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Physical characteristics of forestomach contents from two nondomestic small ruminants, the blackbuck (*Antilope cervicapra*) and the Arabian sand gazelle (*Gazella subgutturosa marica*)

Janine Hertaeg[a], Cathrine Sauer[b,c], Mads F. Bertelsen[c], Sven Hammer[d], Peter Lund[b], Martin R. Weisbjerg[b], Marcus Clauss[a,*]

[a] *Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, CH-8057 Zurich, Switzerland*
[b] *Department of Animal Science, Aarhus University, AU Foulum, Blichers Allé 20, PO Box 50, DK-8830 Tjele, Denmark*
[c] *Center for Zoo and Wild Animal Health, Copenhagen Zoo, Roskildevej 32, DK-2000 Frederiksberg, Denmark*
[d] *Naturschutz-Tierpark Görlitz, Zittauerstr. 43, D-02826 Görlitz, Germany*

A R T I C L E I N F O

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A B S T R A C T

Rumen content stratification and the degree of dissociation of particle and fluid retention in the reticulorumen differ between 'moose-type' and 'cattle-type' ruminant species. These differences are not strictly linked to diet, except for a seeming limitation of 'moose-type' ruminants to a browsing niche. Nevertheless, these differences can be plausibly linked to other observed differences in ruminants, such as the intraruminal papillation pattern, or the size of the omasum. However, many of the corresponding measures are still only available for a restricted number of species. Here, we investigated the dry matter (*i.e.*, the inverse of the moisture) concentration in forestomach contents of 10 blackbuck (*Antilope cervicapra*) and 7 Arabian sand gazelle (*Gazella subgutturosa marica)*, and quantified the rumen papillation pattern. The blackbucks had distinct rumen contents stratification, with more moisture in ventral than in dorsal contents (difference 3.6% units, $P < 0.001$), whereas this difference was much less pronounced in the sand gazelles (0.6% units, $P = 0.227$). While reticulum contents were particularly moist in both species, omasum contents were particularly dry in sand gazelles, but did not differ in moisture from rumen contents in the blackbuck. This species is an outlier among ruminants due to its extremely small omasum. The intraruminal papillation pattern did not differ between blackbucks and sand gazelles and showed a surface enlargement factor (SEF) in the dorsal rumen of 27–28% of the SEF in the *Atrium ruminis*. Compared to data on digesta retention in the same species, the findings are in line with the overall concept of a high fluid throughput causing a distinct stratification of rumen contents and intraruminal papillation, and necessitating a large omasum for fluid re-absorption. However, the data also show that individual species may not correspond to all the assumptions of the concept, suggesting taxon-specific differences between species. Reasons for these differences cannot be linked to a dietary grass-browse spectrum, but may lie in evolutionary contingency.

1. Introduction

Ruminants represent the taxonomic group of large mammalian herbivores with the highest species diversity (Hackmann and Spain, 2010; Pérez-Barbería, 2020). This diversity has spurned investigation into the reasons that facilitate it. Among the most prominent explanations for ruminant diversity is niche diversification according to feeding types. After ascribing ruminant species to predominantly grazing, browsing or intermediate diets (van Zyl, 1965; Hofmann and Stewart, 1972), a large number of studies has addressed putative differences between these feeding types in terms of anatomy, physiology and behaviour (reviewed in Clauss et al., 2008; Codron et al., 2019). Among the many characteristics of grazing and browsing ruminants, those of the digestive tract, and especially those of the forestomach, have received particular attention (Hofmann, 1988), possibly because some of these features show very distinct differences between ruminant species.

* Corresponding author.
E-mail addresses: janine.hertaeg@uzh.ch (J. Hertaeg), csj@zoo.dk (C. Sauer), mfb@zoo.dk (M.F. Bertelsen), s.hammer@tierpark-goerlitz.de (S. Hammer), peter.lund@anis.au.dk (P. Lund), martin.weisbjerg@anis.au.dk (M.R. Weisbjerg), mclauss@vetclinics.uzh.ch (M. Clauss).

