Everything matters: Molar microwear texture in goats (*Capra aegagrus hircus*) fed diets of different abrasiveness

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ABSTRACT

There is an ongoing discourse about whether or not external abrasives influence the microscopic wear in herbivore teeth, including a statement that *"dust does not matter"*. We submitted the maxillary and mandibular second molar of 28 goats (*Capra aegagrus hircus*) to dental microwear texture analysis (DMTA). The study animals were divided into four groups, which received diets of increasing phytolith-based abrasiveness (L: lucerne based pellets, very low phytolith abrasion diet, acting as control; G: grass-based pellets, medium abrasive phytolith diet; GR: grass and rice husk pellets, high abrasion phytolith diet), or a diet with added external abrasives (GRS: the GR diet with addition of large-grained sand as source of external abrasives), for 6 months. Generally, the three diets without sand (L, G, GR) were ranked in the expected sequence by DMTA parameters. For some parameters, in particular those relating to area, complexity, peak sharpness and plateau size of the enamel surface, diet GRS differed from diet GR, whereas the two were not distinct in other parameters, mostly relating to direction, height or volume. Additionally, diets triggered different patterns on the maxillary or mandibular molar for several parameters. For some DMTA parameters, the range covered in the experimental goats corresponded to that observed in free-ranging browsing giraffe (*Giraffa camelopardalis*) and grazing wildebeest (*Connochaetes taurinus*), with goats receiving diet L resembling the giraffe, while the other diets G, GR and GRS more resembled the wildebeest. However, the previously reported mesowear in the goats did not cover the browser-grazer range, and DMTA measurements showed no correlation to the development of mesowear scores or measures of absolute tissue loss in the same animals. In summary, the results confirm DMTA measurements as generally recording properties related to both internal and external abrasives, but also indicate that our understanding of how DMTA characteristics actually originate, and how they relate to other proxies of dental wear, is still very limited.

1. Introduction

Wear traces on teeth have been used for the reconstruction of the diets and the habitats of fossil vertebrates for decades. Usually, these wear traces are grouped according to the level of assessment, into macroscopic (e.g. macro- and mesowear) and microscopic traces (e.g. low magnification, scanning electron microscope, and texture analyses) (Calandra et al., 2019; Davis and Pineda-Munoz, 2016). What really

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matters for their formation remains an open question. Different experiments came to the conclusion that *'dust does not matter'* (Merceron et al., 2016) or that *'dust and grit matter'* (Ackermans et al., 2020c).

The research field of tooth wear is subject to a classic scientific dilemma: on the one hand, substantial catalogues of extant species exist, which are used as references of feeding types – such as browsers vs. grazers. These broad dietary categories can be, in some wear approaches, very reliably differentiated by mesowear (Fortelius and Solounias, 2000), 2D microwear (SEM; Walker et al., 1978) and stereomicroscopic dental microwear (Solounias and Semprebon, 2002), or 3D microwear (dental microwear texture analysis, DMTA) (Calandra and Merceron, 2016; Schulz et al., 2013a; Scott, 2012). The patterns that allow the classification are, in many cases, very convincing, and have a strong differentiation power. Additionally, clear differences between habitats of differing dietary regimes have been demonstrated, especially between free-ranging and zoo animals (Kaiser et al., 2013). Nevertheless, the dietary categories are human-made categories, mainly based on limited feeding observations in the field mostly reflecting species (lifelong) dietary habits. These categories only partly reflect all available adaptive feeding behaviours and have limited power to reflect small-time scale changes on the basis of months or days.

On the other hand, the actual processes that lead to the wear traces have often not been identified and have been described only by hypothetical explanations. In a theoretical approach, we focussed on the presence of abrasives in or on the diet, the putative proportions of abrasion and attrition, and also included other physical aspects of the diet, teeth, and chewing physiology (Kaiser et al., 2016). This approach was a first approximation to combine knowledge from the feeding experiments and surface texture analyses conducted till that time, with the aim to develop a model of tooth wear formation. We want to point out that every dietary reconstruction using general assumptions on tooth wear formation should be more aware of the risk of circular argumentation: when a certain wear type is hypothetically explained to be caused by abrasion, with the derived conclusion that the diet clearly linked to this wear type must be abrasive, and this assumption then obtains factual status without being subjected to experimental testing. In other words, while wear proxies evidently *work*, as can be demonstrated in extant species grouped into diet categories, the hypothetical explanations *why they work* mostly remain speculative, and require testing.

