Bone tool use in termite foraging by early hominids and its impact on our understanding of early hominid behaviour

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ECENT RESEARCH CONDUCTED BY Backwell¹ and Backwell and d'Errico² has confirmed earlier suggestions by Brain and Shipman³ that certain fossil bone fragments found at the Swartkrans and Sterkfontein sites were modified by early hominids. These new studies have also extended earlier research to the potential use of these artefacts, and suggest that the unusual tip modification found on most specimens is not from digging for roots, bulbs and tubers as was previously suggested.3 Rather, recent research suggests that the unique wear patterns were created during termite foraging in epigeal mounds,² where weathered bones were used by hominids to dig into the colony. The implications of this research are many. These results are the first conclusive evidence of tool use linked to a specific food resource at this time depth. Furthermore, this research seems to demonstrate the often predicted link between living chimpanzee and early hominid social and cultural adaptation.4-6 It is also apparent that these tools formed part of an implement-assisted, termite-foraging cultural tradition that persisted unchanged in southern Africa for over half a million years.

Using a multidisciplinary approach to assess the origins of the wear patterns recorded on the 68 bone tools from Swartkrans⁷ (Members 1–3; c. 1.8–1 Myr), we made resin replicas of the tips of the tools^{8,9} and used optical and scanning electron microscopy to identify their surface modifications. Microscopic images of the transparent resin replicas were digitized at ×40 magnification on a sample of 18 fossils from Swartkrans. The orientation and dimensions of all visible striations were recorded using Microware image analysis software.¹⁰ The remainder of the Swartkrans faunal collection was then taphonomically and morphometrically studied in order to establish whether the wear recorded on the tools represented an extreme in variation of a

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taphonomic process affecting, to a lesser degree, the rest of the assemblage. In the course of research, 16 additional specimens that had comparable shape and wear were identified, bringing the total to 85 bone tools.

Microscopic analysis revealed that the Swartkrans specimens had distinctive wear patterns (Figs 1, 2a). Each specimen was found to have a single rounded end with smoothing/polishing confined to an area of between 5 and 50 mm from the tip. Individual striations covered the worn tip, including any recessed areas, but were absent from the remainder of the bone. The striations were 5–40 μ m wide and ran parallel or sub-parallel to the long axis of the bone, decreasing in number away from the tip. All specimens presented a limited number of broader transverse striations orientated subperpendicular to the main axis of the bone. These were generally posterior to the longitudinal parallel striations and ranged between 100 and $400 \,\mu$ m in width.

Thirty-five modern and fossil bone collections from different contexts were examined (Table 1), including those modified by a variety of African carnivores and scavengers, as well as geological processes (such as erosion by river gravel, wind and trampling).¹ From a sample of 13 301 specimens, only 24 pseudo-tools that were grossly similar to the Swartkrans specimens were found. At a microscopic scale, however, they did not have the wear pattern recorded on the fossil tools.

To establish potential hominid activity that might have created this unique wear pattern, and to test the Brain and Shipman hypothesis that these bones were used for digging up tubers, we conducted a series of time-controlled experiments using antelope limb-bone shafts to dig in search of tubers and larvae in a wide range of soil types. We additionally used experimental tools to scrape or pierce animal hides, and to dig in epigeal termite mounds. The experimental tools originally used by Brain and those used by us were replicated and analysed following the same methods applied to the Swartkrans and Sterkfontein bone tools.¹¹

The striations on the fossil bone tools correlate well with those created by digging in epigeal termite mounds (Fig. 2d) and appear significantly different from those produced through other activities. Experimental tools used by Brain and by us for digging tubers from the ground generally recorded superimposed, randomly orientated and relatively broad (c. 30-80µm) striations (Figs 2b,c, 3B). This wear pattern is the result of repeated tangential impact of the tool tip against soil with mixed particle sizes, including angular dolomite blocks. In contrast, the characteristic sub-parallel fine striations (c. 10–30 μ m width) on our experimental tools used in digging termite mounds are the result of repeated abrasion caused by the angular finegrained sediment with a limited range in particle size constituting termite mounds.¹² The sub-parallel striations arise from a motion parallel to the main axis, which is the most efficient action to perforate and flake off the crust of a mound, an activity that encourages the swarming of termites to the surface. Remarkably, the extreme tip wear and distinctive striations were evident on the experimentally created tools after only 15-30 minutes of digging in epigeal termite mounds.

