

Tools and Termites:
Implications for the Foraging Behavior of the Swartkrans Hominids

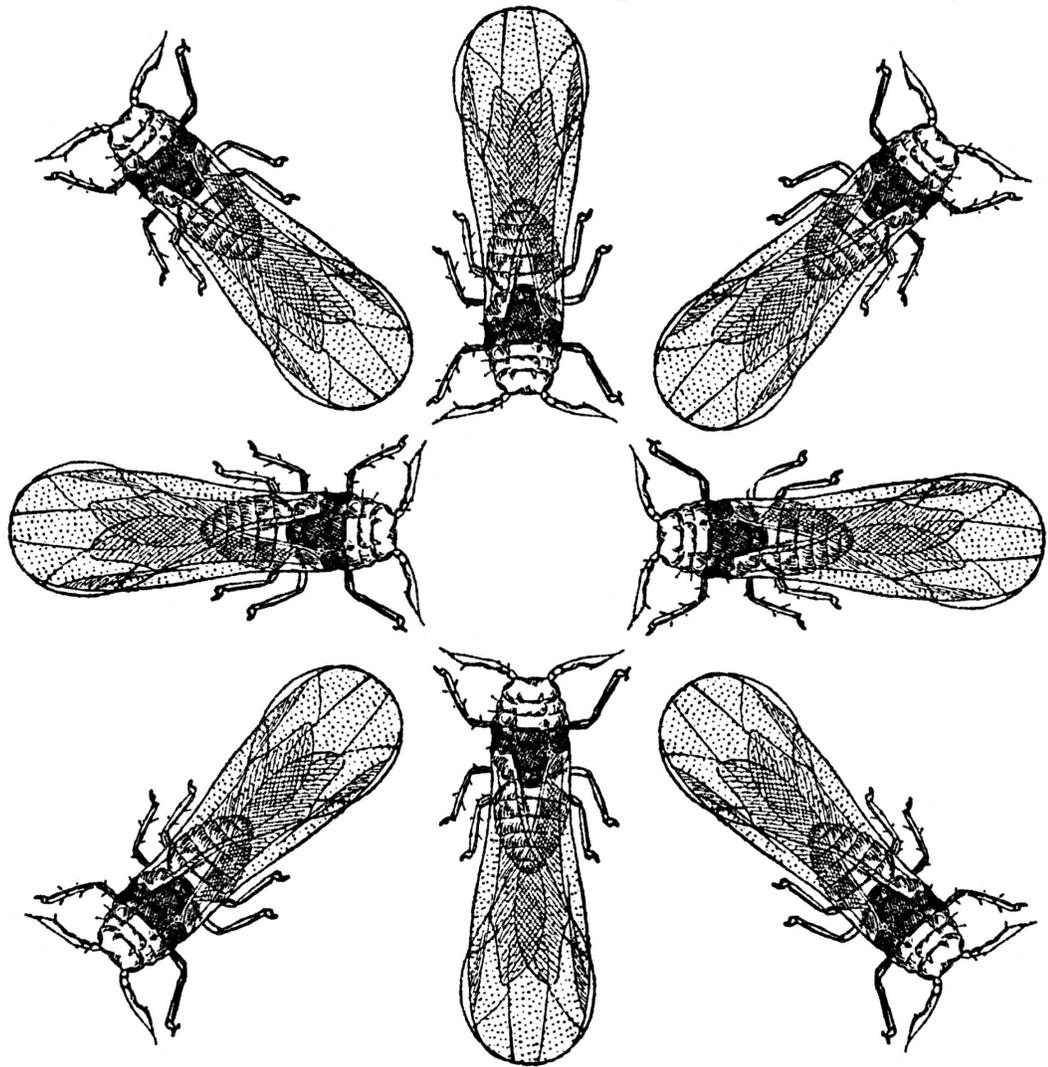
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For Mom

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ABSTRACT

Termites have recently become a subject of interest for paleoanthropologists. In 2001, Backwell and d’Errico reported evidence of termite foraging by the Swartkrans hominids as seen in the wear patterns on bone tools from the site. This conclusion has been credited by some to be a plausible explanation for unexpected carbon isotope signatures present in South African hominid teeth that suggest the diet was different from that of extant non-human great apes, consisting of a significant amount of resources not from woody plants. Grass-eating termites such as the genus *Trinervitermes* are one potential resource that could contribute to the carbon signature. However, not all termites forage for grass, and in fact, *Macrotermes*, the termites most widely consumed by chimpanzees and by many present-day human populations, almost exclusively forage on the remains of woody plants and therefore would not contribute to the signature. This dissertation focuses on *how* the bone tools were being used in order to address which termites were being consumed and their nutritional role in the hominid diet. One possibility is that they were used in a manner similar to “perforating,” a complex action utilized by the chimpanzees of the Goualougo Triangle, Republic of Congo, to use a stick to reopen the exit/entry holes created by termites on their mounds. After analyzing observations of this action, the task was recreated with experimental bone tools and the wear patterns compared to those on the ends of the Swartkrans bone tools. Digging into *Trinervitermes* mounds was also investigated. The wear pattern analyses were

inconclusive, and the best support for which termites would have been consumed comes from behavioral and ethnographic data. Termites of the genus *Macrotermes* may be the most likely resource for Plio-Pleistocene hominids since they are highly selected by both chimpanzees and humans. These termites would not contribute to the surprising carbon isotope signature, but if both the soldiers and alates were being consumed, they would provide a reliable source of protein and fat, which are valuable for larger brained hominids navigating the South African savanna.

Chapter 1

Introduction

The Swartkrans cave, part of the Cradle of Humankind World Heritage Site, is located in the Gauteng province of South Africa, 10 km North-Northwest of Krugersdorp. Formal exploration of the cave began in 1948 by Robert Broom and John Robinson and extensive excavations have continued since. Specimens attributed to *Australopithecus (Paranthropus) robustus* as well as to the genus *Homo* are present in each of the main deposits at the site and tools made of both stone and bone are found in the deposits with both taxa (Brain 2004). The stone tools are similar to contemporaneous Oldowan tools in East Africa but the bone tools are unique to this region of southern Africa (Leakey 1970; Backwell and d'Errico 2005).

Bone tools have been recovered from three sites in the Cradle of Humankind: Swartkrans, Sterkfontein, and Drimolen. Bone tools from all three of these sites share the same elongated shaft fragment shape with a highly worn and polished working end (Backwell and d'Errico 2008). Original assessment of the function of the Swartkrans bone tools by Brain and colleagues (1988) was that of digging implements used to dig for underground storage organs of plants such as *Hypoxis*. 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 and measured magnified striations on the

working ends of the tools. After analyzing experimental tools used to dig into a wide range of soils, scrape and piece animal hides, and break into termite mounds, the authors found that the signature left on bone tools after breaking into termite mounds most closely resembled the Swartkrans bone tools when analyzed with a transmitted light microscope. In 2009, d'Errico and Backwell compared the bone tool assemblage recovered from Drimolen to the one they studied at Swartkrans, this time using three-dimensional optical interferometry. The authors concluded that termite foraging was still the most likely task for the artifacts, but that digging into the soil for tubers cannot entirely be ruled out.

This dissertation is a collection of three papers, each with the purpose of contributing to answering *how* the Swartkrans bone tools were being used by the hominids. Given the evidence discussed above, using the bone tools to forage for termites is a well-supported hypothesis. However, termites are incredibly diverse and abundant, consisting of five living families with over 280 genera and 2,700 species (Abe *et al* 2000); which ones would have been an appealing food resource for the hominids? Backwell and d'Errico chose to conduct their experiments on termite mounds belonging to the genus *Trinervitermes*. However, there are numerous other genera likely available in Plio-Pleistocene Southern Africa, including termites of the genus *Macrotermes*, the genus most commonly preyed upon by chimpanzees and also regularly consumed by many populations of people living in Africa today (Collins and McGrew 1985; Illgner and Nel 2000; Bogart and Pruett 2008). The first paper, presented here in Chapter 2, reviews the availability and nutritional value of different African termite species. The role of termites as a food resource for hominids is dependent on the species, and even the

caste, of termites they would have selected. Chapter 2 constructs a model for hominid termite consumption that can be applied to better understanding hominid diet as a whole.

Using tools to forage for termites is not unique to the human lineage.

Chimpanzees are expert termite foragers, known to use a grass blade to “fish” termites out of their mounds (Goodall 1963). Certain populations of chimpanzees even use tool “kits” that involve using multiple tools; first using a stout stick to perforate the exit/entry holes created by termites on their mounds to aid in the threading of the second fishing tool into the passageway (Sanz *et al* 2004). These stout sticks provide a potential analogy for the Swartkrans bone tools. The second paper of this dissertation, presented in Chapter 3, analyzes the perforation behavior of the Goualougo chimpanzees of the Republic of Congo. Perforation is a more complex task than has been previously reported.

Chimpanzee hands that are specialized for knuckle walking inhibit some manipulative behaviors, but they are still capable of achieving the balance of power and precision that is required to use a stick to reopen the holes on the termite mound. Details of a previously undescribed grip are presented in this chapter. Some chimpanzees at Goualougo utilize a grip intermediate to the classic categorizations of power and precision, here named a “thumb-pocket grip” (Napier 1960). In a thumb-pocket grip, the perforating stick rests on the webbing between the thumb and first finger. The shaft of the tool extends across the palm and the working end of the tool exits the hand between two of the fingers, usually at the flexed intermediate phalanges. Chimpanzees are often seen switching between powerful and precise grips while perforating, but utilization of the thumb-pocket grip appears to eliminate the need for that switch.

Neuromotor control and problem solving cognitive abilities have become highly refined in humans, but tool-use by the great apes, especially the spectacular tool repertoire of the Goualougo chimpanzees, suggests that these skills evolved in the distant past. These behaviors would therefore be within the capabilities of the Plio-Pleistocene hominids, and perforation of termite passageways with bone tools is a plausible function for the Swartkrans bone tools.

The use-wear on the Swartkrans bone tools provides the only direct evidence of the function of the tools for Plio-Pleistocene hominids. Technology for microscopic exploration has advanced greatly in the field of biological anthropology with the development of texture analysis for dental microwear studies (Scott *et al* 2005). Analyzing the Swartkrans bone tools with the combination of confocal microscopy and scale-sensitive fractal analysis may provide clues relating to what type of termite mounds the hominids were breaking in to, such as the low, rounded mounds of *Trinervitermes* or the large, massive mounds of *Macrotermes*, given that the structure of the mounds produce different wear patterns on experimental tools. Different action of the tool could potentially leave a different signature as well, and perforating the holes versus digging holes into the side of the mound can also be investigated. The third paper of this dissertation, presented in Chapter 4, analyzes the texture on the working ends of the Swartkrans bone tools and compares it to the texture present on the ends of experimental tools used to dig into the ground, dig into *Trinervitermes* mounds, dig into *Macrotermes* mounds, perforate exit holes of *Macrotermes* mounds, as well as a combination of these tasks.

Understanding exactly how the bone tools were used is an important step in understanding the diet of the Swartkrans hominids. Recent carbon isotope analyses have suggested that hominids were consuming more foods from resources other than woody plants (Lee-Thorp *et al* 1994; Sponheimer and Lee-Thorp 1999; Van der Merwe NJ 2003). These resources could potentially be grasses or sedges, but also fauna that had consumed grasses or sedges. For instance, consuming grass-eating termites would be one plausible explanation for the reported carbon isotope signatures. However, not all termites forage for grass. The combined three papers presented here investigate the role different termite species could have played in the hominid diet. Chimpanzees show a strong selectivity towards termites of the genus *Macrotermes*, which are not specialized grass-foragers and instead consume a wide range of plant materials including high proportions from woody plants. Plio-Pleistocene hominids may have been following a similar pattern, but also could have been foraging for an array of other available termite genera including the grass-foraging *Trinervitermes*. The conclusion of this dissertation will provide a model of hominid termite consumption that can be applied to future investigations of the evolution of the human diet.

