



Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage

Travis Rayne Pickering^{a*}, Manuel Domínguez-Rodrigo^b, Charles P. Egeland^a,
C.K. Brain^c

^aDepartment of Anthropology and CRAFT Research Center, Indiana University, 130 Student Building, Bloomington, IN 47405, USA

^bDepartamento de Prehistoria, Universidad Complutense, 28040, Madrid, Spain

^cTransvaal Museum, Northern Flagship Institution, Pretoria, 0001, South Africa

Received 10 October 2003; accepted 3 March 2004

Abstract

The ca. 1.0 myr old fauna from Swartkrans Member 3 (South Africa) preserves abundant indication of carnivore activity in the form of tooth marks (including pits) on many bone surfaces. This direct paleontological evidence is used to test a recent suggestion that leopards, regardless of prey body size, may have been almost solely responsible for the accumulation of the majority of bones in multiple deposits (including Swartkrans Member 3) from various Sterkfontein Valley cave sites. Our results falsify that hypothesis and corroborate an earlier hypothesis that, while the carcasses of smaller animals may have been deposited in Swartkrans by leopards, other kinds of carnivores (and hominids) were mostly responsible for the deposition of large animal remains. These results demonstrate the importance of choosing appropriate classes of actualistic data for constructing taphonomic inferences of assemblage formation. In addition, they stress that an all-encompassing model of assemblage formation for the hominid-bearing deposits of the Sterkfontein Valley is inadequate and that each must be evaluated individually using not just analogical reasoning but also incorporating empirical data generated in the preserved fossil samples.

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Keywords: Taphonomy; Carnivores; Early hominids; Carcass body size; Bone surface modifications; Tooth pits

Introduction

Leopards (*Panthera pardus*), often to the near exclusion of many other potential bone-

accumulating carnivores, have featured prominently in taphonomic reconstructions of Plio-Pleistocene fossil sites in South Africa (e.g., Brain, 1968, 1969, 1970, 1974a, 1981, 1993a; de Ruiter and Berger, 2000) and elsewhere (e.g., Cavallo and Blumenschine, 1989). For example, Brain's (1970) demonstration of definitive leopard canine punctures in an early hominid calotte (SK 54) from

* Corresponding author. Tel.: +1-812-856-5260; fax: +1-812-855-4358

E-mail address: trpicker@indiana.edu (T.R. Pickering).

the Hanging Remnant assemblage of Swartkrans Member 1 is especially convincing support of leopard involvement in the collection of that assemblage. That observation, in combination with many others from long-term actualistic research, led to Brain's (e.g., 1981, 1993a) well known hypothesis that leopards were largely responsible for a majority of the Size Class 1 and 2 animal remains from Swartkrans Members 1 and 2. Size Class 1 and 2 animals fall between 4.5–104 kg in live body weight (Brain, 1974b, 1981), the size range of prey preferred by leopards (e.g., Kruuk and Turner, 1967; Pienaar, 1969; Brain, 1981; Wilson, 1981; Bertram, 1982; Scott, 1985; Bailey, 1993; Cavallo, 1997). Brain (e.g., 1981, 1993a) and Vrba (e.g., 1975, 1976) implicated other, larger felids—sabertooth and “false” sabertooth cats—as possibly responsible for the accumulation of larger animal remains (i.e., Size Class 3 and larger: ≥ 100 kg) in the Swartkrans fossil assemblages.

Subsequently, de Ruiter and Berger (2000) studied the faunal accumulation from a modern leopard den on the John Nash Nature Reserve (South Africa). Based on the facts that this assemblage contained the remains of a Size Class 4 eland (*Taurotragus oryx*) and that a Size Class 3 zebra (*Equus burchelli*) was observed in another close-by leopard den, de Ruiter and Berger (2000: 682) concluded: “The [inferred] ability of leopards to kill and cache prey many times their own body weight would imply that perhaps we need not invoke the activity of sabre-tooth cats in the accumulation of bones found in the hominid bearing caves of South Africa.” de Ruiter and Berger (2000: 680, Table 4) supported this claim with reference to the presence of leopard fossils in seven well-known paleontological assemblages from three of the Sterkfontein Valley cave sites, Sterkfontein, Swartkrans and Kromdraai. Other large felid taxa, including *Panthera leo*, *Acinonyx jubatus*, *Homotherium*, *Megantereon*, and *Dinofelis*, are represented sporadically in these various assemblages. Unlike leopards, none is known from all of the assemblages, leading de Ruiter and Berger (2000: 683) to conclude: “While the presence or absence of various carnivore remains in an assemblage does not mean that they

