Bone Tool Texture Analysis and the Role of Termites in the Diet of South African Hominids

JULIE J. LESNIK

Department of Anthropology, Northeastern Illinois University, 5500 N. St. Louis Avenue, Chicago, IL 60625, USA; julie.lesnik@gmail.com

ABSTRACT

The Swartkrans cave, part of the Cradle of Humankind World Heritage Site in South Africa, has yielded bone tool artifacts together with an abundance of hominid fossils attributed to *Australopithecus (Paranthropus) robustus* and some fossils attributed to the genus *Homo*. These bone tools were originally identified as digging implements by Brain and colleagues (1988). More recent studies by Backwell and d'Errico (2001; d'Errico and Backwell 2009) reach the conclusion that they were primarily used to dig into termite mounds. Here, the methods pioneered for dental microwear texture analysis are applied in an attempt to address a narrower question of what genus of termites the hominids were foraging. Texture analysis did not prove to be more informative than previous 3D studies of the Swartkrans bone tools, but the ecology of differing termite genera suggest the conclusion that the genus *Macrotermes* should be further investigated as a hominid food resource.

INTRODUCTION

The heavy masticatory morphology of robust australopithecines was central to Robinson's 'Dietary Hypothesis' that suggested Paranthropus was a dietary specialist, crushing and grinding hard-object food items (Robinson 1954). This hypothesis became a paradigm for explaining the success of the omnivorous genus Homo and the demise of the specialist genus Paranthropus (Wood and Strait 2004). Recent advances such as dental microwear (Grine 1981; Scott et al 2005) and bone chemistry analyses (Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005; Van der Merwe et al 2003) are now suggesting that the diets between Homo and robust australopithecines may not have been as different as previously thought. The South African hominids in the Cradle of Humankind have been central to many of these studies. The site of Swartkrans has a rich assemblage of hominid fossils and associated tools. Learning more about diet helps us understand how these tools may have been used, and vice versa. The tool assemblage at Swartkrans consists of Oldowan type stone tools but also a large number of bone tools that are unlike penecontemporaneous tools in east Africa (Leakey 1970). These bone tools are fragments of animal long bones and appear to be digging implements, based on the presence of wear and polish on one end. This wear and polish has been studied by Brain and colleagues (1988) and Backwell and d'Errico (2001; d'Errico and Backwell 2009) with the intent of identifying the particular task that was being conducted. These studies used different methods, ranging from qualitative analysis of scanning electron microscope (SEM) images (Brain et al. 1988), to quantitative measuring of wear features from light microscope images (Backwell and d'Errico 2001), to three dimensional rendering and measuring of roughness features (d'Errico and Backwell 2009).

In this paper, texture analysis, a combination of confocal microscopy and scale sensitive fractal analysis (SSFA), will be used to assess the wear patterns on the ends of the Swartkrans bone tools. Texture analysis was developed for dental microwear studies as a solution to the errors created by the observer and the two-dimensional images in feature based analyses like SEM. Similar to the work done by d'Errico and Backwell (2009), confocal microscopy generates a 3D image, therefore reducing the loss of information that occurs in converting a 3D surface into a 2D image, as with SEM. The SSFA component of the analysis is based on the principle from fractal geometry that the scale of observation affects the observation of features (Scott et al 2006; Ungar et al 2003). Surface textures that appear smooth at coarse scales can appear rough at fine scales. Using SSFA software to analyze the 3D confocal surface images eliminates the error present when an observer is required to identify the features.

DIET OF SOUTH AFRICAN HOMINIDS

One of the most significant findings in regards to South African hominid diet has been the carbon isotope analyses suggesting that the diets of gracile and robust australopithecines are not only similar but also contain significant resources with the C_4 photosynthetic pathway. In South Africa, the most common C_4 resource is savanna grasses or the meat of animals that consumed C_4 grasses (Sponheimer and Lee-Thorp 1999). Isotope analyses suggest that up to 40% of the diet came from C_4 resources (Sponheimer et al 2005). It was widely agreed at the time that hominids were not adapted to digesting grasses, although recent study of robust australopithecines in East Africa may suggest otherwise (Cerling et al 2011). It was suggested that the hominids were consuming significant amounts of animal foods,

PaleoAnthropology 2011: 268–281.© 2011 PaleoAnthropology Society. All rights reserved.ISSN 1545-0031doi:10.4207/PA.2011.ART57

even though *Australopithecus africanus* was not a tool-user (Sponheimer and Lee-Thorp 1999).

In 2001, Backwell and d'Errico reported evidence of termite foraging at the South African site of Swartkrans. The evidence was in the wear patterns on the ends of bone tools from the 1.7 million year old site. These patterns, combined with the above carbon isotope study, led the authors to suggest that termites may have been contributing to C₄ signature in the hominids. To investigate this idea further, Sponheimer and colleagues (2005) analyzed the carbon signatures of available resources on the South African savanna, including termites. The study found that the different termites available had signatures that ranged from almost entirely C₃ to entirely C₄ resources and everywhere in between. The authors identified a correlation between amount of C₄ in the termites and their location on the savanna; for instance, termites in the more open areas consumed more C₄ resources and those in the closed woodlands consumed more C₃ resources. Termites in the closed riverine environments, however, ate significant C₄ resources despite the availability of woody C₃ plants. The termites that ate the different resources are of different genera. For instance, termites of the genus *Trinervitermes*, the termites used in the Backwell and d'Errico study, are grass foragers, but termites of the genus Macrotermes, the termites most commonly preved upon by chimpanzees, consume woody resources. Since both types of termites are present in the South African habitats associated with hominids, it is difficult to say which they would have eaten. Other factors besides their presence on the landscape could influence choice, such as obtainability, nutritional factors, and palatability.

Across chimpanzee sites, Macrotermes are the most common termite prey (Bogart and Pruetz 2008). The chimpanzees are able to "fish" for the termites by inserting a long grass probe into the exit hole of the termite mound. In this task, the termites' pinching mandibles, which are a defense mechanism against enemies such as ants, are used to the benefit of the forager. The termites attack the grass probes with their pinchers and become attached; the chimpanzees can then retract the grass and remove the attached termites with their mouths (Goodall 1963; Prestwich 1984). Chimpanzees from the Goualougo Triangle in the Republic of Congo use two tools to forage for *Macrotermes* termites. First, the chimpanzees use a stick to perforate the termites' passageways in the mound. After the hole is opened with the first tool, a second grass tool is inserted in order to fish for the pinching insects (Sanz et al 2004). Trinervitermes, on the other hand, do not have pinchers, and instead the soldiers use chemical defenses such as glue spitting or chemical odor. These chemicals repel enemies ranging in size from ants to anteaters; they are irritating and foul tasting (Prestwich 1984). When foraging for Trinervitermes, the hard outer crust of the mound must be broken. Trinervitermes are sensitive to disturbances and will often retreat below ground (Ohiagu and Wood 1976; pers. obs.). These behaviors could account for why chimpanzees do not prey upon this genus.

