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CREATING A CHRONOCLINE OF THE DIET OF *THEROPITHECUS* FROM LOW-
MAGNIFICATION STEREOMICROSCOPY: HOW HAS THE DIET OF *THEROPITHECUS*
CHANGED OVER TIME?

by

Meri Kathryn Hatchett

Under the Direction of Dr. Frank L. Williams

ABSTRACT

The primate genus *Theropithecus* is represented at various Plio-Pleistocene sites including the Pliocene site of Makapansgat (2.9 mya), the early Pleistocene cave of Swartkrans (1.8 mya), the late Pleistocene deposits from Elandsfontein (700,000 ka) and by extant gelada baboons from Ethiopia. To examine how diet has changed over time in this genus, dental microwear features of *Theropithecus darti* (n=2), *Theropithecus danieli* (n=8), *Theropithecus gelada* (n=2) *Theropithecus oswaldi* (n=1) *Parapapio whitei* (n=14), *Papio robinsoni* (n=16) and *Papio ursinus* (n=13) were examined under low-magnification (35x) using light refractive technology. Although there is a significant relationship between small pits and fine scratches, Analysis of Variance followed by Tukey's post-hoc tests failed to demonstrate significant groupings. However, bivariate analyses suggest that as scratch count increases, pit count decreases. The results suggest that there is much dietary variation in modern and extinct gelada baboons, but that extant *Theropithecus* relies somewhat more on grassland resources than did their extinct counterparts.

INDEX WORDS: *Theropithecus*, Dental Microwear, LMS

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An Honors Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Bachelor of Arts in Anthropology

in the College of Arts and Sciences

Georgia State University

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May 2011

DEDICATION

This thesis is dedicated to my father, Billy Roy Hatchett. You were my number one fan and without your support, I would never have accomplished this.

ACKNOWLEDGEMENTS

I would like to thank Frank L. Williams for his continued support and guidance throughout the research and writing of this thesis and the entirety of my undergraduate career. He was both an excellent teacher and a priceless advisor and kindled in me a love for research and a deeper understanding of Anthropology as a science. Without his counsel, this project would have certainly been a much more difficult endeavor. I would also like to thank the Department of Anthropology at Georgia State University for the use of the dental microwear collection without which my research would not have been possible.

TABLE OF CONTENTS

DEDICATION	iv
ACKNOWLEDGEMENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
INTRODUCTION	1
LITERARY REVIEW	
THE ENVIRONMENT OF <i>THEROPITHECUS</i>	2
EXTINCT <i>THEROPITHECUS</i>	3
EXTANT <i>THEROPITHECUS</i>	8
<i>PAPIO</i> AND <i>PARAPAPIO</i> SPECIES	
12	
MATERIALS AND METHODS	14
RESULTS	18
DISCUSSION	
LEAST-SQUARES REGRESSION AND ANOVA	22
COMPARISONS TO THE USE-WEAR TROPHIC TRIANGLE	23
DISCRIMINANT FUNCTION ANALYSIS	23
PALEOENVIRONMENT	24
CONCLUSION	25
REFERENCES	27

LIST OF TABLES

Table 1: Assumed diets of <i>Theropithecus</i> , <i>Papio</i> and <i>Parapapio</i> species	17
Table 2: Canonical Scores Axis	21

LIST OF FIGURES

Figure 1: MP 222 <i>Theropithecus darti</i>	4
Figure 2: SK 561 <i>Theropithecus oswaldi danieli</i>	6
Figure 3: Least Squares Means analysis of small pits among taxa	18
Figure 4: Least Squares Means for fine scratches among taxa	19
Figure 5: Trophic Triangle	20
Figure 6: Canonical Scores Axis	21

Introduction

The genus *Theropithecus* has been found at sites in southern, western and eastern Africa, many of which were also sites of early hominin activity. *Theropithecus gelada*, the only extant species of *Theropithecus*, is a strict granivore, relying on C⁴ grasses to make up more than 90% of its diet (Rowe, 1996). Because of the low nutritional content of the grasses that make up the diet of *T. gelada*, the species must spend the majority of its day grazing in order to fulfill its dietary needs. However, the genus *Theropithecus* was not always the strict granivore that it is today and past species exploited food far outside the range of modern-day *T. gelada*. While *Theropithecus* is not as closely related to *Homo*, it is a relevant non-human primate to study because it has shared much of its evolutionary past with various hominin species. Therefore, it can give the researcher insight into the environments in which the ancestors of modern humans, lived, subsisted and died.

Baboon species like *Theropithecus* can serve as an ecological model for early hominins because of the assumption that both hominids and living African apes are descended from *Dryopithecinae*. In C.J. Jolly's article entitled, "The Seed-Eaters: A New Model of Hominid Differentiation Based on Baboon Analogy," Jolly creates a table comparing various characteristics, "by which either early Pleistocene Hominidae differ from *Pan* or *Theropithecus* from *Papio* and *Mandrillus*," (Jolly, 1970). Twenty-two out of forty-eight characteristics are common between the two adaptive complexes and include adaptations like: open-country habitat, one-male breeding unit, accessory sitting pads (fat deposits of buttocks) present and a reduced premaxilla, (Jolly, 1970). This provides reasonable evidence of parallelism between the evolution of the two species and because of the significantly fewer hominid characteristics that appear in *Papio* as opposed to *Theropithecus*, it is safe to assume that the common characteristics

are not due to chance (Jolly, 1970). These common evolutionary adaptations enable researchers to use the evolution of the genus *Theropithecus* as a model for that of *Homo*. Therefore, by studying *Theropithecus*, its diet and its evolutionary changes, it is possible to get a better picture of the ancestors of modern humans and the changes that occurred in recent *Homo sapiens sapiens*.