can or cannot be considered collecting agents, it seems more probable that the leopards found ubiquitously in all assemblages were responsible for the bones, rather than the variably represented sabre-tooth and false sabre-tooth cats.” This is a provocative conclusion and one that is testable using bone surface modification data; in particular, a consideration of carnivore tooth marks can yield data that might falsify the hypothesis.

There has been considerable effort by taphonomists to establish criteria for distinguishing tooth marks imparted by different African carnivores (e.g., Haynes, 1983; Selvaggio, 1994; Selvaggio and Wilder, 2001; Piqueras, 2002), with the work of Domínguez-Rodrigo and Piqueras (2003) standing as the most recent. Domínguez-Rodrigo and Piqueras (2003) recognized some statistically significant differences in the dimensions of tooth pits left on bones by various carnivores, including lions, leopards, cheetahs, spotted hyenas, jackals, and domestic dogs (bear and baboon tooth pits were also studied but are not discussed here; the leopard and cheetah data are from Selvaggio, 1994). Tooth pits are bone surface modifications imparted by animal chewing and “appear as discrete, roughly circular marks in plan view and result from scarring of bone without [significant] inward crushing of the bone cortex” (Pickering and Wallis, 1997: 1120).

Domínguez-Rodrigo and Piqueras's (2003) results indicate that the lengths and breadths of tooth pits, when considered independently, are reliable criteria for identifying mutually exclusive carnivore groups as the agents of pitting. Finer taxonomic separation is possible for tooth pits imparted on the cancellous bone of limb epiphyses than it is for those left on the denser cortical bone of diaphyses. For mark length on epiphyses, pits <4 mm are observed in samples created by jackals, cheetahs, and leopards, but not in larger dog, spotted hyena, or lion samples; pits 4–6 mm are created by larger dogs, spotted hyenas, and lions (and bears and baboons); and pits >6 mm are usually made only by spotted hyenas and lions. With regard to mark breadth on epiphyses, pits <2 mm are observed mostly in samples from medium-sized felids, leopards, and cheetahs; pits 2–4 mm is a range of great taxonomic overlap; and

Table 1
Distribution of hominid-inflicted bone surface modifications (cutmarks and hammerstone percussion marks) in the Swartkrans Member 3 faunal assemblage on bone specimens across all animal body size classes^a

Size class	Cutmarks	Percussion marks ^b	Total
1	5	9	14
2	32	20	52
3	19	13	32
4	4	3	7
Total	60	45	105

^aAnimal body size classes are based on Brain's (1974b, 1981) classificatory system. Bone surface modification data are from Pickering et al. (in press a, b). Values for each category are number of identified specimens (NISP) preserving each type of damage.

^bPercussion marks=pits and striae, in some cases associated with impact notches. Five additional specimens preserve probable percussion notches only and a separate total of 53 impact flake specimens have been recovered from Swartkrans Member 3.

pits >4 mm are imparted by larger dogs, spotted hyenas, and lions (and bears). In contrast, pit dimensions on diaphyses organize the causal agents into two major groups, carnivores with less robust teeth (including cheetahs, leopards, and jackals) and carnivores with more robust teeth (larger dogs, spotted hyenas, and lions). Carnivores in the first group impart pits that are generally <2 mm in length and <1.5 mm in breadth, while carnivores in the second group impart pits of greater length and breadth. Importantly, even these rather broad distinctions are sufficient to evaluate de Ruiter and Berger's (2000) assertion that leopards were probably responsible for the bulk of bone collection—regardless of carcass body size—in most South African cave sites during the Plio-Pleistocene.

