Senior Honors Thesis

# Microwear Analysis of Five Extant Primate Species in Kibale National Park

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May 14, 2010

## Introduction

The goal of this study was to investigate the microwear patterns on the teeth of five extant primates from Kibale National Park in order to build a microwear description of their dietary habits. This study was undertaken to determine if dental microwear analysis reflects the known dietary habits of the primates living in the park. The five primates each have distinct feeding habits. If dental microwear analysis reflects modern primates feeding habits, it will allow for comparison between other primates and their diets along with reconstructing diet and habitats of extinct primates. Thus, microwear analysis can be used as an independent evaluation of information collected in the field about diet.

Microwear analysis involves identifying and counting features on the enamel surface to determine the types of food that were processed by the tooth (Semprebon *et al.*, 2004b). This type of analysis allows researchers to determine the types of foods an animal ate in the last days of its life. Features that are examined include pits, defined as circular or semicircular scars left on the enamel surface of the tooth (Figure 1), and scratches with straight sides parallel to each other left on the enamel surface (Figure 2). The number of pits and scratches correlate with the types of food consumed. A tooth with a surface that is heavily pitted suggests the animal ate hard food items (e.g., seeds and nuts). A tooth that has many scratches on the enamel surface suggests the animal ate tough food items (e.g., mature leaves and grasses). A tooth with nearly equal numbers of pits and scratches on the enamel surface suggests mixed food items (e.g., a mixture of hard and tough food items).

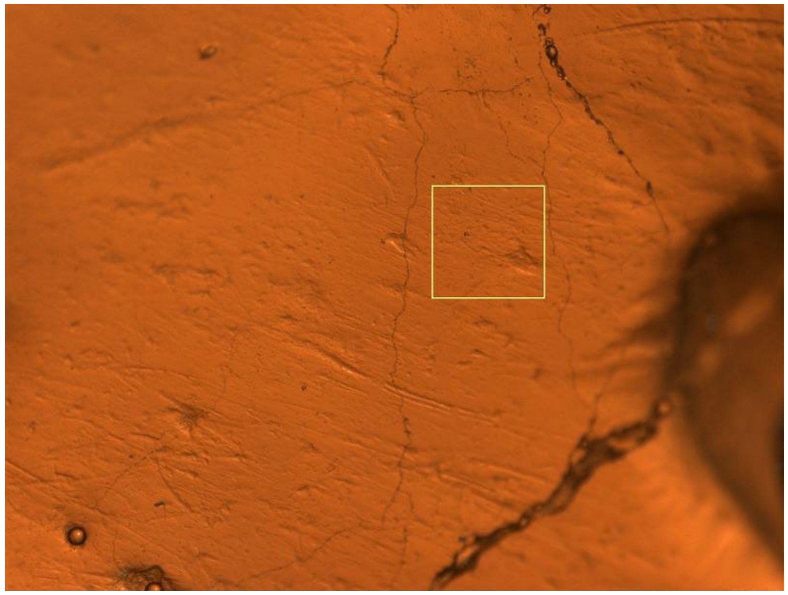

**Figure 1: The photograph is of an orangutan tooth, taken at 35X magnification by Nelson. The square highlights pits seen on the cast.**

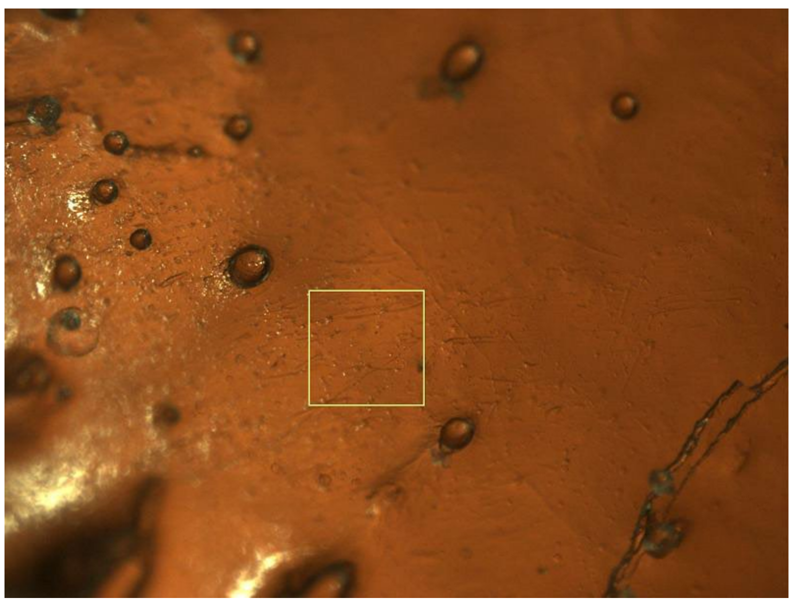

**Figure 2: The photograph is of an orangutan tooth, taken at 35X magnification by Nelson. The square highlights scratches seen on the cast.**

There are two types of magnification analysis that can be used to obtain microwear information, low-magnification refractive light microscopy (35X) and scanning electron microscopy (SEM). Low-magnification techniques will be employed in this study because the costs are negligible when compared to SEM, and the results of a study are obtained in a much shorter amount of time. Low-magnification also allows for a larger sample size and looks at a larger surface of the tooth. In low-magnification, the light refracting through a mold of the tooth, rather than measurements of features on the tooth itself, allows researchers to identify the features (Solounias & Semprebon, 2002).

