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Taxon, Site and Temporal Differentiation Using Dental Microwear in the Southern African Papionins

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TAXON, SITE AND TEMPORAL DIFFERENTIATION USING DENTAL MICROWEAR IN THE SOUTHERN AFRICAN PAPIONINS

By

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Under the Direction of Frank L'Engle Williams

ABSTRACT

The evolutionary history of the South African papionins is a useful analog for the emergence of hominids in South Africa. However, the taxonomic relationships of the papionins are unclear. This study uses low-magnification stereomicroscopy to examine dental microwear and uses the microwear signals to explore the existing classification of these papionins. The results from the species and site level analyses are equivocal. However, the genera and time period results show clear evidence for a dietary change between the extinct and extant forms of *Papio* and *Parapapio*. This adds an additional tool for distinguishing these two groups. The dietary changes witnessed in the papionins are likely found in the hominids from the Plio-Pleistocene. Using the papionin analog, hominid dietary evolution may be explored.

INDEX WORDS: Papionins, South Africa, Plio-Pleistocene, Dental microwear, Hominids, *Papio, Parapapio*

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LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
DFA	Discriminant Function Analysis
DNA	Deoxyribonucleic Acid
HSD	Honestly Significant Differences
LMS	Low-magnification Stereomicroscopy
MYA	Million Years Ago
PCA	Principal Components Analysis
PSC	Phylogenetic Species Concept
SCM	Scanning Confocal Microscopy
SEM	Scanning Electron Microscopy

Chapter One: Introduction

Monkeys, and specifically baboons, have long been linked to humanity from recent television commercials depicting primates in cubicles, to medieval European portrayals of devil monkeys (Schrader, 1986) and to the sacred status of baboons in ancient Egyptian mythology (Carter and Carter, 1999). The link between baboons and humans goes even further than recorded histories and into their common evolutionary past. Both papionins and hominids were evolving in southern Africa during the Plio-Pleistocene epoch (Jablonski, 2002; Jolly, 2001). Jolly (2001) argues that because of this shared past, in terms of time, geography, and complexity of the species relationships within these groups, the papionins can be useful as analogies to hominid evolution.

However, the extinct southern African Plio-Pleistocene papionins are poorly understood in terms of their species designations as are the extant baboons, although the extant baboons are becoming more well understood due to genetic studies (Newman et al., 2003). A variety of methods have been used in previous studies to explore the relationships among the papionins. However, there is still much confusion. Therefore, this study applies the novel method of low-magnification stereomicroscopy (LMS) to the poorly agreed upon species designations in the southern African papionins which extends from the Plio-Pleistocene to the present. Specifically, two genera of baboon-like forms will be investigated: *Parapapio* from southern Africa during the Plio-Pleistocene, extinct *Papio* from Southern Africa during the Plio-Pleistocene, and extant *Papio* from across Africa. *Parapapio* is a generalized baboon form that may be ancestral to modern living

baboons, although that relationship is still unclear (Disotell, 1994; Groves, 2000; Jolly, 1967; Jolly, 1970b; Szalay and Delson, 1979; Williams et al., 2007). The genus *Papio* is somewhat better understood since many species are extant. However, extinct forms such as *Papio izodi* are also addressed here.

Past Research

The literature on these two genera in regards to species differentiation is equivocal with few authors agreeing on what characteristics define each taxon and which specimens belong to which species (Benefit, 1990; Broom, 1940; Delson, 1975; Disotell, 1994; Disotell, 1996; El-Zaatari et al., 2005; Freedman, 1957; Freedman, 1960; Freedman, 1961; Freedman, 1965; Freedman, 1976; Freedman and Stenhouse, 1972; Gear, 1926; Jablonski, 2002; Jolly, 2006; Maier, 1970; Maier, 1971; Proctor and Hudson, 2006; Simons and Delson, 1978; Williams et al., 2006). The debate over species designations is two-fold. In large part, the debate is due to the lack consensus over which species concept to use in the fossil record. Second, there is no methodological agreement for how to categorize the specimens.

One example of the equivocation in the field is evidenced by the work of Freedman (1976) and Maier (1970). Both examined the same specimens (M.3051, M.3060 and M.3061 from Makapansgat) and arrived at different species designations within the genus *Parapapio*. Their designations were based on interpretations of species-specific characteristics. Freedman (1976; pg. 303) notes that having "three morphologically very similar species [of *Parapapio*]…always appeared disturbing." The three species he is referring to, *Pp. broomi*, *Pp. jonesi*, and *Pp. whitei*, appear to be scaled versions of each other. That is, the three species of *Parapapio*, are morphologically

similar, except in their size. Yet, the sizes of the three species all overlap. The varying sizes would be logical if there were a chronological progression or even a significant geographic variation, but they co-occur in the same Pliocene-dated sites (Makapansgat, Sterkfontein and Taung). This suggests that either these size differences may not be indicative of individual species or that the sites have significant temporal depth.

Freedman's (1957, 1960, 1961, 1965; Freedman and Stenhouse 1972) classification of *Parapapio* is largely based on the dimensions of the second and third molars although measurements of the canines, premolars and first molar are occasionally reported (Freedman, 1965). This method has problems. In one instance, Freedman (1960) discusses several specimens that he identifies as belonging to *Parapapio* but cannot identify the species because the molars are missing even though the cranium is largely complete. Freedman (1960) notes that some specimens seem to overlap to which species they could be assigned based on molar dimensions. This lack of agreement and the resulting presence of three scaled species suggests that the species designations may not be accurate. Additionally, Freedman (1960) cites another paper (Leakey and Whitworth, 1958) that states that size differences are not enough to warrant separate species. Even though this paper was written about a different primate genus, *Simopithecus*, it highlights the difficulty of declaring species based solely on the size of cranial remains.

In a later paper Freedman (1965), extends the range of variation in molar dimensions that is permissible in another species, *Papio robinsoni*, despite being unable to find differences between the molar dimensions of *P. robinsoni*, which is a Plio-Pleistocene baboon form and *P. ursinus*, which is extant. In other words, a relatively well-understood living baboon, *P. ursinus*, has less variation in molar dimensions

between individuals than does the extinct *P. robinsoni*. This makes using molar dimensions to distinguish species suspect. Furthermore, the variation in molar dimensions of each of the three co-occurring *Parapapio* forms is greater than the variation found in the extant *Papio ursinus* (Freedman and Stenhouse, 1972). This again suggests that the original methods used to classify these species could not capture distinctions between taxa.

Interestingly, Freedman, whose work is often cited for species designations in *Parapapio*, could not decide how to classify some specimens. First, Freedman (1957) classified a particular specimen from Taung (56604) as *Parapapio antiquus*. Then he decided it was *P. wellsi* (1961) and ultimately decided that it is indeed *Pp. antiquus* (Freedman, 1965). *Pp. antiquus* is a species from Taung that is often described in its similarity to *P. wellsi* and *P. izodi* (Freedman, 1961). If *Pp. antiquus* is so elusive to classify and it bears striking similarities to *P. wellsi* and *P. izodi*, these species may not be real biological units. Clearly this specimen, and perhaps all specimens grouped as *Pp. antiquus*, needs to be reexamined in order to verify the species designations.

Adding to the confusion in the literature about these species is the absence of a consensus on which species concept to use as a reference. Living species are often classified based on soft tissue and behavioral differences. Since all fossil remains consist of hard parts (crania, teeth, etc.) and behaviors cannot be observed, the phylogenetic species concept (PSC) seems most applicable (Groves, 2004). Groves (2004; pg. 1110) defines the PSC as "the smallest cluster of individual organisms within which there is a parental pattern of ancestry and descent and that is diagnosably distinct from other such clusters by a unique combination of fixed character states." This is to say a species is

made up of the smallest group of individuals that all have common traits that differ from other similar animals.

In this study, dental microwear will be used as the fixed character state, or trait with the acknowledgement that dental microwear is not fixed. However, due to the lack of agreement in the literature based on fixed states (i.e. molar size), dental microwear will be explored as a theoretical fixed state. Groves (2004, pg. 1110) continues, " a species has one or more fixed differences from other species; it is 100% different; so one asks not how much difference is necessary to decide whether a population rates as a species, but what proportion of individuals differ? Any kind of character will suffice, be it color, size, vocalization, or a DNA sequence, as long as there is a reasonable supposition that the difference is heritable." It is interesting to note that size is listed as one possible distinguishing feature of a species. However, in the three *Parapapio* species, there is not a 100% difference between the sizes of the species. The three southern African forms of *Parapapio* all overlap in their size ranges. This makes size not a valid argument for different species under the PSC in the context of *Parapapio*.

In this study, it is acknowledged that microwear is not heritable, but the patterns that produce microwear (i.e. the cranial and dental morphologies which correspond to diet) are heritable. Diet, as indicated by various features of teeth, is frequently used in the primate fossil record to infer behavior (Kay et al., 2004; Ungar, 1999; Wolpoff, 1973). Microwear can then be used as a proxy for the requirements of determining species differentiation based on the phylogenetic species concept.

Godfrey and Marks (1991) agree that the phylogenetic species concept is often the only species concept that can be applied to the fossil record. An important caveat that

Godfrey and Marks (1991) note is that there should be no more variation in a fossil species than what is found in their closest living relative. For example, a rough range of the size of third molars can be established for a relatively well-understood living baboon species. That range could then be compared to the range in a fossil baboon species. If the range is either significantly greater or less than the living baboon range, this suggests that the fossil species is not well defined.

However, species concepts in living primates can be just as complex. This is especially true of the papionins, who have natural hybrid zones in the wild (Godfrey and Marks, 1991). Because of these natural hybrid zones, many of the species concepts are difficult to apply to the papionins. The extant papionins are often geographically separated, yet interbreeding occurs when they come into contact in the wild and in captivity. The result is that there are varying opinions on how the closely related baboon groups should be classified. This is further complicated by the natural hybrid zone in which *Papio* hybridizes with *Theropithecus*, who diverged from the *Papio* lineage some 3.75 million years ago (mya) while the remaining baboons had a common ancestor around 1.75 mya (Newman et al., 2003). It is interesting to note that if these two genera that are closely related, but diverged over three million years ago can interbreed, it is likely that the varying species of early hominids could have also interbred (Jolly, 2001). If early species of *Homo* could have interbreed, some Plio-Pleistocene taxonomic designation have little biological value (Scholz et al., 2000).

This study attempts to shed light on these complex genera, *Parapapio* and *Papio* by using dental microwear to 1) determine if the species designations that are assigned to specimens within the genera are statistically real groups, 2) determine what traits of the

microwear differentiate species (if any), 3) determine if there are redundant species labels, 4) determine if *Papio* and *Parapapio* can be distinguished using dental microwear and 5) explore the data to see if there are site or temporal differences among the specimens.

By determining if microwear can differentiate these species, an additional tool will be available to researchers dealing with the complex relationships among fossil primates. Additionally, the temporal variation in papionin diet may be examined and used as a vehicle to explore hominid evolution in Southern Africa because the evolution of *Papio* and *Homo* occurred in the same time period and ecogeographic location. *Papio* and *Homo* are also both encephalized compared to other mammals and are both dietary generalists/opportunists. The rapid dietary shifts in the papionins likely reflects habitat changes caused by climate fluctuations during the Plio-Pleistocene. Therefore, hominid food sources would likely shift just as papionin food sources changed. Thus, the southern African papionins are important to understand in terms of the evolution of cercopithecids, but can also be an important tool for inferring habitat change that affected the Plio-Pleistocene hominids.

Chapter Two: The Context for this Study

In order to fully grasp the complexity of the papionins, a brief introduction to the family Cercopithecidae, and specifically to the papionins, will be given. The evolution of the papionin lineage and the taxonomic relationships of the papionins is also of interest. This is followed by a discussion of the sites at which this study's materials were discovered. The site contexts are important due to their often close proximity to hominid remains. The evolution of papionins and hominids were heavily impacted by Plio-Pleistocene climate change (Vrba 1983, 1993, 1996). Therefore, the climactic and evolutionary theories that are relevant to this region are discussed. Finally, a history of dental microwear is given in order to contrast low-magnification stereomicroscopy with more established methods.

Papionin Relationships and Evolution

The papionins are part of the family Cercopithecidae, otherwise known as the Old World monkeys. The family Cercopithecidae is divided into two subfamilies, the Colobinae, or the leaf eating monkeys, and the Cercopithecinae, which includes *Papio* and *Parapapio*, as well as macaques, guenons, geladas, and other species.

As a subfamily, the Cercopithecinae are relatively homogeneous. There is variation to be sure, but not to the extent that is found in other families. Cercopithecinae includes the most widespread primate genus, *Macaca*, which ranges in northwest Africa, across Asia and even into Japan, and the genus *Papio*.

The genus *Papio*, while not as widespread as the macaque group, is a successful taxon that ranges throughout Africa. The distribution of *Papio* can be seen as a model for the evolution of *Homo* in Africa, since *Homo* emerged in the same places at the same time as *Papio*. The Cercopithecinae tend to be more terrestrial than other groupings of monkeys, which has interesting implications for dental microwear and hominid evolution. Since these groups, specifically the papionins, rely primarily on ground-based or low-hanging food resources their diet may contain more grit than that of arboreal species. That is, terrestrial species tend to consume more sand and non-food particles than arboreal species. The grit in the diet of terrestrial species leads to different patterns of dental microwear than arboreal species.

Papio is the genus that contains all of the living baboons as well as several extinct species. Hominids have been living sympatrically with baboons throughout the fossil record. The oldest hominid remains are typically found in sites that also contain baboon remains (McKee et al., 1995). For example, the Taung child, one of the most famous *Australopithecus* fossils was found at a site that is also known for having deposits of *Papio* and *Parapapio* (Freedman, 1961; Laitman, 1986). The term *Papio* was first used in the scientific literature to identify living baboons by Müller in 1773 (Jablonski, 2002). In contrast, *Parapapio*, the genus that includes fossil baboon forms that are closer to the ancestral form of all the papionins, has a much more recent history in the literature. *Parapapio* was first named by Jones in 1937 (Jablonski, 2002; Jones, 1937). *Parapapio* and *Papio* continue to be confused during the recovery of fossil remains, due to the striking similarities between the forms. *Parapapio* tends to be smaller, and overlaps into the range of the smaller *Papio* taxa. The feature that is most distinguishable between the

two is the slope of the muzzle, which can be difficult to ascertain depending on the state of the fossil when it is retrieved and which portions of the crania, if any, are recovered (Jablonski 2002). Despite the similarities, there is agreement in the literature that *Papio* and *Parapapio* should be maintained as two distinct genera (Jablonski, 2002; Szalay and Delson, 1979).

