

DENTAL MICROWEAR TEXTURE ANALYSIS OF DENTIN: CAN MAMMALIAN
DIETS BE INFERRED WITHOUT ENAMEL?

By

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To my parents, for ensuring that I never had any reason to quit

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LIST OF ABBREVIATIONS

Asfc – Area-scale fractal complexity

epLsar – Anisotropy

Smc – Scale of maximal complexity

Tfv – Textural fill volume

HAsfc – Heterogeneity

DMTA – Dental microwear texture analysis

SSFA – Scale-sensitive fractal analysis

REE – Rare earth elements

SEM – Scanning electron microscope

FLMNH – Florida Museum of Natural History

AMNH – American Museum of Natural History

NMNH – National Museum of Natural History

MCZ – Museum of Comparative Zoology

UABRC – University of Arkansas Biological Research Center

C. hoffmanni – Hoffman's two-toed sloth

B. variegatus – Brown-throated three-toed sloth

D. novemcinctus – Nine-banded or long-nosed armadillo

E. eomigrans – Megatheriid giant ground sloth

H. floridanus – Giant armadillo-like pampathere

M. leptostomus – Megalonychid ground sloth

P. harlani – Harlan's ground sloth

P. concolor coryi – Florida panther, a subspecies of Puma

ANOVA – analysis of variance

CHAPTER I

INTRODUCTION

Understanding an animal's dietary ecology is essential to clarifying their overall ecology and is particularly critical in the face of climate change, where interactions between an animal and their food might be disrupted by changes in temperature, range, or seasonality (Barnosky et al. 2003, Colwell et al. 2008, Sheldon et al. 2011). Therefore, it is important to determine if existing methods of dietary analysis can be applied to understudied groups of animals, such as xenarthrans (i.e., sloths, armadillos and anteaters; Vizcaíno and Loughry 2008). It is only by having a more complete picture of a community's ecology that we can then attempt to predict how these communities might respond in the face of global climate change. Further, if the methods employed herein can reliably record observed diets in extant taxa, then they can potentially be applied to a diverse array of extinct taxa (e.g., giant armadillo-like pampatheres, and ground sloths) which endured periods of dramatic glacial-interglacial climatic shifts (Hulbert 2001).

Although tools such as dental microwear texture analysis (DMTA) of tooth enamel can distinguish between different dietary niches in primates, carnivores, marsupials, and bovids (Prideaux et al. 2009, Schubert et al. 2010, Scott et al. 2006, Scott 2012, Ungar et al. 2007), xenarthrans pose a unique challenge because their permanent teeth lack enamel. We have a reasonable understanding of how enamel is modified in response to food intake and diet (Baker et al. 1959, Teaford 1988b), the same is not true of dentin. Does microwear of dentin reflect diet as it does for enamel? Here we address

this question with a study of dentin microwear texture in teeth with exposed functional dentin and enamel in the form of carnassials, as well by examining extant and extinct xenarthrans with known differences in diet.

Extant xenarthran natural history and ecology

The Magnorder Xenarthra is a group of basal placental mammals endemic to South America (Archibald 2003, Vizcaíno and Loughry 2008). Some xenarthrans, like anteaters, lack teeth entirely (hence the previous polyphyletic name for the clade “Edentata,” meaning tooth-less), whereas all living toothed xenarthrans (i.e., sloths and armadillos), lack enamel on their permanent (Vizcaíno 2009). To compensate for this, toothed xenarthrans have a number of modifications to the more common mammalian dental plan including ever-growing, or hypselodont, teeth (Vizcaíno 2009). Xenarthran teeth are typically composed of two layers of dentin, sometimes with a coating of cementum of varying degrees of thickness, an inner softer layer and a harder outer dentin layer (Fig. 1; Ferigolo 1985, Vizcaíno 2009). The inner dentin (sometimes referred to as orthodentine or vasodentine) is in some taxa similar in hardness to the orthodentine found in other mammals (Ferigolo 1985, MacFadden et al. 2010). The outer dentin (sometimes called osteodentine or hardened/hypermineralized orthodentine) is a more mineralized form of dentin than found in typical mammalian teeth but which is still significantly softer than enamel with an average Mohs’ hardness of 3.8 in contrast to 5.7 (Ferigolo 1985, Kalthoff 2011, MacFadden et al. 2010). When examining xenarthrans in this study,

we only assess the microwear texture of the outer layer of dentin, and to avoid confusion will use the term outer dentin (in keeping with MacFadden et al. 2010).

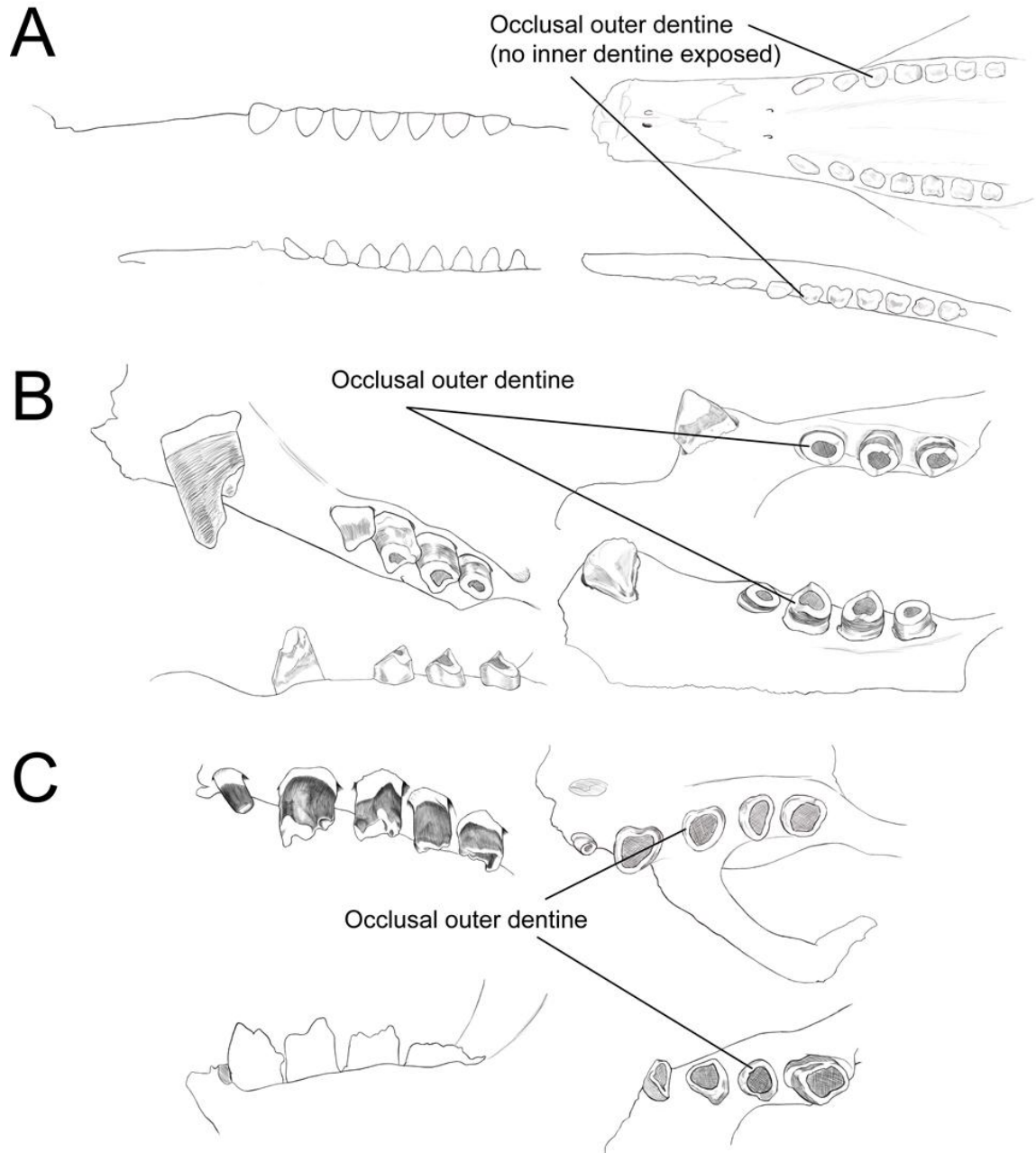


Figure 1: Buccal and occlusal views of the dentition of xenarthran species examined in this study, including: A) *Dasypus novemcinctus*, B) *Choloepus hoffmanni*, C) *Bradypus variegatus*. All views have the anterior direction to the left. Not to scale.

Both extant genera of tree sloths evidently evolved convergently from extinct ground-dwelling ancestors (Gaudin 2004, Webb 1985). The three-toed sloth, *Bradypus variegatus*, is exclusively folivorous with a preference towards young leaves of only a few tree families per individual and is thought to have a more constrained diet when compared to members of the two-toed sloth genus *Choloepus* (Chiarello 2008, Urbani and Bosque 2007). Other than one study of Costa Rican agroforest and other artificial habitats (Vaughan et al. 2007), *Choloepus* lacks dietary data for wild populations but is thought to be primarily folivorous; however, it will consume branches, fruit, flowers, and even eggs when available (Chiarello 2008). The nine-banded armadillo, *Dasypus novemcinctus*, in contrast, is a burrowing terrestrial opportunistic insectivore/omnivore with a preference for ground-dwelling insects, small vertebrates and vegetal/fungal matter with specific diets varying by region and season (Breece and Dusi 1985, da Silveira Anacleto 2007, Redford 1985, Sikes et al. 1990). The armadillo lifestyle and tendency to eat food items found underground indicates that this xenarthran consumes a large amount of dirt and grit (Breece and Dusi 1985), potentially influencing microwear patterns on their teeth.

While modern xenarthrans are elusive and less well understood than many other eutherians, even less is known about the dietary ecology of their fossil relatives (Vizcaíno and Loughry 2008a). Although morphological studies have shed light on xenarthran paleoecology, equivocal dietary interpretations leave large gaps in our understandings of the histories of New World communities containing these animals. Ground sloths were among first immigrants to North American during the Great Biotic Interchange, even predating the connection of the two continents via the Panamanian land bridge (Marshall

1988, Stehli and Webb 1985, Webb 2006). However, as many species of extinct xenarthrans have no extant analogs (Vizcaíno and Loughry 2008a), understanding their paleobiology and paleoecology is challenging.

Paleoecology of extinct xenarthrans from Florida

As mentioned above, the paleoecology of extinct xenarthrans is poorly understood. However, there are various lines of evidence for which basic conclusions about their diet and lifestyle can be drawn including: morphological analysis, scatological analysis, and environmental analysis.