The microwear analyses were done on the right second molar from the maxilla ($M^2$) and in very few cases when the $M^2$ was unavailable for an individual, the right second molar from the mandible ($M_2$) was used. In some cases, the $M^2$ was far too worn for analysis, and the $M^3$ were used as a substitute. The teeth that were analyzed in this study were obtained from chimpanzees (*Pan troglodytes*), olive baboons (*Papio anubis*), red colobus (*Piliocolobus badius*), black-and-white colobus (*Colobus guereza*), and red-tail monkey (*Cercopithecus ascanius*). The samples were obtained from Kibale National Park over thirty years by researchers in the Kibale Chimp Project. From the dietary observations made at Kibale, hypotheses are put forward that describe possible outcomes of the microwear analysis (Table 1).

**Table 1: Species of primates, their preferred and fallback foods, and the expectations for the microwear analysis.**

| Species | Preferred Foods | Expectation | Fallback Foods | Expectation |
|---|---|---|---|---|
| *Pan troglodytes* | Fruits, young leaves, piths, and insects | Coarse scratches along with some small pits. | Stems, bark, and mature leaves | Fine scratches along with cross scratches and large pits |
| *Papio anubis* | Fruits | Coarse scratches along with small pits | Grasses and insects | Fine scratches and small pits |
| *Piliocolobus badius* | Buds, young, leaves, and fruits | Fine and coarse scratches and pits | Mature leaves | Coarse scratches |
| *Colobus guereza* | Young and mature leaves | fine scratches | Seeds and nuts | Large pits and coarse scratches |
| *Cercopithecus ascanius* | Fruits, leaves, and insects | Coarse scratches along with small pits | Mature leaves, insects, bark | Fine Scratches along with cross scratches also large and small pits |

These hypotheses are based on the preferred and fallback foods of each species. Preferred foods are food items that are chosen at a higher rate when compared to their abundance in an animal's habitat. Fallback foods, by contrast, are overly abundant in an animal's habitat, but have low nutritional value and are only selected when preferred foods are limited (Marshall & Wrangham, 2007).

According to Wrangham (1996), *P. troglodytes* consume mostly fruit and piths, but can rely on, leaves, stems, bark, and insects during dry seasons. *P. anubis* also relies heavily on fruits, along with grasses and some insects (Wrangham *et al.*, 1991). *P. badius* feeds off buds, young leaves, and fruit for most of its diet, and may take in mature leaves to supplement their diet (Chapman & Chapman, 2002). *C. guereza* mostly consumes young leaves and some mature leaves and can fall back to nuts and seeds

(Chapman *et al.*, 2004). In addition, *C. ascanius* consumes fruits, leaves, and insects, but can rely on the mature leaves and bark in its environment (Lambert, 2004).

If *P. troglodytes* were eating preferred foods, then the microwear should have small pits and coarse scratches caused by the fruit seeds and the tough exterior of the fruit sliding along the tooth's surface. If *P. troglodytes* were eating fallback foods, then the microwear should have fine scratches, from the leaves and piths processed, along with large pits and cross scratches, from the bark and stems. The hypothesis for the preferred foods for *P. troglodytes* will be applied to *P. anubis,* as they share preferred foods. However, if *P. anubis* individuals were eating fallback foods, then the microwear should have small pits, from the exoskeleton of the insects, and fine scratches, from the grasses. The microwear for *P. badius* should have fine scratches, from leaf buds, and coarse scratches, from leaves and fruit, with some pits, from fruit seeds. However, if *P. badius* were eating fallback foods, it would have coarse scratches, caused by the wear from mature leaves. Microwear evidence of *C. guereza* molars should have fine scratches caused by the mature leaves, its preferred food. Yet if wear on the tooth shows large pits and coarse scratches, *C. guereza* was most likely eating its fallback foods, nuts, and seeds. Lastly, if *C. ascanius* were eating preferred foods, then the microwear would have coarse scratches, from the exterior of the fruit, and small pits, from the seeds and exoskeletons of the insects. On the other hand, if *C. ascanius* were eating their fallback foods, then the microwear should have fine scratches, from the mature leaves, and small pits, left by the exoskeletons of the insects, along with cross scratches, from the bark (See Table 1). Furthermore, the statistical analysis of the three *frugivorous* species should match one another, whereas the two *folivorous* species should match one another.

These hypotheses were created using the information gathered from observations of the feeding habits of the five primates in Kibale. Kibale is in Uganda, next to the Ruwenzori Mountains (Chapman *et al*., 1997; Lwanga, 2006). Within this park, two long-term observation sites (Kanyawara and Ngogo) are dedicated to primate research (Chapman *et al*., 2003) and include information on the feeding habits of the primates across all seasons. The microwear analysis can now provide a basis of comparison between the observations and the physical evidence left on the teeth.

The information gained by this study can help future researchers identify preferred foods among these primates. Because microwear analysis is an independent evaluation of diet, it can be a useful tool for researchers to supplement or disprove the observations made in the field. Contrasting the observed diet with microwear analyses may lead to a better understanding of the dietary habits of extant species. In addition, this comparison will create a description of preferred foods for the five primates that now can be used for comparison of other extant and extinct primates.

## Background

### Primates

All the primates analyzed in this study can be classified into one of three dietary categories: *folivorous* (consuming mainly leaves), *frugivorous* (consuming mainly fruits), or *graminivorous* (consuming mainly grasses) (Godfrey *et al.*, 2004; Nelson, 2003, Semprebon *et al.*, 2004b) (Table 2) (Figure 3 and 4). However, depending on the season, a microwear analysis could notice seasonal changes (Semprebon *et al.*, 2004a) that would classify an animal into a different category due to the reliance on fallback foods.

