M. Clauss, J. Hummel, J. Völlm,
A. Lorenz, R. R. Hofmann

The allocation of a ruminant feeding type to the okapi (*Okapia johnstoni*) on the basis of morphological parameters

Andrea Fidgett,
Marcus Clauss,
Klaus Eulenberger,
Jean-Michel Hatt,
Ian Hume,
Geert Janssens,
Joeke Nijboer
(eds.)

Zoo Animal Nutrition

Vol. III

Filander Verlag

PUBLISHED BY
Filander Verlag, Fürth

Cover photo: Rob Doolaard (Rotterdam Zoo)

ISBN-10 3-930831-57-0
ISBN-13 978-3-930831-57-9

www.filander.com

Printed in the Federal Republic of Germany

M. Clauss[1], J. Hummel[2], J. Völlm[3], A. Lorenz[4], R. R. Hofmann[4]

The allocation of a ruminant feeding type to the okapi (*Okapia johnstoni*) on the basis of morphological parameters

Presented at the Joint Nutrition Symposium at Antwerp, Belgium, 2002

Abstract

As the anatomy of the digestive tract of the okapi (Okapia johnstoni) has not been described in relation to the ruminant feeding type classification to date, we here report anatomical measurements on a complete digestive tract of an okapi euthanised in captivity and measurements of its ingesta particle size and forestomach protozoa species, supplemented with other information on two okapi forestomachs and anatomical literature data. The digestive tract of the okapi is characterised by a comparatively small reticulorumen (wet contents 9.8% of body weight) with weak rumen pillars (thickness 7–10 mm), a shallow reticular honeycomb structure (reticular crest height 1–2 mm) and a small omasum (curvature 28–33 cm); particularly long papillae unguiculiformes have been reported and were found in one forestomach investigated, but are not a consistent finding. The ratio of the length of the small vs. large intestine was low (1.3–1.8). The liver investigated was comparatively large (1.56% of body weight). Faecal particle size investigated was large compared to other ruminant data. Forestomach protozoa were almost exclusively Entodinium species. All these parameters are in accord with a classification as a typical browser according to Hofmann (1989). However, the parotid glands investigated represented only 0.071% of body weight, which is within the range typically reported for grazers. Potential causes and consequences of this finding are briefly discussed.

Key Words

okapi, Okapia johnstoni, anatomy, digestion, nutrition, browser, rumen, reticulum, omasum, intestine, salivary gland

[1] Division of Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland, mclauss@vetclinics.unizh.ch

[2] Zoological Garden of Cologne, and Institute of Animal Science, University of Bonn, Germany

[3] Zoological Garden of Basle, Switzerland

[4] Institute of Zoo and Wildlife Research (IZW) Berlin, Germany

Introduction

Although the ruminant digestive tract has been described in its morphological variety for a very long time (e. g. Flower 1872, Short *et al*. 1965), it was the anatomical work of Hofmann (1969, 1973, 1985, 1988, 1989, 1991, 1999) that not only provided a comparative framework within the ruminant guild by attributing certain morphological peculiarities to one of three feeding types (concentrate selectors/browsers, intermediate feeders, grazers), but also provided a link between the functional anatomy and the ecology of ruminants. Although the major body of morphological observations stems from Hofmann himself, other researchers have contributed to the knowledge of wild ruminant anatomy (e. g. Church and Hines 1978, Kay 1987, Kamler 2001, Clauss *et al*. 2005). This type of research has been particularly fruitful in the Australasian region (Agungpriyono *et al*. 1992, Fraser 1996, Yamamoto *et al*. 1998, Forsyth and Fraser 1999, Jiang *et al*. 2002).

In spite of this scientific output, a large number of species – in particular from the South American and Asian continent – remain to be described. From within the African ruminants, the digestive tract of one flagship species for many zoological gardens in terms of conservation efforts, but also in terms of visual attractivity, the okapi, has not been studied in relation to Hofmann's classification. Nevertheless, the okapi has been used repeatedly as a typical example for a browsing species in morphological, and in particular in palaeontological databases (Janis and Ehrhardt 1988, Gordon and Illius 1988, Janis1990, Solounias and Moelleken 1993, Solounias *et al*. 1995, 2000). This unequivocal classification can be based on solid literature evidence that the okapi is an exclusive browser: Hart and Hart (1988, 1989) and Hart (1992) report that okapis do not include monocots in their diet. Already Burne (1917) reported on remnants of natural food in the oesophagus of an okapi from the wild: a bolus of small fragments of leaves of trees which were identified as fragments of dicotyledonous plants, with grasses being apparently absent. This author cites different other authors who all observed the absence of grass and the complete focus on leaves in the natural diet of the okapi (Wilmet 1913, Christy 1915).

In order to investigate the morphological adaptations of the okapi digestive tract to its strict dicotyledonous diet, and to facilitate a comparison with other ruminant species, we dissected one captive okapi that was euthanised in a zoological collection and inspected the conserved forestomach of another captive individual; additionally, we collated the available data measurements on the okapi digestive tract from the literature.

