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3 Rodent incisor microwear as a proxy for ecological reconstruction

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ABSTRACT

Increasing attention has been directed toward rodents as a source of paleoenvironmental data due to their discrete home ranges and their ubiquity and abundance in many fossil and archaeological assemblages. Further, rodents play a vital role in regulating ecosystem structure and function, and may be closely tied to local habitat. This study assesses the potential of incisor microwear textures of rodents as an environmental proxy, and evaluates the extent to which effects of diet, substrate, and habitat can be parsed from the signal. Microwear textures on lower incisors were analyzed using confocal profilometry and quantified using scale-sensitive fractal analysis. Specimens analyzed ($n=430$) represent omnivorous, herbivorous, and frugivorous species, some arboreal and some terrestrial, collected from African desert, savanna, woodland, and rainforest habitats. Results suggest diet, habitat, and substrate all contribute to rodent incisor microwear patterning, and that this approach holds potential to provide important information about the ecology of past species.

keywords: Muridae; tooth wear; paleoecology; Africa: confocal microscopy; scale-sensitive fractal analysis

1.1 Introduction

Dental microwear texture analysis has proven to be a reliable approach to elucidating dietary behaviors and ecological interactions for many mammalian taxa. Most microwear texture studies have been conducted on larger mammals, such as bovids, carnivorans, and primates (Donohue et al., 2013; Schubert et al., 2010; Schulz et al., 2010; Scott, 2012; Scott et al., 2012, 2006; Ungar et al., 2012, 2010, 2007a, 2007c). Only a handful of studies have applied this technique to micromammals thus far (Belmaker and Ungar, 2010; Burgman et al., submitted; Withnell and Ungar, 2014). Here, we assess the potential of rodent incisor microwear texture patterns to reveal habitat, substrate, and diet information.

Dental microwear is microscopic use wear on teeth typically associated with the acquisition and processing of food. As such, it provides a record of an organism's interaction with its environment, making it a potential proxy for reconstructing paleohabitat (Hopley et al., 2006; Merceron and Madelaine, 2006; Merceron and Ungar, 2005; Schubert et al., 2006; Ungar et al., 2007b). Most microwear research has focused on molars because these teeth function in food breakdown and likely reflect diet (e.g., Butler, 1952; Donohue et al., 2013; Simpson, 1926; Van Valkenburgh et al., 1990). Incisors might also reflect habitat since these teeth provide an initial contact point between an animal and its surroundings. Indeed, those few studies that have focused on front teeth (Kelley, 1990; Rivals and Semprebon, 2010; Ryan and Johanson, 1989; Walker, 1976), have shown their potential for microwear study.

1.2 Dietary and Environmental Causes of Microwear

Some researchers have recently suggested that exogenous quartz grit and dust are more likely to cause tooth wear than are foods themselves (e.g., Lucas et al., 2013; Sanson et

al., 2007). Others have maintained that endogenous abrasives in foods (e.g., silicious phytoliths) can cause tooth wear (Baker et al., 1959; Lalueza Fox et al., 1994; Gügel et al., 2001; Rabenold and Pearson, 2011; Teaforde and Byrd, 1989; Ungar et al., in press; Walker, 1979; Xia et al., 2015). In either case, a recent study of molar microwear of rodents from a variety of habitats found diet to contribute more to pattern differences than does environmental grit per se (Gomes Rodrigues et al., 2009). This may be due to the fact that, regardless of whether grit and dust or phytoliths are the agents of wear, molar microwear patterning reflects masticatory movements associated with specific food properties (Hua et al., 2015).

But what about incisors? These teeth are often used as “tools” for food acquisition, digging, etc. (Ungar, 2010). Rodents use their front teeth to gnaw so much, in fact, that they have evolved ever-growing incisors to offset extreme wear. Unlike molars, incisors are used for more than just chewing food, and they come into direct contact with the environment. This means that incisor microwear might be especially well suited to be a habitat proxy, but also that its interpretation is likely complicated by the fact that a number of factors may contribute to texture patterns.

1.3 Rodent Incisors as a Proxy

Rodents, the quintessential lab mammals, are also ready candidates for studies in the natural world. A principal obstacle to using faunal assemblages for reconstruction of paleoenvironments is taphonomic bias (Winder, 2012). However, rodents are typically *r*-selected organisms, and reproduce early and often (Churakov et al., 2010). This makes them, despite taphonomic preservation issues related to their generally diminutive size, very common in many fossil assemblages.

