

# Tooth Root Morphology in the Early Pliocene African Bear *Agriotherium africanum* (Mammalia, Carnivora, Ursidae) and its Implications for Feeding Ecology

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**Abstract** Tooth root surface areas serve as proxies for bite force potentials, and by extension, dietary specialization in extant carnivorans. Here, we investigate the feeding ecology of the extinct large-bodied ursid *Agriotherium africanum*, by comparing its root surface areas (reconstructed with the aid of computed tomography and three-dimensional image processing) and bite force estimates, with those of extant carnivorans. Results show that in absolute terms, canine and carnassial bite forces, as well as root surface areas were highest in *A. africanum*. However, when adjusted for skull size, *A. africanum*'s canine roots were smaller than those of extant solitary predators. With teeth being the limiting factor in the masticatory system, low canine root surface areas suggest that *A. africanum* would have struggled to bring down large vertebrate prey. Its adjusted carnassial root sizes were found to be smaller than those of extant hard object feeders and the most carnivorous tough object feeders, but larger than those of extant omnivorous ursids and *Ursus*

*maritimus*. This and the fact that it displayed its highest postcanine root surface areas in the carnassial region (rather than the most distal tooth in the tooth row) suggest that *A. africanum* consumed more vertebrate tissue than extant omnivorous ursids. With an apparent inability to routinely bring down large prey or to consume mechanically demanding skeletal elements, its focus was most likely on tough tissue, which it acquired by actively scavenging the carcasses of freshly dead/freshly killed animals. Mechanically less demanding skeletal elements would have been a secondary food source, ingested and processed mainly in association with muscle and connective tissue.

**Keywords** Ursidae · Tooth root surface area · South Africa · Early Pliocene · Feeding ecology

## Introduction

*Agriotherium africanum*, which was originally discovered in 1965 at the South African early Pliocene site of Langebaanweg (LBW) 'E' Quarry (32°58'S, 18°7'E), represents the first pre-Pleistocene ursid to be identified in sub-Saharan Africa (Hendey 1972, 1977). Ever since its discovery, it has generated scientific interest due to its relatively unusual morphology (Hendey 1972, 1974, 1977, 1980; Sorkin 2006; Oldfield et al. 2012). While resembling extant ursids in overall form, it displayed certain adaptations, particularly those related to feeding ecology, that are absent or rare in extant ursids. Aspects of its postcranial skeleton, particularly its long limbs and metapodials, suggest a greater cursorial ability than modern bears (Hendey 1980). With regards to its skull, its muzzle was relatively short and broad, its zygomatic arches were particularly wide, and its neurocranium featured a high sagittal crest. Its P<sup>4</sup> and

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maxillary molars possessed pointed, high crowned buccal cusps that were coupled with reductions of the lingual cusps, forming what could be regarded as a shearing complex that functioned like a “second carnassial” (Fig. 1) (Hendey 1980). The abovementioned morphological features can be considered indicative of a hypercarnivorous lifestyle (Van Valkenburgh 1989, 2007; Wroe et al. 1998) and not surprisingly, *A. africanum* has been characterized as a felid-like predator on large terrestrial vertebrates (Hendey 1972, 1974, 1977, 1980) and more recently, a bone-cracking scavenger of large terrestrial vertebrate carcasses (Sorkin 2006). Notwithstanding the results of these previous studies, there still remains much to be learned with regards to the feeding ecology of this fossil bear. To further investigate this issue, we compared *A. africanum*'s tooth root surface areas (RA) with those of a wide range of extant carnivorans. Tooth root surface area, as we recently showed (Kupczik and Stynder 2012), is a strong indicator of bite force production, and by extension, dietary specialization in extant carnivorans. This potentially makes it a useful tool for reconstructing the feeding ecology of extinct taxa, particularly those without any modern descendants such as *A. africanum*.

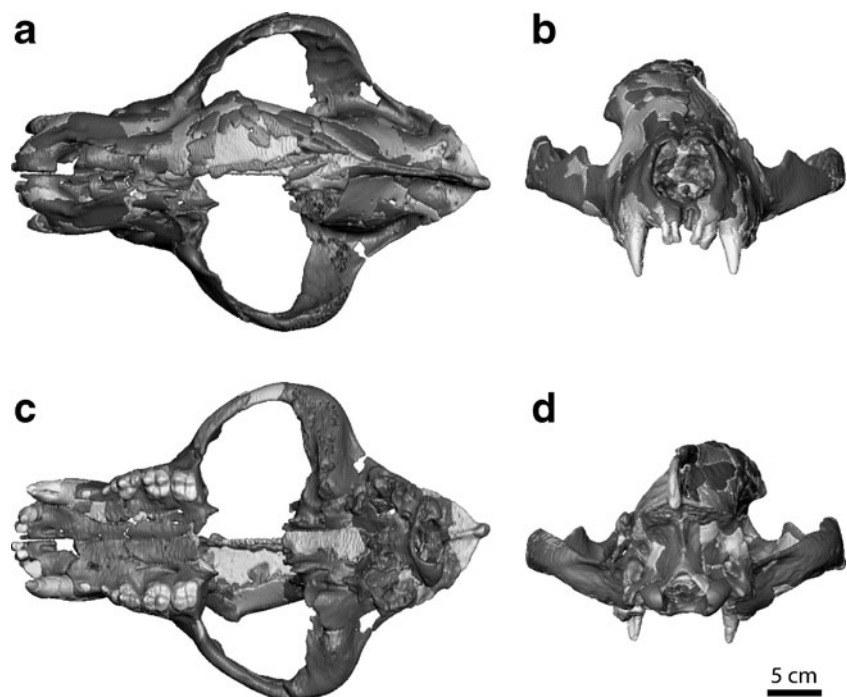
#### Tooth Root Surface Area and Dietary Ecology

Occlusal forces exerted on teeth during mastication can lead to their failure if not effectively dissipated into the jaw, particularly when hard foods are consumed (Spencer 2003; Kupczik and Dean 2008; Lucas et al. 2008). How effectively teeth are able to release these occlusal forces depend on the length, shape, and especially surface area of their roots

