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Quantitative macroscopic digestive tract anatomy of the beira (*Dorcatragus megalotis*)

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Keywords:
abomasum, intestine, gazelle, omasum, reticulum, rumen, salivary glands

Article history:
Received: 4 January 2016
Accepted: 27 September 2016
Published online: 3 November 2016

Abstract
The digestive system of the beira (*Dorcatragus megalotis*), a small East African antelope, has not been described previously. We present anatomical data collected from the only known captive population of the species, allowing for a first understanding of the morphophysiological 'type' of this species. The gastrointestinal anatomy was quantified by weights, dimensions and areas, measured in a total of 19 beiras (ranging in body mass from 3.5 to 13.5 kg; not all measures taken in all animals). These characteristics were then evaluated against a comparative dataset consisting of data from both browsing and grazing ruminants. Overall, for example, in terms of reticular crest height, masseter mass and omasal laminar surface area, the beira digestive tract resembled that of the browsing 'moose-type' ruminants. A diet of dicotyledonous plant material was further supported by the carbon isotope composition ($\delta^{13}C$ = -27.5‰) typical for C_3 plants of a faecal sample collected from a wild specimen, as well as the limited ecological information available for the species.

Introduction

The digestive anatomy of ruminants has been an object of continuous attention, due to the enormous diversity in morphological details across species (Garrod 1877; Neuville and Derscheid 1929; Langer 1973). While much of this work was motivated by the aim of inferring phylogenetic relationships (reviewed by Clauss 2014), it was the work of Hofmann (1968, 1973, 1988, 1989) that introduced the potential of digestive tract characteristics for studies of convergence, by linking the variation of a large number of morphological details with the three feeding types of browser, intermediate feeder and grazer. Convergence was more recently formally confirmed for several of these details (e.g. Hofmann et al. 2008; Clauss et al. 2010a). In order to enhance the clarity of the concept of comparing morphology on the one hand to the natural diet on the other hand, the terms 'moose-type' and 'cattle-type' were coined as descriptors of anatomy and physiology that can be juxtaposed to the botany-focused descriptors of the natural diet (browser vs intermediate feeders and grazers) (Clauss et al. 2010b). While a varying number of morphological details have been published for up to 90 ruminant species, the addition of any new species to the catalogue is welcome in order to increase the power of future investigations of convergence. Here, we used the opportunity of access to digestive tracts of beira antelope (*Dorcatragus megalotis*) for the description of the macroscopic digestive anatomy of the species.

The beira is a small antelope from East Africa, with an area of distribution from the southern coast of the Gulf of Aden to the Horn of Africa in the east, to the borders of Somalia, Ethiopia and Djibouti in the west, and to the Marmar Mountains in north-eastern Ethiopia (Künzel and Künzel 1998; Nowak 1999; Heckel et al. 2008; Giotto et al. 2009). So far, only one population of beira antelopes has been maintained in captivity (Hammer 2011). The scarce information on the species derives from limited observations in the wild and extensive study of this captive group (Hammer and Hammer 2005; Giotto et al. 2008; Giotto et al. 2009; Hammer 2011). In their review of diets of African bovids, Gagnon and Chew (2000) estimated that beira consume 90% of dicot material, 5% fruit and only 5% grass in their natural diet, but considered the underlying information inadequate and hence the estimation unreliable. During sporadic observations, Giotto et al. (2008) recorded a list of 19 dicot and one monocot plant species that were ingested by beiras. Based on the literature cited, we hypothesised that the anatomical characteristics of the digestive tract should place the beira among the 'moose-type' ruminants.

Methods

Data were collected from 19 beiras (six males and 13 females, body mass [BM] range 3.5–13.5 kg) housed at the Al Wabra Wildlife Preservation (AWWP, Qatar). At AWWP, beiras were kept on a diet of browse and fresh lucerne supplemented with pelleted feeds, vegetables and mineral supplements (Hammer 2011). After a period in which it prospered, the captive population suffered from an epidemic of *Mycoplasma* that led to a drastic decline in population size (Hammer 2011; Müller et al. 2013; Gull et al. 2014). Most animals investigated in the present study originated from that pool of deceased animals. The beiras were submitted to standard dissection protocols as described in other species (e.g. Sauer et al. 2016b), including the dissection of the masseter muscle (Axmacher and Hofmann 1988; Clauss et al. 2008), the parotid gland (Hofmann et al. 2008), and the tongue (Meier et al. 2016). Depending on the status of the animals and the necessary pathological investigations, not all measurements could be taken in all animals. The number of animals available for each measure is indicated in the tables. All dissections and measurements were performed by the same investigator (M. Clauss). Terms were used in agreement with the Nomina Anatomica Veterinaria (I.C.V.G.A.N. 2012).

