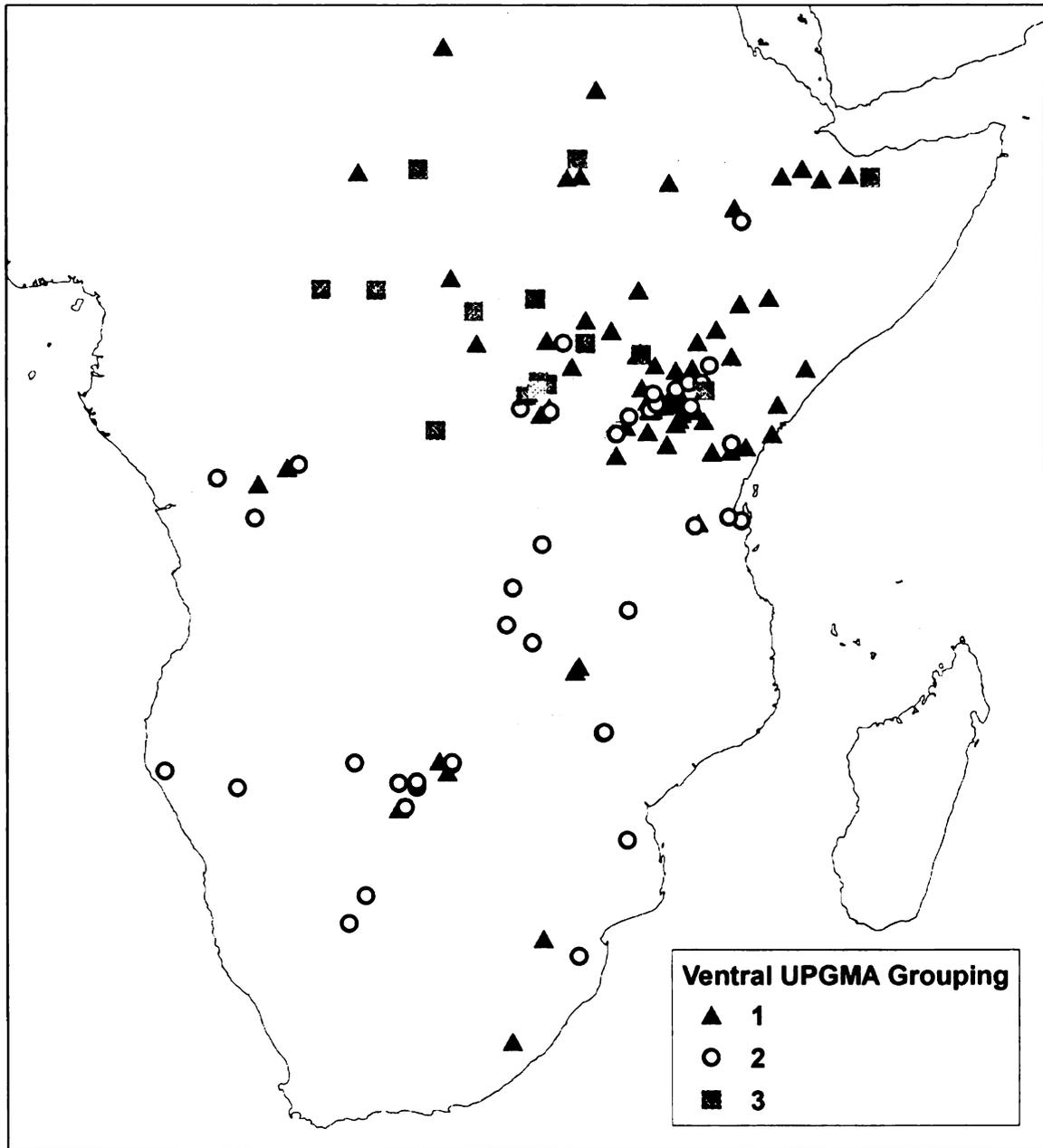


Figure 4.6. Plot of the three groups realized by the UPGMA clustering, for the ventral cranial view. The Equator and the Tropic of Capricorn are indicated by the upper and lower lines, respectively.

Deformations showing pairwise differences between all three groups reinforce the notion that the groups exist in a cline. In the ventral view (Figure 4.8), shape change along this cline is dominated by a relative shortening and narrowing of the palate, and the anterior displacement of the jugal-squamosal suture on the zygomatic arch. The anterior displacement of landmark 9 relative to landmark 10 highlights a shift from a U-shaped palatal margin to a V-shaped margin. Shape change along the cline in the lateral cranium view (Figure 4.9) is mainly in the anterior displacement of the ventral jugal-squamosal suture on the zygomatic arch. The angle of this suture is not as oblique in the northern skulls. This displacement seems to be coupled with a dorsad flare of the squamosal bone that is not captured by the deformation due to a lack of landmarks in this area. In the lateral mandible view (Figure 4.10), there is a decrease in relative breadth of the coronoid process, and the apex is displaced posteriorly, such that the entire process seems to slope backward. Additionally, the angular process is shortened, and the posterior portion of the mandibular ramus loses depth.

DISCUSSION

Allometric shape variation

Skull size makes a small but significant contribution to shape variation in the spotted hyena. Thus, the allometry in adult skulls is not merely a continuation of the shape trajectory seen with growth in early ontogeny (Tanner et al., 2009), where the skulls experience global changes to allow for an increase in jaw adductor mass, as well as an increase in surface area for muscle attachment.

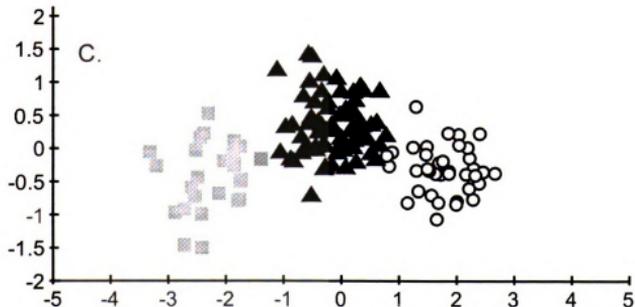
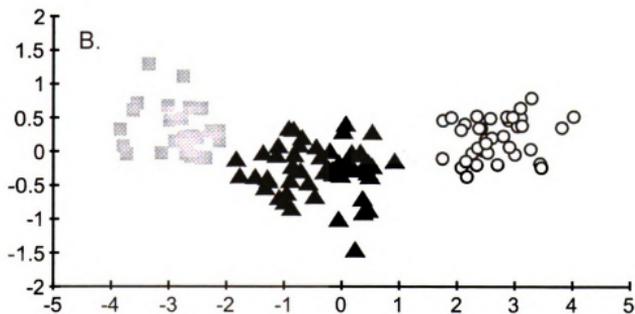
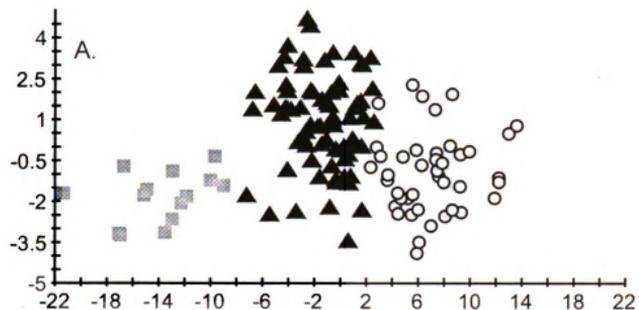


Figure 4.7. Canonical variate analysis results for each view on groups 1 (triangles), 2 (circles), and 3 (squares) identified using UPGMA clustering; A) ventral cranium, B) lateral cranium, and C) lateral mandible.

