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Dental Microwear Analysis of *Cercopithecoides Williamsi*

Elise Geissler

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DENTAL MICROWEAR ANALYSIS OF CERCOPITHECOIDES WILLIAMSI

by

ELISE GEISSLER

Under the Direction of Dr. Frank L'Engle Williams

ABSTRACT

Cercopithecoides williamsi, a Plio-Pleistocene primate, is believed to have been a terrestrial colobine monkey. Dental microwear analysis of *C. williamsi* specimens from South African cave sites was employed to test these assumptions. Analysis of the features shows that although the microwear signature of *C. williamsi* is similar to that of folivorous primates, there are also similarities with terrestrial papionins. Overall, the dental microwear analysis demonstrates that *C. williamsi* could have indeed been a folivorous, terrestrial monkey. A high amount of puncture pits also points to a substantial amount of grit in the diet. Similarities between the microwear features of *C. williamsi* and *Cebus apella* indicate that fruit or hard objects could have been a supplemental food of *C. williamsi*. The consumption of underground storage organs covered in grit would explain the heavy pitting of *C. williamsi* teeth. Being terrestrial, *C. williamsi* would have been in direct competition with terrestrial papionins.

INDEX WORDS: Dental microwear analysis, *Cercopithecoides williamsi*, Terrestrial leaf-monkey, Plio-Pleistocene monkey

DENTAL MICROWEAR ANALYSIS OF CERCOPITHECOIDES WILLIAMSI

by

ELISE GEISSLER

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

Master of Arts

in the College of Arts and Sciences

Georgia State University

2013

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Elise Geissler
2013

DENTAL MICROWEAR ANALYSIS OF CERCOPITHECOIDES WILLIAMSI

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May 2013

DEDICATION

In memory of Mathilde Carmen Hertz (1891-1975) who studied fossil teeth long before my heart started beating and who, by overcoming gender barriers in academia, helped create a path for women who follow her footsteps.

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1 INTRODUCTION

South African Plio-Pleistocene cave sites, known as “Cradle of Humankind”, have not only preserved fossils of gracile and robust Australopithecines but also numerous other primate fossils. Cercopithecoid monkeys are more common in the fossil record than hominid remains. They share many behavioral, dietary and ecological features with humans (Elton, 2006). Thus they offer useful analogues to human ancestors.

C. williamsi is one of the primates found at these sites and understanding more about this monkey will help researchers understand the environment in which humans evolved.

Although there is no terrestrial leaf-eating monkey alive in Africa today, the extinct Plio-Pleistocene monkey *C. williamsi* appears to have been a ground-dwelling colobine. Moreover, *C. williamsi* shows no muscular adaptation to heavy chewing (Elton, 2000) and yet has heavily worn teeth (Benefit, 1999). There are, therefore, many questions which need to be answered for this species.

1.1 Purpose of the Study

This study employs low-magnification light stereomicroscopy to analyze microwear pit and scratch features on the occlusal tooth surface of several *C. williamsi* specimens. The aim is to solve some of the apparent contradictions noted for *C. williamsi* and to test whether they are connected to the Plio-Pleistocene climatic shift during which this monkey lived.

The goal of this thesis is to learn more about this primate for three reasons. First, many paleoecological reconstructions based on faunal remains assume a uniformity of habitat. These reconstructions thus assume that a certain species prefers the same habitat today as it preferred in

the past. Should *C. williamsi* indeed be a terrestrial leaf-eater, the idea of habitat uniformity should be critically reviewed. Secondly, *C. williamsi* lived at a time important to human evolution. Learning more about this primate will increase the understanding of flora, fauna and climate of the time. And thirdly, increased knowledge about *C. williamsi* can further the understanding of how climatic shifts can impact primate diets.

1.2 Tested Hypotheses

In order to learn more about *C. williamsi*, the dental microwear of the monkey will be compared to the dental wear of other primate taxa. By comparing *C. williamsi* with folivores, frugivores, granivores and omnivores, this study seeks to determine where exactly the microwear signature of *C. williamsi* falls. Through comparisons, it will be possible to infer diet and habitat. It will be tested whether *C. williamsi* could have been a terrestrial folivore based on its microwear. Moreover, the comparison to other taxa will allow a more nuanced view of diet and habitat of the primate.

Three hypotheses will be tested in this study. The first hypothesis is that the dental microwear patterns of *C. williamsi* are significantly different from those of other primate taxa. Once it becomes clear that there are statistically significant differences, two additional hypotheses can be tested. The second hypothesis which will subsequently be tested is that *C. williamsi* was relying primarily on a folivorous diet. Lastly, the third hypothesis is that *C. williamsi* was primarily terrestrial.

2 CERCOPITHECOIDES WILLIAMSI

Cercopithecoides williamsi is one species among several belonging to the extinct genus *Cercopithecoides*. The genus appears to have been wide-spread in Plio-Pleistocene Africa and remains have been found in South Africa as well as at numerous archaeological sites in Eastern Africa. Characteristics of the genus include a long and narrow face, strong sexual dimorphism, a short premaxilla, a P³ with a reduced protocone and a deep ophryonic groove (Szalay and Delson, 1979).

2.1 The Fossils

The dental microwear analysis presented in this thesis specifically focuses on *C. williamsi* specimens from the South African cave sites of Sterkfontein, Makapansgat and Bolt's Farm. However, in order to draw any conclusions from an analysis of these specimens, it is important to also consider general characteristics of the genus and species. Further, as habitat can be an indicator of diet, all of the the archaeological sites at which the specimens were found should also be considered and thus will be mentioned here.

2.1.1 *Cercopithecoides fossils*

Cercopithecoides williamsi has been identified at a number of African Plio-Pleistocene cave sites. In South Africa, specimens were found at the karstic cave sites Makapansgat, Swartkrans, Sterkfontein, Bolt's Farm, Kromdraai and Coopers (Freedman, 1957, 1960, 1965, 1970; Maier 1970; see Figure 1).



Figure 1: Map of South African Cave Sites

This map illustrates the Plio-Pleistocene cave sites at which specimens of the genus *Cercopithecoides* were discovered.

In East Africa, *C. williamsi* individuals have also been identified in Leba, Angola (Delson, 1984), Olduvai Gorge, Tanzania (Benefit, 1999; Leakey and Roe, 1994), and Koobi Fora, Kenya (Leakey, 1982). The genus *Cercopithecoides* and the species *williamsi* were both defined by Mollett (1947) who based his description on the type specimen AD 1326-3 from Makapansgat in South Africa. Debate continues, however, as to whether the specimens in South Africa and East Africa are really conspecifics (Frost and Delson, 2002). The only post-cranial remains associated with the primate were found in East Africa and include a complete humerus and a partial ulna, radius and scapula (Birchette, 1981).

Although *C. williamsi* is the best known representative of its genus, it is not the only member. There might be a second representative of the genus in South Africa. McKee et al. (2011) reanalyzed a number of specimens stemming from the South African site Haasgat (see Figure 1) which were originally attributed to *C. williamsi*. Based on morphological differences between the Haasgat fossils and those found at other South African sites, McKee et al. (2011) define the species *Cercopithecoides haasgati*.

Other species of *Cercopithecoides* include *Cercopithecoides kimeui* (Leakey, 1982), *Cercopithecoides meavea* (Frost and Delson, 2002), *Cercopithecoides kerioensis* (Leakey, 2003) and *Cercopithecoides alemayehui* (Gilbert and Frost, 2008). All were found at East African sites. Also in East Africa, Harrison (2011) described the remains of a colobine found at Laetoli, Tanzania, that fits into the *Cercopithecoides* genus but not into any of the established species. No additional species has so far been defined.

C. williamsi, *C. kimeui*, and *C. meavea* are all believed to have been terrestrial (Frost and Delson, 2002; Harrison, 2011). The small colobine described by Harrison (2011) was discovered with postcranial remains and appears to have been arboreal.

2.1.2 Questions of Homogeneity of the Taxon

There is some debate as to whether all specimens assigned to the *C. williamsi* taxon really belong to the same species. Fourie et al. (2008) analyzed stable carbon isotopes as well as trace elements and found a dietary division within the *C. williamsi* species. Specimens from Makapansgat Members 3 and 4 have widely differing $\delta^{13}\text{C}$ values. Whereas *C. williamsi* specimen MP3A appears to have eaten mostly C_3 plants, MP36 seems to have preferred a diet of C_4 foods. Fourie et al. (2008) argue that this kind of separation is unusual within a single species

and suggest that the two specimens exploited two different ecological niches. Codron et al. (2005) had previously found a similar discrepancy for individuals from Swartkrans and Sterkfontein.

Freedman (1957) originally constructed a separate species for *Cercopithecoides* remains from Swartkrans and a single specimen from Sterkfontein and labeled them *Cercopithecoides molletti* to separate them from fossils discovered at Makapansgat. He based this separation on differences in dental size. When describing newly discovered specimens from Makapansgat in 1960, however, Freedman (1960) merged *C. molletti* into *C. williamsi*. He argued that the new material bridges the gap in size variation between the two groups. Subsequently, Delson (1984) described the specimens stemming from the Kroomdrai site as well as some from Makapansgat and Sterkfontein as a “large variant” of *C. williamsi*.

With the goal of finally solving the taxonomic problem, Anderson et al. (2013) tested 37 different landmarks of *C. williamsi* crania from Makapansgat, Sterkfontein, and Bolt’s Farm. Anderson et al. (2013) came to the conclusion that although there is a lot of variation between individuals, there is not more variation than one would find within an extant species.

Amidst questions of the homogeneity of the species in South Africa, so far no quantitative study has been conducted comparing South African specimens with those from East Africa.

2.1.3 *The Diet of C. williamsi*

Based on numerous molar characteristics, including high and sharp cusps as well as large body size, *C. williamsi* is generally considered to be a colobine monkey (Benefit, 1999; Simons and Delson, 1978, Szalay and Delson, 1979). Colobine monkeys, in turn, are traditionally

described as leaf-eaters. However, diets among extant colobine species vary considerably (Koyabu and Endo, 2009).

Here, it is important to understand the difference between fallback and preferred foods. Fallback foods are usually relatively abundant foods and readily available when more preferred foods are more scarce. Although fallback foods are frequently low in nutritional value and hard to process, they are important to survival (Marshall and Wrangham, 2007). Marshall and Wrangham (2007) argue that due to their importance to survival, primates tend to be morphologically adapted to processing specific fallback foods. For colobine monkeys, leaves therefore represent a fallback food and colobine tooth shape is consequently adapted to eating leaves. Preferred foods can include various food items like fruits and seeds. They tend to be overselected, but are frequently not important to survival (Marshall and Wrangham, 2007). It is possible that enamel scars caused by fallback foods will be overrepresented in a sample, as a primate has a higher chance of dying during times of food scarcity than during times of abundance (Constantino and Wright, 2009).

Previous dental microwear analyses support the hypothesis that *C. williamsi* was a folivore. The analysis of an East African *C. williamsi* specimen revealed a similar dental microwear signature as that of *Colobus guereza* (Teaford and Leakey, 1992). E-Zataari et al. (2005), in turn, examined South African specimens using an electron microscope and found that *C. williamsi* showed similarities in dental microwear with *Theropithecus gelada* and also *Colobus guereza* (El-Zataari et al., 2005). There are some differences between individuals, however. *C. williamsi* specimens from Makapansgat are characterized by large pits, but pit percentage in the Sterkfontein and Swartkrans specimens is low. El-Zaatari et al. (2005)

concluded that *C. williamsi* was either a leaf or grass eater, with a higher ingestion of hard objects at Makapansgat.

Isotopic analyses show mixed results as well. Whereas some *C. williamsi* specimens have $\delta^{13}\text{C}$ values consistent with a C_3 -based diet, others show a diet based on up to 60% of C_4 -plants (Codron et al., 2005; Fourie et al., 2008). Codron et al. (2005) argue that due to their $\delta^{13}\text{C}$ signature, at least some *C. williamsi* specimens must have eaten grass.

Muscle attachment sites of *C. williamsi* crania offer additional clues to the diet of this primate. *C. williamsi* did not have a strongly developed nuchal crest, sagittal crest or strong temporal muscles (Simons and Delson, 1978). The musculature of the monkey, therefore, does not support an adaptation to heavy chewing.

2.1.4 *The Locomotion of C. williamsi*

Reconstructing the locomotion of the monkey is no easy task, as there is no postcranial material associated with the craniodental remains of South African *C. williamsi* fossils. Moreover, there is no predictable relationship between diet and locomotion among primates (Fleagle, 1984). No modern, fully terrestrial, colobine monkeys exist and extant African colobine monkeys are highly arboreal. There are indications, however, that *C. williamsi* was terrestrial.

C. williamsi has been frequently categorized as a terrestrial monkey (Benefit, 1999; Codron et al., 2005; Elton, 2001; El-Zaatari et al., 2005; Fourie et al., 2008; Jablonski, 2002; Leakey, 1982). Arguments for a terrestrial locomotion of *C. williamsi* include overall body size, an analysis of East African remains and isotopic analyses of diet.

Cercopithecoides williamsi was larger than today's African colobine monkeys (Maier, 1970). Based on this observation, Vrba (1976) was among the first to argue that the monkey must have been terrestrial.

One of the strongest arguments for a terrestrial locomotion of *C. williamsi* is based on the analysis of a complete left humerus found in East Africa (see Birchette 1981). The humerus appears to have been adapted to terrestrial locomotion according to Birchette (1981).

As it is not completely certain that the specimens in Eastern and southern Africa belong to the same species (Frost and Delson, 2002) additional research has been done focusing on the South African specimens.

Because many of the primate cranial remains from South African Plio-Pleistocene cave sites are not matched with postcrania, statistical methods have proven an important tool to study Plio-Pleistocene primate postcrania. Using regression analysis, Ciochon (1993) matched cranial and postcranial remains of South African Plio-Pleistocene fossils. He came to the conclusion that the South African *C. williamsi* monkeys lacked the extreme terrestrial adaptation of *C. williamsi* in East Africa. Instead, Ciochon (1993) argued, *C. williamsi* probably had a much more eclectic locomotor behavior than previously considered.

In a more recent publication, Elton (2001) analyzed South African cercopithecoid postcranial remains independently of any species designations. She found that part of the monkey fossils she studied show terrestrial adaptations and argued that some of those could potentially be *C. williamsi* remains.

Isotopic analysis seems to point into a similar direction. There is evidence of at least some C₄ consumption in *C. williamsi* (Codron et al. 2005; Fourie et al., 2008), which in turn

would suggest the monkey spent at least some time on the ground. Thus, in summary, previous research supports that South African *C. williamsi* specimens were, at least in part, terrestrial.

2.2 Fossil Context

Even though most South African Plio-Pleistocene cave sites are geographically close to each other, they did not form at the same time. Establishing a chronology is not an easy task for these sites. There is no clear stratigraphy at the sites as their depositional histories are complex and irregular (Brain, 1981; Williams and Patterson, 2010). Regional uplifts, limestone mining, irregular deposits and many other factors have contributed to the stratigraphic complexity (Brain, 1981). Attempts are thus made to date the sites based on biochronology, paleomagnetic stratigraphy and other direct dating methods. In order to determine when exactly the first and last appearance dates of *C. williamsi* fall, it is important to consider the chronology and ecology of the sites at which the fossils were discovered.

2.2.1 Cave Site Chronology

El-Zaatari et al. (2005) synthesized age estimates for all *C. williamsi* sites incorporating the results of a variety of dating methods (table 1). Their synthesis will be used for the discussion of this study

Table 1: South African Cave Site Dating Based on El-Zaatari et al. (2005, p 182)

| | |
|------------------------|---------------|
| Makapansgat, Member 3 | 3.2 – 2.7 myr |
| Makapansgat, Member 4 | 3.2 – 2.7 myr |
| Taung | 3.0 – 2.0 myr |
| Sterkfontein, Member 4 | 2.8 – 2.3 myr |
| Bolt's Farm Pit 23 | 2.2 – 2.0 myr |
| Kromdraai-B | 2.0 – 1.5 myr |
| Drimolen | 2.0 – 1.5 myr |
| Bolt's Farm Pit 6 | 1.8 – 1.6 myr |
| Swartkrans, Member 2 | 1.5 – 1.0 myr |
| Coopers A | 1.3 – 1.2 myr |
| Coopers B | 1.3 – 1.2 myr |

The sites Makapansgat, Sterkfontein, Kromdraai, and Swartkrans will later serve as representatives for a discussion of paleoecology.

One of the ways these sites have been dated is by paleomagnetic dating. Paleomagnetic dating is possible because the magnetic field of the Earth changes over time. During rock formation, iron particles will align themselves towards the North Pole. Times of pole reversals and other magnetic changes have been summarized in polarity time scales. With the help of these scales, researchers can make an age estimate based on the orientation of iron particles within of a particular stratigraphic layer.

Uranium-Lead dating (U-Pb dating) is another direct dating method which has been utilized to date South African Plio-Pleistocene cave sites. Uranium-Lead dating relies on the decay of uranium to lead.

Different faunal dating methods indicate an age of 2.2-3.3 myr for Makapansgat Member 3 (Brock et al. 1977; Vrba, 1975). If dates stemming from the analysis of biochronologies as well as paleomagnetic dating are considered together, most publications point to an age of around 3

myr for Member 3 of the Makapansgat site (Cadman and Rayner, 1989). Generally, it can be said that Makapansgat appears to be one of the oldest sites.

Sterkfontein appears to be an older site as well. Based on the occurrence of micromammals recovered at Sterkfontein Member 4, Avery (2001) dates the site to between 2.6-2.8 myr. Dating the same member based on its paleomagnetic characteristics, Herries and Shaw (2011) arrive at a different age range of 2.16-2.58 myr. The site, thus, likely has a more recent depositional history than Makapansgat.

Based on faunal seriation, McKee et al. (1995) determine that the site Kromdraai B is older than Swartkrans. Thackeray et al. (2002) dated calcified flowstones and sediments. They determined that Kromdraai B must have formed close to the Olduvai event and date the site to around 1.9 myr of age.

Swartkrans appears to be much younger than Makapansgat and Sterkfontein. Paleomagnetic dating of the Swartkrans site has remained inconclusive (Curnoe et al. 2001). Instead, U-Pb dating was successfully applied to date the site. Based on U-Pb dating, Balter et al. (2008) date Swartkrans Member 2 to 1.36 ± 0.29 myr.