A single faecal sample of a free-ranging beira was collected during a field trip to Djibouti in 2003. A homogenised aliquot of the faecal sample was analysed for its carbon isotope composition–$^{13}C/^{12}C$ expressed as $\delta^{13}C$ value versus Vienna Pee Dee Belemnite (Coplen 1994), following standard procedures using an elemental analyser coupled to a continuous flow isotope ratio mass spectrometer (Codron et al. 2007). As faecal $\delta^{13}C$ values reflect the composition of ingested plants (Codron et al. 2007), the proportion of C_3 (mainly dicot) and C_4 (monocot) plants in the beira diet, i.e. the percentage of leaves and grass, could be estimated from this faecal sample.

For a comparative evaluation of the anatomical measures of beiras, current data 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. 2016a), with additional comparative data on tongue anatomy from Meier et al. (2016).

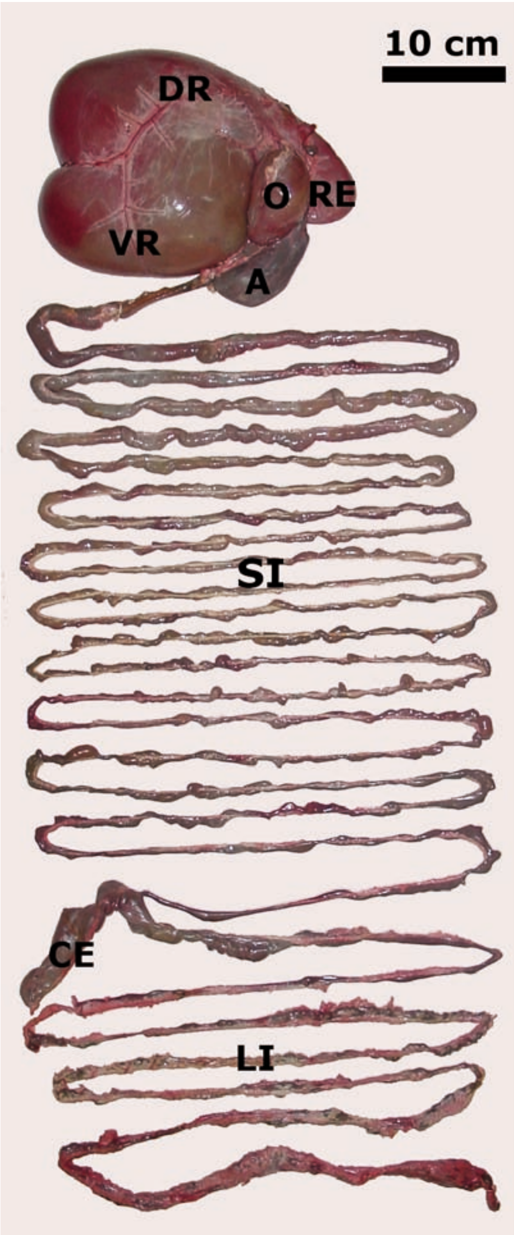

Figure 1. Digestive tract of the beira antelope (*Dorcotragus megalotis*). Abbreviations: DR = dorsal rumen, VR = ventral rumen, RE = reticulum, O = omasum, A = abomasum, SI = small intestine, CE = caecum, and LI = large intestine.

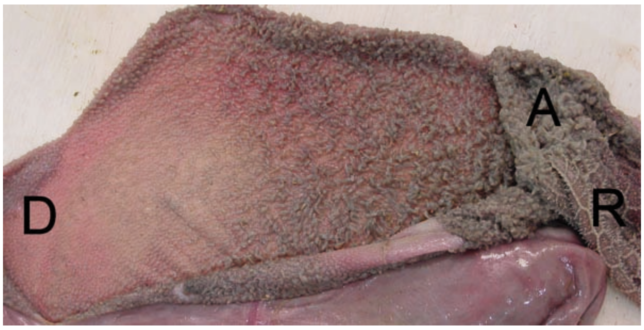

Figure 2. Internal aspect of a reticulorumen of a beira antelope (*Dorcotragus megalotis*). Abbreviations: D = dorsal rumen, A = *Atrium ruminis*, R = reticulum.

