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New data and ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave, South Africa

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New data and interpretations presented in this paper update and augment the previous state of knowledge of early hominid subsistence behaviour at Swartkrans Cave during the formation of the Member 3 depositional unit (c. 1.0 million years ago). Unlike previous reconstructions of passive scavenging by early Pleistocene hominids in the Sterkfontein Valley, our new data lead to an inference of early access by hominids to the carcasses of variously sized ungulates. Early access, in turn, suggests Swartkrans hominids might have possessed the capabilities to hunt and/or scavenge aggressively from primary carnivore predators by c. 1.0 Myr, a pattern that is also increasingly apparent in the pene-contemporaneous archaeological record of other parts of Africa.

Introduction

The last systematic analysis of the Swartkrans Member 3 (c. 1 million years old) zooarchaeology was summarized just over ten years ago by one of us: 'The presence of [17] bones, including four burnt ones, bearing cut and chop marks suggests that hominids were using stone tools for the removal of meat from bones while sitting round their camp-fires.'[1] Here we report on an additional 163 ungulate limb bone specimens from Swartkrans Member 3, with newly identified evidence of hominid butchery activities. This evidence occurs in the form of stone tool cutmarks and hammerstone percussion marks, indicating, respectively, defleshing and demarrowing of bones. In turn, the anatomical patterning of cutmarks indicates early access to carcasses by the hominid butchers, falsifying a hypothesis of passive scavenging and suggesting instead hominid capabilities for hunting and/or aggressive scavenging. This is a novel interpretation of hominid behaviour in the early Pleistocene of southern Africa. Until this study, hominids of the Sterkfontein Valley were reconstructed largely as passive scavengers, reliant on the marginal carcass resources abandoned by primary carnivore predators for flesh and marrow intake.[1–6]

Materials and methods

The total Swartkrans Member 3 faunal assemblage was originally analysed by Brain,[1] Watson[7] and Newman[8] and consists of 108 098 pieces. Of that total, we re-analysed the complete 12 505-piece sub-assemblage that is composed of all the macromammalian limb bone shaft fragments.[9] Further, we selected for more in-depth analysis a sample from that sub-assemblage comprised of all specimens ≥5 cm in maximum dimension and those specimens <5 cm in maximum dimension that also preserve prehistoric bone surface modifications. This sam-

ple consists of 1466 specimens and within it we collected data on bone surface damage as detailed below.

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.[10,11] When possible, specimens were identified to specific skeletal element. When we were unable to identify a specimen to specific element, it was often possible, using the system of Domínguez-Rodrigo,[12,13] to categorize it more generally to a limb segment, as either an upper (humerus or femur), intermediate (radioulna or tibia) or lower (metapodials) limb fragment. Specimens that remained unidentified after these steps were then simply entered into the database as limb bone shaft fragments.

Limb bone shaft fragments were chosen as our unit of analysis for two reasons. First, their high bone mineral density ensures a large proportion of them will have survived the rigours of density-mediated destruction throughout the biostratinomic and diagenetic phases of faunal assemblage formation.[11] Second, experimental and ethnoarchaeological studies have revealed that cutmarks on the midshafts of upper and intermediate bones unambiguously indicate defleshing by hominids.[12–14] Since the meat of these bones is consumed early in carnivore feeding sequences (see details summarized below), defleshing cutmarks on them must indicate early access to carcasses by hominids.

Identification of bone surface modifications was guided by criteria and methods reviewed by Blumenschine et al.[15] Each specimen was inspected under a strong oblique light source with the aid of at least ×10 magnification as recommended by several analysts.[15–22] The following types of damage were observed and recorded: burning, carnivore tooth marks and gastric acid etching, rodent gnaw marks, random linear striae (for example, trampling damage), hammerstone percussion marks, and stone tool cutmarks. Because we concentrate here on presenting data and interpretations of the last two listed types of damage, we now describe in some detail the specific identification criteria used to distinguish percussion marks and cutmarks.