The synthesis of El-Zaatari et al. (2005) gives South African *C. williamsi* specimens a first appearance date of roughly 3.2 myr and a last appearance date of about 1 myr ago. The well-studied sites of Sterkfontein and Makapansgat can thus serve as representatives of early *C. williamsi* sites. Kromdraai and Swartkrans are caves with more recent depositional histories and are representatives of sites dating to a time shortly before the extinction of *C. williamsi*.

2.2.2 *The Plio-Pleistocene Transition*

In order to understand the habitat in which *C. williamsi* lived, it is necessary to reconstruct the overarching climatic trends of the time. With a first appearance date of 3.2 myr and a last appearance date of 1.2 myr (El-Zataari et al., 2005), *C. williamsi* lived during a time of transition from the Pliocene to the Pleistocene. It was a time of climate change and environmental pressures.

The Plio-Pleistocene boundary was initially set at 1.8myr, but most geologists now posit an earlier transition (Anderson et al., 2007). The International Geological Congress has, therefore, officially moved the beginning of the Pleistocene back to 2.58 myr ago. Deep-sea sediment cores confirm a time of major glaciations in the Northern hemisphere around this time (Gibbard et al., 2005).

Temperatures and climates already fluctuated before this time, but the Pleistocene marks the beginning of extreme shifts between maximum glacial expansions and interglacials (Anderson et al., 2007). All of the South African Plio-Pleistocene fossils appear to have been deposited during the time of interglacials when dense vegetation formed a blanket over the soil and thus hindered erosion (Avery, 2001; Brain, 1995).

The climate became periodically cooler and dryer starting roughly 2.8 myr resulting in more arid, open conditions (deMonocal, 1995). The change in climate led to a gradual expansion of C₄ grasslands into South Africa (Reynolds and Kibii, 2011). Wind-blown dust within ocean sediments confirms an increase in aridity with a glacial maximum around 2.8 myr ago (deMonocal, 1995).

The expansion of C₄ plants could have additionally been boosted by the onset of the Walker Circulation (Hopley et al., 2007) around 1.7 myr ago. The Walker Circulation describes a

continuous east-west air stream over the tropics. The circulatory system causes air to rise over Indonesia and to sink over the Pacific. The Walker Circulation is a result of pressure and temperature differences between the eastern and the western Pacific Ocean and results in a continuous flow of air that wraps around the planet.

As all of the *C. williamsi* specimens considered in this study stem from southern African cave-sites, it is important to understand the effect of the Plio-Pleistocene transition on that specific region. Specifically studying South African cave sites, Lee-Thorp et al. (2007) described an overall shift of habitats from relatively closed to more open, drier environments from 3 to 1.5 myr ago. Their conclusion is based on a large-scale carbon isotopic analysis of fossils found at different South African sites.

Climate was not only becoming cooler, but also fluctuating widely while the South African cave sites were forming (Cadman and Rayner, 1989). It was, in fact, when analyzing South African Plio-Pleistocene faunal remains that Vrba (1993) proposed the *Turnover Pulse Hypothesis*. Vrba (1993) argues that punctuated equilibrium – long taxonomic stability interrupted by sudden evolutionary change (see Eldredge and Gould, 1972) – was caused by an outside factor such as climate change. Organisms and species, Vrba (1996) argues, are habitat specific. Once their habitat and therefore their resources change, they are forced to respond. Climatic change will, therefore, inevitably lead to evolution or extinction (Vrba, 1993). As speciation is intimately linked with environmental change, speciation will occur in pulses while species remain stable during times of climatic stability. Many new species appear between 2.9 and 2.5 myr. Vrba (1996) argues that many of the new species have a larger body mass and shorter extremities than their predecessors and seem to be better adapted to colder climate (Vrba,

1996). Vrba (1996) bases her hypothesis on Bergmann's Rule, which argues that a larger body size and therefore a larger body volume to surface ratio is an adaptation to colder temperatures.

Even though the turnover hypothesis has been influential, it has also been criticized. McKee (1996) tested Vrba's turnover pulse hypothesis through computer modeling and compared it to a scenario with purely gradualist change. Using a database of South African Plio-Pleistocene mammals, all of his models of species change fell right into the range of purely gradualist change. He cautioned, however, that although most change can be explained as gradualist according to his model, it does not mean that no turnover pulses occurred.

Partidge et al. (1995) further criticized that it is hard to match evolutionary changes with climate change and that overall climatic trends are often influenced by regional factors. To understand whether the Plio-Pleistocene climate change could have affected *C. williamsi*, it is therefore also important to understand the specific cave-site habitats.

2.2.3 Methods of Reconstructing Paleoecology

As numerous hominin remains have been found at the South African Plio-Pleistocene sites, much research reconstructs the paleohabitat. Analyzing botanical remains might be one the most sensible ways to reconstruct habitat. However, botanical remains are rare at the South African Plio-Pleistocene sites (Bamford, 1999).

Studying faunal remains in order to reconstruct habitats is a widely used alternative. Habitat can be inferred by studying adaptive morphology, for example. Morphological characteristics of an organism can point to the type of environment in which it lived and to which it was adapted (Spencer, 1995). Vrba (1975), for example, studied South African fossil bovids

and by assigning them different feeding habits, reconstructed habitats associated with different sites.

However, many studies reconstructing paleoecology based on fauna assume taxonomic uniformitarianism which can be problematic because closely related taxa do not always share the same type of habitat (Sponheimer et al., 1999). As no extant African colobine monkeys are terrestrial, *C. williamsi* might serve to illustrate this point.

Faunal analysis can, however, reconstruct habitat much more accurately if stable isotopes stemming from the faunal remains are also analyzed. Different isotopes in bone and tooth enamel can be indicators of habitats. Further, oxygen isotopes can be an indirect measure of temperatures, humidity, and precipitation (Sponheimer and Lee-Thorp, 1999).

A dental microwear analysis can also be an indirect indicator of habitat as the characteristics of a habitat can directly influence which foods are available to an organism. Dental microwear analysis is, therefore, another method of faunal habitat reconstruction that does not rely on uniformitarianism. The results of the study presented here thus can be useful for habitat reconstructions as well.

2.2.4 *Isotopic Analyses*

The study of tooth morphology and tooth wear is not the only way to directly infer diet from extinct faunal material. Isotopic analyses have proven useful to study diet, habitat and climate. Much of what is known about the diet of Plio-Pleistocene fauna stems from isotopic analyses. Different methods of isotopic analyses will, therefore, be discussed here in detail.

Isotopes describe variants of the same chemical element which differ in the number of neutrons. One of the elements which has different isotopes is carbon. Stable carbon isotope

analysis has been used on *C. williamsi* and will be utilized to interpret the dental microwear signature of the primate. The method has further been employed for paleoecological reconstructions of South African Plio-Pleistocene sites. Stable carbon isotope analysis will, therefore, be described here in detail.

All plants absorb carbon through photosynthesis. Organisms consuming plants will thus consume carbon, which in turn will be deposited in the tissue of the organisms. There are three different types of photosynthetic pathways, which will result in different ratios of carbon isotopes in plants. Consequently, bone (Sullivan and Krueger, 1981) and tooth enamel (Cerling and Harris, 1999) directly reflect the diet of an organism. Sullivan and Krueger (1981) demonstrated that even fossils will retain specific isotopic signatures.

In order to understand the results of a stable carbon isotope analysis, it is vital to understand photosynthesis. Photosynthesis is a chemical reaction during which plants convert carbon dioxide and water into sugar and oxygen. The carbon atoms of the carbon dioxide are retained by the plant as part of a sugar molecule.

The carbon isotopes ^{12}C and ^{13}C can both naturally be found in the atmosphere. There are equal quantities of ^{12}C and ^{13}C in the atmosphere, but plants tend to discriminate against ^{13}C . So the ratio of $^{13}\text{C}/^{12}\text{C}$ (“ $\delta^{13}\text{C}$ ”) tends to be lower in plants than it is in the atmosphere (O’Leary 1988). The amounts of ^{12}C and ^{13}C absorbed by each plant depend on the photosynthetic pathway of the plant (Smith and Epstein 1971).

There are three different photosynthetic pathways – carbon 3 (C_3), carbon 4 (C_4), and Crassulacean Acid Metabolism (CAM). C_3 plants are the most common and almost all trees, shrubs, and many herbs have a C_3 metabolism (Bocherens et al., 1996) C_4 plants evolved the ability to absorb carbon dioxide very quickly, enabling the plant to close its pores for most of the

day and thus preventing dehydration. They can, therefore, mainly be found in arid regions of warm temperate zones, the subtropics and tropics (Sage, 2004). Sixty percent of all C₄ plants belong to the grass family *Poaceae* (Taylor et al., 2010).

One would, therefore, expect a browser living in a forest habitat to absorb the signature of C₃ plants and a savanna grazer to exhibit a C₄ signature. C₃ plants lead to low $\delta^{13}\text{C}$ values and C₄ plants show a high $\delta^{13}\text{C}$ values. An isotopic signature indicative of diet based on C₄ plants can, therefore, point to the presence of grassland. Carbon-4 plants began to play a role with the grassland expansion of the Miocene, starting around 7 million years ago, but when exactly they moved into South Africa is debated (Luyt and Lee-Thorp, 2003).

The third photosynthetic pathway can be found in CAM plants, which can mimic the isotopic signature of either C₃ or C₄ plants. CAM plants grow in very dry environments like deserts and include cacti, bromeliads and others (Ting, 1985). They will, therefore, not be considered here any further.

One of the problems of carbon isotopic analysis is that even when the presence of C₃ or C₄ plants at a site has been demonstrated, this information by itself cannot be used to reconstruct overall vegetation. C₄ grasses, for instance, can grow in both, grasslands and woodlands (Lee-Thorp et al., 2007). Additional problems with analyzing carbon isotopes come with diagenesis – in this case a chemical overprinting due to different taphonomic processes (Bocherens et al., 1996). The danger of contamination of bones with elements from the environment increases with the age of the fossil (Newesley, 1993) and the South African fossils are very old. Tooth enamel, however, is more resistant to chemical diagenesis (Sponheimer and Lee-Thorp, 2006).

Stable carbon isotopes do not only play a role in the analysis of animal tissue, but also in the analysis of paleosols. Paleosols are soils which formed in the past and have since been

buried. The carbon isotopic signature of paleosols reflects the proportion of C₃ and C₄ plants at the time of soil formation (Sikes, 1999). It, therefore, is also a useful tool for the reconstruction of habitats.

Another frequently employed method is the analysis of stable oxygen isotopes. Two naturally occurring oxygen isotopes, ¹⁶O and ¹⁸O, can be used to reconstruct paleotemperature (Sponheimer and Lee-Thorp, 1999). Both oxygen isotopes can be part of water molecules. Having less neutrons, ¹⁶O is lighter than ¹⁸O and tends to evaporate more readily. Evaporation is directly influenced by temperature and the lower the air temperatures, the less ¹⁸O will evaporate. Ratios of ¹⁶O/¹⁸O ($\delta^{18}\text{O}$) can thus be used as an indirect measure of temperature. Broadly, the colder the temperatures, the lower $\delta^{18}\text{O}$ values are expected to be (Fricke et al., 1998). Hence, ratios of $\delta^{18}\text{O}$ preserved in ice cores can indicate total changes in ice volume and are used to track temperature changes (Mitchell, 2002).

Further, $\delta^{18}\text{O}$ values are used in isotopic analyses of bone and tooth tissue. The $\delta^{18}\text{O}$ composition of faunal material can be an indicator of dietary ecology (Lee-Thorp et al., 2010). Some of the oxygen stemming from water molecules will be incorporated into the bones and teeth of the organism ingesting the water. Different species have different primary sources of water, which in turn will affect the $\delta^{18}\text{O}$ values deposited in their tissues. Plants naturally have higher amounts of ¹⁸O due to a faster evaporation of the ¹⁶O isotope (Bocherens et al., 1996). Herbivores receiving most of their water from plants, will naturally have high $\delta^{18}\text{O}$ values. Browsing herbivores, for instance, receive most of their water from plants, but grazing herbivores drink a lot of supplemental water (Sponheimer and Lee-Thorp, 1999). Stable oxygen isotopes can, therefore, point to a specific diet or habitat of an organism by looking at $\delta^{18}\text{O}$ values in bone and enamel.

2.2.5 South African Cave Site Paleoecology

There is an inevitable connection between the habitat and the diet of a primate. Thus, the specific habitats of the cave sites at which *C. williamsi* was discovered can aid in dietary reconstructions. Several of the South African Plio-Pleistocene cave sites have been studied in depth. Much about the habitat which once characterized these sites is therefore known.

Four well-studied *C. williamsi* sites are Makapansgat, Sterkfontein, Swartkrans and Kromdraai. As discussed earlier, Makapansgat and Sterkfontein both formed around the early stages of the Plio-Pleistocene transition whereas Kromdraai and Swartkrans are representatives of a time when the transition was almost complete. Paleoecological reconstructions suggest that the Plio-Pleistocene shift in climate resulted in a change in habitats.

The site of Makapansgat seems to have been relatively moist compared to the environments of the younger sites (Vrba, 1995). Based on extensive faunal analysis, Reed (1997) suggests that the area around Makapansgat must have been a mosaic of habitats combining woodland, bushland, riverine forests and intermittent edaphic grasslands. Carbon-3 plants likely made up the majority of the vegetation (Sponheimer et al., 1999). However, it appears that, even at this early site, at least some C₄ grasses must have been part of the landscape (Sponheimer and Lee-Thorp, 1994; Sponheimer et al., 2001)

Similarly, the slightly younger site of Sterkfontein Member 4 seems to have been a mosaic of different habitats with nearby forests and grassland (Avery, 2001). Although macroflora is rare at South African Plio-Pleistocene sites, Bamford (1999) described fossilized wood from Sterkfontein. He identified the wood as *Dichapetalim cf. mombuttense*, a liana, and *Anastrabe integerrima*, a shrub. Both of these plants point to dense, humid, forest-like vegetation (Bamford, 1999). A dental microwear analysis of fossil papionins found at the site also point to a

more closed, wetter habitat than what is characteristic for the region today (Williams and Patterson, 2010). Like Makapansgat, Sterkfontein was thus likely characterized by a moister habitat than the younger sites.

There must have been some marginal patches of woodland at the younger site of Kromdraai B (Reed, 1997), but this site appears to have been characterized primarily by grasslands (Vrba 1975). Vrba (1975) characterized Kromdraai B as savanna based on a large number of terrestrial faunal remains. The paleoecology of Kromdraai B, therefore, must have been characterized by a more open habitat than Makapansgat and Sterkfontein.

Swartkrans, which is among the youngest *C. williamsi* sites, also appears to continue the trend towards a more open habitat. Lee-Thorp et al. (2007) observe that the younger deposits of Swartkrans and Kromdraai generally contain faunal material with higher C₄ contents. The lack of fresh grass grazers at Swartkrans Member 2 additionally indicates a relatively dry environment (Reed, 1997). However, it seems that Swartkrans was not a pure savanna. A stable carbon isotope tooth analysis of Australopithecines from Swartkrans points to a combination of a C₃ and C₄ diet of the hominins (Lee-Thorp, 1994) and faunal remains point to body of water close to the cave (Avery, 1995).

Thus, although there is a clear shift in the proportions of C₃ and C₄ habitats, all of the described habitats appear to have been habitat mosaics. The diet of *C. williamsi* can therefore not be conclusively derived from paleoecological reconstructions and other methods such as a dental microwear analysis can bring more clarity.

3 DENTAL WEAR

Teeth are the only parts of an organism that are in constant contact with the outside world (Cuzzo and Sauter, 2012) and yet can survive millions of years. It is, therefore, not surprising that many dietary reconstructions focus on teeth. Studying dental wear in combination with an isotopic analysis provides a powerful tool to reconstruct diet (Walker, 1981). Other methods of dietary reconstruction include the study of tooth and jaw morphology itself (Grine, 2007). There is a clear relationship between molar tooth structure and diet (Kay, 1975).

In order to interpret the dental microwear signature of *C. williamsi*, it is important to understand the influence of diet on teeth. The characterization of *C. williamsi* as a colobine monkey is based on tooth morphology, which in turn is an adaptation to a specific diet. Primate tooth morphologies and primate dietary categories will, therefore, be considered here in more detail. Then, the direct impact of dietary items on teeth and the relationship between macrowear and microwear will be discussed.

3.1 Tooth Morphology and Diet

The most important selective force for teeth is diet. Most primates do not focus on a single dietary item. Instead, primate diets are usually more complex and incorporate different food items such as leaves, fruit and insects. However, although supplementing their diet with different foods, most primates tend to focus on a particular food group more than on other foods. This food group can be used to compare diets of primate taxa.

3.1.1 Dietary Categories

Because primates display a wide range of dietary specializations, primate tooth morphology is frequently studied. Primate dietary categories are “insectivores”, “folivores”, “frugivores” and “omnivores” (Silcox and Teaford, 2002). Primate diets, however, are frequently more complex. Howler monkeys, for instance, are considered classic folivorous monkeys and yet they incorporate fruit and flowers into their diet on a regular basis (Silcox and Teaford, 2002). Primate dietary categories can further be problematic, because there might be dietary variations between different troops of the same species (Winkler, 1984). In addition, items considered “nonfood” can be ingested accidentally or on purpose. Geophagy appears to be widespread among primates. Over 21% of all extant primate species have been seen to deliberately ingest soil (Krishnami and Mahaney, 2000). This is a large number considering that not all extant primate species have been extensively studied. Hence, even though primate species are sorted into categories, actual diets are often complex.

3.1.2 Molar Morphology

When it comes to molar morphology, frugivorous primates often have blunt and flat cusps as well as relatively short crests and broad molars (Benefit, 2000). Insectivorous primates, in contrast, tend to have high cusps with blade-like crests (Bunn and Unger 2009). Typical colobine teeth are bilophodont and have high and sharp cusps that sit close to the buccal and lingual margins resulting in long crests (Lucas and Teaford, 1994). Although an insectivorous and a frugivorous diet will select for a similar tooth shape, leaf-eating and insect-eating monkeys do not overlap in size, making their separation easy (Kay, 1975).

Dental enamel also appears to reflect diet to a limited degree. Taxa with a softer diet tend to have thinner dental enamel than those feeding on tougher dietary items (Schwindler, 2002). Moreover, the overall size of the cheek teeth of a primate appears to be negatively allometrically related to the individuals' metabolic needs (Kay, 1975).

When analyzing morphology, it is always important to remember that the selective force influencing shape is not the food per se, but its mechanical properties (Grine, 2007). Also, tooth morphology does not always precisely reflect the current diet of an individual (Grine, 2007), but can be a reflection of the heritage of an animal (Kay, 1975).

