

Root growth compensates for molar wear in adult goats (*Capra aegagrus hircus*)

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Abstract

One reason for the mammalian clade's success is the evolutionary diversity of their teeth. In herbivores, this is represented by high-crowned teeth evolved to compensate for wear caused by dietary abrasives like phytoliths and grit. Exactly how dietary abrasives wear teeth is still not understood completely. We fed four different pelleted diets of increasing abrasiveness (L: Lucerne; G: grass; GR: grass and rice husks; GRS: grass, rice husks, and sand) to four groups of a total of 28 adult goats, all with completely erupted third molars, over a six-month period. Tooth morphology was captured by medical computed tomography scans at the beginning and end of the controlled feeding experiment, and separation lines between the crown and root segments were defined in the upper right second molar (M2), to gauge absolute wear. Using bootstrapping, significant differences in volume loss between diets L/G and GR/GRS were detected. A small but nevertheless consistent volume gain was noted in the roots, and there was a significant, positive correlation between crown volume loss and root volume gain. This growth could possibly be attributed to the well-known process of cementum deposition and its relation with a putative feedback mechanism, in place to attenuate wear caused by abrasive diets.

KEYWORDS

3D imaging, cementum, controlled feeding experiment, dental wear, ruminant teeth, tooth volume

1 | INTRODUCTION

Teeth are a prime representation of evolution, in which the varying dental morphologies of vertebrates have adapted to cope with diverse diets. In this view, the adaptation of mammalian teeth is one of the main reasons for their evolutionary success (Reilly, McBrayer, & White, 2001). Mammalian teeth are mainly composed of dentin, covered by enamel in the crown and by cementum in the roots.

A pulp canal runs through the hollow inside of the tooth, accommodating the nerves and vessels that supply the dentine core (Ungar, 2010). Whether teeth are brachydont (low-crowned) or hypsodont (high-crowned) depends on crown height and tooth width (Van Valen, 1960). This can also be determined by observing the junction between the root and the crown, although determining where the enamel and dentin layers end and where the cementum begins is not always clear, especially for hypsodont teeth. In many

species of rodents or lagomorphs, teeth may be rootless and thus grow throughout the lifetime of the individual; these are referred to as hypsodont teeth (Hillson, 1986; Koenigswald, 2011).

Hypsodonty has evolved and increased in proportion over time (Jernvall & Fortelius, 2002; Samuels & Hopkins, 2017) as a response to high amounts of wear on the dental tissue related to the ingested diet (Damuth & Janis, 2011; Janis & Fortelius, 1988), where the two main factors causing wear are phytoliths and grit (Damuth & Janis, 2011; Toljagić, Voje, Matschiner, Liow, & Hansen, 2018; Williams & Kay, 2001). Grass contains more phytoliths (hard opaline silicates) than browse (Hodson, White, Mead, & Broadley, 2005; Sanson, Kerr, & Gross, 2007). Phytoliths are thought to cause wear shaping the pattern of tooth facet development (Kaiser et al., 2013), which could facilitate discrimination between grazers and browsers based on the tooth wear pattern. Ruminants with a diet mainly composed of grasses often have high crowned teeth (Simpson, 1955; Williams & Kay, 2001). Because of their lower feeding height compared with browsers, grazers also tend to ingest soil abrasives along with plant matter, further increasing tooth wear (Damuth & Janis, 2011; Janis & Fortelius, 1988). However, exactly how much internal or external abrasives contribute to wear, and how long this takes, is still under debate (Baker, Jones, & Wardrop, 1959; Lucas et al., 2013; Mainland, 2003; Sanson et al., 2007; Xia et al., 2015).

Wear caused by both, internal and external abrasives, can be observed at different levels. Microscopic wear (e.g., dental microwear texture (Grine, 1986; Scott et al., 2005; Ungar, Brown, Bergstrom, & Walker, 2003) and 3D surface texture (Calandra & Merceron, 2016)) measures complex topographic features on the tooth's surface, deemed to represent an animals' diet over the last few days (Percher et al., 2018; Schulz et al., 2013; Scott et al., 2005; Teaford & Oyen, 1989b; Ungar, Merceron, & Scott, 2007). On a macroscopic level, wear is described by mesowear (Fortelius & Solounias, 2000), scoring occlusal relief and cusp shape of the tooth ectoloph to reconstruct an animal's diet. Mesowear is thought to represent more of an average lifetime signal (Ackermans et al., 2018; Brent Jones & Desantis, 2017; Merceron, Schulz, Kordos, & Kaiser, 2007; Yamada, 2012).

Precisely quantifying tooth wear by observing loss of dental tissue on a macroscopic scale is difficult. The established method to quantify species- or population-specific volume loss is to measure the crown height of a series of teeth from individuals that died at various ages and, based on this, estimate a wear rate characterizing the population. These estimated rates have been generated for many species (reviewed in Damuth & Janis, 2014), but recently, more modern techniques are able to provide exact information on volume loss in experimental conditions, using 3D imaging techniques (Karme, Rannikko, Kallonen, Clauss, & Fortelius, 2016). Our approach here consists of using 3D volume analysis of computed tomography (CT) image stacks to define the absolute loss of dental tissue over time, and determine the relation to different diets.