For example, mesowear has been widely shown to differentiate between browsing and grazing ruminants (Fortelius and Solounias, 2000), or between free-ranging and captive individuals of the same species (Clauss et al., 2007). However, experimental approaches (that so far did not include the long-term feeding of grass or browse forages), have not been successful in recreating that differentiation statistically (Ackermans et al., 2018; Solounias et al., 2014; Stauffer et al., 2019). Experimental tests of DMTA measures have yielded unexpected results that contradict traditional explanations, for example suggesting that a more variable signal does not necessarily indicate a more variable diet, but can be triggered by a monotonous diet with certain characteristics (Schulz et al., 2013b). The extent to which species-specific properties influence the wear traces on teeth is another area of debate (Clauss, 2019; DeSantis et al., 2018; Fraser et al., 2018), where it has been difficult to explain patterns across a broad range of species for some measurements (Kaiser et al., 2016; Mihlbachler et al., 2016). Differences between teeth within individuals (i.e. between mandibular or maxillary teeth, or between tooth facets (Arman et al., 2019; Ramdarshan et al., 2017)), further complicate the functional understanding of wear processes. Finally, the extent to which different wear proxies are functionally related, e.g. whether a certain dental microwear texture (DMT) pattern can be expected to be linked to a certain mesowear pattern, remains to be explored. When combining different wear proxies (such as mesowear and DMTA), or combining wear proxies and analyses of the actual diet as derived from stomach contents or isotopes, it appears that the results are often discrepant (Brent

Jones and Desantis, 2017; Ecker et al., 2013; Loffredo and DeSantis, 2014; Louys et al., 2012; Merceron et al., 2010; Mihlbachler et al., 2018; Rivals et al., 2015; Rivals and Lister, 2016; Saarinen et al., 2015; Sánchez-Hernández et al., 2016; Schubert et al., 2006; Strani et al., 2018; Tütken et al., 2013). While this can be explained to some extent by the different time resolution of the respective diet proxies, one would, stochastically, expect these proxies to be more often in accord than not, if they indeed record the same dietary signal in dietary specialists (browsers and grazers), or one would expect the proxy representing the shorter time period to yield a more specific signal (e.g., grass or browse) and the longer-term proxy an intermediate signal – in intermediate feeders. Similarly challenging for our functional understanding of wear proxies, Gailer et al. (2016) found discrepancies between expected and observed tooth form and function in extant bovids based on 3D dental topometry and surface texture.

Perhaps the most prominent scientific debate in the field of dental research revolves around whether internal abrasives (phytoliths) or external abrasives (dust, grit) are the most important, or even the sole entities responsible for wear (Lucas et al., 2013; Rabenold and Pearson, 2014; Sanson et al., 2017; Sanson et al., 2007). The question has a very high relevance, relating to the selective pressures that led to the evolution of hypsodonty and hypseledonty (Jardine et al., 2012; Tapaltsyan et al., 2015). This includes general habitat aridification (increasing dust loads) (Eronen et al., 2010a, 2010b; note that this interpretation is at odds with the finding of Sanson et al., 2017 that grit loads on plants increase during the rainy season due to splash effects), volcanic activity that affects the characteristics of environmental dust (Madden, 2014), or a general spread of plants that contain phytoliths (i.e., monocots), amongst others (Semprebon et al., 2019). For ruminants, the current evidence on effects of internal or external abrasives are not conclusive. Data on hypsodonty, diet, and habitat indicates habitat is an important predictor of the degree of hypsodonty (Damuth and Janis, 2011), but habitat does not appear related to mesowear (Kaiser et al., 2013), suggesting different effects of external abrasives on absolute tooth wear in the form of tissue loss and macroscopic tooth shape.

Different experimental approaches have investigated these questions. With respect to crown tissue loss and mesowear, experimental studies on ruminants, in which diets were supplemented with external abrasives in a controlled manner over periods of 6–15 months, did not detect an effect of these abrasives on absolute crown wear of the maxillary second molar (Ackermans et al., 2019a, 2020b) and mesowear of maxillary and mandibular molars (Ackermans et al., 2020a; 2018). With respect to microwear, Hoffman et al. (2015) documented an effect of external abrasives of 180–425 μm on the maxillary molars of four sheep fed three dietary treatments. In the first larger-scale study with four groups of ten sheep each, Merceron et al. (2016) found that the addition of dust of about 100 μm to natural forages had no significant effect on DMTA measures of mandibular molars. Using a variety of abrasives of different sizes, Ackermans et al. (2020c) largely confirmed these findings, detecting no effect of abrasives of 50 μm, a polishing effect of abrasives of 4 μm, and an abrasion effect of abrasives of 130 μm in DMTA in maxillary and mandibular molars of sheep.

In our view, controlled in vitro and in vivo experimental approaches remain the standard to test our functional understanding of tooth wear, which is originally derived from the epidemiological approaches used when assessing extant specimens whose diet is only assumed. In order to assess how DMT patterns reflect differences in internal- and external abrasive content, and relate to other proxies of wear and tooth position, we applied DMTA to teeth from an experiment in which goats were fed four different diets for a six-month period (Ackermans et al., 2019a; Ackermans et al., 2018). In particular, we were interested in whether the addition of sand to a phytolith-rich diet would have an effect on DMTA results, as it had no discernible effects on absolute tissue loss or mesowear. By using pelleted diets, we exclude variable material properties due to plant leaf geometry or hydration state (Winkler et al., 2019) but focus on the effect of internal and added external abrasives.

We expected the diet of low abrasive content to resemble that of browsers with low overall surface roughness, and the diets of increasing abrasive content to resemble those of grazers with overall high surface roughness (Schulz et al., 2010, 2013a).

