

Short Note

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A preliminary analysis of dental microwear as a proxy for diet and habitat in shrews

Abstract: Dental microwear has been shown to reflect diet in a broad variety of fossil mammals. Recent studies have suggested that differences in microwear texture attributes between samples may also reflect environmental abrasive loads. Here, we examine dental microwear textures on the incisors of shrews, both to evaluate this idea and to expand the extant baseline to include Soricidae. Specimens were chosen to sample a broad range of environments, semi-desert to rainforest. Species examined were all largely insectivorous, but some are reported to supplement their diets with vertebrate tissues and others with plant matter. Results indicate subtle but significant differences between samples grouped by both diet independent of environment and environment independent of diet. Subtle diet differences were more evident in microwear texture variation considered by habitat (i.e., grassland). These results suggest that while environment does not swamp the diet signal in shrew incisor microwear, studies can benefit from control of habitat type.

Keywords: incisors; Soricidae; tooth wear.

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The etiology of mammalian tooth wear has been the subject of much debate in the literature (see Damuth and Janis 2011, Kaiser et al. 2013 for reviews). Some have focused on grit that accumulates on food, whereas others have looked to the food itself, especially siliceous phytoliths that form within plant parts. This discussion has recently extended into the literature on dental microwear, the study of microscopic scratches and pits that form as the result of tooth use. Specifically, it has been suggested that exogenous abrasives on food, rather than endogenous ones within it, are largely responsible for microwear patterns involving removal of enamel from wear facet

surfaces (e.g., Sanson et al. 2007, Lucas et al. 2013). This has led some to speculate that environmental grit levels can affect microwear patterning, complicating or even thwarting efforts to use this as a proxy for reconstructing diets of some fossil species (Wood 2013).

If this is so, animals living in environments with differing exogenous grit loads on their foods should have concomitantly differing patterns of microwear, even if they have similar diets. Here, we test this idea on shrew incisors. Shrews (family Soricidae) provide an opportunity to test this theory, because their diets are reported to be fairly uniform (principally insectivorous, consuming insects and other invertebrates, with a few documented to supplement with varying amounts of vertebrate and/or plant tissue), and they inhabit a broad variety of habitats. Incisors are used because they come into direct contact with the environment and they are not involved in mastication, the mechanics of which might complicate interpretation of microwear patterning.

Dental microwear analysis of molars is often used as a proxy for diet in fossil mammals. Studies of extant species have shown that hard-object feeders, such as nut-crushing mangabey monkeys and bone-crunching hyenas, have more heavily pitted microwear surfaces than do closely related tough-food eaters, such as leaf-eating howlers and flesh-specialist cheetahs, which have facets dominated by long, parallel scratches (e.g., Teaford 1988, Van Valkenburgh et al. 1990). Mammals with broad diets, including both types of food and those with intermediate diets, tend to have scratches and pits on their occlusal surfaces. Microwear has been especially useful for distinguishing browsing from grazing ungulates (e.g., Solounias and Moelleken 1994, Merceron et al. 2005), with more pits in the former and more scratches in the latter. Microwear of fossil ungulates has also been considered an important proxy for habitat reconstruction, as grazers are typically found in more open settings than are browsers (e.g., Merceron and Ungar 2005, Schubert et al. 2006). Some work has also been done on insectivores. For example, bats and strepsirrhine primates that regularly eat hard-shelled beetles evince higher pit-to-scratch ratios on their

incisors than do those that prefer softer moths or caterpillars (Strait 1993). A recent study by Purnell et al. (2013) also showed that 3D microwear surface texture roughness distinguishes hard- from soft-object feeding insectivorous bats.

There have been far fewer such studies on the incisor teeth, but some relationships between patterns of anterior dental microwear and ingestive behavior types have been suggested. Most analyses have focused on primates (e.g., Walker 1976, Ryan 1981, Ungar 1994), though a few have considered other mammals (e.g., Young and Marty 1986, Young et al. 1990). Such studies have found associations between degree of incisor use in ingestion, for example, and density of microwear scratches on these teeth. Other attributes, such as pattern of scratch orientation, seem to relate to specific ingestive behaviors, such as stripping leaves with the front teeth in a specific way. There have been no published studies to the best of our knowledge, however, on shrew incisor microwear and how that might relate to diet, habitat, or tooth use behaviors, such as use of these teeth as forceps for catching prey (*sensu* Churchfield 1990).