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The proximal causes for these differences are not resolved. The initial suggestion that differences in fibre content in the diet might be one of the main drivers (Hofmann, 1989) was not supported by empirical data on the fibre content of natural diets (Woodall, 1992; Codron et al., 2007). The hypothesis that the morphophysiological differences were based on the functional relevance of stratified rumen content for the retention of particles of grass or browse diets (Clauss et al., 2003) was also refuted by empirical testing (Lechner et al., 2010). Additionally, it was increasingly realized that ruminant species often did not follow the strict feeding type categorisation, with animals of a certain morphophysiology also ingesting other forages than expected (Djagoun et al., 2013; Marchand et al., 2013; Clauss and Hofmann, 2014; Przybylo et al., 2019). Such apparent discrepancies led to the statement used in a publication on ruminant dental anatomy that ‘morphology is not destiny’ (Gailer et al., 2016).

But even though the variation in ruminant digestive tract anatomy and physiology thus apparently cannot be causally linked to the diets consumed, it remains fascinating in its own right for being an example of the interplay of anatomy, physiology and digesta characteristics. In an attempt to clearly separate the morphophysiology of a ruminant species from its diet, Clauss et al. (2010) introduced the terms ‘moose-type’ and ‘cattle-type’ ruminants to avoid the circular reasoning that terms like ‘browser anatomy’ or ‘grazer physiology’ implied. ‘Moose-type’ ruminants are characterised by a relatively low throughput of high-viscosity fluid through the forestomach, and appear confined to browse-dominated diets. By contrast, ‘cattle-type’ ruminants are characterised by a relatively higher throughput of low-viscosity fluid through the forestomach, and can live in any kind of diet niche, from strictly browsing to strictly grazing, even though there may be a predominance of intermediate feeders and grazers among them (Przybylo et al., 2019). The differences in fluid throughput can be linked, both by plausible narratives and data correlations, to differences in the stratification of rumen contents (little stratification in ‘moose-type’, distinct stratification in ‘cattle type’). These are also reflected in the stratification of rumen papillation (little in ‘moose-type’, distinct in ‘cattle type’), to differences in the height of the reticular crests (avoiding reticulum emptying during contractions in ‘moose-type’ while facilitating emptying in ‘cattle-type’ – in the latter, re-fill by the low-viscosity fluid is easier), and differences in omasum size (with a higher need for water reabsorption in ‘cattle-type’) (reviewed in Codron et al., 2019; Ehrlich et al., 2019). However, further data, especially on fluid retention, rumen content stratification and papillation pattern are welcome to enlarge the species collection on which the respective relationships can be tested.

Here, we report measurements taken during an anatomical study on two small nondomestic ruminants, the blackbuck (*Antilope cervicapra*) and the Arabian sand gazelle (*Gazella subgutturosa marica*) (Sauer et al., 2016). We compare these data to those taken with identical methods in two other small ruminants, the mouflon (*Ovis ammon musimon*) and the roe deer (*Capreolus capreolus*) from Clauss et al. (2009a). The retention of fluids and particles in the digestive tract of these species had been measured previously in the same individual sand gazelles (Dittmann et al., 2015) and in other individuals of the same species for blackbuck (Hummel et al., 2015). Based on those previous studies, we expected both the blackbuck and the sand gazelles to display ‘cattle-type’ characteristics of clearly stratified rumen contents and rumen papillation.

2. Materials and methods

2.1. Animals and husbandry

Digesta samples were collected from 10 blackbucks (two males and eight females, body mass range 20.1 to 29.3 kg) and seven sand gazelles (all males, body mass range 16.1 to 19.2 kg). The blackbucks were kept at Ree Park Safari, Ebeltoft, Denmark, on a diet of *ad libitum* grass hay, a limited amount of grass haylage and free access to pasture during the day time. Pellets had been gradually removed from the diet at day 5–4 prior to culling and completely withheld on day 3–0. The sand gazelles were kept at Al Wabra Wildlife Preservation (AWWP), State of Qatar, on a diet of *ad libitum* grass hay and limited amounts of fresh lucerne for 4 weeks prior to culling. All animals were adult, clinically healthy, culled for management reasons and fed to carnivore species at the respective collections; this study therefore does not formally represent an animal experiment.