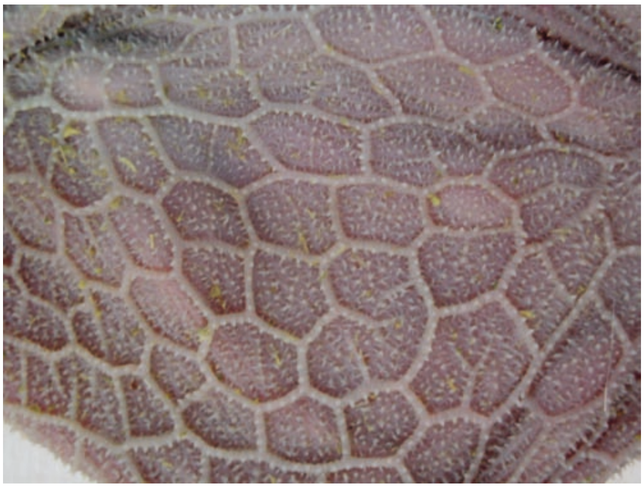

Figure 3. Internal aspect of a reticulum of a beira antelope (*Dorcotragus megalotis*).

Table 1. Regression equations ($y = \alpha * x^{\beta}$; with 95% confidence intervals for parameter estimates) for the relationship of rumen and reticulum size measures to body mass (BM) in beira antelope (*Dorcotragus megalotis*).

Measure		n	BM (kg)	Mean ± SD	BM effect	α	β	R^2
Reticulorumen tissue weight	g	13	4.0–13.5	165.0 ± 55.9	p < 0.001	34.91 [21.24; 57.37]	0.73 [0.50; 0.97]	0.81
Rumen height	cm	12	4.0–13.5	20.3 ± 2.5	p = 0.050	14.56 [10.44; 20.30]	0.16 [0.00; 0.33]	0.33
Dorsal rumen length	cm	12	4.0–13.5	18.0 ± 2.0	p = 0.089	13.61 [9.76; 18.99]	0.14 [-0.03; 0.30]	0.26
Ventral rumen length	cm	12	4.0–13.5	17.3 ± 2.1x	p = 0.094	12.85 [9.01; 18.31]	0.15 [-0.03; 0.32]	0.25
Total rumen diagonal	cm	9	4.0–13.5	20.6 ± 3.1	p = 0.048	13.54 [8.95; 20.48]	0.22 [0.00; 0.43]	0.45
Reticulum height	cm	13	4.0–13.5	9.6 ± 2.0x	p < 0.001	4.05 [2.76; 5.96]	0.42 [0.23; 0.61]	0.69
Reticulum length	cm	12	4.0–13.5	5.0 ± 1.3x	p = 0.051	2.35 [1.13; 4.89]	0.36 [-0.00; 0.72]	0.33
Reticular crest height	mm	14	4.0–13.5	1.0 ± 0.3	p = 0.223	0.59 [0.25; 1.38]	0.24 [-0.17; 0.65]	0.12
Cranial rumen pillar thickness	mm	15	4.0–13.5	3.8 ± 1.0	p = 0.014	1.36 [0.63; 2.95]	0.49 [0.11; 0.86]	0.38
Caudal rumen pillar thickness	mm	15	4.0–13.5	4.9 ± 1.5	p = 0.341	3.08 [1.21; 7.84]	0.21 [-0.25; 0.66]	0.07

To determine the relation between BM and anatomical measures in the beiras, data were ln-transformed and linear regression analysis was used to determine the coefficients of the model: $\ln(Y) = \alpha + \beta \times \ln(BM)$, where Y = the anatomical measure and BM = body mass in kg. The hypothesis of isometric scaling was accepted if 0.33, 0.67 and 1.00 were included in the 95% confidence interval (CI) of the BM exponent (β) of 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). The significance level was set to 0.05.

Results

The stomach of the beira was comprised of a rumen, reticulum, omasum and abomasum as in other ruminants (Fig. 1). The rumen was the largest compartment followed by the abomasum, then the reticulum and the omasum. The rumen had two blindsacs (dorsal and ventral; Fig. 1). The rumen was completely papillated, but there were evident (unquantified) differences in papillae size, with smaller papillae in the dorsal rumen and the most prominent papillae in the atrium ruminis (Fig. 2). The reticulum was characterised by comparatively shallow crests (Fig. 3).