Methods

The anatomical dissection of an okapi (animal I) that was euthanized because of dental wear and disease was performed according to methods described by Hofmann (1969, 1973). As the digestive tract of okapi has been documented visually in excellent form by Burne (1917, 1939) and Neuville and Derscheid (1929), visualisation of anatomical parts was kept to a minimum. Samples of the contents of the reticulorumen and the abomasum were frozen and stored until sieve analysis according to Clauss *et al*. (2002). A sample of fresh rumen contents was fixed in formalin and analysed for protozoa species by microscope (10×) after staining with methylgreen using Ogimoto and Imai (1981) as a reference.

Additionally, the formalin-fixed forestomach of another okapi (animal II) that died of unknown causes was inspected. Further additional data came from Hofmann (unpublished) from the dissection of a captive animal (animal III) in 1988. Other available data on okapi digestive anatomy were collated from the literature. For an overview of the investigated animals, see Table 1.

Table 1: Details of the animals from which data was collated in this study

	this study (I)	this study (II)	Hofmann (unpubl.)/ Werner (1990)
Studbook No.	0329	0385	0224
Sex	Female	male	Female
Body weight (kg)	231	180	190
Body length (mouth to anus, cm)	219		
Age (years)	18 (1984–2002)	9 (1991–2000)	18 (1970–1988)

Burne (1917) investigated a young specimen that came directly from the wild, and Neuville and Derscheid (1929) studied a two year-old female from Antwerp zoo. Burne (1939) gives no indication where the second individual he dissected came from.

Feeding regime of the animals was as follows (all amounts as fresh matter): Animal (I) was offered alfalfa hay *ad libitum*, smaller amounts of browse, 2100 g of a pelleted feed , 450 g carrots, 450 g apples, 450 g banana, 600 g vegetables (each of the latter five distributed over 3 meals). Animal (II) was offered alfalfa hay *ad libitum*, smaller amounts of browse depending on the season, 600 g cattle pellet, 150 g oats, 150 g dried forage meal (alfalfa), 50 g of a mineral pellet, 600 g apple, 600 g banana, 600 g carrots and about 350 g vegetables (the latter eight distributed over 2 meals per day). For animal (III), diet could not be reconstructed in detail.

Results

Data on the forestomach and abomasums of the okapi are collated in Table 2–5.

The rumen is completely papillated, with the exception of the cranial pillar in the specimens investigated for this study. In a similar way, Burne (1939) describes reduced, flattened, almost scale-like nodules on the rumen

Table 2: Measurements taken on the rumen of okapi

	this study (I)	this study (II)	Hofmann (unpubl.)/ Werner (1990)	Burne (1939)	Neuville and Derscheid (1929)	Burne (1917)
Rumen length (cm)	52	64	65	56	33	34
Rumen height (cm)	43	48	52	30.5	36	30
Ostium intraruminale diameter (cm)	19	–	20	–	–	–
Cranial ruminal pillar thickness (mm)	9	7	10	–	–	–
Caudal ruminal pillar thickness (mm)	9	9	10	–	–	–
Rumen papillation	complete	complete	–	com- plete	–	complete
Ostium rumino–reticulare (cm)	14 × 11	15 × 10	–	–	–	–

Table 3: Measurements taken on the reticulum of okapi

	this study (I)	this study (II)	Hofmann (unpubl.)/ Werner (1990)	Burne (1939)	Neuville and Derscheid (1929)	Burne (1917)
Reticulum long diameter (cm)	23	23	–	27	10	15
Reticulum transverse diameter (cm)	19	18.5	–	17.5	8	16
Reticular crest max. height (mm)	1	1.5	–	2	1–2	–
Reticular cellulae max. diameter (cm)	2.4	2.3	2.9	2.5	2	–
Reticulo–omasal orifice (cm)	1.9 × 1.8	2.0 × 1.6	2.4 × 1.0	–	–	–
Pap. unguiculiformes max. length (cm)	0.6	2.0	0.7	1.7	1	–

Table 4: Measurements taken on the omasum of okapi

	this study (I)	this study (II)	Hofmann (unpubl.)/ Werner (1990)	Burne (1939)	Neuville and Derscheid (1929)	Burne (1917)
Omasum length (cm)	13	21	13.6	15.5	–	15.2
Omasum height (cm)	9.5	11.5	11.6	6.4	–	–
Omasum curvature (cm)	31	33.5	28	–	–	–
Number 1st order leaves	13	13	13	13	13	14
2nd	13	12	12	–	–	–
3rd	20	21	24	–	–	–
4th	27	24	46	–	–	–
Size 1st order leaves (max. height cm)	7.0	9.5	7.0	7.5	–	–
2nd	3.0	4.0	3.4	3.6	–	–
3rd	1.5	1.3	1.7	1.3		
4th	0.8	0.5	0.7	0.3		

Table 5: Measurements taken on the abomasums of okapi

	this study (I)	this study (II)	Hofmann (unpubl.)	Burne (1939)	Neuville and Derscheid (1929)
Abomasum diameter at omasum (cm)	–	–	–	18	–
Abomasum diameter at pylorus (cm)	–	–	–	3.8	–
Abomasum length (cm)	42	43	–	44	–
Abomasal folds (No)	22	26	26	23	15

pillars. The shallowness of the reticular honeycomb structure already caught the attention of Burne (1917, 1939), Neuville and Derscheid (1929) and Scheidegger (1950), who all present pictures of this finding in their publications; Langer (1973) reported the maximal reticular crest height in okapi to be 3.9 mm, with a maximal diameter of the reticular cellulae of 2.8 cm. Particularly long *papillae unguiculiformes* had been noted by Burne (1939) and Neuville and Derscheid (1929) who also presented pictures of this finding. One of the two forestomachs examined for this work displayed approximately 30 very long *papillae unguiculiformes* with long, thin, keratineous tips that pointed into the reticulo-omasal orifice. The fact that the omasum appears rather small for a ruminant of this size had been commented upon by Scheidegger (1950), and Clauss *et al*. (2006) measured an average total absorptive surface for the okapi omasal leaves of 2029 cm^2. Langer (1973) counted a total of 18 omasal leaves (all orders combined) in his okapis, a number that appears low compared to the other results on this parameter.