(Kovacs 1971; Spencer 1998, 2003; Kupczik and Dean 2008; Kupczik and Hublin 2010; Hamon et al. 2012; Kupczik and Stynder 2012). Kupczik and Stynder (2012) have shown that among extant large-bodied carnivorans (and irrespective of taxonomic affinity), root surface area is correlated with bite forces and vice versa, which in turn depends on differences in the material properties of foods ingested and masticated. It was found that the greater the amount of hard foods (e.g., bone, bamboo) carnivorans consume relative to soft or tough foods (e.g., skin, muscle, leaves), the higher their bite forces and the larger their postcanine root surface areas (unadjusted and adjusted for skull size). Similarly, the larger the prey species carnivorans focus on (relative to their own body mass), the higher their bite forces and the larger their postcanine root surface areas (unadjusted for skull size). Large root surface areas in carnivorans then, appear to be related to the efficient dissipation of high occlusal forces generated during the mastication of mechanically demanding foods. Within carnivoran species, the postcanine teeth with the largest root surface areas are those having a primary role in food processing, and thus vary with dietary focus (Kupczik and Stynder 2012).

In contrast to postcanine dentition, Kupczik and Stynder (2012) found that canine root surface area in carnivorans is not strictly correlated with bite force, food material properties, or prey size. This notwithstanding, canine root surface area does reflect predatory behavior to an extent. Specifically, predators of powerful, fast-moving prey (e.g., *Panthera leo*) have canines that are well anchored, with large root surface areas. This morphology likely corresponds with the high bending strength required to sustain

**Fig. 1** *Agriotherium africanum* skull, SAM-PQL-45062. **a** superior; **b** anterior; **c** inferior; **d** posterior views. Original skull parts are shown in dark grey, teeth and reconstructed parts in light grey



high bite forces when capturing and killing these types of prey. In contrast, carnivorans that are not carnivorous, or those that hunt prey that are less resistant to capture (e.g., *Ailuropoda melanoleuca*, *Otocyon megalotis*, *Canis simensis*), generally possess poorly-anchored canines with relatively small root surface areas. Canine root surface area then can provide some indication of a carnivoran's predatory ability and nature of its prey (Kupczik and Stynder 2012).

Given the above, we are able to make the following generalizations regarding root surface areas in the main carnivoran dietary groups. Species that are primarily carnivorous (be they predators or scavengers) invariably have large canine and large carnassial root surface areas (except *Ursus maritimus*, which only has large canine root surface areas). Those carnivorans that scavenge (e.g., *Hyaena hyaena*) have the largest carnassial root surface areas, as their diets consist mainly of hard foods such as bone and difficult to process tissue (e.g., thick hide) left unconsumed by predators. On the other hand, those that predate on large prey (e.g., *P. leo*, *Panthera pardus*) as well as those that predate on small- to medium-sized prey (e.g., feral *Canis familiaris*) have intermediate carnassial root surface areas compared to scavengers, as they consume tough, but easier to process prey or body parts. Solitary predators of large prey tend to have the largest canine root surface areas (e.g., felids and *U. maritimus*), while this is not necessarily the case with pack predators of large prey (e.g., *Lycan pictus*). Omnivores generally exhibit the smallest canine and carnassial root surface areas among extant carnivorans, as animal tissue (primarily from small- to medium-sized prey) only constitutes approximately 50 % of their diet. In contrast to predators or specialist scavengers, however, they tend to have a full set of post-carnassial teeth with large root surfaces as they consume significant amounts of non-vertebrate foods requiring crushing (plant material, invertebrates) (Kupczik and Stynder 2012).

By analyzing its tooth root surface areas, we test the following previously suggested hypotheses regarding the feeding ecology of *A. africanum*:

**Hypothesis 1-** *Agriotherium africanum* was a predator on large terrestrial mammals.

Expectation: *Agriotherium africanum* resembles extant tough food feeders that feed on large prey (e.g., *P. leo*) in

possessing large canine and intermediate postcanine (especially carnassial) tooth root surface areas (adjusted for skull size).

**Hypothesis 2-** *Agriotherium africanum* was a bone-cracking scavenger of large terrestrial vertebrate carcasses.

Expectation: *Agriotherium africanum* resembles extant hard food feeders that feed on large prey (*P. brunnea*) in possessing large canine and large postcanine tooth root surface areas (especially carnassial) (adjusted for skull size).