All measurements were positively correlated or tended to correlate with BM (Tables 1–4), except for reticular crest height, thickness of the caudal rumen pillar, length of the lesser abomasum curvature and the ratio of small:large intestinal length. For measurements significantly affected by BM, nearly all included the expected isometric value in the 95% CI of the BM exponent (Tables 1–4). The only exceptions were reticulorumen tissue weight, rumen height, and dorsal and ventral rumen length. These four measures had a lower BM exponent than expected, though the isometric value was numerically close to being included in the 95% CI for all parameters.

The faecal sample collected from a free-ranging beira had a $\delta^{13}C$ value of -27.5‰, indicating a diet consisting only of C_3 plants and no significant intake of C_4 grasses.

Discussion

The data analysed in this study was collected from captive animals, except for the single faecal sample collected from a free-ranging specimen. Although the animals received browse and fresh lucerne on a daily basis, the diet most likely contained lower levels of fibre, and a lower proportion of structurally effective fibre, than the diet of free-ranging animals. While we do not expect this to have an influence on several anatomical measures, such as the height of the reticular crests or the morphology of the tongue, it may well have influenced some other measures such as the linear dimensions of forestomach compartments (due to a lower rumen fill than expected in free-ranging animals). In particular, the size of the omasum has been shown to vary according to the fibre content of the diet in several studies on domestic ruminants (Bailey 1986; Johnson et al. 1987; Fluharty et al. 1999; McLeod and Baldwin 2000). Therefore, these results must be considered with caution.

Table 2. Regression equations ($y = \alpha * x^{\beta}$; with 95% confidence intervals for parameter estimates) for the relationship of omasum and abomasum size measures to body mass (BM) in beira antelope (*Dorcotragus megalotis*).

Measure		n	BM (kg)	Mean ± SD	BM effect	α	β	R^2
Omasum tissue weight	g	11	4.0–11.0	16.0 ± 7.3	p = 0.002	1.50 [0.47; 4.76]	1.14 [0.56; 1.71]	0.69
Omasum height	cm	14	4.0–13.5	5.9 ± 1.5	p < 0.001	1.90 [1.17; 3.11]	0.54 [0.30; 0.78]	0.67
Omasum length	cm	14	4.0–13.5	3.8 ± 1.3	p = 0.011	1.15 [0.49; 2.67]	0.57 [0.16; 0.97]	0.43
Omasum curvature	cm	14	4.0–13.5	10.3 ± 3.4x	p = 0.002	2.57 [1.21; 5.46]	0.66 [0.29; 1.02]	0.56
Number of laminae	-	19	3.5–13.5	28.9 ± 3.4x	p = 0.002	16.94 [12.52; 22.94]	0.26 [0.11; 0.41]	0.45
Surface area of laminae	cm^2	19	3.5–13.5	136.4 ± 4.2	p < 0.001	23.26 [11.12; 48.65]	0.84 [0.48; 1.21]	0.59
Abomasum tissue weight	g	6	4.0–11.0	27.5 ± 47.9	p = 0.013	3.18 [0.82; 12.38]	1.10 [0.38; 1.82]	0.82
Greater abomasal curvature length	cm	9	4.0–11.0	23.4 ± 5.0	p = 0.002	9.68 [6.24; 15.01]	0.44 [0.22; 0.67]	0.76
Lesser abomasal curvature length	cm	7	4.0–11.0	13.2 ± 2.9	p = 0.118	6.83 [2.81; 16.61]	0.35 [-0.13; 0.82]	0.42

Table 3. Regression equations ($y = \alpha * x^\beta$; with 95% confidence intervals for parameter estimates) for the relationship of intestinal size measures to body mass (BM) in beira antelope (*Dorcotragus megalotis*)

Measure		n	BM (kg)	Mean ± SD	BM effect	α	β	R^2
Small intestine length	m	13	4.0–13.5	6.0 ± 0.9	p = 0.028	3.62 [2.34; 5.59]	0.24 [0.03; 0.44]	0.37
Total large intestine length	m	13	4.0–13.5	6.3 ± 0.9x	p = 0.025	3.77 [2.46; 5.79]	0.24 [0.04; 0.44]	0.38
Cecum length	cm	13	4.0–13.5	14.5 ± 2.3x	p = 0.007	7.83 [5.18; 11.84]	0.29 [0.10; 0.49]	0.49
Small : large intestine length	-	13	4.0–13.5	1.0 ± 0.0x	p = 0.419	0.96 [0.94; 0.97]	-0.00 [-0.01; 0.00]	0.06