Previous studies of the jaw biomechanics and morphology of Cingulata, the order within xenarthrans containing armadillos, pampatheres and glyptodonts, found that primitive xenarthrans were likely insectivores (Vizcaíno et al. 2004). However, adaptations including some novel mastication mechanisms with no modern analogues, allowed the group to diversify into herbivory, carnivory, with some examples of highly specialized myrmecophagy, and omnivory (Vizcaíno et al. 2004). A later study was conducted looking only at glyptodonts, and in comparing ratios of relative muzzle width, hypsodonty index, and dental occlusal surface was able to show that smaller more basal glyptodonts were selective herbivores, whereas larger glyptodonts became more generalist feeders (except in the case of the Pleistocene *Glyptodon*, which appears to have shifted back to a more specialized feeding mode; Vizcaíno et al. 2011). The ecomorphology of ground sloths (Tardigrada) has also been examined via similar techniques (Bargo and Vizcaíno 2008). These data instead suggest niche-partitioning in ground sloths based on muzzle-width, with the wider-mouthed taxa as bulk-feeders and

narrow-mouthed taxa as more mixed or selective in their forage (Bargo and Vizcaíno 2008).

Researchers have also begun exploring methods of direct analysis such as stable isotope geochemistry (Czerwonogora et al. 2011, MacFadden et al. 2010, Pérez-Crespo et al. 2011, Ruez 2005) and dental microwear (Green 2009a, Green 2009b, Green and Resar 2012, Oliveira 2001), but issues with both these methods remain (See “Previous work on xenarthran microwear” pg. 11). Specifically, geochemical studies have been limited because permanent xenarthran teeth contain only dentin, which has a higher organic content than enamel and is more prone to taphonomic and diagenetic alteration (Green 2009a, Kalthoff 2011, MacFadden et al. 2010, Vizcaíno 2009, Wang and Cerling 1994). As researchers have shown that rare earth element (REE) analysis can be used as a proxy for testing the amount of chemical alteration to dental material (MacFadden et al. 2010), it is therefore possible that xenarthran teeth may yield biologically meaningful stable isotope values. However, stable isotope geochemistry of teeth provides a longer-term dietary signal representing the average diet at the time of tissue formation and the exact fractionation rates of xenarthrans have yet to be determined (MacFadden et al. 2010), and as such, additional methods of paleoecological investigation should be explored as efficacious alternatives.

In addition to attempting to develop an extant dental microwear texture baseline, we also want to examine extinct taxa to clarify their dietary ecology by comparing them to sympatric extinct taxa and extant relatives. While the hardness of teeth between extant and extinct groups was not shown to be statistically significantly different by MacFadden et al. (2010), it is also not known how subtle differences in hardness might affect

preservation of microwear. There may be some as yet unknown threshold of hardness which limits the use of microwear, and such distinction may only be found by examining taxa with dental materials of varying hardness.

This work focuses on four extinct xenarthran species found at three separate fossil sites in Florida. The sites represent both glacial and interglacial time periods, which gives researchers the opportunity to explore how behavior might change depending on different environments. Further, the presence or absence of a given species at a given site might shed light on preferred environments or overall adaptability through changing climates.

The three sites sampled for this study are Haile 7G, Inglis 1A, and Leisey 1A. Haile 7G is interpreted as a sinkhole which formed within a dense forest, based on the abundance of forest indicator taxa such as tapirs (DeSantis and MacFadden 2007, Hulbert et al. 2006). This interpretation has been confirmed with stable isotope geochemistry, which showed that herbivores found at the locality were consuming primarily C₃ plants, indicating a forested environment (DeSantis and MacFadden 2008). Inglis 1A is a glacial fossil site, determined based on geological evidence and further supported by geochemical studies, and is also dominated by browsing taxa (DeSantis et al. 2009, Morgan and Hulbert 1995). Contrariwise, Leisey 1A is an interglacial site (similarly based on geologic evidence and further supported by isotopic data) and it has a more even distribution of browsers, mixed feeders, and grazers making up the mammalian fauna (DeSantis et al, 2009; Morgan and Hulbert 1995).

Thus, we examined three ground sloths from three separate evolutionary lineages of the suborder Folivora (of the order Pilosa, which includes both sloths and anteaters):

Megatheriidae, Megalonychidae, and Mylodontidae. We also examined the pampathere (i.e. Pampatheriidae) *Holmesina floridanus*. Relationships between the taxa in this study are outlined in a simplified cladogram (Fig. 2). The cingulates *Dasypus novemcinctus* and *Holmesina floridanus* are more closely related to each other than any of the folivorans (i.e. sloths). Amongst the folivorans, *Paramylodon* is a member of the entirely extinct lineage of mylodontid sloths, *Eremotherium* and *Bradypus* are both megatheriid sloths, and *Megalonyx* and *Choloepus* are both megalonychid sloths. Further, we attempted to pick specimens that overlapped with each other in some or all of the localities examined to control for available vegetation and potentially highlight dietary differences between glacial and interglacial habitats.

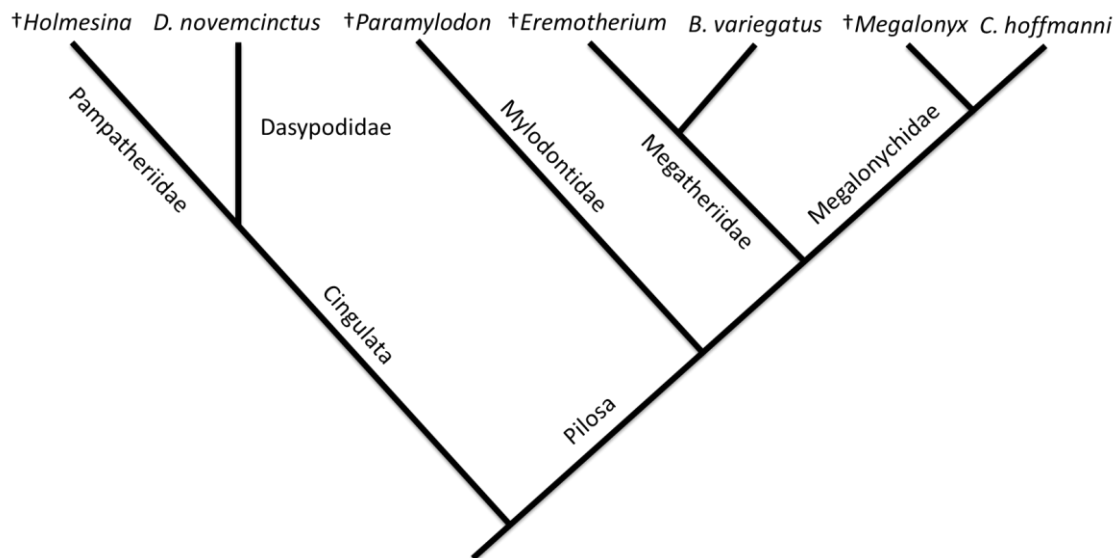


Figure 2: Simplified cladogram showing currently accepted relationships between taxa in this study. Extinct genera designated with †. Use of Pilosa rather than Folivora done to prevent seeming exclusion of myrmecophagous xenarthrans (based on Engelmann 1985, Patterson and Pascual 1968, Webb 1985).

The three ground sloths are thought to have subtle differences in diet and feeding style based on morphology and other paleoecological proxies. For example, the Megatheriid giant ground sloth, *Eremotherium eomigrans*, one of the largest sloths to

ever live, is thought to fill the role of a “high-browser”, similar to an elephant or giraffe; feeding from the tops of trees using both its height and long clawed arms to pull branches towards its mouth (McDonald 2005). This claim is verified by the discovery of branches in tar seeps which match the *Eremotherium*'s unique dentition (McDonald 2005). Further, in North America, fossils of *Eremotherium* are found on coastal plains or along waterways, suggesting a preferred habitat of gallery forests (McDonald 1995).

The Megalonychid ground sloth *Megalonyx leptostomus* is also thought to be a browser, but one that focused on nutrient rich foods relative to *Eremotherium* (McDonald 2005). The genus *Megalonyx* is the most common ground sloth found in North America and while often found in the same localities as *Eremotherium*, it is not restricted to gallery forests (McDonald 1995), possibly indicating a more generalist browse diet. These kinds of differences could yield differences in microwear, as nutrient rich foods could require less oral processing and/or may be softer than other vegetal matter consumed by other ground sloths.

Harlan's ground sloth, *Paramylodon harlani*, was originally interpreted as a grazer by Stock (1925). Since then, there has been much debate on the specific diet of this animal with proponents arguing for the original interpretation, a browser, or a mixed feeder (see Ruez 2005 for summary but also Allen 1913, Brown 1903, Dalquest and Schultz 1992, Lull 1915, Naples 1989, Parker 1885, Stock 1920, Stock 1925, Webb 1978). This original interpretation was based on cranial morphology (Stock 1925). *Paramylodon* has a wider premaxillary region than other ground sloths, and wider mouths in herbivores are generally associated with a grazing lifestyle (Dompierre and Churcher 1996, McDonald 2005). A broader snout in the closely related genus

Glossotherium (Gaudin 1995, 2004) yielded increased surface area for grasping and nipping food, and also allowed for greater freedom for the tongue to manipulate food within the oral cavity (Hirschfeld 1985), which could affect microwear texture. Further, preliminary isotopic work suggests a mixed diet relying heavily on C₄ grasses, but these results did not test for possible diagenetic alteration of the dental tissue (Ruez 2005). Regardless, the lack of specialized morphology does seem to indicate more generalized feeding habits (McDonald 2005). *Paramylodon* also spanned a very large geographical range from Florida to California (McDonald et al. 2004) presumably meaning it was capable of subsisting on a variety of different vegetal matter, even spanning the divide between browsing and grazing. Based upon these inferences, *Paramylodon* might then be expected to show the greatest dietary variation between glacial and interglacial sites, altering its diet from primarily browsing to grazing, depending on floral availability.

The armadillo-like cingulate *Holmesina* has been thought to fall somewhere closer to a pure grazing dietary niche, a lifestyle not achieved by any other group of xenarthrans. Within the genus *Holmesina*, it has been argued that tendencies towards grazing increase with increasing size (McDonald 2005). However, all *Holmesina* possess a jaw structure and inferred masticatory musculature distinct from modern armadillos, including the ability to chew laterally (Edmund 1985). Thus, they are thought to be capable of processing coarse vegetation common in a grazing diet, in contrast to modern armadillos (Edmund 1985, Vizcaíno et al. 1998).

Understanding the paleoecology and paleobiology of extinct megafauna is critical to understanding past environments. However, as the dietary distinctions in xenarthrans noted above are often speculative and difficult to ascertain via geochemical tools,

community ecology is far from well understood in numerous regions that contain an abundance of xenarthrans.

Previous work on xenarthran microwear

High-magnification scanning electron microscope (SEM) dental microwear has been used for decades to analyze animal diets (Teaford 1988a, Walker et al. 1978). Newer methods utilize lower-magnification light images of the wear facet, the area of the tooth being used to process food items, and rely on the same principle as high-magnification microwear by using a human observer to count features such as pits and scratches (Solounias and Semprebon 2002). Analysis of a three-dimensional surface in two dimensions has the potential for distortion and misidentification of features, and the use of human observers increases potential biases (Galbany et al. 2005, Grine et al. 2002, Muhlbachler et al. 2012). Galbany et al. (2005) showed significant inter-observer variation when analyzing microwear striations under high-magnification; as such observations are up to the interpretation of the observer and further vary with observer expertise and experience. On the other hand, Grine et al. (2002) found insignificant differences between observers using the Microware 4.0 with SEM micrographs, but did find higher error rates when other methods were applied. Muhlbachler et al. (2012) demonstrated a potential for sampling bias in the low-magnification methodology through analysis of the same tooth facet by multiple observers under light microscopy, whose relative differences and broad ecological conclusions remained consistent, but nevertheless produced significantly different inter-observer absolute results.