Quantification of the wear pattern facilitated by image analysis was conducted on a sample of eighteen randomly selected bone tools from Swartkrans (i.e. 26% of the original collection), on five tuber-digging tools used by Brain and by us, and six tools to dig termite mounds (Fig. 3). In none of the Swartkrans tools have we observed the variability in orientation of the striations created experimentally by Brain for extracting tubers. Microscopic inspection of the remainder of the Swartkrans and Sterkfontein specimens, including the additional 16 identified by us, confirms that the orientation variability produced by Brain is absent from the wear patterns on these tools. Two of our tuber digging tools (Fig. 3A, G2-3) record an orientation not significantly different from that observed on some Swartkrans specimens (e.g. Fig. 3A, S1, S7). This difference probably depends on the two distinct tasks for which these experimental tools were used. Extraction of Scilla marginata and Hypoxis costata, as carried out by Brain, required scratching out the soil around these large bulbs and the removal of angular dolomitic blocks, an activity implying motions perpendicu-

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Fig. 1. Illustrations in variability in orientation and width of the striations covering the worn areas on the tips of seven Swartkrans bone tools (left) compared with those produced experimentally by digging for tubers (top right) and digging in termite mounds (bottom right) of *Trinervitermes trinervoides* (centre right). On the experimentally created tools used to dig for tubers, striations are composite, randomly orientated and relatively broad. This pattern is the result of repeated tangential impact of the tool tip against coarse ground sediments with mixed particle sizes, including angular dolomitic blocks. On both the experimentally created tools used on termite mounds and the Swartkrans specimens, striations are finer and run parallel or sub-parallel to the long axis of the bone. These striations appear to result from abrasion caused by fine-grained sediment with a limited range of particle size such as that found in the sediment constituting termite mounds. The parallel striations are formed because a motion parallel to the main tool axis is the most efficient way first to pierce and flake off the hard crust of the mound, and then to dig in the softer sediment within the mound. The tool used to dig up tubers is that used by Brain³ in his original experiment. Scale = 1 mm.

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Table 1. Reference collections examined.