Though analyses of dental microwear have been conducted on numerous mammals and other vertebrates, rodents evince several advantages for environmental reconstruction. They can be found in a broad range of habitat types, with individual species often occupying narrowly-defined, distinctive niches. And the distribution of Rodentia is expansive both in terms of space and time. Extant rodents live on all continents except Antarctica, and fossil species are found in deposits spanning most of the Cenozoic. In fact, the first rodents definitively identified in the fossil record date from the late Paleocene, and the clade may extend back to the Cretaceous (Benton and Donoghue, 2007). Further, the order is by far the most speciose among the mammals, accounting for more than 40 percent of all the extant species of mammals (Carleton and Musser, 2005). Indeed, Muridae, the family utilized in this study, is the most speciose in Rodentia (and in fact, in all Mammalia) (Michaux et al., 2001).

Rodents are also important ecological markers because they play an integral role in the larger community of life that surrounds them. Rodents tend to be keystone members of their habitats, either as individual species, such as beaver and prairie dog, or as members of guilds (Brown and Heske, 1990). Rodents act as the trophic glue that holds together food webs, and they serve as ecosystem engineers (Huntly and Inouye, 1988; Jones et al., 1994). They affect community structure by controlling the relative abundance of species in their roles as predator and prey (Howe et al., 2002; Hull Sieg, 1987; Hulme, 1996), and they change ecosystem function in a variety of ways (see discussion in Chew, 1978). Rodents aerate and increase ground water recharge through soil turbation, aid in decomposition and nutrient cycling, control plant productivity and species richness and composition, promote ecological succession, and provide habitats for other species, among other things (e.g., Potter, 1978; Grant et al.,

1980; Inouye et al., 1987; Huntly and Inouye, 1988; Laundre, 1993, 1998; Jones et al., 1994; Hulme, 1996; Weltzin et al., 1997; Davidson and Lightfoot, 2008).

There is no mammalian order more important for regulating biospheric activity than Rodentia, and its adaptive versatility, number of species, cosmopolitan distribution, and overall ubiquity, make it a great model taxon for exploring dental microwear as a proxy for paleoenvironmental reconstruction.

1.4 Dental Microwear as Proxy for Environmental and Diet

Microscopic use-wear on teeth has been considered an indicator of diet and tooth use in studies of fossils since the 1920s, when George Gaylord Simpson noted scratches on the molars of multituberculates (1926). Work on diet-related microscopic tooth wear followed in the 1950s, with contributions by Butler (1952 *et seq.*) and Mills (1955 *et seq.*). These studies set out to examine scratch distribution and direction on cheek teeth to work out details of mastication. Baker and colleagues (1959) followed with the first study of the etiology of microwear, concluding that environmental grit and phytoliths were both capable of abrading enamel. Work continued, and by late 1970's, focus had shifted to the reconstruction of diet. In 1978, Walker and colleagues compared teeth of hyraxes that differ in seasonal availability of food, and found differences in microwear related to both season and dietary preference. The first study to associate diet with microwear in rodents was also published in 1978 (Rensberger, 1978). These early analyses focused largely on molars.

1.4.1 Molar microwear

More recent studies have also focused mostly on molars, but the number of techniques used to identify and characterize microwear patterns and the range of taxa considered has

expanded considerably. Researchers have reported diet-related microwear patterns for ungulates such as pronghorns (Rivals and Semprebon, 2006), antelopes (Schulz et al., 2010; Solounias and Hayek, 1993), bovids (Merceron et al., 2005) and equids (Hayek et al., 1991; Schulz et al., 2010; Solounias and Semprebon, 2002), as well as such small mammals as bats (Purnell et al., 2013; Strait, 1993), moles (Silcox and Teaford, 2002) and lagomorphs (Schulz et al., 2013), various marsupials (Prideaux et al., 2009; Robson and Young, 1989, 1986; Young et al., 1990), predators such as canids and large cats (DeSantis et al., 2012; Schubert et al., 2010; Ungar et al., 2010; Van Valkenburgh et al., 1990), various bear species (Donohue et al., 2013; Peigné et al., 2009; Pinto-Llona, 2013), and many others, including domesticated animals such as pigs and sheep (Mainland, 1998; Ward and Mainland, 1999; Zolnierz, 2014). Results from such studies are clear: species reported to consume harder items tend to have a higher ratio of pits to scratches on their cheek teeth than do closely-related ones that prefer tougher foods. These studies have demonstrated the robustness of rodent molar microwear as a proxy for feeding ecology.

Most rodent microwear studies have been limited been to molars too, and early work focused on relationships between pattern and chewing behaviors (Rensberger, 1978; Teaford and Byrd, 1989; Teaford and Walker, 1983a, 1983b, 1982). More recent analyses of rodent molar microwear have taken a comparative approach to the inference of both diet and paleoenvironmental reconstruction (Firmat et al., 2011, 2010; Gomes Rodrigues et al., 2009; Hautier et al., 2009; Nelson et al., 2005; Townsend and Croft, 2008). In fact, Hopley et al. (2006) and Firmat et al. (2010), actually found molar microwear to better reflect diet and paleoecology than does dental morphology, at least for their study taxa.