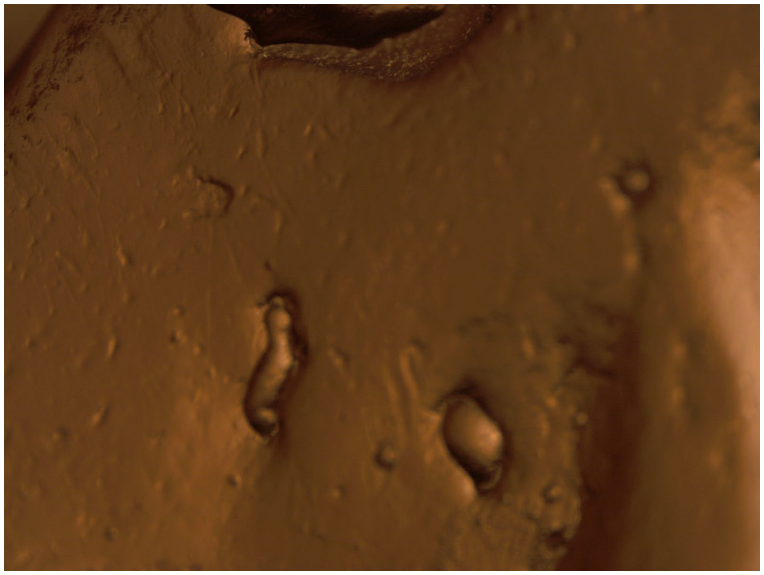

**Figure 3: Microwear expect from a frugivore (picture of a second molar from Pan troglodytes).**

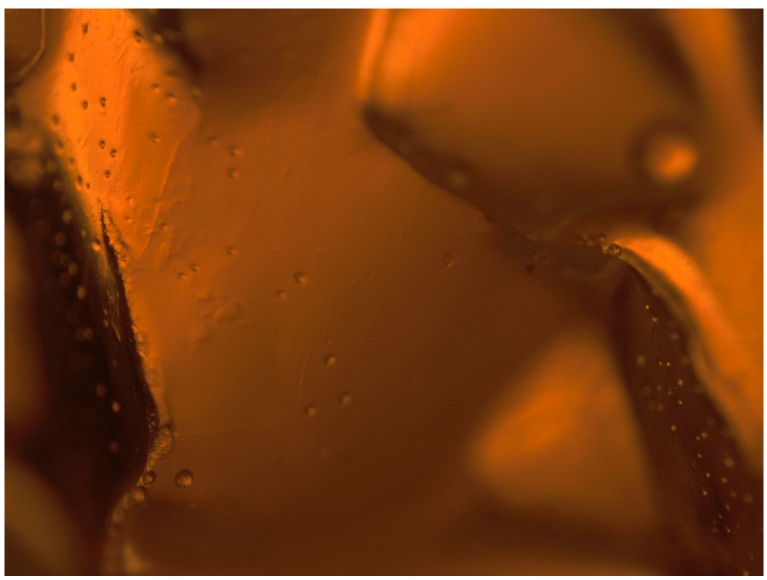

**Figure 4: Microwear expect from a folivore (picture of a second molar from a Piliocolobus badius).**

*Pan troglodytes* have a wide array of foods in their diet. *P. troglodytes* can be found in equatorial rainforests and some open woodland areas. Generally, *P. troglodytes* consume 50 percent fruits along with stems, leaves, and bark. They also consume some insects and small mammals (Kingdon, 1997). According to Wrangham *et al.* (1996), in Kibale, their diet can consist of 67 percent fruits and seeds. This would classify *P. troglodytes* as *frugivorous* during times when its preferred foods are abundant. *P.*

*troglodytes* cranial morphology includes a long palate and long zygomatic arches, giving it a prognathic (long) face. The postcanine tooth row is short compared to other primates. The occlusal surface (surface used for masticating) of the molars of *P. troglodytes* have small, rounded cusps, which are effective at grinding up a range of materials (Pilbrow, 2006).

The diet of *Papio anubis* can vary depending on its habitat. In forested areas, it prefers fruits, but while in open areas, it prefers grasses. This variability suggests that *P. anubis* is *frugivorous* or *graminivorous*, depending on the location it inhabits (Kingdon, 1997). *P. anubis*, in Kibale, consumes fruit as their preferred food because of the rich rainforest area (Wrangham *et al.*, 1991). *P. anubis* possesses the most prognathic face of all the primates in this study due to the large canines the males use in combat. *P. anubis* is characterized by a jaw that contains a long palatine and long zygomatic arch resulting in a prognathic face. *P. anubis* possesses a long postcanine tooth row. The occlusal surface of the molars has small, rounded cusps (Wall, *et al.*, 2006).

*Colobus guereza* and *Piliocolobus badius* feed mostly on leaves in the canopies of trees, classifying them as *folivorous*. *P. badius* are found throughout African forests. They consume mostly flowers, young leaves, buds, and in one area of Africa an ample amount of fruit because there are no other primates (Kingdon, 1997). In Kibale, *P. badius* relies on young leaves when they are around, due to competition from other primates, but can fall back to mature leaves if there is a need (Chapman & Chapman, 2002). *C. guereza* is in equatorial forests in Africa. Their diet is made up almost entirely of leaves, but the proportion of young to old leaves varies according to their location (Kingdon, 1997). In Kibale, *C. guereza* also relies on young leaves and mature leaves for much of its diet (Chapman *et al.*, 2004). Because of the similarity in their preferred foods, Koyabu and Endo (2009) point out that the morphology of their jaw and teeth are similar. Both *P. badius* and *C. guereza* possess a short zygomatic arch, longer palate length, prognathic face, and a long postcanine tooth row. In addition, when compared to other colobus monkeys the occlusal surface of both *C. guereza* and *P. badius* have high crested molars, which are efficient in processing leaves.