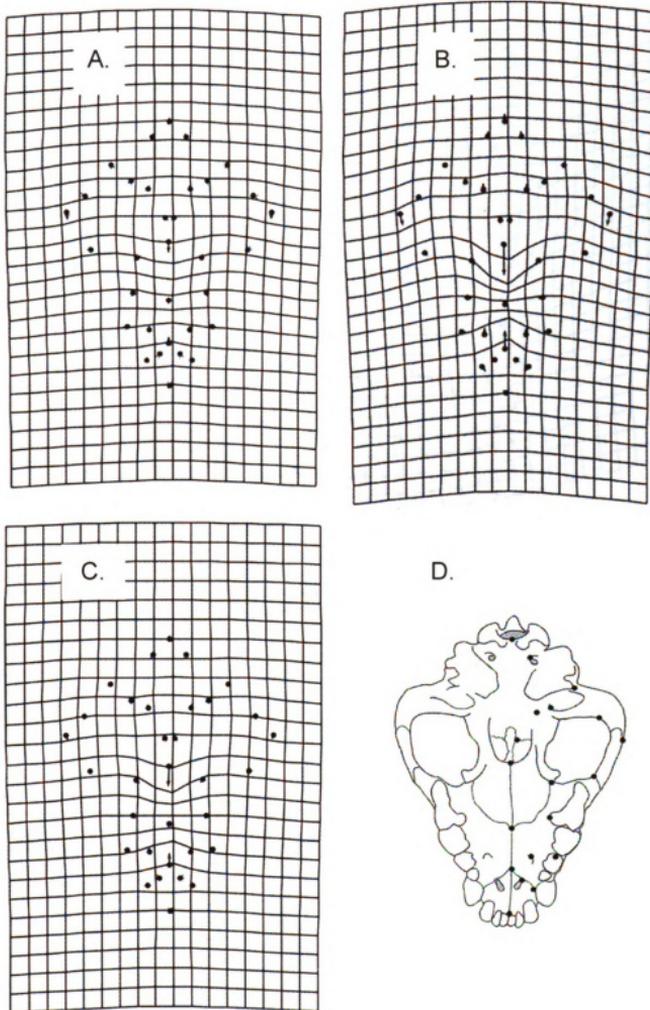


Figure 4.8. Pair-wise deformations of shape change between all groups in the ventral cranial view; A) 2>1, B) 2>3, C) 1>3, D) landmark map. The deformations are exaggerated 3 times for ease of interpretation.

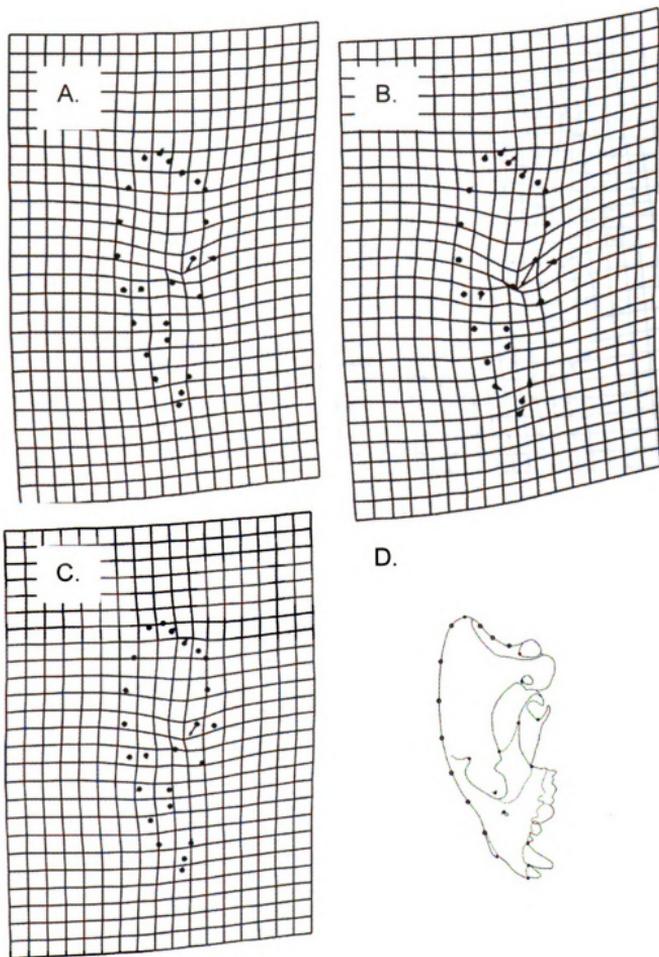


Figure 4.9. Pair-wise deformations of shape change between all groups in the lateral cranial view; A) 2>1, B) 2>3, C) 1>3, D) landmark map. The deformations are exaggerated 5 times for ease of interpretation.

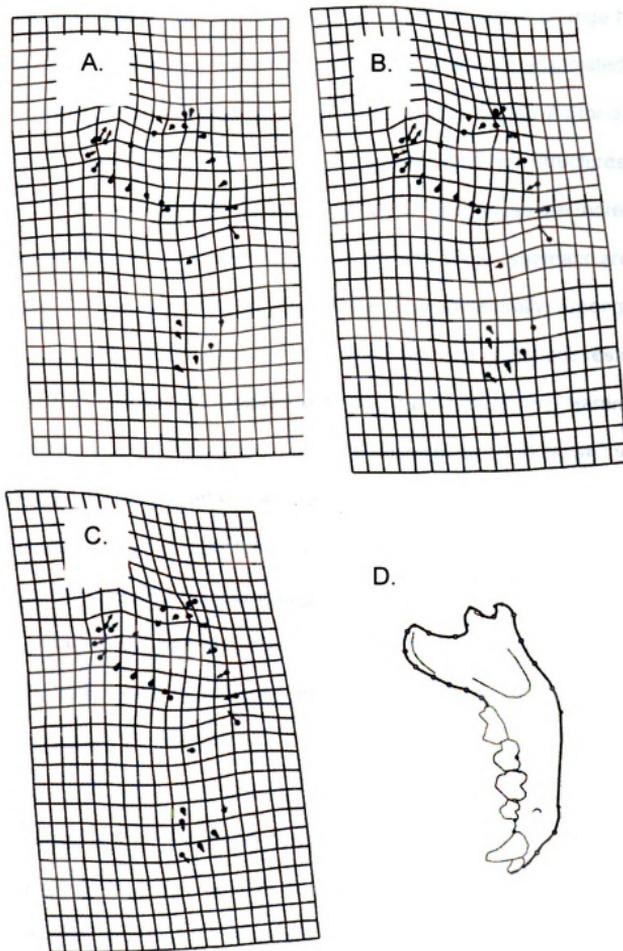


Figure 4.10. Pair-wise deformations of shape change between all groups in the lateral mandible view; A) 2>1, B) 2>3, C) 1>3, D) landmark map. The deformations are exaggerated 5 times for A and C, 3 times for B, for ease of interpretation.