The number of individuals sampled for the various anatomical measures varied from 6 to 19 animals, with a maximum body size range of 3.5–13.5 kg. In spite of this decent sample, the estimates of the exponent for the scaling with body mass often had a very large 95% confidence interval, and interpretations beyond the general finding that expected geometric exponents were mostly included in the interval cannot really be made. Linear dimensions of the rumen scaled somewhat below the expected geometric exponent, which might suggest a limited rumen fill in the larger animals, many of which died from chronic disease (Gull et al. 2014). On the other hand, the mass of the masseter muscles scaled somewhat higher than the expected linear scaling, indicating that during the transition from juvenile to adult, the masseter grows disproportionately, possibly due to the inclusion of a larger proportion of fibrous material in the diet and the corresponding increased chewing activity.

Because few reports on the biology of free-ranging beiras and no anatomical reports exist, the present study is nevertheless a relevant contribution to the ruminant literature, even though morphological measures were taken only from captive animals. The beiras in the present study resembled 'moose-type' ruminants with respect to rumen pillar thickness, reticular crest height and parotid salivary gland weight, and had masseter muscle masses expected for browsers (Fig. 4). In contrast, the heterogenous papillation of the ruminal mucosa (Fig. 2) is qualitatively more reminiscent of 'cattle-type' ruminants, although a certain degree of such heterogeneity does occur among 'moose-type' species (Codron and Clauss 2010). The omasal laminar surface area appeared to fit on the regression line for browsing ruminants if extrapolated to BM < 20 kg; however, at such small body masses, the omasum size of 'moose-type' and 'cattle-type' ruminants appear to converge (Fig. 4). Whether this holds true across many ruminant species remains to be investigated, and reasons for this, such as a minimum size threshold required for omasal function, remain to be explored. As discussed by Sauer et al. (2016a), demonstrating differences in digestive tract anatomy between the feeding types might not be possible at the lower end of the BM range. This is also reflected in the data scatter in Fig. 4 for several measurements such as the salivary gland mass or the freely mobile portion of the tongue, where the intra-specific variation in the beira in the present study is of a similar magnitude to the average difference between 'moose-type' and 'cattle-type' ruminants. The reason for the difficulty in differentiating feeding types at smaller body size via morphology might lie not only in a lack of comparative data from smaller ruminants, but may be equally attributable to the crudeness of resolution of macroanatomical measures in this body size range. Furthermore, anatomical characteristics of individual species need not always reflect those trends commonly considered convergent among feeding types (Jerbi et al. 2016; Sauer et al. 2016a, b). Additionally, there may be physiological thresholds for macroanatomical dimensions below which the functionality of the ruminant forestomach system may be compromised. This hypothesis awaits further testing when data from more small ruminant species becomes available.

Conclusion

The carbon isotope composition of a faecal sample from a free-ranging beira indicates an exclusive C_3 plant-based diet, which supports the observations that beiras mainly consume browse material (Gagnon and Chew 2000; Giotto et al. 2008). This finding matches the overall classification of the anatomical measures of the present study. The present study thus supports the notion that beiras are 'moose-type' ruminants that consume mainly browse.

Acknowledgements

This study was possible because of the kindness of H. E. Sheikh Saoud Bin Mohamed Bin Ali Al-Thani and his support of the Zoo Research Camps 2007-2010 organised by Al Wabra Wildlife Preservation and the Clinic for Zoo Animals, Exotic Pets and Wildlife,

Table 4. Regression equations ($y = \alpha * x^\beta$; with 95% confidence intervals for parameter estimates) for the relationship of tongue dimensions, masseter and salivary gland mass to body mass (BM) in beira antelope (*Dorcotragus megalotis*)

