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Occlusal enamel complexity and its implications for lophodonty, hypsodony, 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 Tarrants, 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 hyposodonty, 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 Museum of Natural History, and the Smithsonian's U.S. Museum of Natural History.

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

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/nih-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. Hyspodonty 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

have yielded OEL measurements. Consequently, every specimen from a species shares the same HI value.

As a common practice in biostatistical analysis (Zar, 2010), we log transformed the OEL and true area data (log base 10) to make distributions homoskedastic (variance does not increase with size). Data for HI were not log transformed because, as a ratio, this metric should not have problems with heteroskedasticity; however, as a ratio, it potentially violates the assumptions of parametric tests. Ideally, we would include true measurements of crown height and occlusal length, but high-crowned teeth are rarely preserved with their full crown height (Famoso and Pagnac, 2011) and would not, in that case, yield meaningful OEL values. Consequently, we must use a species-average HI (Van Valen, 1960; Forsten, 1975; MacFadden, 1984, 1988; Hulbert, 1988a,b; Janis, 1988).

As an initial exploratory analysis, we performed a principal components analysis (PCA), testing for overall correlation of OEL, true occlusal tooth area, and HI (Fig. 2). True occlusal tooth area is measured using the area contained within the surface area of a single tooth rather than taking the product of length and width. JMP uses REML to estimate correlations among variables in the PCA, these correlations are comparable to standard Pearson correlations. As a test of our hypotheses, we performed a multivariate analysis of variance (MANOVA) with evolutionary relatedness, tooth position, true tooth area, and feeding strategy as independent variables and OEL and HI as dependent variables. We accounted for the confounding effects of evolutionary relationships (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Garland, 1991; Garland et al., 1992, 1993) by creating a nested nominal-scale MANOVA axis using the taxonomy of the included specimens. Because genus and species level differences are expected to be strongly different, we excluded them and focused on the tribe, family and order, which should bring out deeper-time differences in the scaling of OEL. We supplemented the MANOVA with a multi-way analysis of variance (ANOVA) testing the effect of taxonomy, tooth position, true tooth area, and feeding strategy on OEL alone (to eliminate the overwhelming effect of HI). In addition, we performed one-way ANOVAs and Tukey tests to explore the origin of significance for the non-nested factors in our MANOVA results.

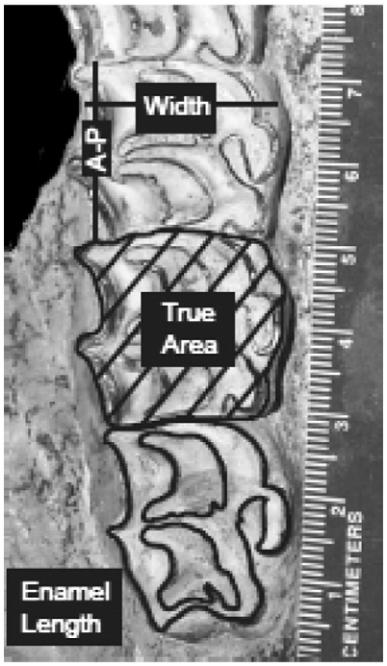

Fig. 1. Examples of true area, occlusal enamel length (OEL), anterior–posterior (A–P) length, and width taken on digital images.

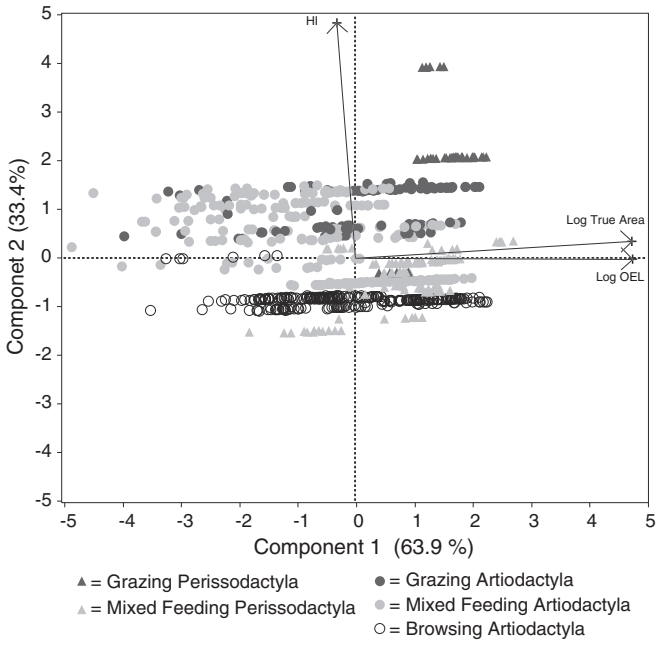

Fig. 2. Plot of PCA results for hypsodonty index, log OEL, and true area. Arrows indicate the direction of correlation. Log OEL and true area are strongly correlated. Symbols represent order (shape) and feeding strategy (color).

