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Quantitative investigation of the intestines in eight species of domestic mammals

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Abstract

Eight species of domestic mammals (dog, cat, horse, pig, cow, goat, sheep, and rabbit) were investigated using quantitative morphometric techniques to determine various functional parameters of the intestines. In addition to lengths and volumes, basal areas were measured directly on the entire large intestines. Histological sections were made from disc-shaped probes punched from predetermined areas of the intestine in order to calculate a factor of increase of the intestinal mucosa due to macroscopically and microscopically visible structures such as folds, mounds, villi, and crypts. Ratios of large intestine to small intestine for the parameters areas and volume as well as area to volume relationships were determined. According to this type of data handling, nonruminant herbivores are set apart from a collective taxonomically unrelated group including faunivores and intermediate feeders plus ruminant herbivores. This latter grouping is discussed in relation to their diet and large intestinal morphology.

Introduction

The availability of morphometric data on the intestines of domestic mammals is surprisingly dearth despite their obvious economic importance. Most data in textbooks are concerned with volumes (Slijper 1946; Flindt 1985) or lengths (Ellenberger and Baum 1943) and the latter are based largely on non-reproducible measurements that are 50 years and older. Although length is the most frequently measured parameter for intestine, it is not necessarily a reliable measurement or is it functionally the most important factor in the intestine. Far more interesting from the functional point of view is the surface area available for absorption and secretion in the various compartments of the intestine. The few data for areas available, for example presented by Chivers and Hladik (1980) from an extensive and heroic compilation of intestinal values for hundreds of species, were largely obtained by extrapolating areas from products of measured lengths times widths. This procedure may well be justifiable for animals whose intestines are uniform throughout their lengths, such as rodent small intestines (Young Owl 1994), however, it does not appear appropriate for large and voluminous intestines. Moreover, intestinal structures such as the spiral fold of the rabbit caecum or the plicae intestinales of the human small intestine, both of which add, respectively, 30 to 50% more surface area over and above the basal surface areas (Snipes 1996), are missed and ignored by such a procedure.

In all methods used to date, only few have taken into account the increase in surface area due to microscopically visible structures such as folds, crypts or villi. Therefore, it

was deemed expedient to employ a newly developed quantitative technique (Snipes and Kriete 1991) to obtain data from domestic animals. The technique should include the advantages of 1) measuring the entire large intestine even for such huge animals as horse or cow and thereby avoiding the obvious disadvantages of sampling and extrapolation, 2) including in these measurements any macroscopically visible and extractable structures (e. g. spiral fold of rabbit caecum) which increases the basal surface area, 3) determining a factor of surface enlargement due to microscopically measurable structures (villi, crypt, folds) and subsequently with this factor, 4) determining a total surface area as the product of the basal area times the microscopic surface enlargement factor.

Material and methods

Three animals each were used in the present study for reasons recently discussed by Snipes (1996). The domestic mammals investigated in the present study include:

dog: *Canis lupus* Linnaeus, 1758
cat: *Felix silvestris* Schreiber, 1777
horse: *Equus przewalskii* Poliakow, 1881
pig: *Sus scrofa* Linnaeus, 1758
cow: *Bos primigenius* Bojanus, 1827
goat: *Capra aegagrus* Erxleben, 1777
sheep: *Ovis ammon* Linnaeus, 1758
rabbit: *Oryctolagus cuniculus* Linnaeus, 1758.
(Nomenclature according to Herre and Röhrs 1990).

Rabbit, dog, and cat were obtained from veterinary physicians practicing all legal forms of euthanasia. Larger animals were obtained from the local abattoir. For the former animals, 4% buffered formol was injected into the lumen of the intestines immediately after death (Fenwick and Kruckenberg 1987). For the latter animals whole intestines were obtained as quickly as possible, opened and flooded with fixative. A thorough discussion of the effects of fixation and each step in the processing of material including reference to possible shrinkage can be found in Snipes (1996, 1997).

A standard methodology for determination of the basal surface areas of the various compartments of the intestines has been described in detail elsewhere (Snipes 1991; Snipes and Kriete 1991; Snipes 1994, 1996). For all animals the entire intestines were measured after having been opened lengthwise and probed for light microscopy (see below). The measurement consisted of tracing contours onto transparent paper of appropriately sized slabs of intestine placed between two glass plates. The contours were subsequently measured for areas (mm^2) using a software especially developed for this purpose and performed on a Kontron semiautomatic imagine analyser (Snipes and Kriete 1991). This procedure gave the basal areas of the tubular or saccular intestinal compartments (small intestine, caecum, colon) and was based on measuring the entire intestine.

To determine an additional increase in the mucosal surface area due to microscopically visible structures, probes were excised according to methods in works cited above. These were processed for light microscopy, the final sections projected via a slide projector onto a digitized tablet for measurement of the factor of increase in surface area due to crypts, villi, and folds. The length of the mucosa surface displaying these surface enlargements was traced with the cursor. This length was set in a ratio to a second length, a straight reference line drawn beneath the mucosal surface to give a Surface Enlargement Factor (SEF), which could then be multiplied times the basal areas to give a final total surface enlargement.