Here, we apply the system to a sample of just one of those assemblages, that from Swartkrans Member 3 (ca. 1.0 Ma). The Swartkrans Member 3 fauna is distinguished from many other Sterkfontein Valley assemblages in preserving abundant taphonomic evidence of hominid involvement in its formation, including stone tool cutmarks, hammerstone percussion damage, and burned bones (e.g., Brain, 1993a; Pickering et al.,

in press a, b, submitted) (Table 1). Because Swartkrans Member 3 holds this unique potential to inform paleoanthropologists about carcass foraging by early hominids in southern Africa, it is particularly important that the assemblage be characterized as accurately and in as much detail as possible. Thus, we offer this contribution in service of that goal and to contextualize arguments we present elsewhere on the reconstruction of hominid behavior at Swartkrans during Member 3 times (e.g., Pickering et al., in press a, b, submitted).

Materials and methods

The fossil sample

The total faunal assemblage from Swartkrans Member 3 consists of 108,098 bone specimens (Brain, 1993a; Watson, 1993). As part of a larger study (Pickering et al., in preparation), we re-analyzed a sample of that total ($n=1466$) that includes *all* the ungulate limb bone shaft specimens ≥ 5 cm in maximum dimension and those <5 cm with observed prehistoric bone surface modifications. Limb bone shaft specimens are defined here as pieces from ungulate humeri, radioulnae, metacarpals, femora, tibiae, and metatarsals that preserve less than their complete, original diaphyseal circumferences and do not possess their articular ends (modified from Pickering, 1999; see also Pickering et al., 2003, in press a, b, submitted). Limb bone shaft fragments were chosen as the analytical sample because most current actualistic models of hominid carcass use focus on limb elements (e.g., Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1991; Marean et al., 1992; Blumenschine and Marean, 1993; Selvaggio, 1994, 1998; Capaldo, 1995, 1997, 1998; Domínguez-Rodrigo, 1999a,b, 2001; Selvaggio and Wilder, 2001; Pickering et al., 2003).

We did not consider limb bone ends in this study because, relative to limb bone shafts, there are very few epiphyseal specimens in the Member 3 fauna. This paucity of limb bone ends probably resulted from the combined effects of at least two major taphonomic processes, one that operated in the biostratinomic phase and the other in the

diagenetic phase. First, as data in this paper indicate, carnivores definitely impacted a substantial portion of the Member 3 assemblage, and a wealth of actualistic research shows that carnivores often destroy or at least substantially reduce and weaken nutrient-laden epiphyses during feeding (e.g., Binford, 1981; Brain, 1981; Bunn, 1983, 1991; Todd and Rapson, 1988; Marean and Spencer, 1991; Marean et al., 1992; Marean and Frey, 1997; Pickering, 2002). Second, the Member 3 sample is derived from a great depth of deposit (Brain, 1981, 1993b; Brain and Watson, 1992). This fact, combined with our observations of pervasive diagenetic breakage in the assemblage (Pickering et al., submitted), suggest that the fauna was subjected to intense sediment pressure during formation, probably eliminating many of the less durable ends of bones that had survived biostratigraphic processes, but not the denser diaphyses (e.g., Lyman, 1994; Pickering et al., 2003).

Twenty-five of the total 532 tooth marked specimens in our sample were chosen at random for tooth pit analysis. A total of 70 individual tooth pits on those selected specimens were molded with Coltène® brand President Fast JET Light Body® polyvinylsiloxane. Following Selvaggio (1994; Selvaggio and Wilder, 2001) and Domínguez-Rodrigo and Piqueras (2003), we measured length and breadth maxima of the molded tooth pit impressions using a Helios® high precision caliper. Measurements were taken on molds rather than on the original bone specimens for two reasons. First, we did not want to risk damaging the fossils by bringing them into contact with our calipers. Second, as Fig. 1 illustrates, tooth pit boundaries are often more clearly delimited on molds, where they appear as prominent convexities, than on fossils, where they sometimes appear as more diffuse concavities.

The modern comparative samples

We used two sets of actualistic data as comparative samples in this study. The first sample is that of Selvaggio (1994; Selvaggio and Wilder, 2001), who presented data on 113 diaphyseal tooth pits. Her subsample of cheetah, leopard, lion, and jackal tooth pits was created under natural feeding