It is unknown whether hominids would find *Macrotermes* more appealing than *Trinervitermes*. It also is unknown how the hominids used the bone tools to obtain the termites. The most likely possibilities for hominid termite foraging are the use of bone tools to dig into *Trinervitermes* mounds, dig into *Macrotermes* mounds, or perforate the exit holes of *Macrotermes* mounds to allow access for fishing probes. These possibilities can be tested experimentally. Here, the wear patterns on the ends of the Swartkrans bone tools will be compared to experimental tools used for the above three tasks, as well as to experimental tools used to dig into the ground for tubers.

First, the null hypothesis needs to be tested:

• H₀: If wear patterns are not significantly different for groups of tools separated by task, then the wielding action and/or soil matrix is not different enough to leave a distinct signature and conclusions about the function of the tools cannot be made.

Rejection of the null hypothesis will allow the following hypotheses to be tested:

- H₁: If the Swartkrans bone tools were used to dig into the termite mounds of the genus Trinervitermes or Macrotermes, then the signature left on the ends of the artifacts will best match that of the experimental tools used on the mounds of Trinervitermes or Macrotermes, respectively.
- H₂: If the Swartkrans bone tools were used to perforate into the exit holes of the mounds of Macrotermes termites, then the signature left on the ends of the artifacts will best match that of the experimental tools used for that task.

THE SWARTKRANS BONE TOOLS

The bone tool assemblage from Swartkrans is housed at the Transvaal Museum (Northern Flagship Institution) in Pretoria, South Africa, and were first identified during the 1976–1988 excavations led by C.K. Brain, although the first reported bone tool in the Cradle of Humankind was found at Sterkfontein in 1959 by Robinson. The artifact was described as a longitudinally split portion of long bone, roughly one centimeter in thickness, with one broken end forming a point and the other end showing a post-depositional break suggesting the implement was originally longer than its preserved 9cm. The surfaces on the pointed end of the artifact had become smooth and polished while the rest of the bone maintained its natural texture. With the rejection of Raymond Dart's "osteodontokeratic culture," Robinson needed to make a convincing case that the implement he was reporting was indeed a bone tool (Dart 1949; 1957; Washburn 1957). Robinson had to refute all natural causes that could produce a pseudo-tool. If the wear and polish were attributed to either water or windblown sand, then it would be expected that the entire bone would be smoothed over. Besides natural weathering, animals are another source of post-mortem alteration to bones. There was no evidence of carnivore or rodent damage, which led Robinson to conclude that hominid activity was the

most likely explanation. He suggested the tool was used to scrape or rub something soft such as the underside of animal skin. Robinson did not believe the tool was used for digging because the surface was polished and did not have the extensive scratching he suspected digging would leave behind (Robinson 1959).

During the 1976–1988 excavations at Swartkrans, Brain and colleagues found 68 artifacts across Members 1-3 that were similar to Robinson's bone implement from Sterkfontein. During these excavations, Brain noticed that the wear produced on the metal implements used for removing the hard Swartkrans breccia resembled the wear seen on the bone tools they were finding. Brain and colleagues decided to test a digging hypothesis, dismissed by Robinson, by conducting digging experiments with bone tools. The tools were fragmented pieces of fresh long bones that resembled the narrow width of the artifacts, sometimes under one centimeter, and had lengths of 10-15cm, based on the assumption that the artifacts were fragments of their initial form. The tools were found to be effective for digging in the hard, dolomitic, South African soil and the continual penetration of a tool into the ground left longitudinal scratches on the end while the tool dragging across hard stones left transverse striations. It also was found that it took hours of digging to match the amount of wear present on the Swartkrans artifacts, suggesting the tools were used multiple times, likely over many days. Scanning electron microscope images were taken of the wear on both the experimental tools and the Swartkrans artifacts. Brain and colleagues concluded that digging could solely be responsible for the wear and polish seen on the artifacts, that the hominids were using the tools to dig for underground storage organs of plants such as Hypoxis, and that the tools were carried around in simple bags to be used multiple times (Brain et al 1988; 1993).

The work done by Brain and colleagues was largely qualitative and, in 2001, Backwell and d'Errico took a quantitative approach to identifying a task for these tools. The authors created experimental bone tools used to dig for tubers in a wide range of soil types, to scrape and pierce animal hides, and to dig into termite mounds. Analysis of the wear patterns present on the ends of the tools, as seen by transmitted light microscopy, showed the termiting tools had a characteristic wear pattern that most closely matched that on the artifacts. The striations were narrower on these tools than those used to dig into the ground, due to the finely sorted sediments of the termite mounds, and the striations ran mostly parallel to the long axis of the tool due to the action of piercing into the hard crust of the mound.

Backwell and d'Errico also provided a comprehensive description of the bone tool sample at Swartkrans. Their analysis of the breakage patterns of the bone tools suggested that the hominids selected heavily weathered, long, straight bone fragments or horn cores that were between 13–19cm long. In general, the bone tools appeared to be longer, wider, and more robust than bone fragments in the faunal sample from Swartkrans (Backwell and d'Errico 2001). These criteria helped the authors identify 16 overlooked bone tools in the Swartkrans faunal sample, bringing the total of identified Swartkrans bone tools up to 84 (Backwell and d'Errico 2003). The tools not only look the same across the deposits, but the authors also noted that the number of tools in each member was proportional to the faunal assemblage, thus ruling it unlikely that they were an intrusion. The dates for the tools can thus be considered consistent with the dates of Members 1–3, spanning almost a million years from 1.8 to 1.0 myr (Backwell and d'Errico 2003).