Kay (1975) introduced the idea of a shearing quotient that is based on relative crest length of cheek teeth. The shearing quotient describes the relationship between molar crest length and diet. The relative length of a molar shearing crest increases with the amount of leaves a particular primate species incorporates into its diet (Kay, 1975). An increased crest length is associated with greater leaf-intake even among leaf-eaters (Lucas and Teaford, 1994). The shearing quotient is very useful method for dietary reconstruction, but heavily depends on precise measurements using specific landmarks. As molar cusps are worn over time, these landmarks disappear, making precise measurements difficult (Bunn and Ungar, 2009).

Dental topographic analysis has therefore been proposed as a solution because it works without specific landmarks (Bunn and Ungar, 2009). Measurements of slope and angularity of occlusal relief can separate different primate species based on their dietary categories (Bunn and Ungar, 2009).

3.2 *Causes of Dental Wear*

In order to fully understand use wear scars on teeth, it is important to consider how these scars are formed. As dental macrowear is a concern in dentistry, it has been extensively studied. Dental microwear formation is not as thoroughly understood, but has been increasingly researched over past decades as a tool to reconstruct diet of extinct species.

3.2.1 *Causes of Dental Macrowear*

The loss of dental enamel and eventually dentin is the result of a number of processes: abrasion, attrition, abfraction, and erosion. Abfraction is the chipping of enamel due to mechanical stress and will not be discussed here any further. Enamel wear during mastication is a combination of abrasion and attrition (Imfeld, 1996). Abrasion is caused by the teeth grinding against each other; attrition results from the friction between teeth and an exogenous element. Abrasivity is influenced by different factors like the properties of the abrasive matter and the sliding medium (i.e. saliva) which can mitigate abrasion (Newesely, 1993).

Unlike attrition and abrasion, erosion is not directly a result of mechanical stress. Erosion refers to an actual mineral dissolution. A common cause of erosion in primate teeth is the contact with acids. Erosion can increase the effect of mechanisms like abrasion and attrition because it softens the enamel surface and makes it more susceptible to other types of wear (Imfeld, 1996; Laurence-Young et al., 2011). Regardless of friction, acids can cause dental lesions on the tooth surface (Zhen et al., 2011). To illustrate how enamel softening due to acids can augment dental wear Zhen et al. (2011) exposed teeth to different acidic solutions and then tested the wear behavior of the teeth using titanium alloy. The titanium alloy caused clear pit and scratch microwear on the teeth.

3.2.2 *Causes of Dental Microwear*

Dental microwear directly leads to dental macrowear. Although there is no clear correlation between the amount of microscopic pits and dental macrowear, there is a positive relationship between scratch width and macrowear (Schmidt, 2010). In addition to macrowear, microwear also plays an important role in dietary reconstruction of primates. Types of microscopic tooth wear are influenced by the direction of force in mastication and by the physical properties of food abrasives (Maas, 1991). Generally, small particles like phytoliths and grit will indent teeth whereas larger particles like seeds can cause microfractures (Calandra et al., 2012).

Based on the effects of phytoliths in teeth, Walker et al. (1978) were the first ones to successfully separate browsers from grazers among hyraxes. Subsequently, Teaford and Walker (1984) distinguished folivores from frugivores by analyzing occlusal dental microwear. Together, the two studies opened the door to paleodietary reconstruction based on dental microwear.

Baker et al. (1959) suggested phytoliths as a possible cause of dental microwear in New Zealand sheep molars. They conducted a hardness test, in which they demonstrated that phytoliths are hard enough to scratch enamel and are probably the source of wear in sheep teeth.

Phytoliths are silica bodies deposited within plant cells or between cell walls (Piperno, 1988). These types of phytoliths are frequently called opal phytoliths. A wider definition of phytoliths includes all microscopic minerals in plants (Muholland and Rapp 1992). Because calcium oxalates have been demonstrated to cause dental microwear (Dennis and Reinhard, 1998), the wider definition of phytoliths will be used here.

The phytolith content of a plant varies by taxa, climate, soil, aridity, age of the plant and other factors (Piperno, 1988). Grine (1986) estimates that phytoliths make up as much as 2% to 4% of a plant. Fruits are more likely to contain phytoliths than leaves (Ungar and Teaford, 1996).

Phytoliths are not the only microwear agent, however, Silcox and Teaford (2002) successfully demonstrated the link between dental microwear and exogenous grit by analyzing dental microwear patterns of moles and tenrecs. The two mammals incorporate earthworms into their diet on a regular basis. As earthworms have soil on the outside and on the inside of their body, a diet based on earthworms is a good way to study the role of grit in dental wear formation. The mole and the tenrec data showed clear dental microwear features that distinguished them from the other mammals (Silcox and Teaford, 2002). Ungar et al. (1995) further demonstrated that grit not only plays a role for terrestrial animals, but that dust also accumulates in forest canopies. Grit, therefore, is a potential cause of dental microwear for terrestrial and arboreal animals. Amount, size, and shape of exogenous grit all have an influence on dental microwear formation (Nystrom et al., 2004).

Although there is consensus that grit can cause dental microwear lesions, not everyone agrees that phytoliths can cause dental microwear. Even though a number of other studies demonstrated that phytoliths are capable of producing microwear (Baker et al., 1959; Calandra et al., 2012; Covert and Kay, 1981; Newesley, 1993) Sanson et al. (2007) were among the first ones to disagree with those studies. Conducting a similar hardness study as Baker et al. (1959), Sanson et al. (2007) concluded that phytoliths are not hard enough to scratch enamel. They concluded that Baker et al.'s (1959) experiment was flawed because the equipment used was

either not sensitive enough or because the method employed to extract the phytoliths altered their chemical properties.

Covert and Kay (1981) determined in an analysis of opossum dental microwear that herbivorous and insectivorous mammals could not be distinguished based on microwear. They fed twelve American opossums a base of cat food with added ingredients simulating abrasive agents of natural foods. The experiment showed that different diets can lead to similar microwear patterns. Their study sparked great controversy and in a response, Gordon and Walker (1983) criticized the experiment as flawed, calling it unrealistic and of insufficient duration. Kay and Covert (1983) responded that an insectivorous or herbivorous diet can easily be distinguished from microwear caused by grit or phytoliths. Microwear caused by insects, however, looks identical to microwear caused by plants and microwear caused by grit is indistinguishable from the microwear caused by phytoliths.

The debate about the causes of dental microwear has recently been reopened. Galbany et al. (2009) as well as Williams and Holmes (2011) have both found that grit could have a disproportionately stronger effect on dental microwear than phytoliths. Lucas et al. (2013) demonstrated that phytoliths merely reposition enamel prisms, only wearing enamel after several occasions of impact. Grit, in contrast, is capable of wearing enamel immediately, thus being a principal cause of dental microwear overshadowing the wear caused by other agents.

Dental microwear patterns of primates have been studied extensively and different microwear features are believed to be indicative of different diets. Fine scratches are a typical microwear pattern of leaf-eaters, for instance (Teaford, 1988; Semprebon et al., 2004). The omnivore *Theropithecus gelada* has also been demonstrated to have a large number of thin striations (Teaford, 1993). Primates incorporating hard objects into their diets usually have a

high proportion of large pits, in contrast (Teaford, 1988, 1993; Teaford and Walker; 1984; Semprebon et al., 2004).

Teaford and Oyen (1989) raised monkeys on different diets to learn more about occlusal dental microwear turnover rates. They came to the conclusion that rates of turnover highly depend on the abrasiveness of a diet, but that most microwear is completely replaced within one or two weeks. In cases of an especially abrasive diet, however, microwear turnover can be a matter of minutes (Teaford and Oyen, 1989).

3.3 *Dental Wear Analysis*

As dental wear is the direct result of food, drink and teeth touching each other during mastication, the study of dental wear is also a study of diet and mastication. Both, dental macrowear and dental microwear can be analyzed and utilized for dietary reconstructions. In situations where the cause of a particular dental wear pattern is not entirely clear, a dental ecology approach can be helpful. Cuozzo and Sauter (2012) proposed that instead of studying isolated aspects of tooth morphology or habitat, the entire dental ecology should be taken into account when reconstructing diets. Dental ecology describes how teeth respond to the environment and how the environment shapes teeth. A thorough dietary reconstruction should, therefore, include analyses of morphology, microwear, macrowear pathologies and so forth.

3.3.1 *Dental Macrowear Analysis*

Dental macrowear is frequently considered in dietary reconstructions. As discussed earlier, *C. williamsi* has heavily worn teeth (Benefit, 1999), which should be considered in

dietary reconstructions for this taxon. Macrowear can indirectly indicate diet as different food items will cause wear at different rates (Janis, 1984).

In primates, shearing wear, caused by tough, fibrous foods, or crushing wear caused by soft and brittle foods, are the two sources of abrasion and in turn macrowear (Janis, 1984). Observations of macrowear can be made rapidly. The disadvantage of dental macrowear analysis is that only individuals of similar tooth morphology and of the same dental age can be compared (Janis, 1984).

Mesowear, a form of tooth wear analysis, is based on the idea that the wear of different tooth facets correlates with the abrasiveness of diet. Hence, when scoring mesowear, a researcher will score the different states of wear of the different tooth facets. Attrition is more common in browsers, whereas abrasion plays a larger role in the tooth wear of grazers which in turn influences which facets are worn (Louys et al. 2012). Louys et al. (2012) found that abrasion will cause low occlusal relief and round cusps, but attrition leads to sharp cusps with high relief. A clear advantage of mesowear analysis is that it is not destructive and rapid, enabling researchers to work with large sample sizes (Louys et al., 2011). So far, however, mesowear analysis has only been developed for ungulate teeth.

3.3.2 *Dental Microwear Analysis*

Dental microwear analysis seeks to pinpoint tooth wear caused by abrasion. Gordon (1982) defines dental microwear analysis to be “the systematic study of microscopic surface damage on skeletal or archaeological materials” (195). There are three types of dental microwear analysis, which are frequently employed: Scanning electron microscopy (SEM), low magnification stereomicroscopy (LMS), and confocal microscopy (CM). In addition, two

different surfaces of a tooth can be analyzed. An analysis of the occlusal surface of the tooth is more common, but studies considering buccal surfaces are gaining in popularity. The study presented here is an LMS dental microwear analysis of the buccal surface of primate teeth. However, as other dental microwear studies are mentioned, the different methods of analysis will be briefly described here.

SEM records electrons reflected by the surface of a tooth and allows for great magnification. Features can, therefore, be observed with great clarity and can even be measured. Most researchers chose a magnification of 500x. The efficacy of the method has been well documented (Semperebon et al., 2004), but the method also has limitations.

Galbany et al. (2005) measured high interobserver error, but low intraobserver error for SEM. Estebananz et al. (2007) added that errors could also be caused by the technology employed and how it is used. Settings can influence the final image produced by the microscope (Rose and Ungar, 1998). Working with SEM, it can take hours to analyze microwear of a single specimen (Rose and Ungar, 1998). The equipment is also expensive. For these reasons, sample sizes are usually very small (Semperebon et al. 2004). Semperebon et al. (2004) also argue that the metric rules applied in the analysis of wear patterns are rather arbitrary.

Compared to SEM, dental microwear texture analysis reduces observer error and opens up the possibility of collecting a larger sample (Scott et al. 2005). Three-dimensional techniques in dental microwear analysis were first introduced in 2003 (Calandra et al., 2012). Confocal microscopy allows the researcher to study tooth morphology, tooth fractures and dental wear (Bunn and Ungar, 2009; Scott et al., 2005). The method works with a point cloud which is created when a tooth is scanned by a laser. Using the software *Geographic Information Systems*, a virtual tooth surface is then constructed based on the point cloud.

Light stereomicroscopy dental microwear analysis, the method used for this study, is a form of microwear analysis relying on less expensive equipment. Here, researchers are working with a light microscope and features are counted at 35x magnification in a 0.4mm^2 area. Microwear features are usually not measured, but are identified and categorized based on their light refractive properties (Godfrey et al. 2004). Semprebon et al. (2004) described the different features. Pits are features which are of similar length and width, and they can be divided into large pits, small pits, and puncture pits. Small pits are shallow, meaning they refract light easily and appear shiny under the microscope. Large pits are much deeper and therefore darker. Puncture pits are a type of large pit and are very symmetrical, “craterlike” features. Scratches, in contrast, are clearly longer than they are wide. Fine scratches are refractive and shiny. Coarse scratches are defined to be wider than fine scratches. Hypercoarse scratches are very deep (Semprebon et al., 2004). One of the strengths of LMS is the external oblique light source, which enhances contrast and can be moved around if necessary.

Mihlbachler et al. (2012) described error rates of LMS to be significant when interobserver error is measured for low magnification stereomicroscopy dental microwear analysis. Interobserver error does, however, become smaller with experience. Intraobserver error is much lower, but might just be lower because of an increased familiarity with different images. Nevertheless, even though every observer collects markedly different data, overall results will describe the same differences between species (Mihlbachler et al., 2012). These findings contrast with Semprebon et al. (2004), who found low observer error associated with LMS.

All of the three methods described above are frequently used to study the occlusal surface of a tooth. Buccal surfaces are also frequently analyzed, however. Buccal wear is believed to be a reflection of abrasion and not attrition (Estebaranz et al., 2007). The cause of buccal wear is

abrasive food particles, which rub against the tooth due to mandibular and cheek movements (Romero et al., 2012). Studying buccal wear is a way to control for attrition as teeth do not touch each other on the buccal surface (Ungar and Teaford, 1996). Buccal microwear can be used as a more cumulative measure of diet, due to its slower turnover rate (Romero et al., 2012). As pits are absent in buccal wear, only scratches can be studied (Estebaranz et al., 2007). Buccal dental microwear can be studied using the same methods as occlusal dental microwear analysis.

Like all tools of dietary reconstruction, dental microwear analysis has some general flaws. A researcher can de facto only observe the last few meals of an individual. Grine (1986) described the problem of dental microwear obliteration with the label “Last Supper” phenomenon. In case of an extremely abrasive food, it might be the very last meal which caused all the visible microwear (Grine, 1986).

Moreover, Estebaranz et al. (2007) cautioned that jaw morphology should not be ignored when studying microwear. Biomechanical differences clearly seem to play a role in dental wear formation (Gordon, 1982). Tightly interlocking facets will lead to more localized microwear, while less tightly locking facets will have a much more random scratch distribution (Gordon, 1982).

Facet type, as well as tooth age also influences microwear formation (Gordon, 1982). Shearing facets seem to have more striations and grinding surfaces tend to have more pits when compared to each other (Gordon, 1982). Further, Gordon (1982) noted that molar and facet position influence pit size and that striation length decreases moving distally from M1 to M3. Age differences in microwear are probably caused by differences in enamel hardness between surface and subsurface minerals (Newesley, 1993).

Dental microwear also does not seem to account for any preparation of food that happens outside of the mouth (Grine, 1986). Food preparation inside the mouth can also skew dental microwear distribution. Seeds, for instance, can result in microfractures if crushed, but many primates will choose to swallow seeds whole or to spit them out (Calandra et al., 2012).

4 METHODS

For this study, dental microwear features were recorded from eighteen *C. williamsi* specimens as well as from a number of comparative taxa. The method used was LMS and different pit and scratch features were counted and recorded.

4.1 The Study Sample

The comparative sample includes extant taxa with known diets as well as extinct taxa, which lived in the same area and around the same time as *C. williamsi*. Extant individuals were included into the study because much about their diet and habitat is known. The extinct individuals, in contrast, likely shared similar living conditions with *C. williamsi*.

4.1.2 The Sample

All of the eighteen *C. williamsi* specimens included in this study were discovered at South African cave sites with the majority of them stemming from Sterkfontein (n = 15). A few specimens also came from Bolt's Farm (n = 2) and Makapansgat (n = 1).

Some of the other extinct taxa included in the comparative sample came from Makapansgat and include *Theropithecus darti* (n = 4), *Parapapio whitei* (n = 2) and *Parapapio broomi* (n = 2). *Parapapio jonesi* (n = 15), some *Parapapio whitei* specimens (n = 6) and ten *Parapapio broomi* specimens (n = 10) all stem from Sterkfontein. Other fossils come from Swartkrans and include *Theropithecus danieli* (n = 6), *Parapapio jonesi* (n = 5), *Papio robinsoni* (n = 11) and *Dinopithecus ingens* (n = 14). A single *Parapapio whitei* (n = 1) specimen was included from Taung.

Extant taxa included in the study are *Papio ursinus* (n = 35), *Papio anubis* (n = 13), *Gorilla gorilla* (n = 5), *Ptilocolobus badius* (n = 2), *Colobus angolensis* (n = 2), *Colobus polykomos* (n = 6), *Theropithecus gelada* (n = 6) and *Cebus apella* (n = 10).

Primate diets are hard to classify because primates are flexible feeders, not restricted solely to one food item or group. However, because the primates in this study are used as a comparative sample, they will be categorized based on most common dietary items consumed so that they can aid in dietary predictions and comparisons.

One of the comparative species, *G gorilla* is an extant representative of terrestrial folivores. Increasing evidence suggests that while foliage is an important fallback food, *G. gorilla* prefers fruit when it is abundant (Remis et al., 2000). This seasonal preference of fruit needs to be kept in mind during interpretation of results.

Three other traditionally folivorous species – *C. polykomos*, *P. badius*, and *C. angolensis* were included in the collection as representatives of extant colobine monkeys. All three species are arboreal leaf-eaters. The dental microwear analysis presented here will, among other things, test whether the dental microwear signature of *C. williamsi* is similar to that of these extant colobine monkeys.

Theropithecus gelada is known to be a granivore and the masticatory apparatus of *T. darti* implies a similar diet (Jablonski, 1993). Based on isotopic analysis, Fourie et al. (2008), also suggested a primarily C₄ based diet for *T. darti*. All *Theropithecus* taxa, considered here serve as representatives of terrestrial granivores.

The sample also includes a number of papionins some of which were sympatric with *C. williamsi*. Benefit (2000) argued that South African Plio-Pleistocene papionins were significantly less frugivorous than their East African counterparts. Studying *P. robinsoni* microwear, Williams and Holmes (2011) observed many scratches, but few pits and classify the taxon as a folivore-frugivore. *Papio ursinus*, an extant species, is known to be an eclectic feeder and omnivore. *Parapapio jonesi* shows many similarities to *P. ursinus* and could have been ancestral to the

taxon (Brain, 1981). *Parapapio broomi* likely consumed larger amounts of C₄ foods compared to extant papionins (Fourie et al., 2008). In general, baboons are such extreme generalists that it seems highly difficult to classify them (Codron et al., 2008). Ultimately, all *Papio spp.* were therefore classified as omnivorous in the database for the purpose of this study.