Sites like Hadar in modern-day Ethiopia, Laetoli in Tanzania, Olorgesailie in southern Kenya and Elandsfontein in South Africa have all been home to *Theropithecus* species, which lived sympatrically with various ancient hominins. By studying the dental remains of *Theropithecus* from these and other Plio-Pleistocene sites, as well as those of modern-day *T. gelada*, researchers are able to form dietary inferences, which can then lead to assumptions about the environments in which *Theropithecus* and hominins existed. Assessing what resources *Theropithecus* was exploiting enables researchers to know what foods were available for *Homo sapiens* who existed in the same regions. In this study, 56 specimens were observed using low-magnification light refractive microscopy (LMS). This allowed for the study of the microwear signals of each individual based on number of pits and scratches on the chewing surfaces. This information was then included in various statistical analyses in order to group the specimens based on number of pits and scratches. From the results, assumptions as to the diets of each group and the environments in which they lived were inferred. This, in turn, afforded a better picture of the environmental pressures that caused them to subsist in the ways in which they did.

Literary Review

The Environment of *Theropithecus*

The genus *Theropithecus* has been in existence for more than 3 million years and has been located at various sites including Swartkrans, Makapansgat and Elandsfontein where fossil

hominins, like various members of the *Australopithecus* genus, have also been discovered. Elandsfontein has also been associated with the genus *Homo*. The information that can be gleaned from the diet of *Theropithecus* can not only lead us to conclusions about its own subsistence, but also about what foods were available in each area and time period in which it has been found. Because human ancestors also inhabited these sites at the same time, it can also lead to conclusions about the diets of humanity's ancestors as well.

In Africa, throughout the Miocene, C⁴ grasses may have been present but closed, wooded, bush-dominated and forested regions were much more prevalent, which indicates a C³ grassland environment (Bobe and Behrensmeyer, 2004). During the Pleistocene, from about 2.6 million to 12,000 years ago, C⁴ grasses became more common, providing a much greater variety of food sources for *Theropithecus* (deMenocal, 2004). C⁴ grasses can include anything from tropical grasses and sedges to rootstocks and herbaceous dicots and are usually found in either disturbed ground or wetlands (Peters and Vogel, 2005). The percentage of C⁴ grasses fluctuated between 20 and 70% and, according to deMenocal (2004), was much higher during glacial periods. The expansion of C⁴ grasses during the Plio-Pleistocene enabled *Theropithecus* to thrive in southern Africa, beginning with its earliest species, *Theropithecus darti*.

Extinct *Theropithecus*

T. darti, located, among other places, at the Plio-Pleistocene site of Makapansgat Valley dated to 2.9 million years ago, had a mixed diet made up of predominantly C⁴ grasses with C³ grasses accounting for a smaller proportion (Fourie et al., 2008). This was at one time thought to be the oldest of the *Theropithecus* deposits but *Theropithecus* has more recently been found at East African sites from close to 4 million years ago, suggesting an earlier origin than the 2.9 million years ago Makapansgat deposits indicate. According to research done on the pitting

incidence and scratch breadth of *T. darti* compared to that of *T. gelada* and *Colobus guereza*, *T. darti* was mainly a grass and/or leaf eater (El-Zaatari et al., 2005). At the time of *T. darti* occupation at the cave site of Makapansgat, the environment was a mix of both C³ and C⁴ grasses but, based on data from flowstones collected from the site, C⁴ grass expansion was a recent development, beginning at the end of the late Neogene (Hopley et al., 2007). Due to local and global climatic fluctuations, after the initial expansion of C⁴ grasses at the end of the late Neogene, southern Africa experienced a greater incidence of variability in the proportion of C³ and C⁴ grasses throughout the Plio-Pleistocene (Hopley et al., 2007).

Figure 1: MP 222 *Theropithecus darti* – lateral view



According to Sponheimer and Lee-Thorpe (2003), the site of Makapansgat was a much more closed environment around 3 million years ago. The percentage of alcelaphini (includes hartebeests, wildebeests, and topis) and antilopini (any of the several ruminants of the family Bovidae having permanent, hollow, unbranched horns), found at Makapansgat suggests

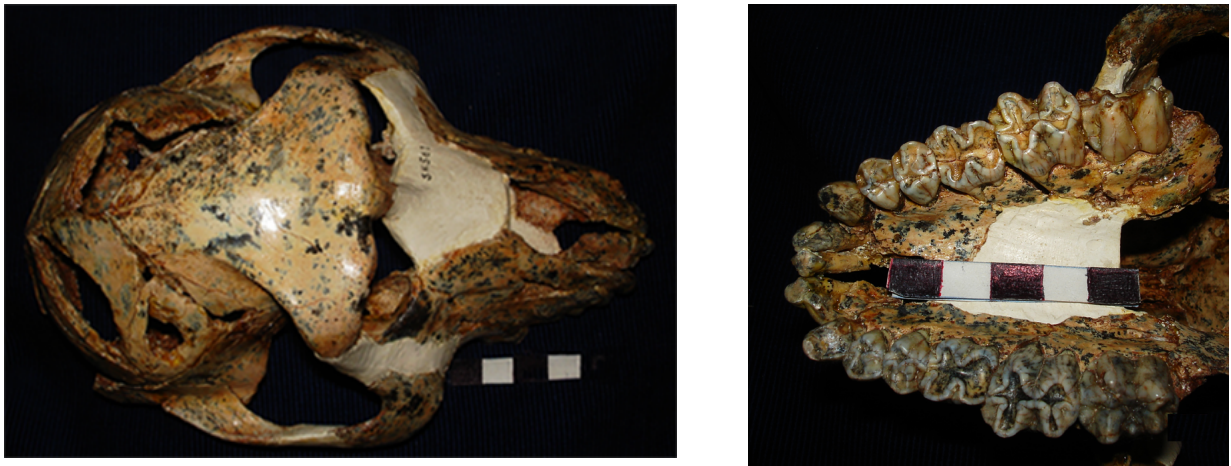
considerable tree and brush cover (Sponheimer and Lee-Thorpe, 2003). The percentage of alcelaphini and antilopini was around 28% and it never exceeds 30% of the total bovid population in areas with extensive tree and brush cover (Sponheimer and Lee-Thorpe, 2003). A closed environment would have much fewer C⁴ resources than an open, savannah-like environment and perhaps explains the reason for the reliance on both C³ and C⁴ resources by *T. darti* at the site of Makapansgat.