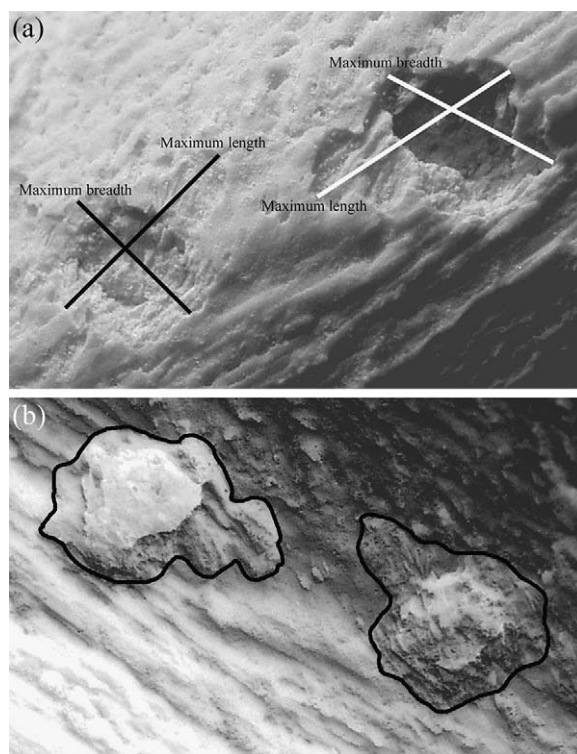


Fig. 1. (a) Tooth pits on a bone diaphysis, with length and breadth maxima indicated. (b) Molds of the same pits are illustrated and outlined to demonstrate how they are often more clearly delimited as convexities rather than as the more diffuse appearing concavities preserved on original bone surfaces.

conditions in the wild, while her spotted hyena subsample was produced by captive animals at the Berkeley hyena colony. It is important to note that Selvaggio's data is slightly biased towards the reporting of larger tooth pits, especially for leopards. This implies that the *overall* range of tooth pit sizes in her sample is small. However, most relevant to our study, this bias also serves to fix the *maximum* range observed in extant leopards. The second sample is that of Domínguez-Rodrigo and Piqueras (2003), who reported on 104 diaphyseal tooth pits (those inflicted by bears and baboons are not considered in this study). In that study, tooth pits from hyenas, jackals, and lions were created under natural feeding conditions, while those inflicted by large dogs were obtained in controlled feeding

Table 2
Maximum dimensions of randomly selected tooth pits on bone specimens from Swartkrans Member 3 ($n=70$ pits)

Statistics	Length (mm)	Breadth (mm)
Mean	2.59	1.98
Standard deviation	1.19	0.87
95% Confidence interval	2.31–2.87	1.77–2.19

experiments. Lions and jackals fed upon bones in a fleshed state while hyenas and large dogs fed upon defleshed bones, reflecting the natural feeding modes of these various taxa.

Results and discussion

The mean length and breadth maxima of randomly selected tooth pits on the Swartkrans Member 3 limb bone shaft sample are shown in Table 2, and the dimensions of each individual tooth pit are listed in Appendix A. When viewed collectively, these data, with mean length >2 mm and mean breadth >1.5 mm, indicate that most tooth pits were imparted by carnivores other than small canids, cheetahs, and leopards. The dimensions fall comfortably within Selvaggio's (1994) modern spotted hyena tooth pit sample. We note, however, that the Swartkrans tooth pit dimensions fall well below the means reported for Domínguez-Rodrigo and Piqueras's (2003) sample of pits created by modern spotted hyenas and lions (Fig. 2a, b). This suggests that even if spotted hyenas were the prominent agent of tooth pitting in the Swartkrans sample, another carnivore taxon/taxa contributed to the creation of that tooth pit profile, which shows smaller dimensions than are seen in samples imparted by extant large predators (brown hyenas, which have slightly less robust teeth than do spotted hyenas and of which a few are represented in Member 3 [Turner, 1993; Watson, 1993], might be implicated). Regardless, the disparity between the fossil data and those from the two modern samples of known origin highlights previous observations that taxonomic identification of tooth pits on the dense cortical bone of limb diaphyses is more equivocal than that of pits on the trabecular bone of limb epiphyses (Domínguez-Rodrigo and Piqueras, 2003).