For this study we included nine species of shrew: *Crociodura leucodon*, *Myosorex varius*, *Neomys fodiens*, *Notiosorex crawfordi*, *Scutisorex congicus*, *Sc. somereni*, *Sorex arcticus*, *So. vagrans*, and *Suncus murinus*. These live in a range of environments, and consume a variety of food types (see Table 1). Species are separated into semi-desert, grassland, forest, and semi-aquatic habitats. We developed broad categories for habitats, given inconsistencies in published characterizations between areas sampled. These allow simple comparisons between areas with similar habitat types differing by vegetative ground cover. Here, semi-desert refers to regions that are arid and have little vegetation. Grasslands refer to open settings dominated by grasses, but with little tree or bush cover. Forest includes closed, wooded habitats with both temperate and rainforest forest types. Semi-aquatic is the

classification given to *Ne. fodiens*, because it spends a substantial amount of its time in or near a water source. Specimens were classified based on metadata on locations of capture for individuals cross-referenced with imagery from Google Earth. All shrew species considered here are primarily insectivorous (consuming insects and other invertebrates, such as spiders, slugs and worms). Those that are reported to supplement their diets with plant matter or vertebrate tissues are classified here as omnivorous and faunivorous, respectively. These categorizations are limited by the number and extent of studies of feeding ecology documented in the literature.

All species have habitat and diet documented to at least some extent in the literature. *Crociodura leucodon* is endemic to Europe and Western Asia, from France to Asia Minor (Barti 2011). It is often associated with dry, upland grasslands (Barti 2011). It eats not only invertebrates (insects, insect larvae and worms), but also small reptiles, mammals and amphibians (Shenbrot et al. 2008). *Myosorex varius* is found in Southern Africa, mostly in moist, densely vegetated habitats such as interior forests (Apps 2000). This species is primarily insectivorous, but supplements its diets with some plant material (Wirminghaus and Perrin 1992). *Neomys fodiens*, the Eurasian water shrew, is native to Eurasia, from Great Britain to Siberia, and exploits both terrestrial and aquatic environments (Churchfield 1985). It too consumes mostly insects, but it also eats sizable fish, amphibians, and small mammals (Churchfield 1985), and so is characterized here as a faunivore. *Notiosorex crawfordi*, the desert shrew, is found in Southwestern and South-Central United States, as well as in Northern and Central Mexico (Armstrong and Jones 1972). The desert shrew prefers semi-desert scrub habitats, and is an opportunistic faunivore, eating whatever small animals it encounters (Hoffmeister and Goodpaster 1962). The armored or hero shrew, *Sc. somereni*, is from Southwestern Uganda, Eastern Congo, and Northern Rwanda (Pennisi 1996). It is also an opportunistic faunivore, eating

Table 1 Shrew details. See text for references and more precise locale data is available in the online supplemental material.

Specimen	N	Diet	Habitat	Location
<i>Crociodura leucodon</i>	13	Faunivore	Grassland	Western Europe
<i>Myosorex varius</i>	17	Omnivore	Forest	South Africa
<i>Neomys fodiens</i>	17	Faunivore	Semi-Aquatic	Western Europe
<i>Notiosorex crawfordi</i>	17	Faunivore	Semi-Desert	Western United States
<i>Scutisorex congicus</i>	7	Faunivore	Forest	Congo
<i>Scutisorex somereni</i>	7	Faunivore	Forest	Congo, Rwanda, and Uganda
<i>Sorex arcticus</i>	17	Insectivore	Grassland	Southern Canada
<i>Sorex vagrans</i>	17	Omnivore	Grassland	Northwestern United States
<i>Suncus murinus</i>	17	Omnivore	Forest	Vietnam

a wide range of small to medium-size invertebrates and vertebrates (Churchfield et al. 2007), and prefers forests. *Sorex arcticus*, the Arctic shrew, is native to Northern North America (Kirkland and Schmidt 1996). It is typically found in grassland but not forest (Perry et al. 2004), and has a diet dominated by insects (Kirkland and Schmidt 1996). *Sorex vagrans*, the vagrant shrew, is from the Central Pacific coast of North America. It too prefers grassland, and is rarely found in closed forest (Gillihan and Foresman 2004). Although principally insectivorous, *So. vagrans* also eats some vegetation, such as grass seeds (Whitaker et al. 1983). *Suncus murinus*, the Asian house shrew, is found throughout Indo-Malayan Asia (Hutterer et al. 2008), and specimens used in this study were all recovered in rainforest/fringe forest settings. This species has been described as an opportunistic omnivore (Prakash and Singh 1999).

