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Convergence of Macroscopic Tongue Anatomy in Ruminants and Scaling Relationships with Body Mass or Tongue Length

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ABSTRACT Various morphological measures demonstrate convergent evolution in ruminants with their natural diet, in particular with respect to the browser/grazer dichotomy. Here, we report quantitative macroanatomical measures of the tongue (length and width of specific parts) of 65 ruminant species and relate them to either body mass (BM) or total tongue length, and to the percentage of grass in the natural diet (%grass). Models without and with accounting for the phylogenetic structures of the dataset were used, and models were ranked using Akaike's Information Criterion. Scaling relationships followed geometric principles, that is, length measures scaled with BM to the power of 0.33. Models that used tongue length rather than BM as a body size proxy were consistently ranked better, indicating that using size proxies that are less susceptible to a wider variety of factors (such as BM that fluctuates with body condition) should be attempted whenever possible. The proportion of the freely mobile tongue tip of the total tongue (and hence also the corpus length) was negatively correlated to %grass, in accordance with concepts that the feeding mechanism of browsers requires more mobile tongues. It should be noted that some nonbrowsers, such as cattle, use a peculiar mechanism for grazing that also requires long, mobile tongues, but they appear to be exceptions. A larger corpus width with increasing %grass corresponds to differences in snout shape with broader snouts in grazers. The *Torus linguae* is longer with increasing %grass, a finding that still warrants functional interpretation. This study shows that tongue measures covary with diet in ruminants. In contrast, the shape of the tongue (straight or "hourglass-shaped" as measured by the ratio of the widest and smallest corpus width) is unrelated to diet and is influenced strongly by phylogeny. J. Morphol. 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

KEY WORDS: browser; grazer; oral processing; lip; muzzle; palate

INTRODUCTION

In herbivores, the tongue is used as a prehensile organ that is involved in grasping diet items. Fundamental differences in feeding modes in grazing and browsing ruminants (Hofmann and Stewart, 1972; Gagnon and Chew, 2000) correspond to differences in the spatial arrangement and physical properties of diet items (reviewed in Clauss et al., 2008b). As part of these adaptations, differences in tongue anatomy between the feeding-types could be expected. Based on the unpublished thesis by Schmuck (1986), Hofmann (1988; 1989) suggested that torus length, in relation to total tongue length, is shorter in browsers than in grazers, and that the freely mobile part of the tongue is longer in browsers than in grazers. This observation appears plausible under the assumption that a long, freely movable part of the tongue is a prerequisite for the manipulation of heterogeneous diet objects as in browse, where selected leaves may be arranged in very close proximity to undesirable plant parts such as thorns or twigs. Grazers, conversely, have often been perceived of showing adaptations of a wide distal snout that allows them to achieve higher bite sizes during grazing (Gordon and Illius, 1988; Fraser and Theodor, 2011; Tennant and MacLeod, 2014), particularly in short-grass grazers (Codron et al., 2008). Such anatomical adaptations could also be reflected in tongues that have wider tips.

Additional Supporting Information may be found in the online version of this article.

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In contrast to the findings that indicate that various browsers may be characterized by tongues with a long freely mobile part (Hofmann, 1988; 1989), Hassanin et al. (2012) used the presence of an "extensible tongue" as a phylogenetic characteristic of giraffids in comparison to other ruminant families. Based on observations of extensible tongues in cattle and tragulids, Clauss (2014) doubted the validity of this approach. Therefore, a comparative evaluation of the proportion of the "freely movable" part of the tongue in different ruminant species is warranted. An important limitation of the original unpublished investigation of Schmuck (1986) had been that the body mass (BM) of the investigated specimens had not been available in most cases. BM is typically included in analyses of comparative anatomy where structures are measured that can be expected to vary, in their dimensions, with BM. Here, we augment this dataset with additional measurements of tongues in specimens with known BM, and with additional literature data, to test for a systematic effect of feeding-type on tongue measurements. In doing so, we also intend to clarify whether macroscopic tongue anatomy is among the soft tissue characteristics suitable for the reconstruction of ruminant phylogeny (Clauss, 2014). The following hypotheses guided our approach:

1. We expected a geometric scaling, with linear measurements scaling against each other (such as the length of a tongue part vs. total tongue length) in a linear fashion, that is, with a scaling exponent of 1.0, and with linear measurements scaling with BM at an exponent of 0.33 (Calder, 1996).
2. Because we consider the tongue to be a comparatively invariable structure that does not respond, in its dimensions, to environmental influence, whereas BM will vary due to a variety of factors, we expect better fit (i.e., lower Akaike Information Criterion [AIC] values) for models relating tongue measurements to tongue length than for models using BM as the independent variable.
3. Ruminants with a lower percentage of grass in their natural diet (i.e., "browsers," Clauss et al., 2003) have higher proportions of a freely mobile tongue part than ruminants with a higher percentage of grass in their natural diet (i.e., "grazers"). We assume convergence of an adaptation to a diet niche to be demonstrated if our proxy for the diet niche (percentage of grass) contributes significantly to models that relate tongue measures to both a body size and a diet proxy, even when controlling for phylogeny.

METHODS

The data originate from a long-lasting effort of the senior author to collect data on as many ruminant species as possible. For the dataset, information on 65 species were available, including 42 from the original thesis of Schmuck (1986), 26 from hitherto unpublished data from the senior author, four from the thesis of Markgraf (2000), after a literature research two from Shao et al. (2010), one from Erdoğan and Pérez (2013) and one from Lönnberg (1900). BM data was available for the same specimens from which the tongue measurements had been taken in 31 species and was extracted from other literature in the other 34 species (sources indicated in Table 1). Species were characterized by the percentage of grass (%grass, a continuous measure) in their natural diet (sources indicated in Table 1).

Measurements were taken on tongues either directly after dissection (some specimens of Schmuck, 1986; Markgraf, 2000 and all specimens of Hofmann unpublished; Shao et al., 2010; Erdoğan and Pérez, 2013), after freezing and defrosting (specimens from Markgraf, 2000), or after formalin fixation at various time points after death (most specimens from Schmuck, 1986). Preservation status of material from Lönnberg (1900) was unknown. The specimens were taken either from the wild during hunting collections or from captivity, either due to fatalities or culling in zoos or from venison slaughtering procedures. We did not expect tongue measurements to be influenced by husbandry conditions or diet and, thus, consider the variation in origin not problematic. With respect to the influence of differences in preservation status of the material from which measurements were taken (e.g., shrinkage due to formalin storage), we assumed such effects to affect all tongue parts in equal proportions; the use of such different material was expected to contribute to the potential result that the total tongue length would yield a better data fit than BM as a basis for comparisons.