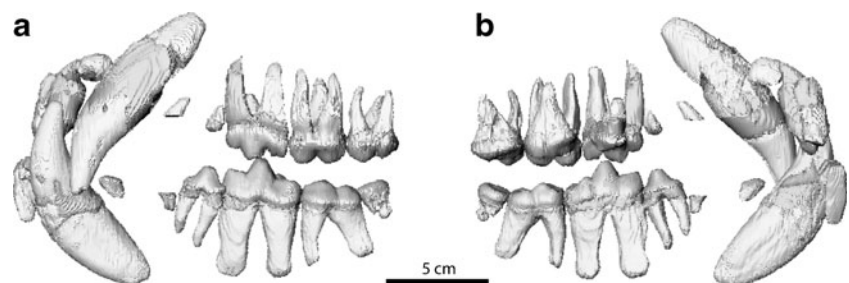
## Materials and Methods

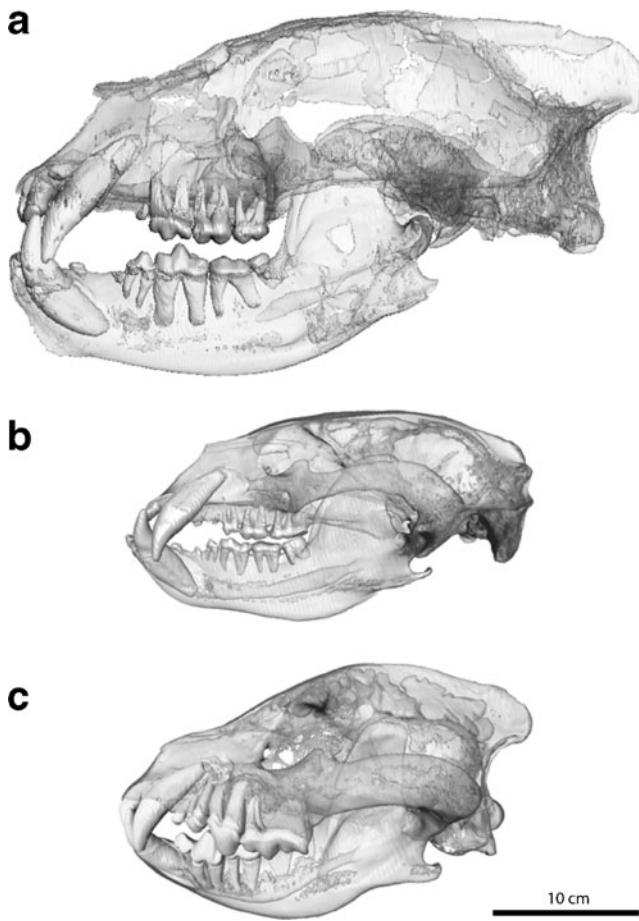
### Sample

The 'E' Quarry *A. africanum* material, which is housed at the Iziko South African Museum, includes a variety of cranial and postcranial elements estimated to belong to approximately 14 animals. Included among the largely fragmentary cranial materials, is a partially reconstructed skull, SAM-PQL 45062 (Fig. 1). Our study focuses on complete and restored tooth roots in the mandible (left side) and maxilla of SAM-PQL 45062. Roots are present on all teeth except for the I<sub>2</sub> and I<sub>3</sub> (Figs. 2 and 3).

The extant carnivoran sample comprised 16 skulls of 13 species previously analyzed by Kupczik and Stynder (2012). Each species was classified into one of three dietary categories based on the material properties of their most relevant foods processed with their postcanine teeth, thus hard food feeders, tough food feeders, and omnivores (supporting literature provided in Kupczik and Stynder 2012). Preferred prey size (small/none, medium, and large) in each case is relative to predator body mass. All specimens were fully adult and are housed at the Iziko South African Museum, Cape Town, South Africa (SAM); the Odontological Collection of The Royal College of Surgeons of England, London, England (RSC); the Field Museum of Natural History, Chicago, USA (FMNH); D.R. Dickey Collection of the University of California, Los Angeles, USA (UCLA); the Texas Memorial Museum of Science and History, Austin, USA (TMM); and the National Museum of Natural History, Washington, USA (USNM). The collection records indicated the sex and provenance in

**Fig. 2** Exposed maxillary and mandibular dentition of *A. africanum*. **a** buccal view; **b** lingual view. Since the P<sub>3</sub> and P<sub>2</sub> are missing or incomplete in this specimen, only the roots are shown. Note the reconstructed parts of the upper and lower canine shown in dark grey





**Fig. 3** *Agriotherium africanum* skull compared to those of an extant ursid and hyaenid (bone is rendered transparent to show the tooth roots). **a** *Agriotherium africanum*; **b** *Ursus americanus*; **c** *Hyaena hyaena*. Note the bulging of the mandibular corpus base in *A. africanum* and *H. hyaena*

most cases. The selection criteria were a full permanent dentition in at least one complete upper quadrant and one complete lower quadrant with fully formed roots.

#### Computed Tomography (CT)

Coronal CT scans were taken of the skull and left mandible of SAM-PQL 45062 using a Toshiba Aquilion CT scanner at the Groote Schuur Hospital, Cape Town, South Africa with the following parameters: FC30 convolution kernel (bone

algorithm); image matrix of 512×512 pixels; 120 kV tube voltage and an exposure of 75 mAs. Scans were taken in helical mode with a slice thickness of 0.5 mm. The resulting in-plane resolution was 0.46 mm for the mandible and 0.62 mm for the skull, respectively. The comparative sample of extant carnivorans comprised CT scans of skulls of ursids, hyaenids, felids, and canids (see Kupczik and Stynder 2012: table 1 for information regarding the comparative sample). More information on these scans, with an in-plane resolution of between 0.17 mm and 0.63 mm, can be found in Kupczik and Stynder (2012).

#### 3D Image Processing

The skull and mandible, as well as the mandibular and maxillary teeth of SAM-PQL 45062, were segmented using Avizo 5.1 (Mercury Computer Systems). In addition, each tooth containing enamel, dentine, and the pulp cavity, was segmented with a semiautomatic threshold-based approach combined with manual editing of the slices. The plaster used to restore fractured teeth was distinguishable from the dental and bone tissues due to their different CT density and added as a separate material in Avizo. Following segmentation, triangulated surface models were generated for each tooth, skull, and mandible using the constrained smoothing algorithm (kernel size of 4) in Avizo. Each tooth was virtually bisected into its anatomical crown and root parts by using a best-fit plane defined by up to ten points along the cemento-enamel junction. Root surface area (RA) was quantified in mm<sup>2</sup>. As a proxy for occlusal area, cervical plane area (CA; in mm<sup>2</sup>) was computed as the area between the bisected crown and root. Both were measured in Avizo. Surface models of the teeth of the extant carnivoran sample were taken from Kupczik and Stynder (2012).