Bone was not the only available material available for digging into termite mounds. Stone tools also exist in the Swartkrans assemblage in all three members, and the stones would not necessarily need to be modified for use on a termite mound. Large stones are abundant in the dolomitic environment, but using stones to dig into a termite mound would not necessarily leave behind evidence in the archaeological record since impact against a termite mound would not leave an identifiable mark on the stone. In experiments comparing the efficiency of unmodified stones versus bone tools for breaking into termite mounds, stones were found to be the more efficient tools for the task (Lesnik and Thackeray 2006). Bone tools were used to dig into the hard outer crusts of termite mounds, following the methodology described by Backwell and d'Errico (2001). Unmodified stones found near termite mounds were used in a similar manner. The stones ranged in size from 0.1kg to 3.5kg, matching the range seen in the modified stone artifacts in the Swartkrans assemblage. Each bone and unmodified stone tool was used to strike an intact termite mound a controlled number of times and the loosened soil was collected and weighed. Tools with more mass removed more soil. Because stone is more massive than bone, the results suggest that stone tools are more effective than bone tools for the task of breaking into the hard outer crust of termite mounds. However, in comparing a bone tool and a stone tool of equal mass, the bone tool was more efficient because of the pointed nature of the bone fragment. This lightweight efficiency may be why the hominids chose bone for tools at least some of the time. This suggestion is not only compatible with Backwell and d'Errico's conclusion of termite foraging with bone tools, but also reemphasizes the lightweight and transportable nature of the tools as originally discussed by Brain and colleagues (1988).

If the tools were being carried around, they would have been available for use on a range of tasks, as Brain and colleagues (1988) suggested. A study by Van Ryneveld (2003), who followed up the Backwell and d'Errico study with more experiments and visual comparisons of SEM images, reached the conclusion that multiple tasks were most likely.

In 2008, Backwell and d'Errico described 22 bone tools from a third Cradle of Humankind site, Drimolen. These tools appear to have been involved in a similar digging task as the Swartkrans tools and share similar features such as bone type, fragment size, break pattern, and position of wear. D'Errico and Backwell (2009) compared these tools to the Swartkrans sample using optical interferometry to produce high quality three-dimensional images of bone tool wear patterns. The sample consisted of eight Swartkrans specimens, seven Drimolen specimens, as well as termite and tuber digging experimental tools and ethnographic tools used for marula fruit processing. Eight scans were taken per tool; the 15 artifacts yielded 120 scans. Ten different variables were studied on the 3D images and showed that termite digging fell within the range of variation for the artifacts from both sites. Termite digging, however, did not account for the total variation seen in the artifacts. The same conclusion was reached for the marula processing tools. Tuber digging fell entirely within Swartkrans variation, but fell partially outside of the Drimolen sample. The tools that fell outside of the range of variation for Drimolen were the tools used in the original Brain and colleagues bone tool study (1988). This result suggests that different users can affect the resulting wear pattern. D'Errico and Backwell state that termite foraging is still the most likely task for these artifact bone tools, but that there is also support for digging into the soil (d'Errico and Backwell 2009).

These previous studies have looked at a maximum of 18 Swartkrans artifacts out of the 84 total in the assemblage, although multiple scans have increased data robustness. The preservation of the artifacts limits the number that can be studied, but a small sample leaves open the possibility of sampling bias. The tools used in each of the studies were not the same and had minimal overlap, therefore the differing conclusions of digging for tubers (Brain et al. 1988) and digging for termites (Backwell and d'Errico 2001) are not necessarily mutually exclusive. In this paper, I look at a larger sample of 38 Swartkrans tools, encompassing the tools used by both groups of researchers in previous studies. From these 38 artifacts, I computer generated ten random samples, each with 10 to 13 artifacts, in order to test the homogeneity of signatures within the Swartkrans bone tools assemblage and the possibility of multiple purposes. Two more hypotheses will be tested, in addition to those listed above:

- H₃: If random samples generated from the Swartkrans assemblage do not have wear patterns that are significantly different from each other and/or are different from the samples used in either the Backwell and d'Errico or Brain and colleagues' studies, then sampling bias is not the cause for the different conclusions of those two studies.
- H₄: If the Swartkrans bone tools were used for multiple tasks, then there will be more than one of the experimental groups that match the tools in the Swartkrans assemblage, i.e., digging for termites and digging for tubers.

MATERIALS AND METHODS

BONE TOOLS EXPERIMENTS

A list of experimental bone tools is presented in Table 1. Some bone tool experiments were conducted on *Trinervitermes* mounds in South Africa, but the majority of experiments for this study were conducted on both *Trinervitermes* and *Macrotermes* mounds in southeastern Senegal at the Fongoli savanna chimpanzee study site 15km north of the town of Kedougou. This area of Senegal is thought to be similar to the open canopy, mosaic, Plio-Pleistocene habitat of early hominids (Pruetz 2007). For this study, the area was ideal because of the presence of both *Trinervitermes* and *Macrotermes* and a rocky soil similar to the dolomitic terrain in the Cradle of Humankind.

Fresh *Bos* bones were obtained from a local butcher. Although it has been shown that the bone tools were created from weathered bone fragments (Backwell and d'Errico 2001), fresh bones were chosen due to availability and the control of their consistency as opposed to different weathering stages of bones exposed to variable environments. A large stone was used to fracture the long bones, usually tibiae, into bone fragments suitable for digging. These fragments ranged roughly in size from 9–19cm length and 15–160g mass. All soft tissue was removed from the working ends of the tools and the grease was washed off with a mild detergent.

A total of 41 tools were used in experiments with varying time and tasks. Tasks were conducted for 10, 20, 40, 60, or 80 minutes. Each tool was used for two tasks except for control tools that were only used for one task. Each tool had its own unique combination of tasks and time. Tasks included:

- Digging into Trinervitermes mounds (TRIN): The bone tool was used to break through the hard outer crust of Trinervitermes mounds. Trinervitermes is the same genus as the termites used in the Backwell and d'Errico studies. This genus is grass foraging and the most common in the Cradle of Humankind today.
- Digging into Macrotermes mounds (MACRO):The bone tool was used to break through the hard outer crust of Macrotermes mounds. Macrotermes are the termites most commonly preyed upon by chimpanzees. This genus consumes woody-plant resources.
- Perforating into Macrotermes mounds (PERF): The bone tool was used to perforate exit holes of Macrotermes mounds. Perforating is the first of a two-step termite foraging process common in the chimpanzees of the Goualougo Triangle. These chimpanzees first use a stick to perforate the exit hole and then use a long blade of grass to "fish" for the termites. The bone tool in these experiments mimicked perforating sticks.
- Digging into the soil (DIG): The bone tool was used to dig into the soil for plant underground storage organs. Some experiments removed a tuber from the ground, but most mimicked the process and yielded no more than a hole in the ground and wear on the tool.