Newer methods, such as DMTA, rely on a three dimensional scan of the wear facet at high magnification which is then quantitatively analyzed with scale-sensitive fractal analysis (SSFA) software (Scott et al. 2006). Boyde and Fortelius (1991) were the first to use tandem scanning confocal microscopy to analyze the microwear texture of molars. Their method involved subtracting a smoothed surface from the actual scan of the surface to obtain the microrelief of the tooth, similar to how textural fill volume (*Tfv*) is calculated with DMTA method used here (see page 15; Boyde and Fortelius 1991, Scott et al. 2006). The light confocal profilers create point cloud matrices in three dimensions at a resolution and depth of field comparable to SEM dental microwear studies (Ungar et al. 2003). Later, Boyde and Jones (1995) suggested the use of confocal mapping on epoxy resins casts of fossil teeth to measure surface tooth-wear features made at the end of an animal's life. Since then, the analysis of microwear texture using scanning confocal microscopy has been shown to differentiate diets in groups such as bovids, carnivores, marsupials, and primates, (Prideaux et al. 2009, Schubert et al. 2010, Scott et al. 2006, Scott 2012, Ungar et al. 2007). DMTA characters, which are described in detail below, have been used to differentiate between browsers and grazers, with browsers having greater complexity and lower anisotropy than grazers in taxa as disparate as bovids and macropodid marsupials (Prideaux et al. 2009, Scott 2012). Frugivores, similarly, demonstrate greater complexity and lower anisotropy than folivores in primates and bovids (Scott et al. 2006, Scott 2012).

Furthermore, carnivores consuming a greater proportion of brittle bone have greater complexity and higher average textural fill volume, and lower anisotropy and scale of maximum complexity than carnivores avoiding bone (Schubert et al. 2010).

Schubert et al. (2010) established this correlation by looking at the enamel microwear texture on the lower m1 carnassial tooth of cheetahs (*Acinonyx jubatus*), African lions (*Panthera leo*), and spotted hyenas (*Crocuta crocuta*). These carnassial teeth are specialized for shearing meat, and occlude with the upper carnassial in a motion similar to a pair of scissors closing. Over the animal's lifetime, this motion wears away at the outer layers of enamel, eventually exposing dentin. This creates one of the few examples of a tooth where enamel and dentin can be found on the same tooth being exposed to the same food items and bite forces and it is thus relevant to our study of xenarthran microwear because it allows us to directly compare the wear texture of two different dental materials from one tooth.

While the microscopic surfaces of xenarthran teeth have been analyzed in conjunction with mandibular biomechanics to reconstruct how certain extinct taxa may have chewed (Bargo et al. 2009, Fariña and Vizcaíno 2001, Vizcaíno et al. 1998, and Vizcaíno and Fariña 1997), the use of xenarthran microwear for interspecific comparisons has been limited. Previous studies have used high- and low-magnification microscopy to count pits and scratches on teeth and have revealed significant differences in the microwear patterns, but not the microwear texture, of extant tree sloths and armadillos (Green 2009b, Green and Resar 2012, Oliveira 2001). Techniques have been developed to help control and account for observer bias in these 2D analyses (i.e., re-coding specimen images so that observers are not aware of the taxon being examined; Green and Resar 2012); however, herein we aim to further distinguish dietary classifications by studying dental microwear in three dimensions, using a more automated method that is less prone to interobserver differences.

DMTA characteristics

Scale-sensitive fractal analysis (SSFA) relies on the idea that the texture of a surface changes with the scale of observation (Scott et al. 2006). A surface that appears smooth at a gross scale may evince a rougher texture at a finer scale; consider a hill as observed from space versus walking it on the ground. Area-scale fractal complexity ($Asfc$) is a measure of how much surface roughness changes with the scale of observation; animals that eat more brittle food, such as bone or nuts, tend to have more complex microwear textures (Fig. 3a; Scott et al. 2005, Scott et al. 2006, Ungar et al. 2003). Scale of maximal complexity (Smc) is the point wherein roughness increase begins to tail off with decreasing scale of observation and can help differentiate between coarse deep wear features and small fine wear features (Scott et al. 2006, Schubert et al. 2010). Heterogeneity of complexity ($HAsfc$) is determined by subdividing the scanned area and assessing variance in complexity among the subdivisions (Fig. 3c-d; Ungar et al. 2003). Thus, a heterogeneous surface texture will show a high $HAsfc$ value (Fig. 3c) whereas a more uniform surface texture will show a low $HAsfc$ (Fig. 3d; Scott et al. 2006). Here we report and analyze heterogeneity using 3x3 and 9x9 subdivided grids.

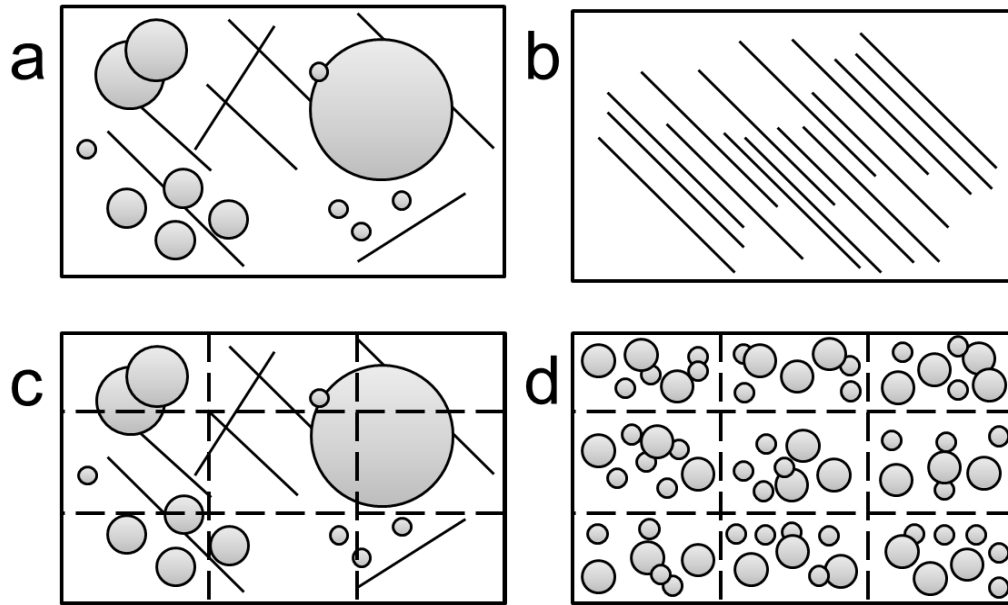


Figure 3: Idealized reconstructions of DMTA surface characteristics showing: a) high complexity, b) high anisotropy, c) low heterogeneity, d) high heterogeneity (modified from Scott et al. 2006).

Length-scale anisotropy of relief (*epLsar*) is a measure of the extent to which microwear surface texture is aligned in a specific direction, with higher anisotropy indicating a greater proportion of features with similar orientations, e.g., Fig. 3b (Prideaux et al. 2009, Scott et al. 2006, Ungar et al. 2003, Ungar et al. 2007). Textural fill volume (*Tfv*) is determined by filling the scanned area with cuboids of known volumes to obtain the aggregate volume of the surface. The volume is first determined at a coarse scale (in this case, 10 μm), and again at a finer scale (2 μm); then the coarse scale volume is subtracted from the finer scale volume to remove the background shape information (e.g., facet curvature) to obtain the volumes of the smaller features themselves (Scott et al. 2006). Animals have higher *Tfv* values when there are many individual features in that 2 – 10 μm range (Schubert et al. 2010).

Goals and objectives

The aim of this study is to explore whether or not dentin is a suitable dental material for microwear texture analysis. We attempt to answer this by asking the following questions: i) are there consistent differences between dentin and enamel from individual teeth that have been subjected to the same food items and chewing mechanisms (e.g., carnassial teeth); ii) can DMTA be used to differentiate between extant xenarthrans with known differences in diet; iii) can DMTA be used to differentiate between the same fossil taxa at different localities (i.e., different environments), iii) can DMTA differentiate between extinct xenarthrans presumed to have differences in diet; iv) does dental microwear differ between like taxa from different sites; and ultimately, vi) is dentin microwear a reliable and comparable indicator of dietary ecology?

CHAPTER II

MATERIALS AND METHODS

Acquisition and preparation of specimens

All tooth specimens for this study were acquired from museum collections. Florida panther (*Puma concolor coryi*) samples ($n = 14$) were obtained from the mammalogy collection of the Florida Museum of Natural History (FLMNH; Table 1). All xenarthran teeth samples were obtained from the collections of FLMNH, the American Museum of Natural History (AMNH), the Harvard Museum of Comparative Zoology (MCZ), and the University of Arkansas Biological Research Center (UABR). For this study, we analyzed 12 brown-throated sloths (*Bradypus variegatus*), 9 Hoffman's two-toed sloths (*Choloepus hoffmanni*), and 12 nine-banded armadillos (*Dasypus novemcinctus*; Table 2). Extinct specimens were obtained from the vertebrate paleontology collection of FLMNH. We analyzed 4 *Eremotherium*, 20 *Holmesina*, 12 *Megalonyx*, and 15 *Paramylodon*. Some specimens could be identified to species level, in which case they are presented as one of the following in Table 3: *Eremotherium eomigrans*, *Holmesina floridanus*, *Megalonyx leptostomus*, or *Paramylodon harlani*. Original specimens were borrowed from collections when possible so that teeth could be scanned directly (Table 2). When this was not possible, original specimens were cleaned with acetone-soaked cotton swabs and molded with regular body polyvinylsiloxane dental impression material (President's Jet, Coltène-Whaledent Corp., Cuyahoga Falls,

OH, USA). Texture analysis was done on replicas prepared from these molds using an epoxy resin and hardening catalyst (Epotek 301, Epoxy Technologies Corp., Billerica, MA, USA).

Scanning

Scans of Florida panther teeth were taken on the buccal side of the anterior cusp of the mandibular first molar (m1) carnassial in keeping with Van Valkenburgh et al. (1990) and Schubert et al. (2010). Each tooth was scanned twice, once on the enamel portion of the tooth, per Schubert et al. (2010), and again on the exposed dentin immediately above the enamel scan (Fig. 4). For xenarthrans, we scanned the outer dentin's occlusal surface on molariform teeth. Armadillo teeth have a cap of orthodentin, whereas sloths have an external coating of cementum with a ridge of outer dentin (composed of orthodentin) around a center of inner dentin (or orthovasodentin) (Fig. 1; Green 2009a, Ungar 2010). All analyses were conducted on the outer dentin of molariform teeth. Whenever possible, the molariform tooth used followed Green (2009a, 2009b); however, some of our specimens were isolated teeth, so specific identification beyond molariform was not possible. Tooth number, if known, is listed in Table 2.