Rather, among the adult spotted hyenas examined here, shape change from smaller to larger skulls is highlighted by changes in structures associated with the origin or insertion of one or more muscles of the head and neck. As for early ontogeny, allometric shape change in adults is associated with structures that are acted upon by muscles, but unlike early ontogeny, the changes are more localized. Instead of the anterior-posterior expansion of the zygomatic arches seen in subadults, the zygomae in adults expand dorso-ventrally. Among adult spotted hyena skulls, larger specimens show evidence of epigenetic restructuring in response to the action of increased adductor muscle mass (e.g. Herring, 1993). The increase in the height of the vault, however, is not likely an increase in surface area for muscle attachment (Joeckel, 1998), but may be related to an allometric increase in the size of the fronto-parietal sinus, which has been shown to dissipate stress during bone-cracking while feeding (Tanner et al., 2008). The dramatic changes in shape with increasing skull size most likely contributed to the difficulty early researchers experienced in attempting to document a geographic pattern in skull shape.

*Shape variation and the taxonomy of *Crocuta crocuta**

Many wide-ranging mammalian species containing multiple subspecies described in the late 18th, 19th, and early 20th centuries have since been collapsed such that they now contain far fewer subspecies. Wider sampling has allowed for more rigorous descriptions of species and subspecies based on both morphological and molecular studies. In the spotted hyena, variation in body

size, coloration, and skull morphology were the bases for many subspecific assignments. It was the individual nature of this variation that led Matthews (1939b) to conclude that subspecific patterns could not be identified. Within a group of 103 specimens collected from one geographical locality in Tanzania, Matthews (1939b) found specimens that he claimed could have been placed in any of four subspecies (*C.c. germinans*, *C.c. fisi*, *C.c. leontewi*, *C.c. fortis*), based on their original descriptions. Matthews' Tanzania sample undoubtedly contained individuals from more than one clan, but there is evidence that variation exists at even lower levels. Within a single clan in the Masai Mara National Reserve, Tanner (2007) found that skulls from adult females low in the dominance hierarchy are larger than those from adult females of higher rank.

Large-scale sampling of skulls across the African continent has revealed a pattern of morphological variation formerly obscured by a high level of individual variation. The three groups indicated by UPGMA analysis represent a cline of variation running from north-central Africa, through northeastern Africa, and southward. While the variation in skull characteristics does not fall into distinct groups that permit delineation of clear subspecies, the pattern of shape variation does correspond to previously described subspecies. Group 2, the northwestern group, allies with *Crocuta crocuta fortis* (Allen, 1924). This subspecies, originally described from the northeastern extreme of the democratic republic of the Congo, was invoked on the basis of its large size, inflated auditory bullae, straight-sided braincase, and palate with a deeply incised, V-shaped posterior border. While the auditory bullae and the shape of the braincase were not

evaluated here, the V-shaped palatal border of Group 2 dominates the shape deformations between this group and Groups 1 and 3 (Figure 4.8).

The historic subspecies from the areas dominated by Groups 2 and 3 are *C.c. germinans* to the northeast, and *C.c. crocuta* to the south. The distinction made between these two groups was based on size and coloration (Matschie, 1900), and no skull characteristics have been described. There is no evidence for the additional taxa described for northern Kenya (*C.c. fisi*) or Ethiopia/Somalia/Uganda (*C. c. habessynica*).

Pleistocene refugia hypothesis

The shape data described here parallel results of *Crocuta* cytochrome b analysis by Rohland et al. (2005), who found two clades, northeastern and southern, with overlap through Kenya and Tanzania. With shape, I found a cline stretching from the north-central part of the continent, through the northeast, to the south. A phylogeographical pattern with an eastern/southern Africa split has been demonstrated for many African mammals (e.g., Arctander et al., 1999), often with an additional western lineage (Flagstad et al., 2000; Muwanika et al., 2003). The driving force behind this disjunct pattern in geographical range and/or genetic variation is suggested to be range restriction at the end of the Pleistocene. Global warming likely restricted savannah habitat (Flagstad et al., 2000), resulting in 2–3 (depending upon the species in question) Pleistocene refugia. The inhospitable habitat separating eastern and southern Africa in the Pleistocene may have left a footprint on the ranges and in the DNA of modern

taxa. However Werdelin (2008) suggested that large carnivores are not likely to show such distinct patterns, owing primarily to their dispersal abilities and catholic feeding habits.

Similar to spotted hyenas, African wild dogs have an eastern/southern clade pattern to mtDNA and microsatellite data, but with a larger zone of admixture (Girman et al., 2001). African wild dogs have larger home range sizes than spotted hyenas (Creel and Creel, 2002), and this larger zone of haplotype overlap may reflect a higher level of mobility in African wild dogs. Geographical skull size variation among African wild dogs is similar to that among spotted hyenas in that the specimens collected in east Africa are smaller than those from central and southern Africa (Girman et al., 1993), but to date, there have been no morphological analyses examining associated variation in shape.

The cline in shape described here for *Crocuta* strengthens the Pleistocene refugia hypothesis suggested by Rohland et al. (2005). More genetic analyses, with both wider sampling, and more genes sequenced, are needed to elucidate the phylogeographic pattern between northern and southern spotted hyenas. Matched genetic and skull samples will allow for further development of the thesis that skull morphology follows a cline in shape that is a remnant of geographic isolation in Pleistocene refugia.

APPENDIX

Table A.1. Catalogue numbers of specimens examined in Chapter One.

*included in cranium analysis, †included in mandible analysis.

AMH 114226*†	BM 39.414*†	MSU 36077*†
AMH 114227*†	BM 39.415*†	MSU 36078*†
AMH 114256*†	BM 39.416*†	MSU 36079*†
AMH 147880*†	BM 39.417*†	MSU 36080*†
AMH 165118*†	BM 39.419*†	MSU 36081*†
AMH 165119*†	BM 39.420*†	MSU 36082*†
AMH 173511*†	BM 39.421*†	MSU 36083*†
AMH 187769*†	BM 39.422*†	MSU 36084*†
AMH 187770†	BM 39.423*†	MSU 36094*†
AMH 187771*†	BM 39.424*†	MSU 36156*†
AMH 187772*†	BM 39.425*†	MSU 36160*†
AMH 187773*†	BM 39.426*†	MSU 36161*†
AMH 187774*†	BM 39.427*†	MSU 36163*†
AMH 187776*†	BM 39.428*†	MSU 36165*†
AMH 187777*†	BM 39.428a*†	MSU 36168*†
AMH 187778*†	BM 39.429*†	MSU 36550*†
AMH 187779*†	BM 39.430*†	MSU 36551*†
AMH 187780*†	BM 39.431*†	MSU 36552*†
AMH 187781*†	BM 39.432*†	MSU 35553*†
AMH 187782*†	BM 39.433*†	MSU 36558*†
AMH 205150*†	BM 39.435*†	MSU 36568*†
AMH 20809*†	BM 39.436*†	MSU 36569*†
AMH 20810*†	BM 39.437*†	MSU 36570*†
AMH 216355*†	BM 39.438*†	MSU 36571*†
AMH 27765*†	BM 46.8.3.3†	MSU 36581*†
AMH 27767*†	BM 5.4.3.4*†	MSU 8048*†
AMH 36389*†	BM 58.208*†	MSU F987*†
AMH 36390†	BM 59.272*†	MSU BFT*†
AMH 36391*†	BM 62.706*†	MSU ECO*†
AMH 52059*†	BM 62.707*†	MSU VGS*†
AMH 52060*†	BM 65.537*	MSU NHM114*†
AMH 52062*†	BM 66.790*†	MSU NHM115*†
AMH 52063*†	BM 66.791*†	MVZ 165159*†
AMH 52064*†	BM 66.792†	MVZ 165160*†
AMH 52065*†	BM 69.2.2.13*†	MVZ 165162*†
AMH 52067*†	BM 70.706*†	MVZ 165163*†
AMH 52068*†	BM 73.1955*†	MVZ 165165*†
AMH 52069*†	BM 8.7.24.13*†	MVZ 165166*†
AMH 52097*†	BM 8.7.24.14*†	MVZ 165167*†
AMH 54243*†	BM 9.6.1.14*†	MVZ 165169*†
AMH 54244*†	BM 92.8.1.4*†	MVZ 165170*†
AMH 54312*†	BM 92.8.1.5*†	MVZ 165171*†
AMH 55467*†	Cambridge 4064*†	MVZ 165173*†

Table A.1. Chapter One specimens, continued.