MOLDING AND CASTING

Experimental tools were cleansed after use with Liqui-Nox (Alconex, Inc.), a phosphate free cleanser appropriate for

Tool #	Task 1	Time	Task 2	Time
1	DIG	Unknown*	-	-
2	DIG	Unknown*	-	-
3	DIG	Unknown*	-	-
4	DIG	20	-	-
5	DIG	20	-	-
6	DIG	20	-	-
7	DIG	40	-	-
8	TRIN	20	-	-
9	TRIN	40	-	-
10	TRIN	20	-	-
11	TRIN	40	-	-
12	TRIN	20	-	-
13	TRIN	40	-	-
14	TRIN	20	-	-
15	MACRO	20	-	-
16	MACRO	20	-	-
17	MACRO	40	-	-
18	MACRO	40	-	-
19	MACRO	20	-	-
20	PERF	20	-	-
21	PERF	20	-	-
22	PERF	20	-	-
23	PERF	20	-	-
24	DIG	20	MACRO	40
25	DIG	40	MACRO	20
26	DIG	20	MACRO	20
27	DIG	20	MACRO	20
28	DIG	20	MACRO	40
29	DIG	40	MACRO	20
30	DIG	20	TRIN	20
31	DIG	20	TRIN	40
32	DIG	40	TRIN	20
33	MACRO	20	DIG	40
34	MACRO	20	DIG	20
35	MACRO	40	DIG	20
36	MACRO	20	DIG	20
37	MACRO	40	DIG	20
38	MACRO	20	DIG	40
39	TRIN	40	DIG	20
40	TRIN	20	DIG	40
41	TRIN	20	DIG	20

*denotes the three experimental tools used in the original Brain *et al.* Study and thus the unknown length of time for their use.



Figure 1. Area of observation for confocal microscopy. The digging end is oriented to the right. The anterior surface is oriented towards the objective lens. The 1.020mm x 1.380mm field of view (yellow rectangle) is on the flat surface superior of the digging tip, but still in the range of wear and/or polish.

use in the field. The working ends of the tools were molded using President Jet (Coltène-Whaledent) polyvinylsiloxane dental impression material. Positive replicas of the bone tools were prepared using Epotek 301 (Epoxy Technologies) epoxy resin. This procedure has been shown to successfully reproduce surface features to a fraction of a micron (e.g., Beynon 1987).

The same molding and casting procedure was used to replicate 38 of the Swartkrans bone tools. The artifacts were clean, so only a soft brush and water were used to remove any surface dust before molding.

TEXTURE ANALYSIS

The casts of the experimental bone tools and the casts of the Swartkrans artifacts were taken to the University of Arkansas where they were studied using texture analysis under the supervision of Dr. Peter Ungar. Texture analysis combines confocal microscopy and scale sensitive fractal analysis to produce a three-dimensional image that can be analyzed without observer error through scale sensitive fractal analysis.

Confocal Microscopy

Confocal scanning microscopy measures z-values, or heights, at fixed x and y intervals to construct a matrix of x, y, and z coordinates. The microscope objective is scanned in the vertical direction to generate a series of optical sections that contain information about which points were in focus at a given z level on the surface. Combining these images produces a matrix of x, y, z coordinates and creates a point cloud (Scott et al 2006; Ungar et al. 2003).

The high resolution casts of artifact and experimental bone tools were observed using a Sensofar Plµ Confocal Imaging Profiler microscope. The specimen was mounted on plasticine with the working end oriented right and the anterior surface facing the objective lens. The scanning surface needs to be flat to the objective lens in order to obtain accurate z-coordinates and the specimens were adjusted until the degree of tilt was less than 30µm. Achieving a level surface can be a challenge for a worn area on a bone tool. For this reason, only one scan was taken for each tool, each one being as close to the same position as possible. The position chosen was superior of the working tip of the tool while still in the highly worn or polished field. The position was as medial on the anterior surface as possible (Figure 1). Once features were identified in the scan area,

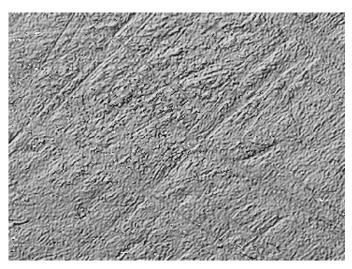


Figure 2. Thresholded photo simulation in SolarMap. White patches are areas where defects were removed from the point cloud and thus the analysis.

the specimen was scanned using the 10x objective resulting in an image with a field of view of 1.020mm x 1.380mm.

The confocal microscope produced three-dimensional point clouds of the bone tools' surfaces. These point cloud files were imported into SolarMap Software (Mountains). After normalization, the images were leveled and displayed as photo simulations where the contrast could be adjusted to highlight features for the observer. Thresholding and erase operators were used to remove obvious defects from the image caused by dust or dirt on the original specimen or air bubbles in the mold or cast. These erased areas appear as white spots on the image. There are no longer data left at these erased positions in the point cloud so they are not factored into the analysis (Figure 2).

Scale Sensitive Fractal Analysis

The corrected point clouds were run through two statistical software packages created by Surfract (Surfract.com). The fractal analysis program Toothfrax, software designed collaboratively with Peter Ungar and the University of Arkansas, was used to measure the following variables: complexity, scale of maximum complexity, anisotropy, and heterogeneity.A second program, Sfrax, was used to measure fill volume of the features.

These software packages are based on the principles of fractal geometry and can be applied to length profiles (length-scale analysis) or to three-dimensional surfaces (area-scale analysis, volume filling v. scale analysis). The basic principle for length-scale fractal analysis is that relative length is measured as the length of the convoluted line divided by the projected straight-line distance between the endpoints. This method is useful for detecting the directionality, or anisotropy, of the features. Area-scale is similar but works with triangular patches as representations of the surfaces. As scale decreases, more triangular patches per unit area are identified. Area-scale fractal analysis is useful for identifying the complexity of the surface. Similarly, volume fill of surface features can be measured by filling a wear surface with varying sized cuboids and summing their volumes.

These methods identify five variables of potential interest. These variables, defined in Scott et al. (2006) and Ungar et al. (2008) are as follows:

Complexity (*Asfc*). Complexity is a measure of change in surface roughness with a change in scale of observation. Relative area is a measure of surface roughness at a given scale and calculated by laying virtual triangular tiles of varying sizes over the surface. Changes in relative area with scale can then be used to characterize the complexity of surface roughness. Area-scale fractal complexity (*Asfc*) is measured as the steepest part of a curve fit to a log-log plot of summed tile area over tile size multiplied by -1,000. Complexity has been shown to distinguish differences in the dental microwear of primates that eat more hard, brittle foods from those that consume more tough foods and has been applied to hominid dentition (Scott et al. 2005). This variable has potential for distinguishing different digging matrices for bone tools.