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Chapter 2

Termites as a food resource for Plio-Pleistocene South African hominids

ABSTRACT

Termites have recently become a subject of interest for paleoanthropologists. In 2001, Backwell and d'Errico reported evidence of termite foraging by Swartkrans hominids as seen in the wear patterns on bone tools from the site. This conclusion has been credited by some to be the explanation for the unexpected carbon isotope signatures present in South African hominid teeth that suggest the diet was different from that of extant non-human great apes, consisting of a significant amount of resources that are not from woody-plants. Grass-eating termites are one potential resource that could contribute to the carbon signature. However, not all termites eat grasses, and in fact, the termites that are most widely consumed by chimpanzees and by many present-day human populations at best have a mixed diet that includes a small amount of grasses. Here I review the ecology of termites and how it affects their desirability as a food resource for hominids. Termites are very diverse, even within species, and this variability affects their carbon signatures and nutritional value, invalidating broad statements regarding the contribution of termites to the hominid diet. It is suggested here that both soldiers and alates of the genus *Macrotermes* be used to model the insectivory component of the Plio-Pleistocene diet. These termites would not contribute to the

unexpected carbon isotope signature, but are of interest since they offer significant amounts of energy-yielding nutrients, providing a potentially critical savanna resource for supporting larger-brained hominids.

INTRODUCTION

In the last decade, there has been much advancement in research related to reconstructing the hominid diet. Dental topography and texture analysis of dental microwear have shown that there are significant differences between the gracile and robust australopithecines in South Africa, but that these differences are likely related more to the fallback foods each species chose when their preferred resources were unavailable. *Australopithecus (Paranthropus) robustus* was better adapted to crush hard, brittle foods, while *Australopithecus africanus* likely relied on tougher foods that required shearing and slicing (Scott *et al* 2005; Ungar *et al* 2007). More remarkable, though, is carbon isotope research that suggests (1) the diets of the two species were more similar than previously thought and (2) the hominids were expanding their diets from the presumed ancestral condition to include more savanna resources (Lee-Thorp *et al* 1994; Sponheimer and Lee-Thorp 1999; Van der Merwe *et al* 2003).

The latter conclusion is related to the proportion of C₃ versus C₄ resources consumed by the hominids as evidenced by the atomic mass of ¹²C and ¹³C isotopes. C₄ photosynthetic pathway plants are adapted to environments with high temperatures and large amounts of sunlight and do not discriminate strongly against the heavier isotope ¹³C. Grasses and other savanna plants, such as sedges, commonly utilize the C₄ pathway. The diets of South African hominids consisted of about 35-40% C₄ resources

(Sponheimer *et al* 2005; Sponheimer *et al* 2006). It has been widely discussed as to what resources these hominids were utilizing. Consuming grasses, sedges, or animals that ate these foods would contribute to this signature. Peters and Vogel (2005) suggested that omnivorous hominids could utilize many different resources on the savanna ranging from ungulates to birds and reptiles, to invertebrates such as termites.

If termites were to be credited with contributing to the unexpected C₄ signature in hominids, then termites should have a high ¹³C to ¹²C ratio. However, Sponheimer and colleagues (2005) found that the different termites they collected in South Africa's Kruger National Park had a highly variable carbon isotope signature ranging from pure C₃ to pure C₄, with most having a mixed signal. As will be demonstrated below, termites are highly variable by species and caste. Different termite species have different diets, from soil, to grass, to wood. Additionally, within-species variation can also be high. Different castes within a species store nutrients differently. Understanding this broad range of termite variation is the first requirement in understanding which termite species would be the most desirable as a hominid food resource and what nutritional value they would have provided.

Recent carbon isotope data for East African hominids suggest reinterpretation of the South African chemical signatures. Previous microwear and isotope data have alluded to the possibility that the robust australopithecines in East Africa had a different diet than South African robusts, but the sample sizes were small and the results questioned (Ungar *et al* 2008; van der Merwe *et al* 2008). Cerling *et al* (2011) published the isotope analysis of 22 *Australopithecus (Paranthropus) boisei* specimens and found that their diets were dominated by C₄ resources. This signature, which strongly differs

from that of their South African counterparts, suggests that these hominids could have been specialized sedge foragers, utilizing tools to acquire a little-exploited underground resource. However, the authors note that there are no known large-bodied sedge specialists and the nutritional value of sedges may be dubious without cooking. Grasses are widely available on the savanna, and despite the competition with other grazers as noted by Peters and Vogel (2005), grasses may be the simplest suggestion for a primary food resource for the East African robust australopithecines.

The existence of a hominid species with a predominantly C₄ diet suggests that the diet of their counterparts in South Africa does not need to be explained by feeding on marginal resources such as birds, lizards, and insects; however, it does now leave the degree of omnivory present in the South African hominids more uncertain as it cannot be determined by carbon isotopes alone. Termites may play a critical role as a resource for hominids since we know that they are a highly sought after prey for many animals, including great apes and humans. Their potential role in the hominid diet is best understood by investigating the desirability, availability and nutritional value of different termite species to their modern day ape predators.

TERMITES

Termites are distributed worldwide, with greatest biomass and diversity in tropical forests (Abe *et al* 2000). Termites coevolved with intestinal ecosystems that allow them to feed on cellulose-dense plant material. In the primitive condition, still present and characteristic of the “lower termites,” wood-feeding flagellates inhabit the intestines. The loss of the symbiosis with these protists marks the evolution of “higher

termites,” or the family Termitidae, which adapted to a wider range of diets as evidenced by the explosive diversity in this family. The higher termite gut remains a source of microbial diversity, and these intestinal bacteria still aid the termites in the breaking down of cellulase and lignin to fulfill the important role of detritivores in the food chain (Breznak and Brune 1994).

Termites are incredibly diverse and abundant, consisting of five living families with over 280 genera and 2,700 species. Most of this diversity is attributable to higher termites, comprising more genera and species than the other termite families combined (~236 g., ~1,958 sp.) There are four subfamilies in Termitidae: Apicotermitinae, Nasutitermitinae, Termitinae, and Macrotermitinae (da Cunha 2000). Abe *et al* (2000) characterize the subfamilies as follows: Apicotermitinae is an enigmatic termite group of soldierless soil feeders. They can make up 30-40% of the entire fauna in tropical forests, but many genera and species remain undescribed. Nasutitermitinae is the largest, most diverse, and most speciose of all termite clades. The subfamily includes genera in all feeding groups and is commonly divided into the soil feeders (*Subulitermes*-branch) and the non-soil feeders (*Nasutitermes*-branch). Non-soil foods include a large variety of living and dead plant material. The subfamily Termitinae is also commonly broken down into two groups, the *Cubitermes*-group, which is an endemic African soil-feeding clade, and the *Termes*-group, which comprises soil-wood interface feeders as well as soil-feeding termites. Finally, Macrotermitinae are the fungus-farming termites that feed on a wide range of dead and living plant material that is processed first by fungus growing within their nests.

Eusocial behavior is another phenomenon of termites. Pheromone trails are used to communicate within the nest and to keep separate foraging areas between different populations (Kaib 1982). The social network is broken down into a caste system that includes one queen and generally one king who reproduces and takes care of the young, soldiers who protect the colony and workers who care for the eggs while they incubate. Young termites undergo one of two developmental pathways: the nymphal line (winged reproductives) and the apterous line (non-winged workers and soldiers). Upon nymphal maturity to alates, the winged sexuals will swarm and begin to establish new colonies. Swarming patterns normally follow rainfall patterns, but can become disconnected in the event of irregular rains. Development of the last nymphal stage is held back until the first rain of the season; if the conditions are not right for leaving the mound and settling a new colony, the winged individuals can wait within the nest for months (Abe *et al* 2000).

The collective biomass within the mound can be impressive, reaching numbers up to 2,000,000 and mass of 20 kg (McGrew 1979). These large numbers make termites a desirable food source for predators, and termites have evolved an array of morphological, chemical, and behavioral defense mechanisms. Despite these mechanisms, many animals still regularly feed on termites, such as chimpanzees who often use tools to bypass the defenses.

MACROTERMES AND CHIMPANZEES SELECTIVITY

Chimpanzees are very choosy when it comes to their termite prey. Of the 664 genera of termites present in Afrotropical habitats, only the consumption of only eight genera has been recorded, with the genus *Macrotermes* being markedly the most common (Abe *et al*

2000). A list of species of termites consumed by chimpanzees is presented in Table 2.1. Chimpanzees primarily feed on termites from the genus *Macrotermes*, often choosing them over more abundant termite species in the area. Collins and McGrew (1985) describe chimpanzees of the Mahale B Group's (Tanzania) preference for *Macrotermes* over the widely available *Odontotermes* as due to longer swarming periods, larger soldiers, and numerous and easy to find exit holes (Collins and McGrew 1985). However, rehabilitated chimpanzees released on Rubondo Island, Tanzania, are known to include *Odontotermes* in their diets (Moscovice *et al* 2007). In fact, most of the genera of termites consumed in rescue reserves are not the same as those selected by natively wild chimpanzee groups. At Rubondo Island, chimpanzees eat *Microtermes* as well as *Odontotermes*. These genera are still in the Macrotermitinae subfamily unlike at Ipassa where the genera include *Microcerotermes* and *Proculitermes* from Termitinae and *Nasutitermes* from Nasutitermitinae, even though *Macrotermes muelleri* are widely available (Hladik 1973; Moscovice *et al* 2007). Other genera of termites regularly consumed by chimpanzees are *Pseudacanthotermes*, also of the Macrotermitinae subfamily, and *Cubitermes* from Termitinae.

Table 2.1

Species	Sites	Reference
Macrotermes subhyalinus	Fongoli, Senegal	Bogart and Pruetz, 2008
	Gombe, Tanzania	Collins and McGrew, 1987
	Tai, Cote d'Ivoire	Boesch and Boesch, 1990
	Mt. Assarik, Senegal	McBeath and McGrew, 1982
Macrotermes bellicosus	Fongoli, Senegal	Bogart and Pruetz, 2008
	Gombe, Tanzania	McGrew, 1992
	Bossou, Guinea	Sugiyama and Koman, 1897
Macrotermes muelleri	Ndoki, Congo	Suszuki, Koroda, and Nishihara, 1995
	Dja, Cameroon	Deblauwe and Janssens, 2008
	Okorobiko, Guinea	McGrew, Tutin, and Baldwin, 1979
Macrotermes nobilis	Goulougo, Congo	Sanz, Morgan, and Gulick, 2004
	Belinga, Gabon	McGrew and Rogers, 1983
	Dja, Cameroon	Deblauwe and Janssens, 2008
Macrotermes lilljeborgi	Dja, Cameroon	Deblauwe and Janssens, 2008
	Okorobiko, Guinea	McGrew, Tutin, and Baldwin, 1979
Macrotermes herus	Mahale B, Tanzania	McGrew and Collins, 1985
Macrotermes renouxi	Dja, Cameroon	Deblauwe and Janssens, 2008
Psuedacanthotermes spiniger	Mahale K, Tanzania	Nishida and Uehara, 1980
Pseudacanthotermes millitaris	Mahale K, Tanzania	Uehara, 1982
	Gombe, Tanzania	Goodall, 1968
Cubitermes spp	Budongo, Uganda	Newton-Fisher, 1999
Microcerotermes spp	Ipasa, Gabon	Hladik, 1973
Nasutitermes spp	Ipasa, Gabon	Hladik, 1973
Procubitermes spp	Ipasa, Gabon	Hladik, 1973
Microtermes spp	Rubondo Island, Tanzania	Moscovice <i>et al</i> , 2007
Odontotermes spp	Rubondo Island, Tanzania	Moscovice <i>et al</i> , 2007

Table 2.1. Species of termites consumed by chimpanzees. This list is not exhaustive of all the sites where chimpanzees consume termites. Only sites with *Macrotermes* identified to the species level are included as well as sites with consumption of termites that belong to other genera.

Mound structure is one factor affecting chimpanzee choice of termite prey. The basic architecture of *Macrotermes* mounds is a conical mound with a ventilation shafts down the center, which splits near ground level into a number of branches that trail down into the subsoil. At the surface of the conical mound are entry/exit holes that tunnel into the many inter-communicating chambers (Abe *et al* 2000). Chimpanzees breach the walls of the fort-like mounds by threading a blade of tall grass into the holes and into the chambers. *Macrotermes* soldiers defend the breach by attacking the grass with their mandibular pinchers. The nature of the soldier caste is to be dispensable. If the mound is disturbed, soldiers will leave to defend against the attack, but during this time, workers begin to repair the damage to the mound and may seal the entryways before the soldiers are able to return. This dispensability can also be seen in their mandibular pinching (Abe *et al* 2000). Soldiers will remain attached to their target, and in chimpanzee foraging, be easily removed from the mound attached to the blade of grass and consumed without much risk of being pinched.