1.4.2. Incisor microwear

Studies of microwear on incisors have been conducted mostly, though not exclusively, on primates. Walker (1976), for example, compared patterns on the incisors of Old World monkeys, and related differences between samples to both diet and substrate. Subsequent studies of primates have focused on these things and on specifics of ingestive behaviors (Kelley, 1990, 1986; Rose et al., 1981; Ryan, 1981; Schmid, 1983; Teaforde, 1983; Ungar, 1996, 1994, 1990).

There have also been several microwear studies of hominins, including *Homo sapiens* (e.g., Bax and Ungar, 1999; Dahlberg and Kinzey, 1962; Krueger, 2015; Krueger and Ungar, 2012, 2010; Lalueza Fox and Frayer, 1997; Lozano et al., 2008; Lukacs and Pastor, 1988; Ryan, 1993, 1981, 1980; Ryan and Johanson, 1989; Ungar and Grine, 1991; Ungar and Spencer, 1999). This work has identified patterns related to both ingestive behaviors, and non-diet anterior tooth functions, such as hide preparation.

There have been fewer studies of anterior dental microwear of non-primate mammals, but those species that have been sampled, represent a very broad range of taxa. Plains zebra (*Equus quagga*) incisors and molars have been compared with each other to confirm that the two types of teeth record diet signals differently. Incisor microwear in moose (*Alces alces*) has been used to distinguish pathological from physiological tooth wear (Young and Marty, 1986). Incisor (tusk) microwear in dugongs (*Dugong dugon*) has been related to use in seagrass harvesting (Domning and Beatty, 2007). Microwear on incisiform teeth of sauropod diplodocoids (Diplodocoidea) has been used to infer diet and foraging strategies (Whitlock,

2011). And finally, a recent study by Withnell and Ungar (2014) showed incisor microwear textures can separate shrews by diet too.

There has been less work done on rodent incisor microwear. Stefen (2011) considered the European beaver (*Castor fiber*), nutria or coypu (*Myocastor coypus*), and muskrat (*Ondrata zibethicus*) to identify markers of diet and wood chewing. While that study was unable to separate species by incisor microwear pattern, perhaps because the analysis was qualitative, it was clear that incisors had different microwear patterns than molars. And indeed, a pilot quantitative study of incisor microwear textures of New World rodents by Belmaker and Ungar (2010) did find differences between granivorous and frugivorous groups. Such analyses provide just enough evidence to make clear that much more work needs to be done to determine the utility of rodent incisor microwear for reconstructing diets and habitats of fossil rodents.

This paper reports on a study of incisor microwear textures for a large sample of rodents representing species with known differences in diet, habitat, and substrate preferences. It represents an attempt to begin to determine effects of each on incisor microwear textures of African rodents, and to assess the potential utility of this approach for paleoecological inference.

2.1 Materials and Methods

In this study, we examined incisor microwear of 430 specimens representing 16 species of extant rodent. Microwear texture attributes were compared for samples grouped by diet, substrate, and habitat type. Groups were expected to vary independent of species classifications, and a taxon-free approach was employed in analysis (see Scott, 2012 for discussion). Basic information on diet and substrate were obtained from the literature,

191 whereas habitat provenance came from recorded capture locations and other original records
192 cross-referenced with Google Earth imagery. We avoided specimens from present-day habitat
193 margins and transitional zones to minimize the effect of anthropogenic and natural
194 environmental change between the date of capture and date of imagery. Summary details for
195 each species are presented in Table 1.

196 Habitats were classified into basic desert, savanna, woodland, and rainforest types.
197 These reflect generalized vegetation zones across the African continent that differ in plant
198 community structure. Because of discrepancies in the way habitats were described by the
199 original collectors and resolution limitations of vegetation maps, precise definitions of habitat
200 categories based upon published sources was not practical. For this study, habitat categories
201 are internally consistent, and are used for heuristic purposes only to separate groups. Here
202 savanna is defined as land where the groundcover is mostly grasses and other herbaceous
203 plants with sparse or absent canopy. Woodland applies to forests dominated by deciduous
204 trees, while the term rainforest is used for tropical evergreen forest. Desert encompasses arid
205 and semi-arid zones with relatively little vegetative groundcover. These habitat categories
206 loosely follow White (1983), and were selected because they could be used with available
207 satellite imagery to assess ground and canopy cover. Preference was also given for species
208 collected in large numbers from given locations within habitat types to maximize statistical
209 power. Most specimens from individual species used in this study derived from a single habitat
210 type. However, *Mastomys natalensis* specimens have been included from savanna, woodland,
211 and rainforest habitats, and *Praomys jacksoni* specimens have been included from woodland
212 and rainforest habitats.

2.2 Sample

Individuals included in this study are stored in the Department of Mammalogy at the National Museum of Natural History in Washington, DC. Only well-provenienced individuals of known species and location were used. Species sampled and specimen numbers for each are presented in Table 1. With the exception of *Merriones spp.*, which have ranges that extend outside of Africa, the species used in this study are endemic only to Africa.

