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PALEOECOLOGICAL RECONSTRUCTIONS OF THE SOUTH AFRICAN PLIO-PLEISTOCENE BASED ON LOW-MAGNIFICATION DENTAL MICROWEAR OF FOSSIL PRIMATES.

by

BRIAN CARTER

Under the Direction of Frank L'Engle Williams

ABSTRACT

Cercopithecines are common in hominid producing deposits and are a useful proxy for determining the ecological context of the early hominids. For this study, dental microwear is examined through low-magnification stereomicroscopy and used to reconstruct the diets of sampled primates. Those from the earliest sites, predominantly *Parapapio,* are primarily frugivorous while the incidence of gramnivory increases in the later *Dinopithecus, Gorgopithecus,* and *Papio* individuals denoting a general cooling and drying trend over the South African Plio-Pleistocene with a distinct pulse between 1.9-1.8 million years ago (mya). *Australopithecus* is reconstructed as a primary gramnivore which indicates that hominids adapted early in their evolution to expanding grasslands.

INDEX WORDS: Paleoecology, dental microwear, *Australopithecus*, *Parapapio*, *Dinopithecus, Papio, Gorgopithecus*.

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BRIAN CARTER

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Arts

In the College of Arts and Sciences

Georgia State University

2006

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by

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December, 2006

For Buddha

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Chapter I

Introduction

An ecological theory for evolutionary change has always played a predominant role and has been applied specifically to early hominid evolution of the Plio-Pleistocene. Vrba (1975) has proposed that past climate changes in South Africa led to shifts in habitat availability, particularly towards the expansion of grasslands, and assumed that the major hominid events of the Plio-Pleistocene, the divergence of the gracile and robust australopithecines, appearance of early *Homo*, increases in cranial capacity, and the development of stone tool technologies, can all be explained through global patterns of cooling and drying and their effects on local habitat.

There are four cave sites that have produced the richest fossil collections in South Africa. Sterkfontein and Makapansgat are generally assumed to be the oldest sites; Swartkrans and Kromdraai date later into the Pleistocene. Vrba (1999) observed differences in the ecological conditions between these two periods and proposed that these differences may be a causal factor in the observed changes in faunal composition. However, one of the primary problems of the South African caves is the lack of absolute dating methods, making the exact and relative biochronology ambiguous for most of these sites.

The best method for evaluating ecological models of early hominid evolution would be to test the available hominid fossils. The problem, however, is the relative

scarcity of hominid fossils and poor methods of dating for the South African caves. Compared to rich diversity of fossil fauna found at these sites, the early hominids make up only a small percentage. Furthermore, there are gaps in the fossil record for the early hominids, most notably between 2.6-1.9 mya and that makes theories surrounding their evolution problematic.

Thus, other species must serve as proxies for understanding the evolutionary context of the early hominids, and fortunately the South African caves provide a rich diversity of fauna for comparison, the only issue being which species should serve as the best proxy. Researchers have proposed various taxa, bovids (Vrba, 1974; 1975; 1999), suids (Bishop, 1999), microfauna (Denys, 1999), and cercopithecines (Benefit, 1999), but have not necessarily come to the same conclusions. Vrba (1975) sees a definitive pulse in local cooling as indicated by proliferation of grassland adapted bovids, but Reed (1997) argues that the perseverance of so many arboreal and frugivorous species suggests that the ecological changes were not sudden and drastic until well into the Pleistocene.

The most direct evidence of a South African ecological change would be shifts in trophic preferences across taxa. Darwin wrote, "The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or distinct species, which subsist on the same kind of food" (Darwin, 1978:86). Other researchers have examined possible trophic shifts in the fossil record, but this study represents the first application of a new method to cercopithecines found in the South African caves.

The cercopithecines represent the best proxy for understanding early hominid evolution. Hominids and monkeys undoubtedly shared the same geographical areas, they are the most closely related, competed for similar resources, and were hunted by the same predators. The large sample sizes of cercopithecines here allow a reconstruction of the Plio-Pleistocene ecologies in South Africa. Included in the analysis are *Australopithecus africanus* and *Australopithecus robustus*, which provide a means of evaluating the adaptive strategies of the early hominids which allowed them such evolutionary success.

Finally, this study is aimed at evaluating a new method proposed by Semprebon et al. (2004) of examining dental microwear through low-magnification stereomicroscopy. Other lines of evidence have determined the diets of the South African cercopithecines fairly well, and if low-magnification microwear readings can delineate diet comparatively, it will represent a new method in distinguishing trophic differences in the fossil record. These variations in microwear signals across sites will be used to evaluate the hypothesis that if there are large scale shifts in diet across *Cercopithecinae* between older and younger temporal periods, one can assume they are a result of ecological change.

Low-magnification stereomicroscopy has its advantage over other methods. It does not involve destruction of fossil remains like isotopic work, and does not require the intensive preparation and specialized equipment required for electron microscopes. With only a little training, the method is quick and easy. Only a few minutes must be devoted to each tooth and extremely large sample sizes can be generated rapidly. However, it does not include many of the quantitative measurements involved in other microwear methods. Surface features are merely counted and scored, absolute lengths and widths of

pits and scratches are ignored. Despite this, the method has proven useful reconstructing the diets of fossil lemurs (Godfrey et al., 2005), and presumably can do the same for Plio-Pleistocene primates and hominids.

Chapter II

The South African Plio-Pleistocene Caves

The caves in South Africa's Sterkfontein Valley are among the richest paleoanthropological regions in the world, producing most of the fossils integral to our understanding of early hominid evolution. They are somewhat enigmatic for researchers, however, because despite the beautiful hominid fossils regularly discovered there, there is no direct way to situate these finds in time. Many other hominid localities, such as East Africa and Indonesia, are volcanic deposits and can be dated using chemical dating methods. The caves have been dated in the best possible ways, although different methods have provided varying dates for each stratum. Although challenging, accurate dating is fundamental to the early hominid evolutionary context. Additionally, the relative biochronology of these deposits is indistinct which makes the paleoecological reconstructions presented here problematic. Specifically discussed are the rates and severity of climate change in the South African Plio-Pleistocene which has been proposed as a causal factor in the major events of hominid evolution. Various researchers have observed speciation and extinction events during this period that cannot adequately be discussed without understanding the depth of time and degree of overlap of each of these caves.

The South African cave deposits are stratigraphically ambiguous with periods of deposition followed by erosion between strata while providing few techniques for

establishing absolute deposition dates in contrast to the volcanic East African sites. At the present, the most common dating method has been biostratigraphic correlations of first and last appearances with well dated East African sites. Essentially, biostratigraphy assumes that southern taxonomic appearances are roughly contemporaneous with those in the east as long as care is taken with the choice of species (McKee et al. 1995).

There are, however, attempts to apply some absolute dating techniques to the South African caves. Electron spin resonance (ESR) dating works because electrons are trapped in a crystalline lattice and remain unchanged once buried underground. Dental enamel is separated from the dentin and ground into a powder and subsequently bombarded with a known dose of gamma rays to separate electrons from their atoms. This changes the magnetic field in a measurable way and predicts the age of mineralization of the sample (Schwarcz et al., 1994; Curnoe et al. 2001).

Paleomagnetic dating is based on changes that occur naturally in the orientation of the Earth's magnetic field. When rocks are formed, the iron in them aligns with the direction of the magnetic pole at the time. Correlations to sites with well known radiometric dates have been used to construct a rough chronology of when these magnetic reversals occurred. The magnetic polarity record of the past few million years can provide the means of dating geologic materials where isotopic determinations are unavailable (Audin et al. 2004).

A newer technique examines the decay rate of aluminum-26 and beryllium-10, common isotopes found in quartz. Muzikar and Granger (2006) explain that surface sediments are bombarded with cosmic rays at a constant rate and atoms of silicone are split into ^{26}Al and ^{10}Be, both of which have half-lives of around a million years. When

buried, the cosmic bombardments stop and given that the decay rate is so slow, biological samples can be dated that are much older than those within the reach of carbon-14 techniques. Aluminum isotopes decay slightly faster than beryllium and comparing the ratios of the two determines the date of burial.

All these methods have been used in conjunction to provide age ranges for the South African deposits. Most agree that Makapansgat Members (Mbrs) 3 and 4 are the oldest at 3.3-2.5 mya based primarily on biostratigraphic correlations with East African sites (Vrba, 1974; Vrba, 1975; Rayner et al. 1993; Schubert, 2006) and paleomagnetic dates (Clarke et al. 2003; Partridge et al 2003). McKee et al. (1995) determined from faunal composition that both strata were roughly contemporaneous although Mbr. 3 produces the most fossils (Reed, 1997). The Taung site, far to the southwest of the rest of the South African sites, is maybe only slightly younger than the Makapansgat deposits. Faunal dating places the famous Taung *Australopithecus* fossil at between 2.8-2.6 mya (McKee, 1993; McKee et al. 1995), although Williams et al. (2006) have suggested that it may be younger, dating closer to the Plio-Pleistocene boundary based on cercopithecine morphological differences from the older sites.

Sterkfontein Mbrs. 2, 4, and 5 are among the richest of the hominid producing sites. Clarke and Tobias (1995) have uncovered an australopithecine, STS 573, in Mbr. 2 that possibly predates Makapansgat, although the dating techniques have generated much controversy. Biostratigraphy has placed Mbr. 2 at 3.5-3.0 mya (Clarke 2002; Clarke et al., 2003) which agree with paleomagnetic dates (Partridge et al., 1999). However, $^{26}Al/^{10}Be$ dating of the sediments in Mbr. 2 with revised paleomagnetic correlations situates STS 573 at greater than 4 mya. Berger et al. (2002), however, suggest that the

ancient dates for Mbr. 2 have been determined through a flawed dating of Mbr. 4. Mbr. 4 has been previously dated by Vrba's bovid biostratigraphic correlations (1974; 1975; 1995; 1999) to be around 2.5 mya, although McKee (1993) mentions that the inclusion of additional fauna and paleomagnetic dates place it a little older. However, Berger et al. (2002) mention that the faunal samples included by McKee et al. (1995) used species that have since been found in much younger sites and were not temporally sensitive. Berger et al. (2002) further explain that the depositional history of Mbr. 4 must have been longer and overlapped some of the later sites. ESR dates from tooth enamel suggest that Mbr. 4 should be dated significantly younger at 2.0 mya (Schwarcz et al., 1994) but that different samples from the site predict remarkably different time periods and that there may either be a long depositional history or admixture from the earliest excavations.

Berger et al. (2002) conclude that Mbr. 4 should be assigned a 1.5-2.5 mya age range and restrict Mbr. 2's age to around 2.5 mya. Clarke (2002) disagrees and concluded that Sterkfontein Mbr. 4 is older and must predate the 2.0 mya Olduvai Bed 1 deposits in East Africa because there is no *Homo*, or early stone tools found that are common at Olduvai. Williams et al. (2006) would also disagree with Berger et al. (2002) and point out the extreme intraspecific variation, small body size, and subtle sexual dimorphism of *Parapapio* as indicative of a late Pliocene deposit.

Although Berger et al. (2002) argue for a much more recent Sterkfontein at 1.5-2.5 mya, their conclusions differ with almost all other lines of evidence and are presented here only to explain the controversy generated in dating the South African sites. Preference here is given to Vrba (1999) and McKee (1993) and situate Sterkfontein Mbr. 4 around 2.5 mya

The chronology of Swartkrans is quite convoluted. Mbr. 1 dates to around 1.8-1.5 mya and consists of a basal level and hanging remnant presumably deposited contemporaneously through different openings in the cave. After a period of erosion creating a cavity between the two, Mbr. 2 was deposited around 1.5 mya, and Mbr. 3 was deposited in a crevice created by more erosion between Mbrs. 1 and 2 (Brain 2004a; Brain 2004b; Churcher and Watson 2004; Watson 2004). Vrba (1975) dates the cave between 2.0-1.0 mya based on biostratigraphic associations with East African bovids. McKee et al. (1995) and Watson (2004) observe a faunal change between Mbrs . 1 and 2 but not 2 and 3, and conclude that two and three are roughly contemporaneous. A minimum of eight *Parapapio jonesi* individuals are found in the hanging remnant of Mbr. 1 which have been found in the older South African deposits but not in the other strata at Swartkrans (Brain, 2004).

Absolute dating methods have been attempted but remain questionable. Curnoe et al. (2001) remark that paleomagnetic dates for Swartkrans were inconclusive due to instability of the samples. Their work on dating the deposits through ESR placed the age of the cave substantially younger than faunal correlations; enamel taken from SKW 11 in the hanging remnant on Mbr.1 dates to 1.6 mya and situate bovids from Mbrs. 2 and 3 between 100-200kya. Curnoe et al. (2001) remark that these dates are significantly younger than biostratigraphic ages due to geochemical processes which produced errors in the sample. Alternatively, they note that the derivation of some of the fossils used in the analysis is unclear; the bovid samples from Mbrs. 2 and 3 could perhaps have been from the significantly younger Mbr. 5 dating very late into the Pleistocene.

For the purpose of this study, the relative chronologies of the South African sites are more important than their absolute dates because it is imperative that the sampled individuals be situated in a relative context to interpret the ecological conditions surrounding cercopithecine and hominid evolutionary change. McKee et al. (1995) explain that faunal assemblages are searched for time sensitive species that can be associated with strata where absolute dating is impossible and then used to create a relative chronology of these cave deposits. McKee et al. (1995) place Makapansgat Mbrs. 3 and 4 as the oldest of the sites with Taung only slightly younger and roughly concurrent with Sterkfontein Mbr. 4. Sterkfontein Mbr. 4 deposits produce primarily late-Pliocene fauna and are definitely younger than Makapansgat Mbr. 4 since many species from Makapansgat have their last appearances there. Williams et al. (2006) noted considerable morphological variation in the primates found at these cave deposits. They proposed that this variation indicated that the depth of time exhibited was substantial at Sterkfontein and Makapansgat.

Sterkfontein Mbr. 5 has the strongest faunal affinities with the earliest Kromdraai deposits. Kromdraai A and B are very similar but B is slightly older and exhibits the first appearance of the robust australopithecines and extant South African species (McKee et al. 1995). Swartkrans is considered the youngest; Mbr. 1 is clearly distinct from the other two and is the last to show definite faunal associations with the earlier sites. Mbrs. 2 and 3 are the youngest and have very few faunal differences and are probably similar in age.

The old world monkeys found at the South African sites are useful as analytical tools because they comprise a large proportion of the faunal remains in these deposits. In the Swartkrans hanging remnant, for example, cercopithecines make up 26.4% of the

individuals found (Brain, 2004). The South African caves contain a range of cercopithecoid forms and display some continuity between sites with deep depositional histories. For instance, *Parapapio* species have been found in multiple strata of Makapansgat, Sterkfontein, Bolts Farm, and Taung and one of these species, *Pp. jonesi*, has been identified in the Swartkrans hanging remnant (Brain, 2004); although, the amount of intraspecies variation is high between sites and temporal ranges and the exact taxonomy is unclear (Williams et al. 2006). *Cercopithecoides williamsi* is found at Makapangat, Sterkfontein, and Bolts Farm (Frost and Delson, 2002; Reed, 2002; Watson, 2004) and the earliest South African *Papio* are found at Sterkfontein Mbr. 4 and date to around 2.8 mya (El-Zaatari et al., 2005) although most are found later at Kromdraai and Swartkrans. *Gorgopithecus major* and *Dinopithecus ingens* are found exclusively in the later Pleistocene deposits of Kromdraai and Swartkrans respectively. The diversity and histories of these cercopithecines allows them to serve as a proxy towards understanding the paleoecological contexts of the Plio-Pleistocene faunal evolution in South Africa.

With a few exceptions, there is a stark change between the older and younger South African sites with regards to cercopithecine fossil assemblages. *Parapapio* and *Cercopithecoides williamsii,* make up a majority of the primate individuals found at Sterkfontein, Makapansgat, and Taung, while the younger Kromdraai, Swartkrans, and Coopers Cave sites have a wider diversity of the larger *Papio, Dinopithecus ingens*, and *Gorgopithecus major*.

Frost and Delson (2002) describe the variation of Plio-Pleistocene cercopithecines in South and East African sites and describe *Parapapio* as an extinct medium sized papionin closely resembling modern *Cercocebus*. *Parapapio* is distinguished from other

Papio by a shorter snout, lack of an anteorbital drop, thin browridges, absence of maxillary fossae or a sagittal crests, and only slight sexual dimorphism. There are four recognized species, *Pp. jonesi*, *Pp. whitei*, *Pp. broomi*, and *Pp. antiquus*, but these taxonomic designations have generated some controversy. Traditionally, these species have been distinguished based on molar size with *Pp. jonesi* being the smallest and *Pp. whitei* the largest. However, Williams et al. (2006) note that variation in molar size in *Pp. broomi* overlaps the other two. Frost and Delson (2002) distinguish *Pp. jonesi* as having a more squarish muzzle than *Pp. whitei* but more rounded than *Pp. broomi* and explain that these are only subtle differences and express the need for better diagnostic criteria.

Some authors argue for a flawed taxonomy in *Parapapio* but disagree with the reclassifications. Thackary et al. (2005) notice no significance difference between mean tooth sizes or isotopic signatures in *Pp. broomi* and *Pp. jonesi* and Thackary and Myer (2004) suggest that *Pp. broomi* and *Pp. jonesi* represent a single sexually dimorphic species. Williams et al (2006) observe, however, that *Pp. jonesi*, represented by STS 565, has distinctive facial characteristics from other *Parapapio* and argue that the range of variation in *Pp. broomi* and *Pp. whitei* overlap.

The genus *Papio* is represented by a number of extant morphospecies, the exact number of which depends on the source. Traditionally, *Papio* has been considered to be five distinct species (Grubb et al., 2003): *P. papio, P. anubis, P. hamadryas, P. cynocephalus,* and *P. ursinus*, although this view is perhaps overly conservative. In captivity, all baboons will hybridize (Jolly, 2001) and in the wild there are hybrid zones, most distinctly between hamadryas and olive baboons where their ranges overlap. This

has led many researchers to conclude that *Papio* represents only a single biological species with many subspecies, *P. hamadryas ssp.* (Phillips-Conroy et al., 1986; Phillips-Conroy and Jolly, 1991; Jolly, 2001). However, there is a considerable amount of morphological variation between forms both in size and shape while hybrid zones are limited in the wild (Grubb et al., 2003). Chacma baboons (*P. ursinus*) of Southern Africa are considerably larger than the pygmy baboons (*P. kindae*) of Angola and Zambia, and southern species have narrower crania than those in the north (Frost et al., 2003). Despite the extreme morphological variation in *Papio*, the case can be made for only subspecific classification. Patterson (1993) would argue that species are defined through affirmation; a species should be classified as such if the members recognize each other as potential mates despite geographical isolation and regardless of whether this actually happens in the wild. Alternatively, Godfrey and Marks (1991) would define the species more broadly than just genetic compatibility. *Papio* could be distinguished at the species level on morphological and ecological considerations; although each form may mate in captivity, most are geographically isolated and do not contribute to each others' gene pools (Grubb et al. 2003).

In the fossil record, *P. angusticeps* and *P. robinsoni* have been found at the Pleistocene sites of Swartkrans, Coopers Cave, and Kromdraai and are distinguished from other papionins with longer and more concave shaped nasals. Pleistocene *Papio* has a higher browridge at glabella than *Theropithecus* although it is less prominent (Frost et al., 2003). Their dentition is similar to *Parapapio* but less derived than *Dinopithecus, Gorgopithecus*, and *Theropithecus*. The early Pleistocene papionins, *Dinopithecus ingens,* and *Gorgopithecus major* are found at Kromdraai A and Swartkrans and are

much larger than contemporaneous *Papio*, with *G. major* being the largest and *D. ingens* being the most prognathic (Jablonski, 1994; Williams et al., 2006).

