



The effect of the rumen washing mechanism in sheep differs with concentration and size of abrasive particles

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ABSTRACT

Measures of tooth wear have widespread use as proxies in palaeobiological reconstructions. In order to apply these proxies, an understanding of potential influence factors on wear is important. The processes during the digestion in the ruminant organism lead, possibly inadvertently, to a washing of material before it is regurgitated for rumination chewing. Therefore, ruminants might experience less tooth wear from external abrasives such as dust and grit, which can be washed off, compared to nonruminant herbivores. Details of the washing mechanism, including its efficiency in relation to abrasive size, have not been explored so far. Here, we describe the location and quantity of external abrasives in the gastrointestinal tract of sheep fed seven diets containing external silica abrasives varying in concentration (0, 4, and 8%) and size (4, 50, and 130 μm). As typical for ruminants, external abrasives accumulated mainly in the fourth stomach section, the abomasum. Compared to the diet, the dorsal rumen contents – from where material for regurgitation and rumination is recruited – were depleted of external abrasives for the 130 μm silicates, and for the 8% concentration of 50 μm silicates, but not for the 4 μm silicates or the 4% concentration of 50 μm silicates. These results suggest that the rumen washing mechanism is probably more protective against abrasion from grit and sand, and potentially less efficient against fine dust.

1. Introduction

In herbivores, particle size reduction has a momentous influence on the rate of digestion (Bjorndal et al., 1990), and the ability to reduce ingesta particle size is therefore typically considered a prerequisite for the high energy intake rate required to fuel endothermy (Fritz et al., 2010). Across mammals, this is achieved by comminution of ingesta with an enormous variety of teeth via chewing (Fortelius, 1985; Lucas, 2004; Ungar, 2010; von Koenigswald, 2018). Teeth are exposed to wear and hence in danger of losing functionality, and the actual causes of tooth wear remain under debate. The pendulum of opinion swings between those suggesting mainly an effect of external abrasives ingested involuntarily alongside food, typically termed ‘grit’ or ‘dust’ (e.g.,

Jardine et al., 2012; Lucas et al., 2013), and those suggesting mainly an effect of internal abrasives in the form of phytoliths, or of other physical or mechanical properties of food itself (e.g., Merceron et al., 2016). Apart from the inclusive view that both sources of abrasives may be important, there is also the standpoint that neither can have a decisive wear effect (e.g., Sanson et al., 2017). Various morphophysiological characteristics are considered adaptations against premature functionality loss (Janis and Fortelius, 1988), including high tooth crowns (hypsodonty; Damuth and Janis, 2011), ever-growing teeth (hypsodonty; Ungar, 2010), tooth elongation (Kullmer, 1999), or increased enamel thickness (Rabenold and Pearson, 2011). While there is typically consensus that these characteristics all serve to increase the functional durability of teeth, the direct selective force – ‘grit’, ‘dust’,

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phytoliths or other structural components of natural diets, is still speculative. Elucidating the physiology of abrasion thus remains important for the understanding of putative adaptive value of the large variety of dental morphophysiology, and hence our ability to use dental wear as a proxy in palaeobiological reconstructions.

The ruminant stomach offers an additional mechanism by which tooth wear may be reduced. Traditionally, the microbial digestion of plant material is considered as the main function of the ruminant stomach complex (Van Soest, 1994). At the same time, the microbes that grow during this process are passed on into the lower digestive tract and are likewise digested by the ruminant host (Van Soest, 1994). An important peculiarity that sets the ruminant forestomach apart from the forestomach of nonruminant foregut fermenters is a sorting mechanism, which ensures a differential treatment of particles that are well-comminuted and digested, and larger particles that require further chewing activity (Dittmann et al., 2015). The sorting mechanism utilizes the floating and sedimenting properties of the digesta in a liquid medium (Lechner-Doll et al., 1991). During all these processes, the digesta is subjected to peristaltic movements as well as soaking in, and mixing with, the forestomach fluid.

One side-effect of these processes is that digesta are washed by the forestomach fluid, and one can expect dense material, such as 'grit', to sediment in such an environment. Sedimentation of sand or 'grit' in corresponding forestomach sections occurs in foregut fermenters regardless of whether they are ruminants or non-ruminants (e.g. in hipopotamus: Wings et al., 2008; in Pecari: Schwarm et al., 2010). In ruminants, however, this should lead to a situation where the majority of particle-size reducing chewing, i.e. rumination, is performed on material that is not only softer, but also contains fewer external abrasives than the ingested diet. In return, it may contain, due to the expedient digestion of easily digestible substances and the concomitant concentration of less digestible plant parts, potentially higher concentrations of internal abrasives (phytoliths). This assumption was used to explain differences in the anatomy, physiology and behaviour associated with the chewing process between ruminants and nonruminants (Dittmann et al., 2017; Fletcher et al., 2010; Janis et al., 2010; Williams et al., 2011; Zhou et al., 2019), as well as differences in tooth wear patterns (Mihlbachler et al., 2016). The actual depletion of external abrasives of the dorsal rumen contents (from where digesta is regurgitated for rumination) was shown in a fistulated sheep by Baker et al. (1961), and more comprehensively in goats fed an experimental diet that contained sand of a grain size of 230 µm (Hatt et al., 2019).

In detail, the ruminant stomach is typically considered composed of four compartments (Fig. 1): the rumen, the reticulum, the omasum, and the abomasum (the following description is based on the review by Clauss and Hofmann, 2014, and references therein). The rumen, reticulum and omasum represent the 'forestomach', and the abomasum corresponds to the (glandular) 'stomach' of simple-stomached mammals. The rumen can be further divided into a dorsal part and a ventral part, that are linked by a large intra-ruminal orifice, and that both have their own 'blind sac' at their rear ends (visible towards the back in Fig. 1). Additionally, the rumen comprises the 'atrium', a section that links the dorsal rumen to the reticulum. In terms of function, fermentation of plant material occurs throughout the rumen, and material is constantly exposed to peristalsis and may repeatedly move from the dorsal to the ventral rumen and vice versa, to the atrium and back, and into the reticulum and back. In the reticulum, material is sorted by density; during its contractions, lighter (and typically larger) material is propelled back towards the atrium (from where it may pass to the dorsal rumen), whereas denser (and typically finer) material is passed on into the omasum, together with fluids. Generally, it is thought that material may enter the reticulum and be directed back towards the rumen repeatedly, but once material has passed into the omasum, it will not move back to the reticulum. An important function of the omasum, with its many lamellae or 'leaves', is to absorb the fluid that carries dense, small particles and microbes out of the reticulum, so that the

secretory action of the glandular stomach, the abomasum, does not have to compensate for the dilution of the digesta by that fluid. The abomasum consists of a larger fundic region, with high longitudinal mucosa folds and a focus on the secretion of gastric acid and enzymes, and a more muscular, narrower pyloric region that regulates the outflow of digesta towards the small intestine. Material from the dorsal rumen is regurgitated for rumination. There is no simple, defined way of movement for digesta, but individual digesta fractions may repeat movements between rumen sections, the reticulum and towards the oral cavity for rumination more often than others.

As mentioned above, the ruminant digestive tract treats external abrasives differently than other parts of the digesta. In particular, external abrasives are washed out of the contents of the dorsal rumen, first accumulate somewhat in the ventral rumen, and are passed on via the reticulum and omasum to the abomasum. Here, the dense material accumulates but is also passed on continuously into the lower digestive tract, usually without evident problems, and is finally excreted via faeces. Accumulation of silica in the abomasum has been reported not only in experimental goats (Hatt et al., 2019), but also in free-ranging and captive wild ruminants (Fig. 2), and its presence in the faeces of ruminants has been described in a variety of species (reviewed in Hummel et al., 2011).