Extinct and extant *Papio* are known from sites across sub-Saharan Africa. *Parapapio* is primarily known from South Africa, but is also found in East and North African early Pliocene through early Pleistocene deposits (Frost and Delson, 2002; Jablonski, 2002; Szalay and Delson, 1979). The fossil specimens in this study all come from southern African locations but the extant forms range from across Africa. (See Appendix for list of specimens and locations).

Sites

The materials for this study are primarily from the southern African cave sites of Bolt's Farm, Cooper's Cave, Kromdraai, Makapansgat, Sterkfontein, Swartkrans and Taung. However, comparative material from extant species was also used and grouped into the regional sites of South Africa (*P. ursinus*), Central Africa (*P. kindae*) and East-Central Africa (*P. anubis*). See Appendix for the locations at which materials were acquired.

The sites of Bolt's Farm, Cooper's Cave, Kromdraai, Sterkfontein and Swartkrans are all found in the Sterkfontein Valley of southern Africa, which is located near the city of Krugersdorp, just west of the capital of Johannesburg. Makapansgat is located further to the north near the city of Potgietersrust. Taung is southwest of Johannesburg, south of the city of Vryburg.

The chronology of the southern African cave sites is very difficult to ascertain due to the complex geologic history. This convoluted history has resulted in lack of a clear stratigraphy for which to date the sites (Brain, 1981; Williams et al., 2007). As a result, inferential comparative dating methods must be used to place these sites in temporal context. First, an examination of faunal remains at these sites can be compared to similar faunal remains in East Africa, where there is well-dated stratigraphy. Second, biochronology, or relative dating based on the specimens found within the site, can be established.

Vrba (1975) examines faunal (antelope) remains to date the sites of Sterkfontein, Swartkrans and Kromdraai. Vrba (1975) finds Sterkfontein to be the oldest site having remains that are dated to 2.5 to 1.6 million years ago (mya). Swartkrans Member 1 is dated from 1.7 to 1.0 mya, while Swartkrans Member 2 is dated to be much more recent, from 500,000 years ago. Kromdraai A dates from 1.3 to 0.7 mya, with Kromdraai B dating from 0.7 to 0.2 mya. Vrba's (1975) dating has been refined in more recent publications. Based on U-Pb chronometry Swartkrans Member 1 has been dated to 2 mya, Member 2 to 2.02 to 1.44 mya and Member 3 to 0.988 mya (Albarede et al., 2006).

In more recent publications, these estimates have been refined by using biochronology (Delson, 1984). Delson (1984) dates Kromdraai A and Swartkrans Member 1 to 1.5 mya, Bolt's Farm and Taung to 2 mya, Sterkfontein Member 4 to 2.5 mya and Makapansgat Member 3-4 to 3.0 mya. Another study (Williams et al., 2007) examines papionin remains in the South African cave sites to determine their age. Williams and colleagues (2007) state that Sterkfontein may bridge the Plio-Pleistocene boundary due to the presence of certain papionins. Similarly they suggest that

Makapansgat may also have extended from the middle Pliocene into the early Pleistocene.

The dating of these sites is an important issue to be addressed because it plays a central role in understanding the evolution of both the papionins and hominids. A clear chronology must be established in order to theorize about possible extinction and speciation events. Additionally, some chronology must be established to understand the effect of climate change on both papionins and hominids.

Dental microwear may be able to help elucidate some of the dating problems. As dental microwear is evidence of diet, changes in dental microwear reflect changes in diet. Thus, dietary reconstruction may be able to supplement other inferential methods such as faunal dating and biochronology.

Climate Change and Evolutionary Theories

It is widely agreed that the sites where *Parapapio* are found should be dated to the Pliocene (Benefit, 1990; Benefit, 2000; Broom, 1940; Delson, 1975; Jablonski, 2002; Szalay and Delson, 1979; Teaford and Leakey, 1992; Williams et al., 2007). There are two issues that make this time period particularly interesting. First, it is the time period in which some of the earliest hominids are found (Laitman, 1986; Leakey and Walker, 1997). Second, southern Africa, and most of the world, was experiencing a dramatic climate change during this period (Reed, 1997). Therefore, this climate change affected both the papionins that were living in southern Africa as well as the early hominids. Theoretical models have been developed to account for the evolution and extinction events seen during this time period.

Several evolutionary theories that relate to reconstructing the evolution of primates, as represented in the South African primate fossil record, are relevant. These include Vrba's turnover pulse (Vrba, 1983; Vrba, 1993; Vrba, 1996), Potts' variability selection hypothesis (Potts, 1998), Reed's use of paleocommunity and taphonomy (Reed, 2002), as well as a variety of methods that relate more specifically to diet and dentition.

Vrba (Vrba, 1983; Vrba, 1993; Vrba, 1996) builds her turnover pulse hypothesis from the framework of punctuated equilibrium that was postulated by Eldredge and Gould (1972). According to Vrba (1993), punctuated equilibrium implies that all species' diversification is a result of physical environmental change. Vrba suggests, "if evolution within established species commonly produces net statis and if significant phenotypic change is associated with rare speciations, then what other special *initiating cause* [emphasis from original] can be invoked but physical environmental change?" (Vrba 1993; pg. 427). Following this logic, all speciation and extinction events are a result of environmental change. Vrba goes on to conclude that Plio-Pleistocene South African evolutionary events are concentrated in a series of turnover pulses that stem from the cooling and drying of global climate change.

One of the strengths in Vrba's (1993, 1996) argument is that the turnover pulse hypothesis can also work with phyletic gradualism. Under a gradualist theory, lineage splitting and extinction are rare events, which would require special explanation. The turnover pulse theory could serve to explain these rare events by using rapid climate change as the mechanism for the rare speciation events. Another factor that strongly supports the idea of a turnover pulse is the dramatic climate shift that occurred during the Plio-Pleistocene as evidenced by ocean core samples (Denton, 1999) and the

corresponding speciation events that are seen in hominids and other primates during this time (deMenocal, 1995; Reed, 1997).

The turnover pulse hypothesis posits that the physical environment, and the species within it, stay static most of the time. However, periods of environmental change and the corresponding changes in species adaptation and composition should be marked by groups of pulses, or periods of rapid change (Vrba, 1993; Vrba, 1996). The implication for fast dietary change on the part of primates is much the same here as it is for punctuated equilibrium. Namely, adaptation to changing environmental conditions must be rapid or extinction may occur.

In contrast to Vrba (1993, 1996), Potts suggests in his variability selection hypothesis that lengthy environmental changes over hundreds of thousands of years results in lineages of organisms facing multiple and substantial disparities in selective environments over time (Potts, 1998). The variability selection hypothesis, attempts to explain the "evolutionary cause of versatility in longer intervals of more dramatic change in an organism's survival regime" (Potts, 1998). In other words, species will be more successful if they can adapt to long-term pressures rather than adapting quickly to dramatic events. This implies that species do not change their adaptations in response to one short-term environmental change as Vrba's (1993, 1996) turnover pulse hypothesis suggests, but rather species adapt to a series of environmental fluctuations that occur over successive generations. Potts seems to suggest that turnover pulses occur, but that they are spread out over evolutionary time rather than being relatively concentrated. This theory is supported by the long-term climactic shifts, such as ice ages, that can be seen throughout the history of the Earth and the corresponding changes in flora and fauna

(Zachos et al., 2001). The implication for primate dietary adaptation is that over time, dietary adaptations shift as they respond to long-term environmental fluctuations.

Moving from broad evolutionary theory to other approaches, Reed (2002) presents a way to examine the evolutionary past through the use of paleocommunity, the study of ancient communities and ecosystems, and taphonomy, the study of what happens to remains after an animal dies. The purpose of tying paleocommunity and taphonomy together are to examine information from across time in context and examine ecological patterns that may have influenced primate behavior (Reed, 2002). That is, contextual evidence can supplement the morphological evidence from the fossil record in order to gain a more complete understanding of evolutionary pressures. Reed (2002) shows that each type of ecosystem (forest, desert, etc.) is occupied by different mammals in different locations, but the mammals fill a similar ecological niche regardless of the ecosystem. Thus, most mammalian communities can be placed into varying ecological niches based on food availability and competition. The behavior of primates can be inferred based on the fact that individuals interact with the vegetation around them and influences the ecological outcomes of other mammalian species. When combined with morphological studies, the biological role of certain structures in fossil primates may be glimpsed. For example, many of the behavioral inferences made for extinct species are based on living analogues with similar ecological characteristics. Without a clear understanding of how a feature affects living primates, it is impossible to determine what behaviors would have been present in fossil primates.

An inherent problem in examining paleocommunities and taphonomy is the comparative method, which is understanding fossil forms through their extant relatives

(Reed, 2002). It can be difficult to ascertain the biological role of certain morphological features of living primates even though behaviors can be observed. Without an extant analogue for comparison, the comparative method can be problematic. Dental microwear can be used in the context of the comparative method because living and extinct primate use wear patterns can easily be compared.

History of Dental Microwear

Dental microwear arose out of the need to study primate diets in the fossil record. It is well established that studying diet in living primates can give significant insight into most aspects of primate behavior (Krebs and Davies, 1993). Since behavior cannot be observed directly in the fossil record, other methods must be used to infer diet and then infer behavior. Understanding diet in fossil primate forms helps to inform the evolution of dietary behaviors. Ecological change can also be inferred. Additionally, dental microwear provides an independent test on inferences of diet based on cusp form, such as shearing crest length (Benefit, 2000).

In living primates, researchers can watch what primates eat and perform fecal analysis to discover any food sources that their observations may have missed (McGrew et al., 2005; Moreno-Black, 1978; Tutin and Fernandez, 2005; Williamson et al., 2005). Since observations and fecal sampling are not an option for extinct and fossil primates, diet has to be inferred using comparative methods (Ungar, 1998; Ungar, 2002). Using the comparative method, anatomical features that relate to diet in living forms can be examined and compared to fossil forms with the same features. If a trait is found to have a particular function in living primates that have a diet type, it is hypothesized that the trait in the fossil record would also indicate that diet.

Within the comparative method for examining diet in primates, there are two broad approaches that can be used (Ungar, 2002): adaptive, or anatomical traits (morphology) and measurements (allometry), and non-adaptive, or evidence that relates to the actual foods that were eaten (see Ungar 2002).

The adaptive evidence can be divided into evidence from allometry and from morphology. Allometry, or differences related to scaling, has been examined in regards to broad dental allometry (Groves and Napier, 1968; Robinson, 1954), cheek tooth allometry (Gould, 1971; Kay, 1975; Kay, 1978; Pilbeam and Gould, 1974), and incisor allometry (Eaglen, 1986; Jolly, 1970a; Jolly, 1970b; Kay and Hylander, 1978). While issues of scaling can be important in understanding broadly different primate diets, such as insectivores and frugivores, it is not useful when comparing species with similar tooth morphologies and similar diets. Additionally, broad dental allometry, that is macro scaling comparisons, cannot reveal which teeth the selection pressures act upon. Moreover, both cheek tooth and incisor allometry do not explain what is seen in living primates without controlling for phylogenetic relationships, or how the species in question are related (Ungar, 2002).

Fortunately, adaptive morphological evidence has been more successful than allometric evidence for inferring diet in the fossil record (Ungar 2002). This includes dental morphology (Crompton and Sita-Lumsden, 1970; Gregory, 1922; Kay, 1984; Simpson, 1933), molar shearing quotient studies (Kay, 1978; Kay, 1984; Kay and Covert, 1984; Kay and Hylander, 1978), dental biomechanics (Lucas and Luke, 1984; Lucas et al., 1994; Lucas and Teaford, 1994), enamel thickness (Kay, 1981; Simons, 1976; Simons and Pilbeam, 1972), enamel structure (Maas, 1991; Maas, 1993; Maas, 1994; Maas and

O'Leary, 1996), and mandibular form (Greaves, 1988; Greaves, 1993; Hiiemae and Kay, 1972; Rosenberger, 1986). Each of these methods examines the underlying structures of the dentition in order to determine which foods were the focus of the diet and how those structures and diets evolved (Ungar 2002). However, they must often be used in conjunction with other measures such as body size to arrive at any correlations with living primates (Kay, 1984). Additionally, these methods often require fossil specimens that are more complete, as in using mandibular form, or require some invasive techniques as in using enamel structure and enamel thickness. These requirements often make these methods unsuitable for fossil specimens due to their rarity and incomplete nature.

There are fewer non-adaptive signals for diet in the primate fossil record. The main non-adaptive signals include tissue analyses, such as stable isotope (Ambrose and DeNiro, 1986; DeNiro and Epstein, 1981) and trace element analysis (Lee-Thorp et al., 1994; Sillen, 1992), and tooth wear analysis both on a macro (Meikle, 1977; Teaford, 1982) and micro (Rensberger, 1978; Walker et al., 1978; Walker, 1976) level. Tissue analyses can be quite difficult with fossils. This is due to lack of adequate samples as well as the difficulty in predicting the environment based on these ratios and elements. This is largely because different environments can have the same results in the analyses (Ungar 2002). Macro tooth wear may prove useful if calibrated to living analogs. However few scientists are actively using this method.

Dental microwear, which examines the use wear patterns on teeth at a microscopic level, eliminates many of the problems evidenced in the above methods. First, since dental microwear is based solely on the marks left behind by broader dietary strategies (i.e. frugivory, folivory, etc.), there is no need to account for allometric

differences in most comparisons (Godfrey et al., 2004). Second, there is little difficulty comparing across regions and time because the broader dietary categories apply throughout space and history. For example, a frugivorous primate from the Pliocene would have similar microwear patterns to a living frugivore. This is largely because the structure of fruit has not changed over time (Barlow, 2000). Since the structure of food sources has not changed, living and extinct diets can be reliably compared using dental microwear.

As a result, dental microwear is useful in tracking the dietary changes of a species through time. This can shed light into both how the species evolved and how the environment influenced those changes. In the southern African papionins and hominids, changes in dental microwear may reflect the changing climate during the Plio-Pleistocene and demonstrate how these species coped with altering food availability by changing their diets. This may also tie into discussions of extinction and speciation events, such as Vrba's (1983, 1993, 1996) turnover pulse by demonstrating an ecological factor that may have resulted in these events.