The histological probes were extracted from the small animals (rabbit, cat, dog) according to a scheme developed previously (Snipes and Kriete 1991). This consisted of three areas of the caecum (apex, corpus, caecocolical ampulla) and five equidistant areas of the colon. The probes were punched out with a cork borer, including at least 3/4 the circumference of the intestine. For the remainder of the animals (sheep, goat, pig, cow, horse) this procedure was not appropriate. The histological probes were taken according to a scheme such that the caecum/colon was divided into 20 equidistant lengths. Likewise, the opened intestinal circumference was divided into 20 equivalent sectors. Probes were then extracted with the largest cork borer according to the following protocol. Probe 1 was taken from length # 1 and circumferential sector # 1; probe 2 from length # 2 and circumferential sector # 2 etc. All probes

were taken as discs and embedded according to the principle of vertical sectioning (Baddley et al. 1986). It should be noted here that all macroscopically visible structures such as folds or plicae were excised with scissors and measured as a part of the basal area.

Using this protocol it was felt that an optimal measurement was carried out: for the basal area the entire intestine and for the microscopic surface enlargement factor determination, large probes according to predetermined sampling sites.

Results

In table 1 the lengths and volumes of small intestine, caecum, colon and the total of these three regions are presented according to increasing body weight. The percentage of each parameter to the total is also given. Volumes were calculated from the measured areas. For all species, small intestines represent over 50% of the total intestinal length. For volume, the caecum and colon of rabbit and horse account for a greater percentage than small intestine.

Table 1. Morphometric values, length and volume.
Measured lengths and the percentage of each compartment to total intestinal length. Species name and body weights in kg given for the eight species studied, listed according to increasing body weight. Calculated values of volume in ml and their percentage to total volume of intestine for small intestine, caecum, colon, and total intestine. sm int = small intestine

Species Body Weights kg	Length cm				Volumes ml			
	sm. int	caecum	colon	total	sm. int	caecum	colon	total
Rabbit (*Oryctolagus cuniculus*) 3.6	196.3 55.9%	40.7 11.6%	114.2 32.5%	351.2	79.3 12.3%	514.2 79.9%	50.1 7.8%	643.6
Cat (*Felis silvestris*) 3.7	148.3 86%	2.0 1%	22.3 13%	172.5	48.3 77.8%	2.9 4.7%	10.9 17.6%	62.1
Dog (*Canis lupus*) 13.6	270 86.5%	42 13.5%	75 24%	312	373 70.7%	34.5 6.5%	120 22.7%	527.5
Sheep (*Ovis ammon*) 42.5	2 153 77%	25 0.9%	615 22%	2 793	1 503 59%	284 11%	766 30%	2 553
Goat (*Capra aegagrus*) 52.5	953 68.4%	21 1.5%	420 30.1%	1 394	1 187 71.1%	1 140.6 8.4%	340.9 20.4%	1 668.5
Pig (*Sus scrofa*) 111.9	1 823.3 74%	28.2 1.2%	610.7 24.8%	2 462.2	4 406.6 50.2%	564.8 6.4%	3 808.1 43.4%	8 779.5
Cow (*Bos primigenius*) 474.3	4 073.3 80.1%	57 1.1%	954.7 18.8%	5 085	14 662.8 72.9%	857.7 4.3%	4 598.8 22.9%	20 119.3
Horse (*Equus przewalskii*) 520.0	3 020 77.8%	120 3.1%	740 19.1%	3 880	46 897.3 25.1%	56 083 30%	83 892.7 44.9%	186 873

Table 2. Morphometric values, areas.
Basal areas, second order enlargement factor (SEF) and total areas for small intestine, caecum, colon, and total intestine for the 8 species studied, listed according to increasing body weights. Percents give the proportion of each segment to total intestinal values. Total areas were arrived at by multiplying basal areas times SEF factor.