Diet-related differences in dental wear have been reported experimentally in a range of species, including goats (*Capra aegagrus hircus*, Linnaeus 1758; Ackermans et al., 2018; Solounias, Tariq, Hou, Danowitz, & Harrison, 2014), rabbits (*Oryctolagus cuniculus* Linnaeus

1758, Müller et al., 2014), guinea pigs (*Cavia porcellus* Linnaeus 1758, Müller et al., 2015) and vervet monkeys (*Chlorocebus pygerythrus* Cuvier 1821; Teaford & Oyen, 1989a). Concerning external abrasives, fine dust has been suggested to create a volume loss effect without affecting the macroscopic mesowear pattern (Kaiser et al., 2013), and in experimental microwear studies on sheep (*Ovis aries* Linnaeus 1758), in which fine dust (<100 µm) was added to forage, Merceron et al. (2016) noted little effect of the extrinsic dust on microwear. Additionally, when adding sand to experimental diets, Hoffman, Fraser, and Clementz (2015) observed microwear pitting for medium grain-sized silica sand (250–425 µm), but no grit effect was evident when smaller fine-grained silica sand (180–250 µm) was added. Large-grained sand originating from ingested soil, on the other hand, creates severe, even pathological tissue loss, often reshaping wear-facets entirely. This was first described in New Zealand sheep where high wear, recorded as incisor volume loss, was related to soil ingestion on very eroded pastures (Barnicoat, 1957; Healy, 1967; Ludwig, Healy, & Cutress, 1966; Madden, 2014), and also seen in zoo animals feeding on sandy soils (Martin Jurado, Clauss, Streich, & Hatt, 2008). In small mammals, as part of the experiments mentioned above (Müller et al., 2014; Müller et al., 2015), diets containing coarse sand resulted in larger amounts of dental tissue loss on incisors and cheek teeth than the same diet without added sand. Using these same diets in an in vitro study on horse molars subjected to mechanical standardized chewing, Karme et al. (2016) found the diet with added sand to cause the most volume loss when observed with a micro-CT.

In a previous publication (Ackermans et al., 2018) we reported mesowear signal development in goats during a controlled feeding experiment over six months. Additional 3D data from this study was used here to report total tooth volume of the upper right second molar (M2) of 26 adult female goats using CT imaging and 3D visualization, to record variations in tooth volume over time in relation to diets of increasing abrasiveness. Tooth crown volume is expected to decrease according to the abrasiveness of the diet; in other words, the group fed the most abrasive diet (GRS > GR > G > L) is expected to show the most absolute volume loss.

2 | MATERIALS AND METHODS

2.1 | Animals

Animal experiments were performed with the approval of the Swiss Cantonal Animal Care and Use Committee Zurich (animal experiment license N°115/2009). Twenty-eight adult female domestic goats (*C. aegagrus hircus*, Linnaeus 1758) of mixed breeds and varying ages (Saanen goats, Chamois colored goats, and Toggenburger goats; average body mass = 60 ± 8 kg, estimated age = 3–10 years, exact ages unknown but all with erupted third molars) were acquired from various sources across Switzerland. For logistic and financial reasons, we were not able to acquire animals of the required age class, and with the obligatory specification of not being pregnant, with reliably registered birth dates. The animals were divided randomly into four

groups, consisting of seven individuals each, and kept in an indoor stable (40 m²/group) covered by industrial carpet, with access to a concreted outdoor compartment (12 m²/group). The feeding experiment was from 182 to 198 days long for 24 of the animals, as euthanasia had to be staggered to facilitate a detailed dissection of each animal for another study, and from 107 to 176 days long for four other animals that were euthanised before the end of the experiment because of reasons unrelated to the study. At the end of the experimental period, the animals were slaughtered and the skulls were skeletonized by enzymatic maceration at the Center of Natural History, University of Hamburg, where they are permanently curated in the Mammalogy Collection.

2.2 | Diets

Experimental diets were designed to contain different levels and types of abrasives between groups, with abrasiveness increasing from lucerne pellets (L), grass pellets (G) to grass pellets with rice husks (GR), and grass pellets with rice husks with an addition of sand (GRS; playground sand, grain size 0–1 mm, REDSUN garden products BV, Heijen, Denmark; mean particle size measured by sieve analysis of 0.233 mm). These diets were of the same batch as those used in experiments with rabbits (Müller et al., 2014), guinea pigs (Müller et al., 2015), and in vitro with horse teeth (Karme et al., 2016). The pelleted diets were designed so the proportion of indigestible silica abrasives in the GRS diet was mimicked by a similar proportion of indigestible, nonabrasive filler (pure lignocellulose, Arbocel, JRS Pharma, Rosenberg, Switzerland) in the other diets, to ensure comparable levels of energy and nutrients per amount of pellets (Müller et al., 2014). Grass hay was provided to all groups except for the lucerne group, which was fed lucerne hay. Each animal received 1,500 g of pelleted food and 100 g of hay daily. It should be noted that in this experiment the diets were designed to mainly comprise pellets, and the provided proportion of hay was, therefore, lower than the normal forage ration for ruminants. Water was available for ad libitum consumption at all times. Samples of all diet items and fecal samples of all animals before slaughter were analyzed for acid-detergent insoluble ash as a measure for silica (abrasives) content (Hummel et al., 2011); a nutritional analysis of the pelleted diets and the silica concentrations have been reported previously (Ackermans et al., 2018; Müller et al., 2014).