Both modern and extinct *Theropithecus* are medium sized papionins and are the most easily distinguished from other baboons primarily by their distinctive dental morphology (Frost and Delson, 2002). The first appearance of *Theropithecus* is 4.0-3.5 mya in East Africa and is rare in South Africa, only occurring at Makapansgat and Swarkrans (Benefit, 1999). Fossil and modern *Theropithecus* have very noticeably high crowned teeth and small incisors. They are distinguished from *Papio* with a more deeply concave face when viewed laterally, a more superiorly oriented nasal aperture, less arched browridges, wide zygomatic arches, a narrow premaxilla, shallow incisal arch, deeper post-orbital constriction, and a smaller brain (Jolly, 1970; 2001; Jablonski, 1994; Williams et al. 2006).

In addition, there is a single species of colobine monkey found in the same strata as the papionins. Fossil colobines are common in East-African Plio-Pleistocene sites (Leakey, 1982) but only *Cercopithecoides williamsi* is found in South Africa (Benefit, 1999; El-Zaatari, 2005) It is assumed to be terrestrial, based on post-cranial morphology, and is distinguished by globular calvaria, broad interorbital distances, thick browridges, thick mandibular corpi, and short muzzles (Frost and Delson, 2002).

Two species of *Australopithecus* are found in the South African sites: *A. africanus* has been found at Sterkfontein, Makapansgat, and Taung (McKee, 1993; Clarke 1995; 2003; Partridge et al., 1999); *A. robustus* has been found at Swartkrans, Drimolen, Sterkfontein Mbr. 5, and Kromdraai (Kuman and Clark, 2000; Grine, 2004). *A. robustus* has massive masticatory structures, extremely large teeth and zygomatic arches, with

reduced canines and prognathism (de Ruiter et al., 2006). The more gracile *A. africanus* has a comparatively prognathic face with parabolic dentition, no diastema, and reduced canines, and a small body size, some retaining arboreal adaptations (Rayner, 1993; Clark and Tobias, 1995; Clark 1995; Partidge et al., 2003). The two species are never found in the same deposits; *A. robustus* is only found in the younger sites.

Reconstructing the ecology of the South African sites is important in understanding the evolutionary context of Plio-Pleistocene fauna. Vrba's (1999) turnover pulse hypothesis claims that events in evolutionary change can be linked to major shifts in climate; specifically, the split between the gracile and robust australopithecines, the evolution of early *Homo*, and the shift from the smaller bodied *Parapapio* to larger *Gorgopithecus* and *Dinopithecus* forms, can be explained by the cooling and drying trends occurring in pulses over the Plio-Pleistocene.

In Vrba's original research (Vrba, 1974; 1975) she plotted a correlation between percentages of bovids in African national parks exploiting different trophic niches, either browsers or grazers, and the types of ecologies, open or closed, occupied by each. Interpreting the South African fossil bovid assemblages within this context, she concluded that there was an environmental change that could accurately account for the faunal turnover between the older and younger sites. The hypothesis could be tested by observing the numbers of first and last appearances (FADs and LADs) and the types of fauna affected. Specifically, she noticed that the bovid genera *Alcelaphini* and *Antilopini* and were predictive of open ecologies in modern Africa and assumed their presence would indicate the same in the Plio-Pleistocene. She found that Sterkfontein Mbr. 4 had the lowest percentage (51%) of grazing bovids and that this corresponded to medium

density woodland. Sterkfontein Mbr. 5, Kromdraai, and Swartkrans produced an observed speciation of open adapted bovids at 1.9-1.8 mya and 0.9-0.6 mya that indicated an expansion of grasslands and increasing vicariance of wooded ecologies.

Vrba is justified in proposing a climate driven model for evolutionary change in South Africa because the Plio-Pleistocene is a period of dramatic global climate fluctuations. Studies taken in Japan (Momohara 1994), Italy (Negri et al. 2003), and New Zealand (Johnson and Curry 2001), and ocean core samples taken from the Atlantic and Pacific (Denton, 1999) demonstrate that perturbations in climate occurred simultaneously across the globe with peaks of change occurring in rough correlation with Vrba's observed speciation and extinction events.

But other researchers have been ambivalent about this proposed turnover-pulse theory for South Africa and question Vrba's methods and environmental reconstructions of which she based on her observed faunal turnovers. Reed (1997) questions whether it was prudent to assume that extinct taxa would necessarily resemble their extant descendants. This faunal uniformitarianism across millions of years is somewhat of an irresponsible assumption; there is no reason to believe that *Alcelaphini* and *Antilopini* would have necessarily occupied the same environments that they prefer today. Isotopic studies of bovid remains at Makapansgat showed that the taxa used in Vrba's analysis did not necessarily correspond to their modern descendants. Sponheimer et al. (1999) examined seven bovid species isotopically and revealed that the ecological assumptions based on comparisons between extinct and extant taxa were flawed. Moreover, even if the bovids indicated an adaptive radiation into grasslands, that does not necessarily mean that there were pulsed climate changes. No one argues that there were not ecological

fluctuations during the Plio-Pleistocene; however, even a slight change would have opened up ecologies into which some species could radiate. The proliferation of open adapted bovids only really indicates that they were among the first and most successful groups to exploit new ecologies. Reed (1997) argues that a more holistic approach must be made to assess the environmental changes of the Plio-Pleistocene which include more taxa and additional methodologies.

A number of different techniques are available for reconstructing past ecologies. Most simply, examining fossilized pollen remains is a direct indicator of vegetation in the surrounding area (Momohara, 1994; Potts, 1998). Pollen is produced by both arboreal and non-arboreal vegetation and is collected in these fossil deposits just like everything else. Ratios of pollen remains from both types of vegetation serve as a direct assessment of paleoecologies. If a layer yields high ratios of pollen from arboreal species, one can assume a higher density of woodlands compared to strata with more grass pollen.

Stable isotopes contain atomic weights heavier or lighter than their more common counterparts. Carbon-13 differs from carbon-12 by only a single neutron and does not naturally decay over time. The ratios of all isotopic variants of carbon are well known in the atmosphere, for every X-number of ^{12}C atoms, there are Y and Z-numbers of ^{13}C and ^{14}C (Potts, 1998; Cloern et al., 2002). ^{13}C is an important indicator of past climates because it is incorporated into the photosynthesis cycle at predictable ratios in various types of plants. Primarily, photorespiration follows one of two distinct pathways, C_3 or C_4 types which describe the number of carbon atoms in the intermediate compounds used to create sugars by each. Each step of photosynthesis requires fractionally less energy to

select lighter isotopes over heavier ones, and after enough cycles, plants invariably result in higher ratios of ^{12}C over ^{13}C (Byrd and Brown 1989).

C_3 and C_4 plants are predominant in different climates; C_3 photosynthetic plants are trees and shrubs and include most fruit bearing plants that are best adapted to environments with warm temperatures and ample rainfall. C_4 plants are better adapted for cooler, drier conditions and include most grasses (Byrd and Brown 1989). The photosynthetic cycles for C_3 and C_4 plants integrate isotopes of carbon in predictable and non-overlapping ratios and remain stable over time after plants decompose and are incorporated into the soil chemistry (Potts, 1998; Sikes et al. 1999). Atmospheric carbon ratios are presumed stable and constant over time, so determining the deviation ($\delta^{13}C$) from atmospheric normal $\delta^{13}C$ value, indicates the predominant vegetation of an area.

Oxygen isotope ratios fluctuate depending on local ecological conditions and allow researchers to take direct measurements of climatic changes over time. During evaporation ^{18}O is enriched in the water while ^{16}O preferentially released into the atmosphere more easily due to its lighter weight (Potts, 1998). At times of high precipitation, land areas receive disproportionately high levels of ^{16}O enriched rainwater and these levels are preserved in geologic deposits as more negative $\delta^{18}O$ values compared to hotter, drier ecologies (Denton, 1999).

When $\delta^{13}C$ and $\delta^{18}O$ values are plotted next to each other, researchers are able to reconstruct the past climate for an area. For instance, Sikes et al. (1999) plotted the $\delta^{13}C$ and $\delta^{18}O$ for Pleistocene deposits in East African fossil beds. The $\delta^{13}C$ values were very high indicating that during the period of deposition, the local ecology was an open C_4 grassland with a significant C_3 vegetation while $\delta^{18}O$ values indicated that the area was

cool with moderate amounts of yearly rainfall. Sikes et al. (1999) compared the isotopic concentrations to modern East Africa and concluded that these deposits represented a cooler and moister environment that the grasslands found in the area today.

Somewhat more indirectly, one can examine the faunal remains recovered from a site and judge the ecologies from the relative abundances of species adapted for particular niches. This is the basis behind Vrba's (1974; 1975; 1999) approach discussed earlier. However, as mentioned, her methods have been criticized for using limited faunal samples and making ecological assumptions based on extant proxies.

Reed (1997) proposes that the entire fossil collections for these sites should be utilized without making assumptions based on faunal uniformitarianism. Instead, she examines species' trophic and locomotor adaptations to reconstruct the types of environments that must have existed in order for these traits to exist. Reed (1997) used this method to analyze modern African environment and found that the total number of frugivorous species was the best predictor of ecological conditions. Frugivory, when combined with the total number of arboreal species in an area, was able to easily distinguish the degree of open or close ecologies down to very slight variations.

Sponheimer et al. (1999) would argue, however, that Reed's faunal analysis still relies on assumptions that would skew ecological reconstructions. They would point out that morphologically, species present with traits that are often times just a product of phylogeny and not necessarily adapted to an ecological niche. Therefore, faunal analysis, only when used in conjunction with direct methods, provides an excellent means for reconstructing the ecologies of the South African fossil record while controlling for phylogeny and without making assumptions based on modern faunal populations.

The ecological reconstructions of Makapansgat have run the range of deserts to forests based on pollen, faunal collections, and isotopic analyses (Rayner et al., 1993). Reed (1997; 2002) notice a high numbers of frugivorous, arboreal, and some aquatic species at Makapansgat Mbrs. 3 and 4. Sponheimer et al. (1999) observe that isotopic evidence places Makapansgat as a primarily wooded environment based on isotopic samples taken from the faunal collections while Bamford (1999) examined fossilized plant remains at Makapansgat and concluded that the vegetation necessitated considerable yearly rainfall. However, McKee (1999) points out that there are a number of grazers and cheetahs which indicate that Makapansgat may have been wooded but still would have included open areas and should thus be considered a mosaic environment.

Sterkfontein Mbr. 4 was considered to have an almost identical faunal composition as Makapansgat (McKee et al. 1995), but Reed (1997) points out that there are fewer arboreal species comparatively but plenty of frugivores and mixed terrestrial/arboreal species. Stable carbon isotopes point to a wide variety of available C_3 resources (Lee-Thorpe et al. 2003) and would agree with Vrba (1974) that Mbr. 4 was a medium density forest. Ecological reconstructions based on the microfaunal remains do not agree, however, and indicate that Mbr.4 was a mixture of grasslands or savanna (Denys, 1999). Reed (1997) found no arboreal or frugivorous species in Mbr. 5 and would agree with Vrba (1975) that it was an open habitat.

Kromdraai B yields only a moderate number of frugivorous and not a single arboreal species and is reconstructed as an open grassland with patchy nearby woodlands (Reed, 1997). Stable carbon isotopes indicate that species relied on predominantly C_4 diets, but some, including *Australopithecus robustus*, still included C_3 resources in its diet

(Lee-Thorpe et al., 1994; 2003; Sponheimer, 2005). Reed (1997) observed that Kromdraai A had just as many frugivorous and a few arboreal species and reconstructed the younger deposit as scrub woodland.

Swartkrans deposits produce no arboreal, but some aquatic and many frugivores but yield progressively fewer frugivores through Mbrs. 2 and 3. Reed (1997) reconstructed the ecology as open grassland with a nearby river and woodland. Isotopic samples of Mbrs. 2 and 3 agree and show no substantial change in vegetation and indicate that the two strata were deposited under similar ecological conditions (Lee-Thorp and van der Merwe, 2004). The isotopic and faunal reconstructions of Swartkrans ecology differ slightly from Vrba's (1975) original bovid study arguing that Swartkrans was an open savanna.

Environmental reconstructions that use holistic evidence examine faunal turnover ecologically rather than taxonomically and point to a definite change towards open habitats between 3.0-2.0 mya, but it is interesting to note that the total numbers of frugivores remain high until the sites dating younger than 1.8 mya. The gradual rise in grazers and parallel fall in arboreal and frugivorous species indicates that climate change in South Africa prior to 1.8 mya was gradual and the major pulses that Vrba (1999) observed in bovids was not representative when examined across taxa. The biggest spikes in grasslands do not occur until 1.8 mya at Swartkrans and Sterkfontein Mbr. 5 (Luyt and Lee-Thorp, 2003).

This is where an excellent sampling of the changes in cercopithecine diets over the Plio-Pleistocene can supplement and clarify ecological models of South African evolutionary change. Extant baboons are known from field studies to prefer fruit sources

before they choose leaves and grasses (Jolly, 2001; Dirks 2003; Nystrom et al., 2004) and may be a good indicator of past ecologies (Benefit, 1999). If a deposit yields a significant percentage of frugivorous baboon, it is evidence that there are still generous woodland resources during those periods of deposition and would mean that the ecology was still relatively warm and had plenty of rainfall.

The diets of fossil primates have been reconstructed using dental morphology, stable isotopes, and occlusal surface microwear analyses. Each of these methods have their attributes and deficiencies, but all point towards a similar line of evidence, that most Plio-Pleistocene cercopithecines were primary frugivores and that the ecologies of the time still included abundant C_3 resources.

Dental morphology is a natural indicator of preferred diets because certain shapes and structures are presumably selected for over time (Bonis and Viriot 2002). Folivorous primates generally have small incisors and sharp crested molars, while frugivores have large incisors and flat gnashing molars. In order to quantify these differences, Ungar (2002) devised a regression for predominately frugivorous extant primates describing the relationship between sheering crest length and the mesial-distal length of M_2. Using the frugivores as a standard he claimed that the deviation from this regression can be described as a sheering-quotient that indicates the amount of leaves in a species' diet. Benefit (1999) created similar regressions of dental morphologies for extant primates against the relative amounts of fruit and leaves included in their accepted diets and found that measurements of sheer crest lengths and degree of flare in molar cusps are reliable at predicting the diets of extant species. These regressions do not discriminate between leaf

and grass eating, but Benefit (1999) makes inferences based on post-cranial morphology as to which a species is likely to prefer.

Stable isotopes of tooth enamel are used to directly quantify dietary components in much the same way they are used to reconstruct past ecologies. Percentages of ^{13}C are the best indicators of primary diet because ratios in bone and tooth enamel are deposited only through food consumption (Lee-Thorp et al., 1989). Other isotopes of oxygen, nitrogen, and strontium are indicators of trophic level but are not quite as well correlated (Sponheimer and Lee-Thorp, 1999; Lee-Thorp et al. 1994; 2003).

Most microwear analyses have been performed using a scanning electron microscope (SEM) and are a direct indicator of diet. Different foods mechanically abrade the occlusal surface of teeth in different quantifiable patterns. Ungar (2006) explained that dental molds are coated with a thin layer of gold and are examined under SEM at 500x. Microwear features can be counted and measured; the number and size of the pits and scratches are able to distinguish between large scale trophic categories. It should be mentioned that microwear has been proven to be ephemeral, sometimes only resulting from the last few days meals. Teaford and Oyen (1989) fed captive monkeys hard and soft diets and compared the rate of microwear turnover and found that microwear signals were obliterated in short periods of time. This makes microwear analyses problematic because if small sample sizes are used, errors will be introduced based on diets that vary with season or geographic range.

Microwear, stable isotopes, and dental morphology have all been used to reconstruct the diets of Plio-Pleistocene primates. For some of these species, isotopic and microwear analyses do not correspond to those of dental morphology and demonstrate

how morphology does not always reflect behavior. Dental regressions based on extant species do not take phylogenetic differences into account. Among extant primates, folivores do display more pronounced cusp lengths, but cercopithecines all have higher cusps than hominoids, none of which are dependent on actual dietary differences (Ungar, 1998)

Previous dietary reconstructions for *Papio angusticeps* collected from Kromdraai and Coopers Cave have been based primarily on dental morphology. Benefit (1999) estimated that *P. angusticeps* was a primary frugivore based on sheer crest lengths. Isotopic and SEM microwear studies on this species are absent from the literature.

Papio robinsoni recovered from Swartkrans and Bolts Farm has been analyzed through dental regressions, isotopic, and SEM microwear methods. Benefit (1999) determined that *P. robinsoni* was a primary frugivore, with only 22% of its diet composed of grasses and leaves. SEM microwear reconstructions, however, place it most similar to modern *Theropithecus gelada* (El-Zaatari et al., 2005) although accepted $\delta^{13}C$ values assign it as a C_3 browser (Lee-Thorp and van der Merwe, 1993). On the other hand, more recent studies find significantly high enough isotopic levels to predict that *P. robinsoni* incorporated between 20-40% C_4 grasses in its diet and that it was an eclectic feeder that capitalized on the increasingly open ecologies of the Pleistocene (Codron et al., 2005).

Benefit (1999) determined that *Cercopithecoides williamsi* was a highly derived folivore and concluded from post-cranial remains that it was terrestrial. Terrestrial locomotion combined with a high rate of dental wear, indicated that it was most likely a gramnivore. El-Zaatari et al. (2005) concluded from their SEM analyses that *C. williamsi*

was indistinguishable from modern *T. gelada* and agreed that it was probably a gramnivore. However, $\delta^{13}C$ reconstructions by Codron et al. (2005) provide mixed results and show a polarization of *C. williamsi*, some being classified as the most gramnivorous and some with the most C_3 based values of any South African cercopithecine. They concluded that *C. williamsi* may represent two species based on such stark differences in diets.

Gorgopithecus major and *Dinopithecus ingens* samples from Kromdraai and Swartkrans are primarily frugivorous based on dental morphology (Benefit 1999) although $\delta^{13}C$ ratios and SEM analyses indicate that both were significantly more folivorous. *G. major* presented with microwear characteristics that pointed to a substantial folivorous component but that it probably preferred fruit. $\delta^{13}C$ values indicate that *D. ingens* also included considerable C_4 resources (Codron et al., 2005) and SEM denoted a primary gramnivorous diet more similar to modern *Theropithecus gelada* and *Papio cynocephalus* (El-Zaatari et al. 2005).

Parapapio diets are nearly impossible to differentiate based on dental characteristics but are usually classified as primary frugivores. Isotopically they are considered C_3 browsers and *Pp. jonesi* and *Pp. broomi* are indistinguishable (Lee-Thorp and van der Merwe, 1989; van der Merwe, 2003; Thackeray and Myer, 2004). SEM microwear analyses conclude that all three shared a similar preference for fruit but indicate that *Pp. jonesi* found at Swartkrans was more frugivorous than other species (El-Zaatari et al., 2005). None of these methods distinguish along taxonomic lines.

