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ORIGINAL ARTICLE

Macroscopic digestive tract anatomy of two small antelopes, the blackbuck (*Antilope cervicapra*) and the Arabian sand gazelle (*Gazella subgutturosa marica*)

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Summary

The digestive tract anatomy of 14 blackbucks (*Antilope cervicapra*) and seven Arabian sand gazelles (*Gazella subgutturosa marica*) was quantified by dimensions, area and weight. Data from the two small-sized antilopinae were evaluated against a larger comparative data set from other ruminants classified as having either a 'cattle-type' or 'moose-type' digestive system. The digestive anatomy of the blackbuck resembled that of 'cattle-type' ruminants, which corresponds to their feeding ecology and previous studies of solute and particle retention time; however, a surprising exception was the remarkably small omasum in this species, which makes the blackbuck stand out from the general rule of a relatively large omasum in grazing ruminants. Sand gazelles had morphological features that corresponded more to the 'moose type' or an intermediate position, although previous studies of solute and particle retention time had led to the expectation of a more 'cattle-type' anatomy. The results show that outliers to general morphological trends exist, that findings on physiology and anatomy do not always match completely and that differences in the digestive morphology among ruminant species are more difficult to demonstrate at the lower end of the body mass range.

Introduction

Most ruminant species of small body size are classified as 'concentrate selectors' or 'browsers' (Hofmann, 1989). Of the exceptions, the majority are classified as 'intermediate feeders' (e.g. many species of deer and gazelles), while a few are 'bulk and roughage eaters' or 'grazers' (e.g. the oribi (*Ourebia ourebi*) and the mountain reedbuck (*Redunca fulvorufula*)). With a body mass (BM) of 20–55 kg (males being larger than females), the blackbuck is one of the few small ruminants considered to be a strict grazer, including approximately 80% grass in their diet (reviewed by Dittmann et al., 2015). Arabian sand gazelles, another member of the Antilopinae subfamily with a small BM (15–30 kg), are considered intermediate feeders including an average of around 40% grass in their diet (reviewed by Dittmann et al., 2015), though with large seasonal variation in forage type preference (Cunningham, 2013).

The classification of ruminants into feeding types has traditionally been based on either observations of feeding ecology, morphophysiological traits of the gastrointestinal tract, or a combination of the two. However, recent studies indicate that digestive anatomy is not necessarily a reliable proxy for the diet of a species, though some traits appear to be more common among browsing than grazing species and vice versa. Instead, it has been suggested to classify ruminants as either 'cattle type' or 'moose type' according to their digestive strategy (Clauss et al., 2010b), with 'cattle types' having a stratified rumen content, a fast flow of fluid through the reticulorumen (RR) and an uneven pattern of ruminal papillation. In contrast, 'moose-type' ruminants have a homogenous rumen content, a relatively slower RR fluid flow and an evenly papillated ruminal mucosa.

Fluid throughput and retention of particles in the RR can be measured using indigestible markers, for example Cr- or Co-EDTA as solute marker and Cr-mordanted fibres as particle marker. Using this marker system, the mean retention time of both fluid and solid material has been determined in many ruminant species including blackbucks (Hummel et al., 2015) and sand gazelles (Dittmann et al., 2015). Given the results of these studies, where a clear separation of solute and particle marker excretion was found in both species, we expected both species to have a 'cattle-type' digestive anatomy, for example having high reticular crests, thick rumen pillars and a relatively large omasum. In particular, the omasum of the blackbuck was expected to be large, to reabsorb the high amount of fluid passing from the RR of this species, as documented by Hummel et al. (2015). The aim of this study was to provide quantitative data on the gross gastrointestinal anatomy of blackbucks and sand gazelles and to determine whether predictions regarding digestive tract morphology based on their feeding ecology and previous retention time studies could be confirmed.