Species Body Weight kg	Basal Area				SEF			Total Area			
	sm. int cm^2	caec cm^2	colon cm^2	total cm^2	sm. int	caec	colon	sm. int cm^2	caecum cm^2	colon cm^2	total cm^2
Rabbit (*Oryctolagus cuniculus*) 3.6	442.2 36.2%	512.5 41.9%	268.1 21.9%	1 222.8	3.50	2.18	1.80	1 548.1 49.1%	1 121.1 35.5%	485.2 15.4%	3 154.4
Cat (*Felis silvestris*) 3.7	300 75.6%	8.5 2.1%	88.4 22.3%	396.8	5.97	1.71	1.68	1 791 91.7%	14.5 0.7%	148.5 7.6%	1 954
Dog (*Canis lupus*) 13.6	1 124.8 78.4%	57.7 3.9%	251.6 17.5%	1 434.1	4.04	1.63	1.70	4 544.2 89.7%	94.1 1.9%	427.7 8.4%	5 066.0
Sheep (*Ovis ammon*) 42.5	6 377.4 70.0%	298.9 3.3%	2 433.6 26.7%	9 109.9	2.81	1.69	1.75	17 920.5 79.0%	505.1 2.2%	4 258.8 18.8%	22 684.4
Goat (*Capra aegagrus*) 52.5	3 770.3 71.1%	192.6 3.6%	1 341.2 25.3%	5 304.1	1.30	1.20	1.18	4 901.4 73.0%	231.1 3.4%	1 582.6 23.6%	6 715.1
Pig (*Sus scrofa*) 111.9	10 047.3 63.0%	447.0 3.0%	5 405.3 34.0%	15 899.6	3.36	2.59	2.35	33 758.9 70.9%	1 157.7 2.4%	12 702.5 26.7%	47 619.1
Cow (*Bos primigenius*) 474.3	27 393.5 76.9%	783.8 2.2%	7 426.9 20.9%	35 604.2	2.80	1.44	1.60	76 701.8 85.5%	1 128.7 1.3%	11 883.0 13.2%	89 713.5
Horse (*Equus przewalskii*) 520.0	42 183.4 53.2%	9 195.4 11.6%	27 928.1 35.2%	79 306.9	2.45	1.32	1.46	103 349.3 66.1%	12 137.9 7.8%	40 775 26.1%	156 262.2

In table 2 the species are again listed according to increasing body weights for basal areas, the surface enlargement factor (SEF) determined by measuring the histological sections, and the total area as the product of the basal area times SEF. Percents of areas are also given. For areas, only the rabbit caecum plus colon has a larger surface area than the small intestine. In all other species, including horse the area of the small intestine, as primary intestinal segment for absorption of nutrient, possesses the most extensive mucosal surface.

Table 3 presents some simple handling of the data to illustrate more clearly the relationships of certain areas of the gut to one another. The coefficient of digestion (according to CHIVERS and HLADIK 1980) is a ratio resulting from dividing the basal area or total area of the large intestine by the corresponding value of the small intestine. These values give an estimation of the functional importance of the large intestine in the utilization of the diet. These ratios are multiplied by 100 and scaled according to a scheme developed by CHIVERS and HLADIK (1980, 1984) such that values between 0–30 are considered faunivores (and newly determined in the present study also ruminants), 30–70 as intermediate feeders and +70 as nonruminant herbivores. From the present data rabbit and horse qualify as nonruminant herbivores as regards basal area, only rabbit regarding total area. Pig ranges with its value of 58 (basal) and 41 (total area) as intermediate feeder together with goat (41 and 37, respectively) as well as horse for total area (51), sheep and cat for basal area (43 and 32, respectively). All other species qualify as faunivores or ruminants (values below 30). Amongst all ruminants the goat has the largest hindgut (HOFMANN 1991).

Table 3. Coefficient of Gut Differentiation.
Coefficient of Gut Differentiation (Coef Dig) = Areas of large intestine divided by areas of small intestine. According to CHIVER and HLADIK (1980, 1984) a scale was devised dividing animals (but not considering the ruminants) roughly into three dietary groups (faunivores, intermediate feeders and herbivores). At left calculations using basal areas, at right calculations using total areas. All values ×100. Ratings: faunivores = 0–30; intermediate feeders = 30–70, and nonruminant herbivores above a value of 70. Note that values for ruminants fall either in the faunivore or intermediate feeder ranges.

Coefficient of Gut Differentiation Areas Large Intestine/Areas Small Intestine				
Animals	Basal Area	Rating	Total Area	Rating
Dog	27	Faunivore	1.5	Faunivore
Cow	3	Ruminant	17	Ruminant
Cat	32	Faunivore/Intermediate	9	Faunivore
Goat	41	Ruminant	37	Ruminant
Sheep	43	Ruminant	27	Ruminant
Pig	58	Intermediate	41	Intermediate
Horse	88	Herbivore	51	Intermediate
Rabbit	177	Herbivore	104	Herbivore

The Coefficient of Volume (Tab. 4) is a similar ratio but uses volumes of large and small intestine. Values are multiplied by 10 according to CHIVERS and HLADIK (1980) and scaled accordingly: 0–7 = faunivore (or as ruminants as determined newly in this study), 7–15 = intermediate feeders; and +15 = nonruminant herbivores. According to this status, again rabbit and horse qualify as nonruminant herbivores. All other animals examined range as faunivore or ruminant except for pig (9.9) as intermediate feeder. Values for

Table 4. Coefficient of Volume.

Coefficient of Volume = Volumes of large intestine divided by volumes of small intestine. Ratings divide the animals roughly into three dietary groups (originally excluding ruminant): faunivores (0–7), intermediate feeders (7–15) and nonruminant herbivores (above 15). All values multiplied by 10. Ratings according to Chivers and Hladik (1980, 1984). Ruminants show values in the faunivore range. Note that stomach and in the case of ruminants the fore-stomach were not included in the calculations.