AMH 69447*†	Cambridge 4062*†	MVZ 165174*†
AMH 80103*†	Cambridge 4065*†	MVZ 165175*†
AMH 80621†	Cambridge 4066*†	MVZ 165176*†
AMH 81833*†	Cambridge 4067*†	MVZ 165177*†
AMH 83591*†	CM 2073*†	MVZ 165178*†
AMH 83592*†	CM 20871*†	MVZ 165179*†
AMH 83593*†	CM 5862*†	MVZ 165180*†
BM 0.10.3.1*†	CM 5866*†	MVZ 165181*†
BM 0.3.18.22*†	CM 5873*†	MVZ 165182*†
BM 0.8.6.2*	CM 63108*†	MVZ 173733*†
BM 1.8.9.27*†	CM 6454*†	MVZ 173734*†
BM 11.4.4.1*†	CM 6827*†	MVZ 173735*
BM 11.8.2.10*†	FMNH 104021*†	MVZ 173737*†
BM 11.8.2.9*†	FMNH 104022*†	MVZ 173738*†
BM 1233f*†	FMNH 104981*†	MVZ 173740*†
BM 15.3.6.90*†	FMNH 127825*†	MVZ 173741*†
BM 19.6.1.3*†	FMNH 127826*†	MVZ 173743*†
BM 2.2.8.1*†	FMNH 127829*†	MVZ 173744*†
BM 2.8.5.4*†	FMNH 18855†	MVZ 173745*†
BM 21.29.10.30*†	FMNH 27007†	MVZ 173746*†
BM 23.1.1.81†	FMNH 32933*†	MVZ 173747*†
BM 23.3.4.11†	FMNH 32935*	MVZ 173748*†
BM 23.3.4.14*†	FMNH 34582*†	MVZ 173751*†
BM 23.3.4.15*†	FMNH 34583*†	MVZ 173758*
BM 23.3.4.16*	FMNH 73034*†	MVZ 173759*
BM 23.3.4.19*†	FMNH 73035*†	MVZ 173762*†
BM 25.12.4.233*†	FMNH 93866*†	MVZ 173768*†
BM 27.2.9.10*†	FMNH 98739*†	MVZ 173770*†
BM 27.2.9.9*†	FMNH 98952*†	MVZ 173771*†
BM 27.7.3.8*†	IRSNB 10250†	MVZ 173773*†
BM 27.7.3.8A*†	IRSNB 10336*†	MVZ 175801*†
BM 28.11.6.3*†	IRSNB 11799*†	MVZ 184088*†
BM 28.9.11.133*†	IRSNB 11801*†	MVZ 184089*†
BM 29.11.3.8*†	IRSNB 11802†	MVZ 4823*†
BM 30.12.182*†	IRSNB 21278*†	NMK-OM 2703*†
BM 30.12.2.4*†	IRSNB 21302*†	NMK-OM 2705*†
BM 30.12.2.5*†	IRSNB 21436*†	NMK-OM 2706*†
BM 30.3.6.13*†	IRSNB 4612*†	NMK-OM 2713†
BM 30.3.6.4*†	IRSNB 7705*†	NMK-OM 3444*†
BM 31.1.2.11*†	IRSNB 8632*†	NMK-OM 3445*†
BM 31.4.1.11*	IRSNB 8633*†	NMK-OM 3575*†
BM 31.4.1.12*†	IRSNB 8634*†	NMK-OM 4760*†
BM 31.4.1.13*†	IRSNB 8635*†	NMK-OM 5085*†
BM 34.4.1.136*†	IRSNB 9480*†	NMK-OM 5194†

Table A.1. Chapter One specimens, continued.

BM 34.4.1.137*†	IRSNB 9967*†	NMK-OM 5314*†
BM 34.4.1.138*†	MNHN-AC 1894-54*†	NMK-OM 7189*†
BM 34.4.1.139*†	MNHN-AC 1896-450*	NMK-OM 7465*†
BM 34.4.1.140*†	MNHN-AC 1901-662*†	NMK-OM 7754*†
BM 38.10.18.47†	MNHN-AC 1910-162*†	NMK-OM 7755*†
BM 38.5.10.1*†	MNHN-AC 1927-175*†	NMK-OM 7756*†
BM 38.5.10.2*†	MNHN-OM 1962-1533*†	NMK-OM 7757*†
BM 38.5.10.3*†	MNHN-OM 1962-1535†	NMK-OM 7759*†
BM 39.337†	MNHN-OM 1962-15362*†	NMK-OM 7760*†
BM 39.338*†	MNHN-OM 1962-1537*†	NMK-OM 7761*†
BM 39.339*†	MNHN-OM 1972.399*†	NMK-OM 7762*†
BM 39.340*†	MNHN-OM 1972.400*†	NMK-OM 7850*†
BM 39.341*†	MNHN-OM 1973.125*†	NMK-OM 7893*†
BM 39.342*†	MNHN-OM 1985-1858*†	NMK-OM u*†
BM 39.343*†	MNHN-OM 1986-1090*†	RCSOM137.41*†
BM 39.344*†	MNHN-OM 1996-2514*†	RCSOM137.42*†
BM 39.345*†	MNHN-OM 1997-415*	RCSOM137.421*†
BM 39.346*†	MRAC 11376*†	RCSOM137.43*†
BM 39.347*†	MRAC 11602*†	RCSOM137.60*†
BM 39.348*†	MRAC 11701*†	RCSOM137.61*†
BM 39.349*†	MRAC 1182*†	RCSOM137.62*†
BM 39.350*†	MRAC 1183-m*†	RCSOM137.63*†
BM 39.351*†	MRAC 12096*†	RCSOM16.5*†
BM 39.352*†	MRAC 12442*†	USNM 015202*†
BM 39.353*†	MRAC 12814†	USNM 020874*†
BM 39.355*	MRAC 13843*†	USNM 122544*†
BM 39.356*†	MRAC 14367*†	USNM 161909*†
BM 39.357*	MRAC 14369*†	USNM 162920*†
BM 39.358*†	MRAC 14813*	USNM 162921*†
BM 39.359*†	MRAC 15644*†	USNM 162923*†
BM 39.3599*†	MRAC 15928*	USNM 162924*†
BM 39.360*†	MRAC 16719*†	USNM 163099*†
BM 39.361*†	MRAC 16785*†	USNM 163100*†
BM 39.362*†	MRAC 16786*†	USNM 163101*†
BM 39.363*†	MRAC 16787*†	USNM 163102*†
BM 39.364*†	MRAC 17619*†	USNM 163103*†
BM 39.365*†	MRAC 17701*†	USNM 163104*†
BM 39.366*†	MRAC 17740†	USNM 163299*†
BM 39.367*†	MRAC 18000*†	USNM 163344*†
BM 39.368*†	MRAC 18001*†	USNM 164502*†
BM 39.369*†	MRAC 18495*†	USNM 164506*†
BM 39.370*†	MRAC 18627*†	USNM 164549*†
BM 39.371*†	MRAC 1897*†	USNM 164834*†
BM 39.372*†	MRAC 19272*†	USNM 172924*†

Table A.1. Chapter One specimens, continued.