Measure		n	BM (kg)	Mean ± SD	BM effect	α	β	R^2
Tongue, free part length	cm	6	5.5–13.5	3.3 ± 0.5	p = 0.444	2.18 [0.58; 8.21]	0.18 [-0.42; 0.79]	0.15
Corpus length	cm	6	5.5–13.5	6.4 ± 0.8	p = 0.026	2.79 [1.44; 5.40]	0.37 [0.07; 0.67]	0.75
Corpus minimum width	cm	6	5.5–13.5	1.8 ± 0.1	p = 0.016	1.11 [0.79; 1.55]	0.22 [0.07; 0.38]	0.80
Corpus maximum width	cm	6	5.5–13.5	2.0 ± 0.2	p < 0.001	0.95 [0.76; 1.20]	0.34 [0.23; 0.44]	0.95
Torus length	cm	6	5.5–13.5	4.7 ± 0.3	p = 0.024	2.94 [2.05; 4.22]	0.21 [0.04; 0.37]	0.76
Total tongue length	cm	6	5.5–13.5	11.0 ± 1.2	p = 0.024	5.65 [3.34; 9.53]	0.30 [0.07; 0.54]	0.76
Masseter weight	g	9	4.0–13.5	18.6 ± 8.3	p < 0.001	1.36 [0.91; 2.04]	1.24 [1.04; 1.44]	0.97
Glandula parotis weight (pair)	g	9	4.0–13.5	13.8 ± 7.0	p < 0.001	0.95 [0.32; 2.82]	1.26 [0.73; 1.79]	0.82
Glandula mandibularis weight (pair)	g	9	4.0–13.5	5.9 ± 2.1	p < 0.001	0.84 [0.52; 1.36]	0.93 [0.70; 1.16]	0.93

