



Phylogenetic constraints on digesta separation: Variation in fluid throughput in the digestive tract in mammalian herbivores

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ABSTRACT

The relevance of the mean retention time (MRT) of particles through the gastrointestinal tract (GIT) is well understood and $MRT_{particleGIT}$ is an important parameter in digestion models. Solute markers have been used to estimate $MRT_{soluteGIT}$ (or 'fluid passage') in animals, but the relevance of this measure is less evident and is usually sought in its relation to $MRT_{particleGIT}$. The ratio between the two measures indicates the degree of 'digesta washing', with little washing occurring at ratios of 1, aboral washing at ratios >1 (where the solute marker travels faster than the particle marker), and oral (retrograde) washing at ratios <1 (where the solute marker travels slower than the particle marker). We analysed digesta washing in a dataset of 98 mammalian species including man of different digestion types (caecum, colon and nonruminant foregut fermenters, and ruminants), controlling for phylogeny; a subset of 72 species allowed testing for the influence of food intake level. The results indicate that $MRT_{soluteGIT}$ and the degree of digesta washing are related to digestion type, whereas variation in $MRT_{particleGIT}$ is influenced mainly by effects of body mass and food intake. Thus, fluid throughput and digesta washing emerge as important correlates of digestive anatomy. Most importantly, primates appear constrained to little digesta washing compared to non-primate mammalian herbivores, regardless of their digestion type. These results may help explain the absence of primates from certain herbivore niches and represent a drastic example of a physiologic limitation in a phylogenetic group. More experimental research is required to illuminate relative benefits and costs of digesta washing.

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1. Introduction

Digestion is a time-dependent process (Stevens and Hume, 1995; Karasov and Martínez del Río, 2007); hence the time that ingested food takes to transit the digestive tract is an important factor for digestive efficiency. At a given level of food intake, the more time is

available for digestion, the more complete digestion can be. Therefore, the digesta mean retention time (MRT)¹ is a parameter that is considered crucial in digestive physiology, and that has been measured in vast numbers of digestive studies (Stevens and Hume, 1998; Clauss et al., 2007a). Evaluation of MRT is particularly relevant in herbivorous species (Stevens and Hume, 1998) because the rate of allo-enzymatic digestion of plant fibre is generally slower than that of the auto-enzymatic digestion of other substrates. MRT is usually assessed by administering markers and measuring their appearance at

Abbreviations: BM, body mass; DMI, dry matter intake (also: absolute dry matter intake); rDMI, relative dry matter intake (expressed per unit metabolic body weight); GIT, gastrointestinal tract; GLM, general linear model; MRT, mean retention time; $MRT_{particleGIT}$, mean retention time of a particle marker in the gastrointestinal tract; $MRT_{soluteGIT}$, mean retention time of a solute marker in the gastrointestinal tract; PGLS, phylogenetic generalized least-squares; SF, selectivity factor, the ratio of $MRT_{particleGIT}/MRT_{soluteGIT}$.

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¹ The terminology associated with measuring the time that digesta is retained in (or in other words: passes through) the gastrointestinal tract varies. "Mean retention time (MRT [in hours or days])" is an integrated measure that considers the complete excretion pattern of a digesta fraction; it is often also called "passage time". Unfortunately, the term "passage rate" has often been used for the same measure, although a 'rate' has the unit [fraction per unit time] and hence cannot be equated with a data given in [unit time]. "Transit time" is the time of first marker appearance in the faeces.

a given point along the gastrointestinal tract (GIT) e.g. the faeces, or the termination of a particular gut segment (Warner, 1981b). Whether a marker used is representative of the whole digesta, or of a relevant fraction of it, is an important consideration in such studies. Commonly, at least two digesta phases are considered separately – the particulate or solid phase, and the fluid or solute phase (Warner, 1981b).

The range of MRTs that a particular species can achieve is a major physiologic characteristic of this species (Hume, 2005; Clauss et al., 2007b). In terms of crude mechanics, any MRT is a function of the capacity (or: volume) of the GIT and the food intake level of the animal (Hume, 2005; Clauss et al., 2007a). In terms of engineering science, MRT is a function of the residence time distribution of a processing system (like the GIT) and is governed by Danckwert's law which relates the residence time distribution to the volume of the system (the GIT capacity) and the volumetric flow rate (digesta throughput) through it (Gottschalk et al., 2006). Animals evolve GIT morphologies and metabolic levels in parallel to their dietary niche (McNab, 2002; Hume, 2005); food particle size reduction (via chewing or gizzard grinding) is an important comparative covariate here because smaller particles may require less time for digestion (Clauss et al., 2009b) but exert greater frictional resistance per unit solid volume on the passage of the fluid phase (Lentle et al., 2009). GIT peristalsis – the characteristic GIT motility patterns – will also play another important role but as far as we are aware this has so far not been investigated and incorporated into comparative evaluations in a broad interspecific approach in mammals (Stevens and Hume, 1995).

Conceptually, the MRT of the particulate phase is easy to understand as it represents the fraction of the digesta that is actually 'subjected to digestion' (Warner, 1981b). The MRT of the particulate phase correlates with digestive efficiency in many studies (Foose, 1982; Udén et al., 1982). A marker moving with the particulate phase moves with that fraction of the food that is exposed to digestive action but remains undigested. Digestion models for animals (Demment and Van Soest, 1985; Illius and Gordon, 1992), effects of diet changes (Müller-Lissner, 1988), pharmacological interventions (Stephen et al., 1987), and even disease susceptibility in humans (Lewis and Heaton, 1999; Heaton, 2000) are commonly related to the MRT of a particulate marker.

In contrast, there is no general concept for the use of 'fluid' MRT, regardless of the widespread use of such measurements (Warner, 1981b). Measurements by use of a 'fluid' marker are traditionally interpreted as 'fluid retention' or 'fluid passage' (e.g. Pickard and Stevens, 1972). But a 'fluid' marker recovered in the faeces (or at another endpoint) does *not* represent the fluid/water *ingested* by the organism that is *not absorbed* (Cork et al., 1999; Clauss et al., 2010b). Fluid is constantly excreted and absorbed in the course of the digestive process throughout the GIT (Stevens and Hume, 1995), and any fluid in the faeces represents the sum of the indeterminate fractions of remaining dietary and secretory fluids. A 'fluid marker' is by definition a non-absorbable, yet digesta-fluid soluble marker. Therefore, it has been suggested that the term 'fluid MRT' should be abandoned and replaced by 'solute MRT' (Cork et al., 1999; Franz et al., 2010). However, because the absorption of most solubilised nutrients is generally by an order of magnitude less time-constrained than the digestion of nutrients in the solid phase, the term 'solute MRT' will have no relevance with regard to limiting the time available for digestion. What, then, is the relevance of fluid/solute MRT measurements?

We hypothesise that functional relevance of fluid MRT data will be revealed by comparison with results from simultaneous measurement of particle MRT. Such comparisons have been conducted previously in human subjects, but were limited to considerations of whether a solute marker can be used to adequately describe digesta movements (Heller et al., 1980; Wruck et al., 1983). Possibly, differences between the fluid and particulate phase MRT reflect the

pumping and processing of digesta within the GIT. In situations where the contained particles are in sufficient concentration to interact and form a 'mat' or 'plug', peristaltic constriction will cause local squeezing-out of the fluid phase from the spaces between the particulate elements of the plug, and more fluid to be reabsorbed into the digesta plug during subsequent relaxation (Lentle et al., 2006). This fluid flow into and out of the digesta plug represents a process of effective 'digesta washing'. It promotes mixing within the interparticulate spaces and hence both, the absorption of soluble nutrients from the digesta at the intestinal mucosa and the permeation of digesta with enzymatic secretions (Lentle et al., 2006). If fluid expressed from the plug moves in a consistent oral or aboral direction, then the more this process is continued, the larger the difference between the fluid and particle MRT may become (Lentle and Janssen, 2008). Notably, fine particles (such as bacteria) may also travel with these fluid movements (Lentle et al., 2009). It is important to note that an increase in the volume of fluid transiting through the plug of entangled particles will increase the degree of washing, but that the dilution of the solid volume fraction of the digesta plug by turbulent admixture with fluid can also lead to a dispersion of the particulate elements and hence disintegration of the plug.

It has been shown in previous work that characteristic differences exist in the pattern of particle and solute retention within various animal groups such as caecum fermenters (including lagomorphs, rodents, and some marsupials) (Hume and Sakaguchi, 1991; Cork et al., 1999; Franz et al., 2010), colon fermenters (including equines, tapirs, rhinoceroses and elephants) (Clauss et al., 2010b; Steuer et al., 2010), nonruminant foregut fermenters² (such as kangaroos, hippopotamus, peccaries, colobine monkeys) (Schwarm et al., 2009b), and ruminants (Hummel et al., 2005; Clauss et al., 2006b). Yet, although a significant body of data on solute retention is available for a wide range of species (Stevens and Hume, 1995), few statistical comparisons have been conducted that consider the effect of body mass (BM), food intake, gut morphology or phylogenetic relationships. Such evaluations have been reported repeatedly for particle retention (Owen-Smith, 1988; Illius and Gordon, 1992; Cork et al., 1999; White and Seymour, 2005; Clauss et al., 2007a). To our knowledge, however, Robbins (1993) presented the only allometric analysis of solute retention data so far, indicating that $MRT_{soluteGIT}$ scaled to $BM^{0.28}$ in foregut and $BM^{0.18}$ in hindgut fermenters.