Scale of maximum complexity (*Smc*). The measured scale at which the microwear surface is the most complex has also been informative in dental microwear studies (Scott et al. 2005; 2006) and is measured here on the use-wear on the bone tools. The scale of maximum complexity (*Smc*) is calculated as the fine scale limit of the steepest part of the curve described for *Asfc*.

Anisotropy (epLsar). Anisotropy describes the directionality of wear features. Relative lengths of depth profiles differ with orientation when the roughness of a surface has directionality, or is anisotropic. Relative lengths at given orientations can be defined as vectors. The length of the mean vector is a measure of surface anisotropy called exact proportion length-scale anisotropy of relief (epLsar). epLsar was calculated for each scan using Toothfrax at the 1.8µm scale of observation, the finest scale for which *epLsar* could be determined given the need to balance scale with number of pixels available at all orientations to calculate robust relative length values. In previous Swartkrans tool use-wear studies, directionality of the striations on the tools was significant for identifying task in both two-dimensions (Backwell and d'Errico 2001) and three-dimensions (d'Errico and Backwell 2009). epLsar will test the significant differences of the directionality of wear on these tools at different scales of observation.

Heterogeneity ($Hasfc_9$ and $Hasfc_{81}$). The above vari-

ables provide useful information about texture but the variation of these measures across a surface can also be informative. For example, adjacent scans from the same specimen can yield differing values for *Asfc*. Heterogeneity of area-scale fractal complexity (*Hasfc*) can be calculated by splitting individual scanned areas into a grid with equal numbers and rows by using the autosplit function on Toothfrax. Marked differences in surface texture across these cells would produce high values of heterogeneity. Scott and colleagues (2006) suggest that heterogeneity comparisons based on 3x3 grids (*Hasfc*₉) and 9x9 grids (*Hasfc*₈₁) were most useful for distinguishing molar microwear surfaces and were applied here in this study.

Texture fill volume (*Tfv*). The SSFA program Sfrax creates an algorithm that fills a surface with square cuboids of different volumes. The texture fill volume of interest here must be identified as different from fill volume of a surface depression inherent to the structure of the bone, or the structural fill volume (*Sfv*). Structural fill volume can be estimated on a coarse scale using cuboids with surface faces of 10µm. When the volume is calculated on a finer scale, using cuboids with surface faces of 2µm, the small texture features also are included in the total volume. Textural fill volume (*Tfv*) can be calculated by subtracting the structural fill volume from the total fill volume.

STATISTICAL ANALYSES

After the scans were analyzed, the resulting data were rank transformed to mitigate assumptions inherent in parametric statistical analyses (Conover and Iman 1981) and then analyzed using multivariate analysis of variance (MANO-VA) model. The MANOVA determined whether groups differed in overall texture patterns. Analyses of variance (ANOVAs) for individual texture attributes and pairwise comparisons tests for the different groups were then used to determine the sources of significant variation. Both Tukey's HSD (honest significant difference) and Fisher's LSD (least significant difference) tests were used to balance the risks of Type I and Type II errors (Cook and Farewell 1996).

RESULTS

Results are illustrated in Tables 2 through 9. There is significant difference in the MANOVA model (Table 2), indicating that use wear textures vary across the samples of interest in this study. The individual ANOVAs (Table 3) indicated that the significant variation among the samples lies entirely in the variable for complexity (*Asfc*).

Fisher's LSD and Tukey's HSD pairwise comparisons of the *Asfc* between all the samples show that most of the difference is between the Swartkrans tools and the Experimental tools (Table 4). The pairwise comparisons of just the experimental tools fail to reject the null hypothesis that task will leave a distinct signature on the ends of the tools (Table 5).

Fisher's LSD pairwise comparisons of the *Asfc* of the Swartkrans samples, including the sample used by Brain and colleagues, by Backwell and d'Errico, and ten randomly generated samples, suggest that when assessing the

TABLE 2. MANOVA MULTIVARIATE TEST OF VARIANCE RESULTS.

	Test Statistic	F	df	p				
Wilks' Lambda	.727	1.524	1,458	.000				
Pillai Trace	.416	1.718	1,319	.000				
Hotelling-Lawley	1.095	1.961	1,418	.000				

Three different test statistics all show a p value of under .05 and suggest that there is significant differences among experimental and artifact bone tools.

signature of the entire Swartkrans assemblage by using a sample, bias is possible. The Brain and colleagues' sample and the randomly generated Swartkrans Sample 8 stand out as significantly different from other samples in the Swartkrans assemblage (Table 6).

Even though the null hypothesis was not rejected, Fisher's LSD and Tukey's HSD pairwise comparisons of the *Asfc* of the Swartkrans tools compared to the experimental tools show some differences in how certain tasks compare to the artifacts. Most of the experimental tools are significantly different from the Swartkrans tools in texture complexity, but the experimental controls for digging into *Trinervitermes* mounds and for perforating into *Macrotermes* mounds are most similar to the Swartkrans sample (Table 7).

Descriptive statistics of the unranked data can be found in Tables 8 and 9. These raw numbers were not used in the scale sensitive fractal analysis but can still be useful in comparing the samples.

DISCUSSION

The results of the SSFA presented here provide insight into the value of use-wear studies and to the possibility of *Macrotermes* as a dietary resource for early hominids. Texture analysis was unable to distinguish wear patterns between experimental tasks, thus failing to reject the null hypothesis. However, there were significant differences among the samples of Swartkrans tools, and some of the samples were better matches to the experimental tools. The experimental tools used for more than one task were the most different from the Swartkrans sample, and the experimental tools used to dig into the ground were also a poor match. The best matches, and thus the most likely tasks were digging into *Trinervitermes* mounds and perforating into *Macrotermes* mounds. Between these two termite genera, *Macrotermes* may be the more likely resource when other evidence, such as termite ecology and great ape predation on termites, is considered.

INTERPRETATION OF THE USE-WEAR RESULTS

The MANOVA test reveals that the entire sample shows significant differences in texture variables but does not identify which variable or what tools. The ANOVA test is necessary to identify where the variation lies. The variables for scale of maximum complexity (*Smc*), textural fill volume (*Tfv*), heterogeneity (*Hasfc*), and anisotropy (*EpLsar*) were not significantly different between the samples. The only variable that was significantly different was complexity (*Asfc*).

