Dental microwear of small mammals as a high resolution paleohabitat proxy: opportunities and challenges

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ARTICLE INFO	ABSTRACT
Keywords: Dental microwear Small mammals Taphonomy	The inter-relationships between hominins and their habitat are some of the key questions in human evolution, and the determination of paleohabitats accurately is the foundation for robust reconstructions. Dental microwear is the study of microscopic submicron wear on dentition and provides a unique opportunity to infer paleodiets and paleohabitats of fossil species. However, the ability to infer paleohabitats from paleodiet is scale sensitive. Thus, dental microwear of small mammals affords us the opportunity to study paleoecology at a finer spatial and temporal scale than microwear analysis of larger mammals. This paper reviews the history of small mammal microwear studies and discusses the relationship between small mammal diet, habitat and dental microwear features and texture. The paper argues that dental microwear on small mammals can provide unique information on paleohabitats not available using dental microwear on larger taxa. Taphonomic biases, the role of dust and grit in the formation of microwear, and variation across tooth and facet in the analysis of dental microwear are discussed. In order to move the field forward and to further clarify the relationship between dental microwear features and diet in small mammals, further studies need to be conducted.

1. Introduction

The current adaptation of humans—occupying habitats as divergent as the arctic and the tropics—is a legacy of the evolutionary history of the species. While global-scale climatic trends are well documented for the early Pleistocene (~2.58–0.78 Ma) (Lisiecki and Raymo, 2007; Raymo et al., 2006; Zachos et al., 2001), the correlation of global to local climatic change remains a challenge (Behrensmeyer, 2006). Indeed, evidence for global climate change is often incongruent with smaller-scale paleohabitat reconstruction (Behrensmeyer, 2006; Kingston et al., 2007). Therefore, bolstering our knowledge of local terrestrial paleohabitats is critical to understanding the selective forces that may have affected early *Homo* (Kingston et al., 2007).

The ability to infer paleo-habitats from morphological proxies is scale-sensitive (Davis and Pineda Munoz, 2016). Ecometric traits such as cranial and tooth measurements reflect the dietary adaptation of the species, i.e., what an individual is adapted to eat. Thus, they reflect adaptations at long evolutionary temporal scales and at larger geographic scales (Gailer et al., 2016). However, it may be of interest to track shorter term habitat changes. These refer to habitat change that can be recorded at the seasonal and ecological time scale of 10^1–10^5 years. The actual diet of an individual depends on food availability, food quality, and predation risks (Calandra and Merceron, 2016). Thus the relationship between food availability and the habitat

provides an excellent paleohabitat proxy. Tracking dietary changes within a life time of an individual or across ecological time scales requires a different group of proxies–use-related dietary proxies.

One of these use-related dietary proxies is dental microwear, which records ante-mortem micro-features on tooth enamel caused by abrasion by food and/or exogenous particles (Teaford and Oyen, 1989). Dental microwear traces derived from use-related morphological changes in tooth morphology reflect what the individual *actually* ate. Indeed, dental microwear reflects the diet of an individual in the last 6 days or so of their life (Gailer et al., 2016; Teaford and Oyen, 1989). Thus, the diet of a population may change in accordance to the availability in forage reflecting the local environment over a very short time scale.

Dental microwear has been used to determine diet in a wide range of taxa including mammals (Covert and Kay, 1981; DeSantis et al., 2013; DeSantis, 2016; Lewis et al., 2000; Merceron et al., 2005; Solounias and Moelleken, 1992; Strait, 1993; Walker et al., 1978), dinosaurs (Fiorillo, 1998; Schubert and Ungar, 2005; Sereno et al., 2007; Varriale, 2016; Williams et al., 2009), fish (Baines et al., 2014; Purnell et al., 2006), conodonts (Purnell, 1995) and invertebrates (Goswami et al., 2005). Since the focus of this paper is the utility of dental microwear in small mammals as paleohabitat indicators, the focus will be on mammalian species.

The dental microwear of a wide range of mammalian taxa have been

studied including primates, marsupials, ungulates and carnivores (Calandra and Merceron, 2016; DeSantis, 2016; Ungar, 2015 and references therein), and used to reconstruct the paleohabitat of both paleontological and archaeological sites (Merceron et al., 2006; Williams and Patterson, 2010). Surprisingly, dental microwear analysis has been primarily limited to large mammals, and the analysis of small mammals has lagged in comparison to that of larger taxa. Indeed, small mammal dental microwear analysis is still very recent and underdeveloped.

While the first dental microwear studies were conducted on small mammals (Rensberger, 1975, 1978; Simpson, 1933; Teaford and Walker, 1984; Walker et al., 1978), subsequent studies over the next two decades focused on larger taxa. Several reasons come to mind: while many taxa were studied, the emphasis of dental microwear since the 1980's onward was on paleodietary reconstructions of non-human primates as modern analogues for the study of hominoids. These studies focused on reconstructing the paleobiology of extinct taxa. Furthermore, results from early microwear studies suggested that best results were obtained for herbivores on the browser – grazer continuum (DeSantis, 2016) leading to a multitude of studies on large-size ungulates. In contrast, many small mammals species were viewed as omnivores (Landry, 1970) and therefore not a focus of these studies. Indeed, several early studies in the 1990's focused on small mammals that were insectivores, faunivores and frugivores (Strait, 1993). Moreover, the earliest rodentia microwear studies conducted in the 1990s and early 2000 focused on muskrat (*Ondatra zibethicus*), which is a primarily herbivorous species (Lewis et al., 2000).