#### Skull Measurements and Bite Force Estimates

The geometric mean of the following four variables was computed as a proxy for cranial/masticatory apparatus size: maximum skull length, bicanine breadth, maximum bizygomatic breadth, and occipital triangle height (see Kupczik and Stynder 2012). In addition, we computed the geometric mean of the following three variables as a proxy for

**Table 1** *Agriotherium africanum* root surface area (RA) and cervical plane area (CA)

		I1	I2	I3	C	P2	P3	P4	M1	M2	M3
Mandibular	RA	610	*	*	4672.5	129	85	1411.6	3307.9	2249.1	546.6
	CA	43	*	*	480.1	170	66	202	625.3	580.9	183.7
Maxillary	RA	774.2	77	322	4460	240	211.2	2990.6	3160.1	2091.7	
	CA	107.5	103.1	355	562.6	67	47.3	497.6	664.4	579.6	

\* no value due to missing tooth

mandible size: mandibular length (condyle to anterior symphyseal margin), coronoid process height (perpendicular distance between angular process and coronoid process), and corpus height at  $M_1$  (perpendicular distance between superior alveolar margin and corpus base). Note that the unit of the geometric mean is in mm. This estimate of masticatory apparatus size is seen here as a biomechanical standard that is related to lever mechanics and muscle size (see Vinyard et al. 2003). We thus computed shape variables as the ratio of the square-root of the maxillary and mandibular root surface areas divided by the geometric mean of the skull and the mandible, respectively. The use of this dimensionless shape variable is a scale-free means to examine variation across a size range by considering differences in form (Jungers et al. 1995). By using skull and mandible size as a biomechanical standard, we were able to compare the tooth root morphology of different carnivorans while holding constant relevant mechanical factors thought to be crucial in influencing skull loading and bite force generation. We also assessed whether *A. africanum* followed the positive allometric scaling pattern observed in extant carnivorans (Kupczik and Stynder 2012) by comparing the residuals from an ordinary least squares regression of  $P^4$  root surface area (square rooted and  $\log_{10}$ -transformed) on the geometric mean of skull size ( $\log_{10}$ -transformed) of the extant carnivorans to the y residual (root surface area) of *A. africanum*.

Maximum bite force at the canine and carnassials of *A. africanum* was estimated based on a 2D lever arm model of the main jaw adducting muscles (the masseter-medial pterygoid muscle complex and temporalis muscles) following the protocol by Wroe et al. (2005) and Christiansen and Wroe (2007) and outlined in Kupczik and Stynder (2012). In brief, the cross-sectional areas of the muscles and the inlever moment arms were computed from screenshot images of the 3D reconstructions of the skulls using IMAGEJ, version 1.44 f (<http://rsbweb.nih.gov/ij/>). By using the outlever moment arm from the jaw joint to the maxillary canine (Ca) and the carnassial ( $P^4$ ), respectively, the bite force (in N) was computed as  $(T \times l_t + M \times l_m)/l_o$ , where T and M are the areas of the temporalis muscle and masseter-ptyergoideus muscle complex, respectively;  $l_t$  and  $l_m$  are the inlever temporalis and masseter-ptyergoideus moment arms and  $l_o$  is the outlever moment arm at Ca and  $P^4$  (at the paracone), respectively.

Statistical Analyses

Root surface areas (cranial and mandible size corrected) of SAM-PQL 45062 were visually compared to published data for extant carnivorans (Kupczik and Stynder 2012). Moreover, bivariate associations between root surface area and cervical plane area, as well as between root surface area and bite force were evaluated with Spearman’s rank correlation. Bivariate trends were modeled with reduced major axis regression line fittings in PAST v. 2.12 (Hammer et al. 2001).

Results

Standard views of the CT based reconstruction of the skull and dentition of SAM-PQL 45062 are shown in Fig. 1. The  $P^4$ ,  $M^1$ , and  $M^2$  are three-rooted (two buccal roots and one lingual root), while the  $P_4$ ,  $M_1$ , and  $M_2$  have two roots each (one mesial, one distal) (Fig. 2). The geometric mean of skull size is 199.26 mm (maximum skull length=449.08 mm, bicanine breadth=113.72 mm, maximum bizygomatic breadth=301.46 mm, and occipital triangle height=102.39 mm). The geometric mean of mandible size is 141.66 mm (mandible length=279.19 mm, coronoid process height=145.89 mm, corpus height at  $M_1$ =69.8 mm). The  $M_1$  of SAM-PQL 45062 has well-developed carnassial cusps and very robust tooth roots with conspicuously thickened root apices (Fig. 2). This corresponds with a bulging of the base of the mandibular corpus in the region of the molars, and is similar to the morphology seen in extant hyaenids and different to that of extant ursids (Fig. 3).

The mandibular and maxillary canines have the largest root surface area in the tooth row (Table 1). Among the maxillary postcanines, RA is largest in  $M^1$  followed closely by  $P^4$  (carnassial). In the mandible, postcanine RA is also largest in the  $M_1$  (carnassial). Peak RA values are higher than any of the published values for extant carnivorans (see Kupczik and Stynder 2012). Metameric variation in mandibular RA in *A. africanum* is the same as in extant ursids, i.e.,  $M_1 > M_2 > M_3$ . In contrast, the metameric pattern of maxillary postcanine root size in *A. africanum* is  $P^4 \leq M^1 > M^2$  compared to  $P^4 < M^1 < M^2$  in extant ursids. The smaller  $M^2$  root surface area of SAM-PQL 45062 is related to the lower number of roots, i.e., three roots as opposed to four found in modern ursids such as *U. americanus* (Fig. 3; Miles and

**Table 2** Inlever moment arms and muscle areas of masseter/medial pterygoid complex and temporalis, and estimated bite forces at maxillary canine (BF<sub>ca</sub>) and P4 (BF<sub>can</sub>) of *A. africanum*

$l_{mp}$ (mm)	$l_t$ (mm)	$A_{mp}$ (mm <sup>2</sup> )	$A_t$ (mm <sup>2</sup> )	BF <sub>ca</sub> (N)	BF <sub>can</sub> (N)
62.72	68.56	2954.77	3344.31	4013.49	5755.14

**Table 3** Product–moment correlation coefficients ( $r$ ) and RMA line fittings (a, slope; b, intercept; 95 % CI, 95 % confidence interval on the slope) of bite force (BF) against root surface area (RA). All data  $\log_{10}$  transformed

Tooth	$r$	$P$	a	95 % CI of a	Intercept b
Canine ( $n=17$ )	0.91358	<0.0001	1.0526	0.7659–1.306	-0.54968
$P^4$ ( $n=17$ )	0.8843	<0.0001	1.0517	0.8059–1.289	-0.16712

Grigson 1990; Kupczik and Stynder 2012). Cervical plane area in the maxilla is largest in the  $M^1$ ,  $M^2$ , canine, and  $P^4$  (carnassial), respectively, while in the mandible it is largest in the  $M_1$  (carnassial),  $M_2$ , and canine, respectively (Table 1).