T. darti was found not only in the Makapansgat Valley but also at the Hadar site in East Africa and was more recently found to have inhabited a site in the Luangwa River Valley (LRV) in eastern Zambia (Elton et al., 2003). A nearly complete, mineralized right femur, which had been fossilized under waterlogged conditions, was found at the LRV site (Elton et al., 2003). While *Theropithecus* was fairly widespread throughout the Plio-Pleistocene, this find extends the known range of *Theropithecus* in Africa (Elton et al., 2003). It is believed that this region of Zambia was used as a dispersal corridor for East and southern African faunas and may provide a link between East and southern African *Theropithecus* populations (Elton et al., 2003).

Theropithecus oswaldi was an exceptionally widespread species throughout the Middle Pleistocene and has been located in East, northern and southern Africa (Frost and Alemseged, 2007). Two subspecies of *Theropithecus oswaldi*, including *T. oswaldi danieli* (Fig. 2) and *T. oswaldi oswaldi*, have been found in Africa. *T. oswaldi oswaldi* was recovered at the Upper Pleistocene site of Elandsfontein, near Hopefield, South Africa (Dechow and Singer, 1984). This *T. oswaldi oswaldi* specimen is a much more recent deposition, with Elandsfontein being dated at around 700,000 years ago. At this point, little is known about *T. oswaldi oswaldi* and much more information is available for *T. oswaldi danieli*. However, it is presumed that *T. oswaldi oswaldi* had a possible omnivorous diet, subsisting on grass seeds, dry and fresh grass blades and

stems, roots and small bulbs (Dechow and Singer, 1984). Around the time of the Elandsfontein deposition, the environment is described as a grassy, “bushveld” (sub-tropical woodland) environment with a warm summer growing season (Luyt et al., 2000). This type of environment is, in most cases, associated with C⁴ grasses, supporting the assumption that *T. oswaldi oswaldi* had a largely graminivorous diet. However, according to Stynder (2009), the environment of Elandsfontein during the Middle and Upper Pleistocene consisted of extensive C³ grasslands as well as trees, broad-leaved bushes and fynbos. Regardless of whether there was a majority of either C³ or C⁴ grasses, it can be assumed that *T. oswaldi oswaldi* relied heavily on grasses for its sustenance, along with smaller amounts of roots, seeds and bulbs.

Fig. 2 SK 561: *Theropithecus oswaldi danieli*, superior view (left) and basilar view (right) – The high shearing crests on the third molars were used to process the grasses that made up much of the diet of *T. oswaldi danieli*.



Theropithecus oswaldi was one of the most widespread of the Plio-Pleistocene primates. It has been found in East Africa, northern and southern Africa, Spain and India (Hughes et al., 2008). Currently, the only proof of *Theropithecus* occupation in Europe is an isolated fossil tooth from the early Pleistocene at Cueva Victoria, Spain (Patel et al., 2006). Patel et al. (2006) also addresses the claim that *Theropithecus* dispersed out of Africa as early as 1.6-1.3 million years

ago based on cervical vertebrae found in Pirro Nord, Italy. According to a study done by Patel et al., they determined that it is extremely difficult to accurately match cervical vertebrae with its proper genus and therefore they reject the claim that *Theropithecus* was present in Italy (Patel et al., 2006). Rook et al. (2004) are in favor of attributing the cervical vertebrae to *Theropithecus*. However, because the only reasoning they have for this assumption is that the sheer size of the vertebrae is indicative of *Theropithecus*, they have yet to be able to properly substantiate their claim (Rook et al., 2004).

Theropithecus in southern Africa also relied heavily on C⁴ grasses with a smaller C³ component (Fourie et al., 2008). However, according to Codron et al. (2005) and El-Zaatari et al. (2005), *T. oswaldi* incorporated a wider variety of food items into its diet than modern-day *T. gelada*, including a greater reliance on fruits and C³ vegetation. *T. oswaldi danieli* has been located at both sites of Swartkrans and Sterkfontein Member 4 (2.6-2.0 million years ago) (van der Merwe et al., 2003). At both sites, the specimens exhibited the thin tooth enamel and reliance on C⁴ resources that characterize *Theropithecus* (van der Merwe et al., 2003). Because of the reliance on a granivorous diet by *Theropithecus*, it is assumed that they possess a need to retain sharp shearing crests for the act of breaking down their food (Macho and Shimizu, 2009). This need for sharp leading edges indicates that *Theropithecus* species in general do not have very wear-resistant teeth (Macho and Shimizu, 2009).

Theropithecus oswaldi danieli has also lent itself to the study of the connection between crown formation time and body mass/brain size in non-human primates. According to Macho (2001), there is a distinct correlation between the pattern and timing of tooth eruption and life history variables like brain size. However, certain non-human primates like *Theropithecus* and *Gorilla gorilla* depart from this pattern by being large bodied but having a more swift crown

formation time (Macho, 2001). *T. oswaldi danieli* dentition has also been studied in order to observe stress during odontogenesis. Eleven *T. oswaldi danieli* molars were studied and while none of them exhibited hypoplasias, they did display accentuated striae of Retzius (Macho et al., 1996). Striae of Retzius, while normal at weekly intervals throughout growth and development, can also manifest during periods of metabolic disturbances (Macho et al., 1996). Accentuated striae of Retzius would appear during times of food scarcity like the height of the dry season for *Theropithecus oswaldi danieli* (Macho et al., 1996).

One of the oldest representatives of the *Theropithecus* genus that has been discovered is an almost complete skeleton of *Theropithecus brumpti* found at the site of Lomekwi, west of Lake Turkana, Kenya dated to around 3.3 million years ago (Jablonski et al., 2002). According to Jablonski et al. (2002), this specimen exhibits some of the key characteristics that set *Theropithecus* apart from many other non-human primates including adaptations for manual grasping and fine manipulation. Features like the proportions of the digital rays and a large, retroflexed medial humeral epicondyle indicate the capability for precise opposition between thumb and forefinger (Jablonski et al., 2002). These unique characteristics of *T. brumpti* indicate that through time, from even one of the earliest recognized remains of *Theropithecus*, they have displayed the food harvesting and processing anatomy that have set *Theropithecus* species apart throughout the entirety of its existence (Jablonski et al., 2002).

