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

## 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, aborad washing at ratios  $N1$  (where the solute marker travels faster than the particle marker), and orad (retrograde) washing at ratios  $b1$  (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.

1 **Phylogenetic constraints on digesta separation: variation in fluid throughput in the**  
2 **digestive tract in mammalian herbivores**

3  
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20  
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22  
23 Running head: Digesta washing

24

25 **Abstract**

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

45

46 **Key words** passage, digestion, fluid, particle, foregut fermenter, hindgut fermenter, ruminant,  
47 nonruminant, caecum fermenter

48

- 49 **List of abbreviations**  
50 BM body mass  
51 DMI dry matter intake (also: absolute dry matter intake)  
52 rDMI relative dry matter intake (expressed per unit metabolic body weight)  
53 GIT gastrointestinal tract  
54 GLM general linear model  
55 MRT mean retention time  
56  $MRT_{\text{particle}}$  GIT mean retention time of a particle marker in the gastrointestinal tract  
57  $MRT_{\text{solute}}$  GIT mean retention time of a solute marker in the gastrointestinal tract  
58 PGLS phylogenetic generalized least-squares  
59 SF selectivity factor, the ratio of  $MRT_{\text{particle}} / MRT_{\text{solute}}$   
60

## 61 **Introduction**

62 Digestion is a time-dependent process (Stevens and Hume 1995; Karasov and Martínez del  
63 Rio 2007); hence the time that ingested food takes to transit the digestive tract is an important  
64 factor in digestive efficiency. At a given level of food intake, the more time is available for  
65 digestion, the more complete digestion can be. Therefore, the digesta mean retention time  
66 (MRT)<sup>a</sup> is a parameter that is considered crucial in digestive physiology, and that has been  
67 measured in vast numbers of digestive studies (Stevens and Hume 1998; Clauss et al. 2007a).  
68 Evaluation of MRT is particularly relevant in herbivorous species (Stevens and Hume 1998)  
69 because the rate of allo-enzymatic digestion of plant fibre is generally slower than that of the  
70 auto-enzymatic digestion of other substrates. MRT is usually assessed by administering  
71 markers and measuring their appearance at a given point along the gastrointestinal tract (GIT)  
72 e.g. the faeces, or the termination of a particular gut segment (Warner 1981b). Whether a  
73 marker used is representative of the whole digesta, or of a relevant fraction of it, is an  
74 important consideration in such studies. Commonly, at least two digesta phases are  
75 considered separately – the particulate or solid phase, and the fluid or solute phase (Warner  
76 1981b).

77

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<sup>a</sup> The terminology associated with measuring the time that digesta is retained in (or in other word: 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.

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

93

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

103

104 In contrast, there is no general concept for the use of 'fluid' MRT, regardless of the  
105 widespread use of such measurements (Warner 1981b). Measurements by use of a 'fluid'  
106 marker are traditionally interpreted as 'fluid retention' or 'fluid passage' (e.g. Pickard and  
107 Stevens 1972). But a 'fluid' marker recovered in the faeces (or at another endpoint) does *not*  
108 represent the fluid/water *ingested* by the organism that is *not absorbed* (Cork et al. 1999;  
109 Clauss et al. 2010b). Fluid is constantly excreted and absorbed in the course of the digestive  
110 process throughout the GIT (Stevens and Hume 1995), and any fluid in the faeces represents  
111 the sum of the indeterminate fractions of remaining dietary and secretory fluids. A 'fluid

112 marker' is by definition a non-absorbable, yet digesta-fluid soluble marker. Therefore, it has  
113 been suggested that the term 'fluid MRT' should be abandoned and replaced by 'solute MRT'  
114 (Cork et al. 1999; Franz et al. 2010). However, because the absorption of most solubilised  
115 nutrients is generally by an order of magnitude less time-constrained than the digestion of  
116 nutrients in the solid phase, the term 'solute MRT' will have no relevance with regard to  
117 limiting the time available for digestion. What, then, is the relevance of fluid/solute MRT  
118 measurements?

119

120 We hypothesize that functional relevance of fluid MRT data will be revealed by comparison  
121 with results from simultaneous measurement of particle MRT. Such comparisons have been  
122 conducted previously in human subjects, but were limited to considerations of whether a  
123 solute marker can be used to adequately describe digesta movements (Heller et al. 1980;  
124 Wrick et al. 1983). Possibly, differences between the fluid and particulate phase MRT reflect  
125 the pumping and processing of digesta within the GIT. In situations where the contained  
126 particles are in sufficient concentration to interact and form a 'mat' or 'plug', peristaltic  
127 constriction will cause local squeezing-out of the fluid phase from the spaces between the  
128 particulate elements of the plug, and more fluid to be reabsorbed into the digesta plug during  
129 subsequent relaxation (Lentle et al. 2006). This fluid flow into and out of the digesta plug  
130 represents a process of effective 'digesta washing'. It promotes mixing within the  
131 interparticulate spaces and hence both, the absorption of soluble nutrients from the digesta at  
132 the intestinal mucosa and the permeation of digesta with enzymatic secretions (Lentle et al.  
133 2006). If fluid expressed from the plug moves in a consistent orad or aborad direction, then  
134 the more this process is continued, the larger the difference between the fluid and particle  
135 MRT may become (Lentle and Janssen 2008). Notably, fine particles (such as bacteria) may  
136 also travel with these fluid movements (Lentle et al. 2009). It is important to note that an  
137 increase in the volume of fluid transiting through the plug of entangled particles will increase  
138 the degree of washing, but that the dilution of the solid volume fraction of the digesta plug by  
139 turbulent admixture with fluid can also lead to a dispersion of the particulate elements and  
140 hence disintegration of the plug.

