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Rodent incisor microwear as a proxy for ecological reconstruction

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ABSTRACT

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

1. Introduction

Dental microwear texture analysis has proven to be a reliable approach to elucidating dietary behaviors and ecological interactions for many mammalian taxa. Most microwear texture studies have been conducted on larger mammals, such as bovids, carnivorans, and primates (Donohue et al., 2013; Schubert et al., 2010; Schulz et al., 2010; Scott, 2012; Scott et al., 2006, 2012; Ungar et al., 2007a, c, 2010, 2012). Only a handful of studies have applied this technique to micromammals thus far (Belmaker and Ungar, 2010; Burgman et al., 2016; Withnell and Ungar, 2014). Here, we assess the potential of rodent incisor microwear texture patterns to reveal habitat, substrate, and diet information. (See Fig. 1.)

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

1.1. Dietary and environmental causes of microwear

Some researchers have recently suggested that exogenous quartz grit and dust are more likely to cause tooth wear than are foods themselves (e.g., Lucas et al., 2013; Sanson et al., 2007). Others have maintained that endogeous abrasives in foods (e.g., silicious phytoliths) can cause tooth wear (Baker et al., 1959; Laluezza Fox et al., 1994; Gügel et al., 2001; Rabenold and Pearson, 2011; Teaford and Byrd, 1989; Ungar et al., 2016; Walker, 1979; Xia et al., 2015). In either case, a recent study of molar microwear of rodents from a variety of habitats found diet to contribute more to pattern differences than does environmental grit per se (Gomes Rodrigues et al., 2009). This may be due to the fact that, regardless of whether grit and dust or phytoliths are the agents of wear, molar microwear patterning reflects masticatory movements associated with specific food properties (Hua et al., 2015).

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

1.2. Rodent incisors as a proxy

Rodents, the quintessential lab mammals, are also ready candidates for studies in the natural world. A principal obstacle to using faunal assemblages for reconstruction of paleoenvironments is taphonomic bias

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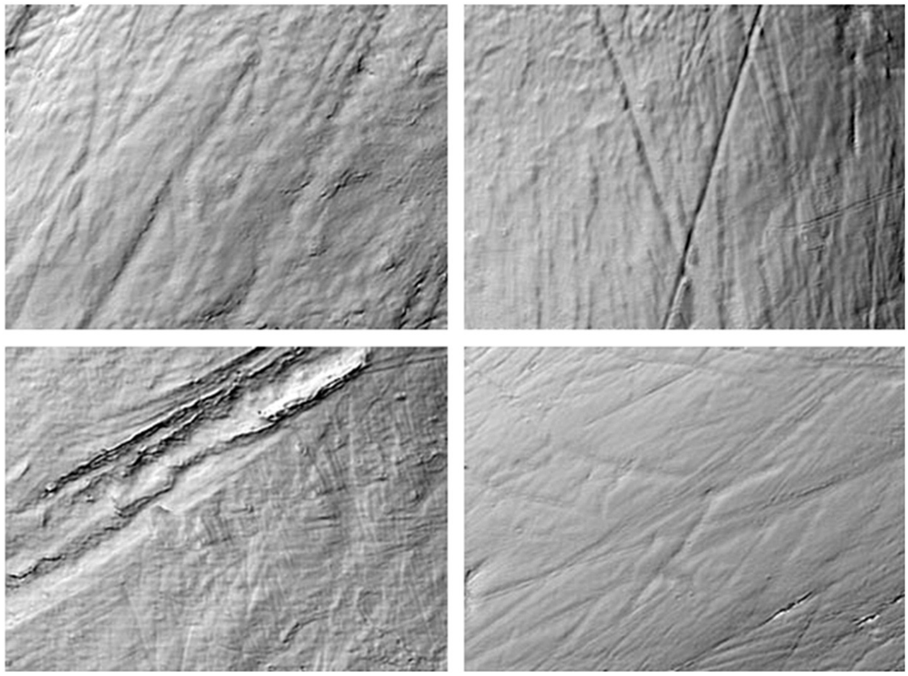

Fig. 1. Photosimulation of microwear surfaces of *Mastomys natalensis* from savanna (upper left), woodland (upper right), and rainforest (lower left) habitats and *Rhabdomys pumilio* from a desert habitat (lower right). Images were generated from point cloud data and represent a planimetric area of 138 μm × 102 μm.

(Winder, 2012). However, rodents are typically *r*-selected organisms and reproduce early and often (Churakov et al., 2010). This makes them, despite taphonomic preservation issues related to their generally diminutive size, very common in many fossil assemblages.

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

Rodents are also important ecological markers because they play an integral role in the larger community of life that surrounds them. Rodents tend to be keystone members of their ecosystems, either as individual species, such as beaver and prairie dog, or as members of guilds (Brown and Heske, 1990). Rodents act as the trophic glue that holds together food webs, and they serve as ecosystem engineers (Huntly and Inouye, 1988; Jones et al., 1994). They affect community structure by controlling the relative abundance of species in their roles as predator and prey (Howe et al., 2002; Hull Sieg, 1987; Hulme, 1996), and they change ecosystem function in a variety of ways (see discussion in Chew, 1978). Rodents aerate and increase ground water recharge through soil turbation, aid in decomposition and nutrient cycling, control plant productivity and species richness and composition, promote ecological succession, and provide habitats for other species, among other things (e.g., Potter, 1978; Grant et al., 1980; Inouye et al., 1987; Huntly and Inouye, 1988; Laundre, 1993, 1998; Jones et al., 1994; Hulme, 1996; Weltzin et al., 1997; Davidson and Lightfoot, 2008).

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

1.3. Dental microwear as proxy for environmental and diet

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

1.4. Molar microwear

More recent studies have also focused mostly on molars, but the number of techniques used to identify and characterize microwear patterns and the range of taxa considered has expanded considerably. Researchers have reported diet-related microwear patterns for ungulates such as pronghorns (Rivals and Semprebon, 2006), antelopes (Schulz et al., 2010; Solounias and Hayek, 1993), bovids (Merceron et al., 2005) and equids (Hayek et al., 1991; Schulz et al., 2010; Solounias and Semprebon, 2002), as well as such small mammals as bats (Purnell et al., 2013; Strait, 1993), moles (Silcox and Teaford, 2002) and lagomorphs (Schulz et al., 2013), various marsupials (Prideaux et al., 2009; Robson and Young, 1986, 1989; Young et al., 1990), predators such as canids and large cats (DeSantis et al., 2012; Schubert et al., 2010; Ungar et al., 2010; Van Valkenburgh et al., 1990), various bear