All specimens included in this study are housed at the US National Museum of Natural History in Washington D.C. First, lower central incisors (I_1 s) were cleaned with cotton swabs soaked in alcohol. Molds of the labial surfaces (right I_1 s when possible) were then made using President's Jet regular body polyvinyl siloxane dental impression material (Coltène-Whaledent Corp., Altstätten, Switzerland). High-resolution replicas were poured using Epotek 301 epoxy resin and hardener (Epoxy Technologies Corp, Billerica, MA, USA), and examined at low magnification under a binocular light microscope, then at higher magnification using a white-light scanning confocal microscope, to confirm presence of unobstructed antemortem microwear. A total of 133 specimens were included in the current study.

Data were collected using a Sensofar PLμ confocal imaging profiler with a 100× objective (Sensofar Corp., Barcelona, Spain). Three-dimensional point clouds were generated for each specimen, with consistent sampling of the distolabial surface near the incisal edge. These point clouds had a lateral (x, y) spacing of 0.18 μm, a vertical resolution of 0.005 μm, and a work envelope reflecting a planimetric area of 138 μm×102 μm (see Scott et al. 2006). First, obvious defects, such as dust particles or casting artifacts, were deleted from the surfaces using thresholding and erase defects operations in Solarmap Universal (Solarius Development Inc., Sunnyvale, CA, USA). Each point cloud (1 per individual) was then analyzed using scale-sensitive fractal analysis software (ToothFrax and SFrax, Surfract Corp. Norwich, VT, USA). Five parameters are used to describe the surface and they include: complexity (*Asfc*), anisotropy (*epLsar*), heterogeneity of complexity (*Hasfc9* and *Hasfc81*), scale of maximum complexity (*Smc*), and textural fill volume (*Tfv*). These attributes together can be

used to characterize microwear surface textures without relying on an observer to count and measure up to hundreds of individual features on a given surface.

These attributes are all described in Scott et al. (2006). *Asfc* is a measure of change of roughness across scales of observation. Surfaces with high *Asfc* values are typically heavily pitted. Anisotropy is a measure of surface orientation concentration. Surfaces dominated by long, parallel scratches typically have high *epLsar* values. *Smc* is the scale at which roughness begins to taper off. Surfaces with high values often lack very small features. *Tfv* is a measure of how much volume is removed from a given surface, measured in this case by features with diameters between 2 μm and 10 μm. A high value reflects a surface dominated by deep features in this size range. Finally, heterogeneity reflects variation in *Asfc* across a surface, subsampled in 3×3 and 9×9 grids. Uniform surfaces have low heterogeneity values, whereas specimens that vary in texture complexity across a surface have higher values.

Data were analyzed using a multivariate analysis of variance model, with separate tests for habitat and diet

Table 2 Summary statistics.

	<i>Asfc</i>	<i>epLsar</i>	<i>Smc</i>	<i>Tfv</i>	<i>Hasfc 3x3</i>	<i>Hasfc 9x9</i>
<i>Crocidura leucodon</i>						
Mean	2.154	0.006	146.19	15759	0.443	0.701
SD	0.873	0.002	271.84	2420	0.111	0.182
<i>Myosorex varius</i>						
Mean	1.446	0.005	0.26	14545	0.579	0.846
SD	0.719	0.003	0.11	4227	0.313	0.445
<i>Neomys fodiens</i>						
Mean	1.994	0.006	143.30	14618	0.584	0.883
SD	1.045	0.003	250.96	7067	0.419	0.522
<i>Notiosorex crawfordi</i>						
Mean	2.386	0.005	70.29	17353	0.502	0.729
SD	1.033	0.002	197.77	2671	0.274	0.257
<i>Scutisorex congicus</i>						
Mean	2.644	0.006	0.22	15752	0.593	0.839
SD	2.234	0.002	0.10	2894	0.213	0.264
<i>Scutisorex somereni</i>						
Mean	1.646	0.004	0.24	14179	0.379	0.696
SD	0.366	0.002	0.06	1913	0.200	0.295
<i>Sorex arcticus</i>						
Mean	1.766	0.006	115.20	15410	0.904	0.936
SD	1.016	0.003	255.76	2529	0.434	0.452
<i>Sorex vagrans</i>						
Mean	1.531	0.009	439.26	15812	0.444	0.640
SD	0.679	0.002	278.89	4294	0.135	0.168
<i>Suncus murinus</i>						
Mean	2.644	0.007	43.40	16055	0.575	0.879
SD	1.083	0.002	149.92	3182	0.304	0.298