Additionally, the taxonomy of the papionins may be clarified by reexamining the existing species designations through dental microwear. Changing dietary signals may provide a chronology of the papionins centering around the Plio-Plesitocene climate shift. Dental microwear may also help differentiate species that lived sympatrically because sympatric species typically occupy slightly different food niches (Harcourt, 1998; Milton, 1981; Porter, 2001; Tutin and Fernandez, 2005).

Ungar (2002) thoroughly reviews dental microwear methods using scanning electron microscopy (SEM). However, he does not address the newer methods of

scanning confocal microscopy (SCM) (Scott et al., 2005; Ungar et al., 2003) nor low-magnification microscopy (LMS) (Godfrey et al., 2004; Semprebon et al., 2004). Since dental microwear is of the most interest here, these three methods of inferring diet will be examined at length.

Chapter Three: Method and Materials

SEM, SCM and LMS

Dental microwear examines the microscopic pits and scratches that are left in the occlusal surface of teeth as food is processed. These data are used to infer diet. Different foods, such as nuts and leaves, will leave measurably different microwear on the tooth surface. The first attempt at using dental microwear was made by Philip Walker (Walker, 1976). He used a light microscope to examine the striations on the incisors of Colobinae and Cercopithecinae and an external light source to highlight striations that were not visible under direct observation. He found that the orientation of the striations differed between these two groups. While his study had the possibility of becoming the seminal work in dental microwear, that honor fell to a different Walker (Walker et al., 1978) and Rensberger (1978), just two years later.

In these seminal works (Rensberger, 1978; Walker et al., 1978), a scanning electron microscope (SEM) was first applied to the examination of dental microwear. Since then the SEM technique of examining dental microwear has become the standard, with numerous studies using the method (Covert and Kay, 1981; Daegling and Grine, 1999; El-Zaatari et al., 2005; Gordon, 1982; Gordon, 1983; Gordon, 1984; Gordon, 1988; Kay and Covert, 1983; Maas, 1991; Teaford, 1985; Teaford, 1988; Teaford, 1993; Teaford, 1994; Teaford and Leakey, 1992; Teaford and Robinson, 1989; Teaford and Walker, 1984; Ungar, 1996; Ungar et al., 1995).

In an effort to explain the techniques employed in using SEM to examine dental microwear, the methods of a recent study by El-Zaatari and colleagues (El-Zaatari et al., 2005) will be summarized here. First, the fossil specimens are cleaned with either acetone or ethyl alcohol. The favored teeth in SEM have been the molars, both maxillary (upper) or mandibular (lower). The location on the tooth does not seem to matter as long as it is a facet that exhibits microwear. Impressions are then made of the molar using polysiloxane vinyl, which is a compound used to make impressions in human dentistry. Casts are made from the molds using an epoxy polymer. Specimens are examined under a standard light microscope to ensure that they are suitable for SEM. If the specimens are usable they are sputter-coated with silver to a thickness of five nanometers in order to be viewed under the scanning-electron microscope. They are then placed under the scanning electron microscope. Micrographs are taken at 500X and scanned into a computer at 200 dots-per-inch. The features of the microwear are examined using the software program MICROWEAR 4.0. The percentage incidence of pitting (pits are defined as microwear scars with a length to width ratio of less than or equal to 4:1), scratch breadth, pit breadth and pit length are all recorded. Then bivariate statistics, analysis of variance, and Mann-Whitney U tests are employed to arrive at the results of the study.

There are a number of problems with using SEM to examine dental microwear. Perhaps the most limiting factor is the expense of sample preparation and of the scanning electron microscope itself (Godfrey et al., 2004; Semprebon et al., 2004). For example, El-Zaatari (2005) examined 50 total specimens from eight species. Of those eight species, two species were examined using only two specimens. Furthermore, large samples would be challenging due to the time-intensive process of quantitatively measuring the width

and breadth of the microwear features (Godfrey et al., 2004). Therefore, any results drawn from these data tend to be based on small sample sizes. Gordon (1988) details a number of problems with the SEM technique in addition to the ones listed by Godfrey et al. (2004). These include the loss of resolution from the scanning electron microscope to the micrograph, the further loss of resolution to scan the micrograph into a computer, differences in magnification levels between studies, and limited visibility depending on the angle of the tooth under the microscope.

A newer method uses a scanning confocal microscopy (SCM) to generate three-dimensional images of the tooth surface. Scale-sensitive fractal analysis is then employed to characterize the microwear (Scott et al., 2005). Similar to SEM, a high quality cast is used. The cast is then placed into a white-light scanning confocal image profiler and recorded at 100X. The employment of graphical computer programs to analyze the results reduces inter-observer error, which is high in SEM. This also increases the sample sizes that may be examined by reducing the time needed to measure the microwear features. However, the SCM method is still reliant on the use of often prohibitively expensive equipment and software.

The newly developed low-magnification stereomicroscopy (LMS) method (Godfrey et al., 2004; Semprebon et al., 2004) is in some regards more closely related to the pioneering study of Walker (1976) than to SEM or SCM. The general techniques summarized here are outlined by Semprebon and colleagues (2004). Molar teeth regardless of their origin (mandible or maxillae) are used for the analysis. The specimen casts are prepared just as in SEM and SCM. In LMS, however, the specimens are examined with a low-magnification stereomicroscope while an external fiber-optic light

source is manipulated to highlight the microwear features. The features are counted in a more categorical way than SEM features although the features that are recorded are similar. Each specimen is sampled twice and averages of those samples are used for the analyses. The purpose of taking two samples is to reduce sampling bias and limit the effect of intra-observer error.

Semprebon (2004) notes that LMS is not meant to replace SEM. However, LMS does overcome a number of the problems that are faced in SEM. In SEM, the most significant limiting factor is cost. LMS is relatively inexpensive. The only equipment needed is a standard microscope, an external light source and an ocular reticle (a 0.4 x 0.4 mm square placed in the eye piece of the microscope to define the sample area). This alone results in larger sample sizes. LMS is also more time efficient than SEM, since data are recorded categorically rather than being measured. Additionally, there is no lost resolution as data are recorded directly from the microscope without taking a micrograph and scanning it in to a computer. Stating a specific magnification in the initial paper on this method also eliminates the variation in magnification between studies. Finally, there is no issue with the angle of the sample under the microscope limiting visibility. The external light source can be manipulated in order to capture all the microwear features.

Microwear and Species Differentiation

Since the ground-breaking work of Semprebon and Godfrey (Godfrey et al., 2004; Semprebon et al., 2004), other researchers have begun to apply this method to questions that address niche and species differentiation (Godfrey et al., 2004; Proctor and Hudson, 2006; Williams et al., 2007). While the relationship between microwear and diet is fairly concrete, the relationship between microwear and niche and species differentiation is less

intuitive. Since microwear is created by the food consumed by the individual, the comparative method can be used to infer diet in extinct forms. Once the dietary signals have been inferred some prediction can be made about the ecological niche that the animal occupied. Godfrey, et al. (2004) and Semprebon, et al. (2004) demonstrate how microwear can help place fossil primates into general dietary categories and then infer an ecological niche. The step to species differentiation is one degree further. Most species occupy a specific niche within their larger ecosystem. This is what allows many similar species to live sympatrically (Harcourt and Nash, 1986; Milton, 1981; Porter, 2001; Tutin and Fernandez, 2005). If differences between dental microwear in similar environments are present, perhaps this can help elucidate species differentiation among closely related forms. Additionally, if the phylogenetic species concept (Groves, 2004) is adhered to, microwear can serve as a proxy for the fixed character state that is needed to differentiate these species.

It should be noted that microwear alone cannot resolve the issue of species differentiation in these forms. However, this study combined with future studies may help to more clearly define the complex relationships of the species within these genera. Microwear can help in proposing niche or species relationships that may serve as hypotheses for researchers investigating other traits.

Materials

A total of 188 individuals of 10 species of papionins, including three extant species of *Papio*, three extinct species of *Papio*, three extinct species of *Parapapio* and four individuals of an indeterminate *Parapapio* species were used in this study. Evidence from SEM studies that show some differences between adult and deciduous wear patterns

(Gordon, 2005; Perez-Perez et al., 2005). However, these findings are considered preliminary. Only adult specimens were used as there has been no published research involving the differences between the adult and deciduous teeth of specimens using LMS. This will also serve to eliminate the possible confounding effects of ontogenetic changes related to diet (Godfrey et al., 2004). In order to maximize the sample size both upper and lower second molars were used. When possible, the paracone, or mesialmost buccal (front-cheekside) cusp was used. However, in some instances the paracone was not available and other locations on the second molar were used. In other studies, no significant differences were found based on molar location (Godfrey et al., 2004; Semprebon et al., 2004). See Appendix for a complete table of the specimens used.

Some species were combined in order to maximize the sample sizes for each species. For example, in the living baboons there are hybrid zones between *Papio anubis* and *Papio hamadryas* (Nystrom et al., 2004; Phillips-Conroy et al., 1991) as well as between *Papio anubis* and *Papio cynocephalus* (Samuels and Altmann, 1986). Some authors consider these baboons members of the same species with differences only at the subspecies level (Newman et al., 2003). Therefore, for this study *P. anubis*, *P. hamadryas*, and *P. cynocephalus* have been combined into the group called *P. anubis*. The two other types of living baboons, *P. ursinus* and *P. kindae* were left as separate groups due to their evolutionary and geographic distance from the other baboons (Newman et al., 2003). In the extinct baboon forms, some species designations (from the museums in which they are curated) were changed to match the current understanding of papionin phylogeny. *P. wellsi* has been eliminated in the literature and has been merged into *P. izodi* (Jablonski, 1994; Jablonski, 2002). *Parapapio antiquus* has also been

eliminated from the literature and reassigned to either *Pp. broomi* or *Pp. whitei* (Jablonski, 2002). However, two specimens of *Pp. antiquus* were unable to be identified as an accepted species and have been placed into the category *Pp.* species indeterminate (*Pp.* (*sp.*)). See table 1 for the individuals that were reassigned.

Table 1 – Reassigned Specimens

Specimen	**Was**	**Is**	**Justification**
MCZ 23082	*P. cynocephalus*	*P. anubis*	Hybrid zones
MCZ 44276	*P. cynocephalus*	*P. anubis*	Hybrid zones
MCZ 169	*P. hamadryas*	*P. anubis*	Hybrid zones
MCZ 5008	*P. hamadryas*	*P. anubis*	Hybrid zones
SAM 11728	*P. wellsi*	*P. izodi*	Condensed in literature
SAM 11730	*P. wellsi*	*P. izodi*	Condensed in literature
SAM 5356	*P. wellsi*	*P. izodi*	Condensed in literature
TP 11	*P. wellsi*	*P. izodi*	Condensed in literature
TP 9	*Pp. antiquus*	*Pp. whitei*	Not a real species
T 17	*Pp. antiquus*	*Pp. broomi*	Not a real species
TP 13	*Pp. antiquus*	*Pp.* (*sp*)	Not a real species
TP 8	*Pp. antiquus*	*Pp.* (*sp*)	Not a real species

Method

The specimens were collected during several Georgia State University research trips in 2005 to South Africa, Belgium, Massachusetts and the Netherlands headed by Dr. Frank Williams. During this trip impressions were taken of the occlusal surface of each specimen using polysiloxane vinyl. Once the materials were curated at Georgia State University, casts were made using epoxy resin and hardener that had been run through a centrifuge to eliminate air bubbles before casting. After allowing time to dry, the casts were examined for microwear features under a standard low-magnification stereomicroscope at 35X magnification. An external oblique (fiber-optic) light source was manipulated to make the microwear features more visible. While under the microscope, features that were within a 0.4 X 0.4 mm ocular reticle (a square that is visible through the eyepiece) were counted following the procedures outlined in

Semprebon et al. (2004). The ocular reticle was positioned over a portion of the paracone of the second molar (if available) that contained readable microwear. For each specimen two samples were taken and then averaged together for use in the analyses.

The microwear features were classified as either pits or scratches. There is no quantitative measurement for a pit, rather they are defined as features that are approximately circular and have similar widths and lengths. Pits are broken into four categories. Small pits are those that are only visible from the light reflected by them as the oblique illumination is altered. Medium pits are those that are larger than a small pit yet take up less than 1/4th of the ocular reticle. Large pits are those that take up at least 1/4th of the ocular reticle. Puncture pits are those that are very deep and craterlike and have regular edges. They appear dark due to their depth. Scratches are also divided into groups. Fine scratches are those that are narrow and finely etched into the surface of the enamel. They are often only visible by manipulation of the light source. Coarse scratches are wider and deeper than fine scratches. Hypercoarse scratches are very deep, wide, and trench-like. They appear dark regardless of the placement of the light source.

Statistical Analyses

After the data were collected statistical methods were employed to 1) determine if the species designations that are assigned to specimens within the genera are statistically real groups and to examine the taxonomic assignments using a new method 2) determine what traits of the microwear can be used to differentiate species (if any), 3) determine if there are redundant species labels, which may elucidate some of the temporal and scaling issues in the papionins 4) determine if *Papio* and *Parapapio* can be distinguished using dental microwear to examine possible ancestry between the genera and 5) to see if any

site or temporal differences exist, which may impact species designations or add information to the turnover pulse theory.

The data are first examined using a bivariate comparison of total pits versus total scratches to explore broad trophic patterns in the data. Determining if the species are statistically real groups is best facilitated by a discriminant function analysis (DFA). Next, to understand which traits of the microwear differentiate species, an analysis of variance (ANOVA) with Tukey's post hoc tests for Honestly Significant Differences (HSD) was used. A principal components analysis (PCA) was utilized to see what groupings emerge from individuals' factor scores. The PCA also identified variables that distinguish individuals. Determining if there are redundant species labels is largely dependent on the interpretation of the results of the analyses listed above, but also includes an examination of the descriptive statistics for each species to determine the amount of variation present in the sample. All of the above procedures were utilized again, but at the genera level to determine if *Papio* and *Parapapio* could be distinguished. Finally, the same procedures were utilized based on site and then on time period. The use of these methods largely followed that of Godfrey et al. (2004). Each of these methods is discussed below.

Bivariate Analysis

Bivariate analyses were utilized in order to examine possible differences at broader levels. For example, total pits and total scratches were plotted in order to explore if species or even genera can be differentiated without breaking the pits and scratches into their components. These graphs include ellipses that represent a 95% confidence interval.