The dimensions and organ and content weights of the intestinal tract are shown in Table 6–7.

Table 6. Dimensions (cm) of the intestine in okapi.

	this study (I)	Burne (1939)	Burne (1917)	Neuville and Derscheid (1929)
Duodenum	98	–	–	–
Jejunum	2025	–	–	–
Ileum	53.5	–	–	–
Small intestine	2176.5	1981.2	–	–
Caecum	46	30.5	–	30
Ansa proximalis	166	127	–	–
Ansa spiralis	894	477.5	289.5	–
Ansa distalis	113	127	–	–
Colon transversum	320	351.7	–	–
Colon descendens	94		–	–
Rectum	80	134.6	–	–
Large intestine length	1713	1097.28	–	–
Total intestine	3889.5	3078.4	–	–

Again, measurements between studies were comparable. Near the ostium ileo-caecale, the ileo-caecal "tonsil" as described by Derscheid and Neuville (1924) and Burne (1939) was evident in our specimen as well. The liver weighed 3.6 kg (1.56 % of body weight) in animal (I) and was reported to weigh 12 lbs (5.45 kg) by Burne (1917). On inspection of the oral cavity,

Table 7: Organ and content weights for the okapi digestive tract from animal (I) investigated for this study

	Organ weight (kg)	Contents wet weight (kg)	Contents % BW	Contents % of total contents
Ruminoreticulum	4.04	22.5	9.8	64.0
Omasum	0.38	0.3	0.1	0.9
Abomasum	1.28	4.8	2.1	13.5
Duodenum	0.14	0.1	0.0	0.2
Jejunum	1.88	3.0	1.3	8.6
Ileum	0.14	0.0	0.0	0.0
Caecum	0.16	0.5	0.2	1.5
Ansa proximalis	0.62	1.5	0.6	4.2
Ansa spiralis	1.1	1.2	0.5	3.3
Ansa distalis	0.2	0.2	0.1	0.5
Colon transversum	0.48	0.4	0.2	1.2
Colon descendesn	0.3	0.2	0.1	0.6
Rectum	0.5	0.5	0.2	1.5
Small intestine	2.2	3.1	1.4	8.9
DFC	0.8	2.0	0.9	5.7
Large intestine	3.4	4.5	2.0	12.8
Total intestine	4.1	6.5	2.8	18.6
Total forestomach	4.42	22.8	9.9	64.8
Total GIT	11.22	35.2	15.3	100

animal (I) showed severe and irregular tooth wear. The incisor arcade, which was reported to measure 43.7 mm by Gordon and Illius (1988), was of similar size with 40.5 mm in this animal. The total weight of both parotid glands was 164 g and of both mandibular glands 144 g (0.071 and 0.062 % of body weight, respectively). Burne (1917) stated that the tongue, which he measured at 35.6 cm, had a free part that was more developed than in any other ruminants except for giraffe. In animal (I), the tongue measured 40 cm with a torus of 15.5 cm and a free part of 17 cm (ratio corpus:torus 1.58; free part 42.5 % of total length).

The rumen contents of animal (I) had a pH of 6.22 and contained only protozoa belonging to the genera of *Entodinium* (*E. dubardi, E. longinucleatum, E. simulans, E. rectangulatum, E. simplex, E. caudatum, C. exiguum, E. parvum, E. rostratum*) and *Dasytricha* (*D. ruminatum*). The particle size distribution of ingesta in the reticulorumen and distal to it is displayed in Table 8.

Discussion

The data collection on the digestive anatomy of okapi shows that in general, data are in good accord across studies. The animals studied by Burne (1917)

Table 8: Particle size distribution in and distal to the ruminoreticulum in animal (I) from this study. MOF = Modulus of fineness calculated according to Poppi et al. (1980). The columns denote the respective sieve sizes (linear dimensions of holes).

		% of all particles						
Contents	MOF	4 mm	2 mm	1 mm	0.5 mm	0.25 mm	0.125 mm	< 0.125 mm
Rumen	3.89	18.4	6.2	15.3	11.5	9.1	7.0	32.5
Distal GIT	3.24	9.3	4.0	13.5	13.4	15.1	9.4	35.2

and Neuville and Derscheid (1929) were evidently younger specimens that had not yet fully matured.

In order to interpret such findings on a quantitative basis, comparative data sets have to be used against which the okapi values can be compared. This method has been used repeatedly, e. g. by Jiang *et al*. (2002) for Mongolian gazelles.

Forestomach parameters

Clauss *et al*. (2003a) showed that the proportion of ruminoreticular (RR) contents on total body weight differs significantly between the ruminant feeding types. Given the data presented by these authors, measurements taken from the animals in this study closely match the regression line for browsing ruminants (Figure 1).

