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Rodent Dental Microwear Texture Analysis as a Proxy for Fine-Scale Paleoenvironment Reconstruction

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by

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ABSTRACT

Dental microwear texture analysis (DMTA) of fossil fauna has become a valuable tool for dietary inference and paleoenvironment reconstruction. Most of this work has utilized larger taxa with larger home ranges. These studies may result in broader-scale habitat inferences that could mask the details of complex mosaic habitats. Rodent DMTA offers an opportunity to work at finer spatial scales because most species have smaller home ranges. Rodents are also keystone species within their ecosystems, abundant, ubiquitous, and found in many fossil deposits. These attributes make them excellent proxies for environmental reconstructions. However, the application of DMTA to rodents remains relatively new. Furthermore, many rodent species are dietary generalists, and individuals available for study in museum collections lack detail on feeding behavior, which makes it difficult to develop strong dietary associations with microwear patterns. The same holds for limited environmental metadata associated with such samples.

This dissertation sought to explore the efficacy of rodent DMTA as a proxy for fine-scale paleoenvironment reconstruction and to establish a baseline of extant incisor and molar textures with detailed metadata associations to aid in future comparisons to fossil taxa. The biomonitoring project at Kolomela Mine, located within South Africa's Northern Cape, provided an ideal opportunity with which to conduct this research. Stomach content analyses conducted on 214 muroid specimens caught within the Kolomela properties examined diets by species, location, and month. These analyses indicated that the Kolomela rodent community mainly consumed grass seed despite the presence of other foodstuff within stomachs.

A confocal profiler scanned high resolution casts to provide microwear textures for 198 incisors and 175 molars, from which SSFA and ISO parameter data were derived. Statistical

tests explored the effects of diet, taxon, and habitat attributes on the central tendencies of these parameters, as well as effects by tooth form. Incisor microwear textures seemed to possess a stronger environmental signal than that of molars, with analyses indicating significant variation by species, macrohabitat, microhabitat, burrowing behavior, soil, and land cover classification. These results suggested that while soil characteristics had a strong influence on parameter central tendencies, incisor microwear textures seem to result from complex interactions with habitat characteristics.

Molar microwear did not parse the considered dietary categories, likely because all individuals had diets dominated by grass seed that swamped any diet signal reflecting the food elements of each group. Significant variation in parameter central tendencies by both species and burrowing behavior were believed to be the result of differing molar topography between Gerbillinae and Murinae specimens. Analyses also separated molar microwear from different dust levels, which indicated that perhaps an environmental signal can be parsed, at least when diets are homogeneous and controlled for. Finally, molar and incisor microwear textures were significantly different from one another, presumably due to a) different roles in food acquisition and process, b) different rates in gross wear and surface turnover, and c) different degrees of interaction with exogenous grit and the outside environment. These results suggest that both tooth types should be considered in future paleoenvironment reconstructions.

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DEDICATION

To my brother, Adam. We might not always see eye to eye, but you've always believed in me anyway. I couldn't ask for a better bro. Thank you.

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CHAPTER ONE: INTRODUCTION

Evolution does not occur in a vacuum. Ecological context is needed to aid in understanding the evolutionary paths that affect species, and the mechanisms behind such paths. Reconstructing past environments provide the background needed in paleoecological studies. Many methods and proxies exist that provide data on climatological and habitat characteristics at differing temporal and spatial ranges. These include broad scaled climatological data, often derived from ocean- and lake- sediment cores (e.g., Owen et al., 2018; Cohen et al., 2016; Kaufman et al., 2020; Kingston et al., 2007; Larrasoaña, 2021; Lyons et al., 2015; Warner & Domack, 2002), which are important in understanding the global patterns that may have influenced environmental change not just on a worldwide scale but at local levels as well. It is also important to consider the more localized ecological data that can be obtained through proxies such as faunal assemblage analysis (e.g., Avery et al., 2010; Belmaker & Hovers, 2011; Bobe et al., 2002; Gomes Rodrigues et al., 2014; Koufos & Vasileiadou, 2015), which provide insight on conditions more directly affecting a community. As such, the complex localized habitats often associated with Plio-Pleistocene hominin sites require the need for both coarse and fine scale methods and proxies.

Dental microwear analysis of faunal remains has become an important tool in reconstructing aspects of paleohabitats. Despite its traditional use in dietary reconstruction, the indirect correlation between diet and the environment provides insights into the vegetative landscape of a given environment. This is in part due to diets being dependent upon the amount and availability of foodstuff within a given area (Calandra & Merceron, 2016). Of particular note in dental microwear studies are that of ungulates, which have proven to be extremely useful

in the application of dental microwear to environmental studies (e.g., Kingston & Harrison, 2007; Merceron et al., 2004; Robinson et al., 2016; Schubert et al., 2006). Scott (2012), for example, established clear differences in microwear textures between extant obligate browsers and grazers, which in turn differentiated between the availability of woody plants and grass species. Larger taxa are great for this kind of analysis: not only are larger teeth typically easier to analyze under a microscope, but their larger body size and terrestrial nature imply that they were subject to similar selective pressures as hominins.

However, when incorporating the temporal and spatial scales of environmental reconstruction, reliance solely on larger taxa can prove problematic (Davis & Pineda-Munoz, 2016). This is because larger animals generally have larger home ranges, and in understanding their diets, we paint a paleoenvironmental reconstruction with broad strokes. These data might mask the details of microhabitats found within the mosaic landscapes associated with many hominin species (Belmaker, 2018). The application of paleoenvironment reconstructive methods to smaller animals with smaller home ranges might help elucidate this masked data and allow for higher spatial resolution. Thusly, this will aid in understanding the complex habitats and environmental dynamics in which early hominins evolved. Unfortunately, the application of dental microwear to smaller taxa is, to date, not as common as it is with other species.

This dissertation provides a new baseline of extant rodent microwear textures and their associated diet and habitat attributes. Furthermore, this project assesses the potential of rodent molar and incisor microwear as a proxy for paleoenvironmental reconstruction through the correlation of dental microwear texture data with known dietary, behavioral, and habitat attributes. Rodents utilized in this dissertation represented seven Muriodea species and were obtained from an on-going environmental assessment program at Kumba Iron Ore's Kolomela

Mine in the Northern Cape Province of South Africa. Given the propensity for rodent species to be categorized as opportunistic generalists, stomach content analysis was conducted on 192 individuals to firmly associate microwear texture with known diet. Both molar (n = 175) and incisor (n = 198) microwear textures were correlated with this dietary data, as well as by burrowing behavior, habitat, microhabitat, and more detailed habitat characteristics: dust accumulation level, soil type, and land cover composition.

Chapter One begins with a brief overview of the role in which environmental dynamics plays in an evolutionary context, as well as a description of some key paleoenvironmental proxies and reconstruction methods. This section is followed by a brief history of the use of rodents and other small mammals as paleoenvironmental proxies, including their use in faunal assemblages and isotope studies. Specific attention is given to rodent dental microwear, followed by a summary of the pilot study that inspired this research. Finally, this chapter concludes with the research objectives and hypotheses that formulated this work, and a short summary of the remaining chapters.

The Importance of Paleoenvironmental Reconstruction

The idea that environmental change acts as a driving force behind human evolution dates back to the mid-20th century (e.g., Robinson, 1963) and has long held importance in paleoanthropological hypotheses. Initial explanations of hominin environmental dynamics were more simplistic in nature, often singling out a key environmental change as the background basis for hominin evolution, such as the switch from forest to savanna settings. The expansion of C4 grasslands in Africa during the Pliocene, for example, was often used to explain the development of bipedalism in early hypotheses (Anderson et al., 2006). However, evolution and climate

change are not so simplistic. As the capability to better reconstruct past environments improved, newer theories have gained prominence. Regardless, the interactions hominins have had with their habitats and their responses to climatic and other environmental changes, are still used in explaining specific biological traits, behaviors, or material cultures of past populations (Marean et al., 2015).

Today, many argue that hominin evolution responded to the increasing fluctuations in climate and habitat that ultimately led to *Homo sapiens*' success in adaptive versatility (e.g., Grove et al., 2015; Kingston, 2007; Potts, 1998; Trauth et al., 2007). This trend is in part due to a shift in stronger understanding of correlations between environment and evolution. It is not the change in temperature or the degree of habitat openness or closeness, per say, that ultimately affects adaptation. Instead, it is the effect these environmental changes have on key functions of life: exploiting resources, reproducing, and any other activity important in survival (Marean et al., 2015). Various hypotheses have been put forward, such as the turnover pulse, variability selection, and the pulsed climate variability hypotheses (see Maslin et al., 2014; Potts, 1998; Potts, 2013; Vrba, 1985), that argue for understanding evolution in context of a fluctuating environment and co-occurring climatic instability.

Acknowledging the nuances of proxies used in paleoenvironmental reconstructions has become extremely important in conducing this kind of research. Specifically, it is important to note what the proxy is looking at, how long a scope of time it covers, and how broad a spatial area it encompasses (e.g., Cohen et al., 2016; Davis & Munoz, 2016; Levin, 2015; Potts, 2013). Thus, to better understand the role of environmental change in hominin evolution and develop clearer hypotheses, paleoenvironmental reconstructions need to be clear and concise, and depicted at both global and localized scales. After all, not all environmental and climatic

changes occur over the same time span, nor effect the same amount of area. Environmental effects may take over hundreds of thousands of years to have an effect (e.g., uplift, changes in ocean circulation), or have a much more immediate (~10-1000 years) effect (e.g., orbital forcing, glacial cycles). These changes may also occur globally or may be restricted to specific locales. Thankfully, there exist several proxies and methods that inform on paleoclimates and paleohabitats at different scales, including, but not limited to, oceanic and lake sediment cores, paleosol isotopic analysis, faunal composition, ecomorphology, enamel isotopic analysis, and dental macro- and microwear. Since these different proxies operate on different scales of both time and space, it is important to continue the development of further proxies and methods that, together, can provide a robust, comprehensive paleohabitat reconstruction.

Rodents as Paleoenvironmental Proxies

Fossil evidence indicates that the order Rodentia dates to the late Paleocene, with developmental origins in Laurasia approximately 55-60 mya (Kay & Hoekstra, 2008). Estimates based on molecular studies push this date further into the Cretaceous, between approximately 75 mya (Springer et al., 2003) and 110 mya (Kumar & Hedges, 1998). Regardless of origins, today rodents are frequently found in terrestrial fossil assemblages, including those that contain hominins and other fossil primates (Denys, 1999). Rodents are speciose, abundant, and the most widely distributed terrestrial mammal aside from humans. Furthermore, rodents easily exploit a broad range of environments. They have a nearly cosmopolitan distribution and are presently found on all continents except Antarctica, as well as comprise more than forty percent of all living mammals (Carleton & Musser, 2005).

Rodents are also important keystone species that are often described as trophic glue that structure their whole biotic community (Huntly & Inouye, 1988; Jones et al., 1994), as well as act as ecosystem engineers (Legagneux et al., 2012). They influence the faunal structure of their ecosystem, controlling predator and prey species abundances. In addition, rodents affect the abiotic characteristics of their habitat. They aerate and increase ground water recharge through soil turbation, aid in nutrient cycling and decomposition, promote ecological succession, impact floral productivity, richness, and composition, and supply habitats for other taxa (e.g., Ballová et al., 2019; Chew, 1978; Lanudre, 1998; Potter, 1978; Prugh & Brashares, 2012; Tschumi et al., 2018; Zhang et al., 2003).

Rodents, and micromammals in general, are short lived and restricted in home range. As such, it is difficult for them to simply leave an area subjected to rapid environmental changes. Alterations in vegetation cover, which influence the distribution and abundance of many micromammal species (Batzli, 1992), therefore readily affect micromammal communities. Either the population adapts (typically observed with generalists that are catholic in their habitat range) or it dies out (as seen with specialist species usually confined to a narrow niche). This trend has been observed among extant species that are currently dealing with the fallout of anthropogenic impacts (e.g., Renaud et al., 2015). It has also been observed in the fossil record, specifically in relation to the instability of the Plio-Pleistocene (e.g., Gómez Cano et al., 2013), where the turnover patterns depict rodent communities that fluctuate in generalist to specialist ratios that correlate with rapid climate changes.

Unsurprisingly then, rodents have been used in environmental reconstruction for decades. Although most research has focused on analyzing rodent assemblages within fossil sites (e.g., Avery, 1981; Belmaker & Hovers, 2011; Cano et al., 2014; Reed, 2008), more recent work with

this taxon has expanded into ecomorphology (e.g., Gómez Cano et al., 2017; Kimura et al., 2013; Paine et al., 2019), isotope analyses (e.g., Arppe et al., 2015; Codron et al., 2015; Leichliter et al., 2017), and dental mesowear analyses (e.g., Kropacheva et al., 2017; Ulbricht et al., 2015; Ungar et al., 2020). Although dental microwear studies have been conducted utilizing rodent molars and incisors (e.g., Burgman et al. 2016; Caporale & Ungar, 2016; Nelson et al., 2005; Gomes Rodrigues et al., 2009), the potential of rodent use in this paleoecological methodology has just begun to scratch the surface.

Rodent Dental Microwear

Dental microwear can best be categorized as the microscopic pits and scratches on the enamel surface of a tooth, typically a result of the acquisition and processing of food. These textures allow for a comparative methodology that associates the microwear pattern with a known diet and the associated physical properties of that food. Several studies amongst various mammalian taxa have established the precedent of using dental microwear texture analysis (DMTA) as a tool to infer the diets of fossil species (e.g., Grine, 1986; DeSantis, 2016; Ungar et al., 2008; Walker et al., 1978) and its use in paleoenvironmental reconstruction (e.g., Kingston & Harrison, 2007; Merceron et al., 2004; Scott, 2012). However, to date, most applications of dental microwear to paleoenvironmental reconstructions have remained focused on large mammals, such as ungulates.

Despite the abundance of micromammal remains at fossil and archeological sites, less work has been conducted using these teeth. This lack of published studies is in part due to the size of micromammal teeth; small teeth can be extremely difficult to work with or even fill the entirety of a microscope's field of view. Furthermore, the diets of extant taxa are often not as

well documented as those of larger mammals. This is in part due to the opportunistic and generalist nature of many species, especially that of rodents, as diets fluctuate depending upon habitat and food availability. What one species might eat in one locale would not necessarily be what the same species would eat in another location (e.g., Abu Baker & Brown, 2012; Curtis & Perrin, 1979; Kerley, 1992).

Until recently, many rodent microwear studies have utilized a scanning electron microscope (SEM) to adjust for small enamel surface area and have been based on individual feature measurements. Many earlier SEM rodent studies have focused on mastication mechanics and microwear etiology. Differences in food properties, along with differences in mastication, were argued to explain the differences in microwear patterns on rodent molars observed using an SEM (Rensberger, 1973). In another example, Teaford and Walker (1983a, 1983b) published a series of short communications utilizing *Cavia porcellusx* (guinea pig) specimens to better understand jaw movement and tooth use in the formation of microwear. Other studies have since successfully analyzed microwear patterns for dietary and, by extension, environmental reconstruction. For example, Hopley et al. (2006) analyzed rodent molar microwear from Makapansgat, South Africa to suggest that these individuals were largely omnivorous but still showed some preference for browsing material. This dietary interpretation led to the inference that mid-Pliocene Makapansgat was a woodland-savanna mosaic. Dental microwear patterns observed on rodent teeth from a fossil assemblage in Ulantatal, China noted, meanwhile, were explained by a high level of insect and grass consumption among the different taxa analyzed (Gomes Rodrigues et al. 2012). According to the authors, these findings implied evidence towards an open habitat with some sort of nearby water source in Oligocene Ulantatal.

There have been even fewer studies done on rodents using the newer microwear analytical approach of whole-surface texture analysis, be it either scale-sensitive fractal analysis (SSFA) or International Standards Organization (ISO) surface metrology. But those that have applied DMTA techniques to rodent microwear have seen success in using rodents to parse diet and environmental differences. For example, a preliminary study of incisors from various rodent taxa hinted at distinct dietary and environmental effects (Caporale & Ungar, 2016). In this study, omnivore specimens tended to have slightly more anisotropic surfaces than those of herbivores while omnivores had slightly more heterogeneous surfaces than that of frugivores. Overall, they authors concluded that incisors better reflected habitat and substrate than food. The application of DMTA methods to the molars of Malagasy rats also separated populations by habitat (Winkler et al., 2016). In this case, the patterns reflected significant variation between village and rainforest populations. DMTA of *Microtus agrestis* (vole) molars from Finnish Lapland indicated a seasonal signal in texture patterns, presumed to have occurred due to differences in endogenous abrasive concentrations within foods consumed in spring/summer and fall/winter (Calandra et al., 2016b).

More recent studies have used rodent dental microwear to better understand the effects of exogenous and endogenous abrasives on microwear formation. Winkler et al. (2019) conducted a controlled feeding experiment with *C. porcellus* specimens that demonstrated that plant hydration alters phytolith abrasives enough to alter microwear patterning. Another controlled feeding experiment indicated the effects the varying properties of exogenous particles (e.g., size, shape, hardness, concentration) have on microwear (Winkler et al., 2020). Yet, Adams et al.'s (2020) comparison of *Talpa europa* (mole) microwear to that of bats indicated that exogenous particles do not influence dietary signal in molar microwear. However, while rodent molar

microwear remains popular, incisor microwear remains underutilized despite their potential for reflecting habitat characteristics. Ungar et al.'s (2021) work analyzing *Lemmus sibiricus* (lemmings) and *Lasiopodomys gregalis* (vole) incisor microwear indicated that differences in textures between high tundra and forest-tundra habitats reflects changes in abrasive loads, as well as differences in how the two taxa utilize their environment. A more comprehensive review of rodent dental microwear is provided in Chapter 2, as well as in Belmaker (2018).

Pilot Study

Prior to this research, a pilot study was conducted to examine molar microwear textures of three sympatric mice (*Rhabdomys pumilio*, *Mastomys coucha,* and *Micaelamys namaquensis*) living in three distinct biomes (Dry Highveld grasslands, Afromontane grasslands, and Nama-Karoo shrublands) within South Africa and Lesotho (Burgman et al., 2016). The aim of this project was to assess variation between taxa when controlling for habitat, and between habitats when controlling for taxa. While multivariate test results indicated a statistically significant interaction between location and species, these differences varied based on taxa and habitat (Figure 1.1). Neither *R. pumilio* or the Dry Highveld grassland samples differed by central tendency or dispersion for the six SSFA variables considered. However, the *Ma. coucha* samples and the samples from the Nama-Karoo and Afromontane differed by both central tendencies and dispersion. *Mi. namaquensis* only differed by dispersion between locations. Furthermore, not all SSFA attributes proved capable of parsing differences in microwear texture.

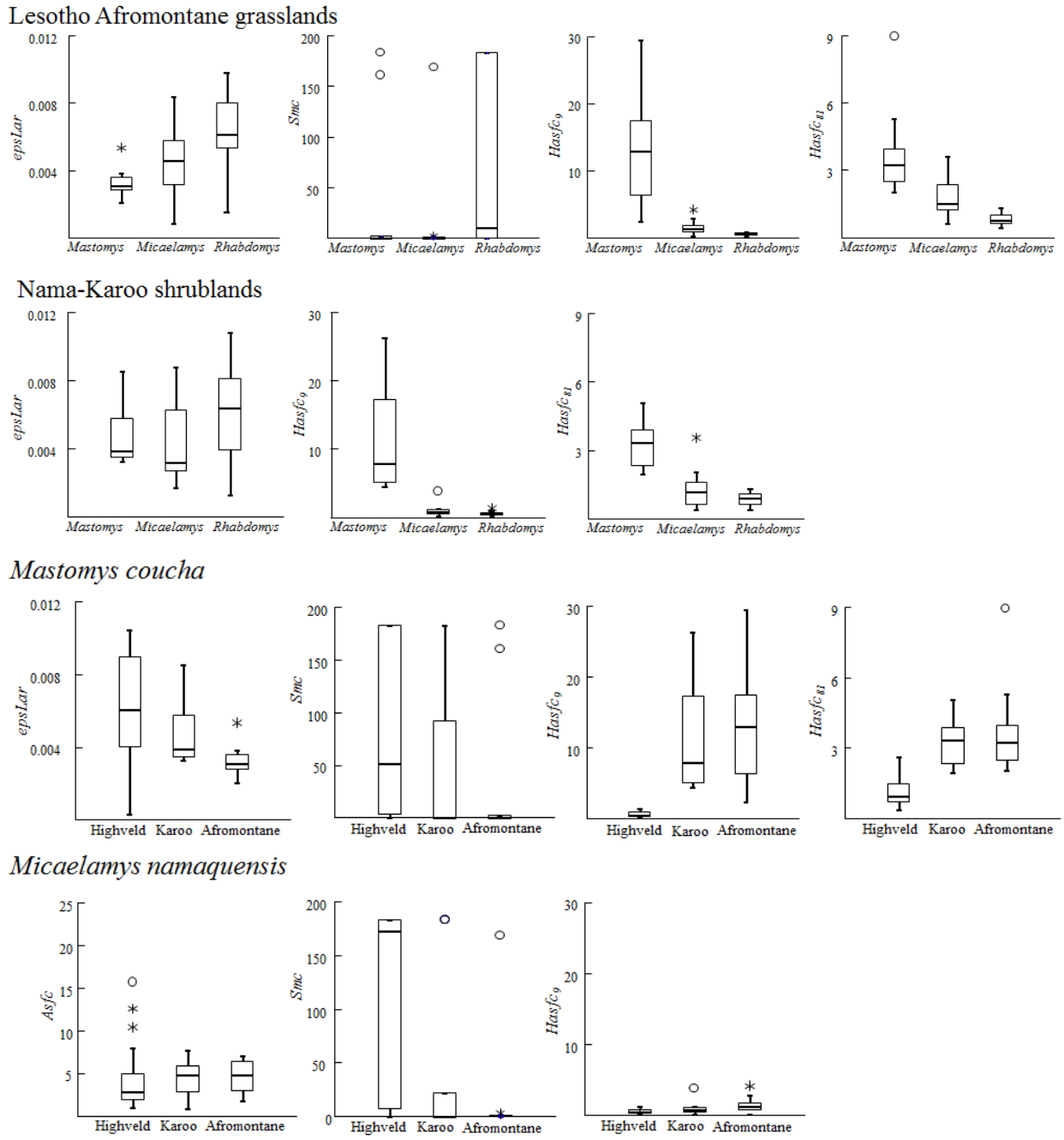

Figure 1.1: Box charts of statistically significant microwear texture variables for three sympatric species (*Mastomys coucha*, *Micaelamys namaquensis*, and *Rhabdomys pumilio*) within a given habitat, and for *Ma. coucha* and *Mi. namaquensis* within three different environments (Dry Highveld grassland, Nama-Karoo shrublands, and Afromontane grasslands). The boxes represent the central 50% of values, with first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers. From Burgman et al. (2016).

Burgman et al. (2016) highlighted the potential of microwear texture analysis of rodent molars. The lack of consistency among results suggested that environmental characteristics such as grit level were probably not the main influencer in molar microwear formation. Were this the case, there should have been consistent and statistically significant differences among all three species. Instead, molar microwear patterns were probably reflecting the adaptation of *Ma. coucha* and *Mi. namamquensis* toward differing resource availability. Both the Nama Karoo shrubland and the anthropogenically disturbed Afromontane were hypothesized to have more limited resources, thus leading to the need for a more varied diet to compete among sympatric species. Despite the dietary similarities of the three species, all categorized as opportunistic omnivores, these results still reflected subtle microwear differences within the Afromontane and the Nama Karoo. Ultimately, it was concluded that while the causation of rodent molar microwear might have stemmed from the combination of diet with other environmental factors, the dietary signal could still be parsed out through analysis.

While this study showed the potential of applying DMTA to rodent molars, it lacked important information on the microhabitats of trap sites and dietary details for species often described as opportunistic, with shifting diets. In addition, the previously mentioned rodent study conducted by Caporale and Ungar (2016) indicated that, for these teeth, microwear texture patterns better separated groups by habitat than diet. Incisor microwear particularly highlighted differences between open and closed habitats. They hypothesized that the incisors of desert and savanna rodents had higher complexity values and rougher surfaces at a finer scale resulted from a greater exposure to abrasive particles in these open habitats.

The difference between these two studies is unsurprising. Rodent incisors have direct contact with the environment and as such, it stands to reason that microwear textures could

reflect non-dietary environmental qualities. Molar microwear patterns, meanwhile, should relate more directly to diet, given interactions between masticatory mechanics and the physical properties of foodstuff (Hua et al., 2015). Together, the analysis of rodent microwear for incisors and molars holds potential to reveal information about both vegetation and landcover within a given location, thus forming the basis of this dissertation.

Research Objectives

The purpose of this research is to determine whether the dental microwear of rodent incisors and molars make an effective proxy for paleoenvironmental reconstructions. To accomplish this task, four objectives needed to be met:

H1. The diets of the individual rodent specimens will reflect the floral characteristics of their specific microhabitats and the dietary nature (i.e., generalist or specialist) of their specific species.

Relying solely on previous research for rodent diets, as done in the pilot study, becomes an issue when trying to parse the dietary signal of generalist species. Many rodents tend to be flexible and opportunistic feeders, and their diets vary based on food availability in space and time. While it allows rodents to be successful in their global distribution and numbers, it makes it difficult to associate DMTA characteristics with specific taxa because their diets are so broad and variable. This is not an issue typically encountered when utilizing other species such as bovids as environmental proxies, since their feeding choices are more predictable. To adjust for the catholic foraging behavior of rodents, the stomach contents of 214 individuals captured at Kolomela Mine and its surrounding properties were analyzed and quantified to the nearest 5% of each of eight food types. These data were then utilized in a brief dietary analysis to better

understand the effects of anthropogenic disruption on the foraging of sympatric rodent species, in which individuals from more disturbed areas ought to supplement their diets with less preferred foods to meet metabolic requirements.

H2: As incisors interact more directly with the environment and lack the influence of masticatory movements, the microwear of rodent incisors ought to reflect the non-dietary characteristics of their microhabitat.

These results provide the other information important to the comparative baseline built by this dissertation. Individuals exposed to higher levels of grit, both within and nearer to Kolomela mine ought to have higher microwear texture complexity values and larger textural fill volume averages than those exposed to less grit. Incisor patterns should also reflect non-dietary aspects of incisor use by rodents, such as those which burrow into soil for nesting. Like with exposure to higher levels of grit, burrowers should have equally complex surfaces with lots of pitting.

H3: Species and individual dietary differences will be reflected through differences in molar microwear texture patterns.

Although most rodent species favor propalinal chewing, previous work has indicated that diet-based microwear patterns follow the same trends that have been observed for other mammalian species (Gomes Rodrigues et al., 2009). As such, it was predicted that the consumption of tougher foods such as grass blades will be associated with higher anisotropy values while the consumption of harder or brittle foods such as insects or seeds will be associated with higher complexity values. As seen in the pilot study, grit levels of the different habitats will not obscure the dietary signal. The data obtained from this portion of the project is one step in constructing a comparative baseline of rodent microwear texture patterns to use in future comparisons with fossil rodents.

H4: Due to their different roles in mastication and other functions, molar microwear patterns will significantly differ from that of incisor microwear patterns.

As previously stated, molar microwear ought to reflect the dietary differences based on the material properties of foods consumed and the masticatory movements of occlusal surfaces. Meanwhile, incisor microwear patterns will reflect any variation in environmental grit load or interactions with soils. The work at Kolomela provided a unique opportunity to obtain environmental characteristics such as dust level, ground cover, and soil type that can be used in analysis of both incisors and molars. Ultimately, these data will provide a baseline with control over dietary and habitat details that ought to allow for closer associations between rodent DMTA and environment.

Structure of the Dissertation

This dissertation is divided into eight chapters, followed by an appendix containing the raw data of the rodent microwear textures and corresponding metadata that form the comparative baseline for future research. Following this first introductory chapter, Chapter 2 delves into the relevant background to this project in a comprehensive literature review of paleoenvironment reconstruction. Specific attention is given to the role dental microwear, especially that of micromammals, can play in this effort. The third chapter discusses Kolomela Mine and its associated properties, the rodent species studied, and details the methods used for both stomach content analysis and dental microwear texture analysis. Chapter 4 provides the results of the stomach content analyses conducted on the Kolomela rodents, as well as the interpretations of these data and the final dietary assignations to be used in the microwear portion of this dissertation. Chapters 5 and 6 both focus on the dental microwear analysis. Chapter 5 discusses

the results and interpretations of the incisor study, broken down by environmental variables, and Chapter 6 follows a similar format for the molar analysis, along with a comparison between the molar and incisor data, and whether they indeed record different aspects of rodent ecology. Finally, Chapter 7 synthesizes the research conducted in this project, discussing whether the objectives outlined in Chapter 1 were achieved and the significance of the results. This chapter concludes the dissertation by providing future avenues of research before final remarks.

CHAPTER TWO: LITERATURE REVIEW

Climate Change and Hominin Evolution

Within the past decade or so, several papers have been published detailing the impact of environment on human evolution (e.g., Bonnfille, 2010; deMenocal, 2011; Galway-Witham et al., 2019; Kingston, 2007; Levin, 2015; Maslin et al., 2015; NRC, 2010; Pisor & Jones, 2020; Potts, 2007, 2012, 2013). Climate change holds the potential to introduce new evolutionary pressures to any given population through alteration of the ecosystem composition and resource availability of their habitat (deMenocal, 2011). This often leads to the need for adaptation by means of behavioral or genetic changes if a population cannot leave to find a habitat in which they are better suited (Davis et al., 2005; Holt, 1990). Over time, these accumulated changes may result in speciation or, if the population is unable to adapt, localized extinction events. The evolution-environment null hypothesis argues that evolution occurs without the influence of climate or environmental change (NRC, 2010; Potts, 2012). However, it is more likely that environment has influenced the evolutionary history of hominins and other organisms on Earth (Potts, 2013). As such, the capability to reconstruct paleoenvironment and paleoclimate during the Plio-Pleistocene is important in understanding the complex interactions hominins have had with their environments.

In the late Miocene, the hominin line diverged from a last common ancestor shared with chimpanzees (Steiper & Young, 2006). During this time, the world was much warmer than today, and at the precipice of undergoing a cooling period (Billups et al., 2008). Tectonic uplift in East Africa joined the Congo with East Africa, leading to the emergence of several endemic species (Couvreur et al., 2008; Maslin et al., 2015), and the formation of lake-suitable basins

(Maslin et al., 2015). Evaporation of the Mediterranean Sea during the Messinian salinity crisis about 7-5 mya (Rouchy & Caruso, 2006) led to important changes in the regional climates of Africa and Eurasia. These changes had lasting effects for the emergences of the hominin lineage (NRC, 2010; van der Made et al., 2006). Prior to 4 mya, the hominin fossil record begins with the appearance of early hominins such as *Ardipithecus*. The appearance of *Australopithecus* and *Paranthropus* between 4-2.7 mya is then followed by the introduction of early *Homo* at 1.8-2.5 mya. Finally, the last main phase of hominin evolution occurs around 800 kya, with the advent and dispersal of later *Homo* species and anatomically modern humans. Most of these events, as well as other speciation, extinction, and dispersal events that characterize hominin history, correspond to important global and regional climatic changes (Armitage et al., 2011; Bernhart Owen et al., 2018; Carto et al., 2009; Casteneda et al., 2009; deMenocal, 1995; Donges et al., 2011; Larrasoaña, 2021; Maslin et al., 2014; Maslin et al., 2015; Shultz et al., 2012; Trauth et al., 2005; Trauth et al., 2021).

The shift from the Pliocene to the Pleistocene saw a global change from the warmer climate of the Pliocene to a colder, varying climate in the Pleistocene. Cyclical influxes of warm interglacials in the Pleistocene became interspersed with cool glacial periods (Bonnefille, 2010; Utescher et al., 2011; Wright, 2009; Zachos et al., 2001). DeMenocal (2004, 2011) cites two major processes affecting African climate change during the Plio-Pleistocene: (1) increasing dry and variable conditions superimposed upon (2) orbital precession forcing that influenced wet and dry cycles (at approximately 20 k year intervals). Furthermore, Milankovitch cycling, cyclic variations in Earth's orbit, induced cycles of change that varied over a 10-100k year time scale (Berger, 1978; deMenocal, 1995).

The Pleistocene also saw the beginning of glaciation in the Northern Hemisphere; analysis of sediment cores off the coasts of West and East Africa indicate continued glaciation variability at 2.8 mya, 1.7 mya, and 1 mya (e.g., Clemens et al., 1996; deMenocal, 2004; Haug et al., 1999; Tideemann et al., 1994; Trauth et al., 2009). During the mid-Pleistocene Revolution, approximately 1.25-0.7 mya, glacial cycles changed from that of a 41 k year periodicity to that of varying cycle lengths with an average of 100 k year periodicity (Berger & Jansen, 1994; Brovkin et al., 2019; Chalk et al., 2017; Clark et al., 2006; Maslin & Ridgwell, 2005). Africa became more arid, with an unstable climate that fluctuated between wet and dry phases (Ashley, 2007; Clemens et al., 1996; Deino et al., 2006; deMenocal, 1995, 2004; Kingston, 2007; Kingston et al., 2007; Larrasoaña, 2021; Maslin & Trauth, 2009; Tiedemann et al., 1994; Trauth et al., 2007; Trauth et al., 2009). This shifting climate influenced the spreading of C3 to C4 vegetation (Brachert et al., 2010; Cerling, 1992; Cerling & Hay, 1986; Feakins et al., 2005; Feakins et al., 2013; Harris et al., 2008; Levin et al., 2004; Segalen et al., 2007) and influenced fluctuations in lake appearances and disappearances (Ashley et al., 2014; deMenocal, 2004; Deino et al., 2006; Hopley et al., 2007; Hopley & Maslin, 2010; Joordens et al., 2011; Kingston et al., 2007; Lepre et al., 2007; Wilson et al., 2014).

Hypotheses of Hominin Evolution and Environment Change

The correlation between global climatic events to the appearance of significant hominin species, morphological developments, or behaviors has long existed in paleoanthropology (e.g., Butzer, 1977; Brain, 1981; deMenocal, 1995; Potts, 1998; Vrba, 1985, 1988). In fact, the idea that there is some connection between evolution and the environment has persisted for over 200 years. In the nineteenth century, Lamarck first wrote of bipedalism developing because of a

primitive ancestor wanting to see a "large and distant view," and passing on this "habit" of bipedalism through generations (Bender et al., 2012). Fifty years later, Charles Darwin and Russel Wallace theorized on the existence of variations within populations and the effects these variations have on survival – the natural selection of a species – subsequently tying evolution and environment together (Darwin & Wallace, 1858). A simplistic definition of natural selection is that of a population's ability to adapt to its surroundings. Though he did not necessarily believe that large scale climate change was necessary to promote natural selection, Darwin still understood that climate possessed some influence on species: "The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals…" (Darwin, 1872, p. 68).

During the twentieth century, various hypotheses were developed that correlated trends in hominin evolution with environmental and climatic changes. Of all ideas conjectured, few have influenced the history of paleoanthropology as the savanna hypothesis (Bender et al., 2011; Domínguez-Rodrigo, 2014). The central theme of the savanna hypothesis, that key events in hominin evolution were tied to a need to adapt to open savanna settings, has been utilized in explaining aspects of hominin morphology since Lamarck's 1809 conjecture on bipediality (Bender et al., 2012; Domínguez-Rodrigo, 2014; Keith, 1923). In the early twentieth century, a German geologist built on this idea by incorporating climate change as a reason for spreading savannas and the adoption of bipedalism (Steinmann, 1908; Bender et al., 2012). The adaptation to open environments remained central in the ecological theories behind hominin evolution for most of the century (e.g., Bartholomew & Birdsell, 1953; Coppens, 1991; Leakey, 1934; Robinson, 1963).

Research has since indicated that bipedality started prior to the widespread C_4 grass expansions (e.g., Bonnefill 1983; Cerling, 1992; Cerling et al., 1997; deMenocal, 1995; Potts, 1996; Reed, 1997; Senut et al., 2001), debunking the long-taught concept of hominin bipedality evolving in response to increased grasslands. Instead, other ecologically based hypotheses attempted to fill the gap, such as the idea that bipedality evolved as an adaptation of forest life (e.g., Rayner et al., 1993). Another hypothesis, the aridity hypothesis, updated the savanna hypothesis by suggesting that the increased presence of xeric environments influenced behavioral and evolutionary adaptations for a variety of mammalian taxa. However, this influence was not tied to specific traits in the same way bipedalism was in the savanna hypothesis (deMenocal, 1995, 2004; Maslin et al., 2015; Reed, 1997;). This idea was especially influenced by a better understanding of an aridification shift around 2.3 – 2.6 mya in the mid-Pliocene (deMenocal 1995, 2004) and evidence of a landscape dominated by C_4 grass and grazer assemblages (e.g., Bobe & Behrensmeyer, 2004; Bobe et al., 2007; Bonnefille, 2010; Cerling et al., 2011; Cerling et al. 2015; Reed, 1997).

More recent hypotheses have suggested that fluctuation in climate and habitat types are responsible for hominin evolution and the adaptive versatility of humans. The first of these, the turnover pulse hypothesis, suggests that speciation and extinction events occur within a short duration due to fundamental shifts in the environment and climate (Vrba, 1985, 1988, 1995). The idea behind this hypothesis is that habitat changes hurt specialists more than generalist species. Often, this results in more rapid evolution and increased speciation events for specialist species due to higher extinction rates. Meanwhile, generalist species can either utilize new environmental changes to their advantage or move someplace more accommodating. Vrba

(1995) in part developed this hypothesis after analyzing a series of bovid fossils, in which the first and last appearance dates of certain species echoed important shifts in the African climate.

The variability selection hypothesis, meanwhile, builds on the turnover pulse hypothesis by suggesting that hominin evolution occurred because of the overall climatic instability of the Cenozoic rather than directional environmental change (Grove, 2011, 2014; Grove et al, .2015; Potts, 1996, 1998, 2013). Rather than reacting to one specific climatic or environmental change, the variability selection hypothesis instead considers a species ability to react to an ever-shifting, unpredictable, and varying environment. Hominins capable of adapting to a constantly changing environment, be it through evolutionary or cultural adaptations, would be able to out-compete those adapted to a particular environmental niche (Potts, 1998). Furthermore, the more adaptable species would be able to disperse to new regions given their flexibility (Grove et al., 2015). The level of speciation events, therefore, should increase during periods of greatest environmental instability.

Conversely, other hypotheses build on climate stability as an important factor in human evolution and dispersal (Grove, 2012; Shultz & Maslin, 2013; Trauth et al., 2015). For example, the Red Queen hypothesis says that for a species to maintain its fitness within co-evolving systems, it must continue to adapt to compete with changing biotic interactions (Pearson, 2001). The pulsed climate variability hypothesis (Maslin & Trauth, 2009; Maslin et al., 2014; Maslin et al. 2015; Shultz & Maslin, 2013; Trauth et al., 2007; Trauth et al., 2010; Trauth et al., 2015) incorporates short periods of extreme climate variability into longer periods of relative climate and environmental stability. Specifically, periods of increased humidity interrupted the trend towards aridification in eastern Africa. As a result, this environmental variability influenced hominin speciation and extinction events.

Finally, it is important to touch on the influence of mosaic habitats, or habitat heterogeneity, on hominin evolution. A mosaic habitat is one in which various smaller habitats, comprised of different vegetation types, are randomly dispersed within a larger region (Elton, 2008; Reynolds et al., 2015). The concept of habitat heterogeneity has its roots in plant ecology (e.g., Cavers, 1914; Pound & Clements, 1897) and proved to be important within the discipline of landscape ecology, especially for metapopulation analysis and spatial dynamics (Reynolds et al., 2015). It was not until the late 1970s that the concept of mosaic habitats reached prominence in hominin paleohabitat reconstructions (e.g., Butzer, 1977; Peters, 1979). The degree of habitat heterogeneity is thought to affect mammalian species richness (Kerr & Packer, 1997), and as such, would influence the selective pressures experienced by hominins in response to changes in diversity (Kingston, 2007). Recent reconstructions of hominin paleohabitats have supported the idea that they were complex, mosaic environments through use of faunal analysis (e.g., Haile-Selassie, 2001; Leakey et al., 2001; Reed, 2008; Vignaud et al., 2002), stable isotope analysis (e.g., Hopley et al., 2006; Kingston & Harrison, 2007; Schoeninger et al., 2003; Sponheimer & Lee-Thorp, 1999), sediment analysis (e.g., Fiebel, 2011), and vegetation analysis (e.g. Andrews & Bamford, 2008).

Issues of Scale

Any given environment is a complex system involving relationships between abiotic and biotic factors (Kearney, 2006). Abiotic environmental changes occur as a response to internal (e.g., increased output of greenhouse gasses) and external (e.g., increased bombardment of solar radiation) forcing mechanisms. These changes are variable and complex, and exist on differing temporal and spatial scales, such as regional versus global or seasonal versus millennial (Hare,

1991; Smithers & Smit, 1997). When determining the proper scale in which to focus for an ecological study, it is therefore important to keep in mind the shifting scales of environmental patterns and the effect this has on populations and ecosystems (Levin, 1992).

Scale is not just an issue when considering abiotic forcing mechanisms. It is also an important influence in biotic reactions. In Rahel's (1990) hierarchical model of taxa response to habitat change, different populations respond to alterations in their habitats at different temporal and spatial scales. Rahel bases the effects of climate change on amplitude (low or high), duration (short or long), and spatial scale (regional or global). At low amplitude changes, there are often few changes in biological community, at either the organismal or population levels (Rahel, 1990). As environmental change becomes more intense, populations begin to react in varying degrees. High amplitude changes at short durations often result in small, plastic changes in organisms, such as a dietary shift. As these changes last longer, or spread beyond a localized habitat, more groups begin to respond more drastically. Changes in species relative abundance may be observed but the overall community structure remains the same (Rahel, 1990). Populations may disappear completely at the highest levels of climate change, resulting in shifts in not just species abundance, but species and niche compositions as well (Rahel, 1990). The reactions of these populations are not just based on climate change, but on life history characteristics as well, with specialists or smaller animals often more sensitive to lower amplitude changes.

Given the intricacies of climate change and the effects it has on different species, it is unsurprising that that careful attention needs to be applied when reconstructing the environmental dynamics of the past. It is important to obtain an understanding of climate change at coarser spatial and temporal levels as they are influential mechanisms that may drive regional

and localized habitat shifts. However, global paleoclimate reconstructions are too broad to provide a clear picture of the local environments directly affecting hominins (Blumenthal, 2016). Thus, there is a need for environmental reconstruction on finer spatial scales as well (Birks et al., 2015; Kingston et al., 2007). There remain issues in correlating global changes to that of regional (Behrensmeyer, 2006), especially as global trends do not match the trends observed in local or regional paleohabitat reconstruction or in the temporal scale of a hominin lifespan (Behrensmeyer, 2006; Behrensmeyer et al., 2007; Blumenthal, 2016; Kingston et al., 2007). Scale-sensitivity applies as much to proxies used in paleohabitat reconstruction as it does to the effects of environmental change (Davis & Pineda Munoz, 2016).

Diet is an excellent proxy for paleohabitat reconstruction, as there is a correlation between community structure within a habitat and food availability. However, the information gleaned from diet easily varies both temporally and spatially (see Davis & Pineda Munoz, 2016). Diet is influenced by ecological factors other than food availability, such as food quality and predation risk (Calandra & Merceron, 2016). Although diet is not the only scale-sensitive proxy, it is an extremely relevant example for this dissertation, and one that is utilized in a variety of methodologies. For example, craniodental ecomorphology can be utilize in determining the potential diet of an organism, such as high-crested molar cusps in primates often correlating with folivorous diets (Kay, 1975; Kay & Hiiemae, 1974; Kay & Hylander, 1978). Yet, when using ecomorphology to reconstruct environmental characteristics, it is important to keep in mind that this proxy represents evolutionary adaptations that exist at large temporal and geographic scales (Gailer et al., 2016). Another way to utilize diet in paleoenvironmental analyses is through isotopic analysis. This represents a smaller temporal scale than that of ecomorphology and instead looks at the results of tissue (e.g., hair, bone, or enamel) over the course of a lifetime

(Davis & Pineda Munoz, 2016). Dental microwear, meanwhile, provides the shortest temporal scale, reflecting diet over the last days of an individual's life. But even then, taxon size also affects spatial scale: smaller organisms possess much smaller habitats in which to obtain food from than those of larger. As such, analyzing the diets of smaller taxa, such as rodents, may reveal data on microhabitats within a larger mosaic landscape that might be lost in the analysis of larger ones.

Dental Microwear Analysis

Dental microwear describes the microscopic features that form on the surface of tooth enamel during mastication. Typically, these features are simplified in form as pits and scratches. This fine-scale wear results from interactions of how an organism chews (Hua et al., 2015) and the physical properties of the ingested material (Crompton & Hiiemae, 1970; Hiiemae & Kay, 1973). Dental microwear is considered to record a "last supper", or an animal's dietary choices from the days prior to death (Grine, 1986; Teaford & Oyen, 1989), and can take at least two weeks for the pattern to be overwritten by a shift in diet (Winkler et al., 2020a). Unlike dental morphology, which reflects what an organism is adapted to eat, dental microwear textures reflect what an organism ate. As such, dental microwear provides information on the diets of extinct species (through comparison to microwear patterns of extant species with known diets), from which information on ecosystem and evolutionary processes can be extrapolated.

Questions remain pertaining to the etiology of dental microwear and its use in reconstructions, be they dietary or ecological in nature (e.g., Lucas et al., 2013; Strait et al., 2012; van Castern et al., 2020). Initial forays into microwear formation indicated that phytoliths, the endogenous silicates within plant cells, were responsible for dental wear on the enamel

surface of mammalian teeth (Baker et al., 1959; Rensenberger, 1978; Walker et al., 1978). Others have argued that the accretion of dust and other exogenous particles on food sources is the sole cause in development of microwear abrasions (e.g., Galbany et al., 2009; Healey & Ludwig, 1965; Kay & Covert, 1983; King et al., 1999; Rabenold & Pearson, 2014; Sanson et al., 2007; Sanson et al., 2017). This is in part due to hardness tests that indicate phytoliths and other hard plant tissues are not strong enough to wear enamel surfaces (Lucas et al., 2013) and sliding tests that similarly indicated a failure on the behalf of hard woody tissue to scratch enamel surface (van Castern et al., 2020). Because of these experiments, it is argued that differences of dust accumulation on an ingested surface is the main contributor to dental microwear patterns.

Accumulation of grit is impossible to avoid. Ungar et al. (1995) indicated that dust levels can vary with season and habitat, along with different accumulations on differing food surfaces. They argue that while this may be influential when it comes to seasonal microwear complexity, it does not obscure and is not the main cause of wear patterns. Other studies confirm that the accumulation of dust and grit on plants is dependent upon environmental influences such as rain, volcanic activity, and anthropomorphic disturbances (e.g., Kretinin & Selyanina, 2006; Madden, 2014; Prusty et al., 2005; Spradley et al., 2015). Furthermore, work by Spradley et al. (2015) and Martin et al. (2020) indicated that grit does not seem to affect the wear of all teeth equally.

Recent work has also shown that microwear results do not depend so much on the hardness of whatever is being chewed. Rather, all that is needed is enough force to break the protein “glue” that holds enamel hydroxyapatite crystals together (Xia et al., 2015; Xia et al., 2017). Furthermore, phytolith-enamel interactions vary based on plant and animal combinations. While the results of hardness values obtained for bunch grass by Lucas et al. (2013) were softer than the primate enamel sample in which they compared it to, it was still harder than that of the

ungulate enamel used by Erickson (2014) within their own tests. While some species of plants might possess softer tissues in comparison to certain enamel samples, this cannot be said of all phytolith-enamel combinations and comparison (Erickson, 2014; Rabenold & Pearson, 2014), and as such, phytoliths can still drive microwear patterns. Finally, *in vitro* feeding experiments testing the influence of phytoliths and grit on microwear formation have resulted in contradictory conclusions. Either dust and grit do not impinge on diet-related microwear patterns (e.g., Adams et al., 2020; Daegling et al., 2016; Merceron et al., 2016), microwear results from a combination of both grit and food stuff (e.g., Hedberg & DeSantis, 2016; Schulz-Kornas et al., 2020), or external abrasives are the principal factor in microwear pattern formation, albeit due more to the size of the particles than the concentration there of (e.g., Ackermans et al., 2020; Hoffman et al., 2015; Martin et al., 2020).

Regardless, dental microwear has proved repeatedly to be an invaluable tool in dietary reconstruction for a variety of animals: herbivores (e.g., DeSantis, 2016; Merceron et al., 2010; Prideaux et al., 2009; Schulz et al., 2010; Schulz et al., 2013; Scott, 2012; Ungar et al., 2007; Ungar et al., 2012; Walker et al., 1978); carnivores (e.g., DeSantis et al., 2012; DeSantis, 2013; DeSantis & Haupt, 2014; Donohue et al., 2013; Jiang & DeSantis, 2014; Schubert et al., 2010; Ungar et al., 2010); and those with more complex diets such as primates (e.g., Scott et al., 2005; Scott et al., 2006; Ungar et al., 2003; Ungar et al., 2008; Ungar et al., 2012) and rodents (e.g., Burgman et al., 2016; Calandra et al., 2016a; Caporale & Ungar, 2016; Gomes Rodrigues et al., 2009; Nelson et al., 2005; Winkler et al., 2016). The importance of dental microwear has increased as methods have shifted away from user-based two-dimensional (2D) analyses to automated three-dimensional (3D) quantifications of microwear texture.

Dental Microwear Texture Analysis

Dental microwear analysis has been conducted through various methodologies since its conception. Two-dimensional approaches to dental microwear utilized SEM microscopy (e.g., Teaford, 1985) or low magnification stereomicroscopy (e.g., Solounias & Semprebon, 2002). These 2D analyses consider the number of individual features and categorize dietary types based on numbers and ratios of pits and scratches. However, in addition to issues with user variability, 2D methods do not consider the depth and size of features that may also indicate dietary differences (DeSantis, 2016). Applying three-dimensional analysis to microwear textures and automated computer analysis, dental microwear texture analysis (DMTA) is at the forefront of current dental microwear research. Using confocal microscopy, scans of the enamel surface are obtained that provide elevation a three-dimensional point cloud rendering to use in the application of repeatable and automated scale-sensitive fractal analysis (SSFA) or International Organization for Standardization (ISO) analysis to three-dimensional surface scans produced by confocal light profilers (Calandra et al., 2016; Schulz et al., 2010; Scott et al., 2005; Ungar et al., 2003). Although DMTA has revolutionized the microwear field, it is not without its own limitations. Namely, variability between confocal microscopes may produce different data sets for the same enamel surface. However, much of this variability can be reduced through the application of 'recipes' that can minimize differences between confocals (Arman et al., 2015).

Scale-Sensitive Fractal Analysis

Scale-sensitive fractal analysis automatically characterizes surface texture independent of measurements of the individual features that were key in 2D studies. This form of dental microwear texture analysis has become an accepted and widely used method for dietary and

environmental reconstruction since its introduction at the start of the twenty-first century (Ungar et al., 2003, 2007; Scott et al., 2005, 2006). SSFA is based on the concept that surface texture varies with scale of observation. While a road may be smooth at a normal perspective, when Ant-Man uses Pym particles to shrink in the Marvel comics, that smooth road becomes a rough terrain. In other words, at coarse scales of observation, a surface will appear smooth while at finer scales of observation, that same surface will appear rough (Scott et al., 2005, 2006). Five variables are typically considered when conducting SSFA analyses: complexity (*Asfc*), anisotropy (*epLsar*), the scale of maximum complexity (*Smc*), textural fill volume (*Tfv*), and heterogeneity (*HAsfc*). These parameters will be discussed in further detail in the following chapter (Chapter 3: Methods).

ISO Analysis

The application of International Standard Organization's 3D parameters to dental microwear analysis was first established in Schulz et al. (2010). This method was based on 2D standardization parameters (ISO 4287, 1997) as established by Kaiser and Brinkmann (2006). The ISO parameters used in microwear analysis are specifically chosen to describe diet by analyzing the geometric characteristics of surface textures (Calandra et al., 2012). Each parameter is meant to describe a particular aspect of the texture that results from mechanical interactions at the food-enamel surface. The ISO parameters used in describing microwear texture vary by study but derive from ISO/FDIS 25178-2 (International Organization for Standardization, 2010; Ţălu et al., 2013). In the case of this dissertation, eight parameters will be described in further detail: *Sdr* (developed interfacial area ratio), *Sdv* (mean dale volume), *Vvv* (pit void volume), *Sda* (mean dale area), *Sv* (maximum pit height), *S5v* (five-point pit height), *Str*

(texture-aspect ratio), and *Ssk* (skewness). As with the SSFA parameters, these variables will be discussed in further detail in the following chapter (Chapter 3: Methods)

Microwear Use in Paleoenvironment Reconstruction

Given that food availability varies under different ecological conditions, as does the concentration of exogenous particles that could be ingested alongside the food, there has been an adoption of dental microwear as a paleoenvironmental proxy rather than just a dietary one. Review papers have been written that specifically discuss how dental microwear analysis can be incorporated into paleoecological studies (e.g., Belmaker, 2018; Calandra & Merceron, 2016; Cuozzo et al., 2012; Grine et al., 2012). Dental microwear has mainly been utilized as a paleoenvironmental proxy using a variety of large taxa (e.g., Aiglestorfer & Semprebon, 2019; Jones & DeSantis, 2016; DeMiguel et al., 2008; DeMiguel et al., 2011; Lewis et al., 2000; Merceron & Ungar, 2005; Merceron et al., 2004; Merceron et al., 2005; Merceron et al., 2007; Merceron et al., 2016; Patnaik, 2014; Sewall et al., 2019; Solounias & Dawson-Sanders, 1988; Solounias et al., 2010; Strani et al., 2019; Ungar et al., 2007; Ungar et al., 2012).

Bovids, particularly, have been key for most dental microwear paleoenvironmental reconstructions. Aside from being commonly found at fossil assemblages, bovids fall into clear dietary categories that can be readily observed within microwear and are often highly dependent upon vegetation. Correlations between grazing and grasses, and between browsing and woody plants, can be seen within microwear signatures (Schubert et al., 2006). Similarly, this coincides with grazing being more prominent in open habitats that have a greater amount of exogenous grit, which some people argue to be more influential in microwear formation. The more abrasive enamel surfaces on animals living in open and arid environments, for example, are thought to

partially stem from greater amounts of exogenous grit in the diet (Solounias & Semprebon, 2002). Regardless of the etiology of microwear, Scott (2012) used microwear textures to break down bovid diet even further by separating obligate grazer, variable grazer, browser/grazer, generalist, browser, and frugivores from one another.

By applying these kinds of associations, an analysis of bovid and other large mammal microwear may be used to indicate environmental change, specifically in terms of vegetative cover within a habitat. For example, reconstruction of the paleodiets for three extinct bovid species in Greece indicated a shift in abundance from grazers towards mixed feeders (Merceron et al., 2005). From this shift, the researchers concluded that bushes and wooded areas began to replace the grassy, open habitat in northern Greece during the late Miocene. Meanwhile, a study of extant African great apes by Galbany et al. (2009) indicated that changes in dental wear texture and complexity within populations of a species could arise due to differences in environment rather than just diet. In addition to different habitats offering different availabilities of dietary choices, they also possess varying levels of dust and other particulates that influence the development of microwear complexity.

Micromammals

Small mammals, or micromammals, are defined in this dissertation as mammals weighing less than 1 kg (Andrews, 1990), though others define this category with an even smaller upper weight limit of < 150 g (Avery, 2007). Micromammals are an historically diverse group that have appeared in the fossil record since the origin of mammals in the late Triassic and tend to be found at many Cenozoic fossil and archaeological sites worldwide. Despite taphonomic issues that act against their preservation, small mammals still tend to be highly

abundant, with a minimum number of individuals often reaching into the hundreds (Avery, 1990). These numbers are in part due to *r*-selected behaviors that include short generation times and large numbers of offspring (Churakov et al., 2010). In fact, their relative abundance at a paleontological site is often larger than that of the large mammal fossils, with higher species richness as well (Fernández-Jalvo et al., 2016). Extant micromammals remain highly diverse and abundant, and are represented in several orders, including Afrosoricida (golden moles), Chiropetra (bats), Eulipotyphla (hedgehogs, gymnures, solenodons, desmans, moles, shrew-like moles, and true shrews), Lagomorpha (hares, rabbits, and pikas), Primates (tarsiers, galagos), Macroscelidea (elephant shrews), Rodentia (most rodent species), and Scandentia (tree shrews). Today, these small mammals represent approximately 80% of all mammalian species (Fernández-Jalvo et al., 2016).

In addition to their frequent appearance in the fossil records, micromammals have been used as paleoecological proxies due to their small home ranges, limited migration, species richness, short lifespan, and rapid evolution (Andrews & O'Brien, 2000, 2010; Belmaker & Hovers 2011; Chaline, 1977;). As such, they provide high resolutions both temporally and spatially, especially in comparison to the resolution of scale obtained from larger mammals. As larger taxa have larger home ranges, the accumulation of these fossils at a given site often represent a larger radius of area (Lyman & Lyman, 1994) and, in many cases, may be more representative of predator accumulation, especially at hominin sites (Belmaker, 2018). Although the presence of micromammals at a site is also often due to predator accumulation (Andrews, 1990; Fernández-Jalvo & Andrews, 1992; Matthews et al., 2006; Mondini, 2002; Gomez, 2005; Reed, 2003; Verzi et al., 2008), predators of micromammals (e.g., raptors) typically have small home ranges in comparison to those that prey on larger taxa, and comprise a radius of 1 – 5 km

(Andrews, 1990). Therefore, analyses of micromammal assemblages still represent a narrower spatial scale than that of larger taxa. Their narrower temporal resolution, on the other hand, stems from their shorter lifespan, which becomes extremely beneficial when methods such as isotope analysis are used for higher resolution reconstructions.

In addition, small mammals react more quickly to climate change and the subsequent changes in their habitat. This sensitivity is in part due to their limited home range and limited dispersal potential, which limits the migration distance of an individual. Because of their *r*-selected qualities of greater offspring and shorter lifespans, shifts in micromammal communities are thought to follow climatic fluctuations closer than other species (Belmaker, 2018). As different taxa and populations respond to environmental changes across different scales (Rahel, 1990), smaller environmental disturbances are more likely to affect micromammal populations than that of other mammals occupying the same region. In addition, small mammal species richness has been shown to correlate with the species richness of local vegetation (Andrews & O'Brien 2000, 2010), with vegetation types influencing the distribution and abundance of many species (Batzli, 1992).

Rodentia

Although micromammals extend across a range of orders and include many different taxa, rodents have had the greatest proliferation and success. The order Rodentia dates to 55-60 mya (Kay & Hoekstra, 2008) or even further back in time, approximately 75-110 mya (Kumar & Hedges, 1998; Springer et al., 2003), based on fossil or molecular analysis, respectively. Like micromammals, they are frequently found in fossil assemblages, including those that contain hominins and other fossil primates (Denys, 1999). Today, rodents are perhaps the most widely

distributed mammal in part from humans, exploiting a large range of environments. They are also speciose, making up 40% of all living mammal species, and are found everywhere except for Antarctica (Carleton & Musser, 2005; Churakov et al., 2010).

Their abundance levels are also very sensitive to climate and habitat change (Fufachev et al., 2019; Gilg et al., 2009; Hernández Fernández, 2001; Hernández Fernández, 2006; Hernández Fernández et al., 2007; Ims et al., 2011; Morris et al., 2012; van der Meulen & Daams, 1992; van Dam & Weltje, 1999). This is especially true for populations of specialist species (Goméz Cano et al., 2013), which are thought to have higher speciation and extinction rates than generalist species due to an inability to find their required resources in another location (Cantalapiedra et al., 2011; Vrba, 1987). One such way in which rodents are affected by the changes in environment is by changes in precipitation level. Rodent species diversity and community composition are particularly influenced by precipitation (Spevak, 1983). Studies conducted by Avery (1982, 1988) and Ernest et al. (2000) indicate a positive correlation between levels of species richness and species diversity and increased level of precipitation.

Sensitivity to climate change has been also recorded in the rodent fossil record. For example, the composition of Iberian sympatric rodent communities changed in correlation to significant climate change events that limited resource use in the Plio-Pleistocene (Goméz Cano et al., 2013). Similar trends are also observed among extant rodent populations. Both recent and historic morphological changes in jaw morphology, an adaptation to changing dietary resources, have been observed in an invasive population of *Mus musculus domesticus* (house mice) on Guillou Island in the Sub-Antarctic (Renaud et al., 2015). This shift in morphology, meant to accommodate the incorporation of invertebrates into their diet, phenotypically separated this population from their continental cousins. However, these changes to the mandible also

reflected increased dietary quality that correspond with the eradication of their only competitor (rabbits) on the island (Renaud et al., 2015).

Furthermore, rodents are intrinsic and important keystone members of their ecosystems (Brown & Heske, 1990; Legagneux et al., 2012) that often act as trophic glue. Many rodent species act as ecosystem engineers (Huntly & Inouye, 1988; Jones et al., 1994). They influence prey and predator species abundance levels (Howe et al., 2002; Hull Sieg, 1987; Hulme, 1996) and alter their habitats through direct interactions with their abiotic environments (Chew, 1978; Davidson & Lightfoot, 2008; Hulme, 1996; Inouye et al., 1987; Jones et al., 1994; Laundré, 1993, 1998; Potter, 1978; Weltzin et al., 1997). They have been known to assist in decomposition and nutrient cycling, as well as engage in soil turbation, which can aerate and increase ground water recharge. Rodents also influence ecological succession, control plant productivity, and provide habitats for other species.

The combination of all these qualities makes rodents prime and precise representations of paleoenvironmental conditions (Avery, 2007; Grimes et al., 2008; Hernández Fernández et al., 2007; Reed, 2003; van der Meulen & Daams, 1992). To date, micromammals have been used to reconstruct paleoenvironmental and paleoclimatic conditions in a variety of different ways. These include, but are not limited to, analyses of faunal assemblages (e.g., Avery, 2001; Avery et al., 2010; Legendre et al., 2005; Montuire et al., 1997; Reed, 2008;), fossil mammal successions (e.g., Calede et al., 2011; Goméz Cano et al., 2013; van Dam & Weltje, 1999) isotope analyses derived from tooth or bone (e.g., Arppe et al., 2015; Hynek et al., 2012; Yeakel et al., 2007), bioclimatic analyses (e.g., Hernández Fernández, 2001; Hernández Fernández, 2006; Hernández Fernández et al., 2007), and dental-wear based analyses, both macro- and micro- (e.g., Burgman et al., 2016; Caporale & Ungar, 2016; Cervantes-Barriga et al., 2021; Firmat et al., 2010; Gomes

Rodrigues et al., 2009; Hopley et al., 2006; Kaya & Kaymakçı, 2013; Kimura et al., 2013; Lewis & Simons, 2007; Oliver et al., 2014; Ungar et al., 2021a; Ungar et al. 2021b).

Micromammal Microwear Studies

Even though the history of dental microwear analysis is dominated by larger taxa, initial foray into this technique involved smaller mammals. The focus on these larger organisms occurred due to the emphasis in microwear use as a paleodietary proxy for hominins. Larger mammals, like most early hominins, are large-bodied, terrestrial, and often herbivorous, and as such, subjective to similar selective pressures. Non-human primates, in particular, served a key role in this pursuit as they are used as extant counterparts for hominins. In addition, larger taxa have been historically easier to analyze. Their diets are better documented than that of smaller mammals, and are also less ambiguous, as many micromammals are opportunistic generalists whose diets vary based on food availability for a particular population (e.g., Abu Baker & Brown, 2012; Curtis & Perrin, 1979; Kerley, 1992). Small mammal teeth are generally 1-2 mm long (Hilson, 2005), with narrow enamel bands that are often < 100 um in width (Patnaik, 2002). Although SEMs could obtain the magnifications needed to fit micromammal molar occlusal surfaces within the envelope of view, these data did not necessarily compare to that obtained at the lower magnifications (Belmaker, 2018). However, modern confocal microscopes utilized with 150x objective have since overcome this issue.

Dental microwear techniques have since been applied to a wide range of micromammal species, including rodents (see Table 2.1 for a list of published studies). These groups have included both extant and extinct taxa, such as Chioptera (e.g., Purnell et al., 2013; Strait, 1993), Multituberculata (e.g., Simpson, 1926; Lazzari et al., 2010), Eulipotyphla (e.g., Adams et al.,

2020; Silcox & Teaford, 2002; Withnell & Ungar, 2014), and a vast variety of rodents that include, but are not limited to, Sciuridae (e.g., Gusovsky & Sinitsa, 2019; Nelson et al., 2005), Cricetidae (e.g., Calanadra et al., 2016; Rensberger, 1978; Ungar et al., 2021), Muridae (e.g., Hopley et al., 2006; Burgman et al., 2016; Winkler et al., 2020b), Gliridae (e.g., Hautier et al., 2009; Oliver et al., 2014), and Caviomorpha (e.g., Teaford, 1983a; Robinet et al., 2020). Belmaker (2018) provides an in-depth review of the nuances of small mammal dental microwear that discusses important studies and necessary considerations for future work in this field.

Early studies

In 1926, dental microwear was used to defend a hypothesis of propalinal mastication in multituberculates, an extinct group of rodent-like micromammals. Simpson (1926) noted that the "longitudinal striations" on the molar occlusal surfaces could only occur from masticatory movements. Decades later, some of the earliest experimental applications of dental microwear to extant micromammals would include *Cavia porcellus* (guinea pigs). Much like Simpson's (1926) study, most of these studies used micromammal microwear to demonstrate mastication mechanics, albeit these through use of scanning electron microscopes. Teaford and Walker (1983a) utilized adult and still-born *C. porcellus* specimens to show that the formation of wear striations requires the presence of some sort of ingested material, as well as to equate the same actions behind mastication to tooth sharpening (Teaford & Walker, 1983b). Another study used guinea pig molar microwear to explore differences in tooth wear based on changes in jaw movements (Teaford & Byrd, 1989). Rodent species, including squirrels, voles, lemmings, geomyoids, and mice, were used by Rensberger (1978) to observe wear effects, including microwear, that resulted from different diets and tooth shape.

Table 2.1: Summary of micromammal and rodent dental microwear studies conducted since 1926.

Study	Species (order: family)	Tooth	Cusp	Procurement	Method
Simpson, 1926	Multituberculata: Ptilodontidae Multituberculata: Cimolomyidae Multituberculata: Plagiaulacidae Multituberculata: Allodontidae	molars			descriptive
Resenberger, 1978	Rodentia: Sciuridae Rodentia: Cricetidae Rodentia: Arvicolinae	M^2 M^1, M^2 M^1	protocone	SEM	descriptive
Teaford & Walker, 1983a	Rodentia: Caviidae	molars		SEM	descriptive
Teaford & Walker 1983b	Rodentia: Caviidae	molars		SEM	descriptive
Teaford & Byrd, 1989	Rodentia: Caviidae	M_1		SEM	scratch orientation
Lee & Houston, 1993	Rodentia: Cricetidae	M^2, M_2		SEM	scratch and pit count
Strait, 1993	Chioptera: Molossidae Chioptera: Hipposideridae Chioptera: Megadermatidae Chioptera: Molossidae Chioptera: Rhinolophidae Chioptera: Phyllostomidae Primates: Galagidae Primates: Tarsiidae Primates: Lorisidae	M_2	protoconid	SEM	scratch and pit count
Crompton et al., 1998	Primates: Tarsiidae	molars	hypoconid	SEM	scratch and pit count
Lewis et al., 2000*	Rodentia: Arvicolinae	M_1	anterior enamel band	SEM	scratch and pit count
Silcox & Teaford, 2002	Chioptera: Noctilionidae Chioptera: Vespertilionidae Primates: Galagidae Primates: Tarsiidae Eulipotyphla: Erinaceidae Eulipotyphla: Talpidae Afrosoricida: Tenrecomorpha	M_1, M_2	hypoflexid, trigonid	SEM	scratch and pit count

Table 2.1 (Cont.)

Study	Species (order: family)	Tooth	Cusp	Procurement	Method
Nelson et al., 2005*	Rodentia: Sciuridae	M^1, M^2	metaconule	stereomicroscope	scratch and pit count
Hopley et al., 2006*	Rodentia: Muridae	lower molar		SEM	scratch and pit count
Charles et al., 2007	Rodentia: Muridae Rodentia: Dipodidae	M_2	entoconid	stereomicroscope	scratch and pit count
Lazzari et al., 2008	Rodentia: Muridae	all available	all available	stereomicroscope	scratch orientation
Townsend & Croft, 2008	Rodentia: Erethizontidae Rodentia: Cavioidea Rodentia: Hydrochoeridae Rodentia: Octodontoidea Rodentia: Chinchillioidea	M^2, M_2		light microscope	scratch and pit count
Calede & Hopkins, 2009*	Rodentia: Mylagaulidae				
Calede, 2009b	Rodentia: Erethizontidae				
Rodrigues et al., 2009*	Rodentia: Muridae	M^1	hypocone	stereomicroscope	scratch and pit count
Hautier et al., 2009*	Rodentia: Gliridae	M_2	protoconid, hypoconid	stereomicroscope	scratch and pit count
Belmaker & Ungar, 2010	Rodentia: Cricetidae Rodentia: Heteromyidae	lower I		confocal profiler	DMTA: SSFA
Calede, 2010*	Rodentia: Geomyidae Rodentia: Mylagaulidae	M^2, M_2 P^4, P_4	protocone,	stereomicroscope	scratch and pit count
Firmat et al., 2010*	Rodentia: Muridae	M^1	hypocone	stereomicroscope	scratch and pit count
Hautier et al., 2010*	Rodentia: Theridomyidae	M^1, M^2 M_1, M_2	protocone, hypocone protoconid, hypoconid	stereomicroscope	scratch orientation
Lazzari et al., 2010*	Multituberculata: Paulchoffatiidae Multituberculata: Cimolodonta Therapsida: Triylodontidae Rodentia: Muridae	M^1, M_1, P^4, P_4, P^5 M^1 P^4 M^1		x-ray microtomograph	scratch orientation

Table 2.1 (Cont.)

Study	Species (order: family)	Tooth	Cusp	Procurement	Method
Firmat et al., 2011*	Rodentia: Muridae	M^1	hypocone	stereomicroscope	scratch and pit count
Stefen, 2011	Rodentia: Castoridae	all available		SEM and light microscope	scratch and pit count
	Rodentia: Echimyidae			light microscope	
	Rodentia: Cricetidae				
Rodrigues et al., 2012*	Rodentia: Cricetidae Rodentia: Ctenodactylidae	M^1, M^2	protocone, hypocone	stereomicroscope	scratch and pit count
Kaya & Kaymaçı, 2013*	Rodentia: Gliridae	M_2	protoconid	SEM	scratch and pit count
Purnell et al., 2013	Chioptera: Vespertilionidae	M_2	protoconid	confocal profiler	DMTA: ISO
	Chioptera: Rhinolophidae				
Rodrigues et al., 2013	Rodentia: Muridae	M^1	hypocone	stereomicroscope	scratch and pit count
Caporale & Withnell, 2014	Eulipotyphla: Soricidae	lower I		confocal profiler	DMTA: SSFA
	Rodentia: Muridae				
Gill et al., 2014*	Morganucodonta: Morganucodontidae	M_2	main cusp	optical profiler	DMTA: ISO
	Kuehneotheria: Kuehneotheriidae	molars			
	Chiroptera: Vespertilionidae	M_2	protoconid		
	Chiroptera: Rhinolophidae				
Oliver Pérez et al., 2014*	Rodentia: Gliridae	M^1, M^2	anterloph, protoloph	environmental SEM	scratch and pit count
Withnell & Ungar, 2014	Eulipotyphla: Soricidae	mandibular I		confocal profiler	DMTA: SSFA
Zykov et al., 2014*	Rodentia: Cricetidae Rodentia: Muridae	M_1			
Burgman et al., 2015	Rodentia: Muridae	M_2	protoconid	confocal profiler	DMTA: SSFA
Patnaik, 2015*	Rodentia: Muridae	molars		SEM	scratch and pit count
	Rodentia: Spalacidae				
Renaud et al., 2015	Rodentia: Muridae	M^1		stereomicroscope	scratch and pit count
Burgman et al., 2016	Rodentia: Muridae	M_2	protoconid	confocal profiler	DMTA: SSFA
Calandra et al., 2016a	Rodentia: Cricetidae	M^2	anterior enamel band	confocal profiler	DMTA: SSFA

Table 2.1 (Cont.)

Study	Species (order: family)	Tooth	Cusp	Procurement	Method
Calandra et al., 2016b	Rodentia: Cricetidae	M^2	mesial enamel band	confocal profiler	DMTA: ISO
Caporale, 2016	Rodentia: Muridae	mandibular I		confocal profiler	DMTA: SSFA
Caporale & Ungar, 2016	Rodentia: Muridae	mandibular I		confocal profiler	DMTA: SSFA
Winkler et al., 2016	Rodentia: Muridae	M^1	hypocone	confocal profiler	DMTA: ISO
Burgman et al., 2017a*	Rodentia: Muridae	M_2	protoconid	confocal profiler	DMTA: SSFA
Burgman et al., 2017b	Rodentia: Muridae	M_2	protoconid	confocal profiler	DMTA: SSFA
Robinet et al., 2017	Rodentia: Caviomorpha	M^1		confocal profiler	DMTA: SSFA
Zykov & Kropacheva, 2017	Rodentia: Cricetidae	M_1		SEM	scratch and pit count
Robinet et al., 2018*	Rodentia: Caviomorpha	M^1		confocal profiler	DMTA: SSFA
Robson, 2018*	Multituberculata: Taeniolabidoidea	all available		SEM	scratch and pit count
Zykov et al., 2018	Rodentia: Cricetidae	M_1	entoconid, protoconid	SEM	scratch and pit count
Gusovsky & Sinitsa, 2019*	Rodentia: Sciuridae	M_3		SEM	scratch and pit count
Kropacheva et al., 2019	Rodentia: Cricetidae	M_1		SEM	scratch and pit count
Mihlbachler et al., 2019	Rodentia: Muridae	M^2		confocal profiler	DMTA: ISO
Winkler et al., 2019	Rodentia: Caviidae	P^4		confocal profiler	DMTA: ISO
Adams et al., 2020	Eulipotyphia: Talpidae	M_2	protoconid	optical profiler	DMTA: ISO
Menéndez et al., 2020*	Rodentia: Sciuridae	M^1, M^2, P_4, M_2, M_3	protocone, hypocone	Environmental SEM	scratch and pit count
Robinet et al., 2020	Rodentia: Caviidae Rodentia: Echimyidae	M^1	protocone	confocal profiler	DMTA: SSFA
Winkler et al., 2020a	Rodentia: Muridae	M^1, M^2	first enamel band	confocal profiler	DMTA: SSFA DMTA: ISO
Winkler et al., 2020b	Rodentia: Caviidae	right P^4	anterior enamel band	confocal profiler	DMTA: ISO
Cervantes-Barriga et al., 2021*	Rodentia: Cricetidae	M^1	hypocone	SEM	scratch and pit count

Table 2.1 (Cont.)

Study	Species (order: family)	Tooth	Cusp	Procurement	Method
Ungar et al., 2021a	Rodentia: Cricetidae	mandibular I		confocal profiler	DMTA:SSFA DMTA: ISO feature based
Winkler et al., 2021	Rodentia: Caviidae	maxillary P, maxillary M	anterior enamel band	confocal profiler	DMTA: SSFA DMTA: ISO
Yang et al., 2021*	Rodentia: Castoridae	P^4, P_4		stereomicroscope	scratch and pit count

*denotes work that involves fossil specimens

Two-Dimensional Studies

Two-dimensional microwear studies have generally utilized scanning electron microscopy or light stereomicroscopy. Enamel surfaces are scanned at high magnifications and impacts of differences in diet are inferred through quantification of the scratches and pits observed in these images. Reported measurements often included the lengths, breadths, and orientations of features, as well as the ratios between scratches and pits (Ungar, 2015). Aside from the aforementioned studies, three other micromammal microwear studies occurred in the twentieth century, all of which used SEMs. Strait (1993) utilized microwear to distinguish hard-object faunivorous microchiropterans and small-bodied primates from faunivores that preferred softer prey, though she could not differentiate between carnivores and insectivores. Lee and Houston (1993), meanwhile, utilized the microwear of two vole species to determine how well their dentition processed food, noting differences in patterns between leaf-eating voles and those that ate grass. Finally, Crompton et al. (1998) used microwear in part to explore the mastication mechanics of the primate *Tarsius bancanus*.

During the first decade of the twenty-first century, micromammal microwear began to focus on dietary and environmental reconstruction (e.g., Calede, 2009; Calede & Hopkins, 2009; Hautier et al., 2009; Hopley et al., 2006; Lewis et al., 2000; Nelson et al., 2005; Gomes Rodrigues et al., 2009; Silcox & Teaford, 2002; Townsend & Croft, 2008). For example, at Makapansgat, South Africa, isotopic and microwear analyses reconstructed omnivorous diets that showed a penchant towards browsing, thus indicating that the mid-Pliocene environment was likely a woodland-savannah mosaic habitat (Hopley et al., 2006). To regulate user observational bias, Hopley et al. (2006) applied computer software to analyze the number of pits and scratches observed on the surface. In another study, microwear features of subfossil

Ondatra zibethicus indicated that differences in patterns coincided with vegetation shifts that occurred in the strata of Lubbock Lake Landmark in which the fossils were found (Lewis et al., 2000). And in Asia Minor, dormouse dental microwear has been used to infer Miocene conditions of Hayranlı, Anatolia (Kaya & Kaymakçı, 2013). The high number of large pits was considered indicative of a hard diet that, in combination with observations of related extant taxa, Kaya and Kaymakçı considered indicative of a mixed diet that reflected a seasonal environment.

SEM studies also focused on parsing diets of extant and extinct taxa. For example, dental microwear patterns derived from earthworm-eating mole and tenrec species separating from that of other faunivorous species (Silcox & Teaford, 2002). Based on the dental microwear attributes obtained through SEM methods, diets have also been suggested for taeniolabidoid multituberculates (Robson, 2018), Miocene *Armantomys* species (Oliver Pérez et al., 2014), fossil Muridae and Spalacidae species (Patnaik, 2015), extinct Xerinae (Menendez et al., 2020) and *Spermophilinus* (Gusovsky & Sinitsa, 2019) squirrels, and fossilized *Sigmodon* rodents (Cervantes-Barriga et al., 2021).

In addition to SEM microwear analyses, light stereomicroscopy became a popular method for dietary studies. For example, Nelson and colleagues (2005) developed an extant baseline from frugivorous arboreal squirrels and omnivorous terrestrial squirrels, separating microwear patterns by variables based on the presence and absence of pits and scratches, as well as their texture and orientation. This resulted in different groupings between the tree and ground species clear enough to use for comparison of fossil sciurid specimens with unknown diets. Comparable methods were also applied to extant and fossilized caviomorph rodents (Townsend & Croft, 2008). In this case, the individual microwear variables, like pit density, did not individually result in clear differences. However, when all attributes were incorporated together

to form a derived microwear profile, rodents could be separated into three dietary groups that allowed for classification of a fossil species. Another example, Hautier et al.'s (2009) analysis of extinct *Hypnomys morpheus* (Balearic dormouse) molars, indicated that in comparison to its extant cousin, the Balaeric dormouse probably ate harder food items.

Gomes Rodrigues et al. (2009) adapted a protocol (Merceron et al., 2004) meant for the analysis of larger taxa to micromammals that utilized other software to count and measure scratches and pits. They applied this method to a study of extant and extinct murids, which resulted in interspecies differences in dental microwear and clearly separated out grazers from the rest of the group. This method continued to be used into the 2010s and was applied to dietary studies of fossil *Canariomys* rodents (Firmat et al., 2010), fossil *Malpaisomys insularis* (Firmat et al., 2011), extant and extinct *Apodemus* and *Stephanomys* species (Gomes Rodrigues et al., 2013), Oligocene Cricetidae and Ctenodactylidae species (Gomes Rodrigues et al., 2012), and extant *Mus musculus domesticus* (Renaud et al., 2015). Other studies using stereomicroscope analyses include the examination of extant *Castor fiber*, *Myocastor coypus*, and *Ondatara zibethicus* microwear (Stefen, 2011) and the dietary reconstructions of extinct Mylaugaulidae species (Calede, 2010).

Interpretations of these dietary reconstructions can lead to inferences on the immediate environment and ecological niches these animals occupied. For example, within an assemblage of fossil rodents from Ulantatal, China, dental microwear patterns obtained through stereomicroscopy indicated high levels of grass and insect consumption among the different taxa that could be interpreted as an open habitat with some sort of nearby water source (Gomes Rodrigues et al., 2012). More recently, these techniques indicated that the diet of the beaver *Trogontherium cuvieri* varied during the early and middle Pleistocene, thus relying upon a

flexible ecological niche to survive through climate changes in northeastern Pleistocene China (Yang et al., 2021).

Evolutionary research has also applied SEM and stereomicroscopy two-dimensional dental microwear techniques. These studies include using the orientation of scratches to help elucidate parallel and convergent evolutions in molar crown morphology (Lazzari et al., 2008) or changes across an evolutionary lineage based on the direction of mastication (Charles et al., 2007). Microwear studies have also been used to describe mastication activities in extinct multituberculate species (Lazzari et al., 2010) and extinct Issiodoromyinae rodents (Hautier et al., 2010). Another 2D micromammal microwear analysis looked at the evolutionary responses triggered by changing environments and subsequent access to food sources in modern day taxa (Renaud et al., 2015). Stereomicroscopy work detailed how stephanodonty, the configuration of the five posterior cusps of the first and second upper molars into a circular pattern, developed in some Murinae lineages as a partial adaptation to fibrous diets (Gomes Rodrigues et al., 2013). SEM studies of extant *Microtus* species have also been used to show the effects of different abrasives on molar microwear (Zykov et al., 2018) or in taphonomy experiments to understand the effects of digestion on microwear patterns (Kropacheva et al., 2019).

Dental Microwear Texture Analysis: Incisors

Dental microwear texture analysis remains a relatively new method in micromammal microwear research. The first application of DMTA to micromammals was a poster presented at the Annual Meeting of the Paleoanthropology Society to assess incisor microwear texture as a potential paleoenvironmental proxy using scale-sensitive fractal analysis (Belmaker & Ungar, 2010). Since this initial foray, only three more papers have been published using micromammal

incisors. Withnell and Ungar (2014) applied SSFA analysis to shrew incisors to determine whether dental microwear analyses of Soricidae could be used as a proxy for diet and habitat. Among specimens, no strong environmental signal was perceived, nor was a dietary signal perceived when compared across habitats. Within a single environment, however, texture patterns reflected interspecies dietary differences.

Alternatively, when the same approach was applied to rodent incisors, distinct dietary and environmental effects were observed (Caporale & Ungar, 2016). Omnivores stood out as more anisotropic than herbivores and more heterogeneous than frugivores, though overall, dietary differences were difficult to parse. As expected, given incisors' role in food acquisition rather than processing, they better reflected habitat and substrate use. Most recently, Ungar et al. (2021) compared *Lemmus sibiricus* (lemmings) and *Lasiopodomys gregalis* (vole) incisor microwear from different habitats within the Arctic using both SSFA and ISO variables, as well as microwear feature analysis. Results indicated that differences between species probably resulted from how the two taxa utilize their environment, as voles burrow and lemmings do not. Further, differences in microwear textures between the high tundra and forest-tundra samples reflected changes in abrasive load, moisture, and vegetative cover between the habitats. Interestingly, feature analysis better discriminated microwear textures by site than did DMTA.

Dental Microwear Texture Analysis: Molars

The remainder of studies employing DMTA have focused on micromammal molars. Burgman et al. (2016) used SSFA to identify environmental and dietary influences in sympatric rodent species. While differences between habitat types were observed for some of the species, there was an inconsistency in the pattern that suggested that the microwear signals for these mice

were driven by the nuances of diet. That same year, a study by Calandra et al. (2016a) applied SSFA to laboratory and wild voles (*Microtus oeconomus*) to test the influence of phytoliths on microwear patterns. Their results indicated that microwear textures varied based on seasonality. Robinet et al. (2017, 2020) analyzed caviomorph rodents from Brazil and found that scale-sensitive fractal analysis successfully separated rodents with distinct dietary preferences.

SSFA application to fossil rodents occurred as part of a larger dental microwear study of Kanapoi's paleocommunity (Ungar et al., 2017). Due to the lack of an existing baseline, however, only vague hypotheses could be made about the dietary implications of this data. Oligocene caviomorph dental microwear textures have also been described by SSFA parameters (Robinet et al., 2018). These two studies make up the entirety of DMTA work applied to fossil micromammals.

The first application of ISO analyses to micromammals focused on four species of microchiroptera (Purnell et al., 2013). Purnell et al. (2013) considered parameters involving height, space, and volume when analyzing the microwear textures of the bats, as well as a hybrid parameter combining information on height and spatial distributions. A principal components analysis (PCA) of the parameters neatly separated the four bat species with little overlap and clear separation between those species that have a greater component of hard foods in their diet from those that have a greater component of softer foods. Another study incorporated microwear texture analysis as part of a greater ecomorphological and dietary study on stem mammals (Gill et al., 2014). Using bats as extant proxies, the PCA conducted on ISO values separated dietary preference by "soft" and "hard" prey, much like the study conducted by Purnell et al., (2013). From this, the authors were able to infer details on the dietary preferences of stem mammal species.