Measurements taken from the tongues are illustrated in Figure 1 and represent linear distance measurements (i.e., not following any curvatures of the organ) taken with callipers, rounded to the nearest millimetre. They include 1) total tongue length from the tip to the end of the *Radix linguae*, 2) the torus length from the *Fossa linguae* to the end of the *R. linguae*, 3) the width of the torus at its widest point, 4) the corpus length from the tip to the *F. linguae*, 5) the width of the corpus at its narrowest point, 6) the width of the corpus at its widest point, and 7) the length of the free portion of the tongue defined as the part rostral to the most rostral insertion of the *Frenulum linguae* on the ventral side of the tongue. The corpus width ratio represents the proportion of the widest corpus width divided by the narrowest corpus width, with values of 1 indicating no difference between the two. Because in our dataset, the widest corpus part was always anterior to the narrowest corpus part, low values indicate a comparatively straight tongue, whereas high values indicate a "spoon-" or "hourglass-shaped" tongue. The proportion of the free portion of the tongue was calculated as the percentage of the length of the free portion of the total tongue length. Not all measurements were taken in all specimens.

Individual measurements are given in the supporting information. Measurements on individual specimens were summarized as species averages; in doing so, care was taken that averages of the reference measures (BM and tongue length) was always taken only from the same specimens for which the target tongue measures were available. For statistical evaluations, BM and linear measurements (length, width) were $\log_{10}$-transformed. Analyses were performed in *R* 2.15.0 (R Development Core Team, 2011) with Ordinary Least Squares (OLS) using the package nlme (Pinheiro et al., 2011) and phylogenetic generalized least squares (PGLS) using the package caper (Orme et al., 2010). In contrast to a common recommendation (Freckleton, 2009), we display results of both OLS and PGLS analyses, because the comparison is often informative about the structure of the dataset (Clauss et al., 2013; 2014; 2015). For PGLS, data were linked to a supertree of extant mammals with branch lengths (Bininda-Emonds et al., 2007; 2008), assigning the position of *Oryx leucoryx* of that tree to *Oryx beisa* (which was not included in that tree). The tree is displayed in the supporting information (Supporting Information, Fig. S1). When

TABLE 1. Dataset on macroscopic measurements on the tongue of different ruminant species used in this study

Species lat	Species eng	*n*	BM (kg)	Grass (%)	TonL (cm)	TorL (cm)	TorW (cm)	CorL (cm)	CorMax (cm)	CorMin (cm)	FreePort (cm)	%FreePort (%)	Wratio
Giraffa camelopardalis[2]	Giraffe	1	750.0[7]	0.1[9]	46.5	19.5	7.6	27.0	5.7	3.6	17.6	37.9	1.58
Antilocapra americana[2]	Pronghorn	1	40.0[7]	15.0[7]	17.6	7.6	3.9	10.0	3.0		5.5	31.2	
Muntiacus muntjak[2]	Muntjac	1	15.0[7]	10.0[10]	11.3	5.0	2.6	6.3	2.6	2.2	4.3	38.2	1.20
Hydropotes inermis[1]	Chinese water deer	4	10.8	50.0[10]	11.5	5.3	2.8	6.3	2.4	2.1	3.2	28.2	1.13
Capreolus capreolus[2]	Roe deer	12	25.0[7]	5.3[9]	11.0	5.2	2.7	5.8	2.5	2.1	3.4	28.2	1.10
Odocoileus hemionus[2]	Mule deer	1	80.0[7]	12.0[9]	19.5	9.9	3.9	9.6	3.5	3.2	6.3	32.3	1.11
Odocoileus virginianus[2]	White-tailed deer	1	70.0[7]	9.9[9]	15.5		3.9		3.2	2.8	6.7	43.2	1.14
Ozotoceros bezoarticus[4]	Pampas deer	4	14.2	75.0[11]	11.2		2.9		2.5				
Mazama americana[1]	Red brocket	6	12.2	1.0[10]	10.4	4.2	2.5	6.2	2.3	2.0	4.1	33.8	1.01
Pudu puda[1]	Pudu pudu	1	11.0	3.0[9]	12.0	5.0	3.0	7.0		2.5	4.5	37.5	
Rangifer tarandus[2]	Reindeer	2	62.0[7]	33.1[9]	24.0	11.1	5.0	13.0	5.3	4.2	8.1	33.4	1.28
Alces alces[1]	Moose	2	167.0	5.0[9]	32.5	14.0		18.5			11.0	34.0	1.11
Cervus nippon[1]	Sika deer	1	55.0	50.0[10]	19.5	9.0	4.5	10.0	4.5	3.5	5.0	25.6	1.29
Cervus elaphus[2]	Red deer	5	170.0[7]	39.1[9]	24.2	11.0	4.5	13.2	4.1	3.4	8.2	33.2	1.21
Axis axis[1]	Axis deer	1	57.0	70.0[10]	16.5	7.6	4.2	8.9	4.3	3.5	4.5	27.3	1.23
Axis porcinus[1]	Hog deer	2	46.2	50.0[10]	17.3	8.7	3.9	8.6	3.9	3.0	4.8	27.4	1.33
Dama dama[1]	Fallow deer	5	58.3	46.0[10]	17.5	7.8	4.5	9.3	3.8	3.3	6.2	35.2	1.19
Elaphurus davidianus[2]	Père David's deer	1	120.0[7]	75.0[10]	19.6	9.0	4.6	10.7	4.0	3.5	6.4	32.4	1.15
Sylvicapra grimmia[2]	Gray duiker	1	14.0[7]	12.0[9]	9.9	3.3	2.9	6.6	2.2	1.9	3.8	37.9	1.14
Cephalophus monticola[1]	Blue duiker	1	4.0	1.0[12]	8.5	3.5	1.7	4.5	1.6	1.4	3.4	40.0	1.14
Cephalophus natalensis[1]	Red duiker	4	8.3	1.0[10]	12.0	5.3	2.7	6.7	2.4	2.1	4.5	37.2	1.14
Boselaphus tragocamelus[2]	Nilgai	1	220.0[7]	35.2[9]	22.4	10.7	4.6	11.7	5.9	4.0	7.2	32.2	1.50
Tragelaphus angasii[1]	Nyala	3	87.5	20.0[10]	20.7	9.0	4.3	12.2	4.2	3.2	8.5	41.0	1.31
Tragelaphus scriptus[1]	Bushbuck	1	37.5	10.0[10]	15.5	6.5	3.2	9.0	3.1	2.7	7	45.2	1.15
Tragelaphus spekii[1]	Sitatunga	2	55.0	68.0[10]	20.7	8.5	4.6	11.8	3.8	3.6	8.3	39.9	1.06
Tragelaphus strepsiceros[1]	Greater Kudu	2	127.5	5.0[10]	24.3	10.6	5.6	13.6	5.1	3.8	8.5	34.6	1.35
Tragelaphus eurycerus[2]	Bongo	2	250.0[7]	20.0[7]	28.3	12.2	6.1	16.2	5.1	4.7	9.4	33.2	1.10
Taurotragus oryx[2]	Eland	1	200.0*	50.0[10]	21.3	9.6	4.7	11.7			6.3	29.7	
Syncerus caffer[1]	African buffalo	1	880.0	58.1[9]	41.0								
Bos taurus[5]	Cattle	8	275.0	69.7[9]	32.0						12.0	37.5	
Bos grunniens[5]	Yak	8	265.0	80.0[7]	28.0						8.0	28.6	
Bison bison[1]	Bison	1	335.0	84.0[10]	32.5	15.0	7.1	17.5	7.4	6.6	9.5	29.2	1.11
Alcelaphus buselaphus[2]	Coke's hartebeest	1	175.0[7]	96.7[10]	22.3	11.4	4.0	10.9	4.6	3.3	5.9	26.2	1.38
Damaliscus lunatus[2]	Topi	1	119.0[7]	99.3[10]	23.6	11.3	4.3	12.3	4.4	3.3	6.7	28.4	1.34
Damaliscus hunteri[1]	Hirola	1	130.0	90.0[10]	24.5	13.0	4.0	12.0	4.0	2.8	6.4	26.1	1.43
Damaliscus pygargus[1]	Bontebok	1	83.0	100.0[10]	19.5	10.0	4.0	10.0	4.0	3.4	5.5	28.2	1.18
Oryx gazella[2]	Gemsbok	1	100.0*	75.0[9]	16.9	8.9	4.0	8.0	4.2	3.6	4.2	24.6	1.17