Materials and Methods

Data were collected from 14 blackbucks (five males and nine females, BM range 20.1–30.0 kg) and seven sand gazelles (all males, BM range 16.1–19.2 kg). Four of the blackbucks and all sand gazelles were kept at Al Wabra Wildlife Preservation (AWWP), State of Qatar, on a diet of grass hay *ad libitum* and limited amounts of fresh lucerne for 4 weeks prior to culling. In addition, blackbucks were fed a small amount of pellets. The remaining ten blackbucks were kept on a diet of *ad libitum* grass hay, limited amounts of grass haylage and free access to pasture during the day time at Ree Safari Park, Denmark. Pellets had been gradually removed from the diet at days 5–4 prior to culling and completely withheld on days 3–0. All animals were culled for management reasons except for one blackbuck that died from trauma. Dissections followed a previously described protocol (Sauer et al., in press). Not all measures were obtained from each individual animal due to practical limitations or time constraints; in particular, no measurements of omasal laminar surface area and salivary glands of sand gazelles were made. Heads of the blackbucks from Ree Park were frozen prior to dissection of the salivary glands, while salivary gland weight was determined in fresh heads from AWWP blackbucks.

For a comparative evaluation of the anatomical measures of blackbucks and sand gazelles, measurements obtained were plotted against literature data on forestomach anatomy and salivary gland weight of other ruminant species, classified as having either a 'moose-type' or 'cattle-type' digestive tract [for species and literature sources, see Sauer et al. (in press), with additional data from Short (1964), Hofmann and Geiger (1974), Nagy and Regelin (1975), Weston and Cantle (1983), Stafford and Stafford (1993), Staaland et al. (1997) and Wang et al. (2014)].

To determine the relation between BM and anatomical measurements, data were ln-transformed and allometric regression analysis was used to determine the coefficients of the model:

$$\ln(Y) = \alpha + \beta \times \ln(\mathrm{BM})$$

where Y = the anatomical measurement and BM = body mass in kilogram. The hypothesis of isometric scaling was accepted if 0.33, 0.67 and 1.00 was included in the 95% confidence interval of the BM exponent (β) of linear dimensions, areas and weights, respectively. Anova was used for step-wise model reduction. All statistical analyses were performed using the statistical software R (version 3.1.0, R Foundation for Statistical Computing, Vienna, Austria). Significance was accepted at $P \leq 0.05$ with values below 0.1 considered as trends.

Results and Discussion

The stomach of both blackbuck and sand gazelle was comprised of a rumen, reticulum, omasum and abomasum as in all other true ruminants (Fig. 1). The rumen was the largest compartment followed by the abomasum, then the reticulum and the omasum. When dissecting the blackbuck omasa for laminar surface area determination, only the first, most of the second and a few of the third-order leaves were dissectable, i.e., more than just a small ridge on the basal layer of the omasum. On average, the blackbuck omasum had 9.7 ± 1.1 leaves of first order, 9.4 ± 1.4 leaves of second order, 14.4 ± 5.3 leaves of third order, 3.0 ± 2.1 leaves that were positively identified as fourth order and 4.0 ± 0.7 leaves where order could not be determined. The size and position of the parotid and mandibular salivary glands of blackbuck are shown on Fig. 2, while the average anatomical measurements of both species are presented in Tables 1 and 2.

In blackbucks, all RR and omasum size measures correlated poorly to BM (all P-values $\geq$ 0.1), while abomasum tissue weight and greater curvature length tended to increase with BM (P = 0.096 and P = 0.052, respectively). The length of the lesser abomasal curvature was not related to BM (P = 0.203). Small intestine (SI) length did not correlate to BM (P = 0.733), while SI tissue weight increased with BM (P = 0.019). Caecum length and tissue weight tended to increase with BM (P = 0.057 and