2.3 | Computer tomography

CT images were acquired from a helical multislice Siemens scanner (Siemens Medical Solutions, Erlangen, Germany) housed at the University of Zurich Veterinary Hospital. Throughout the experiment, parameters were kept constant: tube voltage at 120 kVp, image matrix of 512 × 512 pixels, field of view of 980 × 332 pixels, slice thickness of 0.6 mm, and B60s convolution kernel. At the start of the experiment, before being assigned to the experimental diets, the animals were CT scanned to have a baseline for the tooth condition upon arrival. Another CT scan was performed at the end of

the experiment, post-mortem. As is the general procedure for CT scans, general anesthesia was achieved by administering ketamine, 10 mg/kg (Ketonarkon®, Streuli Pharma AG, Uznach, Switzerland) and xylazine 0.1 mg/kg (Xylazin Streuli, Streuli Pharma AG, Uznach, Switzerland) intramuscularly. Anesthesia was maintained with isoflurane (Attane®, Provet AG, Lyssach, Switzerland) mixed in oxygen with a facemask.

Following data acquisition, the CT datasets were converted to DICOM medical imaging format and rendered into 3D surface models using Amira 5.6 (Mercury Computer Systems/3D Viz group, San Diego, CA) 3D visualization software and using Horos v3.0.1 (Horos Project 2015) for additional visualization.

Using orthographic CT slices at a dorsoventral projection through the upper right M2 and proceeding apically through the image stack, three landmarks at different levels in the tooth were considered as division planes of the crown-root border (Figure 1). Crown-segment 1 was defined as the volume between the tip of the crown and crown point 1 (C1), set at the coronal–most junction of the inner pulp cavity with the dentin (three visible cavities). Crown-segment 2 was from the tip of the crown to crown point 2 (C2), set at the slice before separation of the central pulp cavity (one visible cavity) into two or more root cavities, and crown-segment 3 was set from the tip of the crown to crown point 3 (C3), defined at the slice where distinct roots became visible. For each crown point, the part of the image stack ranging from the defined crown point to the root tips was defined as

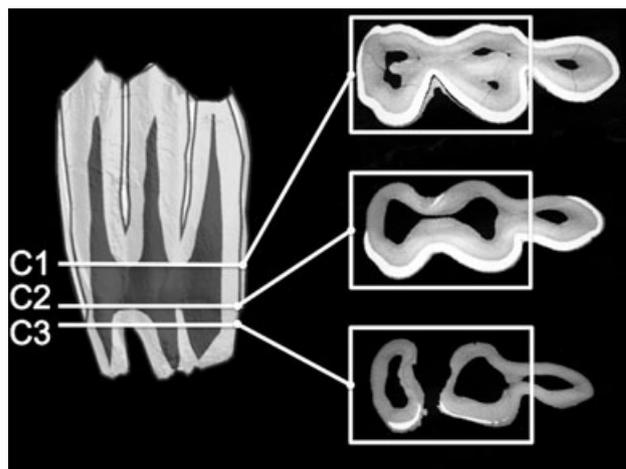


FIGURE 1 Schematic sagittal representation of three possible delimitation lines between molar crown and roots, established to measure crown and root volume in goats (*C. aegagrus hircus*) fed diets of different abrasiveness for six months. Crown segment 1 is defined as the volume between the tip of the crown to crown point 1 (C1), and the volume from C1 to the tip of the roots is defined as root segment 1, idem for crown point 2 (C2) and crown point 3 (C3). White frames represent the transversal tooth-based morphology as seen on X-ray micro-CT slices, used to determine the exact delimitation lines; for C1, one slice further down would show the joint pulpal cavity; for C2, one slice further down would show clearly separated pulp cavities for the two main roots; for C3, one slice further upwards would show the cementum link between the two main roots. The tooth represented is the lower left third molar of animal N°8

root-segment R1, R2, and R3, respectively. Figure 1 was obtained by scanning a lower left m3 (animal N°8; the m3 was used for visualization as it was naturally loosened during maceration, wishing not to damage any other specimens) with an industrial micro-CT scanner (Nikon XT H 225ST) housed at the University of Zurich. Though the m3 has a third cusp, the same method applies.