Locality	Country	Institution	Probable modifying agent	Age	п	Pseudo-points
Botswana Den, G.N.P.,	Botswana	T.M.	Brown hyaena (Hyaena brunnea)	Modern	27	
Kannaguass Den, G.N.P.	Botswana	T.M.	Brown hyaena (Hyaena brunnea)	Modern	54	
Kaspersdraai B Den, G.N.P.	Botswana	T.M.	Brown hyaena (Hyaena brunnea)	Modern	13	
Kwang Den, G.N.P.	Botswana	T.M.	Brown hyaena (Hyaena brunnea)	Modern	56	
Rooikop Den, G.N.P.	Botswana	T.M.	Brown hyaena (Hyaena brunnea)	Modern	17	
Two dens, Central Namib Desert	Namibia	T.M.	Brown hyaena (Hyaena brunnea)	Modern	7 023	
Umfolosi, KwaZulu-Natal	South Africa	T.M.	Cheetah (Acinonyx jubatis)	Modern	108	
Valencia Ranch	Namibia	T.M.	Cheetah (Acinonyx jubatis)	Modern	291	
Irene, Gauteng Province	South Africa	T.M.	Domestic dog (Canis sp.)	Modern	7	
Wits collection	South Africa	W.M.S.	Domestic dog (Canis sp.)	Modern	4	
Randall's	South Africa	T.M.	Hyaena sp.	Modern	70	
Hakos River	Namibia	T.M.	Leopard (Panthera pardus)	Modern	318	
Kruger National Park	South Africa	T.M.	Leopard (Panthera pardus)	Modern	174	
Portsmut	Namibia	T.M.	Leopard (Panthera pardus)	Modern	184	
Quartzberg	Namibia	T.M.	Leopard (Panthera pardus)	Modern	212	
Valencia	Namibia	T.M.	Leopard (Panthera pardus)	Modern	239	
Uitkomst, Gauteng Province	South Africa	T.M.	Mixed Hyaena sp. and porcupine	Modern	234	1
Wright's Den, G.N.P.	Botswana	T.M.	Mixed Hyaena sp. and porcupine	Modern	8	
Wepener, Free State	South Africa	T.M.	Porcupine (Hystrix sp.)	Modern	105	
Kaspersdraai Den, G.N.P.	Botswana	T.M.	Spotted hyaena (Crocuta crocuta)	Modern	15	
Satara, Kruger National Park	South Africa	T.M.	Spotted hyaena (Crocuta crocuta)	Modern	12	
Urikaruus Den, G.N.P.	Botswana	T.M.	Spotted hyaena (Crocuta crocuta)	Modern	69	
Homeb water hole	Namibia	T.M.	Trampling	Modern	93	6
Cornelia, Free State	South Africa	Q.R.D.B.	Fluvial abrasion	1–0.8 Myr	974	
Erfkroon A, Free State	South Africa	Q.R.D.B.	Flood plain context	120 kyr	301	1
Deelpan A, Free State	South Africa	Q.R.D.B.	Brown hyaena (Hyaena brunnea)	200 yr	220	
Elandsfontein Bone Circle, C.P.	South Africa	S.A.M	Hyaena sp.	200–30 kyr	196	
Florisbad, Free State	South Africa	Q.R.D.B.	Spring action	400–100 kyr	216	
Vlakkraal, Free State	South Africa	Q.R.D.B.	Spring action	400–100 kyr	42	
Erfkroon B, Free State	South Africa	Q.R.D.B.	River gravel context	400–300 kyr	263	1
Ysterfontein, C.P.	South Africa	S.A.M	Hyaena sp.	60–300 kyr	150	
Oyster Bay, C.P.	South Africa	Q.R.D.B.	Wind erosion	70–80 kyr	139	
Elandsfontein Main, C.P.	South Africa	S.A.M	Trampling	700–400 kvr	1 1 1 6	
Duinefontein 2 (Melkbos), C.P.	South Africa	S.A.M	Wind erosion	>125 kyr	152	5
Bacon Hole Cave, South Wales	Great Britain	N.H.M.	Spotted hyaena (Crocuta crocuta)	Upper Pleist.	199	10
Total					13 301	24

Abbreviations: T.M., Transvaal Museum, Pretoria; W.M.S., University of the Witwatersrand Medical School;

Q.R.D.B., Quaternary Research Department, National Museum, Bloemfontein; S.A.M., South African Museum, Cape Town;

N.H.M., Natural History Museum, London; B.C., Bone Circle, G.N.P., Gemsbok National Parks; C.P., Cape Province.



Fig. 2. Wear patterns on Swartkrans and experimental bone tool tips photographed in transmitted light using transparent resin replicas. **a**, Bone tool from Swartkrans Member 3 (SKX 38830); **b**, tip of a tool used in Brain's experiment^a to dig up *Scilla marginata* bulbs; **c**, experimental bone tool used to dig the ground in search of tubers and larvae; **d**, experimental bone tool used to dig in a termite mound. Note the similarity in the orientation and the width of the striations in a and d. Scale bar = 2 mm.

lar or oblique to the bone main axis. The random search for tubers and buried larvae made during our experiments was conducted with motions parallel or sub-parallel to the bone axis, resulting in striations approximately parallel to the main axis of the bone. Striation orientation on termite mound digging tools more closely matches that recorded on the Swartkrans tools. This is confirmed by an F-test, indicating that the overall orientation variability of striations on experimental tools used to dig termite mounds is comparable with that recorded on the Swartkrans tools (P = 0.731) and different (P < 0.0001) from the other experimental tools.

A marked difference (Fig. 3B) exists in the striation width variability recorded on the Swartkrans sample (mean = 18 μ m) and termite mound digging tools (mean = 13.7 μ m), as opposed to tools used for extracting tubers (mean = 63.1 and 46.7 μ m for Brain's and our tools, respectively). Optical and SEM microscopic analysis of the remainder of the assemblage shows that enlarging the sample would not have significantly changed the variation in the striation width.