The aim of the present study was to evaluate the digesta washing effect in relation to the size and the concentration of the external abrasives in sheep. Our previous study with goats (Hatt et al., 2019) allowed us to make specific predictions. We expected dorsal rumen contents to be depleted of silica, and accumulation of silica in the abomasum. We expected a clearer signal for a washing effect for the higher concentrations (with a higher potential for clear differences), and for the larger particles. The latter prediction is because, as particles (even of a constant density) become smaller, the adhesive forces that bind these particles to surfaces become stronger. This size effect was poignantly described by Visser (1995): "*Sand on a beach never causes a real adhesion problem; it can just be shaken off from a towel or a swimming suit. Writing on a blackboard with a piece of chalk, on the other hand, is possible because the chalk 'releases' particles which are much smaller than the sand particles. In this case the force of gravity is negligible in comparison to the binding forces keeping the particles to the blackboard.*" Additionally, according to Stoke's law (following to Stokes, 1851), for particles of a given density not adhering to surfaces but freely moving in fluid of a given viscosity, the sedimentation velocity decreases with decreasing particle size. Therefore, any removal of particles from sections of the forestomach that depends on their sedimentation properties should occur at a faster rate for larger particles.

2. Methods

Experiments were performed with approval of the Swiss Cantonal Animal Care and Use Committee Zurich (animal experiment licence 10/2016). Thirty-nine mature, female, non-reproducing sheep were divided into seven groups that received, for 16 months, one of seven pelleted diets varying in the concentration and size of external abrasives (Ackermans et al., 2019a, 2019b, 2020). Note that the number of animals was the result of the initially acquired animals not surviving the whole study period for reasons unrelated to the abrasion experiment. The pellets had a base of lucerne meal, which is naturally low in phytoliths. External abrasives (SCR-Sibelco N.V., Antwerp, Belgium) were added in the form of silica in three different sizes: fine silt (SIRCON® M500, mean particle size of 4 µm, representing 'fine dust'), coarse silt (MICROSIL® M4, mean particle size of 50 µm, representing 'coarse dust'), and fine sand (METTET AF100, mean particle size of 130 µm, representing 'grit'). For each diet of a different abrasive size, abrasives were added in two target concentrations (4% and 8%), resulting in seven different diets (4% fine silt, n = 4 sheep; 8% fine silt, n = 5; 4% coarse silt, n = 7; 8% coarse silt, n = 5; 4% fine sand, n = 6; 8% fine sand, n = 5) and a control diet with no added abrasives

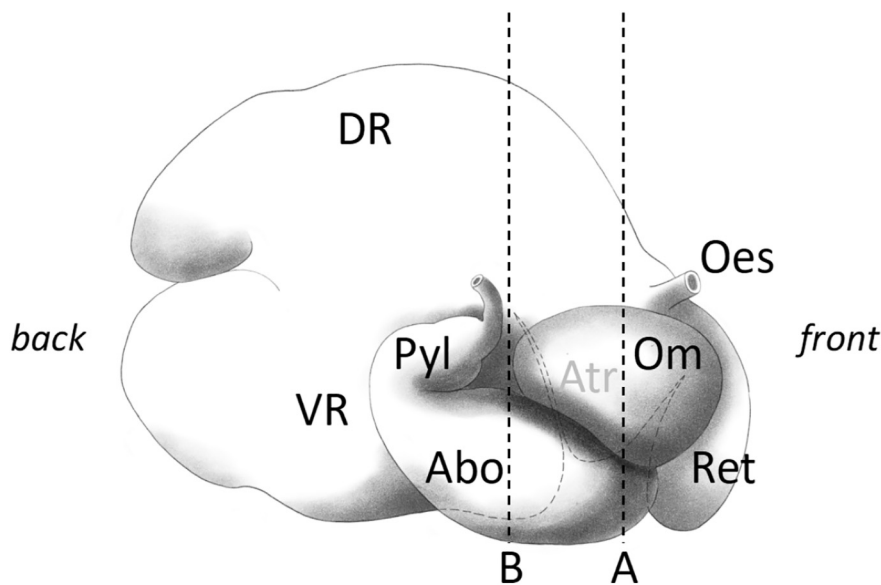


Fig. 1. Schematic representation of the ruminant forestomach, viewed from its right side. The cranial part is to the right, with the oesophagus (Oes), and the caudal part to the left. While the forestomach is positioned next to the left abdominal wall of the animal, the intestines are placed on its right side in the abdominal cavity, between the scheme and the viewer, and are not shown here. DR dorsal rumen (from where contents are regurgitated for rumination), VR ventral rumen (partly overlaid by the abomasum and omasum), Ret reticulum (partially overlaid by the omasum), Om omasum, Abo abomasum (fundus), Pyl abomasum (pylorus). The stippled lines (A, B) indicate the planes of the CT images shown in Fig. 3A and B. Plane A also intersects the dorsal part of the thoracic cavity with the dorsal part of the lungs, not shown here. Drawing modified from Nickel et al. (2004). Note that the pylorus is drawn as pointing dorsally, but in subsequent CT images, rather points to right side of the body (towards the viewer here). After being swallowed, digesta typically moves from the atrium to the dorsal rumen, and travels a variable number of times between the dorsal and ventral rumen compartments, the atrium, and the reticulum. Dense material (typically, small particles) passes

from the reticulum to the omasum and further into the abomasum, whereas lighter material (typically, large particles) is propelled backwards from the reticulum towards the rumen compartments. Material from the dorsal rumen is regurgitated for rumination.

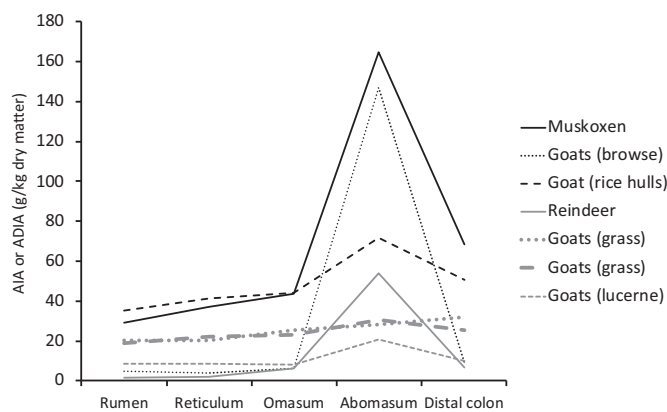


Fig. 2. Reported levels of silica (measured either as acid insoluble ash [AIA] or acid-detergent insoluble ash [ADIA] in dry matter) in the digestive tract of goats (*Capra aegagrus hircus*) fed different diets (Hatt et al., 2019), captive reindeer (*Rangifer tarandus*) fed lichen (Staal and Thing, 1991; read from graph), and free-ranging muskoxen (*Ovis moschatus*) (Staal and Thing, 1991; read from graph). Data displayed for the four sections of the ruminant stomach complex (Rumen, Reticulum, Omasum, Abomasum) as well as the distal colon (equivalent to faeces). Note the accumulation of silica in the abomasum above levels at any other section in many cases, indicating contamination of the ingested material with external abrasives.

($n = 7$). Because in the previous goat study, a coarse sand ($233 \mu\text{m}$) had been used (Hatt et al., 2019), grain sizes were chosen amongst those silica commercially available to span a spectrum below that magnitude, from ‘fine dust’ to ‘fine sand’. The concentrations were chosen to span the range of soil ingestion reported for mammalian herbivores up to 7–8% of the dry matter intake (Beyer et al., 1994).

To ensure all pelleted diets were isocaloric and hence ingested in similar amounts, they were designed so that the proportion of indigestible silica abrasives was matched by a similar proportion of an indigestible, non-abrasive filler (pure lignocellulose, Arbocel, JRS Pharma, Rosenberg, Switzerland) in diets of lesser silica content. The measured concentrations of acid detergent insoluble ash (a proxy for silica) was 12 g/kg dry matter in the control diet, 31 and 52 g/kg dry matter in the fine silt diets, 34 and 66 g/kg dry matter in the coarse silt diet, and 58 and 100 g/kg dry matter in the fine sand diets, respectively

(Ackermans et al., 2019b; Ackermans et al., 2020). Lucerne hay was provided to all groups. Each animal received 1200 g of pelleted food and 200 g of hay daily. Note 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.