*Cercopithecus ascanius* are *frugivorous* primates that gather fruits in the canopy of the forests. *C. ascanius* range in Africa in the equatorial forests along lowland rainforests and secondary bush. They have been known to consume insects and fruit in their home ranges (Kingdon, 1997). The diet of *C. ascanius* in Kibale is composed of mostly fruit and insects, which make up over half of their diet (Lambert, 2004). Specific jaw and tooth morphology of *C. ascanius* was not found, but the morphology for the genus *Cercopithecus* possesses a short zygomatic arch and short palate length, orthognathic (short) face. The postcanine tooth row is short and the occlusal surface contains small, rounded cusps (Table 2).

**Table 2: Species and their dietary classification.**

| Species | Dietary category |
|---|---|
| *Pan troglodytes* | *Frugivorous* |
| *Papio anubis* | *Frugivorous* |
| *Colobus guereza* | *Folivorous* |
| *Piliocolobus badius* | *Folivorous* |
| *Cercopithecus ascanius* | *Frugivorous* |

## Dental Microwear Analysis

Dental microwear analysis has been used since the 1970s (Rensberger, 1978; Walker *et al.*, 1978) to reconstruct diet of extant and extinct species by means of a scanning electron microscope (SEM). In most cases, molds of the teeth are created because they are easier to handle and transport than a whole skull of a specimen (the molding process is not always the same as in low-magnification techniques). The molds are then coated with a reflective metal layer (in most cases gold) that allows the SEM to better detect features. The molds are then placed in an SEM chamber and digitally photographed from 100X to up to 500X magnification (Galbany, 2009). The photographs are then analyzed using metric measurements taken of the features to identify them as pits and scratches (Semprebon *et al.*, 2004b). Besides not being able to analyze large specimen numbers and the high costs, as noted in the introduction, Solounias and Semprebon (2002) also point out that in SEM, many measurements gathered were not useful in determining the dietary behavior of the specimens studied.

These problems led researchers to develop low-magnification (35X) stereomicroscope (Solounias and Semprebon, 2002). They were able to use low-magnification stereomicroscope to classify ungulates into different feeding niches (mixed grazer/browsers, grazers, fruit-dominated browsers, and leaf-dominated browsers). These techniques have also been used to reconstruct past habitats of different primate species in different locations (Godfrey *et al*., 2004, Nelson 2003). In low-magnification, molds are created using clear epoxy that allows light to shine through, allowing for identification of features. The molds are examined under 35X magnification with a 0.5 $mm^2$ viewing area using fiber-optic light, which allows different features to stand out in the examination (Nelson, 2003). The pits and scratches are then counted (e.g. a few pits or scratches seen in 0.5 $mm^2$ area) and qualitatively noted (e.g. fine or coarse scratch; large or small pit and gouges) (Nelson, 2003; Semprebon *et al.*, 2004b). Low-magnification will be used in order to determine the dietary habits of the five-primate species from Kibawe.

## Biases

It must be kept in mind that the specimens collected represent a sample of primates that died from natural causes and were collected on chance encounters during primate observations. There is no way to deduce if these specimens represent the population. Thus, the information gathered will only be relevant to these specimens. In addition, this study works on the assumption that teeth and the jaw are only used for mastication of food. It should be noted that the jaws and teeth of animals are used for many different aspects of their lives. Fighting for territory as well as calls are all functions of the jaw that are overlooked in this study. The second molar is studied since it is assumed that other factors play a small role in creating microwear on this tooth and because it is the middle of the chewing complex (Nelson, 2003; Solounias & Semprebon, 2002; Semprebon, 2004b).

# Methods

Forty-six primate teeth from five species were analyzed (Table 3). All specimens were collected from Kibale National Park over a thirty-year period after they were discovered naturally deceased. Animal specimens were collected by the Kibale Chimpanzee Project researchers and taken back to the field lab where he skeletal remains were then stored at the field lab for future study. Nelson collected the tooth samples in 2002 and 2004 (Nelson, personal commun.). The five primates used in this study are the most common primates observed by teams working for the Kibale Chimpanzee Project (Wrangham *et al.*, 1991; 1996).

**Table 3: Number of teeth specimens of each species.**

| Species | Number of teeth |
|---|---|
| *Pan troglodytes* | 13 |
| *Papio anubis* | 4 |
| *Piliocolobus badius* | 18 |
| *Colobus guereza* | 4 |
| *Cercopithecus ascanius* | 6 |

The specimens' teeth were cleaned with acetone and cotton swabs. Once dry, each tooth was molded twice with a high impression of dental precision material from President Jet®. The reason two molds are created was that the first mold acts as a final step in cleaning the surface of the tooth. A ribbon of putty was then placed around the second mold in order to hold the casting material.

Epoxy resin casts were created using Epo-kwick® resin Buehler®. The epoxy was then poured into the second mold with the putty ribbon and placed into a vacuum chamber, which removes air bubbles from the clear epoxy. The epoxy molds were then removed from the vacuum chamber and left to sit for two days (Nelson, 2003).

The casts were analyzed using a Nikon SMZ1500 Stereoscopic Microscope with low-magnification (35X) refractive light microscopy techniques that are highlighted in Nelson (2003) and in Solounias and Semprebon (2002). The surface of the tooth that was measured is $0.5mm^2$. The surface of the tooth had to be flat when viewed through the microscope so molding clay was used to prop the mold to an appropriate angle. Two surfaces were measured per tooth to obtain an average of features used in the analysis. The features that were counted were the number of pits and scratches (coarse and fine scratches). Large pits, cross scratches, and gouges were noted as to be present or absent if four were viewed in the magnification. A cross scratch runs perpendicular to the other scratches present, while a gouge is a large pit with an irregular shape (Nelson, 2003).