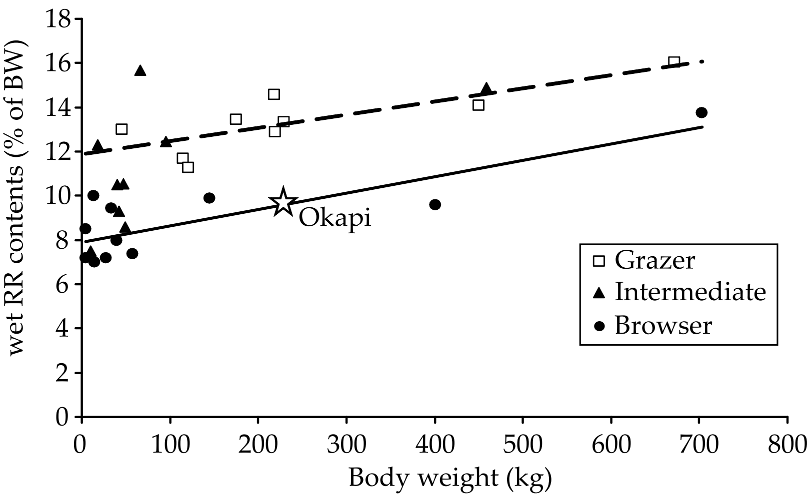

Figure 1: Correlation of body weight and wet ruminoreticular (RR) contents (in % BW) for different ruminant feeding types (from Clauss et al. 2003a). Okapi data measured in this study indicated by the star. Regression lines for grazers (dotted) and browsers (solid).

A similar difference for RR contents between the feeding types was demonstrated by Jiang and Takatsuki (1999), who also found a similar difference in the volume of the RR as determined by water fill. From the data set on African ruminants by Clemens and Maloiy (1983), a proportion of RR contents on the total tract contents of 65 % for browsers and 78 % for grazers can be calculated. This value was 64 % for animal (I) in this study (Table 7). Clauss *et al*. (2003a) showed that the average RR pillar thickness differed systematically between browsers and grazers; again, if the measurements taken on okapi (Table 2) are included into the data provided by these authors, the okapi closely matches the browser regression line (Figure 2).

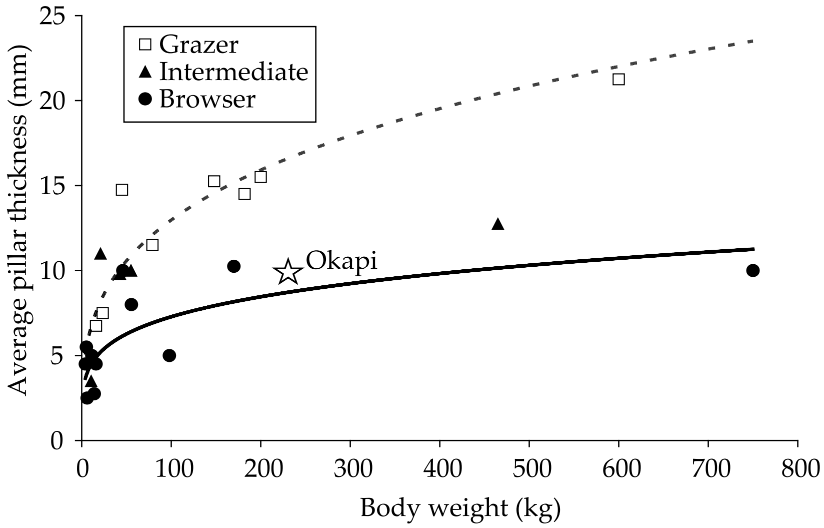

Figure 2: Correlation of body weight and average ruminoreticular pillar thickness (in mm) for different ruminant feeding types (from Clauss et al. 2003a). Okapi data measured in this study indicated by the star. Regression lines for grazers (dotted) and browsers (solid).

Langer (1988) already demonstrated with data sets that included the okapi that browsers had lower reticular crests and a lower number of omasal laminae than grazers (but without correcting for body weight). Correcting for both body weight and phylogeny, Clauss *et al*. (2006) showed that browsers had smaller omasa than grazers; again, the okapi was included in that data set. The size of the omasum can be appreciated by comparing the diagram drawn from animal (I) of this study (Figure 3) to the according drawings in Hofmann (1973, 1989).

The mean absorptive surface of the omasal leaves, reported by Clauss *et al*. (2006) to be 2029 cm^2 for two animals averaging 210 kg, is drastically lower than the 17800 cm^2 reported by McSweeney (1988) for water buffalo (*Bubalus bubalis*) of 164 kg dressed carcass weight.