Manual thresholding of the slice images was performed so as to take the inner pulp cavity of the tooth into account as part of the total volume. From this point on, the upper right M2 was measured in each individual, for each of the two CT scans. The white balance was set at a pixel range of -200 to 2384 pixels and the threshold was set to the full range (-1024 to 3071). The tooth was then delimited manually with the paintbrush tool on multiple slices and interpolated in between for slices with similar morphology. All slices were then checked visually for inconsistencies before the final volume measurement. The total tooth volume was measured, followed by an independent measurement of each section: the tip of the crown to C1, C1 to C2, C2 to C3, and C3 to root tips. The same observer (NLA) performed all of the volume measurements, blinded to the diet groups. Two animals (N°s 11 and 27) were excluded from analysis due to artefacts during the CT process affecting the M2, resulting in a total of 26 animals analyzed. Volume change was calculated by subtraction for all different measures, resulting in data of total volume loss, $\Delta C1$, $\Delta C2$ and so forth for each individual.

2.4 | Statistical analysis

Because all data were not distributed normally, comparisons between treatment groups were performed using ranked data and General Linear Models (GLM) with Tukey's post hoc tests. For all groups, and for each diet group separately, values for C1-3, R1-3 and the total volume were compared between start and end using paired t-tests.

The difference in crown tissue loss and root tissue gain measurements between start and end were compared between groups using analysis of variance (ANOVA) and Sidak's post hoc tests. Because post hoc tests did not always indicate significant differences between groups after a significant ANOVA, the ANOVA was repeated in these cases with bootstrapping (1,000 bootstraps, stratified by diet, 95% confidence intervals of differences), to test whether the confidence interval of the difference between groups included zero. Simple correlations between measures were assessed using Pearson's *R*. The effect of crown tissue loss and diet group on root tissue gain was assessed using GLMs, confirming normal distribution of residuals, with root tissue gain as the dependent variable, crown tissue loss as the independent variable, and diet as cofactor. GLMs were first performed including the crown tissue loss * diet interaction, but this was never significant, and the GLMs were repeated without the interaction. All analyses were performed in SPSS 22.0 (IBM, Armonk, NY), with the significance level set to $P < 0.05$.

3 | RESULTS

The paired t-test of the total M2 volume at the start versus end of the experiment indicated a significant overall decrease in volume (Table 1). This volume loss was also highly significant in t-tests for the crown segments, regardless of the method applied, and a numerical volume gain was visible for all root segments, albeit nonsignificant for R2 (Table 1). When accounting for diet, volume loss was numerically evident, though significant in t-tests only for GR and GRS. Specifically for diet G, $\Delta C1$ is the sole measure showing the numerical loss, though nonsignificant (Table 1). In the roots, the numerical gain in volume is evident overall and significant for the GR and GRS diets (Table 1).

TABLE 1 Mean \pm SD of volume measurements in μm^3 on different crown segment (C) loss and root segment (R) gain, of the upper right second molar (M2) in goats (*C. aegagrus hircus*) fed diets of different abrasiveness for six months

	n	Total volume		C1		C2		C3	
		Start	End	Start	End	Start	End	Start	End
All	26	4,104 \pm 910	4,000 \pm 843**	2,509 \pm 1,080	2,307 \pm 1,043***	2,959 \pm 1,057	2,808 \pm 1,051***	3,535 \pm 1,052	3,392 \pm 959***
L	6	4,121 \pm 1,001	3,982 \pm 870	2,585 \pm 1,136	2,509 \pm 1,238	3,015 \pm 1,118	2,886 \pm 1,171*	3,655 \pm 1,185	3,462 \pm 1,075*
G	6	3,742 \pm 434	3,793 \pm 469	2,352 \pm 466	2,256 \pm 524	2,577 \pm 447	2,652 \pm 580	3,193 \pm 590	3,227 \pm 599
G/R	7	4,033 \pm 1,028	3,884 \pm 952*	2,642 \pm 1,213	2,334 \pm 1,136***	2,938 \pm 1,243	2,682 \pm 1,174**	3,494 \pm 1,251	3,308 \pm 1,105*
G/R/S	7	4,470 \pm 1,052	4,308 \pm 1035*	2,444 \pm 1,441	2,151 \pm 1,289*	3,257 \pm 1,282	3,001 \pm 1,306***	3,766 \pm 1,180	3,559 \pm 1,130**
	n	R1		R2		R3			
		Start	End	Start	End	Start	End	Start	End
All	26	1,595 \pm 764	1,692 \pm 719*	1,145 \pm 408	1,191 \pm 959	569 \pm 379	607 \pm 360*		
L	6	1,536 \pm 227	1,473 \pm 416	1,106 \pm 298	1,095 \pm 342	467 \pm 223	520 \pm 245		
G	6	1,389 \pm 228	1,537 \pm 217	1,164 \pm 223	1,141 \pm 256	549 \pm 221	565 \pm 150		
G/R	7	1,391 \pm 326	1,550 \pm 338*	1,095 \pm 353	1,202 \pm 336*	539 \pm 352	577 \pm 313		
G/R/S	7	2,026 \pm 1,390	2,156 \pm 1,229	1,213 \pm 667	1,306 \pm 735	704 \pm 598	749 \pm 582*		