Most of the chambers within a *Macrotermes* mound also contain fungus combs. The family Macrotermitinae is known as the fungus-farmers. These termites feed on a wide range of dead and living plant materials that are processed by their fungus symbiont on fungus combs in the nest (Abe *et al* 2000). This method requires all food to be brought back to the mound. Storage of food in the mound may correlate with a high density of termites present in the mound at a given time (Sands 1965) and may be an additional reason why termites from Macrotermitinae are the most commonly preyed upon by chimpanzees. Other foraging termites, like those of the subfamily

Nasutermitinae, do not always store their food or live in the same location as their stores (Sands 1965).

The palatability of termites is likely related to their defense mechanisms. *Macrotermes*' defense mechanism is mechanical, using their mandibular pinchers to bite/pierce their enemies. Other termite genera, however, have chemical defenses. Many species of termites have glandular devices that produce and deliver chemical weapons including irritants, contact poisons and glues (Prestwich 1984). Certain species of *Odontotermes* have hypertrophied salivary glands that contain quinines that can be used as nonspecific irritants (Prestwich 1984). Glue spitting is the defense mechanism of termites of the subfamily *Nasutermitinae*, which are also rarely consumed by chimpanzees. This viscous, sticky solution acts as a topical toxicant (Prestwich 1984).

Another factor possibly affecting palatability is the foraging behavior of the termites. Termites from the *Cubitermes*-clade of the subfamily Termitinae feed on soil. The nutritional value of soil-feeding termites is different from foraging termites, mostly related to higher mineral content due to the soil contained in their guts, and is possible that this difference also changes their palatability (Deblauwe and Janssens 2008). The overall nutritional differences amongst termites will be discussed further below.

TERMITE AVAILABILITY ON THE SOUTH AFRICAN SAVANNA

Despite the early understanding that chimpanzee termite foraging was seasonal and occurred mainly during the wet season, termites are a year-round resource (McGrew *et al* 1979; McBeath and McGrew 1982; Goodall 1986). It has now been seen at multiple chimpanzee sites such as the Ndoki Forest and Goulougo, both in Congo, Okorobiko in

Rio Muni, and Fongoli in Senegal that termites are consumed year round (McGrew *et al* 1979; Kuroda *et al* 1996; Pruetz 2006; Sanz *et al* 2007). At the savanna site of Fongoli, termites are consumed during every month of the year and are thought to be a possible compensation for the scarcity of vertebrate prey (Pruetz 2006). When all animal prey is considered, Fongoli chimpanzees eat the same amount as chimpanzees at other sites; however, they consume fewer vertebrates and more invertebrates. In regards to overall diet, the chimpanzees on the savanna do not appear to be employing drastically different subsistence strategies. The Fongoli chimpanzees consume the same amount of fruit as chimpanzees at more lushly forested sites and do not consume more pith and bark, so they are not relying on low-quality fallback foods (Pruetz 2006). At Mt. Assirik, another savanna chimpanzee site in Senegal, the diet contains a higher proportion of low-quality foods, but is still considered to resemble the diets of chimpanzees at forested sites (McGrew *et al* 1988). It appears that the chimpanzees on the savanna are most impacted by having fewer plant species in their repertoires than at other sites (McGrew *et al* 1988; Pruetz 2006).

Although which species of termites were present in Plio-Pleistocene South Africa is unknown, the presence of Termitinae in Africa goes back to the Cretaceous Period (Weesner 1960). The Southern African savanna today has the same termite genera as those at the savanna chimpanzee sites. Six species of *Macrotermes* are known from southern Africa, including *M. subhyalinus*, which are consumed by the savanna chimpanzees at Fongoli and Mt. Assarik, as well as by the chimpanzees of the Tai Forest and at Gombe (McBeath and McGrew 1982; Collins and McGrew 1987; Boesch and Boesch 1990; Uys 2002; Bogart and Pruetz 2008). Other genera that are desirable to

chimpanzees are also present in southern Africa. Both species of *Pseudacanthotermes* consumed by chimpanzees exist in southern Africa as well as 15 or more species of *Cubitermes*. Additional termite families present in Southern Africa, include Hodotermitidae, an ancient group of “lower termites” that are commonly consumed by people currently living in the region (Uys 2002; Nonaka *et al* 1996).

ETHNOGRAPHIC EXAMPLES OF TERMITE CONSUMPTION

Explorers such as Livingstone (1858) noted the consumption of termites across southern Africa with fascination. Today, insects are still widely consumed across Africa, with caterpillars and termites being the most widely eaten and marketed insect groups (DeFoliart 1999). A recent study surveying rural houses in Limpopo, South Africa, found that 93% of households consume insects including termites, grasshoppers and flying ants (Twine *et al* 2003). Johnson (2010) states that there are 61 edible species of termites reported around the world. Many ethnographic accounts of termite consumption use the local definitions and not the taxonomic species names, but Illgner and Nel (2000) list six taxa from ethnographic literature, five of which belong to the genus *Macrotermes*.

Termites are reported as an important part of the diets of people living today in the southern Lunda complex of Midwestern Zambia (Silow 1983). The “big termites,” as they are called locally, belong the genus *Macrotermes*. One method of their capture relies on the same principles used by chimpanzees; *Macrotermes* soldiers will investigate a breach of the termite mound, attack the intruder with their mandibular pinchers, and not let go. The people of Lunda dig open the ventilation shafts of the termite mound, construct a broom out of roots, grass or other available materials and drag it back and

forth inside the open mound. After the soldiers have attacked the bristles, the broom is removed and dunked into a bucket of water where the soldiers release their grip and sink to the bottom. Winged *Macrotermes* sexuals are also consumed when they can be caught during their swarming periods. It takes experience to work fast enough to catch the termites as they emerge from their holes. It is easy to scare them into a retreat and easy to let them slip through fingers. It is also important to mind the attacking soldiers who will bite and draw blood. After collection, the termites are brought back to the camp and roasted. Termites of the genus *Pseudacanthotermes* are also consumed by people in Midwestern Zambia, but only in their winged form. The taste of the *Pseudacanthotermes* is said to be the same as *Macrotermes*, but they are less desired because they are smaller in size (Silow 1983).

An ethnographic account of insectivory in a San group in the central Kalahari revealed that they categorize four groups of edible termites (Nonaka *et al* 1996). One group of termites consumed by the San is identified by its mounds, but the species is unknown. If women come across a mound while out foraging, they will dig into the mound with digging sticks, pick out the nymphs and eat them raw. If the mound yields a large quantity, the women will cease gathering plants, sit down, and eat all day. Two other groups are largely snacks for children, one group belonging to *Hodotermes mossambicus* and the other unidentified. These termites have underground nests near camp and the alates are the only ones consumed when caught by children sitting around their holes waiting for them to emerge.

The termites consumed most by the San also belong to the species *Hodotermes mossambicus* but are bigger in size and their nests are away from camp. The alates are

caught during swarming after heavy showers. If swarms appear near the camp, the women will follow the winged termites to their nests, which are otherwise undetectable underground dwellings. The holes are enlarged with digging sticks, filled with grass to prevent termites from escaping, and the swarm gathered. If only a few termites are caught, they will be eaten raw after removing the heads and wings. If many are caught, the termites are taken home and roasted in hot ash and sand. Soldier and worker termites are not collected, however, because they are less preferable due to their bitter taste (Nonaka *et al* 1996).

Deaths have been reported after the consumption of *Hodotermes* and the reported cause was eating out of season or improperly prepared termites (Fuller 1918). The Khoi of South Africa are reported to eat the nymphs before they reach their winged form, but the soldiers and workers are still ignored. The nests are dug up and the soil brought home and thrown in a bucket of water. The soil, workers and soldiers sink to the bottom while the nymphs float. The nymphs can be skimmed from the top of the water and then fried or boiled and then baked. However, illness is not uncommon when the termites are consumed without the accompaniment of other food, such as bread. It is very possible that consuming large quantities could cause someone to be severely ill (Fuller 1918). The bitter taste of soldiers and workers described by the San (Nonaka *et al* 1996) may be related to toxins present in the non-sexual castes of these lower termites.

NUTRITIONAL VALUE OF TERMITES

Bodenheimer notes in the preface to his book, *Insects as Human Food* (1951), that it is difficult to compile the information on the subject since it is so widely scattered

in “journals and books pertaining to travel, ethnology, geography, medicine, zoology, etc., etc” (pg. 5). Today we have available multiple reviews of the role of insects in the human diet, including works by DeFoliart (1990; 1999), but narrowing the focus to termites can present its own problems. Termites are incredibly speciose, so it is difficult to find the nutritional value of a select species in the literature. Discussions may be better left to the genus level. However, when multiple species within a genus have been sampled, their wide range of variation is apparent (Banjo *et al* 2006; Deblauwe and Janssens 2008). The caste of termite also affects the nutritional content, so chimpanzees who fish for *Macrotermes* soldiers are utilizing a different nutritional source than humans who harvest swarms of alates (Oyarzun *et al* 1996; Deblauwe and Janssens 2008). Different methods used by different authors can also make the values in the literature incomparable, as is seen with estimates of gross energy (Matsumoto 1976; Oyarzun *et al* 1996; Deblauwe and Janssens 2008). Additionally, some studies of termites as food for humans examine their nutritional value *as consumed* which may include being fried in oil (Oliveira *et al* 1976) and thus limits our ability to extend the information to Plio-Pleistocene hominids.

The most comprehensive study of the nutritional value of different species of termites to date is by Deblauwe and Janssens (2008) who compared the insect prey choices of chimpanzees and gorillas who reside in the same forest in Southeast Cameroon. Eight genera and twelve species were analyzed for macronutrients, minerals, and trace elements. The four species consumed most often and designated as ‘important prey’ were analyzed by caste (*Macrotermes lilljeborgi*, *Macrotermes muelleri*, *Cubitermes heghi*, *Thoracotermes macrothorax*). The numbers obtained by Deblauwe

and Janssens are discussed here along with data from two other recent studies: nutritional values of mixed castes of two *Macrotermes* species analyzed by Banjo *et al* (2006) and the nutrients of each caste within a species of *Nasutitermes* analyzed by Oyarzun *et al* (1996). Classic studies that are often referenced also appear here: Oliveira *et al* (1976) analyzed four species of insects *as consumed* in Angola, including *Macrotermes subhyalinus* alates that are fried in palm oil, and Phelps *et al* (1975) investigated the nutritive value of *Macrotermes falciger* alates when fed to white rats.

Table 2.2 shows the nutrients present in different species of termites with mixed castes. *Macrotermes* is the most represented genus with four species. Macronutrients are relatively consistent across the species of *Macrotermes*, and *Macrotermes* tend to be higher in protein than the other genera represented in the table. However, the micronutrients are more variable. The Iron (Fe) content of *M. renouxi* and *M. nobilis* (481 and 440 mg/100g, respectively) is about five times greater than the Iron content of *M. lilljeborgi* and *M. muelleri* (89 and 69 mg/100g, respectively). The inverse pattern is seen for Sodium (Na), which is high in *M. muelleri* (240 mg/100g) and *M. lilljeborgi* (117 mg/100g) and low in the *M. renouxi* (40 mg/100g) and *M. nobilis* (30 mg/100g). Yet, the pattern is not consistent because three of the *Macrotermes* species represent the highest Manganese (Mn) values (72-131 mg/100g), but *M. lilljeborgi* is quite low with only 5 mg/100g. Differences are also noticeable in the two different species of *Cubitermes*. *C. heghi* has over three times the protein as *C. gagei* (43% and 23% of dry matter, respectively). The biggest difference in micronutrients is in the Iron (Fe) content, with *C. gagei* having 950 mg/100g dry matter and *C. heghi* having 141 mg/100g.