After 4 months, CT images were acquired using a helical multislice Siemens scanner (Siemens Medical Solutions, Erlangen, Germany) to image the abdomen of the sheep (tube voltage at 120 kVp, image matrix of 512×512 pixels, field of view of 1329×762 pixels, slice thickness of 0.6 mm, B30s convolution kernel) in a natural (sternal) resting position under general anaesthesia induced with ketamine at 10 mg/kg bodyweight (Ketonarkon®, Streuli Pharma AG, Uznach, Switzerland) and xylazine at 0.1 mg/kg bodyweight (Xylazin Streuli, Streuli Pharma AG, Uznach, Switzerland) intramuscularly, maintained with isoflurane (Attane®, Provet AG, Lyssach, Switzerland) mixed in oxygen via face-mask and dosed to effect. To reverse xylazine, tolazoline (Tolazile® Injection, Akorn Inc., Lake Forest, IL, USA) 2 mg/kg bodyweight was slowly administered intravenously (after minimum anaesthesia time of 45 min) and the animals were closely supervised until fully recovered.

CT data sets were converted to DICOM medical imaging format and evaluated in Horos v3.0.1 (Horos Project 2015, <https://horosproject.org>). Radiodense silica volumes (cm^3) were calculated by manually defining regions of interest (ROIs) on every 6th slice and automated interpolation of missing ROIs. To guide the interpretation of the CT images, please refer to the schematic visualisation of the ruminant forestomach in Fig. 1.

After 16 months, the sheep were euthanised (using the same anaesthetic protocol as for CT followed by intravenous pentobarbital administration until cessation of heartbeat) within 2 h after their last feeding, and the gastrointestinal tract was dissected following a standard protocol (Clauss et al., 2016) while carefully avoiding deviations from the natural position or mixing of the contents (described in Sauer et al., 2017). Samples were taken from the dorsal rumen (from where material is regurgitated for rumination), ventral rumen, reticulum (sorting forestomach), omasum (fluid reabsorption forestomach), abomasum (stomach, initiation of auto-enzymatic digestion), small intestine, caecum, proximal colon, spiral colon, and rectum (faeces). Standard nutrient analyses (AOAC, 1995) were applied. Samples were analysed for the concentration of dry matter (dried at 103°C) and total ash (i.e., including not only silica but also minerals; AOAC no. 942.05), for analyses for acid detergent fibre (ADFom, AOAC no. 973.18) and

acid detergent insoluble ash (ADIA) as a proxy for silica (Hummel et al., 2011).

Statistics were performed using R v 3.5.2 (R Core Team, 2015). For the CT data, for a comparison of the dorsal and the ventral rumen for concentrations of dry matter, total ash and silica (ADIA), and for the calculated differences in silica (ADIA) concentrations between the diets and the contents of the different stomach sections, comparisons between response variables were made using general linear models (LM) where both the dose (0%, 4% or 8%) and size of abrasive materials (small silt, coarse silt, fine sand) were included as effects. However, since this design necessarily excludes various levels of size in the control group, we used a nested model design, with size nested within dose. Significance tests were based on ANOVAs using Type III SS (package car; Fox and Weisberg, 2019). Multiple comparisons, where relevant, were made using Tukey's post hoc tests. Data were ln-transformed to conform to a normal distribution of residuals for CT measurements. For concentrations of dry matter, total ash and silica (ADIA) in all the different sections of the gastrointestinal tract, we used similar model designs, with organ included as another predictor variable, as well as its interaction with the nested terms. In this case, however, because of repeated measures within individuals (and hence non-independence of error terms), we also included individual as a random factor to ensure that ANOVAs (in particular calculations of F-statistics) compared appropriate error terms (Kristensen and Hansen, 2004; Jaeger, 2008). This required use of mixed effects models, using the lmerTest package (Kuznetsova et al., 2017). In all models, residuals were homoscedastic, but were not always normally distributed even after ln-transformation. Trials using ranked data had no qualitative influence on our results, suggesting that absence of normality is not a caveat in this instance, and so we retain the analysis using raw data.

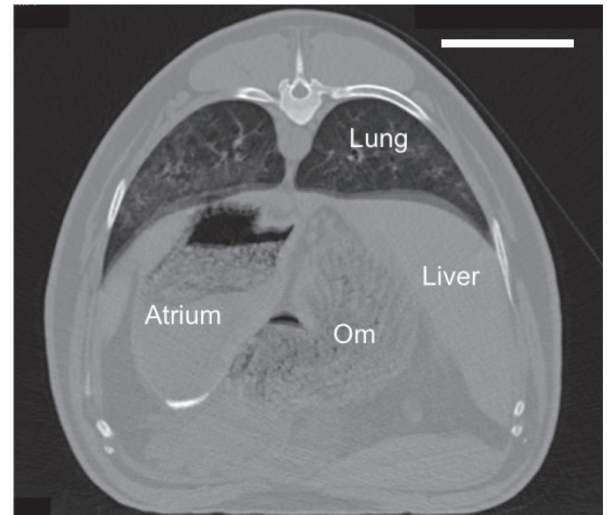
3. Results

Inspection of the CT scans indicated accumulation of radiodense material in the ventral rumen, the *Atrium ruminis*, and the abomasum (Figs. 3 and 4). In the abomasum, two different locations were evident – in the fundic region, where a partitioning of the radiodense material by the folds typical for the fundic mucosa of the abomasum could be observed (Figs. 3B and 4A), and at the pylorus (the exit of the abomasum towards the small intestine) (Fig. 4B, C). Radiodense material was not visible in the dorsal rumen, the reticulum, the omasum or the intestines. The measured dimensions of accumulated radiodense material in the ventral rumen and abomasum showed a numerical pattern with higher values linked to the feeding groups receiving higher concentrations and larger particle size (Fig. 5); the effect of dose was significant for radiodense material visible in the abomasum, and the effects of both dose and size were significant when assessing the whole stomach (Table 1). Note that, as previously reported for goats (Hatt et al., 2019), this accumulation did not cause clinical problems (and the sheep lived for another 12 months on the same diets after the CT scans).

The CT interpretations were corroborated by the analyses of the contents of the different sections of the gastrointestinal tract (Table 2). The highest concentration of silica led to generally higher dry matter values, and differences between sites of the gastrointestinal tract were as expected, with the evident exception of the abomasum that differed from all other sites, in particular for the higher concentration of fine sand. For total ash and silica (ADIA), values increased with concentrations of abrasives in the diet. There were additional statistical effects of abrasives size in the abomasum, with fine sand leading to higher silica (ADIA) values than fine silt. The main significant differences were between the abomasum and all other sites.

The complete findings for dry matter, total ash and silica (ADIA) are displayed in Fig. 6. Dry matter followed the typical ruminant pattern, with drier contents in the dorsal than the ventral rumen, very dry contents in the omasum, higher moisture content in the abomasum and the small intestine, and then a continuously increasing dry matter