Note. L: Lucerne; G: grass; G/R: grass/rice husks; G/R/S: grass/rice husks/sand. Means of start and end differ significantly (paired t-test) at *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

TABLE 2 Mean differences \pm SD (95%CI) [bootstrap confidence interval] on different crown segment (C) loss and root segment (R) gain in the upper right second molar (M2) in μm^3 between start and end volume measurements, in goats (*C. aegagrus hircus*, $n = 26$) fed diets of different abrasiveness for six months

Measure	L	G	G/R	G/R/S
Δ Total volume*	139.5 \pm 176.7 (-45.9;325.0) [1.7; 261.9] ^B	-51.0 \pm 108.9 (-165.3; 63.3) [-132.4; 23.9] ^A	148.9 \pm 143.2 (16.5; 281.3) [53.4; 248.7] ^B	162.5 \pm 115.6 (55.5; 269.4) [87.4; 236.0] ^B
Δ C1*	76.2 \pm 176.3 (-108.8;261.2) [(-46.3;207.8)] ^A	96.5 \pm 129.8 (-39.7;232.7) [6.0;187.9] ^A	308.0 \pm 103.6 (212.2;403.8) [245.2;383.9] ^B	292.8 \pm 233.9 (76.5;509.2) [114.9;438.8] ^B
Δ C2*	129.2 \pm 118.8 ^B (4.8;253.9) [34.4; 200.5] ^B	-74.6 \pm 158.3 ^B (-240.6;91.5) [(-215.0;18.7)] ^A	255.6 \pm 105.0 ^B (158.5;352.7) [188.7; 330.8] ^C	256.0 \pm 87.0 ^B (175.6;336.4) [197.7; 310.5] ^C
Δ C3*	192.7 \pm 140.7 (45.1; 340.4) [100.4; 308.1] ^B	-34.7 \pm 96.4 (-135.9; 66.5) [-98.6; 44.9] ^A	186.4 \pm 198.8 (2.5; 370.2) [58.4; 334.3] ^B	207.4 \pm 144.3 (73.9; 340.9) [93.0; 299.4] ^B
Δ R1	-63.3 \pm 285.7 (-363.2; 236.5) [-]	147.5 \pm 149.5 (-9.4; 304.3) [-]	159.1 \pm 156.2 (14.6; 303.5) [-]	130.4 \pm 269.0 (-118.4; 379.2) [-]
Δ R2	-10.3 \pm 245.4 (-267.8; 247.3) [-]	-23.6 \pm 87.7 (-115.6; 68.4) [-]	106.7 \pm 85.4 (27.7; 185.7) [-]	93.5 \pm 119.4 (-16.9; 204.0) [-]
Δ R3	53.2 \pm 98.8 (-50.5; 156.9) [-]	16.3 \pm 134.1 (-124.5; 157.0) [-]	37.4 \pm 92.2 (-47.8; 122.7) [-]	45.0 \pm 45.2 (3.2; 86.7) [-]

Note. L lucerne ($n = 6$), G grass ($n = 6$), G/R grass/rice husks ($n = 7$), G/R/S grass/rice husks/sand ($n = 7$)

*ANOVA $p < 0.05$.

^{a,b}significant differences (Sidak post hoc test) between groups.

^{A,B}bootstrap 95% confidence interval of difference between groups does not include zero.

Comparing the four diet groups by ANOVA (no bootstrapping), significant differences were apparent for the total volume loss as well as Δ C1, Δ C2, and Δ C3, but without subsequent differences at post hoc testing (except for Δ C2, where the G diet was significantly lower than the other ones; Table 2). Bootstrapping also isolated diet G when observing the total volume loss, Δ C2, and Δ C3. In contrast, L and G were significantly different from GR and GRS for Δ C1 and for Δ C2 after bootstrapping (Table 2).

Pearson's correlation coefficient was highest for the Δ C1- Δ R1 relationship at $R = 0.74$. The correlations between Δ C2- Δ R2 and Δ C3- Δ R3 were also significant, but at decreasing R as the separation line approached the root tips (Tables 2 and 3, Figures 1 and 2). This observation was confirmed using GLMs (Table 4). Finally, the diet cofactor only showed a trend ($p = 0.056$) in the GLMs using the C1/R1 approach, but not for the C2/R2 or C3/R3 approaches. The relationship of Δ R1 to Δ C1 was additionally characterized using linear regression statistics, where the resulting equation (Figure 2) included 0 in the 95% confidence interval of the intercept and 1 in the 95% confidence interval of the slope.