These non-nested factors include feeding strategy, tooth position, and true occlusal area.

Our analysis shows that OEL is strongly dependent on body size therefore future studies would have to include OEL and true area to properly quantify enamel complexity. To simplify future studies we are introducing a new metric along the lines of HI, the occlusal enamel index (OEI) where $OEI = OEL/\sqrt{True\ Area}$. OEI removes the isometric effects of body size and dividing by the root of true area yields a dimensionless unit comparable to the dimensionless HI. See results and discussion for characteristic values of OEI for different feeding classes.

3. Results

Our PCA found a strong correlation ($r = 0.91547$) between true occlusal tooth area and OEL. HI is not correlated with either OEL or tooth area (Fig. 2). We also ran a linear regression with log true occlusal area as the independent variable and log OEL as the dependent. We found an $R^2 = 0.837$and our root square mean error = 0.107. Our nested MANOVA (analyzing both log OEL and HI) found *F*-tests (a test for significance between levels within a factor) of three of the factors (taxonomy, log true occlusal area, and feeding strategy) to be significant at the $p < 0.05$ level (Table 2). These significant results suggest that there is an aspect of allometric scaling on OEL, which may also be an effect of larger animals tending to have more abrasive diets. We see that OEL differs among the different feeding groups when all of the other factors are held constant. The relationship between OEL and true area does change between the three feeding strategies. Tooth position was the only factor without a significant

Table 2
Nested MANOVA Results showing the significant values for the four independent variables on the two dependent variables.

	Nested taxonomy	Tooth position	Diet category	Body size proxy
OEL	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
HI	$p < 0.0001$	$p = 0.1539$	$p < 0.0001$	$p = 0.0011$
F test value	1.5285294	0.0106745	1.0429222	0.0141788

Table 3
One-way ANOVA results showing the significant values for the four independent variables on OEL.

	Nested taxonomy	Tooth position	Diet category	Body size proxy
OEL	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
F test value	0.2002114	0.3173301	0.0284226	1.6770933

result ($p = 0.15$), indicating that when the other factors are held constant there is no significant difference in OEL or HI between tooth positions. The tooth position result for HI is likely a consequence of the way HI was coded for taxa in this analysis; see Discussion for more. Much of the MANOVA result was driven by the strong effect of HI, so we analyzed OEL alone, with a multi-way ANOVA including the same factors, and found taxonomy, Tooth position, log true occlusal area, and feeding strategy to be significant at the $p < 0.05$ level (Table 3). The least square means for feeding strategy from the multiway ANOVA are B = 1.02197, M = 1.00154, and G = 1.05592.

We performed three one-way ANOVAs and Tukey tests to compare the means with OEI as the dependent variable. The independent variables were tooth position, feeding strategy, and taxonomy (Order). The results of the ANOVAs and Tukey tests on tooth position (Fig. 3, A) and feeding strategy (Fig. 3, B) indicate a significant result for each category. Our results show a grouping of premolars and molars with the P2 being most different from the other premolars. With respect to feeding strategy, browsers have the lowest mean, then mixed feeders, and then grazers. These three are distinct from each other. The ANOVA and Tukey test with taxonomy (order) was also significant.

Tukey tests on tooth position vs. OEI were significant and show upper molars one to three (M1–3) grouping together, upper premolar three and four (P3–4) grouping together, and upper premolar two (P2) by itself (Fig. 3B, Table 4). A one-way ANOVA on OEI by feeding strategy is significant at the $p < 0.05$ level; however, Tukey tests on