Analysis of Variance

Godfrey et al. (2004) uses an analysis of variance (ANOVA) with Tukey's post hoc test for HSD. The ANOVA reveals which microwear traits (small pits, coarse scratches, etc.) are significantly different between all of the species. However, this level of detail is not fine enough to determine among which species the differences lie. For that reason a Tukey's post hoc test for HSD is needed to examine all of the pairwise comparisons. Tukey's post hoc test for HSD was used rather than t-tests because for large amounts of data (i.e. 10 species or 55 pairwise comparisons) the likelihood of finding significant results by chance would be greater than the standard acceptable level of 0.05. Tukey's post hoc test for HSD takes into account this increasing likelihood and is thus a more conservative test for large sets of pairwise comparisons (Hill and Lewicki, 2006). This analysis helps identify which microwear traits are useful for distinguishing groups.

Principal Components Analysis

A principal components analysis (PCA) is used to examine the variance/covariance matrix to identify those traits which tend to polarize individuals (Hill and Lewicki, 2006). The PCA reduces the data to fewer dimensions, which reveals how the variation within and across individuals and traits is partitioned. The PCA does not consider the species labels, which have been assigned, but rather groups specimens based solely on the variance/covariance of multiple traits. By extracting principal components from the data, new variables are formed. The purpose of this is to "maximize the variance (variability) of the 'new' variable (factor), while minimizing the variance around the new variable" (Hill and Lewicki, 2006). This allows for the major components of variability to be revealed and graphed against each other. This shows which components polarize

individuals and sheds light into group clusters. The PCA graphs include ellipses that represent 95% confidence intervals.

Discriminant Function Analysis

Following Godfrey et al. (2004), the final statistical analysis employed is a discriminant function analysis (DFA). The DFA assumes that there are "real" groups within the data and then examines which variables are the most predictive of membership in one of the "real" groups. In this way, the individuals were examined to determine if they fell into the group to which they were assigned. If the DFA did not predict group membership, this suggests that the groupings may not be accurate.

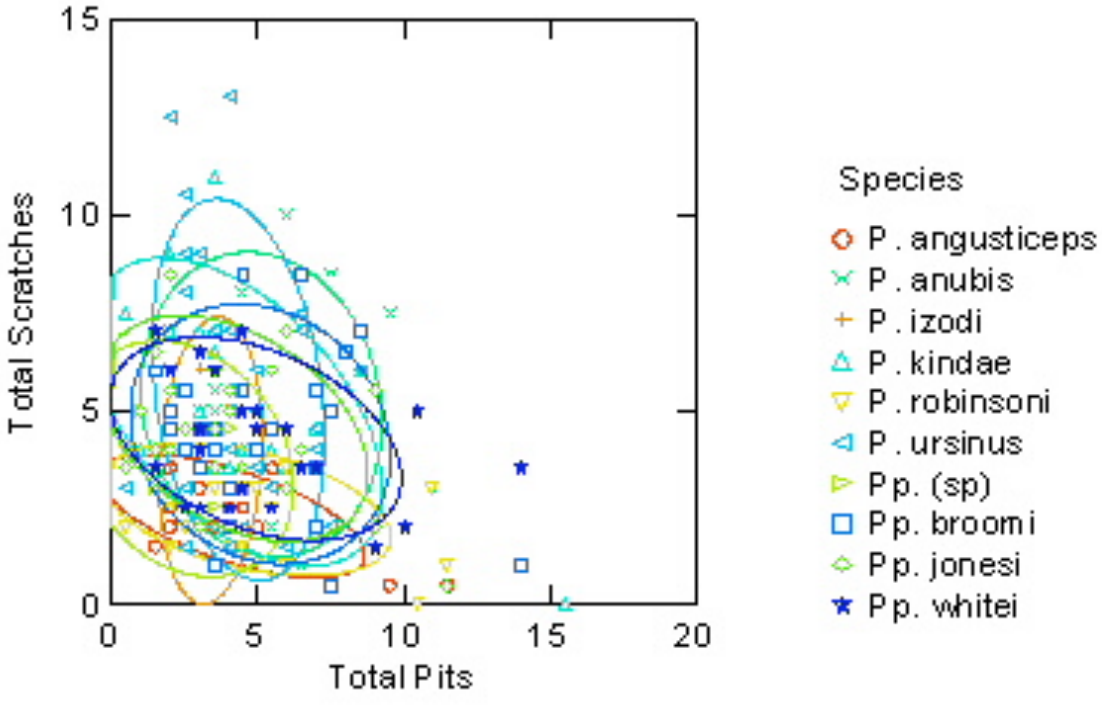
Chapter Four: Results

Results by Species

Bivariate Comparision

The initial comparison of the groups was done by plotting total pits against total scratches, which is standard in the literature. As seen in Figure 1, the relationship among these species is tightly linked. Little can be gathered from this graph beyond a few rough details. *P. angusticeps* appears to have the least variation and is differentiated by having fewer microwear features than other species. *P. robinsoni*, has slightly more variation, but also generally has fewer microwear features. However, the variation of *P. angusticeps* and *P. robinsoni* overlap significantly. In fact, all of the species overlap

Figure 1 – Bivariate Graph of Total Pits and Scratches by Species



to some extent. Two of the extant species, *P. anubis* and *P. ursinus* have the largest amounts of variation. That should be expected due to their relatively large geographic ranges and the larger sample of extant specimens. However, the third extant species, *P. kindae* has a smaller amount of variation and a smaller geographic range than the other living forms. This suggests that *P. kindae* either has a more specialized diet than *P. ursinus* and *P. anubis* and thus lives in a smaller geographic area or that *P. kindae* is restricted to a smaller geographic area that happens to have a slightly different ecosystem resulting in different microwear signals. This supports separating *P. kindae* from other *Papio* taxa because living species that occupy different ecosystems can be classified as different species.

There are also differences between the living forms and the fossil forms. Living forms such as *P. ursinus* and *P. anubis* exhibit more scratches and fewer pits than the extinct forms of both *Papio* and *Parapapio*. These differences are explored in the genera and temporal analyses.

ANOVA with Tukey's HSD

Table 2 shows the sample size, mean and standard deviation by species for each of the microwear traits that were examined. The ANOVA (Table 3) between species revealed significant ($p < 0.05$) differences for the following microwear features: medium pits, fine scratches, coarse scratches, hypercoarse scratches and total scratches. The significant species differences that were revealed in the Tukey's post hoc test for Honestly Significant Differences are shown in Table 4. There were no significant differences found among small pits, large pits, puncture pits and total pits. As such, they will not be included in Table 4 nor any further analyses.

Table 2 – Mean and Standard Deviation of Microwear Features by Species

Species		Sm. Pits	Med. Pits	Lg. Pits	Punct. Pits	Tot. Pits	Fine Scratch	Coarse Scratch	H.coarse Scratch	Tot. Scratch
P. angusticeps	Mean	3.219	0.875	0.063	0	4.156	1.313	0.781	0.188	2.281
N=16	Std. Dev.	2.5428	0.7638	0.1708	0	2.7732	0.9979	0.5154	0.3096	0.9656
P. anubis	Mean	3.75	1.389	0	0	5.139	2.806	1.694	0.639	5.139
N=18	Std. Dev.	2.3964	1.2897	0	0	2.5426	1.8242	1.1264	0.6818	2.412
P. izodi	Mean	2.4	1	0	0	3.4	2.8	0.9	0	3.7
N=5	Std. Dev.	0.8216	0.7071	0	0	0.8216	2.1389	0.7416	0	1.7176
P. kindae	Mean	2.659	1.591	0	0.045	4.295	3.068	1.591	0.295	4.955
N=22	Std. Dev.	2.5232	1.4196	0	0.1471	3.1155	2.1564	1.1916	0.427	2.4684
P. robinsoni	Mean	3.976	0.595	0.048	0.024	4.643	0.929	1.238	0.286	2.452
N=21	Std. Dev.	2.5859	0.7845	0.2182	0.1091	3.0665	0.9258	0.718	0.4351	1.0595
P. ursinus	Mean	3.15	1.183	0	0	4.333	3.817	1.367	0.333	5.517
N=30	Std. Dev.	1.609	1.0379	0	0	1.877	2.4792	1.2861	0.5622	3.1058
Pp. (sp)	Mean	1.625	0.875	0	0	2.5	2.625	0.75	0.375	3.75
N=4	Std. Dev.	1.493	0.4787	0	0	1.472	1.7017	0.6455	0.4787	1.1902
Pp. broomi	Mean	3.48	1.58	0	0.04	5.1	2.02	2.14	0.22	4.38
N=25	Std. Dev.	2.5596	1.3124	0	0.1384	2.8062	1.6361	1.3733	0.4805	2.098
Pp. jonesi	Mean	2.818	1.364	0.023	0	4.205	2.591	1.818	0.114	4.523
N=22	Std. Dev.	1.8228	1.5367	0.1066	0	2.8605	1.5708	1.3848	0.2642	1.8092
Pp. whitei	Mean	2.44	2.5	0	0	4.94	2.02	2.04	0.2	4.26
N=25	Std. Dev.	1.46	2.586	0	0	3.1336	1.2787	1.4356	0.3227	1.6401
Total	Mean	3.106	1.396	0.013	0.013	4.529	2.423	1.58	0.274	4.277
N=188	Std. Dev.	2.1698	1.5168	0.0958	0.0807	2.7107	1.9252	1.2363	0.4633	2.319

Table 3 – ANOVA Results for Species

		Sum of Squares	df	Mean Square	F	Sig.
Sm. Pits	Between Groups	55.696	9	6.188	1.336	0.221
	Within Groups	824.676	178	4.633		
	Total	880.372	187			
Med. Pits	Between Groups	53.212	9	5.912	2.791	**0.004**
	Within Groups	377.016	178	2.118		
	Total	430.227	187			
Lg. Pits	Between Groups	0.088	9	0.01	1.072	0.386
	Within Groups	1.629	178	0.009		
	Total	1.717	187			
Punct. Pits	Between Groups	0.064	9	0.007	1.1	0.365
	Within Groups	1.153	178	0.006		
	Total	1.217	187			
Tot. Pits	Between Groups	49.07	9	5.452	0.732	0.679
	Within Groups	1325.019	178	7.444		
	Total	1374.089	187			
Fine Scratch	Between Groups	146.307	9	16.256	5.292	**0**
	Within Groups	546.825	178	3.072		
	Total	693.132	187			
Coarse Scratch	Between Groups	33.712	9	3.746	2.645	**0.007**
	Within Groups	252.091	178	1.416		
	Total	285.803	187			
H.coarse Scratch	Between Groups	3.827	9	0.425	2.084	**0.033**
	Within Groups	36.316	178	0.204		
	Total	40.142	187			
Tot. Scratch	Between Groups	207.593	9	23.066	5.145	**0**
	Within Groups	798.024	178	4.483		
	Total	1005.617	187			

Table 4 – Significant Results from Tukey's HSD by Species

Dependent Variable	Species	Species	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Medium Pits	*P. angusticeps*	*Pp. whitei*	-1.6250(*)	0.4659	0.021	-3.118	-0.132
	P. robinsoni	*Pp. whitei*	-1.9048(*)	0.4308	0.001	-3.285	-0.524
	P. ursinus	*Pp. whitei*	-1.3167(*)	0.3941	0.033	-2.580	-0.054
Fine Scratches	*P. angusticeps*	*P. ursinus*	-2.5042(*)	0.5426	0.000	-4.243	-0.766
	P. anubis	*P. robinsoni*	1.8770(*)	0.5630	0.034	0.073	3.681
	P. robinsoni	*P. kindae*	-2.1396(*)	0.5347	0.004	-3.853	-0.426
	P. robinsoni	*P. ursinus*	-2.8881(*)	0.4987	0.000	-4.486	-1.290
	Pp. broomi	*Pp. whitei*	1.7967(*)	0.4746	0.008	0.276	3.318
	Pp. broomi	*P. ursinus*	-1.7967(*)	0.4746	0.008	-3.318	-0.276
	Pp. whitei	*P. ursinus*	-1.7967(*)	0.4746	0.008	-3.318	-0.276
Coarse Scratches	*P. angusticeps*	*Pp. broomi*	-1.3588(*)	0.3810	0.016	-2.580	-0.138
	P. angusticeps	*Pp. whitei*	-1.2588(*)	0.3810	0.037	-2.480	-0.038
H.coarse Scratches	*P. anubis*	*Pp. jonesi*	.5253(*)	0.1436	0.012	0.065	0.985
Total Scratches	*P. angusticeps*	*P. anubis*	-2.8576(*)	0.7275	0.005	-5.189	-0.526
	P. angusticeps	*P. kindae*	-2.6733(*)	0.6957	0.006	-4.903	-0.444
	P. angusticeps	*P. ursinus*	-3.2354(*)	0.6555	0.000	-5.336	-1.135
	P. angusticeps	*Pp. jonesi*	-2.2415(*)	0.6957	0.048	-4.471	-0.012
	P. anubis	*P. robinsoni*	2.6865(*)	0.6801	0.004	0.507	4.866
	P. kindae	*P. robinsoni*	2.5022(*)	0.6460	0.006	0.432	4.572
	P. robinsoni	*P. ursinus*	-3.0643(*)	0.6024	0.000	-4.995	-1.134
	P. robinsoni	*Pp. jonesi*	-2.0703(*)	0.6460	0.050	-4.140	0.000

*. The mean difference is significant at the .05 level.

Principal Components Analysis

The data are made complex by a large number of zeros. This may initially appear as missing data. However, since there were zero microwear features observed this is in fact data (Allison, 2001). Fortunately, most of the zeros found in the data set were in the categories of large and puncture pits, which were not significant and were eliminated from the analyses. The other category that has a large amount of zeros is hypercoarse scratches. While this results in a slight positive skew of the variance/covariance matrix, this category does discriminate among species, so it will remain in the data set despite the presence of the zeros.