Asfc, complexity; *epLsar*, anisotropy; *Hasfc*, heterogeneity of complexity; SD, standard deviation; *Smc*, scale of maximum complexity; *Tfv*, textural fill volume.

categories. Data were rank transformed before analysis to mitigate violation of assumptions associated with parametric statistical procedures (see Conover and Iman 1981). Specimens were considered using a taxon-free approach, with published information on species and metadata on provenience from tags on original specimens used to categorize individuals into habitat (semi-desert, grassland, forest, semi-aquatic) and diet (insectivore, faunivore, omnivore) types. Where significance using MANOVA models was found, analyses of variance were computed for each variable to determine the source of variation. A separate ANOVA comparing diet of grassland specimens was also carried out, as this was the only habitat type with individuals representing all diet types. Finally, Tukey's HSD and Fisher's LSD pairwise comparisons were used when needed, to balance the risks of Type I and Type II errors.

Raw data are provided in the online supplement, and statistics are presented in Tables 2 and 3 and Figure 2. For the habitat comparison, both *epLsar* and *Smc* showed significant variation. Forest and grassland individuals differed significantly for both *epLsar* and *Smc*. Neither differed significantly from semi-desert or semi-aquatic specimens, and these did not differ from one another. There were no other differences in microwear texture attributes between habitat types. For the diet comparison, both *epLsar* and heterogeneity (surface broken into 3×3 cells) showed significant variation. Omnivores had a marginally higher average *epLsar* value than insectivores (Fisher's but not Tukey's test result was significant), whereas insectivores had a significantly higher level of heterogeneity (by Tukey's and Fisher's test results) than did faunivores. There were no other differences in microwear texture attributes between diet types.

Table 3 Statistical analysis.

A) MANOVA and ANOVA results							
	<i>Wilks λ</i>	<i>Asfc</i>	<i>epLsar</i>	<i>Smc</i>	<i>Tfv</i>	<i>Hasfc 3x3</i>	<i>Hasfc 9x9</i>
Between habitats							
<i>F</i>	1.992	1.096	3.049	3.227	1.897	0.567	0.699
<i>df</i>	18, 351	3,129	3,129	3,129	3,129	3,129	3,129
<i>p</i>	0.00	0.35	0.03	0.03	0.13	0.64	0.55
Between diets							
<i>F</i>	2.029	1.239	3.003	2.57	0.677	3.006	0.229
<i>df</i>	12, 250	2, 130	2, 130	2, 130	2, 130	2, 130	2, 130
<i>p</i>	0.02	0.29	0.05	0.08	0.51	0.05	0.80
Within grasslands							
<i>F</i>	5.055	2.757	9.647	9.231	0.249	17.573	3.269
<i>df</i>	12, 86	2, 48	2, 48	2, 48	2, 48	2, 48	2, 48
<i>p</i>	0.00	0.07	0.00	0.00	0.78	0.00	0.05
B) Pairwise comparisons probability values							
		Tukey's	Fisher's	Tukey's	Fisher's		
Habitat 1	Habitat 2	<i>epLsar</i>		<i>Smc</i>			
Forest	Grassland	0.03	0.01	0.01	0.00		
Forest	Semi-aquatic	0.65	0.25	0.91	0.51		
Forest	Semi-desert	1.00	0.89	0.97	0.66		
Grassland	Semi-aquatic	0.85	0.43	0.44	0.14		
Grassland	Semi-desert	0.15	0.04	0.32	0.09		
Semi-aquatic	Semi-desert	0.71	0.29	1.00	0.86		
Between diets (all habitats)		<i>epLsar</i>		<i>HAsfc 3x3</i>			
Faunivore	Insectivore	0.79	0.52	0.04	0.02		
Faunivore	Omnivore	0.17	0.08	0.80	0.53		
Insectivore	Omnivore	0.06	0.02	0.15	0.07		
Between diet within grassland		<i>epLsar</i>		<i>Smc</i>			
Faunivore	Insectivore	0.77	0.49	0.53	0.29		
Faunivore	Omnivore	0.00	0.00	0.01	0.00		
Insectivore	Omnivore	0.00	0.00	0.00	0.00		
		<i>HAsfc 3x3</i>	<i>HAsfc 9x9</i>				
Faunivore	Insectivore	0.00	0.00	0.24	0.11		
Faunivore	Omnivore	1.00	1.00	0.66	0.38		
Insectivore	Omnivore	0.00	0.00	0.04	0.02		