The Swartkrans tooth pit sample is enumerated in greater detail in Table 3, where mean mark dimensions are broken down by their occurrences on the bones of small (Size Classes 1 and 2) and large (Size Class 3) animals. Tooth pit dimensions on specimens from small animals show a restricted range of variation and overlap with dimensions observed in modern tooth pit samples created by carnivores with less robust teeth, comparing most favorably to the leopard-derived sample (Fig. 2a, b). In contrast, tooth pit dimensions on Swartkrans specimens from large animals compare very closely to those created by modern large dogs, spotted hyenas, and lions (Fig. 2a, b). This indicates clearly that large carcasses (i.e., Size Class 3) recovered from Swartkrans Member 3 were likely modified predominantly by carnivores other than leopards.

This broad taxonomic view of taphonomic agents at Swartkrans is echoed in recent work on the primate subassemblages of Members 1 and 2. Based on skeletal part representation, Carlson and Pickering (2003) concluded that the primate subassemblage from the Hanging Remnant of Member 1 most closely matches a pattern created by the feeding residues of modern hyenas, while the Member 2 primate remains preserve a pattern like that seen in assemblages composed of bones from modern leopard feces and regurgitations.

In addition, as noted above, bone surface modification evidence indicates a significant hominid contribution to assemblage formation in Swartkrans Member 3 (Pickering et al., in press a, b, submitted). We observed a relatively abundant occurrence of stone tool cutmarks and hammerstone percussion damage on bone specimens *across all animal body sizes*, indicating that hominids exploited a wide range of carcass types (Table 1). This stands in contrast to the variable use of carcasses by different carnivores that is evidenced in the assemblage, with inter-taxonomic partitioning of prey exploitation based on carcass size.

Finally, it is commonly thought that because leopards do not typically break open limbs of prey for marrow extraction, it is unlikely that they will regularly leave tooth marks on diaphyses. If so, it might not be legitimate to exclude leopards as a collector of the large animal sample in Member 3