Both australopithecines have isotopic values that indicate a substantial C_4 component in their diet (Sponheimer et al., 2005) but this does not correspond to

traditional hypotheses of australopithecine morphology. The robust australopithecine hypermasticatory structures have been assumed to be a specialized adaptation to a tough diet (de Ruiter et al., 2006) but $\delta^{13}C$ ratios indicate that it was a generalist eating substantial amounts of grass (Lee-Thorp et al, 1994; 2003; Lee-Thorp and van der Merwe, 2004). Although $\delta^{13}C$ values are higher than contemporaneous papionins, ratios of $\delta^{15}N$ and Sr/Ca indicate that *A. robustus* got much of its ^{13}C from the meat of C_4 grazers or insects (Lee-Thorp et al. 1994; Bonis and Viriot, 2002). Although living in the earlier closed environments, *A. africanus* exhibits similarly high $\delta^{13}C$ ratios that indicating it too included substantial amounts of C_4 grasses in its diet and some have argued that the ability to exploit expanding grasslands of the Plio-Pleistocene was an integral for why the early hominids were so successful (Sponheimer and Lee-Thorp1999; van der Merwe et al. 2003).

A new methodology for determining diet

A new procedure proposed by Semprebon et al. (2004) examines microwear at low magnifications to see if the diets in fossil taxa could be predicted. SEM microwear analysis involves taking quantitative measurements of microwear features. Workers have been able to measure the breadth and length of scratches and diameters of pits to supplement the relative frequencies of each (El-Zaatari et al., 2005; Ungar et al., 2006). Ungar (2002) has found, using SEM analysis, that frugivores have higher ratios of microscopic pits to scratches than folivores and that hard object feeders were even higher. Low magnification stereomicroscopy differs from SEM analyses because observations are made at 35x, rather than 500x for SEM, and includes an inherent subjectivity. The observer must qualitatively define what constitutes a small versus large pits or whether an

apparent scratch is fine, coarse, or hypercoarse and then count each feature. Although the same terminology is used for each method, counting or measuring pits and scratches, SEM and low magnification microscopy are not examining the same features. As Semprebon et al. (2004) note, the small pits only barely visible at 35x under a light microscope are larger than the entire field of view viewed at 500x with SEM.

Despite these warnings, low-magnification stereomicroscopy researchers do not argue that the method is meant to replace standard SEM practices. However, they do claim that the intra/inter observer error is almost identical to SEM methods and that the advantages afforded to the large sample sizes of stereomicroscopy make up for the apparent subjectivity (Godfrey et al. 2004; Semprebon et al. 2004).

With a little bit of training, low magnifications stereomicroscopy is simple and quickly generates large sample sizes. Semprebon et al. (2004) tested inter/intra observer errors using a t-test and observed that there were no statistically significant difference between readings. Additionally, although they standardized their observations on M^2, t-tests proved that there were no differences between maxillary and mandibular readings.

A principal components analysis (PCA) determined that species were separated primarily on the severity of use-wear patterns seen at the eyepiece. Individuals with the lightest patterns (small pits and fine scratches) were separated from those with the heaviest features (large puncture pits and deep trench-like scratches). Both Godfrey et al. (2004) and Semprebon et al. (2004) noticed that traits used in the PCA began to separate extant species along trophic lines.

Discriminant function analyses were used to determine which variables discriminate between two or more naturally occurring groups and tested whether the

method could serve as a valid dietary classification tool in primates. Semprebon et al. (2004) applied three analyses to extant groups with known diets, using dietary categories as their *a priori* classifications. Their first analysis grouped folivores, frugivores, and grazers, and included number of pits, number of scratches, scratch texture, and number of puncture pits as variables. The second analysis distinguished hard-object feeders from the rest and included number of pits, number of scratches, scratch texture, number of large puncture pits, and number of medium puncture pits. Finally, the third analysis was designed to separate seed predators from seed dispersers and included the same variables as the first analysis.

If low-magnification stereomicroscopy is able to delineate broad scale trophic categories in fossil cercopithecines and early hominids, its potential for ecological reconstructions will be invaluable. With extant baboon preferences for frugivory as a premise, microwear signals for Plio-Pleistocene baboons should be useful in predicting the habitats available at each of the South African fossil sites while changes in diet across time will demonstrate the extent of the climate changes proposed by other researchers.

Chapter III

Materials and Methods

Samples Collected

Dental molds were collected on 456 individuals during the summer of 2005 by Frank Williams and Brian Carter in museum collections around South Africa, Europe, and the United States. Of these, 108 were judged to be inappropriate for study due to poor preparation on the part of the collectors or due to taphonomic and preservation processes that degraded the occlusal surfaces and made them unreadable. Microtaphonomic degradation was readily apparent and distinguished from normal dietary microwear. King et al. (1999) studied the effects of acid, alkali, and sedimentary erosion on microwear features. Their conclusions were that taphonomic processes have the ability to alter microwear patterns through complete obliteration but not through formation of new features. Only with the smallest grit was there the formation of 5µm pits, much too small to be seen at the magnifications used here. Rather, of the teeth rejected here, taphonomic degradation appeared as though sand paper had been rubbed over the occlusal surfaces; they were very rough and the microwear features were entirely obliterated. Preparation errors, however, resulted in the majority of the rejected teeth. Most of these errors resulted in improper mixing of the molding material so that the final epoxy casts were completely smooth and transparent. A smaller minority of the sample was rejected because the shellac used to seal the fossil teeth was not removed properly.

Under the microscope these teeth looked like they had a crusty formation on top of the occlusal surface. These were less problematic because most of the time these crusty remnants of shellac were only covering a small portion of the tooth and another area of the surface could be read.

Of the remaining 348 all but 76 were assigned taxonomic designations by the museums and included 11 genera and 31 species. Two species are only represented by one individual, *Pongo* and *Alouatta*. The sample included a mixture of extant and fossil species. Extant species account for 91 individuals with 16 species, the most numerous of which are from *Papio ursinus, Papio kindae,* and *Papio anubis*. Fossil species are listed in Appendix I and included 181 individuals in 15 species dominated by *Parapapio jonesi, Parapapio broomi, Parapapio whitei*, *Australopithecus africanus, Australopithecus robustus, Papio robinsoni, Papio angusticeps, Cercopithecoides williamsii, Gorgopithecus major, Dinopithecus ingens,* and small samples of three recognized species of *Theropithecus*. The fossil specimens were collected from temporally and geographically distinct South African caves including Swartkrans, Taung, Sterkfontein, Bolt's Farm, Coopers Cave, Kromdraai, and Makapansgat, and represent a long temporal sequence spanning the climate changes under question.

Each tooth was read twice and the means taken for each count to produce the final values used in the later analyses. A selection of teeth would be read through a single time and the numbers of microwear features documented and at a later time or date, the same teeth would be read again. This method assumes that error could be introduced by personal bias if the two readings were taken sequentially for each individual. By spacing each reading, preconceptions from a first reading would not be carried over to the second.

Each reading took between two and three minutes and enabled the production of a large sample size.

Methods

The species sampled have been prepared at the museums with a shellac sealant; the first step was its removal so molds of the occlusal surfaces could be made. A solution called 'Zip-Strip' (Star Bronze) was applied to the teeth with a Q-Tip and allowed to sit for a few minutes while it dissolved the shellac. For this analysis, only the mesiobucal cusp of the M_2 was needed, but on many individuals the entire tooth row or another tooth was prepared and molded. The teeth were then cleaned with isopropyl alcohol to remove the 'Zip-Strip' and dissolved shellac. When completely dry the teeth or toothrows were molded using polyvinylsiloxane dental impression material (President Jet, Coltene, Inc). The substance has a viscosity similar to honey and seeped well into spaces along the occlusal surface and between teeth. The dental impressions created a negative image of the teeth that were later used to create a high resolution epoxy cast. The epoxy was blended and poured into test tubes, then placed in a centrifuge until they were adequately mixed. The epoxy could then be poured into the polyvinylsiloxate impressions and allowed to harden overnight.

These epoxy casts were examined at 35x under a stereomicroscope using a 0.4 mm^2 optical reticle as a standardizing guide. A fiber-optic light source was directed at oblique angles adjusted to best illuminate the features examined. The angle of illumination was important because microwear features show up as refracted angles and shadows. The fiber optic light could be adjusted to different angles that were useful at seeing the various features.

The samples were standardized by examining the mesiobuccal cusp of the mandibular second molar. Unfortunately this could not be applied to every tooth examined because some individuals did not have intact second molars, others were not prepared properly, and some were juveniles with unerupted adult molars. In these cases sample site was preferred on the second molar before searching the mesiobuccal cusps of M_1 and M_3. In the case of juveniles the first permanent molar was chosen over deciduous teeth. As a whole, however, a majority of the data were taken from the mesiobuccal cusp of the second molar

Microwear features were counted within the reticle and scored qualitatively for the presence or absence of specific features. The total number of small pits were counted and appeared in the eyepiece as bright white point sources against the darker background and are so small that hundreds could easily fit within the $0.4mm^2$ reticle. At certain angles of the light they were very easy to see as high contrast features. Medium puncture pits were larger than small pits but were dark and low contrast at all angles because they are deeper than small pits and do not reflect light back out towards the eyepiece. Large puncture pits were round and large, usually not as dark as medium puncture pits but easier to distinguish. Many times they were large enough to have other microwear features overlapping them. Large puncture pits were not as common as the other features so a variable was created that distinguished those individuals with either greater or fewer than four large puncture pits. Compiling these three features *post hoc* provided the total number of puncture pits and total number of all pits.

Scratches were counted and scored qualitatively by their texture. Fine scratches are very thin white lines, thin enough to reflect light back out of them, so thin that at 35x

they lack any width. Coarse scratches are also thin but are dark and have some width to them. Hypercoarse scratches are deep and wide, appear as trench-like and sometimes have other microwear features within them. In addition to counting the total number of scratches, the scratch texture was scored (1) fine, (2) mixed fine/coarse, (3) mixed coarse/hypercoarse, and (4) hypercoarse. Although teeth were assigned into the best fit categories and were coded consistently, more individuals fell into the second and third categories because that was where they best fit but not necessarily where they belonged. However, there were no codes provided for 'mixed fine/hypercoarse' or equal amounts of all three types of scratches when the study began. In retrospect, a better method would have been to count each type of scratch individually, much like what was done for the pits, and not use a qualitative coding system for scratch texture. This would have provided more variables for evaluating the variation between taxa and better described what was seen at the eyepiece.

Additionally the presence or absence of gouges were noted, which are somewhat triangular in shape with irregular edges and appear as if something hard and tough dug out a chunk in the enamel. They came in various sizes, some quite small and some nearly 0.2 mm in diameter. Gouges, however, were quite rare in this sample.

This differs subtly from the original method prescribed by Semprebon et al. (2004). Their method included five codes for scratch texture, adding coarse scratches alone. Additionally, there was a distinction made between puncture pits and normal pits that was not made here. Semprebon et al. (2004) counted the total number of small, medium, and large puncture pits separately from non-puncture pits which was not done in

this analysis. The result was that their study included more surface features for the following statistical functions.

Analysis of variance between groups

The analysis of variance between groups (ANOVA) evaluates the null hypothesis that the means for each grouping are equal between populations. The generated ANOVA indicates whether or not the null hypothesis should be accepted, but does not point out which group exhibits significant differences. In this case, all use wear characteristics were used as independent variables: total number of pits, total number of scratches, number of puncture pits, and presence of gouges and cross scratches, scratch texture, number of large pits, medium pits, and small pits, and the ratio of pits to scratches. The resultant ANOVA scores identified microwear features that varied statistically between taxa and would be used in later analyses.

Principal components analysis

For the first multivariate analysis, principal components were generated on the use wear traits that tested as statistically significant in the ANOVA. The variables included were total number of scratches and the percentages of each category of pits to the whole. PCA is useful in reducing multidimensional data sets into functions that are more manageable for analysis and the objective is to reduce the number of variables in the dataset without sacrificing the original variability of the data. A vector is calculated for the dataset that encompasses the maximum amount of variation and a second is calculated that is orthogonal to the first. This results in sets of components that eliminate possible correlations between variables.

PCA also begins to determine which of the microwear features are the most dominant in each dietary category and assess the dietary diversity exhibited in the sample. Presumably, if the species included in the sample have clearly delineated diets, the PCA axes will show an obvious polarization between individuals relying on each dietary category.

Discriminant function analysis

The first discriminant function analysis (DFA) was run on all individuals with all use-wear features in order to see which microwear signs were most prominent in determining diet. Individuals were grouped based by genus, and this also had the advantage of determining if microwear would be useful in delineating taxonomic differences in diet with closely related species.

The second DFA of extant species sampled should be understood with a caveat. Because the majority of the extant individuals are three *Papio* species characterized as having eclectic diets, some compromises must be made with the *a priori* classifications. Field studies of *Papio* conclude that all are frugivorous if given the choice but will exploit all food sources by necessity (Nystrom et al. 2004; Codron et al. 2006), so the real goal of the DFA is to determine the relative weights of alternative food sources.

Although *Papio* is the most generalized of the extant primates included in this sample, there are a few species that could be easily classified as having a specific diet. *Colobus badius, Colobus polykomos*, *Cebus apella, Pan troglodytes, Theropithecus gelada*, and *Gorilla gorilla* could all be fitted neatly into one of three broad categories: frugivory, folivory, or gramnivory. The DFA2 thus had to be performed one of two ways, either diets could be assigned to the best sampled species based on fallback items

(i.e. *P. ursinus* includes more leaves in its diet than the more gramnivorous *P. kindae*) and see if the individuals with clearly defined diets could be accurately predicted, or the species with the most easily defined diets (*Colobus badius, Gorilla gorilla, Pan troglodytes,* and *Cebus apella*) could be used to predict the relative proportions of food items in *Papio*. Both methods had their drawbacks. Assigning *a priori* designations for the better sampled *Papio* individuals was problematic because none can be truly classified as frugivorous, folivorous, or gramnivorous. Making predictions based on the species with easily defined diets risked the possibility of errors being introduced based on small sample sizes. For example, although *C. apella* is traditionally classified as a frugivore, its diet is still variable depending on seasonal food availability (Bionski, 2000). With only three individuals to base a classification system on, there was no way of determining if these three had recently eaten fruit. The same problem is even more apparent in gorillas. Mountain gorillas are specialized folivores, but the more common lowland gorillas have diets much more similar to chimpanzees and are primarily frugivorous (Rogers et al. 1998), but information was not provided to determine which varieties of gorilla were supplied for this sample. The latter method was deemed preferable because extant *Papio* cannot be easily fit into any of the three broad trophic categories. Future analyses would benefit from including larger sample sizes of species with more specialized diets, but in this example, that option was not available.

The independent variables used for the DFA2 were the number of each kind of pit, total scratches, and scratch texture. Predictions for each individual were generated and used to evaluate the proportions of fruit, leaves, and grasses in each species' diets.

Since the three *Papio* species, *P. anubis, P. ursinus,* and *P. kindae*, included can all be classified as generalized browsers with a preference for fruit, this analysis is used to judge the proportion of individuals predicted in each dietary category. The analysis answers the question for these three species, what percentages of grass and leaves are predicted for each of these groups and how does this compare with field studies of baboon diets? In this case the DF2 represents the first test of this method as a diagnostic indicator of primate diets.

DF3 was used to differentiate species with high levels of intentional seed predation from those that do not. In this case two *a priori* classifications were used based on field studies and fecal analyses obtained from the literature; *P. ursinus* and *P. anubis* were classified as intentional seed predators while *T. gelada* and *P. kindae* were classified as non-seed predators (Peters, 1991; Norconk et al., 1998; Nystrom et al. 2004; Codron et al. 2006) The DF3 generated predictions for the remaining unclassified species that were then compared to published observational reports and represents a test for diagnostic viability of this method for predicting levels of seed predation.

The success of the microwear characteristics for reproducing published dietary categories lends credence to the method being applied to the fossil record. The predicted diets for all extant species generated in DF3 and DF4 were used as the *a priori* classifications for predicting the diets of the fossil sample. Each fossil individual with a known species designation was treated as an ungrouped case and dietary classifications were reported as percentages of individuals falling into each category.

Finally each known fossil species was assigned its own category to see if microwear analysis could be used to assign species designations to the 76 individuals

with unknown taxonomic affinities. These unknowns are mostly jaw fragments with not enough material for morphometric classifications. For example, KA 163 is listed as an unknown species in this sample and presented only with a first and second molar on a small chunk of mandible that has not been totally excavated from the encasing material. The amount of morphological overlap for some of these species has been discussed and KA 163 is an example of how this overlap is problematic for researchers working with partial remains and how a trophic designation based on dental microwear may help recognize taxonomic affinity.

Chapter IV

Results

ANOVA

The means of each of the primary use-wear features for each species used in the ANOVA are presented in Appendix II and Table 1 shows the one way ANOVAs used for these and other variables extrapolated from these primary characteristics and grouped by species. Of all the variables tested, only scratch texture, presence of cross scratches, and presence of gouges tested as not being statistically significant between groups. The rest of the values all tested as statistically significant ($p<0.05$) and could be used in the principal components and discriminant functions analyses.

Table 1: ANOVAs for microwear characteristics

	Degrees of freedom Between / Within Groups	Mean Square	F	Significance.
Total Pits	26/243	464.998	3.529	0.000
Total Scratches	26/243	119.720	6.048	0.000
Total Large Pits	26/243	12.149	1.713	0.020
Total Medium Pits	26/243	89.950	2.406	0.000
Total Small Pits	26/243	272.365	3.456	0.000
Total Puncture Pits	26/243	85.080	1.950	0.005
Ratio Scratches/Pits	26/243	0.090	4.449	0.000
Cross Scratches	26/243	0.313	1.487	0.066
Scratch Texture	26/243	0.528	.960	0.523
Gouges	26/243	0.194	.999	0.470
Large Pit %	26/243	0.007	1.518	0.046
Medium Pit %	26/243	0.037	2.714	0.000
Small Pit %	26/243	0.035	2.071	0.002

Principal Components Analysis

The principal components analysis run on all individuals with known species designations included the relative numbers of each category of pits and total number of scratches, all of which tested as statistically significant in the previously run ANOVA. Table 2 displays the component extraction and shows that the first component encompasses 48.5% of the variance and the second, 32.3%, totaling 80.8%. Table 3 displays the resulting components matrix for all known species.

The first component polarizes based on heavy and light use wear patterns. The percentage of medium pits loads most positively while the percentage of small pits load most negatively. Individuals here loaded positively if they had heavier use wear patterns, more medium and large puncture pits compared to small pits. Individuals loaded negatively if they presented with a higher relative proportions of small pits to the rest. The differences between these two could be seen qualitatively at the eyepiece. Some teeth exhibited more heavily textured surfaces with numerous scratches and heavy pitting; others have more delicate wear with finer scratches and many more small pits. The second component polarizes individuals positively with high absolute scratch counts and negatively with those presenting with the heaviest pits.

Table 2: Total variance explained by the PCA

	Initial Eigenvalues			Extraction Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.941	48.534	48.534	1.941	48.534	48.534
2	1.292	32.307	80.841	1.292	32.307	80.841
3	.766	19.159	100.000			

Table 3: Component loading matrix

	Component Loadings	
	1	2
% Large Pits	0.273	-0.809
% Medium Pits	0.931	0.268
% Small Pits	-0.993	0.121
Total Scratches	0.122	0.743

Figure 1 graphs factor axes one and two against each other. Both show only moderate polarization of a few species. The best clustering on the first axis loading positively are *Gorilla gorilla, Papio hamadryas,* and *Theropithecus darti* with the heaviest microwear patterns. Polarized most negatively are *Parapapio sp., Colobus badius, Semnopithecus,* and *Colobus polykomos* with the lightest microwear patterns.