2.2. Digesta samples: collection and analysis

The sampling protocol was initiated within 30 min of slaughter, and was completed within 2 h. Animals were transported and weighed in an upright position, using straps and a hanging electronic scale. After weighing, the digestive tract was removed from the body, taking care to keep the rumen in its physiological position as described by Sauer et al. (2017). Digesta samples for dry matter analysis (the inverse of moisture concentration) were collected from the dorsal rumen (DR), the ventral rumen (VR), the reticulum (RE), and the omasum (OM). Dry matter was determined by drying the samples at 103 °C for 24 h for sand gazelle, while blackbuck samples were dried at 60 °C for 48 h. Because the effects (like the difference between DR and VR) are within species, we consider these different protocols acceptable.

2.3. Rumen mucosa samples: collection and analysis

The sampling of specific locations followed the approach outlined in Clauss et al. (2009c) and Sauer et al. (2017). Mucosa samples in blackbucks were collected from the dorsal rumen wall, the ventral rumen wall, and the *Atrium ruminis* wall at the position marked with squares on Fig. 1. In sand gazelles, the samples were collected only from the dorsal rumen wall and the *Atrium ruminis* wall. All samples were stored in 10% formalin until dissection. We determined the surface enlargement factor (SEF; Schnorr and Vollmerhaus, 1967) of the rumen papillae. The SEF is a dimensionless measure for how much the absorptive surface of the rumen is increased due to the papillae. A round piece of 11 mm in diameter was cut from each mucosa sample using a biopsy punch. All papillae were subsequently cut from the base of the mucosa samples and placed in a container according to size (small, medium, large and narrow, or large and broad) based on visual judgment by the dissector. The number of papillae of each size was counted

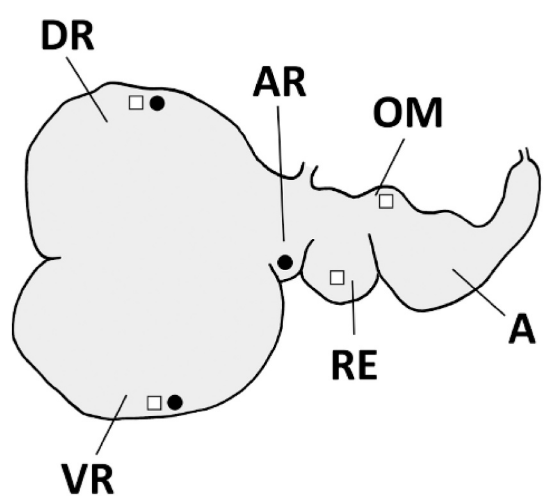

Fig. 1. Locations of sample collection in the forestomach. Figure depicts the forestomach complex of a blackbuck (*Antilope cervicapra*). The omasum of the sand gazelle (*Gazella subgutturosa marica*) was more pronounced.
Locations for digesta sampling are marked with a white square (□), while locations for mucosa sampling are marked with a black circle (●). DR = dorsal rumen, AR = *Atrium ruminis*, RE = reticulum, OM = omasum, A = abomasum, VR = ventral rumen.

and 10 papillae of each size were randomly chosen and measured using digital callipers. The length of each papilla was determined. Papilla width was determined at the midpoint (*i.e.*, length/2). All measurements were recorded to the nearest 0.01 mm. The surface enlargement factor of the rumen mucosa by the papillae was calculated as:

$$SEF = \frac{(no.of\ papillae \times MPSA) + base\ surface\ area}{base\ surface\ area}$$

where MPSA = mean papilla surface area, calculated as 2 × mean papillae height × mean papilla width (MPSA and base surface area are measured as cm^2 or mm^2; the SEF has no unit). Note that an unpapillated area of the rumen wall would thus have a SEF of 1.

2.4. Statistics

Statistical analyses were performed in R (R Core Team, 2017) using the libraries 'lmerTest' (Kuznetsova et al., 2017) and 'plyr' (Wickham, 2016). Within each species, a mixed model was used to assess differences in a measure (like content dry matter, or SEF) between different forestomach regions, while accounting for repeated measures per individual by including individual as a random factor. Model assumptions were assessed as normality of the model residuals, which was given in all cases. Comparisons between individual regions were made using LS-means. The significance level was set to 0.05. For comparison, data on two other small ruminants, the mouflon and the roe deer from Clauss et al. (2009a), were also displayed. Findings on dry matter content and SEF generated in the present study were related with other measurements from available datasets for wild ruminant species (Codron et al., 2019; Ehrlich et al., 2019; Przybylo et al., 2019). Note that in these species comparisons, the natural diet, quantified as the percentage of grass, is considered a species-specific characteristic and does not necessarily reflect the diet to which study animals were exposed.