141

142 It has been shown in previous work that characteristic differences exist in the pattern of  
143 particle and solute retention within various animal groups such as caecum fermenters  
144 (including lagomorphs, rodents, and some marsupials) (Hume and Sakaguchi 1991; Cork et  
145 al. 1999; Franz et al. 2010), colon fermenters (including equines, tapirs, rhinoceroses and

146 elephants) (Clauss et al. 2010b; Steuer et al. 2010), nonruminant foregut fermenters<sup>b</sup> (such as  
147 kangaroos, hippopotamus, peccaries, colobine monkeys) (Schwarm et al. 2009b), and  
148 ruminants (Hummel et al. 2005; Clauss et al. 2006b). Yet, although a significant body of data  
149 on solute retention is available for a wide range of species (Stevens and Hume 1995), few  
150 statistical comparisons have been conducted that consider the effect of body mass (BM), food  
151 intake, gut morphology or phylogenetic relationships. Such evaluations have been reported  
152 repeatedly for particle retention (Owen-Smith 1988; Illius and Gordon 1992; Cork et al. 1999;  
153 White and Seymour 2005; Clauss et al. 2007a). To our knowledge, however, Robbins (1993)  
154 presented the only allometric analysis of solute retention data so far, indicating that  
155  $MRT_{\text{soluteGIT}}$  scaled to  $BM^{0.28}$  in foregut and  $BM^{0.18}$  in hindgut fermenters.

156

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

166

## 167 **Methods**

168 We collated data from the literature from studies that indicated body mass (BM), and the  
169 mean retention time (MRT; as given in the publications) of both particles and solutes. Only  
170 publications that used chromium- or cerium-mordanted fibre (Cr/Ce-f; Udén et al. 1980) or  
171 phenanthroline-ruthenium chloride (RuP; Tan et al. 1971) as markers for measuring  
172  $MRT_{\text{particle}}$  were selected. Similarly, only publications that used cobalt-EDTA or chromium-  
173 EDTA (Udén et al. 1980) as markers for measuring  $MRT_{\text{solute}}$  were used. The only exception  
174 was man (*Homo sapiens*), for whom a study with polyethylene glycol (PEG) as solute marker  
175 was accepted (Wrick et al. 1983). Only data for adult specimens were used. The resulting  
176 dataset included 98 mammal species. This included a set of 16 primate species for which data

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<sup>b</sup> 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..

177 were exclusively available from the unpublished thesis by Judith Caton (1997). A second  
178 dataset was prepared from this first dataset for those sources in which the food intake,  
179 measured as dry matter intake (DMI), were additionally available. This dataset comprised 72  
180 species. Means were calculated for all data points available from each source, and then means  
181 of sources were calculated, if more than one source was available for a species. The full  
182 datasets including all references are given in Table 1.

183

184 Apart from  $MRT_{\text{particleGIT}}$  and  $MRT_{\text{soluteGIT}}$ , the ratio of the two measures was calculated as  
185  $MRT_{\text{particleGIT}} / MRT_{\text{soluteGIT}}$ ; this ratio is referred to as the ‘selectivity factor’ (SF; Lechner-  
186 Doll et al. 1990). A preliminary analysis of the 72 species for which food intake data were  
187 available showed that in the whole dataset, *absolute* DMI (in  $\text{kg d}^{-1}$ ) scaled to  $0.044$  (95%CI  
188  $0.039\text{-}0.049$ )  $BM^{0.77}$  (95%CI  $0.74\text{-}0.80$ ). Therefore, the *relative* DMI ( $rDMI$ ,  $\text{g kg}^{-0.75} \text{d}^{-1}$ ) was  
189 calculated for each species using 0.75 as exponent and used in the comparative analyses.

190

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

204

205 To achieve normality, data on BM were log-transformed. Allometric regressions were  
206 performed as linear regressions on log-transformed data. Statistical analyses were performed  
207 without and with accounting for phylogeny, using General Linear Models (GLMs) with the  
208 passage parameters ( $MRT_{\text{particleGIT}}$ ,  $MRT_{\text{soluteGIT}}$ , SF) as the respective dependent variables,  
209 and with BM,  $rDMI$  and  $MRT_{\text{particleGIT}}$  as the independent variables in different models. As  
210 cofactors, being a primate (yes/no), and the digestion type (caecum fermenter, colon

211 fermenter, nonruminant foregut fermenter, ruminant) were used as categorical variables. First,  
212 conventional GLMs were performed with all cofactors and their interaction (because a  
213 phylogenetic information – belonging to the primate order or not – was already included as a  
214 cofactor, it is not reasonable to perform this model using PGLS). Because the interaction  
215 between being a primate and digestion type was significant in most cases, indicating a  
216 difference in the effects of the different digestion types between primates and nonprimates,  
217 subsequent conventional and PGLS-GLMs were performed separately within nonprimates  
218 and primates, respectively. The statistical calculations were performed with PASW 18.0  
219 (SPSS Inc., Chicago, IL) and COMPARE 4.6 program (Martins 2004). The significance level  
220 was set to  $\alpha=0.05$ . 95% confidence intervals were calculated for coefficients in allometric  
221 regressions.