BM 39.373*†	MRAC 19273*†	USNM 173003†
BM 39.374*†	MRAC 19274*†	USNM 173004*†
BM 39.375*†	MRAC 20325*†	USNM 181516*†
BM 39.376*†	MRAC 2162*†	USNM 181517*†
BM 39.377*†	MRAC 2172*†	USNM 181518*†
BM 39.378*†	MRAC 22802*†	USNM 181519*†
BM 39.379*†	MRAC 2907*†	USNM 181520*†
BM 39.380*†	MRAC 36328*†	USNM 181521*†
BM 39.381*†	MRAC 36543*†	USNM 181522*†
BM 39.382*†	MRAC 36545*†	USNM 181524*†
BM 39.383*†	MRAC 3728*†	USNM 181525*†
BM 39.384*†	MRAC 3788*†	USNM 181526*†
BM 39.385*†	MRAC 3794*†	USNM 181527*†
BM 39.386*†	MRAC 3940†	USNM 181529*†
BM 39.387*†	MRAC 3870*†	USNM 181530*†
BM 39.388*†	MRAC 5934*†	USNM 181533*†
BM 39.389*†	MRAC 6164*†	USNM 181534*†
BM 39.390*†	MRAC 6330*†	USNM 182032*†
BM 39.391*†	MRAC 7964†	USNM 182078*†
BM 39.392*†	MRAC 8005*†	USNM 182082†
BM 39.393*†	MRAC 9292*†	USNM 182084*†
BM 39.394*†	MRAC 9579†	USNM 182085*†
BM 39.395*†	MRAC 9589†	USNM 182091*†
BM 39.396*†	MSU 12391*†	USNM 182095*†
BM 39.397*†	MSU 22401*†	USNM 182101*†
BM 39.398*†	MSU 24292*†	USNM 182103*†
BM 39.399*†	MSU 26055*†	USNM 182105*†
BM 39.400*†	MSU 2714*†	USNM 182110*†
BM 39.401*†	MSU 35852*†	USNM 182113*†
BM 39.402*†	MSU 35853*†	USNM 182114*†
BM 39.403*†	MSU 35854*†	USNM 182117*†
BM 39.404*†	MSU 35855*†	USNM 182210*†
BM 39.406*†	MSU 35856*†	USNM 201010*†
BM 39.407*†	MSU 35857*†	USNM 239161*†
BM 39.408*†	MSU 35858*†	USNM 252774†
BM 39.409*†	MSU 35859*†	USNM 367384*†
BM 39.410*†	MSU 36008*†	USNM 367385*†
BM 39.411*†	MSU 36009*†	USNM 368502*†
BM 39.412*†	MSU 36011*†	USNM 429176†
BM 39.413*†	MSU 36074*†	

Table A.2. Museums visited and abbreviations

Field Museum, Chicago (FMNH)
 Museum of Vertebrate Zoology, Berkeley (MVZ)
 Royal Museum for Central Africa, Tervuren (MRAC)
 Royal Belgian Institute of Natural Sciences, Brussels (IRSNB)
 National Museums of Kenya, Nairobi (NMK-OM)
 Natural History Museum, London (BM)
 National Museum of Natural History, Paris (MNHN)
 American Museum of Natural History, New York (AMH)
 The Smithsonian Institution National Museum of Natural History, Washington, D.C. (USNM)
 Carnegie Museum of Natural History, Pittsburgh (CM)
 Michigan State University Museum, East Lansing (MSU)
 University Museum of Zoology, Cambridge (Cambridge)
 Royal College of Surgeons Odontological Collections, London (RCSOM)

Table A.3. Presence of supernumerary P_1 in *Crocuta crocuta*.

Specimen	Tooth details	Collection locality
Cambridge 4065	Left P_1 present	Hargeisa, Somalia
RCSOM 16.5	Right P_1 present	Samburu, Kenya
USNM 020874	Left P_1 alveolus present	Victoria Falls
USNM 367385	Broken left P_1 present, right P_1 alveolus present	Chioco, Mozambique
BM 39.420	Both P_1 present	Balbal, Tanzania
CMNH 15020	Both P_1 present	Pittsburgh Zoo

Note that the zoo specimen was not included in the total anomaly count.

Table A.4. Specimens used in the study of sexual dimorphism of the spotted hyena. * excluded from mandible analysis. † excluded from ventral analysis.

The Natural History Museum, London				Michigan State University Museum	
Catalogue number	Sex	Catalogue number	Sex	Catalogue number	Sex
BM39 337†	M	BM39 391	F	35852	M
BM39 339	M	BM39 394	F	35853	M
BM39 340	M	BM39 395	F	35854	M
BM39 342	M	BM39 396	F	35856	F
BM39 343	M	BM39 397	F	36008	F
BM39 344	M	BM39 399	F	36011	F
BM39 345	M	BM39 400	F	36074	F
BM39 346	M	BM39 401	F	36077	F
BM39 348	M	BM39 402	F	36078	M
BM39 349	M	BM39 403	F	36079	M
BM39 351	M	BM39 404	F	36080	F
BM39 353	M	BM39 407	F	36083	F
BM39 355*	M	BM39 408	F	36084	M
BM39 356	M	BM39 409	F	36094	F
BM39 358	M	BM39 410	F	36160	F
BM39 359	M	BM39 411	F	36163	M
BM39 360	M	BM39 412	F	36165	F
BM39 361	M	BM39 413	F	36168	M
BM39 362	M	BM39 414	F	36550	F
BM39 363	M	BM39 416	F	36551	F
BM39 364	M	BM39 417	F	36552	F
BM39 366	M	BM39 419	M	36553	F
BM39 368	M	BM39 420	M	36558	F
BM39 369	M	BM39 421	M	36567	F
BM39 370	M	BM39 422	M	36568	F
BM39 373	M	BM39 423	M	36569	F
BM39 375	M	BM39 424	F	36570	F
BM39 376	M	BM39 425	M	36571	F
BM39 378	M	BM39 427	M	36581	F
BM39 381	M	BM39 428	M	486ECO	F
BM39 382*	M	BM39 429	M	897BFT	M
BM39 383	M	BM39 430	F	225VGS	M
BM39 386†	M	BM39 431	F		
BM39 387	M	BM39 432	F		
BM39 388	M	BM39 433	F		
BM39 389	F	BM39 434*	F		
BM39 390	F	BM39 435	F		
		BM39 437	F		

Table A.5. Descriptions of landmark locations.