Table 1. (continued).

Species lat	Species eng	*n*	BM (kg)	Grass (%)	TonL (cm)	TorL (cm)	TorW (cm)	CorL (cm)	CorMax (cm)	CorMin (cm)	FreePort (cm)	%FreePort (%)	Wratio
Oryx beisa[1]#	Beisa Oryx	1	145.0[7]	83.0[7]	27.5	13.4	6.0	14.1	5.0	4.1	7.6	27.6	1.22
Hippotragus niger[1]	Sable antelope	1	235.0	85.0[9]	30.0	15.5	6.0	14.5	5.5	4.5	10.0	33.3	1.22
Pelea capreolus[1]	Vaal Rhebok	2	16.3	7.0[10]	12.3	5.0	2.7	7.6	2.9	2.0	4.3	34.7	1.43
Redunca fulvorufula[2]	Mountain reedbuck	1	24.0[7]	99.0[10]	12.0	5.7	2.2	6.3	2.7	2.0	3.5	28.8	1.38
Redunca redunca[2]	Reedbuck	2	45.0[7]	95.0[10]	15.6	7.8	2.7	7.9	3.6	2.4	3.7	23.5	1.52
Kobus kob[2]	Kob	1	79.0[7]	95.0[10]	16.2	8.1	2.9	8.1	4.0	2.5	4.0	24.7	1.62
Kobus ellipsiprymnus[2]	Waterbuck	1	201.0[7]	84.0[9]	22.3	10.7	4.3	11.6	5.3	3.7	5.9	26.5	1.43
Kobus leche[1]	Lechwe	1	72.0	95.0[7]	17.0	9.0	3.5	8.0	4.5	3.2	5.7	33.5	1.41
Oreotragus oreotragus[2]	Klipspringer	1	11.0[7]	5.0[10]	8.2	3.6	2.1	4.6	2.0	1.7	3.2	39.3	1.18
Ourebia ourebi[2]	Oribi	3	16.0[7]	48.5[10]	10.9	5.4	1.9	5.5	2.0	1.7	3.0	27.9	1.21
Madoqua guentheri[2]	Günther's dikdik	1	4.0[7]	5.0[10]	6.1	2.5	1.6	3.6	1.4	1.2	1.6	26.3	1.17
Raphicerus campestris[2]	Steenbok	2	11.0[7]	10.0[10]	9.6	4.3	2.2	5.3	1.6	1.4	2.8	29.0	1.12
Litocranius walleri[2]	Gerenuk	3	43.0[7]	0.0[10]	13.2	5.5	2.5	7.7	2.2	2.0	3.9	29.0	1.13
Antidorcas marsupialis[1]	Springbok	1	49.5	30.0[10]	14.5	7.0	3.5	7.5	3.0	2.3	4.5	31.0	1.30
Antilope cervicapra[2]	Blackbuck	1	33.0[7]	79.4[9]	10.4	5.1	2.3	5.3	2.3	2.0	3.1	30.3	1.13
Gazella subgutturosa[1]	Goitered gazelle	1	23.0	38.4[9]	11.2	5.5	3.0	5.7		2.3	3.0	26.8	
Gazella thomsonii[2]	Thomson gazelle	5	21.0[7]	75.0[10]	12.4	5.9	2.5	6.5	2.7	2.0	3.4	26.9	1.35
Nanger granti[2]	Grant's gazelle	2	55.0[7]	50.0[10]	16.4	8.0	3.6	8.4	3.6	2.7	4.3	25.9	1.30
Naemorhedus crispus[3]	Serow	1	27.0	70.0[7]	15.8	7.0	3.3	8.8	3.1	2.5	4.6	29.1	1.24
Rupicapra rupicapra[1]	Chamois	1	28.0	74.0[10]	14.0	7.0	3.0	7.0	3.0	2.3	4.0	28.6	1.30
Ovibos moschatus[6]	Musk ox	1	196.0[7]	50.0[9]	27.0	13.5	6.0	13.5	6.0				
Ovis aries[2]	Sheep	3	31.0[7]	55.7[9]	15.6	7.8	3.6	7.9	3.9	3.2	4.3	27.3	1.23
Ovis ammon[1]	Mouflon	1	32.0	35.0[9]	15	7.5	3.8	7.5	3.5	2.5	3.5	23.3	1.40
Pseudois nayaur[3]	Blue sheep	2	34.0	68.0[11]	12.9	6.5	3.2	6.4	3.1	2.4	3.6	28.0	1.30
Hemitragus jemlahicus[3]	Tahr	1	55.0[7]	75.0[7]	16.2	8.4	4.0	7.8	3.9	3.1	4.6	28.4	1.26
Capra aegagrus[3]	Goat	1	36.0	28.0[7]	14.8	7.3	3.3	7.5	4.3	3.0	3.8	25.7	1.43
Neotragus moschatus[2]	Suni	6	6.0[7]	0.0[10]	7.4	3.1	1.8	4.4	1.7	1.5	2.4	31.9	1.11
Aepyceros melampus[2]	Impala	7	55.0[7]	60.0[10]	15.1	7.3	2.8	7.8	2.9	2.3	4.4	29.2	1.26

n = number of individuals studied per species (not all measurments taken in all individuals), BM = body mass, Grass = the percentage of grass in the natural diet, TonL = tongue length, TorL = torus length, TorW = torus width, CorL = corpus length, CorMax = withdth at widest point of corpus, CorMin = width at narrowest point of corpus, FreePort = free portion, %FreePort = free portion as percentage of total tongue length, Wratio = ratio of the width of the corpus at its widest vs. its narrowest point (see Fig. 1 for explanation of measurements).

