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Cautionary lessons from assessing dental mesowear observer variability and integrating paleoecological proxies of an extreme generalist *Cormohipparion emsliei*

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ABSTRACT

Dental mesowear is an inexpensive and expedient method used to characterize the average diet of herbivorous mammals, capturing wear produced over several months in the lifetime of an animal by both attrition and abrasion. Most dental mesowear methods focus on qualitatively categorizing cusp shapes as sharp, round, or blunt with high or low relief, sometimes classifying teeth into numerical categories that integrate these variables (typically 0 to 6, from sharp/high relief to blunt/low relief). As dental mesowear requires an observer to make subjective judgments regarding tooth categories, we assess observer variability and integrate carbon isotope and dental mesowear data to clarify if mesowear similarly records average dietary information in an extreme generalist herbivore (i.e., *Cormohipparion emsliei*). Stable carbon isotope samples of *C. emsliei* from the Bone Valley of Florida (~5 Ma) yield a $\delta^{13}C$ range of 13.7‰, suggestive of highly generalized dietary behavior ranging from primarily browsing to grazing. While average mesowear values for this population are partially consistent with a mixed feeding diet, individual $\delta^{13}C$ values lack significant relationships with all mesowear variables, excluding relief. Further, individuals consuming disparate diets (i.e., individuals with the lowest and highest carbon isotope values of −12.9‰ and 0.8‰, respectively) yield similar dental mesowear values (4.20 and 3.75, respectively). Dental mesowear analyses conducted by experienced versus minimally trained individuals are not significantly different from one another, suggesting that mesowear methods can be easily taught; however, the incorporation of multiple observers can reduce variability. Caution should be exercised when interpreting the diets of individuals based on dental mesowear alone.

1. Introduction

Dental mesowear refers to the macroscopic wear patterns on herbivorous mammal teeth, specifically with regard to the shape and relief of upper premolar and molar cusps. Typically, the consumption of grazing material such as grass (which contains silica bodies, i.e., phytoliths; Butler, 1972) results in the blunting of teeth via abrasive (tooth-on-food) wear (Fortelius and Solounias, 2000). In contrast, the consumption of browse such as tree leaves (which typically contains fewer silica bodies) leads to the sharpening of teeth via attritive (tooth-on-tooth) wear (Walker, 1984; Fortelius and Solounias, 2000). Upon the inception of the technique over a decade ago, dental mesowear was hailed as a quick and cheap method for assessing mammalian diets, as compared to more expensive, time-consuming, and potentially destructive methods such as stable isotope or dental microwear analyses.

Dental mesowear methods were initially used in dietary studies of ungulates (including the orders of Artiodactyla and Perissodactyla), as some members of this group exhibit substantially altered tooth heights potentially coincident with or in response to the expansion of grassland ecosystems (e.g., Janis et al., 2002; Strömberg, 2006). Specifically, dental mesowear of fossil horses in North America demonstrates an immediate shift to blunter/lower relief cusps corresponding with grassland expansion, but at low levels that indicate minimal selection for increased crown height (Mihlbachler et al., 2011). Aside from further clarifying mammalian responses to grassland expansion in the late Cenozoic, mesowear has been used to make various dietary interpretations spanning the Cenozoic, including late Oligocene South American notoungulates (Croft and Weinstein, 2008), Miocene equids in Germany (Kaiser, 2003), and hominoid primates in Hungary (Merceron et al., 2007), among many others (e.g., DeMiguel et al., 2008; Valli and Palombo, 2008; Blondel et al., 2010). While dental mesowear is most commonly employed in conjunction with other dietary proxies such as microwear analysis (e.g., DeMiguel et al., 2008; Valli and Palombo, 2008); it has also been used as a stand-alone method for interpreting ancient diets (e.g., Blondel et al., 2010; Mihlbachler et al., 2011). Most recently, mesowear has been used to analyze dietary differences between extant deer species from Japan, distinguishing browsers from mixed feeders at the same feeding locality (Yamuda, 2013). Mesowear has also been used to clarify the environment in which an

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animal has been eating, with drier environments imparting more dust and particulate matter to plant food and thus potentially begetting a more abrasive mesowear signal (Kaiser and Schulz, 2006; Kaiser and Rössner, 2007).

Initial dental mesowear characters used to categorize tooth cusps included shape (i.e., classifying teeth into sharp, round, and blunt groups) and relief (i.e., classifying teeth into high and low relief groups; Fig. 1A, B). Originally, only upper second molars (M^2) were used for scoring (Fortelius and Solounias, 2000). However, using only one tooth position for analysis was severely limiting due to the need for reasonable sample sizes; thus, the method was eventually expanded to also include upper fourth premolars (P^4), upper first molars (M^1), and upper third molars (M^3; Franz-Odendaal and Kaiser, 2003; Kaiser and Solounias, 2003). Extending analysis to lower teeth is possible, but lower teeth exhibit different mesowear characteristics than uppers in extant specimens, and thus mesowear data from upper and lower teeth should not be used concurrently in analysis (Kaiser and Fortelius, 2003). Dental mesowear qualitative scores were later converted into a numerical spectrum, with increasing numbers reflecting increasing abrasive wear (i.e., higher numerical values correspond with blunter shapes and lower relief; Rivals and Semprebon, 2006; Rivals et al., 2007; Mihlbachler et al., 2011; Fig. 1C). Although methods of quantitatively measuring occlusal relief have been used (i.e., measurements of occlusal cusp height and width, as well as ratios of the two; Croft and Weinstein, 2008; Valli and Palombo, 2008), qualitative categorizations have been more frequently applied.