While some South African *Parapapio. spp.* probably were mainly frugivorous, others could have specialized on harder dietary items (Gommery et al., 2008). Codron et al. (2005) suggest that different *Parapapio.spp.* must have at least eaten some C₄ resources. Like *Papio*, *Parapapio* taxa were, therefore, also entered as omnivores into the comparative database.

There are conflicting dietary categorizations for the baboon-like monkey *D. ingens*. Benefit (1999) argued that *D. ingens* is among the most frugivorous of the South African fossil papionins. However, Codron et al. (2005) found that *D. ingens* must also have ingested a significant amount of C₄ grasses. With an adult male weight of over 45 kg (Brain, 1981), *D. ingens* was most likely a terrestrial primate. Due to the conflicting dietary reconstructions, *D. ingens* was also entered as a terrestrial omnivore into the database.

Cebus apella is an extant species known to be an arboreal frugivore and a hard-object specialist, it therefore serves as representative of arboreal frugivores in the database.

4.1.3 Data Collection

Dental microwear was collected from resin casts using a standard low magnification stereomicroscope with an oblique external light source. Tooth wear was recorded from a 0.4 mm² area of the mesio-buccal cusp using an ocular reticle. While most teeth which were scored are second molars (n = 167), data from several first molars (n = 20) was also collected in order to increase sample size if there was no second molar or if the second molar was not readable. No

deciduous teeth were included in the study. Casts which appeared disturbed or did not have any readable microwear were put aside and not scored. Data were recorded twice on different days and then averaged.

The dental casts are housed at Georgia State University and were collected and prepared by Dr. Frank L'Engle Williams. All of the casts were created from previously collected dental molds using polyvinylsiloxane resin and hardener.

4.2 Statistical Analysis

For comparisons, statistical methods were employed and the software Statistical Package for the Social Sciences (SPSS) was used for all analyses. Statistical analysis was based on the idea that classifications (such as “leaf-eater”) are hypotheses and are therefore testable (Thorington, 1970).

4.2.1 Statistical Analysis of a Sample

When analyzing dental microwear data, it is important to remember that the data are a small sample of a comparatively large population. Working with a sample leaves more room for error. Seasonal and ecological factors can, for instance, influence dental microwear and collection bias of a sample can augment or hide variation (Daegling and Grine, 1999).

In order to test whether the dental microwear of *C. williamsi* is statistically distinct from any other primate groups, the null-hypothesis was “All sampled taxa belong to the same dietary group”. Whenever necessary, the probability value (“p-value”) used was $p = 0.05$. A p-value of under $p = 0.5$ means that the chance of the observed outcome to be accidental is less than 5%. Thus, the chances that the null hypothesis is not true lie above 95%. A probability value can only

reject a null hypothesis, but not confirm an alternative hypothesis (Goodman, 1999). However, as the alternative hypothesis is ideally the opposite of the null hypothesis, it is likely to be true if the null hypothesis is not. Also important to keep in mind is that $p = 0.05$ is an arbitrary threshold commonly used because it is easy to calculate. Generally, the lower a p-value is the higher its significance.

4.2.2 Statistical Tests

An important statistical test which was used during the data analysis phase is an Analysis of Variance test (ANOVA). The ANOVA can compare the means and distributions of several groups for single variables and check whether they are statistically distinct. A Tukey's Honestly Significance Test (Tukey's HSD) can then indicate which means are statistically significantly distinct.

Although the ANOVA and the Tukey's HSD tests indicate where exactly variation lies, it does not indicate how the features are different. Simple boxplots illustrating microwear feature distribution were, therefore, added to visualize differences in microwear feature counts.

Further, a Principal Components Analysis (PCA) was employed to find which features in particular cause a separation of taxa. In order to be able to graph the PCA, two factors were extracted. Naturally, in a PCA the first axis accounts for more variation than subsequent axes. A PCA reduces and rotates a point cloud of data in such a way that variation can be captured and rendered visible.

Following the PCA, a Discriminant Function Analysis (DFA) was run to make predictions about diet, habitat and species designation. A DFA is a tool for classification and can predict dependent variables such as "diet" based on independent variables such as "species".

Keeping in mind that these diets will always be imprecise categorizations for primates, the dietary categories used were “folivore”, “frugivore”, “gramnivore”, and “omnivore”. While it could be argued that all of the primates included in the comparative sample could be described as “omnivorous” to some degree, this category was limited to taxa which were impossible to classify. The three habitat categories employed were restricted to “terrestrial, open/mixed”, “terrestrial, forest” and “arboreal” as many of the extinct taxa came from habitat mosaics.

Lastly, a Mann-Whitney U test was conducted to find whether there are significant differences between the older Makapansgat and Sterkfontein fossils and the two younger specimens from Bolt’s Farm. As the sample size for Bolt’s Farm is only 2, a non-parametric statistical test was chosen. A Mann-Whitney U test, examines whether one part of a sample is significantly different from another without assuming that the sample is representative of a population. The sample size is too small to make any definitive conclusions. However, the Mann-Whitney-U test can indicate trends which can then be further tested with a larger sample size at a later date.

5 RESULTS

Several statistical tools were employed to compare the microwear signatures of the different taxa. Later, nonparametric statistics were utilized to test whether there are differences between *C. williamsi* specimens coming from different sites. The results of the different tests should complement each other and draw a more complete picture.

5.1 Comparison of Taxa

A combination of several different statistical methods was employed to compare the different taxa. An ANOVA in conjunction with a Tukey's HSD test, boxplots, a PCA as well as DFAs were employed and their results will be discussed here. As the different tests are complementary, they will be considered together to draw a more complete picture in the discussion chapter.

5.1.1 ANOVA and Tukey's HSD Test

First, an ANOVA (table 2) in conjunction with a Tukey's HSD test (table 5 in Appendix A) were performed to find which differences between taxa are statistically significant.

Table 2: ANOVA Test Results

| | F | Significance |
|-----------------------------|-------|--------------|
| Small Pits | 1.931 | .023 |
| Large Pits | 4.563 | .000 |
| Puncture Pits | 3.371 | .000 |
| Fine Scratches | 3.246 | .000 |
| Hypercoarse Scratches | 2.205 | .008 |
| Coarse Scratches | 1.096 | .363 |
| Overall number of scratches | 2.849 | .001 |
| Overall number of pits | 1.820 | .035 |

The ANOVA shows that there is significant between-group difference in overall pit and scratch counts. There also is a significant group difference between small pits, large pits, puncture pits, fine scratches, and hypercoarse scratches. The F-value, and, therefore, the between-group variation, is greatest for large pits closely followed by puncture pits. The only dental microwear features for which there is no statistical significance are coarse scratches. Overall, therefore, the ANOVA shows that at least some of the taxa considered in the study have dental microwear signatures which are statistically significantly different from each other.

Following the ANOVA, a Tukey's HSD test was run to find where exactly the significant between-group differences lie (see table 5 in Appendix A). The Tukey's HSD test shows that if the overall number of scratches is compared among the different taxa, there is a clear difference between *C. williamsi* and the different *Parapapio* specimens. A boxplot (Figure 2) shows that the *Parapapio* taxa tend to have more scratches than *C. williamsi*. The other papionins such as *P. ursinus* also show a trend towards more scratches.

The boxplot also shows great overlap of the ranges of *C. williamsi* and *C. apella*. These two taxa do, in fact, have a p-value of 1 when they are compared based on overall scratches. There is, therefore, no statistical difference between the overall scratch counts of *C. apella* and *C. williamsi*.

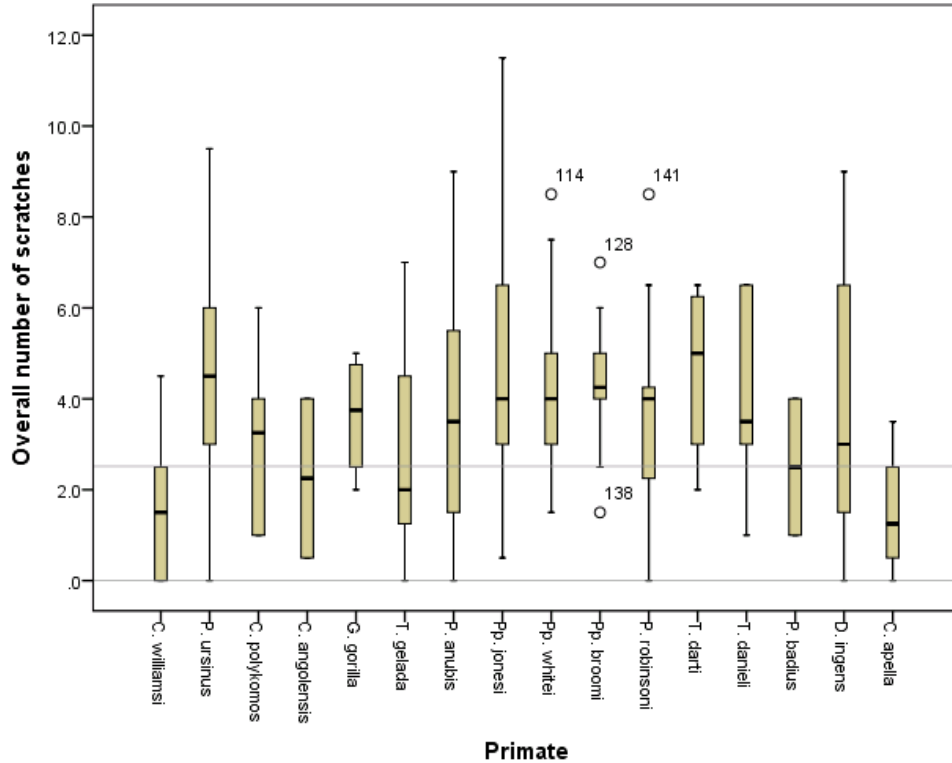


Figure 2: Boxplot of Overall Scratch Counts

The boxplot shows the overall distribution of scratch features. The grey lines indicate the range into which the majority of *C. williamsi* specimens fall.

When it comes to individual scratch features, *C. williamsi* further differs from *P. ursinus* in fine scratch counts ($p = .001$). A boxplot (Figure 3) shows that *P. ursinus* has significantly more fine scratches than *C. williamsi*. Overall, when compared to other taxa, *C. williamsi* has a relatively low fine scratch count.

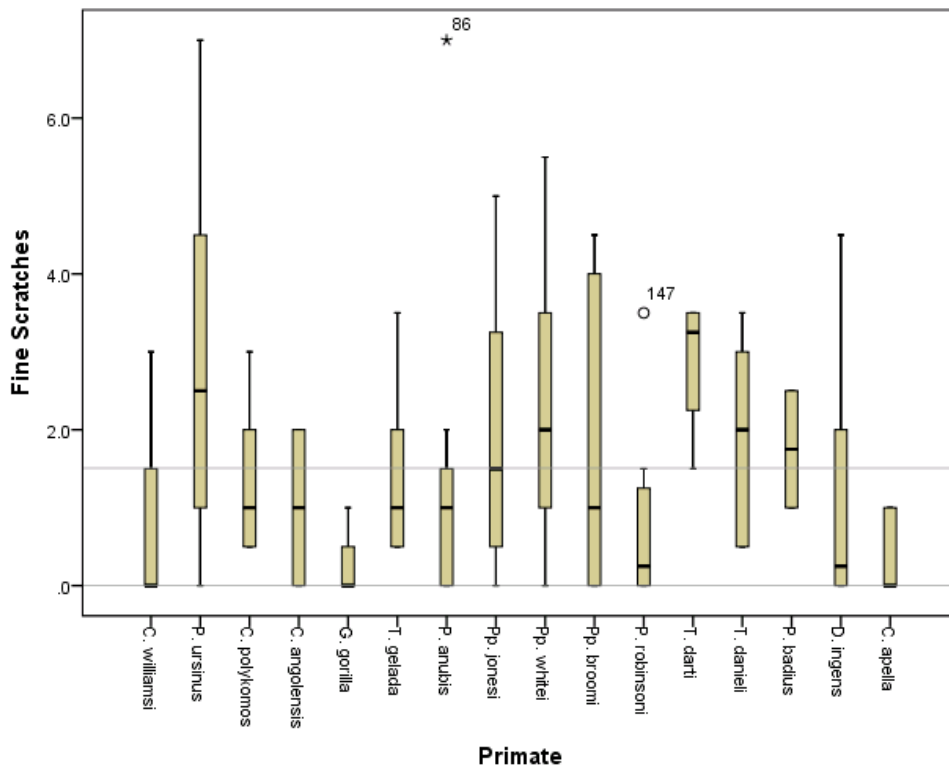


Figure 3: Boxplot of Fine Scratches

The boxplot shows the overall distribution of fine scratch features. The grey lines indicate the range into which the majority of *C. williamsi* specimens fall.

While there are significant in between-group differences for hypercoarse scratches according to the ANOVA, *C. williamsi* is not significantly different from other taxa based on hypercoarse scratches. The Tukey's HSD test resulted in some comparably low p-values, which could be indicators of a trend, however. Probability values for *C. polykomos* ($p = .201$), *P. robinsoni* ($p = .244$) and *T. danieli* ($p = .280$) are all relatively low when hypercoarse scratches are compared to *C. williamsi*. A boxplot (Figure 4) illustrates that *C. williamsi* has a comparably low hypercoarse scratch count and has less hypercoarse scratches than many of the folivores.

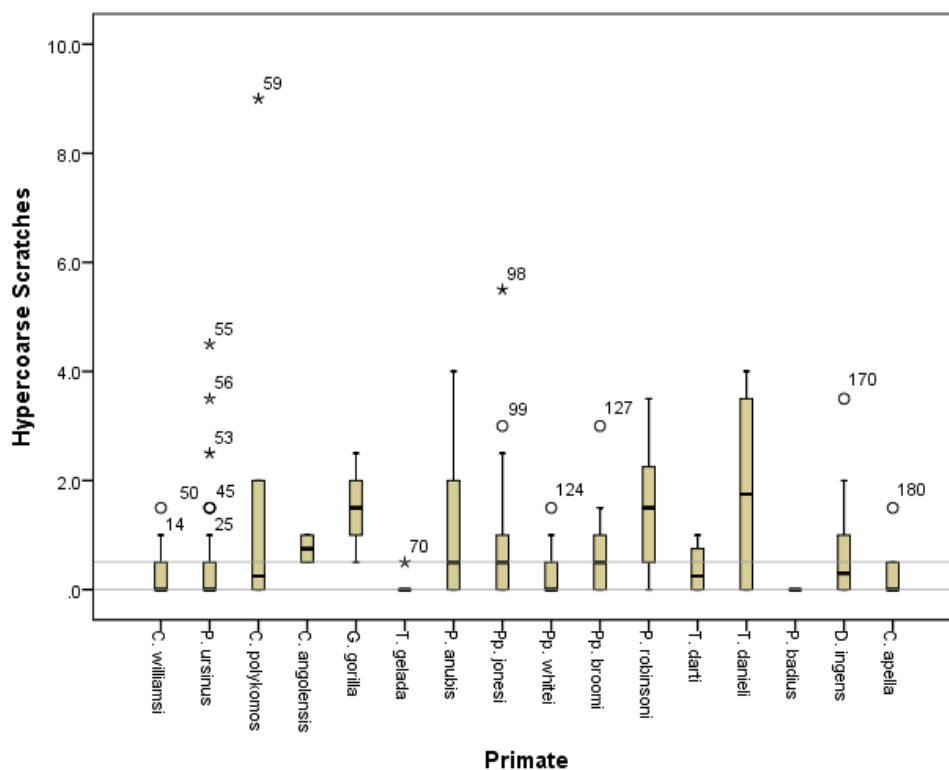


Figure 4: Boxplot of Hypercoarse Scratches

The boxplot shows the overall distribution of hypercoarse scratch features. The grey lines indicate the range into which the majority of *C. williamsi* specimens fall.

Variance for overall pit count is not as large and the only statistically significant difference lies between *C. williamsi* and *Pp. jonesi* at $p = .046$. The Tukey's HSD test also resulted in relatively low p-values when *C. williamsi* was compared to *Pp. whitei* ($p = .200$), *P. robinsoni* ($p = .242$) and *T. danieli* ($p = .273$), possibly indicating a trend. A boxplot (Figure 5) shows that *C. williamsi* specimens tend to have a higher overall pit counts than any of these taxa.

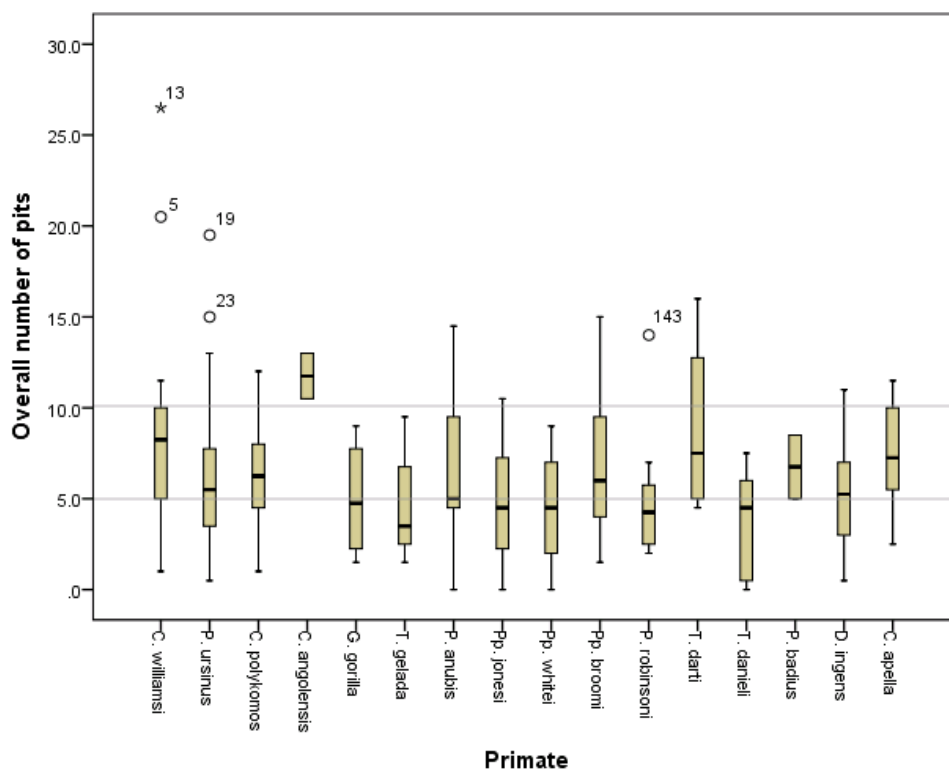


Figure 5: Boxplot of Overall Pit Counts

The boxplot shows the overall distribution of all pit features. The grey lines indicate the range in to which the majority of *C. williamsi* specimens fall.