Table 1 – List of Florida panther (*Puma concolor coryi*) samples from the mammalogy collection at FLMNH.

| Specimen ID | Tooth |
|--------------------|--------------|
| UF20777 | right m1 |
| UF27148 | left m1 |
| UF27370 | left m1 |
| UF27616 | right m1 |
| UF27618 | right m1 |
| UF29263 | right m1 |
| UF29621 | right m1 |
| UF29819 | right m1 |
| UF30391 | right m1 |
| UF30935 | right m1 |
| UF30960 | right m1 |
| UF31021 | right m1 |
| UF31333 | left m1 |
| UF31759 | right m1 |

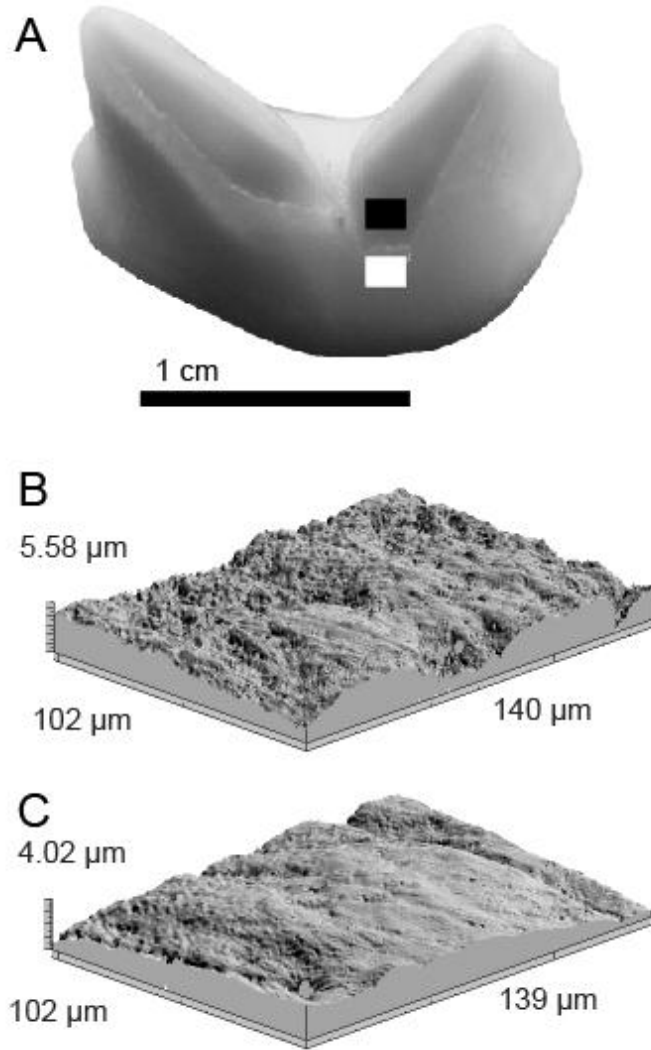


Figure 4: Buccal view of a mandibular m1 carnassial from *P. concolor* (A, UF 31759) including representative 3-D photosimulations of microwear surfaces of enamel (B) and dentin (C) from the same specimen (UF30391). The black and white rectangles (A) are representations 5x greater in magnitude than the actual scanned area of dentin and enamel, respectively.

Table 2 – Sample list of extant xenarthrans, all teeth refer to lower molariforms, loose teeth are identified as ‘m’ for molariform, and asterisks indicate that the scan was of an actual tooth.

| <i>Taxon</i> | Specimen ID | Tooth | <i>Taxon</i> | Specimen ID | Tooth | <i>Taxon</i> | Specimen ID | Tooth |
|----------------------|--------------------|--------------|---------------------|--------------------|--------------|------------------------|--------------------|--------------|
| <i>B. variegatus</i> | AMNH25986 | 2 | <i>C. hoffmanni</i> | MCZ12342 | 2 | <i>D. novemcinctus</i> | AMNH91706 | 2 |
| | AMNH25992 | 4 | | MCZ12344 | 2 | | UABRC885027* | 4 |
| | AMNH96242 | 3 | | MCZ21503 | 2 | | UABRC885028* | 6 |
| | AMNH96244 | 3 | | UF14762 | 3 | | UF3233* | 5 |
| | AMNH96248 | 3 | | UF25984 | m | | UF3236* | 2 |
| | AMNH96251 | 3 | | UF25988 | 3 | | UF4928* | 4 |
| | MCZ34333 | 1 | | UF25990* | m | | UF4929 | 5 |
| | UF14761 | 4 | | UF25993 | m | | UF4934 | 2 |
| | UF24821 | 2 | | UF25994* | m | | UF5091 | 2 |
| | UF25983* | 2 | | | | | UF5092 | m |
| | UF25986 | 2 | | | | | UF5093 | 6 |
| | UF25987 | 2 | | | | | UF7866 | 5 |

Table 3 – Sample list for extinct xenarthrans. Tooth identifications are from the FLMNH database.

| Taxon | Specimen ID | Site | Tooth |
|-------------------------------|--------------------|-------------|--------------|
| <i>Eremotherium</i> | 22S x 45E 1 Nov | Haile 7G | t |
| <i>Eremotherium</i> | 25S x 19E 8 Apr | Haile 7G | t |
| <i>Eremotherium</i> | 20S x 17E 8 Apr | Haile 7G | t |
| <i>Eremotherium eomigrans</i> | UF95868 | Inglis 1A | m |
| <i>Holmesina</i> | Field #HF7 | Haile 7G | t |
| <i>Holmesina</i> | 48S x 37E 5 Apr | Haile 7G | t |
| <i>Holmesina floridanus</i> | UF83713 | Haile 7G | m |
| <i>Holmesina floridanus</i> | UF223812 | Haile 7G | t |
| <i>Holmesina floridanus</i> | UF224650 | Haile 7G | 5 |
| <i>Holmesina floridanus</i> | UF223813 | Haile 7G | 3 |
| <i>Holmesina floridanus</i> | UF20952 | Inglis 1A | 1 |
| <i>Holmesina floridanus</i> | UF227651 | Inglis 1A | t |
| <i>Holmesina floridanus</i> | UF227650 | Inglis 1A | t |
| <i>Holmesina floridanus</i> | UF20948 | Inglis 1A | 7 |
| <i>Holmesina floridanus</i> | UF227649 | Inglis 1A | t |
| <i>Holmesina floridanus</i> | UF256168 | Inglis 1A | m |
| <i>Holmesina floridanus</i> | UF256166 | Inglis 1A | m |
| <i>Holmesina floridanus</i> | UF227653 | Inglis 1A | t |
| <i>Holmesina</i> | UF66422 | Leisey 1A | 9 |
| <i>Holmesina floridanus</i> | UF82000 | Leisey 1A | m |
| <i>Holmesina floridanus</i> | UF86419 | Leisey 1A | m |
| <i>Holmesina floridanus</i> | UF86544 | Leisey 1A | t |
| <i>Holmesina floridanus</i> | UF86575 | Leisey 1A | m |
| <i>Holmesina floridanus</i> | UF93274 | Leisey 1A | 1or2 |
| <i>Megalonyx</i> | MEG #3 | Haile 7G | t |
| <i>Megalonyx</i> | Poyer Oct 2005 | Haile 7G | t |
| <i>Megalonyx</i> | 20S x 42E 27-9 | Haile 7G | t |

| | | | |
|------------------------------|-----------------|-----------|----|
| <i>Megalonyx</i> | 22S x 43E 1 Nov | Haile 7G | t |
| <i>Megalonyx</i> | NFD 9 Aug | Haile 7G | t |
| <i>Megalonyx</i> | 17S x 42E 8 Nov | Haile 7G | t |
| <i>Megalonyx leptostomus</i> | UF227654 | Inglis 1A | c |
| <i>Megalonyx leptostomus</i> | UF227656 | Inglis 1A | c |
| <i>Megalonyx leptostomus</i> | UF227659 | Inglis 1A | m |
| <i>Megalonyx leptostomus</i> | UF227661 | Inglis 1A | m |
| <i>Megalonyx leptostomus</i> | UF227658 | Inglis 1A | Mx |
| <i>Megalonyx leptostomus</i> | UF227660 | Inglis 1A | Mx |
| <i>Paramylodon</i> | UF227662 | Inglis 1A | m |
| <i>Paramylodon harlani</i> | UF95810 | Inglis 1A | 3 |
| <i>Paramylodon harlani</i> | UF95814 | Inglis 1A | m |
| <i>Paramylodon harlani</i> | UF95813 | Inglis 1A | Mx |
| <i>Paramylodon harlani</i> | UF80084 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF80367 | Leisey 1A | 4 |
| <i>Paramylodon harlani</i> | UF67438 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF80214 | Leisey 1A | 3 |
| <i>Paramylodon harlani</i> | UF67448 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF67429 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF67448 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF67748 | Leisey 1A | 1 |
| <i>Paramylodon harlani</i> | UF80175 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF87059 | Leisey 1A | 2 |
| <i>Paramylodon harlani</i> | UF87069 | Leisey 1A | 2 |

All scanning was done based on the methods developed and outlined in Ungar et al. (2003) and Scott et al. (2006). Specifically, carnivore teeth were scanned in accordance with Schubert et al. (2010). Specimens were scanned at the University of Arkansas with a Sensofar Plμ white-light scanning confocal profiler (Solarius Development Inc., Sunnyvale, California) using a 100x objective lens. Resulting point clouds had a 0.18 μm horizontal spacing and vertical resolution of 0.005 μm. Four adjacent scans of each tooth were taken for a total area of 276 μm by 204 μm (Fig. 4). These surfaces were then leveled using SolarMap Universal software (Solarius Development Inc., Sunnyvale, CA) and, if necessary, minor editing was used to exclude dust particles or other artifacts from analysis.

Data processing and statistical analysis

Once all scanning was completed, SSFA analysis was used to calculate $Asfc$, $epLsar$, Smc , Tfv , and $HAsfc$ using ToothFrax and SFrax software (Scott et al. 2005, Ungar et al. 2003, Ungar et al. 2007).

DMTA studies often use non-parametric statistics and/or ANOVAs of ranked data as DMTA data are not typically normally distributed (Schubert et al. 2010, Scott et al. 2006). We too used mostly nonparametric tests, but we also used less conservative parametric tests when Shapiro-Wilk normality test results indicated it appropriate to minimize risk of Type II error. Florida panther samples were compared using the pairwise Wilcoxon signed-rank test, a non-parametric alternative to the Student's paired t-test, to look for significant differences in the means of each DMTA character. We also

used Brown-Forsythe, which tests for significant differences in the variances of two sets of data using the median, as opposed to the mean in Levene's test, because the former is considered more robust against non-normal data than that latter. Additionally, characteristics that are normally distributed were also compared using paired Student's t-tests. Xenarthran data were compared to one another using Kruskal-Wallis tests, which is a non-parametric test equivalent to a one-way analysis of variance (ANOVA), which determines if two sets of independent data originate from the same distribution. A Mann-Whitney U test was used when testing between two samples, but for three or more groups a Kruskal-Wallis analysis is more efficient. As with the Florida panthers, Brown-Forsythe tests were used to test for differences in variance of DMTA characteristics between xenarthran taxa.