Ventral Landmarks

- 1 Premaxilla-premaxilla suture at the posterior edge of the first upper incisor alveoli
- 2 Premaxilla-maxilla suture at the lingual edge of the canine*
- 3 Posterior-most point of the incisive foramen*
- 4 Premaxilla-maxilla suture at the midline
- 5 Posterior edge of the occipital bone at the midline of the foramen magnum
- 6 Metacone of P²*
- 7 Posterior palatine foramen*
- 8 Maxilla-palatine suture at the midline
- 9 Palatine-palatine suture at the posterior edge of the palate
- 10 Maxilla-palatine suture at the posterior edge of the palate*
- 11 Medial-most edge of the protocone of P⁴*
- 12 Medial-most edge of the maxilla-jugal suture*
- 13 Lateral-most edge of the jugal-squamosal suture*
- 14 Anterio-lateral corner of the glenoid fossa*
- 15 Medial-most extension of the postglenoid process*
- 16 Medial aspect of the foramen ovale*
- 17 Palatine-pterygoid suture at the presphenoid*
- 18 Posterior-most edge of the jugular/hypoglossal foramen, medial aspect*
- 19 Anterior edge of the external auditory meatus*
*bilateral landmark

Lateral landmarks

- 1 Anterior-most point of the I³ alveolus
- 2 Anterior-most edge of the canine at the alveolus
- 3 Posterior-most edge of the canine at the alveolus
- 4 Anterior-most edge of the nasal-premaxilla suture
- 5 Dorsal edge of the infraorbital foramen
- 6 Dorsal edge of the lacrimal foramen
- 7 Tip of the postorbital process of the frontal bone
- 8 Dorsal-most edge of the jugal-squamosal suture
- 9 Ventral-most edge of the jugal-squamosal suture
- 10 Ventral-most edge of the maxilla-jugal suture
- 11 Dorsal aspect of the junction of pterygoid hamulus with the body of the pterygoid
- 12 Anterio-dorsal edge of the external auditory meatus
- 13 Anterior-most dorsal edge of the occipital condyle
- 14 Posterior-most extreme of the curvature of the sagittal crest

Table A.5. Descriptions of landmark locations, continued.

Mandibular landmarks

- 1 Anteriodorsal-most point of the mandibular symphysis
- 2 Posterior-most edge of the canine at the alveolus
- 3 Posterior-most edge of M_1 at the alveolus
- 4 Anterior-most edge of P_2 at the alveolus
- 5 Posterior-most extreme of the curvature of the coronoid process
- 6 Posterior edge of the articular facet of the mandibular condyle
- 7 Posterior-most point of the angular process
- 8 Anterior edge of the articular facet of the mandibular condyle
- 9 Ventral apex of the curve of the dentary
- 10 Posterior-most point of the mandibular symphysis
- 11 Dorsal apex of the alveolus between the two roots of P_4
- 12 Dorsal-most aspect of the curve between the angular process and the mandibular condyle
- 13 Dorsal-most projection of the angular process

Table A.6. Catalogue numbers of specimens examined in Chapter Three. *included in ventral centroid size analyses, †included in first lower molar analyses, ‡used for evaluating centroid size, first lower molar length, and condylobasal length as proxies of body size.

AMH 114226†	BM 39.409*†	MSU 36008*†‡
AMH 114227*†	BM 39.410*†	MSU 36011*†‡
AMH 114256*†	BM 39.411*†	MSU 36074*†
AMH 165118*†	BM 39.412*†	MSU 36077*†‡
AMH 165119*†	BM 39.413*†	MSU 36078*†‡
AMH 187769*†	BM 39.414*†	MSU 36079*†
AMH 187771*†	BM 39.416*†	MSU 36080*†
AMH 187772*	BM 39.417*†	MSU 36083*†‡
AMH 187776*†	BM 39.419*†	MSU 36084*†
AMH 187777*†	BM 39.420*†	MSU 36094*†
AMH 187779*	BM 39.421*†	MSU 36160*†
AMH 187782*	BM 39.422*†	MSU 36161*†
AMH 20809*†	BM 39.423*†	MSU 36163*†‡
AMH 20810*†	BM 39.424*†	MSU 36165*†‡
AMH 216355*†	BM 39.425*†	MSU 36168*†‡
AMH 27765*†	BM 39.427*†	MSU 36550*†‡
AMH 27767*†	BM 39.428*†	MSU 36551*†‡
AMH 52059*†	BM 39.429*†	MSU 36552*†
AMH 52060*†	BM 39.430*†	MSU 35553*†‡
AMH 52063*†	BM 39.431*	MSU 36558*†
AMH 52064*†	BM 39.432*†	MSU 36567*†‡
AMH 52065*†	BM 39.433*	MSU 36568*†
AMH 52068*†	BM 39.435*†	MSU 36569*†‡
AMH 52069*†	BM 39.437*†	MSU 36570*†
AMH 52097*†	BM 58.208*†	MSU 36571*†‡
AMH 54243*†	BM 59.272†	MSU 36581*†
AMH 54244*†	BM 62.706*†	MSU 8048*†
AMH 55467*†	BM 62.707*†	MSU BFT*†‡
AMH 81833*†	BM 65.537*	MSU ECO*†‡
AMH 83591*†	BM 66.790*†	MSU VGS*†
AMH 83592*†	BM 66.792†	MVZ 165159*
AMH 83593*†	BM 70.706*	MVZ 165160*†
BM 0.10.3.1*†	BM 9.6.1.14*†	MVZ 165162*†
BM 0.3.18.22*†	BM 92.8.1.4*†	MVZ 165163*†
BM 0.8.6.2*	Cambridge 4062*†	MVZ 165165*
BM 1.8.9.27*†	Cambridge 4065*†	MVZ 165166*†
BM 19.6.1.3*†	Cambridge 4067*†	MVZ 165167*†
BM 2.2.8.1*†	CM 20871*†	MVZ 165169*†
BM 2.8.5.4*†	CM 5862*†	MVZ 165170*†
BM 21.29.10.30*†	CM 63108*†	MVZ 165175*†

Table A.6. Chapter Three specimens, continued.