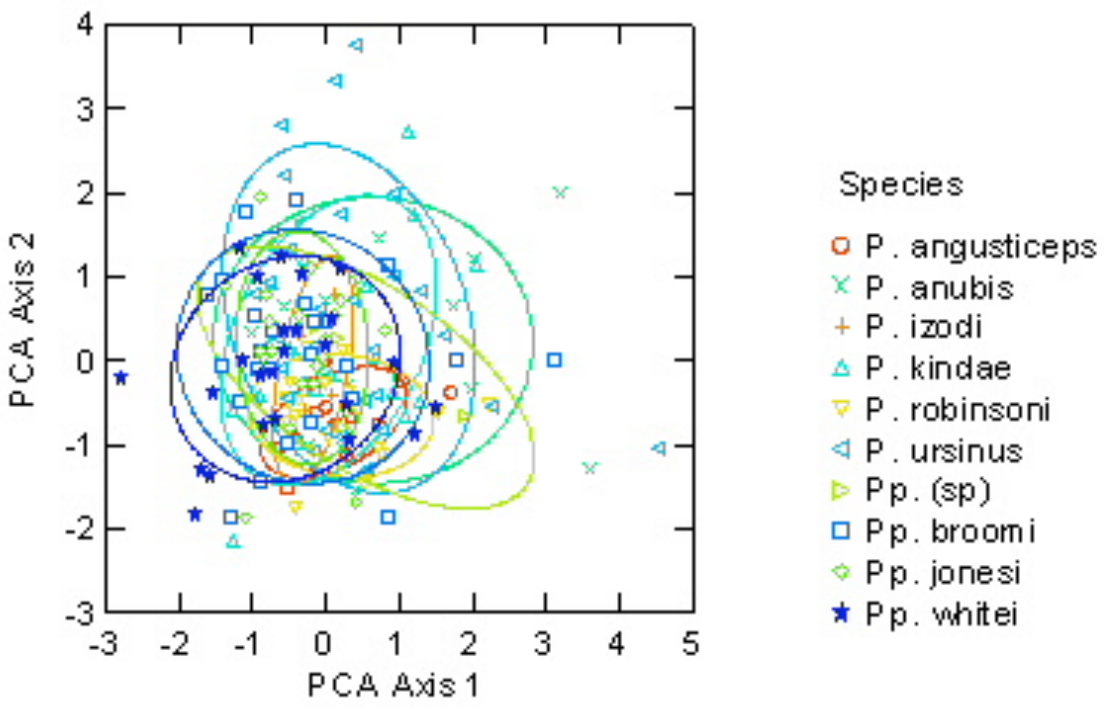
The PCA resulted in five principal components, two of which had Eigenvalues over one. The components with Eigenvalues less than one will not be considered. The first principal component axis polarizes total and fine scratches positively and medium pits negatively (See Table 5 for component loadings). This axis explains 42.24% of the variation. The second principal component axis polarizes hypercoarse scratches positively and coarse scratches and medium pits negatively. This axis explains 21.80% of the variance. See Figure 2.

Table 5 – PCA Component Loadings by Species

	Component	
	1	2
Total Scratches	**0.977**	0.055
Fine Scratches	**0.825**	0.102
Coarse Scratches	0.579	**-0.382**
Hypercoarse Scratches	-0.08	**0.871**
Medium Pits	**-0.369**	**-0.414**

Extraction Method: Principal Component Analysis.
a. 2 components extracted.

Figure 2 – Graph of PCA Axes 1 and 2 by Species



This analysis reveals that *P. angusticeps* is again the species with the least variation and *P. robinsoni* has the second least variation. However, *P. robinsoni* is now differentiated from *P. angusticeps* by being polarized from having more hypercoarse scratches, while *P. angusticeps* is polarized by fine and total scratches. However, these two species still fall within the variation that is present in all the other species. *P. ursinus* and *P. anubis* again have the most variation.

Discriminant Function Analysis

The DFA resulted in four canonical functions, which captured 100% of the variation. The first discriminant function explains 56.0% of the variance in the data. The first three functions together explain 97.0% of the data.

The post hoc classification success for the sample of 188 individuals was 27.1% based on the discriminant functions. In other words, the DFA correctly grouped the species 17.1 percentage points above chance. See Table 6 for a summary of how each species was classified.

Table 6 – DFA Classification Results by Species

			Predicted Group Membership (a)										
		Species	*P. angusticeps*	*P. anubis*	*P. izodi*	*P. kindae*	*P. robinsoni*	*P. ursinus*	*Pp. (sp)*	*Pp. broomi*	*Pp. jonesi*	*Pp. whitei*	Total
Original	Count	*P. angusticeps*	**7**	0	2	0	3	0	4	0	0	0	16
		P. anubis	1	**6**	2	1	1	3	0	1	1	2	18
		P. izodi	1	0	1	0	1	**2**	0	0	0	0	5
		P. kindae	0	**4**	**4**	1	1	3	1	2	2	**4**	22
		P. robinsoni	4	3	2	0	**9**	0	1	1	1	0	21
		P. ursinus	4	5	3	1	3	**10**	0	1	3	0	30
		Pp. (sp)	0	0	**2**	0	1	0	1	0	0	0	4
		Pp. broomi	1	4	4	1	0	2	0	**7**	1	5	25
		Pp. jonesi	1	1	5	0	1	2	1	**6**	2	3	22
		Pp. whitei	0	3	1	1	1	1	2	5	4	**7**	25
	%	*P. angusticeps*	**43.8**	0.0	12.5	0.0	18.8	0.0	25.0	0.0	0.0	0.0	100.0
		P. anubis	5.6	**33.3**	11.1	5.6	5.6	16.7	0.0	5.6	5.6	11.1	100.0
		P. izodi	20.0	0.0	20.0	0.0	20.0	**40.0**	0.0	0.0	0.0	0.0	100.0
		P. kindae	0.0	**18.2**	**18.2**	4.5	4.5	13.6	4.5	9.1	9.1	**18.2**	100.0
		P. robinsoni	19.0	14.3	9.5	0.0	**42.9**	0.0	4.8	4.8	4.8	0.0	100.0
		P. ursinus	13.3	16.7	10.0	3.3	10.0	**33.3**	0.0	3.3	10.0	0.0	100.0
		Pp. (sp)	0.0	0.0	**50.0**	0.0	25.0	0.0	25.0	0.0	0.0	0.0	100.0
		Pp. broomi	4.0	16.0	16.0	4.0	0.0	8.0	0.0	**28.0**	4.0	20.0	100.0
		Pp. jonesi	4.5	4.5	22.7	0.0	4.5	9.1	4.5	**27.3**	9.1	13.6	100.0
		Pp. whitei	0.0	12.0	4.0	4.0	4.0	4.0	8.0	20.0	16.0	**28.0**	100.0

a. 27.1% of original grouped cases correctly classified.

Results by Genera

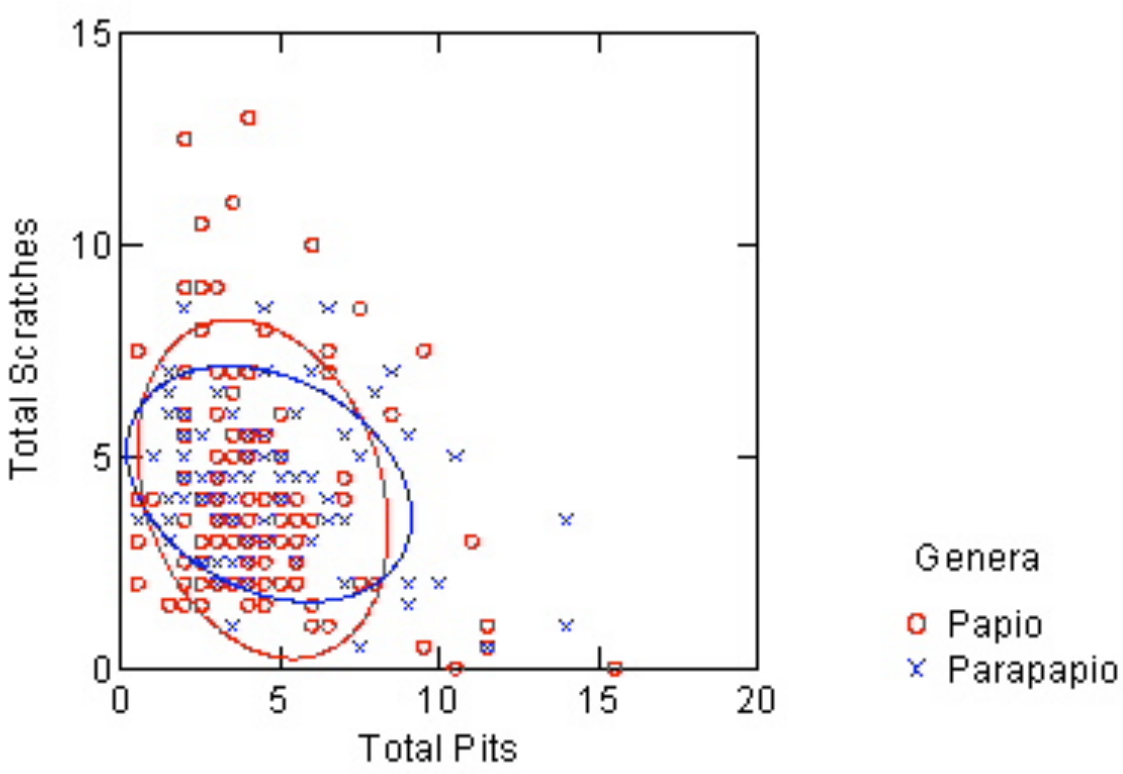
For the analyses by genera the total sample remains the same (n=188). There are 112 specimens of *Papio* and 76 specimens of *Parapapio*.

Bivariate Comparison

Total pits and total scratches were graphed against each other by genera. See Figure 3. This graph reveals a significant amount of overlap between the two genera. However, *Papio* exhibits more scratches and fewer pits than *Parapapio*. Godfrey et al. (2004) found that few scratches and some pits indicate a diet that consists of leaves and

some fruit while more scratches and fewer pits indicate more grasses and less fruit in the diet. This suggests that *Parapapio* may have focused on a more arboreal diet than *Papio*.

Figure 3 – Bivariate Graph of Total Pits and Scratches by Genera



ANOVA

Table 7 shows the results for the ANOVA run at the genus level (*Papio* and *Parapapio*). Significant differences were only found between the genera on the microwear traits of medium pits and coarse scratches. However, hypercoarse scratches approach significance ($p = .052$) and will be considered in the analyses. The microwear features that were not significant will not be considered further.

Table 7 – ANOVA Results for Genera

		Sum of Squares	df	Mean Square	F	Sig.
Sm. Pits	Between Groups	9.303	1	9.303	1.986	0.16
	Within Groups	871.069	186	4.683		
	Total	880.372	187			
Med. Pits	Between Groups	21.015	1	21.015	9.552	**0.002**
	Within Groups	409.212	186	2.2		
	Total	430.227	187			
Lg. Pits	Between Groups	0.005	1	0.005	0.596	0.441
	Within Groups	1.711	186	0.009		
	Total	1.717	187			
Punct. Pits	Between Groups	0	1	0	0	0.996
	Within Groups	1.217	186	0.007		
	Total	1.217	187			
Tot. Pits	Between Groups	2.133	1	2.133	0.289	0.591
	Within Groups	1371.956	186	7.376		
	Total	1374.089	187			
Fine Scratch	Between Groups	5.479	1	5.479	1.482	0.225
	Within Groups	687.653	186	3.697		
	Total	693.132	187			
Coarse Scratch	Between Groups	18.676	1	18.676	13.004	**0**
	Within Groups	267.127	186	1.436		
	Total	285.803	187			
H.coarse Scratch	Between Groups	0.811	1	0.811	3.834	**0.052**
	Within Groups	39.332	186	0.211		
	Total	40.142	187			
Tot. Scratch	Between Groups	1.168	1	1.168	0.216	0.642
	Within Groups	1004.449	186	5.4		
	Total	1005.617	187			

Principal Components Analysis

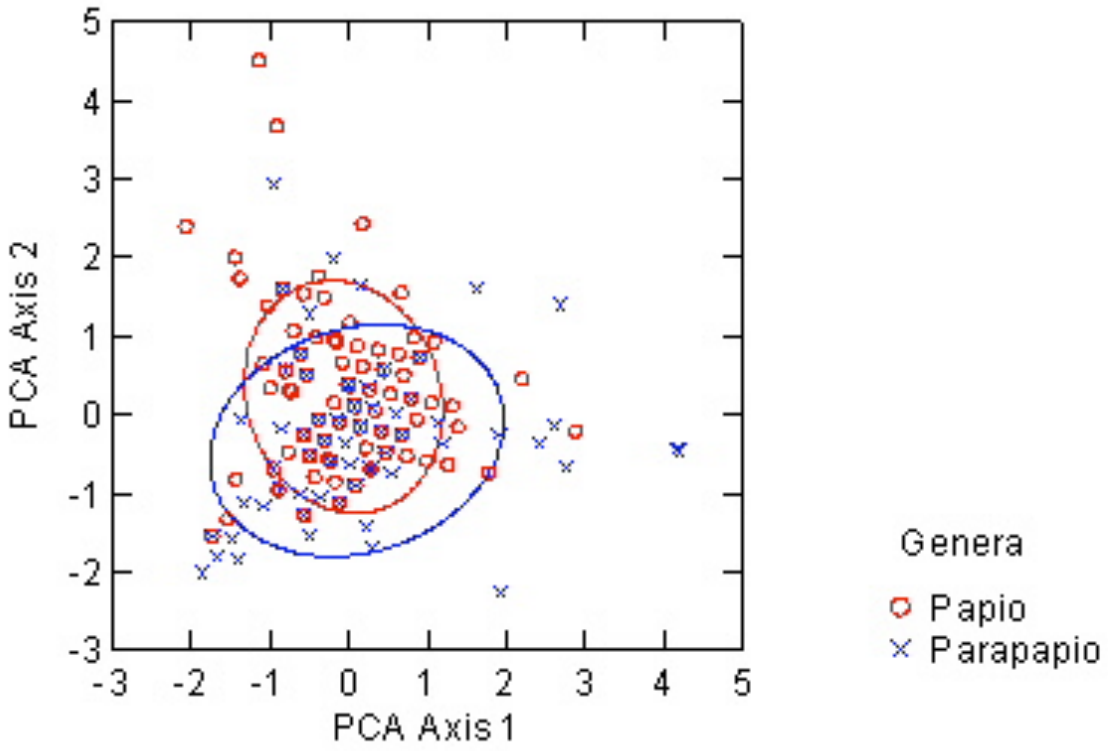
The PCA resulted in three principal components, two of which had Eigenvalues over one. See Table 8 for the component loadings. The first PCA axis polarizes medium pits and hypercoarse scratches positively and coarse scratches negatively. The second PCA axis polarizes medium pits positively and hypercoarse scratches negatively. See Figure 4. Axis 1 explains 38.89% of the variance. PCA axes 1 and 2 together explain 74.64% of the variance.

Table 8 – PCA Component Loadings by Genera

	Component (a)	
	1	2
Coarse Scratch	-0.828	-2.90E-02
Med. Pits	0.454	0.76
H.coarse Scratch	0.525	-0.702

Extraction Method: PCA
a. 2 components extracted.