ISO parameters have been used to characterize the diets of various rodent species. While ISO attributes were unable to distinguish the diets of two populations of *Microtus agrestis* (field voles) from two similar habitats, they did indicate seasonal variation in texture patterns (Calandra et al., 2016c). However, when ISO attributes were applied to the dietary analysis of *Rattus rattus* (black rats) from distinct habitats in Madagascar, there was a clear difference in texture pattern between those from the rainforest and those from a village setting (Winkler et al., 2016).

In addition to dietary studies, rodent DMTA has also been used in experimentation focused on microwear etiology. Winkler et al. (2018) indicated that phytolith and water content (which can affect plant abrasiveness) will alter the microwear texture in *Cavia porcellus*. Guinea pigs were also used to test the influence of the material properties of external abrasives (Winkler et al., 2020b) and foodstuff (Winkler et al., 2021) on molar microwear texture patterns. Winkler et al. (2020b) found that the size, type, shape, and concentration of naturally occurring exogenous abrasives did impact microwear textures, with coarse-grained quartz and volcanic ash resulting in rough textures and high complexity. On the other hand, Adams et al. (2020) indicated that grit did not impact molar microwear dietary signals. Microwear textures did not significantly differ between moles (*Talpa europaea*) and bats with similar diets, even though the latter are considered to have much less interaction with soils than moles. In addition, silicate content within mole stomachs did not correlate with the ISO parameters considered.

Other experiments have used ISO analyses along with SSFA or 2D microwear methods (Mihlbachler et al., 2019; Winkler et al., 2020; Winkler et al., 2021) to provide more comprehensive results. Mihlbachler et al. (2019) applied ISO parameters and scratch and pit counts to analyze the surfaces of *Rattus norvegicus* molars in controlled feeding experiments

meant to test the fidelity of casting techniques under high magnification, such as in using an 150x objective. The original enamel surfaces better separated diets when analyzed either by ISO or 2D variables. When combining data from the two microwear techniques into one analysis, however, cast data more accurately represented data derived from the tooth surface. Winkler et al. (20201) also used *R. norvegicus* specimens to examine the "last supper" effect of dental microwears. The ISO and SSFA data derived from this feeding experiment indicated that textures need between 16 and 24 days to achieve a complete overwrite of the dietary signal (Winkler et al., 2020a). Most recently, work with *C. porcellus* showed how microwear textures varied based on cheek tooth position and the physical properties of ingested foods (Winkler et al., 2021).

While microwear analyses of micromammal teeth span nearly a century of work, most of these studies have been confined to the last twenty years. This body of work is extremely limited in comparison to that of larger taxa. Many of these studies have utilized micromammal microwear to elucidate masticatory adaptations and the etiology of microwear rather than as a proxy for fine-scale paleohabitat reconstruction. This dissertation considers the potential of rodent microwear, both incisor and molar, as a paleoenvironmental proxy and correlates DMTA data to that of known dietary, behavioral, and environmental factors.

CHAPTER THREE: MATERIALS & METHODS

The methods utilized in this dissertation involve: 1) the incorporation of data obtained from other aspects of the Kolomela ecomonitoring project for the 2017 survey year, 2) the stomach content analysis for rodent specimens caught by Dr. Nico Avenant[1, 2] and Dr. Jurie du Plessis[1] during the 2017 survey year, and 3) incisor and molar dental microwear texture analysis (DMTA) of the rodents. From this information, definitive associations can be drawn between rodent dental microwear texture and the environmental and dietary variables through the construction of a baseline to be used in future studies and statistical analyses comparing the various variables to microwear texture. The analysis of stomach contents provides a dietary snapshot that coincides well with the last supper effect documented with dental microwear. This technique is important in creating a better understanding of the molar microwear signal reported for species that are depicted as generalists or opportunists, as is the case for many of the rodents in this study. In these cases, diets can widely vary among separate populations based on the biological and environmental factors surrounding the studied group. The lack of dietary specificity for these species can make it difficult to utilize their microwear as a baseline for paleodietary or paleoenvironmental reconstructions, hence the need for a study such as this one.

This chapter first provides an overview of the study site, Kolomela mine and its associated farms, and the ecomonitoring project that in part made this research possible. This section is followed by an overview of the Gerbillinae and Murinae species used in the project, followed by details on the collection of these specimens, as well as the classification of the environmental data obtained from the other ecomonitoring projects. Finally, this chapter details

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[2] Centre for Environmental Management, University of the Free State, Bloemfontein, South Africa

the methods used to obtain the stomach content and the dental microwear data, and the statistical procedure used to compare all variables.

The Study Region

This study was conducted utilizing specimens captured at Kolomela Iron Ore Mine and its surrounding properties in the Northern Cape Province of South Africa, located approximately 12 to 22 km southwest from Postmasburg (see Figure 3.1). Kolomela is an open-pit cast iron ore mine that covers approximately 16,941.92 hectares of the larger Ghaap Plateau escarpment. This area possesses high plant diversity, with many endemic or near endemic plant species (AngloAmerican, 2014). It is also an area potentially rich in climate data and fossilized material relating to hominin evolution (Doran et al., 2015). The Ghaap Plateau is located within the Eastern Kalahari Bushveld bioregion, one of six main bioregions within the larger savanna biome of southern Africa. It is considered the largest of the savanna bioregions and has the highest average altitude (Mucina & Rutherford, 2006). The area occupied by mine properties is comprised mainly of the Postmasburg Thornveld ecoregion, along with smaller sections of Kuruman Mountain Bushveld, Northern Upper Karoo, Olifantshoek Plains Thornveld, and Southern Kalahari Salt Pans (Mucina & Rutherford, 2006; Smit & van Rensburg, 2018).

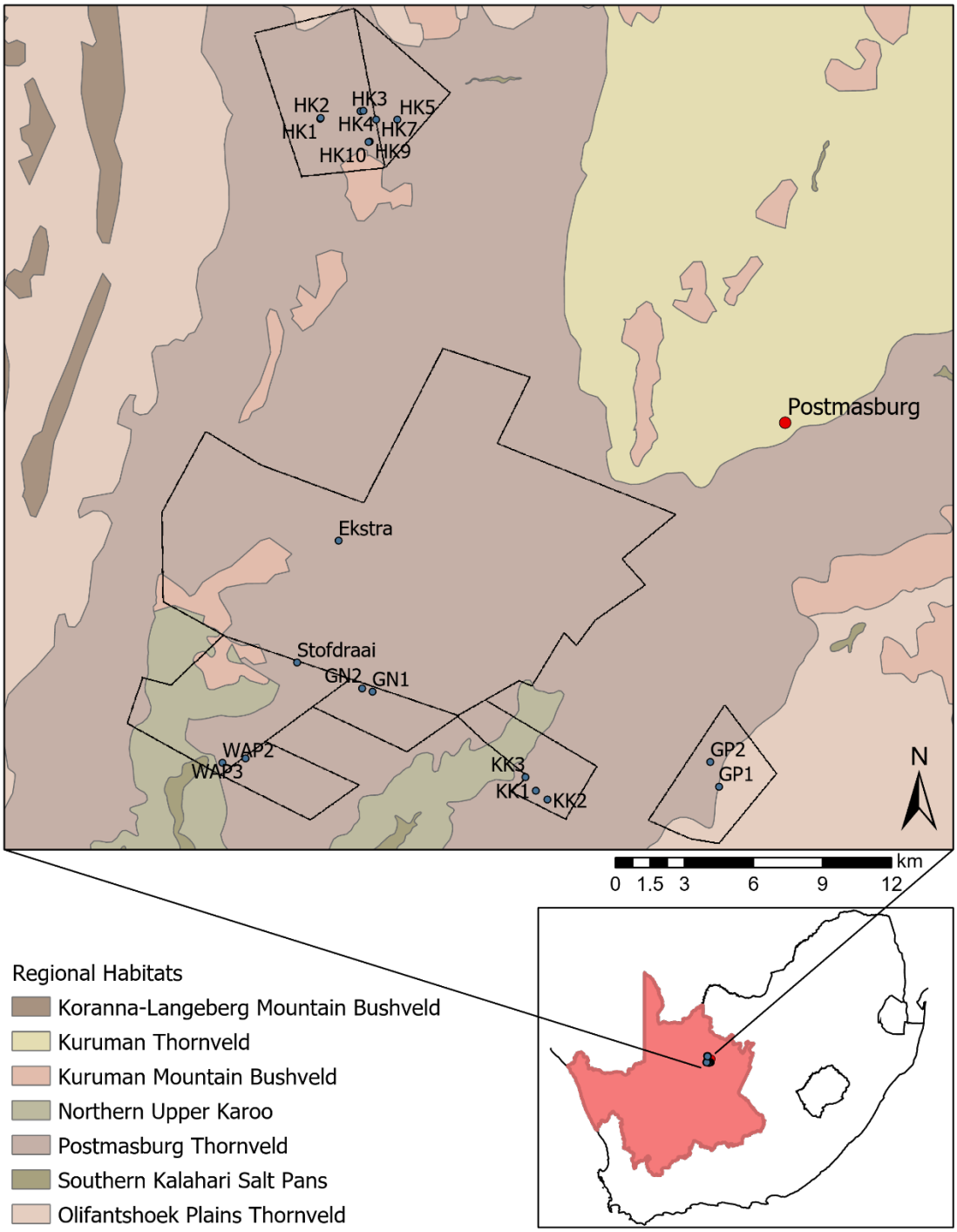

Figure 3.1: Map of Kolomela mine and surrounding areas, with associated ecoregions and the location of each small mammal transect used by Avenant and du Plessis.

Climatically, this region can be described as hot and semi-arid, with an average annual temperature of 18.8º C and intermittently falling rain in the spring and summer months (October to May) that average to 327 mm accumulation. During the summer, temperatures reach up to 42º C. While winters are generally dry, temperatures that drop below freezing at night have the potential to form frost layers (Munica et al., 2006; Smit & van Rensburg, 2018). During the 2017 monitoring season, the average rainfall total recorded 324.7 mm, with a mean rainfall measure of 6.5 mm in May and 0 mm in July (Smit & van Rensburg, 2018). Rodent sampling took place during May and July, providing samples that represent a transitional spring season and a dry winter season.

Kolomela Mine

The Kolomela Iron Ore Mine was established by Sishen Iron Ore Company, a subsidiary of Kumba Iron Ore, and the AngloAmerican mining company. Commercial production began in December 2011, alongside its biomonitoring program. Approximately 16,000 hectares in size, it is estimated to possess a reserve of 209.5 million tons of iron, with a mine lifespan of 29 years (Barradas, 2013). This estimate comes to a production rate of approximately 9 million tons per year, with ore stemming from conglomeratic and laminated hematite of the Proterozoic Griqualand West Supergroup geological formation (Kumba Iron Ore, 2012). Mining is conducted through open pits and blasting, with waste dumped in an adjacent pit. Screened ore is then processed through crushing at the processing plant located on site (Smit & van Rensburg, 2018).

Researchers from the University of the Free State and the National Museum were employed in a joint effort with Kumba Iron Ore to assess the biological and environmental

impact of open pit mining activities. This long-term program was initiated prior to the start of mine operations, with baseline surveys conducted in March 2011. Survey transects and dust fall collectors were established both on the active mine properties and the surrounding farms purchased by Kumba Iron Ore. Kolomela properties have undergone continuous monitoring for bush encroachment, groundwater contamination, dust fall levels, and air quality, and the effects mine operations have had on the local biodiversity. Annual surveys have monitored community changes at multiple trophic levels, in part to serve as bioindicators as to habitat health. Surveys have included the analysis of floral and vegetative composition, and the occurrence and distribution of aquatic invertebrates, birds, reptiles, and small mammals in and around the mine. Results from the 2017 monitoring season were presented at the Kolomela Environmental Symposium Program in April 2018 in Postmasburg, South Africa.

Transect habitats

Transects for the small mammal surveys were established within the Kolomela Mine area (Ekstra) and on seven of the associated farms: Grootpan, Gruispan, Heuningkrantz, Kappies Kareeboom, Sunnyside/Stofdraai, and Wildealsput. These locations were selected based upon the location of transects laid out by the vegetation monitoring team, as well as distance and direction from mining activities (Avenant & du Plessis, 2018). As such, each farm is its own unique habitat within the larger study region. Each transect measured between 250m in length, with snap traps placed about 5m apart (Avenant and du Plessis, 2018). Every transect was considered a microhabitat within the larger farm habitat.

Kolomela Mine (Ekstra).

Site Overview. Only one transect established at the site provided specimens to use in this research. The transect, Ekstra, was located at S28º22'15'' E22º54'02'' within the dwarf karroid shrubveld vegetation unit in the Postmasburg Thornveld ecoregion. According to the 2017 vegetation survey, grasses found within the area included: *Aristida congesta*, *Aristida diffusa*, *Enneapogon cenchroides*, *Enneapogon desvauxii*, *Eragrostis echinochoidea*, *Eragostis truncata*, *Orepetium capense*, *Setaria verticilata*, and *Tragus* species (Smit & van Rensburg, 2018). Other vegetation included the flowering plants *Dicoma capensis*, *Limeum aethiopicum*, *Pentzia globosa*, *Pentzia incana*, *Rosenia* species, woody plant seedlings *Asparagus retrofractus*, *Lycium cinereum*, and *Rhigozum trichotomum*, and trees *Grewia flava*, *Senegalia mellifera*, and *Vachellia karoo*. Avenant and du Plessis (2018) described the soil as sandy and the land cover as 40% bare, 30% grass, 25% bush, and 5% large bushes and trees. The measured dust fall rate for May was 782 mg/m^2/day (Loans, 2018).

Specimen Overview. A total of 19 rodents were trapped at the Ekstra transect in May 2017, comprised of *Gerbilliscus paeba* (*n* =3), *Gerbilliscus leucogaster* (*n* = 13), *Mus minutoides* (*n* =1), and *Rhabdomys bechuanae* (*n* = 2). All 19 individuals provided usable stomach contents for the dietary analysis. Most of these specimens also possessed acceptable surfaces for microwear analysis. Usable incisor surfaces (*n* = 17) were comprised of all *G. leucogaster* and *G. paeba* individuals. These same specimens, alongside one of the *R. bechuanae* molars, provided usable surfaces (*n* =17) for molar microwear analysis.

Grootpan

Site Overview. Grootpan (810 ha) is one of the five farms acquired by Kumba Iron Ore in 2016. This property borders the Kolomela Mine to the south and is separated from the mine by a public gravel road. The farm is located within the Postmasburg Thornveld ecoregion and can be divided into two main vegetation units: dwarf karroid shrubveld in the west, and black thorn bushveld in the east. Two small mammal transects were established in Grootpan, both within the western dwarf karroid shrubveld. GN1 began at S28°25'47.0" E22°54'49.7" and GN2 was established at S28°25'42.2" E22°54'35.3". The soil at both sites was described as clay/loam by Avenant and du Plessis (2018), who further described the land cover at GN1 as 20% bare soil, 14.5% grass, 52.5% bush, and 13% large bushes and trees and at GN2 as 3.5% bare soil, 69% grass, and 27.5% bush. Nearby dust fall rate measured at 697 mg/m^2/day at both Grootpan transects during the May survey, and 1,252 mg/m^2/day during the July collection at GN2. Common grasses reported by Smit & van Rensburg (2018) included *Aristida diffusa*, *Brachiaria serrata*, *Eragrostis lehmanniana*, *Fingerhuthia africana*, *Oropetium capense*, *Enneapogon cenchroides*, *Enneapogon desvauxi*, and assorted *Tragus* species. Other plants reported in the vegetation surveys include the shrub *Rhigozum trichotomum*, the trees *Boscia albitrunca* and *Senegalia mellifera*, seedlings of the fern *Asparagus retrofractus*, various *Appostimum* species, and flowering plants such as *Dicoma capensis*, *Lycium cinereum*, *Pentzia globosa*, *Plinthus karooicus*, *Lycium cinereum.*

Specimen Overview. A total of 81 rodents from Grootpan were used in this research. 33 were trapped at the transect GN1, representing 20 *Gerbilliscus leucogaster*, 1 *Mus minutoides*, and 12 *Rhabdomys bechuanae*. More rodents were obtained at the GN2 transect (*n* = 48), as trapping occurred in May and July. This collection consisted of 2 *Dendromus melanotis*

(both trapped in July), 19 *G. leucogaster* (8 trapped in July), 5 *Mastomys coucha* (3 trapped in July), 2 *Mu. minutoides* (both trapped in July), and 20 *R. bechuanae* (16 trapped in July). As such, Grootpan was represented by a total of 2 *D. melanotis*, 39 *G. leucogaster*, 5 *Ma. coucha*, 3 *Mu. minutoides*, and 32 *R. bechuanae* specimens. Stomach contents were obtained from 75 of these individuals (2 *D. melanotis*, 33 *G. leucogaster*, 5 *Ma. coucha*, 3 *Mu. minutoides*, and 32 *R. bechuanae*). Only 66 specimens possessed adequate incisor surfaces for dental microwear analysis (2 *D. melanotis*, 32 *G. leucogaster*, 3 *Ma. coucha*, 2 *Mu. minutoides*, and 27 *R. bechuanae*). Finally, 50 specimens provided surfaces for the molar microwear analysis (30 *G. leucogaster*, 2 *Ma. coucha*, and 18 *R. bechuanae*).

Gruispan

Site Overview. Gruispan (1,400 ha) was acquired by Kumba Iron Ore in 2012. This farm is located southeast of the mine but does not touch the mine property. Two transects for small mammal surveying were established within the farm: GP1, located at S28º28'00.4'' E23º02'56.5'', and GP2, located at S28º27'25.8'' E23º02'45.0". Unlike some of the other farms, Gruispan's lands occupy two ecoregions. Transect GP2 is located within the Postmasburg Thornveld while GP1 is located on the border of the Olifantshoek Plains Thornveld. The northern region of the farm was described by Smit & van Rensburg (2018) as a relatively flat, open veld with a number of woody plants while the southern area is more closed and dominated mostly by the thorn tree *Senegalia mellifera*. Grasses noted during the vegetation survey of the farm include *Aristida diffusa, Aristida congesta, Cymbopogon pospischilii, Enneapogon scoparius, Eragrostis lehmanniana, Heteropogon contortus, Microchola caffra, Oropetium capense*, *Sporobolus fimbriatus*, and *Tragus* species. Other vegetation includes trees such as

Tarchonanthus camphoratus, *Senegalia mellifera*, *Phymaspermum pavifolium*, and *Ziziphus mucronata*, seedlings of *Asparagus retrofractus* and *Lycium cinereum*, and shrubs like *Cadaba aphylla*, *Eriocephalus ericoides*, *Grewia flava*, and *Pentzia incana* (Smit & van Rensburg, 2018). Soils at the two transects were recorded as loam mixtures, with a loam and sand combination noted at GP1 and a loam and clay combination noted at GP2 (Avenant & du Plessis, 2018). The nearest dust fall monitor recorded the average May dust accumulation at 700 $mg/m^2/day$. However, Smit & van Rensburg (2018) did not observe any strong influence of mining-related dust at this farm. Avenant and du Plessis (2018) described land cover at GP1 as 19% bare soil, 41% grass, 27.5% bushes, and 12.5% large bushes and trees. At GP2, they described it as 5% bare, 11% grass, 83.75% bush, 0.25% tall bushes and trees.

Specimen Overview. All 6 specimens trapped at Gruispan were obtained during the May sample survey. Of these, 5 specimens were classified as *Gerbilliscus leucogaster* and 1 was classified as *Gerbilliscus paeba*. Transect GP1 only provided 2 of these rodents, both *G. leucogaster*. GP2, meanwhile, provided the other 3 *G. leucogaster* specimens and the 1 *G. paeba*. All six gerbils provided both stomach contents and molar surfaces to use in their respective analyses. Only rodents from GP2 possessed clean incisor surfaces for microwear analysis.

Heuningkrantz

Site Overview. Heuningkrantz (2,214 ha) was obtained by Kumba Iron Ore in 2015. Located north of the mine, it is also the furthest away from Kolomela or any of the other associated farms. The farm lies within the Postmasburg thornveld ecoregion and can be described as an area of high vegetative diversity. Its northeast sector contains a variety of woody

vegetation that surround a larger open grassland while the southeast is more mountainous. Dwarf karroid shrubs were noted along a drainage that runs through the farm. The farm is dominated by *Senegalia mellifera* grass. Noted woody vegetation includes *Diospyros lyciodes*, *Grewia flava*, *Searsia cilliata*, *Tarchononthus camphoratus*, *Vachella erioloba*, and *Ziziphus mucronata* (Smit & van Rensburg, 2018). Unfortunately, there were no dust fall collectors on the site in 2017 and as such, no dust data was obtained. Ten transects for small mammal trapping were established within Heuningkrantz's boundaries: HK1 (S28º12'22.0" E22º53'36.1"), HK2 (S28º12'20.6" E22º53'37.0"), HK3 (S28º12'11.4" E22º54'33.1"), HK4 (S28º12'11.0" E22º54'37.2"), HK5 (S28º12'23.0" E22º55'24.7"), HK6 (S28º12'25.0" E22º55'25.0"), HK7 (S28º12'22.9" E22º54'54.8"), HK8 (S28º12'21.8" E22º54'54.7"), HK9 (S28º12'54.1" E22º54'45.9"), and HK10 (S28º12'54.7" E22º54'44.1"). Six of these transects, HK1 – HK6, were established on sandy soils while the other four, HK7 – HK10, were located on rockier soil. Land coverage varied by transect. Both HK1 and HK2 were identical in distribution, with 30% bare soil, 50% grass, 10% bushes, and 10% large bushes and trees throughout the transect. HK3 and HK4 were also similar, recorded as 5% bare soil, 70% grass, 15% bushes, and 10% large bushes and trees. The land distribution at HK5 and HK6 was 20% bare soil, 60% grass, 5% bush, and 15% larger bush and trees. HK7's land cover consisted of 30% bare soil, 30% grass, 20% bushes, and 20% large bushes and trees. HK8, meanwhile, had 20% bare soil visible, 70% grass, and 10% large bush and trees. Finally, HK9 and HK10 showed 30% bare soil, 60% grass, and 10% large bushes and trees (Avenant & du Plessis, 2018).

Specimen Overview. A total of 72 specimens gathered from Heuningkrantz were utilized, collected in May and July. These individuals represented three species: *Gerbilliscus leucogaster* (*n* = 20), *Micaelamys namaquensis* (*n* = 49), and *Rhabdomys bechuanae* (*n* = 3). Of

the ten transects, HK6 and HK8 were the only two not to yield any usable rodents. HK1 and HK10 each yielded 2 specimens a piece, with *G. leucogaster* (*n* = 1) and *R. bechuanae* (*n* =1) trapped at HK1 and *Mi. namaquensis* (*n* = 2) trapped at HK10. Traps at HK2 and HK4 resulted in a loan *R. bechuanae* being caught along each transect. HK3's traps only resulted in *G. leucogaster* species (*n* = 14). HK5 (*n* = 6) provided 5 *G. leucogaster* individuals and 1 *Mi. namaquensis*. Finally, the remaining two successful transects, HK7 and HK9, solely provided *Mi. namaquensis* specimens. 39 were trapped at HK7, with 12 provided by the May survey and 27 by the July, and 7 trapped at HK9, 3 from May and 6 from July. Of these individuals, 59 specimens provided good contents for the stomach content analysis, 51 possessed acceptable molar surfaces for microwear analysis, and 62 possessed acceptable incisor surfaces.

Kappies Karrieboom

Site Overview. Kappies Karrieboom (990 ha), abbreviated as Kappies Karrie, borders the mine along its southern boundary. It is the other farm acquired by Kumba Iron Ore in 2012 and has been included in the ecological monitoring program ever since. Located within the Postmasburg thornveld ecoregion, three small mammal survey transects were established for trapping purposes. All three are located within the eastern part of the farm (KK1 at S28º28'06.0'' E22º58'39.2'', KK2 at S28º28'18.2'' E22º58'55.7'', and KK3 at S28º27'46.8'' E22º58'24.6'') which has been described by Smit & van Rensburg (2018) as flatter with open vegetation. They described the western part of the farm as part of the Kolomela mine panveld vegetation unit. Surveys indicated a prominence of *Aristida diffusa*, *Astrida congesta*, *Enneapogon desvauxii*, *Eragrostis bilfora*, and *Eragrostis lehmanniana* grass species within Kappies Karrie, alongside lesser amounts of *Brachiaria serrata*, *Digitaria eriantha*, *Enneapogon*

scoparius, Eragrostis echinochoidea, Eragrostis obtusa, *Fingerhuthia africana, Heteropogon contortus, Oropetium capense, Schmitia paraorophoides, Enneapogon cenchroides*, and *Setaria verticilata*. Flowering plant species found around the transects include *Dicoma capensis*, *Limeum aethiopicum*, *Lycium cinereum*, *Pentzia globosa*, *Pentzia incana, Phymaspermum parvifolium, Plinthus karooicus*, and various *Rosenia* species. Also noted in the survey were various *Cyperus* sedge species, and woody species such as *Asparagus retrofractus*, *Boscia albitrunca, Diospyros lyciodes, Ehretia rigida, Rhigozum trichotomum, Searsia burchelli, Senegalia mellifra, Tarchonanthus camphoratus*, and *Ziziphus mucronata* (Smit & van Rensburg, 2018).

While dust fall rates measured at 739 mg/m^2/day in May 2017, Smit & van Rensburg (2018) did not notice any visible influence of mining activities during their surveys. Soil type varied between the rodent transect locations. KK1's soil was described by Avenant and du Plessis (2018) as a mix of loam and clay, while KK2 and KK3 were only classified as loam. At KK1, land cover was described as 40% bare soil, 11% grass, 26.5% bush, and 22.5% large bush and trees. KK2 possessed a landscape of 32.5% barre soil, 40% grass, 22.5% bush, and 5% large bush and trees. Finally, KK3 was made up of 32.5% aerial, 25% grass, 12.5% bush, and 35% large bush and trees.

Specimen Overview. Only 43 rodents trapped at Kappies Karrie were utilized in stomach contents and dental microwear analysis. Of these 43, the majority were *Gerbilliscus leucogaster* (n = 27). Also caught were *Gerbilliscus paeba* (n = 2) and *Micaelamys namaquensis* (n = 14). Transect KK1 provided 4 usable specimens, an even mix of *G. leucogaster* and *G. paeba*. KK2 produced 15 specimens, all *G. leucogaster*. Finally, 24 specimens came from transect KK3, a mix of *G. leucogaster* and *Mi. namaquensis.* Of this collection, stomach

contents were obtained from 36 rodents and represented all three species caught. Although the individuals used varied in each analysis, usable surfaces for incisor and molar microwear were similarly represented by a total of 36 individuals apiece, stemming from *G. leucogaster*, *G. paeba*, and *Mi. namaquensis.*

Sunnyside (Stofdraai)

Site Overview. The transect Stofdraai was located at S28º25'06'' E22º53'04'' within the greater Sunnyside farm area. Sunnyside farm was acquired in 2016 and covers 2,497 ha southernly adjacent to Kolomela mine. Sunnyside is located within the Postmasburg thornveld ecoregion and can be divided into distinct vegetation units. The eastern part of the farm is dominated by Dwarf Karroid Shrubveld, while the western area is considered a rocky bushland and the southern area an open grassland. The northern part of the farm, where the Stofdraai transect is located, is considered an open area comprised mainly of sandveld species. The land cover for Stofdraai, as documented by Avenant and du Plessis (2018) was dominated by loam soil and grassy plants: 4% bare soil, 93% grass, 2% bush, and 1% large bush and trees. The small mammal transect was located between two of the vegetation transects, SSM1B and SSM2B. Smit and van Rensburg (2018) reported a variety of grasses along these two transects, including *Aristida diffusa*, *Aristida congesta*, *Brachiaria serrata*, *Cymbopogon pospichilii*, *Eragrostis lehmanniana*, *Heteropogon contortus*, *Oropetium capense*, *Enneapogon cenchroides*, *Enneapogon desvauxii*, *Eragrostis biflora*, *Setaria verticillata*, *Stipagrostis ciliata*, and different *Tragus* species. Woody vegetation within the area consisted of *Asparagus retrofractus*, *Grewia flava*, *Nenax microphylla*, *Rhigozum trichotomum*, *Senegalia mellifera*, and *Vachellia erioloba*. Finally, flowering species included *Felicia muricata*, *Lycium cinereum*, *Monechma incanum*,

Pentzia globosa, and miscellaneous *Pteronia* species. Dust fall rate varied by month: 752 mg/m^2/day in May and 1293 mg/m^2/day in July.

Specimen Overview. A total of 12 rodents were trapped at the Stofdraai transect, with 10 trapped in May and 2 trapped in July. Both rodents trapped in July were attributed to *Gerbilliscus leucogaster*, while eight more *G. leucogaster* specimens were trapped, bringing the total number used to $n = 10$. In addition, *Mus minutoides* ($n = 2$) was also trapped during the May collection. Eight of these rodents, a mixture of *G. leucogaster* with the 2 *Mu. minutoides*, provided stomach contents. Incisor dental microwear was obtained from one of the *Mu. minutoides* and six of the *G. leucogaster* specimens. Finally, the molar microwear data from Stofdraai was obtained solely from the 10 *G. leucogaster* specimens.

Wildealsput

Site Overview. Wildealsput (813 ha) is located south of the main Kolomela property, as well as south of the farm Sunnyside, in which it shares a border. Three small rodent transects were established at the farm: WAP1 (S28°26'47.3", E22°51'16.2"), WAP2 (S28°27'26.8", E22°51'55.1"), and WAP3 (S28°27'20.9", E22°51'51.2"). The farm is located within the Postmasburg thornveld ecoregion and possesses three distinct vegetation units. The northern section of Wildealsput lacks a high quantity of woody plants and is dominated by species like *Rhigozum trichotomum*. *Rh. trichotom* is also found within the eastern section of the farm alongside *Senegalia mellifera* and shallow soils. Finally, the western section of Wildealsput, where the small rodent transects were located, was defined as a lower-lying area with a lot of broad-leaved species such as *Diospyros lyciodes*, *Tarchononthus camphoratus*, and *Ziziphus mucronata* (Smit & Rensburg, 2018). The transect area at Wildealsput lacked a high tree

presence and was mostly dominated by grass and bush. WAP1's land cover was described as 21% bare soil, 75% grass, 3% bush, and 1% tall bush and trees, whereas WAP2 and WAP3 were more similar in composition; 15% bare soil, 35% grass, 44.5% bush, and 6.5% tall bush and trees along WAP2 and 22% bare soil, 32.5% grass, 42.5% bush, and 3% tall bush and trees (Avenant & du Plessis, 2018). No recorded dust fall level could be found for Wildealsput. However, soil types were recorded by Avenant and du Plessis (2018), with loam reported at WAP1, a clay and loam mixture at WAP2, and a clay, loam, and sand mix at WAP3. Wildealsput's grass composition included *Aristida congesta*, *Chloris vigrata*, *Enneapogon desvauxii*, *Eragrostis biflora*, *Eragrostis echinochoidea*, *Oropetium capense*, *Setaria verticillata*, and various *Tragus* species (Smit & Rensburg, 2018). Woody plants such as *Diospyros lycioides*, *Grewia flava*, *Senegalia mellifera*, *Tarchonanthus camphoratus* were also common around Wildealsput, as well as *Asparagus retrofractus*, *Dicoma capensis*, *Grewia flava*, *Lycium cinereum*, *Pentzia globosa*, *Rosaria* species, and *Senegalia mellifera*.

Specimen Overview. Eight specimens were trapped at Wildealsput, seven of which were *Gerbilliscus leucogaster* and one *Gerbilliscus paeba*. WAP1 produced 1 *G. leucogaster*, 3 *G. leucogaster* specimens were caught at WAP2, and 4 specimens were caught at WAP3, both *G. leucogaster* (n = 3) and *G. paeba* (n = 1). All rodents provided stomach contents for analysis. Surfaces for incisor microwear analysis were obtained from *G. leucogaster* (n =7) while surfaces for molar microwear (n = 5) came from both gerbil species, *G. leucogaster* (n = 4) and *G. paeba* (n = 1).

Specimen Summary

The specimens utilized in this study were obtained and processed by Dr. Avenant and associates at the National Museum of the Free State for their small mammal biomonitoring survey during the 2017 monitoring season. Collection followed all applicable South African laws regarding use of animal subjects. Following previously established methods, multiple transects of snap traps were laid out within Kolomela and its farms based upon distance and direction from various mining activities, wind direction, dust fallout concentration, and vegetation (Avenant, 2011; Avenant & du Plessis, 2016). Bait consisted of a mixture of peanut butter, sunflower oil, marmite, and rolled oats. All transects had 50 traps that were checked and rebaited daily for four continuous days in May 2017 and three continuous days in July 2017. A total of 240 specimens obtained during the May and July surveys were sampled for stomach content and microwear analyses. These specimens represented seven species of superfamily Muroidea: *Dendromus melanotis* (*n* = 2), *Gerbilliscus leucogaster* (*n* = 119), *Gerbilliscus paeba* (*n* = 7), *Mastomys coucha* (*n* = 5), *Micaelamys namaquensis* (*n* = 64), *Mus minutoides* (*n* = 6), and *Rhabdomys bechuanae* (*n* = 37). A summary of key characteristics for each species can be found in Table 3.1. Due to an inherent trap-shyness of certain species and an inability to control rodent behavior, a sampling bias towards specific species, diets, burrowing habitats, and environments could not be controlled. Furthermore, not all specimens provided microwear surfaces free of antemortem wear. As such, the distribution of specimens and genera varied among the three aspects of analysis.

Table 3.1: Key characteristics of the Muroidea species utilized in stomach content and microwear analyses.

Family	Subfamily	Species	Common name	Mass (g)	Size (mm)	Habitat preference	Nesting behavior	Diet
Muridae	Gerbillinae	*Gerbilliscus leucogaster*	Bushveld gerbil	48 - 100	224 - 346	savanna, open woodlands, thornveld, bushveld	complex burrows	omnivorous
Muridae	Gerbillinae	*Gerbilliscus paeba*	Pygmy hairy-footed gerbil	21 - 36	174 - 230	arid, semi-arid areas, light woodland, areas of low plant diversity	simple burrows	opportunistic omnivore
Muridae	Murinae	*Mastomys coucha*	Southern multimammate mouse	24 - 73	152 - 325	grassland, woodland savanna, fields, disturbed areas	occupies nests and burrows built by other species	opportunistic omnivore
Muridae	Murinae	*Micaelamys namaquensis*	Namaqua rock mouse	28 - 88	178 - 229	rocky outcrops, savanna, semi-arid areas	builds grass and stick nests in crevices	omnivorous, granivorous
Muridae	Murinae	*Mus minutoides*	Tiny pygmy mouse	3 - 12	67 - 129	afromontane and ripeean forests, grasslands, rocky outcrops, woodlands, disturbed areas	excavates burrows and uses those made by other species	omnivorous
Muridae	Murinae	*Rhabdomys bechuanae*	Four-striped grass mouse	32 - 55	202 - 227	arid savanna	shallow burrows	omnivorous
Nesomyidae	Dendromurinae	*Dendromus melanotis*	Gray climbing mouse	8 - 17	135 - 220	savannas, grass-bush biotypes, moist habitats	grass nests above ground or burrows	granivorous, insectivorous

In total, this collection yielded 192 individuals with usable stomach contents, 198 individuals with acceptable surfaces for incisor microwear analysis, and 175 individuals with acceptable molar microwear surfaces. Stomach contents were obtained from *D. melanotis* (*n* = 2), *G. leucogaster* (*n* = 88), *G. paeba* (*n* = 7), *Ma. coucha* (*n* = 5), *Mi. namaquensis* (*n* = 56), *Mu. minutoides* (*n* = 5), and *R. bechuanae* (*n* = 29). The incisor surfaces were comprised of *D. melanotis* (*n* = 2), *G. leucogaster* (*n* = 101), *G. paeba* (*n* = 6), *M. coucha* (*n* = 3), *M. namaquensis* (*n* = 53), *M. minutoides* (*n* = 3), and *R. bechuanae* (*n* = 30). Finally, the surfaces used in molar microwear analyses were comprised of *G. leucogaster* (*n* = 103), *G. paeba* (*n* = 6), *M. coucha* (*n* = 2), *M. namaquensis* (*n* = 40), and *R. bechuanae* (*n* = 23). Table 3.2 highlights this breakdown of usable stomachs, incisors, and molars for each collection site.

Table 3.2: Breakdown of usable specimens for stomach content and dental microwear analyses from each collection site

			n		
Collection Site	**Taxon**	**Specimens**	**Stomachs**	**Incisors**	**Molars**
Kolomela	*Gerbilliscus leucogaster*	13	13	13	13
	Gerbilliscus paeba	3	3	3	3
	Mus minutoides	1	1	0	0
	Rhabdodmys bechuane	2	2	0	1
	total:	19	19	16	17
Grootpan	*Dendromus melanotis*	2	2	2	0
	Gerbilliscus leucogaster	39	33	32	30
	Mastomys coucha	5	5	3	2
	Mus minutoides	3	3	2	0
	Rhabdodmys bechuane	32	32	27	18
	total:	81	75	66	50
Gruispan	*Gerbilliscus leucogaster*	5	5	3	5
	Gerbilliscus paeba	1	1	1	1
	total:	6	6	6	6
Heuningkrantz	*Gerbilliscus leucogaster*	20	12	18	18
	Micaelamys namaquensis	49	44	41	31
	Rhabdodmys bechuane	3	3	3	2
	total:	72	59	62	51
Kappies Karrie	*Gerbilliscus leucogaster*	27	22	23	26
	Gerbilliscus paeba	2	2	1	1
	Micaelamys namaquensis	14	12	12	9
	total:	43	36	36	36
Sunnyside	*Gerbilliscus leucogaster*	10	6	6	10
	Mus minutoides	2	2	1	0
	total:	12	8	7	10
Wildealsput	*Gerbilliscus leucogaster*	7	7	7	4
	Gerbilliscus paeba	1	1	0	1
	total:	8	8	7	5

Muroidea Superfamily

The Muroidae superfamily (order: Rodentia, suborder: Myomorpha) includes three families within Africa, Muridae (mice, rats, and gerbils), Neosmyidae (pouched rodents, climbing mice, Malagasy rodents), and Spalacidae (fossorial muroids), as well as families occurring outside of this continent. Although the oldest evidence of African rodents dating back to the early Eocene (Colbert, 1969; McKenna & Bell, 1997; Hartenberger, 1998, Winkler et al., 2010), the first muroids did not appear in Africa until the mid to late Miocene. The closing of

the Tethys seaway during the Oligocene-Miocene boundary created landbridges that reconnected Africa to Eurasia. This allowed early Muroidea to enter the continent and diversify into multiple lineages (Happold, 2013; Koufos et al., 2005; Monadjem et al., 2015; Musser & Carleton, 2005). The earliest known muroids in Africa are from the extinct Afrocricetodontinae and occurred for the first time in the early Miocene of East Africa (Lavocat, 1973; Monadjem et al., 2015; Schenk et al., 2013). These arrivals were followed by more migrations and colonizations during the remainder of the Miocene that ultimately led to the subsequent diversification of today's African rodents and the establishment of extant endemic lineages (Happold, 2013; Jacobs, 1985; Monadjem et al., 2015; Winkler, 1994, 2002). Regionalization and speciation within these lineages followed during the Pliocene-Pleistocene due to rifting in East Africa and a global cooling climate (Denys et al., 1985; Monadjem et al., 2015; Reed & Geraads, 2011; Wesselman, 1995). In this study, the Muroidea are presented by individuals from the Muridae and Neosmyidae families.

Muridae Family

The Pakistani muroid *Potwarmus* is considered one of the first Muridae taxa to migrate into Africa, reaching Libya around 18 mya, followed by the Euraisian murid *Progonomy*, which rapidly spread across Africa between 12 – 10 mya (Monadjem et al., 2015). Today, murids can be found globally, comprising of five sub-families: Deomyinae (spiny mice, brush furred mice, link rat), Gerbillinae (gerbils, jirds, and sand rats), Leimacomyinae (Togo mouse), Lophiomyinae (maned rat), and Murinae (Old World rats and mice). These subfamilies are comprised of 150 genera and 730 species. (Happold, 2013). Within Africa, the Muridae can be divided into 50 genera, and 264 species, of which 41 genera and 250 species are endemic (Happold, 2013).

Murids range in size from 5 g to 210 g, found in almost all biotic zones in Africa - both natural and anthropogenic, and represent a diverse dietary range. For this study, specimens represent two sub-families: Gerbillinae (*n* = 126) and Murinae (*n* = 116).

Gerbillinae Sub-Family. These species represent two of the 71 species in Africa, derived from 12 genera. Globally, this sub-family is represented by 16 genera and 101 species found throughout Africa and Asia (Musser & Carleton, 2005). The group diverged sometime in the mid Miocene, approximately 18-16 mya (Michaux et al., 2001), with the earliest African gerbil, *Abudhabia*, stemming from Miocene Kenya (Manthi, 2007; Mein & Pickford, 2006; Winkler, 2003). The extant genus *Gerbilliscus*, of which two species are utilized in this study, first appears in the late Miocene, either in Ethiopia (Wesselman et al., 2009) or Kenya (Denys, 1987). Today, gerbils are typically found in semi-arid to arid environments. Within Africa, these environments include deserts, bushvelds, semi-deserts, grasslands, and woodlands. Gerbillinae species are small to medium sized rodents that are terrestrial, mostly granivorous, and usually nocturnal. They are in part defined by their dentition, with flat-crowned and rooted molars that, dependent upon species, are in part anchored by accessory rootlets (Butler, 1985; Charles et al., 2007; Happold, 2013; Lazzari et al., 2008a). Occlusal patterns are either lophate, planar, or prismatic in nature. Finally, M3s are reduced in size in comparison to other murids, and cylindriform in shape (Happold, 2013). Gerbillinae are represented in this study by *Gerbilliscus leucogaster* (*n* = 119) and *Gerbilliscus paeba* (*n* = 7).

Gerbilliscus leucogaster (Peters 1852). The bushveld gerbil is a common and widely distributed savanna species endemic to Africa. Within South Africa, *G. leucogaster* reaches its southern most limit at about 30º S (Happold, 2013) and has been documented within the north-eastern section of KwaZulu-Natal, the western and southern sections of the Free State, areas of

the Northern Cape north of the Orange River, and throughout the North West, Limpopo, Gauteng, and Mpumalanga provinces (Skinner & Chimiba, 2005). They are usually found in savanna grasslands and woodlands, typically those with sandy soils in which they can dig complex burrows of 40-45 mm in diameter (Happold, 2013). However, *G. leucogaster* distribution is not restricted to sandy substrates and can be found in areas associated with other soils (Happold, 2013). This gerbil is also nocturnal and terrestrial. They are omnivorous and opportunistic, with variations in diet dependent on season (Griffin & Griffin, 1990; Monadjem, 1997; Monadjem et al., 2015; Neal, 1991; Perrin & Swanepoel, 1987). Like other *Gerbilliscus* species, *G. leucogaster*'s upper incisors are narrow, grooved, and slightly opsithodont (Monadjem et al., 2015; Skinner & Chimiba, 2005). Their molars are lophodont, with round, high cusps that fuse together along the transverse laminae (Monadjem et al., 2015).

Gerbilliscus paeba (Smith 1836). The pygmy hairy-footed gerbil is widespread throughout Southern Africa (Monadjem et al., 2015). It extends east from the Limpopo River into the Mozambique region, occupying arid and semi-arid environments (Happold, 2013; Monadjem et al., 2015). Both substrate and vegetation play an influence habitat preference. *G. paeba* is associated with sandy substrate and areas of low plant diversity that usually consist of sparse grass, scrub, of woodland cover (Happold, 2013). It is terrestrial and nocturnal in nature and excavates simple to complex burrows within habitat substrate. *G. paeba* varies its diet based on localized food availability, which in turn tends to affect plant growth and production (Happold, 2013). It has been observed to consume insects, seeds, and other plant material in varying quantities (Kerley, 1989; Nel, 1978; Perrin et al., 1992).

Murinae Sub-Family. The Murinae sub-family, that of Old World mice and rats, is one of the most diverse and abundant groups of extant rodents, consisting of 124 genera and 543

species (Happold, 2013). Although indigenous to Eurasia and Africa (Musser & Carleton, 2005), today they have a global distribution. They have their origin with the migration of *Progonomys* from Pakistan into northern Africa approximately 10.5 – 11.5 mya (Bernor et al., 1987). In eastern Africa, Murinae appear in the fossil record in the late Miocene (Geraads, 2001). They reached southern Africa around 5 – 6 mya, noted by representatives of the extant *Aethomys* genus (Denys, 1999; Manthi, 2007; Mein et al., 2004). The African Murinae continued to radiate and evolve into modern genera throughout the Pliocene (Monadjem et al., 2015). Today, 31 genera and 145 species can be found within Africa, of which 27 genera and 139 species are endemic (Happold, 2013). They range in size from small to large and fill a variety of dietary and terrestrial niches. Dentition is a defining hallmark of the sub-family: its upper and lower molars do not have longitudinal enamel crests between lamina, with cusps located opposite each other on the lower molars (Flynn et al., 1985; Happold, 2013; Jacobs et al., 1989). In this study, four species of murines are used: *Mastomys coucha* (*n* = 5), *Micaelamys namaquensis* (*n* = 64), *Mus minutoides* (*n* = 6), and *Rhabdomys bechuanae* (*n* = 37).

Mastomys coucha (Thomas 1915). The southern multimammate mouse is an extreme generalist, consuming plant and animal material and is even known to be cannibalistic when other food sources are lacking (Monadjem et al., 2015). As such, they can populate disturbed habitats, thus making a good indicator species for level of disturbance (Avenant, 2011; Happold, 2013). The multimammate mouse is endemic to Africa and found within grasslands, woodlands, and savannas, as well as fields and human dwellings (Happold, 2013; Skinner & Chimimba, 2005). They are generally terrestrial and nocturnal. However, detailed information specific to the species tends to be lacking due to conflation with sympatric species *Mastomys natalensis*, from whom it is difficult to distinguish from based solely on appearance (Happold, 2013).

Rather than digging their own burrows for nesting, they occupy those abandoned by other species (Bronner, 1992; Eckard, 1998). Their upper incisors lack grooves, and they have small to average sized molars (Monadjem et al., 2015).

Micaelamys namaquensis (Smith 1834). The Namaqua rock mouse is endemic and widely distributed throughout South Africa, with a preference towards rocky outcrops found in savanna, scrublands, open woodlands, and semi-arid habitats (Skinner & Chimiba, 2005; Happold, 2013; Monadjem et al., 2015). This mouse does not construct burrows and are nocturnal and terrestrial, with some semi-arboreal qualities. They prefer shrubby areas, or habitats of thicker graces or creviced rocks where they can construct nests from grass, twig, or other debris (Happold, 2013). *Mi. namaquensis* is omnivorous, with diets reported to have consist of grass, foliage, seeds, and insects in varying proportions (Bond & Breytenbach, 1985; Gliwicz, 1987; Kerley et al., 1990; Monadjem, 1997; Withers, 1979). Cusps on the molars are rounded and well-separated, with ungrooved, opisthodont upper incisors (de Graaf, 1981; Monadjem et al., 2015).

Mus minutoides (Smith 1834). The tiny pygmy mouse is the smallest rodent utilized in this study. It is an extremely widespread and endemic species, found in a wide range of habitats including savanna, forest, semi-arid, Afromontane forests, and human structures (Skinner & Chimiba, 2005; Happold, 2013; Monadjem et al., 2015). The pygmy mouse is an omnivorous species, known to eat insects, seeds, and other plant material (Kerley, 1992; Monadjem, 1997; Rowe-Rowe, 1986; Wilson, 1975). Their incisors are ungrooved and typically notched on the posterior surface, and their third molars are highly reduced (Monadjem et al., 2015). Although *M. minutoides* is known to utilize burrows from other species, they will also excavate their own

in soft soils to place nests constructed from grass and other fibers (Happold, 2013; Skinner & Chimiba, 2005). They are nocturnal and terrestrial.

Rhabdomys bechuanae (Thomas 1893). Historical ecological data on the four-striped grass mouse are often derived from information on *Rhabdomys* spp. given debate as to whether the genus is comprised of one or multiple (see Castigila et al., 2011; du Toit et al., 2012; Happold, 2013; Hill & Carter, 1941). *R. bechuanae* is considered the more arid and western species of the *Rhabdomys* genus, found in the Nama Karoo and the savannas of the Northern Cape Province (Happold, 2013; Monadjem et al., 2015). In addition to seeds, dietary studies of *Rhabdomys* spp. have indicated variation among seasons (Perrin, 1980) and an omnivorous diet that also includes insects, worms, snails, and plant material (Monadjem et al., 2015; Skinner & Chimiba, 2005). While the literature generally describes *Rhabdomys* as a burrowing genus (Bronner, 1992; Johnson, 1980; Shortridge, 1934; Smithers, 1971), populations of *Rhabdomys* have also been observed to nest aboveground (Brooks, 1974; Choate, 1972). No data could be found on *R. bechuanae*'s specific burrowing habits. Their upper incisors are pro-odont and ungrooved (Monadjem et al., 2015).

Nesomyidae Family

The earliest Nesomyidae rodent to be found in Africa belongs to the Afrocricetodontinae and date back to the Early Miocene (Lavocat 1973; Monadjem et al., 2015; Schenk et al., 2013). In the mid-Miocene, these rodents went extinct, replaced by new taxa such as Myocricetodontinae and Megacricetodontinae, which spread throughout eastern and southern Africa (Monadjem et al., 2015; Winkler et al., 2010). Extant Nesomyidae are endemic to the Africa and Madagascar and consist of six sub-families: Cricetomyiane (pouched mice and rats),

Delanymyinae (swamp mouse), Dendromurinae (climbing mice, fat mice, large eared mouse), Mystromyinae (white-tailed rat), Nesomyinae (Malagasy rodents), and Petromyscinae (rock mice). These sub-families consist of 21 genera and 61 species, of which 12 genera and 34 species are found on the main continent. The nesomyids is not defined by specific diagnostic features like the Muridae and instead represents a wide range of morphological features, as well as niches and habits (Happold, 2013; Musser & Carleton, 2005). As such, they range in size from 5.2 g to 2.8 kg. They are found in both temperate and tropical ecosystems and can even be found in montane habitats with altitudes as high as 4,300 m (Corbert, 1984, Kingdon, 1974; Nowak, 1999). Diets also vary, and include herbivory, insectivory, and omnivory. For this study, specimens represent one sub-family: Dendromurinae (n = 2).

Dendromurinae Sub-Family. This taxon consists of 8 genera and 24 species, all endemic to Africa (Musser & Carleton, 2005). Denndromurinae are thought to have derived from an ancestor in the early Miocene, with the first true dendromurine, *Ternania*, appearing in mid Miocene Kenya, approximately 14 – 13.9 mya (Musser & Carleton, 2005; Tong & Jaeger, 1993). The first fossil evidence of genus *Dendromus*, from Ethiopia and Nambia, date back to 10 – 8 mya (Geraads, 2001; Mein et al., 2004; Musser & Carleton, 2005). Today, dendromurines are found only in Subsaharan Africa in a variety of habitats such as grasslands, scrublands, alpine forests, swamps, and agricultural fields (Carleton & Musser, 2005; Nowak, 1999). Dendromurinae are small rodents that are mouselike in appearance and are either terrestrial or arboreal. Diets are species dependent, and include herbivory, carnivory, and omnivory. They are mostly granivorous, and usually nocturnal. Molar cusps are not well defined but are typically arranged in two longitudinal rows for the first and second molars, with extremely reduced third

molars. Upper incisors are grooved, with the groove located closer to the outer margin of the tooth (Skinner & Chimimba, 2005).

Dendromus melanotis (Smith 1834). The grey pygmy climbing mouse is not actually arboreal in nature but terrestrial with a preference towards grassy habitats (de Graaf, 1981). It is also nocturnal. *D. melanotis* is widespread throughout the southern part of Africa. They have narrow molars with typical murine molars (Ellerman, 1941) and grooved, yellow incisors (de Graaf, 1981). It has been observed to be a dedicated granivore and insectivore (Dieterlen, 1971; Happold, 2013; Rowe-Rowe, 1986; Shortridge, 1934; Smithers, 1971). This species has been observed to build grass nests (Stuart, 1999) as well as dig simple open-ended burrows (Jacobsen, 1977; Nowak 1999).

Stomach Content Analysis

During the processing of animals for curation in the Bloemfontein National Museum, stomachs were removed and stored in 70% ethyl alcohol solution for later analysis. Stomach content analysis was chosen as the means in which to determine rodent diet as it provides a "snapshot" of foods eaten by individuals prior to death, much like dental microwear. This method is a standard method in ecology to study the feeding habits of many taxa, from rodents to fish, that allows for an easy and direct study of what an animal has eaten (Hyslop, 1980; Manko, 2016). Stomach contents were divided into eleven categories: grass blade, grass seed, dicot (i.e., stems and leaves), dicot seed, annelids, curculionids, caterpillars, feathers, hair, or artificial objects (i.e., strings and plastics). Using a Nikon SMZ-745t stereozoom dissection microscope, the percentage abundance of each item type to the overall volume of that stomach's contents was

estimated to the nearest 5%. Any item comprising less than 5% of the contents was automatically rounded up following Smith et al. (2002).

Statistical Analysis

Mean and standard deviation data for volumetric contribution (%) of stomach contents were calculated by species, habitat, and season based on the individual counts. In addition, the frequency of occurrence of a food item was also calculated by species and by habitat (Kerley, 1989). Frequency of occurrence (%) was obtained by dividing the number of stomachs in which the item appeared by the total amount of stomachs examined. As data failed to meet presumptions of normality, Kruskal-Wallis tests were applied to test for differences among species, location, and collection month for percent volumetric contribution (R Development Core Team, 2016). When significance occurred, post-hoc Mann-Whitney U tests were applied to assess significance among species, locations, and collection month (Kerley, 1989; Shiels et al., 2013).

Environmental Metadata

Details from the stomach content analysis were utilized to assign diets to specimens in the microwear analysis, when applicable. If one food type comprised ≥ 70% of the stomach contents, this food was labeled as the sole diet for this specimen. Primary and secondary dietary components were considered in all other cases, with the secondary diet based on the next most frequently occurring food. Associated environmental metadata, such as dust levels, soil type, and percent land cover (grass, shrub/bush, trees, and aerial – defined by the lack of any of the other three floral depicters) were obtained from the 2017 biomonitoring publications. Fallout

dust levels recorded were divided into three groups: low, medium, high. Values below 600 $mg/m^2/day$ were considered low while those above 1200 $mg/m^2/day$ were considered high. The third category of 'medium' included specimens that fall between these two thresholds. A similar classification was used to qualify land cover percentages into low (0-33%), medium (34-66%), and high (67-100%).

In addition, land cover data were used to develop habitat designations based on the hierarchal land cover classification system developed by Grunblatt et al. (1989). This system considers four levels of classification: (a) density of primary life form, (b) density of secondary life form, (c) height class, and (d) dominant taxon. Only the first two levels were used in classifying transect habitats as to mitigate the occurrence of $n = 1$ for each habitat classification. Definitions for life form and density classifications are given in Table 3.3. Based on Grunblatt et al.'s classification system (1989), if an area had less than 2% of vegetative cover, it was considered bare. To be considered a primary life form, vegetation cover should be ≥ 20%. If more than one vegetation category met this threshold, preference was given to trees, then shrubs, and then grass. A density modifier was applied based on the percentage of coverage for this primary life form (see Table 3.3). If none of the vegetation categories comprised ≥ 20%, the life form with the greatest canopy cover was used along with the density sparse. Determining the second level of classification worked much in the same way. Preference was given to trees, then shrubs, and then grass if these categories were ≥ 20%. If not, and if the density of trees or shrubs was between 2 – 19%, one of these vegetations (with trees preferred to shrubs) described the secondary life form. Otherwise, the secondary life form was designated as the second most dominant life form (Grunblatt et al., 1983). As such, an example transect comprised of 45% aerial cover, 35% grass cover, 25% shrub cover, and 5% tree cover would be described as an

open grassed shrubland (oGS). Summary details for habitat metadata are presented both by property (Table 3.4) and by trapping transect (Table 3.5).

Table 3.3: Definitions used in Grunblatt et al.'s (1989) classification system.

(A) Primary life form:		
Term	**Symbol**	**Definition**
Forest	F	trees comprise ≥ 50% of land cover
Woodland	W	trees comprise ≥ 20% and < 50% of land cover
Shrubland	S	bush and shrubs comprise most of land cover
Grassland	G	grasses comprise most of land cover
Bare	B	vegetation only comprises > 2% of land cover
(B) Density modifier:		
Term	**Symbol**	**Definition**
Closed	c	80 - 100% canopy cover
Dense	d	50 - 79% canopy cover
Open	o	20 - 49% canopy cover
Sparse	s	2 - 19% canopy cover
(C) Secondary life form		
Term	**Symbol**	**Definition**
treed	T	trees comprise second most amount of land cover
shrubbed	S	shrubs and bushes comprise second most amount of land cover
grassed	G	grasses comprise second most amount of land cover

Table 3.4: Habitat characteristics for sampling areas in Kolomela Mine and surrounding farms.

Habitat	Area (ha)	Ecoregion	Dominant vegetation	Mean dust level ($mg/m^2/day$)	Soil
Kolomela Mine	16000	Postmasburg Thornveld	dwarf karroid shrubveld	May: 782	sandy
Grootpan	810	Postmasburg Thornveld	dwarf karroid shrubveld, black thorn bushveld	May: 697 July: 1252	loam/clay
Gruispan	1400	Postmasburg Thornveld, Olifantshoek Plains Thornveld	*Senegalia mellifera* , *Tarchonathus camphoratus*	May: 700	loam mixtures
Heuningkrantz	2214	Postmasburg Thornveld	dwarf karroid shrubveld, *Senegalia mellifera*	n/a	sandy to rocky soils
Kappies Karrieboom	990	Postmasburg Thornveld	panveld vegetation	May: 739	loam to loam/clay
Sunnyside	2497	Postmasburg Thornveld	dwarf karroid shrubveld, rocky bushland, sandveld species	May: 752 July: 1293	loam
Wildealsput	813	Postmasburg Thornveld	*Rhigozum trichotomum* , *Senegalia mellifera* , broad-leaved species	n/a	loam mixtures

Table 3.5: Habitat characteristics for rodent transect lines.

Habitat	Transect	Coordinates	Dominant vegetation	Mean dust level ($mg/m^2/day$)	Soil	Land cover (%)				Land cover classification
						Aerial	Grass	Bush	Tree	
Kolomela	Ekstra	S28º22'15" E22º54'02"	dwarf karroid shrubveld	May: 782	sand	40	30	25	5	open grassed shrubland
Grootpan	GN1	S28°25'47.0" E22°54'49.7"	dwarf karroid shrubveld	May: 697 July: 1252	clay, loam	20	14.5	52.5	13	dense treed shrubland
	GN2	S28°25'42.2" E22°54'35.3"	dwarf karroid shrubveld	May: 697 July: 1252	clay, loam	3.5	69	27.5	0	open grassed shrubland
Gruispan	GP1	S28°28'00.4" E23°02'56.5"	open veld, woody plants	May: 700	clay, loam	19	41	27.5	12.5	open grassed shrubland
	GP2	S28°27'25.8" E23°02'45.0"	*Senegalia mellifera*	May: 700	clay, loam	5	11	83.8	0.25	closed grasssed shrubland
Heuningkrantz	HK1	S28º12'22.0" E22º53'36.1"	*Senegalia mellifera*	n/a	sand	30	50	10	10	dense treed grassland
	HK2	S28º12'20.6" E22º53'37.0"	*Senegalia mellifera*	n/a	sand	30	50	10	10	dense treed grassland
	HK3	S28º12'11.4" E22º54'33.1"	*Senegalia mellifera*	n/a	sand	5	70	15	10	dense treed grassland
	HK4	S28º12'11.0" E22º54'37.2"	*Senegalia mellifera*	n/a	sand	5	70	15	10	dense treed grassland
	HK5	S28º12'23.0" E22º55'24.7"	*Senegalia mellifera*	n/a	sand	20	60	5	15	dense treed grassland
	HK6	S28º12'25.0" E22º55'25.0"	*Senegalia mellifera*	n/a	sand	20	60	5	15	dense treed grassland
	HK7	S28º12'22.9" E22º54'54.8"	*Senegalia mellifera*	n/a	rocky	30	30	20	20	open shrubbed woodland
	HK8	S28º12'21.8" E22º54'54.7"	*Senegalia mellifera*	n/a	rocky	20	70	0	10	dense treed grassland
	HK9	S28º12'54.1" E22º54'45.9"	*Senegalia mellifera*	n/a	rocky	30	60	0	10	dense treed grassland
	HK10	S28º12'54.7" E22º54'44.1"	*Senegalia mellifera*	n/a	rocky	30	60	0	10	dense treed grassland

Table 3.5 (Cont.)

Habitat	Transect	Coordinates	Dominant vegetation	Mean dust level ($mg/m^2/day$)	Soil	Land cover (%) Aerial	Grass	Bush	Tree	Land cover classification
Kappies Karrieboom	KK1	S28º28'06.0" E22º58'39.2"	open vegetation	May: 739	clay, loam	40	11	26.5	22.5	open shrubbed woodland
	KK2	S28º28'18.2" E22º58'55.7"	open vegetation	May: 739	loam	32.5	40	22.5	5	open shrubbed grassland
	KK3	S28º27'46.8" E22º58'24.6"	open vegetation	May: 739	loam	32.5	25	12.5	35	open grassed woodland
Sunnyside	Stofdraai	S28º25'06" E22º53'04"	dwarf karroid shrubveld	May: 752 July: 1293	loam	4	93	2	1	closed shrubbed grassland
Wildealsput	WAP1	S28°26'47.3" E22°51'16.2"	broad-leaf species	n/a	loam	21	75	3	1	dense shrubbed grassland
	WAP2	S28°27'26.8" E22°51'55.1"	broad-leaf species	n/a	clay, loam	15	35	44.5	6.5	open grassed shrubland
	WAP3	S28°27'20.9" E22°51'51.2"	broad-leaf species	n/a	clay, sand, loam	22	32.5	42.5	3	open grassed shrubland

Microwear Analyses

The mandibular incisors and the mandibular molar rows of each specimen were cleaned using cotton swabs soaked in 95% isopropyl alcohol to remove any debris from the tooth surface. High-resolution impressions were taken at the Bloemfontein National Museum using President's Jet regular body polyvinylsiloxane dental impression material (Coltene/Whaledent, Alstätten, Switzerland). High-resolution replicas were produced from these molds at the University of Arkansas using Epotek 301 epoxy resin (Epoxy Technologies, Billerica, MA, USA) and examined under lower magnification for the presence of unobstructed antemortem microwear. Those that met criteria developed by Teaford (1988) and King et al. (1999) were then examined using methods based on those described in Scott et al. (2006) and a Sensofar Plμ Neox confocal profiler (Sensofar Corporation, Barcelona, Spain).

A single lower incisor from each specimen was scanned alongside the distal edge of the labial enamel, right below the incisal surface (Figure 3.2; Belmaker & Ungar, 2010; Withnell & Ungar, 2014; Caporale & Ungar, 2016). The enamel rim of the second lower molar mesial loph provided the surface for molar microwear analyses (Figure 3.3). Preference was given to the protoconid as it provides a large and relatively level surface (Silcox & Teaford, 2002; Hautier et al., 2009; Burgman et al., 2016; Ungar et al., 2017). The metaconid was utilized to maintain preserve scanning in the mesial loph when the protoconid lacked sufficient enamel to fill the field of view. Burgman et al. (2016) argued for the justification of utilizing the entire mesial loph in analysis for murid rodents. Propalinal mastication on flattened molars have produced continuous wear facets across the enamel surface (Lazzari et al., 2008), with a lack of variation among facets in scratch orientation (Charles et al., 2007). As such, murids do not appear to

engage in mastication that results in distinct buccal and lingual phases, which implies justification for sampling of the entire mesial loph.

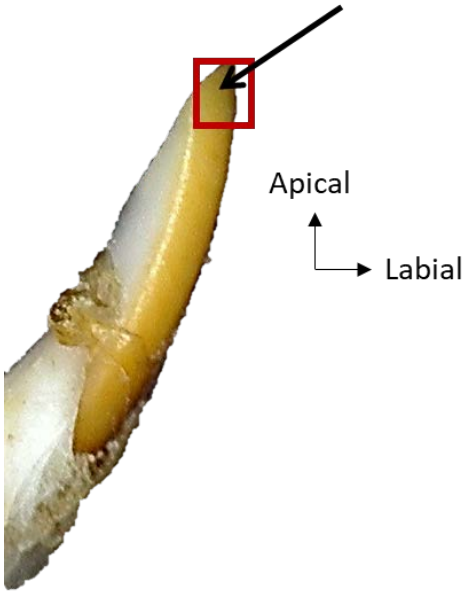

Figure 3.2.: Distal view of murid lower incisor, indicating the area to be scanned below the incisal edge.

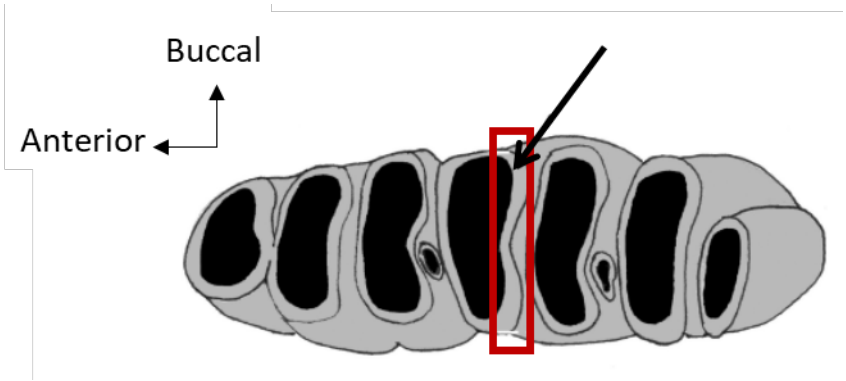

Figure 3.3.: Occlusal view of worn murid molars, M_1-M_3, indicating the area to be scanned on the medial loph. From Burgman et al., 2016.

Scanning occurred under white light and utilized a 100x objective for incisors, and under blue light and the utilization of a 150x objective lens for molars (following Burgman et al., 2016, Caporale and Ungar, 2016). These scans produced three-dimensional point clouds for each

incisor, with a lateral point spacing of 0.18 µm, a published vertical resolution < 0.005 µm, a vertical step of 0.2 µm, and a field of view of 138 by 102 µm. For molars, these scans produced three-dimensional point clouds with a lateral point spacing of 0.13 µm, a published vertical resolution < 1 nm, a vertical step of 0.2 µm, and a field of view of 85 by 64 µm. Raw point clouds were processed using MountainsMap software (DigitalSurf Corporation, Besançon, France) by surface leveling and the manual deletion of any dust or other particles obscuring the surface. Two forms of characterizing dental microwear texture were considered in this study: scale-sensitive fractal analysis (SSFA) and International Standards Organization (ISO) surface metrology. For SSFA, missing data remained unfilled and excluded from analysis. These resulting point clouds were then run through SSFA software packages (Toothfrax and SFrax, Surfract Corporation, Norwich, Vermont, USA) to obtain values for the considered variables. For ISO data collection, the missing data points were filled, and the curvature of the scanned surface was removed using the "form removal" operator in Sensomap v. 7 prior to obtaining the values for these variables.

Although the application of dental microwear texture analysis (DMTA) procedures to rodent teeth has become more prominent in the past few years, the majority of rodent microwear studies have still focused on feature-based analysis (e.g., Gusovsky & Sinitsa, 2019; Renaud et al., 2015; Zykov et al., 2018). Surfaces have typically been characterized through summary statistics of the average number and sizes of microscopic pits and scratches that could accrue high observer-error rates lacking in automatic characterizations of whole microwear surface textures found in DMTA procedures (Galbany et al. 2005; Grine et al., 2002; Mihlbachler et al. 2012). Limiting noise, including that resulting from measurement error, is important when working with subtle signals such as microhabitat and minute nuances in diet. Both SSFA and

ISO methods have proven useful in this sense and provide complimentary data to parse microwear signals (e.g., Calandra et al., 2016b).

Characterization of texture surfaces for SSFA procedures utilize five variables: complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*), textural fill volume (*Tfv*) and heterogeneity of complexity across the surface *(HAsfc*). *Asfc*, or area-scale fractal complexity, examines how surface roughness changes with scale (Scott et al., 2005, 2006). First, the relative area (RelAscale) is calculated through the area-scale tiling algorithm, which determines changes of relative areas over changing scales. This algorithm first determines the surface area through placement of triangles that continually decrease in size with finer scales. These values are then divided by the planometric area of the enamel surface (Scott et al., 2006). The scale in which relative areas are calculated ranges from 7200 μm^2 to 0.02 μm^2. These values are then plotted in a log-log plot multiplied by -1000. From this, *Asfc* is determined through the calculation of the steepest part of curve fit to the plot (Scott et al., 2006). High *Asfc* values tend to be associated with a high number of different sized pits and scratches, which are thought to stem from harder and more brittle foods (Scott et al., 2006; Ungar et al., 2003).

The scale of maximum complexity is taken from the scale range of the *Asfc* value. In other words, *Smc* reports the finest scale associated with the highest degree of microwear complexity (Scott et al., 2006). As such, high *Smc* values are associated with larger features at coarser scales. Heterogeneity of area-scale fractal complexity is calculated by splitting the surface into smaller equal-sized subsets at different scales. *Asfc* is calculated for each of these cells, and the median absolute deviation of *Asfc* values are divided by the median *Asfc* to produce the *HAsfc* value for that grid (Scott et al., 2006). Most microwear analyses consider two measures of *HAsfc*: a coarser scale value of $HAsfc_9$ (a 3x3 grid of 9 cells) and a finer scale value

of *HAsfc*$_{81}$ (a 9x9 grid of 81 cells). Higher *HAsfc* values are indicative of a greater amount of feature variation across the enamel surface.

Length-scale anisotropy of relief measures the orientation of wear features at the finest scale of observation in which anisotropy can be measured, 1.8 µm (Scott et al., 2006). For this parameter, the length-scale rotational algorithm is applied to the surface to determine the relative length (RelLscale). This algorithm takes the total value of line segments at a given scale (longer in length at coarser scales and shorter at finer scales) and divides it by the by estimated profile length (Scott et al., 2006). The resulting values, vectors of relative lengths at specific orientations, are calculated at 5° intervals and normalized through the exact proportion method. The *epLsar* value of the surface is then obtained from the length of the mean vector obtained by plotting the calculated vectors in a rosette diagram (Scott et al., 2006). High *epLsar* values are associated with high amounts of parallel scratches that typically associate with tougher foods.

Finally, texture fill volume measures surface volume through the volume filling versus scale square cuboid filling algorithm (Scott et al., 2006). This calculation measures the surface volume by filling it with square or rectangular cuboids that vary in size based on scale, with larger cuboids associating with coarser scales and smaller cuboids associating with finer scales. *Tfv* is calculated using square cuboids of 2 µm while structural fill volume is a coarser fill volume based on 10 µm cuboid facets. The greater structural fill volume is associated with more concave or convex surface shapes. The structural fill volume can also be used to calculate *Tfv* by subtracting it from the total fill volume. As such, this parameter is influenced both by surface shape and surface texture (Scott et al., 2006). A high *Tfv* value is associated with a greater number of large and deep features on the enamel surface (Scott et al., 2006).

ISO values provide further quantifiable characterizations of surface textures. Such parameters have been increasingly employed in microwear analyses (e.g., Calandra et al., 2012; Schulz et al., 2013) to complement SSFA. The ISO parameters used were: five-point pit height (*S5v*), maximum pit height (*Sv*), mean dale area (*Sda*), mean dale volume (*Sdv*), pit void volume (*Vvv*), texture-aspect ratio (*Str*), developed interfacial area ratio (*Sdr*), and skewness (*Ssk*) (ISO/FDIS 25178-2; Ţălu et al., 2013).

Vvv and *Sdv* represent two measures of feature volume. The pit void volume of the scale limited surface, *Vvv*, is the void volume of valleys and is presented as a percentage. *Vvv* determines the volume based on the lowest valley depth to an 80% material ratio level. The material ratio is a measure of the area of a plane at a given height to the cross-sectional area (Michigan Metrology, 2014). As such, the height aspect of *Vvv* measures the lowest point to the point in which the material ratio is equal to 80%. It provides the potential remaining volume of the surface after significant wear (Michigan Metrology, 2014). Closed dale volume, *Sdv*, quantifies the average volume of dales present in the scanned surface (Schulz et al., 2010), in which a dale is the indented area on a surface that surrounds a minimum low point, the pit (Blateyron, 2020). Dale characteristics are also represented by the closed dale area, *Sda*. This parameter quantifies the area of dales present in the scanned surface (Schulz et al., 2010). High *Sda* values are typically associated with surfaces in which valleys possess large area cross-sections (Calandra et al., 2012).

Meanwhile, two measures of feature depth were used from the ISO parameters: *Sv* and *S5v*. The maximum pit height, *Sv*, parameter measures the depth of the deepest valley from the mean surface plane (Schulz et al., 2010). It is a single point measurement, rather than a measurement reflective of the whole surface (Michigan Metrology, 2014). Five-point pit height

(*S5v*), measures valley depth by averaging the depths of the five deepest valleys on the surface. A high *S5v*, therefore, coincides with the presence of many deep valleys on the tooth surface (Calandra et al., 2012).

Sdr is the ISO parameter represented feature complexity. It is a measurement of the developed interfacial area ratio and measures additional surface area created by texture in the form of a percentage (Michigan Metrology, 2014). *Sdr* is measured by first calculating the overall surface area (texture surface area) of the enamel surface and the cross-sectional area of the surface. The cross-sectional area is subtracted from the texture surface area. This value is then divided by the cross-sectional area to obtain a *Sdr* measurement. As such, *Sdr* is affected by the amplitude and spacing of textures (Michigan Metrology, 2014). The greater the value of *Sdr*, the more intricate the texture is.

Texture-aspect ratio, *Str*, is an ISO spatial parameter that indicates the anisotropy of the surface. It is a ratio of the shortest length at 0.2 from the autocorrelation to the greatest length, with reported values between 0 and 1 (Schulz et al., 2010). Values closer to one are indicative of isotropic surface while those closer to zero indicate that microwear scratches are more anisotropic in nature.

Finally, *Ssk* is a measure of density scratches or skewness of the surface. It considers the symmetry of surface heights around a mean plane. The higher the value of *Ssk*, the more the degree of surface heights vary from that of a normal distribution (Michigan Metrology, 2014). The sign of *Ssk* is also important. A negative *Ssk* is indicative of a surface skewed towards pitting while a positive *Ssk* is indicative of a surface with more peaks. When *Ssk* is equal to zero, the surface heights are considered normally distributed (Michigan Metrology, 2014).

Overall, each microwear surface was defined by three measures of feature complexity (*Asfc*, *Smc*, *Sdr*), two measures of heterogeneity ($HAsfc_9$, $HAsfc_{81}$), three measures of feature volume (*Tfv*, *Vvv*, and *Sdv*), one measure of feature area (*Sda*), two measures of feature depth (*Sv*, *S5v*), two measures of feature anisotropy (*Str*, *epLsar*), and one measure of scratch density (*Ssk*).

Statistical Analysis

Using wild caught specimens resulted in an extremely skewed distribution of individuals across all factors analyzed. In an ideal world, thirty specimens per species per plot would be easy to obtain, with specimens providing comparable sample sizes for a diverse group of diets and other considered variables. Unfortunately, working with field caught specimens does not satisfy this ideal. Transects did not result in even collection of species or specimens, with some locations favored over others. The inability to control the behavior of wild animals was one reason for this problem. For example, trap-shyness created a sampling bias towards specific species. While *Gerbilliscus leucogaster* specimens were easily caught, species like *Dendromus melanotis* proved more difficult to trap and thus resulted in much lower sample sizes. In addition, anthropogenic disturbances at the mine and farm influenced rodent community structures. The 2017 collection period saw an increase in trapping success, species richness, and species diversity (Avenant & du Plessis, 2018). Still, the rodents residing at the Kolomela mine and farms remained subject to prolonged anthropogenic disturbances that typically resulted in a greater presence of generalist species like those used in this study (Avenant 2011).

While sampling bias is a common part of ecology (see Biro & Dingermanse, 2009; Stuber et al., 2013), the imperfect sampling conditions and results made running the analytical

models difficult. To mitigate these circumstances, some caveats needed to be made towards the statistical analyses used in the pilot study, Burgman et al. (2016). Given sampling biases, not all levels could be used for each factor. For example, despite the overall sample including a total of 7 species, only three (*G. leucogaster*, *Mi. namaquensis*, and *R. bechuanae*) were used in species analysis in attempt to provide a biologically meaningful comparison. As a general guideline, only levels with $n \geq 10$ were considered for each factor. Statistical analyses tested for central tendencies. Interactions between factors could not be tested for due to the number of factors examined and the non-orthogonal sampling inherent in this study. Dispersion analyses, following Burgman et al. (2016), were also excluded from this dissertation due to the potential of extremely uneven sampling sizes for the different factor levels driving these results.

Analyses were conducted by species and by metadata factors. A taxon-free approach was utilized to increase sample size for the environmental and behavioral factors, under the assumption that texture patterns resulted from interaction with food and the environment rather than any inheritable characteristics of the rodents used (Andrews & Hixson, 2014; DeSantis et al., 2018). This taxon-free analytical model tested for the effects of macrohabitat, microhabitat, environmental dust load, soil type, diet, burrowing behavior, collection month, and land cover on microwear texture attributes. It also compared microwear differences between incisors and molars.

A general linear model was used to determine where variation occurred, with follow-up tests to document the sources of that variation (R Development Core Team, 2016). First, data were ranked transformed to mitigate the violation of assumptions inherent in parametric statistical analyses (Conover & Iman, 1981). Multivariate analysis of variance tests were individually applied for dust level, soil type, diet, and the percentage of each land cover variable.

Each test was followed by individual ANOVAs to determine which microwear texture variables produced significant results. Both Tukey's HSD and Fisher's LSD pairwise tests were used to identify distinct sources of variation while balancing risks of type I and type II error (Cook & Farewell, 1996). If Fisher's tests revealed significance while Tukey's did not, then the result was only considered to be of marginal significance.

CHAPTER FOUR: STOMACH CONTENT ANALYSIS

Results

A total of 212 rodents collected for the Kolomela biomonitoring project provided usable specimens for stomach content analysis. These specimens spanned two collection periods, May (*n* = 146) and July (*n* = 66), and were obtained from the mine property and six of the surrounding farms. Most specimens came from farms Grootspan (*n* = 76), Heuningkrantz (*n* = 59), and Kappies Kareeboom (*n* = 36). Trap success was much lower at the mine and remaining farms: Kolomela Ekstra (*n* = 19), Wildealsput (*n* = 8), Strofdraai (*n* = 8), and Gruispan (*n* = 6) (see Chapter 3, Figure 3.1 for a map of these locations). Species collection was skewed against trap shy species. *Gerbilliscus leucogaster* (*n* = 99) provided nearly half of the stomachs analyzed, with *Micaelamys namaquensis* (*n* = 56) and *Rhabdomys bechuanae* (*n* = 37) also providing substantial samples. *Gerbiliiscus paeba* (*n = 7*), *Mus minutoides* (*n* = 6), *Mastomys coucha* (*n* = 5), and *Dendromus melanotis* (*n* = 2) comprised the remainder of analyzed stomachs. Appendix I provides the breakdown of stomach contents for each specimen.

Stomach contents were divided into one of three broad categories: plant, insect, or other. Plant material was identified either as grass or miscellaneous dicot, and as either seed or grass blade and dicot stem or leaf. Insects were identified as annelid, curculionid, or caterpillar. Any stomach item that did not fall into the plant or insect category was clumped into that of other. The other category included feather and flesh, both of which were considered dietary in nature, and two non-dietary components: hair and artificial, or man-made, material. Results of stomach content analyses will be presented in context of 1) species, 2) location, and 3) collection month.

For each set of comparisons, frequency of occurrence and volumetric comparisons are considered separately.

Species

Frequency of Occurrence

The frequency of occurrence for ingested items is broken down by species in Table 4.1 and Figure 4.1. Plant matter, specifically grass seed, appeared in 100% of the stomachs analyzed. The presence of other plant material varied in frequency. Apart from *D. melanotis*, all other species had pieces of grass blades within their stomachs (> 16.67%). Grass blades occurred most often in *Mi. namaquensis* (66.07%). All species except for *Ma. coucha* consumed some part of dicot plants. Because grass seed was found in the stomachs of all individuals, the frequency of monocot occurrence was higher than that of dicot. When present in a species, dicot seeds occurred in > 64.9% of individuals with other dicot material, mainly parts of leaves or stems, occurring less often (> 28.57%). Both dicot and dicot seed were found most frequently in *D. melanotis* stomachs (50.00% and 100.00%, respectively). Seeds typically appeared chewed, represented in stomachs as integument pieces or, in the case of grass, clumps of starch.

Table 4.1: Frequency of occurrence (%) for stomach contents in each rodent species.

Ingested material	*Dendromus melanotis*	*Gerbilliscus leucogaster*	*Gerbilliscus paeba*	*Mastomys coucha*	*Micaelamys namaquensis*	*Mus minutoides*	*Rhabdomys bechuanae*
Plant							
Grass blade	0.00	59.60	28.57	40.00	66.07	16.67	48.70
Grass seed	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Dicot stem & leaf	50.00	31.30	28.57	0.00	30.40	33.33	35.14
Dicot seed	100.00	72.70	57.14	0.00	78.57	66.67	64.86
Insect							
Annelid	0.00	7.10	0.00	0.00	1.79	16.67	16.22
Curculionid	100.00	88.90	85.71	60.00	83.93	50.00	91.89
Caterpillar	0.00	4.00	0.00	40.00	5.36	0.00	10.81
Other							
Feather	0.00	1.00	0.00	0.00	1.80	0.00	2.70
Flesh	0.00	14.10	42.86	0.00	16.07	16.67	18.92
Hair	100.00	85.90	100.00	100.00	87.50	100.00	86.49
Artificial	100.00	42.40	57.14	80.00	46.43	83.33	43.24
n =	2	99	7	5	56	6	37

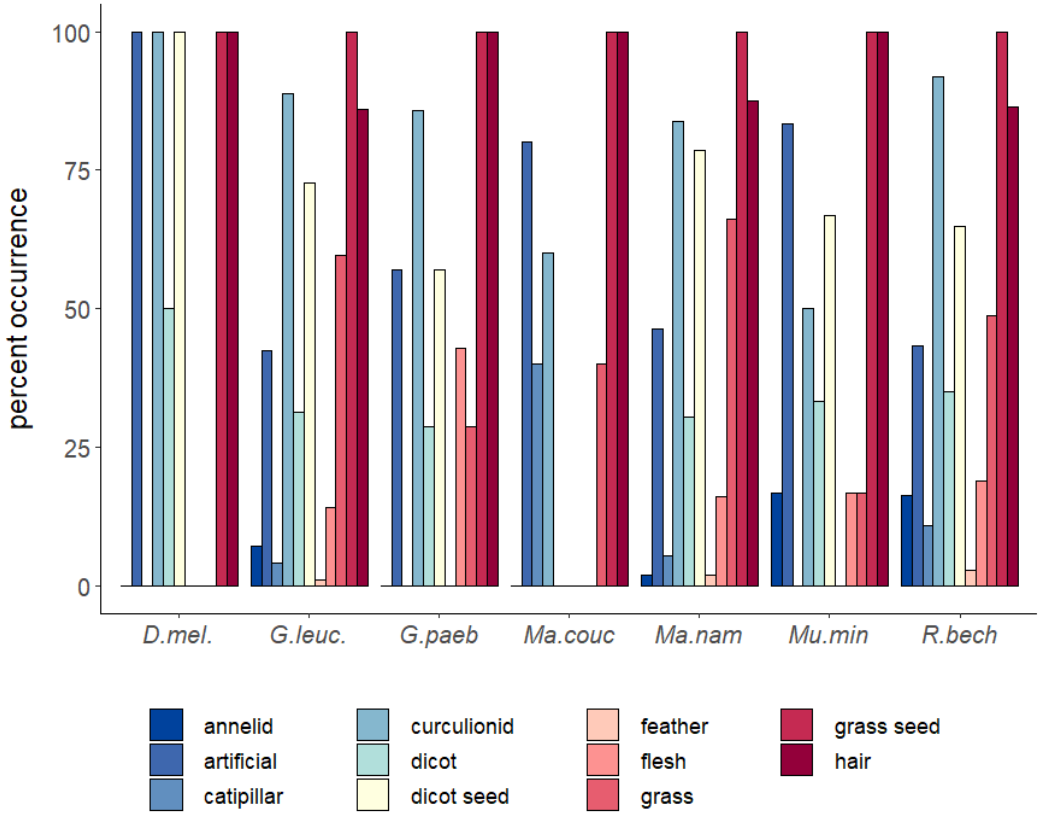

Figure 4.1: Percent occurrence for each ingested item by species: *Dendromus melanotis* (*D. mel.*), *Gerbilliscus leucogaster* (*G. leuc.*), *Gerbilliscus paeba* (*G. paeb*), *Mastomys coucha* (*Ma. couc*), *Mus minutoides* (*Mu. min.*), *Micaelamys namaquensis* (*Mi. nam*), and *Rhabdomys bechuanae* (*R. bech*).