2. Methods

The feeding experiment from which samples were analysed was performed with approval of the Swiss Cantonal Animal Care and Use Committee Zurich (animal experiment licence N° 115/2009), and details on absolute tooth wear, mesowear, and diet preference have been reported previously (Ackermans et al., 2019a; Ackermans et al., 2019b; Ackermans et al., 2018). In brief, 28 adult domestic goats (*Capra aegagrus hircus*) were divided randomly into four groups of seven individuals, and kept for half a year on one of four isocaloric, isonitrogenous pelleted diets designed to contain different levels and types of abrasives. Abrasiveness increased from lucerne pellets (L, silica content measured as acid detergent insoluble ash: 5 g/kg dry matter), grass pellets (G, 16 g/kg dry matter) to grass pellets with rice husks (GR, 24 g/kg dry matter) and grass pellets with rice husks with an addition of sand (GRS, 77 g/kg dry matter; mean particle size of sand 233 μm). For a more detailed description of the diets as well as the concentration of silica in the faeces and digestive tracts of the goats, refer to previous publications (Ackermans et al., 2018; Hatt et al., 2019; Müller et al., 2014); for the effects of the diets on rabbits and guinea pigs see as Müller et al. (2014, 2015) well as Martin et al. (2020). At the end of the experimental period the animals were euthanized, and the skulls were prepared by enzymatic maceration at the Center of Natural History, University of Hamburg, where they are permanently curated in the Mammals Collection.

DMTA of the samples was performed following the standard technique in Schulz et al. (2013a). We applied 46 DMT parameters using the ISO 25178 (roughness), motif, furrow, isotropy, ISO 12871 (flatness), and Scale-sensitive fractal analysis (SSFA). Parameters were grouped into the following categories for simplification: area (*Sda, Sha, mea*), complexity (*Sdr, nMotif, Asfc*), density (*Sal, Spd, medf*), direction (*Std, Str, Tr1R, Tr2R, Tr3R, IsT, epLsar*), height (*S10z, S5p, S5v, Sa, Sku, Sp, Sq, Ssk, Sv, Sxp, Sz, meh, madf, metf, FLTt, FLTp, FLTq, FLTv*), peak sharpness (*Spc*), plateau size (*Smc, Smr*), slope (*Sdq*), and volume (*Sdv, Shv, Vm, Vmp, Vmc, Vv, Vvc, Vvv*) (Table S1).

For each specimen, up to three target sites were analysed, when possible: the posterior facet of the anterior cusp on the second enamel band (from buccal) for the right maxillary second molar (M2) (i.e. the distolingual enamel facet of the paracone, PA-dl; Fig. S1), (nomenclature according to Schultz et al., 2018). In the case the target sites could not be used in a right tooth, the left side was measured. The facet on the mandibular second molar (m2) antagonistic to the facet of the M2 was selected with priority: If possible the anterior facet of the posterior cusp on the first enamel band (from buccal) on the m2 (i.e., the mesiobuccal enamel facet of the hypoconid, hy-mb; Fig. S1) was selected; in case it was not intact, the third enamel band was selected on the m2 (i.e., the mesiobuccal enamel facet of the entoconid, en-mb; Fig. S1). Defects that led to selection of an alternative facet were either broken enamel bands or attached dirt that could not easily be removed, which occurred once each on diets L and G, and three times each on diets GR and GRS. Note that Schulz et al. (2010) neither found mesiodistal (cusp-sides) gradients along the tooth row in the ruminant *Connochaetes taurinus* nor bucco-lingual gradients along the enamel ridges; we therefore did not expect large differences between the two enamel ridges of the same tooth position in the goats. However, Ramdarshan et al. (2017) showed that different facets of a maxillary molar yield different DMTA signals, and that results of comparisons with DMTA signals of mandibular molars may depend on which specific facets are used for the comparison. Ideally, all comparisons would be made with exactly the same set of facets, but this is often not a realistic aim, including in the present study. Ramdarshan et al. (2017) showed that the

overall discrimination power of a DMTA approach is reduced if data from different teeth and facets are lumped in one analysis. Thus, the findings of the present study, where two different facets on one lower molar are analysed, might represent an underestimation of the differences between diets that would have been more distinct if the same facet had been available in all animals.

Target sites were cleaned by with rubbing with an alcohol-soaked cotton swab and then moulded using dental silicone (Provil® novo vinylpolysiloxane type 3 dental putty). A copper wire was inserted into the mould to indicate anatomical orientation, and moulds were placed in a microtiter plate (Schulz et al., 2013a). The plate was then fixed to the table of the confocal disc scanning microscope μsurf custom (NanoFocus AG, Oberhausen, Germany) with a blue LED (470 nm) and high-speed progressive-scan digital camera (984 × 984 pixel), set to a 100× long distance lense (resolution in x, y = 0.16 μm, step size in z = 0.06 μm), housed at the Center of Natural History of the University of Hamburg. Four scans of 160 × 160 μm were rendered per facet, taking care not to overlap scanning areas. In some cases only three scans could be acquired. The data scans and the photosimulations (axiomatic meshed models) of selected target sites were processed with MountainsMap Premium v. 7.4.8803 Software (DigitalSurf, Besançon, France, www.digitalsurf.com).

