



Occlusal enamel complexity and its implications for lophodonty, hypsodonty, body mass, and diet in extinct and extant ungulates



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ABSTRACT

Tooth morphology and rates of wear have strong controls on how well mammals survive in their habitats. Herbivorous mammals, specifically ungulates, combat the effects of wear through a combination of changing the occlusal (chewing surface) enamel length, and changing hypsodonty (relative height of tooth). Changes in these two attributes are most notably seen in the fossil record of ungulates as they adapted to living in cooler, drier, and more open habitats. We expect enamel length and hypsodonty to be greater in ungulate taxa that feed on grasses than in non-grass feeders. We tested this hypothesis by digitally photographing 213 maxillary tooth rows from 84 species of extinct and extant ungulates ($n = 1083$ teeth) and measuring their occlusal enamel length and true occlusal area. We then statistically compared the influences of taxonomy, feeding strategy, tooth position, and tooth area on both hypsodonty and occlusal enamel length using principal components analysis (PCA) and a nested multivariate analysis of variance (MANOVA). The results of our PCA indicated a strong correlation between enamel length and tooth area, but little correlation of either with hypsodonty. Our nested MANOVA showed that tooth position had no significant relationship with hypsodonty ($p = 0.1539$), while all other factors were significant for both hypsodonty and occlusal enamel length. Our results suggest that the occlusal enamel length in ungulate teeth is constrained by both the size of the tooth (and, by proxy, the mass of the individual) and diet. Absolute tooth crown height is similarly affected by a combination of body size and diet, leading to the use of a ratio, hypsodonty index, to characterize the diet component. We propose a similar ratio, the occlusal enamel index (OEI) which reduces the effect of body mass to clearly indicate the component of enamel length determined by abrasiveness of ingested material.

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1. Introduction

Paleobiologists reconstruct the dietary ecology of fossil taxa to gain a better understanding of the complex interactions between organisms and their environments on an evolutionary time scale. Diet is more easily ascertained in extant taxa through observation, while the question of diet is normally more complicated with respect to extinct taxa. Generally, teeth are used to assist in answering the question of diet for extinct vertebrates, because teeth are used in feeding and are typically the only portion of the digestive system that is fossilized. Aspects of tooth morphology have been shown to be excellent proxies for interpreting dietary ecology in ancient mammals, particularly herbivores (Evans et al., 2007; Damuth and Janis, 2011). For example, the height of the tooth crown (hypsodonty, measured as the hypsodonty index [HI], or the mesostyle crown height divided by occlusal length [Forsten, 1975; MacFadden, 1984, 1988; Hulbert, 1988a,b]) is

thought to be indicative of level of abrasives in the diet (i.e., consumption of grasses and/or grit on forage from drier environments (Stirton, 1947; McNaughton and Tarrant, 1983; McNaughton et al., 1985; Janis, 1988; MacFadden, 1998; Strömberg, 2004, 2006; Damuth and Janis, 2011)). We have investigated the relationship between diet and another aspect of dental morphology: the degree of enamel complexity on the grinding surface of the tooth as represented by occlusal enamel length (OEL). Specifically, we analyze ungulates (Perissodactyla and Artiodactyla) and how the three basic herbivore feeding strategies, browsing (B), grazing (G), and mixed feeding (M), influence dental morphology.

Besides increasing hypsodonty, ungulates could combat tooth wear by enlarging tooth area and changing the pattern of enamel on the surface of the tooth. Increased tooth area appears to be a function of increasing body mass and relates to the volume of food comminuted (Fortelius, 1985, 1987, 1988, 1990; Damuth and MacFadden, 1990; Shipley et al., 1994). Herbivores in the Miocene had to cope with increased tooth abrasion, possibly from additional grit from a drying climate and/or grass phytoliths (Strömberg, 2004, 2006; Heywood, 2010; Kaiser et al., 2010; Damuth and Janis, 2011). Increasing the

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relative proportion of enamel, the hardest material in a tooth, could have been one adaptive strategy to deal with this increased abrasion. The aspects of the enamel cutting edge that influence functional efficiency of a tooth are the length of the enamel edge and its orientation relative to the chewing direction (Rensberger et al., 1984; Perez-Barberia and Gordon, 1998a,b; Heywood, 2010; Kaiser et al., 2010). Many ungulates, as well as other taxa such as rodents, have the enamel cutting edges oriented perpendicular to chewing motion, which increases chewing effectiveness and ultimately limits tooth abrasion (Rensberger, 1973; Rensberger et al., 1984; Fortelius, 1985, 1987, 1988, 1990; Damuth and MacFadden, 1990; Shipley et al., 1994). The change in the orientation of the visible enamel bands has been suggested to be an adaptive response to a diet inclusive of grasses and a change in the chewing motion from a compression-and-shear motion to an exclusively shear motion (Rensberger et al., 1984).

Such links between functional efficiency of the occlusal enamel edge with its orientation suggest that changes in OEL might also be an adaptive response to tooth abrasion. Basically, the more cutting edge available, the more perimeter over which to distribute abrasion, so wear should proceed slower. That this adaptive response may have operated is suggested by groups such as the Equidae, in which enamel bands become more complex over time with an increase in the number and shape of plications on the fossettes (Simpson, 1951; Rensberger et al., 1984; Kaiser, 2002; Famoso and Pagnac, 2011), but whether or not the increased enamel complexity is the result of a combination of changes in enamel band orientation and increased OEL has yet to be empirically determined.