Maximum bite force of *A. africanum* is estimated to be 4013.49 N and 5755.14 N at the maxillary canine and carnassial, respectively (Table 2). There is a positive scaling relationship and significant correlation between bite force and root surface area at both tooth positions among extant carnivorans (Table 3; Fig. 4). However, *A. africanum* has relatively small canine root surface areas for its estimated bite force, which is similar to the relationship seen in *A. melanoleuca* (Fig. 4a).

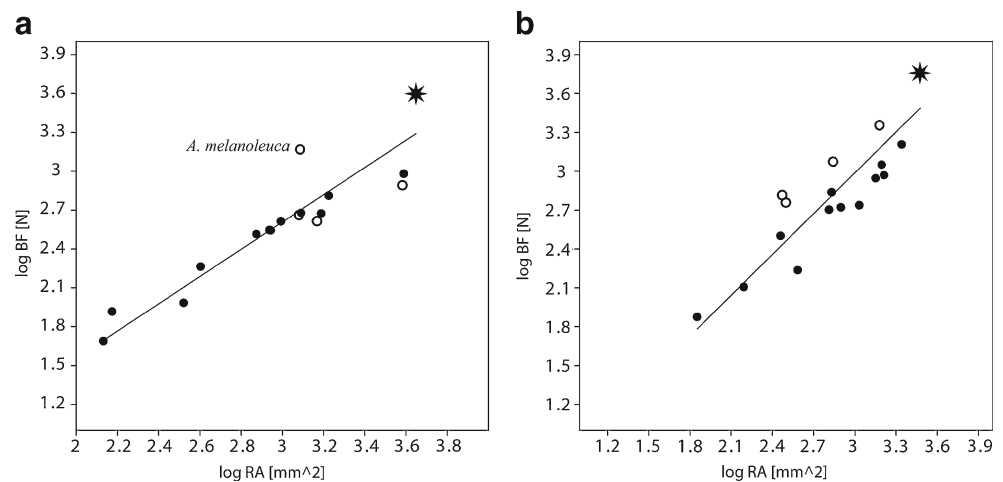
When the skull size adjusted RA values are considered, *A. africanum* has maxillary canine roots that are larger than those of most canids (excluding *Vulpes vulpes*), *A. melanoleuca*, and *Parahyaena brunnea*, but smaller than those of *Crocota crocuta*, *Hyaena hyaena*, the rest of the ursids, and the felids (Fig. 5). In particular, the two predatory species, *U. maritimus* and *P. leo*, have relatively larger canines than *A. africanum*. While *A. africanum* resembles most extant ursids with respect to its  $P^3$  RA value, it exhibits a markedly higher  $P^4$  (carnassial) RA value than them (including the carnivorous *U. maritimus*). Interestingly, its  $P^4$  RA value is most similar to those of canids, particularly the *C. familiaris* specimen included in our study. This is unlikely to be an anomaly, as the range of residuals from an ordinary least

squares regression of the geometric mean of skull size on the  $P^4$  root surface area of the extant carnivorans (-0.215 to 0.153; based on the data provided in Kupczik and Stynder 2012: Tables 3 and 4) encompasses the y residual of *A. africanum* (-0.021). The  $P^4$  tooth root surface area of *A. africanum* is thus well within what is expected for its skull size. In terms of  $M^1$  RA value, *A. africanum* also surpasses those of most ursids (excluding *A. melanoleuca*). Its  $M^2$  RA value, however, is smaller than those of most ursids in the extant sample (excluding *U. maritimus*). It is noteworthy that, in terms of post- $P^3$  root surface area, *A. africanum* resembles the dominant canid pattern rather than the ursid one.

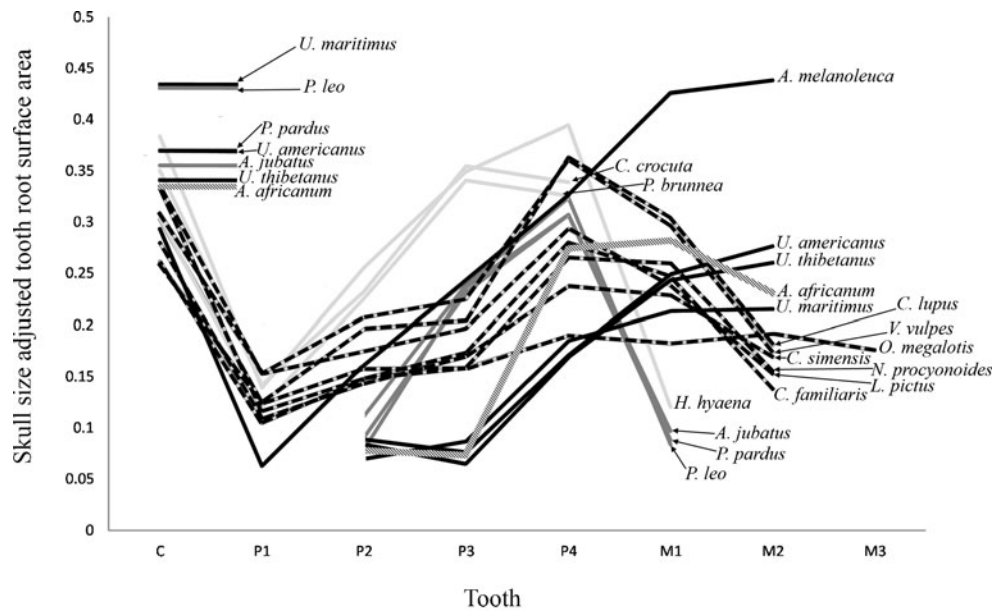
To determine the extant dietary category into which *A. africanum* would best fit given its tooth root surface areas, we compared its (adjusted) maxillary canine and carnassial root surface areas with those of extant hard object feeders, tough object feeders, and omnivores (Fig. 6). Hard object feeders, which include the two bone-cracking scavengers *P. brunnea* and *H. hyaena*, and the bone-cracking scavenger/predator *C. crocuta*, exhibit the highest carnassial RA values in the study sample. Their canine RA values are indistinguishable from those of tough food feeders and certain omnivores though. Omnivores, on the other hand, exhibit the lowest carnassial RA values and amongst the lowest canine RA values in the study sample. Tough food feeders, which include most of the predators, fall between hard food feeders and omnivores in terms of carnassial RA values (excluding *U. maritimus*). *Agriotherium africanum* is indistinguishable from hard food feeders, tough food feeders, and certain omnivores with respect to its canine RA value; however, it clearly resembles tough food feeders with respect to its carnassial RA value.