The supplementary material contains the descriptive statistics for all measurements (Table S1) and the results of statistical tests (Table S2), as well as all data visualisation in boxplots (Fig. S2). Bivariate scatter plots are additionally given for measurements often put into context in DMTA studies: a measure of anisotropy (*epLsar*) vs. a measure of complexity (*Asfc*), and a measure of furrow density (*medf*) vs. a measure of furrow height (*metf*) (Fig. S3).

Statistical analysis was carried out using R software (R Core Team, 2017) using the packages xlsx (Dragulescu, 2014), rJava (Urbanek, 2016), doBy (Højsgaard and Halekoh, 2016), and R.utils (Bengtsson, 2016). Significance was tested using a combination of three statistical tests following Calandra et al. (2012) and Schulz et al. (2013a). As DMT data is generally non-normally distributed, we used the procedure of Wilcox (Wilcox, 2012), applying a robust T1 way heteroscedastic Welch-Yuen omnibus test, coupled with a heteroscedastic pairwise "Dunnett's T3 test", with significances confirmed using the robust heteroscedastic rank-based test according to Cliff (pairwise comparison with bootstrap). Data were assessed, for each jaw separately, for a difference between the feeding groups, and for each feeding group separately for a difference between the jaws. The significance level was set to 0.05. To delineate the expected reference magnitudes, the corresponding measurements for giraffe (*Giraffa camelopardalis*), an exclusive browser, and wildebeest (*Connochaetes taurinus*), a strict ground-level grazer, taken from Schulz et al. (2013a), were included in some of the graphics.

In order to facilitate different statistical approaches to data analysis by other researchers, the original data are given as a supplementary file.

3. Results

The visual impression of the photosimulations of the surface scans was that of increasing roughness from L < G < GR < GRS, with no evident difference between the maxillary and mandibular molars (Fig. 1).

Nevertheless, both the DMTA parameter values given in the boxplots and the scatter plots (Figs. S2, S3) indicate that the maxillary and mandibular molars often deviate in their surface texture pattern. Using Dunnett's T3, many differences between the jaw positions were significant, although this was only once confirmed using Cliff's method (for height parameter *Sz*, Table S3). In particular, the visual pattern across the diets differed distinctively for some complexity (*nMotif*), density (*Spd, medf*), and direction (*Std, Tr1R*) parameters (Fig. S2). Specifically focussing on a difference in the effect of diet GRS as compared to GR, the ranking of the diets in the upper vs. the lower jaw
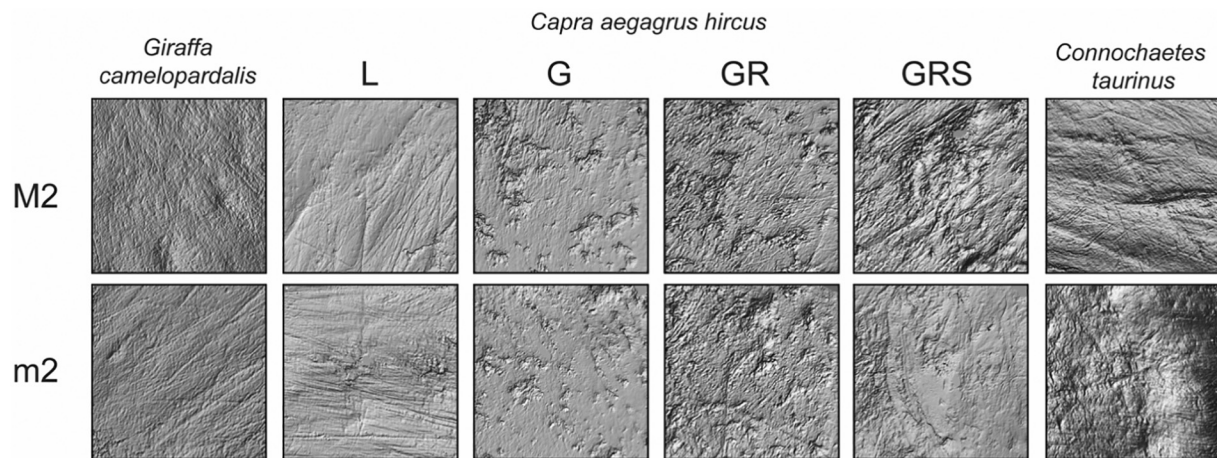
Fig. 1. Surface texture photosimulations at target sides of the enamel facets of goats (*Capra aegagrus hircus*, *n* = 28) fed diets of varying abrasiveness for 6 months. Specimens imaged here are ZMH-S-1161715 (Lucerne L), ZMH-S-1116806 (Grass G), ZMH-S-1298140 (Grass and rice husks GR), ZMH-S-1421691 (Grass, rice husks and sand GRS), showing the maxillary M2 and antagonist for the mandibular m2. All surface scans are taken with the same orientation with anterior to the top and buccal side to the left of the figure, each image represents an area of 160 × 160 μm. All images of M2 taken on the lingual enamel facet of the paracone (PA-dl.), and all images of m2 on the buccal enamel facet of the entoconid (en-mb). Images from the same facets in a giraffe (*Giraffa camelopardalis*) and wildebeest (*Connochaetes taurinus*) from Schulz et al. (2013a) added for visual comparison. See the provided original data file for the measurements corresponding to these images.

appeared mostly similar, but was notably different for categories direction *IsT*, height *Sa*, *Spd*, *Sq*, *metf*, peak sharpness *Spc*, plateau size *Smc*, and volume *Vvc* (Fig. S2).