Coefficient of Volume Volume Large Intestine/Volume Small Intestine			
Ruminant Rating: 0–7	Faunivore Rating: 0–7	Intermediate Rating: 7–15	Nonruminant Herbivore Rating: +15
Cow 3.7	Cat 2.9	Pig 9.9	Horse 29.8
Goat 4.1	Dog 4.1		Rabbit 71.2
Sheep 7.0			

goat are borderline between intermediate and ruminant (7.0, see explanation above). The nomination according to the classical three dietary types: faunivore (carnivore), intermediate (omnivore) and nonruminant herbivore given by Chivers and Hladik (1980) must now be altered such that values for faunivores are shared by the ruminants.

Another helpful mode of handling data represents the use of area to volume ratios (Tab. 5). This relative area designation illustrates the functionally important relationship of the potential contact of luminal content to the surface mucosa. In table 5 these values are given for small intestine, caecum, colon, and total intestine for relative basal area to volume and relative total area to volume. Large values represent a favourable relationship of area to volume. In this case a tendency for higher values to occur in the smaller animals (body weights) compared to large animals is apparent.

Table 5. Relative areas (areas to volume ratios).

Area to Volume Ratios = Areas of small intestine, caecum and colon divided by their respective volumes. Smaller animals have larger values commensurate with their higher metabolic rates reflecting a more advantageous area to volume relationship. For each region of the intestine (small, caecum and colon as well as total intestine) values using basal areas and total areas are given. Animals are listing according to increasing body weights.

Area (cm^2) to Volume (ml)								
Animals + body weights kg	Small intestine		Caecum		Colon		Total Intestine	
	Basal	Total	Basal	Total	Basal	Total	Basal	Total
Rabbit 3.6	5.8	19.5	1.0	2.2	5.3	9.7	1.9	4.9
Cat 3.7	6.2	37.1	2.9	5.0	8.1	13.6	6.4	31.5
Dog 13.6	3.0	18.0	1.7	2.9	2.1	3.5	2.7	13.7
Sheep 42.5	4.2	11.9	1.1	1.8	3.2	5.6	3.6	8.9
Goat 52.5	3.2	4.1	1.4	1.6	3.9	4.6	3.2	4.0
Pig 111.9	2.3	7.6	0.8	2.0	1.4	3.3	1.8	5.4
Cow 474.3	1.9	5.2	0.9	1.3	1.6	2.6	1.8	4.5
Horse 520.0	0.9	2.2	0.2	0.2	0.3	0.5	0.4	0.8

Table 6. Comparative Percentage Values.
Values from the literature (source given in small print beneath each animal name) converted to percentages of each compartment (small intestine, caecum, colon) to total intestine for the parameters basal area and volume compared to values obtained in the present study.

Animal	Basal area %			Volume %		
Source	small int.	caecum	colon	small int.	caecum	colon
Rabbit						
Chivers and Hladik (1980)	50%	27.6%	22.5%	31.3%	51.6%	17.1%
Neumayer (1990)				71.5%	28.5%	
Flindt (1985)				44.4%	37%	18.6%
present study	36.2%	41.9%	21.9%	12.3%	79.9%	7.8%
Cat						
Chivers and Hladik (1980)	71.7%	2.0%	26.3%	57.3%	2.0%	40.7%
Custor (1873)	68.4%	31.6%				
present study	75.6%	2.1 %	22.5%	77.8%	4.7%	17.6%
Dog						
Chivers and Hladik (1980)	82.4%	2.9%	14.7%	77.5%	3.6%	18.9%
Custor (1873)	79.9%	20.1%				
Neumayer (1990)				71.5%	28.5%	
Flindt (1985)				61.8%	3.4%	34.7%
present study	78.4%	3.9%	17.5%	70.7%	6.5%	22.7%
Sheep						
Chivers and Hladik (1980)	79.9%	2.3%	17.9%	77.4%	6.4%	16.2%
Custor (1873)	60.3%	39.7%				
Ellenberger and Baum (1943)					10.0%	
Flindt (1985)				61.6%	6.9%	31.4%
present study	70.0%	3.3%	26.7%	59.0%	11.0%	30.0%
Goat						
Chivers and Hladik (1980)	66.9%	2.5%	30.6%	56.4%	5.6%	38.0%
Custor (1873)	58.8	41.2%				
Flindt (1985)				61.6%	6.9%	31.4%
present study	71.1%	3.6%	25.3%	71.1%	8.4%	20.4
Pig						
Chivers and Hladik (1980)	67.4%	2.6%	30.0%	55.0%	5.6%	39.3%
Slijper (1946)	63.7%	4.4%	31.9%	46.2%	5.1%	48.7%
Custor (1873)	64.8%	35.2%				
Flindt (1985)				47.3%	7.9%	44.8%
present study	63.0%	3.0%	34.0%	50.2%	6.4%	43.4%

Table 6. (Continued)