BM 23.3.4.11†	CM 6827†	MVZ 165176*†
BM 23.3.4.14*†	FMNH 104021*†	MVZ 165179*†
BM 23.3.4.15*†	FMNH 104981*†	MVZ 165180*†
BM 23.3.4.16*	FMNH 127825*†	MVZ 165181*†
BM 23.3.4.19*†	FMNH 127826*†	MVZ 165182*†
BM 24.8.3.4†	FMNH 127829*†	MVZ 173733*†
BM 24.8.3.74†	FMNH 135072*	MVZ 173734*†
BM 25.12.4.233*†	FMNH 32933*†	MVZ 173737*†
BM 27.2.9.9*†	FMNH 34582*†	MVZ 173741†
BM 27.7.3.8*†	FMNH 34583*†	MVZ 173743*†
BM 27.7.3.8A*†	FMNH 73034*†	MVZ 173744*†
BM 28.11.6.3*†	FMNH 73035*†	MVZ 173745†
BM 29.11.3.8*†	FMNH 93866†	MVZ 173746*†
BM 30.12.182*†	FMNH 98739*†	MVZ 173747*†
BM 30.12.2.5*	FMNH 98952*†	MVZ 173748*†
BM 30.3.6.13*†	IRSNB 10250*†	MVZ 173751*†
BM 31.1.2.11*†	IRSNB 10336*†	MVZ 173754*
BM 31.4.1.13*†	IRSNB 11799*†	MVZ 173758*
BM 34.4.1.134†	IRSNB 11801*†	MVZ 173759*
BM 34.4.1.136*†	IRSNB 11804†	MVZ 173768*†
BM 34.4.1.137*†	IRSNB 21278*	MVZ 173770*
BM 34.4.1.138*†	IRSNB 21302*†	MVZ 173771*†
BM 34.4.1.139*†	IRSNB 21436*†	MVZ 175801*†
BM 34.4.1.140*†	IRSNB 4612*†	MVZ 184089*†
BM 38.10.18.47*†	IRSNB 7705†	NMK-OM 2703†
BM 38.5.10.2*†	IRSNB 8632*†	NMK-OM 2705*†
BM 38.5.10.3*†	IRSNB 8633*†	NMK-OM 3580*
BM 39.337†	IRSNB 8634*†	NMK-OM 7189*†
BM 39.339*†	IRSNB 9480*†	NMK-OM 7755*†
BM 39.340*†	IRSNB 9967†	NMK-OM 7757*†
BM 39.342*†	MNHN-AC 1894-54*†	NMK-OM 7761*†
BM 39.343*†	MNHN-AC 1896-450*	NMK-OM 7762*†
BM 39.344*†	MNHN-OM 1962-1537*†	NMK-OM 7850*†
BM 39.345*†	MNHN-OM 1972.400*†	RCSOM137.41*†
BM 39.346*†	MNHN-OM 1996-2514*†	RCSOM137.42*†
BM 39.348*†	MNHN-OM 1997-415*	RCSOM137.43*†
BM 39.349*†	MRAC 11376*†	RCSOM16.5*†
BM 39.351*†	MRAC 11602*†	USNM 020874*†
BM 39.353*†	MRAC 11701*†	USNM 122544†
BM 39.355*	MRAC 12096*†	USNM 162920*†
BM 39.356*†	MRAC 12442*†	USNM 162924*
BM 39.359*†	MRAC 14367*	USNM 163099*†
BM 39.360*†	MRAC 14369*†	USNM 163100*†
BM 39.361*	MRAC 14813*	USNM 163101*†

Table A.6. Chapter Three specimens, continued.

BM 39.362*†	MRAC 16719*	USNM 163102*†
BM 39.363*	MRAC 17619*†	USNM 163103*†
BM 39.364*†	MRAC 18000†	USNM 164502*†
BM 39.366*†	MRAC 18495*†	USNM 164506*†
BM 39.368*†	MRAC 18627*†	USNM 164549*†
BM 39.369*†	MRAC 1897†	USNM 181516*†
BM 39.370*†	MRAC 19272†	USNM 181518*†
BM 39.373*†	MRAC 19273†	USNM 181519*†
BM 39.375*	MRAC 20325*†	USNM 181520*†
BM 39.376*†	MRAC 2162*†	USNM 181521*†
BM 39.378*†	MRAC 22802*†	USNM 181524*†
BM 39.381*†	MRAC 2907*†	USNM 181525*†
BM 39.382*	MRAC 36328*†	USNM 181526*†
BM 39.383*†	MRAC 36543*†	USNM 181527*†
BM 39.385†	MRAC 36545*†	USNM 181530*†
BM 39.386†	MRAC 3728*†	USNM 181533*†
BM 39.387*†	MRAC 3788*†	USNM 181534*†
BM 39.388*†	MRAC 384†	USNM 182032*†
BM 39.389*†	MRAC 3870*†	USNM 182085*†
BM 39.390*†	MRAC 5934*†	USNM 182091*†
BM 39.391*†	MRAC 9292*†	USNM 182095*†
BM 39.394*†	MRAC 9579†	USNM 182103*†
BM 39.395*†	MSU 12391*†	USNM 182105†
BM 39.396*†	MSU 22401*†	USNM 182113*†
BM 39.397*†	MSU 24292†	USNM 182117†
BM 39.399*†	MSU 26055*	USNM 182210*†
BM 39.400*†	MSU 2714*†	USNM 201010*†
BM 39.401*†	MSU 35852*†	USNM 239161*†
BM 39.402*†	MSU 35853*†	USNM 367384*†
BM 39.403*	MSU 35854*†	USNM 367385*†
BM 39.404*†	MSU 35856*	USNM 368502*†
BM 39.407*†	MSU 35857*†	USNM 429176*†
BM 39.408*	MSU 35858*†	

Table A.7. Catalogue numbers of specimens examined in Chapter Four.
 *included in ventral analysis, †included in mandible analysis, ‡ included in lateral analysis.

AMH 114226†	BM 39.408*†‡	MSU 36008*†‡
AMH 114227*†‡	BM 39.409*†‡	MSU 36011*†‡
AMH 114256*†‡	BM 39.410*†‡	MSU 36074*†‡
AMH 165118*†	BM 39.411*†‡	MSU 36077*†‡
AMH 165119*†‡	BM 39.412*†‡	MSU 36078*†‡
AMH 187769*†‡	BM 39.413*†‡	MSU 36079*†‡
AMH 187771*†‡	BM 39.414*†‡	MSU 36080*†‡
AMH 187772*†‡	BM 39.416*†‡	MSU 36083*†‡
AMH 187776*†‡	BM 39.417*†‡	MSU 36084*†‡
AMH 187777*†‡	BM 39.419*†‡	MSU 36094*†‡
AMH 187779*‡	BM 39.420*†‡	MSU 36160*†‡
AMH 187780‡	BM 39.421*†‡	MSU 36161*†‡
AMH 187782*†	BM 39.422*†‡	MSU 36163*†‡
AMH 20809*†‡	BM 39.423*†‡	MSU 36165*†‡
AMH 20810*†‡	BM 39.424*†‡	MSU 36168*†‡
AMH 216355*†‡	BM 39.425*†‡	MSU 36550*†‡
AMH 27765*†‡	BM 39.427*†‡	MSU 36551*†‡
AMH 27767*†‡	BM 39.428*†‡	MSU 36552*†‡
AMH 52059*†‡	BM 39.429*†‡	MSU 35553*†‡
AMH 52060*†‡	BM 39.430*†‡	MSU 36558*†‡
AMH 52063*†‡	BM 39.431*†‡	MSU 36567*†‡
AMH 52064*†‡	BM 39.432*†‡	MSU 36568*†‡
AMH 52065*†‡	BM 39.433*†‡	MSU 36569*†‡
AMH 52068*†‡	BM 39.435*†‡	MSU 36570*†‡
AMH 52069*†‡	BM 39.437*†‡	MSU 36571*†‡
AMH 52097*†‡	BM 58.208*†‡	MSU 36581*†‡
AMH 54243*†‡	BM 59.272†	MSU 8048*†‡
AMH 54244*†‡	BM 62.706*†‡	MSU F987‡
AMH 55467*†‡	BM 62.707*†‡	MSU BFT*†‡
AMH 81833*†‡	BM 66.792†	MSU ECO*†‡
AMH 83591*†‡	BM 9.6.1.14*†‡	MSU VGS*†‡
AMH 83592*†‡	BM 92.8.1.4*†‡	MSU NHM115†‡
AMH 83593*†‡	Cambridge 4062*†‡	MVZ 165159*‡
BM 0.10.3.1*†‡	Cambridge 4065*†‡	MVZ 165160*†‡
BM 0.3.18.22*†‡	Cambridge 4067*†‡	MVZ 165162*†‡
BM 0.8.6.2*‡	CM 20871*†‡	MVZ 165163*†‡
BM 1.8.9.27*†‡	CM 5862*†‡	MVZ 165165*†‡
BM 15.3.6.90†‡	CM 63108*†‡	MVZ 165166*‡
BM 19.6.1.3*†‡	CM 6827†	MVZ 165167*†‡
BM 2.8.5.4*†	FMNH 104021*†‡	MVZ 165169*†‡
BM 21.29.10.30*†	FMNH 104981*†‡	MVZ 165170*†‡
BM 23.3.4.11†	FMNH 127825*†‡	MVZ 165175*†‡

Table A.7. Chapter Four specimens, continued.