For each species, insect parts were present and identifiable within stomachs (> 50.00%), driven mostly by the presence of Curculionidae species (> 50.00%). *D. melanotis* had the highest frequency of occurrence for curculionid (100.00%), with *G. leucogaster* having the second highest occurrence (88.90%). Curculionid was typically identified by the presence of antennae, leg, or small pieces of exoskeleton. Annelids were observed in only three species, *G. leucogaster, Mu. minutoides,* and *Mi. namaquensis,* and in low frequencies (1.79% to 16.67%). Pieces of these segmented worms were easy to differentiate from parasitic worms, which were not included in analysis as their presence did not result from ingestion. Caterpillars also occurred rarely. *D. melanotis, G. paeba,* and *Mu. minutoides* showed no indication of eating caterpillar. While *Ma. coucha* displayed the greatest frequency of caterpillar occurrence (40.00%), caterpillar was not common in the stomachs of *G. leucogaster* (4.00%) or *Mi. namaquensis* (5.36%).

The presence of feathers, albeit infrequently observed, were considered indicative of consuming small avians. Feathers were only found in stomachs of *G. leucogaster* (1.00%) and *Mi. namaquensis* (1.80%). Except for *D. melanotis* and *Ma. coucha,* pieces of flesh were more frequently observed (> 14.10%) than feathers. Flesh was especially common in *G. leucogaster* stomachs (42.86%). Although some pieces of flesh had hair still attached, these pieces were classified under the flesh category rather than hair as the presence of attached hair was a byproduct of flesh consumption. As such, the hair category encompassed individual, free-floating strands that would be the expected result of grooming activity. Hair occurred regularly in the stomachs of all species (> 85.90%), and in every *D. melanotis, G. paeba, Ma. coucha,* and *Mu. minutoides* stomach dissected. Artificial materials were also found in each rodent species (>

42.40%). Artificial materials were anything that appeared anthropogenic in origin, typically as pieces of colored string and small bits of plastic.

Volumetric Contribution

Table 4.2 provides the descriptive statistics for percent volumetric contribution of each stomach content item for the rodent species. Mean data are also depicted graphically in Figure 4.2. Grass seed comprised most of the food stuff in the stomachs of all rodent species. On average, *Ma. coucha* specimens had the lowest contribution of grass seed to stomach contents (57.00%) while *G. paeba* had the highest amount (77.86%). However, no significant differences among species were reported for the concentration of grass seed found within the stomachs ($p = 0.153$) (Table 4.3). Although the amount of grass within the stomach cavity resulted in a significant difference ($p < 0.05$) for the Kruskal-Wallis test, Mann-Whitney post-hoc tests only indicated $p < 0.05$ for a comparison between *G. paeba* and *Mi. namaquensis* (Table 4.3 and Table 4.4, Figure 4.3). Among species that ingested grass, *G. paeba* stomachs had the lowest amount of grass (a mean of 1.43% contribution) and *G. leucogaster* stomachs had the highest (6.97%). The amount of dicot seed and other dicot plant material in stomachs were < 10%, with no significant differences occurring among species (Table 4.3).

Table 4.2: Descriptive statistics for volumetric contribution (%) of plant, insect, and other items found in Kolomela rodent stomachs.

Ingested material	*Dendromus melanotis*	*Gerbilliscus leucogaster*	*Gerbilliscus paeba*	*Mastomys coucha*	*Micaelamys namaquensis*	*Mus minutoides*	*Rhabdomys bechuanae*
Plant							
Grass blade							
Mean	0.00	6.97	1.43	2.00	5.98	1.67	4.46
SD	0.00	9.31	2.44	2.74	6.35	4.08	8.06
Grass seed							
Mean	62.50	64.24	77.86	57.00	67.00	58.33	67.30
SD	17.68	15.46	8.59	24.90	14.65	15.71	15.88
Dicot stem & leaf							
Mean	2.50	1.77	1.43	0.00	1.96	1.67	1.76
SD	3.54	3.06	2.44	0.00	3.65	2.58	2.42
Dicot seed							
Mean	5.00	5.20	2.86	0.00	6.52	5.00	5.00
SD	17.68	15.46	8.59	24.90	14.65	15.71	15.88
Insect							
Annelid							
Mean	0.00	0.76	0.00	0.00	0.09	0.83	4.32
SD	0.00	3.87	0.00	0.00	0.67	2.04	14.20
Curculionid							
Mean	20.00	11.82	4.29	13.00	9.29	7.50	7.84
SD	21.21	11.19	1.89	12.55	7.47	10.37	4.94
Caterpillar							
Mean	0.00	0.20	0.00	6.00	0.27	0.00	0.68
SD	0.00	0.99	0.00	10.84	1.14	0.00	2.10
Other							
Feather							
Mean	0.00	0.61	0.00	0.00	0.09	0.00	0.14
SD	0.00	6.03	0.00	0.00	0.67	0.00	0.82
Flesh							
Mean	0.00	1.46	3.57	0.00	0.98	1.67	1.76
SD	0.00	4.53	5.56	0.00	2.42	4.08	4.89
Hair							
Mean	5.00	4.79	5.00	18.00	5.00	18.33	4.59
SD	0.00	3.11	0.00	14.40	2.70	23.38	2.17
Artificial							
Mean	5.00	2.17	3.57	4.00	2.32	5.00	2.16
SD	0.00	2.59	3.78	2.24	2.52	3.16	2.51
n =	2	99	7	5	56	6	37

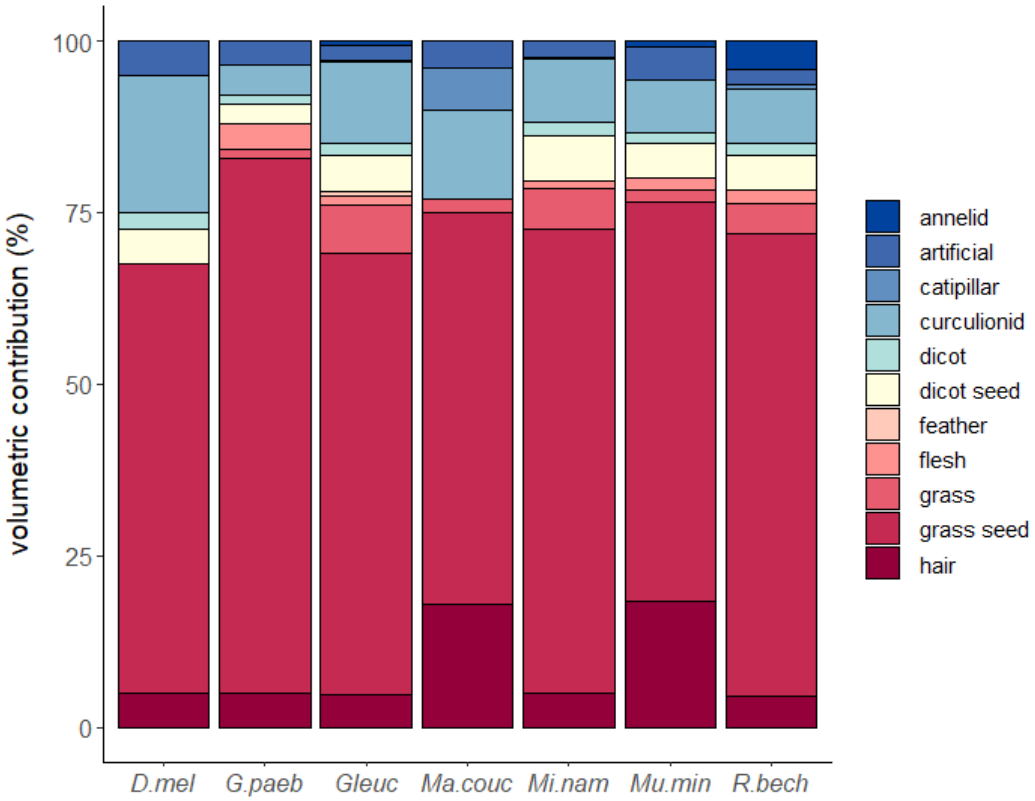

Figure 4.2: Stomach contents depicted by mean percent volumetric contribution for the seven species collected: *Dendromus melanotis* (*D. mel.*), *Gerbilliscus leucogaster* (*G. leuc.*), *Gerbilliscus paeba* (*G. paeba*), *Mastomys coucha* (*Ma. coucha*), *Micaelamys namaquensis* (*Mi. nam.*), *Mus minutoides* (*Mu. min.*), and *Rhabdomys bechuanae* (*R. bech*.).

Table 4.3: Kruskal-Wallis analyses for percent volumetric contribution of food contents for species comparisons.

Ingested material	H-Value	df	*p* -value
Plant			
Grass blade	**11.31**	**5**	**0.046**
Grass seed	9.380	6	0.153
Dicot stem & leaf	0.437	5	0.994
Dicot seed	3.909	5	0.563
Insect			
Annelid	7.601	3	0.055
Curculionid	9.373	6	0.154
Caterpillar	**11.872**	**3**	**0.008**
Other			
Feather	0.508	2	0.776
Flesh	3.914	4	0.418
Hair	**25.911**	**6**	**0.000**
Artificial	10.536	6	0.110

Statistically significant results, in which $p < 0.05$, are bolded.

Table 4.4: Mann-Whitney U tests comparing volumetric contribution of ingested material for rodent species.

Ingested material	Comparison	W	*p*	Ingested material	Comparison	W	*p*
Grass	*G. leucogaster - G. paeba*	488.0	0.059	Hair	*D. melanotis - G. leucogaster*	91.0	0.792
	G. leucogaster - Ma. coucha	330.0	0.191		*D. melanotis - G. paeba*	7.0	0.999
	G. leucogaster - Mi. namaquensis	2756.5	0.953		*D. melanotis - Ma. coucha*	9.0	0.156
	G. leucogaster -Mu. minutoides	420.0	0.075		*D. melanotis - Mi. namaquensis*	55.0	0.977
	G. leucogaster - R. bechuanae	**2161.0**	**0.009**		*D. melanotis - Mu. minutoides*	9.0	0.336
	G. paeba - Ma. coucha	15.5	0.766		*D. melanotis - R. bechuanae*	34.0	0.812
	G. paeba - Mi. namaquensis	**106.5**	**0.040**		*G. leucogaster - G. paeba*	318.5	0.607
	G. paeba - Mu. minutoides	22.5	0.847		***G. leucogaster - Ma. coucha***	**54.0**	**0.000**
	G. paeba - R. bechuanae	97.5	0.260		***G. leucogaster - Mu. minutoides***	**139.5**	**0.003**
	Mi. namaquensis - Ma. coucha	192.5	0.149		*G. leucogaster - Mi. namaquensis*	2622.0	0.435
	Mi. namaquensis - Mu. minutoides	91.5	0.056		*G. leucogaster - R. bechuanae*	1833.0	0.994
	Mi. namaquensis - R. bechuanae	821.5	0.074		***G. paeba - Ma. coucha***	**3.5**	**0.009**
	Ma. coucha - Mu. minutoides	12.5	0.641		*G. paeba - Mi. namaquensis*	199.5	0.926
	Ma. coucha - R. bechuanae	106.5	0.562		*G. paeba - Mu. minutoides*	10.5	0.053
	Mu. minutoides - R. bechuanae	80.0	0.233		*G. paeba - R. bechuanae*	140.0	0.614
Caterpillar	***G. leucogaster - Ma. coucha***	**156.5**	**0.001**		***Ma. coucha - Mi. namaquensis***	**34.5**	**0.000**
	G. leucogaster - Mi. namaquensis	2735.5	0.709		*Ma. coucha - Mu. minutoides*	12.5	0.707
	G. leucogaster - R. bechuanae	1705.5	0.132		***Ma. coucha - R. bechuanae***	**19.0**	**0.000**
	Ma. coucha - Mi. namaquensis	**90.0**	**0.006**		***Mi. namaquensis - Mu. minutoides***	**252.5**	**0.009**
	Ma. coucha - R. bechuanae	64.0	0.074		*Mi. namaquensis - R. bechuanae*	977.5	0.525
	Mi. namaquensis - R. bechuanae	1094.0	0.324		***Mu. minutoides - R. bechuanae***	**171.0**	**0.005**

Statistically significant comparisons, in which $p \leq 0.05$, are bolded.

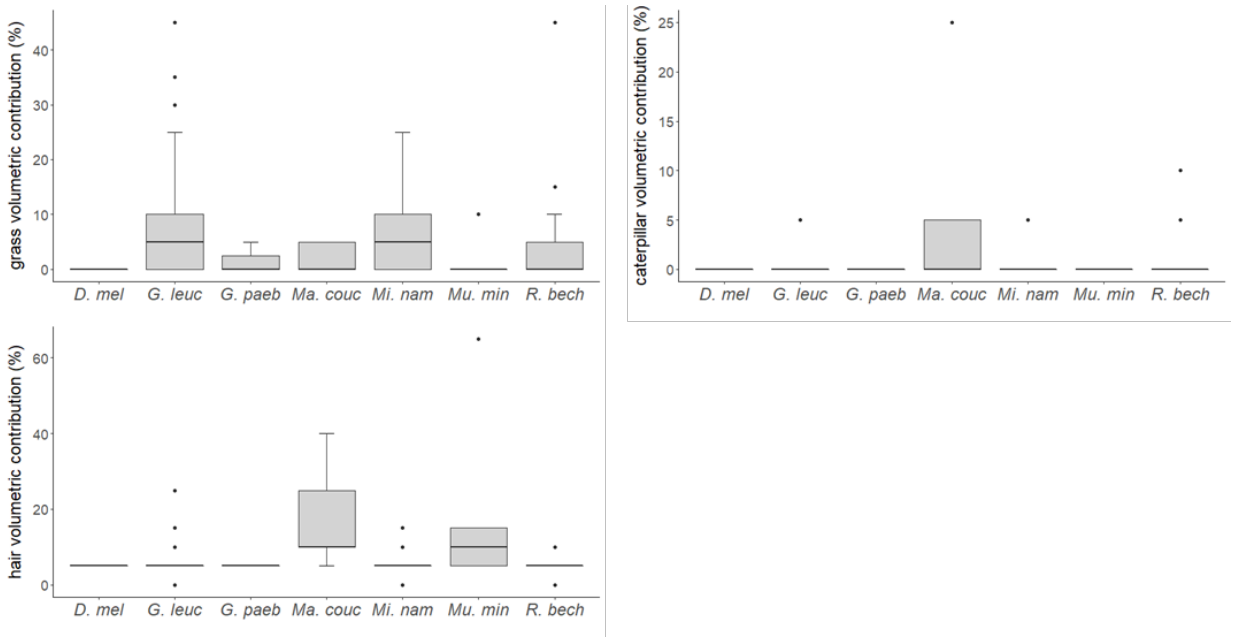

Figure 4.3: Boxplots of statistically significant stomach contents when percent volumetric contribution is analyzed by species: *Dendromus melanotis* (*D. mel.*), *Gerbilliscus leucogaster* (*G. leuc.*), *Gerbilliscus paeba* (*G. paeb*), *Mastomys coucha* (*Ma. couc*), *Micaelamys namaquensis* (*Mi. nam.*), *Mus minutoides* (*Mu. min.*), and *Rhabdomys bechuanae* (*R. bech*.). The boxes represent the central 50% of values, with first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Of the three insect categories, curculionid pieces contributed the most to stomach content abundance. This value was lowest in *G. paeba* and highest in *D. melanotis*, with a mean of 4.3% and 20.0% curculionid, respectively, contributing to stomach contents. When present, caterpillar showed up in low amounts within rodent stomachs. Yet, comparisons among rodents resulted in $p < 0.05$ and statistically significant differences between *G. leucogaster* and *Ma. coucha* and *Mi. namaquensis* and *Ma. coucha* (Table 4.3 and Table 4.4, Figure 4.3). The highest mean percent contribution was within stomachs of *Ma. coucha* (6.0%). Similarly, annelids provided little volumetric contribution and contributed most to *R. bechuanae* stomach contents, with an average of 4.32%. Otherwise, annelids made up < 1% of ingested material when present in other species.

The amount of feather and flesh in stomachs were extremely low (< 1.00% and < 5.00% mean contribution, respectively) and Kruskal-Wallis tests reported no significant variation among species (Table 4.3). The percent volume of artificial material found in stomachs ranged from an average of 2.17% in *G. leucogaster* specimens to 5.0% in *D. melanotis* and *Mu. minutoides* specimens. Once again, no significant variation was recorded (Table 4.3). However, the amount of hair ingested did result in statistically significant differences among species (Tables 4.3 and 4.4, Figure 4.3). Most species had a mean percent contribution of < 5.00% of hair, including *D. melanotis*, *G. leucogaster*, *G. paeba,* and *Mi. namaquensis,* with *R. bechuanae* having the lowest average at 4.59%. *Ma. coucha* and *Mu. minutoides* had the highest amount of hair in stomach contents, 18.0% and 18.33% respectively.

Sampling Location

Frequency of Occurrence

The frequencies of occurrence for ingested items are broken down by location in Table 4.5 and Figure 4.6. Plant material, both monocot and dicot, were found within stomachs from every sampling location (Table 4.5). Grass seed occurred in 100.00% of stomachs collected while the frequency of other plant types varied by location. As such, monocots were more prevalent in stomachs than dicots, regardless of location. Stomachs from Kolomela mine had the highest frequency of occurrence for grass blades (79.00%), while Wildealsput had the lowest (50.00%). Dicot seed also occurred frequently in stomachs regardless of location (> 62.50%), with it being most common in stomachs collected at the transect in Sunnyside (87.50%) and least common at Wildealsput (62.50%). Other pieces of dicot plant were found less frequently in stomachs, ranging from 16.67% at Gruispan to 50.00% at Wildealsput.

Insects were also common at every site. Over half of the stomachs obtained from the mine and surrounding farms contained evidence of curculionid consumption (>66.67%). At Wildealsput, for example, all stomachs contained curculionid parts (100.00%). Annelids were not in any of the stomachs from Kolomela mine or the farm Wildealsput. When worms did appear in stomach contents, they were of relatively low frequency: annelid presence ranged from 3.39% of stomachs at Heuningkrantz to 16.67% at Gruispan. Caterpillar remains were also found infrequently, and only within stomachs from four of the farms. Heuningkrantz stomachs had the lowest occurrence of caterpillars (3.39%) while Wildealsput had the highest (12.50%).

Feathers were only found in stomachs from Kolomela mine (5.26%) and Heuningkrantz farm (3.39%). Flesh was present with a relatively constant frequency at all farms except Sunnyside, which lacked any signs of flesh ingestion. Frequency of occurrence for flesh ranged in value from 12.50% at Wildealsput to 19.44% at Kappies Karee. Hair was consistently found > 75.00% of stomachs from each sampling location, with 100.00% of stomachs from Gruispan containing hair strands. Artificial materials were also found in stomachs from every sampling location (> 25.00%). These frequencies varied more by location than the other three sub-categories in the other category. Artificial items were rare in stomachs from Wildealsput (25.00%) but more common in samples from Sunnyside (62.50%) and Gruispan (100.00%).

Table 4.5: Frequency of occurrence (%) for stomach contents by sampling location

Ingested material	Grootpan	Gruispan	Heuningkrantz	Kappies Karee	Kolomela mine	Sunnyside	Wildealsput
Plant							
Grass	54.00	83.33	59.32	38.89	79.00	62.50	50.00
Grass seed	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Dicot	27.63	16.67	33.90	33.33	26.32	37.50	50.00
Dicot seed	64.47	83.33	72.88	77.78	68.42	87.50	62.50
Insect							
Annelid	10.53	16.67	3.39	8.33	0.00	12.50	0.00
Curculionid	82.89	66.67	88.14	91.67	89.47	75.00	100.00
Caterpillar	9.21	0.00	3.39	8.33	0.00	0.00	12.50
Other							
Feather	0.00	0.00	3.39	0.00	5.26	0.00	0.00
Flesh	17.11	16.67	15.25	19.44	15.79	0.00	12.50
Hair	86.84	100.00	86.44	88.89	94.74	75.00	87.50
Artificial	47.37	100.00	40.68	47.22	47.37	62.50	25.00
n =	76	6	59	36	19	8	8

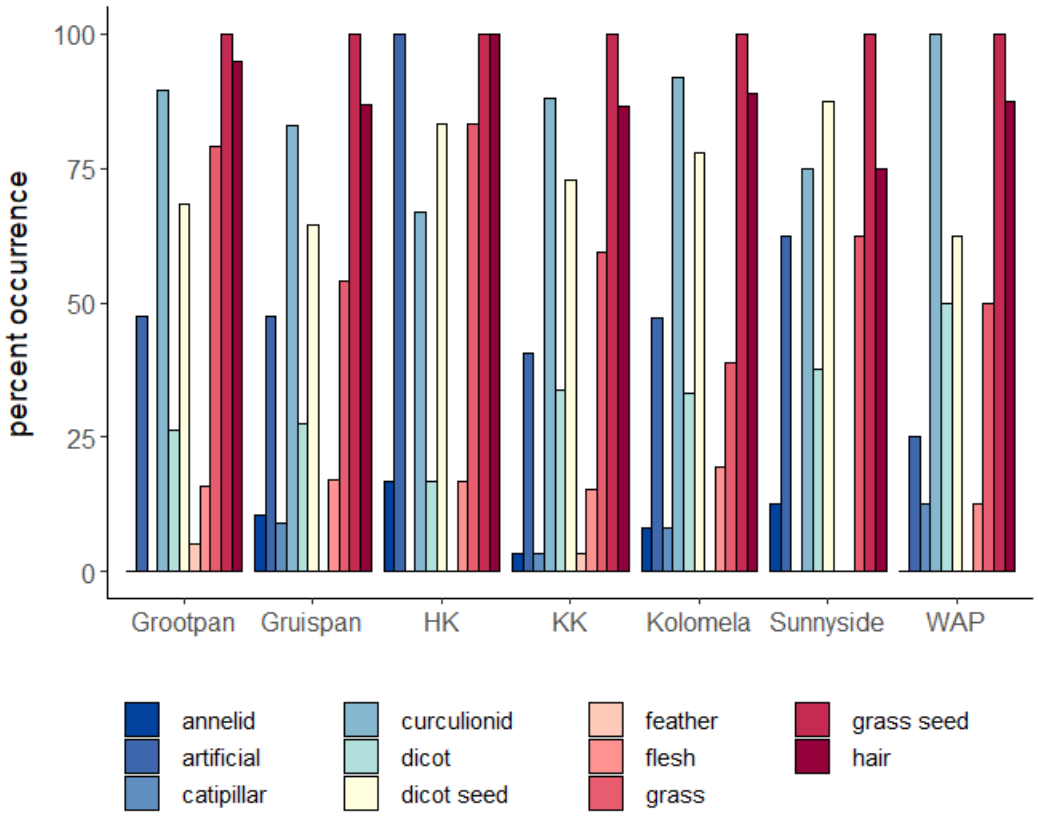

Figure 4.4: Percent occurrence for each ingested item by sampling location: Grootpan, Gruispan, Heuningkrantz (HK), Kappies Kareeboom (KK), Kolomela mine, Sunnyside, and Wildealsput (WAP).

Volumetric Contribution

Table 4.6 provides the descriptive statistics for percent volumetric contribution of each stomach content item based on collection location. Mean data are also depicted graphically in Figure 4.5. Regardless of sample location, grass seed contributed the most to stomach contents of any food type. Mean grass seed amounts were lowest in stomachs from Stofdraai (60.00%) and highest at Wildealsput (71.88%). Other grass material comprised, on average, < 15% of stomach contents at each location. Grass blade was the only ingested material in which the Kruskal-Wallis test reported significance, with $p = 0.019$ (Table 4.7). The amount of grass consumed was lowest at Kappies Karee (3.06%) and highest at Kolomela (13.42%). Pairwise comparisons indicated differences in grass blade contribution between stomachs from the Kolomela mine and those from Grootpan, Heuningkrantz, and Kappies Karee. In addition, Kappies Karee stomachs also differed significantly from Gruispan and Heuningkrantz stomachs (Table 4.8, Figure 4.6). Dicot seed, stem, and leaf comprised < 10.00% of stomach contents when analyzed by location, with dicot seed contributing more to locational diets than other parts of the plants. Dicot seed had the lowest average percent contribution at Wildealsput (3.83%) and highest at Stofdraai (8.75%). Other parts of dicot plants, meanwhile, contributed the last to stomach contents from the Kolomela mine and Kappies Kareeboom farm (1.88%) and highest in those from Wildealsput (2.50%).

Table 4.6: Descriptive statistics for volumetric contribution (%) of plant, insect, and other contents found in rodent stomachs by sampling location.

Ingested material	Grootpan	Gruispan	Heuningkrantz	Kappies Karee	Kolomela Mine	Sunnyside	Wildealsput
Plant							
Grass blade							
Mean	4.93	6.67	5.76	3.06	13.42	8.75	3.75
SD	7.19	4.08	6.49	4.52	13.65	15.06	5.18
Grass seed							
Mean	66.38	62.50	64.24	70.69	59.21	60.00	71.88
SD	14.18	22.08	16.99	12.02	17.89	20.18	9.23
stem &							
Mean	1.38	2.12	2.22	1.32	1.32	1.88	2.50
SD	2.25	2.04	3.62	4.04	2.26	2.59	2.67
Dicot seed							
Mean	4.01	5.00	7.63	4.44	4.21	8.75	3.75
SD	3.83	3.16	12.26	3.11	3.44	9.16	3.54
Insect							
Annelid							
Mean	2.24	0.83	0.25	0.56	0.00	4.38	0.00
SD	10.08	2.04	1.45	1.99	0.00	12.37	0.00
Curculionid							
Mean	10.26	13.33	10.76	9.44	10.00	8.13	8.75
SD	9.62	23.17	9.14	7.63	10.00	5.94	5.18
Caterpillar							
Mean	0.79	0.00	0.17	0.42	0.00	0.00	0.63
SD	3.27	0.00	0.91	1.40	0.00	0.00	1.77
Other							
Feather							
Mean	0.00	0.00	1.10	0.00	0.26	0.00	0.00
SD	0.00	0.00	7.83	0.00	1.15	0.00	0.00
Flesh							
Mean	1.64	0.83	1.02	1.94	1.32	0.00	1.88
SD	4.50	2.04	2.59	5.64	3.67	0.00	5.30
Hair							
Mean	5.92	5.00	4.92	4.72	7.89	5.00	5.00
SD	5.81	0.00	2.71	2.05	13.88	4.63	2.67
Artificial							
Mean	2.43	5.00	2.03	2.50	2.37	3.13	1.88
SD	2.64	0.00	2.48	2.80	2.56	2.59	3.72
n =	76	6	59	36	19	8	8

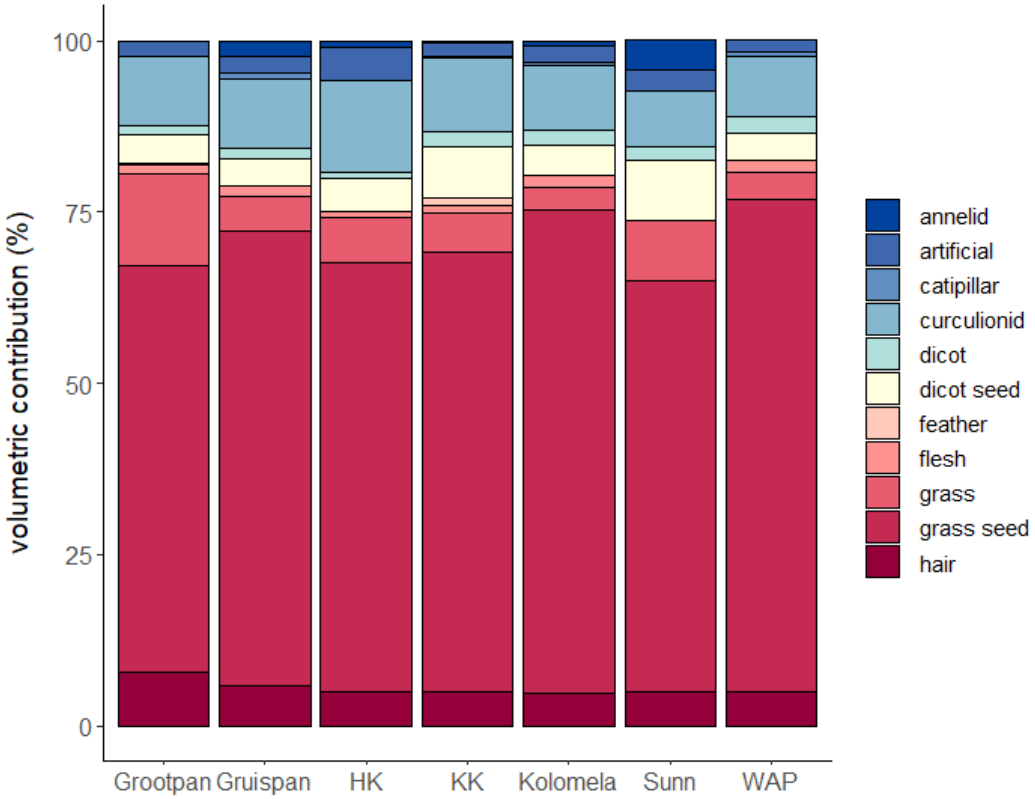

Figure 4.5: Stomach contents depicted by mean percent volumetric contribution for the different sampling locations: Grootpan, Gruispan, Heuningkrantz (HK), Kappies Kareeboom (KK), Kolomela mine, Sunnyside, and Wildealsput (WAP).

Table 4.7: Kruskal-Wallis analyses for percent volumetric contribution of food contents for sampling location comparisons.

Ingested material	H-Value	df	*p* -value
Plant			
Grass blade	**15.182**	**6**	**0.019**
Grass seed	8.624	6	0.196
Dicot stem & leaf	3.236	6	0.778
Dicot seed	6.181	6	0.403
Insect			
Annelid	3.174	4	0.529
Curculionid	1.629	6	0.951
Caterpillar	2.563	3	0.464
Other			
Feather	3.819	2	0.727
Flesh	0.387	5	0.996
Hair	0.891	6	0.989
Artificial	8.961	6	0.176

Statistically significant results, in which $p < 0.05$, are bolded.

Table 4.8: Mann-Whitney U tests comparing volumetric contribution of ingested material for sampling location.

Ingested material	Comparison	W	*p*
Grass	**Kolomela - Grootpan**	**1005**	**0.006**
	Kolomela - Gruispan	66.5	0.558
	Kolomela - Heuningkrantz	**741**	**0.03**
	Kolomela - Kappies Karee	**518**	**0.001**
	Kolomela - Sunnyside	96	0.275
	Kolomela - Wildealsput	111	0.058
	Grootpan - Gruispan	152.5	0.155
	Grootpan - Heuningkrantz	2030	0.319
	Grootpan - Kappies Karee	1578	0.155
	Grootpan - Sunnyside	275	0.642
	Grootpan - Wildealsput	326.5	0.712
	Gruispan - Heuningkrantz	212.5	0.406
	Gruispan - Kappies Karee	**159**	**0.045**
	Gruispan - Sunnyside	30	0.457
	Gruispan - Wildealsput	34	0.197
	Heuningkrantz - Kappies Karee	**1317**	**0.036**
	Heuningkrantz - Sunnyside	235.5	1.000
	Heuningkrantz - Wildealsput	275.5	0.427
	Kappies Karee - Sunnyside	109	0.240
	Kappies Karee - Wildealsput	131	0.666
	Sunnyside - Wildealsput	37.5	0.573

Statistically significant comparisons, in which $p \leq 0.05$, are bolded.

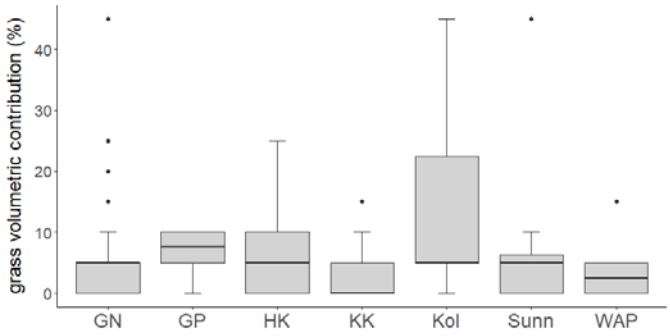

Figure 4.6: Boxplot of statistically significant stomach content when percent volumetric contribution is analyzed by species: Grootpan (GN), Gruispan (GP), Heuningkrantz (HK), Kappies Kareeboom (KK), Kolomela mine (Kol), Sunnyside (Sunn), and Wildealsput (WAP). The boxes represent the central 50% of values, with first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Statistical analysis of insect and other food types did not result in any significant differences by location (Table 4.7). When present, annelid amounts within stomachs were less than 5.00% on average. It was lowest within Kappies Karee stomachs (0.56%) and highest in those from Stofdraai (4.38%). Caterpillar mean contributions were < 1.00% to stomachs from Grootpan, Heuningkrantz, Kappies Karee, and Wildealsput. Curculionid concentrations varied from 8.13% at Stofdraai to 13.33% at Gruispan. Feather, flesh, hair, and artificial materials all provided minuscule amounts to stomach contents as well. Feather and flesh had the lowest percent contributions by location: feathers amounted to 0.26% at the mine and 1.10% at Heuningkrantz while the mean amount of flesh was lowest at Gruispan (0.83%) and highest at both Kappies Karee (1.94%). Hair and artificial materials were found to occur in higher amounts. The amount of hair in stomachs varied from 4.72% at Kappies Karee to 7.89% at Kolomela. Finally, artificial materials comprised < 5.00% of stomach contents at all sampling locations, ranging from 1.88% at Wildealsput to 5.00% at Gruispan.

Sampling Month

Frequency of Occurrence

The frequencies of occurrence for ingested items are broken down by sampling season in Table 4.9 and Figure 4.7. Plant material, both monocot and dicot, were found in stomachs from both months. Evidence of grass seed consumption existed in 100.00% of stomachs sampled in both May and June. The frequency of occurrence for grass blades was higher in July, found in 66.67% of stomachs, and lower in in May (60.96%). Conversely, May stomachs possessed a greater occurrence of dicot seed (74.66%) and dicot stem and leaf (32.19%) than July stomachs (62.12% and 30.30%, respectively).

Insect presence was also greater in May than in July. Annelids were found in 7.53% of May collected stomachs, curculionids in 87.67%, and caterpillars in 6.85%. In July, 6.06% of stomachs contained annelid, 83.33% contained curculionid, and 4.55% contained caterpillar. Feathers were only found in May stomachs (2.05%). Flesh made up < 20.00% of stomachs from either month. Most stomachs sampled from both months contained hair (87.67% in May and 87.88% in July). Finally, the frequency occurrence of artificial materials in stomachs was higher in July at 42.42% than May (10.96%).

Table 4.9: Frequency of occurrence (%) for stomach contents by sampling month

Ingested material	May	July
Plant		
Grass	60.96	66.67
Grass seed	100.00	100.00
Dicot stem & leaf	32.19	30.30
Dicot seed	74.66	62.12
Insect		
Annelid	7.53	6.06
Curculionid	87.67	83.33
Caterpillar	6.85	4.55
Other		
Feather	2.05	0.00
Flesh	14.38	19.70
Hair	87.67	87.88
Artificial	10.96	42.42
n =	146	66

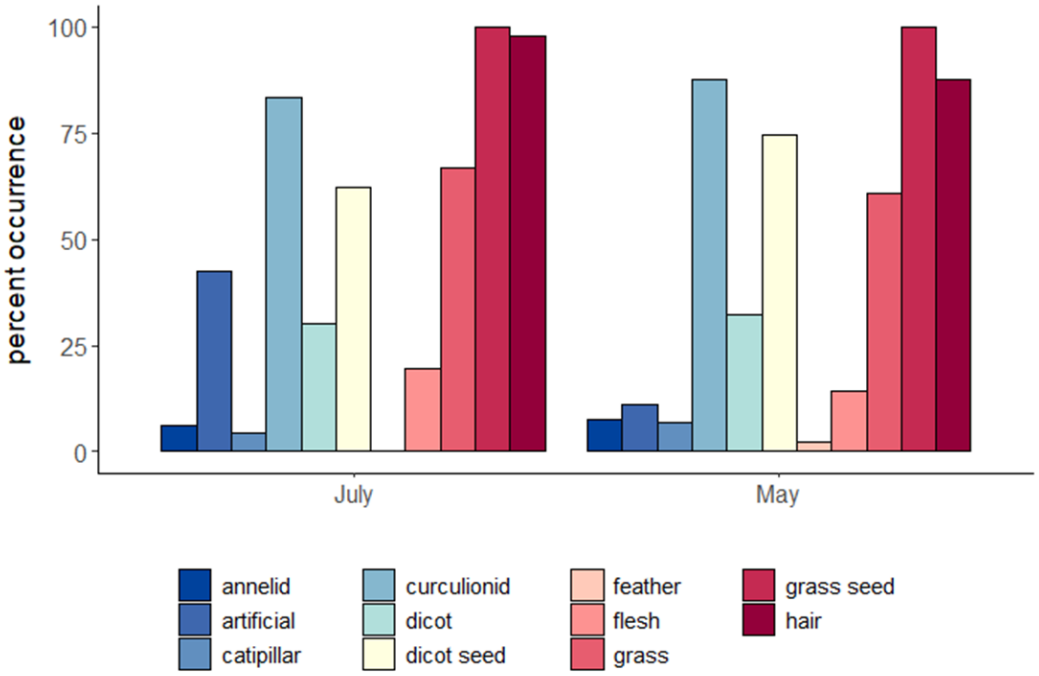

Figure 4.7: Percent occurrence for each ingested item by sampling month.

Volumetric Contribution

Table 4.10 provides the descriptive statistics for percent volumetric contribution of each stomach content item based on sampling month. Mean data are also depicted graphically in Figure 4.8. The mean contributions of food types did not statistically differ between the months of May and July (Table 4.11). Grass seed contributed most to stomach contents regardless of month, with a mean of 64.79% contribution in May and 67.80% contribution in July. The other plant material ingested comprised < 10.00% of stomach contents. While curculionid comprised an average of 11.06% of stomach contents in May and 8.26% in July, annelid and caterpillar amounts were < 5.00% Feathers were not found in any July stomachs and only provided 0.48% of mean stomach contents in May. Flesh and artificial materials made up < 5.00% of stomach contents for both months. Hair also contributed very little to percent volume, varying from 5.15% in July to 5.68% in May.

Table 4.10: Descriptive statistics for volumetric contribution (%) of plant, insect, and other contents found in rodent stomachs, by sampling month

Ingested material	May	July
Plant		
Grass blade		
Mean	5.27	6.82
SD	7.67	8.89
Grass seed		
Mean	64.79	67.80
SD	15.58	15.40
Dicot stem & leaf		
Mean	1.75	1.82
SD	2.91	3.36
Dicot seed		
Mean	5.34	5.23
SD	6.37	9.46
Insect		
Annelid		
Mean	1.30	0.83
SD	7.38	4.52
Curculionid		
Mean	11.06	8.26
SD	10.24	7.16
Caterpillar		
Mean	0.48	0.30
SD	2.37	1.49
Other		
Feather		
Mean	0.48	0.00
SD	4.99	0.00
Flesh		
Mean	1.34	1.59
SD	4.00	4.31
Hair		
Mean	5.68	5.15
SD	6.66	2.77
Artificial		
Mean	2.20	2.50
SD	2.64	2.65

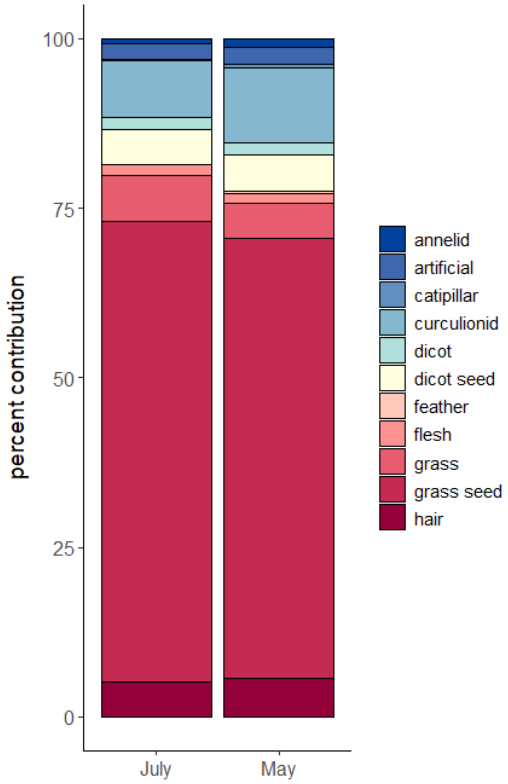

Figure 4.8: Stomach contents depicted by mean percent volumetric contribution for the different sampling months.

Table 4.11: Kruskal-Wallis analyses for percent volumetric contribution of food contents for season comparisons.

Ingested material	H-Value	df	*p* -value
Plant			
Grass blade	2.979	1	0.084
Grass seed	2.059	1	0.151
Dicot stem & leaf	0.016	1	0.901
Dicot seed	1.743	1	0.187
Insect			
Annelid	0.149	1	0.699
Curculionid	3.356	1	0.067
Caterpillar	0.395	1	0.530
Other			
Feather	n/a	n/a	n/a
Flesh	0.747	1	0.388
Hair	0.492	1	0.483
Artificial	0.657	1	0.418

Statistically significant results, in which $p < 0.05$, are bolded.

Discussion

These results provide insight into the dietary ecology of a sympatric muroid community within a region of varying anthropogenic disturbance. As such, these data not only contribute to the existing literature on South African rodent diets but also highlight the potential effects mining activities might have on these species. Regardless of species, location, or collection month, grass seed occurred in every stomach dissected. Often, this food item comprised the greatest percent volume as well. Following the organization of the results section, the interpretations of these data will be discussed individually by species, location, and month effects.

Species Dietary Effects

Of the seven species considered in this study, all but *Dendromus melanotis* have been previously assigned the label of omnivore (see Table 3.1 in Chapter 3). While data indicate that all species leaned towards a more granivorous diet within the Kolomela mine and its surrounding farms, the presence of other food types in the stomach cavities support the omnivorous nature of these rodents. In fact, mean percent contribution to total stomach content rarely differed among species for the various ingested items. Significant differences among species only occurred for the quantity of grass blade, caterpillar, and hair consumed. These differences appeared inconsistently across species.

As grass blades were not found in the stomachs of the *D. melanotis* specimens, it was excluded from statistical analysis. Generally, grass blades contributed < 10.00% to stomach contents, yet significant differences in volume did occur between the *Gerbilliscus paeba* and *Micaelamys namaquensis* populations. Few statistically significant differences were found in

caterpillar consumption as well. *Dendromus melanotis*, *G. paeba*, and *Mus minutoides* were excluded from analysis due to a lack of caterpillar in the sample stomachs. Significant differences occurred in volumetric contribution between *Mastomys coucha* and both *Gerbilliscus leucogaster* and *Mi. namaquensis*. Overall, dietary differences in volumetric contribution were rare. This result may stem from the availability, or lack thereof, of a given food within the Kolomela properties, or the preferences of the individuals within each species. It is also possible that soft tissues, such as those of annelid or caterpillar, may be more susceptible to rapid breakdown from stomach acids in comparison to harder tissues, such as the chiton of curculionids. While this issue would be consistent across species, it would skew stomach content proportions to favor harder tissues and not truly reflect ingesta volume. But given the generalist and opportunistic nature of most of these species, it is unsurprising that diets were extremely similar and lacked any indication of dietary specialization.

In fact, the percent volume of hair ingested led to the greatest occurrence of significant differences among species. However, these differences were probably more indicative of grooming behavior, as suggested by Shiels et al. (2013) in their study Hawaiian rodent behavior and diet. While grooming was evident for each species, not all individual stomachs contained hair. Without further analysis, it is difficult to say whether the hair came from the same individual or resulted from allogrooming. However, it is unlikely that grooming behavior was influenced by dust exposure as the percent contribution of hair in stomachs did not differ by location or month, the two variables that would represent fluctuating dust levels. Most likely, varying hair consumption among species are an artifact of individual or species-specific behavior. That is not to say dust or soil wasn't consumed; on the contrary, these particles were filtered out prior to stomach content analysis. Other non-dietary items, specifically artificial

items, were also found within most stomachs. However, this is unsurprising given that all sampling habitats were anthropogenically affected in some form.

Dendromus melanotis

When compared to previous studies (Abu Baker & Brown, 2014; Rowe-Rowe, 1986), the results supported occurrence of seed ingestion, with regards to the two specimens of *D. melanotis* analyzed. Rowe-Rowe's (1986) analysis of 14 stomachs collected in Grant's Castle Game Reserve indicated 100.00% seed occurrence, as well as the remains of arthropods in 25.00% of the specimens examined. In this study, curculionid pieces were found in both stomachs dissected and had the highest average contribution of all species (20.00%). *Dendromus melanotis*'s granivorous tendencies have also been supported by a controlled foraging study in which these mice showed a preference towards seeds over alfalfa or worms (Abu Baker & Brown, 2014). Non-seed and non-arthropod items contributed very little to stomach contents in this sample, indicating that the *D. melanotis* population within the Kolomela properties follow the expected granivorous diet, along with potential for insectivorous supplementary.

Gerbilliscus leucogaster

Gerbilliscus leucogaster provided the greatest number of stomachs to analyze (n = 99). Once again, grass seed made up most stomach contents for most specimens (a mean of 64.24%). Each food category was found in at least one stomach, with curculionid providing the next highest average percent volume. Only one study, to date, has analyzed *G. leucogaster* dietary behavior. Despite the high percentage of foliage in the diet, this study concluded that the gerbil

species was an omnivore due to the presence of seeds and arthropods within the stomachs (Monadjem, 1997). Although foliage did not generally make up a large quantity of stomach contents in this study, the presence and varying amounts of different food types consumed at the Kolomela properties does supports the omnivorous nature of *G. leucogaster*.

Gerbilliscus paeba

Gerbilliscus paeba had the smaller sample size (n = 7) of the two gerbil species. It also had the highest mean volume of grass seed for all of the Muroidea considered in this study (77.9%), with a mean contribution of ≤5% for all other categories. This highly granivorous activity coincides with other analyses, in which seeds were predominantly found within stomach contents (Nel et al.1984; Van Deventer & Nel 2006). Other studies indicated that *G. paeba* possesses a more omnivorous diet (Ascaray, 1986; Kerley, 1989; 1992) or insectivorous one (Boyer, 1987). The data from the specimens in this study, however, does not support these dietary categories.

Mastomys coucha

Previous studies have described *Ma. coucha* as very opportunistic, willing to eat a relatively large array of foods (Avenant, 2011; Leirs, 2013). Others have indicated a more granivorous diet (Skinner & Chimimba, 2005). However, more dietary studies have been conducted on *Ma. coucha*'s sister species *Mastomys natalensis* (e.g., Iwuala et al., 1980; Kerley, 1992; Koekemoer, 2000; Monadjem, 1997; Mulungu et al., 2011a, b; Mulungu et al., 2014). As explained in Chapter 3, often these two species cannot be distinguished without DNA sequencing (Green et al., 1980; Kruppa et al., 1990). As such, it could be feasible that some of these studies

inadvertently included *Ma. coucha* specimens. Much like *Ma. coucha*, *Ma. natalensis* is considered an opportunistic feeder, with diet differing based on food availability and location. Stomach content analysis of *Ma. natalensis* indicated a high preference towards seeds among some populations (Iwuala et al., 1980; Koekemoer, 2000; Monadjem, 1997). In other populations, herbage and insects dominated stomach contents (Kerley, 1992; Mulungu et al., 2011a, b; Mulungu et al., 2014).

The five *Mastomys coucha* specimens here had, on average, the lowest grass seed contribution to stomach contents (57.00%). Given that the mean volumetric contribution was above 50.00%, these data still align with studies that indicate a granivorous diet for *Mastomys* (Iwuala et al., 1980; Koekemoer, 2000; Monadjem, 1997; Skinner & Chimimba, 2005). The *Mastomys* individuals captured in this study were not solely granivorous, and consumed grass blades and insects as well. It is the only species in this sample not to have any presence of dicot plant within stomachs (Table 4.1), indicating some level of individual preference against dicot. These results lend credence towards labeling the species as more of a generalist.

Micaelamys namaquensis

All ingested food groups, as well as hair and artificial materials, were found within the stomachs of *Micaelamys namaquensis* (n = 56). Like the other species collected at the Kolomela mine and farms, grass seed contributed the majority of foodstuff to stomach contents (67.00%). The dominance of seed in the stomachs of this mouse coincides with that of other studies. A behavior experiment by Abu Baker and Brown (2012) indicated a preference towards seeds over other foods. Seeds also dominated the ingested items found in *Mi. namaquensis* feces (Lancaster, 2009) and stomachs (Van Deventer & Nel 2006).

Alternatively, Monadjem (1997) indicated a greater percent contribution of foliage than seeds in their sample, even though seeds made an average of 40.20% of stomach content contribution. This result led the authors to ascribe a designation of herbivore-granivore to the species. Fecal samples from Kgalagadi Transfronteir Park also supported a high level of herbage in this mouse's diet (Kerley et al., 1990). Gliwicz (1985; 1987) indicated that *Mi. namaquensis* is primarily an herbivore that does not eat insects during the dry season. Data collected at Kolomela indicates otherwise. Although low in comparison to grass seed, the mean volumetric contribution of 9.29% curculionid to stomachs collected in May and July does indicate some preference towards insects during this season (Table 4.2). Other texts have simplified *Mi. namaquensis*'s diet as omnivorous when describing the species (e.g., Happold, 2013; Skinner & Chimimba, 2005). This designation appears appropriate as *Mi. namaquensis* diet appears to vary by population and includes so many different foods. Even at Kolomela, despite the dominance of seeds in the stomachs of many *Mi. namaquensis* specimens, the presence of non-seed material furthers a generalist and omnivorous diet that appears opportunistic in nature.

Mus minutoides

The *Mus minutoides* sample size was also small ($n = 6$) and possessed one of the lower average concentrations of grass seeds (58.33%). Except for caterpillar and feathers, the other categories of ingested material were found in at least one of the five *Mu. minutoides* stomachs. In other studies, seeds were a primary component of this mouse's diet (Iwuala et al. 1980; Net et al. 1984; Kerley 1989, Koekemoer 2000). And while foliage and insects provided relatively little to mean stomach contents at the Kolomela properties, it has been more prominent in other locations (Rowe-Rowe 1986; Kerley 1989; Monadjem 1997). As such, the prominence of either

foliage or seeds within its diet seems location and population dependent. In this study, *Mu. minutoides*' diet leans more towards that of seeds than that of other parts of foliage.

Rhabdomys bechuanae

Little research has previously been conducted on the dietary ecology of *Rhabdomys bechuanae*. This is possibly in part due to debate over *Rhabdomys* as a multi-species genus, as discussed in Chapter 3. As no other data could be found for comparison, the *Rhabdomys* samples from Kolomela will be compared to sister species *R. pumilio*. Grass seed contributed the most to ingested material (a mean of 67.30%) and items from all food categories were found in at least one stomach in the sample. After grass seed, curculionid parts made up the next greatest mean contribution at 7.84%. The high prominence of seed in *R. bechuanae* stomachs does coincide with some *R. pumilio* analyses. For example, Kerley (1989) reported an *R. pumilio* population in which average percent composition of seeds was 62.00%. Other studies indicated a preference towards seeds and insects when available (Brooks, 1974; Nel et al., 1984; Perrin 1980; Taylor & Green, 1976;), especially that of dicot seeds (Curtis & Perrin, 1979; David, 1980; King, 1976; Shelton, 1975). The preference of *R. pumilio* towards dicot seeds is in stark contrast to that of the *R. bechuanae* population analyzed in this study, in which monocot seeds were of greater preference.

Sampling Location Dietary Effect

Little variation in diet was found between farm habitats, or even with the Kolomela mine. Regardless of sample habitat, mean grass seed percent volume comprised ≥ 50.00% of the stomach contents. While other ingested materials were found at most sampling locations, such

as grass blade, curculionid, or dicot plant and seed, these were typically present in starkly lower quantities (Table 4.6). The frequent occurrence of grass alongside trap transects could in part count for a diet high in grass seed for these generalist species. Grass coverage comprised at least 10.00% land cover at each rodent transect, with a mean of approximately 48.50% coverage among all transects (see Chapter 3, Table 3.4). Meanwhile, bush and tree coverage averaged to only 20.40% and 10.20%, respectively. As such, monocot material may simply have been easier to obtain than that of dicot at most sample habitats. Yet, there did not appear to be a correlation between percent grass cover and the ingestion of grass vegetation and seed. For example: while the trapping transects at Kappies Karrie had the lowest grass cover, averaging at 58.00%, its collected sample possessed one of the highest mean grass seed contributions, 70.69%. At the Kolomela mine, where grass coverage alongside the trapping transect was 30.00%, specimens had the highest mean grass contribution (13.4%) and the lowest mean grass seed contribution (59.2%) to stomach contents.

Only the percent volumetric contribution of grass blades to stomach contents exhibited statistical significance when analyzed by sampling location. The stomachs from the Kolomela mine property had the highest mean percent contribution of grass blades despite the smaller sample size. The Kolomela specimens significantly differed in grass percent volume from those from three farms: Grootpan, Heuningkrantz, and Kappies Kareeboom. Given that the Kolomela transect had a lower percent coverage of grass (see Table 3.4, Chapter 3), it is unlikely that high availability of grass is a reason for the significant differences. The transect on the mine property is considered the most disturbed habitat within this study due to its proximity to its proximity to mining activities. The rodent biomonitoring survey indicated that more habitats at Kolomela are more degraded due to the higher presence of generalist and opportunistic species and the

infrequent capture of specialists within the property (Avenant & du Plessis, 2018). Nutrient poor, difficult to digest grass blades are not ideal in comparison to more nutrient rich and easily digestible foodstuff. But if preferred items are unavailable, opportunistic species will eat whatever they can. As such, it is possible that higher grass ingestion at the mine could be explained by a need to eat whatever resources are available, in whatever quantity.

Opportunistic and generalist species have been observed to change their diet based on location. For example, Mulungu et al. (2011a) noted that *Mastomys natalensis* altered their diets based on the availability of their preferred food, grain, in a habitat. When unavailable, their dietary niche broadened to include whatever foods satisfied caloric requirements. Similarly, comparing two different studies of *Micaelamys namaquensis* populations indicated a more granivorous diet in Swaziland (Monadjem, 1997) and a more herbivorous one in the southern Kalahari (Kerley et al., 1990). Key microhabitat characteristics that determine vegetation structure and plant, and therefore food availability, highly influence rodent, and other small mammal, communities (Van Deventer & Nel, 2006). However, in this study, the differences in microhabitats are not enough to cause stark differences in food availability. All habitats are located within the same overarching bioregion, the Eastern Kalahari Bushveld bioregion, with most transects located within the Postmasburg Thornveld ecoregion. While vegetation at Heuningkrantz was unable to be recorded during the 2017 biomonitoring season, all other farms and the Kolomela mine property had the presence of *Aristida*, *Enneapogon*, *Eragrostis*, and *Orepetium* grass species and the tree species *Senegalia* (Smit & van Rensburg, 2018). Thus, these rodent populations were often exposed to the same floral and faunal species regardless of location.

Seasonal Dietary Effects

There were no significant differences in diet breakdown for the sample collected in May or July. However, it is interesting to note that the only occurrence of feathers appeared in three individual stomachs (two from Heuningkrantz, one from the Kolomela mine) that were collected during the May sampling period. Sample collection took place during May, a transitional month between wet to dry, and at the beginning of the dry season in July. In a molar microwear study, no seasonal dietary difference was evident from texture patterns when comparing *R. pumilio* specimens from the wet summer, dry winter, and transitional seasons in the Dry Highveld grasslands (Burgman et al., 2016). While the vegetation present in May might reflect the wet season abundance and composition (Van der Westhuizen, 2006), July is still relatively early for a dry season that lasts through September. However, rains that occurred in December were noted to have led to increased primary productivity throughout the region, and as such more food and better breeding of rodents, ultimately led to a higher trap success rate in 2017 than in previous years (Avenant & du Plessis, 2018). This increase in summer rains could have also led to the continued availability and quantity of similar foods in July as in May.

Conclusion

The stomach contents of rodents collected at Kolomela mine and its surrounding farm properties indicated a highly granivorous diet based on the high presence of grass seed in the stomach cavities. These results occurred regardless of species, location, or month sampled. However, it is important to note that while grass seed was identified in every stomach, these seeds were not identified to species level. Given the diversity of grasses in the region, noted in the vegetation surveys to include various species of *Aristida*, *Enneapogon*, *Eragotis*, and *Tragus*,

rodent species sharing overlapping home ranges may be dividing resource on a species-specific level. This logic can be applied to the remainder of ingested materials identified in this study, as stomach contents were only identified on a general level.

Food preference is based on several characteristics, varying by species and even individual, and is not just restricted to general food categories. Some studies have indicated that more granivorous rodents, such as the *D. melanotis* and *Mi. namaquensis* mice sampled at Kolomela, opt for larger seeds as they provide greater nutrition and more digestible energy during metabolism (Cruise, 2013; Garb et al., 2000; Kelrick et al., 1986; Kerley & Erasmus, 1991; Van der Wall, 2003). Rodents may also consume certain species of seeds based on other factors, such as dispersion, seed densities, toxicity, taste, and ease of obtainment (Cruise, 2013; Kelrick et al., 1986). Even within a given species, preference may vary. Cruise (2013) suggested that within *G. leucogaster*, individuals may have their own individual tastes and display unique preference towards and against specific seed types. While the majority within his testing group preferred sunflower seeds, the food with the highest caloric, fat, and carbohydrate content, others still preferred oat or sorghum seed. Ultimately, the author concluded that these preferences were due solely to individual personalities (Cruise, 2013). This dietary individuality is also reflected by all specimens, regardless of species, in this study.

Aside from *D. melanotis*, the species used in this study are usually described as generalists and opportunists. Yet while the stomach content analyses presented here indicate granivorous diets for all seven species, these results do not contradict previous dietary classifications. Optimal foraging theory states that an animal's best foraging strategy maximizes the net energy gained by searching for food that provides the greatest energy at the lowest cost (Pyke et al. 1977; Schoener, 1971). This theory is especially pertinent for small mammals given

their high metabolic rates. Muroid rodents, like other small mammals, require foods high in calories and nutritious content to maintain their metabolisms, with muroids often opting for higher caloric foods (Gliwicz & Taylor, 2002). While insects provide similarly high caloric value to grass seed, more energy may need to be expended to obtain this prey. This extra expenditure of energy becomes especially relevant when considering the availability of seed caches created by certain rodent species. *G. paeba*, for example, has been known to cache and scatter hoard seeds (Weighill et al., 2017; White et al., 2017) while *R. pumillio* has been known to steal from the caches of other rodents (Rusch et al. 2013). Thus, the presence of a more easily attainable high nutrition food, such as seed, in stomach contents is understandable for generalist species.

Indeed, data from the stomach content analysis indicated that every rodent ingested grass seed. More than just grass seed was found in the stomachs of many individuals, however. Although these other foods were not consistently present in this sample, curculionid parts were found in approximately 80.00% of the overall sample. Averages of curculionid volumetric contribution were relatively low (as were all other stomach content categories in comparison to grass seed) but in some individuals, insects did occupy most of the stomach cavities. One *G. leucogaster* specimen caught within the Gruispan farm had curculionid pieces contribute 60% to its stomach contents. This supports the notion that posits individual preference (Cruise, 2013) as well as the opportunistic nature of this species to eat whatever is available. Similar could be said about dicot seed, which was found in 62.8% of the overall sample but for one *Mi. namaquensis* mouse from Heuningkrantz, contributed 70% to its stomachs.

Generally, the other items that were consumed provided less than 25% mean volumetric contribution to stomach contents regardless of sample division by species, farm, or month. The

presence of different foods in smaller amounts within the sample stomachs could be considered evidence of partial sampling. This behavior is considered common in rodents and is thought to allow assessment of the nutritional quality of various available resources (Barnett et al., 1978; Clark, 1982; Cruise, 2013; Murray & Dickman, 1997). Sampling does indeed explain the high occurrence of foods such as curculionid and dicot seed but the overall low average volume contribution. Opportunistic species will also supplement preferred foods with whatever resources are available to meet their metabolic requirements.

Alternatively, the percentages of different ingested materials may have differed because of interactions with gastric acid. Easily digestible items such as vegetative reproductive tissues or soft animal tissues may be more quickly broken down than less digestible items, like artificial strings, fibrous plant tissue, or insect exoskeletons. As such, these easily digestible items would be harder to identify, creating a bias towards less digestible items. This possibility could explain the higher occurrence and volume of curculionid parts in comparison to annelid and caterpillar. Following this argument, however, one would also expect seed amounts to be lower within stomachs than what was recorded. Still, were this the case, at least the effects of digestibility would be consistent across all specimens.

There were limitations to this study. As this stomach content analysis was meant to provide dietary information for a microwear study, there was no need to identify past general categories to species, or even genera, level. Dental microwear patterns form in part due to food material properties; the mastication of a hard food like nuts or chitin-shelled insects is thought to result in a different pattern than tougher foods like grass blades (Ungar & Sponheimer, 2011). Regardless, the dietary categories used in this dissertation allow for the development of more specific dietary designations than generally used in dental microwear for rodents. While this is

helpful for better elucidating the dental microwear of generalist rodent species, it is not as helpful in elucidating the details of diet on a more species-specific level. In addition, while estimating the percent volume of different food items is an accepted method, it is considered highly subjective in nature and far from exact (Sagar et al., 2018). However, restricting analysis to one person, as done here, does help to mitigate subjectiveness.

The aim of this chapter was to provide a more comprehensive understanding of the dietary ecology of the rodent population at Kolomela mine and farms. It was hypothesized that the diets of individual specimens would reflect the vegetative characteristics of their given microhabitat and the dietary nature of their specific species. The sampled species were previously classified in the literature as granivores or generalists that would eat any available food (see Table 3.1, Chapter 3; Happold, 2013; Monadjem et al., 2015; Skinner & Chimimba, 2005). Sampling habitats were in veld ecosystems, with several grass species recorded in the vegetative survey. As such, the diets recorded from stomach contents, with their high levels of grass seed, match microhabitat characteristics and dietary behaviors of these animals. Even if most species ate grass seed, the dietary labels ascribed to individuals based on their stomach contents are more informative for a microwear study than the label of opportunistic generalist.

Furthermore, the data gathered in this chapter does contribute to the overall dietary knowledge of these sympatric rodent species. While the diets of some species, such as *Mu. minutoides* and *Mi. namaquensis*, have been studied more often, the dietary analysis of other rodents such as *G. leucogaster* and *Ma. coucha* are infrequently found in the literature. Ascertaining dietary details also allows for better understanding of ecological relationships, specifically providing insight on food availability and competition, as well as population

dynamics and the roles played by primary consumers within a given habitat (Batzli & Cole 1979; Iwuala et al., 1980; Taylor & Green 1976).

In the case of this study site, these data also illuminate the effect mining and other anthropogenic activity have on rodent diets and compliment the small mammal biomonitoring data. Avenant and du Plessis (2018) noted a difference in small mammal trap success and species composition between the sampled habitats, with an overall lack of dietary specialists in the 2017 collection. That diets between species were so similar speaks in part to the environmental disturbance at these sites. While enough resources were available to provide usable stomachs for analysis, it is important to note that the presence of high food availability is not indicative of high ecosystem integrity when looking at rodent populations (Avenant, 2011). This is in part because opportunistic and generalist species change their dietary behaviors alongside food availability in adaptation to habitat disturbance (Bekele & Leirs, 1997). Simply put, the rodents examined in this study ate whatever was available to meet their metabolic requirements.

CHAPTER FIVE: INCISOR MICROWEAR

Results

Only 198 specimens collected during the 2017 season of the Kolomela biomonitoring project provided preserved visible antemortem microwear on the incisor surface that was suitable for analyses. These individuals comprised six different species from two Muroidea families, Nesomyidae (*Dendromus melanotis*) and Muridae (all other species). While these specimens spanned both collection periods, various mine properties, species, and diets, not all individuals could be utilized for each analysis. This limitation was in part due to an inability to control rodent behavior, as was explained in Chapter 3. Only groups of sample size $n \geq 10$ were considered when structuring the MANOVAs for each independent variable. Analyses for behavioral and environmental variables were conducted using a taxon-free approach. Statistically significant differences in central tendency did occur, with groups separated by both scale-sensitive fractal analysis (SSFA) and International Standards Organization (ISO) texture parameters. MANOVAs for resulted in $p < 0.05$ when species, habitat, microhabitat, burrowing behavior, and soil type were considered. Results are discussed separately for each: species, macrohabitat, microhabitat, diet, burrowing behavior, soil type, land cover, dust level, and season. Appendix II provides SSFA and ISO parameter values for each specimen utilized.

Species Microwear Effects

Although the total sample contained six species, only three possessed sufficient sample sizes to utilize in species analysis: *Gerbilliscus leucogaster* (n = 101), *Micaelamys namaquensis* (n = 53), and *Rhabdomys bechuanae* (n =30). These species stemmed from two Muridae sub-

families: Gerbillinae (*G. leucogaster*) and Murinae (*Mi. namaquensis* and *R. bechuanae*). Table 5.1 provides descriptive statistics for all species, with representative photosimulations provided in Figure 5.1. Multivariate test results indicated significance variation in central tendencies ($p < 0.005$) when restricting the species sample to *G. leucogaster*, *Mi. namaquensis*, and *R. bechuanae* (Table 5.2). Individual ANOVAs resulted in statistically significant differences for five parameters: complexity (*Asfc*), anisotropy (*epLsar*), five-point pit depth (*S5v*), pit void volume (*Vvv*), and maximum pit height (*Sv*).

Post-hoc comparisons for *Asfc* central tendencies showed significant variation between *G. leucogaster* and *Mi. namaquensis* values, with marginal differences between *G. leucogaster* and *R. bechuanae.* Central tendencies for *G. leucogaster* and *Mi. namaquensis* also differed for *epLsar* and the ISO parameters *S5v, Vvv,* and *Sv* (Table 5.3, Figure 5.2). Compared to the murines, *G. leucogaster* individuals possessed the highest measures of complexity (*Asfc*), pit depth (*S5v* and *Sv*), and valley volume (*Vvv*), and the lowest measure of anisotropy (*epLsar*). Tukey's HSD and Fisher's LSD also separated *Rhabdomys bechuanae* and *Mi. namaquensis* samples for *epLsar* central tendency, with the *Mi. namaquensis* sample having significantly higher values than *R. bechuanae* (Table 5.3, Figure 5.2). Table 5.4 provides microwear descriptions for each species based on these statistically significant parameters.

Table 5.1: Descriptive statistics of incisor texture parameters by species.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
D. melanotis (n = 2)						
Mean	1.727	0.009	0.937	14881.66	0.251	0.438
SD	0.229	0.003	0.624	4036.32	0.112	0.088
G. leucogaster (n = 101)*						
Mean	1.717	0.008	16.155	12505.75	0.249	0.558
SD	0.705	0.002	76.854	3102.31	0.148	1.166
G. paeba (n = 6)						
Mean	1.672	0.010	145.330	16923.35	0.197	0.470
SD	1.022	0.001	207.609	2513.46	0.062	0.220
Ma. coucha (n = 3)						
Mean	1.814	0.007	0.271	16693.89	0.216	0.357
SD	1.202	0.002	0.127	1299.40	0.067	0.057
Mi. namaquensis (n = 53)*						
Mean	1.352	0.009	73.588	13293.68	0.262	0.485
SD	0.474	0.001	153.950	3363.58	0.102	0.179
Mu. minutoides (n = 3)						
Mean	1.585	0.010	30.247	16519.22	0.293	0.421
SD	0.877	0.002	52.092	878.11	0.284	0.172
R. bechuanae (n = 30)*						
Mean	1.489	0.008	17.446	12825.63	0.220	0.429
SD	0.677	0.002	76.194	2678.986	0.094	0.128

ISO:	*Ssk*	*Sdr*	*S5v*	*Str*	*Sdv*	*Vvv*	*Sv*	*Sda*
D. melanotis (n = 2)								
Mean	0.429	1.606	0.851	0.326	7.781	0.056	2.048	320.738
SD	0.340	0.728	0.154	0.205	8.554	0.014	0.578	261.157
G. leucogaster (n = 101)*								
Mean	-0.053	1.507	0.897	0.290	2.785	0.050	1.639	227.775
SD	0.389	0.712	0.272	0.152	2.197	0.019	0.681	125.790
G. paeba (n = 6)								
Mean	-0.141	2.098	1.013	0.399	3.219	0.050	1.658	170.041
SD	0.477	1.171	0.310	0.194	3.631	0.022	0.591	76.681
Ma. coucha (n = 3)								
Mean	0.101	1.640	0.867	0.277	0.737	0.044	1.283	111.014
SD	0.088	1.097	0.289	0.134	0.075	0.016	0.304	59.415
Mi. namaquensis (n = 53)*								
Mean	0.031	1.362	0.754	0.267	2.178	0.048	1.526	180.717
SD	0.315	0.559	0.228	0.134	1.803	0.045	1.054	115.994
Mu. minutoides (n = 3)								
Mean	0.094	1.766	0.733	0.340	0.957	0.031	0.962	94.839
SD	0.375	0.558	0.167	0.140	0.516	0.010	0.273	44.302
R. bechuanae (n = 30)*								
Mean	0.004	1.320	0.838	0.324	4.487	0.045	1.524	266.155
SD	0.402	0.626	0.267	0.161	10.169	0.012	0.650	305.825

*denotes groups used in statistical analyses

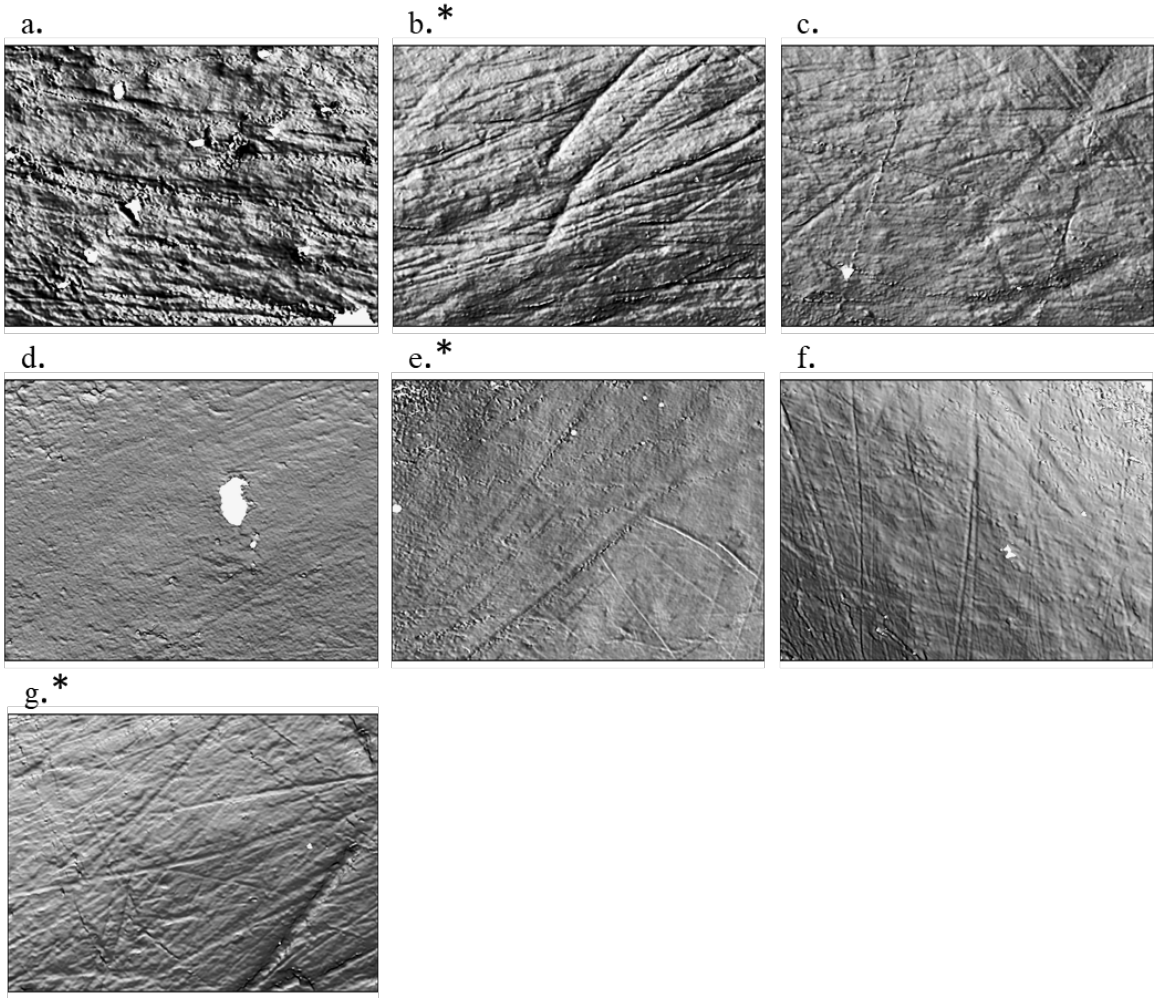

Figure 5.1: Representative incisor microwear photosimulations for the seven rodent species found at Kolomela and its surrounding farms: *Dendromus melanotis* (a), *Gerbilliscus leucogaster* (b), *Gerbilliscus paeba* (c), *Mastomys coucha* (d), *Micaelamys namaquensis* (e), *Mus minutoides* (f), and *Rhabdomys bechuanae* (g). Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Table 5.2: Statistical analyses for incisors by species (n = 184).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.745	**1.900**	**2, 28**	**0.005**

(B) ANOVA results

	F- ratio	*p* -value
Asfc	**5.169**	**0.007**
epLsar	**14.645**	**0.000**
Smc	1.420	0.244
Tfv	1.139	0.322
$HAsfc_{9}$	1.982	0.141
$HAsfc_{81}$	1.756	0.176
Ssk	0.724	0.486
Sdr	1.517	0.222
S5v	**4.447**	**0.013**
Str	1.416	0.245
Sdv	1.236	0.293
Vvv	**3.460**	**0.034**
Sv	**3.458**	**0.034**
Sda	1.790	0.170

Statistically significant results, in which p < 0.05, are bolded.

Table 5.3: Pairwise comparisons for incisors by species.

Variable	Comparison	difference
Asfc	***Mi. namaquensis - G. leucogaster***	**-25.579****
	R. bechuanae - G. leucogaster	**-23.340***
	R. bechuanae - Mi. namaquensis	2.239
epLsar	***Mi. namaquensis - G. leucogaster***	**44.285****
	R. bechuanae - G. leucogaster	2.929
	R. bechuanae - Mi. namaquensis	**-41.456****
S5v	***Mi. namaquensis - G. leucogaster***	**-26.306****
	R. bechuanae - G. leucogaster	-12.279
	R. bechuanae - Mi. namaquensis	14.026
Vvv	***Mi. namaquensis - G. leucogaster***	**-23.168****
	R. bechuanae - G. leucogaster	-12.235
	R. bechuanae - Mi. namaquensis	10.933
Sv	***Mi. namaquensis - G. leucogaster***	**-23.222****
	R. bechuanae - G. leucogaster	-11.776
	R. bechuanae - Mi. namaquensis	-11.446

Statistically significant results, in which p < 0.05, are bolded.

**p* < 0.05 using Fisher's LSD test only; ***p* < 0.05 using both Tukey's HSD and Fisher's LSD tests.

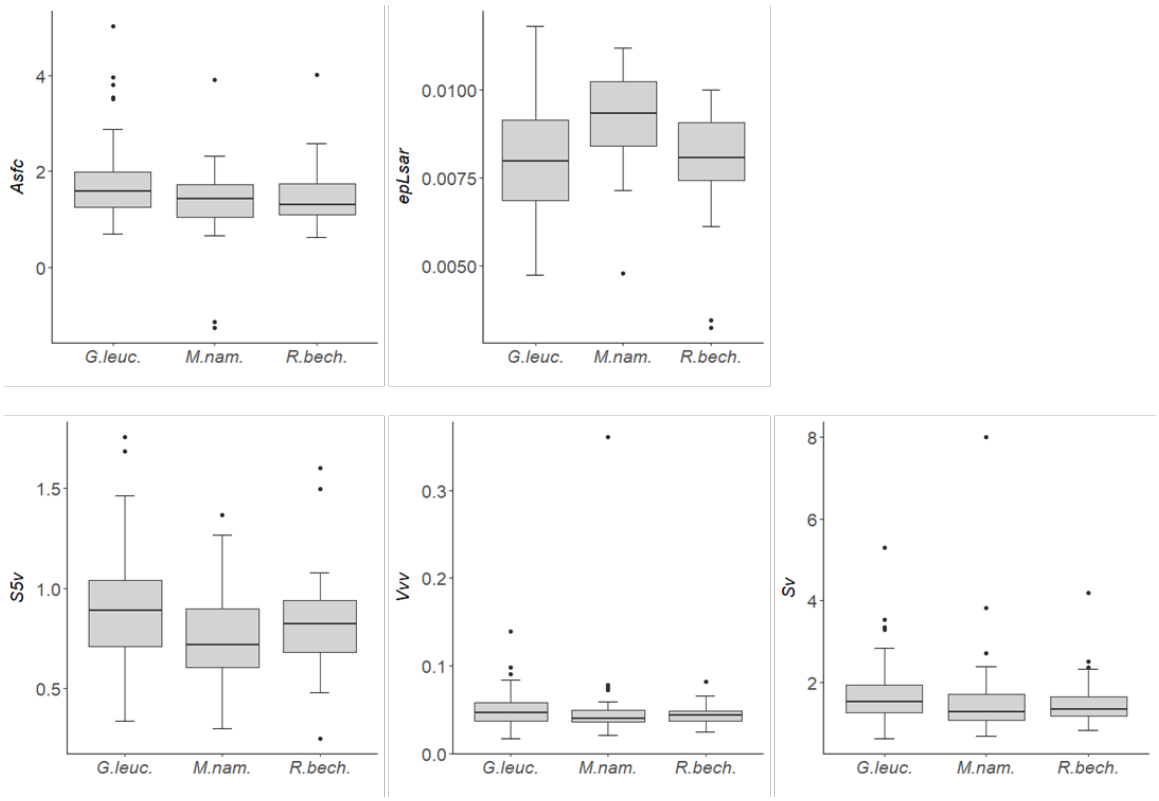

Figure 5.2: Box charts of statistically significant microwear texture parameters when analyzed by species: *Gerbilliscus leucogaster* (*G.leuc.*), *Micaelamys namaquensis* (*M. nam*), and *Rhabdomys bechuanae* (*R.bech*.). The boxes represent the central 50% of values, with first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 5.4: Incisor microwear descriptions for species based on significant microwear parameters.

Species	Significant parameter trends	Microwear description
G. leucogaster	highest *Asfc* , *S5v* , *Sv* , and *Vvv* lowest *epLsar*	complex, isotropic microwear pattern possessing large and deep features
Mi. namaquensis	highest *epLsar* mid-range *Sv* lowest *Asfc* , *S5v* , *Vvv*	anisotropic and generally shallow microwear pattern that lacks the complexity of *G. leucogaster* microwear
R. bechuanae	mid-range *S5v* , *Vvv* low *Asfc* , low *epLsar* lowest *Sv*	not particulary complex or anisotropic in comparison to the other two species, with features that are not particularly large or small, deep or shallow, even though it possess the feature with the smallest depth

Macrohabitat Microwear Effects

The rodent specimens were obtained from seven sampling habitats owned by Kumba Iron Ore: the Kolomela mine and six farms (see Table 3.3 in Chapter 3 for key characteristics of each habitat). Descriptive statistics for each habitat are provided in Table 5.4 while descriptive micrographs are depicted in Figure 5.3. Four habitats were used in statistical analyses: Grootpan (n = 66), Heuningkrantz (n = 62), Kappies Kareeboom (n = 36; also abbreviated as Kappies Karee), and Kolomela mine (n = 16). MANOVA results indicated statistically significant variation in central tendencies for microwear texture parameters among the four macrohabitats ($p < 0.005$; Table 5.5). Univariate tests revealed that differed complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*), developed interfacial area ration (*Sdr*), mean dale volume (*Sdv*), and pit void volume (*Vvv*) among the samples (Table 5.5).

Table 5.5: Descriptive statistics of incisor texture parameters by farm habitats.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
Kolomela Mine (*n* = 16)*						
Mean	1.358	0.009	26.226	11442.57	0.301	0.469
SD	0.459	0.002	102.970	3791.290	0.162	0.161
Grootpan (*n* = 66)*						
Mean	1.660	0.008	20.765	12974.25	0.225	0.598
SD	0.712	0.002	81.716	3174.960	0.104	1.431
Gruispan (*n* = 4)						
Mean	1.468	0.009	0.682	13648.87	5.000	0.557
SD	0.530	0.001	0.666	3523.630	0.144	0.190
Heuningkrantz (*n* = 62)*						
Mean	1.299	0.009	74.818	13007.02	0.244	0.464
SD	0.590	0.001	156.873	3409.470	0.109	0.188
Kappies Karrieboom (*n* = 36)*						
Mean	1.868	0.008	14.925	13426.29	0.233	0.454
SD	0.930	0.002	70.391	2533.140	0.104	0.193
Sunnyside/Stofdraai (*n* = 7)						
Mean	2.228	0.008	0.386	13387.62	0.472	0.635
SD	0.863	0.001	0.226	3399.270	0.273	0.325
Wildealsput (*n* = 7)						
Mean	1.844	0.009	7.015	15126.58	0.164	0.319
SD	0.490	0.002	17.346	2568.130	0.085	0.073

ISO:	*Ssk*	*Sdr*	*S5v*	*Str*	*Sdv*	*Vvv*	*Sv*	*Sda*
Kolomela (*n* = 16)*								
Mean	0.098	1.264	0.875	0.338	1.295	0.037	1.508	175.875
SD	0.223	0.851	0.340	0.146	0.794	0.011	1.077	113.032
Grootpan (*n* = 66)*								
Mean	-0.049	1.441	0.876	0.288	3.623	0.047	1.613	244.606
SD	0.401	0.633	0.278	0.158	6.988	0.016	0.683	227.801
Gruispan (*n* = 4)								
Mean	-0.200	1.228	0.957	0.251	3.122	0.040	1.604	255.314
SD	0.577	0.595	0.311	0.141	1.472	0.012	0.587	96.331
Heuningkrantz (*n* = 62)*								
Mean	0.065	1.341	0.767	0.274	2.696	0.045	1.428	208.862
SD	0.326	0.536	0.214	0.132	2.356	0.015	0.543	121.588
Kappies Karrieboom (*n* = 36)*								
Mean	-0.099	1.794	0.904	0.306	2.395	0.061	1.788	183.511
SD	0.337	0.883	0.280	0.153	1.931	0.056	1.182	88.159
Sunnyside/Stofdraai (*n* = 7)								
Mean	-0.053	1.497	0.849	0.304	3.217	0.045	1.501	240.665
SD	0.434	0.504	0.176	0.199	4.807	0.014	0.369	196.312
Wildealsput (*n* = 7)								
Mean	-0.061	1.754	0.938	0.355	3.300	0.056	1.825	231.539
SD	0.639	0.786	0.235	0.195	2.156	0.011	0.409	174.802

*denotes groups used in statistical analyses

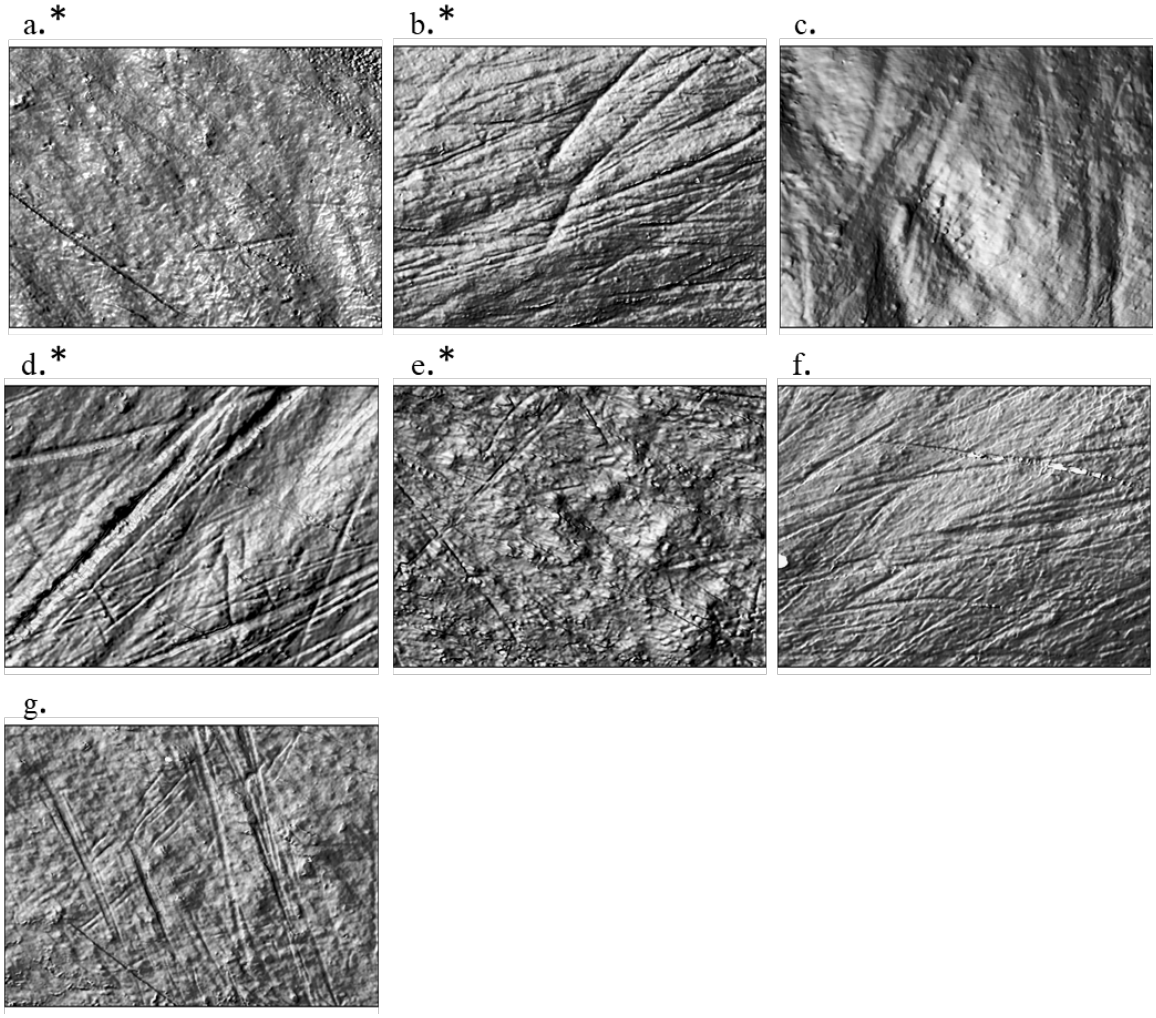

Figure 5.3: Representative incisor microwear photosimulations for each sampling habitat, the mine and the six farms: Kolomela (a), Grootpan (b), Gruispan (c), Heuningkrantz (d), Kappies Kareeboom (e), Sunnyside (f), and Wildealsput (g). Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Table 5.6: Statistical analyses for incisors by farm habitats (*n* = 180).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.665	**1.703**	**3, 42**	**0.005**

(B) ANOVA results

	F- ratio	*p*-value
Asfc	**4.028**	**0.008**
epLsar	**3.779**	**0.012**
Smc	**3.494**	**0.017**
Tfv	1.137	0.336
$HAsfc_9$	1.304	0.275
$HAsfc_{81}$	0.302	0.824
Ssk	2.321	0.077
Sdr	**4.068**	**0.008**
S5v	2.108	0.101
Str	1.016	0.387
Sdv	**3.757**	**0.012**
Vvv	**3.806**	**0.011**
Sv	2.320	0.077
Sda	0.826	0.481

Statistically significant results, in which $p < 0.05$, are bolded.