On the second factor axis, separating individuals based on pits versus scratches, *Theropithecus danieli, Australopithecus africanus, Australopithecus robustus, Colobus polykomos, Papio kindae,* and *Theropithecus darti* are polarized positively with the highest numbers of scratches. Loading most negatively were *Semnopithecus, Colobus badius,* and *Papio hamadryas* with the greatest relative large pit counts. The PCA did not generate clear polarization of the individuals in this sample for a number of different reasons. First, the species used in this sample all have very similar and generalized diets; almost all can be categorized as mixed browsers without clear distinction. Second, the PCA results produced here are only the means for each species and do not accurately account for the range of variation exhibited by each species. The most polarized individuals on either axis tend to be those with the smallest samples and the least opportunity to exhibit much variation. Those species that remain unpolarized may be so because the means calculated place them intermediately.

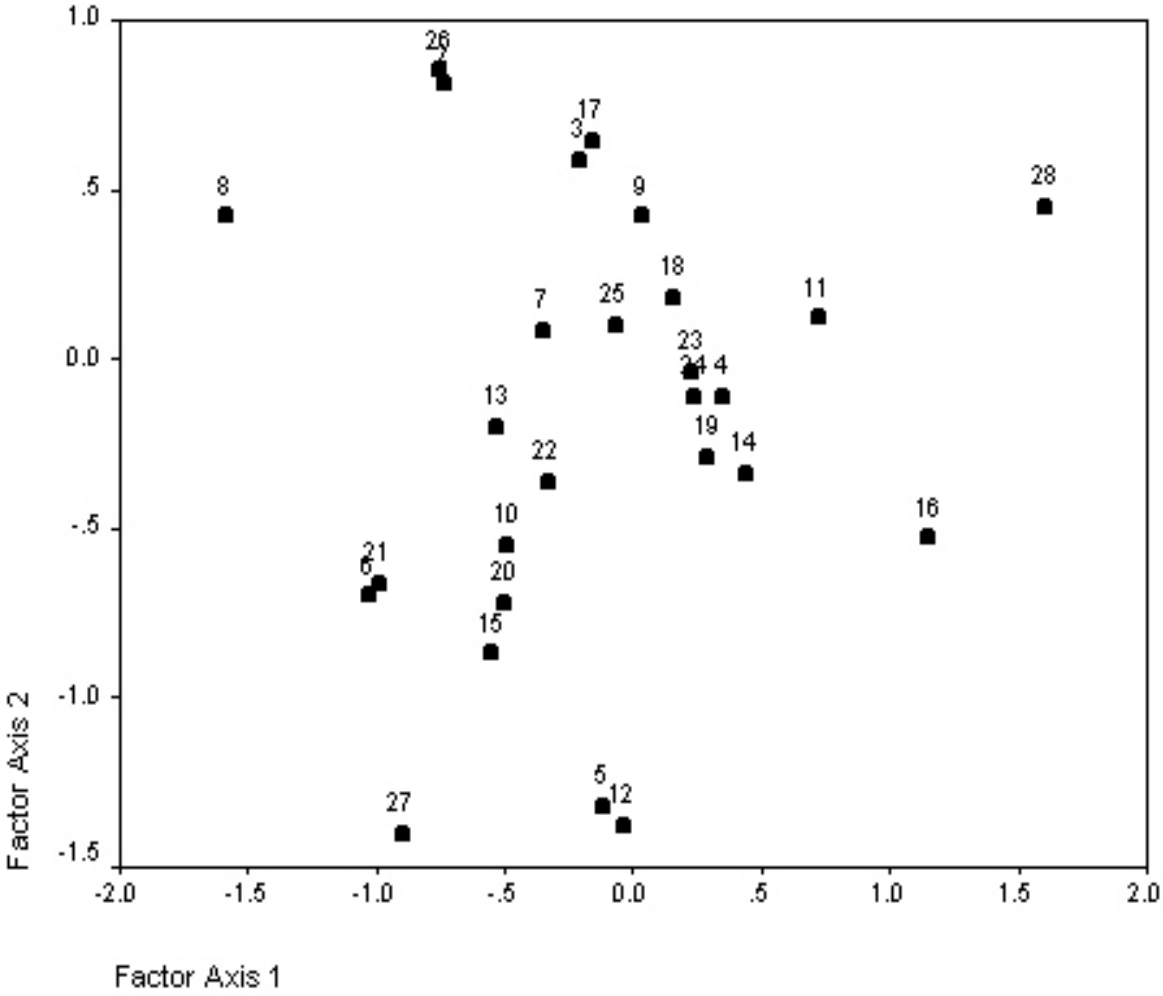

Figure 1: PCA Factor axes one and two (2) *A. africanus* (3) *A robustus* (4) *C. apella* (5) *C. williamsi* (6) *C. badius* (7) *T. gelada* (8) *C. polykomos* (9) *D. ingens* (10) *G. major* (11) *G. gorilla* (12) *P. troglodytes* (13) *P. angusticeps* (14) *P. anubis* (15) *P. cynocephalus* (16) *P. hamadryas* (17) *P. kindae* (18) *P. robinsoni* (19) *P. ursinus* (20) *P. wellsi* (21) *Parapapio sp.* (22) *Pp. antiquus* (23) *Pp. broomi* (24) *Pp. jonesi* (25) *Pp. whitei* (26) *T. danieli* (27) *Semnopithecus* (28) *T. darti*

Table 4 indicates the means and standard deviations of the factor axis scores for each species. The standard deviations for each species indicate that the plotting the means in Figure 1 hides the variation exhibited by each species. The problem with plotting the individual values was the sheer number of data points which precluded an accurate reading of the graph.

Table 4: Factor axis scores and standard deviations for PCA

Species (N)	Mean Factor Axis 1 (Standard Deviation)	Mean Factor Axis 2 (Standard Deviation)
Australopithecus africanus (9)	-0.73 (0.69)	0.81 (0.68)
Australopithecus robustus (16)	-0.21 (0.57)	0.59 (0.65)
Cebus apella (3)	0.35 (0.76)	-0.11 (0.32)
Cercopithecoides williamsi (13)	-0.12 (0.79)	-1.32 (0.33)
Colobus badius (3)	-1.03 (0.53)	-0.70 (0.53)
Colobus polykomos (2)	-1.58 (0.68)	0.42 (1.06)
Dinopithecus ingens (14)	0.04 (0.93)	0.42 (1.06)
Gorgopithecus major (7)	-0.49 (0.68)	-0.55 (1.17)
Gorilla gorilla (3)	0.72 (1.44)	0.12 (0.16)
Pan troglodytes (3)	-0.04 (0.84)	-1.38 (1.49)
Papio angusticeps (12)	-0.53 (0.87)	-0.20 (0.90)
Papio anubis (21)	0.44 (0.69)	-0.34 (1.01)
Papio cynocephalus (4)	-0.55 (0.85)	-0.87 (0.71)
Papio hamadryas (2)	1.15 (0.21)	-0.53 (0.21)
Papio kindae (24)	-0.16 (0.91)	0.64 (0.68)
Papio robinsoni (18)	0.16 (0.85)	0.18 (0.61)
Papio ursinus (19)	0.29 (1.67)	-0.29 (1.13)
Papio wellsi (3)	-0.50 (0.94)	-0.72 (0.66)
Parapapio sp. (3)	-0.99 (0.39)	-0.66 (1.69)
Parapapio antiquus (3)	-0.33 (0.82)	-0.36 (1.19)
Parapapio broomi (31)	0.23 (0.96)	-0.04 (1.17)
Parapapio jonesi (18)	0.24 (0.73)	-0.11 (1.06)
Parapapio whitei (19)	0.07 (1.07)	0.10 (0.89)
Theropithecus gelada (6)	-0.35 (.90)	0.08 (.45)
Theropithecus danieli (5)	-0.75 (1.2)	0.85 (0.23)
Semnopithecus (4)	-0.90 (.82)	-1.40 (0.66)
Theropithecus darti (2)	1.61 (0.68)	0.45 (0.23)

Discriminant Function Analysis

DF1 grouped individuals by genus and was only moderately capable of distinguishing genus level differences in microwear frequencies. Seven canonical functions were generated and only the first tested as statistically significant. Figure 2 plots the group centroids for the first two canonical functions.

Of the use-wear features, total number of scratches and small pits tested as the most highly correlated variables with the canonical functions. Genera were deemed

correctly classified 19.6% of the time, but individuals were most often misclassified into genera with similar diets. Genera with the most specialized diets, *Theropithecus, Cebus,* and *Colobus* had the highest success rates nearing 100%. *Papio* was misclassified as *Gorilla*, *Pan, Dinopithecus, Cercopithecoides*, or *Parapapio* over 60% of the time. It was interesting that *Papio* was misclassified most often based on dietary similarities. *G. gorilla* and *P. troglodytes* are both frugivorous, *Parapapio* has been linked most closely with extant baboons, and *Dinopithecus* and *Cercopithecoides* are most likely mixed gramnivores/folivores and it makes sense that many *Papio* would be associated most closely with folivory since that is a preferred fallback food. Although the DF1 does not reproduce generic designations particularly well, it does begin to point out that microwear features group individuals with like diets and begins to group the most closely related taxa.

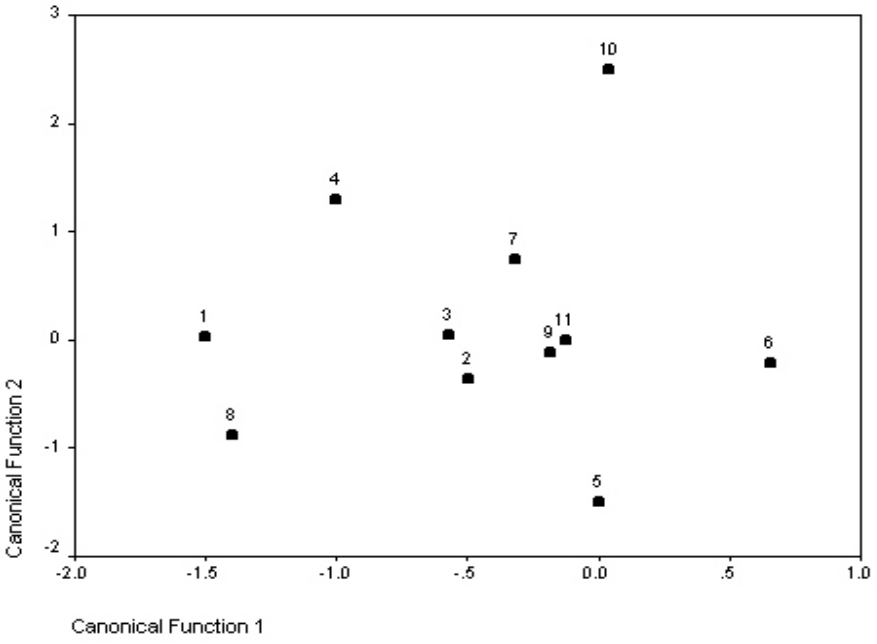

Figure 2: Group centroids for DF1. (1) *Australopithecus*; (2) *Cebus*; (3) *Cercopithecoides*; (4) *Colobus*; (5) *Theropithecus*; (6) *Dinopithecus*; (7) *Gorgopithecus*; (8) *Gorilla*; (9) *Papio*; (10) *Pan*; (11) *Parapapio*.

In the DF2, the independent variables chosen were the total of each sized pit, total scratches, and scratch texture. In the univariate ANOVA, all but scratch texture tested as statistically significant. The analysis generated two discriminant functions seen in Table 5, the first encompassing 77.9% of the variance. Table 6 is the generated Wilks' Lamda evaluating the significance of the first two functions and showing that only the first tests as statistically significant ($p<.05$).

Table 5: Generated canonical functions for DF2

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.673	77.9	77.9	0.791
2	.475	22.1	100.0	0.568

Table 6: Wilks' lambda significance of DF2

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 2	.254	20.585	10	0.024
2	.678	5.834	4	0.212

The generated canonical functions in Table 7 load most positively with total number of small pits and most negatively with total numbers of medium pits. The functions of group centroids generated in Table 8 show that frugivores are most clearly distinguished from folivores in this sample. Individuals judged as frugivorous load the most negatively with high counts of medium pits and scratches while folivores load most positively with the greatest number of small pits. Figure 3 plots the group centroids with the grouped and ungrouped cases and shows that there is a wide variation in the DF scores generated for this analysis.

Table 7: Structure matrix for DF2

	Function 1	2
Total Small Pits	.786	.606
Total Large Pits	.083	-.064
Scratch Texture	-.073	-.026
Total Scratches	-.159	.683
Total Medium Pits	-.310	.584

Table 8: Functions at group centroids

Dietary Category	Function 1	2
Frugivores	-1.142	-.351
Gramnivores	.201	.965
Folivores	1.815	-.526

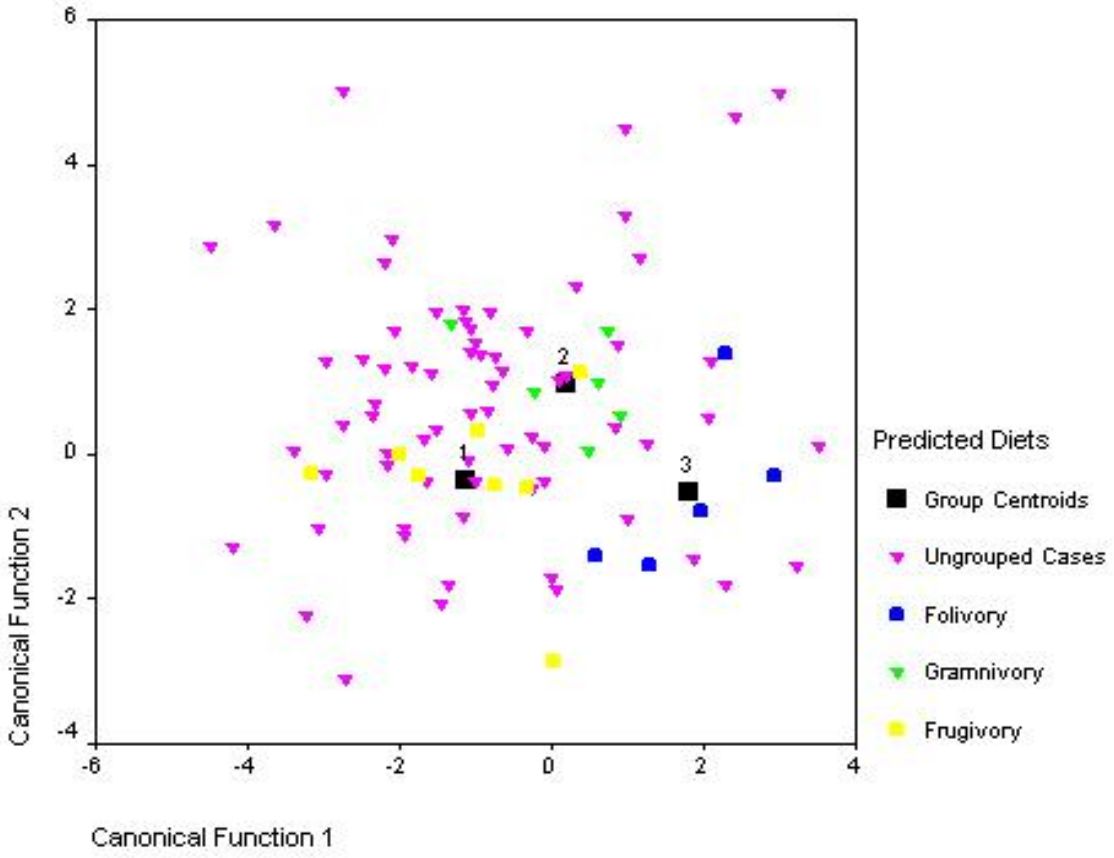

Figure 3: Group centroids for DF2. (1) Frugivory; (2) Gramnivory; (3) Folivory.

The *a priori* classifications proved to be correct in 95% of the cases. Additionally, the second function, although not statistically significant, shows that gramnivores scored most positively because they had the highest scratch counts.

The discriminant analysis predictions in Table 9 distinguish the diets of the *Papio* species extremely well. As expected, all three include a significant amount of fruit in their diets. *P. kindae* and *P. anubis* are predicted as being the most gramnivorous of the three and *P. ursinus* was predicted as including more leaves in its diet and is the most frugivorous. These results are in agreement with the field studies (Philips-Conroy, 1986; Peters, 1991; Nystrom, 2004; Codron et al., 2006).

Table 9: Predicted diets generated in DF2

Species (N)	*A priori* designations	Fruit %	Grass %	Leaf %	Diet Classification/ fallback
Gorilla gorilla (3)	Fruit	1.000	0.00	0.00	Fruit
Colobus badius (3)	Leaves	0.00	.000	1.00	Leaves
Therapithecus gelada (6)	Grass	0.00	1.00	0.00	Grass
Pan troglodytes (3)	Fruit	0.66	0.33	0.00	Fruit
Cebus apella (3)	Fruit	1.00	.000	0.00	Fruit/Leaves
Colobus polykomos (2)	Leaves	.000	0.00	1.00	Leaves
Papio ursinus (20)		0.65	0.15	0.20	Fruit/Leaves
Papio anubis (21)		0.52	0.43	0.05	Fruit/Grass
Papio kindae (24)		0.38	0.58	0.04	Grass/Fruit
Papio cynocephalus (4)		0.25	0.25	0.50	Mixed/Leaves
Papio hamadryas (2)		1.000	0.00	0.00	Fruit
Pongo pygmaeus (1)		1.000	0.00	0.00	Fruit

The DF3 separates seed predators from those that do not specifically seek out seeds. The ANOVA performed shows that all variables except for scratch texture tested as having statistically significant differences between the groups.

One canonical function was obtained and tested as significant in Table 10. The Structure matrix (Table 11) and group centroids (Table 12) show species that rely heavily

on seed predation score low primarily due to higher incidence of puncture pits. *A priori* classification "success" was good at 78.9%; 82.9% of species classified as relying heavily on seed predation were grouped as successful. Figure 4 plots the DF3 scores against the DF1 scores and illustrates that the most negatively loading species for DF3 have the highest predicted intensity of seed predation presented in Table 13 as well as illustrating the high degree of variation in the DF scores.

Table 10: Wilks' Lambda Significance of DF3

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1	0.726	21.496	4	.000

Table 11: Structure matrix for DF3

	Function
Total Pits	0.799
Total Scratches	0.581
Total Puncture Pits	.435
Surface Texture	.087

Table 12: Functions at group centroids for DF3

	Function
Seed Predators	-0.519
Non seed predators	0.709

The percentages of individuals predicted as seed predators served as a means of determining the frequency of seeds as a main dietary component. *P. ursinus* and *P. anubis* are assigned as heavy seed predators based on observational studies (Peters, 1991; Nystrom 2004), *Theropithecus gelada* is assigned as a non-seed predator (Jolly, 1970).