2.3 Specimen preparation and analysis

A single lower incisor was examined for each individual, preferentially the left unless unavailable. Each tooth was cleaned with a cotton swab soaked in 95% isopropyl alcohol to remove any dirt or debris from the surface of the enamel. An impression of each selected incisor's distolabial surface, from the tip to the alveolar bone margin, was taken using polyvinylsiloxane (President Jet Regular Body, Coltene/Whaledent) dental impression material. This material has been shown to faithfully reproduce microwear surface textures to a fraction of a micron (Goodall et al., 2015). Resulting molds were then poured with a high-resolution epoxy (Epotek 301, Epoxy Technologies) to create high-resolution positive replicas of each specimen.

Each cast was first examined using a Sensofar Plμ white-light scanning confocal imaging profiler at 10× magnification for postmortem tooth damage in the region of interest, the area on the distal edge of the labial enamel just below the incisal surface. This region has been shown in the past to preserve diet-related microwear features (Belmaker and Ungar, 2010). Specimens preserving unobscured antemortem microwear (criteria following Teaford, 1988) were then analyzed using a 100× objective lens and white light. First, a planimetric area of 138 μm × 102 μm was scanned to generate a three-dimensional data point representation of the

surface. The lateral point spacing was 0.18 μm , and the published vertical resolution of the instrument is $<.005 \mu\text{m}$. Artifacts, such as dust particles, evident on resultant point clouds, were deleted prior to analysis, and surface models were leveled using Solarmap Universal software (Solarius, Inc.), version 3.1. The resulting point clouds were then analyzed using the Toothfrax and Sfrax scale-sensitive fractal analysis (SSFA) software packages (SurFract Corp). These packages do not require filling of missing data (only data present are used in analysis).

2.4 Scale-Sensitive Fractal Analysis

This study used the standard suite of SSFA texture variables: complexity ($Asfc$), scale of maximum complexity (Smc), heterogeneity ($HAsfc_9$, $HAsfc_{81}$), anisotropy ($epLsar$), and texture fill volume (Tfv). These attributes in aggregate offer a characterization of surface texture that often allows us to distinguish patterns by diet (see Scott et al., 2006 for a detailed description of each variable). $Asfc$ is measured as the slope of a plot of surface roughness over scale of observation. A surface that becomes progressively rougher at finer scales is considered complex. An example is a heavily pitted surface with both large and small features. Smc is the scale at which the change in roughness begins to taper off. A low Smc value follows from surfaces with many fine-scale features. $HAsfc$ is a measure of variation in $Asfc$ across a surface divided into cells of equal size, in this case 3×3 ($HAsfc_9$) and 9×9 ($HAsfc_{81}$). Surfaces that vary in complexity across the field of view have high $HAsfc$ values. Tfv is a measure of volume of small square cuboids (in this case 2 μm across) used to fill a surface divided by volume of larger ones (10 μm across). A surface with many deep features 2 - 10 μm in diameter has a high Tfv value. Finally, $epLsar$ represents directionality of surface texture. It is measured as variation in lengths of depth profiles sampled at different orientations across the surface. A microwear

surface with aligned striations has a higher *epLsar* value than one lacking features with preferred orientation.

2.5 Statistical analyses

Statistical analyses employed a general linear model. First, data were rank transformed for each variable prior to analysis to mitigate the effects of violation of parametric test assumptions (Conover and Iman, 1981). Multivariate Analysis of Variance tests were employed separately for diet, habitat, and substrate, and each was followed by ANOVA tests to find the sources of significant variation in the models. These could not be considered using a factorial model that assesses interactions between variables because of missing cells (e.g., there are no arboreal rodents in the desert). Both Tukey's honestly significant difference (HSD) and Fisher's least significant different (LSD) post-hoc tests were then used to identify sources of variation while balancing risks of Type I and Type II error (Cook and Farewell, 1996). Additional tests were run to assess effects of substrate for diet-habitat combinations with both arboreal and terrestrial representatives (rainforest-omnivores and woodland-herbivores).

3.1 Results

Descriptive statistics are presented in Tables 2 and 6. Analytic statistics are reported in Tables 3 through 5, and Table 7. Results showed significant variation among samples classified by diet, habitat, and substrate.

3.1.1 Diet

While there was significant variation by diet (see Table 3), the differences between omnivores, herbivores and frugivores, as designated for species in the literature (see Table 1), were minimal compared with those typical for molars of mammals with radically differing diets

(Donohue et al., 2013; Schubert et al., 2010; Scott, 2012; Scott et al., 2012). Still, omnivores did have significantly higher *epLsar* values on average than did herbivores. And omnivores had marginally higher average *HAsfc₈₁* values than herbivores, and especially frugivores. While the ANOVA result indicated variation in heterogeneity by diet, pairwise comparison tests were significant by Fisher's LSD but not Tukey's HSD tests and so we can consider these results "suggestive" or of marginal significance.