In this study, hammerstone percussion marks include pits and striae, which are sometimes but not always associated with percussion notches. Diagnostic morphology and configuration of percussion pits and striae are described and illustrated by Turner[23] and Blumenschine and Selvaggio.[21,22] Pits are often closely associated with and/or have emanating from them patches of striae that result from slippage of stone against bone during impact events (Fig. 1a). Cutmarks usually occur as deeply incised linear damage, with V-shaped cross sections.[24,25] Microscopic examination reveals that cutmarks also often preserve such important distinguishing features as internal microstriations, Herzian cones and small lateral striations (that is, shoulder effects) (Fig. 1b).[25–29]

Because it has been demonstrated that various abiotic processes hold the potential to mimic the form of especially

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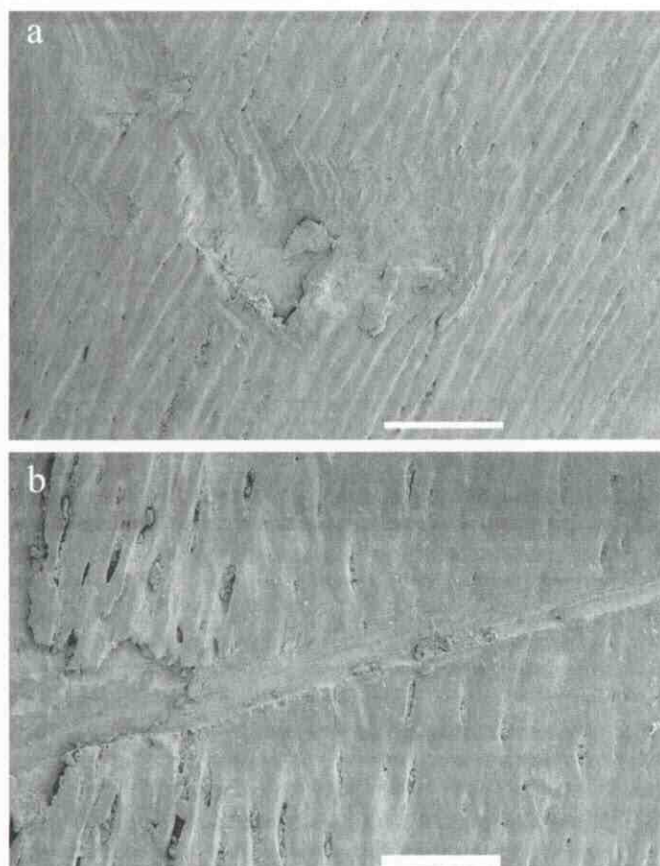*Author for correspondence. E-mail: trpicker@indiana.edu

Fig. 1. Scanning electron microscope micrographs showing representative examples of hominid-imparted hammerstone percussion marks (**a**) and cutmark (**b**). Note the patches of striations emanating from the percussion pit and the internal microstriations within the main groove of the cutmark.[21,22,25]

stone tool cutmarks,[25,29-34] every incidence of suspected hominid-imparted damage was examined macro- and microscopically by each co-author, discussed and a consensus opinion reached. This exhaustive approach was particularly important given that the sedimentary matrix from which the assemblage derives is coarse grained, and the approach also makes us confident of our identifications of hominid-imparted bone surface damage. If there was any doubt in the attribution of damage as hominid-derived, we removed the specimen preserving that damage from the sample. Thus, if anything, our sample of hammerstone-broken and cutmarked specimens is an underestimate of the actual total number of hominid-modified pieces in Swartkrans Member 3.