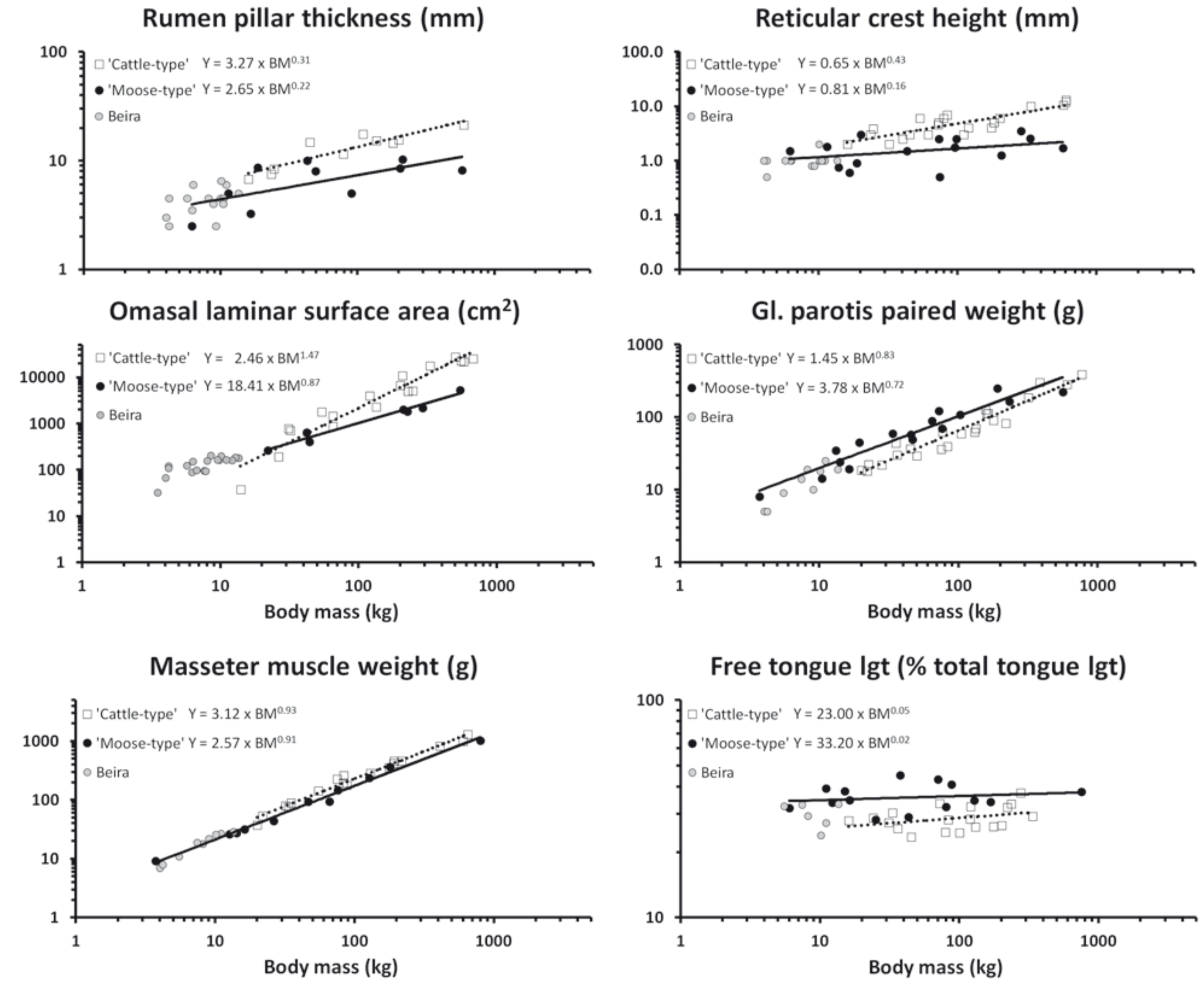

Figure 4. Comparison of selected measures of beira (*Dorcotragus megalotis*) digestive anatomy to other ruminant species (for sources, see methods). Each species is represented by a point, except for the beiras. Solid line: trend line for 'moose-type' ruminants, dashed line: trend line for 'cattle-type' ruminants. Abbreviations: Gl. = Glandula, lgt = length.

Vetsuisse Faculty, University of Zurich, and research at his facility. The assistance of Dr. Abdi Arif during dissections was invaluable. Jakob S. Jørgensen is gratefully acknowledged for developing the segmentation algorithm and image analysis software used to determine surface area of the omasal leaves.

References

Axmacher H., Hofmann R.R. (1988) Morphological characteristics of the masseter muscle of 22 ruminant species. *Journal of Zoology* 215: 463–473.

Bailey C.B. (1986) Growth of digestive organs and their contents in holstein steers: relation to body weight and diet. *Canadian Journal of Animal Science* 66: 653–661.

Clauss M., Hofmann R.R., Streich W.J., Fickel J., Hummel J. (2008) Higher masseter mass in grazing than in browsing ruminants. *Oecologia* 157: 377–385.

Clauss M., Hofmann R.R., Streich W.J., Fickel J., Hummel J. (2010a) Convergence in the macroscopic anatomy of the reticulum in wild ruminant species of different feeding types and a new resulting hypothesis on reticular function. *Journal of Zoology* 281: 26–38.

Clauss M., Hume I.D., Hummel J. (2010b) Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal* 4: 979–992.

Clauss M. (2014) Soft tissue characteristics for the reconstruction of ruminant phylogeny. *Zitteliana* B 32: 1–14.

Codron D., Codron J., Lee-Thorp J.A., Sponheimer M., de Ruiter D., Sealy J., Grant R., Fourie N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology* 273: 21–29.

Codron D., Clauss M. (2010) Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. *Canadian Journal of Zoology* 88: 1129–1138.

Coplen T.B. (1994) Reporting of stable hydrogen, carbon, and oxygen isotopic abundances (technical report). *Pure and Applied Chemistry* 66: 273–276.

Fluharty F.L., McClure K.E., Solomon M.B., Clevenger D.D., Lowe G.D. (1999) Energy source and ionophore supplementation effects on lamb growth, carcass characteristics, visceral organ mass, diet digestibility, and nitrogen metabolism. *Journal of Animal Science* 77: 816–823.

Gagnon M., Chew A.E. (2000) Dietary preferences in extant African Bovidae. *Journal of Mammalogy* 81: 490–511.

Garrod A.H. (1877) Notes on the visceral anatomy and osteology of the ruminants, with a suggestion regarding a method of expressing the relations of species by means of formulae. *Proceedings of the Zoological Society of London*: 2–18.

Giotto N., Laurent A., Mohamed N., Prevot N., Gerard J.F. (2008) Observations on the behaviour and ecology of a threatened and poorly known dwarf antelope: the beira (*Dorcatragus megalotis*). *European*

Journal of Wildlife Research 54: 539–547.

Giotto N., Obsieh D., Joachim J., Gerard J.F. (2009) The population size and distribution of the Vulnerable beira antelope *Dorcatragus megalotis* in Djibouti. *Oryx* 43: 552–555.

Gull J.M., Hebel C., Deb A., Arif A., Clauss M., Hatt J.-M., Hammer S. (2014) Blood values of captive beira antelope (*Dorcotragus megalotis*) prior and during an outbreak of fibrinous pleuopneumonia syndrome (FPPS). *Journal of Zoo and Wildlife Medicine* 45: 735–743.