4 | DISCUSSION

After six months on experimental diets, an overall volume loss was recorded in the upper right M2 for the four diet groups, predominantly in the crown segment. Most interesting, a slight but consistent volume gain in the root segment that was correlated to crown tissue loss was observed; a finding to our knowledge which has not been reported so far in hypsodont teeth. Diets higher in

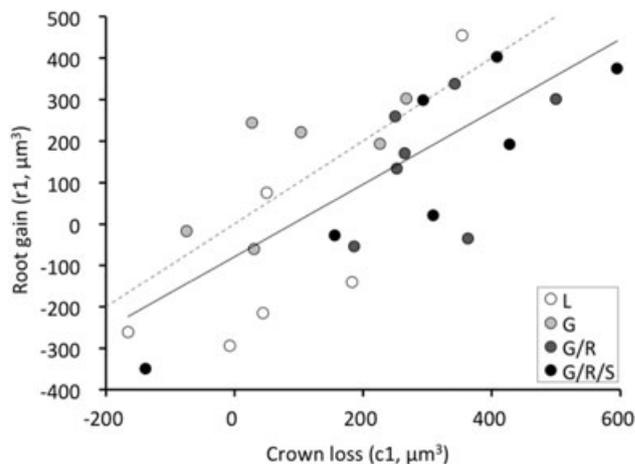


FIGURE 2 The relationship between crown tissue-loss (wear; using method C1) and root tissue-gain (growth, using method R1), in goats (*C. aegagrus hircus*, $n = 26$) fed diets of different abrasiveness for six months. The regression equation, with 95% confidence intervals, was $y = -79 [-172;14] + 0.87 [0.54;1.21] x$ ($R^2 = 0.55$). L lucerne ($n = 6$), G grass ($n = 6$), G/R grass/rice husks ($n = 7$), G/R/S grass/rice husks/sand ($n = 7$). The dotted line denotes $y = x$.

TABLE 3 Pearson's correlation coefficients between different crown segment (C) volume gain and root segment (R) volume loss in the upper right second molar (M2) in μm^3 in goats (*C. aegagrus hircus*) ($n = 26$) fed diets of different abrasiveness for six months

	ΔC2	ΔC3	ΔR1	ΔR2	ΔR3
ΔC1	$R = 0.56$ $P = 0.003$	$R = 0.28$ $p = 0.170$	$R = 0.74$ $p < 0.001$	$R = 0.50$ $p = 0.009$	$R = 0.26$ $p = 0.195$
ΔC2		$R = 0.54$ $p = 0.004$	$R = 0.068$ $p = 0.742$	$R = 0.55$ $p = 0.004$	$R = 0.00$ $p = 0.985$
ΔC3			$R = -0.35$ $p = 0.081$	$R = -0.26$ $p = 0.205$	$R = 0.45$ $p = 0.022$
ΔR1				$R = 0.66$ $p < 0.001$	$R = 0.28$ $p = 0.165$
ΔR2					$R = 0.09$ $p = 0.647$

phytoliths led to more crown loss and root growth; surprisingly, GRS did not cause more wear than the GR.

4.1 | Limitations of study design

The animals used in this experiment were of variable ages and breeds, with varying tooth conditions. A more homogenous sample would have been ideal. But because breeding-animals of the required age class are comparatively expensive, the logistics of keeping such animals until they gave birth, before our experiment, were considered prohibitive, and nonbreeding animals are mostly not kept up to the age we required for the study, we therefore accepted a non-homogenous sample. The requirement of erupted (and in-use) third molars was met by all animals. Additionally, in an effort to simulate "normal" pasture conditions, the amount of added grit in the GRS diet was 5%, as the average amount of soil ingested for sheep ranges from 5% to 9% of daily intake, and up to 33% in extreme cases (reviewed in Damuth & Janis, 2011). Incorporating sand into a pelleted diet is not an accurate representation of natural forage, though consistently adding external abrasives to forage diets would have been impractical over the long term. Evidently, the sand used in

our experiment cannot represent all forms of grit found in nature; nevertheless, it is a valid experimental representation of a highly abrasive substrate. Finally, there can be little doubt that a pelleted diet, while allowing standardized conditions over a long period of time, will evoke different chewing patterns than natural forages, in particular, chewing intensity (chews per dry matter intake) will be lessened on a pelleted diet (Kennedy, 1985). Therefore, it is possible that natural forages of similar nutrient and abrasives content would have a greater effect on tooth wear than pelleted diets.

A further consideration is that the use of a higher resolution CT scanner would have yielded more precise results and higher quality renderings; however, the necessity to scan live, sedated animals only allowed for the use of a medical-grade CT scanner. Further improvements may include the manual segmenting method used in the Amira 3D visualization software, which had a standard error of $\pm 200.57 \mu\text{m}^3$. An automated technique might have served to reduce this error, though detecting the difference between root material and alveolar bone automatically is complicated and furthermore, this technique would not have taken into account the pulp cavity as part of the total volume.

With regard to ANOVA and bootstrapping tests (Table 2), the grass group was often different from the other groups. This could be a chance finding of these particular animals having higher amounts of cementum deposition, as also evident in Figure 2.