A



B

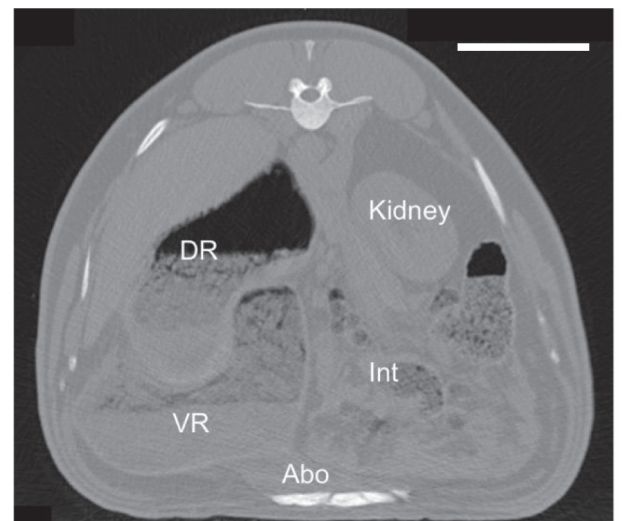


Fig. 3. Computed tomographic scans of a sheep (*Ovis aries*) fed a diet of lucerne meal pellets containing external abrasives (4% coarse silt) for four months. Animal in sternal recumbency. Images represent vertical slices through the thorax and abdomen (A) or, more caudally, through the abdomen only (B), as indicated in Fig. 1. Images are from a caudal point of view, with the dorsal rumen (DR) and ventral rumen (VR) filling the left body cavity. Silica accumulation is visible as hyperattenuating (white) agglomerations in the atrium and abomasum (Abo). Note the partitioning of the sand in the abomasum, which is caused by the fundic mucosal folds. Other radiodense structures correspond to vertebrae and ribs. Sand is not visible at other locations. The typical stratification of rumen contents is visible, with larger particles and air entrapment in the dorsal rumen as opposed to more homogenous, fluid contents of the ventral rumen, and the lamellar structure of the omasum (Om). The white scale bar represents 15 cm.

content along the large intestine (Fig. 6A). In the present study, the only exception to the typical ruminant pattern was the dry matter content in the abomasum that was particularly high on the high concentrations of coarse silt and fine sand, indicating massive silica accumulation. Total ash concentrations (Fig. 6B) as well as silica (ADIA) concentrations (Fig. 6C, Fig. 7) were generally lower in the forestomach (rumen, reticulum, omasum) than in the lower intestinal tract (Table 2), and were extremely high in the abomasum.

When comparing only the dorsal and the ventral rumen, the ventral rumen contents had numerically higher silica (ADIA) concentrations again for fine sand, and for 8% coarse silt, but not for 4% coarse silt or fine silt. Actually, on 8% fine silt, it even seemed that the dorsal rumen

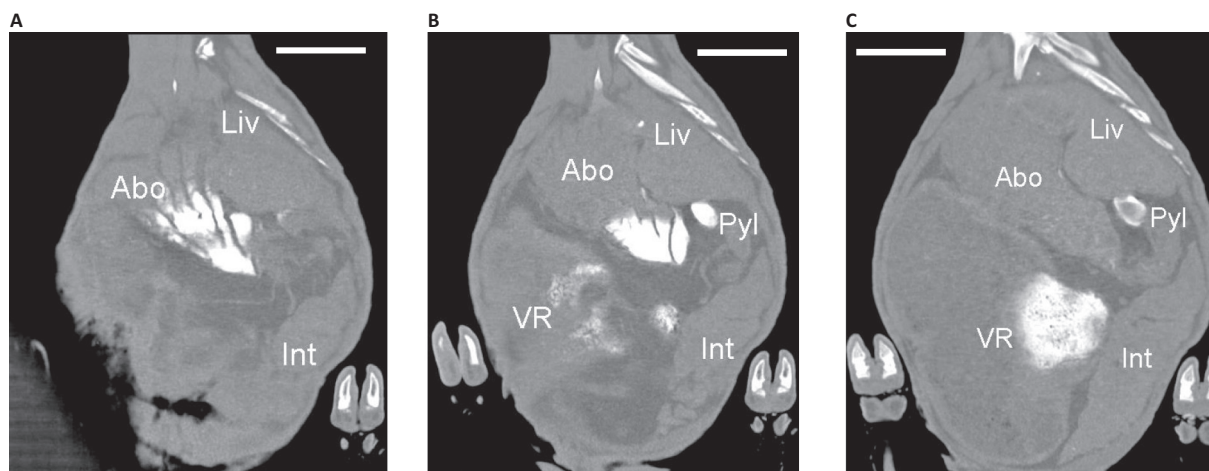


Fig. 4. Computed tomographic scans of a sheep (*Ovis aries*) fed a diet of lucerne meal pellets containing external abrasives (4% fine silt) for four months. Animal in sternal recumbency. Images represent horizontal-oblique slices through the thorax and abdomen at a more dorsal (A), intermediate (B) or ventral (C) position. The hind feet are visible on the lower part of the images. Silica accumulation is visible as hyperattenuating (white) agglomerations in the fundic region of the abomasum (Abo), partitioned by the abomasal fundic mucosal folds (A), in the aboral fundic region of the abomasum as well as in the pylorus (Pyl) of the abomasum, and, in outlines, in the ventral rumen (VR) (B), and more ventrally only in the pylorus and the ventral rumen (C). Note the outline of the abomasum in (C). Other radiodense structures correspond to vertebrae and ribs. Sand is not visible at other locations. Liv liver, Int intestines. The white scale bar represents 10 cm.

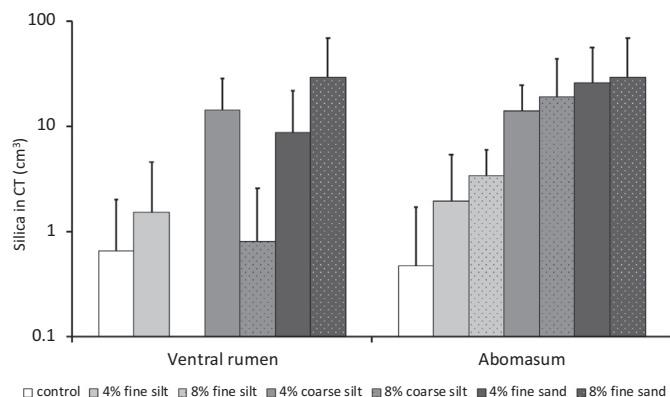


Fig. 5. Average accumulation of radiodense material, as quantified on CT images, in the ventral rumen and abomasum in sheep (*Ovis aries*) fed diets of different abrasive concentrations.

Table 1
Statistical results for CT measurements.

Effect	df	Effect F	Effect P	Post hoc P
<i>Radiodense volume (cm³) ventral rumen</i>				
Dose	2	2.19	0.128	0.126 to 0.599
Dose/size	4	3.44	0.019	0.195 to 1.000
<i>Radiodense volume (cm³) abomasum</i>				
Dose	2	3.71	0.036	0% ≠ 4% (0.030); others 0.084 and 0.856
Dose/size	4	1.21	0.324	0.264 to 1.000
<i>Radiodense volume (cm³) whole stomach</i>				
Dose	2	5.82	0.007	0% ≠ 4%/8% (0.005 and 0.033); other 0.655
Dose/size	4	3.15	0.027	0% ≠ 8% fine sand (0.046); others 0.052 to 1.000

Analyses with linear models for differences between diets in the accumulation of radiodense material in the ventral rumen, the abomasum and the whole stomach of sheep (*Ovis aries*) fed diets of different doses and sizes of abrasives (4% fine silt, 8% fine silt, 4% coarse silt, 8% coarse silt, 4% fine sand, 8% fine sand, and a control diet with no added abrasives) for four months.

contents did not release the abrasives as readily as for the other groups (Fig. 7). In statistical assessments of differences in dry matter, total ash or silica (ADIA) between the dorsal and ventral rumen (nested in abrasives concentration and size), there was always a significant effect of organ site (Table 3); for dry matter, dose and size had significant effects on the difference. For total ash and silica (ADIA), the silica concentration in the diet but not the grain size had an effect on the concentrations measured at the sites (Table 3).

Finally, we calculated the difference in silica (ADIA) concentration between the diets and the different stomach sections. The difference between diet and dorsal rumen contents was significantly greater (i.e., indicating a wash-out effect) for 8% diets, but similar for 4% diets and control; within the 8% diets, the difference increased with increasing abrasive size; within the 4% diets, it was greater for the fine sand than for the silts (Fig. 8A, Table 4). An identical pattern was evident for the difference between diet and reticulum contents (Fig. 8A, Table 4). For the difference between diet and ventral rumen contents, a similar numerical pattern only yielded a significant difference for the 8% diet, but no effect of particle size (Fig. 8A, Table 4). The difference between diet and omasum contents did not indicate a clear pattern (Fig. 8B, Table 4). Compared to the diet, the abomasum contents appeared enriched in silica, which was significant for the 8% diets (Fig. 8C, Table 4).