222

223

## 224 **Results**

225 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  
226  $0.11-0.19$ ) ( $R^2=0.41$ ) (Fig. 2ab); PGLS resulted in a similar relationship of  $25.1$  (95%CI 20.0-  
227  $31.6$ )  $\text{BM}[\text{kg}]^{0.13}$  (95%CI  $0.07-0.19$ ) ( $R^2=0.21$ ).  $MRT_{\text{soluteGIT}}[\text{h}]$  showed a lower allometric scaling  
228 with an even weaker fit, scaling to  $23.9$  (95%CI 20.6-27.7)  $\text{BM}[\text{kg}]^{0.08}$  (95%CI  $0.04-0.12$ ) ( $R^2=0.21$ )  
229 (Fig. 2cd); PGLS resulted in a similar relationship of  $24.5$  (95%CI 18.6-32.4)  $\text{BM}[\text{kg}]^{0.07}$   
230 (95%CI  $0.01-0.13$ ) ( $R^2=0.06$ ). These results support previous findings in a similar dataset that the  
231 scaling relationship between retention parameters and body mass are not particularly distinct  
232 (Clauss et al. 2007a).

233

234 In the conventional GLMs that tested for the influence of BM, being a primate, and digestion  
235 type (and food intake level rDMI), a systematic effect of being a primate as well as a  
236 difference in the effect of digestion type between primates and nonprimates (i.e. a significant  
237 interaction term) were evident (Table 2). The only exception was when both BM and rDMI  
238 were included in a GLM to test for the effect on  $MRT_{\text{particleGIT}}$ , where neither being a  
239 primate, nor the digestion type, nor the interaction between the two was significant (Table  
240 2b). This indicates that  $MRT_{\text{particleGIT}}$  depends mainly on body mass (Fig. 2ab) and food  
241 intake level (Fig. 3ab), but not so much on digestion type or being a primate within  
242 herbivores. Note that if food intake level was not included in the analysis in the larger dataset,  
243 the primate\*(digestion type) interaction did have a significant effect on  $MRT_{\text{particleGIT}}$  (Table  
244 2a). This underlines the importance of including food intake level in investigations of

245 retention parameters. When repeating the GLM with BM and rDMI as covariates for the  
246 whole dataset (n=72 species) using PGLS without cofactors or the interaction, both BM  
247 ( $t=7.88$ ,  $p<0.001$ ) and rDMI ( $t=4.10$ ,  $p<0.001$ ) were highly significant.

248

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

260

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

276

277 The main difference between primates and nonprimates was that in nonprimates, the digestion  
278 type always had a significant effect on  $MRT_{\text{soluteGIT}}$  and the SF (Table 3); in primates,

279 however, SF or the effect of  $MRT_{\text{particleGIT}}$  on  $MRT_{\text{soluteGIT}}$  was not influenced by digestion  
280 type (Table 4). Because the effect of BM on MRT varied between the three primate digestion  
281 types (Fig. 2bd), digestion type did have a significant effect on MRTs when only BM was  
282 considered (Table 4a).

283

## 284 **Discussion**

285 This study indicates differences in the degree of ‘digesta washing’ between mammalian  
286 herbivores. Colon fermenters, nonruminant foregut fermenters and ruminants all achieve  
287 comparatively high ratios of  $MRT_{\text{particleGIT}}$  to  $MRT_{\text{soluteGIT}}$  (i.e., high SF). Caecum  
288 fermenters have been classified as those with a colonic ‘mucous trap’ (SF ~ 1; i.e. gut bacteria  
289 are separated from the digesta by entrapment in a colonic groove and retrograde transport,  
290 without involvement of fluid movements) and a colonic ‘wash-back’ mechanism (SF < 1; i.e.  
291 gut bacteria are flushed in an orad direction from the colon into the caecum by fluid that is  
292 actively secreted in the colon and reabsorbed in the caecum), respectively (Hume and  
293 Sakaguchi 1991; Franz et al. 2010). Because only few animals with a ‘wash-back’ mechanism  
294 were available in the literature and could be included in this dataset, the caecum fermenters  
295 were not divided into additional categories. ‘Wash-back’ species (koala *Phascolarctos*  
296 *cinereus*, common ringtail possum *Pseudocheirus peregrinus*, rabbit *Oryctolagus cuniculus*)  
297 occur in Fig. 2c, 3c, 4a and 4c as evident outliers of the caecum fermenter pattern.

298

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

306

307 Most interestingly, this interplay between digestion type and retention parameters is not  
308 observed among primates, raising the question whether the various digestion types – caecum  
309 fermenters, colon fermenters and foregut fermenters – should really be considered convergent  
310 adaptations between primates and nonprimate mammals. It was previously recognized that  
311 humans apparently do not fit passage patterns documented in other species. Van Soest (1984,  
312 p.27) stated that in human subjects “*the rates of liquid and particulate passage were very*

313 *similar, a surprise since in many animal species liquid has a shorter retention time than*  
314 *particles*". Our evaluation that includes data for other primates suggests that this statement  
315 should be broadened to include the whole primate order: regardless of the digestive strategy,  
316 primates do not display SFs distinctively different from 1, not even the foregut-fermenting  
317 species. This strongly suggests a phylogenetic constraint in the primate order, which  
318 apparently cannot increase its relative fluid throughput in the GIT.

319

320 It should be noted that in previous analyses on more limited sets of species, the natural diet of  
321 the species investigated was used as a covariate (e.g. Clauss et al. 2008b; Steuer et al. 2010).  
322 Omitting the natural diet as a covariate in this study does not suggest that adaptations to the  
323 natural diet are not important. Instead, it reflects the difficulties in finding appropriate diet  
324 proxies: On the one hand it is problematic to describe the diets of such a variety of animals  
325 with a continuous variable that appropriately reflects the dietary choices of all groups (e.g.,  
326 the percentage of grass vs. browse for hoofed mammals, or the percentage of fruit vs. browse  
327 for primates). On the other hand, differences between botanical descriptions are not always as  
328 self-evident as they may seem. For example, regardless of a widespread view that fruit  
329 represent, by default, diet items that are more digestible than leaves (e.g. Sailer et al. 1985),  
330 empirical data collections often show that 'wild fruits' contain fibre levels that are within the  
331 range of browse leaves (Oftedal and Allen 1996; Schwitzer et al. 2009). Therefore, we  
332 suggest that evaluations of the influence of natural diets on retention measurements should  
333 remain limited to certain subgroups at this stage.

