5-2015

Comparison of Microwear on Rodent Molars from Differing Species and a Wide Range of Environments

Mikko Joiner
University of Arkansas, Fayetteville

Comparison of Microwear on Rodent Molars from Differing Species and a Wide Range of Environments

An Honors Thesis submitted in partial fulfillment of the requirements of Honors Studies in Biology

By

Mikiko Joiner

2015

Biology
J. William Fulbright College of Arts and Sciences
The University of Arkansas

Acknowledgements

Thank you to Dr. Ungar for helping me through this process and always answering any questions I had, which were many. Thank you also to the people in lab such as Sarah Livengood, Jenny Burgman, and Anna Ragni who taught me how to cast, use the confocal microscope, and helped me any time I experienced problems. Thank you also to Dr. Delezene for help with data analysis and for advice on writing this paper.

Abstract

Dental microwear analysis is a very useful tool when trying to infer the diet of a particular organism. By studying the use-wear scars left on the enamel of the tooth due to eaten objects, one can infer the diet of the organism because certain types of food leave certain types of scars. For example, the consumption of tree parts produces pits, while the consumption of grasses produces striated scratches (Ungar et al., 2007). Thus, based on the type of microwear, the diet of the organism in question can be deduced, which indicates the type of environment that it lives in. In this study, rodents of three different species (*M. natalensis, M. libycus,* and *P. jacksoni*) from differing environments were examined. Scale-sensitive fractal analysis was used to compare the microwear of these three species in order to determine if there were any differences in microwear, and if there were, the source of these differences were examined. This study showed that the central tendencies of the microwear did not differ significantly, but the variation in dispersion of microwear did.

Table of Contents

Introduction

Dental microwear

Dental microwear is the study of the microscopic use-wear scars left on the enamel of the tooth. Over the past three decades, dental microwear has been used to characterize the feeding habits of extinct animals and has proven useful in reconstructing the environments of those extinct animals (Merceron et al., 2010). Previous methods included scanning electron microscopy (SEM), which did not provide a true representation of teeth surfaces in three dimensions. Measurement of features using this method proved to be time consuming, subjective, and susceptible to interobserver error (Ungar et al., 2003). Thus, a more accurate and useful method known as dental microwear texture analysis (DMTA) was developed. This method provides three-dimensional coordinates representing surfaces at resolutions equivalent to that of SEM studies, and with this method, much of the errors common in previous studies were reduced (Ungar et al., 2003). Using the data collected from DMTA, researchers were able to expand their knowledge on what the environment was like for other extinct animals in the same deposits, including our ancestors, the early hominins. Because DMTA is applicable to a wide range of species, it has proven to be a useful tool in the paleoanthropological world (Ungar et al., 2003).

Diet is recognized as an important factor in determining underlying behavioral and ecological differences among living animals (Ungar et al., 2007). What an organism eats throughout its lifetime is apparent when examining the microwear. For instance, animals that browse on tree parts tend to have more pitted surfaces, whereas those that graze on grasses have more striated ones (Ungar et al., 2007). Also, the amount of grit or

dust in a given environment has a dramatic effect on tooth wear, which should also help to understand the amount of vegetation cover (Ungar et al., 1995). Therefore, using the knowledge about a particular organism's diet allows researchers to reconstruct the environment that the organism resided in. Rodents are particularly useful to study, because they are abundant, found in many different environments, and found in large numbers at fossil sites. This shows that they have and do, even to this day, live in close proximity to humans. In this study, the microwear of three rodent species (*M. natalensis, M. libycus,* and *P. jacksoni*) from varying environments were compared. Their general diets and preferred habitats are known. This study attempts to determine whether environment or the differences in diet because they are different species or both has a major impact on the type of microwear found on their teeth based on their diet. This study aims to develop a baseline of microwear related to specific environments that can be used to compare with fossil rodents found in early hominin sites. Once the patterns in the fossil rodents are documented, they can be compared with the patterns in the living ones, and then the environments in which the extinct ones lived can be reconstructed, and by extension, the habitats of our own ancestors inferred.

Environments/Species

Three terrestrial rodent species, *M. natalensis*, *M. libycus*, and *P. jacksoni*, were chosen because they are from a wide range of environments. Both *P. jacksoni* and *M. natalensis* live in moist environments, such as the rainforest or the woodlands, with some living in the savannah. *M. libycus,* however, live in drier environments, such as the desert. In this study, the *M. libycus* species were all from the desert, *P. jacksoni* were

divided between woodland and rainforest, and *M. natalensis* were divided between savannah and rainforest. *M. natalensis* rodents, more commonly known as the Natal multimammate mouse, typically are omnivorous. Under field conditions, they eat mainly seeds of grass and other plants, dried acacia pods, or the pulpy exterior of wild fruits. As populations increase and food supplies dwindle, they become cannibals (Skinner & Chimimba, 2005). *P. jacksoni* are also omnivores and eat invertebrates, fruits, seeds, and leaves. *M. libycus* eat seeds, stems, roots, and bulbs (Kingdon, 2004; Kingdon, 1974). Overall, the diets of each of these three species are very similar with only one species not being an omnivore.