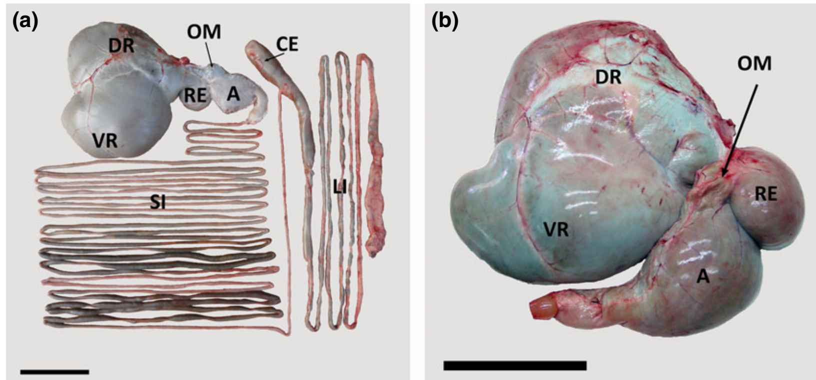

Fig. 1. Digestive tract of the blackbuck. DR, dorsal rumen; VR, ventral rumen; RE, reticulum; OM, omasum; A, abomasum; SI, small intestine; CE, caecum; LI, large intestine. (a) Blackbuck from Ree Park. (b) Blackbuck from Al Wabra Wildlife Preservation. Note the similar omasum size in animals from both institutions. Scale bars represent 15 cm.

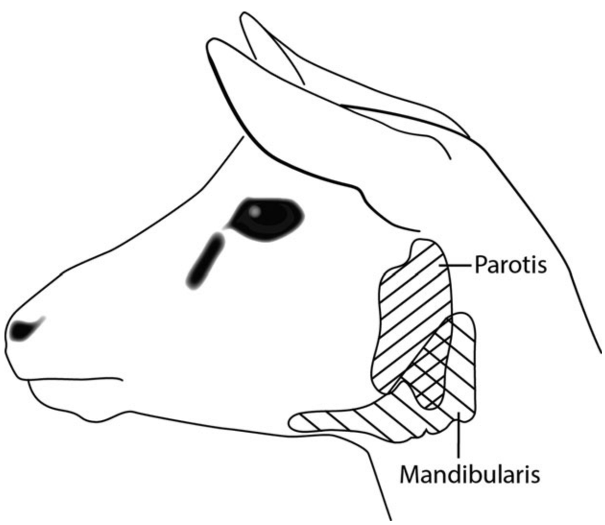

Fig. 2. Position of the parotid and mandibular salivary glands of the blackbuck. The mandibular glands were positioned medially to the parotid glands. Courtesy of Jeanne Peter.

$P = 0.059$, respectively). Total large intestine (total LI, defined as caecum, colon and rectum) was both longer and heavier in larger animals (both $P < 0.03$), while the SI : total LI length ratio did not correlate to BM ($P = 0.149$). Weight of the parotid salivary glands ($n = 10$, BM: 25.0 ± 3.3 kg, weight: 15.2 ± 3.0 g) tended to increase with BM ($P = 0.051$), while the mandibular glands weight ($n = 6$, BM: 24.1 ± 3.3 kg, weight: 13.0 ± 2.8 g) was unaffected by BM ($P = 0.574$). The expected isometric value was included in the 95% confidence interval for all measures correlating or tending to correlate to BM, though the confidence intervals were very wide in many cases.

The BM range of the seven sand gazelles (16.1–19.2 kg) was not wide enough to correlate anatomical measurements to BM. Consequently, only means and standard deviations are presented for this species (Tables 1 and 2). Even though the BM range of the blackbucks was wider than that of the sand gazelles, the fit of the allometric regression model for most anatomical measurements was poor. Thus, to describe the relation between BM and digestive anatomy, data from animals of a wider range of body masses and stages of maturity are needed from both species. Actually, this demonstrates that for species with an inherently narrow range of body masses, intraspecific allometries may be difficult to achieve.

Diet can possibly influence some measures of digestive tract gross anatomy in ruminants, such as omasum size (Lauwers, 1973), and weight of the digestive tract (McLeod and Baldwin, 2000) and of the salivary glands (Mathiesen et al., 1999). Therefore, using captive animals to investigate the digestive anatomy of any species adds a risk of an unintentional effect of an unnatural diet. To mimic a natural diet as much as possible given the captive conditions, pelleted feed was either withheld or only fed in limited amounts in the time up to culling for both species in the study. However, after a life in captivity with higher quality diets, no periods of fasting and free access to drinking water, long-term adaptations to captivity may exist in the animals investigated in this study.