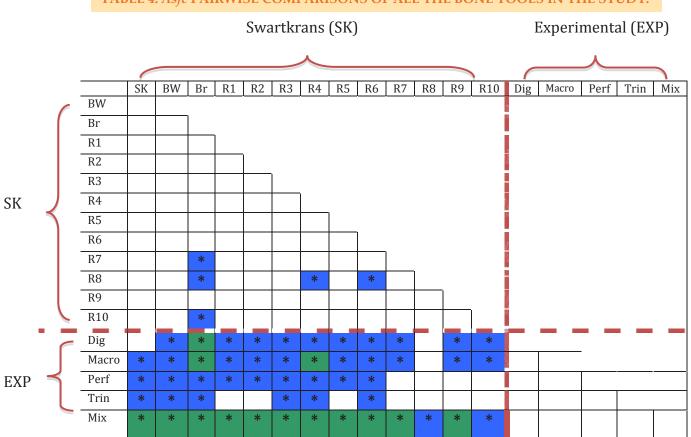
The variable for heterogeneity (*Hasfc*) was not found to be significantly different across the samples but is still informative for this study. For both the experimental tools and the Swartkrans artifacts, the heterogeneity was low, suggesting that the wear pattern was consistent across the scan's field of view. This result confirms the validity of using only one scan for each tool. If the heterogeneity levels were high, there would have been discrepancies across the scanning area suggesting the possibility of a more mosaic wear pattern and the need for more scans to address the pattern.

The lack of significance of the anisotropy (EpLsar) vari-

	F	df	p
Asfc (complexity)	6.297	22	.000
<i>Smc</i> (scale of max. complexity)	1.134	22	.311
<i>EpLsar</i> (anisotropy)	.557	22	.947
Hasfc9 (heterogeneity)	1.013	22	.449
Hasfc ⁸¹	.630	22	.901
<i>Tfv</i> (texture fill volume)	.980	22	.490
The texture complexity (Acte) is the only sign	aificantly di	fforont	wariabl

TABLE 3. ANOVAS OF INDIVIDUAL VARIABLES.

The texture complexity (*Asfc*) is the only significantly different variable with a p value below .05.

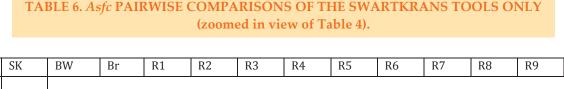


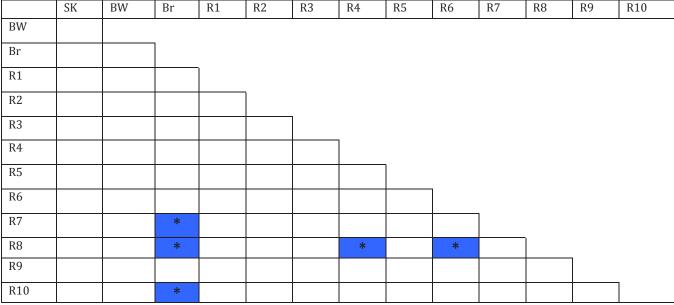
Colored boxes represent significant differences at the .05 level between the two samples in the pairwise analysis. Blue * boxes are significant using Fisher's LSD test and green * boxes are significant using Tukey's HSD test. Sample abbreviations are as follows: SK=Swartkrans entire sample; BW=Sample used in the Backwell and d'Errico (2001) study; Br=Sample used in the Brain et al. (1988) study; R#=Randomly generated sample from the Swartkrans assemblage; Dig=Experimental tools used for digging into the ground only; Macro=Experimental tools used for digging into the mounds of *Macrotermes* termites only; Perf=Experimental tools used to perforate the exit holes of *Macrotermes* mounds; Trin=Experimental tools used to dig into the mounds of *Trinervitermes* only; Mix=Experimental tools used for more than task.

able is also important. Anisotropy measures directionality of the wear pattern striations. Both Brain and colleagues (1988) and Backwell and d'Errico (2001; d'Errico and Backwell 2009) identified directionality as a key to identifying task. Brain and colleagues suggested that longitudinal scratches were a result of continual plunging into the

TABLE 5. Asfc PAIRWISE COMPARISONS OF THE EXPERIMENTAL TOOLS ONLY (zoomed in view of Table 4). Dig Macro Perf Trin Mix Dig Macro Perf Trin Mix Mix Image: Im

TABLE 4. Asfc PAIRWISE COMPARISONS OF ALL THE BONE TOOLS IN THE STUDY.





The Brain et al. sample and the randomly generated Swartkrans sample 8 are significantly different at the .05 level from other Swartkrans samples using Fisher's LSD analysis (blue highlighted boxes).

ground and the transverse scratches were from ripping past sharp stones while digging open the hole. Backwell and d'Errico (2001) described the wear pattern on tools used to dig into the ground for tubers or insects to have randomly oriented striations of various widths and tools used to dig into termite mounds to have striations that were finer and mostly parallel to the longitudinal axis of the bone. In their 3D study, d'Errico and Backwell (2009) noted that tools used to dig for tubers had a range of patterns depending on the user. The tools used in the original study by Brain and colleagues had more random striations than the tools they used in their experiments. In this study, the entire range of variation for digging fits within that of the Swartkrans sample.

The variable for complexity (*Asfc*) is the most informative in this study. Complexity measures how the surface roughness changes with changing scale of observation and is a variable unique to SSFA. The most prominent pattern in the study is that the significant differences in variation of *Asfc* are mostly between the Swartkrans artifacts and the experimental tools, with the experimental tools having lower complexity values (see Table 4). It is possible that these differences are due to taphonomy of the artifacts and selection of weathered fragments by the hominids versus the author's recent use of fresh bone; however, the other texture variables do not follow the same division so there is

TABLE 7. Asfc PAIRWISE COMPARISONS OF THE SWARTKRANS SAMPLESVERSUS THE EXPERIMENTAL SAMPLES (zoomed in view of Table 4).

	SK	BW	Br	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
Dig		*	*	*	*	*	*	*	*	*		*	*
Macro	*	*	*	*	*	*	*	*	*	*		*	*
Perf	*	*	*	*	*	*	*	*	*				
Dig	*	*	*			*	*		*				
Trin	*	*	*	*	*	*	*	*	*	*	*	*	*

The blue highlighted *x* boxes show significant difference at the .05 value using Fisher's LSD and the green * boxes show significant differences at the .05 level using Tukey's HSD. Experimental control samples for digging into *Trinervitermes* mounds and perforating *Macrotermes* mounds appear to be the most like the Swartkrans sample in texture complexity.