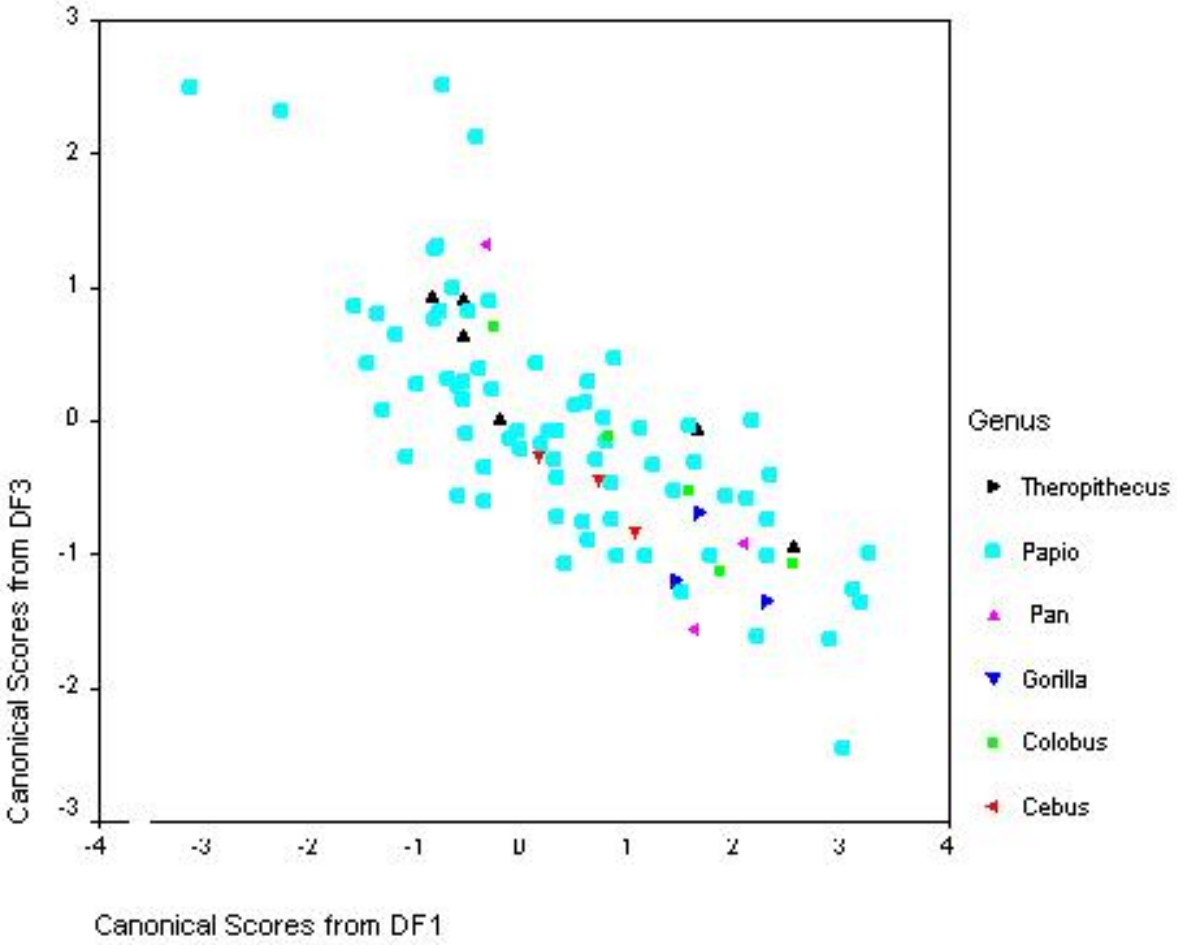

Figure 4: DF3 scores for extant species

Table 13: Predicted intensity of seed predation based on DF3

Species (n)	Assigned Seed predator	Percentage of seed predation	Intensity of seed predation
Papio ursinus (20)	Yes	.85	Heavy
Theropithecus gelada (6)	No	.50	Moderate
Papio anubis (21)	Yes	.75	Heavy
Papio kindae (24)	No	.25	Light
Colobus badius (3)		1.00	Heavy
Colobus polykomos (2)		.50	Moderate
Gorilla gorilla (3)		1.00	Heavy
Cebus apella (3)		1.00	Heavy
Pan troglodytes (3)		.66	Moderate
Papio cynocephalus (4)		.75	Heavy
Papio hamadryas (2)		1.00	Heavy

The predictions for all cases are very similar to observed diets found in the literature based on field studies. All of the *Cebus apella* sampled here were predicted as seed predators and in agreement with published observations (Bionski et al. 2000). Gorillas and chimpanzees are also predicted as heavy seed predators and agree with others' conclusions (Doran, 1998; Rogers et al. 1999). Notable here is the predicted intensity of seed predation for the two colobine monkeys. Norconk et al. (1998) found that *C. badius* and *C. polykomos* incorporated unripe seeds for 65-75% of their diets, while Kirkpatrick (1999) makes a distinction between the two, placing *C. polykomos* as the more intensive seed predator. These results agree more closely with Norconk et al. that these two species of *Colobus* rely heavily on seeds in their diets.

Extinct Taxa

The apparent success of the DFA predictions of determining broad trophic categories and distinguishing extant species justifies applying the same method to the fossil sample.

ANOVA tests for the variables showed that all traits showed statistically significant differences in each of the groups. The analysis generated two discriminant functions, the first capturing 72.3% of the variance (Table 14) and each tested as statistically significant (Table 15).

Table 14: Generated canonical function for DF4

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.598	72.3	72.3	.784
2	.611	27.7	100.0	.616

Table 15: Wilks' lambda Significance of DF4

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 2	.239	125.998	10	.000
2	.621	41.979	4	.000

The first canonical function generated is similar to the extant-only analysis and the structure matrix is presented in Table 16. On the first function, small pits loaded most positively; total medium pits loaded most positively on the second function. Table 17 presents the position of the group centroids and confirms that in this fossil population, frugivores are most easily distinguished from folivores on the first function, and folivores and gramnivores are most easily distinguished on the second. The resultant predictions concluded that 94.6% of the *a priori* classifications were correct. Figure 5 plots the distribution of ungrouped cases in relation to the group centroids and illustrates the amount of variation included in this sample.

Table 16: Structure matrix of DF4

	Function	
	1	2
Total Small Pits	.928	.263
Scratch Texture	-.233	.064
Total Medium Pits	.019	.800
Total Scratches	-.054	.504
Total Large Pits	-.003	-.367

Table 17: Functions at group centroids for DF4

	Function	
Predicted Group for DF4	1	2
Frugivores	-1.218	-.191
Gramnivores	.927	.836
Folivores	1.888	-1.509

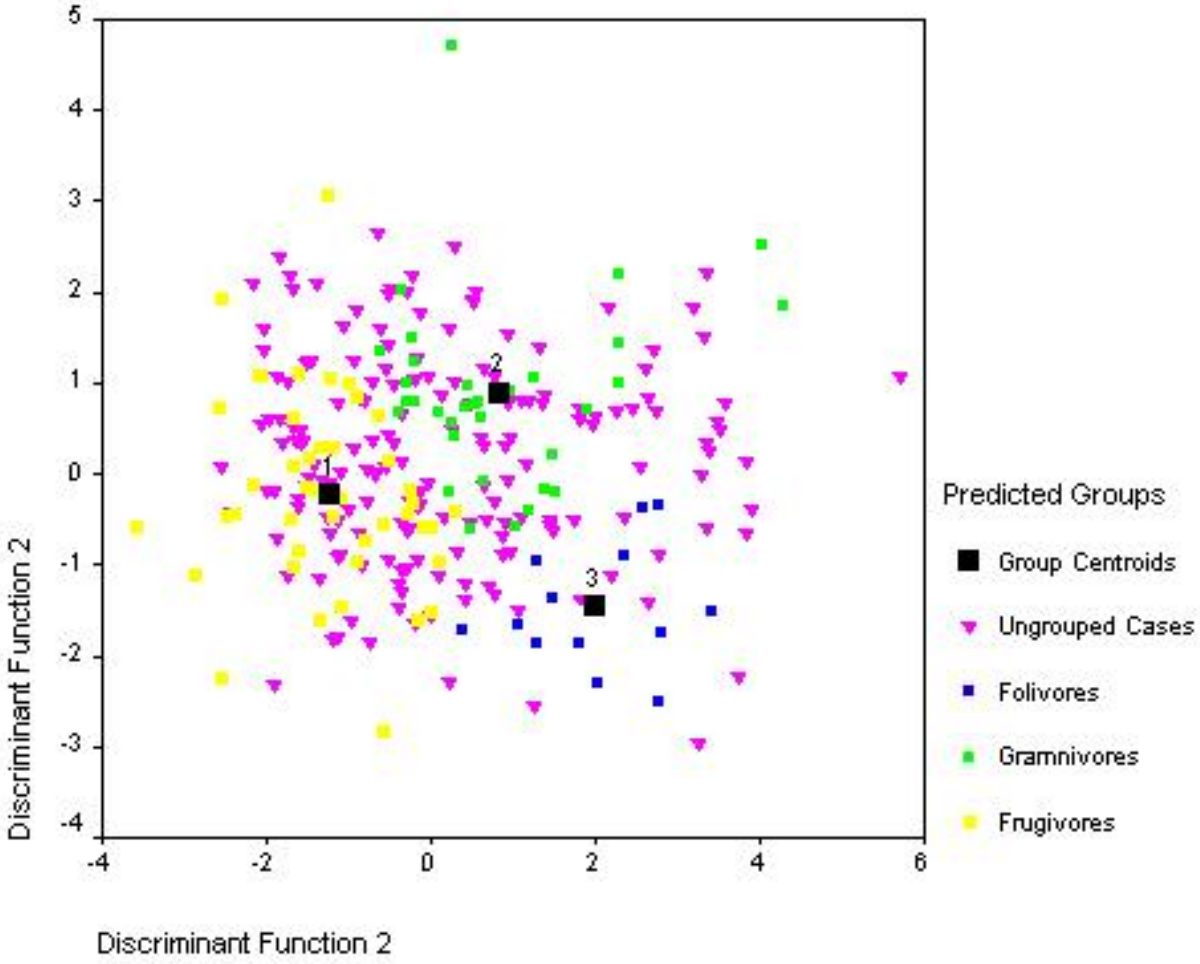

Figure 4: DF4 distribution around group centroids. (1) Frugivory; (2) Gramnivory; (3) Folivory

Table 18 shows the percentages of individuals in each species predicted as falling into one of the three broad tropic groups. *Australopithecus robustus* is predicted as including more fruit in its diet than the gracile form and this is in agreement with isotopic reconstructions made by Sponheimer and Lee-Thorp (1999).

Cercopithecoides williamsii is predicted as a predominant grass eater for the individuals at Sterkfontein, the individuals from Makapansgat and Bolt's Farm were predicted as fruit eaters, and agrees with dental regressions (Benefit, 1999) but differ somewhat from El-Zaatari et al (2005) and isotopic values. Codron et al. (2005) indicate

that *C. williamsii* represents a wide variation of isotopic values and his sample includes different individuals than those presented here; however, three of them overlap, STS 394B, STS 282, and STS 300, and agree exactly with the predictions based on DF4.

Table 18: Predicted diets for fossil species from DF4

Species (N)	Predicted as fruit eating	Predicted as grass eating	Predicted as leaf eating	Overall predicted diet
Australopithecus africanus (9)	0.00	0.88	0.12	Grass
Australopithecus robustus (16)	0.38	0.62	0.00	Grass/Fruit
Cercopithecoides williamsii (13)	0.38	0.47	0.15	Grass/Fruit
Dinopithecus ingens (14)	0.36	0.57	0.07	Grass/Fruit
Gorgopithecus major (7)	0.14	0.43	0.43	Grass/Leaf
Papio angusticeps (12)	0.33	0.33	0.33	Mixed
Papio robinsoni (18)	0.88	0.06	0.06	Fruit
Papio wellsi (3)	0.33	0.00	0.66	Leaf/Fruit
Parapapio sp. (3)	0.00	0.33	0.66	Leaf
Parapapio antiquus (3)	0.33	0.33	0.33	Mixed
Parapapio broomi (31)	0.81	0.03	0.16	Fruit
Parapapio jonesi (19)	0.47	0.32	0.21	Mixed Fruit
Parapapio whitei (19)	0.53	0.26	0.21	Mixed Fruit
Theropithecus danieli (5)	0.20	0.80	0.00	Grass
Semnopithecus sp. (4)	0.00	0.00	1.00	Leaf
Theropithecus darti (2)	1.00	0.00	0.00	Fruit

Most of the *Dinopithecus ingens* individuals from Swartkrans were predicted as mixed gramnivores/frugivores and contrast with predictions that *D. ingens* was a primary frugivore based on dental regressions (Benefit, 1999) and carbon isotopes (Codron et al. 2005), but agree with El-Zaatari et al. (2005) that C4 grasses made up a substantial part of its diet.

Gorgopithecus major, in contrary to previous studies predicting it as a primary frugivore (El-Zaatari et al., 2005; Benefit, 1999), was predominantly folivorous with equal numbers of individuals reported as grass or leaf eating. *Papio angusticeps* was

predicted as being the most omnivorous of the well sampled fossil papionins and agrees nicely with Benefit's (1999) conclusions. *Papio robinsoni* individuals from Swartkrans were predicted as predominantly frugivores, disagreeing with SEM reconstructions (El-Zaatari et al. 2005) and $\delta^{13}C$ ratios (Lee-Thorp and van der Merwe, 1993; Codron, 2005).

Parapapio broomi individuals from Makapansgat and Sterkfontein agree well with Benefit's (1999) regressions of dental characteristics that it was a primary frugivore. Studies based on isotopic carbon (van der Merwe 2003; Lee-Thorpe and van der Merwe 1989) suggest that *Pp. broomi* and *Pp. jonesi* are nearly indistinguishable, but this analysis predicts more *Pp. jonesi* individuals as gramnivorous. Instead, *Pp. jonesi* is most similar to *Pp. whitei*, both primarily frugivorous but still eating significant amounts of foliage.

Theropithecus danieli from Swartkrans was predicted to be most similar to modern gelada baboons as a primary gramnivore and in agreement with $\delta^{13}C$ studies (Codron et al., 2005) while both *Theropithecus darti* from Makapansgat were predicted as frugivores which seems anomalous because the dental morphology is that of a strict folivore (Benefit, 1999) and may be the product of a such a small sample size (n=2).

DF5 was run to distinguish the level of seed predation in the fossil species. The same variables were used as in the extant example and all variables tested as significant as well as the discriminant function generated. Figure 6 plots the distribution of canonical scores generated from DF5 against those for individuals from DF1 and illustrates the wide range of variation in the canonical scores between individuals.

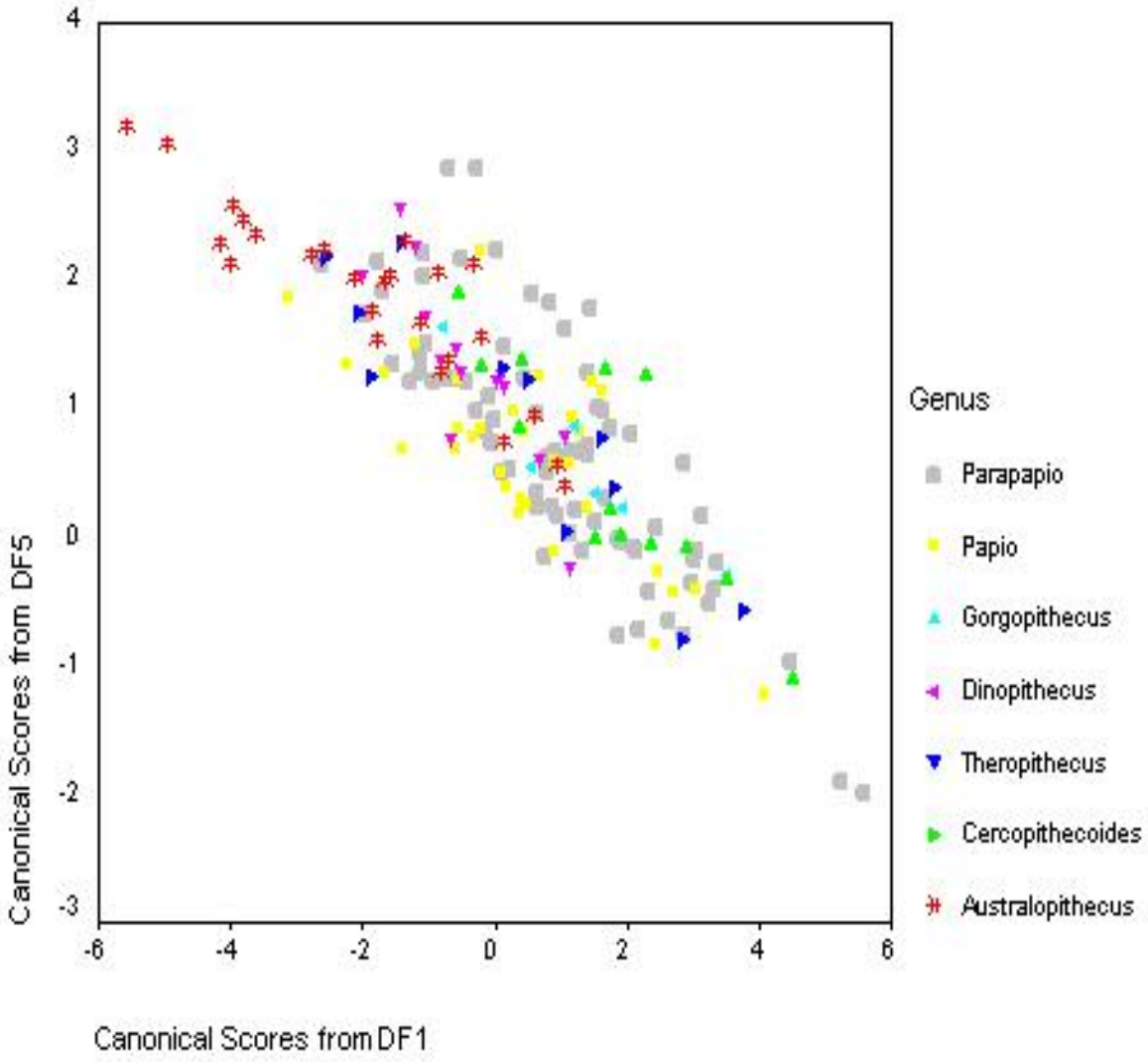

Figure 6: DF5 distribution of scores for extinct species

Table 19 shows the percentages of individuals in each species testing as seed predators through the DF4. *C. williamsi, G. major, P. angusticeps, P. wellsi,* and *Pp. broomi* result in the highest levels of seed predation in the fossil sample. In this analysis, *Pp. broomi* is still easily distinguished from *Pp. jonesi* and *Pp. whitei*, but the latter two cannot be distinguished from one another.

Table 19: Predicted intensity of seed predation based on DF5

Species (N)	Frequency of Positive Score	Level of seed predation
Australopithecus africanus (9)	0.23	Light
Australopithecus robustus (16)	0.00	None
Cercopithecoides williamsi (13)	0.62	Strong
Dinopithecus ingens (14)	0.21	Light
Gorgopithecus major (7)	0.85	Heavy
Papio angusticeps (12)	0.67	Strong
Papio robinsoni (18)	0.50	Moderate
Papio wellsi (3)	0.66	Strong
Parapapio sp. (3)	0.66	Strong
Parapapio antiquus (3)	0.33	Moderate
Parapapio broomi (31)	0.74	Heavy
Parapapio jonesi (19)	0.37	Moderate
Parapapio whitei (19)	0.37	Moderate
Theropithecus danielli (5)	0.20	Light
Semnopithecus sp. (4)	0.50	Light
Theropithecus darti (2)	1.00	Heavy

Finally, a bivariate plot of mean pit and scratch counts for each species (Figure 7) shows that the relationship between pits and scratches alone is enough to distinguish broad trophic categories. The lower center of the plot groups all the primary frugivores predicted in DF2, *G. gorilla, T. darti, P. hamadryas, P. robinsoni, P. ursinus,* and *Pp. broomi*. The upper right corner groups species mostly classified as gramnivores, *T. gelada, T. danieli, D. ingens, A. africanus,* and *A. robustus*. Stretching from the lower left at a slope, the rest of the species are grouped together that represent mixed diets, most species, including *Pp. jonesi* and *Pp. whitei,* are grouped here. The results are more clearly seen when overlaying the average pit and scratch counts for individuals predicted as each of the broad trophic groups by the DF4. Means of pits vs. scratches clearly delineate broad scale trophic patterns that are easily seen under the eyepiece.