For all five primates, the microwear measurements were taken from facet nine, located on the distobuccal surface of the upper molar's protocone and on the lingual surface of the lower molar's hypoconid (Figure 5)(Nelson, 2003). The second molars were used in microwear analysis because it is believed that they are representative of the whole mouth during mastication (Solounias and Semprebon, 2002). Once the features of each tooth were counted and analyzed for kinds of dietary preferences, the information was compared to the observations made by primatologists working in Kibale. The microwear analysis should be an independent analysis of information on the diets of the primates in this study.


**Figure 5: Occlusal surface from a left second maxillary molar (right) and a left mandibular molar (left) showing facet nine circled in red. The mesial surface is on the left for both teeth.**

Once the features of the teeth were collected, the pits and scratches were averaged for each species. The standard deviation was also taken for each species based on their pits and scratches. The qualitative data is based on the percentage observed for each species. The data was then entered into an ANOVA analysis. The ANOVA analysis looks for a variance by finding the Chi-Square of all the primates in order to test the criteria of pits and scratches. A Mann-Whitney analysis was then performed on the data, which assesses whether two of the species come from the same distribution based on their pits and scratches (Samuels, 1989). Statistical Package for the Social Sciences (SPSS) performed both statistical analyses.

## Results

The microwear results for each tooth are available in appendix 1. Out of the original 46 teeth, only 36 were able to produce wear that could be counted. The remaining ten teeth had one of two problems. The first was that the tooth was not correctly molded. Because the molds of the teeth were poor quality, the counts could not be used from those teeth because they were not being representative of the natural microwear, but of the molding process. The second reason was some of the teeth were so badly worn that facet nine was no longer observable on any of the three molars.

The quantitative values were then averaged for each species and the standard deviation was found for each species. The qualitative values were then averaged to produce a percentage of how often it appeared for each species. Table 4 shows the qualitative measurements of the pits and scratches found on the teeth. Figure 6 shows the averages found for the pits and scratches for the five species of primates, while Figure 7 shows the standard deviation for the same data. The results can be compared against the predictions made from the observations in Kibale.

**Table 4: Present of qualitative features seen.**

| Averages | N | Large pits | Gouges | Cross Scr | Fine Scr | Course Scr | Mixed |
|---|---|---|---|---|---|---|---|
| *Pan troglodytes* | 13 | 62% | 31% | 69% | 33% | 8% | 58% |
| *Papio anubis* | 4 | 100% | 0% | 33% | 33% | 33% | 33% |
| *Piliocolobus badius* | 18 | 8% | 8% | 8% | 85% | 0 | 15% |
| *Colobus guereza* | 4 | 0% | 0% | 25% | 100% | 0% | 0% |
| *Cercopithecus ascanius* | 6 | 25% | 0% | 25% | 25% | 0% | 75% |

In a microwear analysis, pits and scratches are both counted and noted for the features they possess. The percentages seen in Table 4 represent the percent of the times each of those features were observed. All five species show the expected wear produced by their diet for the qualitative features. The *folivorous* species show a high percent of fine scratches, with only a few cases of mixed. The *frugivorous* species show a high percentage of mixed scratches. Large pits appear in a higher percentage in the *frugivorous* species. The only species that produced any evidence of course scratches alone were the *frugivorous* species, *Cercopithecus ascanius* being the exception. P. *troglodytes* and *P. badius* were the only two species to show signs of gouges, but *P. troglodytes* had a far higher appearance of gouges (31%).