Animal	Basal area %			Volume %		
Source	small int.	caecum	colon	small int.	caecum	colon
Cow						
Slijper (1946)	69.5%	5.7%	24.8%	63.5%	9.5%	26.9%
Ellenberger and Baum (1943)					13.1%	29.2%
Flindt (1985)				63.4%	10.0%	27.1%
present study	76.9%	2.2%	20.9%	72.9%	4.3%	22.9%
Horse						
Chivers and Hladik (1980)	22.8%	19.2%	58.0%	7.3%	33.3%	59.4%
Slijper (1946)	38.0%	13.0%	49.0%	30.9%	20.5%	48.6%
Ellenberger and Baum (1943)				35.3%	16.7%	47.9%
Flindt (1985)				33.0%	17.4%	49.6%
present study	53.2%	11.6%	35.3%	25.1%	30.0%	44.9%

In table 6 data from four different sources were compared with data from the present study. It was necessary to convert and conform these data into percentages so that a comparative basis could be created. As stated previously, the functionally important parameters are considered to be area and volume. Although lengths of intestines have in the past been more commonly compiled these are considered to be of lesser relevance functionally.

Discussion

The large intestine of ruminants has been largely ignored in the literature except for a few interesting reviews (e. g. Janis 1976; Sibly 1981; Hofmann 1989, 1991), most probably due to the prominence and importance of the rumen-reticulum. It is interesting to note in the present study that values measured for most of the ruminants fall into categories with faunivores. The categorisations should not be taken as necessarily showing functionally similar utilization of diets in these cases but rather that in both ruminants and faunivores the large intestine plays a lesser functionally important role compared to nonruminant herbivores and intermediate feeders.

Comparison with data in the literature is rendered extremely difficult due to the lack of uniformity in the mode of obtaining the data and the handling of the data. Despite this lack of uniformity of data in the literature an attempt at comparing the few compilations available was undertaken. It can be seen that most of the values from different authors range relatively close together. The present values for rabbit, however, differ from previous studies. This is most likely due to the fact that in our study we considered the basal area due to the spiral fold in the caecum of the rabbit which previous authors ignored. This fold accounts for up to 53% of the area in the caecum (Snipes 1996). This most certainly accounts for the difference in the values for rabbit and emphasizes the importance of careful consideration of the structures to be selected for measurement.

The present values for the horse are also slightly divergent from those of previous authors with respect to the proportion due to small intestine. The volumes of large intes-

tine are all very close (44 to 49%). The percentages of area and volume for the large intestine for both horse and rabbit are the highest amongst the studied animals as would be expected for nonruminant herbivores. Only the pig (as true intermediate feeder) possesses values for colon that approach those for the two afore-mentioned animals. All other listed animals, the faunivores (cat and dog) and the ruminants (sheep, goat, and cow) have lower values for percentages of the large intestine.

The only other complete source of data for comparative purposes is that of Chivers and Hladik (1980, 1984). In addition to measured values, we have emphasized the relative proportions or the use of coefficients. Coefficients for total areas include the second-order enlargements of the surface area due to such structures as crypts, microscopic folds, and villi. This form of categorisation shows that such structures are more highly developed in the large intestines of nonruminant herbivores (larger values for rabbit and horse), which correlates with their voluminous macroscopic forms. Ruminants and faunivores have lower values emphasizing the greater functional importance of the intestinal compartments oral to the large intestines. Coefficients of volume are also higher in the two nonruminant herbivores reflecting the fermentation chamber function of their caecum plus colon compartments.

The relative surface area related to volume displays a general tendency for animals with smaller body weights to possess higher values, indicative of a more advantageous mucosal surface area relationship to luminal content, which may be more effective for rapid absorption of nutrients. This has been interpreted as reflecting the higher energy requirements of metabolically more active smaller animals (Karasov and Diamond 1985; Snipes 1996). In a previous study (Snipes and Kriete 1991) comparing 19 different mammalian species this tendency was even more obvious. This weight-dependent association is more apparent using a larger sample of animals of wider weight ranges. This can be visualized to better advantage via linear regression curves (and a wider range of animals) which correlate closely to metabolic body weights (Snipes 1996).

The fact that herbivores whose fermenation chambers are set before the large intestine (ruminants) can be grouped with faunivores based on morphometric parameters is upon initial consideration perhaps a surprising finding, and may even seem contradictory. However, this grouping is a consequence of the functional importance of that portion of the intestinal tract lying proximal to the ileocaecal junction, be it the rumen-reticulum in ruminants or the small intestine in faunivores. This finding is corroborated by several physiological data.