In this study, we collated data on solute and particle retention in 98 mammal species, investigating not only the scaling with body mass, but also differences between the four major herbivore digestion types – caecum fermenters, colon fermenters, nonruminant foregut fermenters, and ruminants. Additionally, because a preliminary analysis had suggested a fundamental difference in retention patterns between primates and other mammals, differences between these two groups were also evaluated. All evaluations were performed with conventional methods as well as with a method that accounts for the non-independence of data originating from species that are related to each other to various degrees via common ancestors in evolutionary time.

2. Methods

We collated data from the literature from studies that indicated body mass (BM), and the mean retention time (MRT; as given in the

² Note that the term "foregut fermenter" does not necessarily exclude additional fermentation in the hindgut, as occurs for example in colobine monkeys Caton, J., 1999. Digestive strategy of the Asian colobine genus *Trachypithecus*. *Primates* 40, 311–325. or ruminants Van Soest, P.J., 1994. Nutritional ecology of the ruminant. Cornell University Press, Ithaca.

publications) of both particles and solutes. Only publications that used chromium- or cerium-mordanted fibre (Cr/Ce-f; Udén et al., 1980) or phenanthroline-ruthenium chloride (RuP; Tan et al., 1971) as markers for measuring MRT_{particle} were selected. Similarly, only publications that used cobalt-EDTA or chromium-EDTA (Udén et al., 1980) as markers for measuring MRT_{solute} were used. The only exception was man (*Homo sapiens*), for whom a study with polyethylene glycol (PEG) as solute marker was accepted (Wrick et al., 1983). Only data for adult specimens were used. The resulting dataset included 98 mammal species. This included a set of 16 primate species for which data were exclusively available from the unpublished thesis by Judith Caton (1997). A second dataset was prepared from this first dataset for those sources in which the food intake, measured as dry matter intake (DMI), was additionally available. This dataset comprised 72 species. Means were calculated for all data points available from each source, and then means of sources were calculated, if more than one source was available for a species. The full datasets including all references are given in Table 1.

Apart from $MRT_{\text{particleGIT}}$ and $MRT_{\text{soluteGIT}}$, the ratio of the two measures was calculated as $MRT_{\text{particleGIT}}/MRT_{\text{soluteGIT}}$; this ratio is referred to as the 'selectivity factor' (SF; Lechner-Doll et al., 1990). A preliminary analysis of the 72 species for which food intake data were available showed that in the whole dataset, *absolute* DMI (in kg d^{-1}) scaled to 0.044 (95%CI 0.039–0.049) $\text{BM}^{0.77}$ (95%CI 0.74–0.80). Therefore, the *relative* DMI ($r\text{DMI}$, $\text{g kg}^{-0.75} \text{d}^{-1}$) was calculated for each species using 0.75 as exponent and used in the comparative analyses.

In order to account for ancestry-based correlations in the datasets (i.e., finding a significant result simply because similar species are closely related) (Felsenstein, 1985; Pagel, 1999), the data were controlled for phylogenetic influences using the "Phylogenetic Generalized Least-Squares" method (PGLS; Martins and Hansen, 1997; Rohlf, 2001). This procedure estimates a covariance matrix of the species due to their ancestral roots and includes these interrelationships in a generalised least squares algorithm to determine the model parameters. The phylogenetic trees for the two datasets were derived by pruning the mammal supertree from Bininda-Emonds et al. (2007) for those species not represented in the datasets, using Mesquite (Maddison and Maddison, 2006). Because the resulting trees were not based on our own calculations of branch lengths using consistently the same characters, we used trees without branch lengths. The resulting phylogenetic tree is shown in Fig. 1. PGLS methods supported the definition of $r\text{DMI}$ using an exponent of 0.75, because the respective regression equation scaled DMI (in kg d^{-1}) to 0.046 (95%CI 0.036–0.058) $\text{BM}^{0.75}$ (95%CI 0.71–0.79).

To achieve normality, data on BM were log-transformed. Allometric regressions were performed as linear regressions on log-transformed data. Statistical analyses were performed without and with accounting for phylogeny, using General Linear Models (GLMs) with the passage parameters ($MRT_{\text{particleGIT}}$, $MRT_{\text{soluteGIT}}$, SF) as the respective dependent variables, and with BM, $r\text{DMI}$ and $MRT_{\text{particleGIT}}$ as the independent variables in different models. As cofactors, being a primate (yes/no), and the digestion type (caecum fermenter, colon fermenter, nonruminant foregut fermenter, ruminant) were used as categorical variables. First, conventional GLMs were performed with all cofactors and their interaction (because a phylogenetic information – belonging to the primate order or not – was already included as a cofactor, it is not reasonable to perform this model using PGLS). Because the interaction between being a primate and digestion type was significant in most cases, indicating a difference in the effects of the different digestion types between primates and nonprimates, subsequent conventional and PGLS–GLMs were performed separately within nonprimates and primates, respectively. The statistical calculations were performed with PASW 18.0 (SPSS Inc., Chicago, IL) and COMPARE 4.6 programme (Martins, 2004). The significance level was set to $\alpha = 0.05$. 95% confidence intervals were calculated for coefficients in allometric regressions.

3. Results

In the overall dataset, $MRT_{\text{particleGIT}}[\text{h}]$ scaled to 23.0 (95%CI 20.1–26.2) $\text{BM}[\text{kg}]^{0.15}$ (95%CI 0.11–0.19) ($R^2 = 0.41$) (Fig. 2a,b); PGLS resulted in a similar relationship of 25.1 (95%CI 20.0–31.6) $\text{BM}[\text{kg}]^{0.13}$ (95%CI 0.07–0.19) ($R^2 = 0.21$). $MRT_{\text{soluteGIT}}[\text{h}]$ showed a lower allometric scaling with an even weaker fit, scaling to 23.9 (95%CI 20.6–27.7) $\text{BM}[\text{kg}]^{0.08}$ (95%CI 0.04–0.12) ($R^2 = 0.21$) (Fig. 2c,d); PGLS resulted in a similar relationship of 24.5 (95%CI 18.6–32.4) $\text{BM}[\text{kg}]^{0.07}$ (95%CI 0.01–0.13) ($R^2 = 0.06$). These results support previous findings in a similar dataset that the scaling relationship between retention parameters and body mass is not particularly distinct (Clauss et al., 2007a).

In the conventional GLMs that tested for the influence of BM, being a primate, and digestion type (and food intake level $r\text{DMI}$), a systematic effect of being a primate as well as a difference in the effect of digestion type between primates and nonprimates (i.e. a significant interaction term) was evident (Table 2). The only exception was when both BM and $r\text{DMI}$ were included in a GLM to test for the effect on $MRT_{\text{particleGIT}}$, where neither being a primate, nor the digestion type, nor the interaction between the two was significant (Table 2b). This indicates that $MRT_{\text{particleGIT}}$ depends mainly on body mass (Fig. 2a,b) and food intake level (Fig. 3a,b), but not so much on digestion type or being a primate within herbivores. Note that if food intake level was not included in the analysis in the larger dataset, the primate*(digestion type) interaction did have a significant effect on $MRT_{\text{particleGIT}}$ (Table 2a). This underlines the importance of including food intake level in investigations of retention parameters. When repeating the GLM with BM and $r\text{DMI}$ as covariates for the whole dataset ($n = 72$ species) using PGLS without cofactors or the interaction, both BM ($t = 7.88$, $p < 0.001$) and $r\text{DMI}$ ($t = 4.10$, $p < 0.001$) were highly significant.

The influence of the primate*(digestion type) interaction on $MRT_{\text{soluteGIT}}$ or SF was significant whether or not food intake level was taken into account (Table 2a,b). These results suggest that digestion type is strongly related to $MRT_{\text{soluteGIT}}$ and SF, with differences between primates and non-primates. Fig. 4a shows how the relationship between $MRT_{\text{soluteGIT}}$ and $MRT_{\text{particleGIT}}$ differs between the digestion types; Fig. 4b indicates that no such difference between the digestion types is evident in primates. The influence of $MRT_{\text{particleGIT}}$ on $MRT_{\text{soluteGIT}}$ was, correspondingly, significantly modified by the primate*(digestion type) interaction (Table 2c). Across all species, SF increased with increasing $MRT_{\text{particleGIT}}$ (Table 2c), but again this relationship was modified by the primate*(digestion type) interaction (Table 2c), with evident differences between primates and non-primates (Fig. 4c,d).