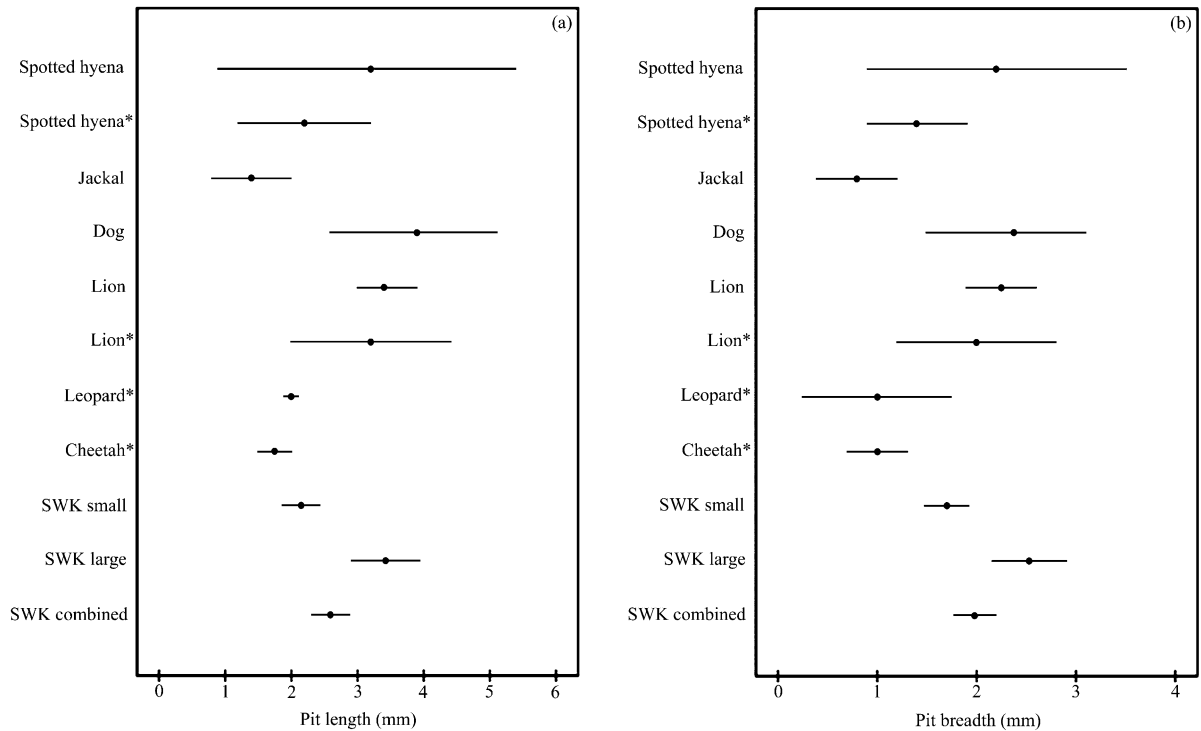


Fig. 2. Tooth pit lengths (a) and breadths (b) created by modern carnivores on dense cortical limb bone diaphyses compared to those variables of randomly selected tooth pits in the Swartkrans Member 3 faunal assemblage. SWK small=tooth pit distributions for 46 individual pits on bone specimens of Size Class 1 and 2 animals from Swartkrans; SWK large=tooth pit distributions for 24 individual pits on bone specimens of Size Class 3 animals from Swartkrans; SWK combined=tooth pit distributions for the entire combined Swartkrans fossil sample of 70 individual pits (for animal size classes see Brain, 1974b, 1981). Circles indicate means, range bars indicate 95% confidence intervals. Data indicated with asterisks (*) are from Selvaggio (1994); all other modern carnivore data are from Domínguez-Rodrigo and Piqueras (2003).

Table 3

Maximum dimensions of randomly selected tooth pits on bone specimens from Swartkrans Member 3, separated by occurrence on the bones of small- and large-sized animals^a

Statistics	Small (<i>n</i> =46 pits)		Large (<i>n</i> =24 pits)	
	Length (mm)	Breadth (mm)	Length (mm)	Breadth (mm)
Mean	2.15	1.70	3.43	2.53
Standard deviation	0.94	0.73	1.20	0.88
95% Confidence interval	1.87–2.43	1.48–1.92	2.92–3.94	2.16–2.90

^aFollowing Brain's (1974b, 1981) classification scheme based on live body weight: small animals=Size Classes 1 and 2; large animals=Size Classes 3 and larger.

based on an absence of their tooth marks on those remains. Previously, we examined two sets of modern leopard feeding refuse: the first set, from South Africa and Namibia, was originally reported

by Brain (1981) and includes the remains of Size Class 1 and 2 bovids and baboons (Domínguez-Rodrigo et al., in preparation); the second set is from South Africa and consists of baboon remains

(Pickering, 2001a,b; Carlson and Pickering, 2003). Combined with our observations of leopard feeding behavior, data generated in these modern samples indicate that leopards do, in fact, leave tooth marks on limb bone midshafts and that this damage is associated with defleshing rather than with demarrowing activities. It is true that most of the midshaft tooth marks in these datasets cluster on or near metaphyses, but nonetheless, they would still be present in a sample such as that selected for analysis in this study.

Selvaggio (1994) and Cavallo (1997) also provided data on limb bone midshaft specimens preserving leopard tooth marks in actualistic samples. It is noteworthy that leopard tooth marks on limb bone midshafts occur in low frequencies in all these modern samples. However, direct measurements of midshaft tooth marks on the bones of small animals from Member 3 yield a strong leopard “signal.” Thus, had leopards been as comparably active with larger animal carcasses at the same site, we would expect a discernible indication of that in tooth mark dimensions on those bones.

Summary and conclusions

There is little doubt that leopards played a prominent role as agents of faunal assemblage formation at Swartkrans during the Plio-Pleistocene (e.g., Brain, 1968, 1969, 1970, 1974a, 1981, 1993a; Carlson and Pickering, 2003). However, a recent claim (de Ruiter and Berger, 2000) that other types of carnivores probably need not be considered as important bone collectors of the Swartkrans large animals remains does not withstand direct testing using bone surface damage data. That claim rests on the observations of a couple of Size Class 3 and 4 carcasses in two modern leopard dens in South Africa (de Ruiter and Berger, 2000).

Our analysis of a sample of tooth pit dimensions on small (Size Classes 1 and 2) and large (Size Class 3) animal bone specimens from Swartkrans Member 3 indicates that while leopards probably did, in fact, contribute significantly to the deposition of small animal remains,

they were not major contributors of the large animal remains. Instead, the large animal bones were probably collected by carnivores, including large canids, spotted hyenas, and lions, capable of more intense bone modification than are leopards. In addition, it is possible that some of those large animal remains were modified by extinct, non-leopard carnivores for which we do not have good actualistic data on tooth mark dimensions (but see Selvaggio's [1994] extrapolated tooth mark values for several extinct taxa). These results are consistent with Brain's (e.g., 1981; see also Vrba, 1975, 1976) original hypothesis of carnivore activity at Swartkrans, with leopards specializing on smaller prey and other predators concentrating on larger prey.