3. Results

3.1. Dry matter concentration

The digesta DM concentration of each GI section for the three species is presented in Fig. 2. Individual as a random factor was significant in blackbuck ($P = 0.013$), indicating individuals differed in their overall level of digesta DM, but not in sand gazelles ($P = 0.805$). In both species, DM concentration decreased numerically from dorsal to ventral rumen and reticulum, and the difference between dorsal rumen and reticulum was significant in both species ($P < 0.001$). In both species, omasum contents were significantly drier than reticulum contents ($P \leqq 0.005$), but only in the sand gazelle were the omasum contents also significantly drier than the dorsal rumen contents ($P < 0.001$). Compared with other ruminant species in Fig. 2, blackbuck are peculiar in that the omasum contents did not represent the driest material in the forestomach. The difference in dry matter concentration between the dorsal and the ventral rumen, as an indicator for rumen content stratification, was 3.6 ± 1.8% units in blackbuck (significant at $P < 0.001$), 0.6 ± 0.5% units in sand gazelles (not significant, $P = 0.227$).

3.2. Rumen papillation

Characteristics of the rumen papillation are summarized in Table 1. Again, individual as a random factor was significant in blackbuck for papillae number and height ($P < 0.027$), but not for width or SEF ($P > 0.171$). In sand gazelles, the random factor was always not significant (*P*

Table 1
Papillae width, heigth and number, SEF and relative SEF of different sampling locations of blackbuck (*Antilope cervicapra*) and Arabian sand gazelle (*Gazella subgutturosa marica*).

		Blackbuck (n = 10)	Sand gazelle (n = 7)
Papillae width [cm]	Dorsal	0.08 ± 0.02^B	0.07 ± 0.01^B
	Atrium	0.11 ± 0.06^A	0.09 ± 0.01^A
	Ventral	0.10 ± 0.02^A	–
Papillae height [cm]	Dorsal	0.10 ± 0.03^C	0.15 ± 0.02^B
	Atrium	0.40 ± 0.06^A	0.43 ± 0.05^A
	Ventral	0.18 ± 0.05^B	–
Papillae number [/cm^2]	Dorsal	289 ± 90^A	175 ± 31
	Atrium	231 ± 73^B	196 ± 54
	Ventral	232 ± 44^B	–
Surface enlargement Factor (SEF)	Dorsal	5.60 ± 2.04^C	4.75 ± 1.19^B
	Atrium	20.98 ± 3.97^A	17.91 ± 4.32^A
	Ventral	9.67 ± 3.38^B	–
Relative SEF (per *Atrium*)	Dorsal	28.4 ± 13.9	27.2 ± 7.2

^{A,B} values with different superscripts differ between locations within a species.