Extant *Theropithecus*

During the Plio-Pleistocene, the genus *Theropithecus* thrived on both the African and Eurasian continents. However, there is now only one species located in the Ethiopian highlands known as *Theropithecus gelada*, or the gelada baboon (Belay and Shotake, 1998). Gelada baboons live in fairly large groups where it is highly unlikely that each individual recognizes all

the other group members. Therefore, they must have a way of assessing others for reproductive mates. Bergman and Beehner (2009) studied a group of known individuals from a population of gelada baboons in Ethiopia and found that in males, the redness of the “bleeding heart” on their chests was a type of quality signal. They found a distinct correlation between color saturation and status within the group even when controlling for age (Bergman and Beehner, 2009). Leader males, the only ones with reproductive access to the females, had redder chests than other males and within the leader male population, those with the reddest chests had the largest groups (Bergman and Beehner, 2009). It is clear that even within such a small population of primates, quality breeding is still of the utmost importance.

The majority of the *T. gelada* population lives in the northern part of the Rift Valley at altitudes varying from 2,000 to 4,500 meters (Belay and Shotake, 1998). There is also a small population of gelada baboons living in the southern part of the Rift Valley. According to Belay and Mori (2006), the two populations (currently living in four separate groups) actually possess varying genetic information making the two groups living in the northern part of the Rift Valley a distinct subspecies from those living in the southern part of the Rift Valley. The genetic variation of the two groups was investigated using restriction fragment length polymorphism (RFLP) of mitochondrial DNA (D-loop), which informed the researchers that the northern and southern groups formed two distinct gelada haplotype clades distinguished by a 9.8% sequence divergence (Belay and Mori, 2006). This sequence divergence is a magnitude higher than intraspecific population differences reported for mammals. Therefore, it can be assumed that the two populations are distinct subspecies, the northern population referred to as *T. gelada gelada*, and the southern as *T. gelada obscurus* (Gippoliti, 2010). A conservative estimate for the split of the northern and southern *T. gelada* populations would range from 696,000 to 1,637,000 years

with an average of 1.17 million years, giving the two subspecies ample time to form their own genetic variations (Belay and Mori, 2006).

While the differences in *T. gelada gelada* and *T. gelada obscurus* are minimal, there are a few noticeable distinctions like the darker colored dorsal fur and flesh colored face of *T. gelada obscurus* (Belay and Shotake, 1998). In 1990, a third distinct group of *T. gelada* was discovered in the Eastern Highlands of the Arsi Region, close to the Bale National Park (Gippoliti, 2010). Based on preliminary research, it has been proposed that the Arsi Region group can be regarded as yet another distinct subspecies (Gippoliti, 2010). According to Gippoliti (2010), the confusion and lack of clarity as to the correct taxonomy of *Theropithecus* could negatively affect conservation strategies. As of his article in 2010, only a small part of the range of *T. gelada* is currently protected by the Semien National Park (Gippoliti, 2010).

T. gelada has a very similar diet to previous *Theropithecus* species, with more than 80% of their diet made up of grass blades (Mau et al., 2009). They have also been known to seasonally feed on seeds and lesser amounts of herbs and fruits (Mau et al., 2009). Studies have been performed on the salivary composition of *T. gelada* and have produced results pertaining to their inability to feed on dicot plants (Mau et al., 2009). According to Mau et al. (2009), baboons that consume a high dicot to monocot ratio of plant foods have a higher amount of proline-rich salivary proteins with tannin-binding capacity. Dicots produce tannins as a chemical defense system in order to discourage animals from eating them. However, animals with the ability to bind the tannins are able to eat and extract nutrients from dicots with which they supplement their diet (Mau et al., 2009). Studies performed on the salivary compounds of *Theropithecus gelada* showed that they lack the proline-rich salivary proteins and are therefore unable to consume dicots as a food source (Mau et al., 2009). Whether the lack of tannin-binding proteins

evolved because *T. gelada* had no need for them or the lack forced them into their narrow-feeding niche has yet to be discovered, but it is clear that without the ability to consume dicots as well as monocots, *T. gelada* is much more vulnerable to environmental changes than other baboon species (Mau et al., 2009).

While *T. gelada* is unable to consume dicots, they have been observed to, on occasion, practice insectivory (Fashing et al., 2010). During a recent locust outbreak in the gelada territory of Ethiopia, many animals including *T. gelada*, ravens and a wolf on one occasion were seen catching and eating locusts (Fashing et al., 2010). When the outbreak first began, the geladas appeared to be afraid of the locusts, uttering screams and other loud vocalizations, which are generally associated with fear (Fashing et al., 2010). However, once the locust density decreased, they began to catch them from the air as well as pounce on those already on the ground (Fashing et al., 2010). Once in hand, the males ate the locusts whole and in one bite, while the females would first bite off the heads and spit them out, pluck off the wings and then eat the rest of the locust (Fashing et al., 2010). While this was a rare occurrence for *T. gelada*, it showed researchers that, when confronted with a new food source, gelada baboons would occasionally navigate away from their omnivorous lifestyle and practice insectivory.

Theropithecus gelada has adapted to its diet restrictions over its long existence but it has also had to adapt itself to living at high altitudes in the Ethiopian highlands. At such high altitudes, temperatures frequently drop below freezing. Beehner and McCann (2008) studied the glucocorticoid levels of gelada baboons in order to gauge their stress level during cold weather. Glucocorticoids are hormones that affect the metabolism of carbohydrates and they can be used to track changes in food availability or seasonal stressors (Beehner and McCann, 2008). *T. gelada* exhibited elevated glucocorticoid levels during extreme cold weather but not during times

of heavy rainfall, which have also been known to cause stress for gelada populations (Beehner and McCann, 2008). Gelada baboons have at least two adaptations for living in cold climates, an increased hair density and greater food intake during cold weather (Beehner and McCann, 2008). However, based on their elevated glucocorticoid levels, these changes are not enough to completely rectify their cold stress (Beehner and McCann, 2008).

Gelada baboons respond well to cool, dry climates, which is most likely why they are currently thriving in the Ethiopian highlands regardless of the cold stress their bodies experience during times of extreme cold. However, regardless of their seemingly normal glucocorticoid levels, they do not fair well during the severe wet season conditions (Dunbar, 1980). Based on a study conducted by Dunbar (1980), births within groups were timed in order to decrease the exposure of newborns to the conditions of the wet season. Females in the same reproductive groups experienced close reproductive synchrony, thought to be due to both environmental and social factors (Dunbar, 1980). Extinct *Theropithecus* from southern Africa may also have experienced similar adaptations to cold stress in this temperate region.