4. Discussion

The present study corroborates the recently described general concept of a washing mechanism in the ruminant forestomach complex, which depletes the digesta of external abrasives in certain compartments, and concentrates them in the glandular stomach (Hatt et al., 2019). Apparently, the principle is easily replicated. Here, we expand this concept by assessing differences in the mechanism for different concentrations and sizes of abrasives. The results suggest that in particular very small abrasives – of a size that defines them as fine silt, and that we consider ‘dust’ (< 5 to 60 µm; following McTainsh et al., 1997; Zender et al., 2003) – are less efficiently washed off the digesta, and are less selectively retained in the abomasum, than larger abrasives of a size that is closer to our understanding of ‘grit’ (> 100 µm). This observation is in line with expectations based on the relationship of particle size and adhesion forces to surfaces (Visser, 1995), as well as relationships of particle size and sedimentation velocity following Stoke's law.

Whether this difference is a real effect operating in nature, and the

Table 2

Statistical results for nutrient analyses along the whole gastrointestinal tract.

Effect	df1	df2	Effect F	Effect P	Post hoc P
<i>Dry matter (% fresh matter)</i>					
Individual	1		0.37	0.543	
Dose	2	32	9.15	0.001	0%/4% ≠ 8% (< 0.001 & < 0.001); other 0.923
Organ	9	285	81.11	0.000	Dorsal rumen ≠ ventral rumen/reticulum/omasum/small intestine/spiral colon/distal colon Ventral rumen ≠ omasum/proximal colon/spiral colon/distal colon Reticulum ≠ omasum/abomasum/caecum/proximal colon/spiral colon/distal colon Omasum ≠ abomasum/small intestine/caecum/proximal colon/distal colon Abomasum ≠ small intestine/spiral colon/distal colon Small intestine ≠ caecum/proximal colon/spiral colon/distal colon Caecum/proximal colon ≠ spiral colon/distal colon Spiral colon ≠ distal colon (< 0.001 to 0.009); others 0.181 to 1.000
Dose/size	4	32	1.07	0.388	0.897 to 1.000
Dose/organ	18	284	2.72	0.000	0%: Dorsal rumen/ventral rumen ≠ distal colon; reticulum ≠ spiral colon/distal colon; omasum ≠ distal colon; abomasum ≠ spiral colon/distal colon; small intestine ≠ proximal colon/spiral colon/distal colon; caecum/proximal colon/spiral colon ≠ distal colon (< 0.001 to 0.022) 4%: Dorsal rumen ≠ reticulum/small intestine/distal colon; ventral rumen ≠ omasum/spiral colon/distal colon; reticulum ≠ omasum/proximal colon/spiral colon/distal colon; omasum ≠ abomasum/small intestine/caecum/distal colon; abomasum ≠ spiral colon/distal colon; small intestine ≠ proximal colon/spiral colon/distal colon; caecum ≠ spiral colon/distal colon; proximal colon/spiral colon ≠ distal colon (< 0.001 to 0.021) 8%: Dorsal rumen ≠ spiral colon/distal colon; ventral rumen ≠ omasum/abomasum/spiral colon/distal colon; reticulum ≠ omasum/abomasum/proximal colon/spiral colon/distal colon; omasum/abomasum ≠ small intestine/distal colon; small intestine/caecum/proximal colon ≠ spiral colon/distal colon; spiral colon ≠ distal colon (< 0.001 to 0.030); others 0.064 to 1.000
Dose/organ/size	36	285	0.9601	0.539	8%/Abomasum/small silt ≠ fine sand (0.010); others 0.967 to 1.000
<i>Total ash (% dry matter)</i>					
Individual	1		0.13	0.715	
Dose	2	32	27.06	0.000	0 ≠ 4 ≠ 8 (< 0.001)
Organ	9	286	44.11	0.000	Dorsal rumen ≠ omasum/abomasum/small intestine/caecum/proximal colon/spiral colon/distal colon Ventral rumen/reticulum ≠ abomasum/caecum/proximal colon/spiral colon/distal colon Omasum ≠ abomasum/caecum/proximal colon Abomasum ≠ small intestine/caecum/proximal colon/spiral colon/distal colon Small intestine ≠ caecum/proximal colon (< 0.0001 to 0.028); others 0.117 to 1.000
Dose/size	4	32	0.28	0.887	0.999 to 1.000
Dose/organ	18	286	3.43	0.000	4%: Dorsal rumen ≠ abomasum/caecum/proximal colon; ventral rumen ≠ abomasum; reticulum ≠ abomasum/caecum/proximal colon; omasum ≠ abomasum; abomasum ≠ small intestine/caecum/proximal colon/spiral colon/distal colon 8%: Dorsal rumen/ventral rumen/reticulum ≠ abomasum/caecum/proximal colon/spiral colon/distal colon; omasum ≠ abomasum; abomasum ≠ small intestine/caecum/proximal colon/spiral colon/distal colon (< 0.001 to 0.042); others 0.069 to 1.000
Dose/organ/size	36	286	0.84	0.734	0.123 to 1.000
<i>Silica (acid detergent insoluble ash, % dry matter)</i>					
Individual	1		1.00	0.318	
Dose	2	32	30.89	0.000	0 ≠ 4 ≠ 8 (< 0.001)
Organ	9	286	49.02	0.000	Dorsal rumen/ventral rumen/reticulum ≠ abomasum/caecum/proximal colon/spiral colon/distal colon Omasum ≠ abomasum/proximal colon/Distal colon Abomasum ≠ small intestine/caecum/proximal colon/spiral colon/distal colon Small intestine ≠ caecum/proximal colon/spiral colon/distal colon (< 0.001 to 0.049); others 0.078 to 1.000
Dose/size	4	32	0.90	0.478	0.743 to 1.000
Dose/organ	18	286	4.73	0.000	4%: Abomasum ≠ all other sections 8%: Dorsal rumen/ventral rumen/reticulum ≠ abomasum/caecum/proximal colon/spiral colon/distal colon; abomasum ≠ all other sections (< 0.001 to 0.013); others 0.056 to 1.000
Dose/organ/size	36	286	1.42	0.064	8%Abomasum: small silt ≠ fine sand (< 0.001); others 0.853 to 1.000

Analyses with linear models for differences between in dry matter, total ash, and acid detergent-insoluble ash along the gastrointestinal tract of sheep (*Ovis aries*) fed diets of different doses and sizes of abrasives (4% fine silt, 8% fine silt, 4% coarse silt, 8% coarse silt, 4% fine sand, 8% fine sand, and a control diet with no added abrasives) for 16 months. Individual was a random effect. For post hoc tests, only relevant pairs were evaluated. For example, organs were compared within a specific abrasive dose only, i.e. two organs from animals with different combinations of both dose and size, were not included as contrasts.

extent to which it is linked to the production of the artificial diets used in the present study, is difficult to judge. One could argue that smaller silica particles, with higher surface interactions with other particles, may combine more tightly with the general food matrix during the compression of the pelleting process, and may still be contained within swallowed food fractions that are not completely moistened by saliva and require some time to dissolve. Larger particles are less likely to stay contained within pieces of food matrix and may therefore be washed out of the ingested material at a faster rate. Should this reasoning be correct, we would expect a less distinct size-related effect in ruminants consuming natural foods, where all external abrasives are on the outside of the plant material and unlikely to be partially trapped in pieces of food matrix. The high intragroup variation observed in the present

study possibly reflects a certain degree of stochasticity with respect to the interactions of abrasive particles and the diet, which may also occur – or not – on natural diets. Investigating the presence and size of abrasives along the gastrointestinal tract of free-ranging ruminants, with a sampling regime that represents the stratification, and hence the difference between dorsal and ventral rumen contents (Sauer et al., 2017), would be required to further investigate these questions.