Sample	Statistic	n	Complexity	Scale of max complexity	Anisotropy	Heterogeneity 9x9	Texture fill volume
Swartkrans	Mean	38	57.02	15.95	.0033	.3713	1.7E6
	Minimum		19.96	14.99	.0005	.19	1.3E6
	Maximum		108.38	26.68	.0111	.66	2.3E6
	Std. Dev.		19.95	3.18	.0019	.0945	2.8E5
Experimental	Mean	41	32.12	14.84	.0033	.3666	1.6E6
	Minimum		12.91	6.66	.0003	.16	1.3E6
	Maximum		57.71	15.37	.0064	1.13	2.3E6
	Std. Dev.		13.45	1.31	.0016	.15	2.1E5

TABLE 8. DESCRIPTIVE STATISTICS FOR ALL VARIABLES IN THE SWARTKRANS ASSEMBLAGEAND THE ENTIRE SAMPLE.

no other support for taphonomic differences. *Asfc* was used to test the hypotheses of this study.

The null hypothesis of this study states that conclusions about function of the bone tool artifacts cannot be made if different experimental tasks do not leave distinct signatures. The pairwise comparisons of the *Asfc* of experimental tools show that the control groups are not significantly different from each other, suggesting that task cannot be identified by the texture of the use wear pattern (see Table 5). This result fails to reject the null hypothesis, making further investigation into the use of the Swartkrans tools difficult. Nevertheless, despite the lack of difference between tasks, certain groups are better matches for the Swartkrans assemblage.

In order to test the hypotheses of which specific task was conducted with the Swartkrans tools, focus must shift

Asfc	Sample	n	Mean	Minimum	Maximum	Std. Dev.
Experimental	ALL	41	32.12	12.91	57.71	13.45
	Dig	7	32.53	17.53	48.77	11.60
	Macro	6	30.11	12.91	56.25	16.49
	Perf	4	36.17	25.25	53.72	12.90
	Trin	6	38.71	14.15	55.80	17.39
	Mix	18	29.52	15.16	57.71	12.33
Swartkrans	ALL	38	57.02	19.96	108.38	19.95
	BW	13	56.61	19.96	95.35	21.12
	Br	11	65.56	45.43	86.08	12.51
	R 1	13	53.96	20.56	80.18	19.17
	R2	12	52.86	20.56	74.35	15.55
	R3	11	59.58	20.56	108.38	26.83
	R4	12	59.96	38.61	86.08	15.11
	R5	13	53.72	32.80	80.18	14.98
	R6	11	62.26	43.46	108.38	18.66
	R 7	13	54.14	29.51	108.38	23.40
	R 8	10	47.97	19.96	95.35	24.81
	R9	13	54.84	19.96	108.38	22.44
	R10	12	55.51	32.80	108.38	24.15

TABLE 9. COMPLEXITY (Asfc) DESCRIPTIVE STATISTICS FOR THE SAMPLESUSED IN THIS STUDY.

to the pairwise comparisons that were not significantly different. It is important to note that the Fisher's LSD test is not as strong as the Tukey's HSD test; therefore, significant difference using the Tukey's test will most strongly rule out a match. Also notable is that the table of *Asfc* descriptive statistics (see Table 9) is the raw data, not the ranked data. Ranking the data allows for parametric tests to be conducted on the nonparametric data (Conover and Iman 1981); the significant differences are in regards to the ranked data. The differences may not be as apparent when looking at the non-ranked data in the table of descriptive statistics. These descriptive statistics show range and standard deviation of the values but do not address the distribution over the sample like the ranked data.

The pairwise comparisons of Swartkrans artifacts to experimental tools that do not show significant differences include tools used to dig into *Trinervitermes* mounds and tools used to perforate *Macrotermes* mounds. Both of these tasks are significantly different from the "Backwell" and the "Brain" sample, but resemble other random samples generated from the Swartkrans assemblage. Therefore, this study shows the most support for the interpretation of termite foraging with the Swartkrans bone tools but is unable to determine which genus of termites the hominids were foraging for.

The next hypothesis states that the differences in results from previous bone tool studies could be from sampling bias. The Swartkrans bone tools assemblage consists of 84 artifacts and the studies done previously looked at no more than 15 of these tools. Results here show that when random samples of 10 to 13 artifacts were generated from the Swartkrans sample, it was possible to find samples that have significant differences in variation (see Table 6). This result suggests that there is potential for sampling bias. The Backwell and d'Errico sample appears to be representative of the Swarkrans assemblage, but the Brain and colleagues sample was significantly different in *Asfc* from three other Swartkrans samples. The randomly generated Sample 8 shows similar differences from the rest of the assemblage, including being significantly different from the sample used by Brain and colleagues. This result also shows support for the hypothesis that there were multiple tasks being conducted within the Swartkrans assemblage. However, the tools in the "Mix" row are tools that were used for two tasks and are the least likely match for the Swartkrans tools. From these results, it appears that while more than one task was likely for the Swartkrans hominids it was not with the same tool.

TERMITES IN THE SWARTKRANS HOMINID DIET

The evidence for termite foraging is stronger than tuberdigging in this study and is equally strong for termites of the genus *Trinervitermes* and the genus *Macrotermes*. If it was possible to determine which genus of termites the hominids were consuming, our understanding of carbon isotope analyses would greatly improve.

Isotope studies have shown that hominids consume

significant amount of foods with C_4 pathways, which are attributed to grassy resources (Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005; Van der Merwe et al. 2003). One explanation for this carbon signature could be that the hominids were eating significant quantities of grassharvesting termites such as *Trinervitermes*. However, if the hominids were eating wood-foraging termites such as *Macrotermes*, the C_4 signature must be coming from other food items. Sponheimer and colleagues (2006) analyzed the carbon signature of hair samples taken from the Fongoli savanna chimpanzees in southeastern Senegal. These chimpanzees are interesting in regards to hominid evolution because they live in an environment similar to what is reconstructed for Plio-Pleistocene hominids, and therefore have similar resources available to them.

The Sponheimer and colleagues (2006) study compared the chimpanzee carbon isotope signature to that obtained from hominid fossils in previous studies. The hypothesis tested was that the C_3/C_4 ratio would be similar between the two since the habitats are similar. The carbon isotope signature for the chimpanzees, however, did not show a significant quantity of C₄ even though grassy resources are widely available. Therefore, hominid diet must be markedly different from the diet of chimpanzees, whether in rainforest or the savanna. It is possible that hominids would have chosen *Trinervitermes* over the chimpanzee-preferred Macrotermes, but based on the ill-tasting chemical defenses of *Trinervitermes*, it seems more likely that the hominids were exploiting an entirely different C₄ resource. Chemical analyses are now suggesting that robust australopithecines in East Africa had a predominantly C₄ diet (Cerling et al 2011). Further research needs to investigate grasses and sedges that could serve as the staple of the Paranthropus boisei diet. The South African counterparts to these resources, not termites, are the most probable candidates for explaining the C_3/C_4 ratio present in the Swartkrans hominids.