Fisher's LSD test for *Asfc* comparisons evinced marginal significance variation between Kappies Kareeboom and Kolomela, as well as between Heuningkrantz and Grootpan, with Tukey's HSD indicating a significant difference in *Asfc* central tendency between Kappies Karee and Heuningkrantz (Table 5.6, Figure 5.4). Pairwise comparisons indicated differences in *epLsar* central tendency between Grootpan and Ekstra (Fisher's LSD $p < 0.05$) and Grootpan and Heuningkrantz (Tukey's and Fisher's both $p < 0.05$). The Heuningkrantz sample possessed a marginally higher *Smc* than either samples from Kolomela or Kappies Karee. While pairwise comparison tests showed that measures of *Sdr* at Kolomela were significantly lower than those at Kappies Karee, they were only marginally lower than those from Grootpan (Table 5.6, Figure 5.4). In addition, Fisher's test evinced higher *Sdr* measures at Kappies Kareeboom than Grootpan or Heuningkrantz. Kolomela mine incisors also had significantly lower *Sdv* measures

than those from Grootpan, Heuningkrantz, or Kappies Karee. Finally, Fisher's LSD test for *Vvv* comparisons indicated marginal significant variation in central tendency for the Grootpan and Kolomela samples and the Kappies Karee and Heuningkrantz samples, while Tukey's HSD indicated significant differences between the Kappies Karee and Kolomela samples. Table 5.8 provides microwear descriptions for each farm based on these statistically significant parameters.

Table 5.7: Pairwise comparisons for incisors by farm habitats.

Variable	Comparison	difference	Variable	Comparison	difference
Asfc	Grootpan - Kolomela	20.767	*Sdr*	**Grootpan - Kolomela**	**28.750***
	Heuningkrantz - Kolomela	-0.639		Heuningkrantz - Kolomela	22.508
	Kappies Karee - Kolomela	**32.09***		**Kappies Karee - Kolomela**	**49.778****
	Heuningkrantz - Grootpan	**-21.406***		Heuningkrantz - Grootpan	-6.242
	Kappies Karee - Grootpan	11.323		**Kappies Karee - Grootpan**	**21.028***
	Kappies Karee - Heuningkrantz	**32.729****		**Kappies Karee - Heuningkrantz**	**27.27***
epLsar	**Grootpan - Kolomela**	**-29.82***	*Sdv*	**Grootpan - Kolomela**	**47.295****
	Heuningkrantz - Kolomela	-2.788		**Heuningkrantz - Kolomela**	**41.476****
	Kappies Karee - Kolomela	-23.34		**Kappies Karee - Kolomela**	**40.611****
	Heuningkrantz - Grootpan	**27.032****		Heuningkrantz - Grootpan	-5.82
	Kappies Karee - Grootpan	6.48		Kappies Karee - Grootpan	-6.684
	Kappies Karee - Heuningkrantz	-20.552		Kappies Karee - Heuningkrantz	-0.865
Smc	Grootpan - Kolomela	18.916	*Vvv*	**Grootpan - Kolomela**	**4.504***
	Heuningkrantz - Kolomela	**36.525***		Heuningkrantz - Kolomela	-12.857
	Kappies Karee - Kolomela	9.76		**Kappies Karee - Kolomela**	**9.142****
	Heuningkrantz - Grootpan	17.609		Heuningkrantz - Grootpan	-31.482
	Kappies Karee - Grootpan	-9.155		Kappies Karee - Grootpan	-10.841
	Kappies Karee - Heuningkrantz	**-26.765***		**Kappies Karee - Heuningkrantz**	**3.029***

Statistically significant results, in which $p < 0.05$, are bolded.

*$p < 0.05$ using Fisher's LSD test only; **$p < 0.05$ using both Tukey's HSD and Fisher's LSD tests.

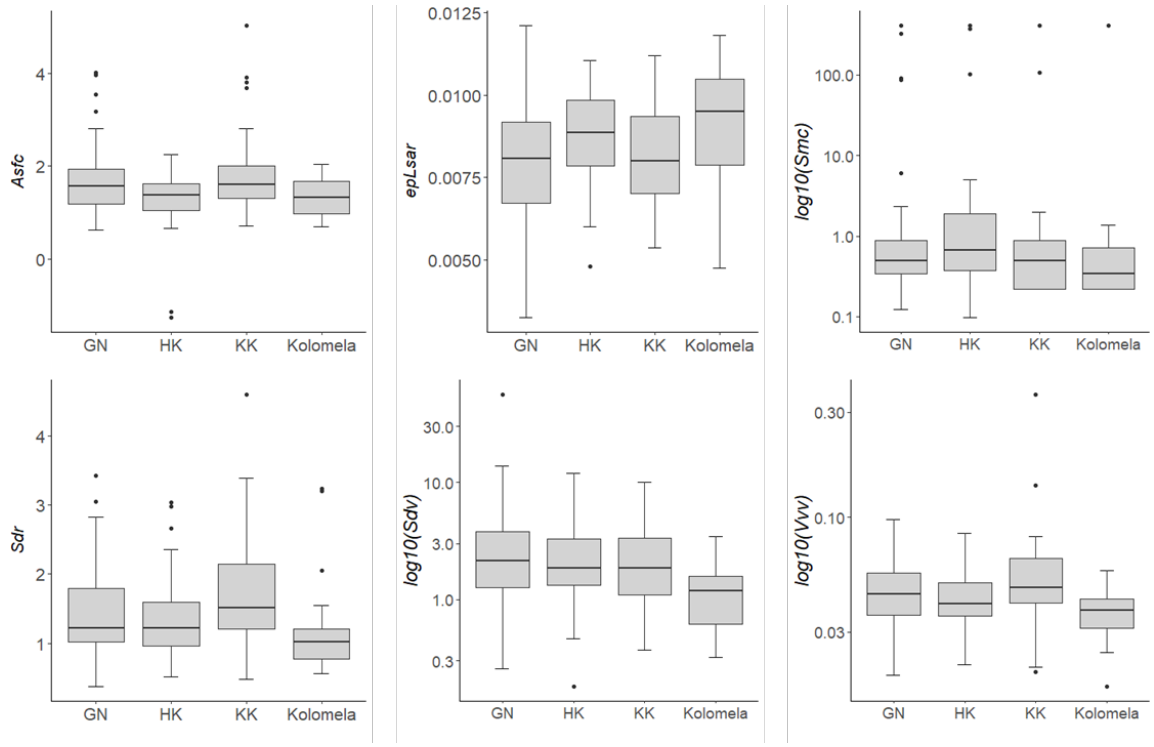

Figure 5.4: Box charts of statistically significant microwear texture parameters when analyzed by habitat: Grootpan (GN), Heuningkrantz (HK), Kappies Kareeboom (KK), and Kolomela. The y-axis for parameters *Smc*, *Sdv*, and *Vvv* is plotted in log space to better clarify the differences among the habitats. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 5.8: Incisor microwear description for habitats based on significant microwear parameters.

Habitat	Significant parameter trends	Microwear description
Kolomela mine	highest *epLsar* low *Asfc* lowest *Smc* , *Sdr* , *Sdv* , *Vvv*	anisotropic microwear features that lacks complexity, with rougher surfaces at finer scales and relatively small and shallow scratches
Grootpan	highest *Sdv* high *Vvv* mid-range *Asfc* , *Smc* , *Sdr* lowest *epLsar*	large and deep isotropic features arranged in microwear patterns that are generally not as complex as those from other sites
Heuningkrantz	highest *Smc* high *epLsar* , *Sdv* mid-range *Sdr* , *Vvv* lowest *Asfc*	relatively anisotropic microwear with larger scratches that are not very complex or deep
Kappies Kareeboom	highest *Asfc* , *Sdr* , *Vvv* high *Sdv* mid-range *Smc* low *epLsar*	most complex and isotropic microwear pattern of the four sites, with some of the largest and deepest features

Microhabitat Microwear Effects

Of the eighteen transects used in collecting the rodent specimens, only seven provided sufficient sample sizes to use in this analysis: Ekstra (on the mine property, $n = 16$), GN1 ($n = 25$) and GN2 ($n = 41$) from Grootpan, HK3 ($n = 14$) and HK7 ($n = 32$) from Heuningkrantz, and KK2 ($n = 12$) and KK3 ($n = 21$) from Kappies Kareeboom. See Table 3.4 (Chapter 3) for key environmental characteristics of each trapping transect. The descriptive statistics for each transect in which rodents were successfully collected are provided in Table 5.9, with representative photosimulations shown in Figure 5.5. MANOVA results indicated statistically significant variation in microwear texture pattern among habitats for central tendencies ($p < 0.05$; Table 5.10). Univariate analyses indicated significant variation for five microwear parameters: complexity (*Asfc*), anisotropy (*epLsar*), developed interfacial area ratio (*Sdr*), mean dale volume (*Sdv*), and pit-void volume (*Vvv*; Table 5.10).

Table 5.9: Descriptive statistics of incisor texture attributes by transect microhabitats.

	SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
Kolomela	Ekstra (*n* = 16)*						
	Mean	1.358	0.009	26.226	11442.571	0.301	0.469
	SD	0.449	0.002	102.970	3791.290	0.162	0.161
Grootpan	GN1 (*n* = 25)*						
	Mean	1.771	0.008	4.228	12446.658	0.214	0.429
	SD	0.633	0.002	17.959	3187.594	0.091	0.116
	GN2 (*n* = 41)*						
	Mean	1.593	0.008	30.848	13295.947	0.232	0.701
	SD	0.755	0.002	101.893	3118.758	0.111	1.814
Gruispan	GP2 (*n* = 4)						
	Mean	1.468	0.009	0.682	13648.872	0.305	0.557
	SD	0.530	0.001	0.666	3523.625	0.144	0.190
Heuningkrantz	HK1 (*n* = 1)						
	Mean	1.388	0.009	0.675	14275.573	0.250	0.421
	SD	n/a	n/a	n/a	n/a	n/a	n/a
	HK2 (*n* = 1)						
	Mean	1.498	0.007	0.675	13709.312	0.149	0.306
	SD	n/a	n/a	n/a	n/a	n/a	n/a
	HK3 (*n* = 14)*						
	Mean	1.402	0.008	30.494	12928.587	0.201	0.453
	SD	0.327	0.001	109.916	2647.807	0.116	0.227
	HK4 (*n* = 1)						
	Mean	1.126	0.009	0.496	13842.841	0.287	0.417
	SD	n/a	n/a	n/a	n/a	n/a	n/a
	HK5 (*n* = 5)						
	Mean	1.482	0.009	84.376	11301.484	0.310	0.621
	SD	0.101	0.001	183.360	3698.286	0.173	0.368
	HK7 (*n* = 32)*						
	Mean	1.241	0.009	105.338	13250.961	0.250	0.451
	SD	0.763	0.001	178.066	3893.807	0.099	0.145
	HK9 (*n* = 6)						
	Mean	1.039	0.009	69.450	14025.758	0.262	0.461
	SD	0.261	0.001	167.992	2902.934	0.950	0.144
	HK10 (*n* = 2)						
	Mean	1.756	0.009	0.282	9457.136	0.244	0.480
	SD	0.340	0.001	0.088	574.369	0.119	0.154
Kappies Kareeboom	KK1 (*n* = 3)						
	Mean	2.079	0.008	137.794	15548.407	0.256	0.442
	SD	1.409	0.001	237.783	3400.579	0.107	0.182
	KK2 (*n* = 12)*						
	Mean	1.777	0.008	0.480	12395.165	0.183	0.356
	SD	1.084	0.002	0.283	2860.009	0.070	0.083
	KK3 (*n* = 21)*						
	Mean	1.889	0.009	5.627	13712.348	0.257	0.511
	SD	0.811	0.002	23.162	2043.249	0.115	0.220

Table 5.9 (Cont.)

	SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$		
Sunnyside	Stofdraai (n = 7)								
	Mean	2.228	0.008	0.386	13387.620	0.472	0.635		
	SD	0.863	0.001	0.236	3399.274	0.273	0.325		
Wildealsput	WAP2 (n = 3)								
	Mean	2.075	0.009	0.303	14041.025	0.201	0.365		
	SD	0.606	0.001	0.072	801.332	0.132	0.101		
	WAP3 (n = 4)								
	Mean	1.670	0.009	12.049	15940.746	0.137	0.284		
	SD	0.377	0.003	22.867	3271.125	0.019	0.014		
	ISO:	***Ssk***	***Sdr***	***S5v***	***Str***	***Sdv***	***Vvv***	***Sv***	***Sda***
Kolomela	Ekstra (n = 16)*								
	Mean	0.098	1.264	0.875	0.338	1.295	0.037	1.508	175.874
	SD	0.223	0.851	0.340	0.146	0.794	0.011	1.077	113.032
Grootpan	GN1 (n = 25)*								
	Mean	-0.026	1.502	0.933	0.275	2.537	0.048	1.637	211.036
	SD	0.375	0.518	0.317	0.179	1.540	0.016	0.711	136.222
	GN2 (n = 41)*								
	Mean	-0.063	1.404	0.841	0.296	4.301	0.046	1.598	265.587
	SD	0.419	0.695	0.250	0.145	8.800	0.015	0.673	269.379
Gruispan	GP2 (n = 4)								
	Mean	-0.200	1.228	0.957	0.251	3.123	0.040	1.604	255.314
	SD	0.577	0.595	0.311	0.141	1.472	0.012	0.587	96.331
Heuningkrantz	HK1 (n = 1)								
	Mean	-0.054	1.211	0.762	0.304	0.715	0.082	1.913	38.490
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	HK2 (n = 1)								
	Mean	0.787	1.136	0.729	0.622	9.534	0.029	1.026	500.593
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	HK3 (n = 14)*								
	Mean	0.045	1.575	0.858	0.290	3.365	0.050	1.501	255.963
	SD	0.352	0.780	0.260	0.105	2.967	0.016	0.527	91.459
	HK4 (n = 1)								
	Mean	0.587	0.939	0.804	0.166	3.705	0.036	1.136	247.780
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	HK5 (n = 5)								
	Mean	-0.231	1.606	0.950	0.302	2.385	0.061	1.716	213.219
	SD	0.532	0.201	0.065	0.118	1.410	0.022	0.359	125.183
	HK7 (n = 32)*								
	Mean	0.060	1.337	0.716	0.258	2.083	0.041	1.411	161.224
	SD	0.259	0.442	0.208	0.142	1.673	0.011	0.606	98.917
	HK9 (n = 6)								
	Mean	0.160	0.871	0.679	0.251	3.834	0.039	1.258	302.263
	SD	0.315	0.245	0.145	0.107	2.835	0.012	0.490	147.804
	HK10 (n = 2)								
	Mean	0.038	1.020	0.838	0.292	1.787	0.041	1.247	248.489
	SD	0.332	0.078	0.197	0.168	1.840	0.007	0.028	202.726

Table 5.9 (Cont.)

	ISO:	*Ssk*	*Sdr*	*S5v*	*Str*	*Sdv*	*Vvv*	*Sv*	*Sda*
Kappies Kareeboom	KK1 (n = 3)								
	Mean	-0.138	2.052	0.948	0.189	4.786	0.069	1.606	134.106
	SD	0.166	1.352	0.036	0.021	4.622	0.021	0.308	14.106
	KK2 (n = 12)*								
	Mean	-0.070	1.731	0.871	0.325	2.127	0.055	0.166	180.614
	SD	0.345	1.141	0.366	0.188	1.443	0.031	0.707	72.669
	KK3 (n = 21)*								
	Mean	-0.111	1.793	0.918	0.312	2.187	0.063	1.887	193.142
	SD	0.360	0.673	0.247	0.138	1.463	0.069	1.461	102.417
Sunnyside	Stofdraai (n = 7)								
	Mean	-0.053	1.500	0.849	0.304	3.217	0.045	1.501	240.665
	SD	0.434	0.504	0.176	0.199	4.807	0.014	0.369	196.312
Wildealsput	WAP2 (n = 3)								
	Mean	-0.321	1.694	0.955	0.251	2.635	0.056	1.820	235.751
	SD	0.294	0.690	0.391	0.133	2.255	0.010	0.416	246.079
	WAP3 (n = 4)								
	Mean	0.134	1.799	0.925	0.432	3.800	0.056	1.790	228.380
	SD	0.800	0.954	0.089	0.213	2.266	0.013	0.464	143.911

*denotes groups used in statistical analyses

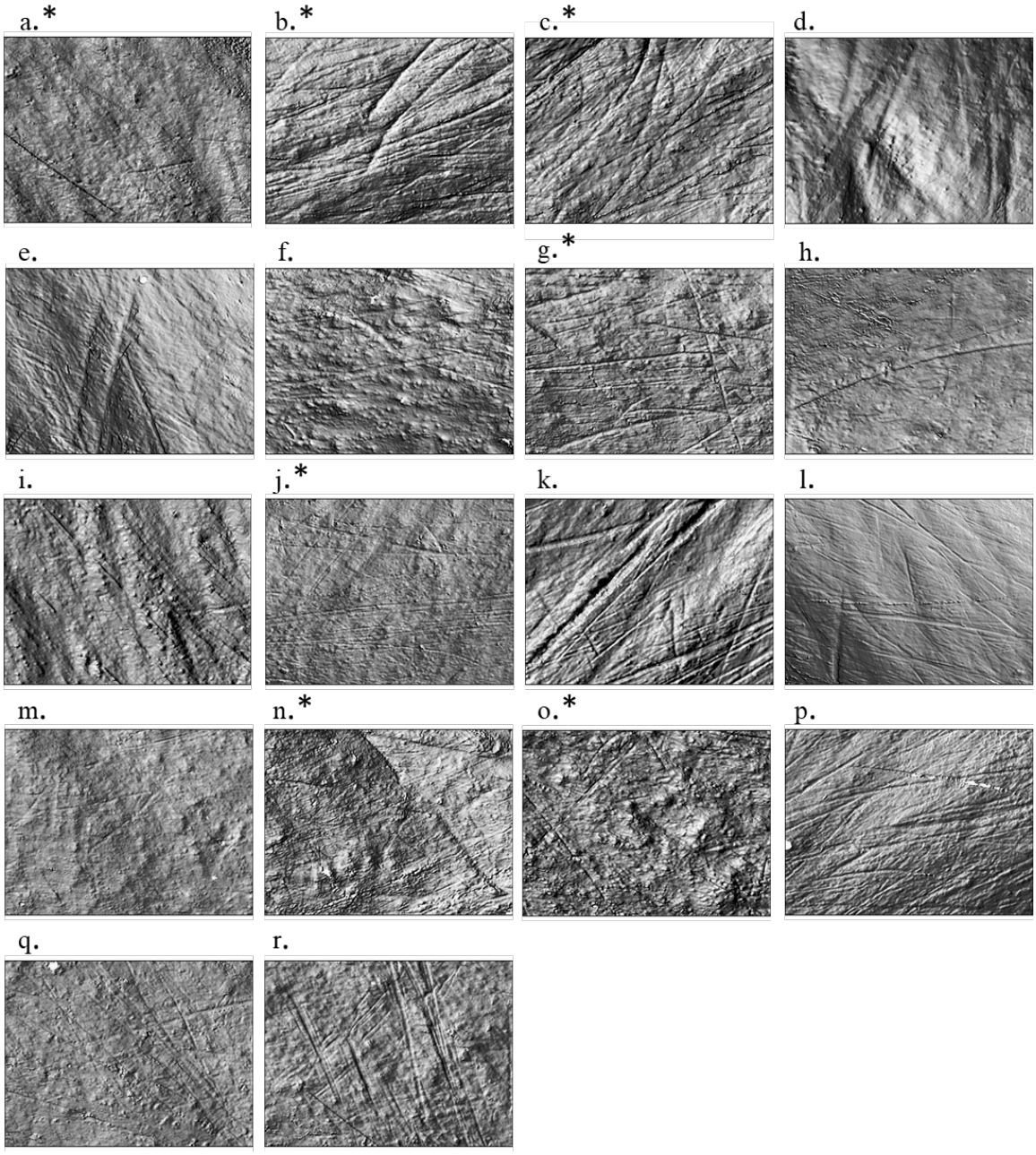

Figure 5.5: Representative incisor microwear photosimulations for each transect within each of the seven habitats: Kolomela, transect Ekstra (a); Grootpan, transects GN1 (b) and GN2 (c); Gruispan, transect GP2 (d); Heuningkrantz, transects HK1 (e), HK2 (f), HK3 (g), HK4 (h), HK5 (i), HK7 (j), HK9 (k), and HK10 (l); Kappies Kareeboom, transects KK1 (m), KK2 (n), and KK3 (o); Sunnyside, transect Stofdraai (p); and Wildealsput, transects WAP2 (q) and WAP3 (r). Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Table 5.10: Statistical analyses for incisors by transect microhabitats (*n* = 161).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.457	**1.424**	**6, 84**	**0.010**

(B) ANOVA results

	F- ratio	*p* -value
Asfc	**2.237**	**0.042**
epLsar	**3.658**	**0.002**
Smc	1.479	0.189
Tfv	1.274	0.273
$HAsfc_9$	2.030	0.060
$HAsfc_{81}$	1.472	0.191
Ssk	0.789	0.580
Sdr	**2.370**	**0.032**
S5v	1.673	0.131
Str	1.234	0.292
Sdv	**2.486**	**0.025**
Vvv	**2.457**	**0.027**
Sv	1.119	0.354
Sda	1.897	0.085

Statistically significant results, in which $p < 0.05$, are bolded.

Fisher's LSD post-hoc comparisons separated the transects with the two highest measures of *Asfc*, GN1 and KK3, from those with the two lowest measures, Ekstra and HK7 (Table 5.11, Figure 5.4). *epLsar* measures were significantly higher for transect HK7 than either KK2 or the two transects from Grootpan, GN1 and GN2 ($p < 0.05$ by both Tukey's and Fisher's tests). However, *epLsar* central tendency was only marginally higher in the Ekstra sample than that of the GN1 or KK2 samples ($p < 0.005$ by Fisher's test). Pairwise comparisons also indicated significant variation between Ekstra and transects GN1 and KK2 for the parameter *Sdr*, with the measure for the Ekstra sample marginally lower than those of the transects. The KK3 sample also had a marginally greater *Sdr* than GN2 or HK7. However, Tukey's HSD indicated that the central tendency for *Sdr* was significantly higher at KK3 than at Ekstra (Table 5.11, Figure 5.4). For parameter *Sdv*, the post-hoc comparisons only separated Ekstra from other transects,

specifically GN1, GN2, HK3, and KK3. Finally, only Fisher's LSD evinced variation between samples for *Vvv* central tendency, indicating that samples from the two transects from Kappies Karee, KK2 and KK3, as well as transects GN1 and HK3 were marginally higher than the sample from Ekstra. Similarly, HK3, KK2, and KK3 had marginally greater *Vvv* measures than HK7. A summary of microwear descriptions for each transect, based on these statistically significant parameters, can be found in Table 5.12.

Table 5.11: Pairwise comparisons for incisors by transect microhabitats.

Variable	Comparison	difference	Variable	Comparison	difference	Variable	Comparison	difference
Asfc	**GN1-Ekstra**	**32.055***	*epLsar*	KK3-GN2	13.079	*Sdv*	HK3-GN1	9.694
	GN2-Ekstra	11.424		HK7-HK3	40.714		HK7-GN1	-14.801
	HK3-Ekstra	4.518		KK2-HK3	-10.369		KK2-GN1	-14.353
	HK7-Ekstra	-1.125		KK3-HK3	16.976		KK3-GN1	-1.663
	KK2-Ekstra	21.542		**KK2-HK7**	**-51.083****		HK3-GN2	5.605
	KK3-Ekstra	**34.851***		KK3-HK7	-23.738		HK7-GN2	-18.891
	GN2-GN1	-20.631		KK3-KK2	27.345		KK2-GN2	-18.443
	HK3-GN1	-27.537	*Sdr*	**GN1-Ekstra**	**37.718***		KK3-GN2	-5.753
	HK7-GN1	**-33.180***		GN2-Ekstra	19.828		HK7-HK3	-24.496
	KK2-GN1	-10.513		HK3-Ekstra	30.152		KK2-HK3	-24.048
	KK3-GN1	2.796		HK7-Ekstra	22.094		KK3-HK3	-11.357
	HK3-GN2	-6.906		**KK2-Ekstra**	**37.271***		KK2-HK7	0.448
	HK7-GN2	-12.549		**KK3-Ekstra**	**52.676****		KK3-HK7	13.138
	KK2-GN2	10.118		GN2-GN1	-17.890		KK3-KK2	12.690
	KK3-GN2	23.427		HK3-GN1	-7.566	*Vvv*	**GN1-Ekstra**	**36.125***
	HK7-HK3	-5.643		HK7-GN1	-15.624		GN2-Ekstra	27.466
	KK2-HK3	17.024		KK2-GN1	-0.447		**HK3-Ekstra**	**42.054***
	KK3-HK3	30.333		KK3-GN1	14.958		HK7-Ekstra	11.500
	KK2-HK7	22.667		HK3-GN2	10.324		**KK2-Ekstra**	**43.375***
	KK3-HK7	**35.976***		HK7-GN2	2.266		**KK3-Ekstra**	**42.982***
	KK3-KK2	13.310		KK2-GN2	17.443		GN2-GN1	-8.659
epLsar	**GN1-Ekstra**	**-31.390***		**KK3-GN2**	**32.848***		HK3-GN1	5.929
	GN2-Ekstra	-24.067		HK7-HK3	-8.058		HK7-GN1	-24.625
	HK3-Ekstra	-27.964		KK2-HK3	7.119		KK2-GN1	7.250
	HK7-Ekstra	12.750		KK3-HK3	22.524		KK3-GN1	6.857
	KK2-Ekstra	**-38.333***		KK2-HK7	15.177		HK3-GN2	14.587
	KK3-Ekstra	-10.988		**KK3-HK7**	**30.582***		HK7-GN2	-15.966
	GN2-GN1	7.323		KK3-KK2	15.405		KK2-GN2	15.909
	HK3-GN1	3.426	*Sdv*	**GN1-Ekstra**	**42.646***		KK3-GN2	15.516
	HK7-GN1	**44.140****		**GN2-Ekstra**	**46.735****		**HK7-HK3**	**-30.554***
	KK2-GN1	-6.943		**HK3-Ekstra**	**52.339***		KK2-HK3	1.321
	KK3-GN1	20.402		HK7-Ekstra	27.844		KK3-HK3	0.929
	HK3-GN2	-3.897		KK2-Ekstra	28.292		**KK2-HK7**	**31.875***
	HK7-GN2	**36.817****		**KK3-Ekstra**	**40.982***		**KK3-HK7**	**31.482***
	KK2-GN2	-14.266		GN2-GN1	4.090		KK3-KK2	-0.393

Statistically significant results, in which $p < 0.05$, are bolded.

*$p < 0.05$ using Fisher's LSD test only; **$p < 0.05$ using both Tukey's HSD and Fisher's LSD tests.

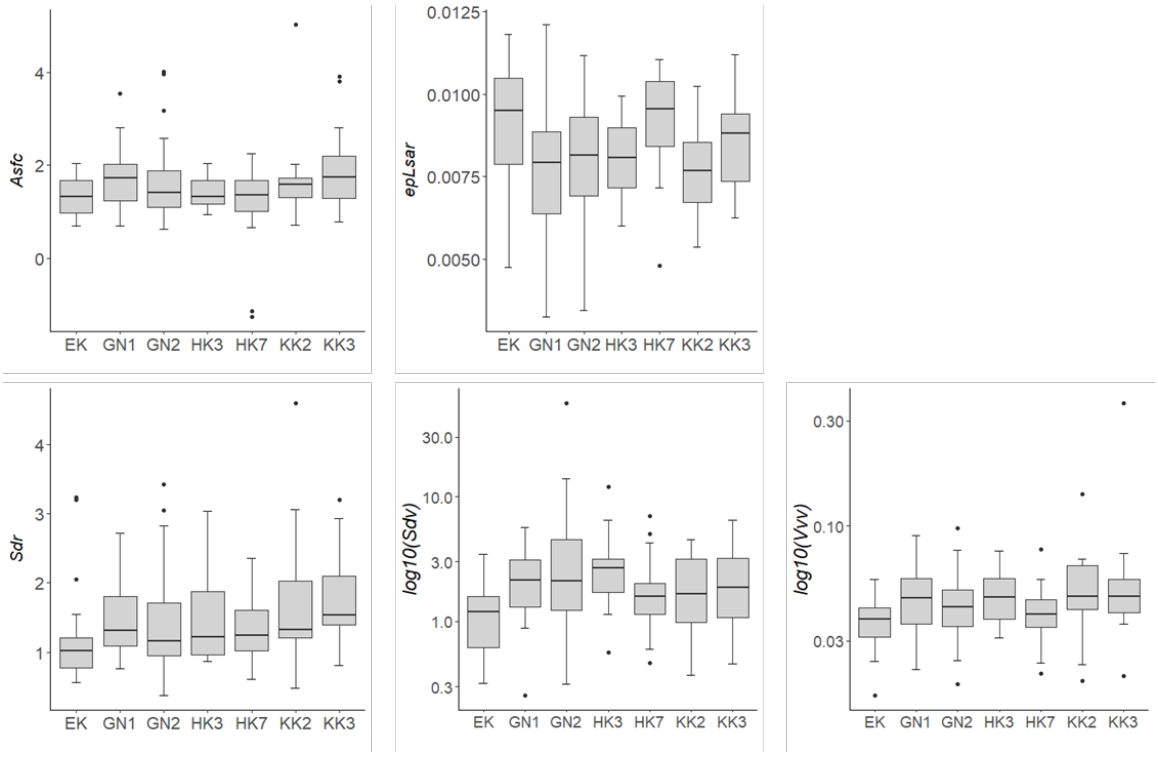

Figure 5.6: Box charts of statistically significant microwear texture variables when analyzed by transect: transect Ekstra (EK) is located within the Kolomela mine, transects GN1 and GN2 in farm Grootpan, transects HK3 and HK7 in farm Heuningkrantz, and transects KK2 and KK3 in farm Kappies Kareeboom. The y-axis for parameters *Sdv* and *Vvv* is plotted in log space to better clarify the differences among the habitats. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 5.12: Incisor microwear description for microhabitats based on significant microwear parameters.

Microhabitat	Significant parameter trends	Microwear description
Ekstra	high *epLsar* low *Asfc* lowest *Sdr* , *Sdv* , *Vvv*	anisotropic microwear features that lacks complexity, with relatively small and shallow scratches
GN1	high *Asfc* , *Sdr* , *Sdv* , *Vvv* low *epLsar*	complex, isotropic microwear texture with large and deep features
GN2	high *Sdv* , *Vvv* low *Asfc* , *epLsar* , *Sdr*	microwear comprised of large, deep features but is generally not as complex or anisotropic as microwear from the other transects
HK3	highest *Sdv* high *Vvv* mid-range *Sdr* low *Asfc, epLsar*	very large and generally deep microwear features that are generally not as complex or anisotropic as microwear from other transects
HK7	highest *epLsar* mid-range *Sdv* low *Sdr* , *Vvv* lowest *Asfc*	microwear textures is the most anistoropic of the samples, with low complexity and smaller, more shallow scratches
KK2	highest *Vvv* high *Asfc* , *Sdr* mid-range *Sdv* lowest *epLsar*	very deep microwear features that are relatively large, with a texture pattern that is complex and isotropic
KK3	highest *Asfc* , *Sdr* high Sdv, Vvv mid-range *epLsar*	most complex microwear pattern among the transect samples, with large and deep features that are somewhat isotropic

Dietary Microwear Effects

Stomach content analysis initially classified species into 13 dietary categories with a primary and secondary component. Rather than follow the traditional omnivore, herbivore, granivore, carnivore scheme, each diet category depended on the food item or items of highest concentration within the stomach cavity. This choice was made to potentially address differences in food physical properties that may affect microwear formation (see Chapter 3). Table 5.13 provides descriptive statistics for each resulting dietary category with representative photosimulations in Figure 5.7. Only three of these groups were considered to have a sufficient sample size for analysis: grass seed-grass (GSGR, n = 21), grass seed-curculionid (GSCU, n =

34), and grass seed-grass seed (GSGS, n = 95). The multivariate test for central tendencies did not report any significance in variation (p = 0.676; Table 5.14).

Table 5.13: Descriptive statistics of incisor texture parameters by diet.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
annelid - annelid (n = 1)						
Mean	1.736	0.009	0.496	14581.93	0.188	0.423
SD	n/a	n/a	n/a	n/a	n/a	n/a
curculionid - grass seed (n = 2)						
Mean	1.653	0.010	3.175	13242.32	0.248	0.733
SD	0.148	0.000	2.543	1481.468	0.048	0.515
feather - grass seed (n = 1)						
Mean	1.335	0.008	0.675	13024.77	0.158	0.300
SD	n/a	n/a	n/a	n/a	n/a	n/a
grass - grass seed (n = 2)						
Mean	1.281	0.008	0.282	14444.64	0.196	0.338
SD	0.060	0.002	0.088	1128.393	0.001	0.048
grass seed - annelid (n = 2)						
Mean	1.757	0.005	0.420	12546.70	0.374	0.507
SD	0.895	0.002	0.107	1633.065	0.273	0.334
grass seed - curculionid (n = 34)*						
Mean	1.544	0.009	49.228	13236.72	0.238	0.431
SD	0.902	0.001	128.241	3032.495	0.112	0.170
grass seed - dicot (n = 4)						
Mean	1.351	0.009	0.665	14169.52	0.445	0.638
SD	0.381	0.001	0.312	3145.682	0.361	0.439
grass seed - dicot seed (n = 7)						
Mean	1.351	0.009	59.450	12293.71	0.261	0.482
SD	0.361	0.001	155.620	1782.449	0.144	0.129
grass seed - flesh (n = 5)						
Mean	1.925	0.008	9.576	11500.68	0.185	0.365
SD	0.645	0.002	20.557	6298.833	0.084	0.087
grass seed - grass (n = 21)*						
Mean	1.456	0.009	42.861	12596.63	0.288	0.470
SD	0.543	0.001	118.156	3087.023	0.151	0.169
grass seed - grass seed (n = 95)*						
Mean	1.626	0.008	32.991	12855.40	0.234	0.450
SD	0.746	0.002	108.458	3373.676	0.104	0.159
grass seed - hair (n = 4)						
Mean	1.843	0.008	0.258	15280.38	0.460	3.348
SD	0.614	0.002	0.107	1930.100	0.231	5.780

Table 5.13 (Cont.)

ISO:	*Ssk*	*Sdr*	*S5v*	*Str*	*Sdv*	*Vvv*	*Sv*	*Sda*
annelid - annelid (*n* = 1)								
Mean	0.291	1.229	0.558	0.567	1.933	0.029	0.831	155.134
SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
curculionid - grass seed (n = 2)								
Mean	-0.358	2.028	1.042	0.157	3.010	0.066	1.628	380.429
SD	0.523	1.419	0.055	0.017	0.615	0.016	0.445	13.377
feather - grass seed (*n* = 1)								
Mean	0.453	1.226	0.715	0.210	3.012	0.042	1.321	324.374
SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
grass - grass seed (*n* = 2)								
Mean	-0.186	1.271	0.673	0.284	2.029	0.040	1.684	210.913
SD	0.551	0.628	0.117	0.185	0.184	0.006	0.961	97.958
grass seed - annelid (*n* = 2)								
Mean	-0.227	1.397	0.852	0.165	2.165	0.049	1.665	198.917
SD	0.105	0.558	0.036	0.017	0.908	0.003	0.086	88.165
grass seed - curculionid (n = 34)*								
Mean	-0.035	1.427	0.804	0.271	2.449	0.045	1.442	211.616
SD	0.361	0.512	0.239	0.140	2.308	0.015	0.499	115.855
grass seed - dicot (*n* = 4)								
Mean	0.091	1.268	0.858	0.355	6.221	0.049	1.450	360.676
SD	0.407	0.496	0.316	0.249	5.313	0.010	0.387	198.987
grass seed - dicot seed (*n* = 7)								
Mean	0.178	1.165	0.781	0.300	2.765	0.046	1.405	182.709
SD	0.359	0.356	0.307	0.101	2.002	0.017	0.559	116.734
grass seed - flesh (*n* = 5)								
Mean	-0.104	2.007	0.867	0.406	1.795	0.049	1.466	173.466
SD	0.416	0.986	0.161	0.218	1.446	0.014	0.386	77.918
grass seed - grass (*n* = 21)*								
Mean	0.006	1.282	0.828	0.304	2.227	0.045	1.454	186.242
SD	0.335	0.565	0.270	0.171	2.157	0.017	0.457	126.726
grass seed - grass seed (*n* = 95)*								
Mean	-0.024	1.515	0.883	0.297	3.266	0.050	1.694	218.319
SD	0.399	0.709	0.275	0.150	6.026	0.036	0.970	199.333
grass seed - hair (*n* = 4)								
Mean	-0.198	1.414	0.748	0.323	1.889	0.043	1.504	195.100
SD	0.160	0.524	0.114	0.188	2.047	0.012	0.620	158.440

*denotes groups used in statistical analyses

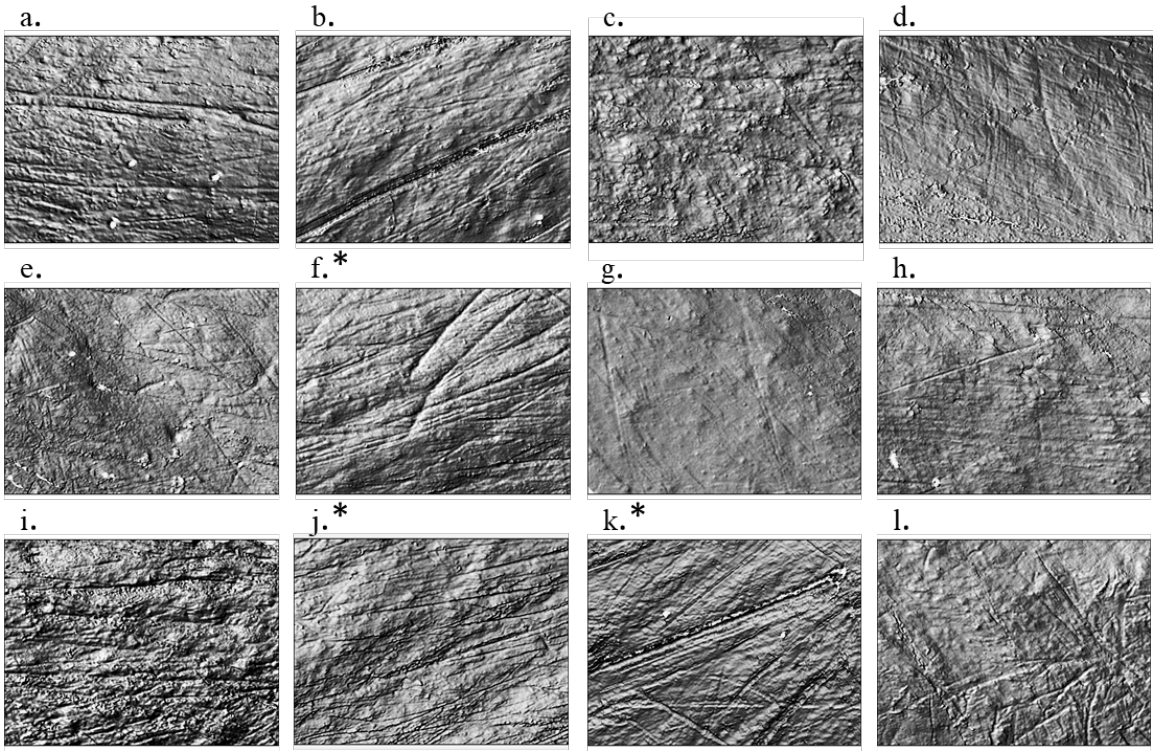

Figure 5.7: Representative incisor microwear photosimulations for each diet based upon stomach content analysis: annelid-annelid (a), curculionid-grass seed (b), feather-grass seed(c), grass-grass seed (d), grass seed-annelid (e), grass seed-curculionid (f), grass seed-dicot (g), grass seed-dicot seed (h), grass seed-flesh (i), grass seed-grass (j), grass seed-grass seed (k), and grass seed-hair (l). Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Table 5.14: Statistical analyses for incisors by diet (*n* = 150).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.842	0.859	2, 28	0.675

Statistically significant results, in which $p < 0.05$, are bolded.

Burrowing Behavior Microwear Effects

Rodents were divided into two behavioral categories based on whether the species constructs underground burrows. *D. melatonis, G. leucogaster, G. paeba, Mu. minutoides,* and *R. bechuanae* formed the burrowing group (*n* = 142) while *Ma. coucha* and *Mi. namaquensis*

comprised the group that did not excavate burrows (n = 56). Table 5.15 provides descriptive statistics for the two categories. Representative photosimulations are provided in Figure 5.8. The MANOVA comparison between the two groups indicated statistically significant variation for central tendencies ($p < 0.05$; Tables 5.8). Univariate analyses reported six texture parameters with statistically significant variation: complexity (*Asfc*), anisotropy (*epLsar*), heterogeneity ($Hasfc_9$), five-point pit height (*S5v*), maximum pit height (*Sv*), and pit void volume (*Vvv*). Specifically, the incisors of burrow-excavating rodents possessed significantly higher central tendencies of *Asfc*, *S5v*, *Sv*, and *Vvv* values than the group of rodents that do not excavate burrows, as well as lower measures of *epLsar* and $Hasfc_9$ (Table 5.8, Figure 5.9). Microwear descriptions based on these statistically significant parameters can be found in Table 5.17 for both groups.

Table 5.15: Descriptive statistics of incisor texture parameters by burrowing behavior.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_9$	***HAsfc*** $_{81}$		
burrower (n = 142)*								
Mean	1.664	0.008	21.969	12878.25	0.242	0.522		
SD	0.710	0.002	87.372	3128.523	0.138	0.986		
non-burower (n = 56)*								
Mean	1.377	0.009	69.661	13475.84	0.259	0.478		
SD	0.769	0.001	150.617	3369.690	0.100	0.177		
ISO:	***Ssk***	***Sdr***	***S5v***	***Str***	***Sdv***	***Vvv***	***Sv***	***Sda***
burrower (n = 142)*								
Mean	-0.034	1.506	0.885	0.303	3.188	0.048	1.610	231.731
SD	0.395	0.730	0.270	0.156	5.114	0.018	0.667	178.362
non-burower (n = 56)*								
Mean	0.035	1.377	0.760	0.268	2.096	0.048	1.513	176.772
SD	0.307	0.586	0.230	0.133	1.782	0.044	1.028	114.362

*denotes groups used in statistical analyses

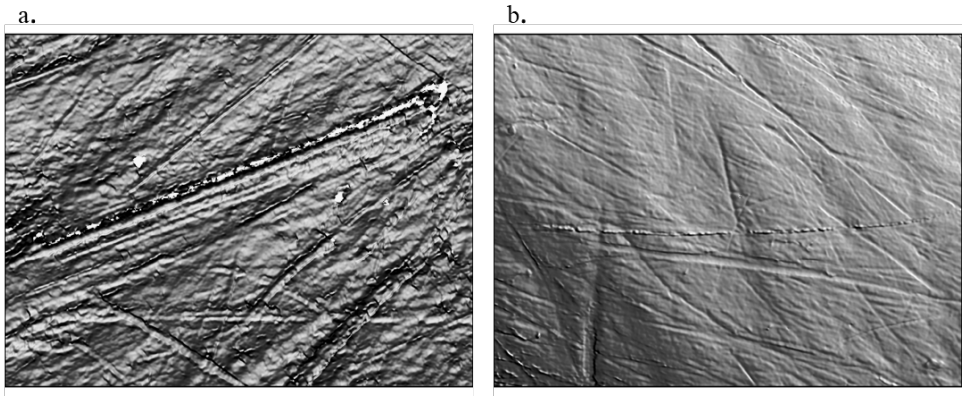

Figure 5.8: Representative microwear photosimulations for species that excavate underground burrows (a) and species that do not (b). Each photosimulation measures an area of 138 µm x 102 µm.

Table 5.16: Statistical analyses for incisors by burrowing behavior (*n* = 198).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.837	**2.542**	**1, 14**	**0.005**

(B) ANOVA results

	F- ratio	*p* -value
Asfc	**5.195**	**0.024**
epLsar	**19.216**	**0.000**
Smc	0.170	0.680
Tfv	1.695	0.194
HAsfc $_{9}$	**4.070**	**0.045**
HAsfc $_{81}$	2.589	0.109
Ssk	1.334	0.250
Sdr	1.142	0.287
S5v	**7.652**	**0.006**
Str	2.030	0.156
Sdv	3.343	0.069
Vvv	**5.156**	**0.024**
Sv	**6.136**	**0.014**
Sda	3.801	0.053

Statistically significant results, in which $p < 0.05$, are bolded.

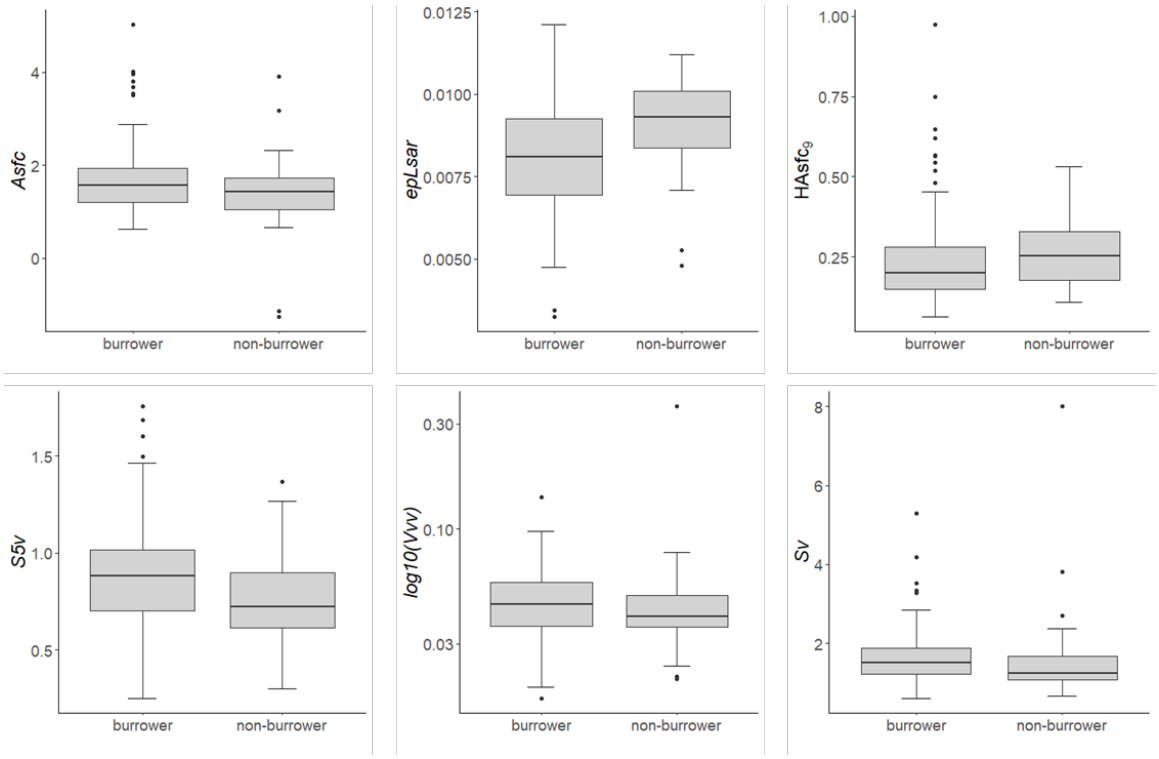

Figure 5.9: Box charts of statistically significant microwear texture variables when analyzed by burrowing behavior. The y-axis for parameter *Vvv* is plotted in log space to better clarify the differences among the habitats. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 5.17: Incisor microwear description using significant microwear parameters for groups based burrowing behavior.

Burrowing behavior	Significant parameter trends	Microwear description
excavates burrows	highest *Asfc* , *S5v* , *Vvv* , *Sv* lowest *epLsar* , *HAsfc* $_9$	Complex, isotropic microwear pattern that is more uniform on across the surface, with deep and large features
does not excavate burrows	highest *epLsar* , *HAsfc* $_9$ lowest *Asfc* , *S5v* , *Vvv* , *Sv*	Anisotropic microwear pattern that is less uniform across the surface, with smaller and shallower features

Soil Microwear Effects

Incisors were divided into soil types based upon Avenant and du Plessis's transect notes: loam (n =40), rocky (n = 40), sand (n = 38), and mixtures of clay-loam (n = 76) and clay-loam-sand (n = 4; Avenant and du Plessis 2018). Descriptive statistics are provided in Table 5.20 for

all categories, with photosimulations of microwear presented in Figure 5.10. Due to the small sample size, clay-loam-sand specimens were excluded from analysis. MANOVA analysis of four other groups resulted in statistically significant differences for central tendencies of microwear parameters ($p < 0.001$; Table 5.19). ANOVAs indicated significant variation for six microwear parameters: complexity (*Asfc*), anisotropy (*epLsar*), developed interfacial area ratio (*Sdr*), five-point pit height (*S5v*), pit void volume (*Vvv*), and maximum pit height (*Sv;* Table 5.19).

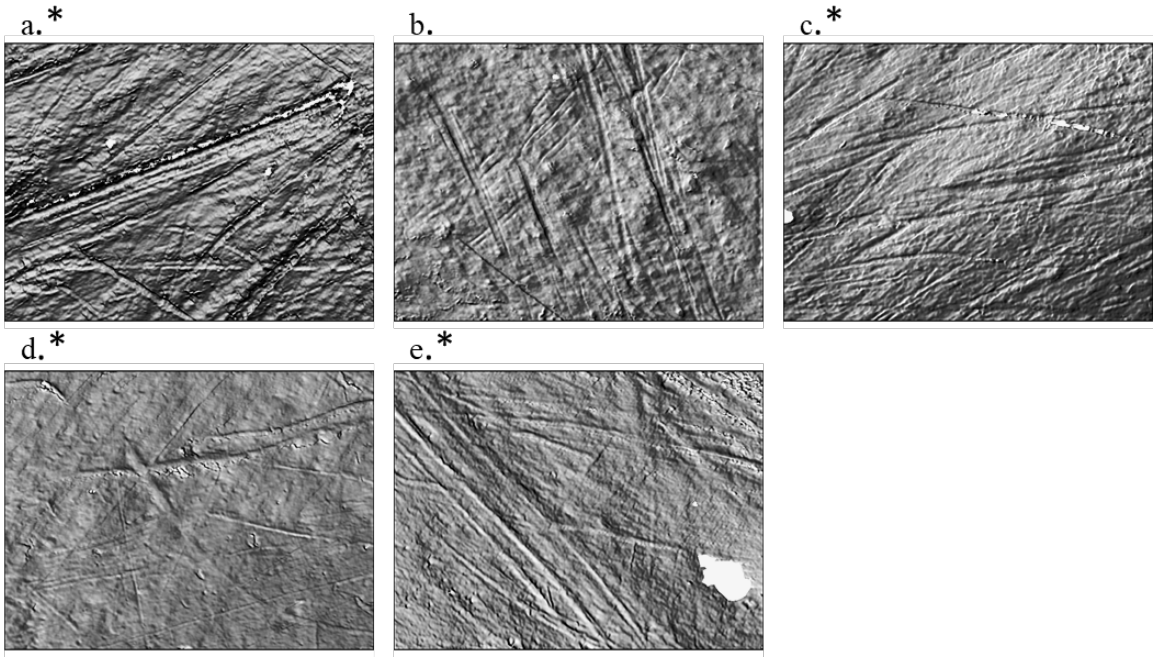

Figure 5.10: Representative microwear photosimulations for the soils found at the different habitats: clay-loam (a), clay-loam-sand (b), loam (c), rocky (d), and sand (e). Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Table 5.18: Descriptive statistics of incisor texture parameters by soil type.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$		
clay-loam (n = 76)*								
Mean	1.683	0.008	23.520	13153.47	0.230	0.581		
SD	0.727	0.002	88.732	3116.533	0.106	1.334		
clay-loam-sand (n = 4)								
Mean	1.670	0.009	12.049	15940.75	0.137	0.284		
SD	0.377	0.003	22.867	3271.125	0.019	0.014		
loam (n = 40)*								
Mean	1.915	0.008	3.165	13260.37	0.273	0.486		
SD	0.898	0.002	16.793	2563.002	0.171	0.229		
rocky (n = 40)*								
Mean	1.236	0.009	94.702	13177.49	0.251	0.454		
SD	0.703	0.001	171.667	3737.032	0.097	0.141		
sandy (n = 38)*								
Mean	1.389	0.008	33.428	12168.86	0.260	0.476		
SD	0.357	0.002	112.436	3252.253	0.146	0.217		
ISO:	***Ssk***	***Sdr***	***S5v***	***Str***	***Sdv***	***Vvv***	***Sv***	***Sda***
clay-loam (n = 76)*								
Mean	-0.072	1.464	0.886	0.281	3.603	0.048	1.622	240.403
SD	0.399	0.665	0.275	0.153	6.568	0.016	0.654	217.682
clay-loam-sand (n = 4)								
Mean	0.134	1.799	0.925	0.432	3.799	0.056	1.790	228.380
SD	0.800	0.954	0.089	0.213	2.266	0.013	0.464	143.911
loam (n = 40)*								
Mean	-0.088	1.722	0.891	0.314	2.358	0.058	1.751	197.940
SD	0.360	0.807	0.274	0.161	2.362	0.053	1.132	115.658
rocky (n = 40)*								
Mean	0.073	1.251	0.716	0.259	2.337	0.041	1.380	187.398
SD	0.265	0.441	0.197	0.135	1.944	0.011	0.571	120.496
sandy (n = 38)*								
Mean	0.070	1.405	0.868	0.318	2.468	0.046	1.516	217.222
SD	0.349	0.748	0.273	0.133	2.459	0.018	0.784	118.908

*denotes groups used in statistical analyses

Table 5.19: Statistical analyses for incisors by soil type (*n* = 194).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.657	**1.908**	**3, 42**	**0.001**

(B) ANOVA results

	F- ratio	*p* -value
Asfc	**5.617**	**0.001**
epLsar	**5.890**	**0.001**
Smc	2.452	0.065
Tfv	1.022	0.384
$HAsfc_9$	0.788	0.502
$HAsfc_{81}$	0.252	0.860
Ssk	2.504	0.061
Sdr	**3.247**	**0.024**
S5v	**3.986**	**0.009**
Str	2.349	0.074
Sdv	1.379	0.251
Vvv	**2.935**	**0.035**
Sv	**2.875**	**0.037**
Sda	0.664	0.575

Statistically significant results, in which $p < 0.05$, are bolded.

Post-hoc comparison tests for *Asfc* central tendency evinced marginal significance variation between incisors from areas of loam to those from areas of rocky soils or sand, with both Tukey's HSD and Fisher's LSD resulting in $p < 0.05$ (Table 5.20; Figure 5.11). In addition, these tests indicated that incisors from clay-loam areas had a significantly higher measure of *Asfc* than those from rocky soils. The rocky soil group also possessed significantly higher *epLsar* central tendency than either the clay-loam or loam groups, and marginally higher *epLsar* central tendency than the sand incisors (Fisher's LSD $p < 0.05$). In contrast, incisors from rocky soils were significantly lower in *S5v* value than both clay-loam and loam incisors, and marginally lower in *S5v* than incisors from sand (Table 5.20; Figure 5.11). While pairwise comparison tests showed that measures of *Sdr* for loam areas were significantly higher than at rocky areas, they were only marginally lower than those from sand. Finally, Fisher's LSD tests for parameters *Vvv* and *Sv* indicated marginally significant variation in central tendencies between the rocky and

clay-loam samples, while Tukey's HSD indicated significant differences between the rocky and loam samples. Table 5.21 provides microwear descriptions for each type of soil based on these statistically significant parameters.

Table 5.20: Pairwise comparisons for incisors by soil types.

Variable	Comparison	difference	Variable	Comparison	difference
Asfc	loam - clay/loam	16.232	*S5v*	loam - clay/loam	3.017
	rocky - clay/loam	**-28.218****		**rocky - clay/loam**	**-33.008****
	sand - clay/loam	-19.895		sand - clay/loam	-1.145
	rocky - loam	**-44.450****		**rocky - loam**	**-36.025****
	sand - loam	**-36.126****		sand - loam	-4.162
	sand - rocky	8.324		**sand - rocky**	**31.863***
epLsar	loam - clay/loam	-0.204	*Vvv*	loam - clay/loam	9.593
	rocky - clay/loam	**41.621****		**rocky - clay/loam**	**-25.232***
	sand - clay/loam	12.158		sand - clay/loam	-7.184
	rocky - loam	**41.825****		**rocky - loam**	**-34.825****
	sand - loam	12.362		sand - loam	-16.778
	sand - rocky	**-29.463***		sand - rocky	18.047
Sdr	loam - clay/loam	20.100	*Sv*	loam - clay/loam	7.063
	rocky - clay/loam	-16.175		**rocky - clay/loam**	**-26.037***
	sand - clay/loam	-9.247		sand - clay/loam	-10.592
	rocky - loam	**-36.275****		**rocky - loam**	**-33.100****
	sand - loam	**-29.337***		sand - loam	-17.655
	sand - rocky	6.938		sand - rocky	15.445

Statistically significant results, in which $p < 0.05$, are bolded.

*$p < 0.05$ using Fisher's LSD test only; **$p < 0.05$ using both Tukey's HSD and Fisher's LSD tests.

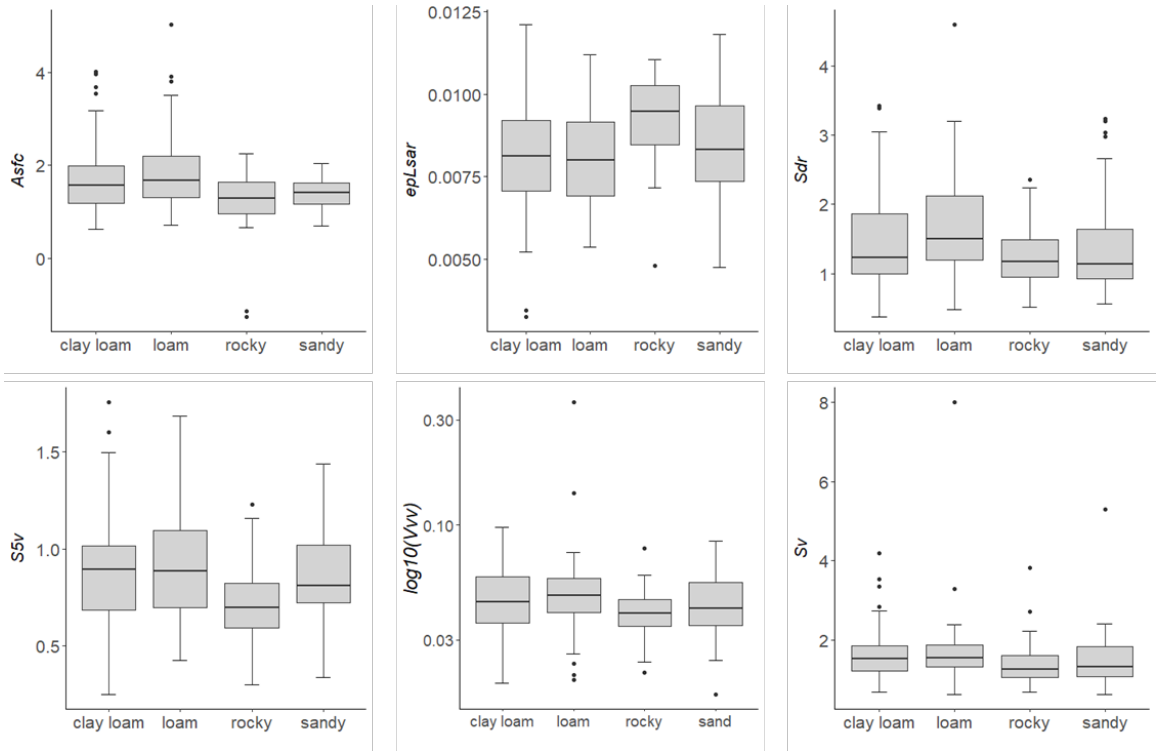

Figure 5.11: Box charts of statistically significant microwear texture variables when analyzed by soil types. The y-axis for parameter *Vvv* is plotted in log space to better clarify the differences among the habitats. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 5.21: Incisor microwear description for soil groups based on significant microwear parameters.

Soil	Significant parameter trends	Microwear description
clay-loam	high *Asfc* , *S5v* , *Vvv* , *Sv* mid-range *Sdr* low *epLsar*	complex, isotropic microwear texture with large and deep features
loam	highest *Asfc* , *Sdr*, *S5v* , *Vvv* , *Sv* lowest *epLsar*	most complex and isotropic microwear texture, with largest and deepest features
rocky	highest *epLsar* low *Asfc* lowest *Sdr* , *S5v* , *Vvv* , *Sv*	most anisotropic microwear texture that lacks complexity and has smaller, shallower scratches
sand	high *S5v* mid-range *Vvv*, *Sv* low *epLsar* , *Sdr* lowest *Asfc*	isotropic microwear texture that's not very complex, with deep features that fall somewhere in between the other groups in size

Land Cover Microwear Effects

Avenant and du Plessis (2018) listed land cover data for each transect as a combination of percent grass, bush/shrub, tree, and exposed soil. These metadata provided the basis for formulating land cover categories based on the hierarchal land cover classification system created by Grunblatt et al. (1989) (see Chapter 3). Based on these data, the incisor sample represented eight distinct land cover categories. Of these groups, five possessed sufficient sample sizes for analyses: dense treed grassland (dTG; $n = 51$), dense treed shrubland (dTS; $n = 25$), open grassed shrubland (oGS; $n = 64$), open grassed woodland (oGW; $n = 32$), and open shrubbed grassland (oSG; $n = 12$). Table 5.22 provides the descriptive statistics of the incisor microwear texture parameters based on these groups, with representative photosimulations in Figure 5.12. The multivariate analysis indicated significant variation among microwear parameter central tendencies (Table 5.23). ANOVAs specifically indicated significant variation for four microwear parameters: complexity (*Asfc*), anisotropy (*epLsar*), and mean dale area (*Sda;* Table 5.23).

Post-hoc comparisons indicated marginal significance for *Asfc* variation, with only Fisher's LSD providing $p < 0.05$ (Table 5.24, Figure 5.13). Specifically, dense treed shrubland (dTS) and open grassed woodland (oGW) incisors both possessed marginally greater central tendencies than those from dense treed grassland (dTG) or open shrubbed woodland (oSW). Open shrubbed woodland incisors possessed marginally higher central tendencies in *epLsar* when compared to incisors from dense treed grassland or open grassed shrubland (Fisher's LSD $p < 0.05$) but significantly higher *epLsar* values when compared to incisors from dense treed shrubland and open shrubbed grassland (both Tukey's HSD and Fisher's LSD $p < 0.005$). Finally, pairwise comparisons for *Sda* separated dense treed grassland microwear from both open

grassed shrubland and open shrubbed woodland, with Tukey's indicating significantly higher *Sda* values latter comparison (Table 5.24; Figure 5.13). Table 5.25 provides microwear descriptions for each land classification group based on these statistically significant parameters.

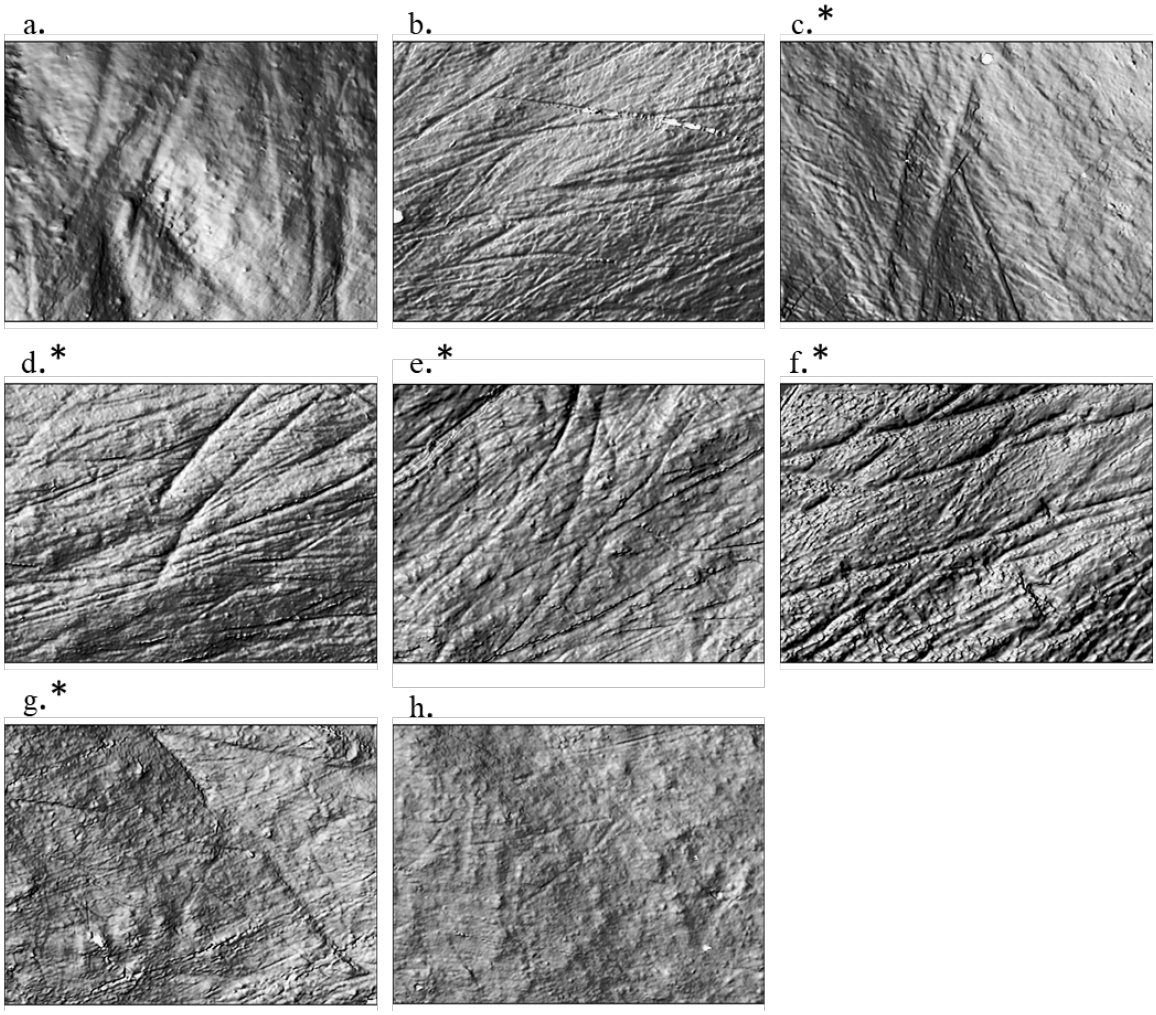

Figure 5.12: Representative microwear photosimulations for land cover classifications: closed grassed shrubland (a), closed shrubbed grassland (b), dense treed grassland (c), dense treed shrubland (d), open grassed shrubland (e), open grassed woodland (f), open shrubbed grassland (g), and open shrubbed woodland (h). Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Table 5.22: Descriptive statistics of incisor texture parameters by land cover classification.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
closed grassed shrubland (cGS; *n* = 4)						
Mean	1.468	0.009	0.682	13648.87	0.305	0.557
SD	0.530	0.001	0.666	3523.625	0.144	0.190
closed shrubbed grassland (cSG; n = 7)						
Mean	2.228	0.008	0.386	13387.62	0.472	0.635
SD	0.863	0.001	0.226	3399.274	0.273	0.325
dense treed grassland (dTG; *n* = 30)*						
Mean	1.360	0.008	42.264	12746.81	0.237	0.477
SD	0.321	0.001	125.481	2847.541	0.119	0.226
dense treed shrubland (dTS; *n* = 25) *						
Mean	1.771	0.008	4.228	12446.66	0.214	0.429
SD	0.633	0.002	17.959	3187.594	0.091	0.116
open grassed shrubland (oGS; *n* = 64)*						
Mean	1.562	0.008	27.086	13032.83	0.242	0.601
SD	0.675	0.002	95.912	3376.468	0.128	1.455
open grassed woodland (oGW; *n* = 21)*						
Mean	1.889	0.009	5.627	13712.35	0.258	0.511
SD	0.811	0.001	23.162	2043.249	0.115	0.220
open shrubbed grassland (oSG; *n* = 12)*						
Mean	1.777	0.008	0.480	12395.17	0.183	0.356
SD	1.084	0.002	0.283	2860.009	0.070	0.083
open shrubbed woodland (oSW; *n* = 35)*						
Mean	1.313	0.009	108.120	13447.89	0.251	0.450
SD	0.839	0.001	179.780	3863.933	0.098	0.145

ISO:	*Ssk*	*Sdr*	*S5v*	*Str*	*Sdv*	*Vvv*	*Sv*	*Sda*
closed grassed shrubland (cGS; *n* = 4)								
Mean	-0.200	1.228	0.957	0.251	3.123	0.040	1.604	225.314
SD	0.577	0.595	0.311	0.141	1.472	0.012	0.587	96.331
closed shrubbed grassland (cSG; n = 7)								
Mean	-0.053	1.497	0.849	0.304	3.218	0.045	1.501	240.665
SD	0.434	0.504	0.176	0.199	4.807	0.014	0.369	196.312
dense treed grassland (dTG; *n* = 30)*								
Mean	0.070	1.502	0.823	0.292	3.351	0.049	1.448	259.665
SD	0.391	0.518	0.212	0.120	2.798	0.017	0.475	124.376
dense treed shrubland (dTS; *n* = 25) *								
Mean	-0.026	1.502	0.933	0.275	2.537	0.048	1.637	211.036
SD	0.375	0.518	0.317	0.179	1.540	0.016	0.711	136.222
open grassed shrubland (oGS; *n* = 64)*								
Mean	-0.023	1.407	0.860	0.313	3.426	0.045	1.600	239.020
SD	0.409	0.746	0.271	0.150	7.141	0.015	0.767	230.618
open grassed woodland (oGW; *n* = 21)*								
Mean	-0.111	1.793	0.918	0.312	2.187	0.063	1.887	193.142
SD	0.360	0.673	0.247	0.138	1.463	0.069	1.461	102.417
open shrubbed grassland (oSG; *n* = 12)*								
Mean	-0.069	1.731	0.871	0.325	2.127	0.055	1.659	180.614
SD	0.345	1.141	0.366	0.188	1.443	0.031	0.707	72.669
open shrubbed woodland (oSW; *n* = 35)*								
Mean	0.043	1.398	0.736	0.252	2.322	0.043	1.427	158.832
SD	0.257	0.572	0.209	0.137	2.109	0.014	0.586	94.700

*denotes groups used in statistical analyses

Table 5.23: Statistical analyses for incisors by land cover classifications.

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
Veg. Cover (*n* = 184)			
0.585	**1.370**	**5, 70**	**0.028**
Aerial (*n* = 198)			
0.888	1.650	1, 14	0.070
Grass (*n* = 198)			
0.847	1.127	2, 28	0.303
Bush (*n* = 190)			
0.934	0.884	1, 14	0.577
Tree (*n* = 198)			
0.912	1.266	1, 14	0.232

(B) ANOVA results

	F- ratio	*p* -value
Land Cover Classification		
Asfc	**2.794**	**0.019**
epLsar	**3.329**	**0.007**
Smc	2.177	0.059
Tfv	1.011	0.413
$HAsfc_{9}$	1.104	0.360
$HAsfc_{81}$	1.642	0.151
Ssk	0.893	0.487
Sdr	2.120	0.065
S5v	1.761	0.123
Str	1.558	0.174
Sdv	0.778	0.567
Vvv	0.199	0.311
Sv	0.913	0.474
Sda	**0.2474**	**0.034**

Statistically significant results, in which $p < 0.05$, are bolded.

Table 5.24: Pairwise comparisons for incisors by land cover classification

Variable	Comparison	difference
Asfc	**dense treed grassland - dense treed shrubland**	**-37.100***
	dense treed grassland - open grassed shrubland	-14.406
	dense treed grassland - open grassed woodland	**-40.452***
	dense treed grassland - open shrubbed grassland	-25.333
	dense treed grassland - open shrubbed woodland	-2.357
	dense treed shrubland - open grassed shrubland	22.694
	dense treed shrubland - open grassed woodland	-3.352
	dense treed shrubland - open shrubbed grassland	11.767
	dense treed shrubland - open shrubbed woodland	**34.743***
	open grassed shrubland - open grassed woodland	-26.046
	open grassed shrubland - open shrubbed grassland	-10.927
	open grassed shrubland - open shrubbed woodland	12.049
	open grassed woodland - open shrubbed grassland	15.119
	open grassed woodland - open shrubbed woodland	**38.095***
	open shrubbed grassland - open shrubbed woodland	22.976
epLsar	dense treed grassland - dense treed shrubland	14.773
	dense treed grassland - open grassed shrubland	-2.329
	dense treed grassland - open grassed woodland	-7.552
	dense treed grassland - open shrubbed grassland	22.317
	dense treed grassland - open shrubbed woodland	**-32.210***
	dense treed shrubland - open grassed shrubland	-17.103
	dense treed shrubland - open grassed woodland	-22.326
	dense treed shrubland - open shrubbed grassland	7.543
	dense treed shrubland - open shrubbed woodland	**-46.983****
	open grassed shrubland - open grassed woodland	-5.223
	open grassed shrubland - open shrubbed grassland	24.646
	open grassed shrubland - open shrubbed woodland	**-29.880***
	open grassed woodland - open shrubbed grassland	29.869
	open grassed woodland - open shrubbed woodland	-24.657
	open shrubbed grassland - open shrubbed woodland	**-54.526****
Sda	dense treed grassland - dense treed shrubland	26.807
	dense treed grassland - open grassed shrubland	**25.132***
	dense treed grassland - open grassed woodland	22.224
	dense treed grassland - open shrubbed grassland	32.950
	dense treed grassland - open shrubbed woodland	**45.795****
	dense treed shrubland - open grassed shrubland	-1.674
	dense treed shrubland - open grassed woodland	-4.583
	dense treed shrubland - open shrubbed grassland	6.143
	dense treed shrubland - open shrubbed woodland	18.989
	open grassed shrubland - open grassed woodland	-2.908
	open grassed shrubland - open shrubbed grassland	7.818
	open grassed shrubland - open shrubbed woodland	20.663
	open grassed woodland - open shrubbed grassland	10.726
	open grassed woodland - open shrubbed woodland	23.571
	open shrubbed grassland - open shrubbed woodland	12.845

Statistically significant results, in which $p < 0.05$, are bolded.

*$p < 0.05$ using Fisher's LSD test only; **$p < 0.05$ using both Tukey's HSD and Fisher's LSD tests.

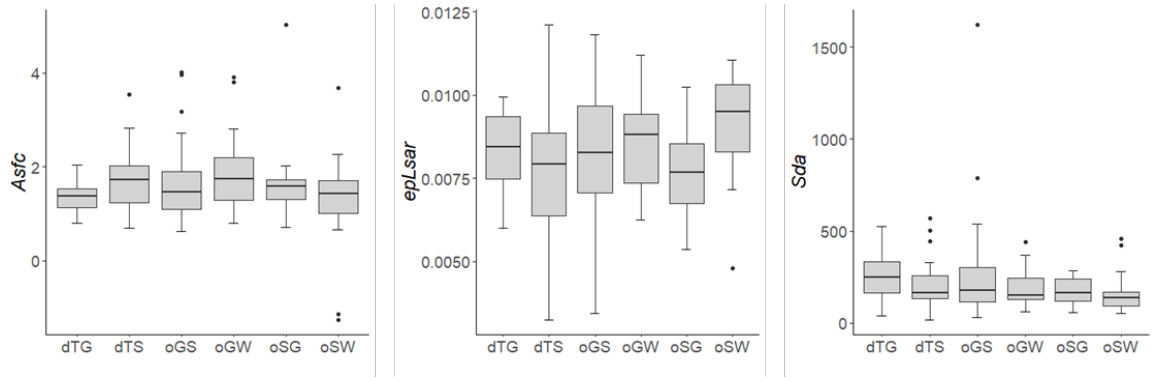

Figure 5.13: Box charts of statistically significant microwear texture variables when analyzed by land cover classification: dense treed grassland (dTG), dense treed shrubland (dTS), open grassed shrubland (oGS), open grassed woodland (oGW), open shrubbed grassland (oSG), and open shrubbed woodland (oSW). Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 5.25: Incisor microwear description for land cover groups based on significant microwear parameters.

Land cover classification	Significant parameter trends	Microwear description
dense treed grassland (dTG)	highest *Sda* low *epLsar* lowest *Asfc*	slightly anisotropic pattern that's the least complex but has the largest feature surface areas
dense treed shrubland (dTS)	high *Asfc* , *Sda* low epLsar	complex, isotropic microwear with features that have large surface areas
open grassed shrubland (oGS)	mid-range *Asfc* low *epLsar* , *Sda*	not particularly complex but somewhat isotropic, with features that have small surface areas
open grassed woodland (oGW)	highest *Asfc* mid-range *epLsar* , *Sda*	most complex microwear pattern that's somewhat isotropic and has features with average surface areas
open shrubbed grassland (oSG)	high *Sda* mid-range *Asfc* lowest *epLsar*	isotropic microwear pattern that's somewhat complex and possesses features with large surface areas
open shrubbed woodland (oSW)	highest *epLsar* low *Asfc* lowest *Sda*	most anisotropic microwear pattern that has low complexity and the smallest feature surface areas

Each of these land cover components were also analyzed as separate factors as to see how they might individually affect incisor microwear signatures. Based on the methods in Chapter 3, each percent coverage group was divided into a low (0 – 33%), medium (34 – 66%), and high

(67 – 100%) category when applicable. The percent of exposed soil was divided into two groups: low (n = 179) and medium (n = 19) coverage levels. Similarly, percent tree coverage consisted of a low coverage level group (n = 177) and a medium group (n = 21), as did percent bush and shrub coverage (n = 162 for low bush coverage and n = 28 for medium bush coverage). Grass cover, however, was comprised of three categories: low (n = 73), medium (n = 62), and high (n = 63). Descriptive statistics for each category are found in Table 5.23, with representative photosimulations in Figure 5.13. MANOVA tests for microwear parameter central tendencies did not result in statistically significant variation for any of the land cover categories: percent exposed soil (p = 0.070), percent grass cover (p = 0.303), percent bush and shrub cover (p = 0.577), or percent tree cover (p = 0.232; Table 5.24).

Table 5.24: Descriptive statistics of incisor texture parameters by percent land cover.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
Percent Aerial						
low (n = 179)*						
Mean	1.595	0.008	34.558	13148.78	0.242	0.515
SD	0.743	0.002	108.885	3107.049	0.125	0.882
medium (n = 19)*						
Mean	1.472	0.009	43.842	12090.86	0.294	0.464
SD	0.685	0.002	129.866	3953.370	0.153	0.159
Percent Grass						
low (n = 73)*						
Mean	1.705	0.008	15.175	12975.49	0.248	0.461
SD	0.693	0.002	69.223	3223.774	0.122	0.171
medium (n = 62)*						
Mean	1.408	0.009	68.032	12942.85	0.238	0.441
SD	0.780	0.001	151.018	3425.733	0.104	0.167
high (n = 63)*						
Mean	1.614	0.008	26.903	13233.18	0.253	0.634
SD	0.721	0.002	96.619	2982.576	0.156	1.468
Percent Bush						
low (n = 162)*						
Mean	1.546	0.008	42.365	13035.25	0.254	0.530
SD	0.762	0.002	121.155	3208.572	0.133	0.926
medium (n = 28)*						
Mean	1.803	0.008	3.807	12617.48	0.213	0.422
SD	0.626	0.002	16.977	3054.756	0.093	0.115
high (n = 8)						
Mean	1.569	0.009	6.365	14794.81	0.221	0.421
SD	0.440	0.002	16.162	3377.530	0.131	0.192
Percent Tree						
low (n = 177)*						
Mean	1.547	0.008	38.997	12968.35	0.245	0.510
SD	0.721	0.002	116.380	3307.213	0.130	0.885
medium (n = 21)*						
Mean	1.889	0.009	5.627	13712.35	0.258	0.511
SD	0.811	0.002	23.162	2043.249	0.115	0.220

Table 5.24 (Cont.)