Figure 4 – Graph of PCA Axes 1 and 2 by Genera



In this analysis *Papio* and *Parapapio* again have a significant amount of overlap. However, there are slight differences. *Parapapio* has a broader range on PCA axis 1, which means there is more variation in the microwear features of hypercoarse scratches and medium pits positively and coarse scratches negatively. *Papio* is polarized by having more medium pits on PCA axis 2.

Discriminant Function Analysis

The DFA resulted in one canonical function, which captured 100% of the variation. The post hoc classification success for the sample of 188 individuals was 66.5% based on the discriminant functions. The classification was 16.5 percentage points above chance. See Table 9 for classification results by genera.

Table 9 – DFA Classification Results by Species

			Membership		
		Genera	*Papio*	*Parapapio*	Total
Original	Count	*Papio*	82	31	113
		Parapapio	32	43	75
	%	*Papio*	72.6	27.4	100.0
		Parapapio	42.7	57.3	100.0

a. 66.5% of original grouped cases correctly classified.

Results by Site

The site locations for all of the extinct specimens are known. However, it is less clear exactly where the living specimens were collected. Therefore, the living species have been grouped into regional sites. In this manner, *Papio anubis* is from East-Central Africa, *Papio kindae* is from Central Africa and *Papio ursinus* is from Southern Africa. While these regional site designations are not as specific as the site locations for the extinct specimens, they will still serve to differentiate the groups. See Table 10 for the sample size by site.

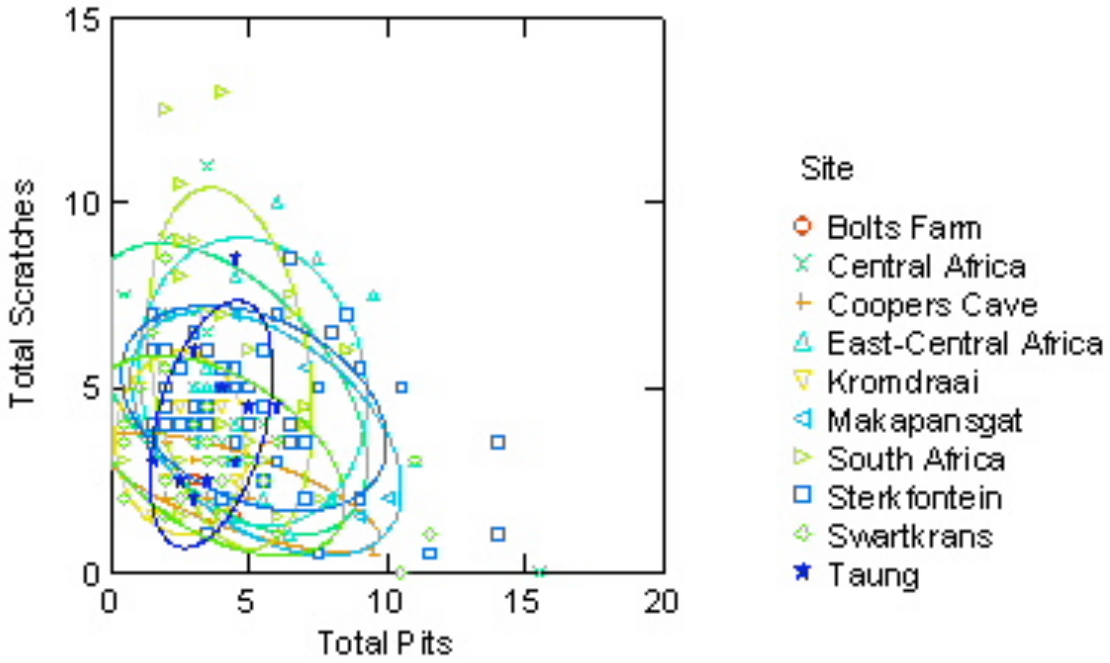
Table 10 – Sample Size by Site

	Frequency	Valid Percent
Bolt's Farm	2	1.1
Central Africa	22	11.7
Cooper's Cave	12	6.4
East-Central Africa	18	9.6
Kromdraai	7	3.7
Makapansgat	8	4.3
Southern Africa	30	16.0
Sterkfontein	49	26.1
Swartkrans	29	15.4
Taung	11	5.9
Total	188	100.0

Bivariate Comparison

The initial comparison was the bivariate graph of total pits and total scratches by site. See Figure 5. At this level of analysis Cooper's Cave, Taung, Bolt's Farm and Kromdraai have the tightest groupings. However, Bolt's Farm has the smallest sample size (n = 2) in the analysis. With only two data points a tight cluster does not seem reliable. Cooper's Cave (n = 12), Taung (n = 11) and Kromdraai (n = 7) are more robust in their clustering. There is once again, significant overlap in these groupings. The sites of Central Africa, East-Central Africa, and Southern Africa have the most variation. Since these are regional sites more variation was expected than what was found in the specific cave sites. When analyzing the data at this level, the extant regional sites do not have the largest sample size as they did in the species and genera level analyses. Sterkfontein has the largest sample (n = 49) and has less variation than the living species. This suggests that there are more dietary similarities between the species found at Sterkfontein than among the living baboon groups.

Figure 5 – Bivariate Graph of Total Pits and Scratches by Site



ANOVA with Tukey's HSD

The ANOVA (Table 11) between sites revealed significant differences ($p < 0.05$) among medium pits, fine scratches, coarse scratches, hypercoarse scratches and total scratches. These are the same microwear features that were found to be significant in the species level analysis. The features that are not significant will not be considered further. The site differences that were revealed in the Tukey's post hoc test for Honestly Significant Differences are shown in Table 12.

Table 11 – ANOVA Results for Site

		Sum of Squares	df	Mean Square	F	Sig.
Sm. Pits	Between Groups	47.725	9	5.303	1.134	0.341
	Within Groups	832.648	178	4.678		
	Total	880.372	187			
Med. Pits	Between Groups	62.002	9	6.889	3.33	**0.001**
	Within Groups	368.225	178	2.069		
	Total	430.227	187			
Lg. Pits	Between Groups	0.09	9	0.01	1.09	0.372
	Within Groups	1.627	178	0.009		
	Total	1.717	187			
Punct. Pits	Between Groups	0.041	9	0.005	0.694	0.714
	Within Groups	1.176	178	0.007		
	Total	1.217	187			
Tot. Pits	Between Groups	87.055	9	9.673	1.338	0.22
	Within Groups	1287.034	178	7.231		
	Total	1374.089	187			
Fine Scratch	Between Groups	127.182	9	14.131	4.445	**0**
	Within Groups	565.95	178	3.179		
	Total	693.132	187			
Coarse Scratch	Between Groups	30.502	9	3.389	2.363	**0.015**
	Within Groups	255.301	178	1.434		
	Total	285.803	187			
H.coarse Scratch	Between Groups	4.041	9	0.449	2.214	**0.023**
	Within Groups	36.101	178	0.203		
	Total	40.142	187			
Tot. Scratch	Between Groups	178.3	9	19.811	4.262	**0**
	Within Groups	827.317	178	4.648		
	Total	1005.617	187			

Table 12 – Significant Results from Tukey's HSD by Site

Dependent Variable	(I) Site	(J) Site	Mean Difference (I-J)	Std. Error	Sig.	Interval	
						Lower Bound	Upper Bound
Med. Pits	Cooper's Cave	Makapansgat	-2.2917(*)	0.6565	0.021	-4.395	-0.188
	Makapansgat	South Africa	1.9417(*)	0.5723	0.029	0.108	3.776
		Swartkrans	2.5388(*)	0.5744	0.001	0.698	4.379
	Sterkfontein	Swartkrans	1.2607(*)	0.3370	0.009	0.181	2.340
Fine Scratch	Cooper's Cave	South Africa	-2.4833(*)	0.6090	0.003	-4.435	-0.532
	South Africa	Sterkfontein	1.7248(*)	0.4134	0.002	0.400	3.049
		Swartkrans	2.3339(*)	0.4643	0.000	0.846	3.822
Coarse Scratch	Cooper's Cave	Sterkfontein	-1.4456(*)	0.3857	0.009	-2.682	-0.210
H.coarse Scratch	Sterkfontein	East-Central Africa	-.4144(*)	0.1241	0.034	-0.812	-0.017
Tot. Scratch	Central Africa	Cooper's Cave	2.7879(*)	0.7737	0.015	0.309	5.267
	Cooper's Cave	East-Central Africa	-2.9722(*)	0.8035	0.011	-5.547	-0.398
		South Africa	-3.3500(*)	0.7364	0.000	-5.710	-0.990
		Sterkfontein	-2.2619(*)	0.6944	0.043	-4.487	-0.037
	South Africa	Swartkrans	2.3615(*)	0.5614	0.002	0.563	4.160

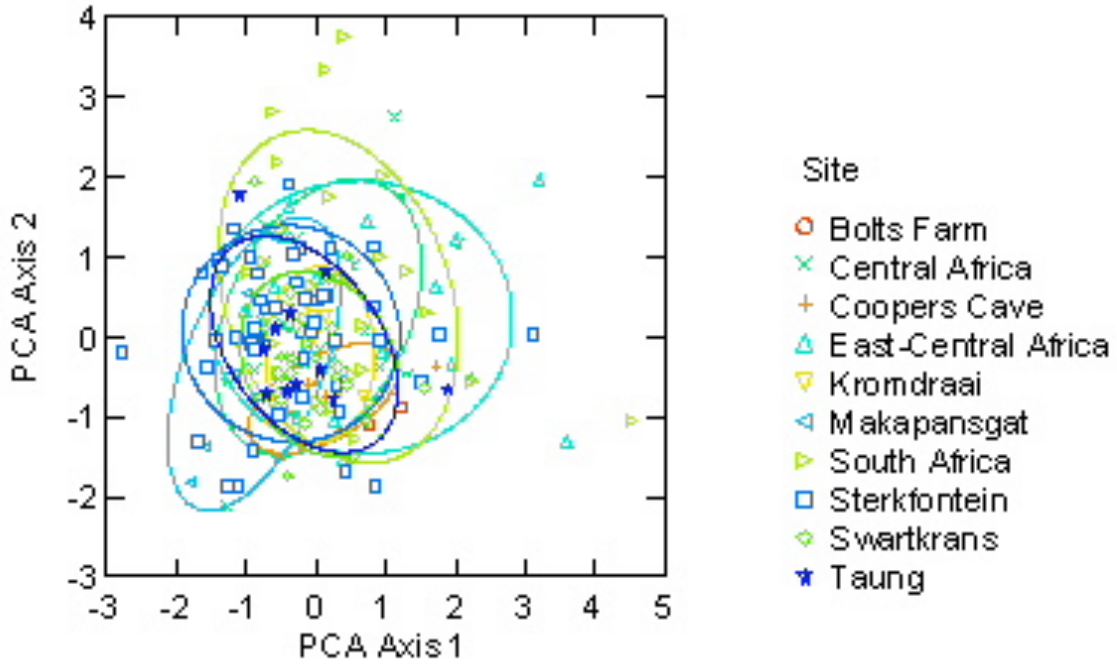
*. The mean difference is significant at the .05 level.

Principal Components Analysis

A separate PCA is not needed in order to examine the results by site because the site level analysis uses the same significant features found in the initial PCA run at the species level. However, those results can be graphed by site (Figure 6).

Bolt's Farm, Cooper's Cave and Kromdraai are the most tightly clustered. This is similar to what was found in the bivariate comparison. However, these tighter clusters are found in the range of all the other sites. East-Central Africa and South Africa have the most variation. Makapansgat is slightly differentiated from the other groupings by being polarized negatively on both PCA axes 1 and 2. That is, Makapansgat specimens tend to have more medium pits and coarse scratches.

Figure 6 – Graph of PCA Axes 1 and 2 by Site



Discriminant Function Analysis

The DFA resulted in four canonical functions, which captured 100% of the variation. The post hoc classification success for the sample of 188 individuals was 30.9% based on the discriminant functions. The classification results are 20.9 percentage points above chance. See Table 13 for classification results by site.

Table 13 – DFA Classification Results by Site

			Predicted Group Membership (a)										
		Site	Bolt's Farm	C. Africa	Cooper's Cave	E.C. Africa	Kromdraai	Makapansgat	S. Africa	Sterkfontein	Swartkrans	Taung	Total
Original	Count	Bolt's Farm	**2**	0	0	0	0	0	0	0	0	0	2
		C. Africa	1	2	0	3	1	3	**5**	3	2	2	22
		Cooper's Cave	1	0	**8**	0	1	0	0	0	1	1	12
		E.C. Africa	3	1	1	**4**	1	1	3	3	0	1	18
		Kromdraai	1	0	1	0	**3**	0	0	0	1	1	7
		Makapansgat	0	1	0	0	0	**3**	0	**3**	1	0	8
		S. Africa	2	2	4	4	0	1	**10**	1	3	3	30
		Sterkfontein	2	0	1	6	6	9	6	**13**	2	4	49
		Swartkrans	4	0	6	1	2	0	0	3	**10**	3	29
		Taung	2	0	1	0	1	1	1	1	1	**3**	11
	%	Bolt's Farm	**100**	0	0	0	0	0	0	0	0	0	100
		C. Africa	4.5	9.1	0	13.6	4.5	13.6	**22.7**	13.6	9.1	9.1	100
		Cooper's Cave	8.3	0	**66.7**	0	8.3	0	0	0	8.3	8.3	100
		E.C. Africa	16.7	5.6	5.6	**22.2**	5.6	5.6	16.7	16.7	0	5.6	100
		Kromdraai	14.3	0	14.3	0	**42.9**	0	0	0	14.3	14.3	100
		Makapansgat	0	12.5	0	0	0	**37.5**	0	**37.5**	12.5	0	100
		S. Africa	6.7	6.7	13.3	13.3	0	3.3	**33.3**	3.3	10	10	100
		Sterkfontein	4.1	0	2	12.2	12.2	18.4	12.2	**26.5**	4.1	8.2	100
		Swartkrans	13.8	0	20.7	3.4	6.9	0	0	10.3	**34.5**	10.3	100
		Taung	18.2	0	9.1	0	9.1	9.1	9.1	9.1	9.1	**27.3**	100

a. 30.9% of original grouped cases correctly classified.