When effects were analysed separately for nonprimates and primates, results of conventional GLMs were generally similar to those of PGLS–GLMs (Tables 3 and 4). However, there were several exceptions amongst the nonprimates. BM ceased to be a significant influence on the SF after phylogenetic correction (Table 3a,b), indicating that its effect in the conventional GLM was due to an uneven distribution of the SF level between different-sized phylogenetic groups, such as generally high SF values in the generally large ruminants (Fig. 2e). The influence of the digestion type on $MRT_{\text{soluteGIT}}$ became significant after phylogenetic correction (Table 3a); this finding represents one of the rarer cases where a nonsignificant finding (here, $p = 0.050$) becomes significant after phylogenetic correction (cf. Fig. 1 on p. 147 in Baker, 2002), because the same effect is observed within individual phylogenetic groups but not so in the whole dataset (Fig. 3c). The influence of the intake level ($r\text{DMI}$) on $MRT_{\text{soluteGIT}}$, close to significance in the conventional GLM ($p = 0.051$, Table 3b), was clearly not significant in the PGLS–GLM ($p = 0.544$), indicating that there is no systematic effect of $r\text{DMI}$ within phylogenetic groups, but that these groups have different levels of $MRT_{\text{soluteGIT}}$ and are distributed unevenly across the $r\text{DMI}$ range.

Table 1
 Datasets used in this study. Species are ordered as in the phylogenetic tree (Fig. 1). GIT denotes digestion type (1 caecum fermenter, 2 colon fermenter, 3 nonruminant foregut fermenter, 4 ruminant); markers include chromium-mordanted fibre (1), cerium-mordanted fibre (2), phenanthroline-ruthenium chloride (3), cobalt-EDTA (4), chromium-EDTA (5) or polyethylene glycol (6); BM body mass, MRT mean retention time, SF selectivity factor, DMI dry matter intake.

Species	GIT	Total dataset (n=98)				Reduced dataset (n=72)					Markers	Source
		BM (kg)	MRT _{particle} GIT (h)	MRT _{solute} GIT (h)	SF	BM (kg)	DMI (kg d ⁻¹)	MRT _{particle} GIT (h)	MRT _{solute} GIT (h)	SF		
<i>Rattus norvegicus</i>	1	0.30	13.1	12.1	1.08	0.30	0.024	13.1	12.1	1.08	14	Sakaguchi et al. (1987)
<i>Phyllotis darwini</i>	1	0.08	8.8	9.1	0.97	0.08	0.009	8.8	9.1	0.97	14	Sakaguchi and Ohmura (1992)
<i>Lasiopodomys brandtii</i>	1	0.04	5.5	7.2	0.76	0.04	0.008	5.5	7.2	0.76	14	Pei et al. (2001b)
<i>Microtus townsendii</i>	1	0.05	13.1	14.8	0.89	0.05	0.008	13.1	14.8	0.89	14	Hume et al. (1993)
<i>Meriones unguiculatus</i>	1	0.05	12.8	9.2	1.39	0.05	0.007	12.8	9.2	1.39	14	Pei et al. (2001a)
<i>Octodon degus</i>	1	0.18	15.5	19.4	0.80	0.18	0.010	15.5	19.4	0.80	14	Sakaguchi and Ohmura (1992)
<i>Hydrochaeris hydrochaeris</i>	1	39.2	33.3	39.2	0.85	39.2	0.605	33.3	39.2	0.85	14	Schwarm et al. (2008) pers. observ
<i>Cavia porcellus</i>	1	0.62	20.5	18.8	1.09	0.62	0.039	20.5	18.8	1.09	14	Sakaguchi et al. (1987), Sakaguchi et al. (1992b), Sakaguchi and Nabata (1992), Sakaguchi and Ohmura (1992) and Franz et al. (2010)
<i>Myocastor coypus</i>	1	4.40	45.0	44.2	1.02	4.40	0.094	45.0	44.2	1.02	14	Sakaguchi and Nabata (1992)
<i>Dolichotis patagonum</i>	1	7.40	27.3	26.8	1.02	7.40	0.185	27.3	26.8	1.02	14	Sakaguchi et al. (1992b)
<i>Lagostomus maximus</i>	1	3.46	27.9	28.7	0.97	3.46	0.125	27.9	28.7	0.97	14	Besselmann (2005)
<i>Marmota caligata</i>	1	2.31	28.9	24.8	1.17	2.31	0.112	28.9	24.8	1.17	14	Hume et al. (1993)
<i>Spermophilus columbianus</i>	1	0.66	22.1	22.5	0.98	0.66	0.026	22.1	22.5	0.98	14	Hume et al. (1993)
<i>Tamias amoenus</i>	1	0.06	14.1	12.7	1.11	0.06	0.008	14.1	12.7	1.11	14	Hume et al. (1993)
<i>Oryctolagus cuniculus</i>	1	1.66	15.9	65.5	0.24	1.66	0.072	15.9	65.5	0.24	14	Sakaguchi et al. (1992a) and Franz et al. (2010)
<i>Cercopithecus neglectus</i>	2	6.30	32.3	28.7	1.12						14	Caton (1997)
<i>Macaca fuscata</i>	2	9.20	22.5	22.7	0.99	9.20	0.251	22.5	22.7	0.99	14	Sakaguchi et al. (1991)
<i>Colobus angolensis</i>	3	7.50	77.0	76.0	1.01	7.50	0.118	77.0	76.0	1.01	14	Schwarm et al. (2009b)
<i>Colobus guereza</i>	3	11.6	54.6	55.3	0.99	10.8	0.154	53.1	48.7	1.09	14	Caton (1997) and Edwards and Ullrey (1999b)
<i>Colobus polykomos</i>	3	12.0	46.0	52.0	0.88	12.0	0.174	46.0	52.0	0.88	14	Schwarm et al. (2009b)
<i>Presbytis thomasi</i>	3	6.00	68.6	61.0	1.12						14	Caton (1997)
<i>Trachypithecus cristatus</i>	3	6.20	54.4	54.0	1.01	5.9	0.089	46.8	44.8	1.04	14	Sakaguchi et al. (1991) and Caton (1997)
<i>Trachypithecus obscurus</i>	3	6.00	62.1	55.4	1.12						14	Caton (1999)
<i>Trachypithecus johnii</i>	3	9.50	42.0	42.0	1.00	9.5	0.157	42.0	42.0	1.00	14	Schwarm et al. (2009b)
<i>Pygathrix nemaeus</i>	3	12.1	33.8	35.5	0.95	12.1	0.429	33.8	35.5	0.95	14	Edwards and Ullrey (1999b)
<i>Gorilla gorilla</i>	2	111	68.9	59.4	1.16	103	1.291	80.6	73.4	1.10	14	Caton (1997) and Remis and Dierenfeld (2004)
<i>Homo sapiens</i>	2	74.8	54.6	51.5	1.06						16	Wrick et al. (1983)
<i>Pan troglodytes</i>	2	47.0	45.6	43.3	1.05	47.0	0.635	42.9	41.4	1.04	14	Milton and Demment (1988)
<i>Pongo pygmaeus</i>	2	70.7	82.1	70.6	1.16						14	Caton et al. (1999)
<i>Hylobates lar</i>	2	5.00	28.6	26.9	1.06						14	Caton (1997)
<i>Hylobates moloch</i>	2	5.00	33.3	30.2	1.10						14	Caton (1997)
<i>Hylobates muelleri</i>	2	5.25	36.1	36.3	1.00						14	Caton (1997)
<i>Hylobates syndactylus</i>	2	10.0	25.4	21.9	1.16						14	Caton (1997)
<i>Hylobates leucogenys</i>	2	5.00	27.8	28.9	0.96						14	Caton (1997)
<i>Alouatta pigra</i>	2	6.15	37.3	32.1	1.16	6.15	0.137	37.3	32.1	1.16	14	Edwards and Ullrey (1999b)
<i>Alouatta seniculus</i>	2	8.03	40.4	55.8	0.72	8.03	0.142	40.4	55.8	0.72	14	Edwards and Ullrey (1999b)
<i>Callithrix pygmaea</i>	1	0.12	18.0	19.7	0.91						14	Caton (1997)
<i>Callithrix jacchus</i>	1	0.37	15.1	16.0	0.94						14	Caton et al. (1996) and Power and Myers (2009)
<i>Leontopithecus rosalia</i>	1	0.64	12.2	14.9	0.82						14	Caton (1997)
<i>Saguinus oedipus</i>	1	0.57	5.4	5.8	0.94						14	Caton (1997)
<i>Saguinus imperator</i>	1	0.54	17.4	21.2	0.82						14	Caton (1997)
<i>Saimiri boliviensis</i>	1	0.88	4.5	7.2	0.62						14	Caton (1997)
<i>Propithecus tattersalli</i>	1	3.24	36.3	32.1	1.13	3.24	0.057	36.3	32.1	1.13	14	Campbell et al. (1999)
<i>Propithecus verreauxi</i>	1	3.58	33.5	32.5	1.03	3.58	0.072	33.5	32.5	1.03	14	Campbell et al. (1999) and Campbell et al. (2004)
<i>Eulemur fulvus</i>	2	2.29	6.3	7.4	0.85	2.27	0.072	7.9	10.4	0.76	14	Caton (1997) and Campbell et al. (2004)
<i>Eulemur mongoz</i>	1	2.00	21.2	19.8	1.07						14	Caton (1997)
<i>Hapalemur griseus</i>	1	1.04	47.5	45.9	1.04	1.04	0.027	47.5	45.9	1.04	14	Campbell et al. (2004)
<i>Lemur catta</i>	1	2.80	23.4	23.0	1.02						14	Caton (1997)
<i>Varecia variegata</i>	2	4.03	6.0	5.8	1.03	4.05	0.132	5.6	5.3	1.05	14	Caton (1997), Edwards and Ullrey (1999a) and Campbell et al. (2004)
<i>Loris tardigradus</i>	1	0.29	43.4	46.7	0.93						14	Caton (1997)