ISO:	*Ssk*	*Sdr*	*S5v*	*Str*	*Sdv*	*Vvv*	*Sv*	*Sda*
Percent Aerial								
low (n = 179)*								
Mean	-0.023	1.478	0.847	0.291	3.002	0.049	1.589	221.810
SD	0.384	0.663	0.260	0.151	4.650	0.029	0.763	169.497
medium (n = 19)*								
Mean	0.061	1.388	0.887	0.314	1.846	0.042	1.523	169.280
SD	0.229	0.945	0.311	0.145	2.147	0.017	0.990	104.469
Percent Grass								
low (n = 73)*								
Mean	-0.029	1.558	0.918	0.304	2.363	0.051	1.686	198.545
SD	0.379	0.728	0.282	0.159	1.762	0.040	1.025	116.971
medium (n = 62)*								
Mean	0.015	1.388	0.776	0.281	2.406	0.046	1.484	192.918
SD	0.329	0.655	0.252	0.149	2.007	0.019	0.589	123.961
high (n = 63)*								
Mean	-0.028	1.445	0.845	0.294	3.957	0.047	1.558	260.313
SD	0.407	0.687	0.240	0.141	7.341	0.015	0.607	228.116
Percent Bush								
low (n = 162)*								
Mean	-0.006	1.458	0.831	0.295	2.920	0.048	1.563	215.881
SD	0.355	0.715	0.255	0.144	4.903	0.030	0.814	170.763
medium (n = 28)*								
Mean	-0.058	1.524	0.935	0.273	2.548	0.049	1.662	213.684
SD	0.374	0.527	0.317	0.173	1.577	0.016	0.684	145.054
high (n = 8)								
Mean	-0.033	1.514	0.941	0.342	3.461	0.048	1.697	241.847
SD	0.670	0.797	0.212	0.194	1.806	0.015	0.500	114.281
Percent Tree								
low (n = 177)*								
Mean	-0.003	1.430	0.843	0.291	2.965	0.046	1.546	219.204
SD	0.370	0.690	0.270	0.150	4.690	0.020	0.660	170.230
medium (n = 21)*								
Mean	-0.111	1.793	0.918	0.312	2.187	0.063	1.887	193.142
SD	0.360	0.670	0.250	0.140	1.460	0.070	1.460	102.420

*denotes groups used in statistical analyses

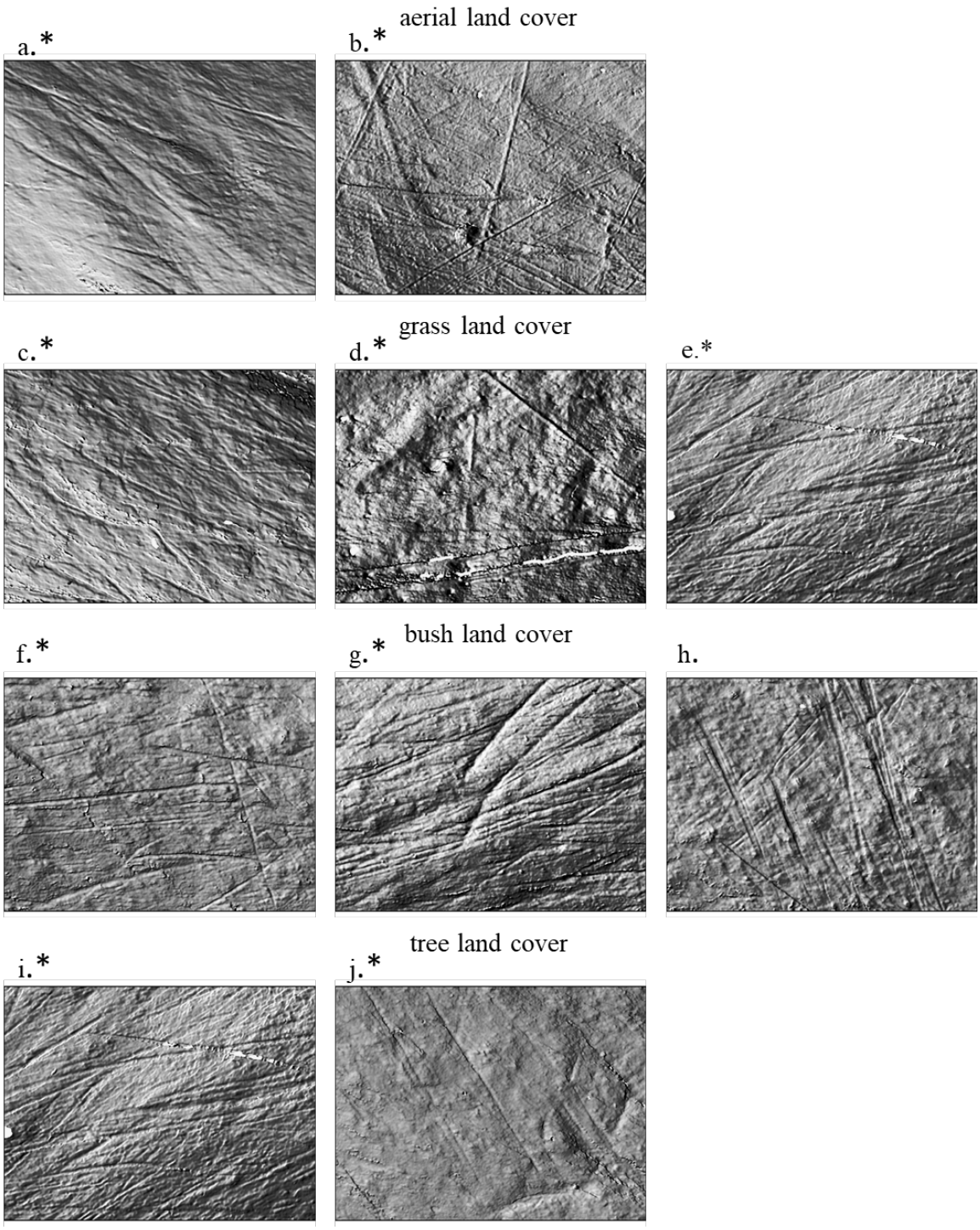

Figure 5.14: Representative microwear photosimulations by different types and levels of land cover. Percent exposed soil is represented by low (a) and medium (b) coverage. Percent grass cover is represented by areas of low, (c), medium (d), and high (e) coverage. Percent shrub and bush cover is represented by low (f), medium (g), and high (h) coverage. And percent cover for trees is divided into low (i) and medium (j) coverage. Each photosimulation measures an area of 138 µm x 102 µm. An * denotes groups used in statistical analyses.

Dust Level Microwear Effects

The 2017 environmental reports from the Kolomela biomonitoring project indicated that dust levels associated with each transect fell into categories of either medium concentration (600 mg/m^2/day < c < 1200 mg/m^2/day) or high concentration (c > 1200 mg/m^2/day). Only 129 specimens could be firmly associated with a high (n = 30) or medium (n = 99) dust level, as any specimen with an unknown dust accumulation was excluded from analysis. Descriptive statistics for the microwear parameters based on these groupings are given in Table 5.25. Figure 5.14 shows representative photosimulations for the two categories. MANOVA analyses indicated a lack of statistically significant variation in microwear central tendencies (p = .629; Table 5.26).

Table 5.25: Descriptive statistics of incisor texture parameters by dust level.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_9$	***HAsfc*** $_{81}$		
medium (n = 99)*								
Mean	1.769	0.008	19.159	12833.62	0.251	0.573		
SD	0.799	0.002	78.737	3091.953	0.126	1.172		
high (n = 30)*								
Mean	1.497	0.008	14.535	13350.27	0.253	0.443		
SD	0.659	0.002	75.145	3193.280	0.175	0.200		
ISO:	***Ssk***	***Sdr***	***S5v***	***Str***	***Sdv***	***Vvv***	***Sv***	***Sda***
medium (n = 99)*								
Mean	-0.053	1.567	0.891	0.304	2.311	0.050	1.640	193.094
SD	0.361	0.774	0.289	0.162	1.666	0.036	0.929	107.019
high (n = 30)*								
Mean	-0.040	1.341	0.866	0.281	5.119	0.047	1.651	307.883
SD	0.416	0.631	0.251	0.132	10.428	0.015	0.720	313.871

*denotes groups used in statistical analyses

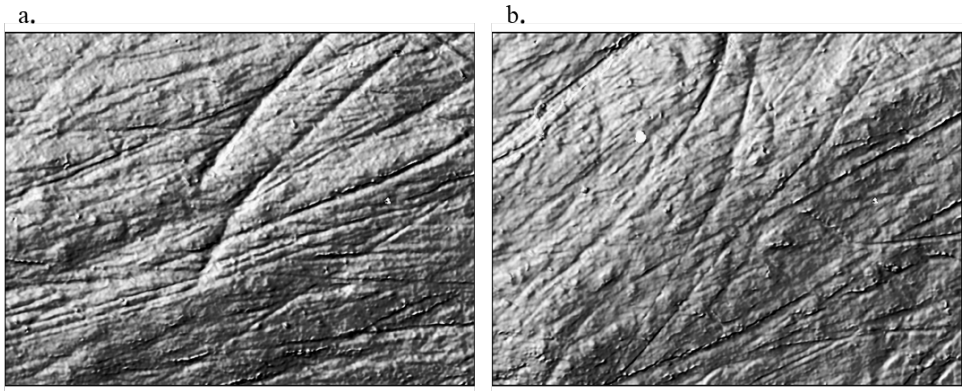

Figure 5.15: Representative microwear photosimulations by dust level, either that of high (a) or medium (b) concentrations. Each photosimulation measures an area of 138 µm x 102 µm.

Table 5.26: Statistical analyses for incisors by dust level (*n* = 129).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.907	0.834	1, 14	0.629

Statistically significant results, in which p < 0.05, are bolded.

Season Microwear Effects

Although the primary sampling occurred during a transitional season (mid-May), Avenant and du Plessis a second, smaller survey in the winter, during mid-July. This extra sampling period resulted in a small group of rodent incisor microwear that could be used to characterize a winter season (July; *n* = 51) in addition to those of a transitional fall period (May; *n* = 146). Descriptive statistics are provided in Table 5.27 while example photosimulations are depicted in Figure 5.15. The MANOVA analysis did not record statistically significant variation in microwear parameter central tendencies ($p = 0.451$; Table 5.28).

Table 5.27: Descriptive statistics of incisor texture parameters by collection month.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_{9}$	*HAsfc* $_{81}$		
May (*n* = 147)*								
Mean	1.640	0.008	32.286	12866.66	0.243	0.525		
SD	0.734	0.002	104.983	2843.813	0.119	0.947		
July (*n* = 51)*								
Mean	1.385	0.009	46.560	13679.35	0.261	0.459		
SD	0.719	0.002	129.594	3282.516	0.157	0.184		
ISO:	***Ssk***	***Sdr***	***S5v***	***Str***	***Sdv***	***Vvv***	***Sv***	***Sda***
May (*n* = 147)*								
Mean	-0.025	1.520	0.857	0.198	2.541	0.049	1.605	203.254
SD	0.368	0.721	0.276	0.155	1.990	0.031	0.818	116.172
July (*n* = 51)*								
Mean	0.020	1.293	0.827	0.275	4.100	0.045	1.504	263.328
SD	0.389	0.557	0.260	0.132	8.695	0.014	0.660	270.906

*denotes groups used in statistical analyses

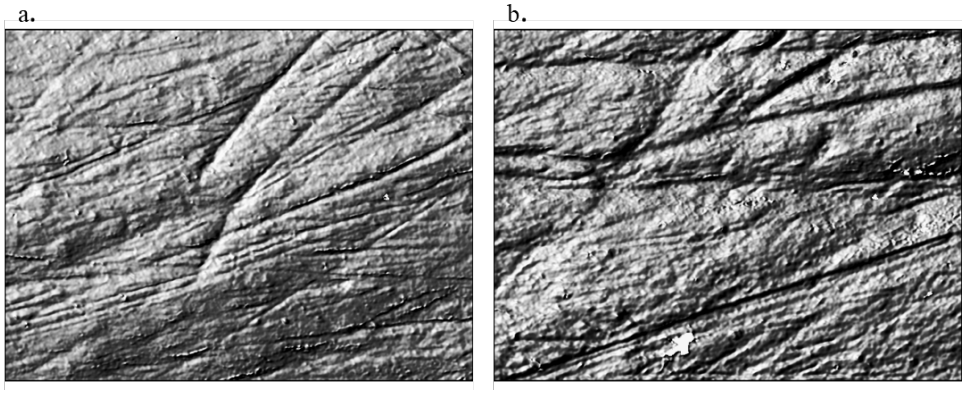

Figure 5.16: Representative microwear photosimulations by collection month: May (a), representing the transitional fall season, and July (b), representing the winter season. Each photosimulation measures an area of 138 µm x 102 µm.

Table 5.28: Statistical analyses for incisors by collection month (*n* = 198).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.940	0.835	1, 14	0.631

Statistically significant results, in which $p < 0.05$, are bolded.

Discussion

The data presented in this chapter builds on existing work (e.g., Belmaker & Ungar, 2010; Caporale & Ungar, 2016; Ungar et al., 2021a) exploring the effects of environmental and behavioral variables on incisor microwear textures in rodents. The incisor sample used in this dissertation displayed a strong environmental signal, with analyses of central tendencies indicating statistically significant variation in microwear parameters for species, macrohabitat, microhabitat, burrowing behavior, soil, and land cover comparisons. It should be noted that the lack of statistical significance for some factors, such as dust level, does not imply a lack of effect on microwear texture. Tested variables may be better parsed by dispersion analyses. Effects on microwear for a single factor may also be obscured by interactions with other variables. Unfortunately, due to the non-orthogonal sampling associated with using field caught specimens, dispersions and interactions between the factors were not tested for (refer to Chapter 3). Still, this chapter provides further insights into a little studied area of dental microwear texture analysis (DMTA). Following the results section, each factor will be discussed separately.

Species Microwear Effects

Species comparison consisted of one gerbil, *Gerbilliscus leucogaster*, and two murines, *Micaelamys namaquensis* and *Rhabdomys bechuanae*. Pairwise comparisons indicated that *G. leucogaster* incisor microwear possessed significantly higher values for complexity (*Asfc*) than those of the other two rodents, while *Mi. namaquensis* incisor microwear possessed the highest anisotropy (*epLsar*) measures in comparison to both other species. In addition, the remaining parameters indicated that the gerbil incisors possessed significantly larger and deeper features (*S5v, Sv, Vvv*) in comparison to *Mi. namaquensis* incisors. These results occurred despite

overlap in habitats (see Chapter 3, Table 3.2) and relatively similar diets dominated by grass seed consumption (see Chapter 4, Table 4.2 and Figure 4.2). It is therefore unlikely that the microwear variation among species results from diet. While incisors are typically only used in procurement and not mastication (Belmaker, 2018; Caporale & Ungar, 2016; Ungar et al., 2021a), the use of incisors to crack open nuts and seeds, for example, may result in a different texture than that observed on the incisors of rodents not eating seeds. However, the granivorous nature of the Kolomela rodent community indicates that observed species effects more likely stem from other behavioral and environmental characteristics.

Micaelamys namaquensis incisor microwear remains distinct from the other two species, possibly due to being the only species in this analysis that does not excavate underground burrows, preferring to build grass nests among rocky outcrops (Happold, 2013). Unsurprisingly, *Mi. namaquensis* was predominately collected along transects marked as 'rocky substrate' and was the only species in this analysis to be found in this soil type. *Micaelamys namaquensis* individuals were also collected in areas consisting of either sand or loam soils, as well as populations of *G. leucogaster* and *R. bechuanae*. Still, pairwise comparisons for central tendencies generally separated *Mi. namaquensis* from the other two Muridae species, and especially from *G. leucogaster*. Incisor microwear for this mouse was highly anisotropic with small and shallow features.

Gerbilliscus leucogaster specimens were easily caught and, as such, comprised the greatest sample size in this analysis. This gerbil species constructs and utilizes underground burrows (Cruise, 2013; de Graaf, 1981; Lotter & Pillay, 2008). A lack of information exists on *R. bechuanae*'s specific burrowing habits, but literature generally describes the *Rhabdomys* genus that constructs its own underground burrows as well as makes use of those constructed by

other species (Bronner, 1992; Johnson, 1980; Schradin & Pillay, 2004; Shortridge, 1934; Smithers, 1975). Populations of *Rhabdomys* have also been observed to nest above ground (Brooks, 1974; Choat, 1972), thus making it not as habitual in burrowing as *G. leucogaster*. Both species, however, dig with their forearms rather than incisors (Giannoni et al., 1996; Webster et al., 1981). Incisor microwear for the gerbil was the most complex and isotropic, with the largest features. *Rhabdomys bechuanae* incisor microwear textures, meanwhile, seemed to fall somewhere in between these two other species, significantly differing from *G. leucogaster* in complexity and from *Mi. namaquensis* in anisotropy measures. *R. bechuanae* was ultimately classified as a burrowing species in this dissertation. That microwear parameters for *R. bechuanae* incisors fall between that of a habitual burrower and a species that only nests aboveground suggests that not all Kolomela *R. bechuanae* populations constructed burrows, supporting previous observations of *Rhabdomys* behavior.

Overall, these results are similar to those from the analysis of burrowing species versus non-burrowing ones, which will be discussed in further detail later in this chapter. It reinforces the idea of substrate interaction as a driving influence in the incisor microwear formation for rodents. Indeed, Ungar et al. (2021a) also argued that differences in substrate use influenced differences in incisor microwear patterns between voles (burrowing) and lemmings (nesting) in the Siberian arctic. Unfortunately, that appears to be the only other study to date that considers burrowing behavior as an influential factor on incisor microwear.

Macrohabitat Microwear Effect

The term *habitat* is inconsistently used throughout ecological literature (see Belmaker, 2018; Kearney, 2006). Following Belamker's (2018) review of rodent dental microwear, this

study uses the definition established in Kearney (2006): a habitat is a physical location in which an organism resides, or has the potential to reside, based on confines of space and time. Within this location are biotic and abiotic factors that affect the distribution and abundance of a given species. This study also incorporates Morris' (1987) division of a given habitat into macro- and micro- elements, the latter of which will be discussed in the next section. Macrohabitats, the focus of this section, incorporate all the location within a given time and space in which an organism conducts biological functions (Morris, 1987), and are represented by the individual Kumba Iron Ore properties in which the Muroidea sample was obtained.

Four of these habitats were considered in the incisor microwear analysis: Kolomela Mine, and the farms Grootpan, Heuningkrantz, and Kappies Kareeboom. Incisor microwear from the mine proper had highly anisotropic features (*epLsar*) that lacked complexity (low *Asfc* and *Sdr* values) and were shallow and small (*Sdv* and *Vvv*), with surfaces appearing rougher at finer scales (low *Smc*). The sample from Heuningkrantz, the farm furthest from mine operations, also possessed lower complexity values (*Asfc*, *Sdr*) but had higher *Smc* values that implied the presence of larger features when examined at coarser scales, as well as high *epLsar* values. Kappies Karee incisors had extremely high *Asfc* and *Sdr* values and low *epLsar* measures, indicating complex and isotropic microwear textures, that also had large and deep features (*Sdv* and *Vvv*). Finally, the Grootpan sample possessed the lowest anisotropy (*epLsar*) values, along with the highest dale volumes (*Sdv*) and high pit void volume (*Vvv*).

Habitats varied in vegetation species and cover, as well as in soil types and dust exposure levels (refer to Chapter 3, Tables 3.4 and 3.5) and in distance from mine activities (Figure 3.1). Diets were relatively consistent among the habitats, with the stomach content analysis indicating a preference for grass seed regardless of location (see Chapter 4, Table 4.5 and Figure 4.7).

Although species composition did differ by location, *Gerbilliscus leucogaster*, was present at all four sites and comprised most of the incisor sample (see Chapter 3, Table 3.2). Despite all habitats being located within the savanna ecosystem of Postmasburg Thornveld, the abiotic differences that exist between these macrohabitats appear significant enough to lead to differences in incisor microwear.

Particularly, habitats were best separated by parameters measuring complexity. Both *Asfc* and *Sdr* parameters indicated that incisors from the habitat of Kappies Kareeboom had the highest complexity, with pairwise comparisons indicating significant variation to incisors from the other three habitats. Biomonitoring activity within Kappies Kareeboom and the Kolomela Mine only occurred during May, while rodent trapping within Heuningkrantz and Grootpan also took place during July. The level of dust exposure was unknown at Heuningkrantz. Rodents from Grootpan were exposed to both medium and high concentrations. However, given the microwear texture differences between Kappies Karee and Ekstra incisors, where dust accumulation was classified as medium level for both sites, it appears that atmospheric grit might not be causing the different signals. It seems more likely that incisor microwear differences stem from other aspects of these habitats.

Kappies Kareeboom and the mine both had similar percentages of exposed soil. However, soils at Kappies Karee were comprised of loam and clay-loam material while specimens obtained from Kolomela were restricted to sandy soils. Given that loam is a mixture of sand, clay, and silt (Schaetzl & Anderson, 2005), this soil contains a greater degree of particle variation in attributes such as hardness, size, and angularity. Studies have indicated that these characteristics are influential on microwear patterns (e.g., Ackermans et al., 2020; Ungar, 1994; Winkler et al., 2020b). It is possible that incisor interaction with soils of mixed components

could increase complexity. Indeed, Winkler et al. (2020b) found that a variation in abrasive particle size potentially led to variation in molar microwear complexity for guinea pigs. Meanwhile, Grootpan also consisted of clay-loam soil, but trapping transects were laid out in areas of much lower percentage of exposed dirt and higher concentration of grass cover in comparison to those at Kappies Kareeboom. This difference in soil exposure could potentially indicate why, despite incisor associations with the same soil, those from Kappies Karee had higher complexity, as measured by *Sdr*. While microwear variation between Kappies Kareeboom and the Kolomela Mine may stem from differences in soil types, microwear variation between Kappies Kareeboom and Grootpan stem from the degree of soil exposure. The effects of both soil type and ground cover on incisor microwear texture will be discussed further in their own sections.

Still, these results do seem to support other suggestions that rodent incisor microwear may be indicative of habitat openness. Caporale and Ungar (2016) compared rodent incisor microwear from varying ecosystems and found that *Asfc* values rose and *Smc* values lowered with more xeric, open locations, marking differences between ecosystems such as deserts and woodlands or savannas and rainforests. Similarly, Ungar et al. (2021a) argued that differences in striation densities for vole incisor microwear between Siberian habitats stemmed from levels of environmental grit, as determined by land composition and cover. The habitats used in this dissertation are not quite as distinct as those from other studies, given that they are all found within the same ecoregion. Still, this gross scale habitat analysis still highlighted the ability of rodent incisor microwear texture analysis to separate savanna macrohabitats from one another in manners like that of these other analyses. In addition to the complexity results, *Smc* values also expressed a similar trend. Specimens from Heuningkrantz were mostly caught within areas of

dense vegetation and possessed a significantly higher *Smc* value than specimens from the Kolomela Mine and Kappies Kareeboom, both consisting of open vegetation cover. Though not the same as a comparison between forest and savanna, the *Smc* parameter still divides open habitats from those of more closed ones, as observed by Caporale and Ungar (2016).

While one would have thought the mine to be the habitat with more complex microwear due to the high degree of anthropogenic activity disturbing the soils, Kolomela incisors had the highest anisotropy measures and the lowest measures for the volume parameters, *Sdv* and *Vvv*. This could be because the transect, Ekstra, was located with sufficient distance from main activity as not to be any more affected than transects at the farms and as such, the incisor microwear of this sample results from variables other than anthropogenic ones. Small feature volumes could stem from the presence of sandy soil at the collection area. While particles size at Kolomela is unknown, it is possible that the sand is made of smaller particles. On molars, controlled feeding experiments of finer quartz abrasives correlated with lower *Vvv* values, as well as higher anisotropy (Winkler et al., 2020b). However, without knowing the precise size of the particles interacting with the rodent teeth at Kolomela, it is impossible to say for certain. Results such as these highlight the need to breakdown the samples by key biotic and abiotic characteristics, as to understand what factors perhaps better are influencing microwear behavior.

Microhabitat Microwear Effects

The previous section discussed the results of the macrohabitat analysis, using specimens captured within four of the Kolomela properties to examine habitat effects on incisor microwear within a grosser spatial scale. However, macrohabitats are usually comprised of multiple smaller microhabitats. These microhabitats differ based on specific biotic and abiotic conditions that influence how an individual might spend its energy and time within that area (Morris, 1987) and

occur at finer spatial resolutions (Jorgensen, 2004). However, microhabitats also need to be defined based upon the studied taxa's concept of scale (Morris, 1987). While microhabitats for a large animal, like an antelope, may include a lake shore within a savanna macrohabitat, that same lake shore may be the entirety of a macrohabitat for a smaller mammal, like the mice and gerbils in this study. Small rodent microhabitats need to be defined on a much smaller spatial scale and should incorporate abiotic differences that would not drastically affect a larger mammal (Belmaker, 2018), such as soil composition or moisture levels.

Locations for the rodent trapping transects were established based on differences in mine activity, vegetation, and dust level. While specific characteristics for each transect microhabitat can be found in Chapter 3 (Table 3.5), each comprise a relatively distinct set of conditions that can be used to define a microhabitat for a small mammal. This analysis allows for the interpretation of data at a finer resolution than that of the macrohabitat analysis by focusing on environmental characteristics distinct to a particular microhabitat rather than the amalgamation of environmental characteristics comprising muroid habitat and home range. Due to their small size and often nocturnal activity patterns, it is difficult to find and follow in rodents the field. As such, African rodent behavior is not studied as frequently as larger mammals and little data exists on the home range extents for these species (Happold, 2013). While information could not be found regarding the taxa used in this dissertation, *Rhabdomys pumilio* and *Mastomys natalensis* home ranges are estimated to be as large as 1500 m^2 and 2666 m^2, respectively (Coetzee, 1975; Schradin, 2006). A linear transect of 250 m, therefore, only comprises a small portion of this overall range. The analysis of microhabitat effect on incisor microwear textures used specimens from six of these transects, with statistically significant parameter variation separating the different microhabitats.

ANOVAs for central tendencies once again indicated significant variation for the *Asfc*, *epLsar*, *Sdr*, *Sdv*, and *Vvv* parameters. Variation in *Smc* central tendency, while significant in the macrohabitat analysis, was no longer significant when comparing samples by a finer spatial scale. Ekstra, as the only transect representing the Kolomela Mine, unsurprisingly possessed the same highly anisotropic features (*epLsar*) that lacked complexity (low *Asfc* and *Sdr* values) and were shallow and small (*Sdv* and *Vvv*). The sample from Heuningkrantz, now divided into HK3 and HK7, varied. HK3 incisors were generally large and deep (*Sdv* and *Vvv*) while the HK7 sample had the most anisotropic texture of the compared microhabitats (high *epLsar* values). KK3 incisor microwear was the most complex (high *Asfc* and *Sdr* values) while microwear from the other Kappies Kareeboom transect, KK2, had the largest measures of pit void volume. Finally, while incisor microwear features from both transects at Grootpan were considered large and deep, complexity parameters for GN1 and GN2 differed in relation other transect samples.

Post-hoc tests for statistically significant variables provided differences among transects that did not appear when comparing larger habitats. For example, while the *epLsar* pairwise comparison between Kappies Karee and Kolomela lacked a significant difference in central tendency, *epLsar* measures from transect KK2 (in Kappies Kareeboom) were marginally significant in comparison to the larger *epLsar* value of the mine transect. Similarly, incisors from HK7, in Heuningkrantz, were significantly higher anisotropy values than those from KK2. Even within the same farm, differences were observed between microhabitats; incisor microwear from HK3 had marginally greater pit void volumes than those from HK7. Indeed, microhabitat incisor microwear analysis seems to reveal details masked in macrohabitat analysis. Incisor microwear from the Kolomela Mine had significantly lower *Sdv* values than incisors from either Kappies Karee or Grootpan. When these habitats are divided into transects, results reflect

differences between the two spatial scales. The *Sdv* central tendency from GN1 incisors, as analyzed by microhabitat, is only marginally greater than the mine incisors, while *Sdv* values from GN2 are significantly greater. In addition, Kappies Karee *Sdv* differences to the mine are restricted to transect KK3 as the comparison in central tendencies between KK2 and the mine samples resulted in a lack of significance.

It is easy to lump specimens from the same habitats or ecosystems into one group when conducting analyses. Yet, a habitat is not necessarily homogenous in every characteristic and often mosaic in composition. Indeed, habitats within the same thornveld ecosystem in this study display varying soil types, vegetation cover, species composition, and so on (refer to Chapter 3, Tables 3.4 and 3.5). And, as these results seem to indicate, such differences may be detected in rodent incisor microwear at different measures of a spatial scale. While the home range of murids is small compared to larger taxa, they still pass through many microhabitats throughout a day range (Morris, 1987), thus making it important to consider habitat effect on multiple spatial scales.

Dietary Microwear Effect

Incisor microwear central tendencies did not significantly differ among the three dietary categories considered: grass seed/grass seed, grass see/curculionid, and grass seed/grass. These results reflect both the similar diets within the Kolomela properties, and the lack of a strong dietary signal for incisor microwear, especially in comparison to that of molar microwear (see Belmaker, 2018). Grass seed comprised ≥ 50% of stomach contents for each dietary category, and as such, any dietary effect would result from the presence of the second greatest contributor to stomach contents, either curculionid or grass. In addition to the other functions of rodent

incisors, they are used in the procurement of food (Belmaker, 2018; Stefen, 2011), with many species using their incisors to crack open nuts and seeds.

If the rodents used in this dissertation were more distinct in dietary preference, possessing sufficient sample sizes of those eating primarily grass blades or curculionids, perhaps dietary differences would have been observed. Belmaker and Ungar (2010) reported higher values of anisotropy and texture fill volume for folivore incisors in comparison to those of granivores, with granivore incisors possessing higher heterogeneity values. Caparole and Ungar (2016), meanwhile, indicated that omnivore incisors had significantly greater heterogeneity values than frugivore incisors, and marginally greater heterogeneity and anisotropy than herbivores. These differences in microwear textures may be influenced by the way in which rodents use their incisors to prepare their food for mastication. Granivore heterogeneity may be reflective of incisor use in opening nuts and seeds. Similarly, omnivore incisors would presumably reflect interactions with chitin, seeds, nuts, and other vegetation. Incisor dietary interactions may also be separated better by dispersion analysis as it may better reflect the variance in the amounts of foodstuff consumed. Unfortunately, rodent dietary behavior is not easily controlled within the field. While previous studies indicate some effect of diet on incisor microwear, this study indicates a stronger environmental influence.

Burrowing Behavior Microwear Effects

Many rodent species interact with soil and substrate in ways that may result in incisor microwear signals that are more indicative of habitat rather than diet (Belmaker, 2018; Kelley, 1990). Of note is the potential influence of burrowing and digging behavior. Indeed, separating the incisor sample based on a species' tendency to excavate underground burrows resulted in

significant differences in microwear parameters. Texture analysis of those species that have been noted to engage in habitual construction or habitation of underground burrows indicated more complex (*Asfc*) and isotropic (*epLsar* and *Str*) microwear patterns that possessed large and deep features in comparison to those of non-burrowers.

From the limited amount of research available, it seems that *Gerbilliscus* species and *R. bechuanae* dig with their forearms rather than incisors (Giannoni et al., 1996; Webster et al., 1981). Nevertheless, it seems reasonable to assume a greater exposure to grit among these burrow excavating individuals. Grit may accumulate on food stored underground or even on their fur as they nest or move through the burrows. From the stomach content analyses conducted in Chapter 4, it appears that all species take part in grooming that leads to the ingestion of hair. Although *Mastomys coucha* has been known to occupy previously constructed burrows (Bronner, 1992; Eckard, 1998), it was classified along with *Micaelamys namaquensis* as a non-burrower due to its lack of active excavation. However, *Ma. coucha* and *Mus minutoides*, a species that actively excavates its own burrows, had the highest mean concentrations of hair in stomachs (~18.0%). As such, the burrowing species, or at least those individuals in this collection, do not appear to groom more or less than those that do not. Still, that does not negate the possibility of incisor-grit interaction stemming from grooming activity, let alone consumption (or burial) of food from underground caches. *Rhabdomys*, for example, has been thought to pilfer from the underground hordes of other rodents (Rusch et al. 2013), while other species from this study, such as *G. paeba*, have been observed to engage in seed scatter-hoarding behaviors (White et al. 2017, Weighill et al. 2017).

The likelihood of greater grit exposure for burrowing species seems a reasonable explanation for the differences in microwear attributes between the two groups. In a controlled

feeding experiment, the addition of sand granules to rabbit diets resulted in deeper molar microwear features that were considered more pronounced than diet lacking added grit (Martin et al., 2020). A similar experiment with goat molars indicated that the addition of sand to diet increased dale area and volume (Schulz-Kornas et al., 2020) while one with guinea pigs showed that varying sizes, shapes, types, and concentrations of external abrasives will alter microwear patterns (Winkler et al., 2020b). However, while these experiments describe microwear features like that of the burrower sample in this study, it is important to note that the different functions of incisors and molars might contribute to different microwear patterns (Belmaker, 2018; Caporale & Ungar, 2016; Stefen, 2011). As such, any comparisons between the two types of teeth must be made considering that molar microwear reflects the masticatory processes not associated with incisors.

Like the higher *Asfc* values found among the burrowers here, Caporale and Ungar (2016) found higher *Asfc* values for incisors analyzed from desert and savanna rodents, which they associated with a potentially higher grit level — as one would also expect burrowers to experience. Terrestrial specimens also had a higher *Asfc* than those arboreal and presumably further away from soil grit (Caporale & Ungar, 2016). Withnell and Ungar (2014) did not find similar environmental trends in shrew incisor microwear. Nor did Adams et al. (2020) note any effect in molar microwear textures based when comparing mole specimens, a subterranean rodent consuming grit-laden earthworms, to bat specimens also consuming soft prey. However, Nelson et al. (2005) did notice that substrate use affected the molar microwear patterns of squirrels. Specifically, they considered that the differences in pit frequency between arboreal and terrestrial squirrels were likely caused by the greater presence of grit in terrestrial diets, in addition to the consumption of more abrasive foodstuff.

Although a comparison of these results to that of Ungar et al. (2021a) indicate that arctic rodents also show a significant difference between burrowers (*Lasiopodomys gregalis*) and non-burrowers (*Lemmus sibiricus*), results between the two studies were contrary. For example, while the Arctic burrowers had higher anisotropy (*epLsar*) values, the South African burrowers were characterized by lower anisotropy and instead tended towards higher complexity (*Asfc*). Similarly, where the burrowing species in this study had deeper and larger dales (*Vvv, S5v*), the data from the Arctic study indicated that non-burrowing species had the deeper and larger dale features. These differences imply that, while burrowing and non-burrowing species can be separated based on incisor microwear, there are other factors at play in addition to whether a rodent nests underground.

It is important to note differences in sample composition: Ungar et al.'s (2021a) burrowing sample was comprised entirely of *L. gregalis* from three different Arctic latitudes. Here, the burrowing sample was dominated by *G. leucogaster,* but included other Muridae species, and collected within a much narrower land range. While *L. gregalis* has a more herbivorous diet, the rodents from Kolomela were clearly generalists that favored seeds (see Chapter 3), with species relying on scatter-hoarding behaviors that would potentially increase the amount of grit on food. Silcox and Teaford (2002) indicated that the ingestion of soil-ladened earthworms by two mole species created a unique molar microwear pattern with a massive number of features not observed among other micromammals. Yet, Adams et al.'s (2020) application of ISO parameters to the molar microwear of bats and moles indicated that exposure to higher grit loads by moles did not obfuscate the dietary signal.

It is possible that other behavioral differences may be at play. *Gerbilliscus* does not utilize its incisors in digging and relies on its forelimbs (Giannoni et al., 1996), although no

recent data could be found confirming or denying incisor use. Meanwhile, Ungar et al. (2021a) conjectured that the use of incisors by *L. gregalis* to loosen soil might explain their higher anisotropy values. On the other hand, *Gerbilliscus* utilizes dust baths to maintain a healthy coat (Hubbard, 1972), which may increase the likelihood of grit particle-incisor interaction within the burrowing group and influence microwear characteristics in a way unrelated to burrowing behavior.

Differences may also be a response to environmental characteristics. The burrowers from Kolomela were collected from a variety of soil types while those from the Arctic were associated mainly with dry and sandy areas (Ungar et al., 2021a). Indeed, when the South African rodents were considered by associated soil type, lower complexity and higher anisotropy values were observed for sandy soil specimens. However, these results were not significant when compared to other soil types occupied by burrowing rodents. Regardless of the reason, more research is needed on the influence of soil and soil-incisor interactions to better elucidate the environmental data that can be obtained in this regard.

Soil Microwear Effects

The soils associated with collection transects at the Kolomela properties possess distinct physical properties that potentially influence the formation of incisor microwear. Results indicate differences in complexity (*Asfc*, *Sdr*), anisotropy (*epLsar*), and feature volume and depth (*S5v*, *Sv*, *Vvv*) parameters by soil type. Incisor microwear from loam soils, including that of the clay/loam mix, possessed more complex and isotropic microwear with large and deep features while incisors from rocky soils had more anisotropic microwear with smaller and shallower

features. The incisor microwear associated with sandy soils were isotropic but not as complex as those from loam soils and had deep features.

Controlled experimental molar microwear work with small mammals has indicated that increasing the size or quantity of exogenous abrasives correlated to an increase for height, volume, and complexity parameters (Ackermans et al., 2020; Winkler et al., 2020b). Soils that contained loam in this study generally possessed more complex and isotropic microwear patterns, with the larger features. Loam is a composite soil comprised of roughly equal proportions of sand, clay, and silt. As such, particle sizes range from < 0.002 mm (clay) to approximately 0.05 mm (larger sand pieces) and are comprised of various materials including red aeolian sands, quartz-based silts and sands, and kaolinite clays (Schaetzl & Anderson, 2005; Smit & van Rensburg 2018; Viljoen et al., 2005). It could be that this mix of particle size is driving the high complexity values. Unfortunately, these experimental studies did not incorporate composites like loam into their work. Further, exposure to silt-sized quartz crystals led to a "polishing effect" on guinea pig molars, with parameters indicating higher anisotropy and lower surface roughness and complexity (Winkler et al., 2020b). Without knowing the size of the particles at the Kolomela properties, only broad assumptions can be made regarding the influence of particle size on incisor microwear.

Significance in *S5v, Sv,* and *Vvv* central tendencies only occurs when these soils are compared to that of rocky soils. There are a couple of possible explanations. First, while rocky soils would contain the largest particle size (> 2mm), given the minute size of the rodent teeth in this sample, it seems reasonable to assume that biting on a rock would potentially due more damage to a tooth. As such, rocks would not have much influence on microwear. Second, and more problematic, is that the sample of rocky soil specimens is composed entirely of *Micaelamys*

namaquensis, a nesting species that does not create or utilize burrows. However, samples from loam soils and sandy soils were comprised mainly *Gerbilliscus leucogaster* specimens and were still separated by complexity parameters. These results indicate that substrate type may influence incisor microwear but also need to be interpreted based on rodent interactions with their environments.

Land Cover Microwear Effects

Both vegetation type and density thereof have been noted to influence grit exposure (Wolf & Nickling, 1993). This leads to more open habitats having higher grit loads and exposure (Caporale & Ungar, 2016; Ungar et al., 2021a) that may be reflected in incisor microwear. The effects of vegetative land cover on incisor microwear were tested in two ways. First, each individual percent cover category was each considered. Second, these data provided the basis for land cover class based on Grunblatt et al.'s (1989) hierarchal vegetation classification system. The results for percent aerial (the amount of exposed soil), grass, bush/shrub, and tree covers did not report statistical significance. However, the central tendencies MANOVA for land cover class did result in $p < 0.05$. Land cover classes were separated by complexity (*Asfc*), anisotropy (*epLsar*), and mean dale area (*Sda*) parameters.

Caution should be taken in interpreting these results, however, as these data are restricted and do not represent the full diversity of land cover characteristics or ecosystems. For example, only low and medium percent coverage for exposed soil cover, bush cover, and tree cover could be compared. It is possible that microwear signals may differ if comparing samples from extremes, such as areas of low soil exposure compared to areas of high soil exposure, as regions with exposed soil percent > 66% might be more reflective of an open area with higher levels of

grit that may adhere to foodstuff. Further, the land cover classification system used gives preference to the degree of cover of the primary vegetation. While both dense and open qualifiers were used in defining a land cover class, these described the percent cover of the primary lifeform. If land cover was considered dense, then the primary vegetation cover comprised 50 – 79% of the trapping area. If open, the primary vegetation cover comprised 20 – 49% of the trapping area.

Incisors from open shrubbed woodlands had the most anisotropic microwear textures in comparison to incisors from all groups except open grassed woodland. These *epLsar* pairwise comparisons appeared to reflect the trend observed with burrowing behavior. Incisors from open shrubbed woodlands, which had the greatest number of incisors from non-burrowing species, had significantly higher central tendencies in *epLsar* than land cover classifications mostly comprised of burrowing specimens. However, results for *Asfc* and *Sda* do not follow the same trend. Nor do they appear reflective of soil composition, as observed within the macro- and microhabitat analyses. Incisor microwear from both dense treed shrublands and open grassed woodlands were more complex than microwear from dense treed grassland or open shrubbed woodlands. In addition, dense treed grassland microwear features had larger dale areas than either open grassed shrubland or open grassed woodland. It could be that the rodent community within areas dense treed grassland are interacting with this environment in such a way that creates incisor microwear with large dale areas and low complexity compared to those rodents from open grassed woodlands. As such, these results appear to indicate that interactions between rodent behavior and abiotic habitat characteristics contribute to differences in incisor microwear.

Dust Level Microwear Effects

Dustfall at Kolomela is comprised of varying proportions of natural quartz, sandy grit, lime calcrete, organics, haematile, road dust, topsoil, ambient soil, and quarzite that stem both from mining and non-mining activities. On average, the majority concentrations of dust particles stemmed from road and mining activity (Loans, 2018). These particulates widely differ in size, shape, and hardness. Unfortunately, the specific compositions of the dust buckets at each transect could not be obtained but Loans' (2018) data indicated that particles are < 100 μm in size. Regardless of dustfall measures, these atmospheric particles could easily be observed as a red layer on top of leaves at most transect sites (personal observation). This observation is unsurprising, given studies along major roadways have indicated the high retention of particulate matter on leaf surfaces (e.g., Dochinger, 1980; Prusty et al., 2005). It is important to note that dust retention depended on material properties of leaf surfaces, and varied based on species (Prusty et al., 2005). As such, the amount of dust in which rodents are exposed to may be more variable than what is indicated by the dust collectors.

However, microwear texture variables did not significantly differ between specimens from medium and high dust collection sites. While these results were surprising, they are also not entirely unexpected given the overwhelming presence of dust the author observed at the Kolomela properties. Specimens were obtained from areas of either medium (734 mg/m^2/day mean) or high (1272.5 mg/m^2/day mean) levels of accumulation. Incisor exposure to dust was relatively likely, and perhaps not so starkly different in accumulation amount as to produce variation in microwear textures. Furthermore, these results may be the result of a conflation of variables. Interactions between factors were not tested due to the non-orthogonal samples and the sheer number of factors examined. Yet, the results from other analyses seem to indicate that

interactions between factors do contribute to rodent incisor microwear formation. It could be that for a comparison of dust level, any variation due to differences in dust accumulation levels may be masked by other variables.

Controlled experimentation with molars has indicated that dietary signals are still distinguishable regardless of grit concentration (e.g., Adams et al., 2020; Merceron et al., 2016), while others have indicated grit concentration affects molar microwear patterns (e.g., Schulz-Komas et al., 2020). Once again, it is important to keep in mind that molars and incisors are not directly comparable. But in the light of the limited research with controlled incisor experimentation, the data remain helpful in attempting to parse the relationship between grit concentration and microwear formation. Indeed, even though Merceron et al. (2016) indicated little effect of dust concentration on dietary signal, they did indicate that the presence of dust did alter microwear texture — just not in a way which would conflate dietary texture on molars given different masticatory dynamics associated with food fracture properties. It is possible that, were this study to contain a low accumulation sample, microwear parameters might have varied based on dust exposure.

Season Microwear Effects

Seasonal differences were tested based upon specimen collection month. Unfortunately, collection took place only during two relatively close periods: May (n =146) and July (n = 51). As such, only two seasons could be compared: winter and transitional (see Burgman et al., 2016). In the Northern Cape, winters are generally dry with temperatures can drop below 0º C at night, resulting in frost layers that disappear during the day (Mucina et al., 2006; Smit & van Rensburg, 2018). The rainy season in Kolomela typically ends in April, and as such, only a

mean of 6.5 mm was recorded during the month of May. In July, no rain fell (Smit & van Rensburg, 2018). The statistical analyses for incisors from these two collection periods did not result in significant variation for microwear parameters.

Burgman et al. (2016) also found a lack of significant difference in *R. pumilio* molar microwear when comparing wet and transitional season samples from the Dry Highveld grassland in the Central Free State of South Africa. Other studies have indicated that seasonality did affect the microwear texture for vole molars, thought to be influenced by seasonal changes in foraging material and the phytolith concentrations within (Calandra et al., 2016a, b). Winkler et al. (2018) further demonstrated plant abrasiveness on rodent molar microwear. This study suggested that in addition to phytolith concentration, water content also affects plant abrasiveness. Guinea pigs fed dry grass possessed significantly rougher molar wear surfaces with large and deep scratches in comparison to the those fed fresh grass (Winkler et al., 2018). As incisors are used in the procurement of foodstuff, it is possible that variation plant hydration and phytolith content may contribute to microwear textures.

Furthermore, while it does not appear that previous work has been done regarding the effects of soil moisture to dental microwear, other tribological studies have indicated that interactions between soil type and moisture have led to differences in wear amounts (e.g., Natis et al., 2008) and soil abrasiveness (e.g., Mirmehrabi et al., 2015). Given the effects both soil type and burrowing behavior have had on incisor microwear in this dissertation, it is possible that microwear parameters might separate incisors collected during wet and dry seasons within the same habitat. However, although May represented a transitional season between the wet and dry period in the Northern Cape Province, rainfall was sparse. The lack of significant variation for

microwear parameters, thus, may be indicative of the similar climate conditions at the Kolomela properties during May and July.

Conclusion

Given dental microwear's application in reconstructing diets, it is unsurprising that little investigation has been done into the efficacy of rodent incisor microwear as an environmental proxy. To date, only four other studies have analyzed micromammal incisor microwear and potential environmental influences on its formation (Belmaker & Ungar, 2010; Caporale & Ungar, 2016; Ungar et al., 2021a; Withnell & Ungar, 2014). This study builds on existing work by not just analyzing differences by habitat and species, but by further breaking down these categories based on important biotic and abiotic variables potentially influential in microwear formation. Results of raw data analysis indicate that incisor microwear does indeed reflect characteristics of habitat much better than it does of diet. Microwear variables were able to separate habitats at both a macro and micro scale within a given ecosystem. And although interactions among factors were not tested, these results seem to indicate their importance as incisor microwear textures were seemingly influenced by non-dietary behavioral interactions with important abiotic characteristics like soil and vegetative cover.

It is important to note that while alterations in microwear patterns can take days to weeks (e.g., Grine, 1986; Teaford & Oyen, 1989; Winkler et al., 2021a), the rate in which the rodent incisors wear is even faster. Rodent incisors are ever-growing and continually erupt during an individual's lifetime, thus requiring deliberate gnawing to maintain shape and size (Happold, 2013). Although the gross wear rates for the Kolomela species could not be found, work with other muroids indicated that the average rate of attrition for rat lower incisors vary between

0.379 mm/day for individuals fed a standard laboratory diet (Weinreb et al., 1967) and 0.483 mm/day (Risnes et al., 1995). In addition, the complete structural turnover of a mouse incisor took 7.2 weeks (Coady et al., 1967). Should similar figures apply to the muroid species at Kolomela, then microwear found on the surfaces of incisor tips would reflect the last 5 to 6 hours prior to death for a field of 0.1 mm in height. While Chapter 6 will discuss the implications of these fast wear rates in comparison to molars, it is still important to touch upon it here. While these results indicate that rodent incisor microwear can parse fine scale spatial comparisons within a larger habitat, this may be in part due to the rapid turnover of rodent incisors.

These data provide important insights into the factors that may influence the formation of rodent incisor microwear, but results need to be interpreted with caution due to limitations in the study. As discussed in Chapter 3, sampling bias due to behavior is a common occurrence in ecological studies (see Biro & Dingermanse, 2009; Stuber et al., 2013). Basing analysis on wild-caught specimens, meant that: a) not all specimens could be utilized when studying a specific independent variable; b) those that were used lacked even sample sizes and could range from $10 > n > 50$; c) dispersion differences were not tested due to such uneven sample sizes; and d) testing for interactions became impractical due to the non-orthogonal samples and sheer number of factors considered. Dispersion analyses may better reflect some of the independent variables considered in this chapter, as previously noted. And individual analyses of these same variables appeared to indicate that interactions could be important in better understanding environmental effects on incisor microwear.

For example, almost all specimens at the rocky soil sites are that of the above ground nester *Mi. namaquensis*. This leads to the possibility that differences between rocky and other soils may, to some degree, be reflecting differences between burrowers and non-burrowers. In

addition, burrow characteristics such as depth and complexity are dependent not just on species but also on the characteristics of available soils (Laundre & Reynolds, 1993). There is a clear interaction between soil and burrowing behavior that needs to be investigated further. Controlled experiments into soil particle effects on microwear could provide complimentary information. These have been done with molars (e.g., Ackermans et al., 2020; Winkler et al., 2020b) but to date, have not been conducted with incisors. Doing so may further elucidate effects of grit, particular that stemming from soil, on incisor microwear.

However, these issues do not dismiss the potential efficacy of incisor microwear as an environmental proxy and highlight the need to continue with future research as to better utilize rodent incisors as a proxy. Based on these data, rodent incisor microwear does appear to be indicative of environmental characteristics rather than diet. Although this cannot be said with certainty given the similar diets among the rodents, it remains a reasonable inference due to the differences between incisors and molars in food acquisition and processing. Instead, habitat characteristics such as soil and vegetative cover, and interactions therewithin, appear to be primary drivers in microwear patterns. Although still preliminary, this research provides additional insight into rodent incisor microwear and adds to the limited extant baseline.

CHAPTER SIX: MOLAR MICROWEAR

Results

Of the rodent specimens collected during the 2017 season of the Kolomela biomonitoring project, only 175 possessed molars that preserved visible antemortem microwear on their mesial loph surfaces. These individuals comprised five different species from two different murid sub-families, Gerbillinae and Murinae, collected from the different Kolomela properties. In addition to analysis by species, taxon-free analyses of microwear texture patterns were conducted for behavioral and environmental variables. However, due to an inability to control rodent behavior, as explained in Chapter 3, a sampling bias occurred towards certain species, diets, and trapping locations. As such, only groups of sample size $n \geq 10$ were considered when running MANOVAs for each independent variable, with analyses for behavioral and environmental variables conducted using a taxa-free approach. Statistical significance in central tendencies occurred when analyzing microwear by species, burrowing behavior, and dust level. Results for each independent variable will be discussed individually: species, macrohabitat, microhabitat, diet, burrowing behavior, soil type, land cover, dust level, and collection month. Appendix III provides scale-sensitive fractal analysis (SSFA) and International Standards Organization (ISO) values for each specimen used. In addition to molar dental microwear texture analysis (DMTA), results are provided in this chapter for a comparison between incisor and molar surfaces.

Species Microwear Effects

Although the molar sample consisted of five species, only those of *Gerbilliscus leucogaster* (n = 105), *Micaelamys namaquensis* (n = 40), and *Rhabdomys bechuanae* (n = 22)

were considered in statistical analyses. As such, analyses compared one Gerbillinae (gerbil) species, *G. leucogaster*, and two Murinae (mouse) species, *Mi. namaquensis* and *R. bechuanae*. Descriptive statistics for all species are provided in Table 6.1 and representative photosimulations in Figure 6.1. Multivariate test results for central tendencies ($p < 0.005$) indicated significant variation among the species (Table 6.2). Individual ANOVAs, also presented in Table 6.2, indicated significance for four parameters: scale of maximum complexity (*Smc)* and textural fill volume (*Tfv),* developed interfacial area ratio (*Sdr),* and five-point pit height (*S5v*). Pairwise comparison tests for each DMTA parameter separated the *G. leucogaster* sample from that of *Mi. namaquensis* and *R. bechuanae* (Table 6.3, Figure 6.2). *Smc* and *Tfv* values were significantly lower for the gerbil than either mouse species, with *Sdr* and *S5v* values only marginally lower (significant by Fisher's but not by Tukey's tests). Microwear variables were not significantly different when comparing *R. bechuanae* to *Mi. namaquensis.* Table 5.4 provides microwear descriptions for each species based on these statistically significant parameters.

Table 6.1: Descriptive statistics of molar texture parameters by species.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc*$_9$	*HAsfc*$_{81}$
G. leucogaster (*n* = 105)*						
Mean	43.784	0.005	10.035	6500.131	0.814	2.794
SD	52.316	0.002	29.565	1245.324	0.955	4.363
G. paeba (*n* = 6)						
Mean	11.844	0.005	0.351	7517.217	0.572	0.827
SD	11.025	0.002	0.185	1531.731	0.243	0.353
Ma. coucha (*n* = 2)						
Mean	17.551	0.005	22.232	7725.067	0.858	2.988
SD	9.950	0.006	31.128	1995.664	0.318	1.926
Mi. namaquensi s (*n* = 40)*						
Mean	55.673	0.006	42.564	7710.602	1.212	1.902
SD	71.806	0.002	67.265	1614.097	1.345	2.017
R. bechuanae (*n* = 22)*						
Mean	78.028	0.005	42.793	7489.636	0.848	2.217
SD	85.024	0.002	68.557	1691.739	0.763	2.485

ISO:	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
G. leucogaster (*n* = 105)*								
Mean	-0.276	2.494	2.816	0.078	1.368	218.692	5.520	0.432
SD	0.365	1.034	1.284	0.026	0.477	146.843	10.417	0.182
G. paeba (*n* = 6)								
Mean	-0.052	2.975	6.324	0.094	1.702	156.526	3.568	0.309
SD	0.278	1.208	4.096	0.043	0.852	73.894	1.918	0.135
Ma. coucha (*n* = 2)								
Mean	-0.369	3.124	3.426	0.096	1.872	65.884	1.138	0.290
SD	0.115	0.902	0.122	0.010	0.053	17.970	0.171	0.032
Mi. namaquensi s (*n* = 40)*								
Mean	-0.217	3.142	3.247	0.090	1.752	192.592	3.612	0.445
SD	0.398	1.810	1.598	0.038	0.915	129.028	4.180	0.199
R. bechuanae (*n* = 22)*								
Mean	-0.205	3.083	4.185	0.097	1.994	224.185	9.295	0.485
SD	0.569	2.130	2.454	0.057	1.516	224.220	16.584	0.207

*denotes groups used in statistical analyses

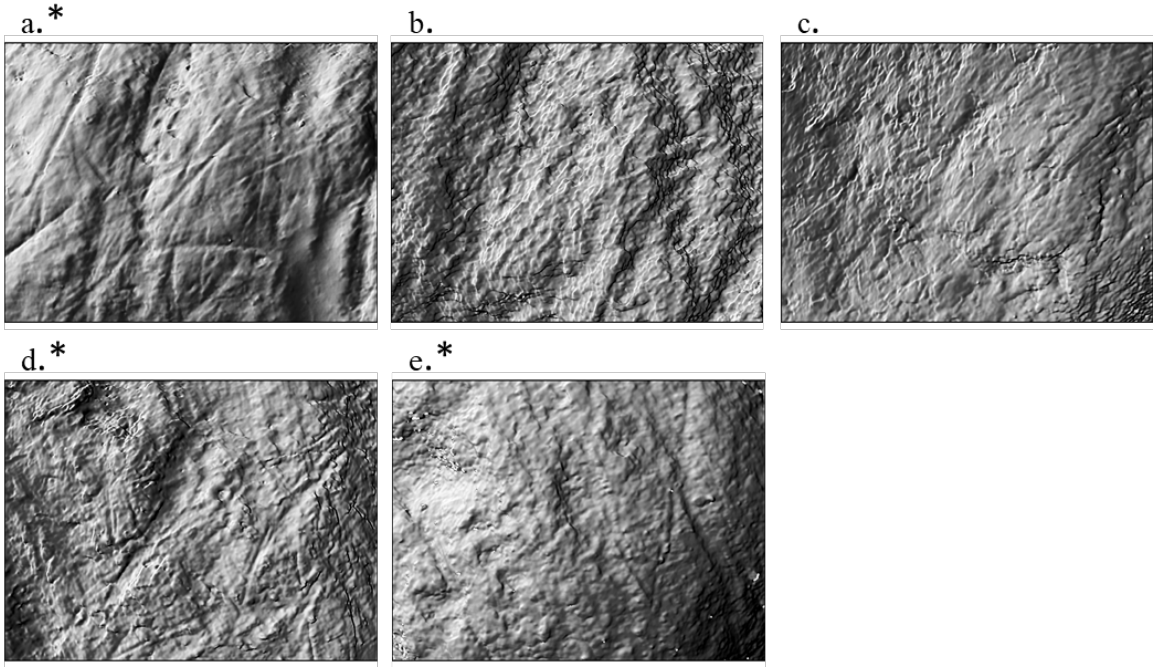

Figure 6.1: Representative microwear photosimulations for the seven rodent species found at Kolomela and its surrounding farms: *Gerbilliscus leucogaster* (a), *Gerbilliscus paeba* (b), *Mastomys coucha* (c), *Micaelamys namaquensis* (d), and *Rhabdomys buchanae* (e). Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Table 6.2: Statistical analyses for molars by species (*n* = 167).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.713	**1.990**	**2, 28**	**0.003**

(B) ANOVA results

	F- ratio	*p*-value
Asfc	1.894	0.154
epLsar	0.140	0.870
Smc	**13.635**	**0.000**
Tfv	**9.310**	**0.000**
$HAsfc_9$	0.862	0.424
$HAsfc_{81}$	0.006	0.993
Ssk	0.669	0.513
Sdr	**3.848**	**0.023**
S5v	**3.887**	**0.002**
Str	0.385	0.681
Sdv	0.181	0.835
Vvv	1.361	0.259
Sv	2.384	0.095
Sda	1.551	0.215

Statistically significant results, in which $p < 0.05$, are bolded.

Table 6.3: Pairwise comparisons for molars by species.

Variable	Comparison	difference
Smc	***Mi. namaquensis - G. leucogaster***	**34.806****
	R. bechuanae - G. leucogaster	**42.085****
	R. bechuanae - Mi. namaquensis	7.280
Tfv	***Mi. namaquensis - G. leucogaster***	**34.517****
	R. bechuanae - G. leucogaster	**25.803****
	R. bechuanae - Mi. namaquensis	-8.714
Sdr	*Mi. namaquensis - G. leucogaster*	9.639
	R. bechuanae - G. leucogaster	**30.405***
	R. bechuanae - Mi. namaquensis	20.766
S5v	***Mi. namaquensis - G. leucogaster***	**20.442***
	R. bechuanae - G. leucogaster	**22.548***
	R. bechuanae - Mi. namaquensis	2.107

Statistically significant results, in which $p < 0.05$, are bolded.

*$p < 0.05$ using Fisher's LSD test only; **$p < 0.05$ using both Tukey's HSD and Fisher's LSD tests.

Table 6.4: Molar microwear descriptions for species based on significant microwear parameters.

Species	Significant parameter trends	Microwear description
G. leucogaster	lowest *Smc* , *Tfv* , *Sdr*, *S5v*	rougher microwear features on a finer scale that are not very large or deep, nor arranged in a complex pattern
Mi. namaquensis	highest *Tfv* high *Smc* , *S5v* low *Sdr*	large and deep features that are not arranged in a very complex pattern
R. bechuanae	highest *Smc* , *Sdr* , *S5v* high *Tfv*	most complex microwear texture, with large and deep features

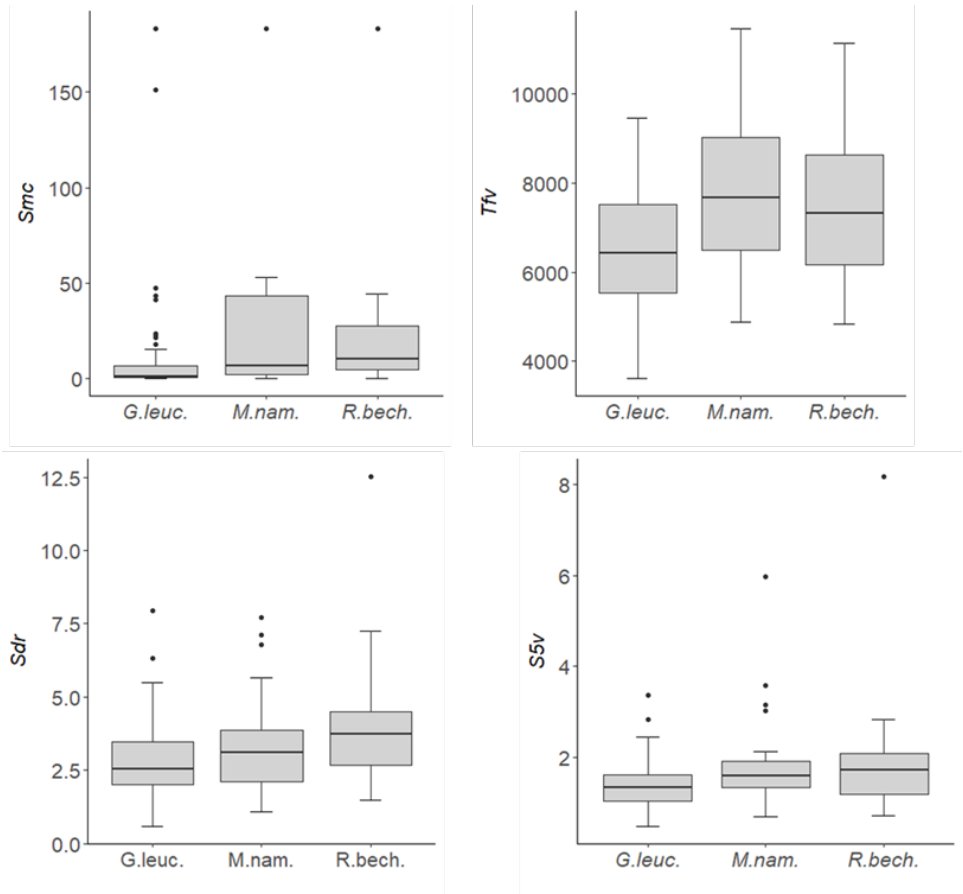

Figure 6.2: Box charts of statistically significant microwear texture variables when analyzed by species: *Gerbilliscus leucogaster* (*G.leuc.*), *Micaelamys namaquensis* (*M. nam*), and *Rhabdomys bechuanae* (*R.bech*.). The boxes represent the central 50% of values, with first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Macrohabitat Microwear Effects

The molar microwear sample was comprised of seven sampling habitats: the Kolomela mine and six farms owned by Kumba Iron Ore. In addition to the Kolomela mine (n = 16), farms Grootpan (n = 51), Heuningkrantz (n = 51), Kappies Karrieboom (n = 36), and Sunnyside/Stofdraai (n = 10) were considered in the statistical analysis. Table 3.3 (Chapter 3) provides key characteristics of each of these habitats. Descriptive statistics for all locations are

provided in Table 6.5, with representative photosimulations provided in Figure 6.3. No significance was found for the MANOVA assessing microwear texture among these macrohabitats (p = 0.845; Table 6.6).

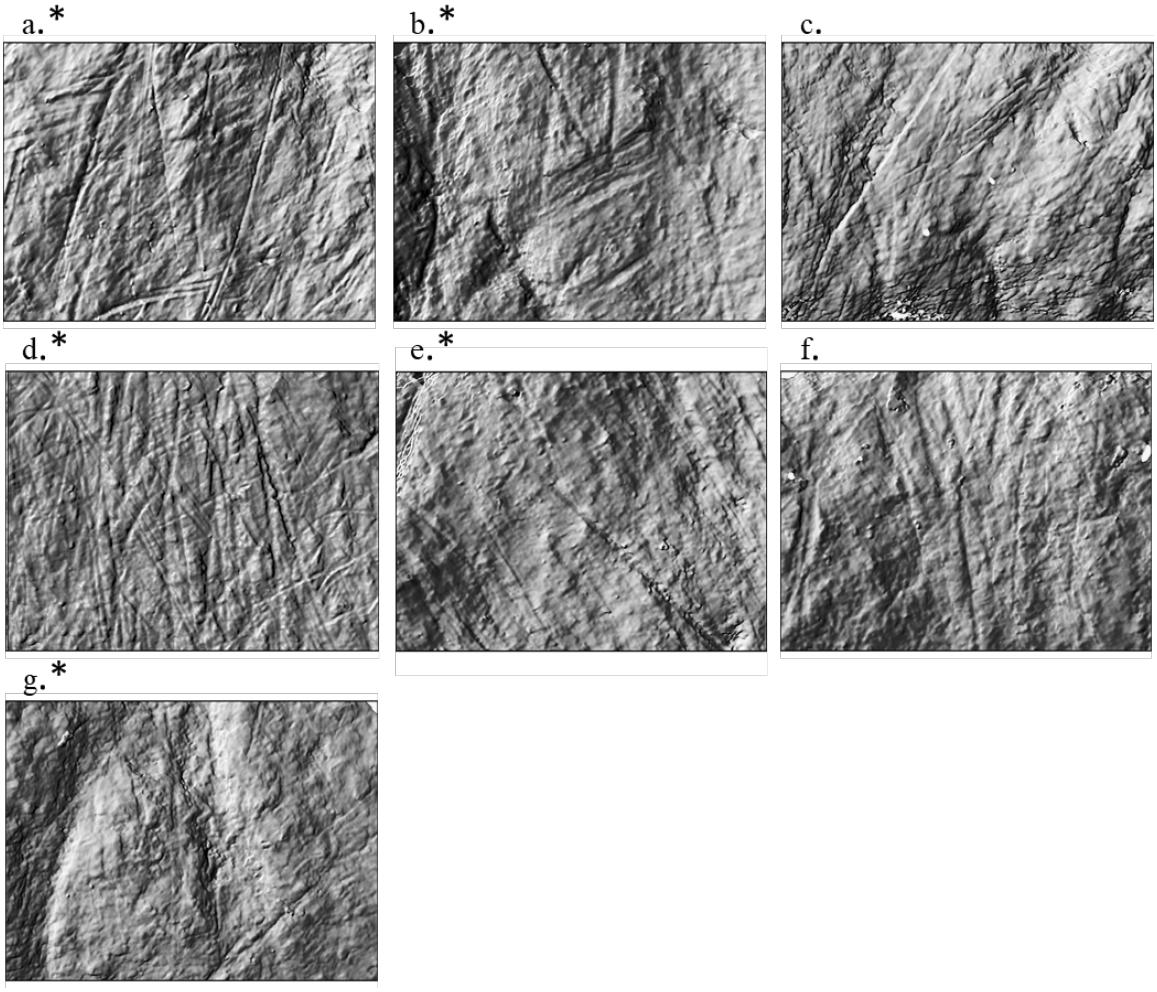

Figure 6.3: Representative incisor microwear photosimulations for each sampling habitat, the mine and the six farms: Kolomela (a), Grootpan (b), Gruispan (c), Heuningkrantz (d), Kappies Kareeboom (e), Sunnyside (f), and Wildealsput (g). Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Table 6.5: Descriptive statistics of molar texture parameters by farm habitats.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
Kolomela (n = 16)*						
Mean	49.262	0.006	14.915	6859.014	0.732	1.991
SD	52.376	0.002	45.079	1240.657	0.555	2.707
Grootpan (*n* = 51)*						
Mean	59.456	0.005	16.644	6820.394	0.705	2.287
SD	68.882	0.002	41.177	1560.679	0.581	2.952
Gruispan (*n* = 6)						
Mean	30.481	0.005	4.940	7050.520	1.385	1.691
SD	49.399	0.002	8.985	1439.439	1.508	1.341
Heuningkrantz (*n* = 51)*						
Mean	44.114	0.006	33.207	6959.721	1.053	2.128
SD	60.693	0.002	61.967	1449.502	1.237	2.967
Kappies Karrieboom (*n* = 36)*						
Mean	57.726	0.006	24.307	7272.422	0.871	3.688
SD	69.430	0.002	50.231	1603.760	0.801	5.669
Sunnyside/Stofdraai (*n* = 10)*						
Mean	12.037	0.005	5.399	6651.602	1.351	1.165
SD	17.544	0.003	8.826	1863.622	2.201	1.019
Wildealsput (*n* = 5)						
Mean	42.208	0.006	2.213	6685.427	0.610	3.423
SD	22.547	0.003	2.265	1197.232	0.104	4.618

ISO:	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
Kolomela (n = 16)*								
Mean	-0.261	2.703	3.383	0.090	1.541	167.840	4.094	0.413
SD	0.235	0.863	1.675	0.034	0.520	54.679	3.186	0.169
Grootpan (*n* = 51)*								
Mean	-0.294	2.810	3.383	0.087	1.668	224.273	7.182	0.432
SD	0.509	1.657	1.965	0.041	1.086	190.330	12.292	0.177
Gruispan (*n* = 6)								
Mean	-0.190	2.476	3.709	0.075	1.506	161.575	2.104	0.443
SD	0.365	1.092	1.065	0.019	0.393	75.747	0.499	0.170
Heuningkrantz (*n* = 51)*								
Mean	-0.216	2.766	2.989	0.083	1.540	228.488	4.836	0.460
SD	0.346	1.554	1.431	0.029	0.813	171.235	9.743	0.208
Kappies Karrieboom (*n* = 36)*								
Mean	-0.182	2.751	3.353	0.083	1.481	198.835	5.881	0.400
SD	0.367	1.232	2.449	0.041	0.654	122.683	12.639	0.195
Sunnyside/Stofdraai (*n* = 10)*								
Mean	19.000	2.977	2.982	0.083	1.567	172.421	3.839	0.472
SD	0.334	1.703	1.283	0.030	0.773	57.483	2.747	0.149
Wildealsput (*n* = 5)								
Mean	-0.049	1.827	2.371	0.062	1.219	170.286	2.452	0.477
SD	0.249	0.260	0.936	0.015	0.330	79.880	1.641	0.234

*denotes groups used in statistical analyses

Table 6.6: Statistical analyses for molars by farm habitats (*n* = 164).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.742	0.812	4, 56	0.845

Statistically significant results, in which $p < 0.05$, are bolded.

Microhabitat Microwear Effects

While eighteen transects were used in rodent trapping, only eight of these provided sufficient samples ($n \geq 10$) for statistical analysis: Ekstra (on the mine property; $n = 16$), GN1 ($n = 25$) and GN2 ($n = 26$) from Grootpan, HK3 ($n = 12$) and HK7 ($n = 28$) from Heuningkrantz, KK2 ($n = 15$) and KK3 ($n = 21$) from Kappies Kareeboom, and the Stofdraai transect ($n = 10$) within the Sunnyside farm (see Table 3.4 in Chapter 3 for environmental summary of each transect). The descriptive statistics for transect microhabitats can be found in Table 6.7 and representative photosimulations in Figure 6.4. MANOVA results indicated a lack of significance for microwear texture central tendency among these macrohabitats ($p = 0.147$; Table 6.8).

Table 6.7: Descriptive statistics of molar texture parameters by transect microhabitats.

SSFA:		*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
Kolomela:	Ekstra (*n* = 16)*						
	Mean	49.262	0.006	14.915	6859.014	0.732	1.991
	SD	52.376	0.002	45.079	1240.657	0.555	2.707
Grootpan:	GN1 (*n* = 25)*						
	Mean	66.744	0.004	12.841	6723.366	0.543	1.546
	SD	77.076	0.002	37.046	1423.271	0.466	2.055
	GN2 (*n* = 26)*						
	Mean	52.729	0.005	20.156	6909.958	0.855	2.971
	SD	61.123	0.002	45.099	1700.877	0.642	3.490
Gruispan :	GP1 (*n* = 2)						
	Mean	69.446	0.004	3.004	7174.315	1.232	1.755
	SD	85.916	0.001	3.546	881.718	0.481	0.959
	GP2 (*n* = 4)						
	Mean	10.998	0.006	5.908	6988.622	1.461	1.660
	SD	9.396	0.003	11.252	1782.930	1.921	1.639
Heuningkrantz:	HK1 (*n* = 2)						
	Mean	7.730	0.005	91.786	6246.214	0.437	0.654
	SD	1.997	0.002	129.381	1514.872	0.282	0.236
	HK2 (*n* = 1)						
	Mean	2.608	0.007	183.272	5360.241	0.193	0.412
	SD	n/a	n/a	n/a	n/a	n/a	n/a
	HK3 (*n* = 12)*						
	Mean	34.026	0.006	9.905	6503.288	0.792	3.308
	SD	47.735	0.001	16.695	1270.310	0.833	4.945
	HK5 (*n* = 6)						
	Mean	22.696	0.006	2.398	6613.994	1.137	1.070
	SD	40.200	0.001	2.257	1317.716	1.297	0.609
	HK7 (*n* = 28)*						
	Mean	58.332	0.006	42.557	7412.191	1.249	1.948
	SD	70.858	0.002	68.324	1484.226	1.446	2.204
	HK9 (*n* = 2)						
	Mean	26.978	0.003	0.937	5914.175	0.662	3.063
	SD	29.682	0.001	0.624	1460.835	0.416	2.131
Kappies Karee:	KK1 (*n* = 3)						
	Mean	31.946	0.004	14.633	7792.398	0.858	2.225
	SD	27.404	0.003	24.746	87.601	0.482	2.358
	KK2 (*n* = 15)*						
	Mean	52.461	0.005	17.081	6300.036	0.565	4.155
	SD	62.376	0.003	46.526	1188.321	0.329	6.717
	KK3 (*n* = 21)*						
	Mean	66.411	0.006	31.940	7996.081	1.129	3.543
	SD	80.065	0.002	56.707	1618.409	1.026	5.270

Table 6.7 (Cont.)

SSFA:		*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$		
Sunnyside:	Stofdraai (*n* = 10)*								
	Mean	12.037	0.005	5.399	6651.602	1.351	1.165		
	SD	17.544	0.003	8.826	1863.622	2.201	1.019		
Wildealsput:	WAP1 (*n* = 1)								
	Mean	43.415	0.002	0.741	4637.612	0.529	1.258		
	SD	n/a	n/a	n/a	n/a	n/a	n/a		
	WAP2 (*n* = 2)								
	Mean	54.528	0.006	2.511	7373.784	0.551	6.379		
	SD	15.367	0.002	2.304	426.468	0.011	7.413		
	WAP3 (*n* = 2)								
	Mean	29.283	0.007	2.652	7020.976	0.709	1.550		
	SD	34.032	0.002	3.533	430.319	0.100	1.078		
ISO:		***Ssk***	***Sv***	***Sdr***	***Vvv***	***S5v***	***Sda***	***Sdv***	***Str***
Kolomela:	Ekstra (*n* = 16)*								
	Mean	-0.261	2.703	3.383	0.090	1.541	167.840	4.094	0.413
	SD	0.235	0.863	1.675	0.034	0.520	54.679	3.186	0.169
Grootpan:	GN1 (*n* = 25)*								
	Mean	-0.278	2.783	3.647	0.088	1.560	224.525	8.201	0.420
	SD	0.433	1.188	1.485	0.026	0.602	163.260	10.452	0.179
	GN2 (*n* = 26)*								
	Mean	-0.310	2.835	3.129	0.087	1.777	224.032	6.204	0.441
	SD	0.581	2.033	2.338	0.052	1.422	216.582	13.980	0.179
Gruispan :	Gruispan								
	GP1 (*n* = 2)								
	Mean	-0.114	2.076	0.078	0.078	1.652	126.484	1.874	0.520
	SD	0.215	0.380	0.290	0.028	0.589	37.051	0.779	0.138
	GP2 (*n* = 4)								
	Mean	-0.228	2.676	3.855	0.074	1.434	184.968	2.258	0.404
	SD	0.447	1.334	1.333	0.019	0.347	93.471	0.326	0.189
Heuningkrantz:	HK1 (*n* = 2)								
	Mean	-0.019	1.906	3.164	0.046	1.006	84.125	0.775	0.339
	SD	0.003	0.207	0.065	0.002	0.746	41.422	0.336	0.228
	HK2 (*n* = 1)								
	Mean	0.071	1.504	2.560	0.051	1.129	157.755	7.652	0.783
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	HK3 (*n* = 12)*								
	Mean	-0.102	2.518	2.730	0.086	1.318	262.652	8.297	0.419
	SD	0.204	1.177	1.351	0.034	0.602	221.608	18.315	0.216
	HK5 (*n* = 6)								
	Mean	-0.337	2.427	3.004	0.083	1.468	287.306	2.802	0.556
	SD	0.310	0.666	1.309	0.027	0.475	216.860	1.542	0.199

Table 6.7 (Cont.)

ISO:		*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
Heuningkrantz:	HK7 (n = 28)*								
	Mean	-0.264	3.113	3.203	0.088	1.747	211.024	3.960	0.462
	SD	0.407	1.854	1.572	0.026	0.942	145.685	4.879	0.216
	HK9 (n = 2)								
	Mean	-0.216	1.919	1.540	0.054	0.934	235.957	4.196	0.352
	SD	0.290	1.042	0.640	0.024	0.334	7.151	0.347	0.021
Kappies Karee:	KK1 (n = 3)								
	Mean	-0.237	2.598	6.176	0.092	1.687	153.803	3.818	0.312
	SD	0.281	1.250	6.687	0.056	0.833	31.781	0.618	0.116
	KK2 (n = 15)*								
	Mean	-0.246	2.508	3.230	0.074	1.357	224.789	4.437	0.393
	SD	0.399	0.705	1.746	0.024	0.413	128.955	2.626	0.194
	KK3 (n = 21)*								
	Mean	-0.115	2.993	2.964	0.088	1.558	182.530	7.768	0.421
	SD	0.358	1.573	1.679	0.050	0.812	128.329	18.832	0.211
Sunnyside:	Stofdraai (n = 10)*								
	Mean	-0.519	2.977	2.982	0.083	1.567	172.421	3.839	0.472
	SD	0.334	1.703	1.283	0.030	0.773	57.483	2.747	0.149
Wildealsput:	WAP1 (n = 1)								
	Mean	-0.208	2.097	2.696	0.087	1.283	190.945	2.137	0.668
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	WAP2 (n = 2)								
	Mean	-0.072	1.952	2.203	0.058	1.460	209.863	2.868	0.493
	SD	0.067	0.168	0.268	0.005	0.144	127.527	2.693	0.259
	WAP3 (n = 2)								
	Mean	0.052	1.565	2.377	0.053	0.946	120.379	2.193	0.364
	SD	0.444	0.026	1.808	0.001	0.382	26.820	1.715	0.300

*denotes groups used in statistical analyses

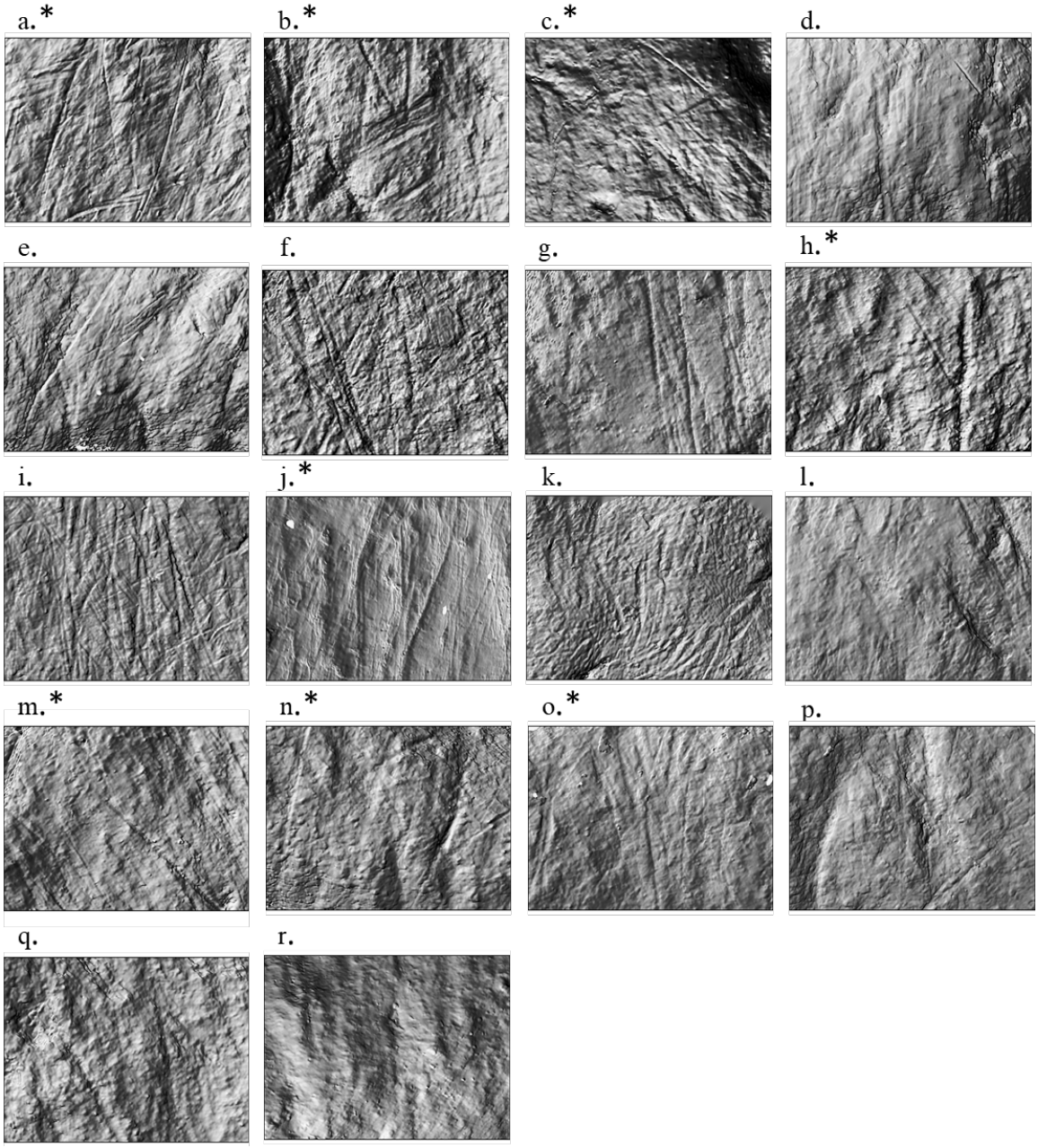

Figure 6.4: Representative incisor microwear photosimulations for each transect within each of the seven habitats: Kolomela, transect Ekstra (a); Grootpan, transects GN1 (b) and GN2 (c); Gruispan, transect GP2 (d); Heuningkrantz, transects HK1 (e), HK2 (f), HK3 (g), HK4 (h), HK5 (i), HK7 (j), HK9 (k), and HK10 (l); Kappies Kareeboom, transects KK1 (m), KK2 (n), and KK3 (o); Sunnyside, transect Stofdraai (p); and Wildealsput, transects WAP2 (q) and WAP3 (r). Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Table 6.8: Statistical analyses for molars by transect microhabitats (*n* = 150).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.441	1.162	7, 98	0.147

Statistically significant results, in which $p < 0.05$, are bolded.

Dietary Microwear Effects

Stomach content analysis separated specimens into 13 dietary categories, each with a primary and secondary component. Rather than follow the traditional omnivore, herbivore, granivore, carnivore labels, the diets examined here depended upon which food item, or items, contributed most to the percent volume of all material within the stomach cavity. This was done to potentially address differences in food physical properties that may affect microwear formation (see Chapter 3). The three diets considered in the statistical analyses were grass seed-grass seed (GSGS, *n* = 85), grass seed-curculionid (GSCU, *n* = 23), and grass seed-grass blade (GSGR, *n* = 20). All other dietary categories were excluded due to a lack of sufficient sample size, although descriptive statistics and representative photosimulations are provided for all (Table 6.9 and Figure 6.5, respectively). The multivariate test for central tendencies did not result in any significance (*p* = 0.069; Table 6.10).

Table 6.9: Descriptive statistics of molar texture parameters by diet.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_{9}$	*HAsfc* $_{81}$
annelid - annelid (n = 1)						
Mean	286.790	0.006	29.154	7684.379	0.445	0.903
SD	n/a	n/a	n/a	n/a	n/a	n/a
curculonid - grass seed (n = 2)						
Mean	15.363	0.004	1.033	5573.878	0.828	1.741
SD	17.704	0.000	0.536	846.473	0.719	1.232
feather - grass seed (n = 1)						
Mean	14.182	0.007	0.496	7798.396	2.851	3.258
SD	n/a	n/a	n/a	n/a	n/a	n/a
grass seed - annelid (n = 2)						
Mean	66.816	0.002	4.807	6965.314	0.412	0.812
SD	87.645	0.000	6.374	765.559	0.219	0.098
grass seed - curculonid (n = 23)*						
Mean	41.353	0.005	5.018	6839.522	1.457	3.495
SD	50.808	0.000	8.701	1122.402	1.729	4.067
grass seed - dicot (n = 4)						
Mean	102.727	0.004	2.564	5524.235	0.527	0.914
SD	88.709	0.000	2.551	864.975	0.354	0.451
grass seed - dicot seed (n = 6)						
Mean	50.407	0.006	33.922	7005.289	0.457	1.436
SD	57.115	0.002	73.389	1614.002	0.149	1.550
grass seed - flesh (n = 5)						
Mean	51.421	0.010	3.854	6653.278	0.495	4.382
SD	43.448	0.003	3.685	1162.267	0.215	8.077
grass seed - grass (n = 20)*						
Mean	40.407	0.010	23.201	7159.374	0.978	2.375
SD	40.522	0.002	55.710	1540.196	0.712	2.822
grass seed - grass seed (n = 85)*						
Mean	49.372	0.010	27.562	7148.692	0.877	2.283
SD	64.639	0.002	54.525	1603.115	0.998	3.608
grass seed - hair (n = 3)						
Mean	110.164	0.000	3.090	6229.170	0.501	4.527
SD	99.188	0.001	3.305	1778.708	0.140	6.490

Table 6.9 (Cont.)