BM 23.3.4.14*†‡	FMNH 127826*†‡	MVZ 165176*†‡
BM 23.3.4.15*†‡	FMNH 127829*†‡	MVZ 165179*†‡
BM 23.3.4.16*†	FMNH 135072*	MVZ 165180*†‡
BM 23.3.4.19*†‡	FMNH 32933*†‡	MVZ 165181*†‡
BM 24.8.3.4†	FMNH 34582*†‡	MVZ 165182*†‡
BM 24.8.3.74†	FMNH 34583*†‡	MVZ 173733*†‡
BM 25.12.4.233*†	FMNH 73034*†‡	MVZ 173734*†‡
BM 27.2.9.9*†‡	FMNH 73035*†‡	MVZ 173737*†‡
BM 27.7.3.8*†‡	FMNH 93866†	MVZ 173741†‡
BM 27.7.3.8A*†‡	FMNH 98739*†‡	MVZ 173743*†‡
BM 28.11.6.3*†‡	FMNH 98952*†‡	MVZ 173745†
BM 29.11.3.8*†‡	IRSNB 10250*†‡	MVZ 173746*†‡
BM 30.12.182*†‡	IRSNB 10336*†‡	MVZ 173747*†
BM 31.1.2.11*†‡	IRSNB 11799*†‡	MVZ 173748*†
BM 31.4.1.13*†‡	IRSNB 11801*†‡	MVZ 173751*†‡
BM 34.4.1.134†	IRSNB 11804†	MVZ 173754†
BM 34.4.1.136*†‡	IRSNB 21278*†‡	MVZ 173758*†
BM 34.4.1.137*†‡	IRSNB 21302*†‡	MVZ 173759*†
BM 34.4.1.138*†‡	IRSNB 21436*†‡	MVZ 173768*†‡
BM 34.4.1.139*†‡	IRSNB 4612*†‡	MVZ 173770*†
BM 34.4.1.140*†‡	IRSNB 7705†	MVZ 173771*†‡
BM 38.10.18.47*†‡	IRSNB 8632*†‡	MVZ 175801*†‡
BM 38.5.10.2*†‡	IRSNB 8633*†‡	MVZ 184088*†‡
BM 38.5.10.3*†‡	IRSNB 8634*†‡	MVZ 184089*†‡
BM 39.337†‡	IRSNB 9480*†‡	NMK-OM 2703†‡
BM 39.339*†‡	IRSNB 9967†	NMK-OM 2705*†‡
BM 39.340*†‡	MNHN-AC 1894-54*†‡	NMK-OM 3580*†
BM 39.342*†‡	MNHN-AC 1896-450*†	NMK-OM 7189*†
BM 39.343*†‡	MNHN-OM 1962-1537*†‡	NMK-OM 7755*†
BM 39.344*†‡	MNHN-OM 1972.400*†‡	NMK-OM 7757*†
BM 39.345*†‡	MNHN-OM 1996-2514*†‡	NMK-OM 7761*†
BM 39.346*†‡	MNHN-OM 1997-415*†	NMK-OM 7762*†
BM 39.348*†‡	MRAC 11376*†‡	NMK-OM 7850*†‡
BM 39.349*†‡	MRAC 11602*†‡	RCSOM137.42*†‡
BM 39.351*†‡	MRAC 11701*†	RCSOM137.41*†‡
BM 39.353*†‡	MRAC 12096*†‡	RCSOM16.5*†‡
BM 39.355*†	MRAC 12442*†‡	RCSOM137.43*†‡
BM 39.356*†‡	MRAC 14367*†‡	USNM 020874*†‡
BM 39.358*†‡	MRAC 14369*†‡	USNM 122544†
BM 39.359*†‡	MRAC 14813*†	USNM 163099*†‡
BM 39.360*†‡	MRAC 16719*†‡	USNM 163100*†‡
BM 39.361*†‡	MRAC 16786†	USNM 163101*†‡
BM 39.362*†‡	MRAC 17619*†‡	USNM 163102*†‡
BM 39.363*†‡	MRAC 17740†	USNM 163103*†‡

Table A.7. Chapter Four specimens, continued.

BM 39.364*†‡	MRAC 18000†‡	USNM 164502*†‡
BM 39.366*†‡	MRAC 18495*†‡	USNM 164506*†‡
BM 39.368*†‡	MRAC 18627*†‡	USNM 164549*†‡
BM 39.369*†‡	MRAC 1897*†‡	USNM 181516*†‡
BM 39.370*†‡	MRAC 19272†	USNM 181518*†‡
BM 39.373*†‡	MRAC 19273†	USNM 181519*†‡
BM 39.375*†‡	MRAC 2162*†‡	USNM 181520*†‡
BM 39.376*†‡	MRAC 22802*†‡	USNM 181521*†‡
BM 39.378*†‡	MRAC 2907*†‡	USNM 181524*†‡
BM 39.381*†‡	MRAC 36328*†‡	USNM 181525*†‡
BM 39.382*†	MRAC 36543*†‡	USNM 181526*†‡
BM 39.383*†‡	MRAC 36545*†	USNM 181527*†‡
BM 39.385†‡	MRAC 3728*†‡	USNM 181530*†‡
BM 39.386†‡	MRAC 3788*†‡	USNM 181533*†‡
BM 39.387*†‡	MRAC 384†	USNM 181534*†‡
BM 39.388*†‡	MRAC 3870*†‡	USNM 182032*†‡
BM 39.389*†‡	MRAC 5934*†‡	USNM 182085*†‡
BM 39.390*†‡	MRAC 9292*†‡	USNM 182091*†‡
BM 39.391*†‡	MRAC 9579†	USNM 182095*†‡
BM 39.394*†‡	MSU 12391*†‡	USNM 182103*†‡
BM 39.395*†‡	MSU 22401*†‡	USNM 182105†‡
BM 39.396*†‡	MSU 24292†‡	USNM 182113*†‡
BM 39.397*†‡	MSU 26055*†‡	USNM 182117†‡
BM 39.399*†‡	MSU 2714*†‡	USNM 182210*†‡
BM 39.400*†‡	MSU 35852*†‡	USNM 201010*†‡
BM 39.401*†‡	MSU 35853*†‡	USNM 239161*†‡
BM 39.402*†‡	MSU 35854*†‡	USNM 367384*†‡
BM 39.403*†‡	MSU 35856*†‡	USNM 367385*†‡
BM 39.404*†‡	MSU 35857*†‡	USNM 368502*†‡
BM 39.407*†‡	MSU 35858*†‡	USNM 429176*†‡

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