Table 2.2

Species	%				mg/100g									Author
	DM	Ash	CP	CF	Ca	P	Mg	Na	K	Fe	Zn	Mn	Cu	
<i>Cubitermes gagei</i>	20	62	13	1	270	250	90	50	980	950	5	12	3	D
<i>Cubitermes heghi</i>	25	35	43	5	227	540	123	100	760	141	15	6	7	D
<i>Macrotermes lilljeborgi</i>	27	6	64	4	192	537	121	117	740	89	14	5	7	D
<i>Macrotermes muelleri</i>	30	7	63	5	403	350	163	240	890	69	61	72	5	D
<i>Macrotermes nobilis</i>	20	3	56	3	770	520	230	30	910	440	23	105	2	D
<i>Macrotermes renoux</i>	22	3	56	2	820	520	240	40	730	481	26	131	3	D
<i>Microtermes parvus</i>	9	5	50	5	330	550	130	50	820	299	16	8	2	D
<i>Nasutitermes lujae</i>	19	4	48	12	130	610	110	80	860	29	13	5	10	D
<i>Nasutitermes spp</i>	21	4	59	7	220	460	130	170	600	97	16	5	5	O
<i>Nasutitermes spp*</i>	32	4	58	18	270	350	143	170	520	55	16	6	3	O
<i>Noditermes indoensis</i>	28	67	18	2	170	320	100	50	840	1264	7	20	3	D
<i>Procupitermes arboricola</i>	21	62	23	3	40	360	80	70	950	624	5	3	1	D
<i>Protermes prorepens</i>	20	7	57	2	700	690	300	450	920	278	107	40	2	D
<i>Thoracotermes macrothorax</i>	25	29	45	9	60	250	70	50	600	2266	23	8	3	D
<i>Thoracotermes macrothorax*</i>	17	59	18	2	233	477	133	890	1137	2169	204	13	2	D

Table 2.2. Nutritional value of termite species with mixed-casted samples. * denotes a mixed caste number calculated by averaging values given by caste. Nutrient codes: DM = Dry Matter; CP = Crude Protein; CF = Crude Fat; Ca = Calcium; P = Phosphorous; Mg = Magnesium; Na = Sodium; K = Potassium; Fe = Iron; Zn = Zinc; Mn = Manganese; Cu = Copper. Author codes: D = Deblauwe and Janssens, 2008; O = Oyarzun *et al*, 1996.

Table 2.3.

%

mg/100g

Species	Caste	%				mg/100g										Author
		DM	Ash	CP	CF	Ca	P	Mg	Na	K	Fe	Zn	Mn	Cu		
<i>Cub. heghi</i>	Larvae	18	8	66	8	880	850	260	4410	2840	1045	1035	10	5	D	
<i>Th. macrothorax</i>	Larvae	22	3	57	21	320	500	120	1720	1050	272	404	2	2	D	
<i>Macro. bellicosus</i>	Alates	91	3	20	-	21	136	0.15	-	-	27	-	-	-	B	
<i>Macro. notalensis</i>	Alates	90	2	22	-	18	114	0.26	-	-	29	-	-	-	B	
<i>Macro. falciger</i>	Alates	-	-	21	22	-	-	-	-	-	-	-	-	-	P	
<i>Nasu. spp.</i>	Alates	41	4	49	40	240	360	150	210	370	25	18	4	2	O	
<i>Cub. heghi</i>	Soldiers	25	29	47	5	210	580	170	860	1520	2100	200	6	3	D	
<i>Macro. lilljeborgi</i>	Soldiers	29	3	68	3	430	360	150	670	1110	42	173	85	5	D	
<i>Macro. lilljeborgi*</i>	Soldiers	28	5	71	2	210	380	120	80	720	26	24	49	4	D	
<i>Macro. muelleri</i>	Soldiers	27	3	72	5	160	370	100	110	760	10	25	45	7	D	
<i>Macro. muelleri*</i>	Soldiers	28	6	67	6	330	310	130	170	890	55	42	94	4	D	
<i>Nasu. spp.</i>	Soldiers	30	4	58	11	370	290	150	60	580	100	16	12	3	O	
<i>Th. macrothorax</i>	Soldiers	26	19	58	4	130	550	140	360	960	1652	74	9	2	D	
<i>Cub. heghi</i>	Workers	31	68	15	3	140	280	110	330	1340	2962	73	11	3	D	
<i>Macro. lilljeborgi</i>	Workers	25	11	54	6	990	450	300	130	850	396	57	102	3	D	
<i>Macro. muelleri</i>	Workers	34	13	50	3	720	370	260	440	1020	142	116	76	3	D	
<i>Nasu. spp.</i>	Workers	25	5	67	2	200	400	130	240	610	39	14	3	5	O	
<i>Th. macrothorax</i>	Workers	27	64	19	3	250	380	140	590	1400	4581	135	29	3	D	

Table 2.3. Nutritional value of termites by caste. * denotes minor soldier. Nutrient codes: DM = Dry Matter; CP = Crude Protein; CF = Crude Fat; Ca = Calcium; P = Phosphorous; Mg = Magnesium; Na = Sodium; K = Potassium; Fe = Iron; Zn = Zinc; Mn = Manganese; Cu = Copper. Author codes: D = Deblauwe and Janssens, 2008; B = Banjo *et al*, 2006; P = Phelps *et al*, 1975; O = Oyarzun *et al*, 1996.

Table 2.3 shows the nutrients in different castes within termite species.

Macrotermes soldiers are the highest in protein of all the termites listed. *Nasutitermes* and *Thoracotermes* soldiers are also high in protein, but the larvae of *Cubitermes heghi* have higher protein than the other castes of that species. Fat content tends to be highest in the larvae and the alates. Workers and soldiers are more variable in fat across the species. As for the micronutrients, Iron (Fe) was generally highest in the workers, with workers and soldiers having more Iron than alates and larvae. Sodium (Na) is highest in the two samples of larvae present in the table (*Cubitermes heghi* and *Thoracotermes macrothorax*). Other micronutrients such as Manganese (Mn) and Potassium (K) did not appear affected by caste but instead by species (Manganese highest in *Macrotermes* and Potassium highest in *Cubitermes*).

Table 2.4 shows the gross energy measured for mixed-caste samples of termite species. The values presented in the table appear to sort by study and is likely due to differing methods. Both Deblauwe and Janssens (2008), and Oyarzun and colleagues (1996), followed sampling methods according to the Association of Official Analytical Chemists (1996 and 1990 volumes, respectively). However, they used different methods for calculating gross energy. The Oyarzun group used an adiabatic bomb calorimeter to determine gross energy. Deblauwe and Janssens calculated gross energy based on a formula developed for use in production animals and state that the formula underestimates the caloric value of chitin since that is not an ingredient present in production animal diets. The Matsumoto (1976) study also used bomb calorimetry and the results are much more comparable to those of Oyarzun and colleagues. Therefore

comparing the caloric value of species across studies does not yield strong results. In the Deblauwe and Janssens study, the value calculated for *Nasutitermes* was equal to or less than that calculated for the four species of *Macrotermes*. However, the *Nasutitermes* value achieved by the Oyarzun group is slightly higher than the value for *Macrotermes carbonarius* calculated by Matsumoto. We can thus expect variation in caloric value at the species level.

Table 2.4

Species	Gross Energy (kcal/g)	Author
<i>Nasutitermes spp</i>	5.87	O
<i>Thoracotermes macrothorax</i>	0.4	D
<i>Protermes prorepens</i>	1	D
<i>Procubitermes arboricola</i>	0.5	D
<i>Noditermes indoensis</i>	0.5	D
<i>Nasutitermes lujae?</i>	1	D
<i>Miicrocerotermes parvus</i>	1	D
<i>Macrotermes nobilis</i>	1	D
<i>Macrotermes muelleri</i>	1.5	D
<i>Macrotermes lilljeborgi</i>	1.4	D
<i>Macrotermes renouxi</i>	1.1	D
<i>Cubitermes heghi</i>	0.9	D
<i>Cubitermes gagei?</i>	0.4	D
<i>Macrotermes carbonarius</i>	5.75	M
<i>Homallotermes foraminifer</i>	5.8	M

Table 2.4. Gross energy of different termite species calculated by different authors. Author codes: D = Deblauwe and Janssens, 2008; O = Oyarzun *et al*, 1996; M = Matsumoto, 1976.

Termites may also be a source for specific fatty acids. Table 2.5 shows the fatty acid contents of termites obtained from the literature. Termites have been found to synthesize linoleic acid (Mauldin 1982; Stanley-Samuelson *et al* 1982). However,

Macrotermes spp. when compared to other edible insects in Africa was much lower for this essential fatty acid with 8.79% linoleic acid as compared to the cricket or weevil that had about 45% (Womeni *et al* 2009). *Macrotermes subhyalinus*, fried in palm oil, were shown to have 43.1% linoleic acid (Oliveira *et al* 1976). Linoleic acid across *Nasutitermes* castes averages to about 11% (Oyarzun *et al* 1996). The high variability of termites appears to apply to fatty acid composition as well.

Table 2.5

	<i>Macrotermes spp</i> Alates	<i>M. subhyalinus</i> Fried Alates	<i>Nasutitermes spp.</i> Alates	Workers	Soldiers
Lauric Acid	-	0.1	0.16	1.93	0.43
Myristic Acid	0.81	0.9	4.89	4.1	4.27
Palmitic Acid	30.47	33	19.15	9.71	7.54
Pamitoleic Acid	2.21	33	1.42	2.11	0.99
Stearic Acid	9.03	1.4	12.68	12.51	11.81
Oleic Acid	47.52	9.5	51.08	48.86	32.63
Linoleic Acid	8.79	43.1	8.51	15.05	11.08
Linolenic Acid	0.63	3.0	0.00	0.00	9.67
Arachidic Acid	-	0.4	1.3	1.66	3.87
Behenic Acid	-	0.1	0.33	1.4	4.38
Author	W	OL	O		

Table 2.5 Termite fatty acids values for different castes and fried versus fresh. Author codes: W= Womeni *et al*, 2009; OL= Oliveira *et al*, 1976; O= Oyarzun *et al*, 1996.

There are yet other nutrients that termites may provide that are currently not fully understood for Afrotropical species. For instance, Wakayama and colleagues (1983) found five species of New World termites were high in vitamin B₁₂, which is apparently synthesized by the bacteria in their guts. Since anaerobic bacteria utilize B₁₂ in many enzymatic reactions, it is likely that termites all over the world are high in this nutrient. Termite consumption in Southern Africa may fulfill B₁₂ requirements.

Humans are able to increase the nutritive value of termites through preparation. A study by Aufferet and Tanguy (1948; results translated in Bodenheimer 1951) compared the fat, calories, and protein present in living termites versus those prepared by the Fullah in French West Africa. The Fullah boil the termites, dry them in the sun, and then fry them (unspecified as to what, if any, oil added). Although the species of termite is unknown, the alates are the caste consumed by the population and were used in their study. Preparation of the termites made the termites higher in all three categories, as seen in Table 2.6. Oliveira and colleagues analyzed *Macrotermes subhyalinus* alates fried in palm oil and found them to contain 38.2 g protein, 46.1 g fat, and 612 kcal per 100 g of the food. Comparing this to the results in Table 2.3, where the numbers were calculated for 100 g of dry matter, it can be seen that the fried alates have more fat than any of the raw termites, and considerably more than other *Macrotermes* alates (*M.s falciger* alates = 22.5 g/100g; *Nasutitermes spp.* = 40.23 g/100g). Gross energy was slightly lower in the fried termites than in the *Nasutitermes* alates, but definitely in the high end of the range, and the protein levels were unremarkable compared to the entire range presented in the table, but it is higher than the other *Macrotermes* alates.

Table 2.6

	Moisture	Fat	Protein	Ash	Calories in 100g
Living termites	44.5%	6.6%	16.9%	-	347
Fried termites	13.0%	36.2%	45.6%	5.0%	508

Table 2.6. Nutritive value of fried versus fresh termite alates, adapted from Aufferet and Tanguy (1948)

DISCUSSION

Although most widely documented for chimpanzees, the other non-human apes also consume termites. Deblauwe and Janssens (2008) show that the different nutritional values of termite species and termite castes may affect prey choice in the great apes. Chimpanzees and gorillas select different prey, and it appears not to be solely because of accessibility issues related to whether tools were used. It is well documented that chimpanzees prefer *Macrotermes* soldiers, and Deblauwe and Janssens found important termite prey for gorillas to be soil-feeding termites such as *Cubitermes* and *Thoracotermes*, with strongest preference for *Cubitermes* workers. Gorillas therefore received much more iron and other micronutrients while chimpanzees received much more protein from their termite resources. Gorillas do not need to supplement protein in their diets because the woody-plants they consume are high in protein (Wrangham *et al* 1991; Deblauwe and Janssens 2008); however, they may not eat enough fruit to fulfill their micronutrient requirements. Conversely, chimpanzees eat plenty of fruit and receive enough micronutrients, but protein is more difficult to obtain for frugivores. The

selection of termite prey for these two apes is appropriate supplementation to their traditional diets (Deblauwe and Janssens 2008).