*BM adjusted; # for phylogenetic analyses, *Oryx beisa* was assigned the position of *Oryx leucoryx* in phylogenetic tree used

Sources: 1 Hofmann (unpublished), 2 (Schmuck, 1986), 3 (Markgraf, 2000), 4 (Erdoğan and Pérez, 2013), 5 (Shao et al., 2010), 6 (Lönnberg, 1900), 7 (Clauss et al., 2009), 8 (Clauss et al., 2011), 9 (Dittmann et al., 2015), 10 (Clauss et al., 2010), 11 (Zerbe et al., 2012), 12 (Gagnon and Chew, 2000).

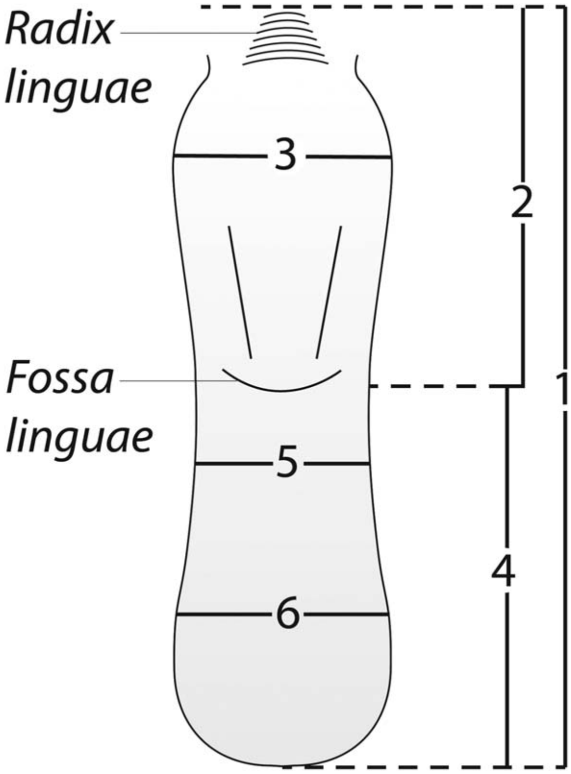

Fig. 1. Tongue measurements taken for this study: (1) total tongue length, (2) torus length, (3) torus width, (4) corpus length, (5) corpus width at narrowest point, (6) corpus width at broadest point. The length of the free portion of the tongue is measured as the distance between the tongue tip and the insertion of the *Frenulum linguae* on the underside of the tongue, not visible in this view. Drawing by Jeanne Peter.

repeating the analyses with a more recent tree based on molecular data from the 10kTree website (Arnold et al., 2010) that is continuously updated, which covered 61 of our 65 species, qualitatively similar results were obtained (not displayed). The phylogenetic signal λ was estimated using maximum likelihood (Revell, 2010) in caper (Orme et al., 2010). λ can vary between 0 (no phylogenetic signal) and 1 (the observed pattern is predicted by the phylogeny; similarity among species scales in proportion to their shared evolutionary time; Pagel, 1999; Freckleton et al., 2002); that is, we assumed Pagel's correlation structure. We analysed first the restricted dataset for which actually measured BM of the investigated specimens were available, and second the complete dataset, including specimens for which BM estimates were based on literature data. In this latter dataset, BM of two specimens that were not fully grown adults were adjusted visually to match the overall pattern (*Oryx gazella*, *Taurotragus oryx*, indicated in Table 1). For each tongue measure, we evaluated the effect of BM and the effect of tongue length, as well as the additional effect of %grass in General Linear Models; that is, according to either

$$\log\, y = a + b\log(\text{sizeproxy})$$

or

$$\log y = a + b\log\ (\text{sizeproxy}) + c\%\,\text{grass}$$

where y is the tongue measurement in question, a is a constant, b the scaling factor of the size proxy (which can be either BM or total tongue length), and c the factor describing the influence of %grass.

Ratios (the corpus width ratio and the proportion of the free portion of the tongue) were additionally also tested against %grass only according to

$$y = a + c\%\,\text{grass}.$$

Models were compared for goodness-of-fit using AIC; following guidelines published for wildlife research, we selected as best-supported models those with a ΔAIC score of ≤ 2, where ΔAIC = AIC—minimum AIC within the candidate model set (Burnham and Anderson, 2001, 2002). The significance level was set to 0.05. For visualisation, length measurements were plotted relative to $\text{BM}^{0.33}$. Results from the dataset limited to specimens with actually measured BM are displayed in the supporting information (Supporting Information, Table S1).

RESULTS

There was a significant positive relationship between BM and tongue length (Tables 2 and Supporting Information, Table S1; Fig. 2). Measurements were according to geometric principles; most measures of length scaled with BM at an exponent that included 0.33 in the confidence interval, or with tongue length at an exponent that included 1.0 in the confidence interval (or the confidence interval came very close to these values; Tables 2 and Supporting Information, Table S1).

In general, results in OLS and PGLS did not differ, in spite of an often significant phylogentic signal. Invariably, PGLS models were better supported as indicated by lower AIC values. Compared with OLS, PGLS reduced significance of the influence of %grass in several cases (Tables 2 and Supporting Information, Table S1) and detected an influence of BM or tongue length on the corpus width ratio where OLS did not indicate it (Table 2).

In general, the results of the two datasets (the smaller dataset with actually measured BM in Supporting Information, Table S1, and the larger dataset with additional measures related to BM data from the literature in Table 2) did not deviate much from each other. The phylogenetic signal did not become systematically stronger with in the larger dataset (no higher values for λ), but was mostly determined with greater confidence as indicated by more frequent significant differences in the estimation of λ from both 0 and 1 (i.e., the confidence interval for λ excluded 0 and 1 more often). In the case of corpus width, BM yielded the best relationship in the smaller dataset (Supporting Information, Table S1), but tongue length in the larger dataset (Table 2). The corpus width ratio was not significantly related to either BM or tongue length in the smaller dataset (Supporting Information, Table S1), in contrast to the larger one (Table 2). The expansion of the dataset never led to %grass being less significant than in the smaller one, but raised %grass to the level of a significant covariable in the case of torus width, corpus width, and the free portion length.