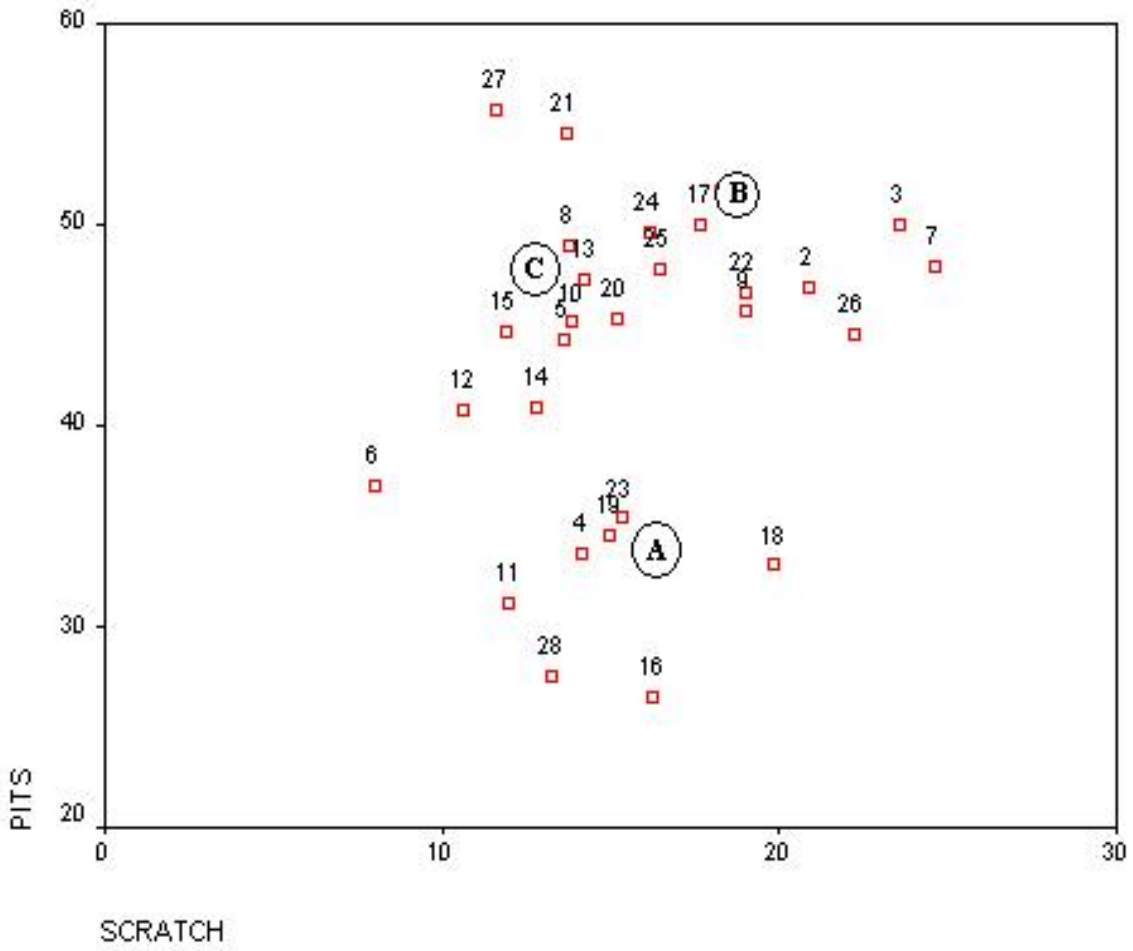

Figure 7: Bivariate scatterplot, total pits versus total scratches (A) Fruigivores; (B) Gramnivores; (C) Folivores; (2) *A. africanus* (3) *A robustus* (4) *C. apella* (5) *C. williamsi* (6) *C. badius* (7) *T. gelada* (8) *C. polykomos* (9) *D. ingens* (10) *G. major* (11) *G. gorilla* (12) *P. troglodytes* (13) *P. angusticeps* (14) *P. anubis* (15) *P. cynocephalus* (16) *P. hamadryas* (17) *P. kindae* (18) *P. robinsoni* (19) *P. ursinus* (20) *P. wellsi* (21) *Parapapio sp.* (22) *Pp. antiquus* (23) *Pp. broomi* (24) *Pp. jonesi* (25) *Pp. whitei* (26) *T. danieli* (27) *Semnopithecus* (28) *T. darti*

Table 20 separates the predictions from DF4 for each site included in this sample and is useful in discussing variation within species and between sites. It is interesting to note the variation in certain species between sites. *Pp. jonesi* uncovered at Makapansgat and Sterkfontein has a mixed diet with roughly equal proportions of fruit, grass, and leaves.

Table 20: Dietary predictions broken down by site

Site - Species	Frugivore	Gramnivore	Folivore	Total Predicted Diet
Makapansgat				
- *Pp. broomi* (n=4)	0.50	0.00	0.50	Fruit/Leaf
- *Pp. jonesi* (n=1)	0.00	0.00	1.00	Leaf
- *Pp. whitei* (n=5)	0.80	0.00	0.20	Fruit
- *T. darti* (n= 2)	1.00	0.00	0.00	Fruit
- *C williamsi* (n=1)	1.00	0.00	0.00	Fruit
-				
Sterkfontein				
- *A. africanus* (n=9)	0.00	0.88	0.11	Grass
- *C. williamsi* (n=10)	0.20	0.60	0.20	Grass/mixed
- *D. ingens* (n=1)	0.00	1.00	0.00	Grass
- *Pp. broomi* (n=28)	0.85	0.03	0.11	Fruit
- *Pp. jonesi* (n=8)	0.37	0.37	0.25	Mixed
- *Pp. whitei* (n=11)	0.46	0.27	0.27	Fruit/Mixed
Taung				
- *Pp. antiquus* (n=3)	0.33	0.33	0.33	Mixed
- *Pp. whitei* (n=2)	0.00	1.00	0.00	Grass
- *P. wellsi* (n=2)	0.50	0.00	0.50	Fruit/Leaf
Bolt's Farm				
- *P. robinsoni* (n=1)	1.00	0.00	0.00	Fruit
- *C. williamsi* (n=2)	1.00	0.00	0.00	Fruit
- *Pp. whitei* (n=1)	1.00	0.00	0.00	Fruit
Coopers Cave				
- *P. angusticeps* (n=9)	0.33	0.33	0.33	Mixed
Kromdraai				
- *G. major* (n=7)	0.14	0.43	0.43	Grass/Leaf
- *P. angusticeps* (n=3)	0.33	0.33	0.33	Mixed
- *Parapapio sp.* (n=3)	0.00	0.33	0.66	Leaf/Grass
- *Pp. jonesi* (n=1)	0.00	1.00	0.00	Grass
Swartkrans				
- *A. robustus* (n=16)	0.38	0.62	0.12	Grass/Fruit
- *D. ingens* (n=13)	0.38	0.54	0.08	Grass/Fruit
- *P. robinsoni* (n=17)	0.88	0.06	0.06	Fruit
- *Pp. jonesi* (n=9)	0.66	0.22	0.11	Fruit/Grass
- *T. danieli* (n=5)	0.20	0.80	0.00	Grass

However, the specimens found at Swartkrans show a definitive shift towards frugivory. *Pp. whitei* is significantly more frugivorous at Makapansgat than those found at Sterkfontein. As a whole there is a general trend toward gramnivory as the sample progresses through time. More species are predicted as gramnivorous at the youngest sites compared to Makapansgat and Sterkfontein; Kromdraai only has three individuals out of fourteen predicted as frugivorous although Swartkrans has quite a number, but still more gramnivores than any of the sites. However, the general trend is an apparent shift in diets chosen by these Plio-Pleistocene baboons towards gramnivory and will bear heavily in the ecological reconstructions discussed below.

Predictions of Unknown Taxa

The discriminant function analyses of microwear features on this fossil sample beautifully separate individuals into their trophic categories and begin to draw distinctions between these species. The last analysis was an experiment to see how well these microwear features could be used for assigning generic or specific classifications to the remaining sample of individuals with unknown taxonomic affinities.

Eleven *a priori* categories were assigned based on all of the extinct species with adequate sample sizes. *P. wellsi* (n=2) and *P. antiquus* (n=3) were left out because of poor sample sizes and neither represent confident taxonomic categories (Williams et al., 2006). The resultant DFA concluded that only 27.1% of individuals actually belonged to their taxonomic group based on the microwear readings. With 11 *a priori* classifications, the random chance at success was 9%, so the variables used represent a three-fold increase in predictive power. Some species were better or worse than others. For example, *Australopithecus africanus,* and the *Parapapio* species were correctly classified

over 33% of the time while only *Australopithecus robustus* and *Papio robinsoni* were over 40% indicating that these species had the most clearly distinct microwear signals in the sample. Many other species fell significantly below the mean of 27.1%, but all were above the random 9% level which indicates that the species used in this analysis have diets that are too similar and cannot attribute species affiliation to single individuals. The microwear signals are useful for distinguishing groups of species and evaluating previously defined taxonomies, but not assigning taxonomic membership to single individuals.

Chapter V

Discussion

The analysis presented here was conducted on 272 individuals comprising eleven genera and thirty-one species. Two species were only represented by one individual (*Pongo pymaeus* and *Alouatta palliate*), and a number of them had only poor sample sizes, *Gorilla gorilla* (n=3), *Pan troglodytes* (n=3), *Colobus badius* (n=3), etc. Ninety-one individuals made up the sixteen extant species, and there were seventy-seven individuals without species designations that were left out of most of the analyses.

Of the remaining sample with known species designations, the majority of the analysis of extant individuals came from three *Papio* and one *Theropithecus* species. For the fossils sample, *Parapapio, Papio*, and *Australopithecus* were best represented. Observational studies discussed earlier demonstrate that extant *Papio* has a highly varied diet and prefers fruit when available but includes a significant amount of supplementary components, and there has, thus far, been no evidence to suppose that fossil papionins would have been any different in this respect. Their dentition is that of a generalized browser and isotopic and SEM microwear analyses agree.

Despite the small sample sizes of the *a priori* designated species, the DFA2 predicted diets for extant species that corresponded well to field studies and indicates the robusticity of low-magnification stereomicroscopy as a method for reconstructing fossil diets. Late Pliocene *Parapapio* is primarily a frugivore, more so than the extant papionins sampled here. There is a remarkable shift in the later Pleistocene cercopithecines that are

still predicted as somewhat frugivorous, but add a substantial gramnivorous component to their diets.

This example left out predictions for hard object feeding described by Semprebon et al. (2004), which is unfortunate because this undoubtedly would have illuminated more variation between the fossil species. However, there were few extant species in this sample that could have been described as hard object specialists. *C. apella* would have been an excellent example, but it did not seem prudent to run the analysis on 272 individuals based on three known hard object feeders. Alternatively, assumptions could have been made on the fossil sample based on previous dietary reconstructions. El-Zaatari et al. (2005) proposed that *C. williamsi* was possibly a hard object specialist due to the abundance of large pits, but mentions that this could also only indicate a terrestrial diet full of grit. However, the purpose of this study was to reconstruct the diets of fossil species based on modern analogues, so predictions of hard object feeding were left out.

Comparing the mean pit/scratch counts for each species illustrated in Figure 7, there is a definite relationship illustrated between microwear frequencies and predicted dietary categories. Frugivores exhibit the fewest total pits and intermediate number of scratches, folivores have a lot of pits but very few scratches, and gramnivores have high pits and scratch counts.

This differs from Semprebon et al. (2004) and Godfrey et al. (2004) who found that frugivores have many pits and few scratches while gramnivores have the opposite. This can be explained in one of a number of different ways. First, the methods used here are different from those described by Semprebon et al (2004). They differentiated pits into large, medium, and small pits, and large, medium, and small puncture pits, and that

differentiation was not done here due to an initial misreading of the method; pits were simply counted as a single type and only distinguished by size. It is quite possible that the difference in methods produced such dissimilar proportions.

Alternatively, the current results could actually reflect different diets. Semprebon et al (2004) primarily examined bovids and only included a few primates in their study. The extant primates used in this analysis that are classified in each category differ from bovids that would be classified the same. For example, extant papionins that are even somewhat gramnivorous are more likely to include a lot of roots in their diet as well as grass (Jolly, 2001; Codron et al., 2006) and it is likely that their fossil counterparts were the same (Codron et al., 2005). Including roots into a diet introduces a lot of grit which would result in the much higher pit counts in many of the gramnivorous species. Large pits are most frequent in folivores, and there seems to be a correlation between folivory and seed eating in this sample. The fossil species with the highest levels of folivory, *G. major* and *P. wellsi* are also listed as being strong seed predators. Whether or not seed predation and folivory are strongly correlated in primates is a different discussion, but some extant colobine monkeys are observed to have a very strong seed component in their diets during certain seasons of the year (Kirkpatrick, 1999) and may serve as an interesting analogue in understanding some of the Plio-Pleistocene cercopithecines.

Finally, as mentioned, this analysis excluded predictions for hard-object feeding, which is certainly associated with some types of feeding more than others. Semprebon et al. (2004) noticed that hard objects leave a distinctive pattern of large pits, deep trench-like scratches, and gouges, and Figure 7 would have certainly captured these

characteristics but was unable to distinguish how much of the variation in the heaviest pits was due to hard-objects specialization.

One of the original goals of this study was to determine whether microwear signals would be useful in assigning species designations for the seventy-seven unknown individuals; however, this proved impossible due to the nature of microwear scarring. The DFA was only moderately capable at reproducing genus level differences in microwear frequencies, but unable to directly predict species level differences between groups. It is important to remember that the microwear features examined here are ephemeral (Teaford and Oyen, 1989) and reflect only the last few meals eaten by an individual. Depending on the time of year or geographical range, individuals in a single species might exhibit a highly varied diet, and this is especially true of papionins. As a result, species only show significant differences when compared as groups and the DFA gives percentages of individuals predicted as falling into one trophic category or another. Because the process of microwear scaring on enamel itself represents a sampling error, i.e., the 'last supper' phenomenon discussed by Teaford an Oyen (1989), only large sample sizes will adequately illustrate large scale taxonomic differences in diet. It is unfortunate that microwear analysis cannot be used to assign individual taxonomic status but it is able to assign broad trophic categories for miscellaneous teeth that could supplement future morphometric studies.

But this begs the question of the taxonomic validity of this fossil sample. Presumably, if we are to assume the traditional species of *Parapapio* indeed reflect true biological affinities, these character traits should infer certain behavioral idiosyncrasies. *Parapapio* species have traditionally been defined by dental size (Frost and Delson,

2002). *Pp. broomi* and *Pp. whitei* are found in the same fossil deposits in Sterkfontein and Makapansgat, some have questioned whether these two represent a single species with wide variation (Williams et al., 2006), or whether they are actually biologically distinct. Alternatively Thackeray and Myer (2004) suggest that similar isotopic ratios indicate that *Pp. jonesi* and *Pp. broomi* are a single species.

The microwear results present two alternate hypotheses: first, traditional taxonomic designations are incorrect and should be revised and that *Parapapio* species are indeed very similar to modern baboons in the amount of intraspecific variation in diet, or that traditional taxonomies are correct.

The multivariate analyses at first glance indicate that there were some marked differences within *Parapapio* between species and sites as predicted by the DF4 (Table 20) which support traditional taxonomic designations. *Pp. broomi* is predicted as being the most frugivorous of the four and not at all similar to the diets of *Pp. whitei*, predicted as eating more grass and leaves. *Pp. jonesi* found in the same deposits is very similar to *Pp. whitei* with equal proportions of grass, leaves, and fruit, and both are more similar to *Pp. antiquus* at Taung than any are to *Pp. broomi*. *Pp. jonesi* found at Swartkrans was much more frugivorous than earlier forms and indicates either that there was a change in diet over time and *Pp. jonesi* exhibits remarkable variation, or that the species *Pp. jonesi* is inadequate.

Other authors have proposed revising the *Parapapio* taxonomy, but the results presented here do not necessarily support any of those particular revisions. Thackeray and Myer (2004) noticed no significant difference between carbon isotope ratios of *Pp. jonesi* and *Pp. broomi* and surmised that this was because they were a single sexually

dimorphic species. Microwear analysis has the ability to differentiate between C_3 leaves and C_3 fruit and will exhibit identical isotopic ratios. Sterkfontein *Pp. jonesi* and *Pp. broomi* trophic predictions (Table 20) indicate that each differ in the amount of fruit, grass, and leaves proportioned, but do not differ in the total amount of C_3 resources in their diets. This would support the evidence that both species are isotopically similar, but suggest that the observed similarity is an artifact resulting from the deficiencies of $\delta^{13}C$ analyses, as microwear signals do differentiate between *Pp. broomi* and *Pp. jonesi*.

Williams et al. (2006) proposed that *Pp. broomi* and *Pp. whitei* were consistently grouped as morphologically separate from other papionins across sites and suggested that the two could be scaled morphologically and should be distinguished only at the subspecies level. The data presented here would not disagree with that conclusion. Although the diets differ remarkably for *Pp. broomi* and *Pp. whitei*, variation between the two is not substantially greater than modern subspecies of *Papio*.

Theropithecus showed inconsistent results but as a whole showed a preference for grass and leaf eating similar to modern gelada baboons. Arguments have been raised for and against the specific classification of fossil *Theropithecus* and these results cannot resolve the dispute (Dechow and Singer, 1984; Jablonski, 1994). There have simply not been enough individuals collected to form any adequate conclusion. It is interesting that both *T. darti* specimens from Makapansgat are predicted as frugivores even though this does not correspond to their dental morphology.

Determining taxonomy based on microwear alone would be purely speculative, but it is useful in evaluating morphometric scenarios. However, modern analogues can prove a useful tool in understanding the variation of fossil samples. Although modern

Papio is often referred as multiple species, evidence of hybrid zones and captive breeding (Phillips-Conroy et al., 1986; Phillips-Conroy and Jolly, 1991; Jolly, 2001) indicates that the modern forms of *Papio* have been described morphologically but do not necessarily reflect biological differences. Modern studies of baboon diets indicate that there is a wide seasonal variation within each group and between forms and this is reflected in the microwear analyses presented here.

These results could be used to support either of the proposed hypotheses, but preference is given here to morphometric studies that indicate similarity of the fossil papionins and suggest a taxonomic revision. The only conclusion that can be made from this study is that there was wide variation in the diets of papionins with little continuity between sites. Additionally, the amount of variation for each species is considerable as seen in the PCA scores (Table 4). The standard deviations for each species indicate that there is a great deal of variability, but the fossil species do not necessarily exhibit more variation than extant *P. ursinus*. The observed variation is greater than other extant baboons and could support the need for taxonomic revision but says nothing of what revisions should be made.

The predictions of diet from low-magnification microwear readings are comparable to those found by other methods. For the most part, isotopic and SEM microwear readings produce nearly identical dietary reconstructs as these. SEM microwear and isotopic signals do not as often correspond to dietary reconstructions based on dental morphology (Benefit, 1999) and this present study tends to agree more strongly with the former methods rather than the latter, and suggesting that dental traits are as often products of phylogeny as they are of behavior. When combined with all

these other lines of evidence, low-magnification microscopy analyses are able to add to the paleoecological reconstructions that have formed the basis of an ecological evolutionary theory of the Plio-Pleistocene in South Africa.