3.1.2 Habitat

There were more differences between groups divided by habitat (see Table 4). Rodents from savanna habitats had more complex microwear surfaces than those from either woodland or rainforest settings. Desert and savanna rodents had significantly lower average scale of maximum complexity than do woodland and rainforest individuals. Woodland rodents had less heterogeneity of complexity on average than either rainforest or desert individuals. When comparing desert and woodland species, results for *Asfc* and *HAsfc* are considered suggestive though of marginal significance given $p < 0.05$ for Fishers but not Tukey's test results.

3.1.3 Substrate

The rodents also varied in microwear texture by substrate (see Table 5). The arboreal species had less complex microwear textures on average, but more anisotropic ones and higher average scale of maximum complexity and texture fill volume. When the woodland-herbivore sample was considered separately, there was no significant substrate effect, but among rainforest-omnivores, the terrestrial sample had significantly higher *epLsar*, *Smc*, *Tfv*, and *HAsfc₉* values than did the arboreal one (Table 6).

4.1 Discussion

Results presented here show differences between samples grouped by diet, habitat, and substrate. It is clear that all three factors contribute to incisor microwear texture variation for the rodents considered in this study. The challenge is to parse these signals.

4.1.1 Diet

It was most difficult to separate the samples by diet. This is unsurprising because the focus here is on incisors, which are used in food acquisition and initial processing, but not mastication. Other studies have shown that molar microwear is more effective at separating rodent species by diet (Gomes Rodrigues et al., 2009; Nelson et al., 2005; Townsend and Croft, 2008). Rodents use their front and back teeth in different ways, and microwear on these tooth surfaces is expected to reflect different etiologies (Stefen, 2011). Nonetheless, incisor microwear surfaces of omnivores in this study were more anisotropic than those of herbivores and their textures were more heterogeneous than those of frugivores. Belmaker and Ungar (2010) likewise found that incisor microwear of folivorous and granivorous rodents differed by these variables, as well as by texture fill volume.

It is not surprising that omnivores have higher heterogeneity, as they likely require greater variation in how they use their incisors during ingestion than do rodents feeding solely on plant matter. Since the differences were not found between herbivores and frugivores, perhaps ingestion of invertebrates explains the differences in anisotropy and heterogeneity. Silcox and Teaford (2002) found that tenrecs and moles had microwear with parallel striations, presumably caused by consuming soil covered soft bodied invertebrates, which would be consistent with the link between anisotropy and invertebrate consumption, but it is important

to remember that Silcox and Teaford considered molars, not incisors, so results are not directly comparable.

The lack of many differences in incisor microwear attributable to diet may actually have more to do with the samples selected and diet characterizations than to limits of the technique itself. The subtle differences in diet within groups and overlap of diet between them pose substantive challenges. Further, when compared to the species most frequently utilized for microwear studies (ungulates, carnivorans, and primates), the diets of rodents typically receive less attention by researchers and are less well understood. Disparities in the methods used to assess diet, which have ranged from analyses of fecal materials to examination of stomach contents, and inconsistencies of how diet is reported, exacerbate the problem. Better control over food choice, and a focus on dietary specialists in future analyses, will hopefully lead to better discrimination.

4.1.3 Habitat

Incisor microwear texture patterns were better separated by habitat type. In pairwise comparisons, *Smc* was able to differentiate between all habitat categories except savanna from desert and woodland from rainforest. The pairwise comparisons for *Asfc* did not yield as many differences, but they did provide some. Again, neither savanna *versus* desert nor woodland *versus* rainforest comparisons yielded significant differences. These variables seem to be identifying habitat openness in a broad sense. Rodents from wetter, more closed settings also tend to have lower complexity and higher average scales of maximum complexity than those from more open habitats.

High *Asfc* values, as seen in the desert and savanna rodents, are typically associated with complex, pitted surfaces. It has been noted that exogenous grit is more prevalent in dry, open environs than in wet/closed ones (Jardine et al., 2012; Solounias and Semprebon, 2002; Stirton, 1947). Indeed, microwear pitting and gouging have been attributed to “dirty browsing” for bovids (Rivals and Semprebon, 2010, 2006; Semprebon and Rivals, 2010, 2007), and grit-laden foods have been suggested to produce high *Asfc* values by Williams (2015). This might also be true for rodent incisors, though the relationship does not seem to hold for molars, at least for those studied to date (Gomes Rodriguez et al. 2009, and Burgman et al., submitted).

Smc values were also higher on average for incisor surfaces of rodents from wet and closed habitats than for those from arid and open ones. Lower *Smc* values suggest more rough surfaces at a finer scale. This pattern could, in principle, relate in part to abrasive size, especially if grit particles present smaller, more angular surfaces for scoring enamel than do other abrasives, such as phytoliths (e.g., Ungar, 1994).