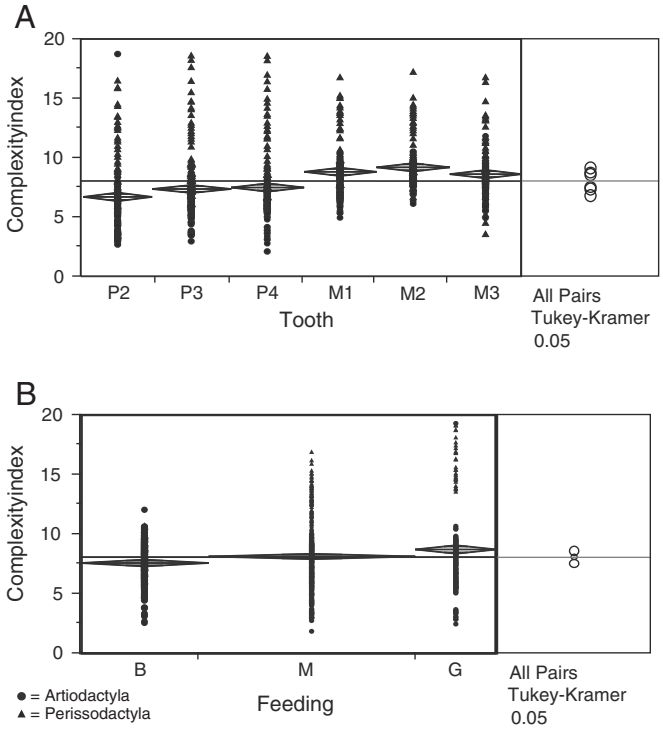

Fig. 3. Plot of ANOVA and Tukey test results. (A) Plots of OEI for tooth position and Tukey test indicating the means for each tooth position. Tukey test shows groupings of teeth. (B) Plots of OEI for feeding strategy (B = Browsing, M = Mixed Feeding, G = Grazing). Tukey tests indicate the means of each feeding strategy and their significant differences from each other.

Table 4
Results for Tukey test of OEI for tooth position.

Level	−Level	Difference	Std err dif	Lower CL	Upper CL	*p*-Value
M2	P2	2.309287	0.2366989	1.63352	2.985053	<.0001
M1	P2	1.956478	0.237349	1.27886	2.634101	<.0001
M3	P2	1.77668	0.2380122	1.09716	2.456196	<.0001
M2	P3	1.692088	0.2286099	1.03941	2.344761	<.0001
M2	P4	1.576559	0.2332235	0.91071	2.242404	<.0001
M1	P3	1.339279	0.229283	0.68468	1.993874	<.0001
M1	P4	1.22375	0.2338833	0.55602	1.891479	<.0001
M3	P3	1.15948	0.2299694	0.50293	1.816035	<.0001
M3	P4	1.043952	0.2345563	0.3743	1.713602	0.0001
P4	P2	0.732728	0.2370223	0.05604	1.409418	0.0249
P3	P2	0.617199	0.2324841	−0.04653	1.280933	0.0855
M2	M3	0.532607	0.2342295	−0.13611	1.201324	0.2057
M2	M1	0.352809	0.2335555	−0.31398	1.019601	0.6575
M1	M3	0.179799	0.2348864	−0.49079	0.850391	0.9732
P4	P3	0.115529	0.2289448	−0.5381	0.769158	0.996

OEI against feeding strategy find B, G, and M insignificant, indicating a significant difference among groups that is small enough that it cannot be discriminated with the Tukey test. When the data are analyzed within each family, we find OEI to be significant for feeding strategy, indicating a strong phylogenetic effect on the relationship of OEI vs. feeding strategy. A one-way ANOVA on OEI by nested taxonomy is also significant at the $p < 0.05$ level ($p < 0.0001$ for each tribe, family, and order).

4. Discussion

Ultimately, this study supports the hypothesis that OEL in ungulates is driven by a combination of body size and feeding strategy. HI appears to be driven exclusively by feeding strategy. It removes body mass as an influence by finding the quotient of mesostyle crown height and tooth length (a proxy for body size), allowing other factors to stand out.

The PCA results showing OEL and tooth area as strongly correlated were expected. From the PCA, we expected that tooth area would have a significant relationship with OEL and not for HI in the subsequent analysis.

It seems apparent from first principles that a taxon that can grind down food to the needed size with fewer strokes would limit its tooth wear, and the results of our MANOVA suggest that, once evolutionary history is controlled, OEL shows a significant relationship to feeding strategy, reflected mostly in a change in its scaling with tooth area, which in turn scales with body mass. It is clear that the effect is much smaller than that for HI (an index which removes body size), so OEL alone will not provide a quick guide to the feeding strategy of an extinct mammal; instead, OEL can be used in concert with taxonomy and HI to reconstruct a more nuanced picture of the feeding strategy of the animal. Our results indicate that OEL was in the suite of characters that evolved to cope with feeding on more abrasive forage. Additionally, OEL appears to have been controlled by increasing body size in concert with feeding strategy: grazers have a larger individual tooth area, and hence a larger inferred body size (Fig. 2).

Differences in OEL scaling are observed between artiodactyls and perissodactyls (Fig. 2). This scaling difference may be related to the groups having different digestive strategies (ruminant versus hindgut fermenter) or simply that they are of different lineages. OEL seems controlled as much by details of diet (grass or browse), as by the size of the animal and its phylogenetic history (particularly the constraints on its digestive strategy). When we use the index, OEI, in our MANOVA the results are the same. Feeding strategy has a more apparent effect on OEI than the combination of OEL and true area, because it clearly emphasizes the non-isometric scaling effects on the occlusal enamel. The ANOVA for OEI verses feeding strategy tests for sensitivity clearly better than OEL alone compared to HI. In future analyses we would like to use

more nuanced metrics of enamel complexity, such as fractal dimensionality or Fourier analysis (Gilbert and Palmqvist, 1995; Ferrario et al., 1999; Bruno et al., 2008). We would expect such metrics to be completely independent of body size scaling.