Results and discussion

Table 1 summarizes ungulate body size and anatomical distribution of hominid-imparted bone surface damage in the Swartkrans Member 3 limb bone sub-assemblage. Ungulates can be divided usefully into three principal sizes for these analyses: small (corresponding to Size Class 1 in Brain's[2,35] well-known classificatory scheme for African bovids), medium (Size Classes 2 and 3), and large (Size Class 4 and larger). Hominid-imparted modifications occur across all size groups, but the remains of medium-sized animals display the highest frequency (8.9%), as measured as a percentage of the total number of specimens (NISP) in each size group. Hominid-modified specimens comprise a smaller percentage (7.0%) of the large-animal total NISP (104) than do they for the medium-animal sample, but the difference between the two size groups is not statistically significant ($\chi^2 = 0.52$, 1 d.f., $P < 0.5$). On the other hand, the

Table 1. Summary of hominid-imparted modifications in the Swartkrans Member 3 limb bone shaft sub-assemblage.[1]

Size class	Skeletal element	NISP	Cutmarks	Percussion marks[2]
1	Humerus	7	1 (14.2)	
	Radioulna	13		
	Metacarpal	14		3 (21.4)
	Femur	15		2 (20.0)
	Tibia	27	1 (3.7)	2 (7.4)
	Metatarsal	12	1 (8.3)	
	Upper	23	1 (4.3)	
	Intermediate	17		
	Metapodial	19	1 (5.3)	
	Limb bone shaft	152		2 (1.3)
	Total	299	5 (1.7)	9 (3.0)
2	Humerus	42	2 (4.8)	3 (7.1)
	Radioulna	32	2 (6.3)	3 (9.4)
	Metacarpal	22	2 (9.1)	2 (9.1)
	Femur	54	5 (9.3)	3 (5.7)
	Tibia	119	6 (5.0)	4 (3.4)
	Metatarsal	44	2 (4.6)	1 (2.3)
	Upper	30	4 (13.3)	
	Intermediate	47	1 (2.1)	
	Metapodial	59	2 (3.4)	
	Limb bone shaft	124	6 (4.8)	4 (3.2)
	Total	573	32 (5.6)	20 (3.5)
3	Humerus	35	2 (5.7)	3 (8.6)
	Radioulna	20	2 (10.0)	
	Metacarpal	15	1 (6.7)	1 (6.7)
	Femur	28	3 (10.7)	2 (7.1)
	Tibia	85	3 (3.5)	4 (4.7)
	Metatarsal	31	3 (9.7)	1 (3.2)
	Upper	24	3 (12.5)	
	Intermediate	14		
	Metapodial	55	1 (1.82)	1 (1.8)
	Limb bone shaft	66	1 (1.5)	1 (1.5)
	Total	373	19 (5.1)	13 (3.5)
4	Humerus	11	2 (18.2)	
	Radioulna	5	1 (20.0)	
	Metacarpal	4		1 (25.0)
	Femur	12		
	Tibia	17		
	Metatarsal	5		
	Upper	9		
	Intermediate	5		
	Metapodial	20	1 (5.0)	2 (10.0)
	Limb bone shaft	16		
	Total	104	4 (3.9)	3 (2.9)
1–4 (total)	Upper total	290	23 (8.0)	13 (4.5)
	Humerus	95	7 (7.4)	6 (6.3)
	Femur	109	8 (7.3)	7 (6.4)
	Indeterminate	86	8 (9.3)	
	Intermediate total	401	16 (4.0)	13 (3.2)
	Radioulna	70	5 (7.1)	3 (4.3)
	Tibia	248	10 (4.0)	10 (4.0)
	Indeterminate	83	1 (1.2)	
	Lower total	300	14 (4.7)	12 (4.0)
	Metacarpal	55	3 (5.5)	7 (12.7)
	Metatarsal	92	6 (6.5)	2 (2.8)
	Metapodial	153	5 (3.3)	3 (2.0)

[1]Animal size classes are based on Brain's[2] well-known system for bovids. Values in brackets in the fourth and fifth columns are percentages of the total number of identified specimens (NISP) for any row. Indeterminately identified pieces are those specimens that could be identified to a limb segment, as an upper (humerus or femur) or intermediate (radioulna or tibia) specimen but no further.
[2]Percussion marks = pits and striae, in some cases associated with impact notches. Five additional specimens preserve notches only and a separate total of 53 impact flake specimens have been recovered from Swartkrans Member 3.