Blackbucks resembled 'cattle-type' ruminants with respect to rumen pillar thickness, reticular crest height and salivary gland weight (Figs 3 and 4), while omasum size parameters were in the range of, and even below, 'moose-type' ruminants (Fig. 5). When the blackbucks were dissected, it was noted that the omasum was small and difficult to identify from the outside of the stomach, i.e., not a separate 'ball-shaped' organ as in other ruminants. This finding was consistent across animals from the two facilities (Fig. 1). In spite of a potential effect of captive diet on

Table 1. Rumen, reticulum, omasum and abomasum size measurements of blackbuck and sand gazelle. All values are presented as mean ± standard deviation

	Blackbuck			Sand gazelle		
	n	BM (kg)	Value	*n*	BM (kg)	Value
Reticulorumen tissue weight (g)	14	25.2 ± 3.3	449.8 ± 64.0	7	17.6 ± 1.1	232.6 ± 20.5
Rumen height (cm)	13	25.2 ± 3.5	26.9 ± 2.8	7	17.6 ± 1.1	19.4 ± 1.6
Dorsal rumen length (cm)	12	24.8 ± 3.3	21.9 ± 2.5	–	–	–
Ventral rumen length (cm)	11	25.2 ± 3.2	22.9 ± 2.6	–	–	–
Total rumen diagonal (cm)	12	25.2 ± 3.5	29.7 ± 3.5	7	17.6 ± 1.1	19.7 ± 1.0
Reticulum height (cm)	13	25.2 ± 3.5	9.4 ± 2.3	7	17.6 ± 1.1	11.0 ± 2.1
Reticulum length (cm)	13	25.2 ± 3.5	7.8 ± 1.3	7	17.6 ± 1.1	5.3 ± 1.7
Reticular crest height (mm)	13	25.2 ± 3.5	4.0 ± 1.3	7	17.6 ± 1.1	1.6 ± 0.3
Cranial rumen pillar thickn. (mm)	14	25.2 ± 3.3	7.2 ± 1.9	7	17.6 ± 1.1	4.7 ± 1.0
Caudal rumen pillar thickn. (mm)	14	25.2 ± 3.3	9.4 ± 2.2	7	17.6 ± 1.1	5.7 ± 0.8
Omasum tissue weight (g)	13	25.2 ± 3.5	20.9 ± 4.0	7	17.6 ± 1.1	18.6 ± 3.4
Omasum height (cm)	13	25.2 ± 3.5	5.0 ± 1.2	7	17.6 ± 1.1	6.6 ± 0.9
Omasum length (cm)	13	25.2 ± 3.5	3.5 ± 0.7	7	17.6 ± 1.1	4.3 ± 0.5
Omasal curvature length (cm)	14	25.2 ± 3.3	6.6 ± 1.7	7	17.6 ± 1.1	9.6 ± 1.4
Number of omasal laminae	5	26.3 ± 2.2	42 ± 3	–	–	–
OLSA (cm^2)	5	26.3 ± 2.2	193.4 ± 28.7	–	–	–
Abomasum tissue weight (g)	13	25.2 ± 3.5	150.4 ± 85.8	7	17.6 ± 1.1	37.9 ± 5.5
Greater abomasal curv. length (cm)	12	25.2 ± 3.5	24.8 ± 3.8	–	–	–
Lesser abomasal curv. length (cm)	12	25.2 ± 3.5	18.2 ± 3.2	–	–	–

BM, body mass; thickn., thickness; OLSA, omasal laminar surface area; curv., curvature.