TABLE 4 Results of general linear models (incl. adjusted R^2) linking root tissue gain (growth) with crown tissue loss (wear), in goats (*C. aegagrus hircus*) ($n = 26$) fed diets of different abrasiveness for six months

Dependent: Root growth	Model	Independent: Crown wear	Cofactor: Diet
$\Delta\text{R1-}\Delta\text{C1}$	$F_{4,21} = 11.150$ $p < 0.001$ $R^2 = 0.62$	$F_{4,21} = 34.330$ $p < 0.001$	$F_{3,21} = 2.950$ $p = 0.056$
$\Delta\text{R2-}\Delta\text{C2}$	$F_{4,21} = 2.786$ $p = 0.053$ $R^2 = 0.22$	$F_{4,21} = 5.988$ $p = 0.023$	$F_{3,21} = 0.489$ $p = 0.694$
$\Delta\text{R3-}\Delta\text{C3}$	$F_{4,21} = 1.514$ $p = 0.234$ $R^2 = 0.08$	$F_{4,21} = 5.460$ $p = 0.029$	$F_{3,21} = 0.223$ $p = 0.879$

4.2 | Absolute volume methodology

The C1/R1 delineation was selected, as it appeared to be the most efficient at excluding interference with root-growth (Tables 3 and 4, Figure 2). According to the results obtained for the different crown point placements, it seems as if volume gain does not only occur in the root tips but also to a certain extent on the sides of the root walls, which most probably indicates lateral cementum deposition, as for example described for bison (Moffitt, 1998). In future experiments, one could consider creating a permanent mark on the teeth, by drilling a small burr for example, so as to define crown loss and root gain based on this mark.

4.3 | Diet

Significant volume loss appeared reliably in the paired *t*-test between feeding groups on diets with high phytoliths content, as in the GR and GRS diets. Using C1, GR showed the highest volume loss and, contrary to expectations, GRS did not show more loss than GR, though GRS contained additional external abrasives. These results correspond to findings in Ackermans et al. (2018), where mesowear scored on these same goats indicated equal or slightly less wear on GRS when compared with GR, which is also similar to observations by Merceron et al. (2016) when observing dental microwear textures. Indeed, the absence of effect from the GRS diet can be explained by the washing mechanism in place in ruminant digestion (Ackermans et al., 2018; Dittmann, Kreuzer, Runge, & Clauss, 2017; Janis, Constable, Houpt, Streich, & Clauss, 2010; Mhlbachler, Campbell, Ayoub, Chen, & Ghani, 2016) where large sand settles to the bottom of the rumen, resulting in a less abrasive bolus upon regurgitation and therefore dampening the potential wear effect of added sand on the teeth. Whether differences noted in the degree of root growth at similar levels of wear, as for example evident between several animals on diets L and G (with less root growth on diet L), are related to differences in the chewing load or intensity (with a hypothesized lower effort on L compared with G) would have to be corroborated by further experiments.

4.4 | Correlation between crown and root volume change

Hypsodonty is positioned on a scale between brachydonty and euhyposodonty, with a varying balance between the formation of the tooth's crown and roots during the animal's life (Koenigswald, 2011). In the euhyposodont incisors of rodents, the crown and roots are controlled by different genetic pathways, flexible between species (Tummers & Thesleff, 2009) indicating that root and crown growth may happen independently. Knowledge concerning the underlying genetic factors that control euhyposodonty is most often restricted to mice and rats, as they are the most accessible models in a laboratory setting, though this leads to poor comprehension of tooth replacement, being that these species are monophyodont (Juuri et al., 2013). The murine incisor is nevertheless the main model for hypo- and euhyposodont studies. As these continuously growing teeth require persistent stem cell presence at the base of the tooth, a developmental regulatory structure called the cervical loop (Jernvall & Thesleff, 2012; Renvoisé & Michon, 2014) promotes tooth growth there when the crown material is lost to wear by attrition (Harada et al., 1999).

The mouth contains a multitude of proprioceptors working to protect the teeth (Sanson, Kerr, & Read, 2017); periodontal ligaments, for example, contain mechanoreceptors that provide feedback on tooth load (Hughes, 2015), at least in humans. Based on a hypothesis by Janis and Fortelius (1988) that the transmission of occlusal stress from tooth to bone will pass through the root to the area of root secretion, Renvoisé and Michon (2014, p. 8) hypothesize that “the physical forces of occlusion, dependent on the animal diet, its

volume, soil grit and/or tooth attrition, might have a mechanical effect on the tooth, and in turn, affects the stem cell niche, through a feedback loop pathway.” The concept of cementum growth compensating for wear has been suggested by Attwell (1980, p. 121): “as [cementum] layers are laid down throughout life, the process may serve to continue eruption and consequently compensate for the loss of crown height resulting from tooth wear”, and also by Klevezal (1996, p. 4): “molars of [...] some ungulates are considered as evergrowing teeth. Their dentin stops growing in length rather early but on the root cementum deposits intensively compensating to some extent [sic] the wear of the crown,” although neither author cited empirical data as proof for the observation. It would thus not be far-fetched to imagine the existence of a tooth-specific feedback mechanism in ruminants, aimed at compensating wear by inducing root growth by means of cementum deposition, as suggested by our findings. The effects of such a mechanism have been shown experimentally in rabbits (Meredith, Prebble, & Shaw, 2015; Müller et al., 2014; Ness, 1956) and guinea pigs (Müller et al., 2015), with independent growth rates between cheek teeth and incisors, where there was a relation between wear and compensatory growth in the incisors and lower premolar p3.