Since the enzyme machinery to breakdown cellulose is missing in many vertebrates, the nutrient value of its breakdown products as well as the cellular contents are deprived to the host animal. Two morpho-physiological modes of coping with this problem were evolved, namely, the development of a fermentation chamber for the breakdown of cellulose via bacteria set before the small intestine (foregut fermenters, ruminants) or distal to the small intestine (so-called hindgut fermenters or better caecal or caecocolical fermenters; Hume and Warner 1980). The obvious advantage of the former is that the breakdown products can be readily digested and absorbed as they pass into the small intestine which lies in direct sequence to the foregut-fermenting chamber. In order for the latter mode to be effective where the fermentation chamber is aboral to the major site of absorption the animals should have to ingest their own faeces, a process known as coprophagy. A special form of coprophagy observed especially in lagomorphs is caecotrophy, ingestion of specially formed faecal pellets directly from the anus usually nocturnally (Hörnicke and Björnhag 1980). Hereby, the nutrients broken down in the large intestine and now held within the pellets are exposed to the small intestine "a second time around" and can be digested and absorbed. Another alternative would be actual absorption in the large intestine itself. Although the small intestine is the major site of absorption in all animals regardless of dietary type some animals indeed do depend largely on absorption in

their large intestines; rabbits account for up to 30% of their energy needs via this route (Parker 1976); in sheep between 4.2% and 26% of digestible energy is accountable by digestion in the large intestine (Ulyatt et al. 1975). Also in pigs, 9.6% to 11.6% of energy requirements depending on carbohydrate diet results from volatile fatty acid production and absorption in the large intestine (Imoto and Namioka 1978). Thus, both hindgut fermenters as well as ruminant forms and intermediate feeders all rely on the fermentation function of their caecum and proximal colon.

Both ruminants and hindgut fermenters use a very similar approach to utilize plant cell walls and cellular content not available to the animals' own hydrolytic enzymes. In both fermentation systems the main end products of ATP-yielding catabolism are volatile fatty acids and microbial biomass (Demeyer and de Graeve 1991), the slight difference being the prominence of methanogenesis in ruminants and acetogenesis in hindgut fermenters.

The major advantages and disadvantages as well as limitations of the two modes of dietary utilization have been established in various comprehensive surveys (e. g. Janis 1976; Hofmann 1989, 1991), size being one limitation (size range for ruminants being between 5 to 1 600 kg) and diet content another (high fibre content can only be tolerated by the ruminant to a certain limit). Here, caecal fermentation becomes advantageous when dealing with high fibre content food, provided intake is not limited (Janis 1976). The larger the herbivore the more fibrous the diet can be. The larger animals have lower energy requirements and thus can tolerate more fibre in their diets. Recent small-sized herbivores are almost all hindgut fermenters (hydraces, rodents, lagomorphs) but usually have developed special dietary adaptations such as eating their own faeces (Hörnicke and Björnhag 1980).

In faunivores (dog and cat), the primary functional role of the large intestine is the aboral transport of undigested nutrient and the absorption of water and electrolytes. The latter function is also a prominent function in all mammals (Höller et al. 1988; Leng 1978; Vernay 1986; Olszewski and Buraczeski 1978).

Through specialization in some species of their selection of nutrient the large intestine has increased in size and differentiation (rabbit, horse). The large intestine has gained an important role in the total digestive process of these animals. In other animals the large intestine has a lesser importance, as in faunivores and ruminants (Drochner and Meyer 1991), at least during normal species-specific nutrition. Accordingly, the percent of total digestibility located in the large intestine for organic substances is lowest for dog and ruminants (both 8%) and highest for horse (25%), and intermediate for pig (17%) (Drochner and Meyer 1991).

The amount of postileal digestion of organic matter depends not only on the species but also the type of food. By feeding pigs and dogs foodstuffs of low digestibility, the postileal digestion increased to 50% and 24%, respecitvely (Kim et al. 1978; Drochner and Meyer 1991).

Other nutrient and physiological similarities of faunivores and ruminants are their crude fibre fermentation (carnivores 7%, ruminants 16%) compared to pigs (17% to 43%) and horses (32%–52%). Degradation of nitrogenous compounds in the large intestine varies from 20% in ruminants to 50% in horses. Net absorption of N/kg body mass$^{0.75}$/day equals 0.1 mg in ruminants and carnivores, and 0.16 mg in pigs, 0.2 mg in horses (Drochner and Meyer 1991; Olszweski and Buraczewski 1978; Niiyama et al. 1979). Thus, microbial digestion in the large intestine in all species serves additional energy supply. Although of lesser differentiation than most large intestines of hindgut fermenters, the caecum of most ruminants is larger and more voluminous than expected (Hofmann 1991). Perhaps the answer to this can be found in the above-mentioned physiological fact that the large intestine of ruminants plays a role in digesting products that have escaped digestion in the forestomach and absorption in the small intestine. This is especially important when overall digestibility decreases.

The present results of a loose grouping of faunivores with ruminants are in compliance with the above-mentioned physiological data. Indeed the present morphometric data simply reflect a predominance of the structural-functional parameters in the large intestine of the hingut nonruminant fermenter compared to the ruminants whose fermentation occurs further orally and faunivores whose selective proteinaceous diets exludes the necessity of a well-developed hindgut fermentative function. This does not, however, exclude the possibility of fermentation taking place in such animals with a greater structural-functional emphasis in the small intestines, like dog, cat, and human. The morphometric parameters for the latter species are such that they also group with faunivores (Snipes 1996). The human large intestine resembles structurally the large intestine of a hindgut fermenter (taeniae, haustra, semilunar folds) as well as possesses resident bacteria and displays production of volatile fatty acids (Bustos Fernández 1983). However, in the case of humans, the small intestine has undergone an enormous structural differentiation, especially in its surface enlargement due to the presence of the plicae circulares (Snipes 1996, 1997). This emphasis in favour of the small intestine which is reflected in the morphometric parameters obscurs the purely structural aspects of the large intestine resembling hindgut fermenting forms. This emphasizes the importance of coordinating morphometrical studies with morphological observation.