Table 2. Intestinal size measurements of blackbuck and sand gazelle. All values are presented as mean ± standard deviation

	Blackbuck			Sand gazelle		
	n	BM (kg)	Value	*n*	BM (kg)	Value
Small intestine tissue weight (g)	13	25.2 ± 3.5	216.0 ± 69.1	7	17.6 ± 1.1	123.7 ± 15.2
Small intestine length (m)	13	25.2 ± 3.4	11.2 ± 1.7	7	17.6 ± 1.1	7.3 ± 0.8
Total LI[a] tissue weight (g)	13	25.4 ± 3.3	177.9 ± 53.3	7	17.6 ± 1.1	128.4 ± 49.9
Total LI[a] length (m)	12	25.1 ± 3.2	4.1 ± 0.4	4	17.7 ± 1.3	2.0 ± 0.4
Caecum tissue weight (g)	13	24.8 ± 3.2	16.0 ± 4.3	7	17.6 ± 1.1	16.9 ± 4.5
Caecum length (cm)	14	25.2 ± 3.3	14.5 ± 2.4	7	17.6 ± 1.1	14.7 ± 3.0
Small intestine : Total LI[a] length	11	25.2 ± 3.3	2.9 ± 0.5	4	17.7 ± 1.3	3.6 ± 1.1

BM, body mass; LI large intestine.
[a]Total large intestine was defined as caecum, colon and rectum.

omasum size, the extent of that effect would have to be enormous to explain the difference between the very small omasum observed and the expected size for a grazing ruminant. The fact that blackbucks had a small omasum at both captive facilities (Fig. 1), i.e., under different diets and husbandry conditions, suggests that this omasum size is not a dietary artefact, but must be an inherent morphological trait of the blackbuck. This was a surprising finding, as the selectivity factor of the RR (SF_{RR}, defined as mean retention time (MRT) of particles in the RR divided by MRT of fluid in the RR) in blackbucks were found to be in the higher end of the range of 'cattle-type' ruminants (Hummel et al., 2015), indicating a relatively high fluid flow out of the RR in this species. Thus, we expected to find a particularly large omasum in the blackbuck to reabsorb this fluid, as predicted by Hummel et al. (2015). A possible consequence of the particularly small omasum of blackbuck could be a particularly large abomasum to accommodate the inflowing digesta and facilitate the presumably larger amount of gastric secretions needed to

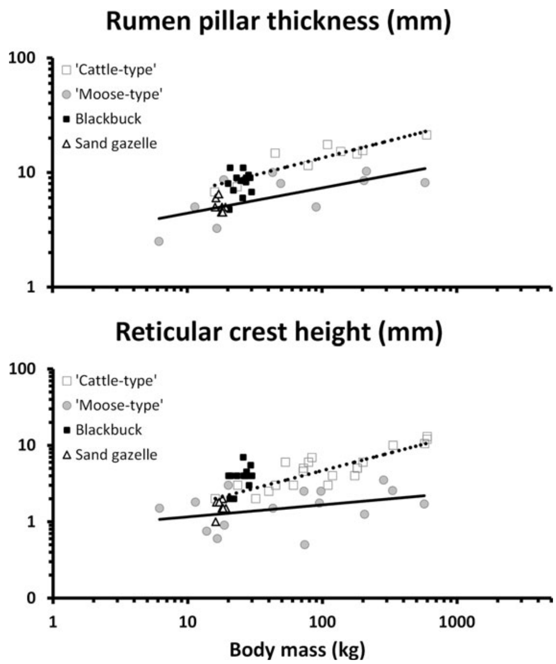

Fig. 3. Comparison of selected internal reticuloruminal measurements of blackbuck and sand gazelle to other species of ruminants. Each species is represented by a point, except for blackbuck and sand gazelle. Solid line: trendline for 'moose-type' ruminants; dashed line: trendline for 'cattle-type' ruminants.