CONCLUSIONS

Texture analysis has been shown to identify differences in diet based on dental microwear, but in this study, the null hypothesis, which stated that tasks would not produce different wear patterns on the ends of bone tools, was not rejected. D'Errico and Backwell's (2009) optical interferometry may be a better tool for analyzing wear patterns, but the conclusion here is that use wear analysis should be done with caution and null hypotheses should always be tested first.

Even without the rejection of the null hypothesis, the comparisons between the Swartkrans bone tools and experimental bone tools provide some insight into how the hominids may have used the tools. The results here do not eliminate the possibility of digging into the ground, but provide additional support for termite foraging being the predominant task. Although the genus of termites cannot be determined because the termite foraging evidence is equally strong for digging for *Trinervitermes* and perforating for *Macrotermes*, this study brings emphasis on the genus *Macrotermes* for the first time. Because chimpanzees

prefer these termites to any other genus, including *Trinervitermes*, their palatability and obtainability should be considered when hypothesizing over termite resources, and further studies should not overlook their possible role in the hominid diet.

ACKNOWLEDGEMENTS

Funding for this work was provided by the University of Michigan Department of Anthropology, the University of Michigan Rackham Graduate School, and the Transvaal Museum, Pretoria, South Africa. For access to materials and overall generosity, I would like to thank Francis Thackeray, Jill Pruetz, Peter Ungar, Crickette Sanz, and Bill Sanders. Additional thanks go out to Milford Wolpoff and Kristin Krueger for their support and guidance.

REFERENCES

- Backwell, L. and d'Errico, F. 2001. Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences USA* 98(4), 1358–1363.
- Backwell, L. and d'Errico, F. 2003. Additional evidence on the early hominid bone tools from Swartkrans with reference to spatial distribution of lithic and organic artefacts. *South African Journal of Science* 99 (5/6), 259–267.
- Backwell, L. and d'Errico, F. 2008. Early hominid bone tools from Drimolen. *Journal of Archaeological Science* 35, 2880–2894.
- Beynon, A.D. 1987. Replication techniques for studying microstructure in fossil enamel. *Scanning Microscopy* 1, 663–669.
- Bogart, S.L. and Pruetz, J.D. 2008. Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology* 70, 605–612.
- Brain, C.K., Churcher, C.C.S., Clark, J.D., Grine, F.E., Shipman, P., Susman, R.L., Turner, A., and Watson, V. 1988. New evidence of early hominids, their culture, and environmefnt from the Swartkrans cave. *South Africa Journal of Science* 84, 828–835.
- Brain, C.K. (ed). 1993. Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph, Pretoria, South Africa.
- Cerling T., Mbua E., Kirera F., Manthi F., Grine F.E., Leakey M., Sponheimer M., and Uno K. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences USA* 108, 9337–9341.
- Conover, W.J. and Iman, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* 35, 124–129.
- Cook, R.J. and Farewell, V.T. 1996. Multiplicity considerations in the design and analysis of clinical trials. *Journal of the Royal Statistical Society* Series A 159, 93–110.
- Dart, R.A. 1949. The predatory implemental technique of the australopithecines. *American Journal of Physical Anthropology* 7, 1–16.

Dart, R.A. 1957. The Osteodontokeratic Culture of Australo-

pithecus Prometheus. Transvaal Museum memoir, No. 10, Pretoria, South Africa.

- d'Errico, F. and Backwell, L. 2009. Assessing the function of early hominin bone tools. *Journal of Archaeological Sci*ence 36, 1764–1773.
- Goodall, J. 1963. Feeding behaviour of wild chimpanzees, a preliminary report. *Symposium of the Zoological Society* of London 10, 39–48.
- Grine, F.E. 1981. Trophic differences between 'gracile' and 'robust' australopithecines: a scanning electron microscope analysis of occlusal events. *South Africa Journal of Science* 77, 203–230.
- Leakey, M.D. 1970. Stone artefacts from Swartkrans. *Nature* 225, 1222–1225.
- Lesnik, J.J. and Thackeray, J.F. 2007. The efficiency of stone and bone tools for opening termite mounds: Implications for hominid tool use at Swartkrans. *South Africa Journal of Science* 103(9/10), 354–358.
- Ohiagu, C.E. and Wood, T.G. 1976. A method for measuring rate of grass-harvesting by *Trinervitermes geminatus* (Wasmann) (Isoptera, Nasutitermitinae) and observation on its foraging behaviour in Southern Guinea savanna, Nigeria. *The Journal of Applied Ecology* 13(3), 705–713.
- Prestwich, G.D. 1984. Defense mechanisms of termites. *Annual Review of Entomology* 29, 201–232.
- Pruetz, J.D, 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. *Primates* 48, 316–319.
- Robinson J.T. 1954. The genera and species of the Australopithecine. *American Journal of Physical Anthropology* 12,181–200.
- Robinson, J.T. 1959. A bone implement from Sterkfontein. *Nature* 184, 583–585.
- Sanz C., Morgan D., and Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist* 154, 567–581.
- Scott R.S., Ungar P.S., Bergstrom T.S., Brown C.A., Grine F.E., Teaford M.F., and Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695.
- Scott R.S., Ungar P.S., Bergstrom T.S., Brown C.A., Childs B.E., Teaford M.F., and Walker A. 2006. Dental microwear texture analysis: technical considerations. *Journal of Human Evolution* 51(4), 339–349.
- Sponheimer M. and Lee-Thorp J.A. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus. Science* 283, 368–370.
- Sponheimer M., Lee-Thorp J.A., de Ruiter D., Codron D., Codron J., Baugh A.T., and Thackeray J.F. 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. *Journal of Human Evolution* 48, 301–312.
- Sponheimer M., Loudon J.E., Codron D., Howells M.E., Pruetz J.D., Codron J., de Ruiter D., and Lee-Thorp J.A. 2006. Do "savanna" chimpanzees consume C₄ resources? *Journal of Human Evolution* 51, 128–133.

Van der Merwe N.J., Thackeray J.F., Lee-Thorp J.A., Luyt, J. 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *Journal* of Human Evolution 44, 581–597.

Van Ryneveld K. 2003. *Bone tools from the early hominid sites, Gauteng; an experimental approach*. M.S. thesis, University of the Witwatersrand, Johannesburg.

Ungar P.S., Brown C.A., Bergstrom T.S., and Walker A.

2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning* 25, 185–193.

- Washburn, S.L. 1957. Australopithecines: The hunters of the hunted? *American Anthropologist* 59(4), 612–614.
- Wood B. and Strait D. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution* 46, 119–162.