C. williamsi is not statistically significantly different from any of the other taxa when small pits are compared. A boxplot (Figure 6) shows that the different *C. williamsi* specimens vary greatly in small pit counts. The wide range in small pit counts could explain why there is no statistical difference between *C. williamsi* and other taxa.

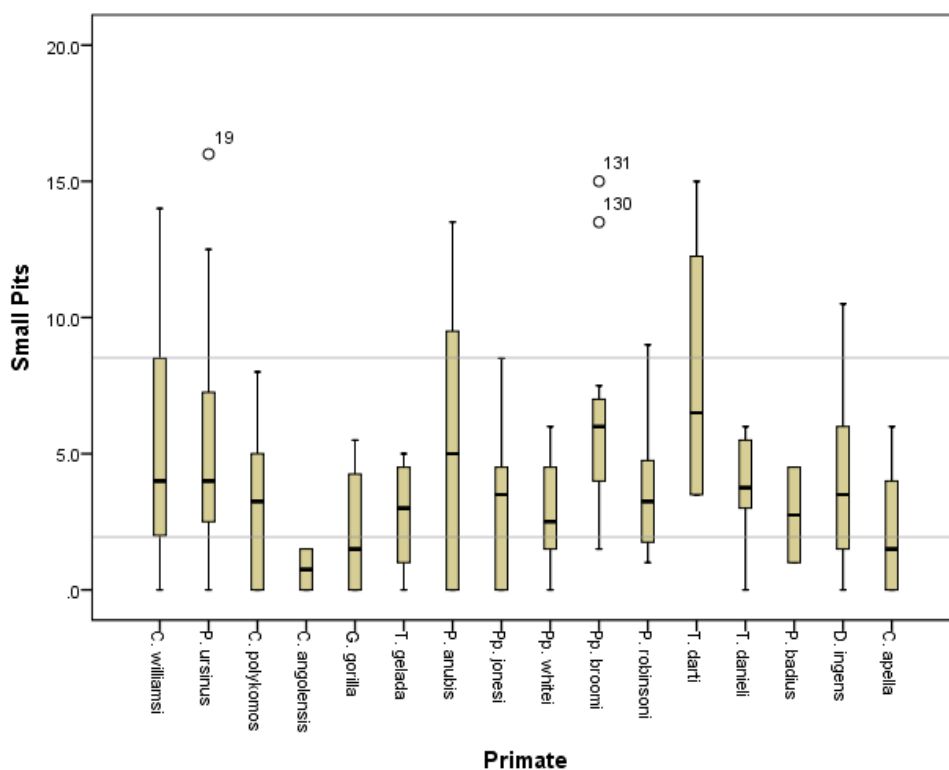


Figure 6: Boxplot of Small Pits

The boxplot shows the overall distribution of small pit features. The grey lines indicate the range into which the majority of *C. williamsi* specimens fall.

The Tukey's HSD test further shows that large pit frequencies are significantly different between *C. williamsi* and *C. angolensis* ($p = .032$). When large pit counts of *C. williamsi* and *C. apella* are compared, the p-value is not statistically significant, but low ($p = .155$). A boxplot (Figure 7) illustrates that *C. williamsi* has less large pits than *C. angolensis* and *C. apella*. The boxplot further shows that *C. polykomos*, also, has a slightly larger amount of large pits when compared to *C. williamsi*.

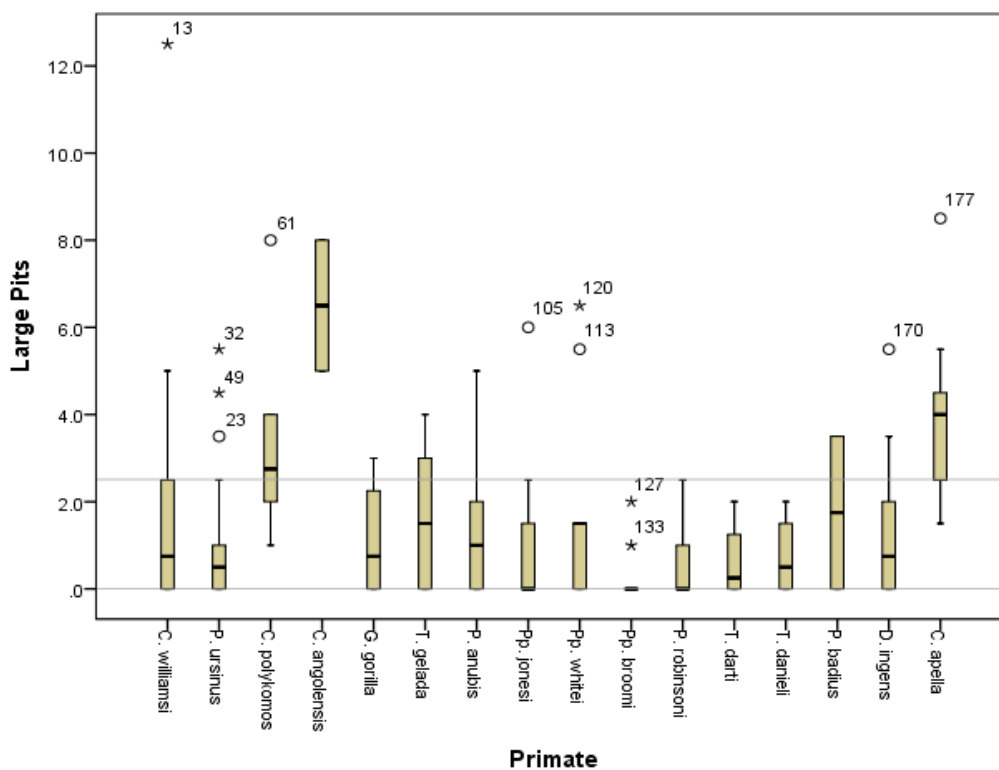


Figure 7: Boxplot of Large Pits

The boxplot shows the overall distribution of large pit features. The grey lines indicate the range into which the majority of *C. williamsi* specimens fall.

While *C. williamsi* is relatively similar to the papionins in large pit counts, this is different for puncture pits counts. There is a statistically significant difference between puncture pit counts when *C. williamsi* is compared to *P. ursinus* ($p = .001$), *P. anubis* ($p = .018$), *Pp. broomi* ($p = .043$) and *D. ingens* ($p = .012$). *Cercopithecoides williamsi* has more puncture pits than the majority of sampled papionins and falls into a similar range of a number of folivorous species as well as *C. apella* (Figure 8). Overall, *C. williamsi* specimens show a great range in puncture pit count.

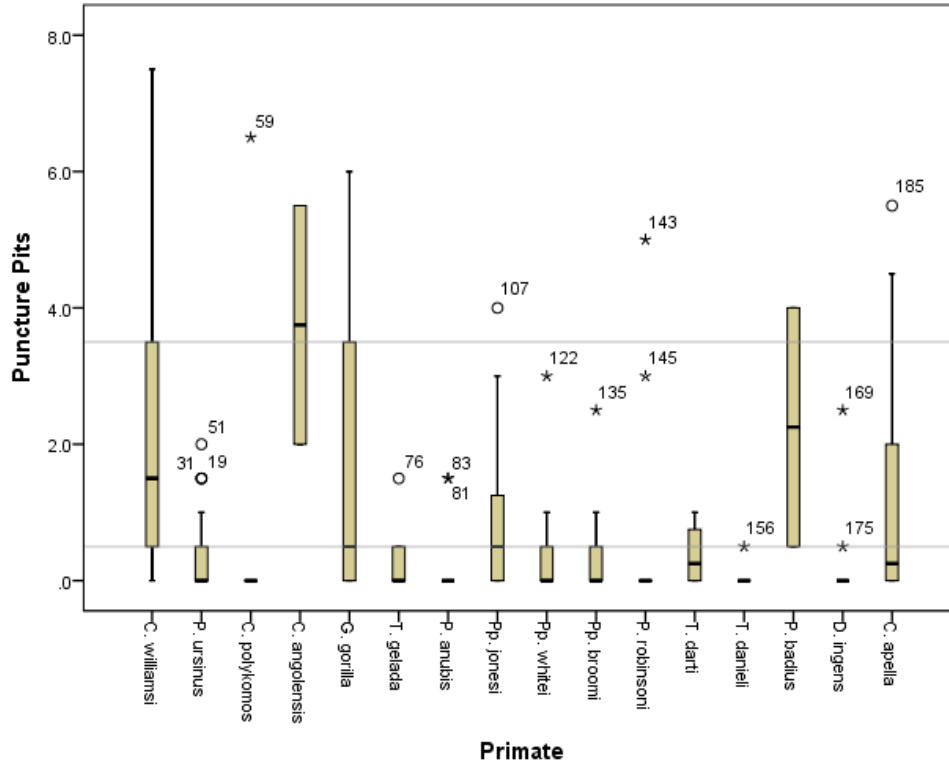


Figure 8: Boxplot of Puncture Pits

The boxplot shows the overall distribution of puncture pits. The grey lines indicate the range into which the majority of *C. williamsi* specimens fall.

5.1.2 Individual Features

While the ANOVA and the Tukey's HSD test compare taxa as a whole an additional simple scatterplot was created to see where individual specimens fall. Overall counts of scratches were plotted against overall counts of pits showing that the amount of pits in *C. williamsi* is much lower than the amount of scratches when compared to other taxa (Figure 9).

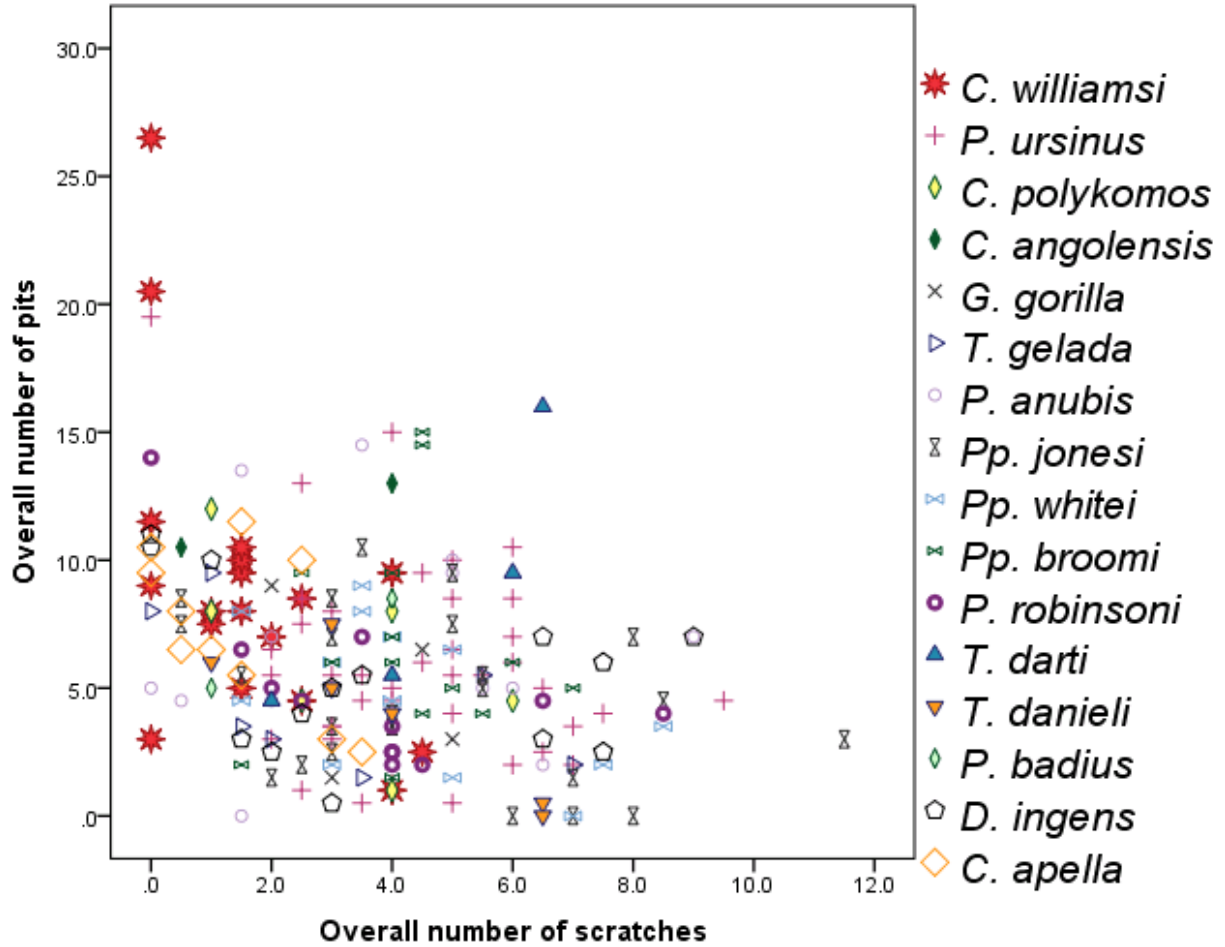


Figure 9: Scatterplot of Overall Pit and Scratch Counts

Overall pit counts are graphed on the y-axis and overall scratch counts are depicted on the x-axis.

5.1.3 PCA

A PCA was utilized to find which microwear features most influence variation between the taxa (Table 3).

Among the first factors, there is a strong positive trend for large pits and puncture pits and a strong negative trend for small pits and fine scratches. Much of the variation in factor 1, therefore, is caused by large and puncture pits on one side and small pits and fine scratches on the other. As demonstrated above, *C. williamsi* has a large amount of puncture pits and small

amount of fine scratches, which therefore both influence where the monkey falls in the comparison.

Factor 2 is influenced by coarse scratches, with a high negative loading, on the one side and small pits, with a high positive loading on the other.

The results of the PCA test, therefore, demonstrate a trend that separates teeth with shallower microwear features from teeth with deeper ones.

Table 3: Component Matrix of Principal Components Analysis

| | Component | |
|-----------------------|-----------|-------|
| | 1 | 2 |
| Small Pits | -.446 | .520 |
| Large Pits | .584 | .112 |
| Puncture Pits | .616 | .368 |
| Fine Scratches | -.699 | .197 |
| Coarse Scratches | -.134 | -.854 |
| Hypercoarse Scratches | .230 | -.161 |

The results of the PCA test were graphed in order to show where exactly individual taxa fall in comparison to the other taxa (Figure 10). Here, *C. williamsi* clearly clusters with *C. apella*, *C. polykomos* and *G. gorilla* on both axes. *P. anubis*, *P. robinsoni* and *P. ursinus* all show a lot of variation in their microwear but none overlap with *C. williamsi*.

On the x-axis, which reflects factor 1, *C. williamsi* together with *G. gorilla*, *C. polykomos*, *T. gelada*, *G. gorilla* and *C. angolensis* are clearly separated from *Pp. broomi*, *P. ursinus*, and *Pp. whitei*. Due to its high amount of puncture pits, therefore, *C. williamsi* specimens cluster with many leaf and grass eaters, but also with the frugivorous *C. apella*.

The y-axis groups *C. williamsi* together with *C. polykomos*, *T. danieli*, *T. darti*, *P. robinsoni*, *Pp. broomi*, and *C. angolensis*. Based on hypercoarse scratches and small pits, *C. williamsi* therefore does not cluster with clear dietary groups.

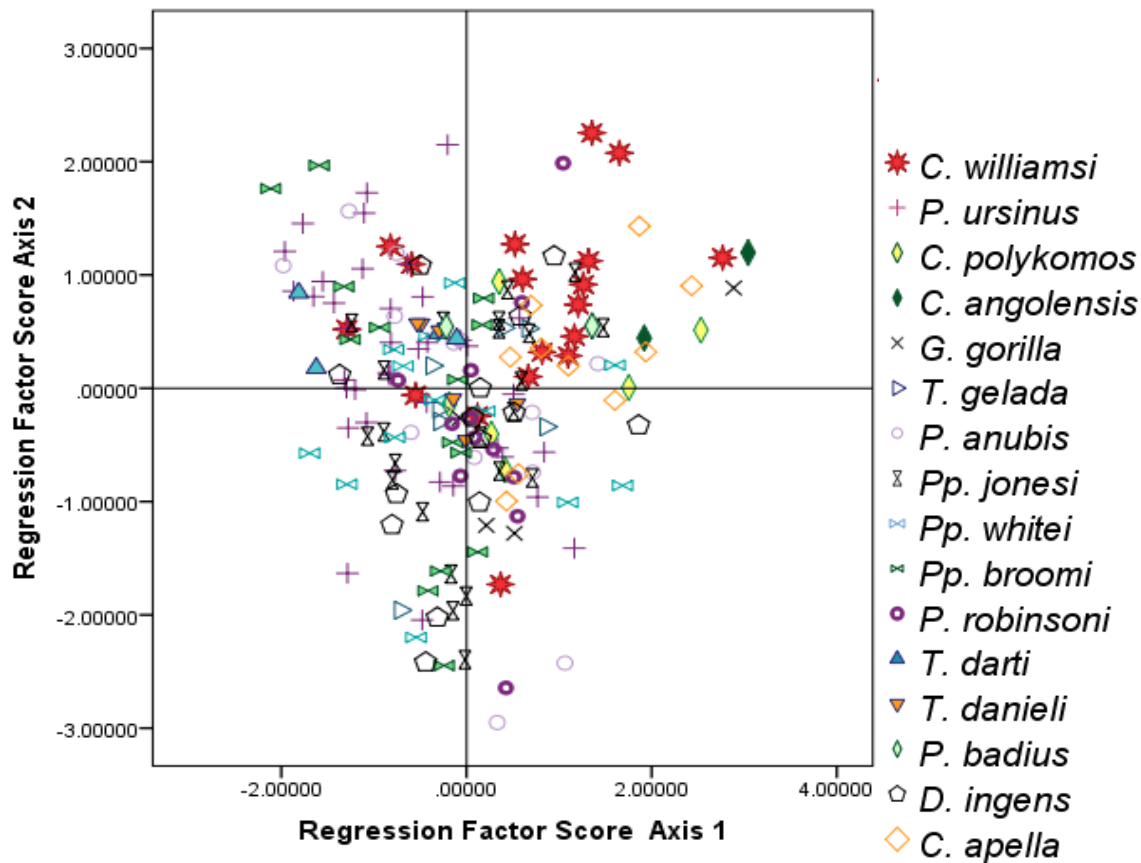


Figure 10: Scatterplot of Principal Components Axes

The PCA scatterplot illustrates similarities and differences of individual specimens based on their microwear features.