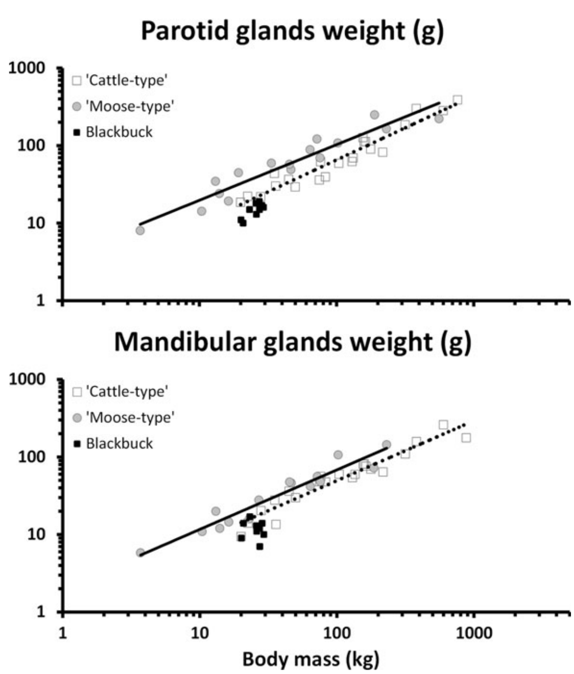

Fig. 4. Comparison of parotid and mandibular salivary gland weights of blackbuck to other species of ruminants. Each species is represented by a point, except for blackbuck. Solid line: trendline for 'moose-type' ruminants; dashed line: trendline for 'cattle-type' ruminants.

counteract the diluting effect of the un-absorbed rumen fluid. Whether ruminant species with a relatively small omasum generally have a relatively large abomasum remains to be investigated. Using the fossil records of pecoran ruminants and tragulids, Clauss and Rössner (2014) speculated that the absence of an omasum in tragulids was a competitive disadvantage that might have contributed to their ecological replacement by pecoran ruminants over time. The example of the blackbuck indicates that the ruminant forestomach system can also function efficiently without a pronounced omasum. The oribi, a grazing ruminant even smaller than the blackbuck, has also been reported as having a smaller omasum than expected (Hofmann, 1973; Stafford and Stafford, 1993). The rareness of this feature, however, with larger omasa present in basically all other ruminant species investigated so far, suggests that this is not a particularly successful adaptation, yet calls for further studies on alternative mechanisms of fluid reabsorption in the few species with small omasa.

Sand gazelles appeared to most resemble 'moose types' for rumen pillar thickness, while the reticular crest height was in the middle range between 'cattle types' and 'moose types' (Fig. 3). In the wild, sand gazelles seasonally include large amounts of browse and hence are classified as intermediate feeders. Based on the apparent differences in SF_{RR} between 'moose-type' and 'cattle-type' ruminants, Hummel et al. (2015) hypothesized that the optimal relation of $MRT_{particles}$ to MRT_{fluid} depends on the type of forage ingested, with higher SF_{RR} in 'cattle types' than in 'moose types'. As SF_{RR} of sand gazelles (2.3, Dittmann et al., 2015) is lower than that of blackbucks (3.2, Hummel et al., 2015), we expect the digestive anatomy of sand gazelle to have less pronounced 'cattle-type' characteristics than that of the blackbuck, though both species are in the SF_{RR} range of 'cattle-type' ruminants (~2.0–4.5, Hummel et al., 2005). The typical range of SF_{RR} for 'moose-type' ruminants is more narrow (~1.0–2.0, Hummel et al., 2005), reflecting the fact that 'moose-type' ruminants predominantly feed on a browse-only diet, while the 'cattle-type' ruminants cover a much wider range of dietary strategies encompassing both intermediate feeders and grazers (Codron and Clauss, 2010).

Several digestive characteristics of browsing and grazing ruminants have been established as examples of convergent evolution, namely the evolution of high reticular crests (Clauss et al., 2010a), greater omasal laminar surface area (Clauss et al., 2006) and smaller parotid salivary glands (Hofmann et al., 2008) in grazing relative to browsing ruminants. However, confirming convergent evolution of a specific trait may be obscured by species in a transition phase, that is species that have changed dietary habits recently with the adaptations of their digestive anatomy 'lagging behind', as discussed by Clauss et al.