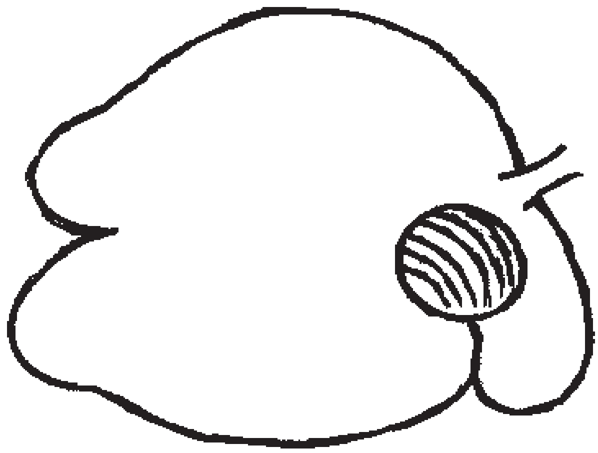

Figure 3: Diagram of the ruminoreticulum and omasum in okapi

Intestine

According to Hofmann (1988), the total intestines of grazers are 25–30 times the body length of the animal, whereas in browsers this factor is only 12–15. In animal (I) of this study, this factor was 18, thus only slightly surpassing the typical browser range. Hofmann (1988) reports ratios of the small intestine:large intestine of 2.2 in browsers and 4.3 in grazers. Okapis seem to have particularly low ratios in this respect, with a value for animal (I) from our study of 1.3 and the animal from Burne (1939) of 1.8.

Liver

Hofmann (unpublished, cited in Duncan *et al*. 1998) gave correlations between body weight (kg) and liver weight (g) to be 22.6 $BW^{0.938}$ for browsers and 13.5 $BW^{0.981}$ in grazers, which would result in calculated liver weights for a body weight of 231 of 3.7 and 2.8 kg, respectively. With an actual liver weight of 3.6 kg, animal (I) from this study was close to the browser value.

Salivary glands

Hofmann (1973, 1988) and Kay (1987) reported that browsers have generally larger parotid glands than grazers. Robbins et al. (1995) confirmed this in principle, finding that parotis weight was about 1.8 g/kg body weight in browsers and 0.5 g/kg in grazers. However, these authors noted that one browser, the Greater kudu (*Tragelaphus strepsiceros*) had a parotid gland weight comparable to that of other grazers. Jiang and Takatsuki (1999) collated data that showed that grazers have a parotid gland weight of about 0.6 g/kg body weight, whereas this value is 1.7–1.8 in browsers. In animal (I) of this study, parotid gland weight was 0.7 g/kg body weight and is thus much closer to the average for grazers than that of browsers. The size and position of the parotis in animal (I) from this study is displayed in Figure 4, which can be compared to the according drawings in Hofmann (1988).

Hofmann (1988) reported mandibular gland weights at 0.4 g/kg body weight for grazers, 0.8 g/kg for intermediate feeders and 1.0 g/kg for browsers. At 0.6 g/kg, animal (I) of this study was closer to the grazer value for the mandibular gland as well.

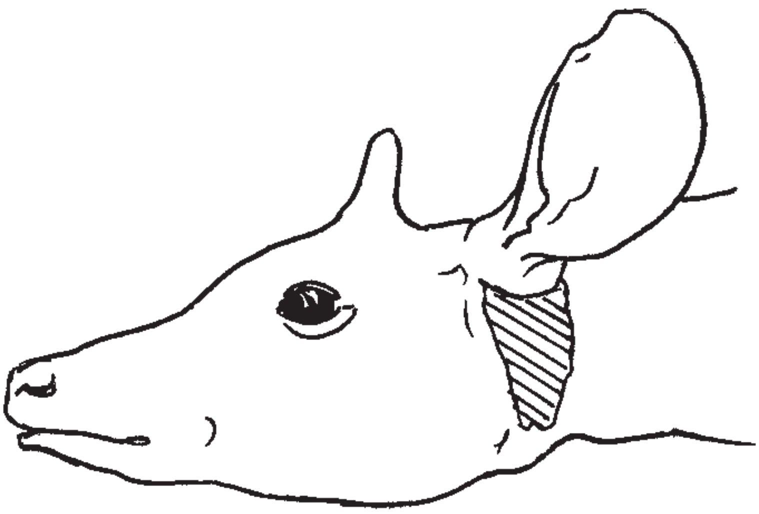

Figure 4: Diagram of the parotid gland in okapi.

Tongue

Hofmann (1988) stated that the free part of the tongue is 28 % of its total length in grazers and 33 % in browsers, and that the ratio of the corpus: torus of the tongue is 1.06 in grazers and 1.24 in browsers. With a ratio of 1.58 and a proportion of the free part at 42.5 % of the total organ length, animal (I) of this study falls well within the browser range.

Physiological parameters

It has been shown that okapi have a comparatively reduced selective particle retention in the forestomach and fast particle passage rates in the total digestive tract (Clauss and Lechner-Doll 2001, Hummel *et al.* 2005). The values achieved for selective particle retention are within the browser range for this parameter. The protozoal fauna of the forestomach of browsing ruminants has been repeatedly described as being dominated by *Entodinium* species only (for a compilation of literature see Clauss and Lechner-Doll 2001, Behrend *et al*. 2004), which were also by far the dominating protozoa in animal (I) of this study. Although large faecal particles and a high modulus of fineness in the faeces of okapi have been reported (Clauss *et al*. 2002), the values obtained from animal (I) even exceed the reported ones. While this can be attributed to the poor condition of the masticatory apparatus of this animal – a condition well-known in aged captive okapis (Raphael 1999) – the fact that such a high proportion of large particles does leave the ruminoreticulum is nevertheless remarkable.