Technical considerations may have also hindered analysis of smaller mammalian taxa. First, archaeological excavation methods have changed over the past century. At the turn of the previous century, archaeologists primarily collected large mammal teeth. In contrast, now we regularly sieve for microvertebrates using small sieve sizes (Zohar et al., 2008), resulting in an increase in the quantity of small mammal teeth from stratified deposits. Second, small mammals have small sized teeth in the range of 1–2 mm in length (Hilson, 2005) and many rodent species tend to have a complex occlusal surface, formed by a narrow, deep in-folds from the sides (Hilson, 2005). As a result, enamel bands are extremely narrow in the range of < 100 μm (Patnaik, 2002). Microscopy required to observe dental microwear on such small areas requires both high magnification and resolution. Scanning electron microscope (SEM) studies used magnifications of up to $1000\times$ for smaller-sized teeth to obtain the needed magnification (Hopley et al., 2006). However, features observed under this high magnification may not be comparable to the ante mortem modification viewed for taxa observed at lower magnifications. With the advent and widespread adoption of low magnification stereomicroscopy (Solounias and Semprebon, 2002), this problem was further confounded as small mammal dental microwear could not be visualized at low magnifications $< 100\times$. Thus, methodological development for small mammal dental microwear analysis was slowed as researchers focused on larger sized animals. Early white light confocal instruments employed an objective with the highest magnification at $100\times$ (Burgman et al., 2016; Scott et al., 2006). This was considered a deterrent to applying dental microwear to small mammal teeth as the enamel bands were often too small to fill a whole work area. Indeed, in the earliest dental microwear texture analysis (Belmaker and Ungar, 2010; Caporale and Ungar, 2016) used incisors given their larger area. However, modern instrumentation allows for up to $150\times$ magnification and objectives with long working distances to overcomes some of these problems (Burgman et al., 2016).

It is within this framework, that this paper reviews the potential of small mammal dental microwear as a paleohabitat proxy. Several possible issues unique to small mammal dental microwear are discussed and suggestions for further research are provided. The paper argues that dental microwear on small mammals can provide unique information on paleohabitats not available using dental microwear on larger taxa. It is important to note that all three methods of dental microwear: SEM, stereomicroscopy, and dental microwear texture analysis are discussed, and not which method is preferable.

2. Paleodietary proxies as paleohabitat indicator

There is a general relationship between diet and habitat (Bodmer, 1991; Jarman, 1974), particularly in herbivores. Fundamental ecological concepts such as "habitat" and "niche" have often been used interchangeably (Kearney 2006 and references therein). It is beyond the scope of this study to discuss different definitions of these concepts here, but for clarification I will use the definitions of Kearney (2006). "Habitat" herein refers to "a description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives" (Kearney, 2006: 187). In contrast, "environment" refers to "the biotic and abiotic phenomena surrounding and potentially interacting with an organism" (Kearney, 2006: 187), and a "niche" is defined as "a subset of those environmental conditions which affect a particular organism, where the average absolute fitness of individuals in a population is greater than or equal to one" (Kearney, 2006: 187).

Traditionally, herbivores have been classified as either browsers, grazers, or frugivores (Bodmer, 1990). While it is obvious that these categories are rather simplistic, it has provided a basis for more complex dietary assignments expressed as percentages of fruits, dicots, and monocots (Gagnon and Chew, 2000). While there is no agreement as to what percent monocots in diet constitutes a grazer (values range from > 50% to > 90%), the general pattern is that grazers consume a majority of graze while browsers consume a majority of their diet in browse (leaves, forbs etc.).

Habitats may vary across landscapes and scales of analysis (Davis and Pineda Munoz, 2016). While all taxa interact with their habitat at different hierarchical scales and levels of ecological resolution, herbivores are particularly susceptible to habitat fluctuations and spatial mosaics given their reliance on vegetation for survival (Senft et al., 1987). The correlation between diet and habitat is not perfect, but there is a general association. For example, grazer herbivores will tend to occupy more open habitats (usually grasslands) than browsers (Gagnon and Chew, 2000). Thus, a high ratio between the number of browser species relative to the number of grazer species within a community is interpreted as evidence for closed habitat (> 80% dense coverage) while a low ratio (i.e., a high proportion of grazer species) is viewed as indicative of the presence of open habitats (Merceron et al., 2004, 2006, 2007; Schubert et al., 2006; Ungar et al., 2007) with both low density coverage of vegetation and low height of trees. Similarly, the rodent community in the desert Frey Jorge (Chile) includes equal numbers of granivorous, insectivorous and herbivores species (Meserve, 1981), while the rodent community in a temperate rainforest in southern Chile includes primarily insectivorous species (Meserve, 1988). When we apply this to the paleontological record, we can use the proportion of taxa with different dietary preferences as a paleohabitat proxy. These represent changes in long-term temporal scales required to evolve a new dietary adaptation and have new taxa disperse into or out of the region. However, mixed feeding herbivores (with a diet of both browsing and grazing at variable proportions) may shift the ratio of grazing to browsing in their diet in proportion to the availability of the vegetation types in their habitat (Bodmer, 1990). Habitats may change across space (microhabitat, ecotones) or across time (intra-annual, decadal).

It is worth emphasizing that identification of habitat via paleodietary proxies, is not based on what an animal eats but how much of every category. A blade of grass is a blade of grass irrespective of the habitat it is consumed in, and a seed is a seed, wherever it is consumed. What matters is the relative proportions of food stuffs with different material properties, and how this varies with habitat. For example, across the spatial scale, the Persian fallow deer (*Dama mesopotamica*) will consume a higher proportion of browse in a closed and wooded habitat than populations living in an open habitat that will consume a higher