lowest frequency of hominid-modified specimens is seen in the small-animal sample (5.0% of the total NISP of 299); the difference in this percentage and that for the medium-animal sample is statistically significant ($\chi^2 = 151.5$, 1 d.f., $P < 0.001$).
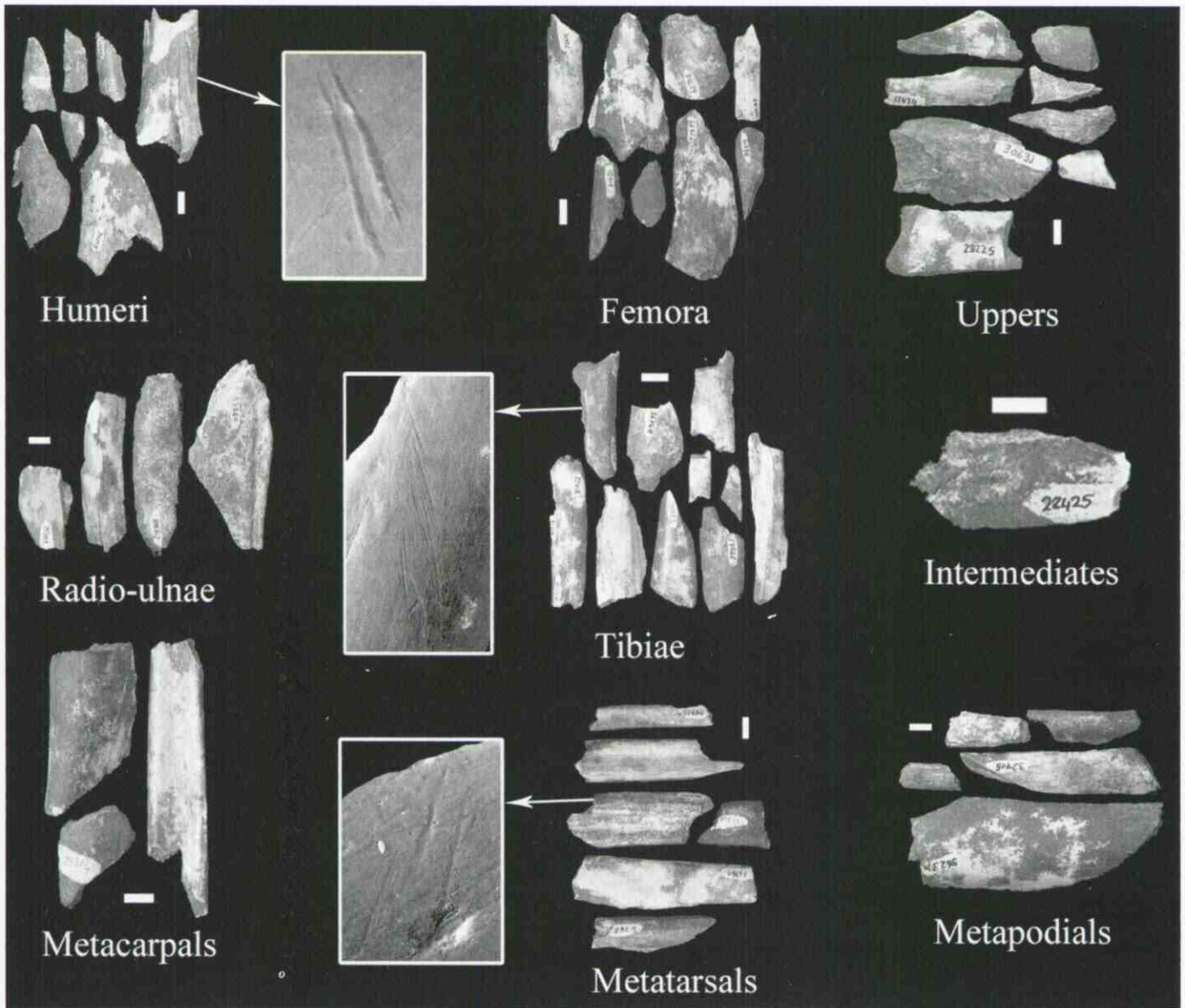
Fig. 2. The sample of identifiable limb bone shaft specimens from Swartkrans Member 3 that bear stone tool cutmarks. Close-ups of cutmarks on three specimens are shown between the first and second column. The third column includes specimens that could only be identified to a lesser precision, as upper (humerus or femur), intermediate (radioulna or tibia) or metapodial specimens. An additional seven cutmarked specimens that could only be identified as limb bone specimens are not shown.