5.1.4 Discriminant Function Analysis

A DFA was employed to predict diet, habitat, and to test species designations (Appendix B.2). Here, the majority of tested *C. williamsi* specimens were predicted to have been terrestrial and folivorous, but species predictions were not as clear.

When habitat was tested, 33% of the *C. williamsi* specimens sampled were predicted to have been terrestrial and to have lived in an open/mixed habitat, another 39% were predicted to

have been terrestrial but living in a forest environment and 25% of *C. williamsi* specimens were grouped in with arboreal primates (Figure 11). Only 28% were predicated to be arboreal.

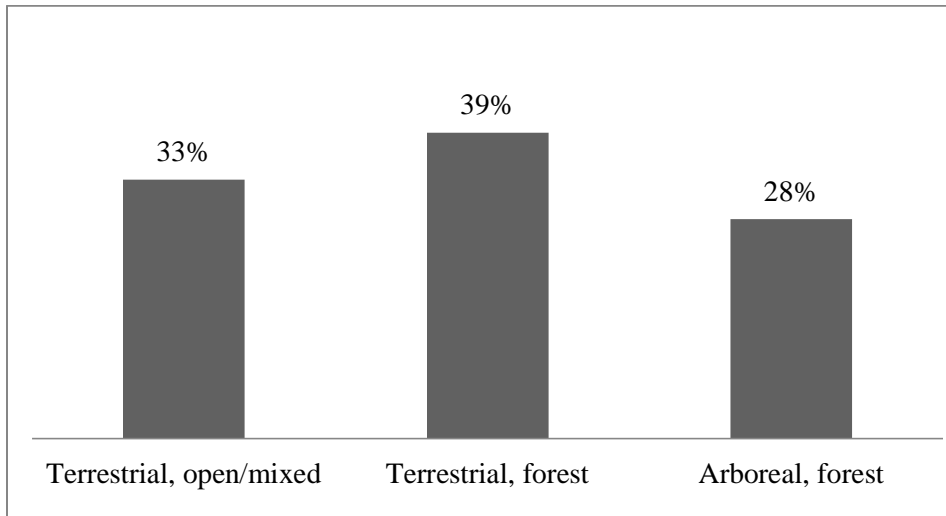


Figure 11: DFA Habitat Predictions

Habitat predictions for *C. williamsi* specimens using a DFA.

A scatterplot illustrating habitat predictions based on the DFA (Figure 12) shows that *C. williamsi* does not clearly cluster with any of the other taxa. A number of *C. williamsi* specimens cluster with arboreal taxa such as the colobine monkeys and *C. apella*. Several *C. williamsi* specimens, however, fall within a large cluster which largely represents the terrestrial taxa of the sample such as the papionins, *T. darti* and *T. danieli*.

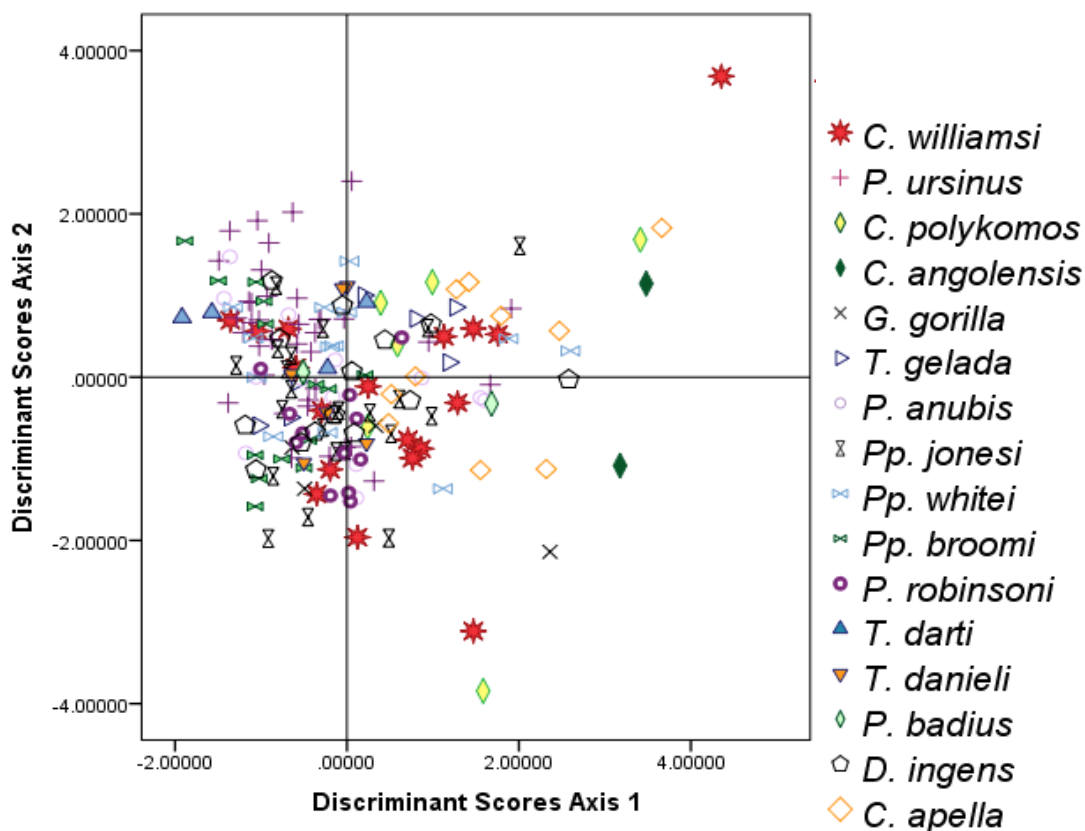


Figure 12: Scatterplot of Habitat Predictions

Habitat predictions for *C. williamsi* specimens using a DFA.

An additional DFA was run to determine predictions of dietary categories. Fifty percent of the recorded *C. williamsi* fossils were predicted to be folivorous, 22% granivorous, 17% as frugivorous, and 11% omnivorous (see table 7 in Appendix A). A scatterplot shows that a large part of *C. williamsi* specimens are similar to the colobines and *C. apella* (Figure 13). Some *C. williamsi* specimens, however, cluster with the papionins.

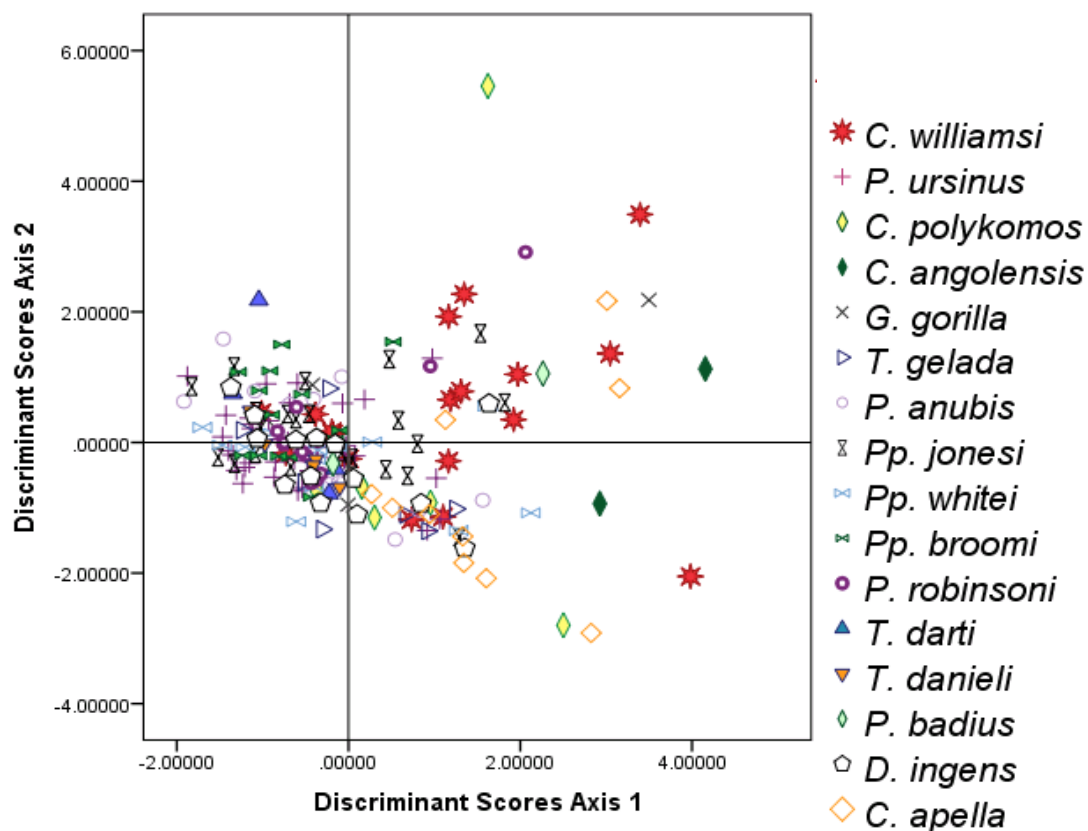


Figure 13: Scatterplot of Dietary Predictions

Predictions of diet of *C. williamsi* specimens using a DFA.

Many of the taxa cluster very closely in the scatterplot which illustrates DFA dietary predictions. Therefore, an additional DFA was run with the goal of creating a graph in which individual taxa can be spotted more easily (Figure 14). The taxa included in the second DFA are *C. williamsi*, *P. ursinus*, *G. gorilla*, *P. anubis*, *Pp. broomi*, *T. danieli*, *C. apella* and a summary of all colobine taxa. The additional scatterplot shows that part of the *C. williamsi* specimens cluster with the colobines and *C. apella* and part of the *C. williamsi* specimens cluster more closely with *P. ursinus*. Here, it becomes apparent that *C. williamsi* and the granivore *T. danieli* do not overlap.

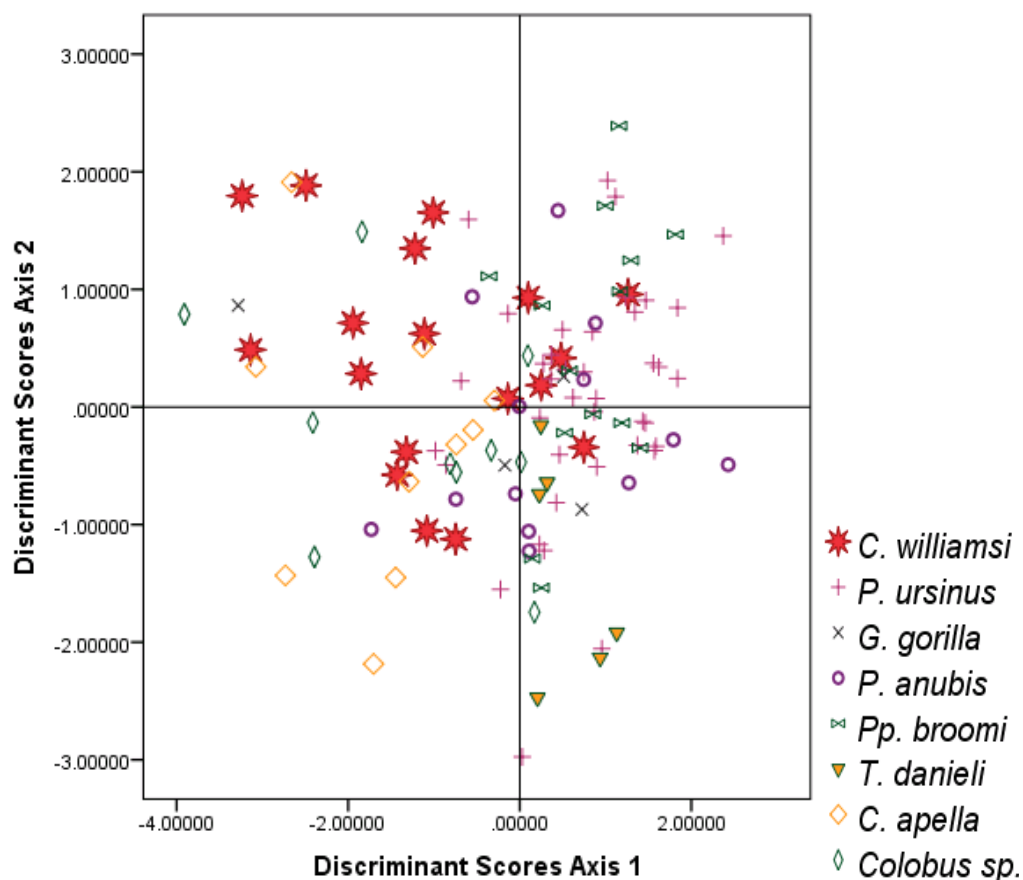


Figure 14: DFA Dietary Predictions with Less Taxa

This graph is also an expression of the DFA results, but is taking less taxa into consideration.

When the specimens were tested for species predictions, only 33% of specimens were listed as *C. williamsi*, 17% each were predicted to be *T. darti* and *P. badius*, 11% *C. apella* and 6% each as *G. gorilla* and *C. angelosis*.

5.2 Comparison of Sites

A Mann-Whitney-U test was employed to test whether there is a difference in microwear between the older sites of Sterkfontein and Makapansgat and two specimens from the younger site of Bolt's Farm (Table 4). While the test did not yield a statistically significant result, a

comparison of puncture pits ($p = .261$) and fine scratches ($p = .327$) results in relatively low p -values. These results should be tested with a larger sample size in the future.

Table 4: Mann-Whitney-U Test

| | Small Pits | Large Pits | Puncture Pits | Fine Scratches | Coarse Scratches | Hypercoarse Scratches |
|--------------------------------|-------------------|------------|---------------|----------------|------------------|-----------------------|
| Mann-Whitney U | 14.500 | 13.500 | 7.500 | 8.000 | 11.500 | 10.000 |
| Wilcoxon W | 150.500 | 149.500 | 10.500 | 11.000 | 147.500 | 13.000 |
| Z | -.212 | -.359 | -1.207 | -1.235 | -.697 | -1.008 |
| Asymp. Sig. (2-tailed) | .832 | .719 | .228 | .217 | .486 | .314 |
| Exact Sig. [2*(1-tailed Sig.)] | .837 ^b | .732 | .261 | .327 | .549 | .471 |

6 DISCUSSION

The statistical analysis shows that the microwear signature of *C. williamsi* falls between that of colobine monkeys and papionins and is very similar to that of *C. apella*. Frugivorous primates generally tend to have a higher amounts of pitting than folivorous primates (Lucas, 2004). One would, therefore, expect low amounts of pitting and high amounts of scratches in *C. williamsi* microwear. However, when pit counts are compared with other primates, *C. williamsi* has a relatively high number of pits. Large pits are fewer in *C. williamsi* than in *C. polykomos*, *C. angolensis* and *C. apella*. Puncture pits, in contrast, are among the highest for *C. williamsi*. The Tukey's HSD test confirms that puncture pit counts of *C. williamsi* are statistically significantly different from several papionins.

At the same time, *C. williamsi* has a relatively low number of scratches. For instance, *C. williamsi* has a lower fine scratch count than the *Theropithecus* species or *P. ursinus* and a lower hypercoarse scratch count than most folivores. Scratch counts for *C. williamsi*, therefore, are more similar to those of the papionins than those of folivores and gramnivores. Overall, *C. williamsi* and *C. apella* show many similarities when their microwear features are compared.

The PCA shows that *C. williamsi* has many similarities with the folivores and *C. apella* and the analysis separates *C. williamsi* from several papionins and gramnivores. In the PCA *C. williamsi* clearly clusters with *C. apella*, *C. polykokomos*, *P. badius* and *C. angolensis*. Furthermore, *C. williamsi* is separated from the gramnivores *T. darti* and *T. danieli* based on small pits and fine scratches.

Overall, the microwear of *C. williamsi* appears to be a mix between the wear typical to terrestrial papionins and that of the arboreal leaf-eaters. This result is not surprising for a

terrestrial leaf-eater and the DFA confirms the hypothesis that *C. williamsi* was terrestrial and folivorous.

Only 33% of the specimens were correctly classified when tested for species, however. While sharing the same diet and tooth morphology with other folivores, *C. williamsi* shared a habitat with the papionins as confirmed by the DFA. This dichotomy between habitat and diet as compared to other taxa is probably also the reason why so many specimens were misclassified when tested for species affiliation.

As so many studies point to terrestriality of *C. williamsi*, it was important to also compare *C. williamsi* to granivores. The dental microwear analysis presented here could not confirm that grasses played a role in the diet of *C. williamsi*. In particular, *T. darti* and *T. danieli* have a much higher scratch count than *C. williamsi*. El-Zaatari et al. (2005), in contrast, found great similarities between the microwear of *C. williamsi* and *T. gelada* in their dental microwear study. There are different possible explanations for the differing results of the two microwear studies.

While one would expect a large fine scratch count for *T. gelada*, this study did not show a particularly high amount of fine scratches for the extant granivore. As *T. gelada* is a relatively rare animal, many museum specimens stem from zoos. It is possible that this or previous studies unknowingly incorporated zoo specimens into the analysis. Zoo specimens, in turn, can have atypical microwear signatures as a result of different types of food.

Further, in a molar microwear texture analysis of *T. gelada* stemming from undisturbed Ethiopian habitats, Shapiro et al. (2013) found that *T. gelada* microwear is much more complex than indicated by previous studies. The authors criticize that previous studies often sample animals from disturbed, marginal habitats. The authors attribute the higher complexity in microwear to either grit or seasonal fallback foods.

Differences between studies could also be explained by the Plio-Pleistocene climatic shift. Most of the *C. williamsi* specimens considered here were relatively old specimens originating from Sterkfontein. Based on an SEM dental microwear analysis, El-Zataari et al. (2005) suggested that there might have been a temporal diet change between *C. williamsi* specimens from the even older site of Makapansgat to *C. williamsi* found at Sterkfontein.

The study presented here also looked for possible temporal shifts. However, the dental microwear analysis did not show a significant shift between the older sites of Sterkfontein and Makapansgat and two specimens from the younger site Bolt's Farm. The sample size is too small, however, to make a definitive conclusion.