TABLE 2. Statistical results for the dataset including also specimens with BM ascribed based on literature data; models tested were y = a + b log(sizeproxy), y = a + b log(sizeproxy) + c %grass, or y = a + c %grass, with either BM or tongue length as size proxies

y	Stats	λ	AIC	ΔAIC	log a	95%CI		t	P	b	95%CI		t	P	c	95%CI		t	P
log Tongue length ($n = 65$)										**log BM**					**%grass**				
	OLS	(0)	−166.7	17.7	0.65	0.60	0.70	26.089	**0.000**	0.33	0.30	0.36	23.647	**0.000**					
	PGLS	0.150*	−184.5	**0.0**	0.66	0.61	0.72	23.991	**0.000**	0.33	0.30	0.36	22.372	**0.000**					
	OLS	(0)	−151.3	33.2	0.66	0.61	0.70	26.200	**0.000**	0.34	0.31	0.37	22.358	**0.000**	−0.00028	−0.00074	0.00018	−1.188	0.239
	PGLS	0.090*	−183.3	**1.2**	0.66	0.61	0.71	24.706	**0.000**	0.33	0.30	0.36	21.386	**0.000**	−0.00022	−0.00070	0.00025	−0.926	0.358
log Torus length ($n = 60$)										**log BM**					**%grass**				
	OLS	(0)	−143.3	108.6	0.27	0.21	0.33	9.310	**0.000**	0.36	0.33	0.39	21.604	**0.000**					
	PGLS	0.110*	−159.9	92.0	0.27	0.21	0.33	8.744	**0.000**	0.36	0.33	0.39	21.174	**0.000**					
	OLS	(0)	−128.5	123.4	0.27	0.21	0.33	9.383	**0.000**	0.35	0.31	0.39	19.423	**0.000**	0.00036	−0.00016	0.00087	1.358	0.180
	PGLS	0.110*	159.9	411.8	0.27	0.21	0.33	8.860	**0.000**	0.35	0.31	0.39	18.880	**0.000**	0.00038	−0.00016	0.00092	1.388	0.171
										log tongue length					**%grass**				
	OLS	(0)	−204.7	47.2	−0.41	−0.48	−0.34	−11.801	**0.000**	1.06	1.01	1.12	37.422	**0.000**					
	PGLS	$0.644^{\dagger}$	−234.7	17.3	−0.44	−0.51	−0.37	−12.182	**0.000**	1.08	1.02	1.13	38.266	**0.000**					
	OLS	(0)	−217.8	34.1	−0.39	−0.44	−0.33	−14.417	**0.000**	1.02	0.97	1.06	44.170	**0.000**	0.00075	0.00052	0.00098	6.396	**0.000**
	PGLS	0.172*	−251.9	**0.0**	−0.40	−0.46	−0.34	−13.991	**0.000**	1.03	0.98	1.07	42.646	**0.000**	0.00069	0.00045	0.00094	5.517	**0.000**
log Corpus length ($n = 60$)										**log BM**					**%grass**				
	OLS	(0)	−129.8	144.7	0.41	0.35	0.48	12.608	**0.000**	0.31	0.28	0.35	16.689	**0.000**					
	PGLS	$0.392^{\dagger}$	−151.2	123.2	0.44	0.37	0.51	11.889	**0.000**	0.30	0.27	0.34	15.884	**0.000**					
	OLS	(0)	−125.0	149.5	0.41	0.35	0.47	13.824	**0.000**	0.34	0.30	0.38	18.230	**0.000**	−0.00097	−0.00150	−0.00044	−3.586	**0.001**
	PGLS	0.111*	−156.1	118.4	0.42	0.36	0.48	13.311	**0.000**	0.33	0.30	0.37	17.428	**0.000**	−0.00086	−0.00142	−0.00031	−3.056	**0.003**
										log tongue length					**%grass**				
	OLS	(0)	−228.3	46.2	−0.22	−0.28	−0.17	−7.885	**0.000**	0.96	0.91	1.00	41.421	**0.000**					
	PGLS	$0.503^{\dagger}$	−254.0	20.4	−0.20	−0.26	−0.14	−6.604	**0.000**	0.95	0.90	0.99	40.109	**0.000**					
	OLS	(0)	−239.8	34.6	−0.24	−0.28	−0.20	−10.838	**0.000**	1.00	0.96	1.03	52.543	**0.000**	−0.00061	−0.00080	−0.00042	−6.239	**0.000**
	PGLS	0*	−274.4	**0.0**	−0.24	−0.28	−0.20	−10.838	**0.000**	1.00	0.96	1.03	52.543	**0.000**	−0.00061	−0.00080	−0.00042	−6.239	**0.000**
log Torus width ($n = 61$)										**log BM**					**%grass**				
	OLS	(0)	−133.3	62.4	0.09	0.02	0.15	2.704	**0.009**	0.27	0.24	0.31	14.708	**0.000**					
	PGLS	$0.593^{\dagger}$	−160.2	35.5	0.11	0.03	0.18	2.870	**0.006**	0.26	0.23	0.30	13.989	**0.000**					
	OLS	(0)	−120.5	75.2	0.09	0.03	0.15	2.773	**0.008**	0.29	0.25	0.33	14.563	**0.000**	−0.00055	−0.00111	0.00001	−1.918	0.060
	PGLS	$0.557^{\dagger}$	−158.4	37.3	0.11	0.03	0.18	2.854	**0.006**	0.27	0.23	0.31	13.381	**0.000**	−0.00016	−0.00073	0.00041	−0.548	0.586
										log tongue length					**%grass**				
	OLS	(0)	−173.6	22.1	−0.47	−0.56	−0.38	−9.930	**0.000**	0.84	0.76	0.92	21.603	**0.000**					
	PGLS	$0.540^{\dagger}$	−195.7	**0.0**	−0.45	−0.55	−0.35	−8.656	**0.000**	0.82	0.74	0.90	20.097	**0.000**					
	OLS	(0)	−159.9	35.8	−0.48	−0.57	−0.39	−10.303	**0.000**	0.87	0.79	0.94	21.353	**0.000**	−0.00038	−0.00078	0.00002	−1.865	0.067
	PGLS	$0.486^{\dagger}$	−194.2	**1.5**	−0.46	−0.56	−0.35	−8.734	**0.000**	0.83	0.75	0.92	19.360	**0.000**	−0.00015	−0.00058	0.00027	−0.722	0.473
log Corpus width ($n = 58$)										**log BM**					**%grass**				
	OLS	(0)	−130.3	37.8	0.03	−0.04	0.09	0.802	0.426	0.30	0.26	0.34	16.317	**0.000**					
	PGLS	0.453*	−148.4	19.6	0.03	−0.04	0.11	0.915	0.364	0.29	0.25	0.33	15.091	**0.000**					
	OLS	(0)	−116.4	51.7	0.02	−0.04	0.09	0.783	0.437	0.29	0.25	0.33	14.676	**0.000**	0.00046	−0.00009	0.00101	1.627	0.110
	PGLS	0.475*	−150.2	17.9	0.03	−0.04	0.11	0.941	0.351	0.28	0.24	0.32	13.896	**0.000**	0.00056	−0.00001	0.00113	1.910	0.061
										log Tongue length					**%grass**				
	OLS	(0)	−144.9	23.1	−0.53	−0.64	−0.41	−9.218	**0.000**	0.88	0.78	0.97	18.637	**0.000**					
	PGLS	$0.731^{\dagger}$	−165.6	2.4	−0.52	−0.65	−0.39	−8.100	**0.000**	0.86	0.76	0.96	17.207	**0.000**					
	OLS	(0)	−135.2	32.9	−0.51	−0.61	−0.40	−9.244	**0.000**	0.83	0.74	0.92	17.655	**0.000**	0.00064	0.00018	0.00111	2.732	**0.008**
	PGLS	0.621*	−168.1	**0.0**	−0.51	−0.63	−0.39	−8.219	**0.000**	0.83	0.74	0.93	16.674	**0.000**	0.00054	0.00005	0.00103	2.170	**0.034**