<i>Nycticebus coucang</i>	1	0.40	29.0	36.1	0.80						14	Caton (1997)
<i>Galago moholi</i>	1	0.20	30.1	41.3	0.73						14	Caton et al. (2000)
<i>Addax nasomaculatus</i>	4	87.4	58.5	35.8	1.64	87.4	1.710	58.5	35.8	1.64	14	Hummel et al. (2008)
<i>Ovis ammon</i>	4	44.2	46.6	31.0	1.50	46.3	1.018	48.3	31.6	1.53	1345	Dellow (1982), Dellow and Hume (1982), Udén et al. (1982), Udén and Van Soest (1982), Rutagwenda (1989), Luginbuhl et al. (1990), Cherney et al. (1991), Bartocci et al. (1997), Behrend et al. (2004) and Pearson et al. (2006)
<i>Capra hircus</i>	4	30.4	41.8	31.9	1.31	30.5	0.831	42.6	32.2	1.32	12,345	Udén et al. (1982), Udén and Van Soest (1982), Rutagwenda (1989) and Freudenberger and Hume (1992)
<i>Capra nubiana</i>	4	35.4	39.3	22.4	1.75	35.4	0.989	39.3	22.4	1.75	14	Gross et al. (1996)
<i>Ovibos moschatus</i>	4	276	72.5	41.5	1.75	276	3.850	72.5	41.5	1.75	14	Lechner et al. (2010)
<i>Cephalophus silvicultor</i>	4	65.0	40.5	34.5	1.17						14	Clauss et al. (2011)
<i>Sylvicapra grimmia</i>	4	13.0	27.5	25.0	1.10						14	Clauss et al. (2011)
<i>Cephalophus monticola</i>	4	3.93	29.7	20.4	1.46	3.85	0.147	24.4	14.8	1.65	14	Luginbuhl et al. (1990) and Clauss et al. (2011)
<i>Bos taurus</i>	4	563	66.4	32.4	2.05	585	8.549	66.7	34.3	1.95	14	Udén et al. (1982), Udén and Van Soest (1982), Mathers et al. (1989), Bartocci et al. (1997), Burns et al. (1997), Pearson et al. (2006) and Lechner et al. (2010)
<i>Bos javanicus</i>	4	432	54.2	24.3	2.23	432	4.655	54.2	24.3	2.23	14	Schwarm et al. (2008)
<i>Bubalus bubalis</i>	4	537	56.9	30.8	1.85	537	8.000	56.9	30.8	1.84	14	Mathers et al. (1989) and Bartocci et al. (1997)
<i>Bubalus depressicornis</i>	4	90.0	39.0	25.0	1.56	90.0	1.767	39.0	25.0	1.56	14	Flores-Miyamoto et al. (2005)
<i>Alces alces</i>	4	345	58.7	55.0	1.07	345	4.167	58.7	55.0	1.07	14	Lechner et al. (2010)
<i>Capreolus capreolus</i>	4	22.4	24.7	21.2	1.17	24.7	0.405	27.0	23.9	1.13	1245	Holand (1994) and Behrend et al. (2004)
<i>Rangifer tarandus</i>	4	96.0	48.0	32.0	1.50	96.0	2.700	48.0	32.0	1.50	14	Lechner et al. (2010)
<i>Giraffa camelopardalis</i>	4	763	44.9	37.2	1.21	763	9.344	44.9	37.2	1.21	14	Clauss et al. (1998) and Schaub (2005)
<i>Okapia johnstoni</i>	4	227	46.8	36.4	1.29	227	3.529	46.8	36.4	1.29	14	Hummel et al. (2005)
<i>Hexaprotodon liberiensis</i>	3	229	78.7	29.2	2.70	229	1.816	78.7	29.9	2.63	14	Clauss et al. (2004) and Schwarm et al. (2008)
<i>Hippopotamus amphibius</i>	3	2175	71.4	27.8	2.57	2175	11.600	71.4	27.8	2.57	14	Clauss et al. (2004)
<i>Pecari tajacu</i>	3	20.7	34.1	25.7	1.33	20.7	0.512	34.1	25.7	1.33	14	Schwarm et al. (2009b)
<i>Camelus bactrianus</i>	4	687	85.2	50.1	1.70	687	2.600	85.2	50.1	1.70	14	Cahill and McBride (1995)
<i>Camelus dromedarius</i>	4	225	76.3	38.7	1.97						14	Heller et al. (1986b)
<i>Lama guanicoe</i>	4	135	52.0	36.2	1.44						14	Heller et al. (1986a)
<i>Ceratotherium simum</i>	2	2175	43.8	27.8	1.58	2175	20.781	43.8	27.8	1.58	14	Schwarm et al. (2008) pers. observ, Steuer et al. (2010)
<i>Diceros bicornis</i>	2	1222	38.3	32.5	1.18	1222	15.697	38.3	32.5	1.18	14	Clauss et al. (2005a), Schwarm et al. (2008) pers. observ, Steuer et al. (2010)
<i>Rhinoceros unicornis</i>	2	2125	60.1	41.4	1.45	2125	22.064	60.1	41.4	1.45	14	Clauss et al. (2005b)
<i>Tapirus terrestris</i>	2	192	54.7	42.0	1.30	192	2.244	54.7	42.0	1.30	14	Clauss et al. (2010b)
<i>Tapirus indicus</i>	2	278	53.1	38.9	1.36	278	3.947	53.1	38.9	1.36	14	Clauss et al. (2010b)
<i>Equus asinus</i>	2	202	40.5	37.3	1.09	202	3.443	40.5	37.3	1.08	14	Pearson and Merritt (1991) and Pearson et al. (2001, 2006)
<i>Equus caballus</i>	2	217	30.6	30.9	0.99	217	4.918	30.6	30.9	0.99	134	Orton et al., (1985a,b), Pearson and Merritt (1991) and Pearson et al. (2001, 2006)
<i>Loxodonta africana</i>	2	2680	23.5	22.8	1.03						14	Hackenberger (1987)
<i>Petauroides volans</i>	1	1.05	34.5	50.0	0.69	1.05	0.046	34.5	50.0	0.69	135	Foley and Hume (1987)
<i>Pseudocheirus peregrinus</i>	1	0.62	73.9	136.6	0.54	0.62	0.024	73.9	136.6	0.54	135	Chilcott and Hume (1985) and Sakaguchi and Hume (1990)
<i>Trichosurus vulpecula</i>	1	2.32	51.4	50.5	1.02	2.32	0.054	51.4	50.5	1.02	35	Wellard and Hume (1981), Foley and Hume (1987) and Sakaguchi and Hume (1990)
<i>Aepyprymnus rufescens</i>	3	2.98	36.5	32.3	1.13	2.98	0.078	36.5	32.3	1.13	35	Wallis (1994)
<i>Bettongia penicillata</i>	3	1.07	33.5	27.0	1.24	1.07	0.046	33.5	27.0	1.24	35	Wallis (1994)
<i>Lagorchestes hirsutus</i>	3	1.23	38.0	30.9	1.23	1.23	0.039	38.0	30.9	1.23	14	Bridie et al. (1994)
<i>Macropus eugenii</i>	3	5.65	21.9	13.1	1.67	4.80	0.117	24.8	15.0	1.66	35	Warner (1981a), Dellow (1982) and Dellow and Hume (1982)
<i>Macropus rufus</i>	3	32.0	28.4	14.7	1.93	32.0	0.478	28.4	14.7	1.93	14	Munn and Dawson (2006) and Schwarm et al. (2009b)
<i>Macropus robustus</i>	3	18.2	30.2	19.0	1.59	18.2	0.471	30.2	19.0	1.59	35	Dellow (1982), Dellow and Hume (1982) and Freudenberger and Hume (1992)
<i>Macropus giganteus</i>	3	20.8	30.3	14.4	2.10	20.8	0.540	30.3	14.4	2.10	35	Dellow (1982) and Dellow and Hume (1982)
<i>Thylogale thetis</i>	3	4.05	22.4	11.9	1.88	4.05	0.141	22.4	11.9	1.88	35	Dellow (1982) and Dellow and Hume (1982)
<i>Potorous tridactylus</i>	3	0.96	25.0	24.0	1.04	0.96	0.045	25.0	24.0	1.04	35	Wallis (1994)
<i>Lasiorhinus latifrons</i>	2	26.2	60.5	39.5	1.53	26.2	0.394	60.5	39.5	1.53	34	Barboza (1993)
<i>Vombatus ursinus</i>	2	29.5	68.5	43.0	1.59	29.5	0.433	68.5	43.0	1.59	34	Barboza (1993)
<i>Phascogale carterii</i>	1	5.96	39.0	121.0	0.32	5.96	0.228	39.0	121.0	0.32	15	Krockenberger and Hume (2007)