A nonparametric Mann-Whitney *U* test clearly detects this disparity, thereby ruling out tuber extraction, as performed in Brain's and our experiments, as a viable function for the Swartkrans tools. However, this test also detects a difference between the Swartkrans and termite mound striations. This may be due to known variability in the sedimentological composition of termite mounds located in different areas and belonging to different species¹² or, alternatively, to a function not yet identified.

We favour, for the moment, the termite foraging hypothesis. First, alternative interpretations require the identification of a digging activity exclusively performed in a fine-grained, stoneless soil matrix, such as that of termite mounds, a feature unlikely to occur in the colluvial or fluviatile deposits of the Sterkfontein Valley or inside the caves of this area. Secondly, while limb-bone shaft fragments are suitable for breaking the hard crusts of termite mounds, they appear



Fig. 3. Image analysis of the wear patterns on Swartkrans and experimental bone tools. A, variability (top graph) and mean (bottom graph) in the orientation of the striations on the Swartkrans tools (S), on experimental tools used to dig termite mounds (T), to excavate the ground in search of tubers and larvae (G), and to extract bulbs (B) (Brain's experimental tools⁵). B, striation width as measured at ×40 magnification on all of the striations visible.

inefficient for other digging activities when compared with the long, stout, and often heavy digging sticks used by modern hunter-gatherers to extract buried tubers, larvae and small game.

Analysis of the breakage patterns on the Swartkrans bone tools, and of the single specimen from Sterkfontein (Member 5; c. 1.7–1.4 Myr) indicates that the early hominid users selected heavily weathered bone fragments of a particular size range (13–19 cm) and shape (long, straight bone flakes and horn cores). Almost all the bone tools from long bone shaft fragments (82 = 97%) show longitudinal fractures typical of weathered bone, and some specimens have use-wear overlying carnivore damage.

Metric analysis of the Swartkrans faunal collection also suggests that the bone tools are a discrete population within the assemblage in that the lengths of the few complete tools fall outside the range of the length of the unworn long bone fragments from the site, and even the broken tools are generally longer.² A similar result is obtained when the widths of the tools and the thickness of the compact bones are compared with those of the other fragments from the site, suggesting that longer, wider and more robust bone fragments were selected for.

The various species of the genus of harvester termite, *Trinervitermes* spp., are common to the grassland and savanna

biomes of southern Africa.13 This genus is recognized by its nest-building activity, giving rise to epigeal mounds that, in the Sterkfontein Valley, are built on shallow soils overlying bedrock. The mounds are characteristically dome-shaped, less than 70 cm high and covered with a crust of consolidated sediment. The structure of the mound is such that the hard crust functions not only in a thermo-regulatory capacity, but also as a protective device against predators.¹³ The existence of these termites in the Sterkfontein Valley during the deposition of Swartkrans Members 1–3, dated to between 1.8 and 1.0 million years ago, is evidenced by the presence of termite-feeding taxa such as Proteles sp. (aardwolf), Orycteropus afer (aardvark) and Manis sp. (pangolin) in the Swartkrans faunal collection.¹⁴ Circumstantial evidence is provided by termite damage identified on some fossils in the Swartkrans faunal remains.¹⁵ It is likely that the termites found in the Sterkfontein Valley today (Trinervitermes trinervoides) are of the same type as those existing there in the Plio-Pleistocene, as palaeoecological reconstructions suggest a similar environment.7

Chimpanzees are known to 'fish' for termites in epigeal mounds using grass stalks as well as to perforate and dig termite mounds in a variety of ways using short robust sticks.¹⁶ Pioneering statements predicting termite foraging by early hominids were made as far back as 1963,⁴ but empirical support has remained elusive until now. The potential role of insectivory in early hominid diets has been comprehensively discussed in the last decade.^{17–19} These studies show that termites are a valuable source of protein, fat, and essential amino acids in the diets of both primates and modern humans. Whereas a rump steak yields 322 calories per 100 grams, and cod fish 74, termites provide 560 calories per 100 grams.²⁰ By digging termites out of their nests, hominids would have made use throughout the year of a rich food source inaccessible to most other large mammals.