Materials and Methods

Sample Collection

Molds of the specimens (n=31) were obtained by Dr. Peter Ungar and Salvatore Caporale from the Smithsonian Museum of Natural History. Before molding, the specimens were cleaned with cotton swabs soaked with acetone and ethyl alcohol. Molds of the fossil teeth were taken with a hydrophobic polyvinylsiloxane silicone (Coltène President's Jet, regular body) impression material (Ungar, 1996). This material reproduces features with resolutions to a fraction of a micron (Beynon, 1987; Teaford & Oyen, 1986*b*). Once the molds were brought back to lab, high-resolution epoxy casts were created using the protocol described in previous papers (Grine and Kay, 1987). Then, pouring of the replicas involved using Epotek 301 resin and hardener (Ungar, 1996).

The rodents are from different areas in Africa. The *P. jacksoni* specimens from the rainforest (n=4) are from Irangi, Kenya, and the woodland species (n=6) are from Kaimosi, Kenya. The *M. natalensis* specimens that live in the rainforest (n=5) are from the Democratic Republic of the Congo, and the savanna specimens (n=4) are from South Africa. *M. libycus* species (n=10) are from the deserts of Africa.

Surface Data Collection

A Sensofar Plμ NEOX scanning confocal profiler (Solarius Development Inc., Sunnyvale, CA) was used to scan the lower second molar with a 150x objective. Generally, the distal, buccal cusp on the tooth was scanned, unless there were problems gathering images there. Problems included lack of microwear, unclear molds, or surfaces that were too steep for images to be taken. If there were problems, other cusps on the second molar were then examined and other molars after that. Three-dimensional point clouds were produced for each specimen using a field of view of 84.88 x 63.63μm^2. Each had a lateral spacing (x,y) 0.13μm and a vertical resolution of <1 mm. After the scanning, each scan was then edited in Sensomap software following standard procedures (Ungar et al., 2003; Scott et al., 2005; Scott et al., 2006; Ungar and Scott, 2009). Any identifiable defects were removed by using the "retouch surface points" feature and non-measured points were then filled in using the "fill non-measured points" feature in Sensomap. The same feature was utilized when generating the ISO data.

Data Analysis

Scans of the tooth surface were analyzed using scale-sensitive fractal analysis programs known as Toothfrax and Sfrax (Surfract Corp., Worchester, MA). These

programs allow for the measurement and calculation of the complexity, anisotropy, scale of maximum complexity, textural fill volume, and surface texture heterogeneity of the specimen being examined. Observer error is reduced through the use of these programs, and more accurate results are generated in comparison to older methods such as scanning electron microscopy. These variables have been shown to be relevant to microwear analysis (Ungar et al. 2003; Scott et al., 2005, 2006).

The scale sensitive fractal analysis variables used in this study are Asfc, Smc, Tfv, Lsar, and HAsfc. Asfc (Area-scale fractal complexity) is a measure of complexity and is measured by the variation in the roughness of the enamel surface when measured at different scales. When pits and scratches on the tooth's surface overlap and have differing sizes, the Asfc measurement increases (Ungar et al., 2007). Smc (Scale of maximum complexity) is the steepest part of the curve used to measure Asfc. This is a measure of features size, and thus a larger Smc is indicative of less wear at fine scales and more wear at course scales. Tfv (Textural fill volume) is the summed volumes of square cuboids of a given scale that fills a surface (Ungar et al., 2007). A surface with a high Tfv would be dominated by moderate-sized deep features. EpLsar (Length-scale anistotropy) is a measurement of the directionality of the wear on the surface. It is measured via vectors and is the length of the mean vector. Surfaces that have scratches running in the same direction have a higher epLsar value, which is characteristic of animals that feed on tough objects (Pontzer et al., 2011). Lastly, HAsfc (heterogeneity) is the variation in complexity across a surface (Pontzer et al., 2011).

ISO parameters were also utilized to analyze the data. They describe the basic geometric properties of surface textures (Calandra et al., 2012). There are thirty

parameters total that can be analyzed, but the ones used in this study were Sdr, Str, and Sv. Sdr is the developed interfacial ratio, which tells how much surface area is added by the texture of the surface. Str is the texture aspect ratio used to identify the uniformity of texture. Sv is the maximum pit height, the depth between the mean plane and the deepest valley (Cohen, 2004; Shulz et al., 2013).

Statistical Analysis

The statistics in this study were generated using SYSTAT software. A multivariate analysis of variance model (MANOVA) was utilized for the variables generated in Toothfrax and Sfrax. The raw data utilized are in Appendix I. After the central tendencies were analyzed, variance tests were performed. Two variance tests were used to analyze the data, Bartlett's test and Levene's test. These are two standard measures of equality of sample variances (Zar, 1984).

Results

Scale Sensitive Fractal Analysis

When examining the data collected from Toothfrax and Sfrax variables, the central tendencies in their microwear did not differ in either species or environment, as shown in Table 1. Table 2 shows that there are, however, significant differences in the dispersion of microwear according to taxon and environment. The graphs below show the significant variation within each category of Asfc, Smc, Tfv, and HAsfc9x9 by either environment or taxon. For Asfc, significant variation was found with Bartlett's test in both environment and taxon. For Smc, both the environment and taxon showed

significant variation with Levene's test. Then, for Tfv, significant variation was found in environments. For HAsfc9x9, significant variation in dispersion was found between taxon. After the equality of several variances tests were performed, pairwise two-sample variance tests were performed on those variables that showed significant variation among environments or taxa in order to determine the sources of significant variation (i.e. which pairs of environments or taxa varied significantly from one another). The results of these tests showed that significant variation occurred between the either *M. natalensis* or *P. jacksoni* with *M. libycus*. When comparing by environments, the most variation occurred between organisms from contrasting environments, as shown in Table 3 and 4.