Macrotermes are an important termite prey for humans. However, human preference seems to be for the alate caste, as opposed to chimpanzees' preference for soldiers. The termite prey choices of humans may be providing a significant source of fat since alates and larvae tend to have more fat than the other castes in their species. If nutritional value is affecting termite prey choice for humans, then it appears that macronutrients may be more important than micronutrients. Although 61 species are reported to be consumed by humans worldwide, the genera of the prey they choose in Africa appear to align more closely with chimpanzees than gorillas. Genera like *Cubitermes* and *Thoracotermes* are not highly selected by humans. The desirability of these genera for gorillas is likely due to their high micronutrient content resulting from their soil-based diet.

Termites would be a desirable food resource for earlier hominids, but with the species and caste diversity in nutritional value, it is difficult to reconstruct the role termites would have had in the hominid diet. In essence, we have three extant models to work from 1) chimpanzee-like, protein-rich choices, 2) gorilla-like, micronutrient-rich choices, and 3) modern human-like, fat-rich choices.

In order to determine which of these models works best for hominids, a baseline hominid diet must be assumed. It will be assumed that 1) the Swartkrans robust australopithecines were foraging for termites (Backwell and d'Errico 2001; d'Errico and Backwell 2009). 2) The diet of the Swartkrans hominids consisted of 65% C₃ foods and 35% C₄ foods, as calculated by Sponheimer and colleagues (2005). 3) The C₃ resources

consisted of woody-plant derived foods with over half of the signature (thus >1/3 the total diet) coming from fruit. The homogeneity of extant great ape diets suggests hominids would have utilized similar resources (Rodman 2002). Savanna chimpanzees therefore provide the best model for the proportion of these resources utilized by early hominids on the South African savanna. According to Pruettz (2006), roughly 55% of observations of chimpanzees feeding in dry environments were of fruit. 4) The C₄ resources were savanna grasses, as suggested by the carbon isotopes of East African hominids presented by Cerling and colleagues (2011). Additionally, the pith of herbaceous plants, such as elephant grass (*Pennisetum purpureum*), is an important energy-yielding fallback food for chimpanzees when fruit is scarce (Wrangham *et al* 1991). Although other resources could have contributed to the signal, such as sedges, but those are being considered here as supplemental, just as the termites being assessed.

Table 2.7

	Crude Protein (% DM)	Crude Fat (% DM)
Fruit	7.7	1.7
Leaves	16.8	2.6
Fig	3.5	3.4
Pith	10.5	1.6

Table 2.7. Mean values of protein and fat present in important chimpanzee foods. As calculated by Wrangham *et al* (1991) based on studies by Hladik (1977), Watts (1984), Calvert (1985), Malenky (1990) and Rogers *et al* (1990). DM = Dry Matter.

Wrangham and colleagues (1991) summarized the nutrient composition of major items consumed by chimpanzees and calculated means across food species within studies by Hladik (1977), Watts (1984), Calvert (1985), Malenky (1990), Rogers and colleagues

(1990). The mean values for crude protein and crude fat appear in Table 2.7 and will be used as the basis for discussion of the hypothetical hominid diet.

Codron and colleagues (2007) assessed the nutritional content of savanna plant foods in South Africa's Kruger National Park. Results show consistently higher protein in browse foods, however the grasses have higher fiber digestibility. Some fruits were shown to have large amounts of poorly digestible fiber and lignins, suggesting that browse foods are not necessarily higher quality. Crude fat present in four species of savanna grasses in Sudan average 1.4% of dry matter, lower than the values presented by Wrangham and colleagues for chimpanzee foods (Savadogo *et al* 2009). Considerable amounts of phosphorous, calcium, magnesium, and potassium can be obtained from savanna grasses, with amounts being significantly higher near or under the tree canopy as compared to the open grassland (Ludwig *et al* 2008). Therefore, the inclusion of grasses in the hominid diet would likely act as a source of gross energy and minerals and not fat and protein.

If the hominid diet was ~30% leaves, ~35% fruit and ~35% grasses, as outlined above, then it appears that protein deficiency could pose a real threat. Even if sedges were contributing to the hominid C₄ signature, Codron *et al* (2007) calculated the protein in sedges to be more similar to grasses than to fruit or leaves, so total protein would still be low. Additional micronutrients, such as iron, may also be low in the hominid diet.

Deblauwe and Janssens (2008) estimated the amount of termite dry matter (DM) consumed per day for the different important termite species consumed by chimpanzees and gorillas in Dja Biosphere Reserve, Cameroon. The lowest estimate was for *Thoracotermes macrothorax* with an estimated average intake of 0.25g DM/day and a

maximum of 4.4g DM/day. The highest estimate was for *Macrotermes muelleri* with an estimated average intake of 2.12g DM/day and a maximum of 58.5g DM/day. Based on these numbers I calculated the nutritional content received when consuming 5g DM of each species/caste of termite listed above in Table 2.2. I also calculated the nutritional content received when consuming 50g DM of each. These results are presented in Tables 2.8 and 2.9.

Recommended dietary allowances (RDA) and adequate intakes (AI) calculated for each nutrient by the National Research Council, Food and Nutrition Board (1989) provide an overestimate of the requirements needed by the smaller-bodied hominids, but these numbers can be compared to the estimated intake of the nutrients from termite prey to assess their nutrient content and their role as a supplemental food. Table 2.8 is the estimate for consuming 5g of termite DM, which is a quantity on par with field observations of termite consumption by the great apes. Consuming 5g DM of select termites would fulfill certain micronutrient requirements. The soil-feeding termites, *Thoracotermes* and *Cubitermes* are rich in iron and zinc and consuming any of the castes would essentially meet requirements for those trace elements. Consuming 5g of *Macrotermes* soldiers or workers would fulfill manganese dietary recommendations.

Table 2.8

Species	Min RDA/AI Caste	g/5g DM		mg/5g DM									Author
		CP 34	CF 65	Ca 1000	P 700	Mg 310	Na 500	K 1600	Fe 8	Zn 8	Mn 1.8	Cu 0.9	
<i>Cub. heghi</i>	Larvae	3.3	0.4	44	43	13	221	142	52	52	0.5	0.3	D
<i>Th. macrothorax</i>	Larvae	2.8	1.1	16	25	6	86	53	14	20	0.1	0.1	D
<i>Macro. bellicosus</i>	Alates	1.0	-	1.1	7	<0.01	-	-	1.4	-	-	-	D
<i>Macro. notalensis</i>	Alates	1.1	-	0.9	6	0.01	-	-	1.5	-	-	-	D
<i>Macro. falciger</i>	Alates	1.1	1.1	-	-	-	-	-	-	-	-	-	D
<i>Nasu. spp.</i>	Alates	2.4	2.0	12	18	8	11	19	1.2	0.9	0.2	0.1	D
<i>Cub. heghi</i>	Soldiers	2.4	0.3	11	29	8.5	43	76	105	10	0.3	0.1	D
<i>Macro. lilljeborgi</i>	Soldiers	3.4	0.2	22	18	8	34	56	2.1	9	4.2	0.2	D
<i>Macro. lilljebori*</i>	Soldiers	3.6	0.1	11	19	6	4	36	1.3	1.2	2.5	0.2	O
<i>Macro. muelleri</i>	Soldiers	3.6	0.3	8	19	5	6	38	0.5	1.2	2.2	0.4	O
<i>Macro. muelleri*</i>	Soldiers	3.4	0.3	17	16	7	9	45	2.7	2.1	4.7	0.2	D
<i>Nasu. spp.</i>	Soldiers	2.9	0.6	19	15	8	3	29	5	0.8	0.6	0.2	D
<i>Th. macrothorax</i>	Soldiers	2.9	0.2	7	28	7	18	48	83	3.7	0.5	0.1	D
<i>Cub. heghi</i>	Workers	0.8	0.2	7	14	6	17	67	148	3.6	0.6	0.1	D
<i>Macro. lilljeborgi</i>	Workers	2.7	0.3	50	23	15	7	43	20	2.8	5.1	0.1	D
<i>Macro. muelleri</i>	Workers	2.5	0.2	36	19	13	22	51	7	5.8	3.8	0.1	D
<i>Nasu. spp.</i>	Workers	3.4	0.1	10	20	7	12	31	2	0.7	0.2	0.3	D
<i>Th. macrothorax</i>	Workers	1.0	0.2	13	19	7	30	70	229	7	1.5	0.1	D

Table 2.8. Estimate of nutrients for consumption of 5 grams termite dry matter. Shaded cells indicate recommended dietary allowance (RDA) has been met. Nutrient codes: DM = Dry Matter; CP = Crude Protein; CF = Crude Fat; Ca = Calcium; P = Phosphorous; Mg = Magnesium; Na = Sodium; K = Potassium; Fe = Iron; Zn = Zinc; Mn = Manganese; Cu = Copper. Author codes: D = Deblauwe and Janssens, 2008; O = Oyarzun *et al*, 1996.

Table 2.9

Species	Min RDA/AI Caste	g/50g DM		mg/50g DM									Author
		CP 34	CF 65	Ca 1000	P 700	Mg 310	Na 500	K 1600	Fe 8	Zn 8	Mn 1.8	Cu 0.9	
<i>Cub. heghi</i>	Larvae	33	4	440	425	130	2205	1420	523	518	4.8	2.5	D
<i>Th. macrothorax</i>	Larvae	29	11	160	250	60	860	525	136	202	1.1	1.0	D
<i>Macro. bellicosus</i>	Alates	10	-	11	68	0.08	-	-	14	-	-	-	D
<i>Macro. notalensis</i>	Alates	11	-	9	57	0.1	-	-	15	-	-	-	D
<i>Macro. falciger</i>	Alates	11	11	-	-	-	-	-	-	-	-	-	D
<i>Nasu. spp.</i>	Alates	24	20	120	180	75	105	185	12	9	1.9	0.9	D
<i>Cub. heghi</i>	Soldiers	24	2.5	105	290	85	430	760	1050	100	3	1.3	D
<i>Macro. lilljeborgi</i>	Soldiers	34	1.5	215	180	75	335	555	21	86	42	2.3	D
<i>Macro. lilljebori*</i>	Soldiers	36	1.0	105	190	60	40	360	13	12	25	2.2	O
<i>Macro. muelleri</i>	Soldiers	36	2.5	80	185	50	55	380	5	12	22	3.7	O
<i>Macro. muelleri*</i>	Soldiers	34	3.0	165	155	65	85	445	27	21	47	2.2	D
<i>Nasu. spp.</i>	Soldiers	29	5.6	185	145	75	30	290	50	8	6	1.7	D
<i>Th. macrothorax</i>	Soldiers	29	2.0	65	275	70	180	480	826	37	4.5	1.0	D
<i>Cub. heghi</i>	Workers	8	1.5	70	140	55	165	670	1481	36	6	1.4	D
<i>Macro. lilljeborgi</i>	Workers	27	3.0	495	225	150	65	425	198	28	51	1.4	D
<i>Macro. muelleri</i>	Workers	25	1.5	360	185	130	220	510	71	58	38	1.3	D
<i>Nasu. spp.</i>	Workers	33	1.1	100	200	65	120	305	20	7	1.6	2.6	D
<i>Th. macrothorax</i>	Workers	10	1.5	125	190	70	295	700	2291	67.3	14	1.4	D

Table 2.9. Estimate of nutrients for consumption of 50 grams termite dry matter. Shaded cells indicate recommended dietary allowance (RDA) has been met. Nutrient codes: DM = Dry Matter; CP = Crude Protein; CF = Crude Fat; Ca = Calcium; P = Phosphorous; Mg = Magnesium; Na = Sodium; K = Potassium; Fe = Iron; Zn = Zinc; Mn = Manganese; Cu = Copper. Author codes: D = Deblauwe and Janssens, 2008; O = Oyarzun *et al*, 1996.

Consuming 50g of termite dry matter is a maximum estimate based on field observations of wild chimpanzees fishing for *Macrotermes muelleri*. However, if 50g of DM of almost any termite species in this study were consumed, trace element requirements would be fulfilled. Consuming this quantity of larvae would meet sodium requirements, and most notable is that eating this quantity of *Macrotermes* soldiers fulfills all protein dietary requirements.