In addition, our results highlight the hazards of blanket statements based on the application of inadequate actualistic criteria in complicated taphonomic settings, such as that at Swartkrans. The indirect evidence of modern leopard killing and carcass transport capabilities is by itself not sufficient to explain the deposition of variably sized animals during the Plio-Pleistocene in South African cave sites. More particularly, direct paleontological evidence, in the form of taxon-specific carnivore tooth marks, better informs investigators on this matter in the Swartkrans Member 3 fauna. We suggest that the same will probably hold true for other assemblages as well.

Acknowledgements

The first three authors thank Bob Brain for his continued support of this program of zooarchaeological re-analysis of Swartkrans Member 3, and for his groundbreaking work that laid the foundation for this new round of research. Thanks to Kathy Kuman, Ron Clarke, and the Department of Archaeology, University of the Witwatersrand, for their hospitality and the continued support of our research. Very special thanks go to the Northern Flagship Institution (formerly the Transvaal Museum) and especially Stephany Potze for granting us permission to study the material and for facilitating its convenient accessibility. We thank Bill Kimbel, Yin Lam, and two other referees for

helpful comments that improved this paper. TRP thanks Henry Bunn for much discussion of taxonomic specificity of carnivore tooth marks and for inspiration to tackle this topic. TRP also thanks his family and Nick Toth and Kathy Schick for their continued unconditional support of his work, and the College of Arts and Sciences, Indiana University, for a Summer Faculty Fellowship to conduct the research. MD-R thanks TRP for inviting him to participate in this research on the Swartkrans fauna and Complutense University for funding. CPE thanks the Graduate and Professional Student Organization, Indiana University, for a Summer Research Award, which partially funded his participation in this research.

Appendix A. Tooth pit maximum length and breadth measurements for randomly selected tooth pits on bone specimens from Swartkrans Member 3

Specimen	Small		Large		
	Length	Breadth	Specimen	Length	Breadth
SWK 25888	1.9	1.6	SWK 19683	3.2	2.7
	2.0	1.4		2.4	1.3
	2.8	1.8	SWK 27684	5.3	3.3
	3.7	1.9		4.5	3.4
SWK 25918	1.7	1.0		3.6	2.2
	2.0	1.0		2.5	2.1
	2.2	1.2		3.1	1.8
SWK 26386	1.2	1.2	SWK 28732	4.2	3.0
	1.4	1.3		2.3	1.5
	1.9	1.8	SWK 29283	3.2	2.5
SWK 26963	1.3	0.8		1.9	1.8
SWK 27681	3.0	1.8		1.6	1.4
	1.8	1.5		2.6	1.7
	1.5	1.5		3.0	1.8
	1.5	1.2	SWK 30555	6.8	4.0
	2.2	1.5	SWK 30628	2.3	1.9
SWK 27724	4.6	2.5		2.2	1.9
	3.2	3.0	SWK 35153	3.4	2.4
	1.9	1.9		3.3	3.0
	1.9	1.4			
SWK 29249	1.5	1.5	SWK 36073	3.8	3.2
	1.4	1.2	SWK 36361	4.9	4.5
	1.4	1.2	SWK 36675	4.0	2.8
SWK 30113	2.3	2.0		4.1	4.0
SWK 30860	3.6	2.4		4.1	2.6
	2.3	2.2			
	2.6	1.4			
	1.8	1.5			
	2.1	1.9			
	1.2	1.2			

Specimen	Small		Large		
	Length	Breadth	Specimen	Length	Breadth
SWK 33605	3.3	2.4			
	2.9	2.1			
	3.0	2.3			
	5.1	4.8			
SWK 34506	1.2	1.1			
	1.2	1.2			
SWK 34577	3.2	3.0			
	2.5	2.2			
	1.5	1.5			
	1.4	1.4			
SWK 36290	1.2	1.0			
	1.5	1.1			
	1.1	1.0			
	1.2	1.0			
SWK 37535	3.2	2.9			
SWK 37575	1.8	1.7			
	1.0	0.9			

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