These results suggest that environmental grit may indeed play an important role in incisor microwear patterning. Habitat openness evidently contributes to at least some of the differences in *Asfc* and *Smc* values for incisors of individuals from xeric compared with mesic settings. It is also possible that intrinsic properties of foods in these different settings contribute to the variation, since different foods are available in different settings (e.g., there is more grass available in savannas than in rainforests). But a finer-scale analysis of diets in each environmental setting, including resource availabilities, phytolith loads, and food material properties, would be necessary to separate out the effects.

Groups are distinguished by heterogeneity of complexity too, though there is no evidence for a consistent directional habitat-related gradient in *HAsfc* values (rainforest and desert samples were both more heterogeneous than those from the woodland). The implication of this is not clear since heterogeneity also varied by diet.

4.1.4 Substrate

Substrate also had an effect on incisor microwear textures. Terrestrial rodents had higher *Asfc* values, but arboreal ones had higher *Smc*, *epLsar*, and *Tfv* values. The arboreal substrate group consisted of two species, woodland *Grammomys dolichurus* and rainforest *Hylomyscus stella*, while the terrestrial group included species from all habitat types, so substrate results are clearly not independent of habitat. Even though we were unable to assess interactions given empty cells, we were able to gain some control over effects of environment and diet by comparing arboreal and terrestrial specimens for woodland herbivores and rainforest omnivores (the only diet-habitat combinations with both arboreal and terrestrial individuals). Results showed no significant substrate effect for the woodland sample, but a strong effect for the rainforest specimens, with *epLsar*, *Smc*, *Tfv*, and *HAsfc9* higher for arboreal than terrestrial individuals.

The lack of a significant variation for *Asfc* for either the woodland-herbivore or rainforest-omnivore sample and the new significant difference in *HAsfc9* for the rainforest-omnivore sample when compared with results from the overall model may in part reflect interactions among factors in the latter case. The differences among substrates in *epLsar*, *Smc* and *Tfv* for the rainforest-omnivore combination, on the other hand, are consistent with results

for the overall model. These findings indicate that there is likely a substrate effect (e.g., more small features on or near the ground), which might be consistent with a grit difference.

The few other studies comparing substrate effects on rodent microwear have focused on molars and used different analytical techniques, so are not directly comparable with the results presented here. Nevertheless, differences by substrate have been identified in the past (Nelson et al., 2005; Townsend and Croft, 2008). It is therefore likely that further study will help us better understand this effect on incisor microwear textures.

5.1 Conclusions

The study presented here suggests that rodent incisor microwear pattern differences result from a combination of factors related to habitat, substrate, and diet. While much work remains to be done, it seems likely that these factors can be teased apart, and provide important information on the ecology of fossil species. The habitat effect was strongest, affirming predictions that rodent incisor microwear signature reflects environment. While it is unclear whether this relates to grit load or food availability in different habits, it is evident that rodent incisor microwear texture holds the potential to be a valuable addition to the slate of proxies available for paleoenvironmental reconstruction.

The fact that there are fewer associations between diet and rodent incisor microwear texture pattern than typical for molar studies underscores the importance of considering both tooth types, as they can provide different yet complementary information. Rodent incisor microwear seems to be especially valuable for separating more open habitats (desert and savanna) from more closed ones (woodland and rainforest). Nevertheless, more work on more groups of rodents with better control over habitat, substrate use, diet, and other niche

attributes, such as temperature (Legendre et al., 2005; Montuire et al., 1997) are needed to determine the limits of rodent incisor microwear as a proxy for each of these effects.

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706

Figure

Figure 1

Table

Table 1

Species	Habitat	Diet	Substrate	<i>n</i>
<i>Acomys cahirinus</i>	Desert	Omnivore _c	Terrestrial _a	29
<i>Aethomys chrysophilus</i>	Savanna	Herbivore _c	Terrestrial _{a,d}	29
<i>Micaelamys namaquensis</i>	Savanna	Herbivore _a	Terrestrial _a	18
<i>Grammomys dolichurus</i>	Woodland	Herbivore _b	Arboreal _{a,b,d}	25
<i>Hybomys univittatus</i>	Rainforest	Frugivore _c	Terrestrial _{a,}	26
<i>Hylomyscus stella</i>	Rainforest	Omnivore _c	Arboreal _{a,}	30
<i>Mastomys natalensis</i>	Rainforest	Omnivore _{c,d}	Terrestrial _{a,d}	22
<i>Mastomys natalensis</i>	Savanna	Omnivore _{c,d}	Terrestrial _{a,d}	26
<i>Mastomys natalensis</i>	Woodland	Omnivore _{c,d}	Terrestrial _{a,d}	26
<i>Meriones crassus</i>	Desert	Herbivore _c	Terrestrial _a	9
<i>Meriones libyacus</i>	Desert	Herbivore _c	Terrestrial _a	17
<i>Mus minutoides</i>	Savanna	Omnivore _{c,d}	Terrestrial _{a,c,d}	29
<i>Mus triton</i>	Woodland	Omnivore _a	Terrestrial _a	19
<i>Parotomys brantsii</i>	Desert	Herbivore _{c,d}	Terrestrial _a	29
<i>Praomys jacksoni</i>	Rainforest	Herbivore _c	Terrestrial _a	40
<i>Praomys jacksoni</i>	Woodland	Herbivore _c	Terrestrial _a	30
<i>Rhabdomys pumilio</i>	Desert	Herbivore _c	Terrestrial _a	26