Table 2. (continued).

y	Stats	λ	AIC	ΔAIC	log a	95%CI		t	P	b	95%CI		t	P	c	95%CI		t	P
Corpus width ratio ($n = 56$)										**log BM**					**%grass**				
	OLS	(0)	−55.0	30.5	1.09	0.97	1.22	17.492	**0.000**	0.09	0.02	0.17	2.652	**0.011**					
	PGLS	0.787†	−84.1	**1.3**	1.09	0.94	1.23	14.785	**0.000**	0.10	0.03	0.17	2.833	**0.006**					
	OLS	(0)	−43.6	41.8	1.09	0.97	1.21	17.948	**0.000**	0.07	−0.01	0.14	1.776	***0.082***	0.00106	0.00002	0.00210	2.005	0.050
	PGLS	0.783†	−82.1	3.3	1.09	0.94	1.23	14.665	**0.000**	0.10	0.03	0.17	2.634	**0.011**	0.00005	−0.00103	0.00113	0.096	0.924
	OLS	(0)	−47.3	38.2	1.19	1.13	1.24	41.311	**0.000**						0.00141	0.00043	0.00239	2.824	**0.007**
	PGLS	0.792†	−77.3	8.2	1.25	1.16	1.34	27.773	**0.000**						0.00050	−0.00058	0.00158	0.913	0.365
										log Tongue length					**%grass**				
	OLS	(0)	−55.5	29.9	0.97	0.73	1.21	7.821	**0.000**	0.23	0.04	0.43	2.310	**0.025**					
	PGLS	0.821†	−85.4	**0.0**	0.89	0.64	1.15	6.962	**0.000**	0.30	0.11	0.49	3.054	**0.004**					
	OLS	(0)	−45.0	40.4	1.00	0.77	1.24	8.314	**0.000**	0.16	−0.04	0.37	1.589	0.118	0.00116	0.00014	0.00217	2.234	**0.030**
	PGLS	0.820†	−83.4	**2.0**	0.89	0.64	1.15	6.844	**0.000**	0.30	0.10	0.50	2.892	**0.006**	0.00002	−0.00104	0.00108	0.032	0.974
log Free portion length ($n = 62$)										**log BM**					**%grass**				
	OLS	(0)	−90.8	66.2	0.16	0.07	0.25	3.460	**0.001**	0.32	0.27	0.37	12.235	**0.000**					
	PGLS	0.656†	−108.9	48.0	0.21	0.10	0.32	3.680	**0.001**	0.31	0.25	0.36	11.002	**0.000**					
	OLS	(0)	−91.2	65.7	0.16	0.08	0.24	3.851	**0.000**	0.37	0.32	0.42	14.456	**0.000**	−0.00160	−0.00233	−0.00087	−4.316	**0.000**
	PGLS	0.364*	−112.0	44.9	0.19	0.09	0.28	3.780	**0.000**	0.34	0.29	0.40	12.244	**0.000**	−0.00109	−0.00188	−0.00030	−2.703	**0.009**
										log Tongue length					**%grass**				
	OLS	(0)	−136.6	20.3	−0.51	−0.64	−0.39	−8.055	**0.000**	1.00	0.90	1.10	19.364	**0.000**					
	PGLS	0.709†	−149.2	7.7	−0.43	−0.57	−0.29	−6.035	**0.000**	0.95	0.84	1.06	17.327	**0.000**					
	OLS	(0)	−145.1	11.8	−0.56	−0.66	−0.45	−10.605	**0.000**	1.09	1.00	1.18	24.218	**0.000**	−0.00129	−0.00174	−0.00084	−5.581	**0.000**
	PGLS	0.282*	−156.9	**0.0**	−0.50	−0.62	−0.38	−8.183	**0.000**	1.04	0.94	1.13	20.409	**0.000**	−0.00104	−0.00155	−0.00053	−3.992	**0.000**
Free portion (% tongue) ($n = 62$)										**log BM**					**%grass**				
	OLS	(0)	379.4	56.4	32.29	27.71	36.87	13.821	**0.000**	−0.63	−3.22	1.96	−0.479	0.633					
	PGLS	0.697†	331.5	8.4	34.53	28.80	40.25	11.812	**0.000**	−1.12	−3.93	1.68	−0.785	0.436					
	OLS	(0)	365.8	42.7	32.10	28.25	35.95	16.341	**0.000**	1.93	−0.46	4.32	1.584	0.119	−0.09083	−0.12579	−0.05587	−5.092	**0.000**
	PGLS	0.333*	324.8	**1.8**	33.74	29.02	38.47	13.998	**0.000**	0.72	−1.97	3.40	0.524	0.603	−0.07098	−0.10989	−0.03208	−3.576	**0.001**
	OLS	(0)	368.5	45.5	34.84	33.01	36.68	37.219	**0.000**						−0.07915	−0.11139	−0.04691	−4.812	**0.000**
	PGLS	0.381*	323.1	**0.0**	34.80	32.32	37.27	27.546	**0.000**						−0.06527	−0.10122	−0.02932	−3.558	**0.001**
										log tongue length					**%grass**				
	OLS	(0)	377.6	54.5	30.39	21.35	39.43	6.590	**0.000**	0.67	−6.69	8.04	0.180	0.858					
	PGLS	0.710†	331.7	8.6	35.54	25.32	45.76	6.813	**0.000**	−2.41	−10.29	5.48	−0.599	0.552					
	OLS	(0)	362.3	39.2	27.27	19.69	34.85	7.052	**0.000**	6.67	0.18	13.16	2.014	**0.049**	−0.09084	−0.12428	−0.05740	−5.324	**0.000**
	PGLS	0.292*	324.5	**1.4**	31.28	22.49	40.08	6.971	**0.000**	3.08	−4.24	10.41	0.825	0.413	−0.07386	−0.11159	−0.03613	−3.837	**0.000**

Analyses were performed in ordinary least squares (OLS, where no phylogenetic signal λ is assumed) or phylogenetic generalized least squares (PGLS, where λ is estimated by maximum likelihood). Parameter estimates are given with their 95% confidence interval (95%CI), and the corresponding t-statistic and P-value. Data fit of the models is compared using AIC among models for a given y. Significant P-values (<0.05) and the ΔAIC values representing the best models are set in bold. Best-supported models are shaded in gray.