In agreement with the previous study on goats (Hatt et al., 2019), the main accumulation sites of the silica particles were again in the abomasum, and to a lesser extent in the ventral rumen. For the abomasum, the major accumulation site was between the fundic laminae, but also partially in the pylorus. The fact that these animals lived on these diets for 16 months, and that variation in dietary abrasives levels

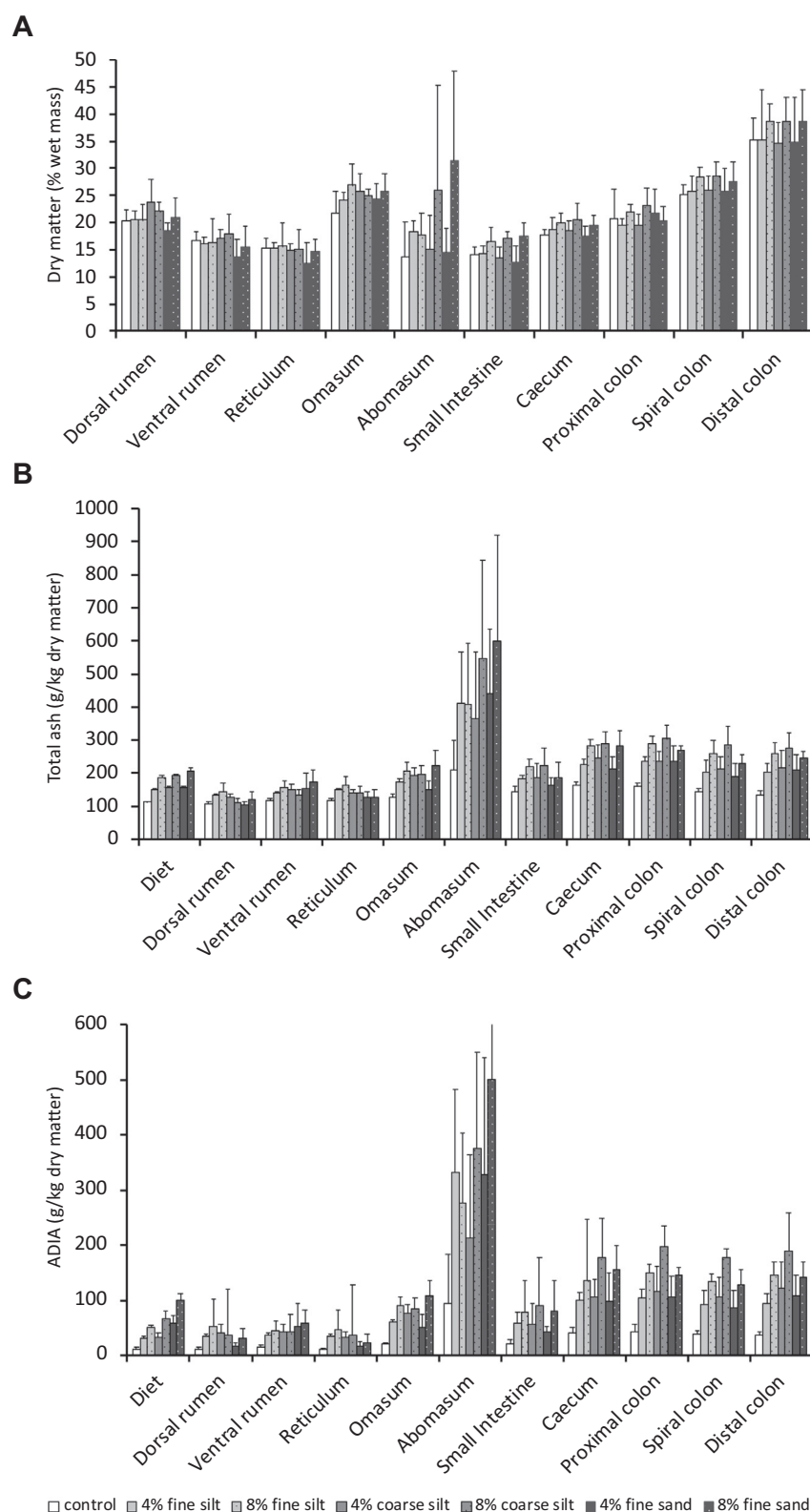


Fig. 6. The (mean + SD) concentration of (A) dry matter, (B) total ash, (C) acid detergent insoluble ash (ADIA; a measure for silica) in the diet and digestive tract of sheep (*Ovis aries*) fed diets of different abrasive concentrations and sizes. For a more detailed look at (C) see Fig. 7.

between the groups corresponded to differences in levels in the faeces, indicates that the accumulation is only temporary, and eventually an equilibrium develops. In other words, the inflow of abrasives into the abomasum must, at least when integrated over longer time periods, match the outflow from this organ. Even though the abomasal surface

does not consist of a keratinized epithelium like the preceding forestomach sections, but rather consists of a soft, glandular epithelium, it is most likely protected by the mucous produced by stomach glands, which also protects the mucosa against the hydrochloric acid produced by the deeper parietal cells (Goff, 2015). The findings in wild and

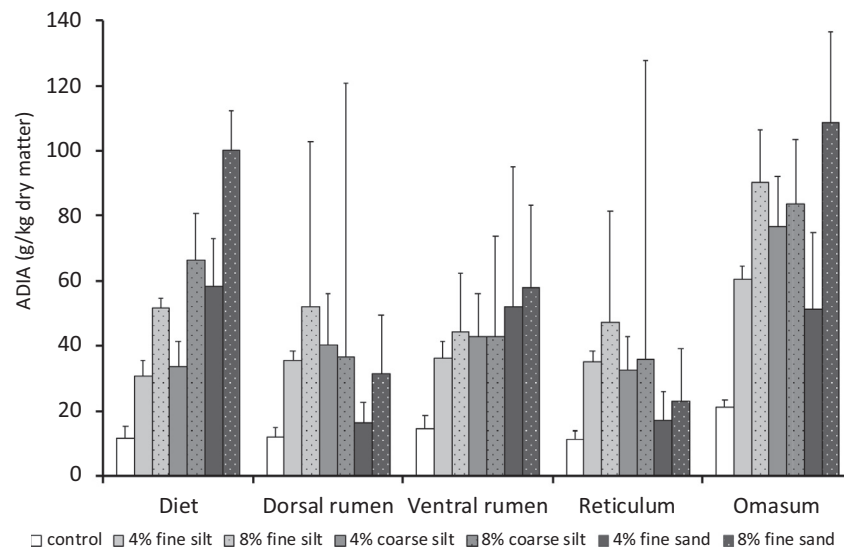


Fig. 7. Concentration of acid-detergent insoluble ash (ADIA, in dry matter; means + SD) in the diet and different sections of the forestomach in sheep (*Ovis aries*) fed diets of different abrasive concentrations and sizes.

Table 3

Statistical results for nutrient analyses between the dorsal and the ventral rumen.