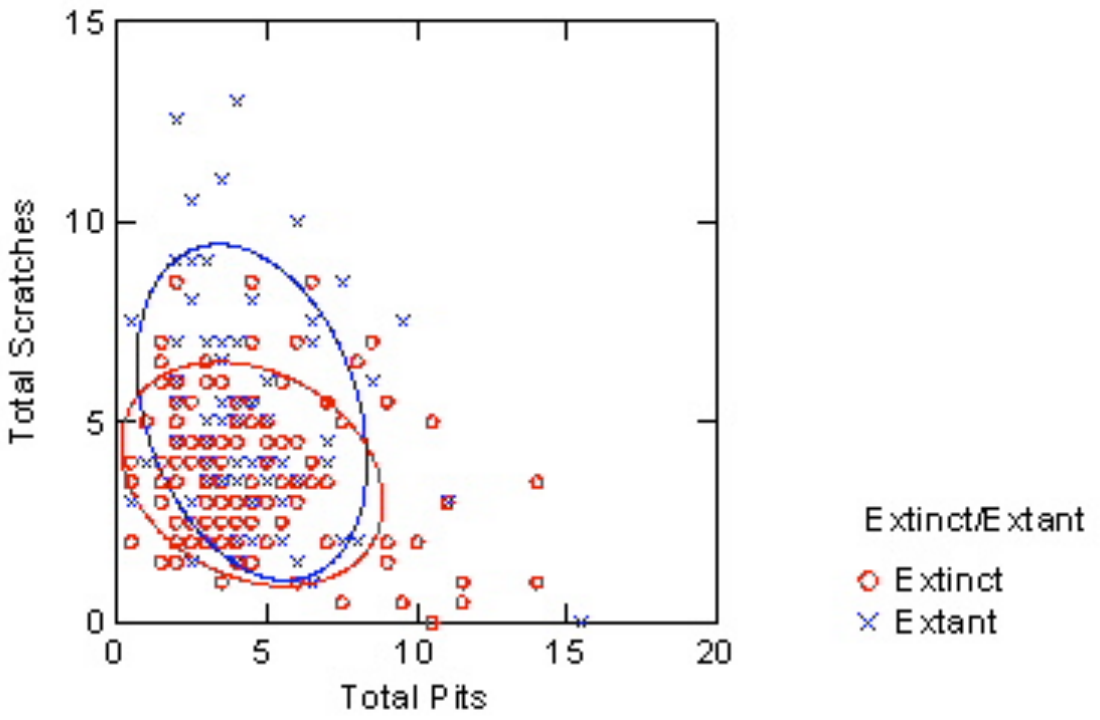
Results by Time Period

The dating of these sites is imprecise, so grouping species by absolute time is difficult. The best estimates for the dates of these sites come from Delson (1984) and Williams et al. (2007). To simplify the complex temporal relationships a bivariate grouping of extinct and extant is used to represent relative time periods. There are 118 extinct specimens and 70 extant specimens.

Bivariate Comparison

The initial comparison was done by plotting total pits and total scratches by status (extinct or extant). See Figure 7. The extinct specimens have fewer scratches than the extant specimens. This could support Vrba's (1983, 1993, 1996) turnover pulse hypothesis by demonstrating that extinct species have less grit in their diet than extant species species. This suggests that the Plio-Pleistocene climate shift from a wetter, more wooded environment to a drier more savanna habitat had an impact on the diet of these species. Additionally, the dietary categories presented by Godfrey et al. (2004) support these data. Grass eaters have a high number of scratches and low numbers of pits, while leaf eaters have fewer scratches and slightly more pits. If these categories are accepted, extant species with more scratches could be classified as more grass-eating, which is indicative of their savanna habitat, while the extinct species with fewer scratches and more pits could be considered more leaf-eating, which would support them living in a more wooded environment.

Figure 7 – Bivariate Graph of Total Pits and Scratched by Time Period



ANOVA

The ANOVA (Table 14) between extinct and extant species revealed significant differences ($p < 0.05$) for the microwear features of fine scratches, hypercoarse scratches, and total scratches. The microwear features that are not significant will not be considered further.

Table 14 – ANOVA Results for Time Period

		Sum of Squares	df	Mean Square	F	Sig.
Sm. Pits	Between Group	0.212	1	0.212	0.045	0.833
	Within Groups	880.16	186	4.732		
	Total	880.372	187			
Med. Pits	Between Group	0.114	1	0.114	0.049	0.824
	Within Groups	430.113	186	2.312		
	Total	430.227	187			
Lg. Pits	Between Group	0.02	1	0.02	2.162	0.143
	Within Groups	1.697	186	0.009		
	Total	1.717	187			
Punct. Pits	Between Group	0	1	0	0.017	0.898
	Within Groups	1.217	186	0.007		
	Total	1.217	187			
Tot. Pits	Between Group	0	1	0	0	0.998
	Within Groups	1374.089	186	7.388		
	Total	1374.089	187			
Fine Scratch	Between Group	90.046	1	90.046	27.771	**0**
	Within Groups	603.086	186	3.242		
	Total	693.132	187			
Coarse Scratch	Between Group	0.38	1	0.38	0.248	0.619
	Within Groups	285.423	186	1.535		
	Total	285.803	187			
H.coarse Scrat	Between Group	1.772	1	1.772	8.592	**0**
	Within Groups	38.37	186	0.206		
	Total	40.142	187			
Tot. Scratch	Between Group	104.127	1	104.127	21.484	**0**
	Within Groups	901.49	186	4.847		
	Total	1005.617	187			

Principal Components Analysis

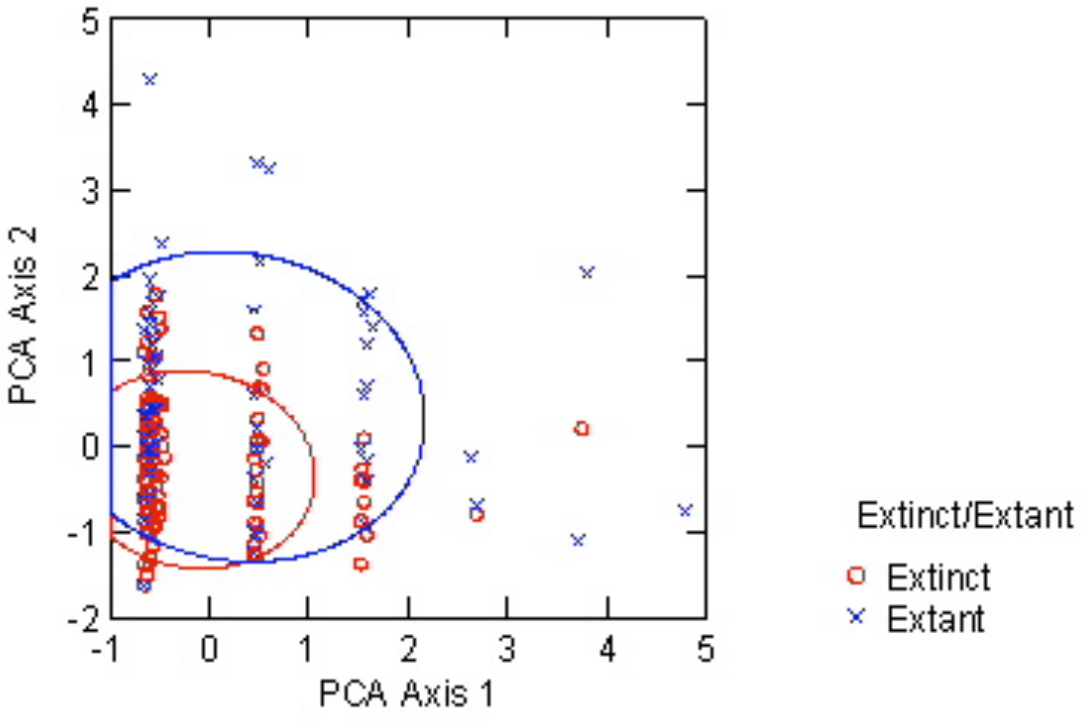
The PCA resulted in three principal components, two of which had Eigenvalues over one. The component loadings are shown in Table 15. PCA axis 1 polarizes fine and total scratches positively and hypercoarse scratches negatively. PCA axis 2 polarizes hypercoarse scratches positively and fine scratches negatively. See Figure 8. Axis 1 explains 61.40% of the variance. Axes 1 and 2 together explain 95.07% of the variance.

Table 15 – PCA Component Loadings by Time Period

	Component (a)	
	1	2
Fine Scratch	0.961	-5.34E-02
Tot. Scratch	0.957	0.108
H.coarse Scratch	-5.22E-02	0.998

Extraction Method: Principal Componen
a. 2 components extracted.

Figure 8 – Graph of PCA Axes 1 and 2 by Time Period



As in the bivariate graph, the extant species are polarized by fine and total scratches positively on PCA axis 1 and hypercoarse scratches positively on PCA axis 2. In other words, the extinct species have fewer scratches than the extant species. Once again this supports the turnover-pulse hypothesis (Vrba 1983, 1993, 1996) and the dietary categories presented by Godfrey et al. (2004).

Discriminant Function Analysis

The DFA resulted in one canonical function, which explained 100% of the variance. The post hoc classification success for the sample of 188 individuals was 66.0% based on the discriminant functions. Since only two time states, extinct and extant, were used, a random distribution of the specimens would have resulted in a 50% success rate. The actual classification success is 16 percentage points above chance. See Table 16 for a summary of the classification results.

Table 16 – DFA Classification Results by Time Period

			Predicted Group Membership		
		Living or Dead	Extinct	Extant	Total
Original	Count	Extinct	81	37	118
		Extant	27	43	70
	%	Extinct	68.6	31.4	100
		Extant	38.6	61.4	100

a. 66.0% of original grouped cases correctly classified.

Chapter Five: Discussion and Conclusions

Discussion

This study has attempted to answer a number of questions regarding the taxonomic and temporal differences of the southern African papionins from the Plio-Pleistocene to the present using dental microwear. A number of arguments can be made based on the results. The extinct forms of *Papio* have less variation than would be expected and may be representative of one species. *Parapapio* forms cannot be distinguished based on dental microwear and may represent one species with temporal variation. Makapansgat appears older than the other sites examined due to the relatively high frequency of pits, representing fruit, found in the specimens from that site. Finally, a turn-over pulse is evident when the extinct forms are compared to the extant forms. These results are discussed at length below.

Species

The bivariate analysis and the PCA resulted in graphs with large amounts of overlap in the data. All of the species fall within the same general range of pits and scratches with no species having a clearly different microwear signature from any other species. However, three species, *P. angusticeps, P. robinsoni*, and *P. izodi*, which are the extinct *Papio* forms, are more tightly clustered than the rest of the species. This may be problematic in their classification as separate species. Godfrey and Marks (1991) noted that extinct species should have no more variation than their extant relatives. The inverse may also be true. *P. robinsoni*, *P. angusticeps*, and *P. izodi* fall within the range of

variation of the extant species examined and have less variation than those extant species. It may be possible that these species should be reexamined to see if, when combined, these three species would form one species whose variation would mirror that found in extant species. The DFA somewhat confirms that the three extinct forms of *Papio* may be indicative of one group, as they are misclassified at least 18.8% of the time as each other (Table 6). This is even more compelling taken in light of their respective locations. There is no duplication of extinct *Papio* from any one site in this study. In light of the dental microwear evidence, it may be possible that researchers have seen site differences in these forms and have attributed that incorrectly to species differences.

A similar issue arises when looking at the three *Parapapio* forms. These forms evidence significant overlap in their variation and the variation is essentially the same when examined both in a bivariate manner and with PCA. The variation in these forms is more similar to what is found in the extant species, but could encompass more variation. This suggests they belong to a single species. However, this is complicated by the fact that these species often occur at the same sites. The past differences that have been observed may not be attributed to site differences. The literature acknowledges that with *Parapapio* there are concerns about these species since they are essentially scaled versions of each other (Freedman, 1976) and may represent either chronological or ecogeographic differences rather than species differences. The DFA confirmed these results as the species *Pp. jonesi* (27.3%) and *Pp. whitei* (20.0%) are often identified as *Pp. broomi*. The three species of *Parapapio* should be reexamined in light of this new evidence to determine if there are enough differences to warrant three species.

This result contradicts the findings of El-Zaatari et al. (2005) and supports the findings of Williams et al. (2007). El-Zaatari et al. (2005) found site differences between the *Parapapio* specimens using SEM but did not address the range of variation that is acceptable within a species. However, the sample sizes used by El-Zaatari et al. (2005) are much smaller than those used here.

Williams et al. (2007) uses facial affinities to form a biochronology of *Parapapio*. They argue that there are no significant differences in facial traits between *Pp. broomi* and *Pp. whitei,* corroborating this study. Williams et al. (2007) finds a facial difference in one specimen (STS 565) of *Pp. jonesi*, but argues that difference is likely due to temporal variation.

Genera

The bivariate and PCA graphs of genera also reveal significant overlap of the specimens. However, there are noticeable differences between the genera. *Papio* has more scratches and fewer pits than *Parapapio*. According to the dietary categories of Godfrey et al. (2004), this implies that *Papio* is more dependent on grasses while *Parapapio* was somewhat more reliant on leaves and fruit. This confirms the results of El-Zaatari et al. (2005) who also found fewer pits and more scratches in the living forms than the extinct forms. It should be noted, however that the same specimens were not used.

This result may support Vrba's (1983, 1993, 1996) turnover pulse hypothesis. The older forms (*Parapapio*) consume foods that are indicative of a more wooded habitat while the younger forms (*Papio*) consume foods that are indicative of a more savanna-like habitat. However, there are extinct forms of *Papio* included in this analysis that

confound the results. That is, because extinct forms of *Papio*, that lived before or during the Plio-Pleistocene climate shift, had similar features to extant forms of *Papio*, that lived after the climate shift, either climate change did not influence *Papio* as strongly as would be suggested by the turnover pulse hypothesis or an even stronger result would be found by examining explicit temporal differences.

Site

The bivariate comparison resulted in groups that significantly overlapped. The tightest groupings were from the sites with the fewest samples. However, the site with the most samples, Sterkfontein, had less variation than the regional sites of the extant species. This may suggest an ecological microniche at Sterkfontein that results in less dietary variation than would be expected or that specimens from Sterkfontein had a more focused diet than the modern papionins.

The PCA revealved similar results that included significant overlap and the greatest variation found in the regional sites of the extant forms. However, Makapansgat is slightly differentiated by having more medium pits and coarse scratches than the other sites. The only species observed here from Makapansgat are *Pp. broomi* and *Pp. whitei*. This may support the climactic and dietary differences found between the older and more recent forms by suggesting that this site with only *Parapapio* shows more of a concentration on fruit than the other sites. This further suggests that Makapansgat is an older site than the others since the microwear features from specimens at this site are indicative of a more frugivorous diet. However, this is difficult to ascertain due to the range of species that occur at other sites.