Thus, although structurally very different, the large intestines of ruminants and faunivores display morphometric parameters that allow them to be classified together. These data expressed in the form of coefficients and ratios reflect solely the proportion and the importance of small intestine in the carnivore and ruminant, and the relative lesser importance of the large intestine in the utilization of their dietary regime. This is the foundation of the similarity and reason for being able to be classified together. The nomenclature for the coefficients adopted from Chivers and colleagues (Chivers and Hladik 1980) is perhaps now misleading (i. e. faunivore now together with ruminant herbivores; omnivores now called intermediate feeders; and herbivores actually meaning only nonruminant herbivores). In their studies ruminants were not included. For the first time then ruminants have been considered under such a categorisation. The terms coefficient of digestion and fermentation express physiological processes, although being determined by morphometrically measurable parameters. Perhaps the latter would more appropriately be termed Coefficient of Relative Volume as practised in the present study (Snipes and Kriete 1991), the former Coefficient of Surface Area. Categorisation is merely an attempt to bring some order into a mass of measurements. It must not be seen as a strigent restrictive grouping but rather as a continuum between two extremes for better visualisation of comparative aspects.

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Zusammenfassung

Quantitative Untersuchung an Därmen von acht verschiedenen Haustierarten

Acht verschiedene Haustierarten (Hund, Katze, Pferd, Schwein, Kuh, Ziege, Schaf und Kaninchen), wurden mit quantitativen morphometrischen Methoden untersucht um verschiedene funktionelle Parameter des Darmes zu erläutern. Zusätzlich zu Länge und Volumen, wurden die Grundfläche des gesamten Darmes gemessen. Histologische Schnitte von scheibenförmigen Proben, die aus vorbestimmten

Bereichen des Darmes gestanzt wurden, dienten zur Bestimmung eines Faktors der Zunahme der Darmoberfläche, die durch Falten, Zotten oder Krypten hervorgerufen sind. Aus den morphometrisch gewonnenen Daten wurde der sogenannte Koeffizient der Verdaulichkeit bzw. der Koeffizient der Fermentation bestimmt. Das Verhältnis Fläche zu Volumen als funktionell wichtige Parameter wurde ebenfalls bestimmt. Werte für Ruminantia fallen in die gleiche Kategorie wie für Faunivoren. Kaninchen und Pferd zeigen Werte, die für Herbivoren charakteristisch sind. Alle anderen untersuchten Tierarten gelten als Faunivoren oder Ruminantia. Das Verhältnis Fläche zu Volumen zeigt die Tendenz, daß kleinere Tiere höhere Werte besitzen (Kaninchen, Katze, Hund).

References

Baddley, A. J.; Gundersen H. J. G.; Cruz-Orivet, L. M. (1986): Estimation of surface area from vertical sections. J. Microscopy **142**, 259–276.

Bustos-Fernández, L. (1983) Colon. Structure and Function. New York London: Planum Med Book Co.

Chivers, D. J.; Hladik, C. M. (1980): Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. J. Morphol. **166**, 337–386.

Chivers, D. J.; Hladik, C. M. (1984): Diet and gut morphology. In: Food acquisition and processing in primates. Ed. by D. J. Chivers, B. A. Wood and A. Bilsborough. New York: Plenum Press. Pp. 213–230.

Custor, J. (1873): Über die relative Grösse des Darmkanales und der hauptsächlichsten Körpersysteme beim Menschen und bei Wirbelthieren. Arch. Anat. Phys. **1873**, 478–504.

Demeyer, D. I.; de Graeve, K. (1991): Differences in stoichiometry between rumen and hindgut fermentation. In: Physiology of the Hindgut. Ed. by M. Kirchgessner. Advances in Animals Physiology and Animal Nutrition. Suppl. to J. Anim. Nutr. **22**, 50–61.

Drochner, W.; Meyer, H. (1991): Verdauung organischer Substanzen im Dickdarm verschiedener Haustierarten. In: Physiology of the Hindgut. Ed. by M. Kirchgessner. Advances in Animals Physiology and Animal Nutrition. Suppl. to J. Anim. Nutr. **22**, 18–40.

Ellenberger-Baum, (1943): Handbuch der vergleichenden Anatomie der Haustiere. 18. Auflage. Heidelberg: Springer Verlag. Pp. 400–401.

Fenwick, B. W.; Kruckenberg, S. (1987): Comparison of methods used to collect canine intestinal tissues for histologic examination. Am. J. Vet. Res. **48**, 1276–1281.