The predominant numbers of robust australopithecines at Swartkrans and Drimolen (associated at the latter site with 23 undescribed bone tools), and the fact that no stone tools have been found at Drimolen,²¹ might suggest that the bone tool culture belonged to *Paranthropus* (*Australopithecus*) robustus. It is still a matter of debate, however, whether this hominid was a stone tool maker.^{22–24} Only the discovery of future sites with bone tools associated with a single hominid type will clarify this issue.

The ability to demonstrate the consumption of a specific food resource by hominids has implications for many areas of study in the field of palaeoanthropology. Past research has mostly relied upon the analysis of chemical and physical signatures in the fossils themselves, on the study of the associated fauna, and comparison with modern primates to predict early hominid diet and cultural adaptation.^{17,25,26} With our results in mind, researchers may now examine the associated fossil hominid samples for chemical and physical evidence related to Trinervitermes consumption. Recent isotopic analyses of early hominid fossils²⁵ demonstrated a significant proportion of C₄ dietary carbon (indicative of protein consumption) in the remains of both Homo and Paranthropus (Australopithecus) robustus, the latter of which is traditionally considered to have been vegetarian.²⁷⁻³² However, only analyses of hominid remains from southern Africa have been published thus far. The widening of the sample to East African remains might identify regional trends suggesting development of distinct cultural adaptations, as observed amongst present-day chimpanzee communities.¹⁶

A relatively small number of putative bone tools is reported from the Plio-Pleistocene in East Africa.^{33,34} The East African tools are markedly different from those found in South Africa with regard to shape, size and presumably function. Future research will explore the extent of bone tool cultures in East Africa, and attempt to identify the purposes for which these implements were used. East African termite mounds are much bigger and more hardy than those of *Trinervitermes*¹³ and the soldiers are highly aggressive. It is probable, on this evidence, that if termites were a regular component of the East African early hominid diet, they did not forage for them using bone tools.

Additionally, there may be unique micro-wear features on hominid dentition associated with the consumption of termites, including the possibility of formic acid etching, silica-derived abrasion and keratin wear marks. The high silica intake associated with the consumption of termites may also contribute to the unusually rapid tooth wear observed in *Paranthropus (Australopithecus) robustus*, and these areas deserve closer examination.

The effect of termite chemical defences upon hominids is unknown, but it is clear that they may have influenced consumer seasonality. Where the chemical defences of Trinervitermes spp. upon the feeding patterns of aardvark appear limited, this may not be the case for hominids. Historical documents relate the severe consequences of eating Hodotermes (a species of termite widespread throughout Africa) out of season and without proper preparation. Extracts from The Journal of the Cape *Entomologist* (1906)³⁵ report how a family of five all fell ill after eating a meal of termites. They complained of dizziness, distention, a dismal feeling, shaking and trembling. They died before dawn.

Finally, the bone tools are found at three sites that span a relatively long period. Based on the form and wear patterns recorded by us on the single specimen from Sterkfontein (Member 5, *c*. 1.7–1.4 Myr), 85 from Swartkrans (Members 1–3, *c*. 1.8–1.0 Myr), and pre-liminary observation of 23 bone tools from the Drimolen early hominid site (2.0–1.50 Myr),²¹ it would appear that the bone tools from southern African sites are all of the same type, suggesting that one implement-assisted, termite-foraging tradition existed unchanged for nearly a million years.

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In the forthcoming issue

Marine science in the Benguela Current region

In the next issue, we will publish articles based on research conducted in 1999 as part of the **BENguela Environment Fisheries** Interaction & Training (BENEFIT) Programme. BENEFIT is a partnership between government departments in Angola, Namibia and South Africa, and involves the participation of tertiary institutions bordering the Benguela Current system, as well as farther afield. The programme initiates region-wide research and capacity development activities to ensure the long-term sustainability of the living resources of the region.

In 1999, shipboard-based research and training permitted 59 individuals from the SADC countries and Kenya to receive hands-on instruction aboard research vessels from Namibia, Germany and South Africa, at the same time generating much new information about the marine environment off the southwest coast of Africa.