MANOVAs based on Ranked data

Multivariate Test Statistics- based on species				
Statistic	Value	F-ratio	df	p-value
Wilks's Lambda	0.635	0.976	12, 46	0.485
Pillai Trace	0.375	0.924	12, 48	0.531
Hotelling-Lawley Trace	0.558	1.022	12, 44	0.446
Multivariate Test Statistics- based on environment				
Statistic	Value	F-ratio	df	p-value
Wilks's Lambda	0.55	0.819	18, 62	0.671
Pillai Trace	0.521	0.841	18, 72	0.647
Hotelling-Lawley Trace	0.692	0.794	18, 62	0.699

Table 1: Multivariate Test Statistics

Variance test results							
	Test	Asfc	epLsar	Smc	Tfv	HAsfc 3x3	HAsfc9x9
Taxon	Bartlett	**8.484***	0.308	2.717	4.698	1.197	**7.926***
	Levene	0.615	0.98	**4.49***	1.826	0.156	0.4
Environment	Bartlett	**10.843***	0.87	6.454	**8.311***	0.894	5.669
	Levene	0.548	1.003	**3.621***	1.955	0.136	0.215
*p < 0.05							

Table 2: Equality of Several Variances

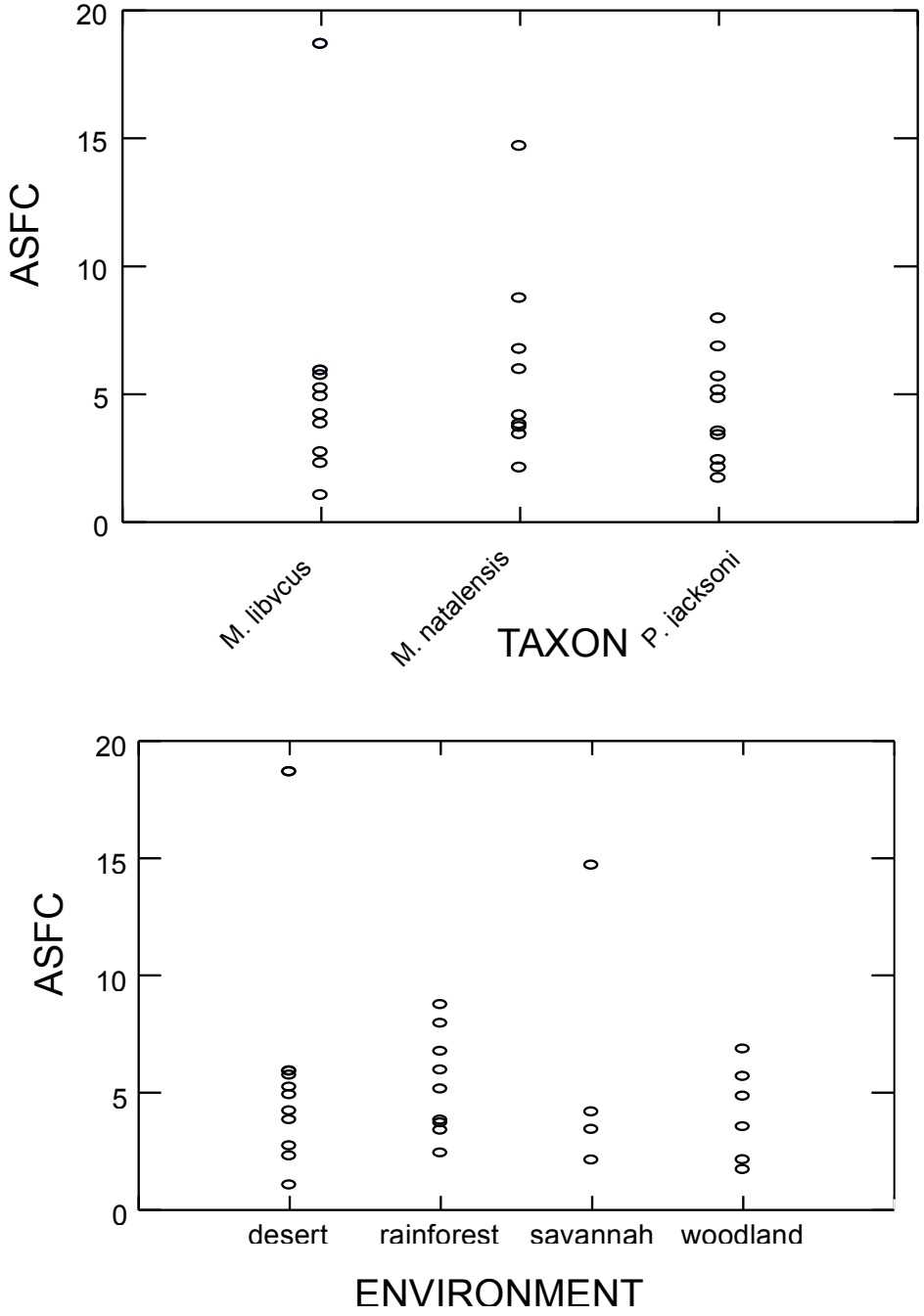


Figure 1: Asfc variation by taxon and environment

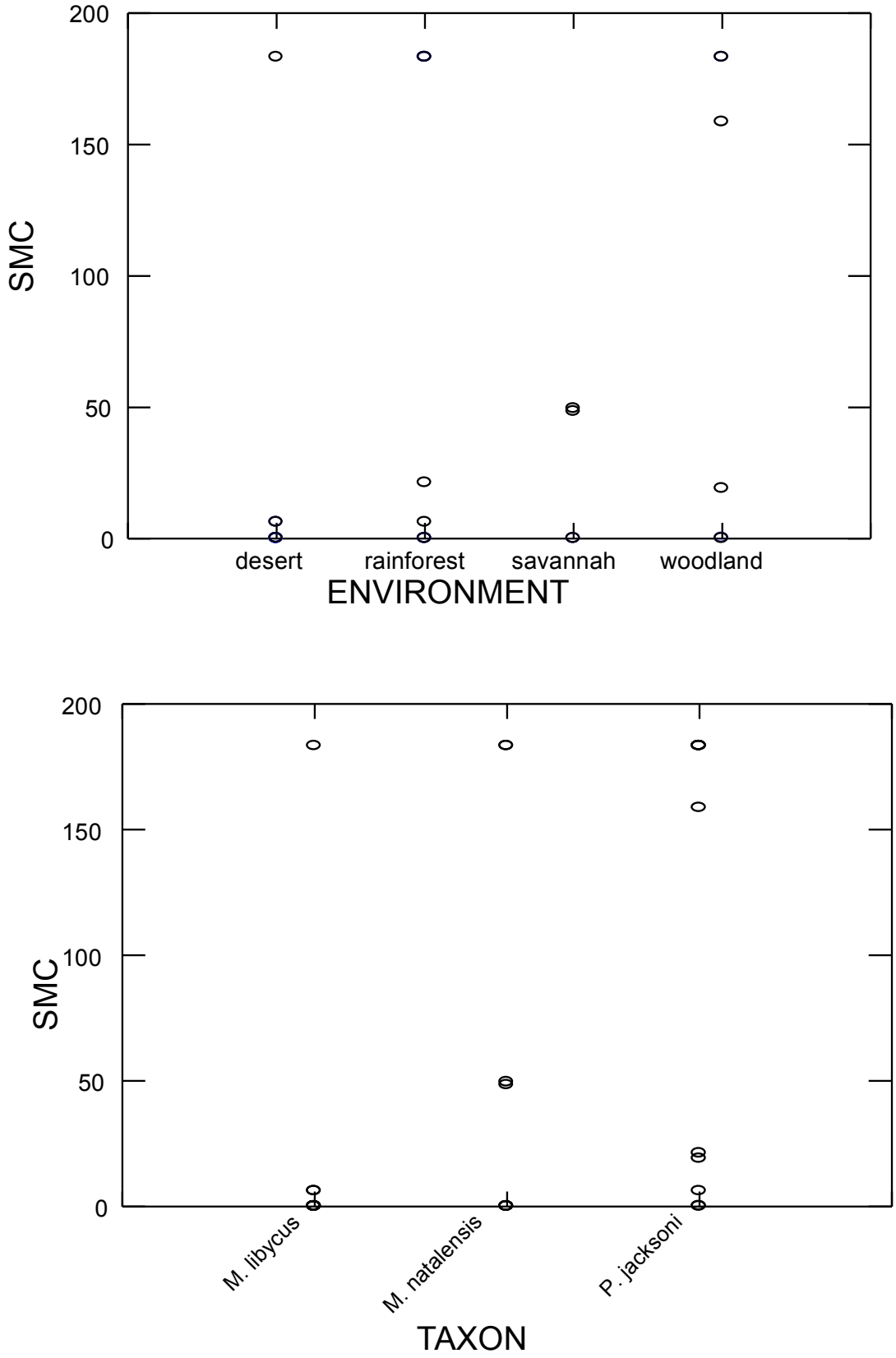


Figure 2: Smc Variation by environment and taxon