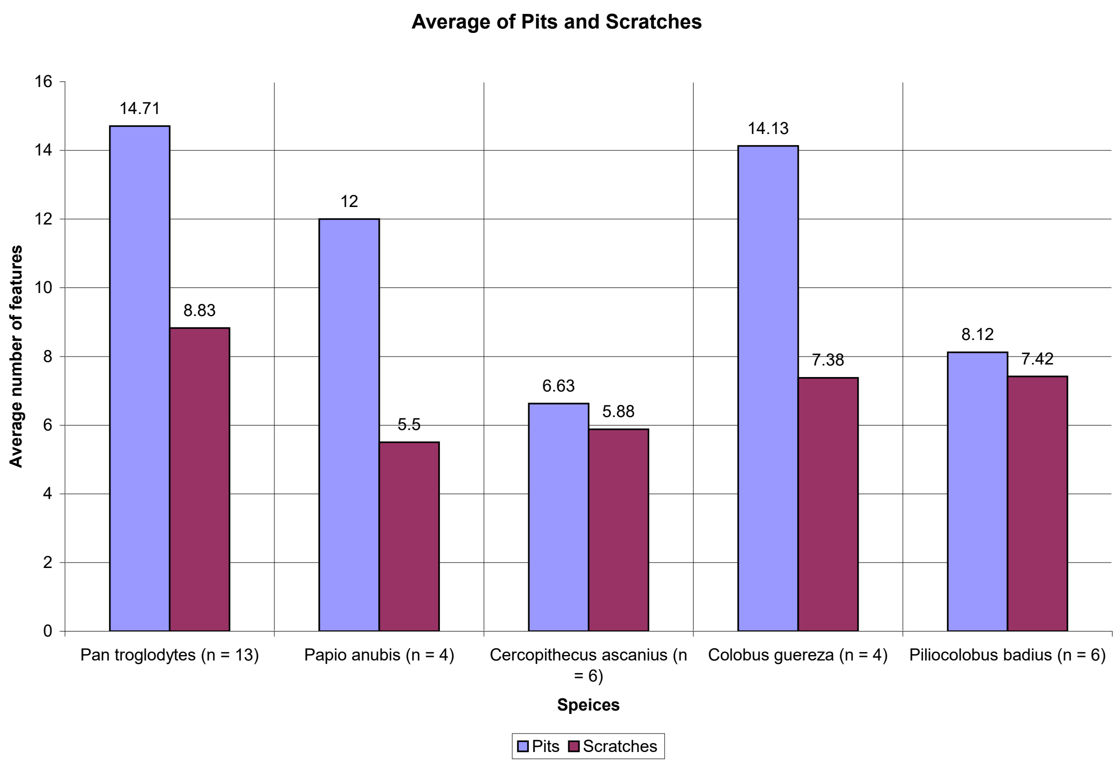


**Figure 6: Graphs of the averages for the pits and scratches for all five-primate species.**

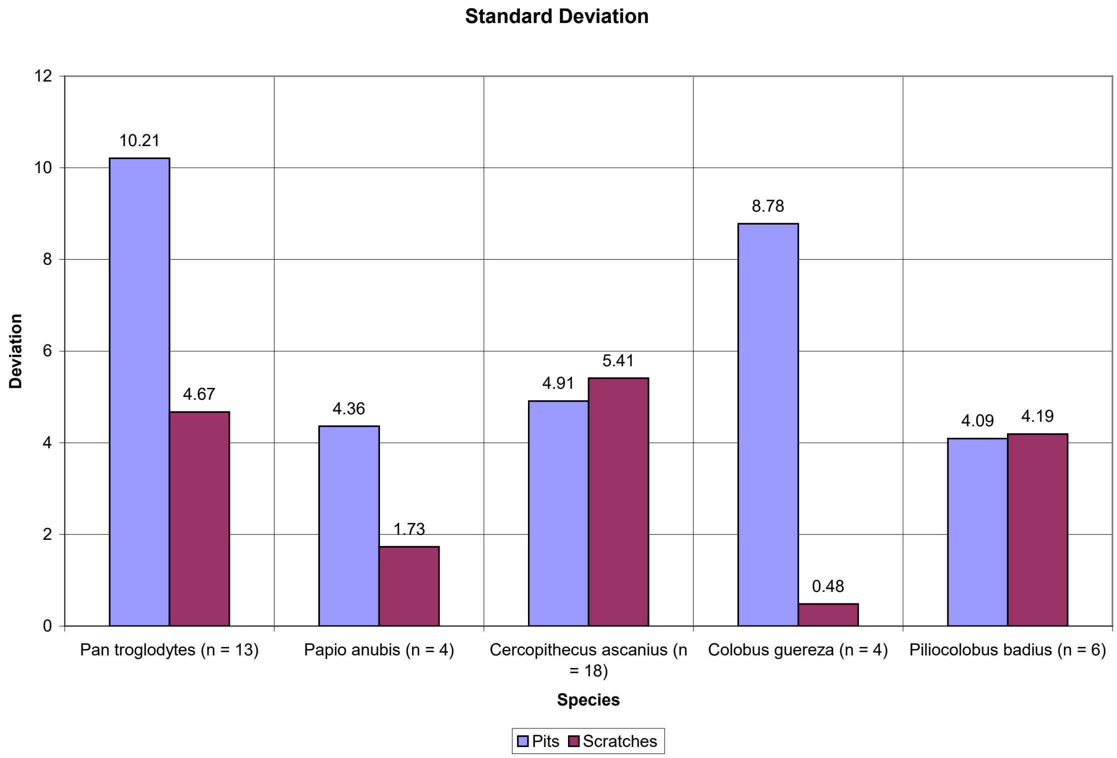


**Figure 7: Graph of the standard deviation for the five species analysis in this study. Pan troglodytes and Colobus guereza show the highest standard deviation among the five primates and only for the pits.**

The averages for *Pan troglodytes* and *Papio anubis* look very similar, which also lines up with the predictions based on their observed feeding habits. However, *P. anubis* and *Colobus guereza* are the most similar out of all five primates. This does not seem to line up with the prediction made about *C. guereza* because *C. guereza* is *folivorous*. The explanation for *C. guereza* having such high pits could be due to grit found in the leaves it consumed. Ungers et al. (1995) showed that dust collects at different rates at different times of the year. They also showed that dust accumulated at the tops of the canopy at a slightly higher rate than within the canopy. This means that *C. guereza* could have a high pit count from the grit on the leaves.

*C. ascanius* matches *Piliocolobus badius* in that they both have low averages of pits and scratches, and the difference between pits and scratches is less than one percent.

*P. badius* was predicted to have low pit averages because it was observed to be folivorous, but it was thought that the scratches would be high because of that same factor. *C. ascanius* was thought to have high pitting because of the observations made of it being *frugivorous*.

The data were then entered into an analysis of variance using SPSS software. The One-Way ANOVA analysis gave the results of Chi-Squared 6.39 with an Asymp Sig of .172 for pits and Chi-Squared 2.47 with an Asymp Sig of .561 for scratches. Nevertheless, A One-Way ANOVA indicated no significant difference in the number of pits or scratches between all species. However, Man-Whitney analysis correlated for there found a couple of marginally significant difference (see table 5 and 6).