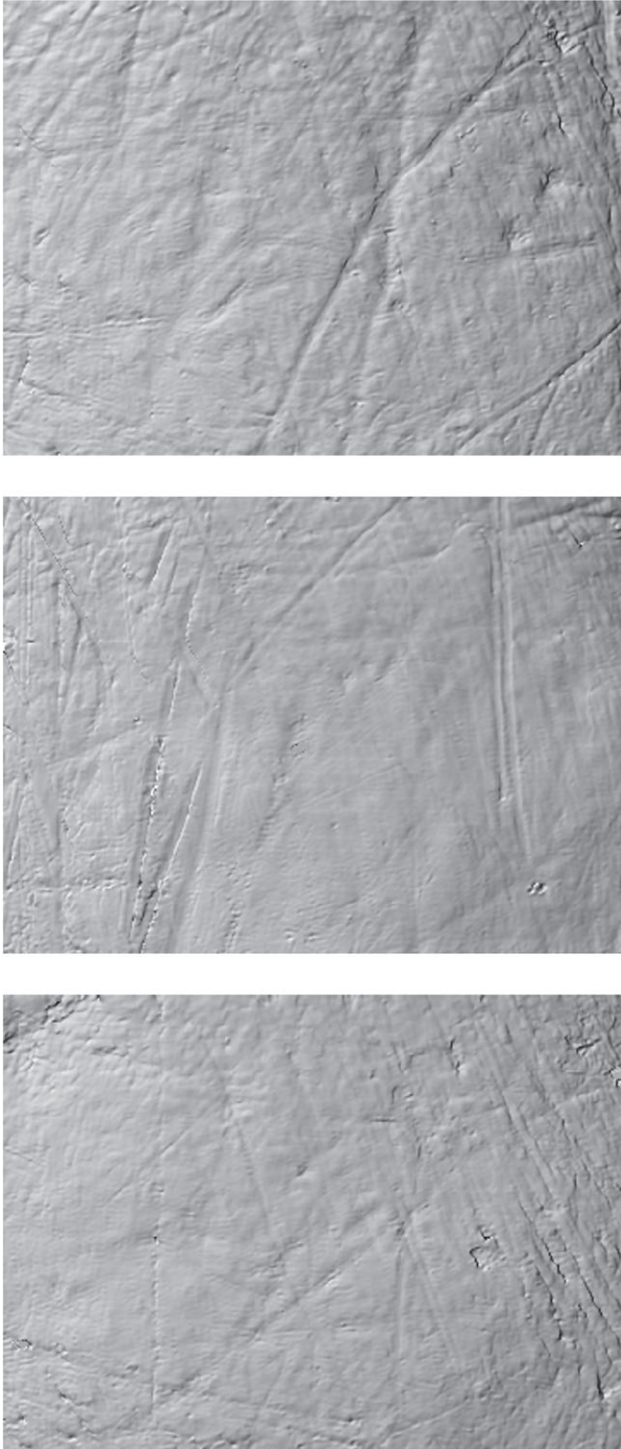


Figure 1 Sample photosimulations of microwear on the incisors of grassland shrews: *Sorex vagrans* (top), *Sorex arcticus* (middle), and *Crocidura leucodon* (bottom). Each represents an area $138\ \mu\text{m} \times 102\ \mu\text{m}$.