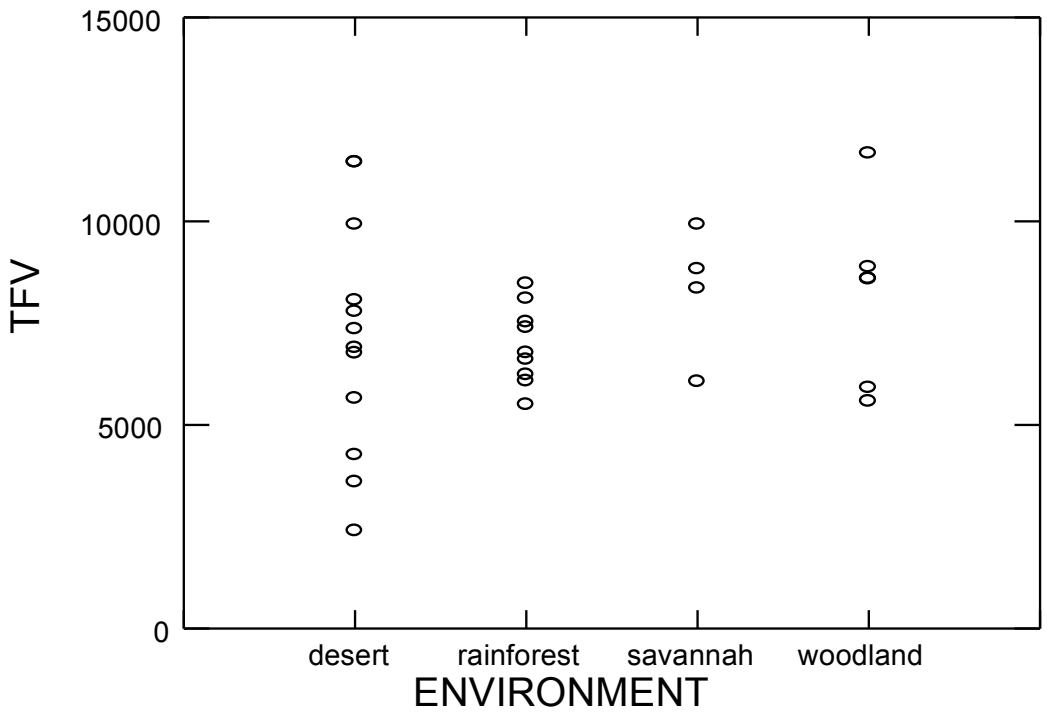


Figure 3: Tfv variation by environment

Pairwise two-sample variance test			
Environment	Asfc	Smc	Tfv
Desert vs. Savannah	1.020	0.241	0.220
Desert vs. Woodland	**1.267***	0.320	0.256
Savanna vs. Woodland	**8.157***	0.092	0.068
Desert vs. Rainforest	**7.171***	0.314	**8.704***
Rainforest vs. Savanna	**0.142***	11.050	0.364
Rainforest vs. Woodland	1.160	1.018	**0.193***
*p<0.05			

Table 3: Pairwise two-sample variance test -Environment

Pairwise two-sample variance test			
Taxa	Asfc	Smc	HAsfc9x9
M. natalensis vs. P. jacksoni	3.416	0.746	0.235
M. libycus vs. P. jacksoni	**7.871***	0.345	1.961
M. libycus vs. M. natalensis	2.304	0.462	**8.349***
*P<0.05			

Table 4: Pairwise two-sample variance test - Taxa

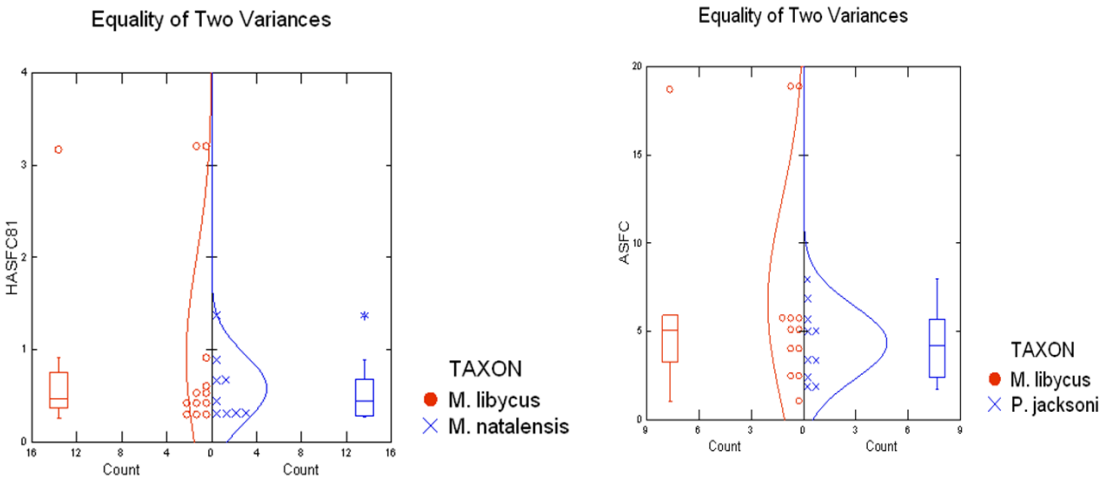


Figure 4: Equality of two variances by HAsfc9x9 and Asfc

ISO Parameters

ISO parameters were also utilized to characterize the nature of the microwear found on the specimen. First the equality of several variances was measured, and then the Pairwise two-sample variance tests were performed with each variable based on either environment or the taxon. The variables studied were STR, SDR, and SV. SDR and SV were found to have the most variation. . Table 5 shows that the variation between SDR and SV occur more in contrasting environments and Table 6 shows that the variation occurs in either *M. natalensis* or *P. jacksoni* with *M. libycus*.

Equality of Several Variances				
Category	Test	STR	SDR	SV
Taxon	Bartlett	0.445	**15.742***	**46.609***
	Levene	0.268	1.516	3.081
Environment	Bartlett	1.304	**19.445***	**57.624***
	Levene	0.439	2.184	**10.798***
*p<0.05				

Table 5: Equality of Several Variances

Pairwise two-sample variance test		
Environment	SDR	SV
Desert vs. rainforest	**0.194***	**5.539***
Desert vs. Savanna	**0.048***	7.663
Desert vs. Woodland	**0.039***	**0.020***
Rainforest vs. Woodland	**0.199***	**0.004***
Rainforest vs. Savanna	0.247	1.384
Savanna vs. Woodland	0.805	**0.003***
*p<0.05		