Conclusions

The number of anatomical parameters measured in this study is smaller than that listed by Hofmann (1988) for the comparative investigation of ruminant digestive morphology. Among these are the masseter muscles, the sublingual salivary glands, and most notably histological parameters, all of which were not measured on animal (I) in this study. Nevertheless, the measured and reported parameters indicate that major anatomical and physiological parameters in okapi are within the typical browser range, and probably reflect adaptations to the peculiarities of its natural diet, which have been described in detail by Hofmann (1973, 1988, 1989, 1999), Clauss and Lechner-Doll (2001) and Clauss *et al*. (2002, 2003a). Admittedly, the method of allocating a feeding type on the basis of anatomical parameters appears especially reliable if the respective opposite (grazer or browser) shall be ruled out. A differentiation between any extreme feeding type and the intermediate feeders would be more speculative in this respect.

The notable exception in this unanimous classification is the size of the salivary glands measured in this study. One of the functions of the salivary glands in browsing ruminants is the production of tannin-binding proteins (Austin *et al*. 1989, Hagerman and Robbins 1993, Juntheikki 1996, Fickel *et al*. 1998). One might speculate that the lack of natural forage with its secondary plant compounds in captivity could mean that the salivary glands are not developed according to their potential in captive animals; however, experimental work has shown that in contrast to rodents, the secretion of salivary tannin-binding proteins is not induced by tannin ingestion in ruminants (Austin *et al*. 1989, Clauss *et al*. 2003b). Therefore, the salivary glands of captive okapi might well represent the state natural for this species. When dissecting two captive giraffes that showed morphological adaptations to long periods of grass hay feeding (Hofmann and Matern 1988), Hofmann and Matern (unpubl.) observed relatively small salivary glands in these specimens. While it cannot be ruled out that captive individuals have less developed salivary glands than free-ranging individuals, these findings could also indicate relatively smaller salivary glands in giraffids as compared to other browsers. Although the relatively larger salivary glands of browsing ruminants are a robust finding in comparative anatomy (Kay 1987, Hofmann 1988) that has been confirmed by statistical evaluations of available data (Robbins *et al*. 1995, Jiang and Takatsuki 1999), it has been observed that the Greater kudu (*Tragelaphus strepsiceros*) is an exception to this rule, and that other members of the Tragelaphinae have salivary glands that are not as large as would be expected because of their dietary habits (Robbins *et al*. 1995). The Greater kudu is the only browsing ruminant species which has been reported to suffer losses in ecological situations where overbrowsing leads to increased dietary tannin levels in their natural forage (Van Hoven 1991). In this context, one might speculate that the large variety of plants included in the natural diet of okapi (Hart and Hart 1989) is an adaptation to reduce the intake of any one particular secondary compound in large amounts (c.f. Westoby 1974), and that a low ability to cope with such secondary compounds confines the okapi to its narrow natural habitat. Evidently, data on the tannin-binding capacity of okapi (and kudu) saliva is warranted, as well as a larger survey of ruminant salivary gland anatomy and analyses of tanninc levels in wild ruminant forages.

Knowing the morphophysiological adaptations of ruminants can help to understand the limitations to the survival (and breeding success) of a species both in captivity and in the wild. For captive management, the typical "browser" digestive anatomy should caution against a common health problem in this feeding type, rumen acidosis (Marholdt and Hofmann 1991), due to the fact that these animals seem to be particularly reluctant to ingest traditional roughage sources used in zoos – hays – in sufficient proportions (Clauss *et al*. 2003c). The data collection of this study demonstrates that the criteria defined by Hofmann (1969, 1973, 1988, 1989) allow a classification of okapi that is in good accord with reports on its natural diet. Further comparative studies on ruminant digestive anatomy should be encouraged.

Acknowledgements

We thank Nadia Robert and Christian Wenker for their cooperation, and B. Peters and C. Witte for support in literature acquisition.

References

Agungpriyono, S.; Yamamoto, Y.; Kitamura, N.; Yamada, J.; Sigit, K.; Yamashita, T. (1992): Morphological study on the stomach of the Lesser mouse deer (*Tragulus javanicus*) with special reference to the internal surface. *J. Vet. Med. Sci.* 54: 1063–1069

Austin, P.J.; Suchar, L.A.; Robbins, C.T.; Hagerman, A.E. (1989): Tannin-binding proteins in saliva of deer and their absence in saliva of sheep and cattle. *J. Chem. Ecol.* 15: 1335–1347

Behrend, A.; Lechner-Doll, M.; Streich, W.J.; Clauss, M. (2004): Seasonal faecal excretion, gut fill, and solute and particle marker retention in mouflon (*Ovis ammon musimon*), and a comparison with roe deer (*Capreolus capreolus*). *Acta Theriol.* 49: 259–267

Burne, R.H. (1917): Notes on some of the viscera of an okapi (*Okapia johnstoni*). *Proc. Zool. Soc. Lond.*, pp. 187–208

Burne, R.H. (1939): Description of the stomach, intestine, liver, and pancreas of the okapi (*Okapia johnstoni*). *Proc. Zool. Soc. Lond.* 109: 451–479

Christy, C. (1915): The okapi. *Nature* 95: 506–507

Church, D.C.; Hines, W.H. (1978): Ruminoreticular characteristics of elk. *J. Wildl. Manage.* 42: 654–659

Clauss, M.; Lechner-Doll, M. (2001): Differences in selective particle retention as a key factor in the diversification of ruminants. *Oecologia* 129: 321–327

Clauss, M.; Lechner-Doll, M.; Streich, W.J. (2002): Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer-dichotomy from the other end. *Oecologia* 131: 343–349