Interestingly (and perhaps significantly), the small-animal sample is also the size group most heavily damaged by carnivore chewing; 73.6% of Size Class 1 limb bone specimens preserve carnivore tooth marks.[9,36] Previously reported metric data on tooth marks also highlight another important distinction between hominid and carnivore carcass-modifiers at Swartkrans Member 3. The consistent representation of hominid-imparted modifications on bone specimens across all body size groups stands in contrast to the more strictly delimited distribution of taxon-specific carnivore tooth marks. For example, leopard tooth marks are restricted largely to Size Classes 1 and 2 remains, while those tooth-marked Size Class 3 and larger remains were damaged predominantly by carnivores with more robust dentitions and jaws, such as spotted hyaenas, large canids and lions.[36]

It is apparent that cutmarks are fairly consistently distributed across all limb segments, upper, intermediate and lower (Fig. 2). The very occurrence of cutmarks indicates that soft tissues were present on bones at the time of hominid acquisition and processing. Had any of the elements been devoid of soft tissues upon

procurement by hominids, there would have been no reason to put a stone tool cutting edge to the bones; in fact, there would have been every reason to avoid cutting into exposed bone, as such an activity dulls a tool's cutting edge unnecessarily.[17,37–40]

For further comparative analyses of the anatomical distribution of cutmarks, it is sensible to combine upper and intermediate limb data versus lower (metapodial) limb data. The midshaft sections of ungulate upper and intermediate limb bones are covered largely by substantial musculature, while metapodial midshafts are devoid of overlying meat. Thus, as experimental and ethnoarchaeological observations indicate,[12–14,37,41–44] cutmarks on upper and intermediate limb bone midshafts reflect defleshing activities, while cutmarks on metapodial midshafts are usually associated with skinning and/or the removal of tendons. In the Member 3 sample, there is no statistically significant difference in cutmark frequencies between meat-bearing elements (upper plus intermediate) and non-meat-bearing metapodials ($\chi^2 = 0.41$, 1 d.f., $P < 0.5$). Thus, it seems probable that Swartkrans hominids at least occasionally gained access to whole limb units of variously sized ungulates and processed

them thoroughly for overlying soft tissues.

Cutmarks on meat-bearing limbs indicate the maximal carcass acquiring abilities of the Swartkrans hominids. Domínguez-Rodrigo,[45] in a sample of 28 modern ungulate carcasses from Kenya, observed that upper and intermediate limb bones display a paucity of adhering flesh after ravaging by lions (*Panthera leo*). Further, midshaft sections on upper limbs in that modern dataset displayed a *complete* lack of flesh scraps, while flesh scraps on the midshaft portions of intermediate limb bones were poorly represented after lion ravaging.[45] Selvaggio[46] observed a similar pattern of lion feeding behaviour: 'limbs were abandoned by lions with little or no flesh on humeri and femora' (p. 54). Based on these findings, there would have been no reason for hominids to have imparted cutmarks on the midshafts of upper and intermediate limb bones at Swartkrans, had those hominids been relegated to the role of passive scavengers.[37-40] If hominids were denied access to large mammal carcasses until after abandonment by the predators and primary consumers of those carcasses (that is, large carnivores), as the passive scavenger model of early hominid foraging implies,[43,47-49] then the midshafts of upper and intermediate limb bones would already be defleshed at the time of the delayed access by hominids.