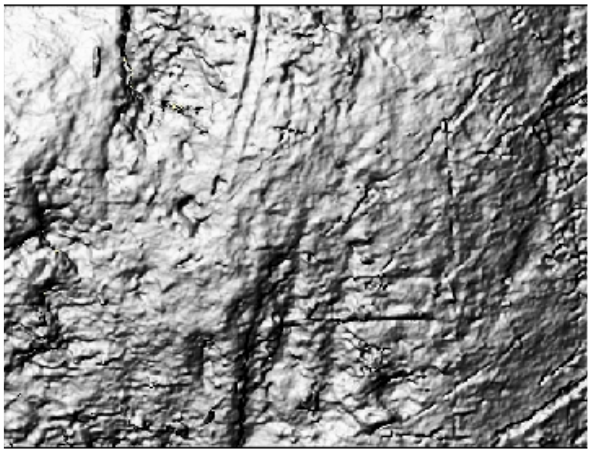
Table 6: Pairwise two-sample variance test - Environment

Pairwise two-sample variance test		
Taxon	SDR	SV
M. libycus vs. *M. natalensis*	**0.085***	**6.097***
M. natalensis vs. *P. jacksoni*	0.717	**0.005***
M. libycus vs. *P. jacksoni*	**0.061***	**0.027***
*P<0.05		

Table 7: Pairwise two-sample variance tests - Taxa

a.)

b.)



c.)

Figure 5: Examples of microwear on a) *M. natalensis*, b) *M. libycus*, and c) *P. jacksoni*