**Table 5: Results from the Mann-Whitney analysis for scratches.**

| | *P. troglodyte* | *P. anubis* | *C. ascanius* | *C. guereza* | *P. badius* |
|---|---|---|---|---|---|
| *P. troglodyte* | X | NS | NS | NS | NS |
| *P. anubis* | 0 | X | NS | NS | NS |
| *C. ascanius* | 0 | 0 | X | NS | NS |
| *C. guereza* | 0 | 0 | 0 | X | NS |
| *P. badius* | 0 | 0 | 0 | 0 | X |

*0 =redundant data, X = no data. NS = not statically significant.*

**Table 6: Results from Mann-Whitney analysis for pits.**

| | *P. troglodyte* | *P. anubis* | *C. ascanius* | *C. guereza* | *P. badius* |
|---|---|---|---|---|---|
| *P. troglodyte* | X | NS | NS | NS | z = -1.88, p = .06 |
| *P. anubis* | 0 | X | NS | NS | z = -1.82, p = .069 |
| *C. ascanius* | 0 | 0 | X | NS | NS |
| *C. guereza* | 0 | 0 | 0 | X | NS |
| *P. badius* | 0 | 0 | 0 | 0 | X |

*0 =redundant data, X = no data. NS = not statically significant.*

According to the Mann-Whitney analysis, there were only two instances when the data was statistically significant. The two examples are when the pits of *P. troglodytes* are compared to *P. badius* (z = -1.88, p = .06) and when the pits of *P. anubis* are compared to *P. badius* (z = -1.82, p = .069). These results agree with what has been observed in the field. *P. troglodytes* and *P. anubis* are both *frugivorous*, while *P. badius* is *folivorous*. However, the three *frugivorous* species should have matched one another, while the two *folivorous* species should have matched, however, a Mann-Whitney analysis showed no statistical significance between the two groups. *C. ascanius* matched with the other four primates being studied when it should have only match with the *frugivorous* species, and *C. guereza* matched had the same results but should have only match with *P. badius*. This result does not agree with the predictions made.

## Discussion

The results from this study are inconclusive. Although there should be an agreement between observations made in the field and microwear analysis, there are several reasons why the results do not agree. The field observations were made over several years across all seasons, while the tooth wear reflects enamel wear over the last few days before the animal's death. The qualitative data seems to agree with what is observed in the field. The quantitative data do not seem to agree with the field observations. Only one of the *folivorous* species was excluded from only two of the *frugivorous* species analyses. None of the *folivorous* analyses excluded any of the other primates.

A potential bias in the results can be due to dental microwear reflecting only the last few meals of any given animal because the surface of the tooth is always being reformed. Unfortunately, what the animal ate last may not be representative of what is normally consumed, leading to what some have called "Last Supper" phenomenon (Grine, 1986). The "Last Supper" phenomenon could account for the inconclusive results showing that *Piliocolobus badius* was the only *folivorous* species being excluded by two of the *frugivorous* species. Nevertheless, this may not be able to account for the reason

*C. ascanius* agrees with all the *frugivorous* species as well as *P. badius*. In addition, according to Semprebon *et al.* (2004a), "…despite the potential for relatively rapid change in microwear patterns, the association between diet and enamel scar patterns in extant animal studies has been demonstrated to be very concordant" (p. 428).

Because the different features that were identified are not metrically measured, one potential bias comes from the misidentification of features (e.g. one observer observes a large pit, while another observes a small pit). According to Semprebon *et al.* (2004b) between individual observers, a variation of features is very low, and the average of two feature counts are used in order to counter within individual observation variation (Nelson, 2003).

Another further bias in this study may have come from a limited number of individuals in the analysis. There were only 47 teeth for the five-primate species. *P. troglodytes* and *P. badius* made up much of the sample; the other three species totaled 15 teeth. The samples for the other three species may not be representative of the whole population. This bias seems to be the most likely cause of the inconclusive results.

Future studies performed on these five species should be carried out on equal numbers of teeth. This may allow for a better data set to work from that would produce conclusive results that agree with the observations made in the field. Once more microwear information is collected for primates of this site, a microwear pattern can be constructed to act as a key for the observation made of fossil assemblages. Fossil assemblages that match the pattern created using a study like this can shed light into the habitat of fossil life forms.

## Acknowledgments

This would not be possible without the support of Dr. Sherry V. Nelson who provided me with the use of her lab and collection, plus the training on her equipment. Further thanks to Dr. Ann Ramenofsky for the helpful ideas and advice during the writing process for this honors thesis. In addition, thanks to the other honors students in the Anth 498 for the helpful feedback in the evolution of this thesis.

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# Appendix 1: Data for the five primates