It is true that some attempts have been made to accommodate evidence of cutmarks on upper and intermediate limb bone midshafts within scenarios of passive scavenging by hominids. For instance, it was suggested that hominids might have scavenged fairly complete carcasses of Size Classes 1 and 2 bovids that were cached in trees and then temporarily abandoned by leopards.[50] Further, the specialized 'slicing' dentition of sabertooth cats was supposed to have precluded their ability thoroughly to deflesh large carcasses that they obtained for food.[2,51,52] In turn, this assertion was used to suggest that cutmarks on upper and intermediate limb bones of larger bovids might reflect passive scavenging by hominids who exploited the substantial amounts of flesh still remaining on these elements once abandoned by sated sabertooth predators.[52-54]

However, more recent research does not support these proposals. For example, in his long-term study of tree-stored leopard kills, Cavallo[55] demonstrated that those felids never abandon cached carcasses without some degree of initial consumption, which includes feeding on the flesh of upper limb bones. This means that a sample of cutmarked limb bone specimens created by hominids scavenging from leopard kills should show a lower proportion of cutmarked upper specimens relative to intermediate and lower specimens. As discussed above, this is clearly not the case in Swartkrans Member 3. Similarly, Marean and Ehrhardt's[56] taphonomic analysis of the fauna from a fossil *Homotherium* den indicates that these sabertooths were very efficient defleshers of large prey carcasses. It is apparent that to test the sabertooth-passive hominid scavenger hypothesis more completely, similar studies need to be conducted on faunas securely inferred to have been collected by other sabertooth taxa. At present, however, that hypothesis is not well supported by the available data. Finally and more generally, we note very few limb bone specimens in the Member 3 assemblage preserve evidence of both carnivore and hominid imparted bone surface damage ($n = 12$), suggesting significant independence in the accumulation of the carnivore and hominid components of the assemblage as a whole.[9]

Turning to the lower limb specimens in our sample, Swartkrans hominids may have imparted cutmarks on metapodials to prepare them for marrow extraction, the major source of edible tissue associated with these elements. Skinning and tendon removal would have facilitated hammerstone percussion directed at metapodials. We note here that, like metapodials, upper and intermediate limb bones acquired by hominids were also probably processed fairly completely, because percussion mark frequencies by individual element and limb segment are not significantly different from cutmark frequencies (for example, for limb segment: $\chi^2 = 1.45$, 2 d.f., $P < 0.5$). Future refitting studies, with the potential to identify the co-occurrence of both percussion marks and cutmarks on the same individual elements, may elucidate this hypothesis more fully.

Summary and conclusions

Although hominid contribution to the large faunal assemblage from Swartkrans Member 3 is minimal,[9,57,58] the newly expanded sample of cutmarked and hammerstone-percussed limb bone shafts is informative about behaviour. A high frequency of cutmarked upper and intermediate limb bone midshafts in this sample falsifies the hypothesis of exclusive passive scavenging by the Member 3 hominids. Had hominids been relegated to scrounging the marrow from felid-killed and defleshed carcasses, there would have been no reason for them to impart cutmarks on skeletal parts consumed early in the feeding sequences those large cats.

This new interpretation of the carcass foraging capabilities of Pleistocene hominids at Swartkrans agrees with early access to large-animal carcasses by hominids inferred from the analyses of other important archaeofaunas, such as FLK 22 *Zinjanthropus* and BK (Olduvai Gorge, Tanzania), FxJj 50 (Koobi Fora, Kenya), and the ST site complex (Peninj, Tanzania).[16,18,24,37,57-60] Our continued work on the zooarchaeology of Swartkrans Member 3, including the analysis of other skeletal parts, holds the potential to elucidate this pattern more clearly in the future. For now, we anticipate our findings will serve the important goal of bringing the South African data more fully into the larger discussion of early hominid foraging behaviour, a topic that has been dominated previously by East African evidence.

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