Dental microwear texture studies typically focus primarily on *Asfc* and *epLsar* as ways of assessing the proportion of hard object feeding in various taxa, and these traits are usually sufficient to parse out dietary niche space in enamel-bearing taxa. However, as each DMTA character represents a distinct aspect of the animal's diet (Scott et al. 2006), in our comparisons of dentine and enamel in carnassials we compared all characteristics between the two materials. For the xenarthrans, we also compared all DMTA characteristics but did attempt to make distinctions of niche space based on *Asfc* and *epLsar* in keeping with previous studies of enamel-bearing taxa.

CHAPTER III

RESULTS

Florida panther dentin versus enamel

The only two characters to show significant variation in central tendency, i.e. mean values, between enamel and dentin are *Tfv* and *Hasfc_{9x9}* (Table 4). All parametric tests, when performed, confirmed results of non-parametric analyses. Dentin *Tfv* and *Hasfc_{9x9}* values were significantly higher and lower for dentin than enamel *Hasfc_{9x9}* respectively (Table 4). In contrast, comparisons of variance failed to show significant variation between enamel and dentin for any texture attribute.

Table 4 – Descriptive and comparative statistics of Florida panther samples ($n = 14$) noting means, standard deviations (SD), and P -values for normality of both enamel and dentin data. Samples were compared by looking at the mean absolute deviation between characters and using both a Wilcoxon signed-rank test (non-parametric) and a two-sample paired Student’s T-test (parametric), when normally distributed according to a Shapiro-Wilk test.

| | | enamel | dentin | deviation | P -value _(np) | P -value _(p) |
|-------------------------------|----------------------|-------------------|-------------------|-----------|----------------------------|---------------------------|
| <i>Asfc</i> | Median | | | | | |
| | Mean | 3.941 | 4.847 | 2.184 | 0.346 | 0.244 |
| | SD | 1.670 | 2.762 | 1.862 | - | - |
| | Normality P -value | 0.230 | 0.573 | | - | - |
| <i>epLsar</i> | Median | | | | | |
| | Mean | 0.0029 | 0.0036 | 0.0014 | 0.149 | 0.171 |
| | SD | 0.0014 | 0.0015 | 0.0010 | - | - |
| | Normality P -value | 0.6050 | 0.6320 | | - | - |
| <i>Smc</i> | Median | | | | | |
| | Mean | 1.108 | 2.399 | 3.189 | 0.286 | - |
| | SD | 2.614 | 7.463 | 7.615 | - | - |
| | Normality P -value | <0.0001 | <0.0001 | | - | - |
| <i>Tfv</i> | Median | | | | | |
| | Mean | 9020 | 13258 | 5589 | 0.001 | 0.008 |
| | SD | 4625 | 3466 | 3370 | - | - |
| | Normality P -value | 0.982 | 0.543 | | - | - |
| <i>HAsfc</i> _(3x3) | Median | | | | | |
| | Mean | 0.443 | 0.384 | 0.194 | 0.286 | - |
| | SD | 0.193 | 0.186 | 0.140 | - | - |
| | Normality P -value | 0.221 | 0.013 | | - | - |
| <i>HAsfc</i> _(9x9) | Median | | | | | |
| | Mean | 0.968 | 0.621 | 0.451 | 0.020 | - |
| | SD | 0.530 | 0.308 | 0.446 | - | - |
| | Normality P -value | 0.027 | 0.028 | | - | - |

Significant P -values are in bold.

Extant xenarthrans

Example photosimulations of extant xenarthran microwear texture can be seen in Fig. 5. No significant differences in texture central tendencies were found between the two extant sloth species, *B. variegatus* and *C. hoffmanni* however, *C. hoffmanni* has significantly lower variation than *B. variegatus* in *Smc* (Table 5, 6). We also combined the two sloth species into the group Folivora. This was done based on the lack of significant differences between the central tendencies in the majority of their microwear characters, as well as the known overlaps of their arboreal diets in contrast to the terrestrial and therefore distinct *D. novemcinctus*. Further, *D. novemcinctus* does have significantly greater *Asfc* than Folivora. *B. variegatus*, the obligate folivore, also has significantly lower mean *Tfv* values than *D. novemcinctus* (Table 6), consistent with the latter consuming harder objects (including invertebrate exoskeletons) than the former. As for analyses of dispersion, *Smc* variation was significantly higher in *C. hoffmanni* than *B. variegatus* ($P=0.044$). And, $HA_{sfc(9 \times 9)}$ varied more in *D. novemcinctus* than *B. variegatus* and Folivora (Table 6). A plot of *Asfc* vs. *epLsar* for extant xenarthran (Fig. 6) shows considerably overlap between all three taxa.

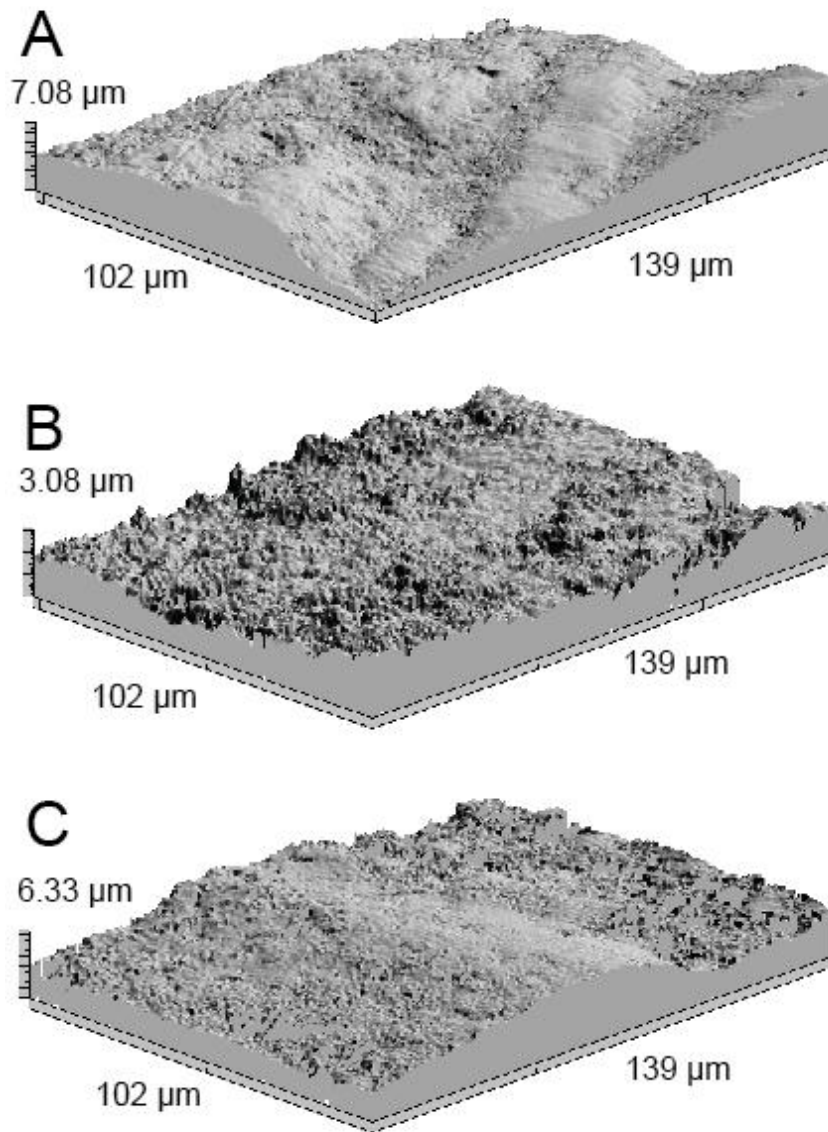


Figure 5: 3D simulation of surface texture scans. A) *Dasypus novemcinctus* (UF4934) , B) *Choloepus hoffmanni* (UF25984), and, C) *Bradypus variegatus* (UF14761).

Table 5 – Descriptive statistics of extant xenarthran samples including mean, standard deviation (SD), median, and *P*-values for normality. Normality *P*-values were calculated using a Shapiro-Wilk test.

| <i>Taxon</i> | Statistic | <i>n</i> | <i>Asfc</i> | <i>epLsar</i> | <i>Smc</i> | <i>Tfv</i> | <i>HAsfc</i> (3x3) | <i>HAsfc</i> (9x9) |
|-----------------------------|-------------------------------|----------|-------------|---------------|--------------------|--------------|--------------------|--------------------|
| <i>Bradypus variegatus</i> | mean | 12 | 3.783 | 0.0024 | 1.662 | 11166 | 0.306 | 0.582 |
| | SD | | 2.605 | 0.0012 | 3.392 | 4218 | 0.089 | 0.139 |
| | median | | 4.062 | 0.0021 | 0.154 | 12197 | 0.268 | 0.575 |
| | <i>P</i> -value for normality | | 0.370 | 0.003 | < 0.0001 | 0.655 | 0.029 | 0.992 |
| <i>Choloepus hoffmanni</i> | mean | 9 | 3.673 | 0.0020 | 33.131 | 12159 | 0.358 | 0.660 |
| | SD | | 2.607 | 0.0006 | 50.960 | 4370 | 0.132 | 0.230 |
| | median | | 3.860 | 0.0019 | 0.213 | 13476 | 0.315 | 0.648 |
| | <i>P</i> -value for normality | | 0.509 | 0.442 | 0.001 | 0.018 | 0.467 | 0.390 |
| <i>Dasypus novemcinctus</i> | mean | 12 | 7.521 | 0.0030 | 9.970 | 14333 | 0.390 | 0.868 |
| | SD | | 5.853 | 0.0012 | 32.350 | 2059 | 0.192 | 0.447 |
| | median | | 5.552 | 0.0033 | 0.154 | 14311 | 0.324 | 0.690 |
| | <i>P</i> -value for normality | | 0.023 | 0.273 | < 0.0001 | 0.007 | 0.035 | 0.055 |

Significant *P*-values are in bold.