ISO:	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
annelid - annelid (*n* = 1)								
Mean	0.003	2.782	6.741	0.106	2.039	129.694	1.891	0.536
SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
curculonid - grass seed (*n* = 2)								
Mean	-0.290	2.282	2.553	0.088	1.343	172.232	1.563	0.364
SD	0.292	1.029	1.150	0.031	1.026	101.748	0.339	0.112
feather - grass seed (*n* = 1)								
Mean	0.096	5.454	5.099	0.133	2.454	12.933	0.306	0.189
SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
grass seed - annelid (*n* = 2)								
Mean	-0.271	2.573	3.063	0.087	1.695	345.092	12.347	0.539
SD	0.237	1.337	1.045	0.055	0.577	328.779	16.068	0.161
grass seed - curculonid (*n* = 23)*								
Mean	-0.334	2.574	2.819	0.082	1.339	216.840	6.756	0.434
SD	0.395	1.196	0.848	0.023	0.545	148.581	15.259	0.163
grass seed - dicot (*n* = 4)								
Mean	-0.462	3.229	3.785	0.081	1.685	278.082	13.947	0.472
SD	0.328	0.242	1.171	0.013	0.449	157.422	17.267	0.227
grass seed - dicot seed (*n* = 6)								
Mean	-0.144	2.123	2.337	0.063	1.319	144.625	2.245	0.401
SD	0.255	0.868	1.024	0.019	0.538	60.212	1.429	0.190
grass seed - flesh (*n* = 5)								
Mean	-0.226	2.021	2.419	0.067	1.075	136.797	2.685	0.292
SD	0.513	0.875	1.063	0.031	0.360	31.232	1.250	0.237
grass seed - grass (*n* = 20)*								
Mean	-0.228	3.010	2.853	0.073	1.728	199.471	5.427	0.433
SD	0.326	2.210	1.682	0.023	1.205	135.183	7.281	0.178
grass seed - grass seed (*n* = 85)*								
Mean	-0.217	2.887	3.559	0.091	1.700	188.179	4.916	0.459
SD	0.458	1.521	2.157	0.042	0.908	142.612	8.697	0.194
grass seed - hair (*n* = 3)								
Mean	-0.323	1.675	2.031	0.066	0.988	188.798	2.016	0.481
SD	0.398	0.721	1.595	0.030	0.420	23.462	1.063	0.160

*denotes groups used in statistical analyses

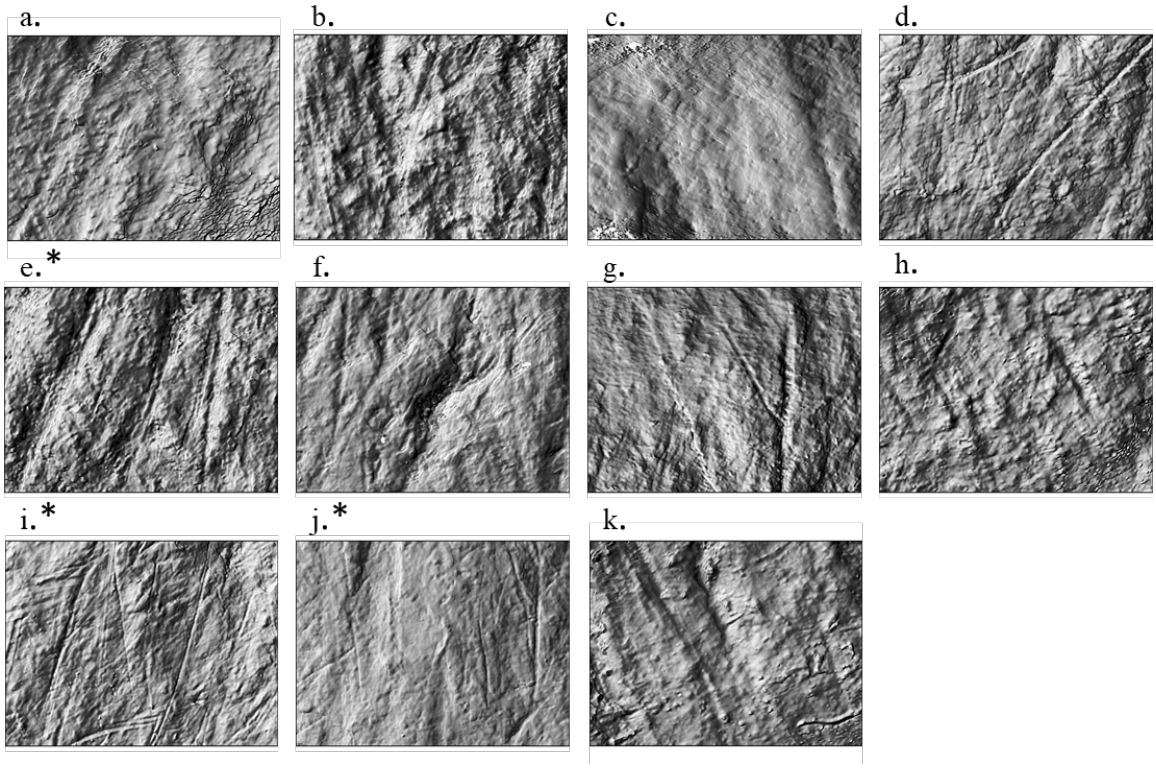

Figure 6.5: Representative microwear photosimulations for each diet based upon stomach content analysis: annelid-annelid (a), curculionid-grass seed (b), feather-grass seed (c), grass seed-annelid (d), grass seed-curculionid (e), grass seed-dicot (f), grass seed-dicot seed (g), grass seed-flesh (h), grass seed-grass (i), grass seed-grass seed (j), grass seed-hair (k). Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Table 6.10: Statistical analyses for molars by diet (*n* = 128).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.713	1.476	2, 28	0.065

Statistically significant results, in which $p < 0.05$, are bolded.

Burrowing Behavior Microwear Effects

Rodents were divided into two categories based upon whether they engage in excavating underground burrows (*G. leucogaster*, *G. paeba*, and *R. bechuanae*, n = 133) or refrain from such activity (*Mastomys coucha* and *Mi. namaquensis*, *n* = 42). Table 6.11 presents the descriptive statistics for each group, with representative photographs provided in Figure 6.6. The

MANOVA comparison between the two groups indicated statistical significance for central tendencies ($p < 0.05$; Table 6.12). Individual ANOVAs indicated that these differences occurred for three texture parameters: scale of maximum complexity (*Smc*), texture fill variable (*Tfv*), and five-point pit height (*S5v*; Table 6.12 and Figure 6.7). The molar surfaces obtained from burrowing species possessed lower values for statistically significant parameters than those molars obtained from specimens that do not engage in burrowing activity. Microwear descriptions based on these statistically significant parameters are provided in Table 5.17.

Table 6.11: Descriptive statistics of molar texture parameters by burrowing behavior.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_{9}$	***HAsfc*** $_{81}$		
burrower (n = 133)*								
Mean	48.040	0.005	15.054	6711.280	0.808	2.609		
SD	59.505	0.002	39.998	1390.894	0.903	4.020		
non-burrower (n = 42)*								
Mean	53.867	0.006	41.595	7711.291	1.195	1.953		
SD	70.530	0.003	65.929	1604.796	1.315	2.004		
ISO:	***Ssk***	***Sv***	***Sdr***	***Vvv***	***S5v***	***Sda***	***Sdv***	***Str***
burrower (n = 133)*								
Mean	-0.254	2.616	3.210	0.082	1.492	216.573	6.119	0.435
SD	0.404	1.299	1.912	0.035	0.804	160.694	11.591	0.187
non-burrower (n = 42)*								
Mean	-0.224	3.141	3.256	0.090	1.758	185.352	3.470	0.438
SD	0.390	1.771	1.559	0.037	0.893	128.720	4.097	0.197

*denotes groups used in statistical analyses

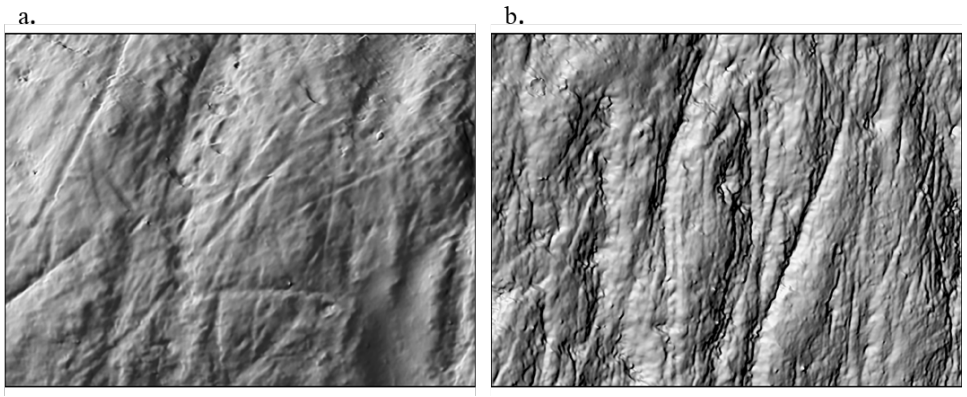

Figure 6.6: Representative microwear photosimulations for species that excavate underground burrows (a) and those that do not (b). Each photosimulation measures an area of 85 µm x 64 µm.

Table 6.12: Statistical analyses for molars by burrowing behavior (*n* = 175).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.845	**2.900**	**1, 14**	**0.015**

(B) ANOVA results

	F-ratio	*p*-value
Asfc	0.266	0.607
epLsar	2.394	0.124
Smc	**11.517**	**0.001**
Tfv	**12.198**	**0.001**
$HAsfc_9$	2.044	0.155
$HAsfc_{81}$	0.235	0.629
Ssk	0.175	0.676
Sdr	0.131	0.718
S5v	**4.181**	**0.042**
Str	0.014	0.906
Sdv	0.235	0.629
Vvv	1.733	0.190
Sv	3.464	0.064
Sda	0.005	0.945

Statistically significant results, in which $p < 0.05$, are bolded.

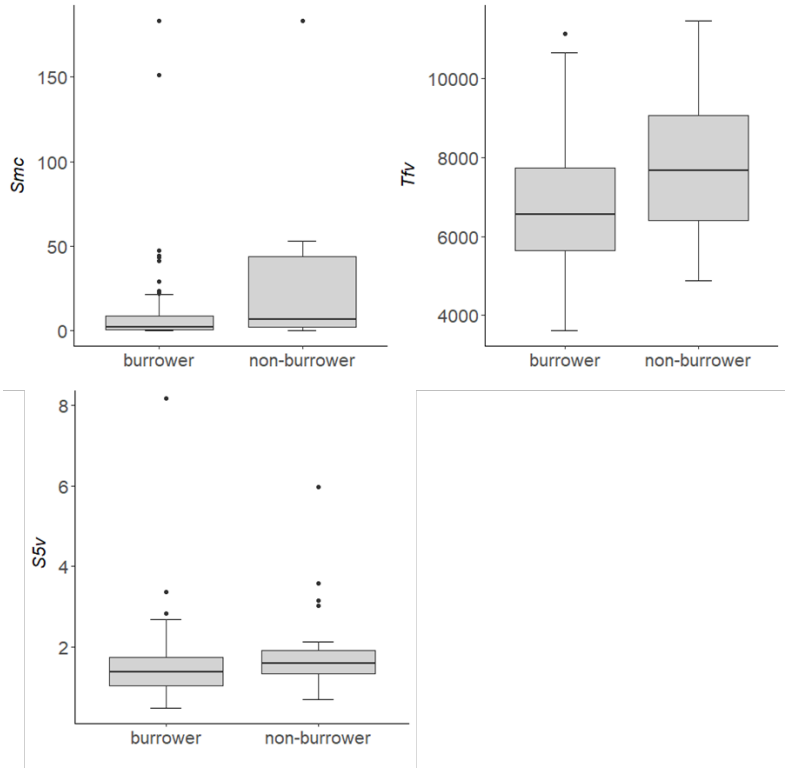

Figure 6.7: Box charts of statistically significant microwear texture variables when analyzed by burrowing behavior. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 6.13: Molar microwear descriptions for species based on significant microwear parameters.

Burrowing behavior	Significant parameter trends	Microwear description
excavates burrows	lowest *Smc* , *Tfv* , and *S5v*	Microwear patterns appear rougher at finer scales, with small and shallow features
does not excavate burrows	highest *Smc* , *Tfv* , and *S5v*	Microwear features are large and deep

Soil Microwear Effects

Transect notes from Avenant and du Plessis (2018) detail the soils associated with each trapping transect. A total of five soil classification types are used: loam (n = 44), rocky, (n = 30),

sand (n = 37), and mixtures of clay-loam (n = 62) and clay-loam-sand (n = 2). Descriptive statistics for molar texture attributes by each of these soils is provided in Table 6.14. Representative photosimulations are given in Figure 6.8. Statistical analyses utilized molars from loam soil, clay-loam mix, rocky substrate, and sand groups. MANOVA results for central tendencies indicated a lack of significance in molar microwear attributes considered by soil type (p = 0.855; Table 6.15).

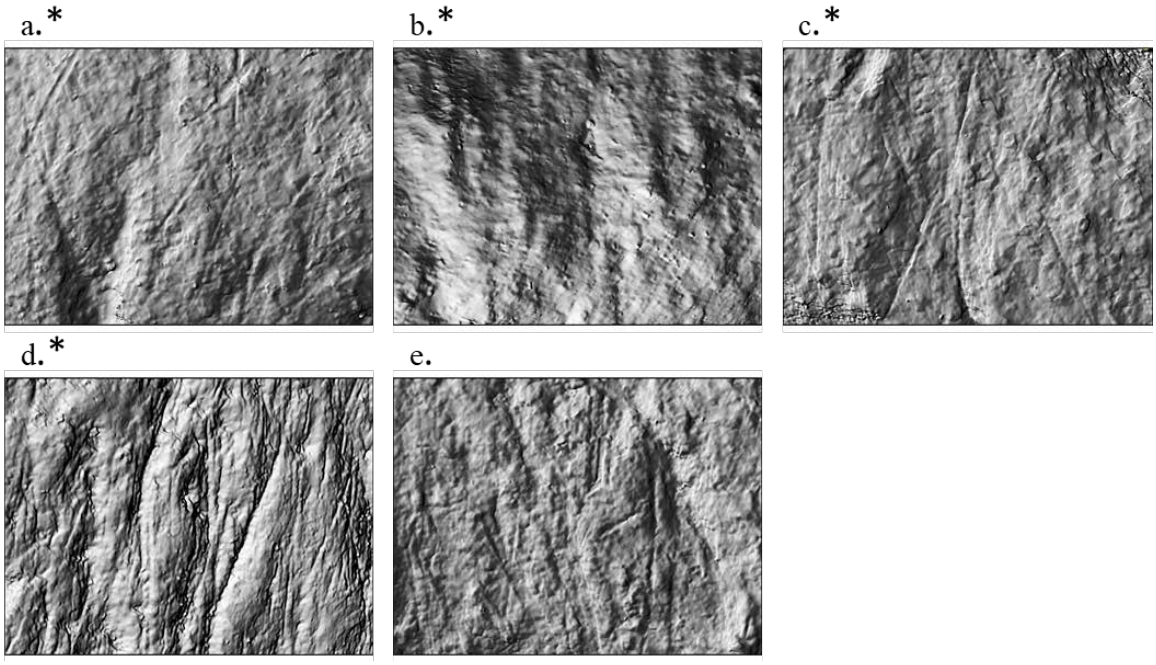

Figure 6.8: Representative microwear photosimulations for the soils found at the different habitats: clay-loam (a), clay-loam-sand (b), loam (c), rocky (d), and sand (e). Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Table 6.14: Descriptive statistics of molar texture parameters by soil type.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_9$	***HAsfc*** $_{81}$		
clay-loam (*n* = 62)*								
Mean	55.092	0.005	14.931	6908.977	0.775	2.359		
SD	64.888	0.002	37.809	1497.121	0.718	2.992		
clay-loam-sand (*n* = 2)								
Mean	29.283	0.007	2.652	7020.976	0.709	1.550		
SD	34.032	0.002	3.533	430.319	0.100	1.078		
loam (*n* = 44)*								
Mean	48.775	0.006	20.134	7035.992	0.973	3.159		
SD	65.689	0.003	45.970	1721.956	1.253	5.225		
rocky (*n* = 30)*								
Mean	56.242	0.006	39.782	7312.323	1.210	2.023		
SD	69.052	0.002	66.766	1506.331	1.405	2.182		
sand (n = 37)*								
Mean	36.507	0.006	19.966	6630.279	0.787	2.154		
SD	47.412	0.002	50.214	1233.288	0.784	3.382		
ISO:	***Ssk***	***Sv***	***Sdr***	***Vvv***	***S5v***	***Sda***	***Sdv***	***Str***
clay-loam (*n* = 62)*								
Mean	-0.274	2.739	3.511	0.085	1.647	214.888	6.435	0.429
SD	0.478	1.560	2.269	0.040	1.001	176.647	11.317	0.175
clay-loam-sand (*n* = 2)								
Mean	0.052	1.565	2.377	0.053	0.946	120.379	2.193	0.364
SD	0.444	0.026	1.808	0.001	0.382	26.820	1.715	0.300
loam (*n* = 44)*								
Mean	-0.251	2.795	3.056	0.082	1.480	196.562	5.506	0.428
SD	0.387	1.329	1.575	0.037	0.661	114.505	11.636	0.192
rocky (*n* = 30)*								
Mean	-0.261	3.033	3.093	0.086	1.693	213.102	3.980	0.455
SD	0.397	1.825	1.579	0.027	0.934	139.393	4.663	0.203
sand (n = 37)*								
Mean	-0.198	2.518	3.067	0.084	1.406	217.284	5.200	0.445
SD	0.247	0.930	1.425	0.032	0.541	168.604	10.892	0.200

*denotes groups used in statistical analyses

Table 6.15: Statistical analyses for molars by soil type (*n* = 173).

(A) MANOVA results

Wilks' λ	***F*-value**	**df**	***p*-value**
0.819	0.770	3, 42	0.851

Statistically significant results, in which p < 0.05, are bolded.

Land Cover Microwear Effects

The ground composition for the trapping transects set by Avenant and du Plessis were also described based upon the percent cover of grass, bush/shrub, tree, and exposed soil at each location. Utilizing these metadata and the hierarchal land cover classification system created by Grunblatt et al. (1989), it was determined that rodents were trapped in nine distinct land cover categories (see Chapter 3). Of these categories, five possessed sufficient sample size to be used in analysis: dense treed grassland (dTG; $n = 41$), dense treed shrubland (dTS; $n = 25$), open grassed shrubland (oGS; $n = 48$), open shrubbed grassland (oSG; $n = 15$), and closed shrubbed grassland (cSG; $n = 10$). Descriptive statistics of the molar microwear texture parameters are listed in Table 6.16 and representative photosimulations can be found in Figure 6.9. No statistical significance was reported by the MANOVA ($p = 0.057$; Table 6.17).

Table 6.16: Descriptive statistics of molar texture parameters by land cover classification.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc* $_9$	*HAsfc* $_{81}$
closed grassed shrubland (cGS; *n* = 4)						
Mean	10.998	0.006	5.908	6988.622	1.461	1.660
SD	9.396	0.003	11.252	1782.930	1.921	1.639
closed shrubbed grassland (cSG; n = 10)*						
Mean	12.037	0.005	5.399	6651.602	1.351	1.165
SD	17.544	0.003	8.826	1863.622	2.201	1.019
dense shrubbed grassland (dSG; *n* = 1)						
Mean	43.415	0.002	0.741	4637.612	0.529	1.258
SD	n/a	n/a	n/a	n/a	n/a	n/a
dense treed grassland (dTG; *n* = 23)*						
Mean	26.805	0.005	21.825	6408.888	0.814	2.346
SD	40.491	0.002	52.452	1222.195	0.896	3.735
dense treed shrubland (dTS; *n* = 25) *						
Mean	66.744	0.004	12.841	6723.366	0.543	1.546
SD	77.076	0.002	37.046	1423.271	0.466	2.055
open grassed shrubland (oGS; *n* = 48)*						
Mean	51.368	0.006	16.230	6927.943	0.811	2.676
SD	55.562	0.002	41.994	1437.922	0.580	3.303
open grassed woodland (oGW; *n* = 18)*						
Mean	66.411	0.006	31.940	7996.081	1.129	3.543
SD	80.065	0.002	56.707	1618.409	1.016	5.270
open shrubbed grassland (oSG; *n* = 15)*						
Mean	52.461	0.005	17.081	6300.036	0.565	4.155
SD	62.376	0.003	46.526	1188.321	0.329	6.717
open shrubbed woodland (oSW; *n* = 21)*						
Mean	55.778	0.006	39.854	7448.985	1.121	1.975
SD	68.057	0.003	65.670	1427.996	1.382	2.180

Table 6.16 (Cont.)

ISO:	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
closed grassed shrubland (cGS; *n* = 4)								
Mean	-0.228	2.676	3.855	0.074	1.434	184.968	2.258	0.404
SD	0.447	1.334	1.333	0.019	0.347	93.471	0.326	0.189
closed shrubbed grassland (cSG; n = 10)*								
Mean	-0.519	2.977	2.982	0.083	1.567	172.421	3.839	0.472
SD	0.334	1.703	1.283	0.030	0.773	57.483	2.747	0.149
dense shrubbed grassland (dSG; *n* = 1)								
Mean	-0.208	2.097	2.696	0.087	1.283	190.945	2.137	0.668
SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
dense treed grassland (dTG; *n* = 23)*								
Mean	-0.159	2.345	2.728	0.077	1.288	245.951	5.712	0.458
SD	0.248	0.964	1.220	0.031	0.540	195.387	12.998	0.213
dense treed shrubland (dTS; *n* = 25) *								
Mean	-0.278	2.783	3.647	0.088	1.560	224.525	8.201	0.420
SD	0.433	1.188	1.485	0.026	0.602	163.260	10.452	0.179
open grassed shrubland (oGS; *n* = 48)*								
Mean	-0.260	2.669	3.151	0.085	1.649	198.333	5.072	0.436
SD	0.462	1.607	1.996	0.044	1.119	170.952	10.805	0.176
open grassed woodland (oGW; *n* = 18)*								
Mean	-0.115	2.993	2.964	0.088	1.558	182.530	7.768	0.421
SD	0.358	1.573	1.679	0.044	0.812	128.329	18.832	0.211
open shrubbed grassland (oSG; *n* = 15)*								
Mean	-0.246	2.508	3.230	0.074	1.357	224.789	4.437	0.393
SD	0.399	0.705	1.746	0.024	0.413	128.955	2.626	0.194
open shrubbed woodland (oSW; *n* = 21)*								
Mean	-0.261	3.063	3.491	0.089	1.742	204.158	3.943	0.448
SD	0.393	1.795	2.450	0.028	0.920	137.897	4.568	0.205

*denotes groups used in statistical analyses

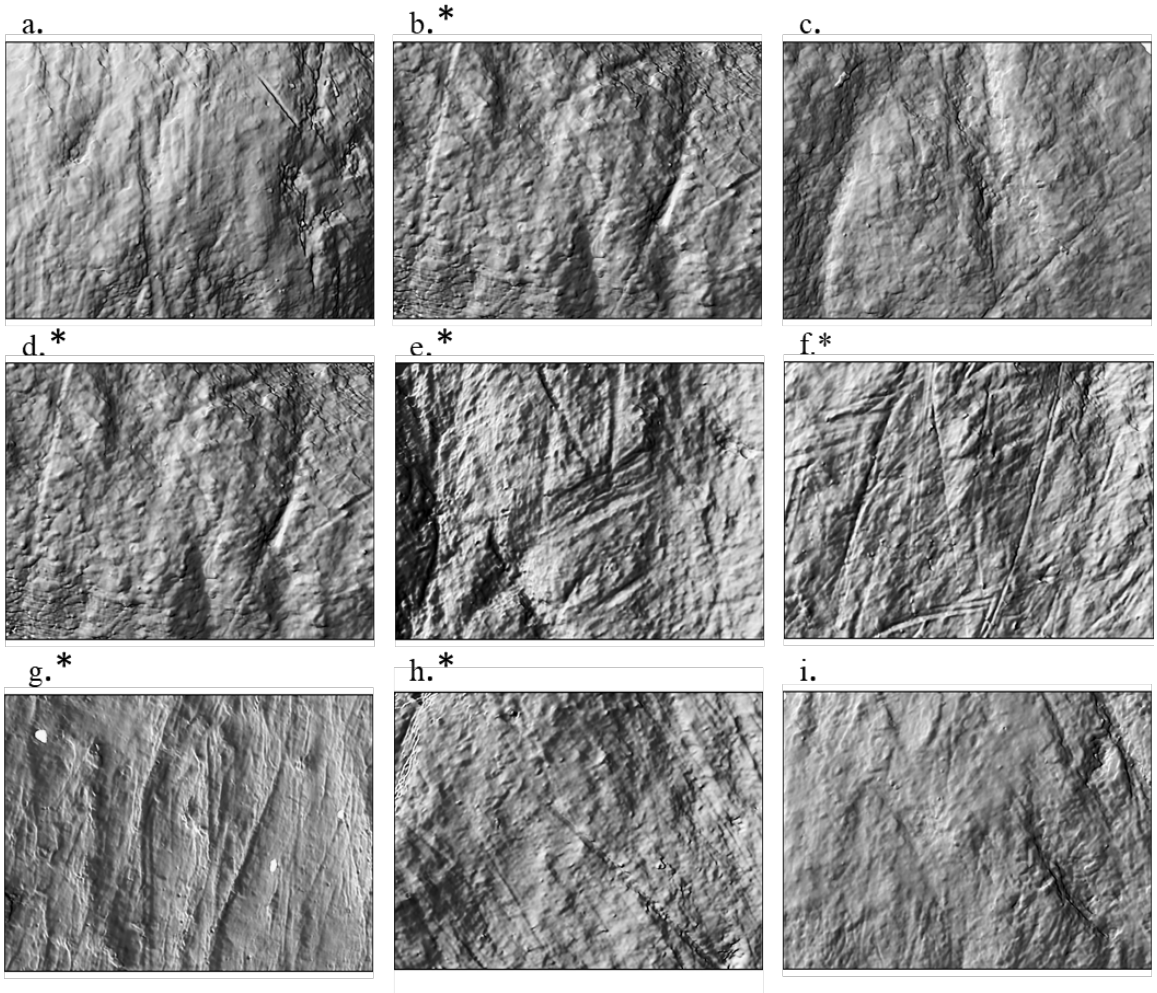

Figure 6.9: Representative microwear photosimulations for the different classifications of land cover at Kolomela and the surrounding farms: closed grassed shrubland (a), closed shrubbed grassland (b), dense shrubbed grassland (c), dense treed grassland (d), dense treed shrubland (e), open grassed shrubland (f), open grassed woodland (g), open shrubbed grassland (h), and open shrubbed woodland (i). Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Table 6.17: Statistical analyses for molars by land cover.

(A) MANOVA results

	Wilks' λ	*F*-value	df	*p*-value
Land cover classification (*n* = 139)				
	0.519	1.253	6, 84	0.069
% Exposed soil (*n* = 175)				
	0.956	0.527	1, 14	0.914
% Grass (*n* = 175)				
	0.871	0.813	2, 28	0.739
% Shrub/Bush (*n* = 169)				
	0.892	1.336	1, 14	0.192
% Tree (*n* = 175)				
	0.872	1.674	1, 14	0.066

Statistically significant results, in which $p < 0.05$, are bolded.

The four components of land cover described by Avenant and du Plessis (2018) were also analyzed separately to see how they might individually affect molar microwear signatures. Each percent coverage was divided into a low (0-33%), medium (34-66%), and high (67-100%) group when applicable. The percent of exposed soil could only be divided into low (*n* = 156) and medium (*n* = 19) coverage levels. The percent of tree cover likewise only had the two categories: low (*n* = 157) and medium (*n* = 18). All three levels were analyzed for grass cover: low (*n* = 68), medium (*n* = 62), and high (*n* =49). Finally, only the low (*n* = 142) and medium (*n* = 27) groups were considered for the percent bush cover, as the high level did not have a sufficient sample size. Table 6.18 provides the descriptive statistics for DMTA parameters for the percent cover groups of each type of land cover category and Figure 6.10 provides representative photosimulations. MANOVA tests for central tendencies did not result in statistical significance for any of the land cover categories: exposed soil (*p* = 0.914), percent grass cover (*p* = 0.739), percent shrub/bush cover (*p* = 0.192), or percent tree cover (*p* = 0.066; Table 6.17).

Table 6.18: Descriptive statistics of molar texture parameters by percent land cover.

SSFA:	*Asfc*	*epLsar*	*Smc*	*Tfv*	$HAsfc_9$	$HAsfc_{81}$
Percent Exposed Soil						
low (n = 156)*						
Mean	49.801	0.005	22.269	6946.076	0.920	2.502
SD	63.721	0.002	49.517	1537.894	1.072	3.754
medium (n = 19)*						
Mean	46.528	0.006	14.871	7006.390	0.752	2.028
SD	49.108	0.002	41.970	1315.498	0.534	2.595
Percent Grass						
low (n = 68)*						
Mean	56.475	0.005	17.830	7170.270	0.819	2.226
SD	68.134	0.002	43.294	1483.185	0.820	3.359
medium (n = 62)*						
Mean	49.592	0.006	31.758	6905.225	0.970	2.542
SD	62.238	0.002	62.158	1403.764	1.136	4.039
high (n = 49)*						
Mean	39.654	0.005	14.238	6711.265	0.934	2.650
SD	52.777	0.002	34.374	1627.972	1.153	3.579
Percent Bush/Shrub						
low (n = 142)*						
Mean	47.815	0.006	23.888	6983.510	0.954	2.583
SD	60.509	0.002	51.451	1535.912	1.070	3.838
medium (n = 27)*						
Mean	65.805	0.004	12.046	6773.398	0.544	1.917
SD	74.067	0.002	35.647	1379.188	0.447	2.794
high (n = 6)						
Mean	17.093	0.007	4.822	6999.407	1.210	1.623
SD	19.333	0.002	9.016	1394.495	1.539	1.359
Percent Tree						
low (n = 157)*						
Mean	47.486	0.005	20.252	6832.267	0.876	2.325
SD	59.792	0.002	47.747	1446.906	1.027	3.407
medium (n = 18)*						
Mean	66.411	0.006	31.940	7996.081	1.129	3.543
SD	80.065	0.002	56.707	1618.409	1.026	5.270

Table 6.18 (Cont.)

ISO:	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
Percent Exposed Soil								
low (n = 156)*								
Mean	-0.245	2.751	3.148	0.083	1.556	214.273	5.677	0.441
SD	0.415	1.493	1.648	0.035	0.857	160.807	10.293	0.191
medium (n = 19)*								
Mean	-0.257	2.686	3.848	0.090	1.569	165.033	4.039	0.396
SD	0.234	0.893	2.953	0.036	0.558	50.271	2.836	0.163
Percent Grass								
low (n = 68)*								
Mean	-0.217	2.767	3.500	0.087	1.534	193.365	6.506	0.411
SD	0.366	1.217	2.021	0.036	0.629	127.634	11.480	0.181
medium (n = 62)*								
Mean	-0.239	2.699	3.093	0.080	1.540	215.373	3.787	0.455
SD	0.367	1.420	1.488	0.026	0.747	141.677	3.645	0.202
high (n = 49)*								
Mean	-0.295	2.767	2.992	0.086	1.609	223.562	6.205	0.448
SD	0.477	1.747	1.909	0.043	1.134	195.333	13.658	0.182
Percent Bush/Shrub								
low (n = 142)*								
Mean	-0.248	2.768	3.153	0.084	1.571	208.581	5.170	0.440
SD	0.397	1.502	1.903	0.037	0.887	155.922	10.650	0.191
medium (n = 27)*								
Mean	-0.263	2.722	3.540	0.085	1.553	223.397	7.791	0.425
SD	0.420	1.163	1.478	0.027	0.579	158.707	10.144	0.180
high (n = 6)								
Mean	-0.135	2.306	3.363	0.067	1.271	159.132	2.232	0.391
SD	0.425	1.182	1.517	0.018	0.406	76.156	0.889	0.200
Percent Tree								
low (n = 157)*								
Mean	-0.261	2.717	3.249	0.084	1.557	212.172	5.292	0.438
SD	0.402	1.428	1.847	0.034	0.837	156.662	9.263	0.187
medium (n = 18)*								
Mean	-0.115	2.993	2.964	0.088	1.558	182.530	7.768	0.421
SD	0.358	1.573	1.679	0.050	0.812	128.329	18.832	0.211

*denotes groups used in statistical analyses

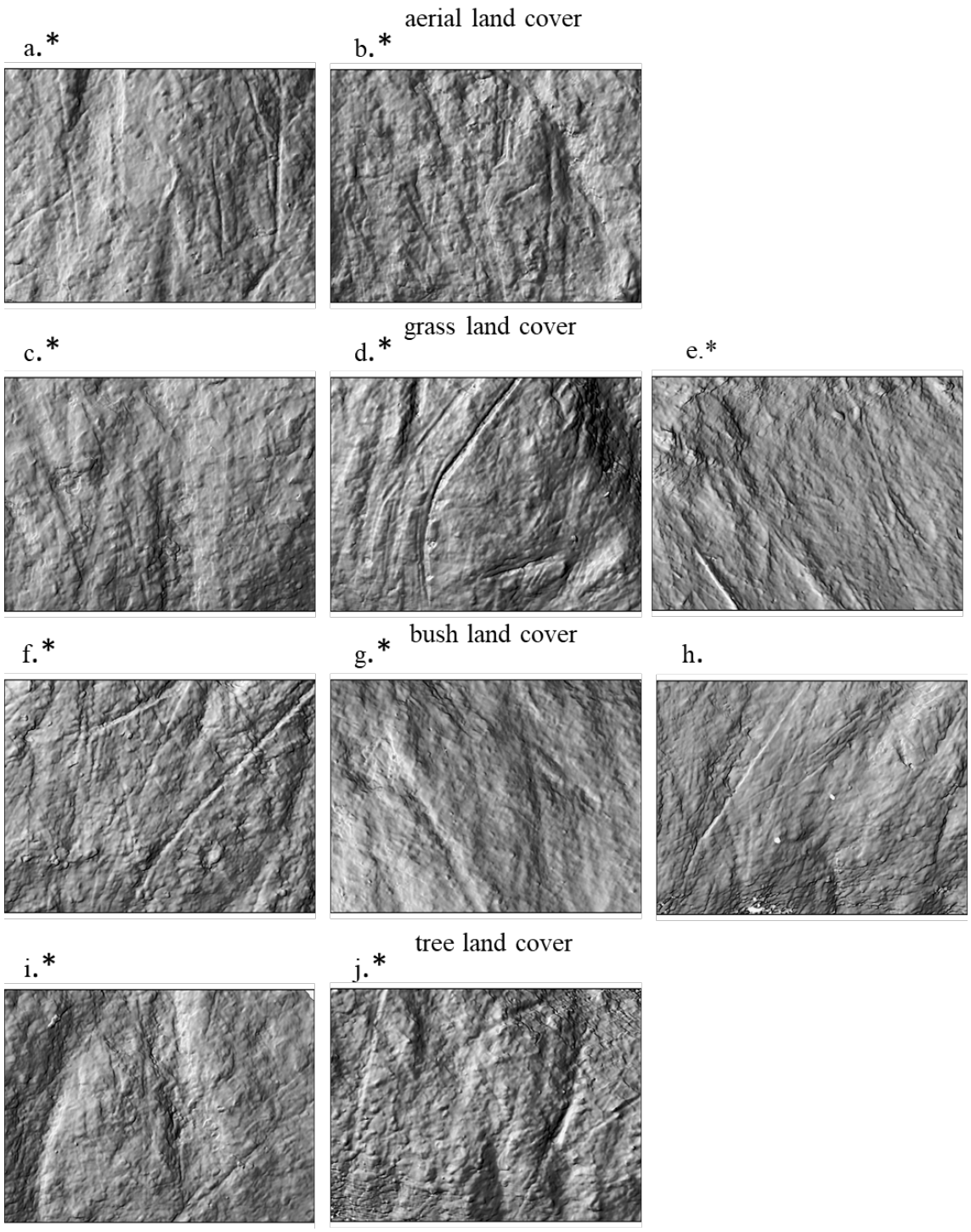

Figure 6.10: Representative microwear photosimulations by different types and levels of land cover. Percent exposed soil is represented by low (a) and medium (b) coverage. Percent grass cover is represented by areas of low, (c), medium (d), and high (e) coverage. Percent shrub and bush cover is represented by low (f), medium (g), and high (h) coverage. And percent cover for trees is divided into low (i) and medium (j) coverage. Each photosimulation measures an area of 85 µm x 64 µm. An * denotes groups used in statistical analyses.

Dust Level Microwear Effects

Rodent molars were divided into two dust level categories based on data from the 2017 Kolomela environmental reports: those from areas of high dust concentration ($c > 1200$ mg/m^2/day, $n = 20$) and those from areas of medium dust concentration (600 mg/m^2/day $< c <$ 1200 mg/m^2/day, $n = 99$). The descriptive statistics for molars when analyzed by dust accumulation are given in Table 6.19 and representative photosimulations can be found in Figure 6.11. MANOVA analyses were significant for the central tendencies ($p < 0.05$; Table 6.20). Individual ANOVAs indicated that molar microwear from areas of medium dust concentration had higher central tendencies for mean dale volume (*Sdv*) and average two-dimensional dale area (*Sda*; Table 6.20 and Figure 6.12). Table 6.21 provides microwear descriptions for grouping based on dust concentrations using these statistically significant parameters.

Table 6.19: Descriptive statistics of molar texture parameters by dust level.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_9$	***HAsfc*** $_{81}$		
medium (n = 99)*								
Mean	55.404	0.005	17.911	7028.239	0.826	2.583		
SD	67.066	0.002	43.664	1551.654	0.989	4.123		
high (n = 20)*								
Mean	35.642	0.005	13.713	6631.141	0.962	2.382		
SD	44.351	0.002	33.999	1514.321	0.685	2.402		
ISO:	***Ssk***	***Sv***	***Sdr***	***Vvv***	***S5v***	***Sda***	***Sdv***	***Str***
medium (n = 99)*								
Mean	-0.248	2.746	3.383	0.085	1.519	213.620	6.598	0.413
SD	0.369	1.198	1.894	0.033	0.611	159.139	11.987	0.180
high (n = 20)*								
Mean	-0.362	2.911	3.247	0.088	1.862	159.846	3.188	0.476
SD	0.632	2.210	2.472	0.059	1.547	88.490	3.058	0.160

*denotes groups used in statistical analyses

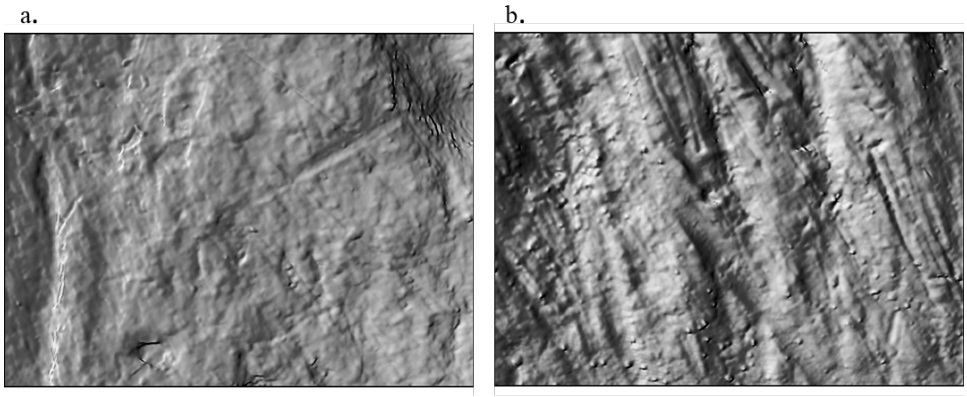

Figure 6.11: Representative microwear photosimulations by dust level, either that of high (a) or medium (b) concentrations. Each photosimulation measures an area of 85 µm x 64 µm.

Table 6.20: Statistical analyses for incisors by dust level (*n* = 119).

(A) MANOVA results

Wilks' λ	*F*-value	df	*p*-value
0.804	**1.807**	**1, 14**	**0.047**

(B) ANOVA results

	F- ratio	*p*-value
Asfc	1.448	0.231
epLsar	0.473	0.493
Smc	0.469	0.495
Tfv	2.362	0.127
$HAsfc_{9}$	3.216	0.076
$HAsfc_{81}$	2.384	0.125
Ssk	0.346	0.558
Sdr	1.518	0.220
S5v	0.120	0.729
Str	1.797	0.183
Sdv	**7.221**	**0.008**
Vvv	0.643	0.424
Sv	0.116	0.735
Sda	**4.177**	**0.043**

Statistically significant results, in which $p < 0.05$, are bolded.

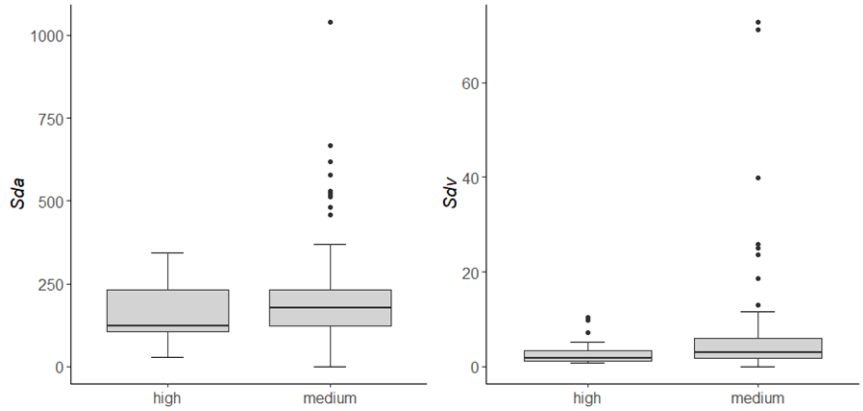

Figure 6.12: Box charts of statistically significant microwear texture variables when analyzed by level of dust accumulation. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 6.21: Molar microwear descriptions for dust level groups based on significant microwear parameters.

Dust level	Significant parameter trends	Microwear description
high	lowest *Sda* , *Sdv*	microwear features are small and shallow
medium	highest *Sda* , *Sdv*	microwear features are large and deep

Season Microwear Effects

Although the primary sampling period occurred during a transitional season in mid-May, Avenant and du Plessis conducted a second, smaller survey in the winter, during mid-July. This extra survey resulted in a small group of rodent molar microwear that could be used to characterize a winter season (July; n = 37) in addition to those of the transitional fall period (May; n =135). Table 6.22 provides the descriptive statistics of molar texture parameters by month and Figure 6.13 provides representative photosimulations. No statistical significance was found for central tendencies in the MANOVA analysis (p = 0.323; Table 6.23).

Table 6.22: Descriptive statistics of molar texture parameters by month.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_9$	***HAsfc*** $_{81}$		
May (n = 135)*								
Mean	49.075	0.005	18.520	6957.740	0.847	2.557		
SD	61.279	0.002	45.528	1495.250	0.951	3.936		
July (n = 37)*								
Mean	51.582	0.006	33.744	7019.292	1.137	2.200		
SD	67.212	0.003	59.298	1572.761	1.280	2.489		
ISO:	***Ssk***	***Sv***	***Sdr***	***Vvv***	***S5v***	***Sda***	***Sdv***	***Str***
May (n = 135)*								
Mean	-0.227	2.700	3.204	0.083	1.511	212.106	6.172	0.430
SD	0.345	1.359	1.771	0.032	0.705	155.919	11.670	0.183
July (n = 37)*								
Mean	-0.308	2.920	3.158	0.089	1.730	180.606	3.274	0.462
SD	0.561	1.745	2.041	0.045	1.176	113.496	3.143	0.199

*denotes groups used in statistical analyses

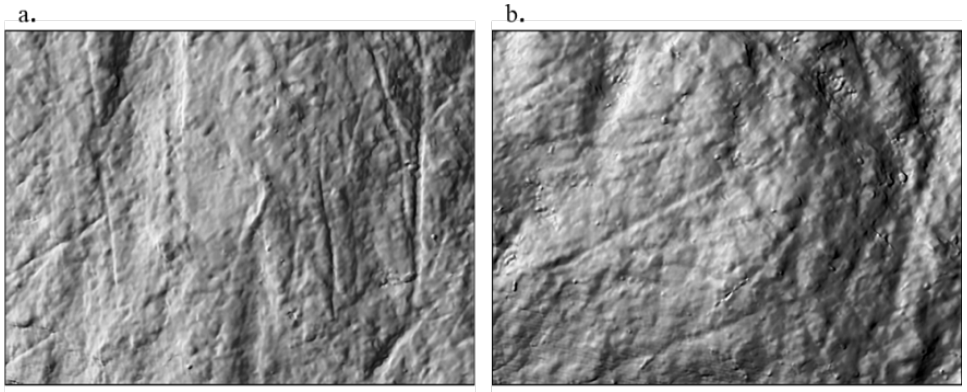

Figure 6.13: Representative microwear photosimulations by collection month: May (a), representing the transitional fall season, and July (b), representing the winter season. Each photosimulation measures an area of 84 µm x 64 µm.

Table 6.23: Statistical analyses for molars by collectcion month (n = 172).

(A) MANOVA results

Wilks' λ	***F*-value**	**df**	***p*-value**
0.907	1.145	1, 14	0.323

Statistically significant results, in which $p < 0.05$, are bolded.

Tooth Microwear Effects

The descriptive statistics for incisors (n = 198) and molars (n = 175) are provided in Table 6.24, with representative photosimulations in Figure 6.14. MANOVA tests indicated statistically significant variation when comparing incisor and molar values ($p < 0.001$; Table 6.25). Subsequent ANOVAs indicated significant difference between incisors and molars for every texture variable except that of the average two-dimensional dale area (*Sda*; Table 6.25 and Figures 6.15 and 6.16). Incisors possessed significantly higher measures of anisotropy (*epLsar*), textural fill volume (*Tfv*), and skewness (*Ssk*). All other parameters, complexity (*Asfc*), scale of maximum complexity (*Smc*), heterogeneity at both a 3x3 and 9x9 grid ($HAsfc_9$ and $HAsfc_{81}$), developed interfacial area ratio (*Sdr*), five-point pit height (*S5v*), texture-aspect ratio (*Str*), mean dale volume (*Sdv*), pit void volume (*Vvv*), and maximum pit height (*Sv),* were significantly higher for the molar sample than incisor. General microwear descriptions for incisors and molars based on these statistically significant parameters are given in Table 6.26.

Table 6.23: Descriptive statistics of dental microwear texture parameters by tooth type.

SSFA:	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc*** $_9$	***HAsfc*** $_{81}$		
Incisors (n = 198)*								
Mean	1.583	0.008	35.458	13047.261	0.247	0.510		
SD	0.737	0.002	110.729	3201.298	0.128	0.840		
Molars (n = 175)*								
Mean	49.444	0.005	21.461	6952.662	0.902	2.451		
SD	62.180	0.002	48.696	1503.144	1.027	3.643		
ISO:	***Ssk***	***Sv***	***Sdr***	***Vvv***	***S5v***	***Sda***	***Sdv***	***Str***
Incisors (n = 198)*								
Mean	-0.015	1.583	1.469	0.048	0.851	216.638	2.889	0.293
SD	0.372	0.785	0.693	0.028	0.265	164.790	4.476	0.150
Molars (n = 175)*								
Mean	-0.246	2.744	3.221	0.085	1.557	209.477	5.517	0.436
SD	0.399	1.441	1.828	0.035	0.832	154.174	10.421	0.189

*denotes groups used in statistical analyses

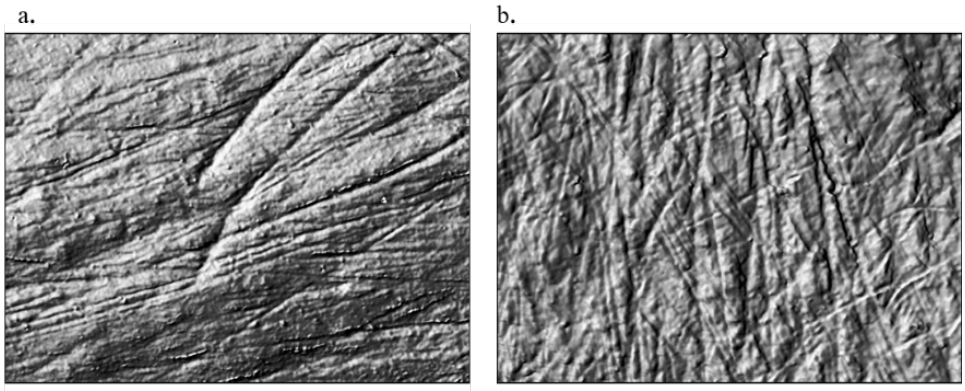

Figure 6.14: Representative microwear photosimulations of *Gerbilliscus leucogaster* incisors (a) and molars (b). The incisor photosimulation measures an area of 138 µm x 102 µm while the molar photosimulation measures an area of 85 µm x 64 µm.

Table 6.25: Statistical analyses for differences in tooth type (*n* = 373).

(A) MANOVA results

Wilks' λ	*F* -value	df	*p* -value
0.154	**140.42**	**1, 14**	**0.000**

(B) ANOVA results

	F- ratio	*p* -value
Asfc	**957.510**	**0.000**
epLsar	**203.920**	**0.000**
Smc	**46.116**	**0.000**
Tfv	**522.710**	**0.000**
$HAsfc_{9}$	**218.400**	**0.000**
$HAsfc_{81}$	**287.250**	**0.000**
Ssk	**34.059**	**0.000**
Sdr	**249.390**	**0.000**
S5v	**244.520**	**0.000**
Str	**72.119**	**0.000**
Sdv	**24.989**	**0.000**
Vvv	**259.660**	**0.000**
Sv	**207.550**	**0.000**
Sda	1.311	0.288

Statistically significant results, in which $p < 0.05$, are bolded.

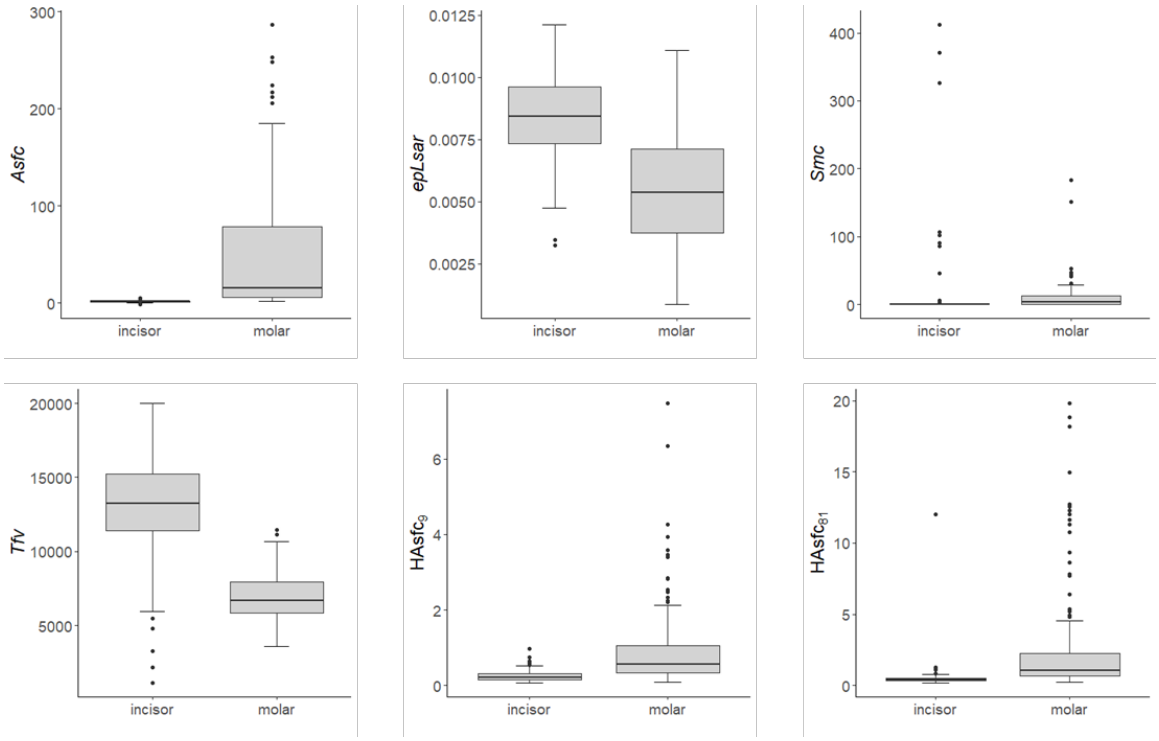

Figure 6.15: Box charts of statistically significant microwear SSFA variables when analyzed by tooth. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

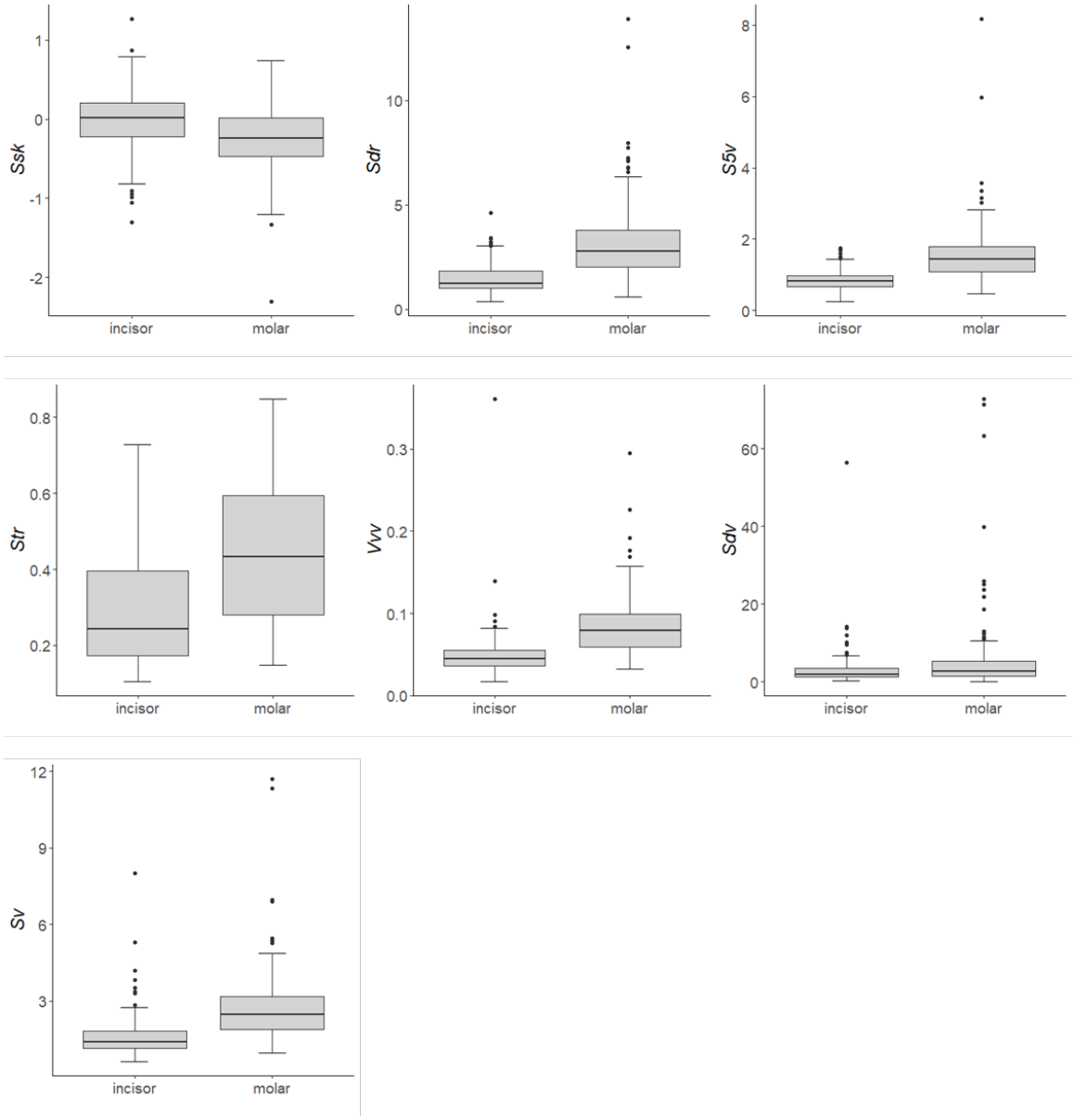

Figure 6.16: Box charts of statistically significant microwear ISO variables when analyzed by tooth. Each box represents the central 50% of values, with the first and third quartiles indicated by the edges of the box. The median is represented by the horizontal line within the box. Whiskers provide the range of values within 1.5 times the interquartile range, with the dots indicating outliers.

Table 6.26: Molar microwear descriptions for incisors and molars based on significant microwear parameters.

Tooth	Significant parameter trends	Microwear description
incisor	highest *epLsar*, *Tfv*, *Ssk* lowest *Asfc*, *Smc*, $HAsfc_9$, $HAsfc_{81}$, *Sdr*, *S5v*, *Str*, *Vvv*, *Sdv*, *Sv*	Microwear texture is anisotropic and relatively uniform across the surface, with large and broad scratches
molar	highest *Asfc*, *Smc*, $HAsfc_9$, $HAsfc_{81}$, *Sdr*, *S5v*, *Str*, *Vvv*, *Sdv*, *Sv* lowest *epLsar*, *Tfv*, *Ssk*	Microwear pattern is very complex and isotropic, with a greater degree of pattern variation, more pits, and features that are large and deep

Discussion

Initial research into rodent molar microwear indicated the potential to differentiate between the nuances of rodent diets and environments (see Burgman et al., 2016). However, data presented in this dissertation did not quite parse behavioral and environmental signals to the same degree as in the pilot study. In fact, analyses of central tendencies only indicated statistically significant microwear texture attributes among species, their burrowing behaviors, and differences in dust levels. The lack of statistical significance for some factors, such as vegetation cover, does not imply a lack of effect on microwear texture, however, as only central tendencies were compared. Individual factor effects may also be obscured by interactions with other variables. Unfortunately, due to the non-orthogonal sampling associated with using field caught specimens, dispersions and interactions between the factors were not tested for (refer to Chapter 3). Once again, each independent variable tested will be discussed individually.

While molar microwear did not parse the dietary categories used in this analysis, these results are understandable as the stomach content analyses from Chapter 4 indicated that all individuals possessed similar diets – dominated by grass seed. In comparison to incisors, molar

microwear analyses did not parse samples by most environmental variables, indicating that incisor microwear remain more useful for direct environmental interactions while molar microwear reflect dietary signal. Both tooth types ought to be considered in future microwear studies as complimentary aspects that paint a more complete picture of rodent interactions with their environment than could incisors, and especially molars, alone.

Species Microwear Effects

Gerbilliscus leucogaster possesses significantly lower values for scale of maximum complexity (*Smc*), textural fill value (*Tfv*), and five-point pit height (*S5v*) in comparison to the two murine species, *Micaelamys namaquensis* and *Rhabdomys bechuanae*. In addition, the gerbil sample has lower central tendencies for developed interfacial area ratio (*Sdr*) than *R. bechuanae*. These results indicate that gerbil molar microwear consists of smaller and shallower features that are slightly less complex than those of the mice, despite a similar diet dominated by grass seed consumption (see Chapter 4, Table 4.2 and Figure 4.2).

Species differences appear to be driven primarily by burrowing behavior in the incisor analysis. Likewise, non-burrower molar microwear had significantly higher central tendencies for *Smc*, *Tfv*, and *S5v*, much like the two murine species analyzed. If molar microwear differences among species were solely associated with burrowing behavior, however, one would also expect statistically significant differences in parameter measures not just between the burrowing *G. leucogaster* and grass nesting *Mi. namaquensis*, as observed, but also between the other burrowing species, *R. bechuanae,* and *Mi. namaquensis*. Instead, molar microwear signals follow sub-family lines: with the two Murinae species (*R. bechuanae* and *Mi. namaquensis*) differing in texture from the Gerbillinae (*G. leucogaster*).

Molar microwear records the interaction between how an organism chews and the physical properties of the ingested materials (Crompton & Hiiemae, 1970; Hiiemae & Kay, 1973; Hua et al., 2015). As such, this microwear data can be used to elucidate both dietary behaviors and masticatory processes. Many rodent studies have used microwear for chewing mechanics research rather than dietary reconstruction (e.g., Charles et al., 2007; Lazzari et al., 2008; Teaford & Byrd, 1989; Teaford & Walker, 1983a). Stomach content analysis revealed that grass seed comprised the greatest mean volumetric contribution for each species, ranging from an average of 64.2% for *G. leucogaster* to 67.5% for *Mi. namaquensis* (Table 4.2). Microwear analysis by diet (considered further in a later section) revealed a lack of statistical significance for microwear texture parameters when diet consisted of ≥ 50% grass seed. As such, it seems unlikely that dietary differences between these three generalist species are driving the observed differences in microwear. Nor does it seem likely that these results are influenced by burrowing behavior, as previously explained.

It is plausible to suggest that the observed results for species analysis may relate more to masticatory dynamics driven by molar morphology than diet. Most murids favor propolinal chewing, in which molars slide against each other in a postero-anterior direction. This is the case for the three species considered here. Differences, however, stem from the shape of the molars: Gerbillinae have flat-crowned molars while Murinae are considered more cuspidate (Butler, 1985; Charles et al., 2007; Lazzari et al., 2008a). Both cuspidate and flat-crowned rodent molars produce little difference in scratch orientation when engaging in propolinal mastication, producing features oriented in similar anteroposterior directions (Charles et al., 2007). Murinae facets develop along longitudinal gutters of upper and lower molars as cusps interlock during occlusion and mastication. On the other hand, the flattening of Gerbillinae molars prevents

interlocking during occlusion and allows upper and lower molar wear facets to remain relatively parallel to one another during mastication (Lazzari et al., 2008a, b). This difference means that the cusps and wear facets of *G. leucogaster* molars lack the slope and interlocking nature of *Mi. namaquensis* and *R. bechuanae* molars.

The influence of tooth topography on microwear formation has been explored in other species (e.g., Purnell et al., 2017; Ungar et al., 2017) but not, as far as the author is aware, for rodents. These analyses have met with different results. For the primate *Sapajus apella*, the average slope, angularity, or relief of the upper second molars had no significant influence on SSFA texture variables (Ungar et al., 2017). Conversely, an odontocete (*Delphinapterus leucas*) study indicated that microwear texture, defined by ISO variables, did vary based on tooth characteristics that included a combination of tooth location, wear, and facet slope and orientation (Purnell et al., 2017).

Murid molars are morphologically different from primates and odontocetes, adapted to breaking down high-fiber plant material (Happold, 2013; Landry, 1999; Mess et al., 2001). And their masticatory dynamics are clearly different too; primates chew transversely while odontocetes do not chew at all. Yet, all else equal – diet, mastication direction, habitat composition, and the fact that both burrowing and non-burrowing murine molar microwear differed from the gerbil — results seem to suggest that differences in tooth topography and morphology may be driving the observed differences in microwear texture. The interlocking of cusps in the Murinae dental plan may serve to better hold food particles within the tooth borders during mastication, thus resulting in the presence of deeper features. Studies that specifically measure and define topographical aspects of rodent molars in relation to microwear should be conducted to explore this hypothesis in further detail.

It should be noted that, except for burrowing behavior, the other factors considered in this chapter possess sample specimens that represent a mix of gerbils and murines. The inclusion of individuals of both subfamilies within these samples should minimize the impact of occlusal topography on results for other factors, particularly when patterns are consistent among the taxa. Arguments have been made for the incorporation of intraspecific variation in DMTA to improve dietary inference, albeit by using a Linear Mixed Effects model not utilized here (Arman et al., 2019). The remaining discussion sections will follow the same rationale: so long as the sample is represented by a mix of both murid subfamilies, consistent patterns in microwear attributes for taxa with differing molar topography are likely a result of the factors considered.

Macrohabitat Microwear Effect

The definition of *habitat* often varies across the ecological literature (see Kearney, 2006). For this study, habitat refers to a physical location in which an organism resides, or has the potential to reside, that is confined by scales of space and time (Belmaker, 2018; Kearney, 2006). This location is comprised of biotic and abiotic factors that affect the distribution and abundance of a given species. This study also incorporates Morris' (1987) division of a given habitat into macro- and micro- elements, the latter of which will be discussed in the next section. Macrohabitats are the locations within a given scale of time and space in which an organism can conduct all biological functions (Morris, 1987) and are represented by the individual Kumba Iron Ore properties in which rodent trapping occurred. All macrohabitats are located within the Postmasburg Thornveld ecoregion. Habitats varied in vegetation species and cover, as well as abiotic factors such as soil and dust exposure (refer to Chapter 3, Tables 3.4 and 3.5) and distance from mine activities (Figure 3.1). Despite variations in macrohabitat characteristics,

statistically significant differences in central tendencies were not reported for the molar microwear variables.

Diet did not differ by location; grass seed remained the greatest contributor to stomach contents for these specimens (see Chapter 4, Table 4.5 and Figure 4.7). If diet does not significantly differ by habitat, neither then should molar microwear. This idea is consistent with long-standing suggestions that molar dental microwear is driving largely by diet (Adams et al., 2020; Calandra et al., 2016b; Merceron et al., 2016). Even though species composition of vegetation, and quantity of each taxon, may have differed within macrohabitats, the types of food available (e.g., grass blades, gras seed, dicot seed, curculionid) did not. All foodstuffs were those that could be found within the Postmasburg Thornveld and these generalist species ate whatever best met their metabolic requirements.

The different biotic and abiotic characteristics represented by each macrohabitat were not sufficient to affect unique signals for molar microwear texture as they were for incisors. The only environmental variable to result in significance was dust concentration, and even soil comparisons lacked significance (both variables will be discussed in a later section). Dust results align with experimental data indicating that specific properties of exogenous grit effect molar microwear (e.g., Martin et al., 2020; Winkler et al., 2020b). However, soil results agree with experiments that indicate otherwise (e.g., Merceron et al., 2016; Hua et al., 2020) despite many of these species relying on foods from underground scatter or larder hoards (Evans, 2003; Rusch et al., 2013; Weighill et al., 2017; White, 2013; White et al., 2017), where this foodstuff would be directly exposed to soils.

While this study failed to result in much significant variation by habitat proxies, molar microwear should not be entirely dismissed when considering environmental applications. In the

pilot study, rodent molars from three distinct South African ecoregions used scale-sensitive fractal analysis to separate rodent molar microwear within the same habitat and to separate microwear texture by habitat for two of the three species used (Burgman et al., 2016). Though possible that abiotic characteristics such as varying dust and soil exposure influenced these data, the inconsistency in results indicated that resource availability and partitioning was more influential. In Madagascar, texture variables clearly distinguished between molar microwear collect from rainforest and village *Rattus rattus* specimens, with similar conclusions drawn about interactions between dietary and exogenous grit influences (Winkler et al., 2016).

Unlike those studies, however, this study lacks truly distinct and separate environments that may lend themselves to differing resource availability detectable through an analysis of molar microwear texture central tendencies. The amalgamation of factors that make up the Kolomela mine and farm macrohabitats may ultimately be too alike to one another in aggregate to be separated here. Further, future dispersion analyses might better reflect the idiosyncrasies of the individual and reflect how habitats within the same bioregion influence resource partitioning and therefore habitat-driven dietary differences between rodents. As such, the lack of differing microwear signals among habitats here may not be a failure of rodent molar microwear to parse macrohabitats but an artifact of data and analysis constraints.

Microhabitat Microwear Effects

The previous section discussed the results of macrohabitat analysis and used data from all specimens captured within each Kumba Iron Ore property. However, each macrohabitat may be comprised of multiple smaller microhabitats. These microhabitats differ based on specific biotic and abiotic conditions that influence how an individual might spend its energy and time within

that area (Morris, 1987). These microhabitats occur at a finer spatial resolution than that of the macrohabitats (Jorgensen, 2004), with multiple microhabitats comprising the larger habitat. However, microhabitats also need to be defined based upon the studied taxa's concept of scale (Morris, 1987). Take an antelope, for example. Microhabitats for this larger animal may include a lake shore within a savanna macrohabitat. But for smaller mammals, like the mice and gerbils in this study, the lake shore may be the entirety of their habitat. The microhabitats for a rodent need to be defined on a much smaller scale and consider environmental differences that would mean nothing for the antelope (Belmaker, 2018), such as soil composition or moisture levels. Each trapping transect was established based on differences in mine activity, vegetation, and dust level (Avenant & du Plessis, 2017) and therefore varied in properties that might affect how murids utilize each area. As such, each transect was considered a separate microhabitat. Specific characteristics for each transect microhabitat can be found in Chapter 3 (Table 3.5).

Microhabitat analysis allows for a breakdown of the larger habitat in which rodents reside and as such, provides data at a finer resolution and results driven by characteristics distinct to that microhabitat rather than the entirety of the murid's home range. Unfortunately, African rodent behavior is not studied as much in the field as that of larger mammals, and thus it is difficult to determine home range size for each species (Happold, 2013). Still, data available for the sister taxa of *R. bechuanae* and *Ma. coucha*, *Rhabdomys pumilio* and *Mastomys natalensis*, respectively. Studies estimate that home ranges can be as large as 1500 m^2 for *R. pumilio* and 2666 m^2 for *M. natalensis* (Coetzee, 1975; Schradin, 2006). These estimates indicate that an individual linear transect of 250 m length may comprise a small portion of a rodent's day range. However, much like with the molar macrohabitat analysis, the multivariate analysis lacked statistically significant differences in microwear texture among the eight transects analyzed.

Once again, similar arguments may be made as in the macrohabitat discussion. Grass seed remained the primary stomach content in individuals analyzed in Chapter 4, with volumetric means ranging between 53.12% (HK3) to 71.00% (KK2) among transects. Based on this analysis, most individuals captured at transects Ekstra, GN1, GN2, HK7, KK2, and KK3 were assigned a diet of grass seed-grass seed. At HK3 and Stofdraai, however, most molars used corresponded with unknown diets since time constraints in the field did not allow for every stomach to be dissected. Given the predominance of grass seed consumption at the Kolomela mine and at the farms, it is very likely that individuals with unknown diets were also ingesting grass seed. An overall lack of major dietary difference should still be reflected by a lack of significant difference in the central tendencies for molar microwear texture variables. But dispersion may once again better capture the range of diets of trapped individuals. Or it may be that these microhabitats are not those in which murids are engaging in dietary behavior that would lead to distinctive molar microwear. These rodents may be foraging anywhere within their greater home range and without direct observation, there is no certainty that these areas are included.

Although more specific in abiotic characteristics (e.g., each transect reflected a specific vegetative cover, soil type, and dust concentration), these factors were not influential in parsing molar microwear central tendencies as they were for incisors (see Chapter 5). Instead, results for this microhabitat analysis continue to align with those of the stomach content analysis and macrohabitat DMTA. Regardless of distinct abiotic and biotic characteristics, rodent molar microwear and rodent stomachs indicate similarities in ingested material. Unlike incisors, which act as a multitool in the rodent cosmos, molars are a specialized instrument that are used only in mastication. Thusly, molar microwear for these murids remains reflective of interactions

between teeth and ingested food. And when foodstuff does not drastically differ, it seems, neither does molar microwear pattern.

Dietary Microwear Effects

Stomach content analyses indicated a preference for grass seed consumption, although individuals also ingested other foodstuff such as grass blades, dicot seeds and leaves, curculionid, flesh, and annelids (see Chapter 4). However, the three dietary groups with sufficient sample sizes all possessed grass seed as their main dietary contributor. This bias meant that molar microwear was likely dominated by a grass seed signal, and any differences found likely depended upon the second greatest contributor to stomach contents, which made up < 50% of stomach contents (for example, see Table 4.2 and Figure 4.2). The three dietary groups considered — grass seed/grass seed, grass seed/grass, and grass seed/curculionid — did not produce different molar microwear texture signatures.

Molar microwear is considered to reflect the interactions between mastication and the physical property of the ingested food (Crompton & Hiiemae, 1970; Hiiemae & Kay, 1973; Hua et al., 2015), providing a window into dietary reconstruction. Indeed, both feature-based and textural analyses have been used in previous studies of rodent molar microwear and have been met with greater success than this sample (e.g., Burgman et al., 2016; Nelson et al., 2005; Robinet et al., 2020; Townsend & Croft, 2008; Winkler et al., 2016). Winkler et al. (2016), for example, used DMTA techniques to suggest that black rats living within the villages of Madagascar had very different diets from those residing in rainforests, with the village rats presumably eating a lot of human food waste. Dietary differences, based on the differing physical properties of foodstuff, were noted for the molar microwear of caviomorph rodents from

South America (Robinet et al., 2020). Specifically, diets of grass and mature leaves had higher *Asfc* and *Tfv* values than those rodents eating young leaves. Feature-based analyses also indicated diet-based microwear differences for rodent molars. While Nelson et al. (2005) suggested that the differences in pit frequency between arboreal and terrestrial squirrels were likely caused by the greater presence of grit in terrestrial diets, they also noted that their results could be a result of diet. The consumption of seeds or insects by ground squirrels potentially increased pit frequency for the terrestrial omnivores. Meanwhile, discriminant function analysis of low-magnification microwear characteristics separated fruit-leaf and fruit-seed eaters from those grass and leaves, also discriminating between fruit-leaf and fruit-seed eaters (Townsend & Croft, 2008).

The pilot study for this research also used SSFA variables to parse molar microwear textures in an analysis of rodent species within the same habitat (Burgman et al., 2016). Although the three species used (*Rhabdomys pumilio*, *Mastomys coucha*, and *Micaelamys namaquensis*) are all classified as generalists, the microwear textures of these species differed within the Lesotho Afromontane grasslands and within the South African Nama-Karoo shrublands. The study did not rule out environmental factors, suggesting that the greater grit loads found in the anthropogenically disturbed Lesotho grasslands and the Nama-Karoo shrublands could be influencing microwear patterning. However, differences in food consumption and dietary resource partitions were considered the main reason for these differences.

This conclusion was in part highlighted by the lack of significant differences among species within the third environment, the South African Dry Highveld bushlands. Unlike the other two sampling locations, the Dry Highveld were thought to possess greater resource

availability, thus allowing rodents to seek out preferred (and potentially similar) foods (Burgman et al., 2016) – like the results reported here. Similarly, a comparison of vole molar microwear from two different localities in Poland also lacked significant differences in DMTA parameters (Calandra et al., 2016b). As the vole species considered is primarily a grass blade eater, the authors concluded that the lack of significance did not indicate a limitation in vole molar microwear to interpret diet but, instead, that the animals from both sites were primarily eating grass.

Methodology may also explain why the MANOVA for central tendencies in this study failed to distinguish between the secondary diets of the Kolomela rodents. As previously mentioned, stomach content analysis revealed remarkably similar diets among individuals from Kolomela and the surrounding farms. On average, grass seed made up 64.96% of stomach contents for this sample (Chapter 4). Furthermore, the methods used to define a secondary component in diet meant that grass or curculionid comprised less than 50% of stomach contents for each rodent -- typically a lot less. Therefore, it could be that the amount of grass blade and curculionid ingested was not enough to affect microwear texture in comparison to the amount of grass seed consumed. Or diet may be separated better by dispersion analysis, which may better reflect variance in the amounts of foodstuff consumed. Unfortunately, rodent dietary behavior could not be controlled as to provide a more meaningful array of diets.

Finally, it is also possible that the scan size, 85 x 64 um, is too small to parse the more minute aspects of diet being swamped by such a large intake of grass seed. Scans sampling larger areas on tooth facets (e.g., 200 x 200 um) have been shown to provide clearer discrimination among SSFA variables for more similar diets in sheep as opposed to smaller (e.g., 50 x 50 um) fields (Ramdarshan et al., 2017; Robinet et al., 2020). However, between the small

size of rodent molars and the even more confining formation of enamel rims around dentin lakes for most species, larger scans were impossible to obtain in many cases for the current study. As such, there may simply be limitations in the degree of dietary resolution able to be parsed from small mammal molars.

Controlled feeding experimentation indicated that it took at least two weeks for a diet switch to completely overwrite previous microwear patterns on rat molars, although noticeable changes in texture started appearing early on after a dietary switch (day 2 of the new diet; Winkler et al., 2020a). Obviously, rodent stomachs do not possess two weeks' worth of food. This difference in temporal scale suggests that the use of stomach content analysis as a complimentary method to microwear might be limited. That said, the lack of difference in microwear textures for specimens with similar stomach contents (e.g., mostly grass seed) suggests these diet proxies may offer consistent results. Thus, the potential exists for further use of stomach contents in ascribing better defined diets to the microwear of generalist and opportunistic rodent species.

Burrowing Behavior Microwear Effects

Parsing the rodent molar sample by burrowing behavior resulted in significant differences in central tendencies for scale of maximum complexity (*Smc*), textural fill value (*Tfv*), and five-point pit height (*S5v*). The microwear pattern for the sample including rodents that did not engage in burrowing (*Micaelamys namaquensis* and *Mastomys coucha*) possessed greater tendencies towards deeper and larger features than those rodents that did engage in burrowing behavior (*Gerbilliscus leucogaster*, *G. paeba*, and *Rhabdomys bechuanae*) and may be the result of an interaction with the taxonomic occlusal morphology signal (see below). These results align

with those from the species analysis, in which gerbil molar microwear separated from the two Murinae species. Given that the sample of rodents who build and occupy underground burrows is mostly comprised of gerbils (83.46% of *n*), it is not too surprising that the Gerbillinae microwear texture signal associated with occlusal dynamics might be swamping that of the Murinae for the burrowing sample. As discussed in the species section, there appears to be a microwear signature resulting from differences in molar morphology and topography between the two sub-families. Indeed, a comparison of the summary statistics for species (Table 6.1) and for burrowing behavior (Table 6.11) shows that the *Smc*, *Tfv*, and *S5v* means for the non-burrower sample are comparable to that of the *R. bechuanae* and *Mi. namaquensis* samples, while those of the burrower sample compare with *G. leucogaster*.

From the limited amount of research available, it appears that both *Gerbilliscus* species and *R. bechuanae* engage in digging with their forearms rather than incisors (Giannoni et al., 1996; Webster et al., 1981). Regardless, with digging burrows comes an overall increased exposure to grit. Further, given the hoarding (food storage) behaviors of these species, one might expect the food to be covered with greater amounts of exogenous abrasive particles. The expected rodent microwear signals that generally accompany higher exposures to exogenous abrasives, such as higher complexity and larger and deeper features (Martin et al., 2020; Nelson et al., 2005; Winkler et al., 2020b), appear to be lacking on molars. These results are very different from that of the incisor comparison, in which the microwear of the burrowing sample depicted the larger, deeper features. Unlike molars, however, incisors do not radically differ in form among taxa and are free from the influences of occlusal dynamics affected by tooth form., These results appear consistent with the notion that occlusal dynamics, rather than grit exposure, appear to drive the molar microwear texture signatures (see below).

Rodents possess a diastema between their incisors and molars that can be closed by a skin fold on the upper lips to separate gnawing activities from those of mastication (Happold, 2013; Skinner & Chimimba, 2005). During non-dietary incisor activity, the diastema remains open to allow indigestible material to fall out of the sides of the mouth rather than be ingested (Skinner & Chimimba, 2005). Likewise, when chewing, the fold of skin closes the diastema to keep the food within the buccal cavity (Skinner & Chimimba, 2005). This biological adaptation likely in part explains differing effects of exogenous grit on incisors and molars and thus differences in burrowing signals. The grit studies conducted by Martin et al. (2020) and Winkler et al. (2020b) involved feeding rodents pellets filled with grit of varying types and concentrations. As such, molar exposure to grit was inevitable. While these studies clarify the influence of different physical properties for abrasive particles, they are not necessarily a reflection of how rodent molar interactions with exogenous grit occurs.

Instead, exposure to exogenous abrasives during mastication is dependent upon what clings to food surfaces as well as the food texture itself (Hua et al., 2020). An analysis of field trapped *Talpa europea* molar microwear generally indicated a lack of correlation between texture parameters and environmental abrasives, with mole microwear indistinguishable from that of bats also consuming soft prey (Adams et al., 2020). Other experimental studies also conclude that grit effects on molar microwear remain highly dependent upon diet (e.g., Hua et al., 2020; Merceron et al., 2016). Much like with the moles and bats, diet does not significantly differ between the two groups considered here, as grass seed made up most stomach contents regardless of species (Chapter 4; Table 4.2 and Figure 4.2). While murid incisors may be more sensitive to behavioral characteristics that increase grit exposure, it appears that molars are not.

These data suggest, then, that rodent molars may be utilized in dietary construction without the need to consider behavioral differences such as nesting above or below ground.

Soil Microwear Effects

Four soil types were considered in this analysis: sand, rocky, loam, and clay-loam soils. Each possess distinct physical particle properties (e.g., size, hardness, shape) that may influence the formation of incisor microwear. Indeed, controlled laboratory experimentation has indicated that an increase of the size or quantity of abrasives correlates to an increase in height, volume, and complexity parameters (Ackermans et al., 2020; Schulz-Kornas et al., 2020; Winkler et al. 2020b). In processing stomach contents for analysis, ingested particles in wastewater were observed when filtered through a 500 μm sieve (personal observation). However, the concentration and composition of these particles were not analyzed, leaving it unknown as to whether this material stemmed from atmospheric dust, soil, foodstuff, or some combination thereof. In analyzing molar microwear central tendencies by the type of soil in which specimens were obtained, no statistically significant results occurred for texture parameter central tendency. This result is starkly different from that of the incisor microwear analysis, where nearly half of the texture parameters separated incisors based on soil, as well as the aforementioned laboratory experiments with grit.

Incisors and molars interact with soil in different ways, with morphological adaptations meant to reduce the amount of non-edible material ingested, as explained in the previous section. Although none of these species were reported to use incisors in digging, these teeth are still the first to contact the surrounding environment. Remember, the presence of the diastema between the incisors and molars reduces the amount of indigestible material from entering the buccal

cavity during incisor use while folds of skin block this gap during mastication to keep foodstuff from falling out (Skinner & Chimimba, 2005). As such, molar interaction with soil or other exogenous grit stems mainly from particles adhered to ingested material.

Rodent incisors are also ever-growing and have high rates of eruption and attrition that lead to fast turnover of the enamel surfaces (e.g., Coady et al., 1967; Risnes et al., 1995; Weinreb et al., 1967). Under a field of 0.1 mm in height, microwear on some murid incisor tips would only be reflective of the previous five to six hours. Conversely, molars for these taxa are rooted and become worn out over time, forming dentin pools surrounded by enamel rims. Alterations in microwear textures on molar enamel take days (e.g., Grine, 1986; Teaford & Oyen, 1989) with full turnover taking up to two to three weeks (Winkler et al., 2021a). In the same duration it takes molar microwear textures to be rewritten, mouse incisors are nearly halfway towards complete replacement (Coady et al., 1967). Molars therefore likely have much more accumulation of microwear on their enamel surfaces, representing a longer temporal period than those of incisors.

Laboratory experimentation has indicated that the size or quantity of abrasives correlated to differences in height, volume, and complexity parameters for molar microwear (Ackermans et al., 2020; Schulz-Kornas et al., 2020; Winkler et al., 2020b). These abrasives in these studies included materials seen in the soil composition of this study area, such as quartz and kaolin clay (Schaetzl & Anderson, 2005; Smit & van Rensburg, 2018; Viljoen et al., 2005), thus adding to their relevance. Yet, despite differences between incisor and molar morphology and usage, results from these studies were much more applicable to the incisor study in Chapter 5 than the data presented here. It may be that pellet feeding experiments do not necessarily mimic wild conditions. The guinea pigs in Winkler et al. (2020b), consumed pellets with added indigestible

abrasives as fill material that ensured interactions between molars and abrasives. Indeed, a study of gross dental wear for *Alouatta palliata* primate populations indicated that atmospheric volcanic ash had more of an impact on anterior tooth wear than molar (Spradley et al., 2015).

Other research has indicated that the effect of exogenous grit is in part reliant upon the material properties of the foods with which they are ingested and does not obfuscate dietary signal (Adams et al., 2020; Hua et al., 2020; Merceron et al., 2016). It may be such in this scenario, where the mechanical properties of the preferred grass seed supersede any effect caused by adhered soil. However, this reasoning does not account for the statistically significant differences in central tendencies that occurred in the dust analysis (to be discussed later in this chapter).

Land Cover Microwear Effects

The concentration of aeolian-borne grit (i.e., dust) is in part dependent upon the characteristics of land cover, with both vegetation type and density influencing grit exposure (Wolf & Nickling, 1993). As such, it is presumed that areas with less vegetative cover and more exposed soil should have greater accumulation of dust (see below for a more direct comparison of molar microwear by dust accumulation level). In addition, so should decreasing the height of vegetative cover. This leads to more open habitats having higher grit loads and exposure (Caporale & Ungar, 2016; Ungar et al., 2021a) that may be reflected in microwear. However, central tendencies MANOVAs of the influence of land cover on molar microwear signals failed to result in statistical significance for analysis by both vegetation classification (see Grunblatt et al., 1989) and by individual percent land cover for tree, shrub/bush, grass, and exposed soil.

Results here indicate that vegetation concentration is not influencing molar microwear texture formation for the Kolomela rodents.

Caution should be taken in interpreting these results, however, as these data are restricted and do not represent the full diversity of land cover characteristics. As a reminder, trapping transects were laid out based upon representative vegetation species, distance and direction from mining activities, wind direction, and potential differences in dust fall out (Avenant & du Plessis, 2018). Each trap also had no guarantee of successfully trapping rodents. Specimens used in this analysis were dependent upon these two variables, as this research builds off data collected for the Kolomela mine environmental impact assessment. As such, only low and medium percent coverage for exposed soil cover, bush cover, and tree cover could be compared. It is possible that microwear signals may differ if comparing samples from extremes, such as areas of low soil exposure compared to areas of high soil exposure, as regions with exposed soil percent > 66% might be more reflective of an open area with higher levels of grit that may adhere to foodstuff. Conversely, results are consistent with the notion that molar microwear is driven by mostly by diet as the vegetation species comprising land cover were all representative of those found in the Postmasburg Thornveld (see Chapter 3, Table 3.5).

Dust Level Microwear Effects

As described in Chapter 5, dust accumulation at the Kolomela mine and surrounding properties results primarily from mining activity and road use. Dust collectors indicate a mixture of quartz, sand, lime calcreate, hematite, road dust, ambient soil, quartzite, and various organics -- often < 100 μm in diameter (Loans, 2018). Although the specific compositions at sites of interest could not be ascertained, much of this dust appeared as thin red coatings on plants and

other objects regardless of location (personal observation). Molars with associated dust metadata fell in one of two categories: those from mid-level accumulation areas ($697 > x > 782$ mg/m^2/day) and those from higher-level areas ($1252 > x > 1293$ mg/m^2/day). As previously mentioned, particulates were observed during the preparation of stomach contents for analysis and likely resulted from the ingestion of atmospheric dust or ground soil in addition to foodstuff (personal observation).

When analyzing incisor microwear (see Chapter 5), the MANOVA conducted did not indicate significance for textural parameter central tendencies based upon a comparison of mid- or high- dustfall accumulations; nor did an analysis of molar microwear by soil group. The MANOVA analyzing molar microwear patterns based upon dust accumulation, however, did result in statistical significance. Specifically, the molars collected from sites with medium measures of dustfall possessed higher central tendencies in dale volume and area. Since dale measures reflect the region surrounding a pit, the microwear on these molars can be interpreted as having larger features than the molars from areas of higher dust concentration. These results are surprising given that other environmental variables did not influence molar microwear, nor did dust levels affect variation in incisor microwear. While it is likely that aeolian dust plays more of a role in microwear signature, that the Kolomela molars display only this environmental effect, especially while incisors do not, is puzzling and difficult to explain.