Flindt, R. (1985): Biologie in Zahlen. Eine Datensammlung in Tabellen mit über 9 000 Einzelwerten. Ernährung, Verdauung. Stuttgart: Gustav Fischer Verlag.

Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart: Gustav Fischer Verlag.

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

Hofmann, R. R. (1991): The comparative morphology and the functional adaptive differentiation of the large intestine of the domestic mammals. In: Digestive Physiology of the Hindgut. Ed. by M. Kirchgessner. Advances in Animals Physiology and Animal Nutrition. Suppl. to J. Anim. Nutr. **22**, 7–17.

Höller, H.; Figge, A.; Richter, J.; Breves, G. (1989): Nettoresorption von Calcium und von anorganischem Phosphat aus dem perfundierten Colon und Rectum von Schafen. J. Anim. Physiol. Nutr. **59**, 9–15.

Hörnicke, H.; Björnhag, G. (1980): Coprophagy and related strategies for digesta utilization. In: Digestive Physiology and Metabolism in Ruminants. Ed. by Y. Ruckebusch and P. Thivens. Lancaster: MTP Press.

Hume, I.; Warner, C. I. (1980): Evolution of microbial digestion in mammals. In: Digestive Physiology and Metabolism in Ruminants. Ed. by Y. Ruckebusch and P. Thivens. Lancaster: MTP Press.

Imoto, S.; Namioka, S. (1978): Volatile fatty acid production in the pig large intestine. J. Anim. Sci. **47**, 467–478.

Janis, C. (1976): The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution **30**, 757–774.

Karasov, W. H.; Diamond, J. M. (1985): Digestive adaptations for fueling the cost of enothermy. Science **228**, 202–204.

Kim, K.-I.; Benevenga, N. J.; Grummer, R. H. (1978): Lactase activity and volatile fatty acid production in the caecum and colon of pigs fed a corn-soy or 40% whey diet. J. Anim. Sci. **46**, 1648–1657.

Leng, E. (1978): Absorption of inorganic ions and volatile fatty acids in the rabbit caecum. Brit. J. Nutr. **40**, 509–519.

Neumayer, H. (1900): Über Capacität des Verdauungscanales. Sber. Jes. Morph. Physiol. München.

Niiyama, M.; Duguchi, E.; Kagota, K.; Namioka, S. (1979): Appearance of 15N-labeled intestinal microbial amino acids in the venous blood of the pig colon. Am. J. Vet. Res. **40**, 716–718.

Olszewski, A.; Buraczewski, S. (1978): Absorption of amino acids in isolated pig caecum in situ. Acta Physiol. Pol. **29**, 167–176.

Parker, D. S. (1976): The measurement of production rates of volatile fatty acids in the caecum of the conscious rabbit. Br. J. Nutr. **36**, 61–70.

Sibly, R. (1981): Strategies of digestion and defecation. In: Physiological Ecology. Ed. by C. R. Townsend and P. Callow. Oxford: Blackwell Scientific Publ.

Slijper, E. J. (1946): Die physiologische Anatomie der Verdauungsorgane bei den Vertebraten. In: Tabulae Biologicae. Ed. by V. J. Koningsberger, E. J. Slijper, and H. J. Vonk. Amsterdam: W Junk.

Snipes, R. L. (1991): Morphology of the mammalian cecum and colon. Microscopic and morphometric considerations. In: Hindgut '91. Ed. by T. Sakata and R. L. Snipes. Tokyo: Senshu University Press. Pp. 1–27.

Snipes, R. L. (1994): Morphometric methods for determining surface enlargement at the microscopic level in the large intestine and their application. In: The Digestive System in Mammals. Ed. by D. Chivers and P. Langer. Cambridge: Cambridge University Press. Pp. 234–263.

Snipes, R. L. (1996): Morphometry of the mammalian intestinal system. A methodological concept to incorporate the functionally important structural parameters of intestinal absorptive surfaces. Habilitationsschrift. Fachbereich Humanmedizin der Justus-Liebig-Universität Giessen.

Snipes, R. L. (1997): Intestinal Absorptive Surface in Mammals of Different Sizes. Adv. Anat. Embryol. Cell. Biol. Vol. 138 Heidelberg: Springer Verlag Pp. 1–88.

Snipes, R. L.; Kriete, A. (1991): Quantitative investigation of the area and volume in different compartments of the intestine of 18 mammalian species. Z. Säugetierkunde **56**, 225–244.

Ulyatt, M. J.; Dellow, D. W.; Reid, C. S. W.; Bauchop, T. (1975): Structure and function of the large intestine of ruminants. In: Digestion and Metabolism in Ruminant. Armidale: Univ. of New England Publish Unit. Pp. 119–133.

Vernay, M. (1986): Colonic absorption of inorganic ions and volatile fatty acids in the rabbit. Comp. Biochem. Physiol. **83 A**, 775–784.

Young Owl, M. (1994): A direct method for measurement of gross surface area of mammalian gastrointestinal tracts. In: The Digestive System in Mammals. Ed. by D. Chivers and P. Langer. Cambridge: Cambridge University Press. Pp. 219–233.

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