The DFA correctly classifies nine out of 10 sites (at least 26.5% and up to 100%, or 20.9 percentage points above chance, see Table 13) the majority of the time. This is the strongest result of all the DFA's in the study. This indicates that site location must be taken into account in any further studies that examine these species. Because the DFA is most successful at grouping species by site, there must be microwear features that are site specific.

It is possible that the site differences actually show temporal variation. Just as Makapansgat appears to be an older site based on the microwear dietary signals, other Pliocene sites, such as Bolt's Farm, Sterkfontein and Taung, may be differentiated from the younger Pleistocene sites of Kromdraai and Swartkrans (Williams et al., 2007).

Time Period

Perhaps the clearest results come from the analysis by gross time period, or whether the species is extinct or extant. Both the bivariate analysis and the PCA show clear differences between the extinct and extant forms. This is similar to what was found in the genus level analysis that older forms (*Parapapio*) exhibit microwear features that are indicative of a more frugivorous diet than the younger forms (*Papio*). However, using an extinct/extant comparison eliminates the extinct *Papio* bias found in the genus level analysis. The extinct forms have fewer scratches and slightly more pits than the extant forms. The dietary signal (Godfrey et al., 2004) shown by the extinct forms shows a focus on leaves and some fruit while the signal shown by the extant forms shows more of a reliance on grasses and the accompanying grit in their diet. This clearly shows an ecological shift from a more wooded environment to a more savanna environment and

becomes clear support for Vrba's (1983, 1993, 1996) turnover-pulse hypothesis as well as confirming continued climate deterioration later in the Pleistocene to the present day.

Conclusions

As noted by Carter (2006), a limitation of LMS dental microwear is that it cannot explain individual differences in diet. Rather, it is more appropriate to examine populations with large enough sample sizes. Despite this limitation, LMS still has significant advantages over SEM and SCM. While LMS may not be as precise as other methods, it can increase sample sizes and supplement the results of other methods. However, extreme precision should not be expected for primates, which are often opportunistic feeders. A relatively large amount of variation should be expected within a species. Additionally, LMS examines a larger area of the tooth surface than the other dental microwear methods. This results in a larger sample from which to gather data.

While dental microwear is acknowledged to be a dynamic trait, the morphological structures that lead to dietary specialization are fixed. In the absence of those features, such as crania and mandibles, dental microwear can serve as a proxy for a fixed trait under the phylogenetic species concept. Other studies have shown that LMS can accurately predict the broad dietary specializations of specimens (Godfrey et al., 2004; Semprebon et al., 2004). Using LMS as a proxy for a fixed trait in the fossil record provides a valuable new tool with which to examine complex taxonomic relationships.

As with most papers that address the issue of species designations in the Plio-Pleistocene South African papionins (e.g. Freedman 1965, Groves 2000, Jablonski 2002, Williams et al. 2007), the results presented here are somewhat equivocal at the species level. The most significant insight into the species designations comes from the lack of

variation found in the extinct forms of *Papio* compared to the extant forms of *Papio*. In light of the site differences, this is suggestive that the extinct forms of *Papio* do not have enough variation in them for several species designations and should be collapsed into one species with known site differences. However, this study examines dental microwear exclusively and does not take into account any morphological differences.

Similarly, there was little variation found among the species of *Parapapio*, again suggesting that if there are differences between the species they represent differences other than those found from dietary signals. For example, those differences may be temporal or they could be a result of misclassification of these three species that are scaled versions of one another. It is possible that *Parapapio* is marked by more extreme sexual dimorphism than previously considered and that the scaled species of *Parapapio* are actually large males, small females, and moderately sized individuals.

The site analyses were similarly equivocal. There was little differentiation between sites except Makapansgat, where only *Parapapio* was found. However, the DFA was most successful at classifying specimens by site. The site level DFA resulted in the highest percentage points above chance, which is unexpected because species designations should be stronger than site differences. Since the difference seen at Makapansgat is indicative of substantial time depth, it is likely that the site differences represent temporal differences.

The most revealing result was from the temporal (extinct versus extant) analysis and to a lesser extent the analysis of genera. Here, a clear turnover-pulse can be seen along with a change in diet. The evidence suggests that extinct forms were able to exploit the more wooded habitat while the extant forms adapted to the savanna. This is

particularly important in light of the hominid evolution that was occurring during this time period. Jolly (2001) has argued that papionins are a good analogy for studying hominid evolution due to their similar occurrence both in terms of geography and time. This study further demonstrates that the papionins are good analogs for hominids by showing the clear dietary shift that occurred during the Plio-Pleistocene climate change, which may be useful for addressing some of the questions regarding climate change and the emergence of the genus *Homo* (Bobe and Behrensmeyer, 2003). Other studies (Carter, 2006) confirmed that southern African *Australopithecus* shows a diet that is indicative of a grassland ecology. As earlier hominid fossils are found in southern Africa a comparison of their dietary signals to the signals of older, east African hominid fossils as well as papionin specimens may demonstrate the adaptability of hominids to a grassland ecology.

Further research should continue to expand sample sizes, investigate site differences, elucidate the significance of those differences, make direct comparisons to hominids from southern Africa and expand the investigation to East Africa where a more precise chronology is available. Additionally, future studies should incorporate a more precise temporal analysis using dates based on the biochronologies of Delson (1984) and Williams et al. (2007). As more studies address the evolution of the southern African papionins, a greater understanding of the paleoecology of hominid evolution may be obtained.

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Appendix

Specimens by Species

Specimen	Species	Time	Site	Museum
CO102	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO104	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO106c	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO107a	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO115/103	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO117	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO118	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO134a	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO134b	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO134d	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO135a	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO135a2	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
KA 151	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 156	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 166A	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 194	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
MCZ 15378	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 17342	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 17342	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 21160	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 21161	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23091	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23803	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23805	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 26472	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 26473	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 29728	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 29786	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 31619	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 8304	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23082	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 44276	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 169	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 5008	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
TP 10	*P. izodi*	Extinct	Taung	South African Museum
SAM 11728	*P. izodi*	Extinct	Taung	South African Museum
SAM 11730	*P. izodi*	Extinct	Taung	South African Museum
SAM 5356	*P. izodi*	Extinct	Taung	Witwatersrand University Medical School
TP 11	*P. izodi*	Extinct	Taung	Witwatersrand University Medical School
IRSNB 10616	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique

IRSNB 10618	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10619	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10624	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10625	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10627	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10628	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10629	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10632	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10633	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10634	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10635	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10636	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10639	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10641	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10642	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 12863	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 7885	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 807	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 8531	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 9102	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10626	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
BF 38	*P. robinsoni*	Extinct	Bolt's Farm	Witwatersrand University Medical School
SK 14083	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 406	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 407	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 408	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 416	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 417	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 421	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 423	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 436	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 445	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 458	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 536	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 549	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum

SK 557	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 558	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 560	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 565	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 566	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 571B	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 602	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
ZM 33672	*P. ursinus*	Extant	South Africa	South African Museum
ZM 35953	*P. ursinus*	Extant	South Africa	South African Museum
ZM 36895	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37165	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37273A	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37273B	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37273C	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37274	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37675	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37676	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37678	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38318	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38323	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38335	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38340	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38343	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38354	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38355	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38361	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38363	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38364	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38365	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38366	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38368	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38369	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38371	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38373	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38376	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38380	*P. ursinus*	Extant	South Africa	South African Museum
ZM 40415	*P. ursinus*	Extant	South Africa	South African Museum
KA 157	*Pp. (sp)*	Extinct	Kromdraai	Transvaal Museum
KA 162	*Pp. (sp)*	Extinct	Kromdraai	Transvaal Museum
TP 13	*Pp. (sp)*	Extinct	Taung	Transvaal Museum
TP 8	*Pp. (sp)*	Extinct	Taung	Transvaal Museum
T 17	*Pp. broomi*	Extinct	Taung	Witwatersrand University Medical School
M 3056	*Pp. broomi*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 118	*Pp. broomi*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 151	*Pp. broomi*	Extinct	Makapansgat	Transvaal Museum
STS 413B	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 1237	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 251	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum

STS 256	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 262	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 268	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 274	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 280	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 305	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 325	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 343	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 354	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 362	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 368A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 371	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 374A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 378A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 398A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 414B	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 562	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS unnumb	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
KA 160	*Pp. jonesi*	Extinct	Kromdraai	Transvaal Museum
SK 412	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 414	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 418	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 433	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 437	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 462	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 537A	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 579	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
STS 250	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 287	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 306	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 329	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 333	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 340	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 355	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 367	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 372A	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 381	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 390	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS unnumb max.	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS unnumb	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
SK 550	*Pp. whitei*	Extinct	Swartkrans	Witwatersrand University Medical School
TP 9	*Pp. whitei*	Extinct	Taung	Witwatersrand University Medical School
BF 43	*Pp. whitei*	Extinct	Bolt's Farm	Witwatersrand University Medical School
MP 117	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 221	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 223	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 224	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School

MP 239	*Pp. whitei*	Extinct	Makapansgat	Transvaal Museum
STS 253	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 259	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 263	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 266	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 303	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 323	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 342	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 352	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 353	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 359	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 370A	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 370B	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 414A	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 563	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS unnumbered	*Pp. whitei*	Extinct	Sterkfontein	Witwatersrand University Medical School
TP 12	*Pp. whitei*	Extinct	Taung	Witwatersrand University Medical School
TP 89-154	*Pp. whitei*	Extinct	Taung	Witwatersrand University Medical School

Specimens by Site

Specimen	Species	Time	Site	Museum
BF 38	*P. robinsoni*	Extinct	Bolt's Farm	Witwatersrand University Medical School
BF 43	*Pp. whitei*	Extinct	Bolt's Farm	Witwatersrand University Medical School
IRSNB 10616	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10618	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10619	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10624	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10625	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10627	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10628	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10629	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10632	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10633	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10634	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10635	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10636	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10639	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10641	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10642	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 12863	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 7885	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 807	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 8531	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 9102	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
IRSNB 10626	*P. kindae*	Extant	Central Africa	Institut Royal des Sciences Naturelles Belgique
CO102	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO104	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO106c	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO107a	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO115/103	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO117	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO118	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO134a	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum

CO134b	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO134d	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO135a	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
CO135a2	*P. angusticeps*	Extinct	Cooper's Cave	Transvaal Museum
MCZ 15378	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 17342	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 17342	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 21160	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 21161	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23091	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23803	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23805	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 26472	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 26473	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 29728	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 29786	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 31619	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 8304	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 23082	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 44276	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 169	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
MCZ 5008	*P. anubis*	Extant	East-Central Africa	Museum Comparative Zoology
KA 151	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 156	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 166A	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 194	*P. angusticeps*	Extinct	Kromdraai	Transvaal Museum
KA 157	*Pp. (sp)*	Extinct	Kromdraai	Transvaal Museum
KA 162	*Pp. (sp)*	Extinct	Kromdraai	Transvaal Museum
KA 160	*Pp. jonesi*	Extinct	Kromdraai	Transvaal Museum
M 3056	*Pp. broomi*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 118	*Pp. broomi*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 151	*Pp. broomi*	Extinct	Makapansgat	Transvaal Museum
MP 117	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 221	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 223	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 224	*Pp. whitei*	Extinct	Makapansgat	Witwatersrand University Medical School
MP 239	*Pp. whitei*	Extinct	Makapansgat	Transvaal Museum
ZM 33672	*P. ursinus*	Extant	South Africa	South African Museum
ZM 35953	*P. ursinus*	Extant	South Africa	South African Museum
ZM 36895	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37165	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37273A	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37273B	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37273C	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37274	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37675	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37676	*P. ursinus*	Extant	South Africa	South African Museum
ZM 37678	*P. ursinus*	Extant	South Africa	South African Museum

ZM 38318	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38323	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38335	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38340	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38343	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38354	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38355	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38361	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38363	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38364	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38365	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38366	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38368	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38369	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38371	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38373	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38376	*P. ursinus*	Extant	South Africa	South African Museum
ZM 38380	*P. ursinus*	Extant	South Africa	South African Museum
ZM 40415	*P. ursinus*	Extant	South Africa	South African Museum
STS 413B	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 1237	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 251	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 256	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 262	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 268	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 274	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 280	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 305	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 325	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 343	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 354	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 362	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 368A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 371	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 374A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 378A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 398A	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 414B	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 562	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS unnumbered	*Pp. broomi*	Extinct	Sterkfontein	Transvaal Museum
STS 250	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 287	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 306	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 329	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 333	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 340	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 355	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum

STS 367	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 372A	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 381	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 390	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS unnumb max.	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS unnumbered	*Pp. jonesi*	Extinct	Sterkfontein	Transvaal Museum
STS 253	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 259	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 263	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 266	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 303	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 323	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 342	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 352	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 353	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 359	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 370A	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 370B	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 414A	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS 563	*Pp. whitei*	Extinct	Sterkfontein	Transvaal Museum
STS unnumbered	*Pp. whitei*	Extinct	Sterkfontein	Witwatersrand University Medical School
SK 14083	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 406	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 407	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 408	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 416	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 417	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 421	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 423	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 436	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 445	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 458	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 536	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 549	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 557	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 558	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 560	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 565	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 566	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 571B	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 602	*P. robinsoni*	Extinct	Swartkrans	Transvaal Museum
SK 412	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 414	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 418	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 433	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 437	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum

SK 462	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 537A	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 579	*Pp. jonesi*	Extinct	Swartkrans	Transvaal Museum
SK 550	*Pp. whitei*	Extinct	Swartkrans	Witwatersrand University Medical School
TP 10	*P. izodi*	Extinct	Taung	South African Museum
SAM 11728	*P. izodi*	Extinct	Taung	South African Museum
SAM 11730	*P. izodi*	Extinct	Taung	South African Museum
SAM 5356	*P. izodi*	Extinct	Taung	Witwatersrand University Medical School
TP 11	*P. izodi*	Extinct	Taung	Witwatersrand University Medical School
TP 13	*Pp. (sp)*	Extinct	Taung	Transvaal Museum
TP 8	*Pp. (sp)*	Extinct	Taung	Transvaal Museum
T 17	*Pp. broomi*	Extinct	Taung	Witwatersrand University Medical School
TP 9	*Pp. whitei*	Extinct	Taung	Witwatersrand University Medical School
TP 12	*Pp. whitei*	Extinct	Taung	Witwatersrand University Medical School
TP 89-154	*Pp. whitei*	Extinct	Taung	Witwatersrand University Medical School