We also considered variation between diets within the grassland habitat only, as this was the only habitat with representatives of all three dietary categories; *epLsar*, *Smc*, and *HAsfc* (both 3×3 and 9×9 grids) showed significant

variation in this case. First, omnivores had significantly higher *epLsar* than either faunivores or insectivores. Also, insectivores had significantly higher average heterogeneity than faunivores or omnivores using a 3×3 grid. Insectivores also had significantly higher average heterogeneity than omnivores when a 9×9 grid was used.

Our results suggest no strong environmental signal in shrew incisor microwear when comparing individuals ranging from semi-desert to rainforest. We found no evidence for a strong diet signal across habitats, which is unsurprising given the lack of gross differences in food preference reported among shrew species considered in this study. By contrast, when we limited our analysis to a single environment i.e., grassland, subtle differences in diet (inclusion of some vegetation or vertebrates) are reflected in significant variation in microwear texture patterns. This suggests that while environment will not likely overwhelm microwear signals, control over broad differences in habitat may yield the best diet discrimination.

The results of this study provide important clues about the role of habitat in microwear texture patterning, at least for shrew incisors. If habitat played a substantive role in that patterning, we would expect to have seen marked differences between semi-desert, grassland, forest, and semi-aquatic shrews. We see few differences, and those that there are cannot be readily explained as a function of environmental grit load. Likewise, there were few differences between shrews with differing diets. This is not surprising, given that all shrews studied apparently ate mostly invertebrates, and may have used their incisors as forceps to grasp and trap these animals in a similar manner.

Variation in microwear between diet types within the grassland habitat is noteworthy. By focusing on just grassland species (again, the only habitat category with all three dietary groups), the diet signal is clearer despite the subtlety of differences in food preferences. While no one, to our knowledge, has documented variation among these species in incisal use behaviors, it seems reasonable to speculate that plant matter, vertebrates, and invertebrates each require different ingestive behaviors, and that these likely underlay the differences seen. How these differences translate to the difference in microwear texture attributes documented will require direct observation of incisor use during feeding to determine.

It is also reasonable to speculate that the variation seen between diets when controlling for habitat suggests that environment can introduce noise to the system when looking for subtle differences in microwear related to feed preferences. This suggests that efforts to reconstruct the diets of fossil shrews using incisor microwear