Table 6 – A summary of *P*-value results of Kruskal-Wallis and Brown-Forsythe tests between extant xenarthran taxa. Sloths (*B. variegatus* and *C. hoffmanni*) were compared to *D. novemcinctus* individually, as well as grouped together (suborder Folivora) and compared using a Mann-Whitney U test.

| Kruskal-Wallis Test | | | Brown-Forsythe Test | | |
|--------------------------|---------------------|------------------------|--------------------------|---------------------|------------------------|
| <i>Asfc</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> | <i>Asfc</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> |
| <i>B. variegatus</i> | 0.784 | 0.083 | <i>B. variegatus</i> | 0.786 | 0.247 |
| <i>C. hoffmanni</i> | - | 0.061 | <i>C. hoffmanni</i> | - | 0.272 |
| Folivora | - | 0.038 | Folivora | - | 0.180 |
| <i>epLsar</i> | | | <i>epLsar</i> | | |
| <i>B. variegatus</i> | 0.523 | 0.272 | <i>B. variegatus</i> | 0.708 | 0.304 |
| <i>C. hoffmanni</i> | - | 0.098 | <i>C. hoffmanni</i> | - | 0.063 |
| Folivora | - | 0.120 | Folivora | - | 0.131 |
| <i>Smc</i> | | | <i>Smc</i> | | |
| <i>B. variegatus</i> | 0.630 | 0.673 | <i>B. variegatus</i> | 0.044 | 0.386 |
| <i>C. hoffmanni</i> | - | 0.927 | <i>C. hoffmanni</i> | - | 0.218 |
| Folivora | - | 0.837 | Folivora | - | 0.684 |
| <i>Tfv</i> | | | <i>Tfv</i> | | |
| <i>B. variegatus</i> | 0.228 | 0.027 | <i>B. variegatus</i> | 0.904 | 0.098 |
| <i>C. hoffmanni</i> | - | 0.397 | <i>C. hoffmanni</i> | - | 0.190 |
| Folivora | - | 0.064 | Folivora | - | 0.078 |
| <i>HAsfc(3x3)</i> | | | <i>HAsfc(3x3)</i> | | |
| <i>B. variegatus</i> | 0.335 | 0.191 | <i>B. variegatus</i> | 0.549 | 0.283 |
| <i>C. hoffmanni</i> | - | 0.804 | <i>C. hoffmanni</i> | - | 0.598 |
| Folivora | - | 0.340 | Folivora | - | 0.297 |
| <i>HAsfc(9x9)</i> | | | <i>HAsfc(9x9)</i> | | |
| <i>B. variegatus</i> | 0.325 | 0.069 | <i>B. variegatus</i> | 0.122 | 0.035 |
| <i>C. hoffmanni</i> | - | 0.486 | <i>C. hoffmanni</i> | - | 0.224 |
| Folivora | - | 0.130 | Folivora | - | 0.024 |

Significant *P*-values are in bold.

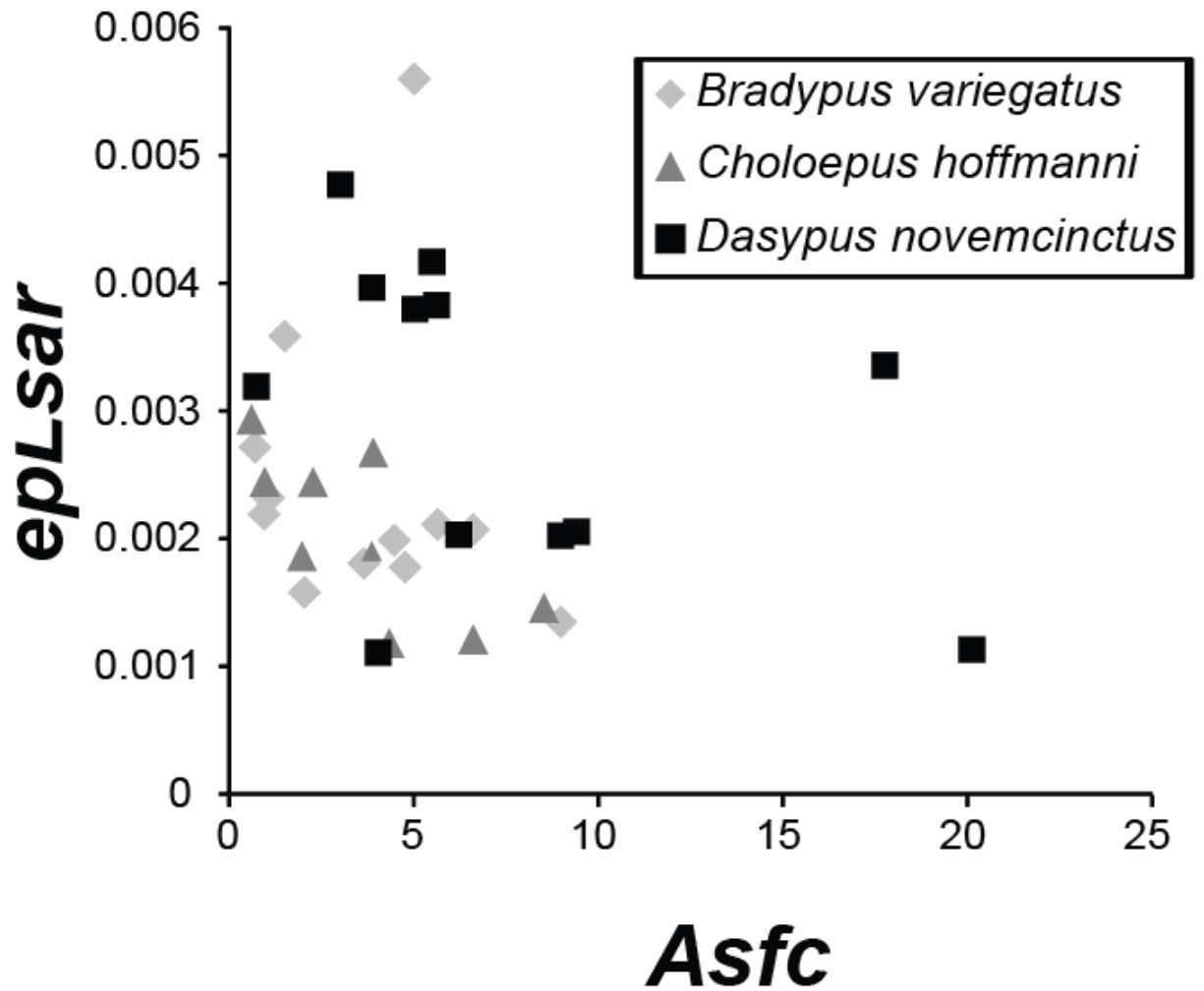


Figure 6: Anisotropy ($epLsar$) versus complexity ($Asfc$) of extant xenarthran samples.

Extinct xenarthrans

No extinct xenarthran species showed statistically significant differences between any sites (for like taxa); therefore, all values referred to herein are combined values for all

sites sampled. *Holmesina* had the highest *Asfc* and the highest *Tfv*, followed by *Megalonyx*, *Paramylodon*, and then *Eremotherium*. *Smc*, *HAsfc*_(3x3), and *HAsfc*_(9x9) show the opposite pattern with *Eremotherium* having the highest value followed by *Paramylodon*, *Megalonyx*, and then *Holmesina*. In terms of *epLsar*, *Paramylodon* had the greatest average *epLsar*, followed closely by *Holmesina*, then *Eremotherium*, and *Megalonyx* (Table 7).

As with the extant xenarthrans, *Tfv* shows the most statistically significant differences amongst taxa. *Holmesina* shows statistically significantly higher *Tfv* than *Eremotherium* ($P=0.001$), *Megalonyx* ($P=0.033$), and *Paramylodon* ($P=0.015$). *Holmesina* also had significantly higher *Asfc* and *epLsar* than *Paramylodon* ($P=0.021$) and *Megalonyx* ($P=0.030$), respectively. There are no significant differences between extinct ground sloths, with the exception of higher *epLsar* in *Paramylodon* than *Megalonyx* ($P=0.014$).

We also compared extant xenarthrans to their extinct ancestors using a Kruskal-Wallis test (Table 8). We found that *Holmesina* has significantly higher *Asfc* than all three extant xenarthrans ($P_{Bv}=0.0003$, $P_{Ch}=0.001$, $P_{Dn}=0.049$). *Holmesina* also had significantly higher *Tfv* than both extant sloths ($P_{Bv}=0.0001$, $P_{Ch}=0.012$). *Megalonyx* has significantly higher *Asfc* than both living sloths ($P_{Bv}=0.024$, $P_{Ch}=0.027$). Alternatively, both *B. variegatus* and *D. novemcinctus* had significantly higher *epLsar* values than *Megalonyx* ($P_{Bv}=0.013$, $P_{Dn}=0.001$). *D. novemcinctus* also has significantly higher *Tfv* than *Eremotherium* ($P=0.021$). Lastly, *Paramylodon* has significantly higher *HAsfc*_(3x3) than *B. variegatus* ($P=0.006$).

Table 7 – Descriptive statistics for all extinct xenarthrans.

| <i>Genus</i> | <i>Site</i> | <i>Statistic</i> | <i>n</i> | <i>Asfc</i> | <i>epLsar</i> | <i>Smc</i> | <i>Tfv</i> | <i>HAsfc</i> _(3x3) | <i>HAsfc</i> _(9x9) |
|---------------------|-------------|------------------|----------|-------------|---------------|------------|------------|-------------------------------|-------------------------------|
| <i>Eremotherium</i> | Haile 7G | median | 3 | 5.806 | 0.00214 | 0.152 | 7253 | 0.419 | 0.588 |
| | | mean | | 4.645 | 0.00224 | 0.190 | 6963 | 0.388 | 0.602 |
| | | SD | | 2.403 | 0.00032 | 0.067 | 6173 | 0.126 | 0.057 |
| | Inglis 1A | median | 1 | 12.643 | 0.00074 | 0.267 | 10979 | 0.667 | 1.413 |
| | | mean | | 12.643 | 0.00074 | 0.267 | 10979 | 0.667 | 1.413 |
| | | SD | | n/a | n/a | n/a | n/a | n/a | n/a |
| | Combined | median | 4 | 6.027 | 0.00206 | 0.209 | 9116 | 0.458 | 0.626 |
| | | mean | | 6.645 | 0.00186 | 0.209 | 7967 | 0.458 | 0.805 |
| | | SD | | 4.454 | 0.00079 | 0.067 | 5426 | 0.173 | 0.408 |
| <i>Holmesina</i> | Haile 7G | median | 6 | 25.361 | 0.00169 | 0.154 | 17035 | 0.396 | 0.587 |
| | | mean | | 25.911 | 0.00206 | 0.154 | 16636 | 0.446 | 0.655 |
| | | SD | | 16.524 | 0.00085 | 0.004 | 2010 | 0.209 | 0.268 |
| | Inglis 1A | median | 8 | 18.375 | 0.00156 | 0.150 | 15822 | 0.315 | 0.627 |
| | | mean | | 21.519 | 0.00187 | 0.158 | 15501 | 0.398 | 0.631 |
| | | SD | | 11.954 | 0.00087 | 0.021 | 1125 | 0.226 | 0.214 |
| | Leisey 1A | median | 6 | 4.725 | 0.00289 | 0.180 | 14305 | 0.407 | 0.554 |
| | | mean | | 12.712 | 0.00266 | 0.212 | 15410 | 0.352 | 0.571 |
| | | SD | | 21.110 | 0.00092 | 0.079 | 2428 | 0.119 | 0.175 |
| | Combined | median | 20 | 17.480 | 0.00180 | 0.151 | 15822 | 0.333 | 0.596 |
| | | mean | | 20.194 | 0.00216 | 0.173 | 15814 | 0.398 | 0.620 |
| | | SD | | 16.447 | 0.00090 | 0.050 | 1840 | 0.188 | 0.212 |
| <i>Megalonyx</i> | Haile 7G | median | 6 | 6.682 | 0.00110 | 0.152 | 11693 | 0.451 | 0.722 |
| | | mean | | 9.105 | 0.00109 | 0.193 | 10988 | 0.558 | 0.821 |
| | | SD | | 7.726 | 0.00045 | 0.077 | 4736 | 0.369 | 0.459 |
| | Inglis 1A | median | 6 | 14.126 | 0.00143 | 0.151 | 15252 | 0.279 | 0.525 |
| | | mean | | 16.672 | 0.00181 | 0.161 | 15475 | 0.294 | 0.544 |