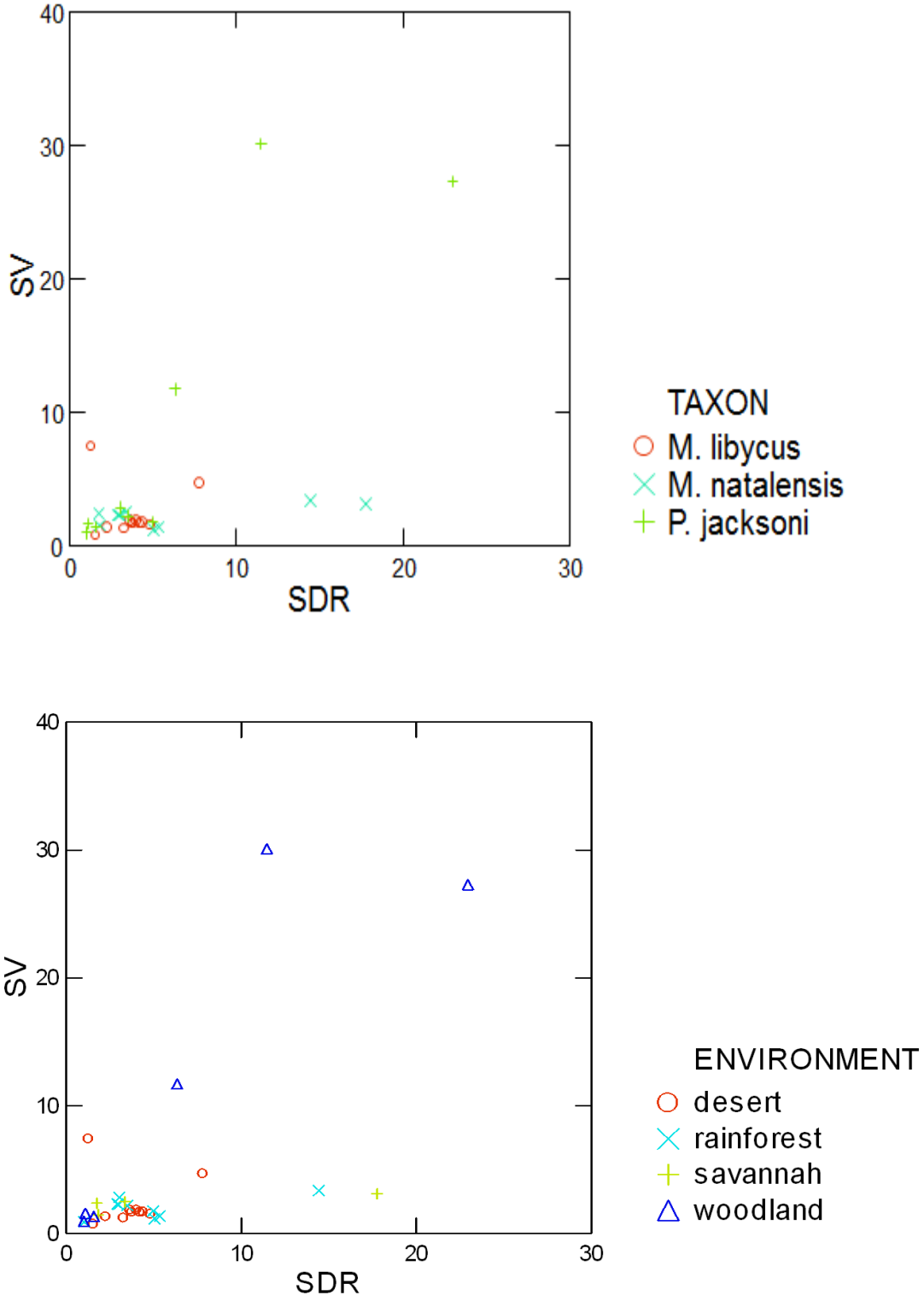


Figure 6: SDR vs. SV by Taxon and Environment

Discussion

Tooth/Sfrax

The fact that central tendencies did not differ was particularly interesting because this result was not expected; more differences were expected. However, looking at the scans in Figure 5, not many differences among species were visible to the casual observer. Any differences would have been in the specific qualities of the features measured, and even there, there were no significant differences. Significant variation in dispersion may be due to the fact that this particular sample size was small. A smaller sample size increases the possibility of more variation within a category, such as environment or taxa. However, after the pair wise two-sample tests were performed, the results showed that the most variation occurred between the two omnivorous species and the herbivorous species. That was to be expected, since the omnivorous species have a different component in their diet that would produce different microwear. With regard to environments, the most variation occurred between species from the most contrasting environments, for example, desert vs. rainforest. These differences were also expected, since those from contrasting environments are more likely to have different microwear present on their teeth. The reason why central tendencies did not differ may be due to the fact that overall, these rodents' diets are very similar; all three species analyzed generally eat fruits, seeds, and leaves. The variation in dispersion may be caused by changing environments and how volatile the weather may be in that particular environment or by the availability of food at that time of collection of species. For example, the variation in Asfc and Smc may be due to the environments' influence on the foods that these rodents

eat. *M. libycus* may eat seeds that are covered with sand as opposed to *P. jacksoni* which may eat seeds covered in dirt. Although both species eat seeds, the physical nature of the sand or dirt that covers them may have a significant impact on the microwear found on the teeth.

ISO parameters

Central tendencies were similar to the results from Tooth/Sfrax. However, significant variation in Sdr and Sv dispersions were apparent. Thus, those two variables were more closely examined. The results suggest that the variation in Sdr and Sv may stem from the environmental influence on the foods that these rodents eat, similar to the results from Toothfrax and Sfrax. The variation in dispersion among species may be attributed to one of the species not being an omnivore, an extra component of diet the other two species have. This is also consistent with the data from Tooth/Sfrax.

Overall, the results suggest that there is a strong environmental component to the microwear found on their teeth that may prove useful in reconstructing the habitats of the rodents, other animals found with them, and our ancestors.

Conclusions and further directions

The purpose of this study was to see if there were major differences in microwear among specimens of differing species of rodents from differing environments. This study found that the central tendencies of the microwear did not differ, but the variation in dispersion within species and environments did significantly differ. This information will be expounded upon later with studies that will include a larger sample size. With a larger

sample size, the central tendencies may differ due to evidence showing that microwear does differ according to diets of animals, as shown in previous papers. This study is the first of many to determine a baseline for microwear in rodents in order to recreate the environment that our ancestors lived in.

References

Beynon, A. D. (1987). Replication technique for studying microstructure of fossil enamel. Scan. Microsc. 1, 663–669.

Calandra I, Schulz E, Pinnow M, Krohn S, Kaiser TM. 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. J Hum Evol 63(1):85-98.

Cohen DK. 2004. Glossary of surface texture parameters. Michigan Metrology, LLC .

Evans AR, Wilson GP, Fortelius M, Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445(7123):78-81.

Grine FE, Ungar PS, Teaford MF. 2002. Error rates in dental microwear quantification using scanning electron microscopy. Scanning 24(3):144-53.

Grine FE and Kay RF. 1988. Early hominid diets from quantitative image analysis of dental microwear. Nature 333(6175):765-8.

Kingdon J. 2004. The kingdon pocket guide to african mammals. Princeton, NJ: Princeton University Press.

Kingdon J. 1974. Soft-furred rats, praomys rats (praomys(praomys)). In: East african mammals. New York, New York: Academic Press, INC. 590 p.

Merceron G, Escarguel G, Angibault J, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? Plos One 5(3):e9542.

Pontzer H, Scott JR, Lordkipanidze D, Ungar PS. 2011. Dental microwear texture analysis and diet in the dmanisi hominins. J Hum Evol 61(6):683-7.

Ren Y, Amin A, Malmstrom H. 2009. Effects of tooth whitening and orange juice on surface properties of dental enamel. J Dent 37(6):424-31.

Schubert BW, Ungar PS, DeSantis LRG. 2010. Carnassial microwear and dietary behaviour in large carnivorans. J Zool 280(3):257-63.

Schulz E, Piotrowski V, Clauss M, Mau M, Merceron G, Kaiser TM. 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. Plos One 8(2):e56167.

Scott RS, Ungar PS, Bergstrom TS, Brown CA, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: Technical considerations. J Hum Evol 51(4):339-49.

Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436(7051):693-5.

Skinner JD and Chimimba CT. 2005. Natal multimammate mouse. In: The mammals of the southern african subregion. van der Horst D, editor. 3rd ed. Cambridge University Press. 149 p.

Ungar PS, Teaford MF, Glander KE, Pastor RF. 1995. Dust accumulation in the canopy: A potential cause of dental microwear in primates. Am J Phys Anthropol 97(2):93-9.

Ungar PS. 1996. Dental microwear of european miocene catarrhines: Evidence for diets and tooth use. J Hum Evol 31(4):335-66.

Ungar PS, Brown CA, Bergstrom TS, Walker A. 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning 25(4):185-93.

Ungar, P.S., Scott, R.S., Scott, J.R., and Teaford, M.F., 2007. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D. and Nelson, G.C. (Eds.), Dental Anthropology. Cambridge University Press, Cambrige.

Zar J. H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs.