It is important to remember that these results only reflect trends in central tendency and do not explore the interactions with other factor or dispersion effects. Because of this narrow analysis, the possibility that incisor microwear is affected by dust concentration or composition cannot be dismissed. It could be that dispersion analyses might better parse incisor microwear based on aeolian grit effects or that interactions, especially with soil and behavior, are obscuring

any wear pattern that might result from dust. As previously discussed, incisor tips experience high rates of attrition to accommodate the continual eruption of the tooth and as such, incisor microwear does not reflect the same duration as molar. This difference in gross wear may also be driving differences between central tendency results for dust, and for other factors as well.

That microwear from molars collected in areas of medium levels of accumulations have larger dale areas and volumes may not be the result of dust concentration as so much as dust composition. While the overall makeup and range of particle size for aeolian grit is known, a breakdown by individual dust collectors was not obtained. As previously stated, the size, shape, and type of particle appear to affect molar microwear texture (e.g., Ackermans et al., 2020; Schulz-Kornas et al., 2020; Winkler et al., 2020). It might be that the aeolian particles associated with the medium level sample, in concert with the material properties of grass seed (see Hua et al., 2020), may be driving the higher central tendencies for the parameters *Sda* and *Sdv*.

However, this does not explain why aeolian dust affects a difference in central tendencies while other aspects of environment have not. The rodents from areas of high dust accumulation were also in areas with low percent soil exposure and all collected in July (see Chapter 3, Table 3.5). Meanwhile, rodents from areas of medium accumulation were all collected in May and vary in the percent soil exposure. Much like conflation with soil and soil interactions may explain the lack of significance in central tendencies for the effects of dust level on Kolomela incisor microwear, perhaps the molar results are also driven by similar interactions. Analyzed independently, land cover and season did not affect molar microwear. This does not, however, rule out interactions among these factors contributing the differences observed here.

While it is unknown whether rodents were consuming food within the areas in which they were captured. Preference could have been given for foraging within a specific substrate over

another. For example, *Micaelamys namaquensis* has been observed to favor foraging in sand rather than in substrates comprised of either sawdust or pebbles (Abu Baker & Brown, 2012). Although foraging substrate preference data are not available for other species in this study, this substrate preferences remain plausible for all taxa. If most of these individuals preferred to forage in sandy environments, similar exogenous abrasives ingested with similar foods (e.g., grass seed) should produce similar microwear textures (Hua et al., 2020). Unfortunately, this also highlights a flaw inherent in this experimental design: without direct observation, be it by cameras or other means, it is difficult to associate behaviors influential in microwear formation with such a specific location as a trapping transect.

Overall, the results of dust accumulation on molar microwear are inconsistent with other results presented in this dissertation, for both molars and incisors, and frankly, puzzling. That there appears to be a weak environmental signal in molars for dust level when diets are mostly controlled for (see Chapter 4) is consistent with the notion that exogenous grit can affect microwear but not enough to overwhelm the dietary signals in taxa with distinct food preferences (e.g., Adams et al., 2020; Hua et al., 2020; Merceron et al., 2016). However, why only aeolian abrasives only appear to affect the central tendencies of Kolomela molars is more difficult to explain – as is why this form of grit is not affecting incisors, too. This could be the result of a lack of dispersion and interaction analyses, conflation of variables, and physiological differences in incisor and molars. Regardless, it emphasizes the need for future research to better address these issues.

Seasonal Microwear Effects

Comparison of microwear by collection season indicated an overall lack of distinct difference in molar textures. This is unsurprising as most stomach contents for both collection periods were comprised of grass seed (64.8% mean contribution in May and 67.8% mean contribution in July; see Chapter 3 for more details). Furthermore, there lacked drastic environmental difference between the two months that could potentially affect food availability, or the material properties of the foodstuff consumed. Both months were relatively dry, with only 6.5 mm of rain falling in May and no rain in July (Mucina et al., 2006; Smit & van Rensburg, 2018). Perhaps the only real variation was in dust accumulation; where measured, amounts were higher in July ($1252 > x > 1293$ mg/m^2/day) than in May ($697 > x > 782$ mg/m^2/day).

When the analysis was restricted solely to microwear with known dust concentration, texture patterns from mid-level concentrations displayed larger dale areas and volumes (Table 6.20, Figure 6.12). Grouping microwear by month incorporated individuals from the farms Heuningkrantz and Widealsput into the mid-level group. Trapping transects within both farms were also located some distance away from the mine property (see Chapter 3, Figure 3.1). However, while dust buckets were not maintained at these sites, presumably, accumulation concentrations at Heuningkrantz and Widealsput would follow the patterns seen at other farms: greater in July during the more arid winter. Given this, it is unclear why the addition of specimens from Heuningkrantz and Widealsput lacked the same statistical significance in central tendency as the dust level comparison. However, these results are consistent with the lack of seasonal effects on molar microwear in the pilot study (Burgman et al, 2016).

The use of transitional periods in comparison to winter or summer periods in South Africa may be inadequate to understand possible effects of seasonality. Testing for the impact of

seasonality on microwear texture might be more valuable if analyzing samples from the wetter summers and the dryer winters. In addition to the results of this study, the comparison between the summer (wet) season and transitional period in the Dry Highveld grassland also indicated a lack of significance for SSFA quantification of *Rhabdomys pumillio* microwear (Burgman et al., 2016). There is potential for rodent molar microwear to elucidate seasonality — especially among opportunistic animals, should a change of seasons be accompanied by a change in food availability. This effect was observed by Calandra et al. (2016a, b), in which the seasonal shift in food availability was reflected in vole microwear attributes. Specifically, differences in the phytolith concentration of available foods were thought to drive the seasonal variation observed (Calandra et al., 2016a, b). In addition, abiotic influences, such as rainfall, may also be influential if seasonal variation is notable enough. During summer and spring months, the Kolomela region receives around 327 mm in accumulation, or around 50 mm/month. This increase in rainfall during spring/summer months may be observed in molar microwear, as rodents would hypothetically be eating plant material that's less brittle in summer months than winter due to increased hydration (Henry et al., 2000; Vincent, 1983; Winkler et al., 2018). Unfortunately, there was no summer collection period at the Kolomela properties in which to test this hypothesis.

Tooth Comparison

While rodents use their molars mainly as a masticatory tool to process foodstuff, the adaptive role of incisors is much more complex. Aside from gnawing, rodents use incisors in activities such as biting, cutting, stabbing, carrying, tearing, slicing, gouging, scraping, grooming, and digging (Happold, 2013). The diastema and associated skin-fold between the

incisors and molars, as previously described, aid in separating incisor activity from that of chewing as to reduce the intake of non-digestible matter (Happold, 2013; Skinner & Chimimba, 2005). Chewing and gnawing activities are further separated by the shifting of the mandible forwards and prevents molars and incisors from being in occlusion at the same time (Cox et al., 2012; Hiiemae & Ardran, 1968). The incisor and molar samples were hypothesized to significantly differ in microwear signal due to these differences in use. Specifically, molar microwear should relate more directly to diet than should incisor microwear and reflect interactions between mastication and the physical properties of foodstuff, while incisor microwear should be reflective of habitat use (Belmaker, 2018; Caporale & Ungar, 2015; Hua et al., 2015; Stefen, 2011; Ungar et al., 2021a).

Comparing the DMTA parameters of the incisor and molar samples indicated stark differences in texture signal, with ANOVAs producing statistically significant results ($p < 0.001$) for nearly every parameter. Mean dale area (*Sda*) was the only texture variable in which statistical significance was not reported. Molar microwear was more complex (*Asfc*, *Sdr*) than that of incisors, while incisors were more anisotropic (*epLsar*, *Str*) with large, broad features (*Tfv*). Molars also possessed larger features on coarser scales (*Smc*), higher pattern variation across the surface ($HAsfc_9$, $HAsfc_{81}$), and a greater presence of pits (*Ssk*). These pits were also significantly deeper than those on incisors (*Sv*, *S5v*) and greater in volume (*Vvv*, *Sdv*).

These results are as expected. Although microwear turnover rates in rodents do not align perfectly with rodent metabolism, changes in pattern may begin one or two days after a change in diet. A complete turnover of microwear signal, however, takes between 8 - 24 days (Winkler et al., 2020a). Still, the lack of statistical significance in the dietary MANOVAs coincide well with the data from the stomach content analysis. Although individual variation might exist, these

murids predominantly fed on grass seed regardless of species, location, or collection month (see Chapter 4). The diet-based signal on rodent molar microwear follow trends observed with larger mammals despite propolinal mastication (Rodrigues et al., 2009). Diets of harder and more brittle foods, such as grass seed, are usually associated with more complex and pitted surfaces (e.g., see Ungar, 2015 for review). As such, the more complex and pitted microwear of molars aligns well with a diet tending towards graminivory.

Furthermore, these results may be driven by differences in gross wear between the two types of teeth. Unlike molars, where the “last supper” microwear effect is more reflective of the last few suppers, incisor microwear truly records that metaphorical last supper. As a reminder, rodent incisors are ever-growing, with high attrition rates that lead to fast turnover of enamel at the tip of the tooth (e.g., Coady et al., 1967; Risnes et al., 1995; Weinreb et al., 1967). Incisor microwear, therefore, only reflects hours of a rodent's life rather than days, or even weeks (see Grine, 1986; Teaford & Oyen, 1989; Winkler et al., 2020b for further on the "last supper" effect on molar microwear). As such, the significantly higher complexity and deeper, larger features associated with the rodent molar sample may also be reflective of wear accumulation on different temporal scales.

The higher anisotropy of the incisor sample may be reflective of the orthal movements associated with this tooth use. Stefen (2011) believed the parallel scratches on beaver incisors to reflect direct contact between the tooth surface and either food or bark. Similarly, Ungar et al. (2021a) cited repetitive orthal movement while digging as an explanation for increased anisotropy on vole incisors in comparison to those of lemmings. Incisor use in digging has not been recorded for any of the species in this study. Still, these specimens gnaw, and presumably use their incisors to groom and to carry food, young, and nesting materials - actions which would

still involve repetitive orthal movements for incisors. While propolinal mastication also incorporates a back-to-forth movement, albeit on the horizontal plane rather than the vertical as is for incisors, the molar microwear observed here lacks the clear anisotropic signal of incisors. It is possible that in the initial occlusion between molar teeth, a crushing action leads to the more complex, pitted texture observed. Meanwhile, the distal labial portion of the incisor analyzed may only slide past the particles of food or grit in which it interacts, causing scratches in the direction of drag (see Hua et al., 2015).

Finally, the large scratches may be a result of incisor interaction with grit throughout an individual's daily activities, including grooming, burrowing, foraging, and eating. Given the location of these specimens within and surrounding an active open pit mining site, and the propensity for most of these species to use underground burrows, it seems inconceivable that incisors would not encounter dust or soil. While analyzing the effects of exogenous abrasives on molar microwear formation, Winkler et al. (2020b) reported that exposure to large quartz particles, which comprise the loam and sandy soils at these sample sites, resulted in higher values for volume parameter.

Differences between mastication and incisor movement need to be considered, as does the "last supper" effect and the gross wear differences between the two forms of teeth. Still, the incisor microwear presented here separated macro- and micro- habitats, burrowing behavior, and soil types, when molars only showed statistical significance for species, burrowing behavior, and dust level. Even then, the first two variables seem to be the result of differing molar topography among taxa. Differences reported by dust accumulation in molars rather than incisors, however, are thought to be the result of an environmental signal highlighted due to the lack of a dietary

differences. This indicates that while rodent molar microwear remains applicable in dietary reconstruction, it is the incisors that will provide more information on the abiotic environment.

Conclusion

Despite a lack of many significant differences in central tendencies and constraints in the experimental design, these data still are not inconsistent with rodent molar microwear as a proxy for diet. Statistically significant differences were observed for analyses by species, burrowing behavior, and dust levels. However, it was the ***lack*** of statistical significance that spoke volumes. The murids collected at the Kumba Iron Ore properties possessed a strong preference for eating grass seed (see Chapter 4). Although individual dietary preferences were observed in stomach content analyses, the three diet groups with sufficient sample sizes for microwear analysis each possessed stomachs with at least 50% volumetric contribution of grass seed. This tendency towards grass seed consumption was clearly reflected in the microwear data, as DMTA of central tendencies could not parse diet groups of grass seed-curculionid, grass seed-grass blade, and grass seed-grass seed. This homogenous signal provided a chance to observe the influence of other factors in molar microwear formation.

Specifically, molar microwear appeared to be affected by differences in taxa and differences in exogenous grit composition. Species differences in microwear occurred across a sub-family line, with the Gerbillinae sample (*Gerbilliscus leucogaster*) separating from the Murinae samples (*Micaelamys namaquensis* and *Rhabdomys bechuanae*) by measures of *Smc*, *Tfv*, *Sdr*, and *S5v*. Except for *Sdr*, these same parameters also separated molar microwear by basis of burrowing activity. Unlike with incisors, where burrower features were larger and

deeper, the molar microwear for burrowers were smaller and shallower like the *G. leucogaster* sample. Rather than reflect burrowing behavior, this result might actually stem from differences in tooth shape and topography, as *Gerbilliscus* species made up most of the burrowing sample. Given that all the murid species used in this study engage in propalinal mastication, thought was not given to differences that may occur based on dentition. But in this study, it appears that the flatter, non-interlocking molars of gerbils produce shallower, less complex microwear than the more sloped, interlocking molars of murine species. If diets had differed more radically among the generalist species, this effect may have been overlooked. Instead, it provides a cautionary tale that not all murid molars are the same. Reasons such as this are why extant taxa with differing dental bauplans are considered separately in microwear analyses (e.g., Ungar et al., 2017). Further, it suggests further research be done on the effects of slope and other topographic differences of murid molars on microwear, similar to that of Ungar et al. (2017) or Purnell et al. (2017).

The lack of a dietary difference in both microwear and stomach content analysis also allowed for a potential exogenous abrasive signal to be reflected. While laboratory experiments have shown the effects varying sizes, quantities, shapes, and types of exogenous abrasives can have on molar microwear formation (e.g., Ackermans et al., 2020; Schulz-Kornas et al., 2020; Walker et al., 2020b), others have indicated that adhered particles of grit work in concert with foodstuff to produce microwear textures that preserve the dietary signal (e.g., Hua et al., 2020; Merceron et al., 2016) or demonstrated that exogenous grit does not affect the dietary effect on microwear (e.g., Adams et al., 2020). Interestingly, while soil type lacked an effect on molar microwear, dust level could be separated by ISO parameters *Sdv* and *Sda*. It is feasible that

exogenous grit does provide an environmental signal when diets are relatively similar, as at Kolomela. However, these results were difficult to explain.

Even though the nuances of rodent diets could not to be separated in this study, rodent molar microwear signals may still reflect diet. However, dietary specifics and many of the other independent variables examined in this study might better be dispersion analyses than central tendencies. However, due to the potential of extremely uneven sample sizes driving dispersion results for many of these comparisons, those analyses were excluded from this thesis. Dispersion differences by habitat and by species were noted for the SSFA variables used in the pilot study (Burgman et al., 2016). It is quite possible that future work in reworking the statistical methods to accommodate sample size issues might indicate better separation for molars in these categories.

Overall, molar microwear lacked a strong environmental signal with a lack of statistical significance occurring in macrohabitat, microhabitat, soil, land cover, and seasonal analyses. Since resource availability, and preferred food, didn't differ among the samples used in analysis of these various variables, molar microwear should not differ (see Calandra et al., 2016b for similar results). In studies in which rodent molar microwear had a perceived environmental signal, it was likely due to differences in available foodstuff (e.g., Burgman et al., 2016; Nelson et al., 2005; Robinet et al., 2020; Winkler et al., 2016;). Rodent incisor microwear, meanwhile, appeared much more influenced by environmental factors. The microwear signals of these teeth indicated statistical significance for habitat, microhabitat, and soil type, as well as by species and burrowing behavior. When comparing the entirety of the incisor microwear sample to that of molars, stark differences were observed. Mainly, incisors were more anisotropic with large and broad scratches, while molar microwear was more complex with larger pits and greater surface

variation. In future research, both teeth should be considered to retrodict environments on basis of abiotic (incisors) and biotic (molars) factors.

CHAPTER SEVEN: CONCLUSIONS

The reconstruction of past environments allows for insight into some of the key forces behind hominin evolution and the context in which evolution occurred. Numerous methods and proxies exist that aid in this goal, ranging from broad-scaled climatological data reflective of the shifting global climates in the Pliocene-Pleistocene to data reflecting more localized conditions within a given time and place. Dental microwear texture analyses (DMTA) help to build datasets on these more localized conditions. Faunal molar microwear analyses reflect dietary behaviors of past animals, and the material properties of ingested materials reflect food availability in a given habitat. However, most of these studies have focused on larger taxa (e.g., Merceron et al., 2004; Schubert et al., 2006; Scott et al., 2012) that may mask the complexities of the mosaic by habitats occupied hominins. As such, focus on smaller taxa with smaller home ranges, like those of many rodent species, becomes important when considering more finely-scaled paleoenvironment data.

The application of DMTA to micromammals and rodents is relatively new, with many studies only conducted during the past decade (see Table 2.1, Chapter 2). While fossil rodent dental microwear has previously been used in paleoecological studies (e.g., Hopley et al., 2006; Kaya & Kaymakçı, 2013; Rodrigues et al., 2012; Ungar et al., 2017; Yang et al., 2021), texture-based analyses remain relatively rare. Indeed, of these studies, only Ungar et al. (2017) utilized DTMA techniques. Still, prior work using extant taxa has indicated that DMTA techniques can be applied to both rodent incisors and molars to successfully parse habitats and diets, respectively (e.g., Burgman et al., 2016; Caprolae & Ungar, 2016; Ungar et al., 2021; Winkler et al., 2016).

This dissertation, therefore, focused on the efficacy of using rodent dental microwear texture analysis as a paleoenvironmental proxy. Using wild-trapped Muroidea species caught at Kumba Iron Ore's Kolomela Mine and associated properties provided an opportunity to better understand both abiotic and biotic influence on rodent microwear formation for both incisors and molars. The preservation of specimen stomachs allowed investigations of dietary microwear effects made based on known stomach contents for species typically referred to as generalist or opportunistic in the literature. In addition, data provided by the biomonitoring program conducted at these sites allowed microwear to be assessed relative to specific abiotic characteristics not always detailed in DMTA studies of wild-caught specimen, such as the effects of dust level, vegetative land cover, and soil composition on both molar and incisor microwear textures. All data also contributed to the construction of a DMTA baseline of extant South African muroids with known dietary, behavioral, and abiotic factors for future interpretations of fossil data.

This chapter summarizes the results of the previous chapters, focusing on key findings from the stomach content and microwear analyses in context of the objectives and hypotheses established in Chapter One. In addition, this chapter discusses limitations of this study, particularly concerning ecological field work, and suggests future directions to further rodent microwear as a proxy for fine-scale environmental reconstruction.

Research Objectives and Hypotheses

This study had four main objectives used to assess the effectiveness of rodent dental microwear texture analysis as a proxy for paleoenvironmental reconstructions: 1) the utilization of stomach content analyses to ascertain specific dietary preferences; 2) the effects of

environmental and behavioral attributes on incisor microwear textures; 3) the effects of environmental and behavior attributes on molar microwear textures; and 4) a comparison of molar and incisor DMTA results. While the biomonitoring project at Kolomela provided most of the relevant metadata for the microwear analysis, the captured Muroidea rodents mainly consisted of generalist species. The lack of dietary specificity for flexible and opportunistic feeders makes it difficult to use extant specimens for comparative microwear studies because the variability makes it difficult to associate dental microwear texture parameters with specific diets.

1. The first objective of this research, the stomach content analyses of 214 specimens captured within the Kolomela properties, created a chance to better establish the diets of these individuals and to compare extant rodent microwear with individual food choices preferences rather than broad species associations.

2. The second objective of this study was the application of incisor microwear texture analysis as a direct proxy for the non-dietary characteristics of macro- and microhabitats. Incisors from 198 individuals provided microwear texture data, consisting of both scale-sensitive fractal analysis (SSFA) and International Standards Organization (ISO) parameters, which were then analyzed based on different behavioral and environmental attributes. This incisor sample was comprised of six Muroidea species of families Nesomyidae and Muridae that were collected in May and in July from seven different properties, including that of the mine proper.

3. The third objective, the molar analysis, was to confirm that rodent molar microwear is reflective of dietary attributes and food availability within a given location. Methods followed those of the incisor DMTA, with 175 specimens providing molar microwear texture data that were analyzed based on the same behavioral and environmental attributes. While this sample was also collected in May and July from the seven Kolomela properties, it only consisted of five Muridae species.

4. Objective four was to confirm the hypothesis that rodent incisors and molars recorded different aspects of rodent ecology, as well as build a baseline of extant rodent incisor and molar microwear with detailed ecological metadata that can be used in future studies. To accomplish this, results from the incisor and molar analyses were compared and consolidated. In addition, statistical analyses compared the texture data for each type of tooth to clarify differences in microwear texture patterns between these teeth.

Objective One: Stomach Content Analysis of Muroidea Rodents

The first objective of this dissertation considered the catholic foraging behavior of generalist rodent species and sought to provide specific diets that could be used within the dental microwear analyses. In addition, stomach content analysis allowed for a chance to better understanding the dietary behaviors of a rodent community impacted by mining and other anthropogenic activities. It was hypothesized that the diets of individual muroid rodents would reflect the vegetative composition of their habitat as well as the dietary nature of their specific species. Further, individuals from more disturbed areas were hypothesized to supplement their diets with less preferred foods to meet metabolic requirements. Ingested materials were

determined to the nearest 5% of overall volume contribution and consisted of eleven reoccurring items: grass blade, grass seed, dicot stem and leaf, dicot seed, annelid, curculionid, caterpillar, feather, flesh, hair, and artificial materials. To test hypotheses, the percent volumetric contribution of plant, insect, and other material to stomach contents were compared by species, collection location, and collection month.

The results of these analyses supported the hypothesis that stomach contents reflect habitat and species dietary behavior. Despite collection occurring at the different Kolomela properties, all were located primarily within the Postmasberg Thornveld among a high diversity of monocots that included various *Aristida*, *Enneapogon*, *Eragotis*, and *Tragus* species (see Smit & van Rensburg, 2018). Furthermore, the breakdown of land cover at each trapping transect typically consisted of a higher percentage of grass cover (Table 3.5 in Chapter 3). Under Grunblatt et al.'s (1989) hierarchal classification system, most of these transects were described as grassed shrublands or grasslands. The high availability of grass material coincides with the high concentrations of grass seed within the analyzed stomachs, regardless of species (mean ≥ 58.33%), location (mean ≥ 59.21%), or collection month (mean ≥ 64.79%). Conversely, grass blades were found less frequently in stomachs, and always contributed far less to the overall stomach contents regardless of species (mean ≤ 6.97%), location (mean ≤ 13.42%), or month (mean ≤ 6.82%). This difference is unsurprising. Grass blades are nutrient poor and harder for unspecialized rodent species to digest, especially in comparison to nutrient rich seeds (Langer, 2002; Verde Arregoitia & D'elia, 2021; Williams & Kay, 2001).

Indeed, *Dendromus melanotis* was the only species in this analysis that is considered a specialist, subsisting specifically on seeds and insects (Dieterlen, 1971; Happold, 2013; Rowe-Rowe, 1986; Shortridge, 1934; Smithers, 1971). The two *D. melanotis* stomachs examined

contained, on average, 62.5% grass seed and 20% curculionid. All the murids represented, *Gerbilliscus leucogaster*, *G. paeba*, *Mastomys coucha*, *Micaelamys namaquensis*, and *Mus minutoides*, are described as generalist omnivores that are often opportunistic (e.g., Happold, 2013; Monadjem et al., 2015; Skinner & Chimimba, 2005). This generalist nature implies that these species will consume whatever is necessary to meet their high caloric requirements. Often, muroids will opt for higher caloric foods, such as seed or insect (Gliwicz & Taylor, 2002). Of the two options, less energy needs to be used to obtain grass seeds than insects, especially in areas of high grass concentration.

However, individual preferences within a species may vary, which may in part explain the few statistically significant differences between taxa observed in the Kruskal-Wallis tests. Aside from differing percent contributions of hair within stomachs, which was thought to be an effect of species grooming behavior, the percent contribution of grass and caterpillar also significantly differed among generalist species. Specifically, significant variation existed between *G. leucogaster* and *R. bechuanae*, as well as *G. paeba* and *Mi. namaquensis* in percent grass contribution to stomach contents, and between *Ma. coucha* and both *G. leucogaster* and *Mi. namaquensis* for percent caterpillar contribution. These results may be indicative of species preferences, sampling behavior, or a reflection of competition between sympatric populations over supplementary food sources.

Generalist rodents alter their dietary behavior based on habitat disturbance and food availability (Bekele & Leirs, 1997) and this flexibility was predicted to be reflected within the dietary analysis. Rodents captured within the Kolomela Mine had the highest percent contribution of grass blade, which significantly differed in comparison to populations from three of the farms. As the most disturbed location sampled, it seems reasonable that the mean

increased amount of grass blade in stomachs stemmed from those rodents needing to eat whatever they could to supplement metabolic requirements. The percent contribution of all other ingested materials did not differ significantly among collection locations. However, these similar diets could be due to ecological similarities within the Postmasburg Thornveld or the compromised environmental integrity at all these collection locations. Although mining activity only took place within the Kolomela boundaries, the other properties are farmlands have experienced their own anthropogenic disturbances, which could have also limited the available dietary resources for rodents.

Aside from exploring dietary ecology hypotheses, Chapter 4 established known diets for 214 individual rodents that could be used in dental microwear analysis. These data are especially important considering the catholic dietary behavior of the capture Murinae specimens. "Opportunistic omnivore," as most of the species used in this study are labeled, is an extremely broad dietary classification that allows for population differences within a species but limits the extent in which an extant baseline of rodent microwear can be used to reconstruct dietary behavior to extinct species. Yet, stomach content analyses at Kolomela revealed muroid diets that were overwhelmingly granivorous. This detail agrees with the vegetation composition of the Kolomela properties and the opportunistic nature of the murine species. In addition, it provides dietary nuance missing in the pilot study (Burgman et al., 2016) and proved to be extremely useful in parsing differences in incisor and molar microwear.

Objective Two: Incisor Microwear Texture Analysis of Muroidea Rodents

The second objective of this dissertation was to establish a comparative baseline of extant incisor microwear textures that includes behavioral and environmental metadata in addition to

SSFA and ISO microwear texture data. It was hypothesized that incisor microwear would reflect the non-dietary characteristics of a habitat due to the lack of influence by masticatory movements and the direct interactions these teeth have with their surroundings. A sample of 198 muroid individuals provided surfaces with antemortem microwear and contributed to the incisor portion of the extant microwear baseline. These individuals comprised seven species: climbing mouse *Dendromus melanotis* (family Nesomyidae, sub-family Dendromurinae), gerbils *Gerbilliscus leucogaster* and *Gerbilliscus* paeba (family Muridae, sub-family Gerbillinae), and mice species *Mastomys coucha*, *Micaelamys namaquensis*, and *Rhabdomys bechuanae* (family Muridae, sub-family Murinae). Analyses of microwear texture parameters indicated statistically significant variation in central tendencies by species, macrohabitat, microhabitat, burrowing behavior, soil type, and land cover classification.

Higher grit exposure was predicted to result in more complex microwear textures with larger features and increased pitting, be it due to increased dust exposure or use of these teeth in constructing underground burrows. This hypothesis was only partially supported by the results in Chapter 5. Statistical differences for species and burrowing behavior appeared driven by increased exposure to soil particles. Indeed, species that engaged in underground burrow excavations had significantly higher complexity (*Asfc*, *Sdr*) values and larger features (*S5v*, *Vvv*, *Sv*) than those that did not. However, microwear texture analysis based on the amount of aeolian dust exposure did not result in statistically significant difference, as was expected. While these results were surprising, they still make sense in light of the overwhelming presence of dust typically present at the Kolomela properties (personal observation). Specimens were obtained from areas of either medium (734 mg/m^2/day mean) or high (1272.5 mg/m^2/day mean) levels of

accumulation, which meant incisor exposure to dust in all study area locations was likely and perhaps not so starkly different as to produce differences in microwear textures.

Dental microwear textures varied significantly by both macro- and microhabitat, however, results appeared to be highly influenced by soil composition. Incisor microwear associated with loam soils were characterized as complex surfaces with large and deep features while microwear associated with rocky soils was more anisotropic with small, shallow features. Similarly, incisor microwear from the farm Kappies Kareeboom, consisting of clay/loam and loam soils, possessed the highest measures of complexity and large, deep features. Yet, incisors from Heuningkrantz, which was a mix of sand and rocky soils, had low measures of complexity that appeared consistent with results from the soil analysis. Similar trends were noted for microhabitat effect. The most complex microwear stemmed from transect KK3 in the Kappies Kareeboom farm, which consisted of loam soils within an open habitat. Microwear from the Heuningkrantz farm transect, HK7, displayed little complexity, reflective of the rocky soil found at the site. That the physical properties of different soils appeared to affect incisor microwear in this study supports previous in vivo experimental studies that showed these properties to influence molar microwear characteristics when exogenous grit was directly fed to test subjects (e.g., Ackermans et al., 2020; Schulz-Kornas et al., 2020; Winkler et al., 2020; but see also Adams et al., 2020; Merceron et al., 2016).

Microwear textures did not vary significantly in land cover analyses by the percent cover for each type of vegetation. Likewise, the percent cover of exposed soil did not significantly vary statistically for each group considered. An analysis of land cover classification, based on Grunblatt et al.'s (1989) hierarchal classification system, however, did indicate statistically significant variation in microwear parameter central tendencies for complexity (*Asfc*), anisotropy

(*epLsar*), and mean dale area (*Sda*). There did not appear to be a trend towards open vegetation areas having increased complexity or larger features, nor any strong associations to soil properties. Interactions with soils may have influenced microwear in some ways, as *epLsar* results reflected the results observed in the burrowing analysis. These results remain difficult to interpret when considering any particular aspect of a given habitat, as observed with the macro- and microhabitat studies. Instead, they seem to imply that rodent diversity and behavior vary based on vegetative cover, even within the same ecoregion, and that incisor microwear will be more dependent on these interactions than any single characteristic of their habitat.

As hypothesized, diet did not appear to influence incisor microwear formation. This result needs to be interpreted with caution, however. The diets of Kolomela rodents were extremely similar, which could have also contributed towards the lack of statistical significance in the dietary analysis. Caporale and Ungar (2016) also had difficulty parsing rodent incisor microwear based on diet, as did Ungar et al. (2021). Indeed, Ungar et al. (2021) explained microwear variation between lemmings and voles as related to microhabitat characteristics and substrate use, which aligned with Caporale and Ungar's (2016) conclusion that habitat had the strongest effect on incisor microwear.

Although Kolomela incisor microwear patters did not reflect every environmental parameter considered, the influence of substrate use and composition was clear in this investigation. These results support the idea that rodent incisor microwear reflects habitat attributes. While it was easy to associate soil and soil interaction effects with incisor microwear patterns, the results of the land cover analysis indicated that incisor microwear formation cannot be broken down so simply. Rodents use incisors for several functions, all of which likely result in the formation of dental microwear on their surfaces. This *in situ* research occurred within a

specific ecoregion, the Postmasburg Thornveld, where climate and vegetation are relatively similar. Yet, incisor microwear parameters indicated variation when ecosystem characteristics did differ, further suggesting their efficacy as a paleoenvironmental proxy.

Objective Three: Molar Microwear Texture Analysis of Muroidea Rodents

Like the second objective of this dissertation, the third objective focused on establishing a comparative baseline of extant rodent microwear. This baseline provides data on molar microwear textures that, once again, includes behavioral and environmental metadata, as well as SSFA and ISO parameters. Unlike the incisor study, the molar microwear analysis was restricted to Muridae species: the two gerbils of sub-family Gerbillinae, *Gerbilliscus leucogaster* and *Gerbilliscus paeba*, and three mice from sub-family Murinae, *Mastomys coucha*, *Micaelamys namaquensis*, and *Rhabdomys bechuanae*. Unfortunately, *Dendromus melatonis* and *Mus minutoides* molars did not possess well-preserved antemortem microwear on the enamel surfaces and were excluded from study. Together, these species comprised a sample of 175 individuals. It was hypothesized that molar microwear would reflect dietary preference, with signals unobscured by grit exposure. The consumption of tough foods (e.g., grass blades) would be associated with higher anisotropy while the consumption of hard, brittle items (e.g., seeds) would be associated with higher complexity.

Analyses for central tendencies did not indicate statistically significant differences in microwear parameters by diet. However, these results were not inconsistent with the initial hypotheses that rodent molar microwear would be indicative of dietary preference given the extreme uniformity of diets among the individuals considered in this study. The stomach content analyses presented in Chapter 4 indicated that the generalist species found within the Kolomela

properties possessed a strong preference for grass seed despite some individual dietary variation. Three diet groups were established to have sufficient sample sizes for the analysis of central tendencies: grass seed/grass seed, grass seed/grass blade, and grass seed/grass seed. However, each group consisted of individuals with at least 50% volumetric contribution of grass seed, which likely resulted in the lack of statistical significance in microwear parameter central tendencies by diet. Indeed, Calandra et al. (2016b) observed similar results for a sample of wild caught voles, indicating that the similar environmental attributes of the two habitats meant that vole diet did not differ. That most of the Kolomela rodents were eating the same thing was not initially expected when developing the dissertation plan. However, the relatively homogenous dietary signal did provide a chance to observe the influence of other factors on molar microwear.

Analyses of microwear texture parameters did indicate statistically significant differences in central tendencies by species, burrowing behavior, and dust level. Both the signals for species and burrowing behavior appear to be driven by differences in molar topography. Samples composed primarily of non-interlocking, flatter molars (gerbils) possessed shallower, less complex microwear textures than those samples consisting of more sloped, interlocking molars (murines). This result was unexpected and may have been masked if diets had significantly differed. Instead, it indicates that the shared trait of propalinal mastication might not be enough of a justification to group muroid species together for molar microwear analyses. Instead, much like with larger taxa (e.g., Ungar et al., 2017), it appears that the dental bauplan of individual species must be considered as well.

That two parameters, mean dale area (*Sda*) and mean dale volume (*Sdv*), parsed specimens by dust level was surprising given that a) this factor did not separate incisor microwear when most other grit related factors produced an effect (which will be discussed in

the next section), and b) no other environmental characteristic affected molar microwear textures, as the burrowing effect was thought to be taxa-driven. Several conjectures were put forward to explain this result. Perhaps the molar microwear textures of wild rodents provide an environmental signal when diet can be controlled for, and food variation does not swamp the signal. Maybe the soil analysis resulted in a lack of effect because these seed-eating rodents were potentially foraging the same foods within the same type of soil, regardless of the soil associated with a trapping transect. These explanations are consistent with previous work establishing that the dietary signal is not obscured by exogenous grit (e.g., Merceron et al., 2016; Hua et al., 2020) because this dust effect occurred among relatively homogenous dietary textures. Furthermore, it is possible that microwear patterns might still differ in dispersion or be obscured by interactions of factors considered here but not included due to issues with sample sizes and the large number of factors considered.

Due to the dominance of grass seed in the diets of the Kolomela rodents, hypotheses regarding tough and hard food associations with DMTA parameters could not be fully evaluated. However, these results are not inconsistent with the hypothesis that molar microwear pattern reflects the dietary ecology at Kolomela and confirm the usefulness of stomach content analysis in this dissertation. Without the degree of dietary specificity provided by stomach contents, these same data could be interpreted as a failure of molar microwear to parse the diets of generalist rodents. Taxa-driven differences may have also been misinterpreted as dietary differences. However, in knowing that the diets of these generalists were mainly granivorous, it seems more likely that the lack of statistical significance in parameter central tendencies by diet aligns with the results of the stomach content analysis, and that rodent molar microwear will indicate dietary signals regardless of exogenous grit.

Objective 4: Comparison of Muirodea Incisor and Molar Microwear Textures

The final objective of this dissertation was to test the hypothesis that rodent incisors and molars record different aspects of rodent ecology. Specifically, molar microwear was predicted to reflect the material properties of ingested foodstuff in concert with the masticatory actions of occlusal surfaces while incisor microwear would reflect aspects of grit exposure (Belmaker, 2018; Caporale & Ungar, 2015; Hua et al., 2015; Stefen, 2011; Ungar et al., 2021a). This comparison was included in Chapter 6 along with the molar microwear analysis. In addition to comparing the effects of the different factors, statistical analyses were conducted on the entire muroid sample to compare directly central tendency variation in microwear texture parameters between the two tooth types.

Results did indeed confirm the hypotheses that rodent incisors and molars substantially differ in microwear textures. Every parameter, except for *Sda*, showed statistically significant differences in central tendency when comparing molars and incisors. Molar microwear was more complex and isotropic than incisors, with heterogeneous patterning across the enamel surface that was composed of large and deep pits and scratches. Incisors, meanwhile, had anisotropic microwear texture comprised mainly of large, broad scratches. Furthermore, the tested factors – species, macrohabitat, microhabitat, diet, burrowing behavior, soil, land cover, dust levels, and season – had different effects on microwear textures for incisors than for molars (see Table 7.1). Incisor central tendency analyses indicated a greater degree of non-dietary influence, as samples could be parsed by macrohabitat, microhabitat, soil, and land cover classification. While diet results for molar microwear lacked statistical significance, this is likely a result of dietary homogeneity within the sample, as grass seed contributed most to each dietary group considered.

Table 7.1: Summary of significant variables for the dental microwear analysis of Kolomela rodents

Factor considered	Tooth	MANOVA results	Signnificant DMTA parameters
Species	I	$p < 0.01$	*Asfc , epLsar , S5v , Vvv, Sv*
	M	$p < 0.01$	*Smc , Tfv , Sdr , S5v*
Macrohabitat	I	$p < 0.01$	*Asfc, epLsar, Smc, Sdr , Sdv, Vvv*
	M		
Microhabitat	I	$p < 0.05$	*Asfc , epLsar , Sdr , Sdv , Vvv*
	M		
Diet	I		
	M		
Burrowing behavior	I	$p < 0.01$	*Asfc , epLsar , HAsfc$_9$, S5v , Vvv , Sv*
	M	$p < 0.05$	*Smc , Tfv , S5v*
Soil	I	$p < 0.001$	*Asfc , epLsar , Sdr , S5v , Vvv , Sv*
	M		
Land cover classification	I	$p < 0.01$	*Asfc , epLsar , Sda*
	M		
Land cover (percent)	I		
	M		
Dust level	I		
	M	$p < 0.05$	*Sdv , Sda*
Collection month	I		
	M		
Tooth comparison		$p < 0.001$	*Asfc , epLsar , Tfv, HASfc$_9$, HAsfc$_{81}$, Ssk , Sdr , S5v , Str , Sdv , Vvv , Sv*

*if p -value is not provided, analysis lacked statistical significance

Although species and burrowing central tendency analyses resulted in statistically significant diferences in both incisor and molar studies, the mechanisms driving these results were thought to differ. For molars, taxon-driven differences in tooth topography and occlusion were believed to be the primary cause of significant differences for these two factors. For incisors, however, burrowing behavior seemed more influential in affecting these results. Surprisingly, dust level affected the central tendencies of molar microwear parameters despite not affecting incisor microwear patterning. However, it is important to remember that both dispersion analyses and interaction tests were not conducted in this dissertation (see Chapter 3). The lack of a statistical difference in central tendency should not imply an overall lack of effect

given these restricted analyses. Dust level effects on incisor microwear may be better expressed through dispersion variation. Or the aeolian grit signal in incisors may be obscured by other factors, such as soil and soil interactions. Clearly, more work needs to be done in understanding the environmental effect on rodent incisors.

While varying interactions with their external habitat do appear to be reflected in dental microwear textures, one cannot divorce aspects of rodent dental development from these results. Incisors are, in essence, multitools for rodents. While gnawing is important in maintaining both the shape of incisors and rates of attrition equivalent to rates of eruption, incisors are also used in functions like food procurement, fighting, digging, grooming, and carrying (Happold, 2013). Molars, however, are only used in mastication. Rodent dentition has evolved to reflect these differences in use. Incisors and molars cannot both be in occlusion at the same time (Cox et al., 2012; Hiiemae & Ardran, 1968). The diastema and associated skin-fold between incisors and molars act to separate incisor activity from that of molars and reduce the intake of non-digestible matter when incisors are used for non-dietary purposes (Happold, 2013; Skinner & Chimimba, 2005). These adaptations, in addition to the results presented here, help support the hypothesis that rodent molar microwear is indicative of diet.

However, the higher complexity values observed for molar microwear might also result from difference in the rate of gross wear for these species. Incisors are ever-growing, and as previously mentioned, attrition rates need to match those of continual eruption. The molars of the muroid species from the Kolomela properties are rooted and once the enamel surface is worn away, it does not regrow. Despite the lack of information on the attrition rates of these species, lab experimentation using murids have indicated that attrition rates range between means of 0.379 mm/day (Weinreb et al., 1967) to 0.483 mm/day (Risnes et al., 1995). These data indicate

that while molar microwear turnover can take days to weeks (e.g., Grine, 1986; Teaford & Oyen, 1989; Winkler et al., 2020b), incisor microwear turnover happens in a matter of hours. This discrepancy in temporal scale indicates that the more complex microwear of rodent molars may result from interactions between the overall accumulation of microwear and diet given more time for microwear to accumulate on and affect the enamel surface. It also indicates that incisor microwear is likely much more reflective of activity in microhabitats occupied during the last hours of an individual's life.

That microwear textures of incisors and molars indicate different aspect of rodent ecology appears to be an accurate assumption, at least within the confines of this dissertation. Despite analyses restricted to central tendencies, results seem to indicate that the incisor microwear signal does relate to exogenous grit in the environment. And while molar microwear might possess an environmental influence when diet is relatively constant, as observed with the dust level factor, this does not obscure the primary determinant of diet. However, these microwear results should be interpreted within the context of the dental adaptations that in part make Rodentia such a successful radiation.

Conclusions

The main purpose of this research was to assess the efficacy of using rodent dental microwear texture analysis as a paleoenvironmental proxy. With the assistance of the Kolomela biomonitoring program, a baseline of extant muroid incisor and molar microwear parameter textures was established with known dietary and environmental characteristics. Analyzing the effects of these characteristics on parameter central tendencies tested hypotheses regarding specific ecological contributions to incisor and molar microwear etiology. This study is also one

of the few to combine the stomach content analysis with dental microwear. And it is the first to apply both techniques to an analysis of rodents within the same study. Stomach content analysis proved particularly important in this dissertation due to a sample consisting mainly of generalist species, and the vagaries associated with these diets as a response to resource availability.

To date, only four studies have examined the incisor microwear of micromammal rodents, with three focusing on rodents (Belmaker & Ungar, 2010; Caporale & Ungar, 2016; Ungar et al., 2021) and one on shrews (Withnell & Ungar, 2014). Although more work has been conducted with rodent molars, the bulk of these studies have only occurred within the last decade (see Belmaker, 2018 for a review). Given the potential of rodent microwear for diet and habitat inference, especially that of incisors, to reflect finer spatial and temporal scales, the formation of such a detailed extant baseline becomes important to use in interpreting fossil rodent microwear textures. In return, these interpretations may further the understanding of the complex, mosaic habitats in the past, such as those in which Plio-Pleistocene hominins are thought to have evolved.

The data presented in this dissertation do substantiate the idea that molars and incisors reflect different aspects of rodent ecology, as previously summarized. Simply, these results are consistent with the notion that molar microwear texture is driven mainly by diet while incisor microwear seems to reflect a more complex interplay of other environmental components and interactions. This study was not without its constraints, many of which associated with the difficulties in using specimens from a wild rodent community.

Study Limitations

While *in-situ* research allowed for detailed and direct associations between rodent dental microwear textures and documented environmental parameters, it also resulted in imperfect sampling conditions that complicated statistical analyses. As discussed in Chapter 3, the use of field caught specimens led to extremely skewed sample sizes given an inability to control the behavior of wild animals. Variation in trap shyness, for example, led to an abundance of *Gerbilliscus leucogaster* specimens while other species, such as *Dendromus melanotis*, were only represented by a couple of individuals. In addition, the prolonged anthropogenic disturbances at the Kolomela properties have led to rodent communities consisting mainly of generalist species (Avenant, 2011). Working with dietary generalists set precedent for stomach content analyses; without utilizing this method, dietary specifics would be unknown at Kolomela given the wide variety of foodstuff a generalist rodent will eat. Conversely, due to potential resource limitations, rodent diets did not vary as much as expected.

Given more time, training, and resources, stomach contents could have been parsed to more specific levels that may have better clarified the dietary overlap of sympatric species rather than the broad categories used. However, this level of specificity was deemed unnecessary for this dissertation as molar microwear formation is dependent upon interactions in mastication and the material properties of foodstuff. Furthermore, stomach content analyses is not a perfect science. Due to issues with timing, stomachs collected during the processing of May animals for curation at the Bloemfontein National Museum were preserved for nearly two months prior to analysis. Differential digestion rates may have resulted in a bias against some food items as some material is more easily digested than others. In addition, estimating the percent volume of stomach contents is subjective, although restricting analysis to an individual person mitigates

interobserver error (Mahesh et al., 2018). Indeed, stomach content analyses are considered a valid dietary determinant that have provided valuable food estimates for many species (Medin, 1970; Kronfeld & Dayan, 1998). Apart from observing rodent foraging prior to death, this method provided the most appropriate dietary analog to the scale represented by microwear. While fecal analyses might also be considered, this method requires being able to associate specific feces with specific individuals and following wild rodents within the veldt is not so easily accomplished.

The statistical analyses used in the microwear chapters were based on those utilized in the pilot study, Burgman et al. (2016). However, these analyses had been applied to orthogonal data that made testing for interaction and dispersion effects possible without possible influence from sample sizes. Due to the imperfect sampling conditions that accompanied the use of wild caught specimens in this study design, as well as the number of factors examined, tests for interactions were excluded from this study. The impracticality of these tests meant that the lack of significance for some of the factors analyzed may be in part due to interactions. Likewise, dispersion effects were not tested due to the potential of uneven sample sizes driving the results (see Parra-Frutos, 2012) despite their potential relevance. For example, the analysis of rodent molars by dietary effect resulted in a lack of statistical significance. That the three diets considered all consisted of grass seed as their primary component was thought to cause this result. However, dispersion analysis may have better parsed such similar diets as specific quantities of grass seed consumed did vary among specimens included in this group.

Despite limitations, this dissertation still succeeded in building a comprehensive baseline of extant rodent incisor and molar microwear, complete with abiotic and biotic details that may

aid in utilizing rodent dental microwear as a paleoenvironmental proxy. Future research, and different statistical methods, will build on the baseline provided here.

Future Directions

This project initiated a detailed baseline of extant Muroid molar and incisor microwear that should assist in interpreting the microwear of fossil fauna and examined the effects of different behavioral and environmental factors on rodent microwear textures. However, much remains to be done. This dissertation sought to address the entirety of the available rodent sample. However, in retrospect, taxon-free analyses may not be as applicable to rodents as previously thought. Differences in dental bauplans appeared to affect molar microwear by sub-family while differences in burrowing behavior appeared to affect incisor microwear by species. These results ought to be accounted for in future work, separating extant taxa for analyses based on these known traits. Furthermore, this study only analyzed data for differences in central tendencies. Analyses of sample dispersion might also yield important insights into effects of the various factors on microwear texture attribute distributions. This analysis is a challenge given the non-orthogonality of the research design given real-world field constrains. Perhaps permutation tests can be run using randomly sub-sampled groups of equivalent size in the future.

Aside from addressing issues in the methodology of this dissertation, this baseline still needs to be used with a fossil sample to test its efficacy for reconstructing diet and environment. In addition, it would be beneficial to build upon the dietary portion of this baseline with more associations between stomach contents and dental microwear data of other generalist rodents. It would also be beneficial to incorporate rodents with similar metadata from other ecosystems into this baseline.

As the majority of rodent dental microwear studies has focused on molars, much more research needs to be done in understanding the environmental signal in incisor microwear. While this dissertation indicates that soil properties affect incisor microwear textures, for example, future experiments should explore the effects of different types and sizes of soil particles on incisor microwear, as well as the effects soil moisture and composition. These experiments might help to clarify the patterns observed in studies of wild-caught rodents. Regardless, this research indicates the potential of rodent dental microwear texture as a paleoenvironmental proxy and suggests that both tooth forms should be used together in future environmental reconstructions.

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Appendix I: Stomach content analysis results for muroid rodents from Kolomela

Field no.	Species	Transect	Month	Grass	Grass seed	Dicot seed	Dicot plant	Annelid	Curculonid	Caterpillar	Feather	Flesh	Hair	Artificial	Diet
13084	*Gerbilliscus leucogaster*	Ekstra	May	5	80	5	0	0	5	0	0	0	5	0	grass seed
13085	*Gerbilliscus leucogaster*	Ekstra	May	45	40	5	0	0	5	0	0	0	5	0	grass & grass seed
13086	*Gerbilliscus leucogaster*	Ekstra	May	30	45	10	0	0	5	0	0	0	5	5	grass seed & grass
13087	*Gerbilliscus leucogaster*	Ekstra	May	5	75	5	5	0	5	0	0	0	5	0	grass seed
13088	*Gerbilliscus leucogaster*	Ekstra	May	25	55	5	5	0	0	0	0	0	5	5	grass seed & grass
13089	*Gerbilliscus leucogaster*	Ekstra	May	0	75	0	0	0	20	0	0	0	5	0	grass seed
13090	*Gerbilliscus leucogaster*	Ekstra	May	30	50	5	0	0	10	0	0	0	5	0	grass seed & grass
13091	*Gerbilliscus leucogaster*	Ekstra	May	10	60	0	0	0	25	0	0	0	5	0	grass seed & grass
13092	*Gerbilliscus leucogaster*	Ekstra	May	15	65	5	5	0	5	0	0	0	5	0	grass seed & grass
13093	*Gerbilliscus leucogaster*	Ekstra	May	20	45	10	0	0	15	0	0	0	5	5	grass seed & grass
13094	*Gerbilliscus leucogaster*	Ekstra	May	35	35	10	5	0	5	0	0	0	5	5	grass seed & grass
13095	*Gerbilliscus leucogaster*	Ekstra	May	5	85	0	0	0	5	0	0	0	5	0	grass seed
13096	*Gerbilliscus paeba*	Ekstra	May	0	85	0	0	0	5	0	0	5	5	0	grass seed
13097	*Gerbilliscus paeba*	Ekstra	May	5	70	5	5	0	5	0	0	0	5	5	grass seed
13098	*Gerbilliscus paeba*	Ekstra	May	5	75	5	0	0	5	0	0	5	5	0	grass seed

13099	*Mus minutoides*	Ekstra	May	0	30	0	0	0	0	0	0	0	65	5	hair & grass seed
13100	*Rhabdomys bechuanae*	Ekstra	May	5	70	5	0	0	10	0	0	0	5	5	grass seed
13101	*Rhabdomys bechuanae*	Ekstra	May	0	50	5	0	0	20	0	5	15	0	5	grass seed & curculionid
13102	*Gerbilliscus leucogaster*	Ekstra	May	15	35	0	0	0	40	0	0	0	5	5	curculionid & grass seed
13103	*Gerbilliscus leucogaster*	GN1	May	10	65	5	5	0	5	0	0	0	5	5	grass seed
13104	*Gerbilliscus leucogaster*	GN1	May	0	60	5	0	0	35	0	0	0	0	0	grass seed & curculionid
13105	*Gerbilliscus leucogaster*	GN1	May	15	50	5	0	0	20	0	0	0	5	5	grass seed & curculionid
13106	*Gerbilliscus leucogaster*	GN1	May	5	75	0	0	5	15	0	0	0	0	0	grass seed
13107	*Gerbilliscus leucogaster*	GN1	May	5	75	0	0	0	15	5	0	0	0	0	grass seed
13108	*Rhabdomys bechuanae*	GN1	May	5	10	0	0	70	10	0	0	0	5	0	annelid
13109	*Rhabdomys bechuanae*	GN1	May	0	60	0	0	5	20	5	0	0	5	5	grass seed & curculionid
13110	*Rhabdomys bechuanae*	GN1	May	0	65	5	5	0	15	5	0	0	5	0	grass seed & curculionid
13111	*Rhabdomys bechuanae*	GN1	May	0	70	5	5	0	5	0	0	5	5	5	grass seed
13112	*Rhabdomys bechuanae*	GN1	May	5	70	5	5	0	5	0	0	0	5	5	grass seed
13113	*Rhabdomys bechuanae*	GN1	May	0	80	5	0	0	10	0	0	0	5	0	grass seed

13114	*Gerbilliscus leucogaster*	Stofdraai	May	0	75	5	0	0	10	0	0	0	5	5	grass seed
13115	*Gerbilliscus leucogaster*	Stofdraai	May	5	65	5	0	0	15	0	0	0	5	5	grass seed & curculionid
13116	*Gerbilliscus leucogaster*	Stofdraai	May	5	65	5	0	0	15	0	0	0	5	5	grass seed & curculionid
13117	*Mus minutoides*	Stofdraai	May	0	65	10	5	0	0	0	0	0	15	5	grass seed & hair
13118	*Rhabdomys bechuanae*	GN2	May	5	70	15	0	0	5	0	0	0	5	0	grass seed & dicot seed
13119	*Rhabdomys bechuanae*	GN2	May	0	90	0	0	0	5	0	0	0	5	0	grass seed
13120	*Gerbilliscus leucogaster*	GN2	May	5	75	0	0	0	10	0	0	0	5	5	grass seed
13121	*Gerbilliscus leucogaster*	GN2	May	5	55	10	5	0	15	0	0	0	5	5	grass seed & curculionid
13122	*Gerbilliscus leucogaster*	GN2	May	10	70	0	0	0	0	0	0	0	15	5	grass seed & hair
13123	*Gerbilliscus leucogaster*	GN1	May	0	65	10	5	0	10	0	0	0	5	5	grass seed
13124	*Gerbilliscus leucogaster*	GN1	May	5	65	5	0	0	20	0	0	0	5	0	grass seed & curculionid
13125	*Gerbilliscus leucogaster*	GN1	May	5	65	5	0	0	15	0	0	0	5	5	grass seed & curculionid
13126	*Gerbilliscus leucogaster*	GN1	May	0	55	0	0	0	35	0	0	0	5	5	grass seed & curculionid
13127	*Gerbilliscus leucogaster*	GN1	May	0	75	0	0	0	15	0	0	0	5	5	grass seed

13128	*Rhabdomys bechuanae*	GN1	May	5	75	5	0	0	5	0	0	0	5	5	grass seed
13129	*Gerbilliscus leucogaster*	GP1	May	5	20	5	0	0	60	0	0	0	5	5	curculionid & grass seed
13130	*Gerbilliscus leucogaster*	GP1	May	5	65	10	5	5	0	0	0	0	5	5	grass seed
13131	*Gerbilliscus leucogaster*	GN1	May	25	50	5	5	0	5	0	0	0	5	5	grass seed & grass
13132	*Rhabdomys bechuanae*	GN1	May	0	50	0	0	50	0	0	0	0	0	0	grass seed & annelid
13133	*Gerbilliscus leucogaster*	GP2	May	10	80	0	0	0	0	0	0	0	5	5	grass seed
13134	*Gerbilliscus leucogaster*	GP2	May	10	65	5	0	0	5	0	0	5	5	5	grass seed
13135	*Gerbilliscus leucogaster*	GN2	May	5	80	5	0	0	5	0	0	0	5	0	grass seed
13136	*Gerbilliscus leucogaster*	GN2	May	5	55	5	5	0	0	0	0	0	25	5	grass seed & hair
13137	*Gerbilliscus leucogaster*	GN2	May	10	70	5	0	0	5	0	0	0	5	5	grass seed
13138	*Gerbilliscus leucogaster*	GN2	May	5	65	5	0	0	15	0	0	0	5	5	grass seed & curculionid
13139	*Rhabdomys bechuanae*	GN2	May	15	55	5	0	0	15	0	0	0	5	5	grass seed & grass
13144	*Gerbilliscus leucogaster*	Stofdraai	May	0	80	5	5	0	5	0	0	0	5	0	grass seed
13145	*Mus minutoides*	Stofdraai	May	10	65	10	5	0	0	0	0	0	5	5	grass seed
13147	*Gerbilliscus leucogaster*	GN1	May	0	40	5	0	0	50	0	0	0	5	0	curculionid & grass seed
13148	*Gerbilliscus leucogaster*	GN1	May	10	50	10	5	0	15	0	0	5	5	0	grass seed & curculionid
13149	*Gerbilliscus leucogaster*	GN1	May	0	85	0	0	0	0	0	0	10	5	0	grass seed

13150	*Gerbilliscus leucogaster*	GN1	May	0	60	5	0	0	5	0	0	15	10	5	grass seed & flesh
13151	*Gerbilliscus leucogaster*	GN1	May	0	75	10	0	0	0	0	0	10	5	0	grass seed
13152	*Gerbilliscus leucogaster*	GN1	May	0	60	5	5	0	25	0	0	5	0	0	grass seed & curculionid
13153	*Mus minutoides*	GN1	May	0	50	5	0	5	25	0	0	10	5	0	grass seed & curculionid
13154	*Gerbilliscus leucogaster*	GN2	May	10	75	5	0	0	0	0	0	0	5	5	grass seed
13155	*Gerbilliscus leucogaster*	WAP3	May	5	60	5	5	0	10	0	0	0	5	10	grass seed
13157	*Gerbilliscus leucogaster*	GP2	May	10	65	5	0	0	10	0	0	0	5	5	grass seed
13158	*Gerbilliscus paeba*	GP2	May	0	80	5	0	0	5	0	0	0	5	5	grass seed
13159	*Gerbilliscus leucogaster*	KK1	May	15	65	5	0	0	5	0	0	5	5	0	grass seed & grass
13160	*Gerbilliscus leucogaster*	KK1	May	0	50	0	0	0	40	0	0	0	10	0	grass seed & curculionid
13161	*Gerbilliscus leucogaster*	KK3	May	0	75	5	5	0	5	0	0	0	5	5	grass seed
13162	*Gerbilliscus leucogaster*	KK3	May	0	55	10	5	0	10	0	0	15	5	0	grass seed & flesh
13163	*Gerbilliscus leucogaster*	KK3	May	0	80	5	0	0	5	0	0	0	5	5	grass seed
13164	*Gerbilliscus leucogaster*	KK3	May	5	80	5	0	0	5	0	0	0	5	0	grass seed
13171	*Rhabdomys bechuanae*	HK4	May	0	65	5	5	10	5	0	0	0	5	5	grass seed
13172	*Gerbilliscus leucogaster*	KK2	May	0	65	0	20	0	5	0	0	0	5	5	grass seed & dicot plant
13174	*Rhabdomys bechuanae*	HK2	May	0	80	0	0	0	10	0	0	0	5	5	grass seed

13179	*Gerbilliscus paeba*	KK1	May	0	90	0	0	0	5	0	0	0	5	0	grass seed
13180	*Gerbilliscus leucogaster*	KK2	May	0	45	0	0	5	15	0	0	30	5	0	grass seed & flesh
13181	*Gerbilliscus leucogaster*	KK2	May	0	75	5	0	0	15	0	0	0	5	0	grass seed
13182	*Gerbilliscus leucogaster*	KK2	May	5	65	5	5	0	5	0	0	5	5	5	grass seed
13183	*Gerbilliscus leucogaster*	KK2	May	0	80	5	0	0	5	0	0	0	5	5	grass seed
13184	*Gerbilliscus leucogaster*	KK2	May	0	80	5	5	0	5	0	0	0	5	0	grass seed
13185	*Gerbilliscus leucogaster*	WAP3	May	15	65	5	5	0	5	0	0	0	5	0	grass seed & grass
13186	*Gerbilliscus leucogaster*	WAP2	May	5	75	5	0	0	10	0	0	0	5	0	grass seed
13187	*Gerbilliscus paeba*	WAP3	May	0	65	0	5	0	5	0	0	15	5	5	grass seed & flesh
13188	*Gerbilliscus leucogaster*	WAP2	May	0	80	0	0	0	10	5	0	0	5	0	grass seed
13189	*Gerbilliscus leucogaster*	WAP3	May	5	80	0	0	0	5	0	0	0	10	0	grass seed
13190	*Gerbilliscus leucogaster*	KK2	May	0	80	5	0	5	5	0	0	0	0	5	grass seed
13191	*Gerbilliscus leucogaster*	KK2	May	0	80	0	5	0	5	0	0	5	5	0	grass seed
13192	*Gerbilliscus leucogaster*	KK2	May	0	65	5	0	10	10	5	0	5	0	0	grass seed
13193	*Gerbilliscus leucogaster*	KK3	May	0	75	5	0	0	10	0	0	0	5	5	grass seed
13194	*Micaelamys namaquensis*	KK3	May	0	70	5	5	0	10	0	0	0	5	5	grass seed
13195	*Gerbilliscus leucogaster*	KK3	May	10	55	5	10	0	10	0	0	0	5	5	grass seed

13196	*Rhabdomys bechuanae*	GN1	May	0	65	15	5	0	15	0	0	0	0	0	grass seed & dicot seed, curculionid
13197	*Rhabdomys bechuanae*	GN1	May	0	70	5	5	0	10	0	0	0	5	5	grass seed
13198	*Gerbilliscus leucogaster*	WAP2	May	0	65	5	5	0	20	0	0	0	5	0	grass seed & curculionid
13200	*Gerbilliscus leucogaster*	KK3	May	0	65	10	0	0	20	0	0	0	5	0	grass seed & curculionid
13201	*Gerbilliscus leucogaster*	KK3	May	5	75	5	0	0	10	0	0	0	5	0	grass seed
13202	*Gerbilliscus leucogaster*	KK3	May	0	90	0	0	0	10	0	0	0	0	0	grass seed
13203	*Micaelamys namaquensis*	KK3	May	0	50	15	0	0	20	0	0	5	5	5	grass seed & curculionid
13205	*Gerbilliscus leucogaster*	KK3	May	10	45	5	5	0	20	0	0	0	10	5	grass seed & curculionid
13206	*Gerbilliscus leucogaster*	KK2	May	0	75	5	5	0	10	0	0	0	5	0	grass seed
13207	*Gerbilliscus leucogaster*	WAP1	May	0	85	10	0	0	5	0	0	0	0	0	grass seed
13208	*Rhabdomys bechuanae*	GN1	May	0	90	5	0	0	0	0	0	0	5	0	grass seed
13209	*Rhabdomys bechuanae*	GN1	May	0	60	5	0	20	10	0	0	0	5	0	grass seed & annelid
13211	*Mastomys coucha*	GN2	May	0	20	0	0	0	25	25	0	0	25	5	curculionid, catipillar, hair
13212	*Rhabdomys bechuanae*	GN2	May	5	65	5	5	0	10	0	0	0	5	5	grass seed
13213	*Mastomys coucha*	GN2	May	5	55	0	0	0	25	0	0	0	10	5	grass seed & curculionid
13214	*Mastomys coucha*	GN2	May	5	50	0	0	0	0	0	0	0	40	5	grass seed & hair

13215	*Gerbilliscus paeba*	KK1	May	0	80	5	0	0	0	0	0	0	5	10	grass seed
13216	*Rhabdomys bechuanae*	HK1	May	10	40	40	0	0	5	0	0	0	5	0	grass seed & dicot seed
13232	*Micaelamys namaquensis*	HK7	May	5	60	5	0	0	25	5	0	0	0	0	grass seed & curculionid
13233	*Micaelamys namaquensis*	HK7	May	0	85	5	0	0	5	0	0	0	0	5	grass seed
13234	*Micaelamys namaquensis*	HK7	May	0	80	5	5	0	5	0	0	0	5	0	grass seed
13235	*Micaelamys namaquensis*	HK7	May	0	65	5	0	0	5	0	5	0	15	5	grass seed & hair
13236	*Micaelamys namaquensis*	HK7	May	15	40	5	0	0	20	0	0	10	5	5	grass seed & curculionid
13237	*Micaelamys namaquensis*	HK7	May	0	55	35	0	0	10	0	0	0	0	0	grass seed & dicot seed
13238	*Micaelamys namaquensis*	HK7	May	0	80	5	0	0	15	0	0	0	0	0	grass seed
13245	*Gerbilliscus leucogaster*	HK3	May	0	30	5	5	0	50	0	0	0	5	5	curculionid & grass seed
13246	*Gerbilliscus leucogaster*	HK3	May	0	70	0	0	0	20	0	0	0	5	5	grass seed & curculionid
13247	*Gerbilliscus leucogaster*	HK3	May	10	75	0	0	0	10	5	0	0	0	0	grass seed
13248	*Gerbilliscus leucogaster*	HK3	May	0	15	0	0	0	15	0	60	10	0	0	feather & grass seed, curulionid
13249	*Gerbilliscus leucogaster*	HK3	May	0	45	40	5	0	5	0	0	0	5	0	grass seed & dicot seed
13250	*Gerbilliscus leucogaster*	HK3	May	10	40	35	5	0	5	0	0	0	5	0	grass seed & dicot seed
13251	*Gerbilliscus leucogaster*	HK3	May	0	75	5	5	0	10	0	0	0	5	0	grass seed

13252	*Gerbilliscus leucogaster*	HK3	May	0	75	5	5	0	10	0	0	0	5	0	grass seed
13253	*Gerbilliscus leucogaster*	HK5	May	10	60	0	0	0	25	0	0	0	5	0	grass seed & curculionid
13254	*Gerbilliscus leucogaster*	HK5	May	0	75	5	0	0	15	0	0	0	5	0	grass seed
13255	*Gerbilliscus leucogaster*	HK5	May	15	70	0	0	0	10	0	0	0	5	0	grass seed & grass
13256	*Gerbilliscus leucogaster*	HK5	May	10	50	5	0	0	25	0	0	0	5	5	grass seed & curculionid
13257	*Micaelamys namaquensis*	HK7	May	5	65	5	0	0	20	0	0	0	5	0	grass seed & curculionid
13258	*Rhabdomys bechuanae*	GN2	July	10	75	5	0	0	0	0	0	0	5	5	grass seed
13259	*Rhabdomys bechuanae*	GN2	July	0	85	5	0	0	5	0	0	0	5	0	grass seed
13260	*Rhabdomys bechuanae*	GN2	July	5	70	0	5	0	5	0	0	5	5	5	grass seed
13261	*Rhabdomys bechuanae*	GN2	July	0	85	0	0	0	5	0	0	0	10	0	grass seed
13262	*Rhabdomys bechuanae*	GN2	July	0	65	0	0	5	15	10	0	0	5	0	grass seed & curculionid
13263	*Rhabdomys bechuanae*	GN2	July	10	80	0	0	0	5	0	0	0	0	5	grass seed
13264	*Rhabdomys bechuanae*	GN2	July	5	65	5	5	0	5	0	0	5	5	5	grass seed
13265	*Rhabdomys bechuanae*	GN2	July	0	75	5	5	0	10	0	0	0	5	0	grass seed
13266	*Rhabdomys bechuanae*	GN2	July	5	75	0	0	0	5	5	0	5	5	0	grass seed
13267	*Rhabdomys bechuanae*	GN2	July	5	65	5	5	0	10	0	0	0	5	5	grass seed
13268	*Rhabdomys bechuanae*	GN2	July	5	50	0	0	0	10	0	0	25	10	0	grass seed & flesh

13269	*Rhabdomys bechuanae*	GN2	July	0	90	0	0	0	5	0	0	5	0	0	grass seed
13270	*Mastomys coucha*	GN2	July	0	80	0	0	0	0	5	0	0	10	5	grass seed
13271	*Mus minutoides*	GN2	July	0	70	0	0	0	5	0	0	0	15	10	grass seed & hair
13272	*Dendromus melanotis*	GN2	July	0	75	5	5	0	5	0	0	0	5	5	grass seed
13274	*Dendromus melanotis*	GN2	July	0	50	5	0	0	35	0	0	0	5	5	grass seed & curculionid
13275	*Mus minutoides*	GN2	July	0	70	5	0	0	15	0	0	0	5	5	grass seed & curculionid
13276	*Mastomys coucha*	GN2	July	0	80	0	0	0	15	0	0	0	5	0	grass seed & curculionid
13277	*Rhabdomys bechuanae*	GN2	July	15	70	0	5	0	5	0	0	0	5	0	grass seed & grass
13278	*Rhabdomys bechuanae*	GN2	July	5	70	15	0	0	5	0	0	0	5	0	grass seed & dicot seed
13279	*Rhabdomys bechuanae*	GN2	July	0	80	5	5	0	5	0	0	0	5	0	grass seed
13280	*Rhabdomys bechuanae*	GN2	July	45	40	5	0	0	5	0	0	0	5	0	grass & grass seed
13281	*Micaelamys namaquensis*	HK7	July	15	70	10	5	0	0	0	0	0	0	0	grass seed & grass
13282	*Micaelamys namaquensis*	HK7	July	0	60	0	0	0	30	0	0	0	10	0	grass seed & curculionid
13283	*Micaelamys namaquensis*	HK7	July	20	60	0	0	0	5	0	0	5	5	5	grass seed & grass
13284	*Micaelamys namaquensis*	HK7	July	0	55	10	5	0	20	0	0	5	5	0	grass seed & curculionid
13285	*Micaelamys namaquensis*	HK7	July	10	55	10	5	0	10	0	0	0	5	5	grass seed
13286	*Micaelamys namaquensis*	HK7	July	0	75	10	0	0	5	0	0	5	5	0	grass seed

13287	*Micaelamys namaquensis*	HK7	July	0	90	5	0	0	0	0	0	0	5	0	grass seed
13288	*Micaelamys namaquensis*	HK7	July	10	80	0	0	0	5	0	0	0	5	0	grass seed
13289	*Micaelamys namaquensis*	HK7	July	20	60	0	0	0	5	0	0	10	5	0	grass seed & grass
13290	*Micaelamys namaquensis*	HK7	July	20	65	0	0	0	5	0	0	5	5	0	grass seed & grass
13291	*Micaelamys namaquensis*	HK7	July	10	65	5	0	0	10	0	0	0	5	5	grass seed
13292	*Micaelamys namaquensis*	HK7	July	10	85	0	0	0	0	0	0	0	5	0	grass seed
13293	*Micaelamys namaquensis*	HK7	July	0	85	0	0	0	10	0	0	0	5	0	grass seed
13294	*Micaelamys namaquensis*	HK7	July	10	65	5	5	0	5	0	0	0	5	5	grass seed
13295	*Micaelamys namaquensis*	HK7	July	5	60	10	0	0	15	0	0	0	5	5	grass seed & curculionid
13297	*Micaelamys namaquensis*	HK7	July	5	35	10	20	0	15	0	0	0	10	5	grass seed & dicot plant
13298	*Micaelamys namaquensis*	HK7	July	5	90	0	0	0	0	0	0	0	5	0	grass seed
13299	*Micaelamys namaquensis*	HK7	July	5	80	0	0	0	10	0	0	0	5	0	grass seed
13300	*Gerbilliscus leocogaster*	Stofdraai	July	45	15	30	0	0	10	0	0	0	0	0	grass & dicot seed
13301	*Gerbilliscus leocogaster*	Stofdraai	July	5	50	0	0	35	10	0	0	0	0	0	grass seed & annelid
13303	*Gerbilliscus leucogaster*	GN2	July	0	70	5	0	0	0	0	0	20	5	0	grass seed & flesh
13305	*Gerbilliscus leocogaster*	GN2	July	5	75	5	0	0	15	0	0	0	0	0	grass seed
13305	*Gerbilliscus leucogaster*	GN2	July	10	75	5	0	0	5	0	0	0	5	0	grass seed

13307	*Gerbilliscus leucogaster*	GN2	July	20	70	0	0	10	0	0	0	0	0	0	grass seed & grass
13308	*Gerbilliscus leucogaster*	GN2	July	0	75	15	5	0	0	0	0	0	5	0	grass seed
13309	*Gerbilliscus leucogaster*	GN2	July	5	75	5	0	0	10	0	0	0	5	0	grass seed
13312	*Gerbilliscus leucogaster*	GN2	July	10	65	5	0	0	10	0	0	0	5	5	grass seed
13314	*Gerbilliscus leucogaster*	GN2	July	10	80	0	0	0	5	0	0	0	5	0	grass seed
13315	*Gerbilliscus leucogaster*	GN2	July	20	60	5	0	0	10	0	0	0	5	0	grass seed & grass
PBHK7 MN10	*Micaelamys namaquensis*	HK7	July	5	70	5	0	0	10	0	0	0	5	5	grass seed
PBHK7 MN12	*Micaelamys namaquensis*	HK7	July	5	65	5	5	5	5	0	0	0	5	5	grass seed
PBHK7 MN2	*Micaelamys namaquensis*	HK7	May	25	55	5	10	0	0	0	0	0	5	0	grass seed & grass
PBHK7 MN3	*Micaelamys namaquensis*	HK7	May	0	85	5	0	0	5	0	0	0	5	0	grass seed
PBHK7 MN4	*Micaelamys namaquensis*	HK7	July	10	60	5	5	0	5	0	0	0	10	5	grass seed
PBHK7 MN5	*Micaelamys namaquensis*	HK7	May	20	65	5	0	0	5	0	0	0	5	0	grass seed & grass
PBHK7 MN6	*Micaelamys namaquensis*	HK7	July	5	80	5	0	0	0	0	0	0	5	5	grass seed
PBHK7 MN7	*Micaelamys namaquensis*	HK7	July	0	65	5	5	0	5	0	0	5	10	5	grass seed
PBHK7 MN7b	*Micaelamys namaquensis*	HK7	July	5	5	70	10	0	0	0	0	0	5	5	dicot seed
PBHK7 MN8	*Micaelamys namaquensis*	HK7	July	0	65	5	0	0	15	0	0	0	10	5	grass seed & curculionid
PBHK7 MN9	*Micaelamys namaquensis*	HK7	July	5	85	0	0	0	10	0	0	0	0	0	grass seed

PBHK9 MN1	*Micaelamys namaquensis*	HK9	May	0	70	15	0	0	10	0	0	0	5	0	grass seed & dicot seed
PBHK9 MN10	*Micaelamys namaquensis*	HK9	July	5	55	5	5	0	25	0	0	0	5	0	grass seed & curculionid
PBHK9 MN2	*Micaelamys namaquensis*	HK9	May	5	65	5	0	0	20	0	0	0	5	0	grass seed & curculionid
PBHK9 MN3	*Micaelamys namaquensis*	HK9	July	5	60	5	5	0	15	0	0	0	5	5	grass seed & curculionid
PBHK9 MN4	*Micaelamys namaquensis*	HK9	July	5	75	5	0	0	5	0	0	0	5	5	grass seed
PBHK9 MN5	*Micaelamys namaquensis*	HK9	July	5	70	5	5	0	5	0	0	0	5	5	grass seed
PBHK9 MN7	*Micaelamys namaquensis*	HK9	July	0	65	5	0	0	20	0	0	5	5	0	grass seed & curculionid
PBKK3 MN1	*Micaelamys namaquensis*	KK3	July	5	80	5	0	0	5	0	0	0	5	0	grass seed
PBKK3 MN11	*Micaelamys namaquensis*	KK3	July	5	65	0	0	0	20	0	0	0	5	5	grass seed & curculionid
PBKK3 MN2	*Micaelamys namaquensis*	KK3	May	5	80	5	0	0	5	0	0	0	5	0	grass seed
PBKK3 MN3	*Micaelamys namaquensis*	KK3	May	0	85	5	0	0	5	0	0	0	5	0	grass seed
PBKK3 MN4	*Micaelamys namaquensis*	KK3	May	5	80	0	0	0	5	0	0	0	5	5	grass seed
PBKK3 MN5	*Micaelamys namaquensis*	KK3	May	0	75	5	0	0	10	0	0	0	5	5	grass seed
PBKK3 MN6	*Micaelamys namaquensis*	KK3	May	5	75	5	5	0	0	0	0	0	5	5	grass seed
PBKK3 MN7	*Micaelamys namaquensis*	KK3	May	15	60	5	5	0	0	5	0	0	5	5	grass seed & grass
PBKK3 MN8	*Micaelamys namaquensis*	KK3	May	10	60	5	0	0	15	5	0	0	5	0	grass seed & curculionid
PBKK3 MN9	*Micaelamys namaquensis*	KK3	May	10	75	5	0	0	10	0	0	0	0	0	grass seed

13305	*Gerbilliscus leocogaster*	GN2	July	5	75	5	0	0	15	0	0	0	0	grass seed
13305	*Gerbilliscus leucogaster*	GN2	July	10	75	5	0	0	5	0	0	0	5	0	grass seed
13307	*Gerbilliscus leucogaster*	GN2	July	20	70	0	0	10	0	0	0	0	0	0	grass seed & grass
13308	*Gerbilliscus leucogaster*	GN2	July	0	75	15	5	0	0	0	0	0	5	0	grass seed
13309	*Gerbilliscus leucogaster*	GN2	July	5	75	5	0	0	10	0	0	0	5	0	grass seed
13312	*Gerbilliscus leucogaster*	GN2	July	10	65	5	0	0	10	0	0	0	5	5	grass seed
13314	*Gerbilliscus leucogaster*	GN2	July	10	80	0	0	0	5	0	0	0	5	0	grass seed
13315	*Gerbilliscus leucogaster*	GN2	July	20	60	5	0	0	10	0	0	0	5	0	grass seed & grass
PBHK7 MN10	*Micaelamys namaquensis*	HK7	July	5	70	5	0	0	10	0	0	0	5	5	grass seed
PBHK7 MN12	*Micaelamys namaquensis*	HK7	July	5	65	5	5	5	5	0	0	0	5	5	grass seed
PBHK7 MN2	*Micaelamys namaquensis*	HK7	May	25	55	5	10	0	0	0	0	0	5	0	grass seed & grass
PBHK7 MN3	*Micaelamys namaquensis*	HK7	May	0	85	5	0	0	5	0	0	0	5	0	grass seed
PBHK7 MN4	*Micaelamys namaquensis*	HK7	July	10	60	5	5	0	5	0	0	0	10	5	grass seed
PBHK7 MN5	*Micaelamys namaquensis*	HK7	May	20	65	5	0	0	5	0	0	0	5	0	grass seed & grass
PBHK7 MN6	*Micaelamys namaquensis*	HK7	July	5	80	5	0	0	0	0	0	0	5	5	grass seed
PBHK7 MN7	*Micaelamys namaquensis*	HK7	July	0	65	5	5	0	5	0	0	5	10	5	grass seed
PBHK7 MN7b	*Micaelamys namaquensis*	HK7	July	5	5	70	10	0	0	0	0	0	5	5	dicot seed

Appendix II: Raw data and metadata for muroid incisor microwear texture analysis

Field no.	Species	Transect	Month	Diet	Nesting	Dust ($mg/m^2/day$)	Soil	% Aerial	% Grass	% Bush	% Tree
13084	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low
13085	*Gerbilliscus leucogaster*	Ekstra	May	GRGS	burrower	782	sand	medium	low	low	low
13086	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13087	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low
13088	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13089	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low
13090	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13091	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13092	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13093	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13094	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sand	medium	low	low	low
13095	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low
13096	*Gerbilliscus paeba*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low
13097	*Gerbilliscus paeba*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low
13098	*Gerbilliscus paeba*	Ekstra	May	GSGS	burrower	782	sand	medium	low	low	low

13102	*Gerbilliscus leucogaster*	Ekstra	May	CUGS	burrower	782	sand	medium	low	low	low
13103	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13105	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13106	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13107	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13108	*Rhabdomys bechuanae*	GN1	May	ANAN	burrower	697	clay loam	low	low	medium	low
13109	*Rhabdomys bechuanae*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13110	*Rhabdomys bechuanae*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13111	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13112	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13113	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13114	*Gerbilliscus leucogaster*	Stofdraai	May	GSGS	burrower	752	loam	low	high	low	low
13115	*Gerbilliscus leucogaster*	Stofdraai	May	GSCU	burrower	752	loam	low	high	low	low
13116	*Gerbilliscus leucogaster*	Stofdraai	May	GSCU	burrower	752	loam	low	high	low	low
13117	*Mus minutoides*	Stofdraai	May	GSHA	burrower	752	loam	low	high	low	low
13118	*Rhabdomys bechuanae*	GN2	May	GSDS	burrower	697	clay loam	low	high	low	low
13119	*Rhabdomys bechuanae*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low

13120	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13121	*Gerbilliscus leucogaster*	GN2	May	GSCU	burrower	697	clay loam	low	high	low	low
13122	*Gerbilliscus leucogaster*	GN2	May	GSHA	burrower	697	clay loam	low	high	low	low
13123	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13126	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13131	*Gerbilliscus leucogaster*	GN1	May	GSGR	burrower	697	clay loam	low	low	medium	low
13132	*Rhabdomys bechuanae*	GN1	May	GSAN	burrower	697	clay loam	low	low	medium	low
13133	*Gerbilliscus leucogaster*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13134	*Gerbilliscus leucogaster*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13135	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13136	*Gerbilliscus leucogaster*	GN2	May	GSHA	burrower	697	clay loam	low	high	low	low
13137	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13138	*Gerbilliscus leucogaster*	GN2	May	GSCU	burrower	697	clay loam	low	high	low	low
13144	*Gerbilliscus leucogaster*	Stofdraai	May	GSGS	burrower	752	loam	low	high	low	low
13148	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13149	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13150	*Gerbilliscus leucogaster*	GN1	May	GSFL	burrower	697	clay loam	low	low	medium	low

13151	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13152	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13153	*Mus minutoides*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13154	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13155	*Gerbilliscus leucogaster*	WAP3	May	GSGS	burrower		clay loam s	low	low	high	low
13157	*Gerbilliscus leucogaster*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13158	*Gerbilliscus paeba*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13159	*Gerbilliscus leucogaster*	KK1	May	GSGR	burrower	739	clay loam	medium	low	low	low
13160	*Gerbilliscus leucogaster*	KK1	May	GSCU	burrower	739	clay loam	medium	low	low	low
13162	*Gerbilliscus leucogaster*	KK3	May	GSFL	burrower	739	loam	low	low	low	medium
13163	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13164	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13166	*Gerbilliscus leucogaster*	KK2	May		burrower	739	loam	low	medium	low	low
13167	*Gerbilliscus leucogaster*	KK2	May		burrower	739	loam	low	medium	low	low
13170	*Gerbilliscus leucogaster*	KK2	May		burrower	739	loam	low	medium	low	low
13171	*Rhabdomys bechuanae*	HK4	May	GSGS	burrower		sand	low	high	low	low
13172	*Gerbilliscus leucogaster*	KK2	May	GSDI	burrower	739	loam	low	medium	low	low

13173	*Micaelamys namaquensis*	HK10	May		non-burrower		rocky	low	medium	low	low
13174	*Rhabdomys bechuanae*	HK2	May	GSGS	burrower		sand	low	medium	low	low
13178	*Micaelamys namaquensis*	HK10	May		non-burrower		rocky	low	medium	low	low
13179	*Gerbilliscus paeba*	KK1	May	GSGS	burrower	739	clay loam	medium	low	low	low
13180	*Gerbilliscus leucogaster*	KK2	May	GSFL	burrower	739	loam	low	medium	low	low
13181	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13182	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13183	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13184	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13185	*Gerbilliscus leucogaster*	WAP3	May	GSGR	burrower		clay loam s	low	low	high	low
13186	*Gerbilliscus leucogaster*	WAP2	May	GSGS	burrower		clay loam	low	medium	medium	low
13187	*Gerbilliscus paeba*	WAP3	May	GSFL	burrower		clay loam s	low	low	high	low
13188	*Gerbilliscus leucogaster*	WAP2	May	GSGS	burrower		clay loam	low	medium	medium	low
13189	*Gerbilliscus leucogaster*	WAP3	May	GSGS	burrower		clay loam s	low	low	high	low
13190	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13191	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13193	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium

13194	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
13195	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13196	*Rhabdomys bechuanae*	GN1	May	GSDI	burrower	697	clay loam	low	low	medium	low
13197	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13198	*Gerbilliscus leucogaster*	WAP2	May	GSCU	burrower		clay loam	low	medium	medium	low
13199	*Gerbilliscus leucogaster*	GN1	May		burrower	697	clay loam	low	low	medium	low
13200	*Gerbilliscus leucogaster*	KK3	May	GSCU	burrower	739	loam	low	low	low	medium
13201	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13202	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13203	*Micaelamys namaquensis*	KK3	May	GSCU	non-burrower	739	loam	low	low	low	medium
13204	*Micaelamys namaquensis*	KK3	May		non-burrower	739	loam	low	low	low	medium
13205	*Gerbilliscus leucogaster*	KK3	May	GSCU	burrower	739	loam	low	low	low	medium
13206	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13210	*Gerbilliscus leucogaster*	GN1	May		burrower	697	clay loam	low	low	medium	low
13212	*Rhabdomys bechuanae*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13213	*Mastomys coucha*	GN2	May	GSCU	non-burrower	697	clay loam	low	high	low	low
13216	*Rhabdomys bechuanae*	HK1	May	GSDS	burrower		sand	low	medium	low	low