| | | | | | | | | | |
|--------------------|-----------|--------|----|--------|---------|-------|-------|-------|-------|
| | | SD | | 14.755 | 0.00125 | 0.025 | 4214 | 0.082 | 0.191 |
| | Combined | median | 12 | 9.510 | 0.00135 | 0.151 | 12895 | 0.344 | 0.562 |
| | | mean | | 12.888 | 0.00145 | 0.177 | 13232 | 0.426 | 0.683 |
| | | SD | | 11.904 | 0.00097 | 0.057 | 4874 | 0.290 | 0.365 |
| <i>Paramylodon</i> | Inglis 1A | median | 4 | 6.743 | 0.00209 | 0.152 | 14023 | 0.391 | 0.768 |
| | | mean | | 12.010 | 0.00257 | 0.180 | 11713 | 0.427 | 0.722 |
| | | SD | | 13.965 | 0.00198 | 0.058 | 5151 | 0.133 | 0.119 |
| | Leisey 1A | median | 11 | 4.202 | 0.00227 | 0.150 | 13628 | 0.414 | 0.654 |
| | | mean | | 7.376 | 0.00227 | 0.189 | 13204 | 0.445 | 0.700 |
| | | SD | | 6.687 | 0.00087 | 0.064 | 3290 | 0.110 | 0.141 |
| | Combined | median | 15 | 4.836 | 0.00227 | 0.150 | 13628 | 0.413 | 0.685 |
| | | mean | | 8.612 | 0.00235 | 0.187 | 12806 | 0.440 | 0.706 |
| | | SD | | 8.845 | 0.00119 | 0.061 | 3726 | 0.112 | 0.132 |

Table 8 – Comparative statistics between extant and extinct xenarthrans.

| Kruskal-Wallis Test | | | | | | | |
|---------------------|----------------------|---------------------|------------------------|---------------------|----------------------|---------------------|------------------------|
| <i>Asfc</i> | <i>B. variegatus</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> | <i>Tfv</i> | <i>B. variegatus</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> |
| <i>Eremotherium</i> | 0.298 | 0.274 | 1.000 | <i>Eremotherium</i> | 0.338 | 0.112 | 0.021 |
| <i>Holmesina</i> | 0.000 | 0.001 | 0.049 | <i>Holmesina</i> | 0.000 | 0.012 | 0.085 |
| <i>Megalonyx</i> | 0.024 | 0.027 | 0.432 | <i>Megalonyx</i> | 0.178 | 0.737 | 0.569 |
| <i>Paramylodon</i> | 0.156 | 0.151 | 0.895 | <i>Paramylodon</i> | 0.137 | 0.680 | 0.594 |
| <i>epLsar</i> | <i>B. variegatus</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> | <i>HAsfc(3x3)</i> | <i>B. variegatus</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> |
| <i>Eremotherium</i> | 0.492 | 0.885 | 0.172 | <i>Eremotherium</i> | 0.069 | 0.290 | 0.347 |
| <i>Holmesina</i> | 0.499 | 0.875 | 0.080 | <i>Holmesina</i> | 0.111 | 0.675 | 0.835 |
| <i>Megalonyx</i> | 0.013 | 0.110 | 0.001 | <i>Megalonyx</i> | 0.296 | 0.975 | 0.847 |
| <i>Paramylodon</i> | 0.860 | 0.567 | 0.234 | <i>Paramylodon</i> | 0.006 | 0.120 | 0.146 |
| <i>Smc</i> | <i>B. variegatus</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> | <i>HAsfc(9x9)</i> | <i>B. variegatus</i> | <i>C. hoffmanni</i> | <i>D. novemcinctus</i> |
| <i>Eremotherium</i> | 0.749 | 0.932 | 0.981 | <i>Eremotherium</i> | 0.320 | 0.845 | 0.776 |
| <i>Holmesina</i> | 0.318 | 0.215 | 0.123 | <i>Holmesina</i> | 0.678 | 0.447 | 0.108 |
| <i>Megalonyx</i> | 0.366 | 0.255 | 0.165 | <i>Megalonyx</i> | 0.688 | 0.507 | 0.160 |
| <i>Paramylodon</i> | 0.214 | 0.145 | 0.079 | <i>Paramylodon</i> | 0.089 | 0.633 | 0.836 |

Significant *P*-values in bold.

CHAPTER IV

DISCUSSION

Differences between enamel and dentin

Statistically significant differences between dentin and enamel can tell us if there are fundamental differences in the way these tissues record microwear texture. However, we found that only two characteristics, *Tfv* and *HAsfc*_(9x9), show statistically significant differences. Dentin had significantly higher *Tfv* than enamel likely because dentin is softer than enamel (MacFadden et al. 2010) and more likely to form deeper scratches at equivalent forces compared to enamel (Lucas 2004). *HAsfc*_(9x9) values in enamel were significantly higher than dentin likely because heavy microwear overprinting, or the stacking of textural features from multiple feeding events over time, may well swamp within facet variation. The lack of differences between dentin and enamel anisotropy (*epLsar*), scale of maximal complexity (*Smc*), and especially complexity (*Asfc*) are more difficult to explain in light of the material properties of these tissues. It may be that dentin and enamel are recording similar food items differently but inconsistently for these attributes that leads to variation that swamps the differences. This is evidenced by the fact that while statistically significant differences failed to be demonstrated, the differences between these two dental materials are not differing in a consistent way. For example, in terms of complexity (*Asfc*), dentin may be either more or less complex than enamel, which suggests that the lack of significant difference is not necessarily due to

actual similarities, but rather inconsistent differences between dentin and enamel (Table 4). Clearly more work needs to be done to understand this, and despite a lack of significant variation between the tissues in some attributes, the differences in others make it clear that we cannot compare results for these different tissues directly.

Extant xenarthrans

As *D. novemcinctus* is known to have the most diverse diet of the three extant xenarthrans sampled, including the consumption of chitinous exoskeletons, larvae, fruits, fungi, soft invertebrates, and small vertebrates (Chiarello 2008, Redford 1985, Urbani and Bosque 2007), this armadillo species is expected to have the highest complexity. Although no significant differences in *Asfc* were apparent between individual species, Folivora data is statistically distinct from *D. novemcinctus*. This suggests that it may be possible to distinguish between the broad categories of arboreal folivory and fossorial omnivory. However, subtler distinguishing, such as varying degrees of folivory between sloths, may not be possible; thus, these data suggest limiting the use of dentin microwear texture analysis to taxa with broad dietary differences.

Lower *Tfv* seen in *B. variegatus* relative to *D. novemcinctus* is expected based on previous studies of the enamel of lemur teeth (Scott et al. 2009). Specifically, folivorous animals typically have low *Tfv* values compared to animals that eat tougher food (Scott et al. 2009). Similarly, *Smc* values corresponds to the scale of the wear causing material (Scott et al. 2006) with greater variation in these values suggestive of greater variation in the size of food objects being consumed by *C. hoffmanni*, as compared to *B. variegatus*.

This is consistent with the individual preference of *B. variegatus* not only for a small number of specific tree species, but also for leaf buds over mature leaves as the former are softer and easier to digest (Urbani and Bosque 2007), whereas *C. hoffmanni* will consume leaves, but also flowers, branches, and fruit (Meritt 1985), i.e., food likely masticated into particles of different sizes.

Mean values for *epLsar* in sloths are on the lower end of the spectrum than mean *epLsar* values typical of browsing taxa (Prideaux et al. 2009, Ungar et al. 2007).

According to Ungar et al. (2007), browsing bovids have average *epLsar* values between approximately 0.002 and 0.005, and Prideaux et al. (2009) similarly found average *epLsar* values of around 0.004 for marsupial browsers. Whereas both *Bradypus* and *Choloepus* had average *epLsar* values of 0.0024 and 0.0020 respectively (Table 5).

Anisotropy is typically lower in browsers than grazers (Prideaux et al. 2009, Scott et al. 2005, Ungar et al. 2007); however, greater anisotropy is also found in folivorous primates as compared to frugivorous primates, and extant sloths have comparable dietary niches to other neotropical arboreal monkeys (Scott et al. 2005). Scott et al. (2005) showed that the folivorous mantled howler monkey (*Alouatta palliata*) has significantly higher *epLsar* and lower *Asfc* than the frugivorous/hard-object feeding tufted capuchin (*Cebus apella*). The mean *Asfc* values of *B. variegatus* and *C. hoffmanni* fall in between the mean values exhibited by the primates. Alternatively, both sloths show mean *epLsar* values below *Cebus apella*. This further suggests the difficulty of direct comparison between enamel and dentin microwear values.

In contrast, *D. novemcinctus*, has the same mean *epLsar* value (0.003; Table 5) as the spotted hyena (*Crocuta crocuta*), and the African lion (*Panthera leo*; Schubert et al.

2010). This is not to say that there is an overlapping dietary niche between armadillos and feliformes, rather that *D. novemcinctus* consumes small vertebrates (Sikes et al. 1990), shelled insects (da Silveira Anacleto 2007), and a considerable amount of grit (McDonough and Loughry 2008); thus, leaving dental microwear consistent with durophagy seen in the aforementioned carnivorans (Schubert et al. 2010) or frugivory (Scott et al. 2012). Or it may be due to a softer diet combined with softer dental tissues. Nevertheless, differences in occlusal morphology and chewing biomechanics among taxa surely complicate the story.

There is substantial overlap between *epLsar* and *Asfc* among the three species. This suggests that dentin DMTA may be less able to differentiate between dietary groups than enamel. In other enamel-bearing taxa with similar levels of dietary difference those two characters, even where there is significant overlap, are sufficient to parse out distinctions in food consumption in bovids, primates, marsupials, and carnivores (Prideaux et al. 2009, Schubert et al. 2010, Scott et al. 2006, Scott 2012, Ungar et al. 2007). Additionally, while we might have expected to see some overlap with the sloths due to the highly variable and opportunistic diet of the armadillo, all but two individuals of *D. novemcinctus* have *epLsar* and *Asfc* values that fall within the range of the sloths. Overall, this high amount of overlap between taxa with known distinct diets casts doubt on the efficacy with which dentin microwear texture preserves dietary information.