Hammer C., Hammer S. (2005) Daten zur Fortpflanzung und Jungtierentwicklung der Beira-Antilope (*Dorcatragus megalotis*). *Der Zoologische Garten NF* 75: 89–99.

Hammer C. (2011) Ex situ management of Beira antelope *Dorcatragus megalotis* at Al Wabra Wildlife Preservation, Qatar. *International Zoo Yearbook* 45: 259–273.

Heckel J.O., Rayaleh H.A., Wilhelmi F., Hammer S. (2008) *Dorcatragus megalotis*. In: *IUCN 2009 IUCN Red List of Threatened Species Version 2009.* www.iucnredlist.org

Hofmann R.R. (1968) Comparison of the rumen and omasum structure in East African game ruminants in relation to their feeding habits. *Symposium of the Zoological Society of London* 21: 179–194.

Hofmann R.R. (1973) *The Ruminant Stomach.* East African Literature Bureau, Nairobi.

Hofmann R.R. (1988) Morphophysiological evolutionary adaptations of the ruminant digestive system. In: Dobson A., Dobson M.J. (eds). *Aspects of Digestive Physiology in Ruminants*. Ithaca, NY: Cornell University Press, 1–20.

Hofmann R.R. (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443–457.

Hofmann R.R., Streich W.J., Fickel J., Hummel J., Clauss M. (2008) Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. *Journal of Morphology* 269: 240–257.

I.C.V.G.A.N. (2012) *Nomina Anatomica Veterinaria.* Revised 5th edn. International Committee on Veterinary Gross Anatomical Nomenclature. http://www.wava-amav.org/Downloads/nav_2012.pdf.

Jerbi H., Bayoudh M., Clauss M., Pérez W. (2016) Gross anatomy of the stomach of the dorcas gazelle (*Gazella dorcas*). *International Journal of Morphology* (in press).

Johnson C.L., Johnson D.E., Rumpler W.V. (1987) Source and level of alimentation effects on visceral organ mass of fat steers. In: Moe P.W., Tyrrell H.F., Reynolds P.J. (eds). *Energy Metabolism of Farm Animals*. Totowa: Rowman and Littlefiled, 50–53

Künzel T., Künzel S. (1998) An overlooked population of the beira antelope in Djibouti. *Oryx* 32: 75–80.

Langer P. (1973) Vergleichend-anatomische Untersuchungen am Magen der Artiodactyla. II. Untersuchungen am Magen der Tylopoda und Ruminantia. *Gegenbaurs Morphologisches Jahrbuch* 119: 633–695.

McLeod K.R., Baldwin R.L. (2000) Effects of diet forage:concentrate ratio and metabolizable energy intake on visceral organ growth and in vitro oxidative capacity of gut tissues in sheep. *Journal of Animal Science* 78: 760–770.

Meier A.R., Schmuck U., Meloro C., Clauss M., Hofmann R.R. (2016) Convergence of macroscopic tongue anatomy in ruminants and scaling relationships with body mass or tongue length. *Journal of Morphology* 277: 351–362.

Müller D.W.H., Hammer S., Hammer C., Hatt J.-M., Clauss M. (2013) A conceptual approach to density-dependent management of zoo animals kept in herds. *International Zoo Yearbook* 47: 208–218.

Neuville H., Derscheid J.M. (1929) Recherches anatomiques sur l'okapi (*Okapia johnstoni*). IV. L'estomac. *Revue de Zoologie et de Botanique Africaine* 16: 373–419.

Nowak R.M. (1999) *Walker´s Mammals of the World*, 6th edn. Baltimore: Johns Hopkins University Press.

Sauer C., Bertelsen M.F., Hammer S., Lund P., Weisbjerg M.R., Clauss M. (2016a) Macroscopic digestive tract anatomy of two small antelopes, the blackbuck (*Antilope cervicapra*) and the Arabian sand gazelle (*Gazella subgutturosa marica*). *Anatomia Histologia Embryologia* 45: 392–398.

Sauer C., Bertelsen M.F., Lund P., Weisbjerg M.R., Clauss M. (2016b) Quantitative macroscopic anatomy of the giraffe (*Giraffa camelopardalis*) digestive tract. *Anatomia Histologia Embryologia* 45: 338–349.