As an indication of the size of prey on which *A. africanum* might have focused, we compared its (adjusted) maxillary canine and carnassial root surface areas with those of extant carnivorans that feed on large-sized prey, medium-sized prey, and no/small-sized prey (Fig. 7). Consumers of

**Fig. 4** Bivariate plots of bite force ( $\log$  BF [N]) and root surface area ( $\log$  RA [ $\text{mm}^2$ ]). **a** maxillary canine; **b** maxillary carnassial. Reduced major axis regression shown. Closed circles=canids, felids, hyaenids; open circles=ursids; asterisk=*A. africanum*



**Fig. 5** Plots comparing skull size adjusted maxillary tooth root surface areas of the carnivorans included in the study

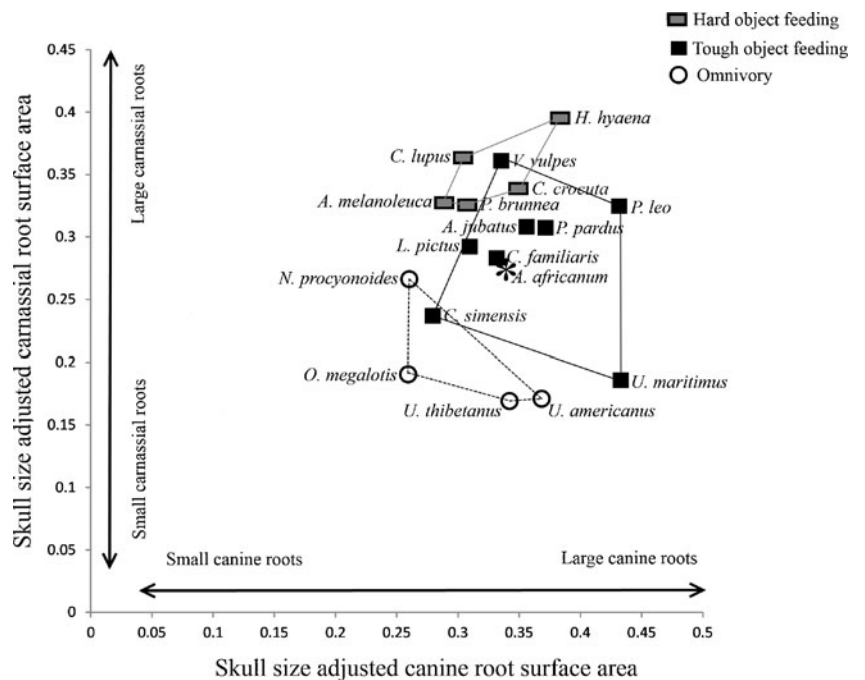


large- and medium-sized prey exhibit relatively large canine roots. Both groups also exhibit similar carnassial RA values (excluding *U. maritimus*). In comparison, consumers of no or small-sized prey generally exhibit low canine and carnassial RA values. *Agriotherium africanum* resembles most closely pack-hunting carnivorans (especially canids) that feed on medium- to large-sized prey with respect to its canine RA value. It displays smaller canine root surface areas than solitary hunters of medium- to large-sized prey, but larger areas than some omnivores and *A. melanoleuca*. In terms of carnassial RA value, it resembles those carnivorans that feed on small- to medium-sized prey.

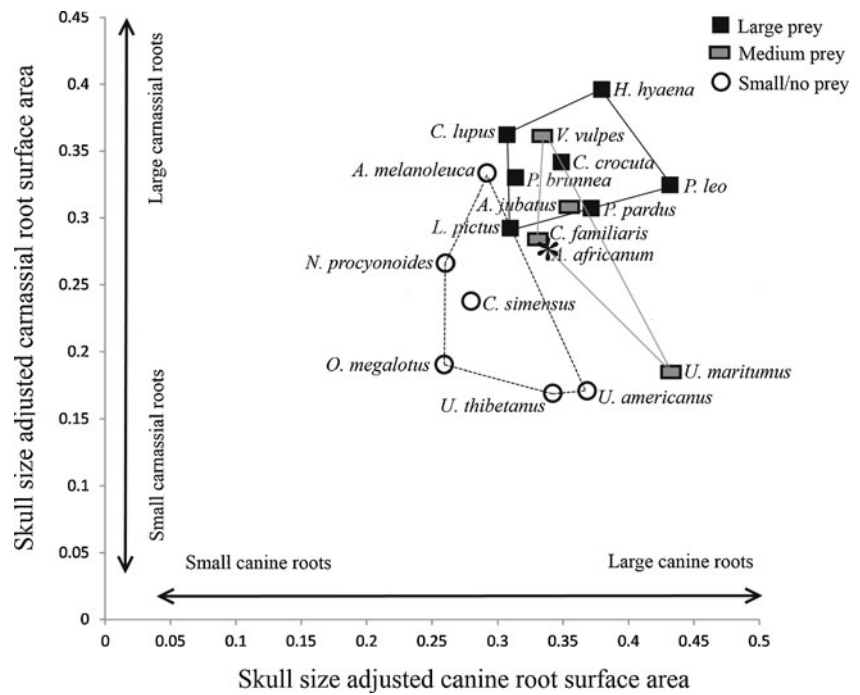
**Discussion**

The *A. africanum* skull analyzed in our study, SAM-PQL 45062, follows the positive allometric pattern between P<sup>4</sup> root size and skull size evident in extant carnivorans. Given the uncertainty surrounding its exact body mass (published estimates vary from 317 kg (Oldfield et al. 2012) to 540 (Sorkin 2006)), we are unable to say for sure whether SAM-PQL 45062’s skull size scales with its body mass. However, as this is predominantly the case in extant carnivorans (Christiansen and Wroe 2007), it likely did.