We hypothesize that OEL evolves in response to changing feeding strategy, potentially acting as a trade off or a compliment with hypsodonty. If so, grass-feeding taxa are predicted to have a longer OEL compared to non-grass feeders of similar body mass within the same clade. To test this prediction it is also necessary to explore how OEL scales to body mass. Tooth area can be used as a proxy for body size; in fact, body size is often calculated from measurements on the tooth row for extinct taxa (MacFadden, 1986). Geometric scaling of specific morphological attributes, specifically allometric, may be the result of physiological or metabolic necessity, but still may have ecological consequences (Pilbeam and Gould, 1974; Gould, 1975; Peters, 1983; Fortelius, 1985). Consequently, we also explore whether the scaling of OEL correlates to feeding strategy. Ultimately, if OEL for a particular body mass does correlate to a particular feeding ecology in ungulates, it would add to the suite of morphological proxies available for determining paleodiet.

1.1. Hypotheses

In this study we test hypotheses related to ancient diets and tooth morphology. First, we test whether OEL alone varies significantly among the three feeding strategies. Second, we test whether the mass-dependent scaling of OEL varies significantly among the three feeding strategies. We tested these hypotheses quantitatively, accounting for phylogenetic relationships when appropriate.

2. Methodology

We digitally photographed the occlusal surfaces of 213 maxillary tooth rows from 84 species from six families (Table 1) of extinct and extant ungulates ($n = 1083$ teeth) with a centimeter scale bar using a Kodak DC290, Fujifilm Finepix A345, Olympus Stylus Tough, and a Canon Digital EOS Rebel SLR. We collected specimens from the University of California Museum of Vertebrate Zoology, University of California Museum of Paleontology, Florida Museum of Natural History, University of Nebraska State Museum, University of Oregon Museum of Natural and Cultural History, Burke Museum of Natural History and Culture, John Day Fossil Beds National Monument, American

Table 1
Families used in this study with number of modern and fossil teeth measured.

Families	# Modern teeth	# Fossil teeth
Giraffidae	18	0
Equidae	56	253
Cervidae	336	0
Camelidae	24	0
Bovidae	378	0
Antilocapridae	18	0

Museum of Natural History, and the Smithsonian's U.S. Museum of Natural History.

2.1. Definition of terms

AMNH F:AM = Frick Collection American Museum of Natural History, AMNH FM = American Museum of Natural History, JODA = John Day Fossil Beds National Monument, MVZ = University of California Museum of Vertebrate Zoology, UCMP = University of California Museum of Paleontology, UF = Florida Museum of Natural History, UNSM = University of Nebraska State Museum, UOMNCH B- = University of Oregon Museum of Natural and Cultural History Biology Collections, USNM = United State National Museum of Natural History (Smithsonian), UWBM = Burke Museum of Natural History and Culture.

2.2. Data collection and statistical methods

We measured OEL and true occlusal tooth area (Fig. 1) on digital photographs using the public domain NIH image program ImageJ (developed at the U.S. National Institutes of Health and available on the internet at <http://rsb.info.nih.gov/ni-image>) on Macintosh iBook and Dell Inspiron laptops. Raw measurements were used for the statistical tests (Supplemental Table 1). For some taxa, both left and right maxillary cheek tooth rows were measured, allowing us to determine individual variability and measurement error. Multiple measurements were taken from one side of the maxilla and compared to the other side. Measurement error was within the individual variability observed between sides. Care was taken to select individuals in medial stages of wear (no deciduous premolars and no teeth in extreme stages of wear). Skulls and complete to nearly complete tooth rows were preferred because we can be more confident in taxonomic identification. We performed statistical analysis with JMP Pro 9 (JMP®, Version 9.0.0. SAS Institute Inc., Cary, NC, 1989–2010). Extinct and extant taxa were analyzed together.

Taxonomy follows McKenna and Bell (1997), MacFadden (1998), and Famoso and Pagnac (2011).

The dietary categories used in this study are based on the three broad diet groupings of Hofmann and Stewart (1973), and were designated as assigned (Supplemental Table 1) in Janis (1988, 1990a,b), Janis and Ehrhardt (1988) and Nowak (1999). These categories were based on the forage composition and stomach structure in modern ungulates, and have been adopted in much of the paleoecological literature for interpretation of ancient ungulate diets (Janis, 1988; Quade et al., 1992; Solounias et al., 1995; MacFadden and Cerling, 1996; Janis et al., 2000, 2002). Selectors of concentrated herbage (herein called "browsers") primarily feed on plants other than grasses. Bulk and roughage feeders (herein called "grazers") concentrate feeding on grasses. Intermediate feeders have a composite diet between that of the browsers and grazers. Hypsodonty Index (HI) for extant taxa, measured as the lower third molar (m3) HI (Van Valen, 1960), was obtained from Janis (1988). Upper first molar (M1) HI for extinct horses were obtained from original data for MacFadden (1988, personal communication April 2002), and from Forsten (1975), MacFadden (1984), and Hulbert (1988a,b). HI values are assigned based on species and not obtained directly from individual specimens, because of the necessity of measuring HI on unworn teeth, which would not

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