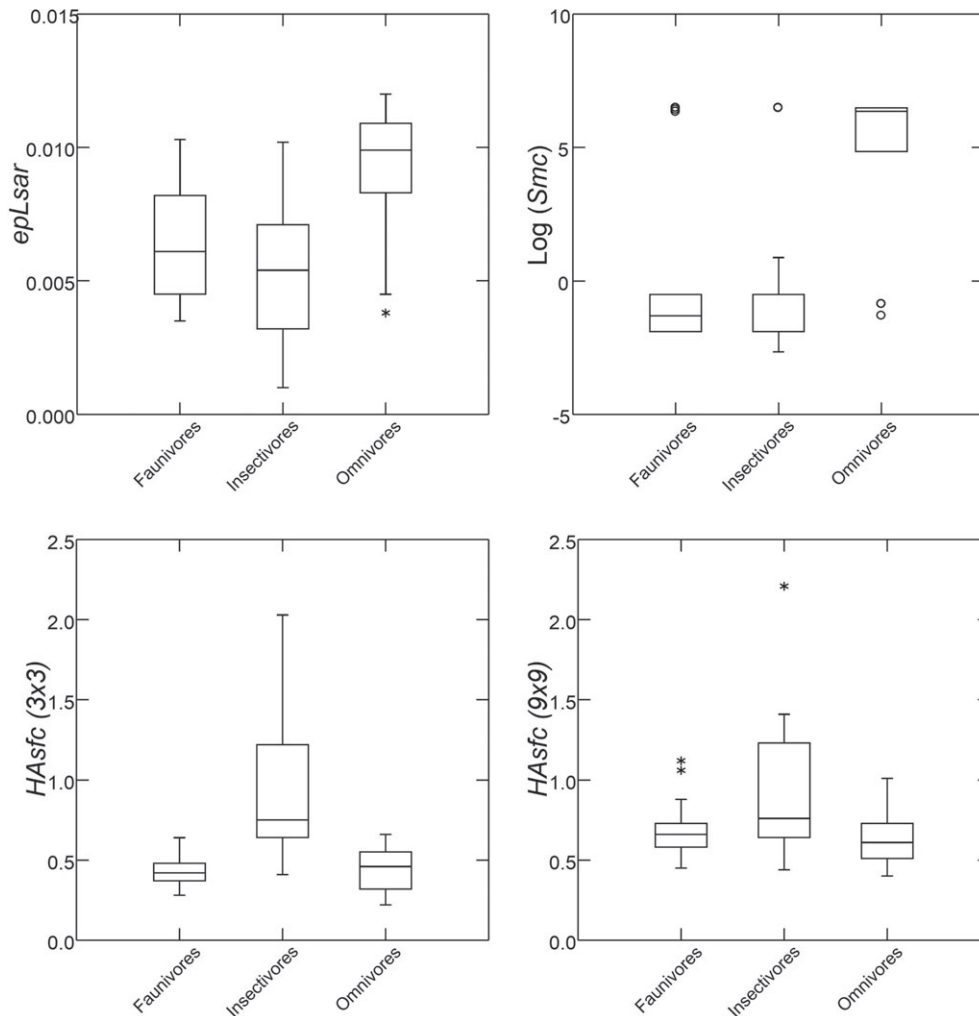


Figure 2 Standard box plot representation of the grassland data for each variable separated by diet category. The boxes represent the central 50% of values, with the edges indicating first and third quartiles and the horizontal lines representing medians. The whiskers are the range of values within 1.5 times the interquartile range from the box edges, the asterisks are values between 1.5 and 3 times the interquartile range from the box edges, and open circles are values beyond that.

analysis would benefit from an independent assessment and control of the paleoenvironments from which they were recovered. That said, the distinct lack of a habitat signal clearly indicates that environment (and presumably grit load) does not swamp or overwhelm microwear texture signatures on shrew incisors.

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References

- Apps, P. 2000. *Smither's mammals of Southern Africa: A field guide*. Struik Publishers, Cape Town, South Africa.
- Armstrong, D.M. and J.K. Jones, Jr. 1972. *Notiosorex crawfordi*. *Mamm. Species* 17: 1–5.