Plotting the parameter anisotropy against complexity (*epLsar* vs. *Asfc*) showed some diet group distinction in the maxillary, but none in the mandibular molar; in particular, diet GR (but not GRS) led to the more complex and anisotropic patterns in the maxillary M2 (Fig. S3). Plotting density and depth of furrows against each other (*medf* vs. *metf*) showed a more pronounced distinction between diets, and even more pronounced in the lower than in the upper molar, with a decreasing density and increasing depth of furrows from L to G, GR and GRS (Fig. S3), a pattern also evident in the facet surface visualisation (Fig. 1).

Two of three parameters of the area category showed a pattern in relation to diet, with a continuous increase from L < G < GR < GRS (*Sda*, *mea*; Figs. 2A, S2); the pattern had statistical support once by Cliff's method (*Sda*; Table S3).

Complexity parameters showed either an increase from L < G < GR, with no additional increase or even a decrease in GRS (*Sdr*, *Asfc*; Figs. S2, S3), or a continuous decline as L > G > GR > GRS (*nMotif*; Fig. 2B). Only the latter decline achieved statistical support by Cliff's method (Table S3).

Density parameters either showed no diet effect (*Sal*, Fig. S2) or a decrease from L > G > GR > GRS in the lower molar with deviating patterns in the upper molar (*Spd*, *medf*; Figs. 2C, S2, S3), but none of these patterns had statistical support by Cliff's method (Table S3).

Direction parameters had several contrasting patterns between the maxillary and mandibular molars (*Std*, *Str*, *Tr2R*, *epLsar*; Fig. S2). Generally, G or GR showed the most extreme values, and GRS either was similar to, or had lower values than, diet G or GR (Figs. 2D, S2, S3). This latter pattern showed one incidence of statistical support by Cliff's method (Table S3).

Most height parameters showed a similar pattern, with a systematic shift from L to G to GR, and GRS being similar as, or less pronounced than, GR (Figs. 2EF, S2, S3). As mentioned above, there were several parameters for which this sequence of diet ranking differed between the maxillary and mandibular molars, typically with the maxillary molar showing a more pronounced value for GRS. The sequence of height parameters found statistical support by Cliff's method (Table S3) in many cases.

In the peak sharpness category the parameter (*Spc*) was lowest on L, and was similar for G, GR, and GRS in the maxillary molar but increased from G to GR in the mandibular molar, with a decrease again for GRS

(Fig. 2G); the pattern had statistical support by Cliff's method (Table S3).

In the plateau size category the parameter *Smc* and in the slope category the parameter *Sdq* also showed similar patterns, including the difference between the jaws (Fig. 2HI), also with support from Cliff's method (Table S3). By contrast, plateau size parameter *Smr* did not yield any pattern (Fig. S2).

In the volume category the parameters generally showed patterns similar to the height parameters, with an increase L < G < GR and GRS being similar to, or higher than, GR in the maxillary molar, and less than GR in the mandibular molar (*Vm*, *Vmp*, *Vmc*, *Vv*, *Vvc*, *Vvv*; Figs. 2J, S2). A continuous increase L < G < Gr < GRS was only evident in dale volume (*Sdv*) (Fig. S2). The patterns had statistical support by Cliff's method in several instances (Table S3).

When compared to previously reported values for giraffe and wildebeest, the measurements in the goats appeared to span the range from a strict browser to a strict grazer feeding close to the ground (Fig. 3).