We noted that OEI was significantly different between different tooth positions. We see three functional units arise in the Tukey test results, P2, P3–4, and M1–3. These functional units may be a selective advantage of keeping a constant amount of enamel in the tooth row at any given eruption period or wear stage (Sisson and Grossman, 1953). It is more likely that the functional units are a result of the genetic development of teeth, with the molars being clones of one another and premolars developing independently of one another (Kangas et al., 2004). Kangas et al. (2004) showed changes in dental characters to be correlated with quantitative changes in genetics in mice suggesting a strong influence of genes on the evolution of teeth. Analyzing tooth position in a MANOVA can serve as a proxy for the genetic control on dental morphology.

While we were able to partially account for the effect of evolutionary relationships on OEL and OEI, it is clear to us that this sort of analysis would be improved by comparative methods that completely account for the details of evolution recorded in an overall phylogenetic hypothesis (Stack et al., 2011; Cayuela et al., 2012). Including taxonomy as a nested factor in the MANOVA allowed only a first-order approximation of the influences of evolutionary history. Ideally we would use a molecular tree-based phylogenetic comparative method, such as phylogenetically informed Monte Carlo computer simulations, for testing our hypotheses, but current methods require known branch lengths and cannot be used with fossil-based phylogenies as in our equid data (Stack et al., 2011; Cayuela et al., 2012). The current state-of-the-art in phylogenetically-informed comparative methods requires phylogenies with consistently-derived branch lengths, an easy task for molecular phylogeneticists, but not yet a common result of morphology-dependent fossil phylogenetics work. We see an important need for a new method for establishing branch-length bounded phylogenetic trees utilizing the fossil record, and it is clear that many workers are moving in this direction (Brown and Slater, 2012; Marcot and Glynn, 2012; Simpson, 2012). Some workers have used first and last appearance data to estimate branch lengths for fossil only phylogenies (Mihlbachler and Solounias, 2006) and we are currently exploring this avenue for additional investigations.

Most of the variation observed in the enamel cutting edges of ungulates can be explained by clade membership, tooth area, tooth position, and feeding strategy. The strong differences between OEL scaling in equids (perissodactyls) as compared to artiodactyls suggest that phylogenetic effects play a key role in OEL scaling. The scaling relationship between OEL and body size ultimately is controlled by the amount of food an animal needs to process to maintain the metabolic demands mandated by a given body size as well as the abrasiveness of ingested items. The character complex ungulates modified in response to selective pressure from abrasive forage include tooth crown height, the orientation of visible enamel bands, and tooth microstructure (Stirton, 1947; Rensberger, 1973, 1975; Rensberger and von Koenigswald, 1980; Rensberger et al., 1984; von Koenigswald et al., 1987; Janis, 1988, 1995; Pfretzschner, 1993).

An alternative hypothesis for the evolution of complexity of the occlusal enamel bands invokes the need to resist grinding against the opposing tooth (upper to lower). This hypothesis could be addressed by investigating the details of enamel complexity for animals with different diets within the grazing niche. We cannot make distinct predictions for this hypothesis given our current dataset but this avenue would be worth further investigation.

5. Conclusions

Our results indicate that, at least in the ungulates we studied, increasing lophodonty, as expressed by OEI, is an adaptation to dietary specialization. Moving forward, we would like to learn whether the same broad relationship holds true for other groups that have coincidentally developed hypsodonty and lophodonty, as in geomyid, aplodontid, and cricetid rodents (Flynn and Jacobs, 2008; Flynn et al., 2008; Lindsay, 2008; van Dam et al., 2011; Becerra et al., 2012), as well as South American notoungulates (Billet et al., 2009). Further studies of the genetic and developmental control of these and other dental features are needed to address the interesting question of mammalian tooth evolution in the face of changing environmental and ecological demands.

Our study suggests that OEL alone and the mass-dependent scaling of OEL varies significantly among the three feeding strategies. However, OEL cannot be used on its own to determine feeding strategy. A combination of OEL, HI, and phylogeny should be used to ascertain the feeding strategy of extant and extinct ungulates. Our OEI is shown to successfully reduce the effect of body-size on the OEL. Further examination of the fractal dimension will assist in completely removing the effects of body size from studies of tooth complexity (Gilbert and Palmqvist, 1995).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2013.07.006.

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