Papio and Parapapio Species

The dietary limitations of *Theropithecus*, while making it difficult for them to subsist in a variety of habitats, have enabled them to be sympatric with other baboon species throughout their existence. Particular physical aspects like the elongated muzzle and reduced anterior teeth size of *Theropithecus* when compared to *Papio* and *Parapapio* species are indicative of their distinct dietary habits (Williams et al., 2007). The preference for fruits and seeds in *Papio* limits the competition with *Theropithecus* for food sources because of the omnivorous diet of *Theropithecus*. Also, grasses as well as the fruits preferred by *Papio* and *Parapapio* respond to the same type of environment so each species can easily find enough of their preferred

sustenance in the same environment (Dunbar, 1992). Many species of both *Papio* and *Parapapio* have been sympatric with *Theropithecus* species in the past and still today, *Papio* species are found in the same habitats as *T. gelada*. Among the species that have been and still are sympatric with *Theropithecus* are: *Papio ursinus*, *Papio robinsoni* and *Parapapio whitei*.

The diet of *Papio ursinus* has enabled it to be sympatric with various *Theropithecus* species because its diet complements the C⁴ grass reliance of *Theropithecus*. *Papio ursinus* relies predominantly on C³ resources for its dietary requirements (Codron et al., 2005) and is considered an underground storage organ (USO) specialist, particularly in the dry season (Ungar et al., 2006). During the dry season, hypogeous tubers, bulbs and roots can account for up to 90% of their diet (Ungar et al., 2006). According to El-Zaatari et al. (2005), *P. ursinus* includes some C⁴ resources in its diet but not enough to force them into competition with *Theropithecus*. The microwear signal for *P. ursinus*, for the most part, arises from the exogenous grit attached to USOs (Daegling and Grine, 1999), which produces a larger amount of pitting and thicker scratches on the chewing surfaces (Ungar et al., 2006).

Papio robinsoni was found along with *Theropithecus oswaldi danieli* at Swartkrans and is dated to about 1.8 million years ago. According to El-Zaatari et al. (2005), *P. robinsoni* consumed a diet made up of predominantly C³ resources and, unlike *P. ursinus*, did not utilize C⁴ resources to supplement its diet. Codron et al. (2005) also noted that *P. robinsoni* had a diet indistinguishable from that of C³-browsing ungulates from Swartkrans. Because of its reliance on C³ resources, one would expect to find a higher pit and scratch frequency and more robust microwear features in general than one would find on *Theropithecus*.

Parapapio whitei, sympatric with *T. darti* at Makapansgat, had an intermediate diet, consisting of both C³ and C⁴ resources with the C³ component being slightly stronger (Fourie et

al., 2008). The diet of *Pp. whitei* consisted of rootstocks, fruits and the underground parts of plants, resources for which *T. darti* had little use (Fourie et al., 2008). It is clear when investigating the diets of these *Papio* and *Parapapio* species why they were so successful at being sympatric partners with various *Theropithecus* species.

Materials and Methods

In order to collect data from primate dentition, casts were made of the molars from museum specimens. In this analysis, 56 specimens were utilized, including *Theropithecus danieli* (n = 8), *Theropithecus darti* (n = 2), *Theropithecus gelada* (n = 2), *Theropithecus oswaldi* (n = 1), *Parapapio whitei* (n = 14), *Papio robinsoni* (n = 16) and *Papio ursinus* (n = 13). Dental impressions were molded on location at the museums where the original specimens are housed, including the Transvaal Museum, the University Witwatersrand Medical School, the South African Museum and the Museum of Comparative Zoology at Harvard University. The impressions were created using polyvinylsiloxane dental impression material (“President Plus Jet Regular Body, Surface Activated 4605” Coltene/Whaledent Inc.) (Semprebon et al., 2004). In some cases, previously applied shellac remained on the dentition. In such instances, they were cleaned with a shellac remover (Zip-Strip, Star Bronze Co.), followed by 95% alcohol (Semprebon et al., 2004). Once the teeth were cleaned and the molds formed, resin casts were created from the molds by mixing resin and hardener and pouring it into the putty receptacles (EpoKwick, Buehler Ltd.) (Williams and Patterson, 2010).

Once the resin casts were prepared, they were examined using the technique of low-magnification light refractive microscopy (LMS). This technique uses an oblique light source in order to illuminate reflective microwear features on the resin casts. With this technique, there is no need to distinguish particular features by measurement. Microwear features were observed

and counted on the paracone of M^2 . Using a standard 0.4×0.4 ocular reticle, features were counted on two occasions and a mean was taken from the two trials. The unique reflective signature of each microwear feature distinguishes it from other features. In the research conducted for this analysis, features including small pits, medium pits, large pits, fine scratches and coarse scratches were observed based on their shape and reflective properties. Small pits are shallow and completely encompassed within the ocular reticle and are fully visible under the external light source. They also easily refract light. Medium and large pits are slightly less refractive and while medium pits are at least 50% larger than small pits, large pits are at least twice the size of small pits. Fine scratches are refractive and shallow while coarse scratches are slightly less refractive and noticeably deeper. Pits and scratches are indicative of particular feeding practices when found in abundance. A high pit count is generally attributed to hard-object feeding in ungulates and primates, while a high fine scratch count is associated with gramnivory. Coarse scratches, however, point to a diet made up of much more than just grasses and could be caused by anything from small rocks and grit, which adhere to underground storage organs or to the hard edges of seeds consumed by seed predators (Williams and Patterson, 2010).

In order to avoid intra-observer error, all of the data were collected by the author. An error study was performed on microwear counts of 8 specimens. On two separate occasions, microwear features were counted on the specimens and were then analyzed by a t-test and a Mann-Whitney U test in order to measure the intra-observer error. For the majority of the microwear features, including small pits, medium pits, large pits and fine scratches, the t-test and Mann-Whitney U test yielded insignificant differences between the two trials (p values = 0.744-0.108 for t-test and 0.898-0.107 for Mann –Whitney U test). The p value for coarse scratches was significant, at 0.019 for the t-test and 0.025 for the Mann-Whitney U test. However, this can be

explained by the fact that no coarse scratches were observed on the first trial, yet they were observed on three specimens in the second trial.