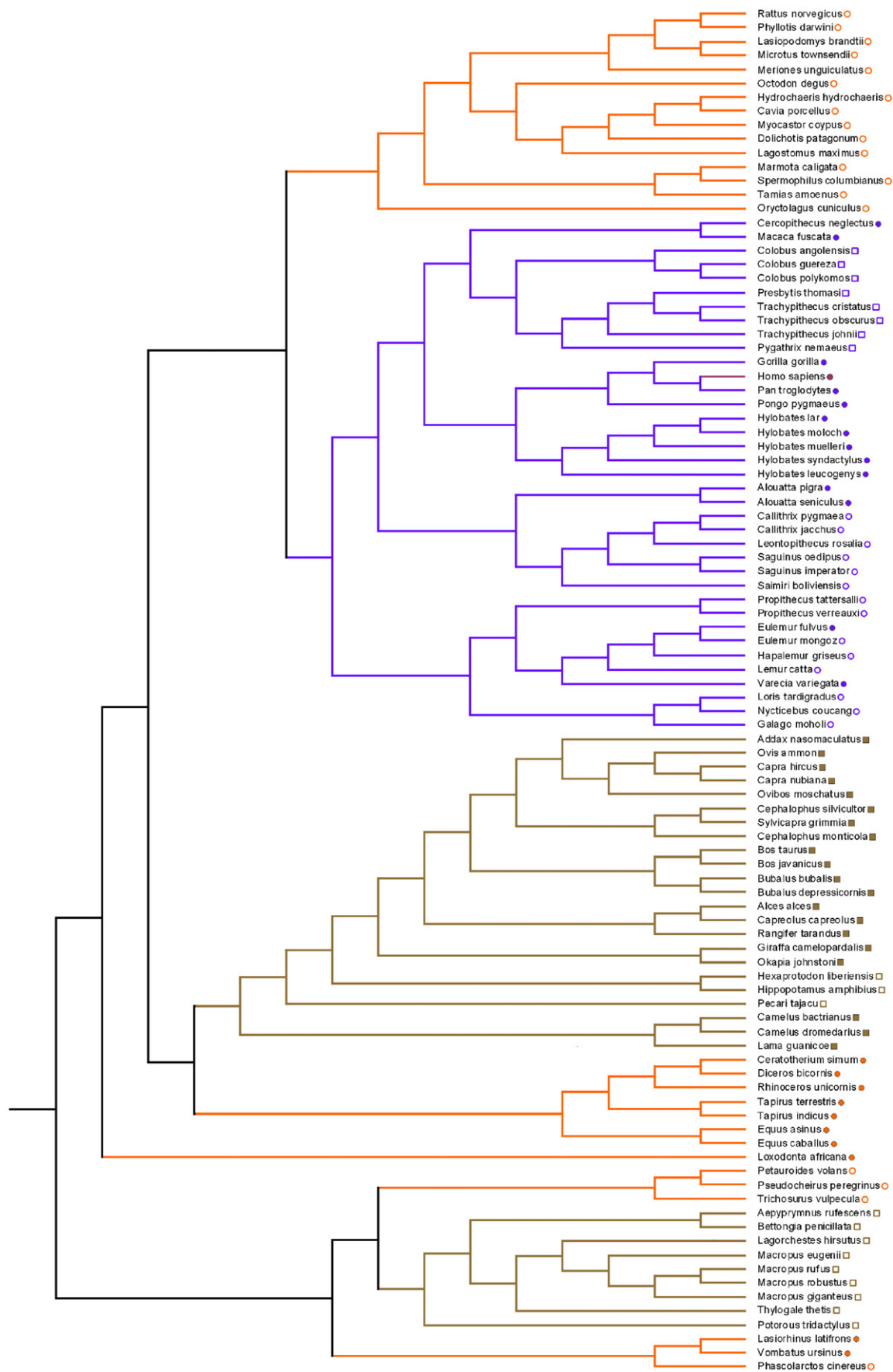


Fig. 1. Phylogenetic tree used in the PGLS analyses (pruned from Bininda-Emonds et al., 2007 with resolved polytomies). Colour codes and symbols correspond to the representation of species in Figs. 2–4.

The main difference between primates and nonprimates was that in nonprimates, the digestion type always had a significant effect on $MRT_{\text{soluteGIT}}$ and the SF (Table 3); in primates, however, SF or the effect of $MRT_{\text{particleGIT}}$ on $MRT_{\text{soluteGIT}}$ was not influenced by digestion type (Table 4). Because the effect of BM on MRT varied between the three primate digestion types (Fig. 2b,d), digestion type did have a significant effect on MRTs when only BM was considered (Table 4a).

4. Discussion

This study indicates differences in the degree of ‘digesta washing’ between mammalian herbivores. Colon fermenters, nonruminant foregut fermenters and ruminants all achieve comparatively high ratios of $MRT_{\text{particleGIT}}$ to $MRT_{\text{soluteGIT}}$ (i.e., high SF). Caecum fermenters have been classified as those with a colonic ‘mucous trap’ (SF ~1; i.e. gut bacteria are separated from the digesta by entrapment in a colonic groove and retrograde transport, without involvement of fluid movements) and a colonic ‘wash-back’ mecha-

nism (SF <1; i.e. gut bacteria are flushed in an oral direction from the colon into the caecum by fluid that is actively secreted in the colon and reabsorbed in the caecum), respectively (Hume and Sakaguchi, 1991; Franz et al., 2010). Because only few animals with a ‘wash-back’ mechanism were available in the literature and could be included in this dataset, the caecum fermenters were not divided into additional categories. ‘Wash-back’ species (koala *Phascolarctos cinereus*, common ringtail possum *Pseudocheirus peregrinus*, rabbit *Oryctolagus cuniculus*) occur in Figs. 2c, 3c, 4a and c as evident outliers of the caecum fermenter pattern.

Our analyses suggest that although patterns of particle retention in mammals are mainly an effect of body mass and food intake but not digestive anatomy as such (Clauss et al., 2007a), digestive anatomy plays an important role in fluid throughput and digesta washing. Digestive anatomy thus is not interpreted as influencing particle passage per se, but as influencing particle passage relative to solute passage. Additionally, digestive anatomy and physiology support the formation of a particulate matrix that can be perfused by fluid, without disintegrating into a dispersion.

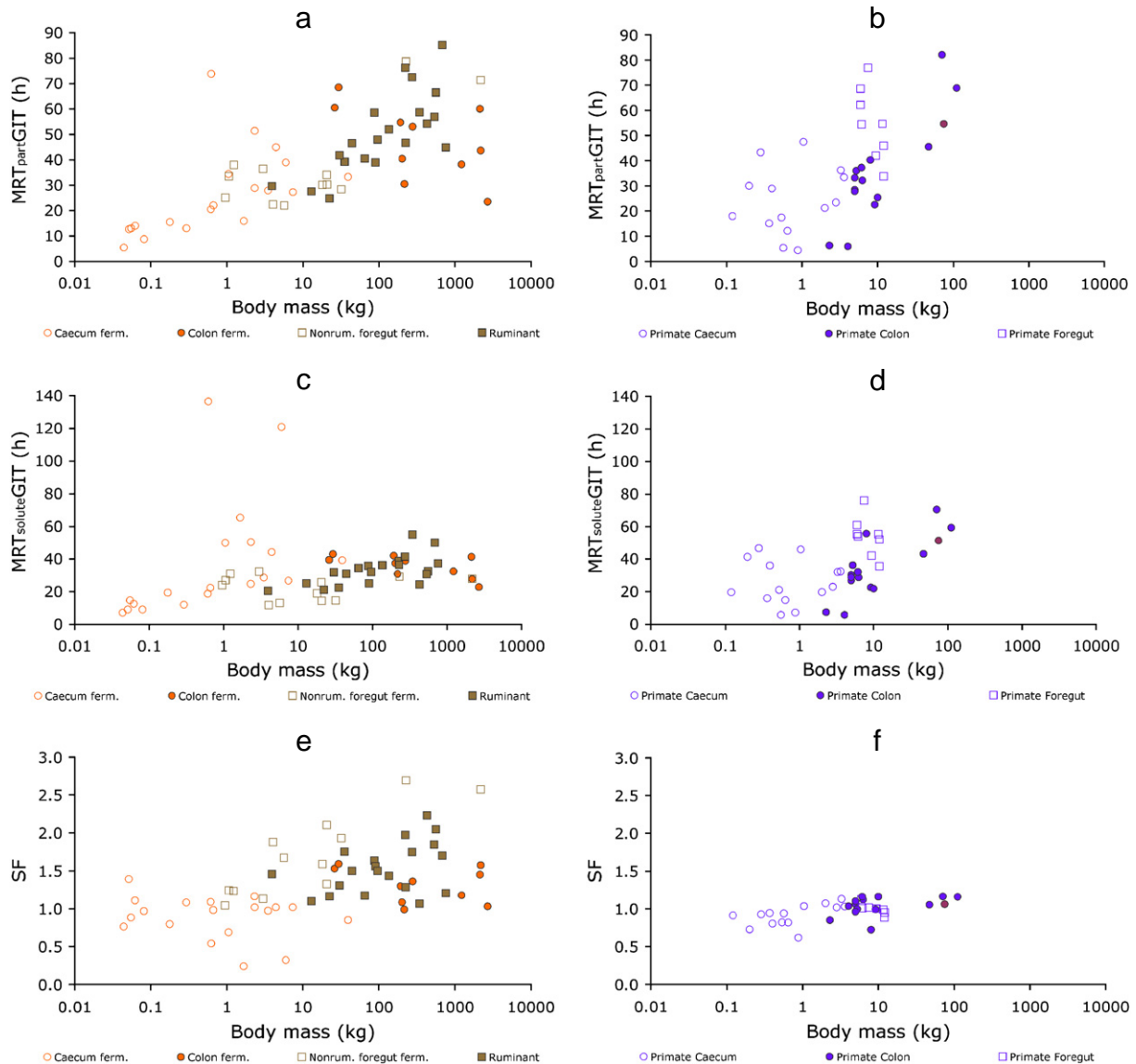


Fig. 2. Relationship between body mass (BM) and mean retention time (MRT) of particles in the gastrointestinal tract (GIT) in a) nonprimate mammalian herbivores and b) primates, between BM and MRT of solutes in the GIT in c) nonprimate mammalian herbivores and d) primates, and between BM and the ratio of $MRT_{\text{particleGIT}}$ to $MRT_{\text{soluteGIT}}$ (SF) in e) nonprimate mammalian herbivores and f) primates. For data sources see Table 1; for statistics, see Tables 2 and 3. The purple dot indicates *Homo sapiens*.