Camelids, suids or hippopotamids are only some examples of animals showcasing the combination of molars with fixed growth and ever-growing incisors or canines, indicating the possibility of euhyposodont teeth present in hypsodont animals (Koenigswald, 2011). Sequential replacement in the form of delayed molar eruption is an evolutionary adaptation to wear (Janis & Fortelius, 1988), although eruption timing can also be delayed by other external factors such as general malnutrition or specific nutritional deficiencies (calcium and phosphorous), especially in younger animals when the dentition is rapidly developing (Greenfield & Arnold, 2008; Moran & O'Connor, 1994; Popkin, Baker, Worley, Payne, & Hammon, 2012). Historically, tooth eruption schedules for ovicaprids (reviewed by Zeder, 2002) show that molar eruption seems to follow a specific time frame, with only slightly longer time periods in wild or feral animals, most likely due to nutritional differences (Caughley, 1965; Silver, Brothwell, & Higgs, 1969; Taber, 1971; Vigal & Machordom, 1985). Still, to date, no continued growth after the final eruption has been reported (Greenfield & Arnold, 2008). Interestingly, seasonal deposition of cementum layers on the root area of teeth has been recorded and used to age animals for many years (Laws, 1952). It is, however, never described as a type of growth, even though the material is clearly being added to the tooth root structure.

Lieberman (1993) tested the effect of changes in diet on cementum microstructure in a controlled feeding experiment on goats, using diets of different hardness (normal or softened pellets) and with a different protein, mineral (calcium and phosphorus) and vitamin content. The diet hardness, before rumination, impacted cementum growth by affecting the orientation of the Sharpey's fibers, which re-align to counter tensile forces that press teeth in the alveoli during occlusion. This difference in orientation altered visual representation of the incremental cementum lines when viewed under polarized light. The differences in diet mineralization affected the formation rate of the collagen matrix, resulting in darker

cementum bands. This demonstrates that diet hardness and mineral content affect cementogenesis. In any case, growth is happening at the root level, although more accurate equipment is necessary to observe precisely which tissue layer of the roots is gaining volume, whether it is indeed cementum that is the main source of growth in reaction to diet, and how exactly the feedback mechanism works.

5 | CONCLUSION

Volume changes in goat molars show the possible existence of a previously undetected feedback mechanism in ruminants, possibly related to the amount of wear inflicted on the tooth, which reacts and changes even in the absence of euhypsodonty. The observed increase in root volume might be linked to the well-described factor of cementum deposition, already known to react differently depending on various seasonal and physiological forces, though this hypothesis would benefit from further physiological-based research. This mechanism suggests itself to be common to any ruminant, and even to all herbivores in which the investigation of cementum deposits has been described as a method for age determination (Klevezal, 1996). Investigating the spread of this mechanism across species, and for example its link to brachyodont or hypsodonty, might shed further light on evolutionary adaptations to tooth wear. Following studies on differential growth of individual teeth in rodents and rabbits (Ness, 1956; Schour & Medak, 1951), performing an experimental manipulation (such as a graded grinding down) of selected teeth of an adult ruminant and a subsequent detailed investigation of the cementum reaction of treated versus nontreated teeth, might help elucidate the feedback mechanism and outline the scope and limits of compensatory cementum deposition. Such approaches might be useful in estimating the respective costs and constraints of the cementum deposition mechanism as compared to other strategies like euhypsodonty.

Measuring absolute volume allows us to better understand the development of tooth wear over time. Here, it confirmed that diets higher in phytoliths cause more wear, whether it is recorded in the form of volume loss or mesowear, as in our previous article, and that in ruminants, large sand has little effect, probably because it is washed off the ingesta before rumination.

Though a medical grade CT scanner was sufficient to observe slight morphological changes in this study, a detailed approach into the precise mechanics of each tooth layer with a higher-resolution technique should be investigated in future research.

The outcome of this study reveals the need to consider the implications of root growth reacting to (putatively diet-specific) wear from many more points of view. Further research may search to tease apart how much of this signal is due to phenotypic plasticity and how much is genetic. The implications for hypsodonty and euhypsodonty from an evolutionary viewpoint are then also to be questioned. This study is a starting point, but wider use of this technique will provide more information on the matter and serve to create a database of tooth volume changes, of the crown and roots, which we believe will help in understanding dental wear

more than the technique of measuring volume on ontogenetic series of teeth, used up to date.

In any case, teeth should be seen not as a dead structure that is just worn away, but more as a part of the living, growing body.

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CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

AUTHOR CONTRIBUTIONS

MC, TMK, DWHM, PRK, and JMH designed the study, DWHM and MC performed the animal experiment, PRK supervised the CT scanning, JH supervised the nutritional analyses, NLA created the 3D renderings and performed volume measurements, NLA and MC analysed the data and drafted the first version of the manuscript which then received input by all other co-authors.

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