Clauss, M.; Lechner-Doll, M.; Streich, W.J. (2003a): Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis. *Oikos* 102: 253–262

Clauss, M.; Lason, K.; Gehrke, J.; Lechner-Doll, M.; Fickel, J.; Grune, T.; Streich, W.J. (2003b): Captive roe deer (*Capreolus capreolus*) select for low amounts of tannic acid but not quebracho: fluctuation of preferences and potential benefits. *Comp. Biochem. Physiol.* B 136: 369–382

Clauss, M.; Kienzle, E.; Hatt, J.M. (2003c): Feeding practice in captive wild ruminants: peculiarities in the nutrition of browsers/concentrate selectors and intermediate feeders. A review. In: *Zoo animal nutrition II* (A.L. Fidgett, M. Clauss, U. Gansloßer, J.-M. Hatt, J. Nijboer, eds.). Fürth: Filander Verlag, pp. 27–52

Clauss, M.; Hummel, J.; Vercammen, F.; Streich, W.J. (2005): Observations on the macroscopic digestive anatomy of the Himalayan tahr (*Hemitragus jemlahicus*). *Anat. Hist. Embryol.* 34: 276–278

Clauss, M.; Hofmann, R.R.; Hummel, J.; Adamczewski, J.; Nygren, K.; Pitra, C.; Streich, W.J.; Reese, S. (2006): The macroscopic anatomy of the omasum of free-ranging moose (*Alces alces*) and muskoxen (*Ovibos moschatus*) and a comparison of the omasal laminal surface area in 34 ruminant species. *J. Zool. Lond.* (in press)

Clemens, E.T.; Maloiy, G.M.O. (1983): Digestive physiology of East African wild ruminants. *Comp. Biochem. Physiol.* A 76: 319–333

Derscheid, J.M.; Neuville, H. (1924): Recherches anatomiques sur l'okapi. I. Le caecum et la glande ileo-caecale. *Rev. Zool. Bot. Afr.* 12: 498–507

Duncan, P.; Tixier, H.; Hofmann, R.R.; Lechner-Doll, M. (1998): Feeding strategies and the physiology of digestion in roe deer. In: *The European roe deer: the biology of success* (R. Andersen, P. Duncan, J.D.C. Linnell, eds.). Stockholm: Scandinavian University Press, pp. 91–116

Fickel, J.; Göritz, F.; Joest, B.A.; Hildebrandt, T.; Hofmann, R.R.; Breves, G. (1998): Analysis of parotid and mixed saliva in roe deer. *J. Comp. Physiol.* B 168: 257–265

Flower, W.H. (1872): Lectures on the comparative anatomy of the organs of digestion of the mammalia. Lecture IX. *Medical Times and Gazette* 2: 319–322

Forsyth, D.M.; Fraser, K.W. (1999): Seasonal changes in the rumen morphology of Himalayan tahr (*Hemitragus jemlahicus*) in the Two Thumb Range, South Island, New Zealand. *J. Zool. Lond.* 249: 241–248

Fraser, K.W. (1996): Comparative rumen morphology of sympatric sika deer (*Cervus nippon*) and red deer (*C. elaphus scoticus*) in the Ahimanawa and Kaweka Ranges, central North Island, New Zealand. *Oecologia* 105: 160–166

Gordon, I.J.; Illius, A.W. (1988): Incisor arcade structure and diet selection in ruminants. *Functional Ecol.* 2: 15–22

Hagerman, A.E.; Robbins, C.T. (1993): Specificity of tannin-binding salivary proteins relative to diet selection by mammals. *Can. J. Zool.* 71: 628–633

Hart, J.A. (1992): Forage selection, forage availability and use of space by okapi (*Okapia johnstoni*) a rainforest giraffe in Zaire. In: *Proceedings International Symposium „Ongulés/Ungulates ‚91"* (F. Spitz, G. Janeau, G. Gonzalez, S. Aulagnier, eds.). Toulouse, p. 18

Hart, J.A.; Hart, T.B. (1988): A summary report on the behaviour, ecology and conservation of the okapi (*Okapia johnstoni*) in Zaire. *Acta Zool. Pathol. Antv.* 80: 19–28

Hart, J.A.; Hart, T.B. (1989): Ranging and feeding behaviour of okapi (*Okapia johnstoni*) in the Ituri forest of Zaire: food limitation in a rainforest herbivore? Symp. *Zool. Soc. Lond.* 61: 31–50

Hofmann, R.R. (1969): Zur Topographie und Morphologie des Wiederkäuermagens im Hinblick auf seine Funktion. Nach vergleichenden Untersuchungen an Material ostafrikanischer Wildarten. *Zbl. Vet. Med.* Suppl. 10: 1–180

Hofmann, R.R. (1973): *The ruminant stomach*. East African Monographs in Biology Volume II. Nairobi: East African Literature Bureau

Hofmann, R.R. (1985): Digestive physiology of the deer – their morphophysiological specialisation and adaptation. *R. Soc. N. Zeal. Bull.* 22: 393–407

Hofmann, R.R. (1988): Morphophysiological evolutionary adaptations of the ruminant digestive system. In: *Aspects of digestive physiology in ru-*

minants (A. Dobson, M.J. Dobson, eds.). Ithaca NY: Cornell University Press, pp. 1–19