334

### 335 *Increasing fluid throughput: possible benefits*

336 The evidence for convergent evolution towards a higher SF, i.e. a higher fluid throughput, in  
337 large herbivores that exploit a grazing niche (Clauss et al. 2010a; Clauss et al. 2010b; Steuer  
338 et al. 2010) is strong indication that adaptations enhancing digesta washing are subject to  
339 natural selection. A large number of old and recent in vitro studies with ruminant inoculum  
340 (Isaacson et al. 1975; Shi and Weimer 1992; Meng et al. 1999; Eun et al. 2004; Fondevila and  
341 Pérez-Espés 2008) and limited in vivo evidence in domestic cattle (Wiedmeier et al. 1987a;  
342 Wiedmeier et al. 1987b; Froetschel et al. 1989; Bird et al. 1993) suggest that an increased  
343 fluid throughput will enhance microbial yield from fermentation chambers, and potentially  
344 also microbial fibre digestion. Provided that the morphological means for maintaining a high  
345 local solid volume fraction at the site of filtration are present and prevent the disintegration of  
346 the digesta matrix into a dispersion, one might add. A likely explanation is that constant

347 washing-out keeps microbial populations in their growth (rather than maintenance) stage  
348 (Isaacson et al. 1975), and that particularly fast-growing strains are selected. In other fields of  
349 biology, such as wildlife or fish population management, it is well-known that harvesting  
350 during the growth stage of a population optimizes the overall yield from that population  
351 (Schaefer 1954; Jensen 1996; Sinclair et al. 2006). While both, increased microbial yield and  
352 fibre digestion represent important selective advantages in foregut fermenters and could  
353 explain convergent evolution towards higher fluid throughput in ruminants (Clauss et al.  
354 2010a), an increase in fibre digestion efficiency alone might represent a selective advantage  
355 even in those hindgut fermenters that do not recycle microbial protein from their fermentation  
356 chamber. The selection of particularly efficient bacterial strains by a high fluid throughput  
357 could explain convergent adaptations for high fluid throughput in this group (Clauss et al.  
358 2010b; Steuer et al. 2010); this may be particularly relevant for species foraging on grass,  
359 because grass generally has a slow fermentation pattern (Hummel et al. 2006).

360

#### 361 *Increasing fluid throughput: mechanisms*

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

372

373 The particle size distribution in digesta plays an important role in considerations on digesta  
374 washing. Digesta composed of mainly small particles will not only have greater surface area  
375 but will also have smaller interparticulate voids when the solid volume fraction is high.  
376 Greater peristaltic pressure will be required to overcome the increased friction with the fluid  
377 phase, and hence particles will tend to move with the fluid phase rather than 'being washed'  
378 as a plug. In other words, high fluid throughput in a system that contains mostly fine-grained

379 digesta likely leads to a state of dispersion<sup>c</sup> (Lentle et al. 2009). Because digesta particle size  
380 is a function of body mass, with smaller particle sizes in smaller animals (Fritz et al. 2009),  
381 digesta washing may therefore be more difficult to achieve in smaller animals. This could  
382 help to explain the tendency of smaller animals to have SF ~ 1 (Fig. 2e), and why many small  
383 herbivores adopt a ‘mucus trap’ colonic separation mechanism that is not based on increased  
384 fluid throughput (Hume and Sakaguchi 1991). Conversely the larger particles in the digesta of  
385 animals of larger body mass are more likely to entangle and form a persistent matrix that  
386 allows the fluid phase to move in relation to the solid phase. Rumination, where a particularly  
387 heterogeneous particle size distribution is maintained in the rumen (cf. mean particle size of  
388 rumen digesta from Clauss et al. 2009a; with the mean faecal particle size in nonruminant  
389 herbivores from Fritz et al. 2009), may thus offer a condition that is particularly favourable  
390 for the formation of a coherent and stable digesta matrix.

391

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

401

#### 402 *Increasing fluid throughput: constraints*

403 While the dilution of digesta may have beneficial effects on certain aspects of digestion, it  
404 may also represent challenges for enzymatic digestion or fluid re-absorption. If, in foregut  
405 fermenters, very dilute digesta reached the sites of auto-enzymatic digestion – the glandular  
406 stomach and the small intestine –, a higher production of digestive enzymes would be  
407 necessary to compensate for this dilution. If, in hindgut fermenters, very dilute digesta  
408 reached the sites of water re-absorption – the distal colon –, a higher water re-absorption  
409 capacity would be required. Macroscopic anatomy supports this reasoning: true ruminants

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<sup>c</sup> 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, L.X., Crison, J.R., Amidon, G.L., 1996. Compartmental transit and dispersion model analysis of small intestinal transit flow in humans. *International Journal of Pharmaceutics* 140, 111-118.)

410 have higher food intakes than camelids (Van Saun 2006) and hence most likely also (at  
411 similar rates of digesta washing) a higher absolute outflow of liquid from the foregut  
412 fermentation chamber. They have evolved a special forestomach compartment – the omasum  
413 – whose main function is fluid (and mineral) re-absorption (Hauffe and Engelhardt 1975;  
414 Clauss et al. 2006a), which prevents the entry of excessively diluted digesta into the glandular  
415 stomach and small intestine.