**Fig. 6** A comparison of maxillary carnassial and canine root surface areas (both skull size adjusted) of hard food feeders, tough food feeders, and omnivores



**Fig. 7** A comparison of maxillary carnassial and canine root surface areas (both skull size adjusted) of large-prey consumers, medium-prey consumers, and small-prey consumers/consumers of no prey. Estimated prey size is relative to predator body size in each case



The estimated absolute bite force potential at the canine and carnassial of SAM-PQL 45062 is higher than that of any of the extant carnivorans reported in Kupczik and Stynder (2012), which is consistent with *A. africanum* being able to consume large prey, either as predator, scavenger, or predator/scavenger. Our computed canine bite force is somewhat lower than that reported by Oldfield et al. (2012) for the same individual (4013.49 N vs. 4566.14 N, respectively), but this may be due to differences in the estimation methods (2D vs. 3D lever arm models). High bite force notwithstanding, when  $P^4$  carnassial root surface area (adjusted to skull size) is taken into account, *A. africanum* falls within the range of variation of tough food feeders. With regards to prey size, *A. africanum* displays carnassial and especially canine root surface areas that are smaller than those of solitary felids that hunt prey equal to or larger than their own body mass (*P. pardus*, *Acinonyx jubatus*, and on occasions *P. leo*). Its canine RA value resembles more closely the slightly lower values of pack-hunting canids that hunt prey at the upper end of the ungulate body size spectrum. As pack hunters, canids such as *Canis lupus* and *Lycaon pictus* are able to bring down prey much larger than themselves, notwithstanding their relatively low canine RA values. In comparison, it appears unlikely that *A. africanum* was a habitual predator on large prey, given that it was probably solitary like extant bears. We thus reject hypothesis 1, which states that *A. africanum* was an active predator of large terrestrial prey. This however does not exclude the possibility that like extant brown bears (*Ursus arctos*) (Sacco and Van Valkenburgh 2004; Christiansen 2007), it occasionally preyed on animals equal to or larger than its

own body mass as part of its feeding strategy. Much of its hunting activity though, would probably have centered on prey smaller than its own body mass.

Our results are consistent with those derived from recent cranial and post cranial evidence that also paint *A. africanum* as an ineffective predator of large vertebrate prey. To test the hypothesis that *A. africanum* and its North American Pleistocene equivalent *Arctodus simus* (Ursidae, Tremarctinae) were felid-like predators (see Kurtén 1967; Hendeby 1980), Sorkin (2006) systematically compared their morphologies with those of extant hunters of large prey. Sorkin (2006) found that the two fossil bears had relatively smaller canines than *P. leo* and *P. tigris*, which would have made it difficult for them to suffocate or sever the spinal cords of large prey. Also, in contrast to the big cats, the orbits of *A. africanum* and *A. simus* were much smaller relative to the size of their skulls, which would have made the visual tracking of prey very difficult. With regards to the postcranial skeleton, both *A. africanum* and *A. simus* were found to be poorly adapted to subdue large prey. Specifically, the forearm and wrist morphology of these fossil ursids were markedly inferior to those of *P. leo* and even the extant brown bear *U. arctos* when it came to grasping and grappling with large prey. Aspects of their limb and vertebral column morphology also suggest that *A. africanum* and *A. simus* were inferior to big cats in their ability to sneak up on prey and accelerate rapidly, which would have made it very difficult to ambush prey. In addition, their poor vision and plantigrade feet (Kurtén 1967; Hendeby 1980) make it highly unlikely that they were pursuit predators (Sorkin 2006).



What of its scavenging ability? Sorkin (2006) proposed that *A. africanum* probably obtained most of the vertebrate animal material in its diet by scavenging in a similar manner to extant bone-cracking scavengers such as *P. brunnea* and *H. hyaena*. A high sagittal crest and stout zygomatic arches suggest that it possessed the large masticatory muscles required to generate high bite forces needed to fracture bone. Indeed, a recent finite element analysis (FEA) of SAM-PQL 45062 by Oldfield et al. (2012) showed that this specimen was very capable of generating exceptionally high bite forces for its size, higher than any extant carnivoran. Its skull was also able to resist both these and high extrinsic loads. With regards to its dentition, its maxillary and mandibular carnassials exhibit buttressed roots and pointed cusps similar to those on the bone-cracking teeth ( $P^3/P_3$ ) of modern hyenas (Fig. 2; Hendeby 1977). In addition, our results indicate that maximum occlusal load in the tooth row of *A. africanum* was applied to the carnassial region as opposed to the most distal tooth in the tooth row as in extant ursids. This would have allowed it to exert relatively high occlusal loads on foods such as bone that require more anterior placement in the jaw to be processed.

While *A. africanum* certainly had many of the morphological attributes required to consume bone, its comparatively low carnassial RA values probably made it less efficient than *P. brunnea* and *H. hyaena* at processing large, mechanically demanding skeletal elements on a consistent basis. This and the very low incidence of cracked and highly worn crowns in the ‘E’ Quarry *A. africanum* dental sample (Hendeby 1977, 1980; pers. obs.) suggest that bone was a secondary food source, ingested and processed mainly in association with its primary food source, namely tough tissue (muscle, connective tissue). A concentration on tough vertebrate tissue would have required regular access to complete or near complete carcasses. These *A. africanum* would only have been able to acquire if it was in a position to drive predators off their kills or actively search for animals that had died of natural causes. Its large body size would arguably have given *A. africanum* the advantage over any predator or competing scavenger that existed at the time with respect to carcass procurement and defense, thus appreciably increasing its chances of acquiring tough tissue on a regular basis. Similarly, its lengthened limbs would have assisted it in covering large tracks of land in search of carrion (Sorkin 2006). Overall then, our results are most consistent with hypothesis 2, which states that *A. africanum* was a scavenger on large vertebrate prey. However, they do not support Sorkin’s (2006) suggestion that it was a habitual bone cracker.