When using a qualitative dietary proxy such as mesowear, it is essential to first determine variability between different observers (inter-observer variability). Observer variability has been examined in other paleoecological methods including dental microwear (i.e., the microscopic examination of tooth wear surfaces indicative of disparate diets; Grine et al., 2002; Semprebon et al., 2004; Galbany et al., 2005; Scott et al., 2008; Mihlbachler et al., 2012; DeSantis et al., 2013). Perhaps because of the relative simplicity and fairly recent development of the dental mesowear method, variability has not yet been analyzed in the same way as with dental microwear methods. Instead, mesowear characters are typically scored by one or two experienced observers. There have only been two studies addressing dental mesowear observer variability. Kaiser et al. (2000) examined a group of experienced mesowear observers and found scores to be consistent. More recently, Mihlbachler et al. (2011) found some significant differences between a set of four observers performing mesowear analysis on fossil horses; however, they stipulate that the differences were minor and random, that practice reduced these differences, and that the differences were not significant when looking at only more experienced mesowear observers. Here, we assess differences between groups of experienced and inexperienced observers, while also analyzing the degree to which each observer's assemblage score deviates from the overall assemblage

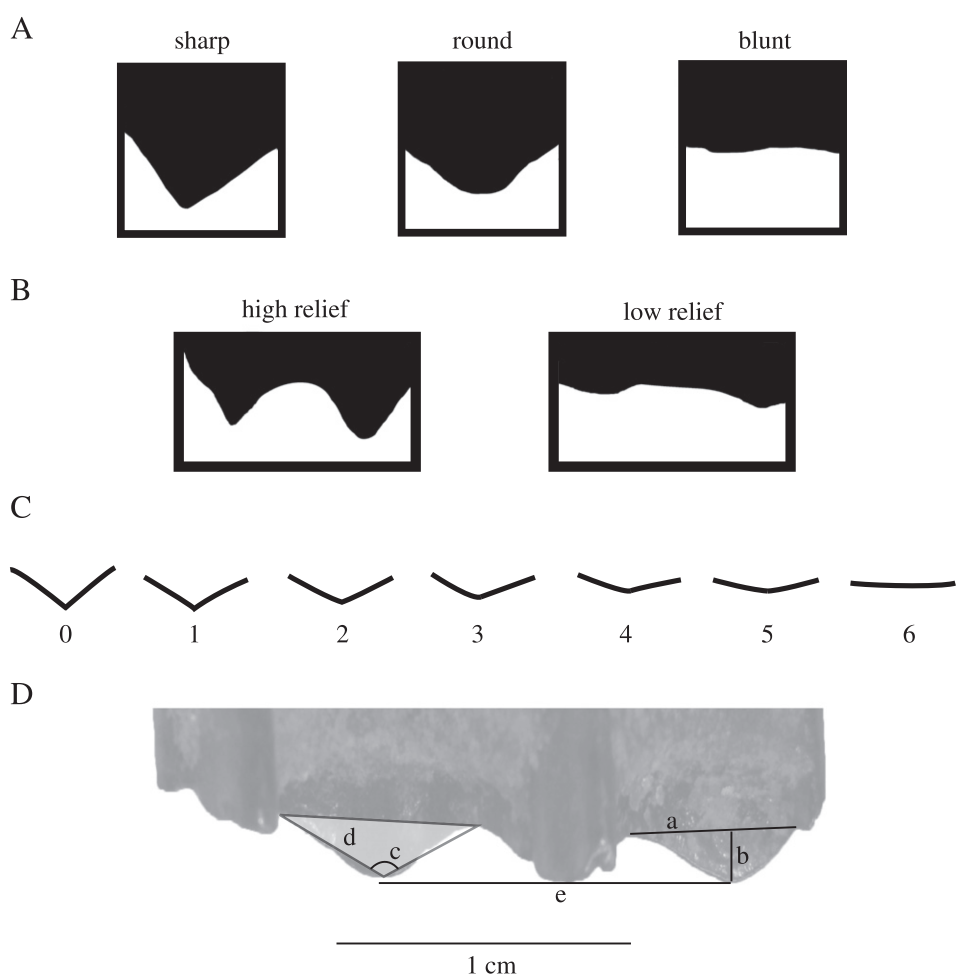

Fig. 1. Visual summaries of the three traditional scales for qualitative mesowear determination, and of the digital measurements taken in an attempt to quantitatively determine mesowear. Shape (A) and relief (B) scales have been adopted from Kaiser and Solounias (2003). The 0–6 (MNS) scale (C) has been adopted from Mihlbachler et al. (2011). The digital measurements taken on *C. emsliei* tooth cusps (D), taken using digital photographs of the samples in labial view and the computer program ImageJ, are classified as: a: cusp width; b: cusp height; c: cusp angle; d: cusp area; and e: intercusp distance. (For the diagram in D, measurements have been separated between the two cusps for ease of viewing, but in calculations only measurements performed on the sharper cusp are used. Occlusal relief refers to sharper cusp height divided by intercusp distance.) All scales were recreated based on digital images of *C. emsliei* teeth from this assemblage.