4. Discussion

The findings of the present study can most conveniently be summarized as *'everything matters'*, with respect to the influence of the different experimental diets, in a twist to the title of Merceron et al.'s (2016) experimental study in sheep that concluded that *'dust does not matter'*. In that study, about 1% of quartz dust had been added to clover or grass silages fed to sheep for 70 days, with no significant effect of the addition on various DMTA measures (reported for mandibular molars only). In the present study, the addition of an external abrasive was not only at a much higher concentration (5% of the pelleted diet), but also contained larger abrasive particles (classifying as 'sand' rather than 'dust'; Kok et al., 2012). Although for some DMTA parameters, there appeared to be no additional effect of this diet (GRS) when compared to the diet with the highest concentration of internal abrasives (phytoliths, diet GR) or, visually, in some cases even a lesser effect, the GRS diet stood out for some other DMTA parameters. Additionally, a pattern showing an effect of GRS was not consistent for all measurements between the maxillary and mandibular teeth, suggesting some functional differences between the jaws in relation to sand. In particular, for some height parameters, sand seemed to leave more distinct traces on the maxillary teeth (though without changing the ranking of the diets), possibly related to the inverted pestle-and-mortar-function (Kaiser and
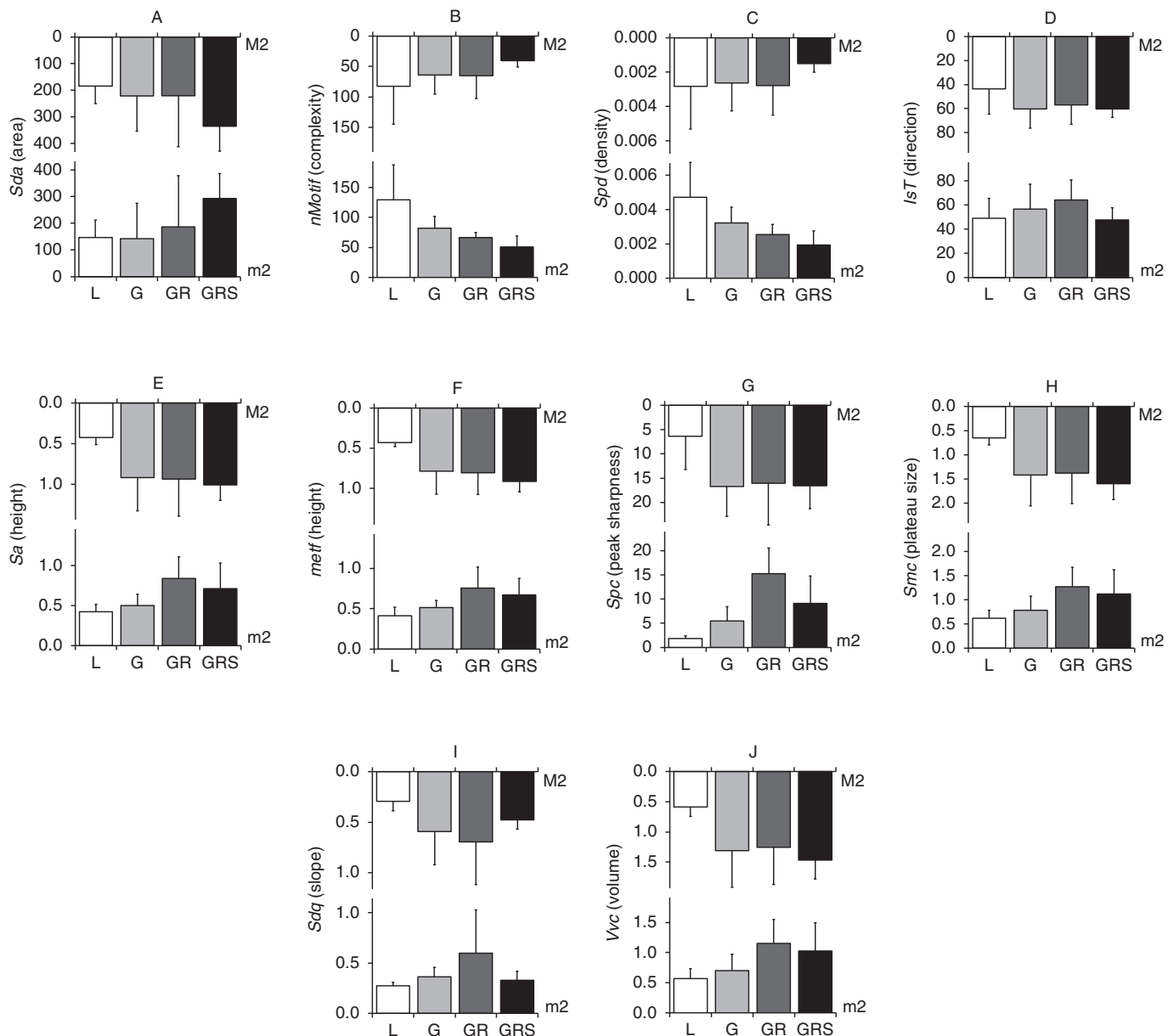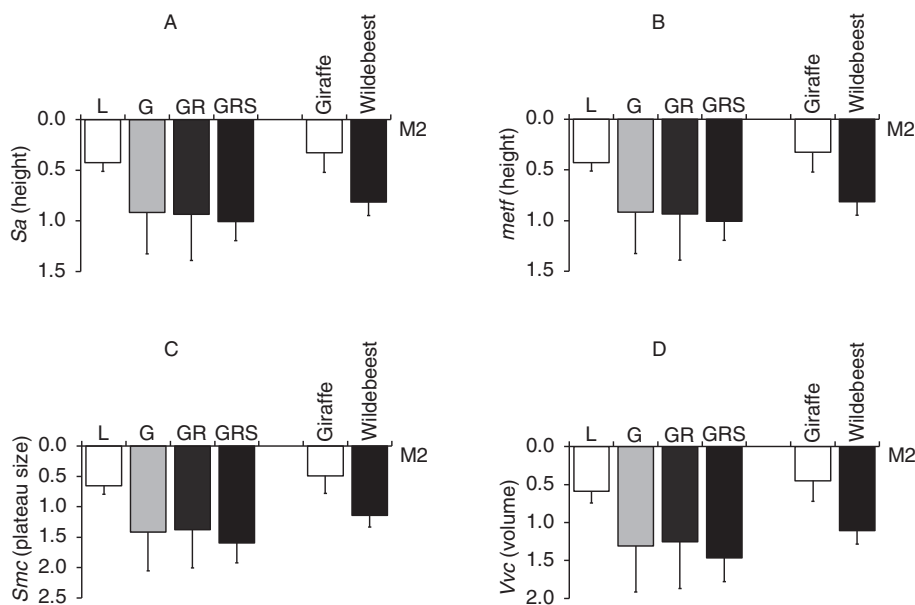
Fig. 2. Selected mean (± SD) abbreviation of DMTA parameters (category) of the maxillary (upper columns) and the mandibular (lower columns) second molar in goats (*Capra aegagrus hircus*, n = 28) fed four different pelleted diets (L lucerne, G grass, GR grass and rice hulls, GRS grass, rice hulls and sand) for half a year. For parameter descriptions see Table S1 and statistics see Table S2. Columns arranged to visually juxtapose maxillary (M2) and mandibular (m2) teeth.