The differences in diet for fossil papionins between sites (Table 20) are readily apparent and justify a discussion of the changing South African paleoecology. Individuals at the older sites, Makapansgat, Sterkfontein, and Taung, are more often predicted as frugivores. At Sterkfontein, 85% of *Pp. broomi* individuals were predicted as frugivores, as well as 80% of *Pp. whitei* from Makapansgat. *Pp. whitei* from both sites combined is indicated as a primary frugivore, and *Pp. jonesi* from Sterkfontein, although more generalized, still includes fruit as a substantial component.

At the younger sites, Coopers Cave, Kromdraai, and Swartkrans, there is a shift towards more generalized and folivorous primates. At Kromdraai, over a third of all individuals were predicted to be gramnivores, all of their diets included substantial leaf components, and only two specimens, *G. major* and *P. angusticeps,* were predicted as frugivorous. At Swartkrans, many more individuals were predicted as fruit eaters; 58% of all the individuals are frugivorous, almost as high as Sterkfontein. However, there were more taxa with a substantial gramnivorous component to their diet than the individuals from the earlier sites.

Reed's (1997; 2002) reconstruction of the ecology of Plio-Pleistocene South African deposits was based on the relative numbers of frugivorous and arboreal species. She found that modern ecosystems could be predicted by the abundances of these kinds of species and concluded that early sites were much more forested, but that the

persistence of frugivorous species indicated that patchy woodlands persevered into the Pleistocene.

The results presented here support that ecological reconstruction. None of the individuals from Makapansgat in this study were predicted as gramnivorous; all were judged as fruit or leaf eaters, with the distinct preference for fruit. This would suggest that Makapansgat was a relatively closed environment, with ample opportunities for primates to forage in the trees. McKee (1999) suggests, however, that grazers and predators that feed on grazers are not rare at Makapansgat and that this points to the presence of available open areas. However, it seems likely that the primates at Makapansgat did not exploit the existing grasslands since none of them were predicted as gramnivorous.

There seems to be a change at Sterkfontein, with more individuals indicated as gramnivores; however, a majority of *Parapapio* are still predicted as frugivorous, although they include more grass and leaves than the same species at Makapansgat. Reed (1997) noted fewer arboreal species at Sterkfontein than Makapansgat and concluded that the site represents a medium density forest and the data presented here agree. *Australopithecus africanus* specimens were almost entirely gramnivorous, while *Cercopithecoides williamsi* and *Parapapio* all indicate that primates were beginning to exploit an expanding open ecology.

Only four individuals from Kromdraai were predicted as frugivores which indicate a remarkable shift from the older sites. Reed (1997) noticed only a moderate number of frugivores and no arboreal species, and this current analysis does not disagree with her reconstruction that it was an open grassland with nearby patches of woodland.

Reed (1997) finds that Swartkrans deposits produce almost no arboreal species, but some aquatic and frugivorous species. The results here agree, most of the individuals in this analysis were predicted as frugivores. It should be noted that this may be a bias resulting from the generous samples of *P. robinsoni* from Swartkrans included here. *P. robinsoni* is indicated as a primary frugivore, but *A. robustus* and *D. ingens* sampled are both predominantly gramnivorous. Isotopic samples of Mbrs. 2 and 3 showed no substantial change in vegetation during the period (Lee-Thorp and van der Merwe, 2004), and most of the individuals analyzed here were gramnivores. This would indicate that although there were some woodlands, grasslands were dominant at Swartkrans and that this ecology was relatively constant through the deposition of Mbrs. 2 and 3.

Taken as a whole, this suggests that there was a cooling and drying trend that spanned the Plio-Pleistocene and that earlier periods were warmer with considerable forested areas, but the later periods were much more open. This general trend noticed by other researchers, suggests that this reconstruction of papionin diets, can be used to assess the relative chronologies of the South African sites. The most frugivorous and fewest gramnivorous species are found at Makapansgat and would date it as the oldest of the sites. Sterkfontein has just as many frugivorous individuals, but more gramnivores and would be somewhat younger. Kromdraai and Swartkrans are the youngest and would have been deposited well into the cooling and drying during the Pleistocene and the expansion of the grasslands at Kromdraai is exaggerated at Swartkrans.

As a whole, different lines of evidence all point towards environmental changes separating the older and younger sites which had a major impact on the local fauna and

form the context of the apparent pulse of hominid evolutionary change seen in southern Africa during the Plio-Pleistocene.

Vrba's (1975; 1999) bovid studies indicated that there was a pulsed speciation event after 2.7-2.5 mya and suggested a major cooling trend surrounding the depositional history for Sterkfontein that would have presumably affected primates as well. However, this is not the case. Primates found at the older Makapansgat deposits survive well past her proposed major cooling period. This either indicates that Makapansgat is significantly younger and roughly contemporaneous to Sterkfontein Mbr. 4 or that the climate changes and corresponding faunal turnover was not so severe. The relative dating of Makapansgat is probably accurate, however, based on faunal associations between sites (McKee et al., 1995) and cercopithecine associations with East Africa (Delson, 1984). The microwear data presented here support the latter proposal because there are no species indicated as gramnivores at Makapansgat although there are a few at Sterkfontein. This indicates that Makapansgat predates the cooling trend from 2.7-2.5 mya and denotes no major turnover for cercopithecines. The only possible conclusion from these results is that Vrba is correct; Sterkfontein represents a cooler period around 2.5 mya, but the ecological changes were only moderate. Perhaps bovids encountered different evolutionary pressures that forced them to radiate into the grasslands, but obviously cercopithecines still had access to their previously preferred resources.

The second turnover pulse Vrba (1999) discerns from bovid assemblages is between 1.9-1.8 mya and indicates another episode of severe cooling and drying. Unlike the event postulated for 2.7-2.5 mya, the data on cercopithecine diets do support Vrba's observations of severe environmental change. Of all the cercopithecines found at the

older sites, only *Pp. jonesi* survives into the Pleistocene deposits at Swartkrans but only in Mbr. 1. All of the Swartkrans/Kromdraai taxa are new and indicate a distinct preference for gramnivory. One can only conclude from this evidence that there was indeed a marked speciation/extinction event around 1.9-1.8 mya resulting from local ecological changes that continued well into the Pleistocene. Pliocene holdovers like *Pp. jonesi* are able to survive because of patchy riparian forests found in the earliest Swartkrans deposits, but did not survive further vicariance of their preferred habitat.

As a result, both periods can be juxtaposed as two distinct scenarios. There was a cooling and drying trend leading up to Vrba's (1999) observed turnover at 2.7-2.5 mya, but it was moderate and gradual. The later climate change was a distinct event with major speciation and extinction of the cercopithecines presented here. The evolutionary perspective should thus focus on how gradual and punctuated climate changes differ in their affects of biotic evolution. Local cooling and drying created open ecologies that had once been a relatively minor part of southern Africa and provided new opportunities for species to evolve and flourish.

These two events of cooler and dryer climates spanning the Plio-Pleistocene allowed an adaptive radiation into the grasslands by primates that previously had remained in forests. The dynamics of adaptive radiation are such that, within a relatively short period of time, many new forms can derive from a few ancestral species and will appear as a speciation event in the fossil record. In this case, a species that can survive an environmental change by exploiting newly opened ecologies has a distinct advantage and the traits that are advantageous to these new ecologies will be selected for. In a sudden climate change, the fossil record would exhibit corresponding punctuated speciation and

extinction events, specialists are hurt by these changes more than generalists and the generalists would be capable of an ecological diaspora and rapidly speciate (Vrba, 1999). Alternatively, a gradual ecological change would still result in some faunal change, but it would not be as dramatic an event. Some species would be less affected than others and be able to adapt behaviorally before biologically. The cercopithecine diets presented here correspond well to this theory and describe a gradual behavioral radiation into the expanding grasslands at Sterkfontein, but more of a punctuated speciation event at 1.9-1.8 mya.

This forms the context for interpreting the results of the *Australopithecus* microwear readings within an evolutionary perspective. Both species exhibited high proportions of individuals predicted as gramnivorous and this matches reconstructions based on isotopic ratios indicating that they included substantial C_4 resources (Lee-Thorpe, 2003). Scott et al. (2005) found that there were differences in microwear texture between *A. africanus* and *A. robustus* but there were significant overlaps. *A. robustus* was found to include more hard and brittle foods in its diet while *A. africanus* had a much tougher diet based on the amount of complexity and anisotropy exhibited by each. The method used by Scott et al. (2005) indicated variability in diet for each individual, which is not possible in low-magnification stereomicroscopy that only classifies individuals in one trophic category or another. Textural analysis indicated that *Australopithecus* varied in different components of their diets, but the substantial proportions were probably quite similar and the differences were perhaps due to seasonal variability. This compares with the results of this analysis that indicated a profound similarity in the two species with *A. robustus* predicted as only slightly more frugivorous. This would agree with Scott et al.

(2005) that the diets were quite similar for the two with differences being only in the more minor dietary components.

Clarke and Tobias (1995) indicate that the oldest australopithecine remains are represented by STS 573 at Sterkfontein Mbr. 2. They observe that STS 573 exhibited a number of postcranial features best adapted for life in trees and that this indicated an early arboreal history for *Australopithecus*. However, *A. africanus* presented here exhibited distinct microwear signals for gramnivory and denotes an early *Australopithecus* radiation into the grasslands even though open ecologies were not yet dominant. The earliest expansion of grasslands based on reconstructions of cercopithecine diets occurred during the depositional history of Sterkfontein Mbr. 4 although it has been discussed that this expansion was probably moderate; however, *A. africanus* was already heavily exploiting grassland resources. It is unfortunate that no *A. africanus* specimens were sampled from Makapansgat because that would have been an indicator of the evolutionary history of gramnivory in *A. africanus*. Makapansgat is distinguished in this analysis with not a single individual predicted as gramnivorous, so one can only speculate if *A. africanus* was able to differentiate from other primates much earlier. Nonetheless, later into the Pleistocene, this early ability to exploit grassland resources proved advantageous when more severe climate changes caused grasslands to become the dominant ecology. *A. robustus* was quite obviously eating grass as a primary staple.

Early hominid ability to exploit grassland resources encouraged their success once ecological pressures forced less adapted species into extinction. Although closed ecologies are still present at the younger sites, they were probably patchy by the

Pleistocene; the early hominids had already radiated into the grasslands and used the inconsistent woodland resources as supplements rather than staples. This adaptation for open ecologies no doubt contributed to later evolutionary developments in *Homo* of South Africa.

Chapter VI

Conclusions

In this study, analyses of dental microwear examined through low-magnification stereomicroscopy largely agree with alternative methods for reconstructing the diets of the fossil cercopithecines from Plio-Pleistocene South Africa. The individuals examined exhibit significantly different microwear signals between taxa and site. Used in conjunction with others' research, these trophic category predictions are useful in reconstructing paleoecologies and evaluating theories surrounding early hominid evolution.

The changes in cercopithecine diets presented here form the basis of the following conclusions. First, low-magnification microwear analysis represents a compelling technique for reconstructing broad scale trophic categories of seed predation, frugivory, gramnivory, and folivory. Other methods, including dental characteristics, isotopic ratios, and SEM microwear signals, all broadly agree with the results of this analysis. Further work should expand the sample sizes, when possible, of the taxa presented here and include more individuals with specialized diets. The biggest advantage of this method over SEM or isotopic techniques is that large sample sizes can be generated in relatively short periods of time without specialized equipment or destruction of the fossil sample.

Second, the diets of extant papionins are by and large frugivorous and the ratio of alternative resources predicts the ecological availability of fruit. Cooler and drier

climates do not produce the forests generally necessary for abundant fruit reserves. Thus, the changes in diets exhibited in this sample, from the older primarily frugivorous species to the younger generalists, indicate that there was a shift in the South African Plio-Pleistocene towards more open ecologies. Although this was a general trend, wooded areas did not disappear and some cercopithecines were still able to subsist on a primary frugivorous diet well into the Pleistocene. The ecological changes are not indicated to be sudden and extreme by this analysis until after 2.0 mya during the deposition of Kromdraai and Swartkrans when grasslands began to be the dominant ecologies of the area. In the sequence between Makapansgat and Sterkfontein, the diets of the cercopithecines indicate a more gradual shift in habitats.

Finally, the diets of the australopithecines indicated by their microwear signals, point towards a habitat theory for their success in the Pleistocene. *A. africanus* predates the worst of the climate changes, but was evidently already exploiting the available grasslands. These adaptations were predisposed for open ecologies and allowed an adaptive radiation of hominids into the dominant grasslands of the Pleistocene. Additional microwear research should be performed on the australopithecines from Makapansgat and later *Homo* remains, but I would speculate that these fossils would also indicate an ability to successfully exploit an open ecology.

Future research should include samples of primates and hominids from earlier and later time periods than included here. It would be interesting to examine the diets of primates predating those presently sampled from Makapansgat to see how recently gramnivory becomes a useful trait in South African primate evolutionary history outside of the primarily gramnivorous *Theropithecus*. Also an expanded sample of microwear

signals would be useful in applying better relative dates to these remains. For this current analysis, individuals were only classified based on site, very little information was available on exactly where in each stratum they were uncovered, and in some cases this information does not exist. This is unfortunate because it would allow for a better understanding of the variation within species and how it corresponds to their position in the cave deposits. With this added dimension, the variation in diets of these species could serve as a test for assertions by Williams et al. (2006) that *Parapapio* represents a biochronological indicator of long depositional histories for Sterkfontein and Makapansgat and would be an excellent application of these data.

The deficiency of low-magnification microwear analyses is that it is unable to examine subtle dietary proportions in individuals. Using the methods here, it can assign an individual a category, but cannot begin to explain the variability in an individual's diet. It is really only a valid method for evaluating populations. In this way it is not as sensitive as examining isotopic ratios which indicate exact proportions of C_3 and C_4 dietary components. This means that low-magnification microwear studies will not replace existing methodologies but serve as a supplement. Despite whatever deficiencies may exist, however, it nonetheless remains easy and low tech, contrasting nicely to SEM and isotopic analyses. These other techniques may excel in precision and sensitivity, but the methods presented here represent sheer quantity. Large sample sizes can be generated very quickly with a low incidence of error which makes low-magnification microscopic evaluation of dental microwear an excellent supplement to others methods.

References Cited

Audin, L., et al.
2004 Palaeomagnetism and K-Ar and $^{40}Ar/^{39}Ar$ ages in the Ali Sabieh area (Republic of Djibouti and Ethiopia): constraints on the mechanism of Aden ridge propagation into southeastern Afar during the last 10 Myr. Geophysical Journal International 158(1):327-345.

Avery, D. M.
2001 The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. Journal Human Evolution 41(3):113-132.

Bamford, M
1999 Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. South African Journal of Science 95:231-237.

Benefit, Brenda R
1999 Biogeography, Dietary Specialization, and the Diversification of African Plio-Pleistocene Monkeys. *In* African Biogeography, Climate Change, and Human Evolution. T.G. Bromage and F. Schrenk, eds. Pp. 172-188. New York: Oxford University Press.

Berger, Lee R., Rodrigo Lacruz, and D. J. De Ruiter
2002 Brief Communication: Revised Age Estimates of *Australopithecus*-Bearing Deposits at Sterkfontein, South Africa. American Journal of Physical Anthropology 119:192-197.

Bernor, RL, and M Armour-Chelu
1999 Toward an Evolutionary History of African Hipparionine Horses. *In* African Biogeography, Climate Change, and Human Evolution. T. Bromage and F.S. Schrenk, eds. Pp. 189-215. New York: Oxford University Press.

Bionski, Sue, Robert P Quatrone, and Hilary Swartz
2000 Substrate and tool use by Brown Capuchins in Suriname: Ecological contexts and cognitive bases. American Anthropologist 102(4):741-762.

Bishop, Laura
1999 Suid Paleoecology and habitat preferences at african pliocene and pleistocene hominid localities. *In* African Biogeography, Climate Change, and Human Evolution. T. Bromage and F. Schrenk, eds. Pp. 216-225. New York: Oxford University Press.

Bobe, Rene, and Anna K. Behrensmeyer
2004 The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus Homo. Palaeogeography, Palaeoclimatology, Palaeoecology 207(3-4):399-420.

Bonis, Louis de, and Laurent Viriot
2002 Evolution: Teeth and Paleoanthropology. Connective Tissue Research 43:87-93.

Brain, C.K
2004a Structure and Stratigraphy of the Swartkrans Cave in the Light of the New Excavations. *In* Swartkrans: A Cave's Chronicle of Early Man. C.K. Brain, ed. Pretoria: Transvaal Museum, Northern Glagship Institution.

—
2004b A Taphonomic Overview of the Swartkrans Fossil Assemblages. *In* Swartkrans: A Cave's Chronicle of Early Man. C.K. Brain, ed. Pretoria: Transvaal Museum, Northern Flagship Institution.

Byrd, GT, and RH Brown
1989 Environmental effects on photorespiration of C_3-C_4 species. Plant Physiology 90:1022-1028.

Clarke, R. J., et al.
2003 Dating the Sterkfontein Fossils. Science 301:596-597.

Clarke, Ron J
2002 On the Unrealistic 'Revised Age Estimates' for Sterkfontein. South African Journal of Science 98(9/10):415-420.

Clarke, Ron J, and Phillip V Tobias
1995 Sterkfontein Member 2 foot bones of the oldest South African Hominid. Science 269(5223):521-425.

Cloern, James E., Elizabeth A. Canuel, and David Harris
2002 Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. Limnology and Oceanography 73(3):713-729.

Codron, Daryl, et al.
2006 Inter- and intrahabitat dietary variability of chacma baboons (*Papio ursinus*) South African savannas based on fecal δ13C, δ^{15}N, and %N. American Journal of Physical Anthropology 129(2):204-214.

—
2005 Utilization of savanna-based resources by Plio-Pleistocene baboons. South African Journal of Science 101(May/June):245-248.

Curnoe, Darren, et al.
2001 Direct ESR dating of a Pliocene hominin from Swartkrans. Journal of Human Evolution 40(5):379-391.

Darwin, Charles
1978 The Origin of Species. Franklin Center: The Franklin Library.

Delson, Eric
1984 Cercopithecid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. Courier Forschungs-Institut Seneckenberg 69:199-219.

De Ruiter, D. J.
2003 Revised faunal lists for Members 1-3 of Swartkrans, South Africa. Annals of the Transvaal 40:29-41.

De Ruiter, Darryl. J., Christine M. Steininger, and Lee R. Berger
2006 A cranial base of Australopithecus robustus from the hanging remnant of Swartkrans, South Africa. American Journal of Physical Anthropology 130(4):435-444.

Dechow, PC, and R Singer
1984 Additional fossil Theropithecus from Hopefield, South Africa: a comparison with other African sites and a reevaluation of its taxonomic status. American Journal of Physical Anthropology 63(4):405-35.

Denton, GH
1999 Cenozoic Climate Change. *In* African Biogeography, Climate Change, and Human Evolution. T. Bromage and F.S. Schrenk, eds. Pp. 94-114. New York: Oxford University Press.

Denys, C
1999 Of Mice and Men: Evolution in East and South Africa during Plio-Pleistocene Times. *In* African Biogeography, Climate Change, and Human Evolution. T. Bromage and F. Schrenk, eds. Pp. 226-252. New York: Oxford University Press.

Dirks, Wendy
2003 Effect of diet on dental development in four species of catarrhine primates. American Journal of Primatology 61:29-40.

Doran, Diane M., and Alastair McNeilage
1998 Gorilla ecology and behavior. Evolutionary Anthropology: Issues, News, and Reviews 6(4):120-131.