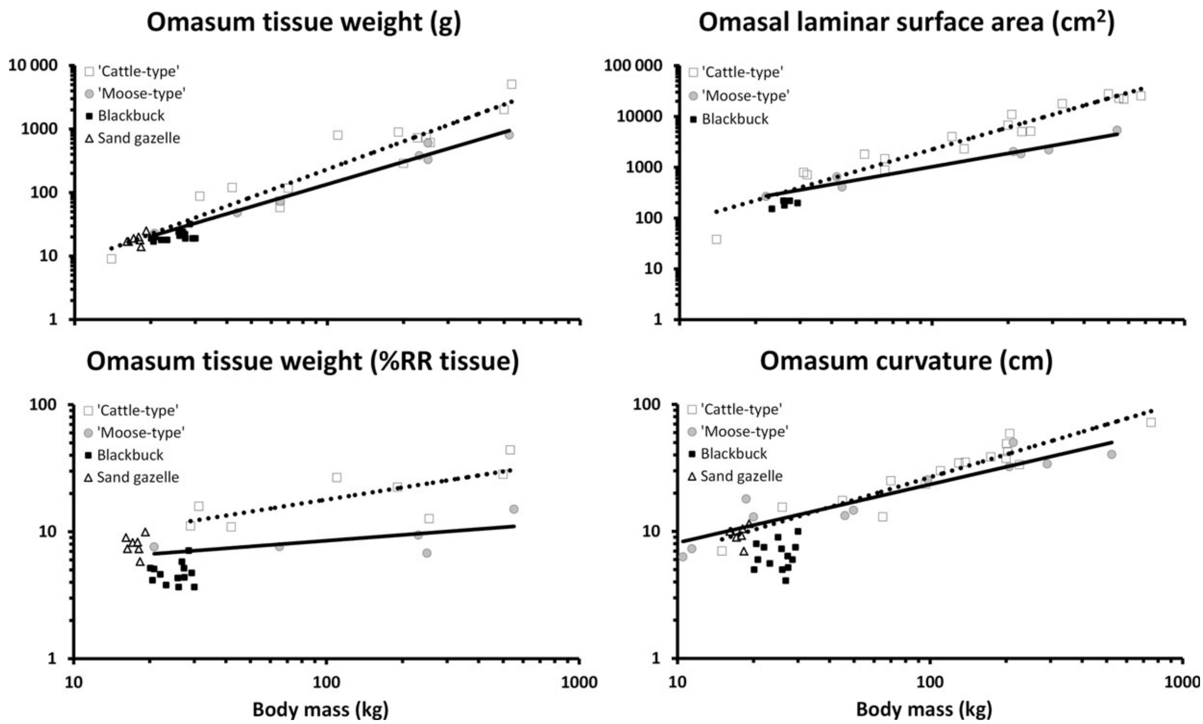

Fig. 5. Comparison of omasum size parameters of blackbuck and sand gazelle to other species of ruminants. Each species is represented by a point, except for blackbuck and sand gazelle. Solid line: trendline for 'moose-type' ruminants; dashed line: trendline for 'cattle-type' ruminants.

(2008). It can only be speculated if the case of the small blackbuck omasum represents a delay in anatomical adaptations to a grass-based diet.

In conclusion, the present study confirmed that many morphological traits of the digestive tract of the blackbuck correspond to the 'cattle-type' anatomy. A notable exception, however, was the surprising discovery of an unusually small omasum in this species, even smaller in size than reported for 'moose-type' ruminants. For sand gazelles, some morphological results were in line with previous findings in 'moose-type' ruminants, such as rumen pillar thickness and omasum size, whereas others were of an intermediate position. These results indicate that differentiation of the ruminant types is difficult to detect at small body masses (as also evident in the converging regression lines in Figs 3 and 5). Additionally, they show that physiology, as measured by digesta retention times, and morphology do not necessarily yield completely matching results, suggesting either that their interplay is not yet fully understood, or that theories linking the two must include a certain degree of flexibility.

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Conflict of Interest

The authors have no conflict of interest regarding the content of this manuscript.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Data set with measurements of the digestive tract anatomy of individual blackbucks and sand gazelles.