*λ significantly different from 1.

$^{\dagger}\lambda$ significantly different from 0 and 1.

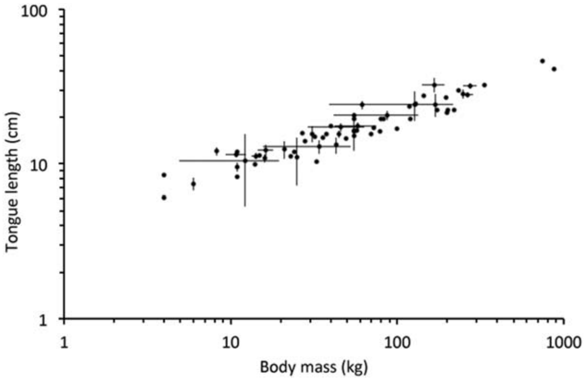

Fig. 2. Relationship between BM (in kg) and tongue length (in cm) in ruminant species (representing the raw data of the complete dataset of Table 1 with specimens whose BM was measured and whose BM was taken from the literature). Error bars indicate standard deviation. For statistics, see Table 2.

Models using tongue length as the independent variable were usually better supported than those using BM (Table 2), with the exception of corpus width and the corpus width ratio in the smaller dataset (Supporting Information, Table S1).

The natural diet, as assessed by %grass, had a significant influence on several measurements (Table 2 and Supporting Information, Table S1). Variation in %grass had no significant effect on total tongue length (Fig. 3A) because animals with a higher %grass had a comparatively a shorter corpus (Fig. 3B) and a longer torus (Fig. 3C). A higher %grass was associated with a wider corpus width, and there was no tendency for an association with a smaller torus width after including phylogeny in the analysis (Table 2). The corpus width ratio (whether tongues were straight or poon-shaped) was not associated with %grass when phylogeny was controlled for (Table 2). Finally, a higher %grass was associated with a lower proportion of the free part of the tongue of its overall length in both the reduced or the expanded dataset (Fig. 4).

DISCUSSION

Comparative studies often rely on data from a variety of sources—for example, BM data is often taken from another source than the measurement in question (Clauss et al., 2008b). The question arises whether this approach is satisfactory, or whether only data from specimens should be included whose BM had been actually recorded in parallel to the measurement in question. Given the lack of principal differences between the dataset using only original BMs, and the one allowing also additional species with literature BM data, accepting literature BM data was acceptable in the case of macroscopic tongue anatomy. However, BM itself may not always be the most useful proxy for body size. BM may be subjected to systematic seasonal variation or other variation related to the nutritional and health status of the animal (e.g., Schwartz et al., 1987; Adamczewski et al., 1992; Lane et al., 2014). Given that many morphological measures that may be of interest can be expected to show less corresponding variation, such as skeletal measures or in our case tongue length, it should always be considered if a less variable reference measure as a proxy for body size is available. For example, rather than using literature

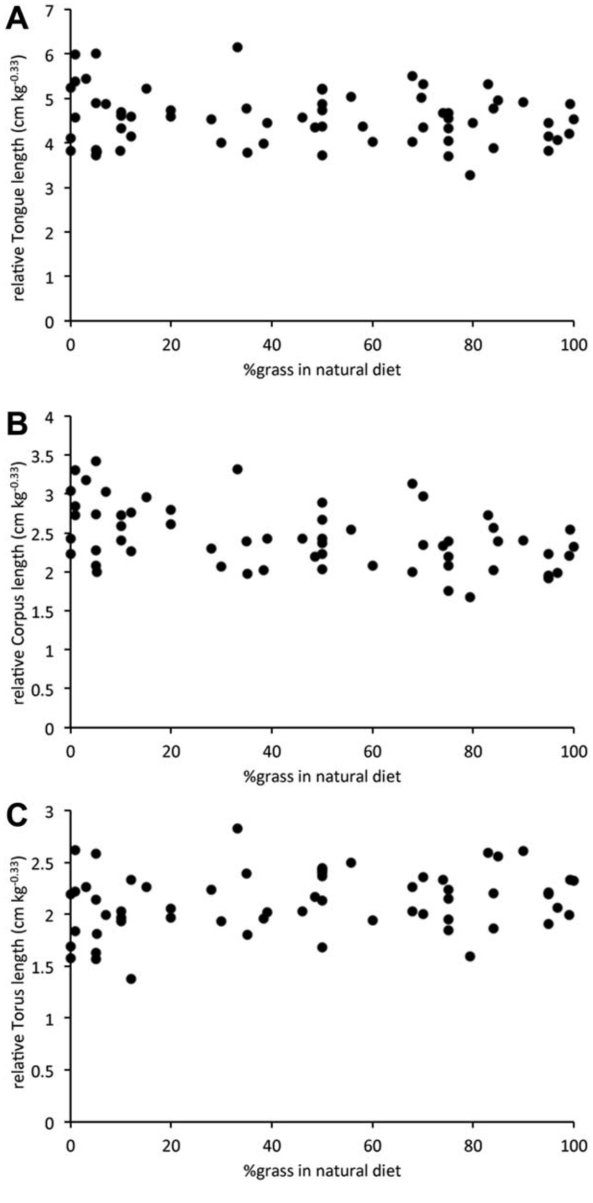

Fig. 3. Relationship between the percentage of grass in the natural diet and **A)** the relative total tongue length, **B)** the relative corpus length, **C)** the relative torus length in ruminant species (all in cm kg$^{-0.33}$; representing the complete dataset of Table 1 with specimens whose BM was measured and whose BM was taken from the literature). For statistics, see Table 2.

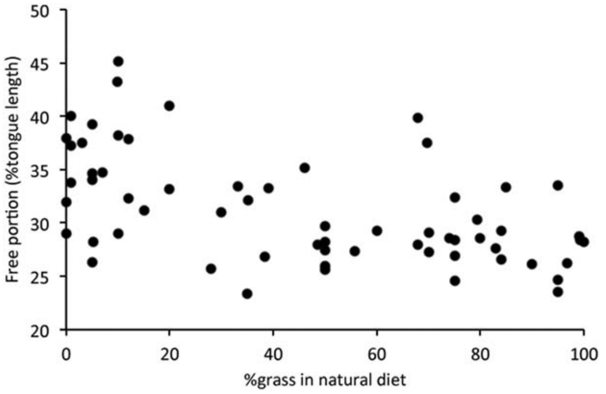

Fig. 4. Relationship between the percentage of grass in the natural diet and the proportion of the free part of the tongue of the total tongue length in all ruminant species in which this measurement was taken. For statistics, see Table 2.