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. (1991): Endangered tropical herbivores – their nutritional requirements and habitat demands. In: *Recent advances on the nutrition of herbivores* (Y.W. Ho, H.K. Wong, N. Abdullah, Z.A. Tajuddin, eds.). UPM Serdang: Malaysia Society of Animal Production, pp. 27–34

Hofmann, R.R. (1999): Functional and comparative digestive system anatomy of Arctic ungulates. *Rangifer* 20: 71–81

Hofmann, R.R.; Matern, B. (1988): Changes in gastrointestinal morphology related to nutrition in giraffes: a comparison of wild and zoo specimens. *Int. Zoo Yb.* 27: 168–176

Hummel, J.; Clauss, M.; Zimmermann, W.; Johanson, K.; Norgaard, C.; Pfeffer, E. (2005): Fluid and particle retention in captive okapi (*Okapia johnstoni*). *Comp. Biochem. Physiol.* A 140: 436–444

Janis, C.M. (1990): Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropodoids and ungulates. *Mem. Queensland Mus.* 28: 349–366

Janis, C.M.; Ehrhardt, D. (1988): Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool. J. Linn. Soc.* 92: 267–284

Jiang, Z.; Takatsuki, S. (1999): Constraints on feeding type in ruminants: a case of morphology over phylogeny. *Mammal Study* 24: 79–89

Jiang, Z.; Takatsuki, S.; Li, J.; Wang, W.; Ma, J.; Gao, Z. (2002): Feeding type and seasonal digestive strategy of Mongolian gazelles in China. *J. Mammal.* 83: 91–98

Juntheikki, M.R. (1996): Comparison of tannin-binding proteins in saliva of Scandinavian and North American moose. *Biochem. Syst. Ecol.* 24: 595–601

Kamler, J. (2001): Morphological variability of forestomach mucosal membrane in red deer, fallow deer, roe deer and mouflon. *Small Rum. Res.* 41: 101–107

Kay, R.N.B. (1987): Weights of salivary glands in ruminant animals. *J. Zool. Lond.* 211: 431–436

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

Langer, P. (1988): *The mammalian herbivore stomach*. Stuttgart: Gustav Fischer

Marholdt, F.; Hofmann, R.R. (1991): Makro- und mikroskopische Veränderungen der Pansenschleimhaut von Zoo- und Wildwiederkäuern – ein Befundbericht mit Hinweisen zur artgerechten Fütterung. *Arbeitstagung der Zootierärzte im deutschsprachigen Raum* 11: 19–34

McSweeney, C.S. (1988): A comparative study of the anatomy of the omasum in domesticated ruminants. *Aust. Vet. J.* 65: 205–207

Neuville, H.; Derscheid, J.M. (1929): Recherches anatomiques sur l'okapi *Okapia johnstoni*. IV. L'estomac. *Rev. Zool. Bot. Afr.* 16: 373–419

Ogimoto, K.; Imai, S. (1981): *Atlas of rumen microbiology*. Tokyo: Japan Scientific Society Press

Poppi, D.P.; Norton, B.W.; Minson, D.J.; Hendricksen, R.E. (1980): The validity of the critical size theory for particles leaving the rumen. *J. Agric. Sci. Camb.* 94: 275–280

Raphael, B.L. (1999): Okapi medicine and surgery. In: *Zoo and wild animal medicine: current therapy 4* (M.E. Fowler, R.E. Miller, eds.). Philadelphia: WB Saunders, pp. 646–649

Robbins, C.T.; Spalinger, D.E.; Van Hoven, W. (1995): Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? *Oecologia* 103: 208–213

Scheidegger, S. (1950): Pathologisch-anatomische Untersuchung des Okapi „Bambe". *Acta Trop.* 7: 133–150

Short, H.L.; Medin, D.E.; Anderson, A.E. (1965): Ruminoreticular characteristics of mule deer. *J. Mammal.* 46: 196–199

Solounias, N.; Moelleken, S.M.C. (1993): Tooth microwear and premaxillary shape of an archaic antelope. *Lethaia* 26: 261–268

Solounias, N.; Moelleken, S.M.C.; Plavcan, J.M. (1995): Predicting the diet of extinct bovids using masseteric morphology. *J. Vertebr. Paleontol.* 15: 795–805

Solounias, N.; McGraw, W.S.; Hayek, L.A.; Werdelin, L. (2000): The paleodiet of the Giraffidae. In: *Antelopes, deer, and relatives. Fossil record, behavioral ecology, systematics, and conservation* (E.S. Vrba, G.B. Schaller, eds.). New Haven: Yale University Press, pp. 83–95

Werner, A. (1990): Vergleichende morphometrische Untersuchungen am Blättermagen von 17 Wiederkäuern unterschiedlicher Ernährungstypen. [dissertation]. Giessen: University of Giessen.

Wilmet (1913): L'okapi. *C. R. Acad. Sci. Paris* 156: 2006–2008

Van Hoven, W. (1991): Mortalities in kudu populations related to chemical defence in trees. *J. Afr. Zool.* 105: 141–145

Westoby, M. (1974): An analysis of diet selection by large generalist herbivores. *Am. Nat.* 108: 290–304

Yamamoto, Y.; Atoji, Y.; Agungpriyono, S.; Suzuki, Y. (1998): Morphological study of the forestomach of the Japanese serow (*Capricornis crispus*). *Anat. Hist. Embryol.* 27: 73–81