13221	*Gerbilliscus leucogaster*	HK3	May		burrower	sand	low	high	low	low
13224	*Gerbilliscus leucogaster*	HK3	May		burrower	sand	low	high	low	low
13225	*Gerbilliscus leucogaster*	HK3	May		burrower	sand	low	high	low	low
13226	*Gerbilliscus leucogaster*	HK3	May		burrower	sand	low	high	low	low
13229	*Gerbilliscus leucogaster*	HK3	May		burrower	sand	low	high	low	low
13230	*Gerbilliscus leucogaster*	HK3	May		burrower	sand	low	high	low	low
13232	*Micaelamys namaquensis*	HK7	May	GSCU	non-burrower	rocky	low	medium	low	low
13233	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower	rocky	low	medium	low	low
13234	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower	rocky	low	medium	low	low
13237	*Micaelamys namaquensis*	HK7	May	GSDS	non-burrower	rocky	low	medium	low	low
13238	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower	rocky	low	medium	low	low
13245	*Gerbilliscus leucogaster*	HK3	May	CUGS	burrower	sand	low	high	low	low
13246	*Gerbilliscus leucogaster*	HK3	May	GSCU	burrower	sand	low	high	low	low
13247	*Gerbilliscus leucogaster*	HK3	May	GSGS	burrower	sand	low	high	low	low
13248	*Gerbilliscus leucogaster*	HK3	May	FEGS	burrower	sand	low	high	low	low
13249	*Gerbilliscus leucogaster*	HK3	May	GSDS	burrower	sand	low	high	low	low
13250	*Gerbilliscus leucogaster*	HK3	May	GSDS	burrower	sand	low	high	low	low

13251	*Gerbilliscus leucogaster*	HK3	May	GSGS	burrower		sand	low	high	low	low
13252	*Gerbilliscus leucogaster*	HK3	May	GSGS	burrower		sand	low	high	low	low
13253	*Gerbilliscus leucogaster*	HK5	May	GSCU	burrower		sand	low	medium	low	low
13254	*Gerbilliscus leucogaster*	HK5	May	GSGS	burrower		sand	low	medium	low	low
13255	*Gerbilliscus leucogaster*	HK5	May	GSGR	burrower		sand	low	medium	low	low
13255	*Micaelamys namaquensis*	HK5	May		non-burrower		sand	low	medium	low	low
13256	*Gerbilliscus leucogaster*	HK5	May	GSCU	burrower		sand	low	medium	low	low
13257	*Micaelamys namaquensis*	HK7	May	GSCU	non-burrower		rocky	low	medium	low	low
13259	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13260	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13261	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13262	*Rhabdomys bechuanae*	GN2	July	GSCU	burrower	1252	clay loam	low	high	low	low
13263	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13264	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13265	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13266	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13267	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low

13268	*Rhabdomys bechuanae*	GN2	July	GSFL	burrower	1252	clay loam	low	high	low	low
13269	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13270	*Mastomys coucha*	GN2	July	GSGS	non-burrower	1252	clay loam	low	high	low	low
13271	*Mus minutoides*	GN2	July	GSHA	burrower	1252	clay loam	low	high	low	low
13272	*Dendromus melanotis*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13274	*Dendromus melanotis*	GN2	July	GSCU	burrower	1252	clay loam	low	high	low	low
13276	*Mastomys coucha*	GN2	July	GSCU	non-burrower	1252	clay loam	low	high	low	low
13277	*Rhabdomys bechuanae*	GN2	July	GSGR	burrower	1252	clay loam	low	high	low	low
13278	*Rhabdomys bechuanae*	GN2	July	GSDS	burrower	1252	clay loam	low	high	low	low
13279	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13280	*Rhabdomys bechuanae*	GN2	July	GRGS	burrower	1252	clay loam	low	high	low	low
13281	*Micaelamys namaquensis*	HK7	May	GSGR	non-burrower		rocky	low	medium	low	low
13282	*Micaelamys namaquensis*	HK7	July	GSCU	non-burrower		rocky	low	medium	low	low
13283	*Micaelamys namaquensis*	HK7	July	GSGR	non-burrower		rocky	low	medium	low	low
13284	*Micaelamys namaquensis*	HK7	July	GSCU	non-burrower		rocky	low	medium	low	low
13285	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13286	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low

13287	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13288	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13289	*Micaelamys namaquensis*	HK7	July	GSGR	non-burrower		rocky	low	medium	low	low
13290	*Micaelamys namaquensis*	HK7	July	GSGR	non-burrower		rocky	low	medium	low	low
13291	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13294	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13295	*Micaelamys namaquensis*	HK7	July	GSCU	non-burrower		rocky	low	medium	low	low
13297	*Micaelamys namaquensis*	HK7	July	GSDI	non-burrower		rocky	low	medium	low	low
13299	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13300	*Gerbilliscus leucogaster*	Stofdraai	July	GSDI	burrower	1293	loam	low	high	low	low
13301	*Gerbilliscus leucogaster*	Stofdraai	July	GSAN	burrower	1293	loam	low	high	low	low
13304	*Gerbilliscus leucogaster*	GN2	July		burrower	1252	clay loam	low	high	low	low
13305	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13307	*Gerbilliscus leucogaster*	GN2	July	GSGR	burrower	1252	clay loam	low	high	low	low
13308	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13309	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13312	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low

13312	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13314	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13315	*Gerbilliscus leucogaster*	GN2	July	GSGR	burrower	1252	clay loam	low	high	low	low
	Gerbilliscus leucogaster	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13308b	*Gerbilliscus leucogaster*	GN2	May		burrower	697	clay loam	low	high	low	low
PBHK7 MN10	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN11	*Micaelamys namaquensis*	HK7	May		non-burrower		rocky	low	medium	low	low
PBHK7 MN12	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN2	*Micaelamys namaquensis*	HK7	May	GSGR	non-burrower		rocky	low	medium	low	low
PBHK7 MN3	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN4	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN5	*Micaelamys namaquensis*	HK7	May	GSGR	non-burrower		rocky	low	medium	low	low
PBHK7 MN6	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN7	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN8	*Micaelamys namaquensis*	HK7	May	GSCU	non-burrower		rocky	low	medium	low	low
PBHK7 MN9	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK9 MN1	*Micaelamys namaquensis*	HK9	May	GSDS	non-burrower		rocky	low	medium	low	low
PBHK9 MN2	*Micaelamys namaquensis*	HK9	May	GSCU	non-burrower		rocky	low	medium	low	low

PBHK9 MN3	*Micaelamys namaquensis*	HK9	May	GSCU	non-burrower		rocky	low	medium	low	low
PBHK9 MN4	*Micaelamys namaquensis*	HK9	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK9 MN6	*Micaelamys namaquensis*	HK9	May		non-burrower		rocky	low	medium	low	low
PBHK9 MN7	*Micaelamys namaquensis*	HK9	May	GSCU	non-burrower		rocky	low	medium	low	low
PBKK3 MN10	*Micaelamys namaquensis*	KK3	May		non-burrower	739	loam	low	low	low	medium
PBKK3 MN2	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN3	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN4	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN5	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN6	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN7	*Micaelamys namaquensis*	KK3	May	GSGR	non-burrower	739	loam	low	low	low	medium
PBKK3 MN8	*Micaelamys namaquensis*	KK3	May	GSCU	non-burrower	739	loam	low	low	low	medium
PBKK3 MN9	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium

Field no.	Species	*Asfc*	*Smc*	*epsLar*	*Tfv*	*HAsfc* $_{9}$	*HAsfc* $_{81}$	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
13084	*Gerbilliscus leucogaster*	1.978	0.220	0.005	1132.676	0.447	0.551	-0.185	1.597	1.089	0.035	0.758	108.522	1.287	0.144
13085	*Gerbilliscus leucogaster*	1.238	0.344	0.007	15242.532	0.195	0.372	0.204	1.005	0.827	0.036	0.755	280.180	2.159	0.415
13086	*Gerbilliscus leucogaster*	1.793	0.220	0.008	11231.271	0.454	0.782	-0.050	1.861	1.068	0.051	1.419	112.692	1.029	0.190
13087	*Gerbilliscus leucogaster*	0.694	1.116	0.011	11858.209	0.256	0.471	0.013	1.100	0.592	0.039	0.812	353.616	1.999	0.352
13088	*Gerbilliscus leucogaster*	0.746	0.220	0.012	11720.534	0.253	0.490	0.332	1.013	0.574	0.017	0.447	293.022	0.626	0.212
13089	*Gerbilliscus leucogaster*	1.421	0.675	0.008	12018.866	0.367	0.563	0.404	5.293	3.202	0.057	1.316	63.942	1.951	0.467
13090	*Gerbilliscus leucogaster*	0.756	0.496	0.010	9601.306	0.231	0.329	0.020	0.622	0.565	0.024	0.339	114.563	0.587	0.249
13091	*Gerbilliscus leucogaster*	0.985	0.220	0.010	11339.150	0.307	0.475	0.561	1.510	0.807	0.039	0.778	260.219	1.467	0.274
13092	*Gerbilliscus leucogaster*	1.628	0.220	0.010	13081.283	0.748	0.743	-0.192	1.832	1.012	0.045	1.215	59.007	0.566	0.176
13093	*Gerbilliscus leucogaster*	2.034	0.344	0.008	8348.060	0.272	0.360	-0.225	1.066	1.547	0.038	0.722	52.272	0.550	0.599
13094	*Gerbilliscus leucogaster*	1.579	0.220	0.008	6814.531	0.453	0.662	0.185	0.826	0.779	0.026	0.508	146.449	1.288	0.435
13095	*Gerbilliscus leucogaster*	1.985	0.882	0.006	11106.748	0.113	0.248	0.144	1.450	2.049	0.042	0.870	109.213	1.049	0.352
13096	*Gerbilliscus paeba*	1.188	412.362	0.011	15389.652	0.206	0.356	-0.029	1.621	3.239	0.037	1.440	38.808	0.320	0.418
13097	*Gerbilliscus paeba*	1.234	0.344	0.009	17041.038	0.127	0.247	0.281	0.703	0.778	0.024	0.576	188.461	1.250	0.603
13098	*Gerbilliscus paeba*	0.919	0.344	0.010	12865.407	0.171	0.480	0.090	1.316	1.067	0.033	1.047	243.140	1.144	0.347

13102	*Gerbilliscus leucogaster*	1.548	1.378	0.010	14289.876	0.214	0.369	0.012	1.313	1.024	0.055	1.003	389.888	3.444	0.169
13103	*Gerbilliscus leucogaster*	2.403	0.344	0.008	18230.928	0.200	0.475	0.258	2.730	2.721	0.074	1.462	58.545	2.577	0.178
13105	*Gerbilliscus leucogaster*	1.610	0.344	0.006	11905.310	0.120	0.299	0.289	0.959	1.263	0.029	0.639	85.298	1.047	0.536
13106	*Gerbilliscus leucogaster*	1.234	0.344	0.010	13250.819	0.131	0.481	0.265	1.640	0.825	0.070	1.091	213.651	1.925	0.178
13107	*Gerbilliscus leucogaster*	2.813	0.496	0.006	12317.772	0.324	0.502	0.035	2.842	1.729	0.059	1.757	86.771	1.537	0.166
13108	*Rhabdomys bechuanae*	1.736	0.496	0.009	14581.928	0.188	0.423	0.291	0.831	1.229	0.029	0.558	155.134	1.933	0.567
13109	*Rhabdomys bechuanae*	0.696	0.882	0.008	10767.899	0.065	0.337	0.154	1.312	0.757	0.043	0.736	445.498	3.607	0.174
13110	*Rhabdomys bechuanae*	1.148	1.984	0.008	12100.184	0.268	0.514	-0.263	1.157	1.213	0.045	0.605	309.494	2.752	0.279
13111	*Rhabdomys bechuanae*	2.018	0.882	0.008	12840.930	0.193	0.300	-0.162	1.163	1.770	0.047	0.944	163.457	2.659	0.729
13112	*Rhabdomys bechuanae*	1.187	0.496	0.010	12613.199	0.215	0.386	-0.198	1.521	0.964	0.044	0.920	201.047	1.277	0.160
13113	*Rhabdomys bechuanae*	1.188	0.496	0.006	17557.998	0.386	0.847	-0.304	2.314	1.833	0.061	1.495	18.564	0.256	0.406
13114	*Gerbilliscus leucogaster*	3.511	0.344	0.008	16295.861	0.354	0.618	-0.253	1.508	2.236	0.056	0.887	164.007	1.537	0.105
13115	*Gerbilliscus leucogaster*	2.079	0.344	0.006	15683.318	0.349	0.408	0.551	1.153	1.106	0.026	0.896	140.178	1.346	0.580
13116	*Gerbilliscus leucogaster*	2.879	0.220	0.008	9620.768	0.164	0.312	0.025	1.850	1.503	0.057	0.783	215.281	1.990	0.172
13117	*Mus minutoides*	2.597	0.220	0.009	15992.855	0.621	0.619	-0.055	0.871	2.160	0.027	0.705	44.408	0.365	0.350
13118	*Rhabdomys bechuanae*	1.198	0.675	0.007	11929.445	0.220	0.445	0.868	0.836	0.949	0.031	0.575	150.049	2.748	0.435
13119	*Rhabdomys bechuanae*	1.684	0.220	0.009	16232.952	0.254	0.427	0.180	1.379	1.417	0.033	0.892	72.517	1.232	0.505

13120	*Gerbilliscus leucogaster*	3.955	0.220	0.008	15657.358	0.329	0.595	-0.155	1.875	2.387	0.041	1.249	266.651	5.508	0.140
13121	*Gerbilliscus leucogaster*	1.638	412.362	0.010	16260.422	0.177	0.307	-0.352	1.585	2.086	0.050	0.959	147.391	5.035	0.288
13122	*Gerbilliscus leucogaster*	1.936	0.344	0.006	14572.005	0.648	12.016	-0.130	1.539	1.158	0.057	0.722	215.199	1.082	0.579
13123	*Gerbilliscus leucogaster*	3.537	0.220	0.006	11514.595	0.243	0.468	-0.948	3.521	2.288	0.091	1.016	501.464	5.622	0.657
13126	*Gerbilliscus leucogaster*	1.576	0.344	0.008	13680.321	0.239	0.343	0.108	0.996	1.023	0.026	0.500	141.577	1.571	0.226
13131	*Gerbilliscus leucogaster*	2.558	0.220	0.009	13491.489	0.194	0.428	0.313	1.744	2.043	0.044	0.971	148.661	1.091	0.170
13132	*Rhabdomys bechuanae*	2.390	0.496	0.003	11391.946	0.181	0.270	-0.153	1.605	1.791	0.047	0.827	136.565	2.807	0.153
13133	*Gerbilliscus leucogaster*	1.582	0.496	0.010	14677.887	0.520	0.578	0.174	1.654	0.976	0.035	1.170	354.680	5.216	0.173
13134	*Gerbilliscus leucogaster*	2.155	0.344	0.010	13583.440	0.240	0.364	0.133	1.363	1.308	0.038	0.820	141.333	1.941	0.461
13135	*Gerbilliscus leucogaster*	2.111	1.667	0.006	12446.203	0.163	0.599	-0.907	2.068	3.051	0.077	0.909	167.604	3.040	0.288
13136	*Gerbilliscus leucogaster*	1.732	0.344	0.008	13023.721	0.423	0.452	-0.424	2.338	0.967	0.047	0.652	408.163	4.910	0.169
13137	*Gerbilliscus leucogaster*	1.453	0.220	0.009	12518.187	0.249	0.404	-0.540	1.688	1.188	0.069	0.689	121.479	1.006	0.162
13138	*Gerbilliscus leucogaster*	0.762	326.759	0.010	14050.104	0.190	0.454	-0.002	0.860	0.868	0.032	0.533	245.740	2.643	0.139
13144	*Gerbilliscus leucogaster*	2.186	0.344	0.007	7671.229	0.274	0.452	-0.730	1.551	1.277	0.044	0.623	201.562	1.702	0.567
13148	*Gerbilliscus leucogaster*	1.232	0.675	0.009	10664.696	0.129	0.458	0.445	1.025	1.711	0.036	0.688	206.670	2.684	0.358
13149	*Gerbilliscus leucogaster*	1.716	0.220	0.009	10624.770	0.392	0.421	-0.160	1.987	1.189	0.044	1.033	142.747	1.177	0.193
13150	*Gerbilliscus leucogaster*	2.271	0.344	0.007	2178.974	0.333	0.391	-0.188	0.978	1.351	0.036	0.617	87.261	0.879	0.167

13151	*Gerbilliscus leucogaster*	1.730	0.344	0.006	8683.303	0.399	0.453	-0.572	2.619	1.088	0.067	0.834	132.339	2.130	0.173
13152	*Gerbilliscus leucogaster*	1.770	0.344	0.009	13126.530	0.177	0.340	-0.127	0.994	0.981	0.035	0.665	236.937	1.650	0.159
13153	*Mus minutoides*	1.049	90.397	0.012	16031.891	0.110	0.340	0.521	0.745		0.022	0.582	127.481	1.307	0.475
13154	*Gerbilliscus leucogaster*	1.246	0.344	0.005	6297.350	0.122	0.409	-0.257	1.252	1.125	0.033	0.719	123.681	2.536	0.621
13155	*Gerbilliscus leucogaster*	1.108	0.675	0.010	16675.661	0.141	0.303	1.268	1.297	1.356	0.039	0.970	29.223	0.593	0.392
13157	*Gerbilliscus leucogaster*	0.928	1.667	0.009	8940.946	0.238	0.476	-0.052	1.010	0.614	0.030	0.585	311.952	3.058	0.170
13158	*Gerbilliscus paeba*	1.207	0.220	0.007	17393.213	0.221	0.810	-1.053	2.391	2.013	0.057	1.252	213.289	2.277	0.199
13159	*Gerbilliscus leucogaster*	0.992	0.344	0.008	12780.982	0.134	0.281	-0.240	1.556	0.690	0.081	0.906	133.674	2.463	0.170
13160	*Gerbilliscus leucogaster*	1.574	0.675	0.007	14519.662	0.331	0.404	0.053	1.326	2.075	0.044	0.965	148.423	1.787	0.212
13162	*Gerbilliscus leucogaster*	2.800	0.344	0.007	13851.036	0.162	0.413	-0.155	1.659	2.930	0.057	0.992	140.672	2.074	0.416
13163	*Gerbilliscus leucogaster*	1.804	0.496	0.007	11051.534	0.099	0.236	0.228	1.352	1.503	0.051	0.717	242.034	6.456	0.516
13164	*Gerbilliscus leucogaster*	1.584	1.984	0.006	16618.217	0.123	0.361	0.149	1.511	2.036	0.048	1.128	241.714	1.504	0.363
13166	*Gerbilliscus leucogaster*	2.027	0.882	0.006	15287.648	0.210	0.507	-0.722	3.285	4.598	0.140	1.684	149.527	4.255	0.146
13167	*Gerbilliscus leucogaster*	1.367	0.220	0.010	17091.290	0.299	0.403	0.082	0.617	0.622	0.020	0.453	59.109	0.373	0.184
13170	*Gerbilliscus leucogaster*	5.025	0.220	0.005	12785.628	0.261	0.366	-0.187	2.162	3.064	0.070	1.226	113.250	1.850	0.365
13171	*Rhabdomys bechuanae*	1.126	0.496	0.009	13842.841	0.287	0.417	0.588	1.136	0.939	0.036	0.804	247.780	3.705	0.166
13172	*Gerbilliscus leucogaster*	1.568	0.220	0.008	12106.306	0.255	0.420	0.298	1.348	1.503	0.043	0.518	267.901	4.529	0.715

13173	*Micaelamys namaquensis*	1.515	0.344	0.009	9863.276	0.159	0.371	0.273	1.267	0.964	0.046	0.977	391.837	3.088	0.173
13174	*Rhabdomys bechuanae*	1.498	0.675	0.007	13709.312	0.149	0.306	0.787	1.026	1.136	0.029	0.729	500.593	9.534	0.622
13178	*Micaelamys namaquensis*	1.996	0.220	0.010	9050.996	0.328	0.589	-0.197	1.227	1.075	0.037	0.699	105.140	0.486	0.412
13179	*Gerbilliscus paeba*	3.671	412.362	0.010	19344.578	0.303	0.640	-0.229	1.935	3.393	0.082	0.971	120.221	10.110	0.184
13180	*Gerbilliscus leucogaster*	1.636	0.496	0.008	11894.434	0.151	0.266	0.432	1.479	1.200	0.048	0.968	285.838	1.033	0.601
13181	*Gerbilliscus leucogaster*	2.001	0.882	0.009	11680.241	0.149	0.266	0.090	1.342	1.949	0.046	0.872	258.971	2.924	0.160
13182	*Gerbilliscus leucogaster*	1.160	0.220	0.009	10337.754	0.173	0.479	-0.565	2.233	1.206	0.048	1.131	121.286	0.871	0.259
13183	*Gerbilliscus leucogaster*	1.303	0.496	0.006	8381.951	0.171	0.321	-0.379	1.938	1.212	0.071	0.595	230.831	1.669	0.184
13184	*Gerbilliscus leucogaster*	0.707	0.220	0.007	8192.748	0.111	0.259	0.018	0.769	0.486	0.023	0.439	165.105	0.736	0.490
13185	*Gerbilliscus leucogaster*	1.920	0.496	0.008	11599.508	0.138	0.280	-0.277	1.540	1.240	0.053	0.979	330.944	4.468	0.546
13186	*Gerbilliscus leucogaster*	1.983	0.344	0.008	14921.465	0.135	0.257	-0.077	1.798	1.264	0.060	0.560	116.259	0.745	0.190
13187	*Gerbilliscus paeba*	1.816	46.349	0.011	19506.227	0.156	0.285	0.091	1.982	3.228	0.069	0.792	216.330	4.212	0.640
13188	*Gerbilliscus leucogaster*	2.722	0.344	0.009	13354.327	0.115	0.457	-0.237	2.319	2.490	0.045	1.342	72.235	2.029	0.404
13189	*Gerbilliscus leucogaster*	1.835	0.675	0.005	15981.589	0.111	0.270	-0.548	2.341	1.373	0.065	0.959	337.022	5.923	0.152
13190	*Gerbilliscus leucogaster*	1.308	0.675	0.010	16295.049	0.240	0.340	0.168	1.367	1.285	0.052	0.997	119.793	3.983	0.348
13191	*Gerbilliscus leucogaster*	1.592	0.345	0.007	10709.688	0.070	0.297	0.089	1.630	1.371	0.039	0.874	232.602	1.646	0.174
13193	*Gerbilliscus leucogaster*	1.934	0.882	0.007	15034.935	0.110	0.354	0.259	1.502	1.531	0.046	0.769	440.758	3.442	0.343

13194	*Micaelamys namaquensis*	1.862	0.675	0.008	10993.039	0.268	0.367	0.130	1.199	1.852	0.036	0.671	124.355	1.931	0.305
13195	*Gerbilliscus leucogaster*	1.991	0.344	0.009	16392.559	0.371	0.536	-0.152	1.995	1.394	0.064	1.200	153.110	1.862	0.138
13196	*Rhabdomys bechuanae*	1.737	0.882	0.008	11448.430	0.185	0.355	-0.506	1.643	1.764	0.058	1.079	237.400	4.029	0.203
13197	*Rhabdomys bechuanae*	1.806	2.328	0.008	9313.865	0.176	0.453	0.204	1.515	2.207	0.049	1.017	330.347	5.021	0.109
13198	*Gerbilliscus leucogaster*	1.520	0.220	0.009	13847.284	0.353	0.382	-0.648	1.498	1.327	0.064	0.962	518.760	5.131	0.160
13199	*Gerbilliscus leucogaster*	1.346	0.882	0.008	16345.621	0.194	0.442	0.403	1.362	1.219	0.053	0.912	570.382	5.664	0.180
13200	*Gerbilliscus leucogaster*	1.747	0.675	0.007	9964.755	0.267	0.466	-0.416	2.288	1.818	0.048	0.941	235.394	3.455	0.444
13201	*Gerbilliscus leucogaster*	1.186	1.116	0.007	16373.509	0.255	0.535	-0.250	2.091	1.539	0.045	1.143	297.810	3.499	0.311
13202	*Gerbilliscus leucogaster*	2.250	0.344	0.011	13606.591	0.189	0.371	0.043	1.343	2.502	0.041	0.931	113.112	0.877	0.113
13203	*Micaelamys namaquensis*	3.910	0.220	0.009	15755.025	0.531	1.113	-0.253	1.810	2.539	0.072	1.366	245.790	3.029	0.198
13204	*Micaelamys namaquensis*	1.588	0.220	0.011	11936.803	0.280	0.523	0.080	1.809	0.834	0.037	0.641	367.928	3.560	0.171
13205	*Gerbilliscus leucogaster*	3.797	0.220	0.006	13267.787	0.201	0.309	-0.487	1.747	2.102	0.066	1.065	137.249	1.283	0.448
13206	*Gerbilliscus leucogaster*	1.628	0.882	0.008	13979.246	0.110	0.351	-0.152	1.742	2.272	0.065	0.689	163.149	1.657	0.269
13210	*Gerbilliscus leucogaster*	1.519	0.882	0.006	14723.825	0.114	0.393	0.270	1.643	2.027	0.049	1.204	256.443	5.138	0.128
13212	*Rhabdomys bechuanae*	0.905	85.989	0.010	12868.063	0.253	0.529	0.177	1.851	0.738	0.042	1.029	305.927	5.698	0.332
13213	*Mastomys coucha*	3.165	0.124	0.005	16586.197	0.154	0.302	0.128	1.614	2.827	0.061	1.191	85.950	0.761	0.209
13216	*Rhabdomys bechuanae*	1.388	0.675	0.008	14275.573	0.250	0.421	-0.054	1.913	1.211	0.082	0.762	38.490	0.715	0.304

13221	*Gerbilliscus leucogaster*	1.152	0.496	0.010	16008.507	0.145	0.364	-0.303	1.276	1.064	0.057	1.018	190.786	1.783	0.300
13224	*Gerbilliscus leucogaster*	1.470	0.882	0.007	17645.148	0.132	0.436	-0.166	1.294	1.529	0.045	0.930	213.157	1.793	0.320
13225	*Gerbilliscus leucogaster*	1.324	0.496	0.009	12484.115	0.173	0.309	0.171	0.999	0.863	0.033	0.579	175.854	1.148	0.302
13226	*Gerbilliscus leucogaster*	1.250	0.882	0.006	11179.118	0.194	0.352	-0.117	2.194	1.224	0.075	0.737	293.406	2.771	0.188
13229	*Gerbilliscus leucogaster*	1.009	1.667	0.008	12903.909	0.155	0.602	0.711	1.639	2.977	0.057	0.510	157.069	2.843	0.176
13230	*Gerbilliscus leucogaster*	0.946	0.882	0.007	16815.971	0.120	0.224	0.098	0.775	0.934	0.031	0.614	274.226	1.675	0.486
13232	*Micaelamys namaquensis*	-1.136	412.362	0.011	16714.855	0.400	0.730	0.092	2.713	2.238	0.050	0.511	52.242	1.902	0.189
13233	*Micaelamys namaquensis*	2.011	0.344	0.008	11798.420	0.191	0.340	0.131	0.931	1.543	0.030	0.730	77.051	0.746	0.477
13234	*Micaelamys namaquensis*	1.549	412.362	0.011	14198.646	0.303	0.485	-0.081	1.059	1.229	0.038	0.791	164.047	2.046	0.137
13237	*Micaelamys namaquensis*	1.493	0.220	0.009	13959.027	0.139	0.329	-0.178	1.373	1.597	0.042	0.531	153.546	1.451	0.155
13238	*Micaelamys namaquensis*	0.654	0.496	0.005	3283.944	0.166	0.343	0.192	1.329	1.347	0.031	0.725	94.394	1.431	0.415
13245	*Gerbilliscus leucogaster*	1.757	4.974	0.010	12194.764	0.282	1.098	-0.727	1.942	3.031	0.077	1.081	370.970	2.574	0.145
13246	*Gerbilliscus leucogaster*	1.765	0.496	0.008	12347.491	0.243	0.345	0.258	1.396	1.640	0.046	0.835	165.078	1.507	0.174
13247	*Gerbilliscus leucogaster*	2.039	0.675	0.007	14805.117	0.123	0.344	-0.036	2.361	2.661	0.070	1.305	298.767	11.921	0.364
13248	*Gerbilliscus leucogaster*	1.335	0.675	0.008	13024.768	0.158	0.300	0.453	1.321	1.226	0.042	0.715	324.374	3.012	0.210
13249	*Gerbilliscus leucogaster*	1.080	412.362	0.009	8951.839	0.140	0.371	0.363	1.058	0.929	0.036	0.700	230.304	3.217	0.392
13250	*Gerbilliscus leucogaster*	1.561	0.220	0.008	13148.799	0.565	0.702	0.081	2.411	1.133	0.049	1.377	404.922	6.511	0.319

13251	*Gerbilliscus leucogaster*	1.719	1.984	0.008	10246.862	0.149	0.555	-0.022	1.264	1.946	0.055	0.869	371.721	5.786	0.252
13252	*Gerbilliscus leucogaster*	1.222	0.220	0.006	9243.810	0.234	0.340	-0.140	1.079	0.895	0.031	0.744	112.844	0.563	0.434
13253	*Gerbilliscus leucogaster*	1.427	0.675	0.008	12112.596	0.105	0.329	-0.086	1.305	1.390	0.036	0.912	165.426	2.279	0.435
13254	*Gerbilliscus leucogaster*	1.368	3.527	0.010	5482.394	0.545	1.247								
13255	*Gerbilliscus leucogaster*	1.451	412.362	0.007	12302.376	0.335	0.529	-0.109	2.015	1.661	0.072	0.979	333.914	4.071	0.262
13255	*Micaelamys namaquensis*	1.621	0.344	0.008	15667.166	0.180	0.384	0.259	1.526	1.858	0.051	1.026	59.500	0.630	0.353
13256	*Gerbilliscus leucogaster*	1.545	4.974	0.010	10942.889	0.383	0.617	-0.989	2.019	1.517	0.084	0.882	294.036	2.561	0.160
13257	*Micaelamys namaquensis*	1.814	0.098	0.009	4782.379	0.162	0.305	0.084	0.984	1.622	0.028	0.592	52.587	0.681	0.181
13259	*Rhabdomys bechuanae*	2.574	1.200	0.008	4774.648	0.164	0.391	0.018	1.317	3.429	0.051	0.851	96.357	1.530	0.198
13260	*Rhabdomys bechuanae*	2.266	0.675	0.007	14977.691	0.070	0.283	0.414	1.505	1.696	0.046	0.935	196.351	1.980	0.203
13261	*Rhabdomys bechuanae*	1.057	0.220	0.010	11344.693	0.389	0.598	-0.359	1.226	0.886	0.051	0.250	69.795	0.315	0.278
13262	*Rhabdomys bechuanae*	1.271	0.675	0.009	12353.780	0.144	0.389	-0.297	1.354	1.061	0.042	0.679	308.946	2.019	0.374
13263	*Rhabdomys bechuanae*	1.072	412.362	0.009	14928.219	0.206	0.294	0.064	1.019	0.375	0.039	0.685	789.158	6.604	0.292
13264	*Rhabdomys bechuanae*	1.330	0.344	0.008	9318.009	0.157	0.283	0.281	1.263	1.071	0.032	0.882	195.590	2.177	0.348
13265	*Rhabdomys bechuanae*	0.925	0.344	0.009	13917.739	0.481	0.661	-0.022	1.225	0.778	0.024	0.478	120.326	1.165	0.528
13266	*Rhabdomys bechuanae*	1.461	0.344	0.008	9732.861	0.101	0.320	-0.605	1.314	1.038	0.047	0.814	140.283	1.350	0.356
13267	*Rhabdomys bechuanae*	1.098	1.116	0.008	15411.235	0.220	0.389	-0.248	1.574	0.918	0.043	0.682	355.886	2.978	0.491

13268	*Rhabdomys bechuanae*	1.100	0.344	0.007	10072.746	0.122	0.469	-0.701	1.232	1.326	0.035	0.968	137.229	0.780	0.207
13269	*Rhabdomys bechuanae*	0.930	0.675	0.008	15929.753	0.186	0.483	0.568	1.789	0.799	0.046	0.823	1622.360	56.305	0.475
13270	*Mastomys coucha*	0.863	0.344	0.007	15451.694	0.206	0.354	0.173	1.016	0.663	0.040	0.638	178.854	0.654	0.432
13271	*Mus minutoides*	1.107	0.124	0.011	17532.920	0.149	0.304	-0.183	1.269	1.372	0.042	0.913	112.629	1.200	0.196
13272	*Dendromus melanotis*	1.889	1.378	0.007	12027.548	0.330	0.500	0.188	1.639	2.121	0.046	0.742	136.072	1.732	0.471
13274	*Dendromus melanotis*	1.566	0.496	0.011	17735.772	0.172	0.375	0.669	2.456	1.092	0.066	0.960	505.405	13.830	0.181
13276	*Mastomys coucha*	1.415	0.344	0.010	18043.784	0.288	0.416	0.003	1.218	1.431	0.031	0.770	68.239	0.798	0.191
13277	*Rhabdomys bechuanae*	0.625	6.076	0.010	13617.188	0.365	0.537	-0.372	2.514	0.561	0.065	0.933			0.173
13278	*Rhabdomys bechuanae*	1.923	0.882	0.007	11975.754	0.255	0.531	0.248	1.118	1.655	0.043	0.984	99.016	1.025	0.310
13279	*Rhabdomys bechuanae*	4.004	0.220	0.003	17293.150	0.277	0.520	0.088	4.178	2.370	0.059	1.601	132.689	2.029	0.182
13280	*Rhabdomys bechuanae*	1.324	0.220	0.010	13646.744	0.196	0.304	-0.576	2.364	1.715	0.045	0.590	141.646	1.898	0.153
13281	*Micaelamys namaquensis*	1.049	1.667	0.008	17329.042	0.380	0.724	-0.169	1.702	1.924	0.035	0.674	80.835	0.978	0.708
13282	*Micaelamys namaquensis*	0.961	0.496	0.008	14877.769	0.125	0.316	-0.142	1.111	1.246	0.046	0.818	160.961	1.612	0.147
13283	*Micaelamys namaquensis*	1.997	370.573	0.009	15121.047	0.238	0.629	0.166	1.721	1.142	0.057	1.159	141.606	1.326	0.222
13284	*Micaelamys namaquensis*	1.091	0.496	0.010	14202.411	0.320	0.401	-0.275	1.783	1.258	0.053	1.231	187.692	1.894	0.586
13285	*Micaelamys namaquensis*	1.918	0.496	0.010	14183.516	0.179	0.230	0.634	1.205	1.711	0.036	0.808	150.151	1.662	0.168
13286	*Micaelamys namaquensis*	1.632	0.220	0.010	12380.637	0.178	0.399	0.500	0.673	0.878	0.021	0.353	168.445	1.353	0.296

13287	*Micaelamys namaquensis*	1.286	0.882	0.007	12296.668	0.491	0.552	-0.430	1.677	0.860	0.046	0.898	460.397	4.245	0.171
13288	*Micaelamys namaquensis*	1.752	412.362	0.011	13781.182	0.392	0.768	0.216	0.825	1.152	0.029	0.619	72.397	0.762	0.143
13289	*Micaelamys namaquensis*	1.479	0.882	0.009	13470.528	0.154	0.333	0.026	1.284	1.419	0.040	0.846	280.053	7.004	0.493
13290	*Micaelamys namaquensis*	0.835	0.344	0.010	11842.905	0.439	0.567	0.467	0.775	1.390	0.024	0.523	63.686	0.466	0.311
13291	*Micaelamys namaquensis*	0.939	0.220	0.011	14215.466	0.254	0.603	-0.029	1.035	1.023	0.034	0.680	119.633	1.574	0.242
13294	*Micaelamys namaquensis*	1.656	0.220	0.007	13752.034	0.231	0.490	0.304	1.293	1.944	0.047	0.598	94.184	0.772	0.161
13295	*Micaelamys namaquensis*	0.856	412.362	0.010	16679.277	0.338	0.566	0.198	0.951	0.997	0.029	0.300	95.579	0.990	0.153
13297	*Micaelamys namaquensis*	0.881	0.675	0.010	18375.502	0.365	0.485	0.180	0.958	0.612	0.038	0.664	279.434	2.269	0.326
13299	*Micaelamys namaquensis*	-1.259	412.362	0.011	16204.494	0.241	0.539	0.272	1.338	1.040	0.050	0.921	120.264	1.904	0.258
13300	*Gerbilliscus leucogaster*	1.217	0.882	0.009	14747.862	0.974	1.292	0.393	1.850	1.194	0.057	1.172	657.968	14.057	0.178
13301	*Gerbilliscus leucogaster*	1.124	0.344	0.006	13701.448	0.567	0.743	-0.302	1.726	1.002	0.051	0.878	261.249	1.523	0.177
13304	*Gerbilliscus leucogaster*	1.204	0.882	0.008	12398.926	0.198	0.300	0.195	1.019	1.231	0.041	0.785	134.381	1.544	0.496
13305	*Gerbilliscus leucogaster*	1.073	0.675	0.008	14541.860	0.151	0.337	0.382	1.153	1.069	0.032	0.688	534.490	3.420	0.144
13307	*Gerbilliscus leucogaster*	1.258	1.378	0.009	6787.905	0.271	0.486	-0.816	1.775	1.102	0.065	1.074	538.040	6.829	0.147
13308	*Gerbilliscus leucogaster*	1.613	0.496	0.005	9873.493	0.217	0.278	0.159	1.055	1.026	0.031	0.836	177.494	1.481	0.246
13309	*Gerbilliscus leucogaster*	2.214	0.882	0.006	11911.221	0.154	0.290	0.208	1.461	2.155	0.040	1.012	214.474	3.781	0.160
13312	*Gerbilliscus leucogaster*	2.054	1.116	0.007	14742.062	0.207	0.453	-0.987	3.342	2.026	0.098	1.248	407.287	4.430	0.169

13314	*Gerbilliscus leucogaster*	1.720	0.675	0.006	16870.064	0.147	0.373	-0.128	2.173	1.895	0.064	1.199	289.999	5.293	0.164
13315	*Gerbilliscus leucogaster*	1.620	0.344	0.009	14847.300	0.169	0.332	0.342	1.399	1.166	0.037	0.901	306.389	5.723	0.520
	Gerbilliscus leucogaster	2.002	0.344	0.009	11779.233	0.193	0.595	-0.633	2.077	1.072	0.051	1.173	282.172	3.095	0.154
13308b	*Gerbilliscus leucogaster*	0.982	0.675	0.009	10633.064	0.332	0.574	0.106	0.672	0.793	0.019	0.448	303.745	2.966	0.195
PBHK7 MN10	*Micaelamys namaquensis*	1.060	0.496	0.010	10964.954	0.254	0.491	0.166	1.228	0.797	0.043	0.984	424.212	3.703	0.175
PBHK7 MN11	*Micaelamys namaquensis*	2.063	412.362	0.010	20015.955	0.137	0.283	-0.218	3.817	0.887	0.078				0.341
PBHK7 MN12	*Micaelamys namaquensis*	1.488	0.344	0.009	16603.603	0.259	0.369	-0.387	2.109	1.228	0.040	0.758	274.954	7.038	0.151
PBHK7 MN2	*Micaelamys namaquensis*	1.822	0.675	0.009	15287.036	0.145	0.314	-0.192	1.249	2.087	0.039	0.699	71.352	0.601	0.159
PBHK7 MN3	*Micaelamys namaquensis*	2.255	0.675	0.007	11003.920	0.271	0.352	-0.234	1.697	2.355	0.050	0.831	134.067	1.310	0.323
PBHK7 MN4	*Micaelamys namaquensis*	1.203	0.496	0.011	10797.013	0.195	0.382	-0.123	1.573	1.015	0.039	0.492	172.075	1.765	0.298
PBHK7 MN5	*Micaelamys namaquensis*	1.128	101.902	0.011	19025.238	0.265	0.396	0.455	1.109	1.469	0.037	0.602	120.689	1.541	0.193
PBHK7 MN6	*Micaelamys namaquensis*	1.605	412.362	0.010	8357.458	0.223	0.399	0.020	1.109	1.060	0.045	0.536	205.709	2.000	0.158
PBHK7 MN7	*Micaelamys namaquensis*	1.177	0.344	0.008	13646.704	0.295	0.571	0.072	1.729	1.204	0.041	0.735	125.839	2.921	0.178
PBHK7 MN8	*Micaelamys namaquensis*	1.026	0.344	0.010	5929.354	0.116	0.221	-0.029	1.418	0.751	0.038	0.614	246.872	1.576	0.180
PBHK7 MN9	*Micaelamys namaquensis*	1.432	0.675	0.008	8949.783	0.155	0.512	0.220	1.385	1.754	0.052	0.959	153.005	5.051	0.166
PBHK9 MN1	*Micaelamys namaquensis*	0.811	1.116	0.009	11815.562	0.255	0.573	-0.083	1.127	0.685	0.040	0.537	202.636	3.686	0.183
PBHK9 MN2	*Micaelamys namaquensis*	1.280	0.882	0.007	11644.696	0.141	0.300	-0.277	2.211	1.215	0.059	0.916	308.104	3.512	0.173

PBHK9 MN3	*Micaelamys namaquensis*	1.422	0.882	0.008	12173.312	0.405	0.436	0.301	0.910	0.904	0.027	0.614	184.738	1.501	0.452
PBHK9 MN4	*Micaelamys namaquensis*	0.789	1.116	0.009	18654.703	0.223	0.353	0.577	0.913	0.515	0.028	0.720	523.944	7.529	0.256
PBHK9 MN6	*Micaelamys namaquensis*	1.035	412.362	0.010	13340.130	0.208	0.416	0.367	1.307	0.899	0.038	0.745	431.730	6.596	0.174
PBHK9 MN7	*Micaelamys namaquensis*	0.894	0.344	0.010	16526.145	0.340	0.686	0.059	1.076	1.007	0.040	0.544	162.429	0.182	0.271
PBKK3 MN10	*Micaelamys namaquensis*	1.133	0.220	0.010	11906.912	0.272	0.857	-0.230	2.021	2.041	0.054	1.157	129.148	0.896	0.344
PBKK3 MN2	*Micaelamys namaquensis*	1.282	0.344	0.011	13564.569	0.266	0.489	0.092	1.072	1.137	0.036	0.899	63.862	0.488	0.162
PBKK3 MN3	*Micaelamys namaquensis*	1.115	0.496	0.009	14584.060	0.348	0.851	-1.305	8.008	3.199	0.361				0.397
PBKK3 MN4	*Micaelamys namaquensis*	2.197	0.220	0.008	12139.633	0.445	0.608	0.419	1.191	1.131	0.041	0.646	153.894	1.760	0.588
PBKK3 MN5	*Micaelamys namaquensis*	1.723	0.220	0.009	11381.399	0.215	0.479	-0.149	0.918	0.804	0.021	0.428	93.031	0.455	0.373
PBKK3 MN6	*Micaelamys namaquensis*	1.507	0.882	0.009	14613.891	0.189	0.429	-0.039	2.371	1.453	0.075	1.267			0.178
PBKK3 MN7	*Micaelamys namaquensis*	2.323	0.882	0.008	14890.526	0.109	0.189	-0.093	1.418	2.667	0.052	0.709	136.780	1.878	0.168
PBKK3 MN8	*Micaelamys namaquensis*	1.156	0.675	0.009	13370.486	0.380	0.553	0.139	1.135	1.459	0.045	0.910	281.330	2.259	0.159
PBKK3 MN9	*Micaelamys namaquensis*	0.790	106.697	0.011	16662.042	0.329	0.697	-0.333	1.196	1.180	0.037	0.784	71.732	0.854	0.422

Appendix III: Raw data and metadata for muroid molar microwear texture analysis

Field no.	Species	Transect	Month	Diet	Nesting	Dust ($mg/m^2/day$)	Soil	% Aerial	% Grass	% Bush	% Tree
13084	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13086	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13087	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13088	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13089	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13090	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13091	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13092	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13093	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13094	*Gerbilliscus leucogaster*	Ekstra	May	GSGR	burrower	782	sandy	medium	low	low	low
13095	*Gerbilliscus leucogaster*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13096	*Gerbilliscus paeba*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13097	*Gerbilliscus paeba*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13098	*Gerbilliscus paeba*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low
13100	*Rhabdomys bechuanae*	Ekstra	May	GSGS	burrower	782	sandy	medium	low	low	low

13102	*Gerbilliscus leucogaster*	Ekstra	May	CUGS	burrower	782	sandy	medium	low	low	low
13104	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13105	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13106	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13107	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13108	*Rhabdomys bechuanae*	GN1	May	ANAN	burrower	697	clay loam	low	low	medium	low
13109	*Rhabdomys bechuanae*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13110	*Rhabdomys bechuanae*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13111	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13112	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13113	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13114	*Gerbilliscus leucogaster*	Stofdraai	May	GSGS	burrower	752	loam	low	high	low	low
13115	*Gerbilliscus leucogaster*	Stofdraai	May	GSCU	burrower	752	loam	low	high	low	low
13116	*Gerbilliscus leucogaster*	Stofdraai	May	GSCU	burrower	752	loam	low	high	low	low
13118	*Rhabdomys bechuanae*	GN2	May	GSDS	burrower	697	clay loam	low	high	low	low
13119	*Rhabdomys bechuanae*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13120	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low

13121	*Gerbilliscus leucogaster*	GN2	May	GSCU	burrower	697	clay loam	low	high	low	low
13122	*Gerbilliscus leucogaster*	GN2	May	GSHA	burrower	697	clay loam	low	high	low	low
13123	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13124	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13125	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13126	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13127	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13128	*Rhabdomys bechuanae*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13129	*Gerbilliscus leucogaster*	GP1	May	CUGS	burrower	700	clay loam	low	medium	low	low
13130	*Gerbilliscus leucogaster*	GP1	May	GSGS	burrower	700	clay loam	low	medium	low	low
13131	*Gerbilliscus leucogaster*	GN1	May	GSGR	burrower	697	clay loam	low	low	medium	low
13132	*Rhabdomys bechuanae*	GN1	May	GSAN	burrower	697	clay loam	low	low	medium	low
13133	*Gerbilliscus leucogaster*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13134	*Gerbilliscus leucogaster*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13135	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
13136	*Gerbilliscus leucogaster*	GN2	May	GSHA	burrower	697	clay loam	low	high	low	low
13137	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low

13140	*Gerbilliscus leucogaster*	Stofdraai	May		burrower	752	loam	low	high	low	low
13141	*Gerbilliscus leucogaster*	Stofdraai	May		burrower	752	loam	low	high	low	low
13142	*Gerbilliscus leucogaster*	Stofdraai	May		burrower	752	loam	low	high	low	low
13143	*Gerbilliscus leucogaster*	Stofdraai	May		burrower	752	loam	low	high	low	low
13144	*Gerbilliscus leucogaster*	Stofdraai	May	GSGS	burrower	752	loam	low	high	low	low
13148	*Gerbilliscus leucogaster*	GN1	May	GSCU	burrower	697	clay loam	low	low	medium	low
13149	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13150	*Gerbilliscus leucogaster*	GN1	May	GSFL	burrower	697	clay loam	low	low	medium	low
13151	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13157	*Gerbilliscus leucogaster*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13158	*Gerbilliscus paeba*	GP2	May	GSGS	burrower	700	clay loam	low	low	high	low
13159	*Gerbilliscus leucogaster*	KK1	May	GSGR	burrower	739	clay loam	medium	low	low	low
13160	*Gerbilliscus leucogaster*	KK1	May	GSCU	burrower	739	clay loam	medium	low	low	low
13161	*Gerbilliscus leucogaster*	KK3	July		burrower	739	loam	low	low	low	medium
13162	*Gerbilliscus leucogaster*	KK3	May	GSFL	burrower	739	loam	low	low	low	medium
13163	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13164	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium

13165	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13166	*Gerbilliscus leucogaster*	KK2	May		burrower	739	loam	low	medium	low	low
13167	*Gerbilliscus leucogaster*	KK2	May		burrower	739	loam	low	medium	low	low
13168	*Gerbilliscus leucogaster*	KK2			burrower	739	loam	low	medium	low	low
13170	*Gerbilliscus leucogaster*	KK2	May		burrower	739	loam	low	medium	low	low
13172	*Gerbilliscus leucogaster*	KK2	May	GSDI	burrower	739	loam	low	medium	low	low
13174	*Rhabdomys bechuanae*	HK2	May	GSGS	burrower		sandy	low	medium	low	low
13179	*Gerbilliscus paeba*	KK1	May	GSGS	burrower	739	clay loam	medium	low	low	low
13180	*Gerbilliscus leucogaster*	KK2	May	GSFL	burrower	739	loam	low	medium	low	low
13181	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13182	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13183	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13184	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13185	*Gerbilliscus leucogaster*	WAP3	May	GSGR	burrower		clay loam sar	low	low	high	low
13186	*Gerbilliscus leucogaster*	WAP2	May	GSGS	burrower		clay loam	low	medium	medium	low
13187	*Gerbilliscus paeba*	WAP3	May	GSFL	burrower		clay loam sar	low	low	high	low
13190	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low

13191	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13192	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13193	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13194	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
13195	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13196	*Rhabdomys bechuanae*	GN1	May	GSDI	burrower	697	clay loam	low	low	medium	low
13197	*Gerbilliscus leucogaster*	GN1	May	GSGS	burrower	697	clay loam	low	low	medium	low
13198	*Gerbilliscus leucogaster*	WAP2	May	GSCU	burrower		clay loam	low	medium	medium	low
13199	*Gerbilliscus leucogaster*	GN1	May		burrower	697	clay loam	low	low	medium	low
13201	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13202	*Gerbilliscus leucogaster*	KK3	May	GSGS	burrower	739	loam	low	low	low	medium
13204	*Micaelamys namaquensis*	KK3	May	GSCU	non-burrower	739	loam	low	low	low	medium
13205	*Gerbilliscus leucogaster*	KK3	May	GSCU	burrower	739	loam	low	low	low	medium
13206	*Gerbilliscus leucogaster*	KK2	May	GSGS	burrower	739	loam	low	medium	low	low
13207	*Gerbilliscus leucogaster*	WAP1	May	GSGS	burrower		loam	low	high	low	low
13216	*Rhabdomys bechuanae*	HK1	May		burrower		sandy	low	medium	low	low
13217	*Gerbilliscus leucogaster*	HK1			burrower		sandy	low	medium	low	low

13218	*Gerbilliscus leucogaster*	HK5			burrower	sandy	low	medium	low	low
13224	*Gerbilliscus leucogaster*	HK3	May		burrower	sandy	low	high	low	low
13225	*Gerbilliscus leucogaster*	HK3	May		burrower	sandy	low	high	low	low
13226	*Gerbilliscus leucogaster*	HK3	May		burrower	sandy	low	high	low	low
13229	*Gerbilliscus leucogaster*	HK3	May		burrower	sandy	low	high	low	low
13230	*Gerbilliscus leucogaster*	HK3	May		burrower	sandy	low	high	low	low
13233	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower	rocky	low	medium	low	low
13234	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower	rocky	low	medium	low	low
13235	*Micaelamys namaquensis*	HK7	May	GSHA	non-burrower	rocky	low	medium	low	low
13237	*Micaelamys namaquensis*	HK7	May	GSDS	non-burrower	rocky	low	medium	low	low
13245	*Gerbilliscus leucogaster*	HK3	May	CUGS	burrower	sandy	low	high	low	low
13246	*Gerbilliscus leucogaster*	HK3	May	GSCU	burrower	sandy	low	high	low	low
13248	*Gerbilliscus leucogaster*	HK3	May	FEGS	burrower	sandy	low	high	low	low
13249	*Gerbilliscus leucogaster*	HK3	May	GSDS	burrower	sandy	low	high	low	low
13250	*Gerbilliscus leucogaster*	HK3	May	GSDS	burrower	sandy	low	high	low	low
13251	*Gerbilliscus leucogaster*	HK3	May	GSGS	burrower	sandy	low	high	low	low
13252	*Gerbilliscus leucogaster*	HK3	May	GSGS	burrower	sandy	low	high	low	low

13253	*Gerbilliscus leucogaster*	HK5	May	GSCU	burrower		sandy	low	medium	low	low
13254	*Gerbilliscus leucogaster*	HK5	May	GSGS	burrower		sandy	low	medium	low	low
13255	*Gerbilliscus leucogaster*	HK5	May	GSGR	burrower		sandy	low	medium	low	low
13255	*Micaelamys namaquensis*	HK5	May	GSGR	non-burrower		sandy	low	medium	low	low
13256	*Gerbilliscus leucogaster*	HK5	May	GSCU	burrower		sandy	low	medium	low	low
13257	*Micaelamys namaquensis*	HK7	May	GSCU	non-burrower		rocky	low	medium	low	low
13259	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13260	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13265	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13267	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13268	*Rhabdomys bechuanae*	GN2	July	GSFL	burrower	1252	clay loam	low	high	low	low
13270	*Mastomys coucha*	GN2	July	GSGS	non-burrower	1252	clay loam	low	high	low	low
13276	*Mastomys coucha*	GN2	July	GSCU	non-burrower	1252	clay loam	low	high	low	low
13277	*Rhabdomys bechuanae*	GN2	July	GSGR	burrower	1252	clay loam	low	high	low	low
13278	*Rhabdomys bechuanae*	GN2	July	GSDS	burrower	1252	clay loam	low	high	low	low
13279	*Rhabdomys bechuanae*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13281	*Micaelamys namaquensis*	HK7	May	GSGR	non-burrower		rocky	low	medium	low	low

13282	*Micaelamys namaquensis*	HK7	July	GSCU	non-burrower		rocky	low	medium	low	low
13284	*Micaelamys namaquensis*	HK7	July	GSCU	non-burrower		rocky	low	medium	low	low
13285	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13287	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13288	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13289	*Micaelamys namaquensis*	HK7	July	GSGR	non-burrower		rocky	low	medium	low	low
13291	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13294	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13295	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13297	*Micaelamys namaquensis*	HK7	July	GSDI	non-burrower		rocky	low	medium	low	low
13298	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
13300	*Gerbilliscus leucogaster*	Stofdraai	July	GSDI	burrower	1293	loam	low	high	low	low
13301	*Gerbilliscus leucogaster*	Stofdraai	July	GSAN	burrower	1293	loam	low	high	low	low
13303	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13304	*Gerbilliscus leucogaster*	GN2	July		burrower	1252	clay loam	low	high	low	low
13305	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13307	*Gerbilliscus leucogaster*	GN2	July	GSGR	burrower	1252	clay loam	low	high	low	low

13308	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13309	*Gerbilliscus leucogaster*	GN2	July	GSGS	burrower	1252	clay loam	low	high	low	low
13315	*Gerbilliscus leucogaster*	GN2	July	GSGR	burrower	1252	clay loam	low	high	low	low
13308b	*Gerbilliscus leucogaster*	GN2	May	GSGS	burrower	697	clay loam	low	high	low	low
PBHK7 MN1	*Micaelamys namaquensis*	HK7	May		non-burrower		rocky	low	medium	low	low
PBHK7 MN10	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN11	*Micaelamys namaquensis*	HK7	July		non-burrower		rocky	low	medium	low	low
PBHK7 MN12	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN2	*Micaelamys namaquensis*	HK7	May	GSGR	non-burrower		rocky	low	medium	low	low
PBHK7 MN4	*Micaelamys namaquensis*	HK7	May	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN5	*Micaelamys namaquensis*	HK7	May	GSGR	non-burrower		rocky	low	medium	low	low
PBHK7 MN6	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN7	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
PBHK7 MN8	*Micaelamys namaquensis*	HK7	July	GSCU	non-burrower		rocky	low	medium	low	low
PBHK7 MN9	*Micaelamys namaquensis*	HK7	July	GSGS	non-burrower		rocky	low	medium	low	low
PBHK9 MN1	*Micaelamys namaquensis*	HK9	May	GSDS	non-burrower		rocky	low	medium	low	low
PBHK9 MN3	*Micaelamys namaquensis*	HK9	July	GSCU	non-burrower		rocky	low	medium	low	low

PBKK3 MN2	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN3	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN4	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN5	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN6	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium
PBKK3 MN7	*Micaelamys namaquensis*	KK3	May	GSGR	non-burrower	739	loam	low	low	low	medium
PBKK3 MN9	*Micaelamys namaquensis*	KK3	May	GSGS	non-burrower	739	loam	low	low	low	medium

Species	*Asfc*	*Smc*	*epsLar*	*Tfv*	*HAsfc* $_{9}$	*HAsfc* $_{81}$	*Ssk*	*Sv*	*Sdr*	*Vvv*	*S5v*	*Sda*	*Sdv*	*Str*
Gerbilliscus leucogaster	3.266	0.496	0.003	4821.558	0.168	0.293	-0.581	1.900	2.143	0.071	1.083	155.159	2.718	0.184
Gerbilliscus leucogaster	11.644	0.612	0.007	7386.279	1.448	1.616	-0.454	3.407	4.304	0.099	2.084	161.524	4.345	0.367
Gerbilliscus leucogaster	143.609	12.400	0.009	6650.906	0.612	2.510	-0.188	1.910	3.280	0.081	1.430	256.124	11.018	0.698
Gerbilliscus leucogaster	127.682	7.936	0.006	6004.432	0.569	0.746	0.146	3.442	2.433	0.082	1.361			0.567
Gerbilliscus leucogaster	70.251	5.511	0.006	7577.619	0.365	1.118	0.026	1.420	1.399	0.057	1.270	216.189	6.351	0.640
Gerbilliscus leucogaster	21.654	0.882	0.004	5281.386	1.495	11.310	-0.311	1.567	1.521	0.057	0.953	157.146	1.170	0.324
Gerbilliscus leucogaster	2.792	0.300	0.006	7755.819	0.149	0.367	-0.110	2.158	1.726	0.050	0.757	245.495	7.408	0.274
Gerbilliscus leucogaster	87.940	4.464	0.005	6309.775	0.676	1.592								
Gerbilliscus leucogaster	96.852	7.936	0.007	6170.035	0.764	1.072	-0.186	2.741	3.425	0.069	1.512	142.502	1.739	0.292
Gerbilliscus leucogaster	13.030	183.272	0.009	6524.819	0.226	0.544	-0.376	2.196	3.693	0.077	1.623	106.175	1.205	0.671
Gerbilliscus leucogaster	8.492	1.200	0.005	6497.227	2.208	4.571	-0.418	3.325	2.177	0.169				0.276
Gerbilliscus paeba	10.367	0.612	0.006	8336.054	0.800	1.188	-0.217	4.657	7.134	0.133	2.682	84.440	1.002	0.212
Gerbilliscus paeba	11.574	0.496	0.003	7979.623	0.664	0.933	-0.358	2.900	5.863	0.094	1.882	107.130	3.653	0.540
Gerbilliscus paeba	7.277	0.153	0.008	8753.803	0.490	0.624	0.146	2.869	5.253	0.066	1.400	202.125	6.850	0.365
Rhabdomys bechuanae	136.335	10.802	0.008	8583.705	0.301	0.897	-0.510	2.781	3.690	0.134	2.001	180.072	1.666	0.354

Gerbilliscus leucogaster	35.433	1.568	0.005	5111.186	0.776	2.473	-0.523	3.278	2.702	0.113				0.435
Gerbilliscus leucogaster	2.564	0.612	0.003	8816.846	0.206	0.427	-0.358	1.909	2.022	0.089	0.988	528.353	25.091	0.290
Gerbilliscus leucogaster	24.567	0.496	0.001	6388.240	0.913	6.408	-1.329	3.143	2.943	0.115	1.785	251.659	3.120	0.407
Gerbilliscus leucogaster	11.075	0.496	0.003	6752.602	0.781	1.013	-0.271	6.957	4.391	0.055	2.823	229.882	18.567	0.444
Gerbilliscus leucogaster							-0.573	2.230	2.996	0.093	1.514	164.281	2.358	0.264
Rhabdomys bechuanae	286.790	29.154	0.004	7684.379	0.445	0.903	0.003	2.782	6.741	0.106	2.039	129.694	1.891	0.536
Rhabdomys bechuanae	22.297	4.140	0.007	7325.005	2.091	3.814	0.289	1.867	2.623	0.075	1.033	115.251	2.664	0.570
Rhabdomys bechuanae	105.275	6.271	0.006	8632.879	0.370	0.823	-0.503	3.282	1.916	0.067	0.710	115.230	2.602	0.294
Rhabdomys bechuanae	6.479	13.527	0.006	9259.727	0.418	0.587	-0.499	3.171	4.072	0.103	1.856	235.757	4.458	0.849
Rhabdomys bechuanae	54.677	21.316	0.010	6377.434	1.323	7.825	0.294	4.644	7.247	0.114	2.831	66.153	1.482	0.177
Rhabdomys bechuanae	9.662	183.272	0.003	8943.247	0.335	0.470	0.344	2.207	3.958	0.054	1.183	163.862	5.907	0.217
Gerbilliscus leucogaster	4.625	0.220	0.004	5199.553	0.114	0.319	-0.362	2.154	3.285	0.103	1.330	217.081	1.412	0.295
Gerbilliscus leucogaster	21.244	7.079	0.007	8100.264	7.484	3.741	-1.178	6.884	5.071	0.137	3.355	154.716	4.304	0.702
Gerbilliscus leucogaster	10.266	0.882	0.007	8022.811	1.558	1.823	-0.548	4.011	4.480	0.103	1.966	120.863	9.148	0.471
Rhabdomys bechuanae	9.608	183.272	0.008	8758.358	0.294	0.571	-0.062	2.494	3.812	0.067	1.692	119.268	0.837	0.180
Rhabdomys bechuanae	248.576	44.243	0.007	11144.466	0.638	1.040	0.389	3.141	5.926	0.098	2.657	1039.841	71.251	0.291
Gerbilliscus leucogaster	96.183	8.842	0.004	7997.233	0.240	0.971	-0.838	5.312	1.924	0.112				0.356

Gerbilliscus leucogaster	48.732	5.885	0.006	6558.173	0.811	12.581	-0.203	2.167	2.085	0.086	1.518	369.694	6.312	0.725
Gerbilliscus leucogaster	14.484	0.153	0.003	4365.474	0.648	12.016	0.116	0.963	0.586	0.033	0.553	178.176	1.039	0.348
Gerbilliscus leucogaster	6.990	0.220	0.002	5802.215	0.243	0.468	0.161	2.012	4.971	0.064	1.368	188.868	6.053	0.399
Gerbilliscus leucogaster	127.650	1.035	0.002	7456.735	0.193	0.595	-0.133	1.705	3.003	0.060	0.991	89.791	1.476	0.394
Gerbilliscus leucogaster	2.997	0.392	0.007	7860.076	0.097	0.352	-0.809	1.933	1.871	0.083	1.188	125.699	1.436	0.460
Gerbilliscus leucogaster	5.116	0.392	0.004	4561.762	0.173	0.335	0.248	1.903	3.457	0.060	1.067	180.833	1.328	0.465
Gerbilliscus leucogaster	2.863	0.300	0.004	5262.699	0.417	0.708	0.068	1.747	1.911	0.059	1.423			0.382
Rhabdomys bechuanae	42.625	9.798	0.004	8524.096	1.350	5.184	-0.355	4.477	4.650	0.149	2.661	225.033	11.600	0.758
Gerbilliscus leucogaster	8.694	0.496	0.004	6550.846	1.572	2.432	0.038	2.345	3.621	0.097	2.068	100.285	1.323	0.422
Gerbilliscus leucogaster	130.198	5.511	0.003	7797.784	0.892	1.077	-0.266	1.808	3.211	0.058	1.235	152.683	2.425	0.618
Gerbilliscus leucogaster	3.109	0.300	0.003	5563.198	0.217	0.411	-0.782	2.644	2.030	0.057	1.036	618.155	25.905	0.705
Rhabdomys bechuanae	128.790	9.314	0.001	6423.983	0.257	0.881	-0.438	3.518	3.801	0.126	2.103	577.574	23.708	0.425
Gerbilliscus leucogaster	5.169	22.786	0.007	7961.740	0.336	0.786	-0.898	4.646	3.458	0.100	1.569			0.469
Gerbilliscus leucogaster	11.602	0.392	0.006	6424.302	1.117	1.620	-0.044	2.343	5.022	0.075	1.710	173.711	2.177	0.639
Gerbilliscus leucogaster	12.660	1.200	0.004	7852.952	1.085	2.478	-0.111	2.126	3.902	0.079	1.646	113.370	3.225	0.707
Gerbilliscus leucogaster	103.483	2.449	0.005	6413.515	0.486	1.026	-0.660	1.658	1.764	0.073	1.019	215.692	1.862	0.437
Gerbilliscus leucogaster	135.592	4.801	0.008	6704.061	0.326	0.959	-0.473	2.641	2.031	0.082	1.332	667.051	12.924	0.154

Gerbilliscus leucogaster	59.390	0.612	0.002	4232.453	0.968	1.122								
Gerbilliscus leucogaster	2.143	0.300	0.005	3618.346	0.155	0.351	-0.442	1.492	1.381	0.043	0.936	104.471	1.000	0.241
Gerbilliscus leucogaster	4.581	22.045	0.009	8443.292	0.542	0.709	-0.255	3.217	3.474	0.073	0.875			0.400
Gerbilliscus leucogaster	3.848	21.316	0.009	8378.073	0.245	0.466	-0.472	1.816	2.033	0.080	1.169	231.005	4.118	0.495
Gerbilliscus leucogaster	3.069	0.496	0.003	7763.076	0.898	1.081	-0.382	2.207	1.489	0.066	1.243	252.021	4.629	0.479
Gerbilliscus leucogaster	142.831	2.449	0.005	6238.648	0.348	0.679	-0.269	1.832	3.650	0.067	1.219	141.424	1.564	0.211
Gerbilliscus leucogaster	75.017	0.882	0.001	5542.702	0.586	1.095	-0.834	2.457	2.083	0.107	1.252	248.185	5.815	0.472
Gerbilliscus leucogaster	86.496	5.511	0.001	6409.680	0.444	0.860	-0.381	2.703	3.368	0.102	1.542	179.646	4.067	0.227
Gerbilliscus leucogaster	168.749	11.322	0.005	5470.072	0.727	0.836	0.237	2.812	3.944	0.098	1.851	47.470	0.443	0.495
Gerbilliscus leucogaster	24.024	0.153	0.009	8807.531	4.270	3.970	0.016	1.915	4.796	0.061	1.530	97.636	1.979	0.211
Gerbilliscus paeba	3.199	0.300	0.003	4760.916	0.120	0.261	0.014	1.802	2.145	0.061	0.926	283.557	2.617	0.299
Gerbilliscus leucogaster	58.578	0.300	0.002	7873.809	1.395	4.926	-0.501	1.887	2.098	0.056	1.163	152.749	4.402	0.439
Gerbilliscus leucogaster	3.830	43.208	0.008	6947.175	0.463	0.577	0.059	1.865	2.537	0.064	1.251	186.097	3.171	0.210
Gerbilliscus leucogaster	216.728	21.316	0.008	9467.342	0.367	0.837	-0.318	2.867	2.358	0.097	1.696			0.772
Gerbilliscus leucogaster	82.729	4.464	0.009	7584.550	0.520	1.004	-0.048	1.242	1.327	0.049	1.021	108.934	1.471	0.179
Gerbilliscus leucogaster	14.715	5.885	0.005	6017.418	1.803	1.372	-0.235	3.402	4.583	0.111	2.005	198.901	5.505	0.243
Gerbilliscus leucogaster	2.531	8.383	0.004	6802.136	0.316	0.485	-0.478	2.039	1.602	0.079	1.075	347.080	1.566	0.598

Gerbilliscus leucogaster	114.054	3.239	0.003	5644.179	0.486	0.749	-0.079	2.285	4.236	0.076	1.609	201.499	4.957	0.431
Gerbilliscus leucogaster	86.783	1.568	0.005	6296.991	0.299	0.936	0.091	1.471	2.018	0.049	0.894	459.150	3.552	0.588
Gerbilliscus leucogaster	18.963	0.882	0.002	5853.772	0.465	4.412	-0.339	1.738	0.986	0.045	0.985	200.599	1.779	0.187
Gerbilliscus leucogaster	7.706	0.153	0.010	5942.048	0.543	0.921	-0.548	2.693	5.477	0.083	1.760	482.279	4.647	0.148
Gerbilliscus leucogaster	5.877	183.272	0.007	6708.914	0.702	0.938	-0.772	3.151	2.636	0.090	1.520	352.374	5.982	0.167
Gerbilliscus leucogaster	62.533	1.035	0.002	4603.734	0.648	1.316	-0.442	2.908	2.650	0.064	1.027	194.047	6.642	0.300
Rhabdomys bechuanae	2.608	183.272	0.007	5360.241	0.193	0.412	0.072	1.504	2.560	0.051	1.129	157.755	7.652	0.783
Gerbilliscus paeba	33.432	0.392	0.003	8556.209	0.716	1.172	-0.267	4.041	13.894	0.157	2.647	122.561	3.882	0.287
Gerbilliscus leucogaster	80.076	8.842	0.008	7725.274	0.712	18.827	-1.012	3.198	2.259	0.098	1.331			0.187
Gerbilliscus leucogaster	4.624	0.153	0.008	6477.834	0.153	0.328	-0.150	2.127	2.755	0.046	1.096	62.262	0.794	0.245
Gerbilliscus leucogaster	205.532	17.856	0.007	9140.744	0.287	0.711	0.230	1.757	4.572	0.058	1.214	156.533	8.918	0.657
Gerbilliscus leucogaster	3.192	0.496	0.004	5457.651	0.516	0.630	-0.333	2.837	2.285	0.075	1.510	262.557	7.593	0.584
Gerbilliscus leucogaster	3.433	23.539	0.002	5140.601	0.276	0.645	-0.698	2.961	2.631	0.124	1.542	190.086	2.292	0.458
Gerbilliscus leucogaster	53.347	5.150	0.008	7325.257	0.779	2.312	-0.262	1.547	1.098	0.053	1.216	101.414	0.980	0.576
Gerbilliscus leucogaster	65.394	0.882	0.005	7675.343	0.558	1.137	-0.119	2.071	2.013	0.055	1.561	119.688	0.964	0.676
Gerbilliscus paeba	5.219	0.153	0.006	6716.695	0.638	0.788	0.366	1.583	3.655	0.052	0.676	139.343	3.406	0.153
Gerbilliscus leucogaster	5.058	0.220	0.005	7416.309	0.132	0.298	-0.080	2.457	3.658	0.085	0.718	146.655	2.634	0.613

Gerbilliscus leucogaster	38.772	2.964	0.006	6285.006	1.096	19.823	0.253	2.281	1.637	0.058	1.780	243.583	7.973	0.219
Gerbilliscus leucogaster	6.873	1.200	0.003	6957.443	1.230	1.002	-0.157	1.692	2.708	0.055	1.087	143.256	2.566	0.463
Gerbilliscus leucogaster	73.358	6.669	0.008	6312.882	0.330	0.890	0.082	1.872	2.268	0.065	1.392	156.217	3.073	0.587
Micaelamys namaquensis	19.024	3.827	0.004	8979.738	3.399	2.288	-0.882	6.928	4.159	0.227	3.024	0.269	0.015	0.704
Gerbilliscus leucogaster	22.840	0.741	0.006	6214.769	1.110	18.186	0.353	1.493	1.034	0.038	0.871			0.247
Rhabdomys bechuanae	212.136	6.271	0.004	6662.595	0.263	0.521	-0.168	3.180	3.790	0.089	1.996	513.338	39.805	0.298
Gerbilliscus leucogaster	63.074	0.496	0.004	4839.337	0.417	1.088	-0.094	1.645	3.406	0.071	0.803	138.788	2.717	0.180
Gerbilliscus leucogaster	43.662	4.140	0.007	7072.226	0.543	11.621	-0.024	1.834	2.392	0.062	1.358	300.038	4.772	0.310
Gerbilliscus leucogaster	10.030	0.220	0.004	4562.635	0.430	0.815	-0.800	2.823	6.334	0.126	1.734	113.672	2.774	0.578
Gerbilliscus leucogaster	22.067	0.220	0.007	7659.651	2.333	12.735	-0.598	3.074	1.329	0.068	0.588	179.273	2.934	0.165
Gerbilliscus leucogaster	185.443	14.109	0.008	6663.042	0.709	1.096								
Micaelamys namaquensis	16.405	5.150	0.003	7288.582	3.469	5.356	-0.309	3.259	1.931	0.077	1.328	176.689	0.782	0.524
Gerbilliscus leucogaster	41.076	6.271	0.008	6012.216	1.623	12.543	-0.063	2.867	2.065	0.082	0.835	520.257	72.785	0.528
Gerbilliscus leucogaster	143.441	10.802	0.008	4850.036	0.928	10.790	0.348	4.060	7.940	0.111	2.289	52.173	1.781	0.651
Gerbilliscus leucogaster	43.415	0.741	0.002	4637.612	0.529	1.258	-0.208	2.097	2.696	0.087	1.283	190.945	2.137	0.668
Rhabdomys bechuanae	9.142	183.272	0.007	7317.390	0.637	0.821	-0.018	2.053	3.118	0.048	1.533	113.414	1.014	0.500
Gerbilliscus leucogaster	6.318	0.300	0.003	5175.038	0.237	0.488	-0.021	1.760	3.210	0.045	0.479	54.835	0.538	0.177

Gerbilliscus leucogaster	104.631	3.527	0.006	6595.038	0.539	0.992	-0.380	3.643	5.504	0.084	1.909	702.360	5.283	0.764
Gerbilliscus leucogaster	4.402	47.421	0.005	5710.543	0.333	0.560	-0.316	2.900	2.335	0.119	1.035	633.653	63.226	0.281
Gerbilliscus leucogaster	10.703	1.984	0.007	8787.669	2.115	1.688	-0.126	1.842	3.454	0.070	0.603	136.738	0.821	0.594
Gerbilliscus leucogaster	50.580	0.392	0.005	5411.813	0.976	2.990	0.014	2.054	2.531	0.069	1.556	696.175	5.644	0.457
Gerbilliscus leucogaster	21.196	0.392	0.004	5899.817	0.659	12.268	-0.221	2.464	1.006	0.079	1.045	388.062	6.330	0.196
Gerbilliscus leucogaster	5.547	41.175	0.007	6440.792	0.328	0.424	0.025	2.859	5.086	0.142	1.593	233.075	3.302	0.283
Micaelamys namaquensis	6.657	4.801	0.008	6595.477	1.797	2.672	0.140	3.194	2.207	0.085	2.123			0.663
Micaelamys namaquensis	59.670	0.220	0.006	5994.354	1.651	1.666	-0.567	2.293	1.332	0.079	1.229			0.436
Micaelamys namaquensis	212.523	6.669	0.004	7908.532	0.370	0.539	-0.425	2.404	3.742	0.091	1.392	172.525	3.148	0.659
Micaelamys namaquensis	2.910	0.220	0.004	8124.344	0.367	0.680	-0.523	1.776	2.006	0.062	0.977	97.850	0.802	0.485
Gerbilliscus leucogaster	1.962	1.035	0.005	5059.601	0.136	0.319	-0.384	1.223	1.335	0.054	0.617	244.179	1.803	0.236
Gerbilliscus leucogaster	128.107	7.079	0.005	6884.040	0.229	0.675	0.088	1.564	3.324	0.051	0.961	111.847	1.418	0.508
Gerbilliscus leucogaster	14.182	0.496	0.007	7798.396	2.851	3.258	0.096	5.454	5.099	0.133	2.454	12.933	0.306	0.189
Gerbilliscus leucogaster	134.660	15.309	0.006	8307.041	0.545	1.117	0.166	3.567	3.179	0.085	2.151	91.229	3.288	0.213
Gerbilliscus leucogaster	2.343	0.392	0.007	6423.319	0.467	0.669	-0.058	1.413	1.512	0.044	0.991	196.141	3.332	0.529
Gerbilliscus leucogaster	31.983	2.964	0.002	6593.510	0.416	14.971	-0.467	3.057	2.074	0.120	1.887			0.795
Gerbilliscus leucogaster	2.642	0.220	0.006	4722.907	0.450	0.763	-0.041	1.820	1.823	0.061	0.921	145.138	1.794	0.745

Gerbilliscus leucogaster	9.490	6.271	0.008	6973.952	3.594	1.621	-0.636	2.234	1.917	0.087	1.393	205.886	1.361	0.290
Gerbilliscus leucogaster	3.828	0.392	0.006	6625.933	0.232	0.816	-0.239	2.242	2.678	0.090	1.492	342.265	4.037	0.618
Gerbilliscus leucogaster	4.302	0.220	0.007	7507.018	0.090	0.283	0.131	1.728	2.313	0.033	0.839	120.380	2.328	0.676
Micaelamys namaquensis	5.749	2.211	0.004	7858.913	0.960	0.761	-0.189	2.649	3.288	0.113	2.087	196.342	2.285	0.323
Gerbilliscus leucogaster	8.175	1.770	0.005	4123.112	1.406	1.945	-0.710	2.067	2.321	0.091	1.086	156.603	1.521	0.662
Micaelamys namaquensis	3.804	0.220	0.002	5979.282	0.255	0.442	-0.497	3.981	3.131	0.102	1.330	50.548	0.514	0.345
Rhabdomys bechuanae	56.406	14.109	0.005	10660.128	0.685	3.917	-0.714	3.623	6.574	0.176	2.646	237.496	7.188	0.485
Rhabdomys bechuanae	13.396	0.220	0.004	7182.968	2.474	2.907	-0.028	2.019	3.455	0.083	1.468	125.383	2.829	0.751
Rhabdomys bechuanae	150.338	22.045	0.002	6111.825	1.326	9.319	-2.305	11.698	12.530	0.295	8.177	27.397	1.374	0.560
Rhabdomys bechuanae	17.947	1.035	0.008	5619.707	1.129	3.576	0.348	1.140	2.760	0.044	0.974	116.243	1.136	0.303
Rhabdomys bechuanae	2.587	0.300	0.004	4830.189	0.158	0.433	-0.052	1.377	1.485	0.035	0.807	119.264	1.798	0.714
Mastomys coucha	24.587	44.243	0.009	9136.215	0.634	4.350	-0.288	3.761	3.512	0.089	1.834	53.177	1.017	0.313
Mastomys coucha	10.515	0.220	0.001	6313.919	1.084	1.626	-0.450	2.486	3.340	0.103	1.909	78.590	1.258	0.267
Rhabdomys bechuanae	86.211	3.527	0.003	6036.999	0.444	1.075	0.048	2.047	1.763	0.059	1.223	148.521	1.890	0.566
Rhabdomys bechuanae	104.952	2.964	0.006	5537.462	0.704	1.007	-0.375	2.309	2.427	0.081	1.402	122.247	1.261	0.664
Rhabdomys bechuanae	9.779	9.314	0.005	7795.216	2.827	1.796	-0.263	2.502	3.177	0.087	1.740	283.278	10.476	0.397
Micaelamys namaquensis	57.595	1.984	0.006	8434.716	2.242	4.164	-0.420	2.769	1.481	0.084	1.632	225.567	2.550	0.298

Micaelamys namaquensis	8.353	1.378	0.007	7973.301	1.382	1.891	-0.382	1.475	3.049	0.052	1.030	98.370	1.643	0.395
Micaelamys namaquensis	153.451	5.511	0.003	6361.906	0.420	0.693	-0.310	2.591	3.416	0.116	1.457	577.133	2.506	0.311
Micaelamys namaquensis	106.388	7.079	0.004	6643.876	0.222	0.719	-0.004	2.529	2.183	0.083	1.399			0.252
Micaelamys namaquensis	19.991	47.421	0.010	9597.063	6.353	4.799	0.036	3.203	3.832	0.148	2.072			0.193
Micaelamys namaquensis	3.913	183.272	0.009	5400.524	0.990	1.108	-0.095	2.045	1.446	0.049	1.010	350.252	1.941	0.662
Micaelamys namaquensis	7.450	1.568	0.004	5537.379	2.538	3.437	-0.563	2.200	1.824	0.112	1.529	204.000	12.280	0.173
Micaelamys namaquensis	8.412	183.272	0.006	7267.817	0.944	1.056	0.132	2.834	3.576	0.102	1.517	159.706	2.312	0.602
Micaelamys namaquensis	8.074	6.271	0.008	9091.341	1.237	2.343	-0.799	4.051	3.253	0.099	1.800	58.887	0.816	0.229
Micaelamys namaquensis	6.808	42.185	0.008	9261.362	1.091	1.070	-0.561	3.255	2.161	0.117	1.870	241.344	9.320	0.603
Micaelamys namaquensis	129.870	2.211	0.006	5699.103	0.224	0.527	-0.313	3.448	5.396	0.078	1.772	218.342	4.226	0.776
Micaelamys namaquensis	4.472	183.272	0.006	5830.784	0.510	0.491	-0.854	2.613	1.072	0.093	1.119	148.741	3.409	0.724
Gerbilliscus leucogaster	6.368	0.741	0.004	5251.509	0.974	1.292	-0.925	3.379	3.305	0.093	1.945	186.601	5.117	0.516
Gerbilliscus leucogaster	4.842	0.300	0.002	7506.646	0.567	0.743	-0.103	1.628	2.324	0.048	1.287	112.610	0.985	0.653
Gerbilliscus leucogaster	5.764	0.220	0.005	6431.050	0.356	0.661	-0.375	2.501	3.473	0.067	1.439	90.300	2.036	0.530
Gerbilliscus leucogaster	4.924	0.220	0.009	7540.691	1.125	1.466	-0.514	3.281	2.114	0.067	1.710	293.569	9.816	0.392
Gerbilliscus leucogaster	71.385	2.700	0.008	5824.910	0.746	1.888	0.627	2.700	2.557	0.049	1.875	344.934	7.290	0.370
Gerbilliscus leucogaster	106.421	10.294	0.007	5355.493	0.617	1.119	0.108	1.931	1.654	0.055	1.076	230.553	1.745	0.522

Gerbilliscus leucogaster	2.298	8.383	0.002	5415.809	0.856	1.496	-1.202	2.913	1.400	0.117	1.342	268.634	1.922	0.605
Gerbilliscus leucogaster	2.619	150.940	0.005	5983.971	0.218	0.400	0.064	1.434	1.556	0.047	0.955	165.977	0.782	0.300
Gerbilliscus leucogaster	25.223	1.984	0.007	8651.112	1.635	7.731	-0.802	3.514	2.244	0.105	1.736	76.269	0.964	0.173
Gerbilliscus leucogaster	6.276	0.496	0.002	5437.004	0.678	0.840	-0.040	1.972	3.292	0.069	1.691	115.880	2.875	0.438
Micaelamys namaquensis	106.692	12.400	0.004	7480.593	0.468	1.341	-0.207	3.146	2.243	0.077	1.537	519.486	5.693	0.193
Micaelamys namaquensis	10.075	183.272	0.008	6546.579	0.413	0.654	0.741	1.921	3.057	0.079	1.599	102.245	3.796	0.781
Micaelamys namaquensis	152.809	11.855	0.002	8916.060	0.242	0.689	0.152	1.796	4.396	0.063	1.585	155.856	3.016	0.571
Micaelamys namaquensis	224.271	30.869	0.007	8988.798	0.264	0.959	-0.695	4.863	3.506	0.087	2.133			0.187
Micaelamys namaquensis	16.432	0.392	0.007	9251.537	1.690	2.202	-0.068	11.318	6.782	0.092	5.981	432.650	21.755	0.608
Micaelamys namaquensis	111.063	14.109	0.005	6923.869	0.508	1.447	-0.529	2.304	2.463	0.077	1.604	83.160	1.245	0.676
Micaelamys namaquensis	6.882	183.272	0.006	6892.033	0.285	0.361	-0.087	2.041	3.426	0.051	1.429	230.417	1.946	0.479
Micaelamys namaquensis	166.688	17.201	0.007	5272.494	0.262	0.772	-0.810	5.294	4.817	0.153	3.145			0.454
Micaelamys namaquensis	6.196	52.963	0.010	10626.626	0.376	0.589	-0.545	3.064	4.007	0.102	1.672	253.276	2.069	0.259
Micaelamys namaquensis	7.724	4.464	0.002	6330.797	3.942	8.624	-0.046	1.615	2.182	0.059	1.048	226.559	1.616	0.740
Micaelamys namaquensis	24.114	3.239	0.011	8610.806	3.942	8.624	0.709	3.130	7.712	0.083	1.938	35.623	0.514	0.187
Micaelamys namaquensis	47.967	1.378	0.002	4881.209	0.368	4.570	-0.011	1.182	1.087	0.038	0.698	241.013	3.951	0.337
Micaelamys namaquensis	5.990	0.496	0.004	6947.141	0.956	1.557	-0.421	2.655	1.992	0.071	1.170	230.901	4.441	0.367

Micaelamys namaquensis	252.682	29.154	0.002	9415.723	0.923	1.511	-0.292	5.275	5.644	0.191				0.373
Micaelamys namaquensis	52.579	1.200	0.007	6628.816	0.392	1.339	0.133	1.186	1.876	0.049	0.752	139.227	1.793	0.715
Micaelamys namaquensis	10.177	183.272	0.006	9589.717	0.336	0.618	0.073	2.519	2.679	0.096	1.932	203.914	7.363	0.548
Micaelamys namaquensis	6.580	41.175	0.009	9510.459	0.548	0.753	0.402	1.698	4.116	0.059	1.357	227.723	2.082	0.288
Micaelamys namaquensis	155.577	12.400	0.003	9365.162	0.485	0.769	0.021	3.191	3.606	0.047	1.638	90.181	0.796	0.202
Micaelamys namaquensis	15.249	47.421	0.009	11467.478	1.342	1.464	0.445	5.396	7.103	0.080	3.571	40.611	2.785	0.194
Micaelamys namaquensis	5.631	183.272	0.005	8949.783	0.315	0.528	-0.246	2.581	2.706	0.085	1.851	166.138	5.804	0.283