416

#### 417 *Consequences for primates?*

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

425

426 Our results raise the intriguing question of whether primates are actually physiologically  
427 limited in their capacity to increase fluid throughput through their GIT in the sense of an  
428 evolutionary constraint (McKittrick 1993). Reasons for this can, so far, only be speculated  
429 upon and might include a relatively low saliva production (Schwarm et al. 2009b). If a high  
430 fluid throughput is important for non-coprohagic herbivores that use a grazing niche, then  
431 the findings of this study could explain why primates do not occupy a grazing niche.

432 However, the exception of the gelada baboon (*Theropithecus gelada*) (Dunbar 1977) and the  
433 recent discovery of a C<sub>4</sub>-dominated diet in *Paranthropus boisei* (an East African hominin)  
434 (Cerling et al. 2011) open up the question whether, under certain conditions, primates can rely  
435 more on grasses than expected based on what is known so far about their digesta passage  
436 characteristics. The conclusion that geladas cannot compete with ruminants (Dunbar and Bose  
437 1991) might partially be explained by the primate order's general constraint to low fluid  
438 throughput. Our results also support the general view that primates are not characterized by  
439 high degrees of morpho-physiological digestive adaptations (Milton 1986) but can  
440 nevertheless successfully occupy various niches due to other reasons such as their behavioural  
441 flexibility (Reader and Laland 2002).

442

#### 443 *Outlook*

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

454

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810 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  
811 colon fermenter, 3 nonruminant foregut fermenter, 4 ruminant); markers include chromium-mordeanted fibre (1), cerium-mordanted fibre (2),  
812 phenanthroline-ruthenium chloride (3), cobalt-EDTA (4), chromium-EDTA (5) or polyethylene glycol (6); BM body mass, MRT mean retention  
813 time, SF selectivity factor, DMI dry matter intake  
814

Species	GIT	----- Total dataset (n=98) -----				----- Reduced dataset (n=72) -----					Markers	Source
		BM (kg)	MRT <sub>particle</sub> (h)	MRT <sub>solute</sub> (h)	SF	BM (kg)	DMI (kg d <sup>-1</sup> )	MRT <sub>particle</sub> (h)	MRT <sub>solute</sub> (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. 2009a)
<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 and Nabata 1992; Sakaguchi et al. 1992b; Sakaguchi and Ohmura 1992; 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; 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; 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; 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; 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; 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; 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; 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; 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; 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	12345	(Udén et al. 1982; Udén and Van Soest 1982; Rutagwenda 1989; Freudemberger 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; 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; 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; 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; 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; 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; 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	(Steuer et al. 2007; 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; Steuer et al. 2007; 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; 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. 1985b; a; Pearson and Merritt 1991; 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; Sakaguchi and Hume 1990)
<i>Trichosurus</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; Sakaguchi and

<i>vulpecula</i>												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; 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; 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; Freudenberg 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; 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; 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>Lasiornhinus 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>Phascolarctos cinereus</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)

816 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  
817 log-transformed body mass (BM [kg]), the relative dry matter intake (rDMI [ $\text{g kg}^{-0.75} \text{d}^{-1}$ ]), or  $\text{MRT}_{\text{particles}}$  in 98 (a, c) or 72 (b) mammal species,  
818 respectively, using “being a primate” and the digestion type (caecum fermenter, colon fermenter, nonruminant foregut fermenter, ruminant) as  
819 cofactors as well as the interaction of the two cofactors. A significant interaction indicates different effects between the digestion types in primates  
820 vs. **nonprimates**.  
821

Dependent variable	Corrected model	R <sup>2</sup>	BM	rDMI*	Primate (yes/no)	Digestion type	Primate*(Dig.type)
a)							
$\text{MRT}_{\text{particle}}$	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
$\text{MRT}_{\text{solute}}$	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)							
$\text{MRT}_{\text{particle}}$	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
$\text{MRT}_{\text{solute}}$	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)							
$\text{MRT}_{\text{solute}}$	<0.001, F=17.62	0.58	$\text{MRT}_{\text{particle}}$ 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

822 \*if rDMI was used as a covariable, then the smaller dataset of 72 species was used.

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826 Table 3. Results of General Linear Models, either calculated conventionally (conv) or using Phylogenetic Generalized Linear Least-Squares (PGLS;  
827 used to correct for non-independence of data originating from species related to each other by evolutionary ancestry), relating passage parameters  
828 (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  
829 (rDMI [g kg<sup>-0.75</sup> d<sup>-1</sup>]), or MRT<sub>particles</sub> in 61 (a, c) or 56 (b) non-primate mammal species belonging to one of the four major digestion types (caecum  
830 fermenter, colon fermenter, nonruminant foregut fermenter, ruminant), respectively. Differences between the conventional and the PGLS GLM are  
831 indicated by grey shading.  
832