- Barti, L. 2011. Unusual occurrence of the bicoloured white-toothed shrew (*Crocidura leucodon*, Soricomorpha, Soricidae) in a mature Beech forest in the Ciomad-Puturosu Mountains (Eastern Carpathians, Central Romania). *Acta Siculica* 2011: 119–124.
- Churchfield, S. 1985. The feeding ecology of the European Water Shrew. *Mammal Rev.* 15: 13–21.
- Churchfield, S. 1990. The natural history of shrews. Cornell University Press, London.
- Churchfield, S., F. Dieterlen, R. Hutterer and A. Dudu. 2007. Feeding ecology of the armored shrew, from the north-eastern Democratic Republic of Congo. *J. Zool.* 273: 40–45.
- Conover, W.J. and R. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35: 124–129.
- Damuth, J. and C.M. Janis. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biol. Rev.* 86: 733–758.
- Gillihan, S.W. and K.R. Foresman. 2004. *Sorex vagrans*. *Mamm. Species* 744: 1–5.
- Hoffmeister, D.F. and W.W. Goodpaster. 1962. Life history of the desert shrew *Notiosorex crawfordi*. *Southwest. Nat.* 7: 236–252.
- Hutterer, R., S. Molur and L. Heaney. 2008. *Suncus murinus*. In: IUCN 2012. IUCN red list of threatened species. Version 2012.2. Available at: www.iucnredlist.org. Accessed March 1, 2013.
- Kaiser, T.M., D.W.H. Müller, M. Fortelius, E. Schulz, D. Codron and M. Clauss. 2013. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mamm. Rev.* 43: 34–46.
- Kirkland, G.L. Jr., and D.F. Schmidt. 1996. *Sorex arcticus*. *Mamm. Species* 524: 1–5.
- Lucas, P.W., R. Omar, K. Al-Fadhalah, A.S. Almusallam, A.G. Henry, S. Michael, L.A. Thai, J. Watzke, D.S. Strait and A.G. Atkins. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *J. R. Soc. Interface* 10: 20120923.
- Merceron, G. and P. Ungar. 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape Province, South Africa. *S. Afr. J. Sci.* 101: 365–370.
- Merceron, G., L. de Bonis, L. Viriot and C. Blondel. 2005. Dental microwear of the late Miocene bovids of northern Greece: Vallesian/Turolian environmental changes and disappearance of *Ouranopithecus macedoniensis*? *B. Soc. Géol. France.* 176: 475–484.
- Pennisi, E. 1996. Superhero Shrew. *Science* 271: 149.
- Perry, N.D., D.T. Stewart, E.M. Madden and T.J. Maier. 2004. New records for the arctic shrew, *Sorex arcticus*, and the newly recognized maritime shrew, *Sorex maritimensis*. *Can. Field Nat.* 118: 400–404.
- Prakash, I. and H. Singh. 1999. Food of a shrew, *Suncus murinus* inhabiting hilly tracts of south and southeastern Rajasthan. *Proc. Natl. Acad. Sci. India* 69: 245–250.
- Purnell, M.A., N. Crumpton, P.G. Gill, G. Jones and E.J. Rayfield. 2013. Within-guild dietary discrimination from 3-D textural analysis of tooth microwear in insectivorous mammals. *J. Zool.* doi: 10.1111/jzo.12068.
- Ryan, A.S. 1981. Anterior dental microwear and its relationship to diet and feeding behavior in three African primates (*Pan troglodytes troglodytes*, *Gorilla gorilla gorilla* and *Papio hamadryas*). *Primates* 22: 533–550.
- Sanson, G.D., S.A. Kerr and K.A. Gross. 2007. Do silica phytoliths really wear mammalian teeth? *J. Archaeol. Sci.* 34: 526–531.
- Schubert, B.W., P.S. Ungar, M. Sponheimer and K. Reed. 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. *Palaeogeogr. Palaeoclimatol.* 241: 301–319.
- Scott, R.S., P.S. Ungar, T.S. Bergstrom, C.A. Brown, B.E. Childs, M.F. Teaford and A. Walker. 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51: 339–349.
- Shenbrot, G., R. Hutterer, G. Amori, B. Kryštufek, N. Yigit, G. Mitsain and L.J. Palomo. 2008. *Crocidura leucodon*. In: IUCN 2012. IUCN red list of threatened species. Version 2012.2. <www.iucnredlist.org>. Downloaded on 27 February 2013.
- Solounias, N. and S.M.C. Moelleken. 1994. Dietary differences between two archaic ruminant species from Sansan, France. *Hist. Biol.* 7: 203–220.
- Strait, S.G. 1993. Molar microwear in extant small-bodied faunivorous mammals: An analysis of feature density and pit frequency. *Am. J. Phys. Anthropol.* 96: 63–79.
- Teaford, M. 1988. A review of dental microwear and diet in modern mammals. *Scanning Microscopy* 2: 1149–1166.
- Ungar, P. 1994. Incisor microwear of Sumatran Anthropoid primates. *Am. J. Phys. Anthropol.* 94: 339–363.
- Van Valkenburgh, B., M.F. Teaford and A. Walker, A. 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. *J. Zool.* 222: 319–340.
- Walker, P.L. 1976. Wear striations on the incisors of cercopithecoid monkeys as an index of diet and habitat preference. *Am. J. Phys. Anthropol.* 45: 299–308.
- Whitaker, J.O., S.P. Cross and C. Maser. 1983. Food of vagrant shrews (*Sorex vagrans*) from Grant County, Oregon, as related to livestock grazing pressures. *Northwest Sci.* 57: 107–111.
- Wirminghaus, J. and M. Perrin. 1992. Diets of small mammals in a Southern African temperate forest. *Israel J. Zool.* 38: 353–361.
- Wood, B. 2013. Gritting their teeth. *Nature* 493: 486–487.
- Young, W.G. and T.M. Marty. 1986. Wear and microwear on the teeth of a moose (*Alces alces*) population in Manitoba, Canada. *Can. J. Zool.* 64: 2467–2479.
- Young, W.G., K.P. Brennan and R.I. Marshall. 1990. Occlusal movements of the Brushtail possum, *Trichosurus vulpecula*, from microwear on the teeth. *J. Zool.* 38: 41–51.