El-Zaatari, Sireen, et al.
2005 Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. Journal of Human Evolution 49:180-205.

Foley, R
1999 Evolutionary Geography of Pliocene African Hominids. *In* African Biogeography, Climate Change and Human Evolution. T. Bromage and F. Schrenk, eds. Pp. 328-348. New York: Oxford University Press.

Frost, Stephen R., and Eric Delson
2002 Fossil Cercopithecidae from the Hadar Formation and surrounding areas of the Afar Depression, Ethiopia. Journal of Human Evolution 43:687-748.

Frost, Stephen R., et al.
2003 Cranial allometry, phylogeography, and systematics of large-bodied papionins (primates: Cercopithecinae) inferred from geometric morphometric analysis of landmark data. The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology 275A(2):1048-1072.

Fruth, Barbara, Gottfried Hohmann, and William C Mcgrew
1999 The *Pan* Species. *In* The Nonhuman Primates. P. Dolhinow and A. Fuentes, eds. Pp. 64-72. London: Mayfield Publishing Company.

Godfrey, Laurie, and Jonothan Marks
1991 The nature and origins of primate species. American Journal of Physical Anthropology 34(S13):39-68.

Godfrey, Laurie R., et al.
2005 New Insights into Old Lemurs: The Trophic Adaptations of the Archaeolemuridae. International Journal of Primatology 26(4):825-854.

Goldsmith, Michele
1999 Gorilla Socioecology. *In* The Nonhuman Primates. P. Dolhinow and A. Fuentes, eds. Pp. 58-63. London: Mayfield Publishing Company.

Grine, Frederick E.
2004 Description and preliminary Analysis of New Hominid Craniodental Fossils from the Swartkrans Formation. *In* Swartkrans: A Cave's Chronicle of Early Man. C.K. Brain, ed. Pretoria: Transvaal Museum, Northern Flagship Institution.

Grubb, Peter , et al.
2003 Assessment of the Diversity of African Primates. International Journal of Primatology 24(6):1301-1367.

Jablonski, Nina G
1994 New fossil cercopithecid remains from the Humpata Plateau, southern Angola. American Journal of Physical Anthropology 94(4):435-464.

Johnson, K.G., and G.B. Curry
2001 Regional biotic turnover dynamics in the Plio-Pleistocene molluscan fauna of the Wanganui Basin, New Zealand. Palaeogeography, Palaeoclimatology, Palaeoecology 172:39-51.

Jolly, Clifford
1970 The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5:5-26.

—
2001 A proper study for mankind: Anologies from the Papionin monkeys and their implications for human evolution. American Journal of Physical Anthropology 116(S33):177-204.

King, Tania, Peter Andrews, and Basak Boz
1999 Effect of taphonomic processes on dental microwear. American Journal of Physical Anthropology 108(3):359-373.

Kirkpatrick, R Craig
1999 Colobine Diet and Social Organization. *In* The Nonhuman Primates. P. Dolhinow and A. Fuentes, eds. Pp. 93-108. Mountain View: Mayfield.

Klaassen, Marcel, Michele Thums, and Ian D. Hume
2000 Effects of diet change on carbon and nitrogen stable-isotope ratios in blood cells and plasma of the long-nosed bandicoot (Perameles nasuta). Australian Journal of Zoology 52(6):635-647.

Kuman, K, and Ron J Clark
2000 Stratigraphy, artifact industries and hominid associations for Sterkfontein, member 5. Journal of Human Evolution 38:827-847.

Lee-Thorp, J.A., Matt Sponheimer, and N. van der Merwe
2003 What do stable isotopes tell us about hominid dietary and ecological niches in the plio-pleistocene. International Journal of Osteoarchaeology 13(1-2):103-113.

Lee-Thorp, J.A., and N. van der Merwe
2004 Stable Carbon isotope Studies of Swartkrans Fossils. *In* Swartkrans: A Cave's Chronicle of Early Man. C.K. Brain, ed. Pretoria: Transvaal Museum, Northern Flagship Institution.

Lee-Thorp, J.A., N. van der Merwe, and C.K Brain
1989 Isotopic evidence for dietary differences between two extinct baboons species from Swartkrans. Journal of Human Evolution 27:361-372.

—
1994 Diet of Australopithecus robustus at Swartkrans from stable carbon isotopic analysis. Journal of Human Evolution 27:361-372.

Luyt, C J, and J.A. Lee-Thorp
2003 Carbon isotope ratios of Sterkfontein fossils indicate a marked shift to open environments c. 1.7 Myr ago. South African Journal of Science 99(5/6):271-274.

McKee, Jeffrey K
1996 Faunal turnover patterns in the Pliocene and Pleistocene of southern Africa. South African Journal of Science 92:281-293.

—
1999 The autocatalytic nature of hominid evolution in African Plio-Pleistocene environments. *In* African Biogeography, Climate Change, and Human Evolution. T. Bromage and F. Schrenk, eds. Pp. 57-75. New York: Oxford.

McKee, Jeffrey K, J Francis Thackeray, and Lee R Berger
1995 Faunal assemblage seriation of southern African Pliocene and Pleistocene fossil deposits. American Journal of Physical Anthropology 96(3):235-250.

McKee, Jeffrey K, Phillip V Tobias, and Ron J Clarke
1996 Faunal evidence and Sterkfontein Member 2 foot bones of early hominid. Science 271(5253):1301-1303.

McKee, Jeffrey K.
1993 Faunal dating of the Taung hominid fossil deposit. Journal of Human Evolution 25(5):363-376.

Momohara, A
1994 Floral and paleoenvironmental history from the late Pliocene to middle Pleistocene in and around central Japan. Palaeogeography, Palaeoclimatology, Palaeoecology 190:243-255.

Muzikar, Paul, and Darryl Granger
2006 Combining cosmogenic, stratigraphic, and paleomagnetic information using a Bayesian approach: General results and an application to Sterkfontein. Earth and Planetary Science Letters 243(3-4):400-408.

Negri, A, C Morigi, and S Giunta
2003 Are Productivity and stratification important to saprope deposition? Microfossil evidence from late Pliocene insolation cycle 180 at Vrica, Calabria. Palaeogeography, Palaeoclimatology, Palaeoecology 190:243-255.

Norconk, Marilyn, Brian Grafton, and Nancy Conklin-Brittain
1998 Seed Dispersal by Neotropical Seed Predators. American Journal of Primatology 45:103-126.

Nunn, Charles L., and Carel P. van Schaik
2002 A Comparative Approach to Reconstructing the Socioecology of Extinct Primates. *In* Reconstructing Behavior in the Primate Fossil Record. J.M. Plavcan, R.F. Kay, W.L. Jungers, and v. Schaik, eds. Pp. 159-215. New York: Kluwer Academic/Plenum Publishers.

Nystrom, Pia, Jane Phillips-Conroy, and Clifford Jolly
2004 Dental Microwear in Anubis and Hybrid Baboons (*Papio hamaryas,* Sensu Lato) living in Awash National Park, Ethiopia. American Journal of Physical Anthropology 125:279-291.

Partridge, T. C., et al.
2003 Lower Pliocene Homind Remains from Sterkfontein. Science 300(5619):607-613.

Partridge, Timothy C, et al.
1999 The new hominid skeleton from Sterkfontein, South Africa: age and preliminary assessment. Journal of Quaternary Science 14(4):293-298.

Patterson, Hugh E. H.
1993 Evolution and the Recognition Concept of Species. Baltimore: The Johns Hopkins University Press.

Peters, Charles R
1991 Shell strength and primate seed predation of nontoxic species in eastern and southern Africa. International Journal of Primatology 14(2):315-344.

Phillips-Conroy, Jane, and Clifford Jolly
1986 Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. American Journal of Physical Anthropology 71(3):337-350.

Phillips-Conroy, Jane, Clifford Jolly, and Frederick L. Brett
1991 Characteristics of hamadryas-like male baboons living in anubis baboon troops in the Awash hybrid zone, Ethiopia. American Journal of Physical Anthropology 86(3):353-368.

Potts, Richard
1998 Environmental Hypotheses of Hominin Evolution. Yearbook of Physical Anthropology 41:93-136.

Rayner, RJ, BP Moon, and JC Masters
1993 The Makapansgat australopithecine environment. Journal of Human Evolution 24:219-322.

Reed, Kaye E.
1997 Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution 32(2-3):289-322.

—
2002 The Use of Paleocommunity and Taphonomic studies in Reconstructing Primate Behavior. *In* Reconstructing Behavior in the Primate Fossil Record. J.M. Plavcan, R.F. Kay, W.L. Jungers, and C.P. van Schaik, eds. Pp. 217-259. New York: Kluwer Academic / Plenum Publishers.

Rogers, M. E. , et al.
1998 Lowland gorillas and seed dispersal: The importance of nest sites. American Journal of Primatology 45(1):45-68.

Schmidt, Christopher W.
2001 Dental microwear evidence for a dietary shift between two nonmaize-reliant prehistoric human populations from Indiana. American Journal of Physical Anthropology 114(2):139-145.

Schubert, Blaine W., et al.
2006 Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 241(2):301-319.

Schwarcz, HP, RC Grun, and PV Tobias
1994 ESR dating studies of the australopithecine site of Sterkfontein, South Africa. Journal Human Evolution 26(3):175-181.

Scott, Rubert S., et al.
2005 Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436(7051):693-695.

Semprebon, Gina M., et al.
2004 Can low-magnification stereomicroscopy reveal diet? Journal of Human Evolution 47:115-144.

Sikes, Nancy E., Richard Potts, and A. K. Behrensmeyer
1999 Early Pleistocene habitat in Member 1 Olorgesailie based on paleosol stable isotopes. Journal of Human Evolution 37(5):721-746.

Sponheimer, Matt, and J.A. Lee-Thorp
2003 Using carbon isotope data of fossil bovid communities for paleoenvironmental reconstruction. South African Journal of Science 99(5/6):273-276.

Sponheimer, Matt, et al.
2005 Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. Journal of Human Evolution 48(3):301-312.

Sponheimer, Matt, and Julia A. Lee-Thorp
1999 Isotopic Evidence for the Diet of an Early Hominid, *Australopithecus africanus*. Science 283(5400):368-370.

Sponheimer, Matt, Kaye E. Reed, and J.A. Lee-Thorp
1999 Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. Journal Human Evolution 36:705-718.

Steele, D. Gentry, and Joseph F. Powell
2005 Paleobiology of the first Americans. Evolutionary Anthropology: Issues, News, and Reviews 2(4):138-146.

Teaford, Mark F., and Ordean J Oyen
1989 In vivo and in vitro turnover in dental microwear. American Journal of Physical Anthropology 80(4):447-460.

Thackeray, Francis, et al.
2005 Stable carbon isotope analyses of Parapapio tooth enamel from Sterkfontein and Swartkrans. South African Journal of Science 110(9/10):483-484.

Thackeray, Francis, and S Myer
2004 *Parapapio broomi* and *Parapapio jonesi* from Sterkfontein: males and females of one species? Annals of the Transvaal Museum 41:79-82.

Turner, A
1999 Evolution in the African Plio-Pleistocene Mammalian Fauna - Correlation and Causation. *In* African Biogeography, Climate Change, and Human Evolution. T. Bromage and F. Schrenk, eds. Pp. 76-87. New York: Oxford university Press.

Ungar, Peter
1998 Dental allometry, morphology, and wear as evidence for diet in fossil primates. Evolutionary Anthropology 6(6):205-217.

—
2002 Reconstructing to Diets of Fossil Primates. *In* Reconstructing Behavior in the Primate Fossil Record. J.M. Plavcan, R.F. Kay, W.L. Jungers, and C.P. van Shaik, eds. Pp. 261-296. Nre York: Kluwer Academic/Plenum Publishers.

Ungar, Peter S., et al.
2006 Dental microwear and diets of African early Homo. Journal of Human Evolution 50(1):78-95.

van der Merwe, N., et al.
2003 The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. Journal of Human Evolution 44:581-597.

Vrba, Èlisabeth S.
1974 Chronological and ecological implications of the fossil bovidae at the Sterkfontein australopithecine site. Nature 250:19-23.

—
1975 Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. Nature 254:301-304.

—
1992 Mammals as a key to evolutionary theory. Journal of Mammology 73:1-28.

—
1995 The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. *In* Paleoclimate and Evolution with Emphasis on Human origins. È.S. Vrba, G. Denton, T.C. Partridge, and L. Burckle, eds. New Haven: Yale University Press.

—
1999 Habitat Theory in Relation to the Evolution in African Neogene Biota and Hominids. *In* African Biogeography, Climate Change, and Human Evolution. T.G. Bromage and F. Schrenk, eds. Pp. 19-34. New York: Oxford University Press.

Watson, V
2004 Composition of the Swartkrans Bone Accumulations, in Terms of Skeletal Parts and Animals Represented. *In* Swartkrans: A Cave's Chronicle of Early Man. C.K. Brain, ed. Pretoria: Transvaal Museum, Northern Flagship Institution.

Williams, F.L. , R.R. Ackermann, and S.R. Leigh
2006 Inferring Plio-Pleistocene southern African biochronology from facial affinities in *Parapapio*and other fossil papionins. American Journal of Physical Anthropology In Press.

Appendix I

List of Specimens

Australopithecus africanus
- STS 1
- STS 12
- STS 1512
- STS 17
- STS 18
- STS 19
- STS 36
- STS 53
- STS 56

Australopithecus robustus
- SK 11
- SK 12
- SK 13
- SK 1586
- SK 23
- SK 25
- SK 34
- SK 46
- SK 47
- SK 48
- SK 57
- SK 6
- SK 79
- SK 83
- SK 858
- SK 876

Cercopithecoides williamsi
- BF 42A
- BF 42B
- MP 3
- STS 270
- STS 282
- STS 288
- STS 295
- STS 300
- STS 344
- STS 352
- STS 357
- STS 366
- STS 394

Dinopithecus ingens
- SB 7
- SK 14004
- SK 401
- SK 404
- SK 413
- SK 415
- SK 428
- SK 492
- SK 546
- SK 574
- SK 578A
- SK 600
- SK 603
- STS???

Theropithecus darti
- M 3073
- MP 222

Gorgopithecus major
- KA 105
- KA 1148
- KA 154
- KA 169
- KA 198
- KA 60B
- KA 626

Theropithecus danieli
- SK 426
- SK 44?
- SK 563
- SK 567
- SK 575A

Papio angusticeps
- CO 100
- CO 102
- CO 104
- CO 104A
- CO 115/103
- CO 116
- CO 117
- CO 118
- CO 134B
- KA 151
- KA 156
- KA 166A

Semnopithecus sp.
- SAM 16647A
- SAM 16647A
- SAM 16648A
- SAM 16648B

Papio robinsoni
- BF 38
- SK 14083
- SK 406
- SK 408
- SK 416
- SK 417
- SK 421
- SK 436
- SK 445
- SK 453
- SK 458
- SK 52
- SK 558
- SK 560
- SK 561
- SK 566
- SK 571B
- SK 602

Parapapio jonesi
- KA 160
- M 3060
- SK 412
- SK 414
- SK 418
- SK 433
- SK 437
- SK 462
- SK 550
- SK 573A
- SK 579
- STS 287
- STS 306
- STS 329
- STS 333
- STS 340
- STS 355
- STS 372A
- STS 381

Papio wellsi
- SAM 11729
- TP 10
- TP 11

Parapapio sp.
- KA 155
- KA 157
- KA 162

Parapapio antiquus
- T 17
- TP 13
- TP 8

Parapapio whitei
- BF 43
- MP 117
- MP 221
- MP 223
- MP 224
- MP 239
- STS 253
- STS 259
- STS 263
- STS 323
- STS 353
- STS 359
- STS 367
- STS 370A
- STS 370B
- STS 414A
- STS 563
- T 89-154
- TP 12

Parapapio broomi
- M 3056
- M 3070
- MP 118
- MP 151
- STS 251
- STS 256
- STS 26?
- STS 262
- STS 274
- STS 280
- STS 294
- STS 305
- STS 319
- STS 324
- STS 343
- STS 343
- STS 350
- STS 362
- STS 368A
- STS 371
- STS 373A
- STS 373B
- STS 374A
- STS 374B
- STS 378 A
- STS 398A
- STS 413B
- STS 414B
- STS 433
- STS 468
- STS 562
- STS 562

Appendix II

Means and standard deviations (SD) of microwear features for each species.

Species (N)	Scratches (SD)	Small Pits (SD)	Medium Pits (SD)	Large Pits (SD)
Australopithecus africanus (9)	20.89 (4.7)	29.33 (5.0)	16.22 (5.3)	1.33 (1.2)
Australopithecus robustus (16)	23.59 (4.7)	27.69 (6.2)	18.16 (4.7)	4.22 (2.7)
Cebus apella (3)	14.16 (1.2)	16.17 (2.5)	15 (3.3)	2.5 (1.5)
Cercopithecoides williamsi (13)	13.58 (3.2)	24.88 (8.5)	17.62 (5.7)	1.81 (1.6)
Colobus badius (3)	8 (0.9)	24.83 (4.6)	9 (2.3)	3.17 (1.6)
Colobus polykomos (2)	13.75 (4.5)	36 (2.12)	9.5 (5.6)	3.5 (1.4)
Dinopithecus ingens (14)	19 (4.3)	23.79 (6.7)	18.86 (6.4)	3.07 (3.2)
Gorgopithecus major (7)	13.86 (4.7)	27.14 (6.5)	14.14 (3.4)	3.86 (2.9)
Gorilla gorilla (3)	12 (2.6)	13.83 (6.0)	16.17 (5.6)	1.17 (1.3)
Pan troglodytes (3)	10.66 (1.3)	20.5 (8.5)	15.67 (13)	4.66 (1.4)
Papio angusticeps (12)	14.25 (3.3)	28.96 (10)	15.88 (6.2)	2.46 (2.3)
Papio anubis (21)	12.83 (4.3)	19.43 (5.3)	18.36 (6.6)	3.12 (2.8)
Papio cynocephalus (4)	11.88 (5.9)	26.5 (3.1)	13.88 (6.3)	4.25 (1.4)
Papio hamadryas (2)	16.26 (5.3)	9.75 (1.8)	12.75 (1.1)	4 (0.7)
Papio kindae (24)	17.69 (4.8)	26.44(11.7)	21.83 (8.3)	1.71 (1.9)
Papio robinsoni (18)	19.83 (4.3)	17.08 (8.1)	12.83 (3.8)	3.14 (1.3)
Papio ursinus (19)	14.98 (3.8)	18.15(10.6)	13.45 (5.1)	2.9 (3.3)
Papio wellsi (3)	15.17 (1.6)	27.67(12.1)	12.5 (2.0)	5.17 (2.9)
Parapapio sp. (3)	13.67 (5.8)	36.17 (7.8)	14 (7.4)	4.33 (4.3)
Parapapio antiquus (3)	19 (2.2)	26.67 (8.0)	14.33 (1.5)	5.67 (4.9)
Parapapio broomi (31)	15.31 (5.4)	17.81 (7.4)	14.88 (5.3)	2.7 (2.7)
Parapapio jonesi (18)	16.13 (4.6)	25.37(11.2)	20.03 (5.7)	4.18 (3.9)
Parapapio whitei (19)	16.45 (5.2)	25.55 (13)	19.32 (8.2)	2.97 (2.0)
Theropithecus gelada (6)	24.58 (4.3)	27.25 (2.9)	17.83 (6.4)	2.83 (2.5)
Theropithecus darti (2)	13.25(2.5)	9.25 (5.3)	17.25 (3.9)	1 (1.3)