The gorilla-model for termite prey selection emphasizes the selection of termites high in micronutrients. Micronutrient deficiency may have been a concern for hominids as well if their diets were only 30% fruit. Consuming a small amount of soil-feeding termites could provide all daily-required iron and zinc and may have been a desirable supplement for hominids. Consuming soil-feeding termites could also have contributed to the C₄ signature present in South African hominid fossils. The soil consumed by these termites contains plant remains from the environment, so would have included a high proportion of C₄ plants.

Micronutrient requirements could also be met by eating larger quantities of other, non-soil-feeding termites. Termites of the genus *Macrotermes*, which is the most selected genus by chimpanzees and highly sought out by human populations in Africa, could fulfill micronutrient requirements if 20g DM were consumed, depending on the species and the caste. Consuming 50g DM of *Macrotermes* soldiers would also fulfill all requirements for dietary protein. Working with our assumption of 30% leaves, 30% fruit, 40% grasses in the hominid diet, a supplemental resource with significant protein would be an appealing choice for hominids. The chimpanzee-model of consuming protein-rich termites may be a good fit for South African Plio-Pleistocene hominids. *Macrotermes*

consumption would most likely contribute to the C₃ portion of the carbon isotope signature for the hominids, although there are a few species like *M. michaelseni* that are known grass foragers (Uys 2002).

The human-model of termite consumption is more variable than both the gorilla and chimpanzee models. Human populations eat a wide variety of termite species, but appear to prefer the alate caste. Alates have higher fat content than soldiers do and workers, so these termites may be selected based on their contribution to the gross energy content of the diet. There is also evidence of modern human consumption of *Macrotermes* soldiers (e.g. Silow 1983). It is possible that hominids were consuming species of termites similar to modern humans as a way to supplement additional macronutrients to their diet.

Hominids could have consumed *Macrotermes* soldiers on the level of chimpanzees but also benefited from exploiting the swarming alates during the wet season like many modern human populations. The hypothesis that suggests that *A. robustus* was obtaining extra nutrients from termites fits with the evidence of brain expansion for the species. *A. robustus* had an average cranial capacity of 587 cubic centimeters, similar to specimens that some associate with early *Homo* (Wolpoff 1999). With the expansion of such an energetically expensive organ, utilization of resources beyond that of chimpanzees is necessary. However, this change does not need to be dramatic, and exploiting multiple castes of *Macrotermes* may provide a significant contribution to these additional resources.

CONCLUSION

Termite species are abundant and diverse. Even the caste system of these social insects produces great variability within a species. Termites eat a wide range of plant materials, including grasses and woody plants, with some species being specialized foragers and others consuming items across the range. This variability makes it difficult to identify the role termites may have had in the diet of Plio-Pleistocene hominids by chemical signature alone. Data compiled from termite ecology, chimpanzee termite-foraging behavior, and preferences of living human populations suggest that termites belonging to the genus *Macrotermes* may have been a desirable prey choice for hominids. *Macrotermes* soldiers contain high levels of proteins, while the alates are high in fat. Eating considerable numbers of termites would also fulfill many micronutrient requirements. It is possible that hominids were able to increase their gross energy intake as well as fulfill nutrient requirements such as protein and iron by regularly consuming termites of the genus *Macrotermes*.

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Chapter 3

Power and precision in the grips of Goualougo chimpanzees when perforating termite mounds

ABSTRACT

The Goualougo chimpanzees are known to have one of the largest and most complex tool repertoires reported for wild populations of chimpanzees. They use a set of two tools, one to perforate the hard outer crust of termite nests, then a second tool to go through the hole to obtain the termite prey. Here I report that the use of the first tool, the perforation stick, is more complex than previously understood. The chimpanzees use a combination of power to break the crust and precision to remove the loosened soil, before switching to the second tool. This sequence can be achieved by switching grips or by using an intermediate grip for the entirety of the bout. The chimpanzees are observed to have success with the intermediate grip that is here named “thumb-pocket grip,” which is similar to how some humans hold a pencil. Thumb-pocket grips are identified by the shaft of the tool extending across the palm of the hand and the working end of the tool exiting the hand between two of the fingers, most commonly at the flexed intermediate phalanges of the third and fourth fingers

INTRODUCTION

Chimpanzees and humans have dramatically different hand morphology. The relatively longer thumb of humans promotes object manipulation while the relatively longer proximal phalanges of chimpanzees are specialized for arboreal behavior and knuckle walking (Preuschoft 1973). Chimpanzees' short thumbs and long fingers hinder object manipulation, yet the genus *Pan* is known to be a habitual tool-user (e.g. Goodall 1963; Boesch 1993). The grips chimpanzees use to bring stability to the tools in their hands reflect the compromise between locomotion and manipulation.

Napier defined two classes of grips, power and precision (Napier 1960; Napier 1963). In humans, the thumb is an essential part of both of these grips, but chimpanzees can manage both power and precision tasks without any aid from the thumb.

Chimpanzees' long proximal phalanges allow them to hook narrow, slender objects under their fingers and produce a power grip that needs neither thumb nor palm (Napier 1960). Humans show a strong preference for using the distal ends of the fingers, especially the pads, against the thumb in precision grips while chimpanzees are more varied, using additional grips such as pad of the thumb to side of the index finger and a no-thumb scissor grip between two adjacent fingers for precision tasks (Napier 1960; Christel 1993).

Chimpanzees can produce large amounts of force with their hands but chimpanzee precision grips are often weak and static (Marzke 1996b). The ease of precise manipulation seen in humans has thus been the focus of studies of hominid evolution and tool-use (Marzke 1996a; Susman 1988). However, recent studies have shown that both chimpanzees and gorillas are capable of complex intermanual object

translation, where the digits are used to move objects within one hand, suggesting this ability was present in the last common ancestor (Byrne 2001; Corp 2002; Crast 2009). These manual skills suggest that complex neuromotor control evolved in the distant past and has been maintained by the non-human African apes during the evolution of specialized knuckle-walking morphology, as well as refined over the course human evolution (Tuttle 1970).

Although chimpanzees are capable of complex object translation they are still handicapped from many precision grips by their knuckle-walking morphology. Chimpanzee grips can be studied to investigate the problem-solving techniques used by these apes to complete a task for which their hands may not be best suited. The chimpanzees of the Goulougo Triangle, Republic of Congo provide an ideal study population for such questions since they are known to have one of the largest and most complex tool repertoires reported for wild populations of chimpanzees (Sanz 2007). Additionally, the remote video footage taken at termite mounds in the study area (Sanz *et al* 2004) provides the ability to re-watch, stop-frame and slow-motion the actions of the chimpanzees, guaranteeing accurate observations of tool manipulation.

The videos taken at the termite mounds show termite mound perforation in addition to termite fishing. Termites will reseal their exit/entry holes, and in order for a chimpanzee to insert a grass probe to fish for the termites, the passageway must be re-opened. If the chimpanzees are not successful using their hands to remove the soil, the chimpanzees will attempt to perforate through the barrier with a stick and recreate the passage (Sanz *et al* 2004). Although the obstruction in the passageway is generally softer than the cemented structure of the nest, its toughness is variable, and perforation is not

always successful (Sanz *et al* 2004). The grips used for holding the perforation sticks have previously been described as precision grips as they resembled the grips used for fishing (Sanz 2004). However, it has been shown that chimpanzees have great individuality in their grip preferences (Christel1993). I hypothesize that upon closer inspection of the grips used by the chimpanzees for perforation, there will be a wide range of grips used by different individuals, and that the chimpanzees will switch away from precision grips to more powerful grips before giving up on a passageway if the obstruction is difficult to open.

This study will identify the grips used by the Goulougo chimpanzees for perforation and address the hypothesis that the most successful perforating chimpanzees will have a range of grips at their disposal to use as the task dictates. In particular, I will look for evidence of five predictions:

- Prediction 1: The most common grip will be the pad-to-side grip, a precision grip translated to this task from its common use in termite fishing.
- Prediction 2: Chimpanzees will begin with the pad-to-side grip, and will switch to a more powerful grip when the obstruction is too tough to perforate easily.
- Prediction 3: The most successful perforators will be the individuals with the greatest grip repertoire for handling obstructions of varying toughness.
- Prediction 4: The most successful juveniles will be those of the most successful mothers.

METHODS

The Goulougo Triangle is located northern Republic of Congo in the southern portion of the Nouabalé-Ndoki National Park, This study area covers 380 km² of evergreen and semideciduous lowland forest, with altitudes ranging between 330 and 600 m. The study site is home to three communities of chimpanzees. The Moto community of 70 individuals is the best habituated and most reported. The climate is transitional between the Congo-equatorial and subequatorial climatic zones. Rainfall is bimodal, with a main rainy season from August through November and a short rainy season in May.

Remote video cameras were used for surveillance of ten termite nests across the three communities between 2003 and 2007. These devices contained a passive infrared sensor triggered by animal movements. If the sensor detected movements, it would begin to record. Recording would continue for two minutes or until motion was no longer detected, at which point the recorder would power down. Each month of the year is represented in the videos collected and there is more activity at Moto than the other two communities.

Each recording was scored for age-sex class of chimpanzees, individual identification, approaches with tool materials, tool type, tool manufacture, tool modification, and tool use. Tapes that include perforation were further scored for the type of grip used to manipulate the perforating tool (e.g. precision, power) and the specific grip (e.g. pad-to-side, hook). A series of perforation is defined as the time between starting and stopping perforation. In this time, the chimpanzees may pause and resume perforating, switch grips, switch hands, switch holes or switch locations on the

mound. 147 series of perforation were viewed and coded. A bout of perforation is defined as the distinct period of tool-use within a perforation series. The end of a bout is defined by either switching grips, switching hands, switching holes, switching location, terminating perforation altogether or successfully obtaining prey. 290 bouts were viewed and coded.

The success of a grip in a perforation bout is defined by the chimpanzee switching tools to a grass stem for termite fishing. This change in tool indicates that the passageway in the mound has been unobstructed with the first tool and that the piece of grass can now be successfully threaded through the hole.

RESULTS

Of the 290 bouts of perforation observed for a minimum of 13 chimpanzees, 157 bouts yielded an unobstructed view of the hand and the grip was identified and recorded. Three types of grips were used by the Goualougo chimpanzees. In addition to power and precision, the Goualougo chimpanzees utilize a third type of grip, intermediate to the above-mentioned. This type of grip is referred to here as “thumb-pocket.” In a thumb-pocket grip, the perforating stick rests on the webbing between the thumb and first finger. The shaft of the tool extends across the palm and the working end of the tool exits the hand between two of the fingers, usually at the flexed intermediate phalanges (Figure 3.1).

Six specific grips were recorded:

- Hook grip. The tool is enclosed by four flexed fingers. A power grip.

- Two-handed grip. The more specific grip of the tool through the hand was usually obscured by the addition of the second hand. Considered here the most powerful grip.
- Pad-to-side grip. The tool is pinched between the pad of the thumb and the side of the index finger. A precision grip.
- Thumb-pocket 2/3. The tool rests between the thumb and index finger and exits under the index finger. Thumb-pocket grips are intermediate to power and precision grips.
- Thumb-pocket 3/4. The tool rests between the thumb and index finger and exits between the third and fourth digits. This is the most common thumb-pocket grip.
- Thumb-pocket 4/5. The tool rests between the thumb and index finger and exits over the pinky finger.

Figure 3.1

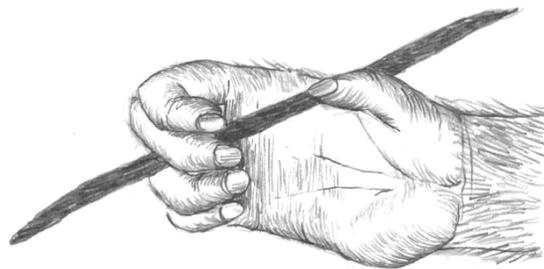


Figure 3.1. Thumb-pocket grip. The tool rests on the webbing between the thumb and index finger, extends across the palm and the working end of the tool exits the hand between flexed intermediate phalanges, usually of the third and fourth fingers.