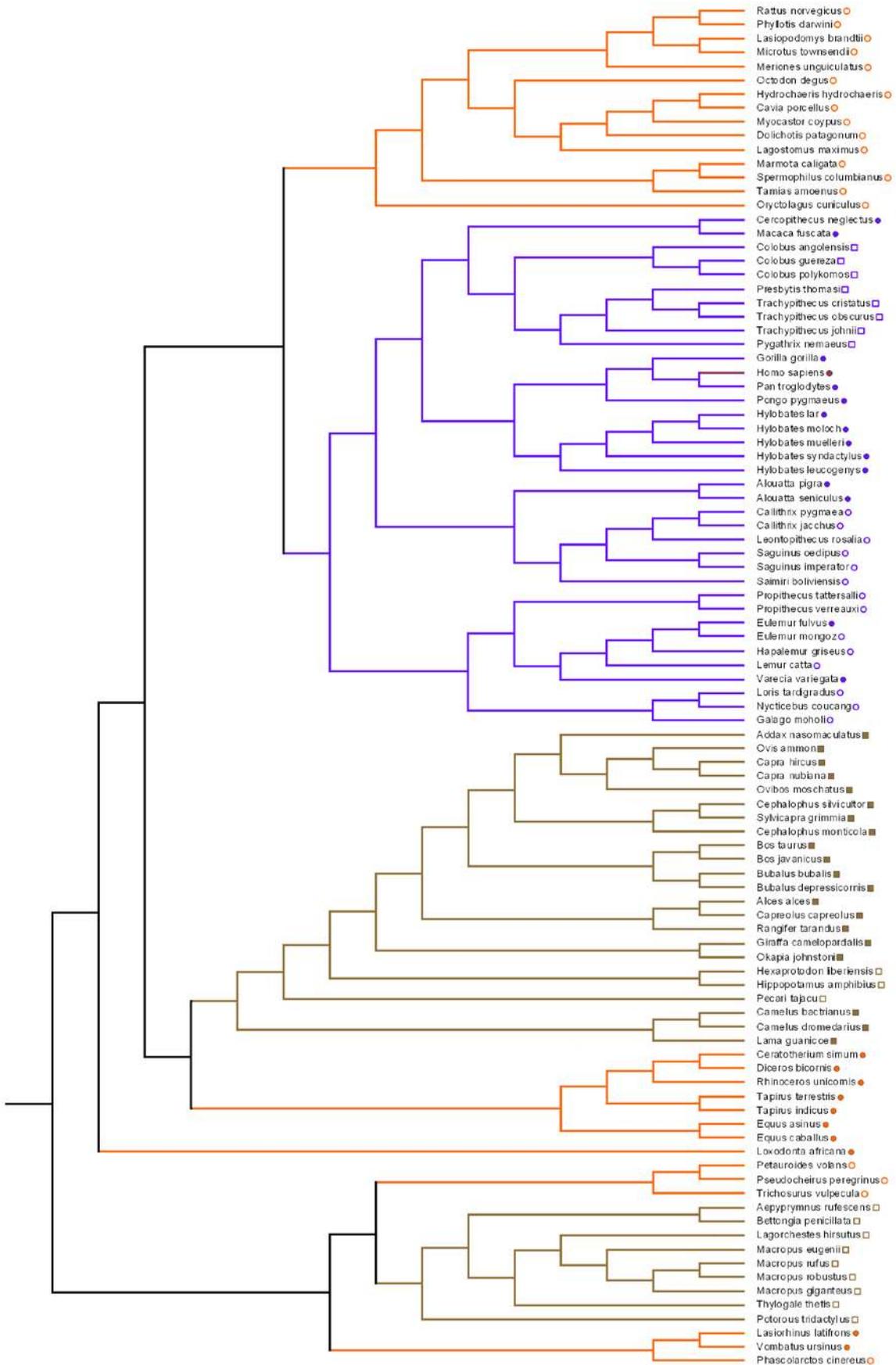
Dependent variable	Statistic	Corrected model	R <sup>2</sup>	BM	rDMI*	Digestion type
a)						
MRT <sub>particle</sub>	conv	p<0.001, F=12.61	0.47	p<0.001, F=19.98	-	p=0.542, F=0.72
	PGLS	p<0.001, F=6.20	0.31	p<0.001, t=3.91	-	p=0.800, x <sup>2</sup> =1.00
MRT <sub>solute</sub>	conv	p=0.064, F=2.37	0.15	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 <sup>2</sup> =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 <sup>2</sup> =14.32
b)						
MRT <sub>particle</sub>	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 <sup>2</sup> =2.36
MRT <sub>solute</sub>	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 <sup>2</sup> =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 <sup>2</sup> =13.46
c)						
MRT <sub>solute</sub>	conv	p<0.001, F=10.07	0.42	MRT <sub>particle</sub> 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 <sup>2</sup> =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 <sup>2</sup> =18.78

833 \*if rDMI was used as a covariable, then the smaller dataset of 56 species was used.  
834  
835

836 Table 4. Results of General Linear Models, either calculated conventionally (conv) or using Phylogenetic Generalized Linear Least-Squares (PGLS;  
837 used to correct for non-independence of data originating from species related to each other by evolutionary ancestry), relating passage parameters  
838 (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  
839 (rDMI [g kg<sup>-0.75</sup> d<sup>-1</sup>]), or MRT<sub>particles</sub> in 37 (a, c) or 16 (b) primate species belonging to one of the three major primate digestion types (caecum  
840 fermenter, colon fermenter, nonruminant foregut fermenter), respectively.  
841