_aHappold, 2013; _bKingdon, 1984; _cKingdon,1997; _dSkinner and Chimimba, 2005

Table 2

		<i>Asfc</i>	<i>Smc</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>	<i>epLsar</i>	<i>Tfv</i>
Diet							
omnivore	<i>n</i> =181						
	median	1.052	1.070	0.557	0.813	0.011	15,452.64
	mean	1.189	231.266	0.745	1.028	0.010	15,574.51
	s.d.	1.712	293.579	0.654	0.693	0.002	3,768.579
herbivore	<i>n</i> =223						
	median	1.217	0.417	0.488	0.723	0.010	15,474.14
	mean	1.298	154.697	0.686	0.900	0.010	15,529.79
	s.d.	1.365	264.375	0.579	0.537	0.001	3,071.633
frugivore	<i>n</i> =26						
	median	1.226	1.351	0.458	0.697	0.010	15,227.75
	mean	1.426	170.59	0.492	0.718	0.010	15,632.45
	s.d.	0.865	268.12	0.238	0.250	0.001	3,245.956
Habitat							
desert	<i>n</i> =110						
	median	1.197	0.268	0.547	0.822	0.011	15,587.59
	mean	1.292	139.850	0.722	0.950	0.011	15,706.97
	s.d.	1.475	257.471	0.572	0.502	0.002	3,204.140
savanna	<i>n</i> =102						
	median	1.349	0.267	0.519	0.697	0.011	16,028.01
	mean	1.666	130.595	0.682	0.985	0.010	16,237.36
	s.d.	1.443	244.003	0.505	0.686	0.002	3,827.777
woodland	<i>n</i> =100						
	median	0.949	1.355	0.456	0.693	0.010	14,807.96
	mean	1.127	243.794	0.572	0.801	0.010	14,967.12
	s.d.	1.379	295.367	0.497	0.447	0.002	3,086.655
rainforest	<i>n</i> =118						
	median	1.010	8.643	0.547	0.798	0.011	15,442.43
	mean	0.991	234.817	0.801	1.019	0.010	15,321.04
	s.d.	1.600	297.921	0.749	0.700	0.002	3,309.610
Substrate							
Terrestrial	<i>n</i> =375						
	median	1.204	0.422	0.505	0.735	0.010	15,344.92
	mean	1.344	166.512	0.670	0.934	0.010	15,425.76
	s.d.	1.397	269.280	0.527	0.596	0.002	3,432.713
Arboreal	<i>n</i> =55						
	median	0.847	413.531	0.616	0.810	0.011	16,741.17
	mean	0.686	333.635	0.900	1.003	0.011	16,434.77
	s.d.	1.979	303.148	0.943	0.636	0.001	2,915.002

Table 3

A. MANOVA results

	Wilks's λ	Pillai Trace	Hotelling's T^2
<i>F</i>	1.921	1.914	1.927
<i>df</i>	12, 844	12, 846	12, 842
<i>p</i> -value	0.029	0.029	0.028

B. ANOVA results

	<i>Asfc</i>	<i>Smc</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>	<i>epLsar</i>	<i>Tfv</i>
<i>F</i>	0.621	2.356	2.801	3.550	6.263	0.033
<i>df</i>	2, 427	2, 427	2, 427	2, 427	2, 427	2, 427
<i>p</i> -value	0.538	0.096	0.062	0.03	0.002	0.968

C. Paired Comparisons

	<i>HAsfc₈₁</i>	<i>epLsar</i>
frugivore × herbivore	-33.471	11.685
frugivore × omnivore	-57.993**	-31.62
herbivore × omnivore	-24.522*	-43.305*

* result was significant for Fisher's LSD test only

** result was significant for both Tukey's HSD and Fisher's LSD test

Table 4

A. MANOVA results

	Wilks's λ	Pillai Trace	Hotelling's T^2
<i>F</i>	4.076	4.014	4.127
<i>df</i>	18, 1,191	18, 1,269	18, 1,259
<i>p</i> -value	0.00	0.00	0.00