Theropithecus species are frequently assumed to be gramnivores because of the high percentage of grasses that comprise the diet of *Theropithecus gelada* (Table 1). However, because of the drastically altered climate in southern, eastern and western Africa where *Theropithecus* has lived, it has relied on a vast array of food types over the past several millions of years. By comparing the microwear signatures of the various species of *Theropithecus* with the *Papio* and *Parapapio* species with which they were once sympatric, one can both better understand the environment in which the primates were living as well as better isolate the plant species that each primate relied upon. When employing LMS, a microwear signature consisting of a high number of scratches and a low number of pits is associated with gramnivory, a low number of each is indicative of folivores and a high number of each signifies what was most likely to be a seed predator or extractive forager. After the microwear data were collected, a series of statistical analyses were run in order to infer the meaning of the data. A one-way analysis of variance (ANOVA), with posthoc Tukey's Honestly Significant Differences (HSD), was utilized to compare differences between the 7 species separately for each feature. In order to determine the significance of the relationship between each pair of microwear features, linear regressions were performed. In order to show the overall variations between the species with respect to the features, a bivariate plot was included. Discriminant function analysis was also included utilizing the three microwear features best represented in the sample to examine the relationship among individuals using multiple variables and to estimate classification rates.

Based on the information in Table 1 as well as information about the environment in southern Africa when *Theropithecus* existed, it is presumed that *Theropithecus gelada*, *T. darti*

and *T. oswaldi* specimens will exhibit fewer microwear features overall and a higher proportion of scratches to pits because of their tendency toward grammivory. However, since *Papio ursinus* and *P. robinsoni*, as well as *Parapapio whitei* have a much more varied diet, the microwear results for each species will differ greatly but show a higher abundance of pits and microwear features in general.

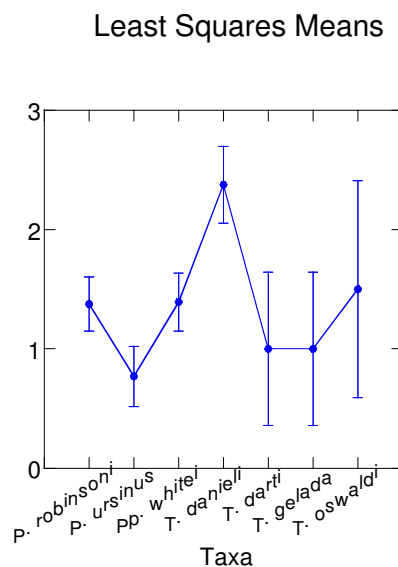
TABLE 1 – Assumed diets of *Theropithecus* species as well as *Parapapio* and *Papio* species.

Genus	Inferred Diet	Source
<i>Theropithecus oswaldi danieli</i>	Largely C ⁴ diet, characteristic of grazers; including tropical grasses and certain sedges. Some reliance on fruits and C ³ vegetation.	Fourie et al. (2008) and Codron et al. (2005)
<i>Theropithecus darti</i>	Largely C ⁴ diet, characteristic of grazers; including tropical grasses and certain sedges.	Fourie et al. (2008)
<i>Theropithecus gelada</i>	Grammivorous; more than 80% of diet made up of grass blades. Seasonally feed on seeds and lesser amounts of herbs and fruits. They very occasionally eat insects.	Mau et al. (2009)
<i>Theropithecus oswaldi oswaldi</i>	Possible grammivorous diet including: grass seeds, dry and fresh grass blades and stems, roots and small bulbs.	Dechow and Singer (1984)
<i>Parapapio whitei</i>	Intermediate diet including both C ³ and C ⁴ resources; rootstocks, fruits and the underground parts of plants.	Fourie et al. (2008)
<i>Papio robinsoni</i>	Predominantly C ³ based diet. Between 20% and 30% leaves and 50%-70% fruits.	Codron et al. (2005)
<i>Papio ursinus</i>	Predominantly C ³ based diet; trees, shrubs and forbs. Very little grass.	Codron et al. (2005)

Results

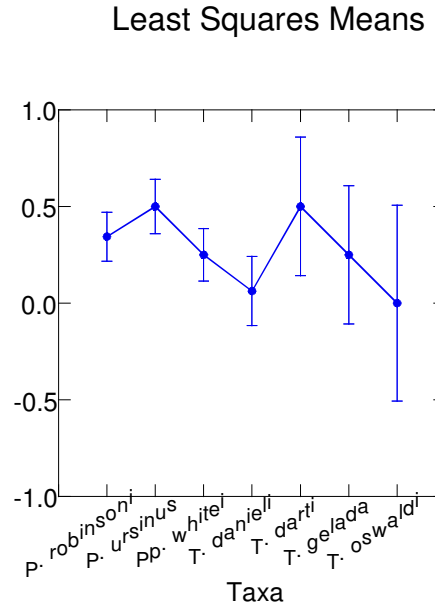
For the statistical analysis, ANOVA and Least Square Means were calculated, along with Discriminant Function Analysis. Least Square Means are estimates and ranges of variation for traits derived from Model 1 regression of each microwear feature for each taxon. They reflect ANOVA F and p values and mimic post-hoc Tukey's Honestly Significant Differences in terms of displaying significant differences in the projected distribution of taxa. Discriminant Function Analysis was conducted with small pits, fine scratches and coarse scratches to show which traits separated taxa. Only small pits showed significant differences among taxa ($p=0.025$). In Least Square Means for small pits, *Theropithecus oswaldi danieli* exhibited the greatest number of pits (Fig. 3). *Papio ursinus* showed the least amount of small pits (Fig. 3). *Papio robinsoni* and *Parapapio whitei* are intermediate between these two extremes. Tukey's significance test shows that the significant p value is actually stemming from significant differences between *P. ursinus* and *T. oswaldi danieli* ($p = 0.005$) with the former exhibiting significantly smaller numbers of small pits than *T. oswaldi danieli*.