Table 2

Results of General Linear Models relating passage parameters (mean retention time MRT of particles or solutes [in h], or their ratio SF) to log-transformed body mass (BM [kg]), the relative dry matter intake (rDMI [$\text{g kg}^{-0.75} \text{d}^{-1}$]), or MRT_{particles} in 98 (a, c) or 72 (b) mammal species, respectively, using “being a primate” and the digestion type (caecum fermenter, colon fermenter, nonruminant foregut fermenter, ruminant) as cofactors as well as the interaction of the two cofactors. A significant interaction indicates different effects between the digestion types in primates vs. nonprimates.

Dependent variable	Corrected model	R ²	BM	rDMI ^a	Primate (yes/no)	Digestion type	Primate*(dig.type)
a)							
MRT _{particle}	$p < 0.001$, F = 12.14	0.49	$p < 0.001$, F = 30.16	–	$p = 0.030$, F = 4.85	$p = 0.028$, F = 3.16	$p = 0.040$, F = 3.35
MRT _{solute}	$p = 0.001$, F = 3.95	0.24	$p = 0.002$, F = 10.19	–	$p = 0.017$, F = 5.90	$p = 0.217$, F = 1.51	$p < 0.001$, F = 8.96
SF	$p < 0.001$, F = 18.14	0.59	$p = 0.001$, F = 11.15	–	$p < 0.001$, F = 11.30	$p = 0.001$, F = 5.34	$p < 0.001$, F = 10.01
b)							
MRT _{particle}	$p < 0.001$, F = 12.29	0.61	$p < 0.001$, F = 28.50	$p < 0.001$, F = 19.31	$p = 0.607$, F = 0.27	$p = 0.419$, F = 0.96	$p = 0.123$, F = 2.17
MRT _{solute}	$p = 0.008$, F = 2.90	0.27	$p = 0.009$, F = 7.19	$p = 0.019$, F = 5.75	$p = 0.651$, F = 0.21	$p = 0.636$, F = 0.57	$p = 0.047$, F = 3.22
SF	$p < 0.001$, F = 10.57	0.57	$p = 0.016$, F = 6.13	$p = 0.751$, F = 0.10	$p = 0.019$, F = 5.77	$p = 0.037$, F = 2.99	$p = 0.008$, F = 5.18
c)							
MRT _{solute}	$p < 0.001$, F = 17.62	0.58	$p < 0.001$, F = 91.60	–	$p = 0.112$, F = 2.58	$p = 0.004$, F = 4.74	$p = 0.003$, F = 6.30
SF	$p < 0.001$, F = 19.13	0.60	$p < 0.001$, F = 14.38	–	$p < 0.001$, F = 24.56	$p = 0.002$, F = 5.34	$p < 0.001$, F = 13.62

^a If rDMI was used as a covariable, then the smaller dataset of 72 species was used.

Most interestingly, this interplay between digestion type and retention parameters is not observed amongst primates, raising the question whether the various digestion types – caecum fermenters, colon fermenters and foregut fermenters – should really be considered convergent adaptations between primates and nonprimate mammals. It was previously recognised that humans apparently do not fit passage patterns documented in other species. Van Soest (1984, p.27) stated that in human subjects “the rates of liquid and particulate passage were very similar, a surprise since in many animal species liquid has a shorter retention time than particles”. Our evaluation that includes data for other primates suggests that this statement should be broadened to include the whole primate order: regardless of the digestive strategy, primates do not display SFs distinctively different from 1, not even the foregut-fermenting species. This strongly suggests a phylogenetic constraint in the primate order,

which apparently cannot increase its relative fluid throughput in the GIT.

It should be noted that in previous analyses on more limited sets of species, the natural diet of the species investigated was used as a covariate (e.g. Clauss et al., 2008b; Steuer et al., 2010). Omitting the natural diet as a covariate in this study does not suggest that adaptations to the natural diet are not important. Instead, it reflects the difficulties in finding appropriate diet proxies: On the one hand it is problematic to describe the diets of such a variety of animals with a continuous variable that appropriately reflects the dietary choices of all groups (e.g., the percentage of grass vs. browse for hoofed mammals, or the percentage of fruit vs. browse for primates). On the other hand, differences between botanical descriptions are not always as self-evident as they may seem. For example, regardless of a widespread view that fruits represent, by default, diet items that are

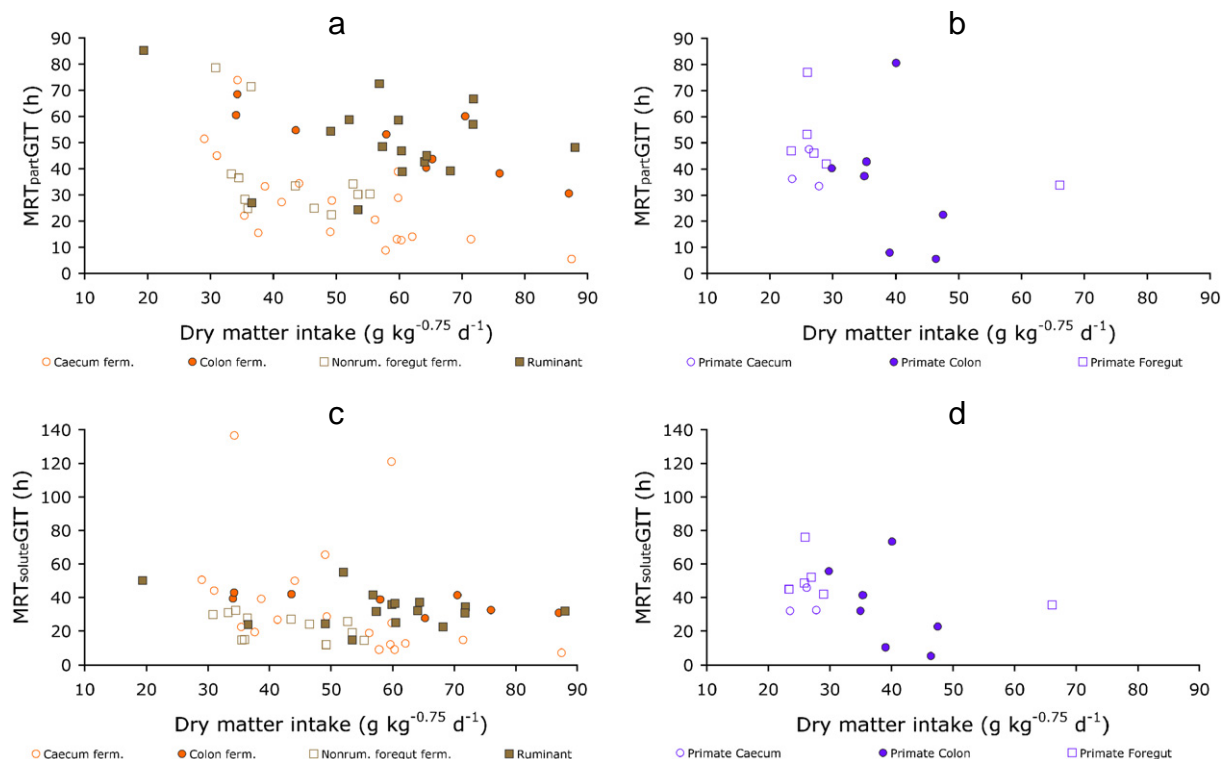


Fig. 3. Relationship between relative dry matter intake (rDMI) and mean retention time (MRT) of particles in the gastrointestinal tract (GIT) in a) nonprimate mammalian herbivores and b) primates, and between rDMI and MRT of solutes in the GIT in c) nonprimate mammalian herbivores and d) primates. For data sources see Table 1; for statistics, see Tables 2 and 3.