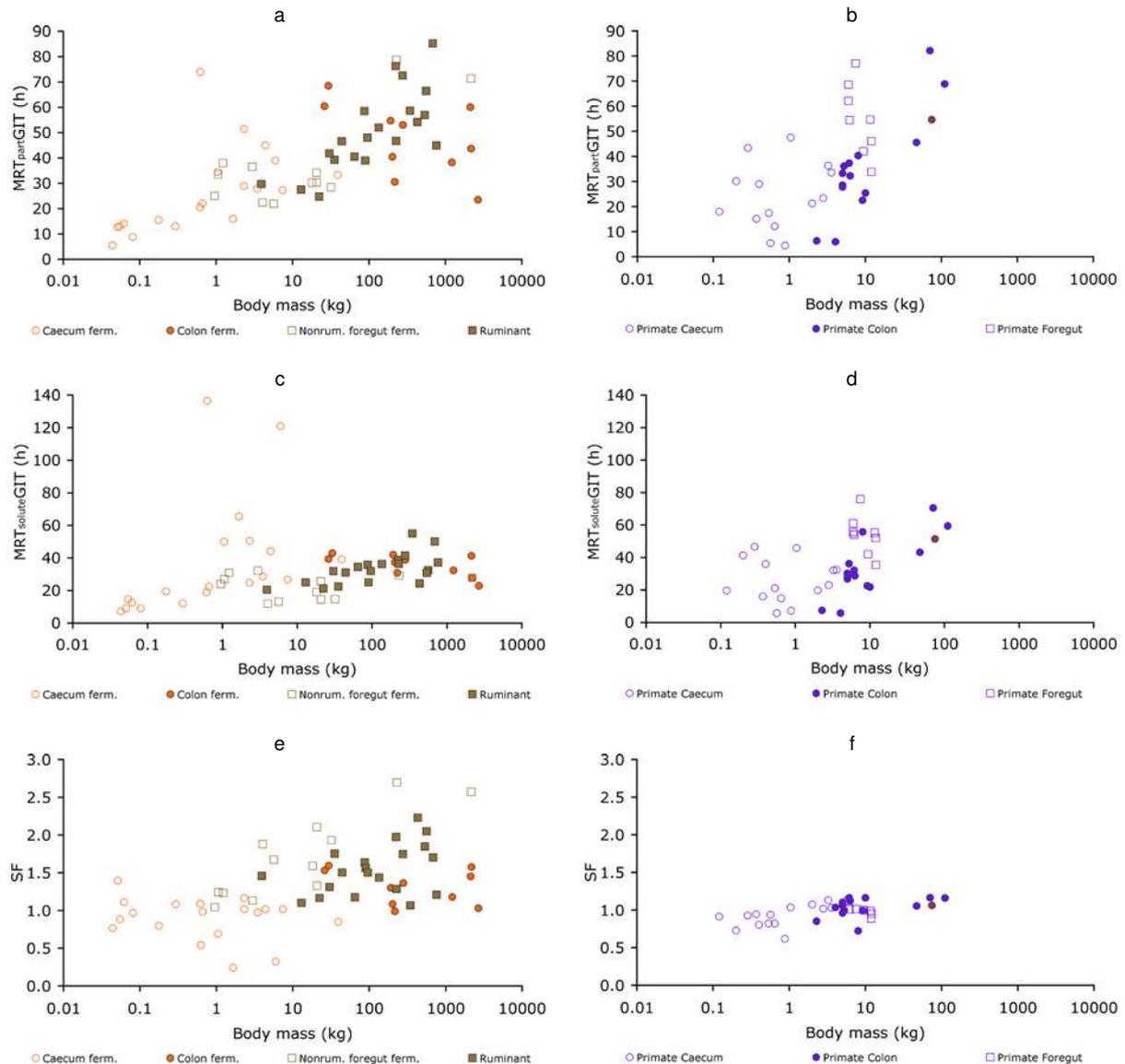
Dependent variable	Statistic	Corrected model	R <sup>2</sup>	BM	rDMI*	Digestion type
a)						
MRT <sub>particle</sub>	conv	p<0.001, F=12.08	0.52	p=0.001, F=13.03	-	p=0.010, F=5.32
	PGLS	p<0.001, F=8.96	0.45	p=0.002, t=3.35	-	p=0.020, x <sup>2</sup> =7.86
MRT <sub>solute</sub>	conv	p<0.001, F=9.21	0.46	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 <sup>2</sup> =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 <sup>2</sup> =0.02
b)						
MRT <sub>particle</sub>	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 <sup>2</sup> =3.88
MRT <sub>solute</sub>	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 <sup>2</sup> =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 <sup>2</sup> =2.16
c)						
MRT <sub>solute</sub>	conv	p<0.001, F=180.6	0.94	MRT <sub>particle</sub> 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 <sup>2</sup> =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 <sup>2</sup> =4.24

842 \*if rDMI was used as a covariable, then the smaller dataset of 16 species was used.  
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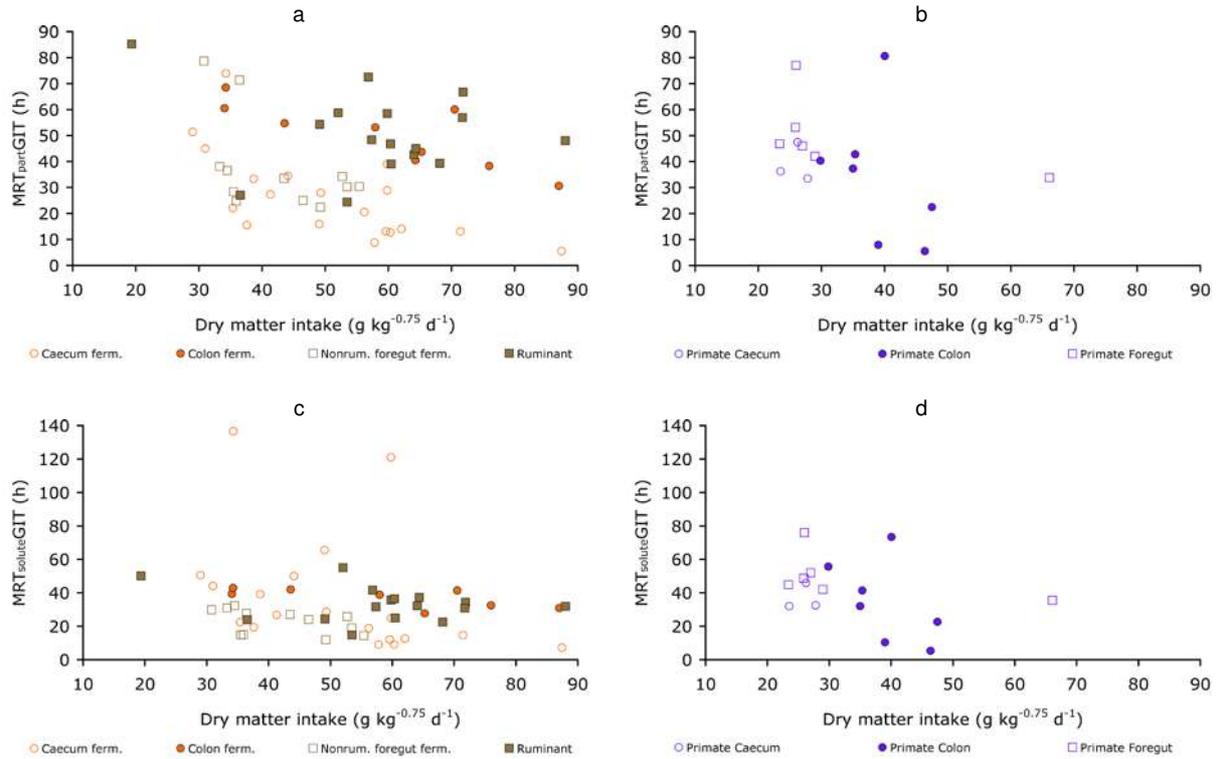
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Figure 1. Phylogenetic tree used in the PGLS analyses (pruned from Bininda-Emonds et al. 2007 with resolved polytomies). Colour codes and symbols correspond to the representation of species in Fig. 2-4.