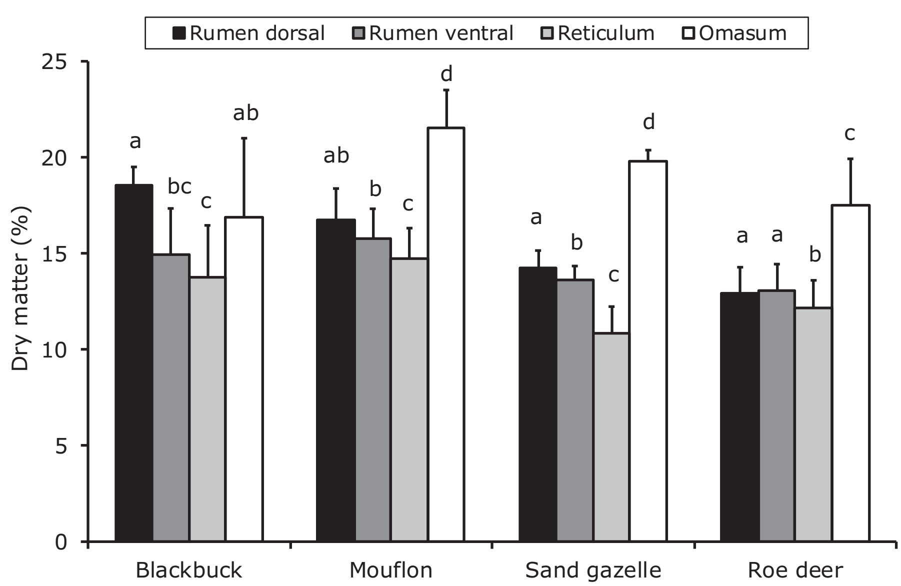

Fig. 2. Dry matter concentration in the forestomach contents of blackbuck (*Antilope cervicapra*, $n = 10$) and sand gazelle (*Gazella subgutturosa marica*, $n = 7$) of the present study as compared to mouflon (*Ovis ammon musimon*, $n = 19$) and roe deer (*Capreolus capreolus*, $n = 23$) from Clauss et al. (2009a). Within species, different letters indicate significant differences between the forestomach regions.

> 0.515). In both species, dorsal papillae were less wide and shorter than those of the *Atrium ruminis*, leading to significantly lower dorsal SEF compared to *Atrium* SEF (Table 1). The relative dorsal SEF (in % *Atrium* SEF) was very similar in both species at 27–28% (Table 1).

4. Discussion

Our study expands the number of nondomestic ruminant species for which physiological and anatomical measurements are available. These results are valuable especially in their contextualisation with previously gathered ruminant data.

The two species included in this study represent two different ruminant feeding types. Blackbuck are considered strict grazers (reviewed in Dittmann et al., 2015; Hummel et al., 2015), whereas sand gazelles are considered intermediate feeders (Dittmann et al., 2015), with an assumed average 80 and 38% of grass in their respective natural diets (Fig. 3A). This spacing across the diet spectrum, however, is not necessarily matched by a parallel distribution over a range of anatomical and physiological measurements.

Compared to the diet data, the two species of the present study followed a trend of higher difference between dorsal and ventral rumen dry matter with increasing percentage of grass in the natural diet (Fig. 3A), and with a larger difference in the retention time of small particles and fluids in the reticulorumen (RR), which was suggested to drive the stratification of rumen contents (Codron et al., 2019) (Fig. 3B). Whereas sand gazelle matched the general ruminant pattern of the difference between dorsal and ventral rumen dry matter and relative omasum size, suggesting that conditions linked to rumen contents stratification require more fluid re-absorption at the omasum, the blackbuck was an outlier to the pattern due to its particularly small omasum (Sauer et al., 2016) (Fig. 3C).

The selectivity factor (SF; Lechner-Doll et al., 1990), representing the ratio of the retention time of small particles to the retention time of fluid in the reticulorumen, increases nearly in parallel to the percentage of grass in the natural diet of the two species, from 2.3 in the sand gazelle (Dittmann et al., 2015) to 3.2 in the blackbuck (Hummel et al., 2015) (Fig. 3B). At these SF_{RR}, blackbuck and sand gazelles are classified as 'cattle-type' ruminants (Clauss et al., 2010).

The SF_{RR} is considered an indication for the degree to which the particulate matter in the reticulorumen is 'washed' by fluid, and thus an increasing SF_{RR} should lead to a more pronounced accumulation of liquid in the ventral rumen and hence a more pronounced rumen contents stratification (Fig. 3B). This applied to the difference between the two species of the present study.

Compared to other ruminant species, the two species of the present study were similar in the relative dorsal SEF but varied more in the difference between dorsal and ventral rumen dry matter (Fig. 4A), the difference in the retention time of small particles and fluids in the reticulorumen (Fig. 4B) and the relative size of the omasum (Fig. 4C). Although the species of the present study largely corresponded to the overall ruminant pattern, the difference between them did not match that pattern (Fig. 4).

It is plausible that a stratification of rumen contents should be reflected in a stratification of the rumen papillation. However, although sand gazelles and blackbuck differed in the stratification as measured by moisture in rumen contents, they were nearly identical in terms of the relative SEF, the measure for stratification in the rumen papillation pattern (Fig. 4). Note that the relative SEF measured in the blackbuck of the present study was, at 28%, basically identical to the 27% previously reported for the species based on other specimens (Clauss et al., 2009c). And although the sand gazelles did not differ in rumen content moisture stratification, they differed in the relative SEF at 27%. The similarity of sand gazelles and the blackbuck in this measure remains unexplained, and cannot even be attributed to low sample sizes.