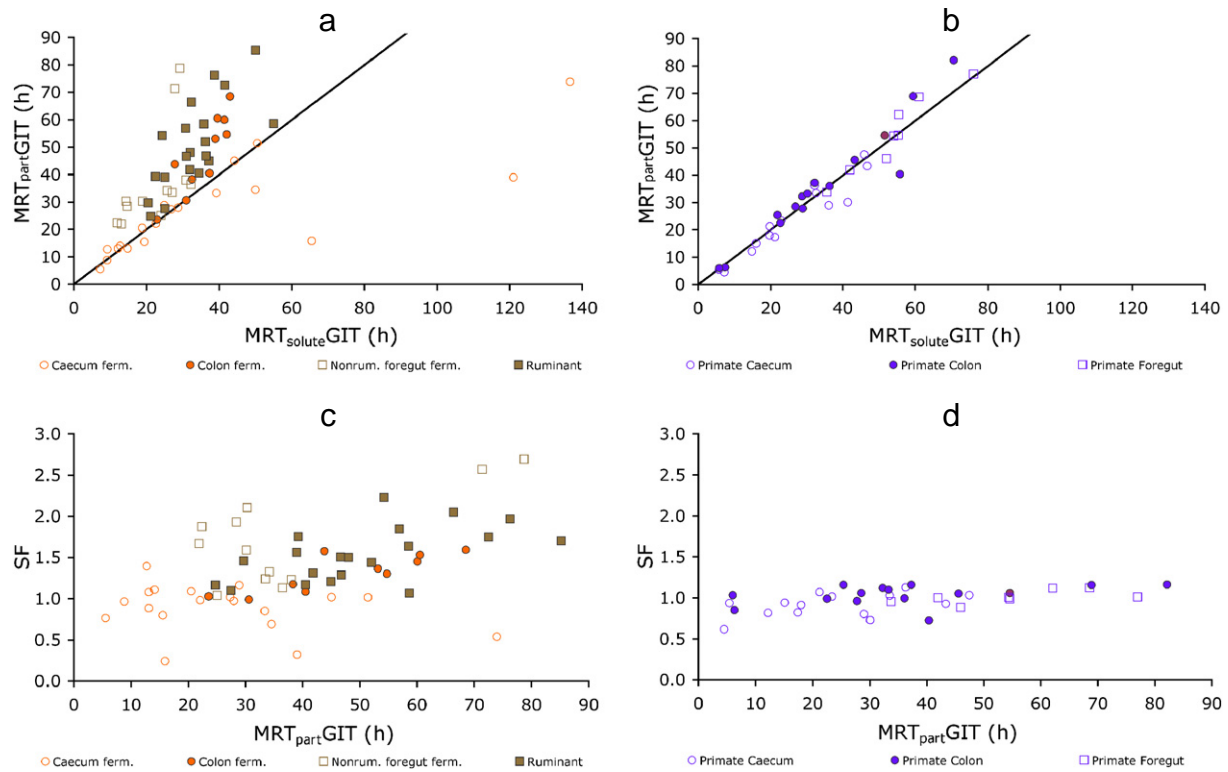


Fig. 4. Relationship between the mean retention time (MRT) of solutes and particles in the gastrointestinal tract (GIT) in a) nonprimate mammalian herbivores and b) primates, and between the MRT of particles and the ratio of $MRT_{particleGIT}$ to $MRT_{soluteGIT}$ (SF) in c) nonprimate mammalian herbivores and d) primates. For data sources see Table 1; for statistics, see Tables 2 and 3. The purple dot indicates *Homo sapiens*.

more digestible than leaves (e.g. Sailer et al., 1985), empirical data collections often show that ‘wild fruits’ contain fibre levels that are within the range of browse leaves (Oftedal and Allen, 1996; Schwitzer et al., 2009). Therefore, we suggest that evaluations of the influence of natural diets on retention measurements should remain limited to certain subgroups at this stage.

4.1. Increasing fluid throughput: possible benefits

The evidence for convergent evolution towards a higher SF, i.e. a higher relative fluid throughput, in large herbivores that exploit a grazing niche (Clauss et al., 2010a; Clauss et al., 2010b; Steuer et al., 2010) is strong indication that adaptations enhancing digesta washing are subject to natural selection. A large number of old and recent in vitro studies with ruminant inoculum (Isaacson et al., 1975; Shi and Weimer, 1992; Meng et al., 1999; Eun et al., 2004; Fondevila and Pérez-Espés, 2008) and limited in vivo evidence in domestic cattle (Wiedmeier et al., 1987a; Wiedmeier et al., 1987b; Froetschel et al., 1989; Bird et al., 1993) suggest that an increased fluid throughput will enhance microbial yield from fermentation chambers, and potentially also microbial fibre digestion. Provided that the morphological means for maintaining a high local solid volume fraction at the site of filtration are present and prevent the disintegration of the digesta matrix into a dispersion, one might add. A likely explanation is that constant washing-out keeps microbial populations in their growth (rather than maintenance) stage (Isaacson et al., 1975), and that particularly fast-growing strains are selected. In other fields of biology, such as wildlife or fish population management, it is well-known that harvesting during the growth stage of a population optimises the overall yield from that population (Schaefer, 1954; Jensen, 1996; Sinclair et al., 2006). Whilst both, increased microbial yield and fibre digestion represent important selective advantages in foregut fermenters and could explain convergent evolution towards

higher fluid throughput in ruminants (Clauss et al., 2010a), an increase in fibre digestion efficiency alone might represent a selective advantage even in those hindgut fermenters that do not recycle microbial protein from their fermentation chamber. The selection of particularly efficient bacterial strains by a high fluid throughput could explain convergent adaptations for high fluid throughput in this group (Clauss et al., 2010b; Steuer et al., 2010); this may be particularly relevant for species foraging on grass, because grass generally has a slow fermentation pattern (Hummel et al., 2006).

4.2. Increasing fluid throughput: mechanisms

The main physiological routes for increasing the amount of fluid that transits the particulate digesta plug in herbivores are increased saliva production (Bailey, 1961) and secretion of fluid into the colon (Argenzio et al., 1974; Snipes et al., 1982). Differences in the degree of digesta washing should be largely due to differences in saliva output and viscosity, or colonic secretions, between species. Schwarm et al. (2009b) hypothesised that ruminating herbivores may have particularly high saliva inputs into their GIT. Unfortunately, however, comparative data on these measurements are lacking. Manipulating saliva secretion has, so far, been performed in ruminants only (Wiedmeier et al., 1987a; Wiedmeier et al., 1987b; Froetschel et al., 1989; Bird et al., 1993), with results that correspond to those of the in vitro studies with an increased bacterial yield from the forestomach at increased salivation.

The particle size distribution in digesta plays an important role in considerations on digesta washing. Digesta composed of mainly small particles will not only have greater surface area but will also have smaller interparticulate voids when the solid volume fraction is high. Greater peristaltic pressure will be required to overcome the increased friction with the fluid phase, and hence particles will tend to move with the fluid phase rather than ‘being washed’ as a plug. In

Table 3

Results of General Linear Models, either calculated conventionally (conv) or using Phylogenetic Generalized Linear Least-Squares (PGLS; used to correct for non-independence of data originating from species related to each other by evolutionary ancestry), relating passage parameters (mean retention time MRT of particles or solutes [in h], or their ratio SF) to log-transformed body mass (BM [kg]), the relative dry matter intake (rDMI [g kg^{-0.75} d⁻¹]), or MRT_{particles} in 61 (a, c) or 56 (b) non-primate mammal species belonging to one of the four major digestion types (caecum fermenter, colon fermenter, nonruminant foregut fermenter, ruminant), respectively. Differences between the conventional and the PGLS GLM are indicated by grey shading.

Dependent variable	Statistic	Corrected model	R ²	BM	rDMI*	Digestion type
a)						
MRT _{particle}	conv	p<0.001, F=12.61	0.47	p<0.001, F=19.98	–	p=0.542, F=0.72
	PGLS	p<0.001, F=6.20	0.31	p<0.001, t=3.91	–	p=0.800, x ² =1.00
MRT _{solute}	conv	p=0.064, F=2.37	0.15	p=0.025, F=5.29	–	p=0.050, F=2.78
	PGLS	p=0.001, F=5.13	0.27	p=0.019, t=2.41	–	p=0.002, x ² =15.30
SF	conv	p<0.001, F=14.84	0.52	p=0.012, F=6.67	–	p<0.001, F=9.56
	PGLS	p<0.001, F=7.19	0.34	p=0.072, t=1.83	–	p=0.003, x ² =14.32
b)						
MRT _{particle}	conv	p<0.001, F=18.88	0.65	p<0.001, F=24.10	p<0.001, F=18.52	p=0.262, F=1.37
	PGLS	p<0.001, F=14.86	0.60	p<0.001, t=4.87	p<0.001, t=3.82	p=0.501, x ² =2.36
MRT _{solute}	conv	p=0.025, F=2.82	0.22	p=0.037, F=4.61	p=0.051, F=4.00	p=0.029, F=3.27
	PGLS	p=0.009, F=3.50	0.26	p=0.013, t=2.59	p=0.544, t=0.61	p=0.004, x ² =13.56
SF	conv	p<0.001, F=11.47	0.53	p=0.034, F=4.76	p=0.771, F=0.09	p<0.001, F=8.10
	PGLS	p<0.001, F=5.74	0.36	p=0.102, t=1.67	p=0.291, t=1.07	p=0.004, x ² =13.46
c)						
MRT _{solute}	conv	p<0.001, F=10.07	0.42	MRT _{particle} p<0.001, F=34.14	–	p=0.001, F=6.13
	PGLS	p<0.001, F=17.46	0.47	p<0.001, t=5.43	–	p<0.001, x ² =20.70
SF	conv	p<0.001, F=16.61	0.54	p=0.002, F=10.52	–	p<0.001, F=11.49
	PGLS	p<0.001, F=12.31	0.39	p=0.003, t=3.11	–	p<0.001, x ² =18.78