Fortelius, 2003), where food 'resting' on the mandibular teeth is moved across the maxillary antagonist, with potentially a higher relative movement of food along the maxillary than the mandibular molar surface.

The GRS diet stood out for some parameter categories (area, complexity, peak sharpness and plateau size parameters), but less in others, such as direction, height or volume parameters. Currently, there appears to be no simple explanation for the variation in the effect of diets on the different parameters, in particular because of a lack of controlled studies allowing a change of only a single factor. Ideally, in vitro chewing systems (Hua et al., 2015; Karme et al., 2016) would be used to determine the effect of different types of abrasives when concentration and chewing pressure is varied, in order to understand how the different DMTA parameters interact. To date, there is no logical method to decide whether, in general, the patterns found indicate an additional effect of GRS as compared to GR (e.g., in *Sda*, Fig. 2A), or whether the diet with the same concentration of internal abrasives but without the

sand had the most pronounced effect (e.g., in *Spc*, Fig. 2G). The L diet consistently showed low values in height and volume parameters, which are also found in wild browsing species like the giraffe. Even though the experimental diets were given in a pelleted form, they reflected the differences in parameter values observed between wild browsing and grazing ungulates (Schulz et al., 2013a). We are thus left with the conclusion that both, internal and external abrasives have an effect on DMTA in our animal model.

One important aspect of our understanding of tooth wear has rarely been addressed in the literature: the extent to which signals detected in microwear or DMTA actually translate into macroscopic tooth wear. Macroscopic tooth wear, or quantitative tissue loss, represents a rate measurement where loss of tooth height is measured per unit time. This can be done by comparing dental measurements of animals of different ages within populations (Damuth and Janis, 2014; Sanson et al., 2017), by measuring changes in the distance between tooth crowns and burr marks (Ackermans et al., 2020b; Meredith et al., 2015; Müller et al.,

Fig. 3. Selected mean (± SD) abbreviations of DMTA parameters (category) of the maxillary M2 in goats (*Capra aegagrus hircus*, n = 28) fed four different pelleted diets (L lucerne, G grass, GR grass and rice hulls, GRS grass, rice hulls and sand) for half a year, as compared to corresponding measurements on the maxillary second molar in free-ranging giraffe (*Giraffa camelopardalis, n* = 7) and wildebeest (*Connochaetes taurinus,* n = 7) from Schulz et al. (2013a). Columns arranged to symbolize maxillary teeth in comparison with Fig. 2.

2014; Müller et al., 2015), or by volumetric measurements of 3D-rendered dental CT scans taken from the same tooth at different time points (Ackermans et al., 2019a; Ackermans et al., 2020b; Karme et al., 2016). Alternatively, macroscopic wear can be described qualitatively between species or populations, e.g. comparing dental dimensions of animals on different diets (Martin et al., 2019), or by mesowear (Fortelius and Solounias, 2000). Mesowear can also be translated into a rate when assessing individuals of different ages in a population (Rivals et al., 2007) or assessing CT scans made in the same individuals over time (Ackermans et al., 2020a; Ackermans et al., 2018). In particular when observing mesowear changes in cusp shape or in occlusal relief, tissue loss can be parsimoniously implied. In contrast to all these examples, microwear or DMTA yield information on the traces on the tooth's surface, and if measured repeatedly within individuals, can inform on the rate at which these traces change their pattern and are hence overwritten (Teaford and Lytle, 1996; Teaford and Oyen, 1989; Teaford et al., 2017). It could be implied that the overwriting a wear pattern (Schulz et al., 2013b), even on a microscopic scale, is necessarily associated with tissue loss. However, it is not possible to infer rates of tissue loss from these measurements so far. Some authors even suggest that some part of the DMTA patterns might be rather due to plastic deformation, rather than to tissue loss (Lucas et al., 2013). Therefore, comparisons of actual tissue loss rates with the associated DMTA measurements would be highly interesting, to test whether a relationship between the two wear proxies can be established.