Colobine monkeys have been observed to have more scratches than pits when compared to cercopithecines (Lucas and Teaford, 1994). Fine scratch count, which is relatively low in *C. williamsi*, is actually typical for leaf eaters (Teaford, 1988). Pits, therefore, are more common in primates specializing in fruit. Teaford and Walker (1984) found that at least 40% of the microwear features of frugivores in their study were pits. Among frugivores, in turn, hard-object feeders tend to have a higher average pit count than animals specializing on soft fruit (Teaford and Ungar, 2000). In particular puncture pits are believed to be a characteristic of hard-object feeders (Godfrey et al., 2004).

Cercopithecoides williamsi demonstrates a lot of similarities with hard-object consumers, especially with *C. apella*. Puncture pits, which are common in *C. apella* and *C. williamsi*, are believed to be typical for hard-object specialists (Godfrey et al., 2004). Further, *C. williamsi* has a lot in common with the two seed specialists *C. angolensis* and *C. polykomos*. Both, *C. angolensis* and *C. polykomos* primarily rely on seeds and mature leaves (Koyabu and Endo, 2009). It has actually been argued that colobine monkey teeth could be adapted to both, leaf and

seed predation (Lucas and Teaford, 1994). Seed predation, in turn, is a form of hard-object feeding.

Based on this initial assessment, one could falsely speculate that *C. williamsi*, therefore, clusters with leaf eaters not because of leaves, but due to hard-object feeding. There are, however, a number of arguments against hard-object feeding of *C. williamsi*. The amount of large pits in *C. apella*, and *C. angolensis*, for example, is much higher than in *C. williamsi*. *C. williamsi* and *P. badius* both have lower large pit counts. *P. badius*, in turn, prefers young leaves and ingests fewer seeds than the other two extant African colobines (Koyabu and Endo, 2009).

While this difference is not statistically significant, there are other reasons why *C. williamsi* was likely not a hard-object specialist. An important adaptation to hard-object feeding are strong chewing muscles (Dominy et al., 2008). *Cercopithecoides williamsi*, however, did not have a strongly developed nuchal crest or sagittal crest (Simons and Delson, 1978), pointing to a relatively weak chewing musculature.

El-Zataari et al. (2005) found a relatively high number of pits in *C. williamsi* from Makapansgat, but not from Sterkfontein or Swartkrans. The authors concluded that the pits were either caused by hard-object feeding or grit adhering to food at Makapansgat. They further argued that the primates at Sterkfontein and Swartkrans likely concentrated on soft foods. Szalay and Delson (1979) have indicated that *C. williamsi* might have fed on soft food items covered in grit. The dental microwear study presented here confirms that the dental microwear signature of *C. williamsi* was, at least in part, caused by soft food covered in grit.

Something *C. apella* and many colobine species have in common is the incorporation of at least some fruit into their diet. Dela (2012) studied Asian colobines in human-modified environments and found that in an environment high in fruit availability and low in competition,

colobine monkeys can incorporate a much larger percentage of ripe fruit into their diet than originally believed. Daegling and McGraw (2001) also observed a high fruit intake of up to 70% of the entire diet for *C. polykomos* in C^ote d'Ivoire .

While tooth morphology and dental microwear clearly indicate that the fallback food of *C. williamsi* must have been leaves, the similarities with the fruit eater *C. apella* indicate that it probably also ate fruit. As *C. williamsi* was terrestrial, the fruit could have been close to the ground or on the ground and therefore covered with grit. Grit can mimic the effects of hard-object-feeding in dental microwear formation (Daegling and Grine, 1999). Soft fruit covered in grit would therefore explain why *C. williamsi* shows so many similarities with hard-object feeders and yet is not adapted to hard-object feeding.

Even if a food item plays a role nutritionally, it will not have an influence on tooth morphology unless it is habitually eaten in large amounts (Kay, 1975). *Cercopithecoides williamsi* could, therefore, have eaten some fruit without showing any adaptations to it. Leaf-eaters are selective feeders even when it comes to leaves themselves (Harris et al., 2009). Because the protein to fiber ratio of a leaf is important for leaf-eating monkeys, they cannot simply choose any type of leaf (Wasserman and Chapman, 2003). Although leaves themselves are abundant in many environments, the same is not true for young leaves, which are preferred by many taxa (Harris et al., 2009).

The heavy pitting of *C. williamsi* teeth, which is not caused by hard-object feeding, is a further indicator that *C. williamsi* was terrestrial. While some of the pitting might have been caused by phytoliths, grit is a significantly more effective microwear agent than phytoliths (Lucas et al., 2013). The heavily worn teeth of *C. williamsi* (Benefit, 1999) point to a rather abrasive diet. While there is evidence of dust in the tree canopy (Ungar et al., 1995), there are

naturally higher amounts of grit closer to the ground. It is, therefore, likely that the foods eaten by *C. williamsi* were found close to the ground.

The consumption of underground storage organs (USOs) such as tubers, corms, bulbs, and rhizomes, could have also played a role as well. Both, Fourie et al. (2008) and Codron et al. (2005) found varied isotopic signatures in *C. williamsi* specimens independently of site. Among the specimens with different isotopic signals are fossils from Sterkfontein (Codron et al., 2005) which were also sampled in this study. Underground storage organs have both C₃ and C₄/CAM isotopic signatures (Yeakel et al., 2007) and, unless washed, will be covered in grit. Daegling and Grine (1999), in fact, found a high incidence of pitting of *P. ursinus* teeth after the animals consumed USOs during the dry season. Underground storage organs, therefore, could be an explanation for the mixed isotopic signals as well as some of the pitting of *C. williamsi* teeth. While African colobine monkeys are fully arboreal and do not include underground storage items into their diet, semi-terrestrial colobine monkeys in Asia have been seen to do so. Sayers and Norconk (2008), for instance, found that 7.7% of the diet of Himalayan *Semnopithecus entellus* consists of USOs. The utilization of USOs has also been witnessed for *Rhinopithecus brelichi* (Xiang et al., accepted to be published).

Jablonski (2002) argued that the reason for the extinction of terrestrial African Plio-Pleistocene colobine monkeys could have been competition with terrestrial papionins. This study could support her suggestion. As discussed in previous chapters, the habitat around the South African cave sites shifted from relatively closed to more open, drier environments from 3 to 1.5 myr ago (Lee-Thorp et al., 2007). With a last appearance date of 1.2 myr (El-Zataari et al., 2005), *C. williamsi* disappeared from the fossil record shortly thereafter. In east Africa *C. williamsi* also suddenly disappeared from the fossil record and the timing also coincides with

climatic changes to a more arid climate (Leakey, 1982). Leakey (1982), therefore, suggested that the large Plio-Pleistocene colobines, such as *C. williamsi*, might have gone extinct due to changes in climate.

The climatic shift likely led to an increased competition between *C. williamsi* and terrestrial papionins. Before its extinction, *C. williamsi* was present at older, more wooded sites, but also younger, more open habitats (El-Zataari et al., 2005) in South Africa. The disappearance of forests must have been an environmental stressor for a derived folivore like *C. williamsi*. *Cercopithecoides williamsi*, possibly, might have had a harder time finding enough adequate leaves as forests started disappearing in Plio-Pleistocene South Africa. *Cercopithecoides williamsi* might have, therefore, supplemented its diet with fruits and USOs and therefore entered into direct competition with the terrestrial papionins.

In fact, the only large colobine which survived this initial wave of extinctions among the genus *Cercopithecoides* was *C. kimuei*. *Cercopithecoides kimuei*, in turn, does not appear to have been as strongly adapted to folivory as the other members of the genus *Cercopithecoides* (Benefit, 2000). *C. kimeui* was likely better suited for a competition with more frugivorous primates, further supporting the idea that *C. williamsi* might have become extinct due to competition with terrestrial papionins.

7 CONCLUSIONS

The statistical analyses showed that there are indeed statistical differences between some microwear features recorded on *C. williamsi* teeth and those of other taxa. These statistical differences indicate that there are statistically significant groups in the data which in turn allows for comparisons of the taxa. The data confirms the hypotheses that *C. williamsi* was likely a folivore and that it is probable the monkey was fully or at least partially terrestrial. Moreover, the similarity to *C. apella* and a high number of enamel pits coupled with a weak chewing musculature support the suggestion of Szalay and Delson (1979) that *C. williamsi* ate soft foods covered in grit.

Cercopithecoides, *Parapapio* and *Theropithecus* coexisted at several South African sites, indicating some kind of niche differentiation between the species (Fourie et al., 2008). The niche of *C. williamsi* was thus likely a diet focusing on leaves. However, as forests retreated in South Africa during the onset of the Pleistocene, suitable leaves must have become scarcer.

Cercopithecoides williamsi shows many similarities with *C. apella*. *Cebus apella* in turn can be characterized as a durophagous and frugivorous. However, *C. apella* exhibits a strong chewing muscles whereas *C. williamsi* had a relatively weak masticatory apparatus (Szalay and Delson, 1979). The teeth of *C. williamsi* are also very worn (Benefit, 1999) which may be a reflection of excessive grit. Grit can, in fact, mimic the effects of durophagy on dental microwear (Daegling and Grine, 1999). Naturally, more grit would adhere to foods found on the ground-level or underground than on foods found in arboreal habitats. Fruit, for instance, can be a soft food item which can easily be covered in grit if picked up from the ground. Fruit is a common food item among colobines, and its incorporation into the diet of *C. williamsi* could explain the similarity with the frugivores *C. apella*.

Alternatively, USOs are covered in grit and their consumption would explain the mixed isotopic signals found by Fourie et al. (2008) and Codron et al. (2005) as well as the similar microwear signatures of *C. williamsi* and the durophagous *C. apella*. In summary, *C. williamsi* probably ate a combination of leaves, fruit, and USOs.

Jablonski (2002) suggested that *C. williamsi* became extinct as a result of competition with more ecologically aggressive terrestrial papionins. Leakey (1982) proposed climate deterioration and also competition with other primates to be the reason for the extinction of large Plio-Pleistocene colobines. The study presented here demonstrates that both, climate change and competition with terrestrial papionins, could have played a role in the extinction of *C. williamsi*.

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APPENDICES

*Appendix A: Statistical Analyses**A.1 Tukey's HSD Test***Table 5: Tukey's HSD Test Results**

| Multiple Comparisons | | | | | | | |
|----------------------|---------------------|----------------------|-----------------|------------|-------|-------------------------|-------------|
| Tukey HSD | | | | | | | |
| Dependent Variable | (I) Primate | (J) Primate | Mean Difference | Std. Error | Sig. | 95% Confidence Interval | |
| | | | | | | Lower Bound | Upper Bound |
| Small Pits | <i>C. williamsi</i> | <i>P. ursinus</i> | .2030 | .9790 | 1.000 | -3.202 | 3.608 |
| | | <i>C. polykomos</i> | 1.8889 | 1.6196 | .999 | -3.744 | 7.522 |
| | | <i>C. angolensis</i> | 4.3889 | 2.5609 | .940 | -4.518 | 13.295 |
| | | <i>G. gorilla</i> | 3.0139 | 1.8992 | .969 | -3.591 | 9.619 |
| | | <i>T. gelada</i> | 2.4246 | 1.5304 | .969 | -2.898 | 7.747 |
| | | <i>P. anubis</i> | -.2073 | 1.2505 | 1.000 | -4.556 | 4.142 |
| | | <i>Pp. jonesi</i> | 2.1824 | 1.0812 | .812 | -1.578 | 5.943 |
| | | <i>Pp. whitei</i> | 2.3697 | 1.2505 | .875 | -1.980 | 6.719 |
| | | <i>Pp. broomi</i> | -1.1111 | 1.2243 | 1.000 | -5.369 | 3.147 |
| | | <i>P. robinsoni</i> | 1.5139 | 1.2804 | .998 | -2.939 | 5.967 |
| | | <i>T. darti</i> | -2.7361 | 1.8992 | .987 | -9.341 | 3.869 |
| | | <i>T. danieli</i> | 1.4722 | 1.6196 | 1.000 | -4.161 | 7.105 |
| | | <i>P. badius</i> | 2.3889 | 2.5609 | 1.000 | -6.518 | 11.295 |
| <i>D. ingens</i> | 1.3175 | 1.2243 | .999 | -2.941 | 5.576 | | |

| | | | | | | | |
|---------------|---------------------|----------------------|----------|--------|-------------|--------|-------|
| | | <i>C. apella</i> | 2.9389 | 1.3551 | .717 | -1.774 | 7.652 |
| Large Pits | <i>C. williamsi</i> | <i>P. ursinus</i> | 1.1068 | .4861 | .641 | -.584 | 2.797 |
| | | <i>C. polykomos</i> | -1.5278 | .8041 | .872 | -4.324 | 1.269 |
| | | <i>C. angolensis</i> | -4.6111* | 1.2714 | .032 | -9.033 | -.189 |
| | | <i>G. gorilla</i> | .7639 | .9429 | 1.000 | -2.515 | 4.043 |
| | | <i>T. gelada</i> | .2460 | .7598 | 1.000 | -2.397 | 2.889 |
| | | <i>P. anubis</i> | .6197 | .6209 | 1.000 | -1.540 | 2.779 |
| | | <i>Pp. jonesi</i> | .9758 | .5368 | .907 | -.891 | 2.843 |
| | | <i>Pp. whitei</i> | .3120 | .6209 | 1.000 | -1.847 | 2.471 |
| | | <i>Pp. broomi</i> | 1.6746 | .6078 | .306 | -.439 | 3.789 |
| | | <i>P. robinsoni</i> | 1.2639 | .6357 | .828 | -.947 | 3.475 |
| | | <i>T. darti</i> | 1.2639 | .9429 | .994 | -2.015 | 4.543 |
| | | <i>T. danieli</i> | 1.1389 | .8041 | .989 | -1.658 | 3.935 |
| | | <i>P. badius</i> | .1389 | 1.2714 | 1.000 | -4.283 | 4.561 |
| | | <i>D. ingens</i> | .4246 | .6078 | 1.000 | -1.689 | 2.539 |
| | | <i>C. apella</i> | -2.0611 | .6728 | .155 | -4.401 | .279 |
| Puncture Pits | <i>C. williamsi</i> | <i>P. ursinus</i> | 1.6774* | .3582 | .001 | .432 | 2.923 |
| | | <i>C. polykomos</i> | .8889 | .5926 | .981 | -1.172 | 2.950 |
| | | <i>C. angolensis</i> | -1.7778 | .9369 | .874 | -5.036 | 1.481 |
| | | <i>G. gorilla</i> | .2222 | .6948 | 1.000 | -2.194 | 2.639 |
| | | <i>T. gelada</i> | 1.6151 | .5599 | .234 | -.332 | 3.562 |
| | | <i>P. anubis</i> | 1.7415* | .4575 | .018 | .150 | 3.333 |
| | | <i>Pp. jonesi</i> | 1.1027 | .3956 | .287 | -.273 | 2.478 |
| | | <i>Pp. whitei</i> | 1.4722 | .4575 | .104 | -.119 | 3.063 |

| | | | | | | | |
|---------------------|---------------------|----------------------|----------|--------|-------------|--------|-------|
| | | <i>Pp. broomi</i> | 1.5794* | .4479 | .043 | .022 | 3.137 |
| | | <i>P. robinsoni</i> | 1.3056 | .4685 | .287 | -.324 | 2.935 |
| | | <i>T. darti</i> | 1.5972 | .6948 | .625 | -.819 | 4.014 |
| | | <i>T. danieli</i> | 1.8889 | .5926 | .113 | -.172 | 3.950 |
| | | <i>P. badius</i> | -.2778 | .9369 | 1.000 | -3.536 | 2.981 |
| | | <i>D. ingens</i> | 1.7579* | .4479 | .012 | .200 | 3.316 |
| | | <i>C. apella</i> | .6722 | .4958 | .993 | -1.052 | 2.396 |
| Fine Scratches | <i>C. williamsi</i> | <i>P. ursinus</i> | -2.0876* | .4485 | .001 | -3.648 | -.528 |
| | | <i>C. polykomos</i> | -.6389 | .7420 | 1.000 | -3.220 | 1.942 |
| | | <i>C. angolensis</i> | -.3056 | 1.1732 | 1.000 | -4.386 | 3.775 |
| | | <i>G. gorilla</i> | .4444 | .8701 | 1.000 | -2.582 | 3.471 |
| | | <i>T. gelada</i> | -.7341 | .7011 | 1.000 | -3.173 | 1.704 |
| | | <i>P. anubis</i> | -.4979 | .5729 | 1.000 | -2.490 | 1.495 |
| | | <i>Pp. jonesi</i> | -1.1534 | .4953 | .603 | -2.876 | .569 |
| | | <i>Pp. whitei</i> | -1.5748 | .5729 | .309 | -3.567 | .418 |
| | | <i>Pp. broomi</i> | -1.0198 | .5609 | .906 | -2.971 | .931 |
| | | <i>P. robinsoni</i> | -.0556 | .5866 | 1.000 | -2.096 | 1.985 |
| | | <i>T. darti</i> | -2.1806 | .8701 | .472 | -5.207 | .846 |
| | | <i>T. danieli</i> | -1.2222 | .7420 | .957 | -3.803 | 1.358 |
| | | <i>P. badius</i> | -1.0556 | 1.1732 | 1.000 | -5.136 | 3.025 |
| | | <i>D. ingens</i> | -.4127 | .5609 | 1.000 | -2.363 | 1.538 |
| | | <i>C. apella</i> | .2944 | .6208 | 1.000 | -1.865 | 2.454 |
| Coarse Scratches | <i>C. williamsi</i> | <i>P. ursinus</i> | -.5278 | .4575 | .999 | -2.119 | 1.063 |
| | | <i>C. polykomos</i> | -.4444 | .7568 | 1.000 | -3.077 | 2.188 |