Figure 3 – Least Squares Means analysis of small pits among taxa.



For fine scratches in the Least Square Means analysis, some substantial differences between taxa exist, the most noticeable being that of *P. ursinus*, which exhibits a greater number of fine scratches when compared to *T. oswaldi danieli*, which shows a relatively small number of scratches (Fig. 4). These differences, however, are not statistically significant.

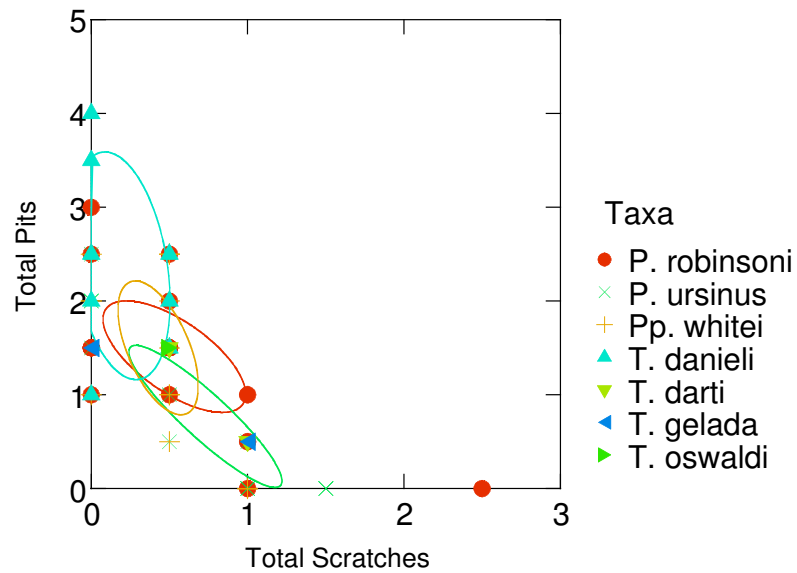
Figure 4 – Least Squares Means for fine scratches among taxa.



A trophic triangle (Semprebon et al., 2004) was created to compare total pits to total scratches across the entirety of the specimens. In Semprebon et al. (2004) the trophic triangle separates grassland foragers with a relatively large number of scratches and few pits from hard-object feeders, which exhibit few scratches and a large number of pits. In the trophic triangle, *P. robinsoni*, *T. gelada* and a few individual *P. ursinus* show the greatest number of scratches relative to pit density. These are distinct from some *P. robinsoni* and *T. oswaldi danieli* specimens, which exhibit relatively large numbers of pits with respect to the density of scratches (Fig. 5). The fact that *P. robinsoni* exhibits such a wide breadth of values for pits and scratches suggests a variable diet with some individuals exploiting primarily grasses and others

concentrating on hard-object foods, possibly including underground storage organs. This variable feeding habit would most likely be related to the changes in food availability during the different seasons. *P. robinsoni* was most likely forced to subsist mainly on grasses during the warm summer months and rely on underground storage organs during the cold winter months.

Figure 5: Trophic triangle – Total pits (y-axis) compared to total scratches (x-axis)

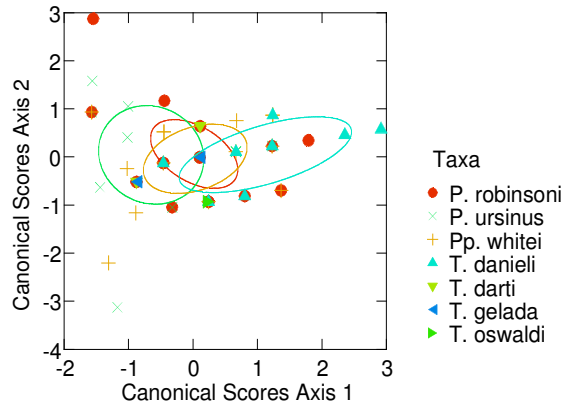


Small pits, fine scratches and coarse scratches were compared together in a Discriminant Function Analysis, and shown on Canonical Scores axes 1 and 2 (Fig. 6 and Table 2). Here, *T. oswaldi danieli* is nearly distinct from *P. ursinus* on the basis of fine scratch count in the former and coarse scratch count in the latter on the first CS axis. On the second CS axis, one *P. robinsoni* individual is polarized on the positive extreme from one *P. ursinus* positioned on the negative extreme (Fig. 6). The rather low function scores (Table 2) prohibit definitive explanations of these extremes, although the relatively high loading for small pits is suggestive of being at least partially responsible for the projection of the lone *P. ursinus* positioned positively on this axis.

Table 2: Canonical Scores Axis

Feature	CS Axis 1	CS Axis 2
Small pits	1.023	0.213
Fine scratches	0.655	1.103
Coarse scratches	0.599	1.013

Figure 6: Canonical Scores Axis



The post-hoc Tukey’s Honestly Significant Differences analysis showed that the specimens had only one real grouping, which occurred between *Theropithecus oswaldi danieli* and *Papio ursinus*. This is most likely an effect of the vast difference between their respective amounts of small pits in the ANOVA and shows that the specimens used in this experiment all had variable diets, which failed to exhibit the clear microwear signals of species with more restrictive diets.

Discussion

The statistical analysis results allow for a number of varied predictions as to the evolution of the genus *Theropithecus* over time and the environment of a myriad of sites in Africa where both *Theropithecus* and a number of australopithecine taxa have resided in the past. The most noteworthy conclusion that can be drawn from the statistical analysis is the sheer variability in the diets of each species. During the Pleistocene, southern and eastern Africa were experiencing drastic changes in temperature and humidity levels, which allowed for the expansion of C⁴

grasses into what had previously been a C³ dominated environment (deMenocal, 2004). This directly affected the food resources of *Theropithecus*, *Papio* and *Parapapio* species enabling them to partake in a more diverse diet. This diverse diet manifested itself in the wide array of microwear scars on the chewing surfaces of each specimen.