Such a test can be done qualitatively, when comparing our DMTA data of experimental goats with data of free-ranging ruminants. Given their natural diets (data collection in Dittmann et al., 2015), giraffe and wildebeest should span the range of diet abrasiveness in ruminants. Giraffe typically ingest phytolith-poor dicot material distant from the ground in the tree crown, whereas wildebeest mainly ingest grass, feeding at ground level and hence on material putatively more contaminated with dust, grit and soil. Silica levels as indicators of quartz grit and dust measured in faeces of free-ranging giraffe and wildebeest corroborate this pattern (Hummel et al., 2011). For several of the DMTA measurements, the range covered by our experimental goats corresponds to that between giraffe and wildebeest (Fig. 3). This correspondence in DMTA is contrasted, however, by the lack of a similar range in mesowear scores achieved after half a year on the experimental diets (Ackermans et al., 2018). These observations suggest that DMTA and mesowear act on very different time scales, and cannot be directly linked, at least within the time period of half a year in goats.

A quantitative test for the relationship between DMTA measurements and mesowear or absolute dental tissue loss is to compare the DMTA results of the present study, on an individual basis, to the changes in mesowear score and crown volume loss of the same teeth (the maxillary M2). Even if mesowear scores did not develop to a full browser-grazer difference, the directionality of the development of the mesowear score could nevertheless show some relationship with the DMTA signal. Scatter plots of the corresponding data are given in Fig. S4-S6, indicating no discernible relationship between any of the wear proxies. We do not know the extent to which the experimental diets used in the present study really represent diets consumed by animals in the wild. Nevertheless, the lack of a coherent pattern throughout different wear proxies suggests that the processes recorded by these methods occur at distinct serial, but non-overlapping and most probably independent geometrical scales. This means that when developing concepts of tooth wear, a direct link from a pattern at microscale to a pattern at macroscale cannot be automatically assumed. It would be highly interesting to investigate longer time spans and quantify the complete duration of wear change including turnover rates for mesowear and tooth volume changes.

Such investigations may reveal counter-intuitive findings. For example, in vitro studies with human enamel found that the concentration of silica particles was not positively correlated with wear – on the contrary (Borrero-Lopez et al., 2018). If this result is robust, then common conceptions about the dosage effect of abrasives need to be reconsidered. Additionally, animals' behavioural reactions to abrasive diets are rarely explored. For the goats of the present study, results from a preference test suggest the capability to detect the sand in the GRS diet (Ackermans et al., 2019b). Humans have been shown to reduce chewing intensity when exposed to external abrasives (Prinz, 2004), and a comparison of faecal particle sizes in chimpanzees (*Pan troglodytes*) between seasons with and without dust contamination (Schulz-Kornas et al., 2019) suggest a similar reaction in that species. Therefore, one possible reason for the GRS diet showing an effect that was lower than expected as compared to GR, could be a reduced chewing intensity at ingestion on the part of the goats (cf. Dittmann et al., 2017), coupled with a washing mechanism in their forestomach that removed the sand from the digesta prior to regurgitation for rumination (Hatt et al., 2019, 2020).

There are only few studies available using individuals for which the diet consumed during the weeks prior to surface texture formation is known, either from observations in the same population from which

dental samples for DMTA were taken (Schulz-Kornas et al., 2019; Stuhlträger et al., 2019), or from stomach contents of the same individuals whose teeth were analysed using DMTA (Merceron et al., 2010), or from feeding experiments. Their results do not fully correspond to expectations derived from our current understanding of the aetiology of surface texture signatures. So far, statistical analyses have mainly focussed on whether categorical differences between groups (either experimental units or assumed feeding categories on species level) are reflected in DMT patterns. These analyses have aimed at identifying measurements with the highest differentiation power (Francisco et al., 2018), or address issues of sampling such as tooth position, or jaw, for diet discrimination (Ramdarshan et al., 2017). Yet, apart from understanding *how* DMTA works for diet differentiation, we also need to know *why* it works.

5. Conclusions

The experimental diets applied in the present study triggered dental microwear texture (DMT) pattern differences resembling differences between free-ranging ruminants of different feeding types - an expected result based on intuitive assumptions regarding the effects of internal and external abrasives. However, results also showed DMT patterns that challenged that same inference, in showing no correlation between DMT patterns and measurements of absolute dental tissue loss or mesowear patterns. The extent to which DMT and macroscopic wear are interrelated, and whether the presence of specific DMT patterns indicate macroscopic tissue loss, requires further investigation.

Our results confirm that DMT measurements generally record properties related to both internal and external abrasives, but the different patterns in upper and lower molars also indicate that our understanding of how DMT characteristics actually originate, and how they relate to other proxies of dental wear, is still very limited. Thus, we conclude that *"everything matters"*, including abrasiveness (internal and external) of the diet, tooth position, and even other factors that we could not consider under the given experimental conditions.

Author contributions

ESK, MC, JMH and TMK designed the study, MC and DWHM performed the animal experiment, DEW and JC performed the texture measurements, JH provided the nutritional analyses of the diets, NLA contributed literature research, LFM supported the data management, ESK, DEW and MC performed data analyses, NLA and LFM devised the graphics design, ESK, DEW and MC wrote the first draft of the manuscript that then received input from all co-authors.

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Data availability

Descriptive statistics and all data evaluation are given in the text supplement. The original data is given as a spreadsheet supplement.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A

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