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851 Figure 2. Relationship between body mass (BM) and mean retention time (MRT) of  
 852 particles in the gastrointestinal tract (GIT) in a) nonprimate mammalian herbivores and  
 853 b) primates, between BM and MRT of solutes in the GIT in c) nonprimate mammalian  
 854 herbivores and d) primates, and between BM and the ratio of  $MRT_{particle\ GIT}$  to  $MRT_{solute\ GIT}$   
 855 (SF) in e) nonprimate mammalian herbivores and f) primates. For data sources see Table  
 856 1; for statistics, see Tables 2 and 3. The purple dot indicates *Homo sapiens*.  
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Figure 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.

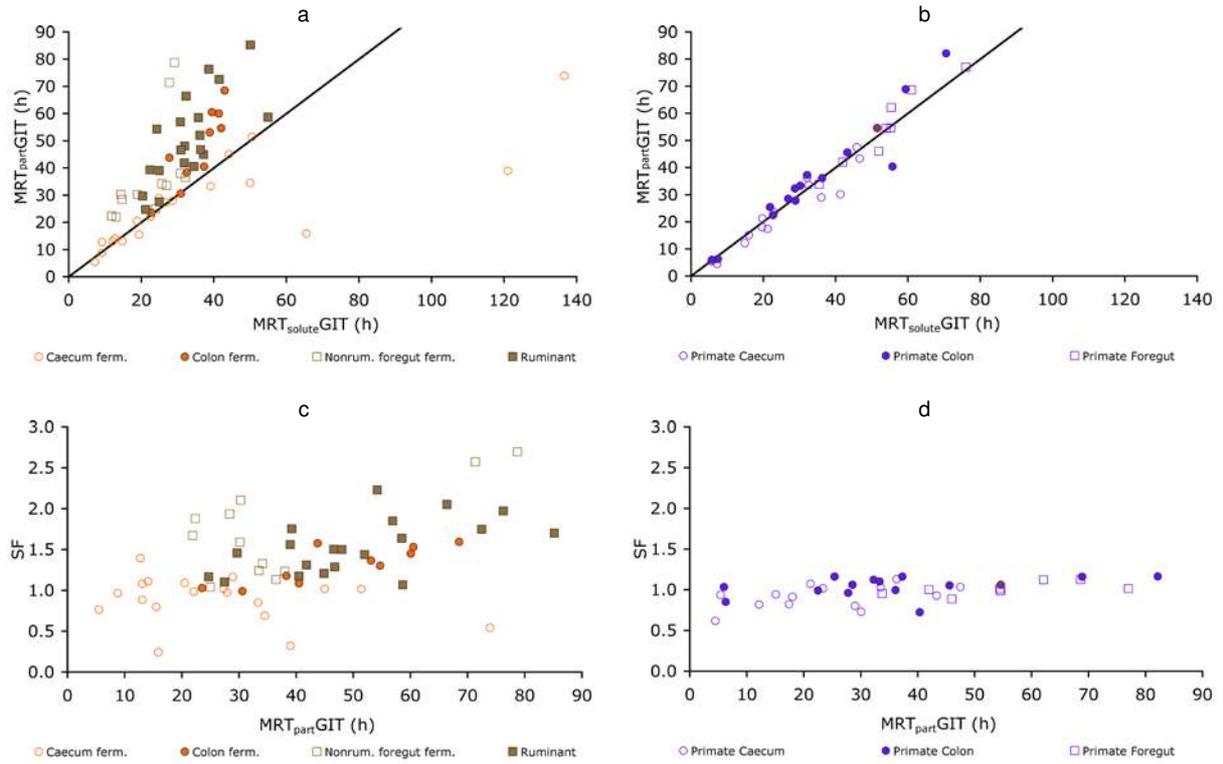


Figure 4. Relationship between the mean retention time (MRT) of solutes and particles in the gastrointestinal tract (GIT) in a) nonprimate mammalian herbivores and b) primates, and between the MRT of particles and the ratio of  $MRT_{particleGIT}$  to  $MRT_{soluteGIT}$  (SF) in c) nonprimate mammalian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