Effect	df1	df2	Effect F	Effect P	Post hoc P
Dry matter (% fresh matter)					
Individual	1		5.63	0.018	
Dose	2	32	1.87	0.171	0.779 to 0.997
Organ	1	32	79.02	0.000	(Dorsal rumen \neq ventral rumen)
Dose/size	4	32	3.05	0.031	4%: coarse silt \neq fine sand (0.014); others 0.827 to 1.000
Dose/organ	2	32	0.55	0.582	4%/8%: Dorsal rumen \neq ventral rumen (< 0.001); other 0.208
Dose/organ/size	4	32	0.50	0.739	0.190 to 1.000
Total ash (% dry matter)					
Individual	1		8.38	0.004	
Dose	2	32	6.04	0.006	0 \neq 4/8 (< 0.001 and 0.016); other 0.573
Organ	1	32	48.65	0.000	(Dorsal rumen \neq ventral rumen)
Dose/size	4	32	2.04	0.112	0.163 to 1.000
Dose/organ	2	32	8.65	0.001	4%/8%: Dorsal rumen \neq ventral rumen (0.001 and 0.002); other 0.941
Dose/organ/size	4	32	5.28	0.002	0.268 to 1.000
Silica (acid detergent insoluble ash, % dry matter)					
Individual	1		3.36	0.067	
Dose	2	32	7.72	0.002	0% \neq 4%/8% (< 0.001); other 0.299
Organ	1	32	6.68	0.015	(Dorsal rumen \neq ventral rumen)
Dose/size	4	32	0.47	0.759	0.994 to 1.000
Dose/organ	2	32	4.51	0.019	0.203 to 1.000
Dose/organ/size	4	32	4.39	0.006	0.699 to 1.000

Analyses with linear models for differences between in dry matter, total ash, and acid detergent-insoluble ash between the dorsal and the ventral rumen of sheep (*Ovis aries*) fed diets of different abrasive concentrations (4% fine silt, 8% fine silt, 4% coarse silt, 8% coarse silt, 4% fine sand, 8% fine sand, and a control diet with no added abrasives) for 16 months. Individual was a random effect. For post hoc tests, only relevant pairs were evaluated. For example, organs were compared within a specific abrasive dose only, i.e. two organs from animals with different combinations of both dose and size, were not included as contrasts.

domestic ruminants, summarized in Fig. 2, additionally suggest that the accumulation of dense material at this site can be considered a normal process. African buffalo (*Syncerus caffer*) were estimated to ingest up to 28 kg of external silicates per year (Sansou et al., 2017), bison (*Bison bison*) ingesting natural forages can apparently withstand daily intake rates of soil of 6% in dry matter (Beyer et al., 1994), and cattle on ranges or pasture have been estimated to ingest up to one kilogram of soil per day (Healy, 1968; Mayland et al., 1975; Mayland et al., 1977), without accompanying reports of clinical problems. The amount of sand accumulating in the abomasum depends on the amount of sand ingested, but also on gastrointestinal motility (Dirksen, 2002). According to this author, healthy cows fed 10 kg sand daily over 35 days with their diet did not show any clinical signs of obstruction, similar to the animals of the present study.

In domestic ruminants, cases and case series of abomasal sand impaction have been reported in the literature. However, the condition seems to be uncommon. Gravel can occasionally be palpated in the abomasum during exploratory laparotomy, but without any signs of obstruction (Cebra et al., 1996). In general, sand impaction of the abomasum in cattle is caused by sand contaminated feed (Erickson and Hendrick, 2011; Hunter, 1975) or water (Simsek et al., 2015), or because of pica (ingestion of non-nutritive substances) apparently triggered by an acidogenic diet (Melendez et al., 2007). Dirksen (2002) suggests that underlying diseases affecting the motility and mucosa of the abomasum, as well as feed quality, are important factors for developing sand impaction in domestic cattle. The clinical signs in cattle with sand impaction are rather unspecific and attributable to forestomach dysfunction or intraluminal intestinal obstruction. In those cases reported in the literature, sand impaction has been diagnosed by exploratory laparotomy or necropsy. To sum up these observations, ruminants appear well able to handle substantial amounts of external silica in their digestive tract.

A result of the CT analyses in the present study that had not been reported previously is the notable accumulation of radiodense material in the *Atrium ruminis*. During dissections, we had not considered it feasible to sample this material separately, due to the large connection between the preceding rumen chambers and this part. The atrium links the dorsal and ventral rumen chambers to the reticulum, and dense material that collects in the ventral rumen should next be passed on to the atrium, and then into the reticulum (Wyburn, 1980). Apparently, more intense contractions in the reticulum, as compared to the atrium, prevent a similar accretion of radiodense material at the former site.

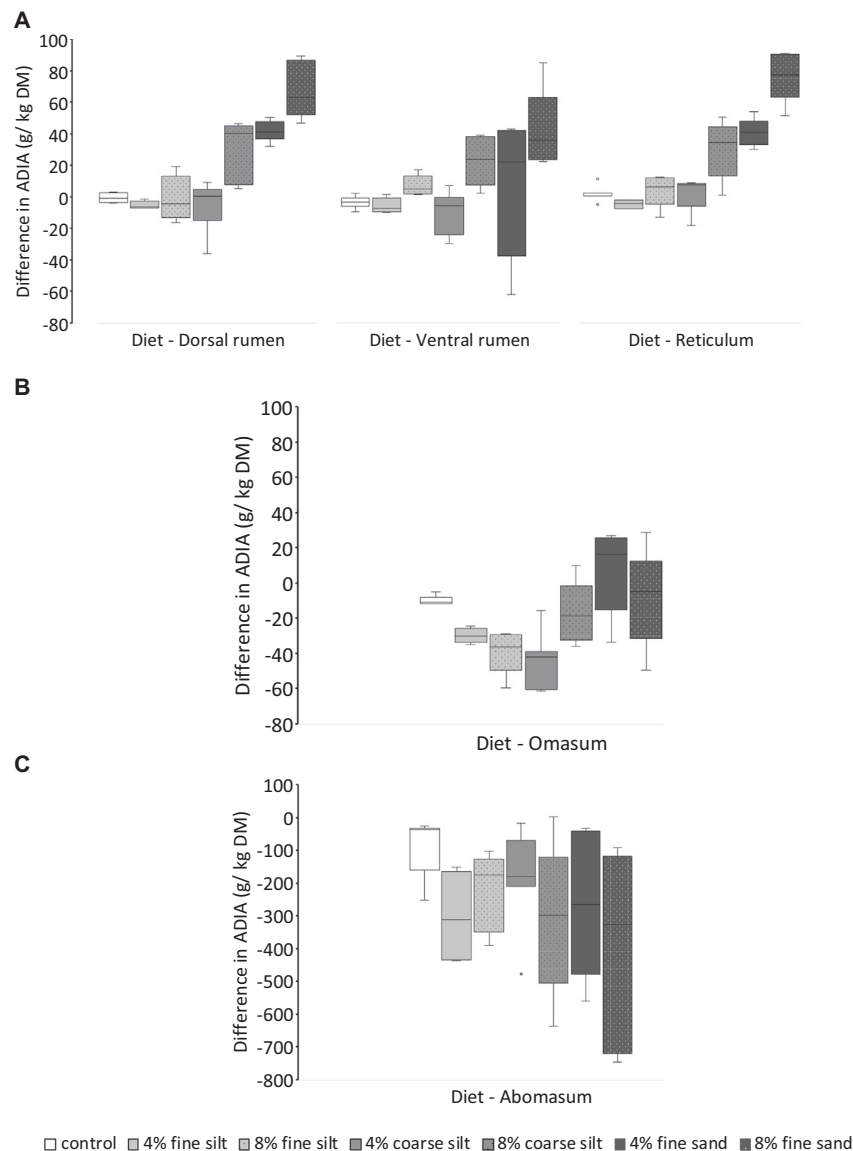


Fig. 8. Differences (median, inner quartiles, minimum/maximum) in the concentration of silica (acid detergent insoluble ash, ADIA in g/kg dry matter) between (A) the diet and digesta in different sections of the rumen and reticulum, (B) the diet and digesta in the omasum, and (C) the diet and digesta in the abomasum. Note that positive values on the y-axes of indicate digesta depleted in ADIA relative to diet, and negative values an enrichment relative to diet.

Why accumulations in the atrium had not been visible in the goats, with the coarsest silica particles, could be related to species-specific differences in motility, or in rumen fluid throughput (Clauss et al., 2006). Differences in the degree of fluid throughput between ruminant species that cannot be explained as adaptations to the natural diet could, in theory, also represent adaptations to the degree to which food is contaminated with dust or grit in the natural habitat (Przybyło et al., 2019), but this hypothesis still awaits testing. It is, however, suggestive that the only two ruminant species in which a very high rumen fluid viscosity (and hence a putatively lesser ‘washing effect’) has been measured, the moose (*Alces alces*) and the roe deer (*Capreolus capreolus*) (Clauss et al., 2009a, 2009b), are strict browsers from mesic habitats with a putatively very low external abrasives intake and brachydont teeth (Mendoza and Palmqvist, 2008).