BM data to correlate with her cranial skeletal measurements, Spencer (1995) or Codron et al. (2008) used the length of the maxillary molar row as a body size proxy. The fact that relationships with tongue length were nearly always better supported than those with BM (Tables 2 and Supporting Information, Table S1) emphasizes the relevance of this approach.

Our results must be considered with caution due to the unknown influence of the different preservation stages of the material from which measurements were taken. As they are, they clearly support the conclusions of Hofmann (1988; 1989) that torus length, in relation to total tongue length, is shorter in browsers than in grazers, and that the tongue of browsers generally has a longer freely mobile part than that of grazers. Our results suggest that using the characteristic of an "extensible tongue" as a phylogenetic peculiarity of giraffids only (Hassanin et al., 2012) is not correct. The estimation of the phylogenetic signal λ in several of the PGLS models indicates a certain phylogenetic structure in tongue morphology, most prominent in the corpus width ratio, that is, whether a tongue is straight or "hourglass-shaped." This characteristic might be particularly useful as a soft tissue phylogenetic signal because it is apparently not subject of convergent evolution as an adaptation to diet.

When discussing tongue function, it should be remembered that the tongue is a muscular hydrostat (Smith and Kier, 1985), and the degree to which it can be protruded from the mouth cannot really be deducted from static macroanatomical measurements. How much the tongue can be elongated will not only depend on its resting shape, but also on the arrangement of internal muscle fibres. In the absence of comparative data on such arrangements, or on measurements of tongue protrusion in live animals, conclusions drawn from macroscopic resting shapes must remain preliminary. Comparative studies on the internal architecture of ruminant tongues, including quantification of the relative contributions of longitudinal, transverse, and perpendicular muscle fibres, would be welcome.

The findings of Hofmann (1973; 1985; 1988; 1989; 2000) on convergent morphological characteristics of the feeding apparatus and digestive tract of different ruminant feeding-types have not only inspired a variety of similar studies (reviewed in Clauss et al., 2008b), but have also been questioned based on a lack of feeding-type differentiation when a large set of morphological variables taken from Hofmann (1973) was analyzed together (Pérez-Barbería et al., 2001). Criticism against that latter work includes the fact that character choice was not based on considerations of functionality but on sheer availability (similar to our approach in this study for some of our characters), and not even backed by speculative explanations (Clauss et al., 2008b). In contrast, a series of tests on selected, putatively functionally relevant measures has confirmed convergence among feeding-types in anatomical measures related to muzzle and snout shape (Fraser and Theodor, 2011; Tennant and MacLeod, 2014), the salivary glands (Hofmann et al., 2008) and the masseter (Clauss et al., 2008a), teeth (Heywood, 2010; Kaiser et al., 2010), the intraruminal papillation (Clauss et al., 2009), the rumen and the reticulum (Clauss et al., 2010) as well as the omasum (Clauss et al., 2006a), and in measures related to digestive efficiency (Pérez-Barbería et al., 2004) and rumen physiology (Dittmann et al., 2015). Similar to the findings of this study, the results of these analyses usually demonstrate convergence, but also indicate an interspecific measurement variability that makes a confident allocation of a feeding-type based on any single measure questionable. In this study, this is evident in the data scatter even in those relationships that are statistically significant. Additionally, adaptations of the digestive tract may also have evolved in response to other selective pressures than the botanical grass-browse dichotomy, in particular among grazers and mixed feeders (Codron et al., 2008; Dittmann et al., 2015), so that a tight correlation between diet and morphology need not be expected within certain sections of the feeding-type continuum (Clauss and Hofmann, 2014). Also, not all morphological adaptations need to be convergent in all phylogenetic groups, as e.g. evident in the comparatively small salivary glands reported in giraffids regardless of the fact that they are strict browsers (Clauss et al., 2006b; Sauer et al., 2016).

A functional interpretation of the findings of this study must remain hypothetical, and will revolve around the process of food ingestion. An intuitive assumption is that browsers, which have to pluck leaves off twigs or from between thorns, may need particularly long tongues, which would fit the results of our study. However, Hofmann (1988) explained, naming cattle and Père David's deer (*Elaphurus davidianus*) as specific examples, that some grazers also use their tongue (rather than their lips or their incisors and the maxillary "dental pad") for harvesting grass. Correspondingly, cattle have a particularly long freely mobile tongue tip. Conversely, other ruminants such as sheep and goats graze with their lips and do not use their tongues to harvest forage (Baumont et al., 2006). To our knowledge, no systematic compilation exists that compares how ruminant species harvest the food they ingest (using either mainly their lips, their tongues, or their incisors). Descriptions of individual species that compare the use of different parts of the oral ingestion apparatus in terms of their relevance for food harvest are also lacking. The overall pattern observed in our study here suggests that the feeding behavior of cattle, that is, the use of a long tongue to harvest grass bundles, is not the most prominent strategy among grazers, which, therefore, mostly have comparatively shorter free tongue tips. Whether differences between the feeding-types in terms of the mobility of the lips, as stated, for example, by Hofmann (1989) or Searle and Shipley (2008), can really be demonstrated in comparative datasets remains to be shown.

A longer free portion of the tongue explains the longer corpus in browsing ruminants (Fig. 3B). It cannot, however, explain observations on the length and width of the torus (Fig. 3C). The distinct appearance of the *Torus linguae* is a characteristic of ruminants (Hofmann, 1988) whose function remains to be elucidated. The increasing corpus breadth with at higher proportions of grass in the natural diet might be related to the concept that grazing ruminants have broader muzzles (Gordon and Illius, 1988; Janis and Ehrhardt, 1988; Solounias et al., 1988; Solounias and Moelleken, 1993; Spencer, 1995) or palates (Hofmann, 1988) than browsers. It must be noted that this concept has been challenged based on phylogenetic independent contrast analysis that did not detect a significant difference in incisor arcade breadth between categorical ruminant feeding-types (Pérez-Barbería and Gordon, 2001). In contrast, both Fraser and Theodor (2011) and Tennant and MacLeod (2014) found that other measures of snout shape actually matched categorical feeding-types, even when corrected for phylogeny, with browsers having more pointed and narrower snout shapes than grazers. It appears reasonable to assume that tongue shape reflects this difference to a certain extent, as suggested by our results. With more data such as ours becoming available, more comprehensive analyses combining various morphological characteristics of the feeding apparatus (e.g., Fraser and Rybczynski, 2014) will become feasible. In particular, data on ingestive behaviour (using lips vs. teeth vs. tongue for harvesting plants) would be an important addition in this respect.

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