| | | | | | | | |
|--------------------------|---------------------|----------------------|---------|--------|-------|--------|-------|
| | | <i>C. angolensis</i> | .1389 | 1.1966 | 1.000 | -4.023 | 4.301 |
| | | <i>G. gorilla</i> | -1.2361 | .8874 | .991 | -4.322 | 1.850 |
| | | <i>T. gelada</i> | -.7897 | .7151 | .999 | -3.277 | 1.697 |
| | | <i>P. anubis</i> | -.8996 | .5843 | .976 | -2.932 | 1.133 |
| | | <i>Pp. jonesi</i> | -1.1872 | .5052 | .588 | -2.944 | .570 |
| | | <i>Pp. whitei</i> | -1.2073 | .5843 | .784 | -3.240 | .825 |
| | | <i>Pp. broomi</i> | -1.2540 | .5721 | .701 | -3.244 | .736 |
| | | <i>P. robinsoni</i> | -.8194 | .5983 | .992 | -2.900 | 1.261 |
| | | <i>T. darti</i> | -.7361 | .8874 | 1.000 | -3.822 | 2.350 |
| | | <i>T. danieli</i> | .3889 | .7568 | 1.000 | -2.243 | 3.021 |
| | | <i>P. badius</i> | -.1111 | 1.1966 | 1.000 | -4.273 | 4.051 |
| | | <i>D. ingens</i> | -1.2183 | .5721 | .744 | -3.208 | .771 |
| | | <i>C. apella</i> | -.0611 | .6332 | 1.000 | -2.263 | 2.141 |
| Hypercoarse Scratches | <i>C. williamsi</i> | <i>P. ursinus</i> | -.1816 | .3299 | 1.000 | -1.329 | .966 |
| | | <i>C. polykomos</i> | -1.6111 | .5458 | .201 | -3.509 | .287 |
| | | <i>C. angolensis</i> | -.4444 | .8629 | 1.000 | -3.446 | 2.557 |
| | | <i>G. gorilla</i> | -1.1944 | .6400 | .887 | -3.420 | 1.031 |
| | | <i>T. gelada</i> | .2341 | .5157 | 1.000 | -1.559 | 2.028 |
| | | <i>P. anubis</i> | -.8868 | .4214 | .760 | -2.352 | .579 |
| | | <i>Pp. jonesi</i> | -.6944 | .3643 | .870 | -1.962 | .573 |
| | | <i>Pp. whitei</i> | -.0406 | .4214 | 1.000 | -1.506 | 1.425 |
| | | <i>Pp. broomi</i> | -.3730 | .4126 | 1.000 | -1.808 | 1.062 |
| | | <i>P. robinsoni</i> | -1.2361 | .4315 | .244 | -2.737 | .265 |
| | | <i>T. darti</i> | -.0694 | .6400 | 1.000 | -2.295 | 2.156 |

| | | | | | | | |
|-----------------------------|---------------------|----------------------|----------|--------|-------------|---------|--------|
| | | <i>T. danieli</i> | -1.5278 | .5458 | .280 | -3.426 | .370 |
| | | <i>P. badius</i> | .3056 | .8629 | 1.000 | -2.696 | 3.307 |
| | | <i>D. ingens</i> | -.4516 | .4126 | .999 | -1.886 | .983 |
| | | <i>C. apella</i> | .0056 | .4566 | 1.000 | -1.583 | 1.594 |
| Overall number of pits | <i>C. williamsi</i> | <i>P. ursinus</i> | 2.9872 | 1.1107 | .346 | -.876 | 6.850 |
| | | <i>C. polykomos</i> | 2.6667 | 1.8375 | .986 | -3.724 | 9.057 |
| | | <i>C. angolensis</i> | -2.7500 | 2.9053 | 1.000 | -12.854 | 7.354 |
| | | <i>G. gorilla</i> | 4.0000 | 2.1546 | .891 | -3.493 | 11.493 |
| | | <i>T. gelada</i> | 4.2857 | 1.7362 | .500 | -1.753 | 10.324 |
| | | <i>P. anubis</i> | 2.2692 | 1.4187 | .966 | -2.665 | 7.203 |
| | | <i>Pp. jonesi</i> | 4.3043* | 1.2266 | .046 | .038 | 8.570 |
| | | <i>Pp. whitei</i> | 4.1923 | 1.4187 | .200 | -.742 | 9.126 |
| | | <i>Pp. broomi</i> | 2.2143 | 1.3890 | .967 | -2.616 | 7.045 |
| | | <i>P. robinsoni</i> | 4.1667 | 1.4526 | .242 | -.885 | 9.219 |
| | | <i>T. darti</i> | .1250 | 2.1546 | 1.000 | -7.368 | 7.618 |
| | | <i>T. danieli</i> | 5.1667 | 1.8375 | .273 | -1.224 | 11.557 |
| | | <i>P. badius</i> | 2.2500 | 2.9053 | 1.000 | -7.854 | 12.354 |
| | | <i>D. ingens</i> | 3.4643 | 1.3890 | .481 | -1.366 | 8.295 |
| | | <i>C. apella</i> | 1.6500 | 1.5373 | .999 | -3.697 | 6.997 |
| Overall number of scratches | <i>C. williamsi</i> | <i>P. ursinus</i> | -2.7991* | .6189 | .001 | -4.952 | -.647 |
| | | <i>C. polykomos</i> | -1.4722 | 1.0238 | .987 | -5.033 | 2.089 |
| | | <i>C. angolensis</i> | -.6389 | 1.6188 | 1.000 | -6.269 | 4.991 |
| | | <i>G. gorilla</i> | -2.0139 | 1.2005 | .950 | -6.189 | 2.161 |
| | | <i>T. gelada</i> | -1.3175 | .9674 | .993 | -4.682 | 2.047 |

| | | | | | | |
|--|---------------------|----------|--------|-------------|--------|-------|
| | <i>P. anubis</i> | -2.0812 | .7905 | .383 | -4.830 | .668 |
| | <i>Pp. jonesi</i> | -3.0628* | .6835 | .001 | -5.440 | -.686 |
| | <i>Pp. whitei</i> | -2.7735* | .7905 | .046 | -5.523 | -.024 |
| | <i>Pp. broomi</i> | -2.6746 | .7739 | .053 | -5.366 | .017 |
| | <i>P. robinsoni</i> | -2.1389 | .8094 | .377 | -4.954 | .676 |
| | <i>T. darti</i> | -3.0139 | 1.2005 | .469 | -7.189 | 1.161 |
| | <i>T. danieli</i> | -2.3889 | 1.0238 | .600 | -5.950 | 1.172 |
| | <i>P. badius</i> | -.8889 | 1.6188 | 1.000 | -6.519 | 4.741 |
| | <i>D. ingens</i> | -2.2103 | .7739 | .249 | -4.902 | .481 |
| | <i>C. apella</i> | .2111 | .8566 | 1.000 | -2.768 | 3.190 |

A.2 Discriminant Function Analysis

Table 6: DFA Habitat Predictions

| Specimen | Habitat Prediction |
|----------|---------------------|
| STS357 | Terrestrial, mixed |
| STS295 | Terrestrial, mixed |
| STS394 | Terrestrial, forest |
| STS541 | Terrestrial, forest |
| STS288 | Arboreal, forest |
| STS282 | Terrestrial, forest |
| STS366 | Terrestrial, forest |
| STS270 | Arboreal, forest |
| STS392 | Arboreal, forest |
| STS300 | Terrestrial, mixed |
| STS344 | Arboreal, forest |
| SWP495 | Terrestrial, mixed |
| BF42B | Arboreal, forest |
| MP3 | Terrestrial, forest |
| STS294 | Terrestrial, mixed |
| STS350 | Terrestrial, mixed |
| BF42A | Terrestrial, forest |
| STS541 | Terrestrial, forest |

Table 7: DFA Dietary Predictions

| Specimen | Dietary Prediction |
|----------|--------------------|
| STS357 | Gramnivore |
| STS295 | Gramnivore |
| STS394 | Folivore |
| STS541 | Folivore |
| STS288 | Folivore |
| STS282 | Folivore |
| STS366 | Folivore |
| STS270 | Frugivore |
| STS392 | Folivore |
| STS300 | Folivore |
| STS344 | Frugivore |
| SWP495 | Omnivore |
| BF42B | Frugivore |
| MP3 | Folivore |
| STS294 | Gramnivore |
| STS350 | Gramnivore |
| BF42A | Omnivore |
| STS541 | Folivore |

Table 8: DFA Species Predictions

| Specimen | Species Prediction |
|----------|----------------------|
| STS357 | <i>P. ursinus</i> |
| STS295 | <i>T. darti</i> |
| STS394 | <i>C. williamsi</i> |
| STS541 | <i>P. badius</i> |
| STS288 | <i>C. williamsi</i> |
| STS282 | <i>C. williamsi</i> |
| STS366 | <i>C. williamsi</i> |
| STS270 | <i>C. apella</i> |
| STS392 | <i>P. badius</i> |
| STS300 | <i>C. williamsi</i> |
| STS344 | <i>C. apella</i> |
| SWP495 | <i>T. darti</i> |
| BF42B | <i>C. angolensis</i> |
| MP3 | <i>C. williamsi</i> |
| STS294 | <i>T. darti</i> |
| STS350 | <i>T. gelada</i> |
| BF42A | <i>G. gorilla</i> |
| STS541 | <i>P. badius</i> |

Appendix B: List of Specimens**Table 9: List of Specimens**

| Specimen | Primate |
|----------|---------------------|
| STS357 | <i>C. williamsi</i> |
| STS295 | <i>C. williamsi</i> |
| STS394 | <i>C. williamsi</i> |
| STS541 | <i>C. williamsi</i> |
| STS288 | <i>C. williamsi</i> |
| STS282 | <i>C. williamsi</i> |
| STS366 | <i>C. williamsi</i> |
| STS270 | <i>C. williamsi</i> |
| STS392 | <i>C. williamsi</i> |
| STS300 | <i>C. williamsi</i> |
| STS344 | <i>C. williamsi</i> |
| SWP495 | <i>C. williamsi</i> |
| BF42B | <i>C. williamsi</i> |
| MP3 | <i>C. williamsi</i> |
| STS294 | <i>C. williamsi</i> |
| STS350 | <i>C. williamsi</i> |
| BF42A | <i>C. williamsi</i> |
| STS541 | <i>C. williamsi</i> |
| NNMcatE | <i>P. ursinus</i> |
| NNMcatF | <i>P. ursinus</i> |
| NNMcatG | <i>P. ursinus</i> |
| NNM1289 | <i>P. ursinus</i> |
| ZM40415 | <i>P. ursinus</i> |
| ZM36895 | <i>P. ursinus</i> |
| ZM37116 | <i>P. ursinus</i> |
| ZM36896 | <i>P. ursinus</i> |
| ZM33675 | <i>P. ursinus</i> |
| ZM37274 | <i>P. ursinus</i> |
| ZM35923 | <i>P. ursinus</i> |
| ZM40898 | <i>P. ursinus</i> |
| ZM38447 | <i>P. ursinus</i> |
| ZM38333 | <i>P. ursinus</i> |
| ZM38323 | <i>P. ursinus</i> |
| ZM38364 | <i>P. ursinus</i> |
| ZM36895 | <i>P. ursinus</i> |
| ZM37165 | <i>P. ursinus</i> |
| ZM38314 | <i>P. ursinus</i> |
| ZM38373 | <i>P. ursinus</i> |

| | |
|----------|----------------------|
| ZM38370 | <i>P. ursinus</i> |
| ZM38380 | <i>P. ursinus</i> |
| ZM38361 | <i>P. ursinus</i> |
| ZM37678 | <i>P. ursinus</i> |
| ZM38351 | <i>P. ursinus</i> |
| ZM38365 | <i>P. ursinus</i> |
| ZM37273 | <i>P. ursinus</i> |
| ZM38225 | <i>P. ursinus</i> |
| ZM38366 | <i>P. ursinus</i> |
| ZM38363 | <i>P. ursinus</i> |
| ZM38342 | <i>P. ursinus</i> |
| ZM38335 | <i>P. ursinus</i> |
| ZM38369 | <i>P. ursinus</i> |
| ZM35921 | <i>P. ursinus</i> |
| ZM6859 | <i>P. ursinus</i> |
| ZM35818 | <i>P. ursinus</i> |
| ZM35919 | <i>P. ursinus</i> |
| ZM33672 | <i>P. ursinus</i> |
| MCZ23120 | <i>P. ursinus</i> |
| MCZ21149 | <i>C. polykomos</i> |
| MCZ21150 | <i>C. polykomos</i> |
| MCZ21151 | <i>C. polykomos</i> |
| MCZ21152 | <i>C. polykomos</i> |
| MCZ21147 | <i>C. polykomos</i> |
| MCZ22356 | <i>C. polykomos</i> |
| MCZ22629 | <i>C. angolensis</i> |
| MCZ22356 | <i>C. angolensis</i> |
| MCZ29048 | <i>G. gorilla</i> |
| MCZ46325 | <i>G. gorilla</i> |
| MCZ38326 | <i>G. gorilla</i> |
| MCZ46413 | <i>G. gorilla</i> |
| NNM39135 | <i>T. gelada</i> |
| NNM39132 | <i>T. gelada</i> |
| NNM11416 | <i>T. gelada</i> |
| NNM1950 | <i>T. gelada</i> |
| MCZ23986 | <i>T. gelada</i> |
| MCZ6377 | <i>T. gelada</i> |
| NNM39130 | <i>T. gelada</i> |
| MCZ21161 | <i>P. anubis</i> |
| MCZ23091 | <i>P. anubis</i> |
| MCZ26472 | <i>P. anubis</i> |

| | |
|----------|-------------------|
| MCZ8304 | <i>P. anubis</i> |
| MCZ17343 | <i>P. anubis</i> |
| MCZ23084 | <i>P. anubis</i> |
| MCZ29729 | <i>P. anubis</i> |
| MCZ29786 | <i>P. anubis</i> |
| MCZ29791 | <i>P. anubis</i> |
| MCZ31619 | <i>P. anubis</i> |
| MCZ17342 | <i>P. anubis</i> |
| MCZ23083 | <i>P. anubis</i> |
| MCZ21161 | <i>P. anubis</i> |
| STS344 | <i>Pp. jonesi</i> |
| STS355 | <i>Pp. jonesi</i> |
| STS329 | <i>Pp. jonesi</i> |
| STS372A | <i>Pp. jonesi</i> |
| STS333 | <i>Pp. jonesi</i> |
| STS381 | <i>Pp. jonesi</i> |
| STS306 | <i>Pp. jonesi</i> |
| STS250 | <i>Pp. jonesi</i> |
| STS340 | <i>Pp. jonesi</i> |
| STS355 | <i>Pp. jonesi</i> |
| STS287 | <i>Pp. jonesi</i> |
| SK412 | <i>Pp. jonesi</i> |
| SK462 | <i>Pp. jonesi</i> |
| SK579 | <i>Pp. jonesi</i> |
| SK414 | <i>Pp. jonesi</i> |
| SK437 | <i>Pp. jonesi</i> |
| SK433 | <i>Pp. jonesi</i> |
| STS390 | <i>Pp. jonesi</i> |
| STS276 | <i>Pp. jonesi</i> |
| SK412 | <i>Pp. jonesi</i> |
| SK579 | <i>Pp. jonesi</i> |
| STS306 | <i>Pp. jonesi</i> |
| STS372A | <i>Pp. jonesi</i> |
| STS370B | <i>Pp. whitei</i> |
| STS259 | <i>Pp. whitei</i> |
| STS303 | <i>Pp. whitei</i> |
| STSunnum | <i>Pp. whitei</i> |
| STS352 | <i>Pp. whitei</i> |
| STS563 | <i>Pp. whitei</i> |
| STS359 | <i>Pp. whitei</i> |
| STS414 | <i>Pp. whitei</i> |

| | |
|---------|---------------------|
| STS370A | <i>Pp. whitei</i> |
| MP239 | <i>Pp. whitei</i> |
| MP47 | <i>Pp. whitei</i> |
| T89-154 | <i>Pp. whitei</i> |
| STS563 | <i>Pp. whitei</i> |
| STS374A | <i>Pp. broomi</i> |
| STS373B | <i>Pp. broomi</i> |
| STS354 | <i>Pp. broomi</i> |
| STS325 | <i>Pp. broomi</i> |
| STS362 | <i>Pp. broomi</i> |
| STS368A | <i>Pp. broomi</i> |
| STS414B | <i>Pp. broomi</i> |
| STS474 | <i>Pp. broomi</i> |
| STS294 | <i>Pp. broomi</i> |
| STS319 | <i>Pp. broomi</i> |
| STS324 | <i>Pp. broomi</i> |
| STS373A | <i>Pp. broomi</i> |
| MP118 | <i>Pp. broomi</i> |
| MP2 | <i>Pp. broomi</i> |
| SK408 | <i>P. robinsoni</i> |
| SK417 | <i>P. robinsoni</i> |
| SK602 | <i>P. robinsoni</i> |
| SK549 | <i>P. robinsoni</i> |
| SK571B | <i>P. robinsoni</i> |
| SK557 | <i>P. robinsoni</i> |
| SK436 | <i>P. robinsoni</i> |
| SK416 | <i>P. robinsoni</i> |
| SK555 | <i>P. robinsoni</i> |
| SK14083 | <i>P. robinsoni</i> |
| SK550 | <i>P. robinsoni</i> |
| SK445 | <i>P. robinsoni</i> |
| MP222 | <i>T. darti</i> |
| MP76 | <i>T. darti</i> |
| MP168 | <i>T. darti</i> |
| M3073 | <i>T. darti</i> |
| SK44? | <i>T. danieli</i> |
| SK575A | <i>T. danieli</i> |
| SK405 | <i>T. danieli</i> |
| SK411 | <i>T. danieli</i> |
| SK402 | <i>T. danieli</i> |
| SK593 | <i>T. danieli</i> |

| | |
|----------|------------------|
| MCZ31940 | <i>P. badius</i> |
| MCZ39400 | <i>P. badius</i> |
| SK600 | <i>D. ingens</i> |
| SK413 | <i>D. ingens</i> |
| SK574 | <i>D. ingens</i> |
| SK603 | <i>D. ingens</i> |
| SK542a | <i>D. ingens</i> |
| SK415 | <i>D. ingens</i> |
| SK428 | <i>D. ingens</i> |
| SK440 | <i>D. ingens</i> |
| SK545 | <i>D. ingens</i> |
| SK578A | <i>D. ingens</i> |
| SK14004 | <i>D. ingens</i> |
| SK401 | <i>D. ingens</i> |
| SK561 | <i>D. ingens</i> |
| MCZ30724 | <i>C. apella</i> |
| MCZ31065 | <i>C. apella</i> |
| MCZ31070 | <i>C. apella</i> |
| MCZ31066 | <i>C. apella</i> |
| MCZ29789 | <i>C. apella</i> |
| MCZ31071 | <i>C. apella</i> |
| MCZ31073 | <i>C. apella</i> |
| MCZ30722 | <i>C. apella</i> |
| MCZ29729 | <i>C. apella</i> |
| MCZ31068 | <i>C. apella</i> |