Differences seen between these groups could be due to differences in mastication, metabolism, and digestion between the two groups. Sloths have simplified dentition (Vizcaíno 2009), and a ruminant-like digestive system (Hintz et al. 1978); they likely spend less time orally processing food items than a sympatric primate eating the

same objects. Further, xenarthrans have low metabolic rates relative to other comparably-sized eutherians (Irving et al. 1942, McNab 1978, Nagy and Montgomery 1980), so they may not be eating as often as primates with similar diets. Dental microwear is dynamic and has been found to vary significantly in as little as 24 hours (Teaford and Oyen 1989). It is also possible that softer dentin preserves a shorter microwear signal than enamel, essentially overwhelming this method's ability to separate and measure individual features; thus, yielding high values in characters such as *Asfc* and *Tfv* and low values for characters like *epLsar*. Further, there are known intertooth variations in low-magnification microwear of xenarthrans (Green 2009a, Green and Resar 2012). Although we attempted to standardize tooth positions, this was not always possible and resulting variation might have contributed noise to the system that swamped actual diet signals. Additionally, it has been shown that there is seemingly random variation in how the dentition is shaped throughout the lifetime of *C. hoffmanni*, with stark morphological differences between individuals from the same region (Hirschfield 1985). This might also yield differences in animals that have similar diets, but different rates of consumption and amount of oral processing of those same food items. These factors could potentially contribute variation in microwear beyond the simple distinction between enamel and dentin.

Extinct xenarthrans

There were initially two reasons for testing extinct xenarthrans even if extant xenarthrans failed to show statistically significant differences in DTMA characters. First, even without a modern baseline statistically significant differences in the texture of

extinct xenarthran teeth still would have indicated differences in diet, even if those differences could not be correlated with living relatives. Second, it was suspected that differences in the hardness of outer dentin amongst xenarthrans might yield more conclusive results for extinct species rather than extant descendants.

MacFadden et al. (2010) showed that there are no statistical differences in the hardness of extinct versus extant xenarthran teeth. However, removing species not included in our analysis (except for *Glossotherium*, which is the closest available relative to *Paramylodon*) does show a trend. All the taxa in our study have average Mohs hardness values of less than 5 and that the extant taxa from our study *Bradypus*, *Choloepus*, and *Dasybus*, have hardness values of 3.5, 3, and 3.6 respectively; whereas the extinct genera, *Eremotherium*, *Glossotherium*, *Holmesina*, and *Megalonyx*, have average hardness values of 3.6, 3.5, 4.8, and 4.3 respectively. Unfortunately, sample sizes are too low for statistical comparisons when taxa are examined at the genus level.

Holmesina showed statistically significantly greater *Tfv* than any other extinct xenarthran. This is consistent with the interpretation that *Holmesina*, unlike the other xenarthrans included in this study, may have been grazing on plants with higher silica contents than the softer browse consumed by the other herbivores examined. *Holmesina* analyzed by MacFadden et al. (2010) showed Mohs hardness values between 4 and 6, on the harder end of the xenarthran teeth sampled. However, *Holmesina* outer dentin (i.e.) is typically poorly preserved, suggesting that it is composed of a softer material (Vizcaíno 2009). High *Tfv* in *Holmesina* could also be due to the way *Holmesina* chews. Unlike other xenarthrans, *Holmesina* is thought to have chewed with a lateral motion, resulting in a dense network of transverse striations on the occlusal surface of the tooth (Edmund

1985). These striations are consistent with the types of patterns expected from grazers (Ungar et al. 2007), but the softness of the tooth relative to enamel seems to have led to much deeper features than see on the teeth of grazers with enamel. However, in other DMTA studies grazing is usually quantified by high *epLsar* and low *Asfc* relative to browsers and hard object feeders (Fig. 7). An alternate explanation is that *Holmesina*, like many modern armadillos, is feeding on hard-shelled insects within grasslands, but insectivores typically have sharp conical teeth, ideal for piercing and gripping the carapace of prey items (Landry 1970). *Holmesina* has completely flat teeth (Fig. 8), which seem poorly suited for an insectivorous lifestyle.

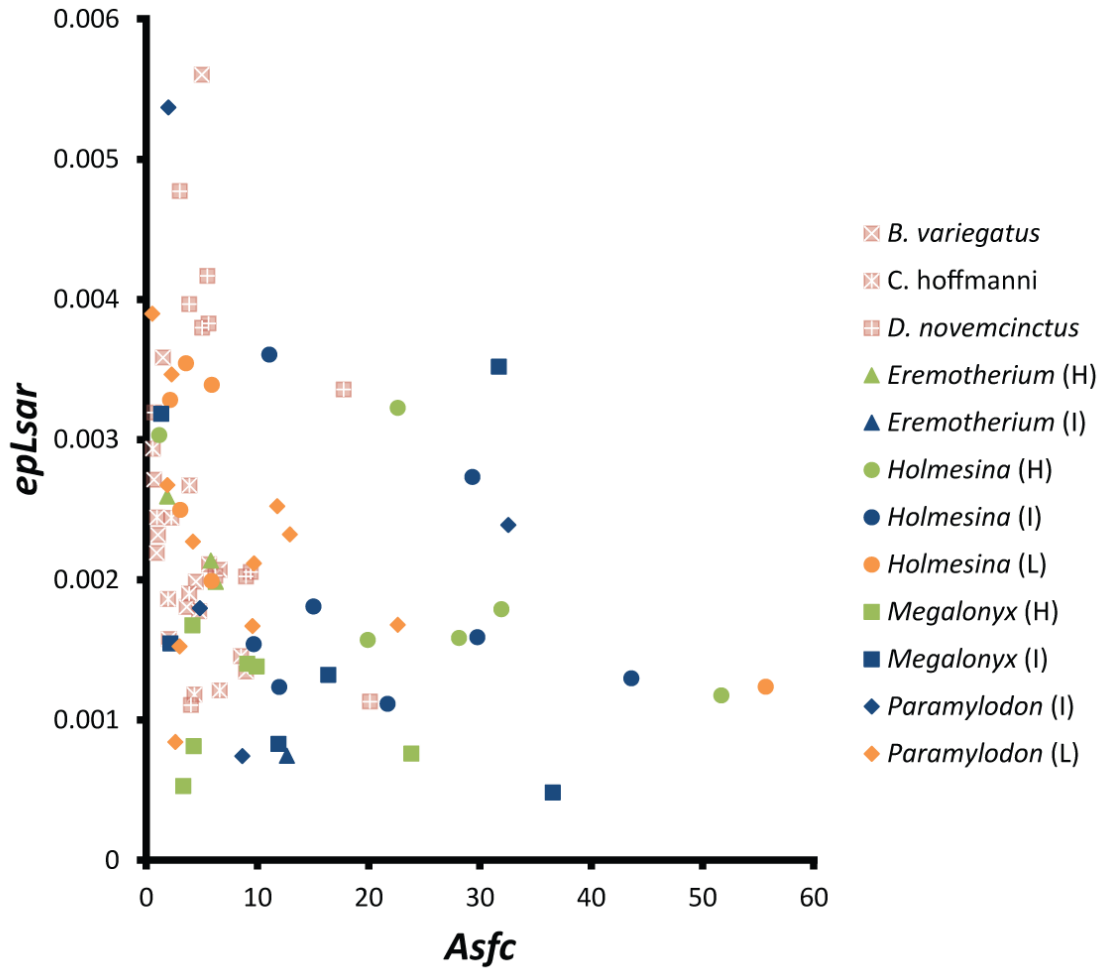


Figure 7: *epLsar* vs. *Asfc* for extinct xenarthrans, showing overlap with extant specimens. (H) indicates a taxa from Haile 7G, (I) indicates taxa from Inglis 1A, and (L) indicates taxa from Leisey 1A.

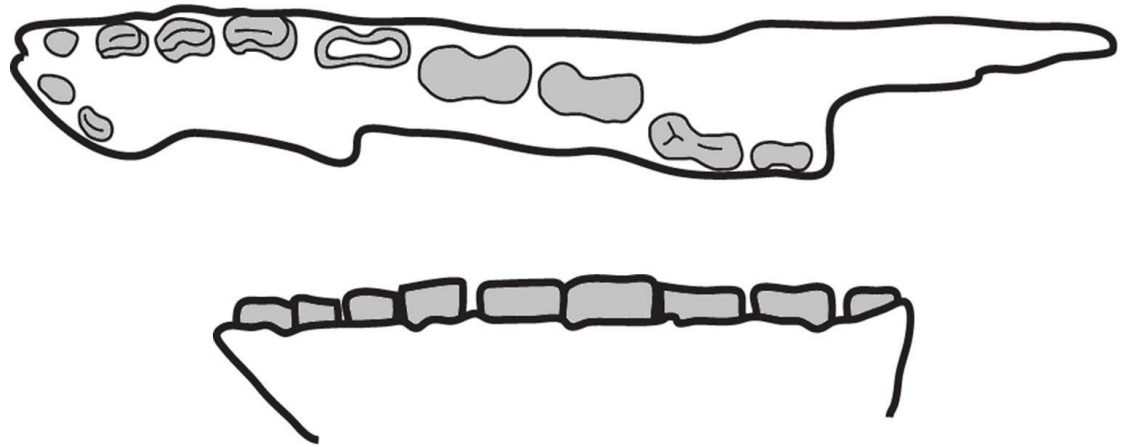


Figure 8: Occlusal and Buccal view of *Holmesina* jaw with teeth (based on Edmund 1985).

All three ground sloths have low *epLsar* values. This is expected for *Eremotherium* and *Megalonyx* due to their morphologically inferred browsing dietary niche, but not necessarily for *Paramylodon* which is inferred to be more of a mixed feeder or grazer. The high degree of overlap between sites for *Paramylodon* also fail to support the idea that *Paramylodon* diet varied with environment or over time, but this idea is still predicated on the presumption that DMTA of dentin is properly characterizing dietary niches in xenarthrans.

Conclusions and applications

This study attempted to address several questions concerning dentin microwear texture (see “Goals and objectives” on page 16). We find that there are not consistent differences between dentin and enamel microwear texture in teeth exposed to the same food items and chewing mechanisms, but further work is needed to evaluate differences

between these tissue types. We also find that while there are some significant differences in the DMTA characteristics of extinct xenarthran teeth, these characteristics are not definitively diagnostic, even given the distinct diets of the taxa examined. This conclusion holds when we examine extinct xenarthrans, but differences between extant and extinct xenarthrans may suggest some level of taphonomic alteration of microwear texture. Dentin microwear texture was not able to distinguish between the same taxa at different sites, even when other lines of paleoenvironmental analysis suggest different food availability at different sites, which undermines the overall utility of dentin microwear texture.

Collectively, these data suggest that dentin microwear texture is able to differentiate between distinct diets in xenarthran taxa with markedly different diets (e.g., sloths versus armadillos) but perhaps not between those with subtly differing diets (e.g., between sloth species). While xenarthran outer dentin is harder relative to typical mammalian orthodontine, it is still soft enough that xenarthran teeth need to grow continuously throughout their lifetime (MacFadden et al. 2010, Vizcaíno 2009). Furthermore, the diets of the animals studied are distinct enough that differences between them should have been obvious using DMTA. These results suggest that there is some useful information being recorded in the outer dentin of xenarthran teeth, but DMTA, as it is applied to enamel, may be limited in its ability to effectively capture and characterize these subtler differences. The combined conclusion from these results is that we should cautiously use dentin microwear texture as a proxy for dietary reconstruction; however, dentin and enamel microwear textures should not be directly compared.

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