Appendix I- Raw Data

Taxon	Bag	Specimen	Environment	Asfc1om	epLsar1.80µm	Tfv (µm³)	LineStart	3x3HAsfc	9x9HAsfc	Sv	Str (s = 0.2)	Sdr
P. jacksoni	PSU3	9	woodland	1.718182	0.002385	8580.703721	0.300054	0.47	0.77	1.322435963	0.719182382	1.569952664
P. jacksoni	PSU4	1	woodland	5.686803	0.001618	8871.623492	0.153089	0.24	0.33	11.69719967	0.445081587	6.331600281
P. jacksoni	PSU4	6	woodland	2.130875	0.005743	5911.821 92	183.271905	0.32	0.45	0.959546973	0.849958821	0.995058834
P. jacksoni	PSU4	6	woodland	4.843209	0.00798	8591.054933	183.271905	0.83	2.17	1.571275956	0.630850849	1.088521141
P. jacksoni	PSU4	7	woodland	3.541664	0.004096	5580.051399	19.203471	0.38	0.47	30.08962015	0.309270974	11.46109287
P. jacksoni	PSU4	7	woodland	6.858067	0.002124	11665.94154	158.728693	0.18	0.54	27.28246923	0.592393518	22.9508204

P. jacksoni	SSC 2	10	rainforest	7.954195	0.001659	8467.016227	183.271905	0.82	2.41	2.189553938	0.659565939	3.476995285
P. jacksoni	SSC 2	6	rainforest	3.397273	0.004092	6769.256375	6.270521	0.21	0.37	2.82889892	0.442434985	3.025997258
P. jacksoni	SSC 2	7	rainforest	5.152971	0.006297	7525.565329	183.271905	0.23	0.56	1.75948695	0.624210235	4.962044697
P. jacksoni	SSC 2	9	rainforest	2.424804	0.003935	5500.459874	21.316098	0.32	1.02	0.906864974	0.688986406	1.008826323
M. libycus	SSC 9	28	desert	2.297161	0.007111	6896.206912	183.271905	0.16	0.32	0.71051698	0.902986435	1.549172218
M. libycus	SSC 9	4	desert	18.681925	0.001585	11447.22539	6.270521	1.06	3.16	1.633469954	0.611898928	3.760374027
M. libycus	SSC 9	18	desert	5.233454	0.005921	9922.582573	0.153089	0.35	0.36	1.812645949	0.097712511	4.018007031

M. libycus	SSC 9	19	desert	4.214175	0.00253	7778.767344	0.153089	0.47	0.42	1.802702949	0.498371621	3.65042949
M. libycus	SSC 9	20	desert	2.727177	0.005246	4263.01555	0.220448	0.33	0.38	1.293821963	0.52211313	2.258577616
M. libycus	SSC 9	21	desert	3.842886	0.006961	8064.432799	0.153089	0.29	0.46	1.191723966	0.460720816	3.274118811
M. libycus	SSC 9	22	desert	1.055677	0.004971	2400.103566	0.153089	0.32	0.57	7.380755791	0.471266494	1.276395738
M. libycus	SSC 9	23	desert	5.920486	0.001555	3603.015855	0.220448	0.29	0.49	1.677878953	0.347586436	4.388622035
M. libycus	SSC 9	24	desert	4.909081	0.007753	7353.266738	0.153089	0.50	0.60	1.643192954	0.371518259	4.206624735
M. libycus	SSC 9	25	desert	5.74299	0.003207	6760.35383	0.153089	0.77	0.91	1.486274958	0.410277465	4.824518525
M. libycus	SSC 9	26	desert	5.921403	0.00365	5650.113173	0.220448	0.28	0.26	4.644610869	0.649175107	7.808258704

M. libycus	SSC 9	4	desert	18.681925	0.001585	11447.22539	6.270521	1.06	3.16	1.633469954	0.611898928	3.760374027
M. natalensis	PSU 5	15	savannah	14.695243	0.001675	9919.750706	0.153089	0.23	0.37	3.105985912	0.260558999	17.75633609
M. natalensis	PSU 5	18	savannah	4.173548	0.004898	8352.494793	49.600803	0.18	0.28	2.376998933	0.613624063	1.743799793
M. natalensis	PSU 5	19	savannah	3.425959	0.004437	6063.106045	48.504686	0.45	0.68	2.47951993	0.301609463	3.353959436
M. natalensis	PSU 5	13	savannah	2.129725	0.004778	8822.57279	0.153089	0.74	0.89	1.458249959	0.723190794	1.819840741
M. natalensis	SSC 5	11	rainforest	3.708093	0.005692	6078.61376	0.153089	0.48	0.67	1.151052967	0.465601729	5.035335121
M. natalensis	SSC 5	12	rainforest	8.745623	0.004356	8099.642928	0.153089	0.32	0.45	3.357287905	0.631956398	14.42587956
M. natalensis	SSC 5	13	rainforest	3.817736	0.004289	6603.739114	183.271905	0.68	1.37	2.264704936	0.727190559	2.982594744

M. natalensis	SSC 5	14	rainforest	5.964034	0.007223	6233.496287	0.153089	0.24	0.28	1.360104962	0.453402668	5.345617204
M. natalensis	SSC 5	15	rainforest	6.759352	0.001001	7390.255364	183.271905	0.17	0.28	2.300219935	0.313557312	2.916300204