Chimpanzees successfully obtained prey in 61% of the perforation series observed (90 of 147). Within these series, there were 290 bouts of perforation and 157 of those bouts had identifiable grips and are the subject of this study. Of the 157 bouts of perforation with identified grips, 41 bouts (26%) led to the successful obtaining of prey. The grip used in the most number of bouts, and by the most individuals, is the two-handed grip. By the definition provided here, this grip, however, was the least successful of the six grips identified. The most successful grip was the other identified power grip, the hook grip, which was successful 45% of the times it was seen utilized (n=31). The one precision grip seen in the sample, the pad-to-side grip, was successful 26% of the time it was used (n=21) (Table 3.1).

Table 3.1

Grip	Grip Type	Number of Individuals	Total Use (n=157)	Success	Grip Type Success
Hook	Power	n=8	n=31; 20%	n=14; 45%	20%
Both Hands	Power	n=10	n=54; 34%	n=3; 6%	--
Pad-to-side	Precision	n=5	n=21; 13%	n=6; 29%	29%
Thumb-pocket, 2/3	Thumb-pocket	n=6	n=12; 8%	n=3; 25%	--
Thumb-pocket, 3/4	Thumb-pocket	n=6	n=37; 24%	n=13; 35%	33%
Thumb-pocket, 4/5	Thumb-pocket	n=1	n=2; 1%	n=1; 50%	--

Table 3.1. Individual grips observed in the Goualougo chimpanzees. Horizontal lines show which type category the grip fits within, the number of individuals recorded using the grip, the number of bouts in which the grip was recorded, and the number of bouts the grip was observed successfully perforating a termite mound. The last column is the success of the grip types: power, precision and thumb-pocket.

There were only 31 of the 157 bouts with identified grips that ended with a switch in grip. Of these, only four were switches from the pad-to-side grip, the only precision grip in the sample. Power grips (hook and two-handed) were switched to the most, 14 times, but were also the grips switched away from the most, 21 times. Thumb-pocket grips were switched to 10 times and switched away from 3 times (Table 3.2).

Table 3.2

First Grip	Switched To	# of times
Hook	Thumb-pocket 3/4	3
	Thumb-pocket 2/3	2
	Both Hands	1
	Unknown	1
Both Hands	Pad-to-side	3
	Thumb-pocket 2/3	1
	Thumb-pocket 3/4	3
	Thumb-pocket 4/5	1
	Hook	1
	Both Hands	2
	Unknown	3
Pad-To-Side	Hook	3
	Both Hands	1
Thumb-Pocket 2/3	Hook	1
Thumb-Pocket 3/4	Both Hands	1
Thumb-Pocket 5/6	Both Hands	1
Unknown	Hook	1
	Both Hands	2

Table 3.2. Chimpanzee grip switches. The chimpanzees were seen switching grips 31 times. These switches were more commonly from a power grip to a more precise grip and not *vice versa*, as was predicted.

The minimum number of chimpanzees seen perforating was thirteen, and over 70% of the video footage with identifiable grips was of six known individuals. Adult

female chimpanzees were the most frequent visitors to the termite mounds. One adult female in particular, Theresa, comprised 25% of the bouts with visible grips. Theresa was also the most successful individual, obtaining prey with 38% of her bouts. Theresa used a wide range of grips, but preferred the power grips. The next most observed individual was an adult male, Talangai, but his success was only 4%. The most seen juvenile was a female, Samantha, and she was recorded with a visible grip the same number of times as her mother, Sarah. In this sample, Samantha was more successful than Sarah was. Maya is another successful adult female, obtaining prey 26% of the time, and she showed a strong preference to the thumb-pocket 3/4 grip, using it 18 of the 19 times she was recorded with a visible grip (Table 3.3).

Table 3.3

Top Users	Age-Sex ID	# Grips	# Bouts	Contribution to Total	Personal Success	# Switches
Theresa	Adult Female	5	40	25%	n=15; 38%	11
Talangai	Adult Male	4	21	13%	n=1; 4%	6
Maya	Adult Female	2	19	12%	n=5; 26%	1
Vanessa	Adult Female	3	11	7%	n=1; 9%	3
Sarah*	Adult Female	3	10	0.4%	n=2; 20%	1
Samantha*	Juvenile Female	3	10	0.4%	n=5; 50%	1
Other	----	6	46	29%	--	8

Table 3.3. Most frequent perforating chimpanzees. Horizontal lines show the individual's age and sex classification, the number of different grips used by that individual, the number of bouts recorded with visible grips for that individual, the percentage of total bouts recorded that were of that individual, and the number of bouts

ending in the successful obtaining of prey for that individual. * denotes mother-daughter.

DISCUSSION

Perforation is more complex than previously reported. Perforating termite mounds requires precision and power; precision to manipulate the stick directly within the exit/entry hole and power to break loose soil that can become tightly packed in the passageways. The chimpanzees of the Goualougo Triangle use multiple grips for perforation, sometimes in sequence. However, this sequence is not the one that was predicted. I expected to see a switch in grips from precision to power when the termite mound appeared too difficult to break. Instead, I saw a different pattern that questions the operational definition of success.

The least successful grip given the operational definition was the two-handed grip, the most powerful in this study and the one employed the most often. This result appears contradictory since I expected that breaking open the entryway would allow for subsequent termite fishing. It appears it is necessary to first clear debris from the passageways after the crust is broken, a task requiring more precision than the two-handed grip could provide. The use of the two-handed grip broke the crust of the termite mound a high percentage of times, but the chimpanzee often switched (thus ending the bout unsuccessfully) to a one-handed grip in order to remove the loosened soil and gain access to the inside of the mound. This sequence of grips brings to question whether the grip that removed the debris can be considered successful if it was not the one that facilitated the opening of the passageway.

If the chimpanzees need precision for removing debris, then I should see more support for the prediction that the pad-to-side grip will be used with high frequencies. The Goualougo chimpanzees utilized the precise pad-to-side grip in 13% of the recorded bouts with visible grips, which is less than predicted. It was expected that the chimpanzees would use this grip for perforation because it is the most common grip used during termite fishing. It appears that perforation requires more power than a precision grip can supply and instead of switching grips a high number of times, some chimpanzees are selecting a more powerful grip such as the thumb-pocket grip. When the chimpanzees switched away from the power grips to grips that are more precise they selected the thumb-pocket type more often than they did precision.

The thumb-pocket type of grip, which includes all three variants where the tool exits between different fingers, was the most successful of the three types observed. The success was 33% (14/51) compared to 20% for power grips (17/85) and 26% for the precision grip (6/21). Chimpanzees rarely switched away from thumb-pocket grips. This type of grip is essentially a powerful precision grip well suited for the task of perforation that requires both forms of manipulation. Marzke (2006) observed chimpanzees using the webbed pocket between the thumb and index finger in a manner similar to a human grasping an apple while opposing the force of a bite. She describes it as the most powerful precision grip and evidence here supports that statement. Additionally, the “advanced human-style grip” in Morris’ *Biology of Art* (1962) is employed by apes using paintbrushes and appears to be similar to the thumb-pocket grip. However, besides anecdotal accounts, this grip has not been formally described.

Although thumb-pocket grips were the most successful type, the most successful specific grip was the hook grip (45%; 14/31). Power grips were not the most successful of the types we observed since our category includes the hook as well as the two-handed grip which had a success rate of only 6% (3/54), thus lowering the average for this group. Although the hook grip is undoubtedly a power grip, hooks allow for some degree of precision unlike using both hands. However, the chimpanzees switched away from this grip to grips that are more precise six times. In one instance, the chimpanzee switched to a two-handed grip in order to get more power but ultimately was unsuccessful at opening that hole and relocated.

The most successful individual chimpanzee was the adult female Theresa. Theresa used five different grips, the most seen for an individual in this sample, providing support for the prediction that the most successful chimpanzee would have the greatest grip repertoire. Theresa, however, was the most frequently observed chimpanzee, appearing in 40 bouts with visible grips and representing 25% of the total sample. Partially contributing to her large number of bouts was the fact that she switched grips more than any other individual, switching 11 of the 31 recorded times. Conversely, the next most successful individual was Maya who was seen using only two different grips during the 19 bouts where they were visible. Maya had a strong preference for the thumb-pocket 3/4 grip and only switched grips one time. These two individuals appear to be employing two different strategies, one that switches between a large number of grips depending on the situation and one that regularly uses an intermediate grip that is successful for a variety of situations.

The most successful female, Theresa, did not have young offspring with her visiting the termite mounds. Maya is the mother of a subadult male named Donny who appeared with her in two of the five videos where she was recorded perforating. In one of these videos, Donny also participated in two bouts of perforation and although successful, did not stay for long. The most successful juvenile was Samantha, the daughter of Sarah. These two individuals perforated together in two videos and each participated in ten bouts of perforation. Samantha was more successful than her mother in these clips, obtaining prey five times to her mother's two. The increased interest of Samantha as compared to Donny in termite foraging is consistent with the findings from Gombe that female juvenile chimpanzees more closely imitate their mothers and begin termite fishing at an earlier age, becoming more proficient than their male counterparts (Lonsdorf *et al* 2004).

The Goualougo chimpanzees are elegant and sophisticated in their tool manipulation for termite foraging. Their apparent ease at the task of perforation led to the development of predictions without fully understanding the complexity of the task. Although the predictions were not explicitly supported as they are currently written, there is strong evidence for the overall hypothesis that the chimpanzees exhibit great problem solving skills in their choice of grip for the task of perforation.

CONCLUSION

The chimpanzees of the Goualougo Triangle use multiple grips for perforation, often in sequence, and the success of an individual grip cannot simply be determined by the obtaining of prey. It appears that the chimpanzees have a feel for what they need to do in order to open a passageway on the mound. If the hole is not opening easily, they

will switch to a more powerful grip. If that powerful grip leaves too much debris, the chimpanzees may use a more precise grip to remove the excess soil from the hole. Since each hole is unique, there is not a consistent pattern, however, the combination of power and precision in the sequences suggests another step to this process of termite foraging. Not only do the chimpanzees switch from one tool to another in order to reach the termites, but they also utilize that first tool in multiple ways. Additionally, the use of the thumb-pocket grips demonstrates these chimpanzees' ability to find different ways of solving the problem of needing both precision and power for perforation. The problem solving skills of the Goualougo chimpanzees are evidenced by the range of grips they use and the different ways they use them to perforate through the hard outer crusts of termite mounds.

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Chapter 4

Texture analysis of the Swartkrans bone tools

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 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; Van der Merwe *et al* 2003; Sponheimer *et al* 2005) 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 (Ungar *et al* 2003; Scott *et al* 2006). 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, 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 preyed 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.

Macrotermes are the primary termite genus consumed by chimpanzees (Bogart and Pruettz 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, as discussed in Chapter 3. 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 is also 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. In this chapter, 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:

- H_0 : 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:

- H_1 : 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.
- H_2 : 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. The bone tools were first identified during the 1976-1988 excavations led by C.K. Brain but the first reported bone

tool in the Cradle of Humankind was found at Sterkfontein in 1959 by Robison. 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 9 cm. 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," Robison needed to make a convincing case that the implement he was reporting was indeed a bone tool (Dart 1949; 1957; Washburn 1957). Robison 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 Robison 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. Robison 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 (Robison 1959).

During the 1976-1988 excavations at Swartkrans, Brain and colleagues found 68 artifacts across Members 1-3 that were similar to Robison'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 Robison, 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 10-15 cm, 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 was also 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 13-19 cm 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 0.1 kg to 3.5 kg, 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. Since 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 TOOL EXPERIMENTS

A list of experimental bone tools is presented in table 4.1. 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 15 km 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 9-19 cm length and 15-160 g 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 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.

Table 4.1

TOOL	TASK 1	TIME (min)	TASK 2	TIME (min)
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

Table 4.1. List of experimental tools and their tasks. * denotes the three experimental tools used in the Brain *et al* study and thus the unknown length of time for their use.

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 (Ungar *et al* 2003; Scott *et al* 2006).

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 (4.1). Once features were identified in the scan area, the specimen was scanned using the 10x objective resulting in an image with a field of view of 1.020 mm x 1.380 mm.

Figure 4.1



Figure 4.1. Area of observation for confocal microscopy. The digging end is oriented to the right. The anterior surface is oriented towards the objective lens. The 1.020 mm x 1.380 mm field of view (shaded rectangle) is on the flat surface superior of the digging tip but still in the range of wear and/or polish.