One peculiarity previously demonstrated for blackbuck is the extremely small omasum in this species (Sauer et al., 2016) making it a

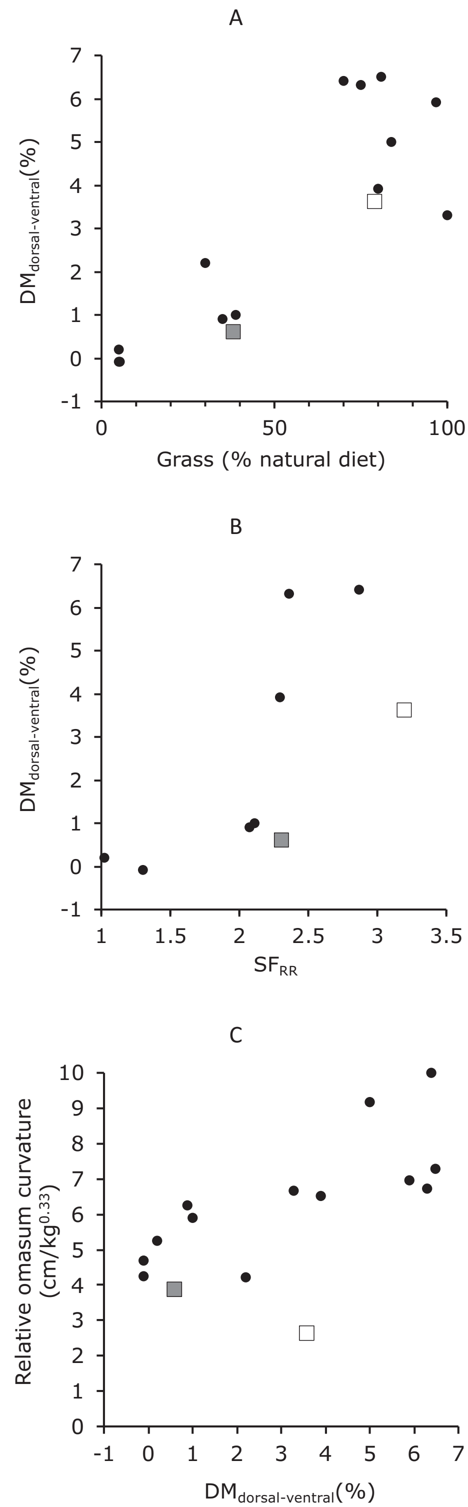

Fig. 3. Relationship between the difference in the dry matter (DM) concentration between the contents of the dorsal and the ventral rumen (a measure of the stratification of the rumen contents) and (A) the percentage of grass in the natural diet; (B) the selectivity factor (SF, the ration of particle to fluid retention in the reticulorumen RR; higher SF mean a higher throughput of fluid per particles); and (C) the relative size of the omasum. Data not generated in the present study were taken from the literature (Codron et al., 2019; Ehrlich et al., 2019; Przybylo et al., 2019). Species of the present study: blackbuck (*Antilope cervicapra*, white square), sand gazelle (*Gazella subgutturosa marica*, grey square). Black dots represent other ruminant species.