Rumination can begin as early as directly after ingesting food, but typically starts about 15–50 minutes after the termination, and hence up to 4 h after the initiation, of a feeding bout (Dulphy and Favardin, 1987). At 1–2 mixing cycle contractions of the rumen per minute (Waghorn and Reid, 1983), this allows for ample time that ingesta is exposed to the washing effect of rumen fluid. For a given amount of

food, ruminants spend about 2–5 times as much time ruminating as ingesting (Ulyatt et al., 1986; Dulphy et al., 1995), they use a more regular chewing pattern during rumination (Dittmann et al., 2017), and they achieve the majority of particle size reduction during rumination (McLeod and Minson, 1988). While the amount of time spent ruminating per day will depend on food intake levels and the concentration of fibre in the ingested diet, there is no effect of body mass or feeding type on rumination activity across species (reviewed in Lauper et al., 2013).

Apart from serving for (i) the microbial fermentation of plant material, (ii) possibly for some microbial detoxification of secondary plant compounds, (iii) for the harvest of microbial biomass, and (iv) for the density sorting of digesta to subject large particles for repeated mastication (Clauss and Hofmann, 2014), the ruminant forestomach additionally reduces the abrasive load on the teeth by washing off abrasives prior to rumination. It is difficult to judge which of these functions is the one mainly selected for, and whether one should consider the ruminant forestomach as a direct adaptation to wash food. For example, whether the presence of a washing mechanism influences the comparative feeding selectivity, with nonruminants avoiding grit-

Table 4
Statistical results for differences in silica (ADIA) content.

Effect	df	Effect F	Effect P	Post hoc P
<i>Diet – Dorsal rumen</i>				
Dose	2	18.71	< 0.001	0%/4% ≠ 8% (< 0.001); other 0.145
Dose/size	4	30.79	< 0.001	4%: small silt/coarse silt ≠ fine sand (< 0.001), other 1.000 8%: small silt ≠ coarse silt ≠ fine sand (< 0.001 to 0.036)
<i>Diet – Ventral rumen</i>				
Dose	2	7.76	0.002	0%/4% ≠ 8% (0.002 and 0.021); other 1.000
Dose/size	4	2.21	0.090	0.304 to 1.000
<i>Diet – Reticulum</i>				
Dose	2	29.69	< 0.001	0%/4% ≠ 8% (< 0.001); other 0.059
Dose/size	4	41.36	< 0.001	4%: small silt/coarse silt ≠ fine sand (< 0.001), other 1.000 8%: small silt ≠ coarse silt ≠ fine sand (< 0.001 to 0.036)
<i>Diet – Omasum</i>				
Dose	2	1.52	0.235	0.235 to 0.990
Dose/size	4	9.36	< 0.001	4%: coarse silt ≠ fine sand (< 0.001), others 0.072 and 0.981 8%: 0.223 to 0.999
<i>Diet – Abomasum</i>				
Dose	2	3.54	0.041	0% ≠ 8% (0.032); others 0.165 and 0.539
Dose/size	4	0.88	0.488	0.935 to 1.000

Analyses with linear models for differences between in dry matter, total ash, and acid detergent-insoluble ash between the dorsal and the ventral rumen of sheep (*Ovis aries*) fed diets of different abrasive concentrations (4% fine silt, 8% fine silt, 4% coarse silt, 8% coarse silt, 4% fine sand, 8% fine sand, and a control diet with no added abrasives) for 16 months.

contaminated food to a higher degree than ruminants, remains to be investigated. Given a putative general life history advantage of some but not all ruminant clades over other large mammalian herbivores (Clauss et al., 2019), the washing effect may possibly be considered one of a large variety of functional peculiarities that make ruminants particularly efficient at transforming environmental resources into offspring.

Hatt et al. (2019) summarized findings in comparative herbivore dental anatomy and dental wear, as well as chewing physiology, that are affected by the existence of a washing mechanism in the forestomach of ruminants. These include differences in mandibular anatomy (Fletcher et al., 2010; Zhou et al., 2019) and chewing forces (Williams et al., 2011) as well as chewing patterns (Dittmann et al., 2017), but also tooth wear-related observations such as the general difference in hypsodonty between equids and ruminants even when ingesting similar natural diets (Damuth and Janis, 2011), differences in wear traces between hindgut fermenting and ruminant ungulates on putatively similar diets (Mihlbachler et al., 2016), distinct differences in feeding experiments between the wear effect of the same diets on live rabbits and *in vitro* assays versus live ruminants (Ackermans et al., 2019a, 2019b; Ackermans et al., 2018; Karne et al., 2016; Müller et al., 2014), or the catching conclusion that for ruminant tooth wear as measured by microtexture, ‘dust does not matter’ (Merceron et al., 2016). The results of the present study and that of Hatt et al. (2019) suggest that abrasives will affect ruminants in different ways than nonruminant herbivores. Generally speaking, (i) external abrasives should have less wear effect in ruminants; (ii) if external abrasives of various sizes are present simultaneously that typically lead to different microtexture patterns (Ackermans et al., 2020), the effect of the larger ones should be less, and that of the smaller ones correspondingly more, (iii) internal abrasives should have a higher effect, because they are embedded in leaf and stem material, and are enriched in the material regurgitated for rumination (Hatt et al., 2019). The general difference in hypsodonty between ruminants and equids mentioned above possibly suggests that

the protection against large external abrasives outweighs the concentration of internal abrasives with respect to dental tissue loss. Anyway, these findings caution against transferring experimental or observational results on tooth wear from ruminants directly to non-ruminant species, and vice versa. By extrapolation from their similar forestomach physiology to taxonomic ruminants (Lechner-Doll et al., 1991; Dittmann et al., 2015; Idalan et al., 2019), these conclusion include camelids as well.

Various reasons may exist why the same abrasives might cause different wear patterns in different species, ranging from dental anatomy, differences in enamel characteristics, to different chewing patterns and forces. For ruminants (and possibly camelids), the forestomach washing mechanism is just another of these reasons. Ideally, addressing the use of tooth wear as a habitat or climate proxy should not cause trench lines between supporters of taxon-specific and taxon-free approaches, but will simply benefit by prudent interpretations (Clauss, 2019; DeSantis et al., 2018; Fraser et al., 2018) and attempts to ensure constancy amongst the species used at different locations. In our opinion, categorically rejecting taxon-free approaches, even if a relative constancy of species distributions has been achieved, may be as unproductive as categorically rejecting the use of methods that account for differences between taxa, such as statistics accounting for the phylogenetic structure of the data. The mechanisms of herbivore tooth wear most likely still hold much to discover.

5. Conclusions

Amongst the many functions the ruminant forestomach fulfils is a washing of the ingested material, a process occurring inadvertently due to the presence of copious amounts of fluids and regular mixing peristalsis. Because the major chewing activity in ruminants processes regurgitated material after it has been exposed to the washing action, external abrasives, such as ‘dust’ and ‘grit’, should affect the ruminants’ cheek teeth to a lesser extent than a similar dietary concentration of ‘dust’ and ‘grit’ is expected to affect the cheek teeth of nonruminant herbivores. The present experiment suggests that this protective effect is more prominent for ‘grit’, and less so for ‘dust’. These findings contribute to explaining discrepancies in the observed effect of similar diets on tooth wear of different herbivore species, and remind us that different taxa may evolve different means to deal with environmental challenges.

Authors' contributions

JMH and MC designed the study, NLA, LFM and MC performed the experiment and dissections, HR and PRK supervised the CT scanning, JH supervised the nutritional analyses, JMH performed the CT measurements, DC analysed the data, JMH and MC wrote the first draft of the manuscript, to which CG contributed a passage on abomasal sand impaction in domestic ruminants; the draft then received input from all co-authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data

The original data measured in this study are available via the Mendeley Data repository linked to this article.

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