Least-Squares Regression and ANOVA

The Least-Squares regression exhibited *Theropithecus oswaldi danieli* as having a higher than expected number of pits, which speaks to its reliance on a variety of food sources, possibly including fruits and USOs. This is in congruence with Codron et al. (2005) and El-Zaatari et al. (2005), who stated that *T. oswaldi danieli* incorporated a wider variety of food items into its diet than modern-day *T. gelada*, including a greater reliance on fruits and C³ vegetation. In the same test, *Papio ursinus* represented the opposite extreme, exhibiting much fewer small pits and a greater number of fine scratches. This finding is in opposition to Daegling and Grine (1999), who observed that the microwear signal of *P. ursinus* was mainly created from the exogenous grit attached to the USOs, which produces a larger amount of pitting and thicker scratches. However, Williams and Patterson (2010) have referred to *P. ursinus* as a habitat generalist and it has been observed that their diet changes drastically depending on the seasons; during the winter months they rely much more heavily on USOs and supplement their summer diet with a much higher concentration of grasses. *Papio robinsoni* and *Parapapio whitei* were intermediate between the two extremes of *T. oswaldi danieli* and *P. ursinus*, between whom the only significant differences were found. The lack of a significant lean toward pits or scratches in *Pp. whitei* is in agreement with the findings of Fourie et al. (2008), who stated that *Pp. whitei* had an intermediate diet, consisting of both C³ and C⁴ resources with the C³ component being slightly stronger.

Comparisons to the Use-Wear Trophic Triangle

A trophic triangle was also created in order to compare total pits to total scratches. The trophic triangle separates grassland foragers with relatively large numbers of scratches and few pits from hard-object specialists with few scratches a large number of pits (Semprebon et al., 2004). As is to be expected, *T. gelada* is shown as having a much greater number of scratches than pits and is also grouped with *P. ursinus*, which coincides with its Least-Squares regression signature showing similar results. *T. oswaldi danieli* appears on the opposite end of the spectrum on the trophic triangle with a greater number of pits in comparison to scratches, which is also congruent with its Least-Squares regression results. *Papio robinsoni* showed much more variable results, with more pits than scratches but not to the extent of *T. oswaldi danieli*. These results differ somewhat from El-Zaatari et al. (2005), who stated that *P. robinsoni* consumed a diet comprising of predominantly C³ resources and did not utilize C⁴ resources to supplement its diet. Codron et al. (2005) noted that *P. robinsoni* had a diet indistinguishable from that of C³-browsing ungulates from Swartkrans. However, the results of both the Least-Squares regression and the trophic triangle for *P. robinsoni* insinuate that it possessed a highly variable diet with some individuals concentrating primarily on grasses as a food source and others subsisting on hard-object feeders, including presumably USOs.

Discriminant Function Analysis

The microwear features that occurred the most, small pits, fine scratches and coarse scratches, were compared in a discriminant function analysis, and shown on Canonical Scores axes 1 and 2. The main information gleaned from this exercise was that *T. oswaldi danieli* is nearly distinct from *P. ursinus* on the basis of fine scratch count in the former and coarse scratch

count in the latter on the first CS axis. This reiterates the trend seen previously, which separates *T. oswaldi danieli* and *P. ursinus* based on scratch and pit counts.

Paleoenvironment

The results of the statistical analysis are in some ways unexpected based on the lack of distinct groupings within the specimens. However, *T. gelada* is the one species that showed the expected results, having a high number of fine scratches and a low number of pits due to its reliance on grasses for more than 80% of its diet (Mau et al., 2009). The results are indicative of a great amount of dietary variation in virtually every specimen, which is congruent with the expansion of C⁴ grasses from about 2.6 million to 12,000 years ago (deMenocal, 2004). This provided a much greater variety of food sources for *Theropithecus* as well as those with whom they were sympatric.

Because *Theropithecus* species have been known to be sympatric with various hominin species, it is possible to use dietary information of *Theropithecus* gleaned from this study in order to create a partial reconstruction of the environment of fossil hominins. Early *T. darti* had a diet made up of a variety of resources including grasses and leaves, and was possibly an occasional frugivore, based on pitting incidence (El-Zaatari et al., 2005). At the time of *T. darti* occupation at the cave site of Makapansgat, the environment was a mix of both C³ and C⁴ grasses, which would lead to the assumption that the australopiths who also inhabited this site may have also had a diet with a large grass component. At sites like Olorgesailie in Kenya, *T. oswaldi danieli* has been found with *Homo erectus* remains, which can provide a number of conclusions: *Homo erectus* was possibly hunting and subsisting on *T. oswaldi danieli* and, based on dietary information from *T. oswaldi danieli*, *H. erectus* was most likely supplementing its diet with fruits and C³ vegetation (Codron et al., 2005 and El-Zaatari et al., 2005).

Conclusion

This dental microwear study supported the claim that *Theropithecus* species have relied on C⁴ resources to supplement their diet from their inception but have become increasingly more gramnivorous over the millions of years of their existence. *T. darti* and *T. oswaldi danieli* both relied on C⁴ grasses for a portion of their diet, but supplemented it to a much greater extent with resources such as fruits and leaves. Therefore, they have a much larger number of pits on their chewing surfaces with respect to fine scratches. *T. gelada*, the only extant species of *Theropithecus*, has been known to consume almost exclusively grasses; this was found to be in agreement with the large number of fine scratches and lower number of pits found on the specimens. This expanding reliance on C⁴ resources is likely caused by a number of circumstances, including the general drying trend of southern and eastern Africa during the Plio-Pleistocene, which led to the expansion of grasslands across the environment, as well as the salivary makeup of *Theropithecus*, which puts constraints on the ability of *Theropithecus* to break down certain folivorous resources. This study provided a glimpse of the environments of *Theropithecus*, which in turn furnished information on foods and resources available to australopithecines and *Homo* species, which inhabited some of the same sites in Africa around the same time periods as *Theropithecus*. In turn, this study can provide information on the evolution of the human species and the many roles non-human primates played in that evolution.

By developing a greater understanding of the dietary constraints and food resources available to the ancestors of modern humans, it is possible to form a greater understanding of how and why modern humans evolved in the manner in which they did. The dietary inferences that were made from this research are just one more step towards recreating the various environments in which the ancestors of modern humans resided. By focusing on non-human

primates as a source for ecological information and morphological comparison, it is possible to form a greater understanding of *Homo sapiens sapiens* as a species.

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