| ID | Specimen | Pits | Large Pits | Gouges | Scratches | Cross Scr | Fine Scr | Course Scr | Mixed | |
|---|---|---|---|---|---|---|---|---|---|---|
| Pan | | | | | | | | | | |
| KBF | SVN7 | N/A | | | | | | | | |
| KBF | SVN7 | N/A | | | | | | | | |
| KBF | SVN8 | 16 | 1 | 1 | 10 | 1 | | | 1 | |
| KBF | SVN8 | 22 | 1 | 1 | 7 | 1 | | | 1 | |
| KFB | 150 | 23 | 1 | 1 | 13 | 1 | | | 1 | M3 |
| KFB | 150 | 25 | 1 | 1 | 11 | 1 | | | 1 | M3 |
| KFB | 70 | 14 | 1 | | 6 | 1 | | | 1 | Juv M1 |
| KFB | 70 | 10 | 1 | | 4 | | | | 1 | Juv M1 |
| KFB | 107 | 12 | 1 | | 1 | | 1 | | | |
| KFB | 107 | 7 | 1 | | 5 | | 1 | | | |
| KFB | 18 | 9 | | | 12 | 1 | | | 1 | |
| KFB | 18 | 8 | | | 10 | 1 | | | 1 | |
| KFB | 153 | 40 | 1 | | 4 | | | 1 | | M3 |
| KFB | 153 | 28 | 1 | | 1 | | | 1 | | M3 |
| KFB | 150 | 5 | | | 10 | | 1 | 1 | | |
| KFB | 150 | 2 | | | 4 | | 1 | 1 | | |
| KFB | 151 | 8 | 1 | 1 | 17 | 1 | | | 1 | |
| KFB | 151 | 8 | 1 | 1 | 13 | 1 | | | 1 | |
| KFB | 155 | 19 | 1 | 1 | 8 | | | | 1 | |
| KFB | 155 | 17 | 1 | 1 | 5 | | | | 1 | |
| KFB | 106 | 10 | | | 13 | 1 | 1 | | | |
| KFB | 106 | 6 | | | 10 | 1 | 1 | | | |
| KFB | 105 | 4 | | | 12 | 1 | 1 | | | |
| KFB | 105 | 5 | | | 22 | 1 | 1 | | | |
| KFB | 17 | 19 | | | 14 | 1 | 1 | | | |
| KFB | 17 | 11 | | | 12 | 1 | 1 | | | |
| KFB | 16 | 12 | 1 | | 6 | 1 | | | 1 | |
| KFB | 16 | 12 | 1 | | 6 | 1 | | | 1 | |
| Papio | | | | | | | | | | |
| KFB | 29 | 17 | 1 | | 4 | 1 | | 1 | | |
| KFB | 29 | 17 | 1 | | 5 | 1 | | 1 | | |
| KFB | 181 | 12 | 1 | | 10 | | 1 | | | |
| KFB | 181 | 8 | 1 | | 5 | | 1 | | | |
| KFB | 181 | 12 | | | 8 | 1 | | | 1 | Lower M2 |
| KFB | 181 | 17 | | | 8 | 1 | | | 1 | |
| Cercopithecus | | | | | | | | | | |
| KFB | 174 | 8 | | | 4 | | | | 1 | |
| KFB | 174 | 15 | | | 7 | | | | 1 | |
| KFB | 14 | N/A | | | | | | | | |
| KFB | 14 | N/A | | | | | | | | |
| KFB | 122 | 7 | | | 0 | | 1 | | | |
| KFB | 122 | 12 | | | 2 | | 1 | | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| KFB | 127 | 8 | 1 | | 13 | 1 | | | 1 | |
| KFB | 127 | 2 | 1 | | 14 | 1 | | | 1 | |
| KFB | 182 | 1 | | | 1 | | | | 1 | |
| KFB | 182 | 0 | | | 6 | | | | 1 | |
| KFB | 40 | N/A | | | | | | | | M3 |
| KFB | 40 | N/A | | | | | | | | M3 |
| Colobus | | | | | | | | | | |
| KFB | 173 | 24 | | | 10 | 1 | 1 | | | |
| KFB | 173 | 22 | | | 6 | 1 | 1 | | | |
| KFB | 121 | 8 | | | 2 | | 1 | | | |
| KFB | 121 | 23 | | | 13 | | 1 | | | |
| KFB | 123 | 0 | | | 8 | | | | | |
| KFB | 123 | 4 | | | 6 | | 1 | | | |
| KFB | 119 | 22 | | | 11 | | 1 | | | |
| KFB | 119 | 10 | | | 3 | | 1 | | | |
| KFB | 172 | 0 | | | 0 | | | | | |
| KFB | 172 | 0 | | | 0 | | | | | |
| Piliocolobus | | | | | | | | | | |
| KFB | 161 | 16 | | | 0 | | 1 | | | |
| KFB | 161 | 1 | | | 4 | | 1 | | | |
| KFB | 112 | 7 | 1 | | 15 | | 1 | | | |
| KFB | 112 | 10 | 1 | | 8 | | 1 | | | |
| KFB | 30 | 9 | | | 8 | 1 | 1 | | | |
| KFB | 30 | 6 | | | 3 | 1 | 1 | | | |
| KFB | 165 | 11 | | | 3 | | 1 | | | |
| KFB | 165 | 3 | | | 10 | | 1 | | | |
| KFB | 59 | 2 | | | 2 | | 1 | | | |
| KFB | 59 | 4 | | | 6 | | 1 | | | |
| KFB | 168 | N/A | | | | | | | | |
| KFB | 168 | N/A | | | | | | | | |
| KFB | 169 | 6 | | 1 | 11 | | 1 | | | |
| KFB | 169 | 8 | | 1 | 9 | | 1 | | | |
| KFB | 157 | N/A | | | | | | | | |
| KFB | 157 | N/A | | | | | | | | |
| KFB | 111 | 9 | | | 1 | | 1 | | | |
| KFB | 111 | 2 | | | 0 | | 1 | | | |
| KFB | 41 (?) | 8 | | | 11 | | 1 | | | |
| KFB | 41(?) | 5 | | | 6 | | 1 | | | |
| KFB | 19 | 9 | | | 10 | | 1 | | | |
| KFB | 19 | 4 | | | 11 | | | | | |
| KFB | 160 | 17 | | | 2 | | 1 | | | |
| KFB | 160 | 7 | | | 5 | | 1 | | | |
| KFB | 170 | 5 | | | 16 | | 1 | | | |
| KFB | 170 | 4 | | | 14 | | 1 | | | |
| KFB | 164 | 24 | | | 12 | | | | 1 | |
| KFB | 164 | 15 | | | 5 | | | | 1 | |
| KFB | 15 | 7 | | | 6 | | | | 1 | |
| KFB | 15 | 12 | | | 15 | | | | 1 | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| KFB | 60 | N/A | | | | | | | | |
| KFB | 60 | N/A | | | | | | | | |
| KFB | 162 | N/A | | | | | | | | |
| KFB | 162 | N/A | | | | | | | | |

The last column indicates if the tooth did not come from the second molar. Blank means second top molar. The text indicates which tooth was analyses if not second top molar.