*if rDMI was used as a covariable, then the smaller dataset of 56 species was used.

other words, high fluid throughput in a system that contains mostly fine-grained digesta likely leads to a state of dispersion³ (Lentle et al., 2009). Because digesta particle size is a function of body mass, with smaller particle sizes in smaller animals (Fritz et al., 2009), digesta washing may therefore be more difficult to achieve in smaller animals. This could help to explain the tendency of smaller animals to have SF ~1 (Fig. 2e), and why many small herbivores adopt a ‘mucus trap’ colonic separation mechanism that is not based on increased fluid throughput (Hume and Sakaguchi, 1991). Conversely the larger particles in the digesta of animals of larger body mass are more likely to entangle and form a persistent matrix that allows the fluid phase to move in relation to the solid phase. Rumination, where a particularly heterogeneous particle size distribution is maintained in the rumen (cf. mean particle size of rumen digesta from Clauss et al., 2009a; with the mean faecal particle size in nonruminant herbivores from Fritz et al., 2009), may thus offer a condition that is particularly favourable for the formation of a coherent and stable digesta matrix.

A further possible means by which herbivores may increase the amount of fluid that transits the particulate digesta plug is by maximising the elastic behaviour of the component particles (Lentle et al., 2009). Systematic mechanical analyses of different forages are missing so far, but the high cellulose to lignin ratio of grass (Hummel et al., 2006) as well as anatomical adaptations of grazing herbivores (Clauss et al., 2008a) suggest that grass is less brittle/more elastic than browse forage; grass also has particular fractionation patterns that result in longish, ‘fibre-like’ particles (Clauss et al., 2003). Grass may thus be more suited to the formation of coherent digesta mats and may in particular aid recovery of the digesta matrix from compression and re-uptake of fluid into the inter-particulate spaces (Lentle et al., 2009).

³ Note that the state of the digesta in the small intestine (in contrast to the stomach or the large intestine), with its secretions of enzyme-containing fluid, is always a dispersion, as observable at any dissection where digesta in this section of the GIT is never in the form of a coherent matrix such as a mat or pellets, and as described in pharmacological modelling (Yu et al., 1996). (Compartmental transit and dispersion model analysis of small intestinal transit flow in humans. International Journal of Pharmaceutics 140, 111–118.)

4.3. Increasing fluid throughput: constraints

Whilst the dilution of digesta may have beneficial effects on certain aspects of digestion, it may also represent challenges for enzymatic digestion or fluid re-absorption. If, in foregut fermenters, very dilute digesta reached the sites of auto-enzymatic digestion – the glandular stomach and the small intestine –, a higher production of digestive enzymes would be necessary to compensate for this dilution. If, in hindgut fermenters, very dilute digesta reached the sites of water re-absorption – the distal colon –, a higher water re-absorption capacity would be required. Macroscopic anatomy supports this reasoning: true ruminants have higher food intakes than camelids (Van Saun, 2006) and hence most likely also (at similar rates of digesta washing) a higher absolute outflow of liquid from the foregut fermentation chamber. They have evolved a special forestomach compartment – the omasum – whose main function is fluid (and mineral) re-absorption (Hauffe and Engelhardt, 1975; Clauss et al., 2006a), which prevents the entry of excessively diluted digesta into the glandular stomach and small intestine.

4.4. Consequences for primates?

One theoretical reason for the low SF measured in primates, when compared to other nonruminant foregut or colon fermenters, could be a lower defecation frequency, which could hypothetically reduce the resolution of passage measurements (which depend on frequent defecations). However, even in other herbivores with low defecation frequencies, such as tapirs (Clauss et al., 2010b) or herbivorous tortoises (Franz et al., 2011), high SFs have been measured, making defecation frequency alone an unlikely candidate to explain the observed difference between primates and non-primates.

Our results raise the intriguing question of whether primates are actually physiologically limited in their capacity to increase fluid throughput through their GIT in the sense of an evolutionary constraint (McKittrick, 1993). Reasons for this can, so far, only be speculated upon and might include a relatively low saliva production (Schwarm et al., 2009b). If a high fluid throughput is important for

Table 4

Results of General Linear Models, either calculated conventionally (conv) or using Phylogenetic Generalized Linear Least-Squares (PGLS; used to correct for non-independence of data originating from species related to each other by evolutionary ancestry), relating passage parameters (mean retention time MRT of particles or solutes [in h], or their ratio SF) to log-transformed body mass (BM [kg]), the relative dry matter intake (rDMI [$\text{g kg}^{-0.75} \text{d}^{-1}$]), or MRT_{particles} in 37 (a, c) or 16 (b) primate species belonging to one of the three major primate digestion types (caecum fermenter, colon fermenter, nonruminant foregut fermenter), respectively.

Dependent variable	Statistic	Corrected model	R ²	BM	rDMI ^a	Digestion type
a)						
MRT _{particle}	conv	p<0.001, F= 12.08	0.52	p= 0.001, F= 13.03	–	p= 0.010, F= 5.32
	PGLS	p<0.001, F= 8.96	0.45	p= 0.002, t= 3.35	–	p= 0.020, x ² = 7.86
MRT _{solute}	conv	p<0.001, F= 9.21	0.46	p= 0.010, F= 7.54	–	p= 0.008, F= 5.63
	PGLS	p= 0.002, F= 5.89	0.35	p= 0.020, t= 2.44	–	p= 0.023, x ² = 7.58
SF	conv	p= 0.004, F= 5.37	0.33	p= 0.013, F= 6.94	–	p= 0.916, F= 0.09
	PGLS	p= 0.005, F= 5.26	0.32	p= 0.005, t= 3.00	–	p= 0.990, x ² = 0.02
b)						
MRT _{particle}	conv	p= 0.018, F= 4.78	0.64	p= 0.006, F= 11.59	p= 0.077, F= 3.80	p= 0.213, F= 1.78
	PGLS	p= 0.018, F= 4.77	0.63	p= 0.006, t= 3.40	p= 0.074, t= 1.97	p= 0.144, x ² = 3.88
MRT _{solute}	conv	p= 0.031, F= 3.99	0.59	p= 0.014, F= 8.48	p= 0.075, F= 3.87	p= 0.312, F= 1.30
	PGLS	p= 0.031, F= 3.98	0.59	p= 0.014, t= 2.91	p= 0.074, t= 1.97	p= 0.252, x ² = 2.76
SF	conv	p= 0.612, F= 0.69	0.20	p= 0.223, F= 1.67	p= 0.941, F= 0.01	p= 0.375, F= 1.07
	PGLS	p= 0.618, F= 0.68	0.20	p= 0.197, t= 1.38	p= 0.951, t= 0.06	p= 0.340, x ² = 2.16
c)						
MRT _{solute}	conv	p<0.001, F= 180.6	0.94	MRT _{particle} p<0.001, F= 351.4	–	p= 0.289, F= 1.29
	PGLS	p<0.001, F= 169.0	0.94	p<0.001, t= 17.60	–	p= 0.343, x ² = 2.14
SF	conv	p= 0.003, F= 5.58	0.34	p= 0.010, F= 7.45	–	p= 0.091, F= 2.58
	PGLS	p= 0.001, F= 8.53	0.33	p= 0.012, t= 2.67	–	p= 0.120, x ² = 4.24

^a If rDMI was used as a covariable, then the smaller dataset of 16 species was used.

non-coprohagic herbivores that use a grazing niche, then the findings of this study could explain why primates do not occupy a grazing niche. However, the exception of the gelada baboon (*Theropithecus gelada*) (Dunbar, 1977) and the recent discovery of a C₄-dominated diet in *Paranthropus boisei* (an East African hominin) (Cerling et al., 2011) open up the question whether, under certain conditions, primates can rely more on grasses than expected based on what is known so far about their digesta passage characteristics. The conclusion that geladas cannot compete with ruminants (Dunbar and Bose, 1991) might partially be explained by the primate order's general constraint to low fluid throughput. Our results also support the general view that primates are not characterised by high degrees of morpho-physiological digestive adaptations (Milton, 1986) but can nevertheless successfully occupy various niches due to other reasons such as their behavioural flexibility (Reader and Laland, 2002).

4.5. Outlook

To date, the benefits of a high fluid throughput and intensive digesta washing represent concepts that can be used to explain the observed patterns in mammalian herbivores. However, these concepts require further experimental testing, including assessments of the physical properties of particulate digesta and its behaviour in relation to digestive fluids (Lentle and Janssen, 2008; Lentle et al., 2009), and modelling of fluid movements in the gastrointestinal tract that has so far been restricted to domestic ruminants (Seo et al., 2007). Additionally, measurements of particle and solute retention in key species missing from the dataset so far, such as the gelada baboon, or the proboscis monkey (*Nasalis larvatus*) that is reported to regurgitate and remasticate digesta in a fashion reminiscent of rumination (Matsuda et al., 2011), can be expected to lead to further insights.

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