If *A. africanum* was not an active predator or regular consumer of large, mechanically demanding bone, why then was it capable of generating the high bite forces attributed to

it in Oldfield et al. (2012) and the current study? The answer might lie with its large body/skull size. As a very large carnivoran, it would have needed to move a bigger jaw mass on top of the force required to break down its food (more muscle/bone mass=more force). Whether it was required to regularly use the maximum muscle force that studies suggest it was capable of producing is not known, but this appears unlikely, given its comparatively small dental root surface areas. In any case, *A. africanum* is not unique in its purported ability to generate bite forces significantly greater than that required to consume its regular diet. The extant Malayan sun bear *U. malayanus* has an omnivorous diet despite the fact that it can generate bite forces in excess of that predicted for its body size and broad rostrum (Christiansen 2007).

Extant bears are known to scavenge; however, they are at best opportunistic in this regard (Beeman and Pelton 1980; Madić et al. 1993; Derocher et al. 2002). *Agriotherium africanum*, given its dental root morphology, was probably more habitual in its scavenging activities. Scavenging could have been a viable subsistence strategy at various times in ursid evolution. Two large Pleistocene bears, the North American *A. simus* (Sorkin 2006; Schubert and Wallace 2009) and South American *Arctotherium angustidens* (Figueirido and Soibelzon 2009; Soibelzon and Schubert 2011) were also hypothesized by some to have scavenged large vertebrates on a regular basis. Interestingly, all three fossil ursids lived in environments with high ungulate diversity (Gentry 1980; Figueirido and Soibelzon 2009; Soibelzon and Schubert 2011), which could explain their apparent focus on vertebrate tissue. They also shared their environments with a variety of saber-toothed felids, which given the specialized nature of their dentition (Christiansen 2008; Slater and Van Valkenburgh 2008), would have left large amounts of soft tissue on their kills. Besides the kills of saber-toothed felids, it is also likely that *A. africanum* had ample access to complete carcasses as a result of mass die-offs. During the early Pliocene, temperatures dropped substantially compared to previous times while the earth’s climate became more turbulent (Cane and Molnar 2001; deMenocal 2004; Sepulchre et al. 2006). Seasonal flooding of rivers may have been commonplace. At ‘E’ Quarry, catastrophic mortality profiles for the giraffid genera *Sivatherium* and *Giraffa* and the bovid *Damalacra* suggest that seasonal flooding was probably an important cause of mortality among these and other herd animals (Klein 1982). Seasonal droughts may also have killed off many herbivores. The high prevalence of linear enamel hypoplasias in the ‘E’ Quarry herbivores suggests that drought-related nutritional stress was common at the time (Franz-Odenaal and Solounias 2004).

Interestingly, the presence of premasseteric fossae on its mandibles, as well as its relatively broad post-carnassial tooth

crowns, suggests that in addition to being a meat eater, *A. africanum* might also have consumed plant material (Sorkin 2006). Premasseteric fossae are indicative of large zygomatico-mandibularis muscles, which facilitate medio-lateral movement of the mandible to produce a grinding component for the mastication of plant foods (Davis 1955; Sorkin 2006) as well as invertebrate exoskeletons. Given that its root surface areas suggest a focus on meat eating (largest in the maxillary carnassial area and not the most distal molar as in extant bears), it probably ate less plant material than most extant bears. This agrees with Sorkin's (2006) suggestion that plants (and invertebrates for that matter) were consumed to supplement a meaty diet.

The ability to shift between carnivory and herbivory (or vice versa) is common among extant omnivorous ursids (Persson et al. 2001; Mowat and Heard 2006; Richards et al. 2008); however, it is also known to occur in ursids that have more specialized diets like the marine vertebrate predator *U. maritimus* (Hobson and Stirling 1997; Derocher et al. 2002) or even the largely herbivorous extinct *Ursus spelaeus* (Bocherens et al. 1990, 1994, 2006; Richards et al. 2008). By being flexible in their diets, ursids are able to survive through seasonal and geographical variability in food resources. This dietary flexibility would have been critical to the survival of *A. africanum* in what is thought to have been climatically and environmentally unstable times.

## Conclusion

Our results suggest that *A. africanum* was more carnivorous than most extant bears. A dietary emphasis on vertebrate animal tissue is most evident in the carnassial region of its tooth row where maximum occlusal load was applied and root surface areas were largest. This and the fact that its canine roots were not larger than those of extant bears (when size-adjusted) suggest that it probably scavenged most of the vertebrate animal tissue it consumed. While its (size-adjusted) carnassial root surface areas were higher than those of most extant bears, they were smaller than those of extant bone-cracking hyenas. Given this, *A. africanum* was probably not a habitual bone cracker of large bones as previously suggested. Bone was likely a secondary food source, ingested and processed mainly in association with tough tissue scavenged from complete or near complete carcasses. The presence of premaxillary fossae on its mandibles suggests that it probably supplemented its carrion-based diet with vegetable matter and invertebrates. The most parsimonious explanation of the evidence presented here, is that *A. africanum* was a mesocarnivore (a carnivore that consumed 50–70 % vertebrate animal matter with the bal-

ance made up of non-vertebrate foods) (Van Valkenburgh 2007; Shrestha et al. 2011). As a large ursid that was able to scavenge, occasionally hunt small- to medium-sized animals, and eat invertebrates and plant foods as circumstances demanded, *A. africanum* would have been well placed to take advantage of the dietary opportunities on offer in a variable, unstable African environment. Its abundance at "E" Quarry relative to the remains of other large terrestrial carnivorans, suggests that it thrived on a continent that is not traditionally associated with ursids.

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