Figure 4.2



Figure 4.2. Thresholded photo simulation in SolarMap. White patches are areas where defects were removed from the point cloud and thus the analysis.

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.

Scale Sensitive Fractal Analysis

The corrected point clouds were run through two statistical software packages created by Surfraft (Surfraft.com). The fractal analysis program Toothfrac, 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, Sfrac, 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 $1.8 \mu\text{m}$ 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 (*Hasfc₉* and *Hasfc₈₁*). The above variables 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 (*Hasfc₉*) and 9x9 grids (*Hasfc₈₁*) 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 10 μm . When the volume is calculated on a finer scale, using cuboids with surface faces of 2 μm ,

the small texture features are also 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 (MANOVA) 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 4.2 through 4.9. There is significant difference in the MANOVA model (Table 4.2), indicating that use wear textures vary across the samples of interest in this study. The individual ANOVAs (Table 4.3) 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 4.4). 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 4.5).

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 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 4.6).

Although the null hypothesis was not rejected, 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 4.7).

Descriptive statistics of the unranked data can be found in Tables 4.8 and 4.9. These raw numbers were not used in the scale sensitive fractal analysis but can still be useful in comparing the samples.

Table 4.2

	Test Statistic	<i>F</i>	<i>df</i>	<i>p</i>
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

Table 4.2. MANOVA multivariate test of variance results. Three different test statistics all show a p value of less than .05 and suggest that there is significant differences among experimental and artifact bone tools.

Table 4.3

	<i>F</i>	<i>df</i>	<i>p</i>
Asfc (complexity)	6.297	22	.000
Smc (scale of max. complexity)	1.134	22	.311
EpLsar (anisotropy)	.557	22	.947
Hasfc ₉ (heterogeneity)	1.013	22	.449
Hasfc ₈₁	.630	22	.901
Tfv (texture fill volume)	.980	22	.490

Table 4.3. ANOVA's of individual variables. The texture complexity (*Asfc*) is the only significantly different variable with a p value below .05.

Table 4.4

		Swartkrans (SK)										Experimental (EXP)							
		SK	BW	Br	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	Dig	Macro	Perf	Trin	Mix
SK	BW		/																
	Br			/															
	R1				/														
	R2					/													
	R3						/												
	R4							/											
	R5								/										
	R6									/									
	R7			*							/								
	R8			*				*		*		/							
EXP	R9											/							
	R10			*									/						
	Dig	*	*	*	*	*	*	*	*	*	*	*	*	*	/				
	Macro	*	*	*	*	*	*	*	*	*	*	*	*	*		/			
	Perf	*	*	*	*	*	*	*	*	*	*	*	*	*			/		
Trin	*	*	*	*	*	*	*	*	*	*	*	*	*				/		
Mix	*	*	*	*	*	*	*	*	*	*	*	*	*					/	

Table 4.4. Complexity (*Asfc*) pairwise comparisons of all the bone tools in the study. 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* 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 one task.

Table 4.5

	DIG	MACRO	PERF	TRIN	MIX
DIG	/				
MACRO		/			
PERF			/		
TRIN				/	
MIX					/

Table 4.5. Complexity (*Asfc*) pairwise comparisons of the experimental tools only (zoomed in view of Table 4.4). There are no significant differences between the tasks; therefore, the null hypothesis is not rejected.

Table 4.6

	SK	BW	Br	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
BW		/											
Br			/										
R1				/									
R2					/								
R3						/							
R4							/						
R5								/					
R6									/				
R7			*							/			
R8			*				*		*		/		
R9												/	
R10			*										/

Table 4.6. Complexity (*Asfc*) pairwise comparisons of the Swartkrans tools only (zoomed in view of Table 4.4). 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).

Table 4.7

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

Table 4.7. Complexity (*Asfc*) pairwise comparisons of the Swartkrans samples versus the experimental samples (zoomed in view of Table 4.4). The blue highlighted 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.

Table 4.8

Sample	Stat	n	<i>Asfc</i>	<i>Smc</i>	<i>epLsar</i>	<i>Hasfc₈₁</i>	<i>Tfv</i>
Swartkrans	Mean	38	57.02	15.95	.0033	.3713	1.7E6
	Min		19.96	14.99	.00	.19	1.3E6
	Max		108.38	26.68	.01	.66	2.3E6
	Std. Dev.		19.95	3.18	.0019	.0945	2.8E5
Experiment	Mean	41	32.12	14.84	.0033	.3666	1.6E6
	Min		12.91	6.66	.0003	.16	1.3E6
	Max		57.71	15.37	.0064	1.13	2.3E6
	Std. Dev.		13.45	1.31	.0016	.15	2.1E5

Table 4.8. Descriptive statistics for all variables in the Swartkrans assemblage and the entire experimental sample: Descriptive statistics (Stat), complexity (*Asfc*), scale of maximum complexity (*Smc*), anisotropy (*epLsar*), heterogeneity 9x9 (*Hasfc₈₁*), and texture fill volume (*Tfv*).

Table 4.9

<i>Asfc</i>	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
	R1	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
	R7	13	54.14	29.51	108.38	23.40
	R8	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 4.9. Complexity (*Asfc*) descriptive statistics for the samples used in this study.

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 amongst 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*) variable 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 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 (Table 4.4). 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 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 (Table 4.5). 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 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 (Table 4.9) 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 that do not show significant differences are primarily in the rows associated with digging into *Trinervitermes* mounds and perforating *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 look 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 (Table 4.6). 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 tuber-digging 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 C₄ pathways, which are attributed to grassy resources (Sponheimer and Lee-Thorp 1999; Van der Merwe *et al* 2003; Sponheimer *et al* 2005). One explanation for this carbon signature could be that the hominids were eating significant quantities of grass-harvesting termites such as *Trinervitermes*. However, if the hominids were eating wood-foraging termites such as *Macrotermes*, the C₄ 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 C₃/C₄ 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 C₃/C₄ 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 since 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. Since 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.

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CHAPTER 5

Conclusion

The purpose of this dissertation was to investigate the possible ways the Swartkrans bone tools were used. The major findings of the three papers all suggest that the Swartkrans hominids were most likely foraging for termites belonging to the genus *Macrotermes*, possibly by perforating the mounds in a manner similar to the Goualougo chimpanzees.

There would have been many taxa of termites available to hominids on the Plio-Pleistocene South African savanna. The genus *Trinervitermes* was of initial interest for researchers since they are currently widespread across the Sterkfontein valley where the site of Swartkrans resides. Additionally, *Trinervitermes* are grass-foraging termites. Consumption of these termites would contribute to the unexpected carbon isotope signatures present in the South African hominid teeth that suggest that the diet was different from that of extant non-human great apes and included resources not from woody-plants. However, these termites are not regularly consumed by any extant apes, so this dissertation investigated the desirability and obtainability of preferred termite prey of chimpanzees, gorillas, and humans in order to determine if another genus would provide a better model for hominid consumption.

Modern human populations in South Africa today regularly utilize insects as a food resource, including termites. 61 edible species of termites have been reported around the world (Johnson 2010) and the genus *Macrotermes* is one of the most common taxa consumed. Many reports describe capturing swarms of flying termites, which are the alate caste in their nuptial flights (e.g. Silow 1983; Nonaka *et al* 1996). Comparisons of the nutritional values of the different castes of termites presented in Chapter 2 suggest the alates have a higher fat content than the other castes within termite species and may be part of the reason why the winged sexuals are highly sought out during swarming periods.

Chimpanzees show a strong preference the soldier caste of *Macrotermes* termites. The chimpanzees of the Goualougo Triangle, Republic of Congo use a tool set to forage termite mounds. Before threading a piece of long grass into the inner chamber to “fish” for *Macrotermes* soldiers, like is commonly seen at chimpanzee sites across Africa, they first use a stout stick to perforate open obstructed entry/exit holes on the mound. The Goualougo chimpanzees forage year round and this behavior may contribute to their ability to access the inside of the mound in every season. The research presented in this dissertation demonstrated that perforating behavior is more complex than was initially reported. The chimpanzees of the Goualougo Triangle demonstrate remarkable dexterity and cognitive skills in choosing the grips they use to hold the perforating tool. The task requires both precision and power to perforate through the small opening on the hard mound crust. The chimpanzees accomplish this by either switching grips or utilizing an intermediate grip like the thumb-pocket grip described in Chapter 3.

The intricate work chimpanzees do in order to obtain *Macrotermes* soldiers may suggest that the termites provide a valuable nutritional resource. Deblauwe and Janssens (2008) compared the nutritional value of the insect prey choices of chimpanzees and gorillas that reside in the same forest in Southeast Cameroon. Their paper, along with other research done on the nutritional value of termites, was reviewed in Chapter 2. *Macrotermes* termites, especially the soldiers, are high in protein. The maximum amount observed being consumed by the chimpanzees at Deblauwe and Janssens' site was 58.5 grams (g) of dry matter (DM) per day. *M. muelleri* soldier dry matter is 67% protein, so when 58.5 g are consumed, 39 g of protein are obtained. The recommended daily allowance estimated for adult humans by the National Research Council, Food and Nutrition Board (1989) is 34 g/day, so it is possible for chimpanzees to obtain all of their protein requirements from termite foraging alone.

The preferred prey of gorillas is soil-feeding termites and consumption of only a small quantity can fulfill the requirements for micronutrients such as iron and zinc (Deblauwe and Janssens 2008). However, consumption of large quantities of most termite species also fulfills these requirements, so chimpanzees consuming *Macrotermes* in larger amounts are also meeting recommended daily allowances of iron and zinc.

The wear patterns on the Swartkrans bone tools supports the possibility of foraging for termites by perforating the termite mounds. The use of texture analysis, which was developed for analyzing dental microwear, did not distinguish between the different tasks conducted with experimental tools; however, two of the tasks produced signatures that were not significantly different from some of the samples of Swartkrans bone tools (digging into *Trinervitermes* mounds and perforating the entry/exit holes of

Macrotermes mounds). Although the texture analysis could not identify a definite match between task and the Swartkrans bone tools, it suggests perforating was one of the closest fits.

d'Errico and Backwell's three-dimensional study (2009) concluded that foraging for *Trinervitermes* was the best match for the wear patterns on the Swartkrans tools, but that there was also support for digging into the ground for tubers. Their study did not investigate *Macrotermes* mounds. The results presented here in Chapter 4 also show support for digging for *Trinervitermes*, but not for digging into the soil. However, with the failure to reject the null hypothesis that experimental tools will all show the same wear patterns, the scope of these questions may be beyond the capabilities of texture analysis that was created for the hard enamel of teeth. It was surprising that the texture analysis did not show support for digging into the soil, and therefore the lack of support for digging into *Macrotermes* mounds does not preclude the task from the hominid repertoire.

The results of the two wear pattern studies above appear to provide the most support for *Trinervitermes* foraging. However, with the lack of evidence of their consumption by extant apes, the conclusion remains unclear. There are also other edible genera of termites besides *Trinervitermes* and *Macrotermes*. For instance, the San in Southern Africa use digging sticks to forage for the alates of *Hodotermes*. Just as the chimpanzee perforating sticks were used as a possible model for the Swartkrans bone tools, the digging sticks used for *Hodotermes* may be another potential analog. It is possible that using bone tools to dig into the underground nests of *Hodotermes* could produce a match to the Swartkrans tools as good as the one produced by digging into

Trinervitermes mounds. If more bone tool wear pattern studies were to be conducted, experiments with *Hodotermes* nests should be of primary importance. Nutritional value of *Hodotermes* appears to be unknown in the literature, but ethnographic accounts suggest that the workers and soldiers may be toxic (Fuller 1918; Nonaka *et al* 1996). The larvae and alate castes would therefore be the ones highly selected, and thus would provide a significant source of fat since these castes tend to be highest in fat content across species.

Overall, the Swartkrans bone tools may have been used for a variety of tasks, including digging into the ground for tubers, but the strongest evidence lies with termite foraging. Wear patterns on bone tools may not be able to be differentiated between the mounds of different termite taxa, so the best support for which termites would have been being consumed comes from behavioral and ethnographic data. Termites of the genus *Macrotermes* are a likely resource for Plio-Pleistocene hominids, in the author's opinion, since both extant humans and chimpanzees regularly consume them, but there are many other taxa of termites that would have been available and a potential valuable food resource for Plio-Pleistocene hominids.

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