B. ANOVA results

	<i>Asfc</i>	<i>Smc</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>	<i>epLsar</i>	<i>Tfv</i>
<i>F</i>	6.442	11.05	3.366	3.276	1.692	2.416
<i>df</i>	3, 426	3, 426	3, 426	3, 426	3, 426	3, 426
<i>p</i> -value	0.000	0.00	0.019	0.021	0.168	0.066

C. Paired Comparisons

	<i>Asfc</i>	<i>Smc</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>
desert × rainforest	27.674	-63.675**	-6.164	4.308
desert × savanna	-32.662	10.359	14.533	25.153
desert × woodland	33.731*	-58.332**	43.307*	47.403**
rainforest × savanna	-60.336**	74.034**	20.697	20.845
rainforest × woodland	6.057	5.343	49.472**	43.094**
savanna × woodland	66.393**	-68.691**	28.774	22.250

* result was significant for Fisher's LSD test only

** result was significant for both Tukey's HSD and Fisher's LSD test

Table 5

A. MANOVA results			
	Wilks's λ	Pillai Trace	Hotelling's T^2
F	5.429	5.429	5.429
df	6, 423	6, 423	6, 423
p -value	0.00	0.00	0.00

B. ANOVA results						
	$Asfc$	Smc	$HAsfc_9$	$HAsfc_{81}$	$epLsar$	Tfv
F	5.127	22.631	1.781	0.459	14.822	4.396
df	1, 428	1, 428	1, 428	1, 428	1, 428	1, 428
p -value	0.024	0.00	0.183	0.498	0.00	0.037

Table 6

		<i>Asfc</i>	<i>Smc</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>	<i>epLsar</i>	<i>Tfv</i>
Rainforest omnivores							
terrestrial	<i>n</i> =22						
	median	0.713	3.547	0.455	0.675	0.008	13796.5
	mean	1.233	209.396	0.644	1.053	0.009	13474.6
	s.d.	1.271	295.401	0.595	1.042	0.002	4203.46
Arboreal	<i>n</i> =30						
	median	0.835	649.555	0.836	0.835	0.012	16883.4
	mean	0.327	438.036	1.165	0.327	0.012	16236.7
	s.d.	2.351	284.232	1.144	2.351	0.001	2998.46
Woodland herbivores							
terrestrial	<i>n</i> =30						
	median	0.918	1.357	0.467	0.684	0.01	14727.6
	mean	1.057	258.237	0.647	0.893	0.01	14834.5
	s.d.	1.36	311.474	0.737	0.648	0.001	2608.17
arboreal	<i>n</i> =25						
	median	1.191	1.066	0.439	0.673	0.01	16671.3
	mean	1.115	208.354	0.582	0.736	0.01	16672.5
	s.d.	1.334	281.388	0.477	0.391	0.001	2854.3

Table 7

A. MANOVA results

Rainforest omnivores

	Wilks's λ	Pillai Trace	Hotelling's T^2
<i>F</i>	7.367	7.367	7.367
<i>df</i>	6, 45	6, 45	6, 45
<i>p</i> -value	0	0	0

Woodland herbivores

	Wilks's λ	Pillai Trace	Hotelling's T^2
<i>F</i>	1.577	1.577	1.577
<i>df</i>	6, 48	6, 48	6, 48
<i>p</i> -value	0.175	0.175	0.175

B. ANOVA

	<i>Asfc</i>	<i>Smc</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>	<i>epLsar</i>	<i>Tfv</i>
<i>F</i>	0.69	8.236	6.869	3.453	39.973	5.363
<i>df</i>	1, 50	1, 50	1, 50	1, 50	1, 50	1, 50
<i>p</i> -value	0.41	0.006	0.012	0.069	0	0.025

Figure Legend

Figure 1. Photosimulation of microwear surfaces of *Mastomys natalensis* from savanna (upper left), woodland (upper right), and rainforest (lower left) habitats and *Rhabdomys pumilio* from a desert habitat (lower right). Images were generated from point cloud data and represent a planimetric area of $138\ \mu\text{m} \times 102\ \mu\text{m}$.

Table legends

Table 1. Summary of sampled species with habitat of collection and diet and substrate information as reported in the literature. Additional information on each species is presented in the supplemental material.

Table 1. Descriptive statistics for *Asfc*, complexity; *epLsar*, anisotropy; *HAsfc₉* and *HAsfc₈₁*, heterogeneity of complexity (3 x 3 and 9 x 9 respectively); *Smc*, scale of maximum complexity; *Tfv*, textural fill volume.

Table 2. Analytical statistics for diet.

Table 3. Analytical statistics for habitat.

Table 4. Analytical statistics for substrate.

Table 5. Descriptive statistics for substrate (rainforest omnivores and woodland herbivores).

Table 6. Analytical statistics for substrate (rainforest omnivores and woodland herbivores).