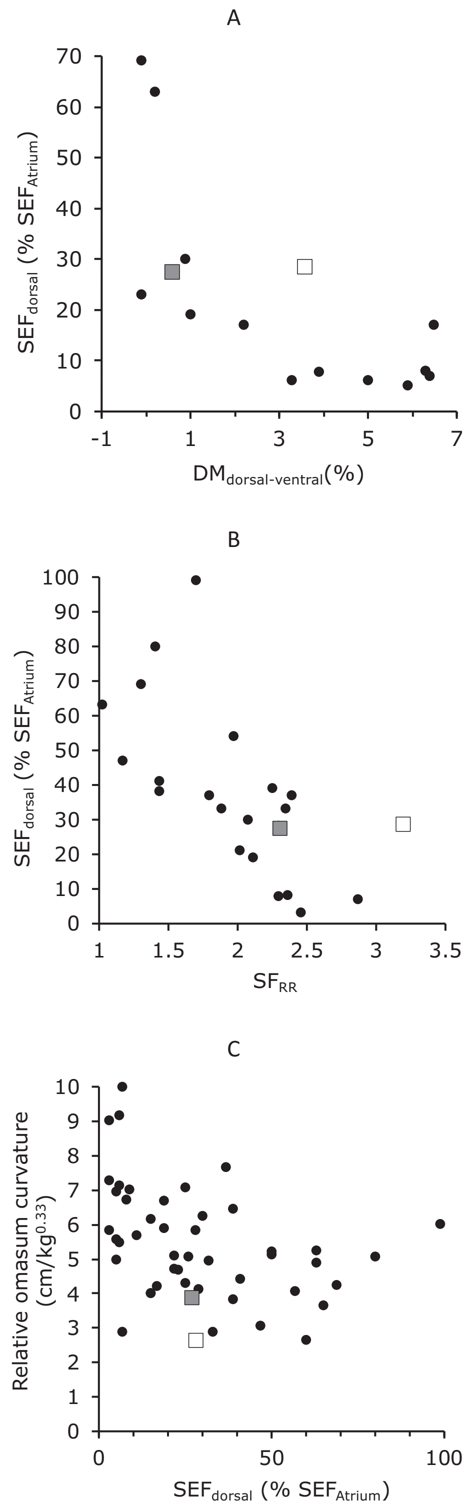

Fig. 4. Relationship between the relative surface enlargement factor (SEF) of the ruminal papillae in the dorsal rumen (expressed as % of the SEF in the *Atrium ruminis*; an anatomical correlate of the stratification of rumen contents) and (A) the difference in the dry matter (DM) concentration between the contents of the dorsal and the ventral rumen (a measure of the stratification of the rumen contents); (B) the selectivity factor (SF, the ration of particle to fluid retention in the reticulorumen RR; higher SF mean a higher throughput of fluid per particles); and (C) the relative size of the omasum. Data not generated in the present study were taken from the literature (Codron et al., 2019; Ehrlich et al., 2019; Przybylo et al., 2019). Species of the present study: blackbuck (*Antilope cervicapra,* white square), sand gazelle (*Gazella subgutturosa marica*, grey square). Black dots represent other ruminant species.

clear outlier among all ruminants (Ehrlich et al., 2019), but especially among those considered either grazers or 'cattle-type' species with a high SF_{RR}. A high SF_{RR}, indicative of a high fluid throughput through the reticulorumen, is typically linked to a larger omasum, which makes sense, given that one of the main functions of the omasum is fluid reabsorption (Ehrlich et al., 2019). In this respect, the blackbuck is a reminder that not every species needs to express all adaptations of its clade. We found that the contents of the omasum of blackbuck are different from all other ruminants measured so far (Clauss et al., 2009a; Clauss et al., 2009b; Clauss et al., 2016; Clauss et al., 2017; Sauer et al., 2017). Blackbuck omasal contents are not distinctively drier than rumen contents (Fig. 2), which supports the functional interpretation of the omasum as a drying organ whose drying capacity is related to its size. In this respect, reticulum contents in all ruminant species investigated so far (Hummel et al., 2009 and citations above) are either less dry than rumen contents, or - in animals with well-stratified rumens - of similar moisture as the ventral rumen contents (Fig. 2). This supports the general concept that the reticulum is the site of density-dependent particle sorting (Lechner-Doll et al., 1991), and requires particularly fluid contents in which particles can either float or sediment.

A reason for the data scatter evident in the relationships of Figs. 3 and 4, also observed previously for the same and other morphological and physiological measures in ruminants (Codron et al., 2019), may not only lie in differences in measurement accuracy between the different methods, and the fact that hardly ever all measurements taken were in the same individuals. It may also lie in the self-evident hypothesis that the interplay of anatomy and physiology varies among species due to evolutionary contingency. Currently, the existing datasets (Figs. 3 and 4) hardly contain sufficient numbers of species for a statistical assessment that includes an accounting for the phylogenetic structure. Given measurements in more species in the future, it may be possible to further explore these questions. To date, the datasets allow a functional interpretation of forestomach function that revolves around the degree of fluid throughput through the forestomach, leading to content and papillation stratification and requiring omasal fluid absorption in many species. The ultimate aim of this fluid throughput may well be not related to diet but to the harvesting of the microbes that are farmed in the forestomach (Clauss et al., 2010), a mechanism different ruminant taxa may have achieved and are using to varying degrees.

Declaration of Competing Interest

The authors declare no conflict of interest.

Acknowledgements

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