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2 # Gross intestinal morphometry and allometry in primates

3 **Running title: Primate intestinal length**

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24 **Abstract**

25 Although it is generally assumed that among mammals and within mammal groups, those

26 species that rely on diets consisting of greater amounts of plant fiber have larger

27 gastrointestinal tracts (GIT), statistical evidence for this simple claim is largely lacking. We

28 compiled a dataset on the length of the small intestine, caecum and colon in 42 strepsirrhine,

29 platyrrhine and catarrhine primate species, using specimens with known body mass (BM).

30 We tested the scaling of intestine length with body mass, and whether dietary proxies

31 (percentage of leaves and the diet quality index) were significant covariates in these scaling

32 relationships, using two sets of models: one that did not account for the phylogenetic

33 structure of the data, and one that did. Intestine length mainly scaled geometrically at

34 exponents that included 0.33 in the confidence interval; Strepsirrhini exhibited particularly

35 long caeca, while those of Catarrhini were comparatively short. Diet proxies were only

36 significant for the colon and the total large intestine (but not for the small intestine or the

37 caecum), and only in conventional statistics (but not when accounting for phylogeny),

38 indicating the pattern occurred across but not within clades. Compared to terrestrial

39 Carnivora, primates have similar small intestine lengths, but longer large intestines. The data

40 on intestine lengths presented here corroborate recent results on GIT complexity, suggesting

41 that diet, as currently described, does not exhaustively explain GIT anatomy within primate

42 clades.

43

44 **Keywords** primate, anatomy, digestive tract, diet, phylogeny

Introduction

Of the various aspects of mammalian biology where a link between form and function has been investigated, the connection between diet and the morphology of the digestive tract has received considerable attention (Chivers and Langer, 1994). Illustrations of the digestive tracts of herbivores and carnivores make it evident that the digestive tracts of herbivores are more complex (Stevens and Hume, 1998) due to the less digestible nature of their natural diets. Though statistical evidence is lacking (Lavin, Karasov, Ives, Middleton and Garland, 2008; Smith, Parker, Kotzé and Laurin, 2017), it is usually thought that the intestines of herbivorous mammals are longer than those of carnivores (Orr, 1976). When considering gastrointestinal complexity across all eutherian mammal clades, however, there is a less clear-cut relationship between intestine morphology and diet. In particular, while complex hindguts are typically associated with (but not obligatory for) herbivores, complex stomachs are not necessarily linked with high-fiber herbivory, as evidenced by the morphology observed in whales and myomorph rodents (Langer and Clauss, 2018).

Among primates, the morphology of the gastrointestinal tract, both macro- and microscopically, has been suggested to be tightly linked to dietary ecology (Chivers and Hladik, 1980; Martin, Chivers, MacLarnon and Hladik, 1985; Lambert, 1998). Understanding aspects of the anatomy of primates' digestive systems is thought to provide information about the diet to which a particular taxon may be adapted (Ferrari and Lopes, 1995) or its dietary constraints, such as why a species may target or avoid certain food items (Lambert, 1998). Despite the value of broad anatomical comparisons across taxa, relatively few studies have taken an interspecific, phylogenetic approach to the gross anatomy of primate gastrointestinal tracts. Quantitative analyses of gut morphology frequently focus on a small range of taxa (e.g., Ferrari and Martins, 1992; Ferrari, Lopes and Krause, 1993 in callitrichines), and some studies (e.g., Hill, 1958) provide illustrations of primate gastrointestinal tracts, but do not

70   provide measurements. The paucity of recent gross intestinal morphology research may be in

71   part related to the fact that the proportions of different components of the gastrointestinal

72   tract can vary intraspecifically with age (Langer, 1988) or with dietary shifts (Gross, Wang

73   and Wunder, 1985). Nevertheless, the use of relative dimensions can provide information

74   about the relative role of different portions of the tract in a particular subset of species

75   (Chivers and Hladik, 1980; Caton, 1998) and can inform hypotheses about adaptations to

76   different dietary regimes. The enlarged caecum and colon of some strepsirrhines, New World

77   monkeys, cercopithecines, and hominoids (Hladik, Charles-Dominique, Valdebouze, Delort-

78   Laval and Flanzy, 1971; Chivers, 1994), for example, act as fermentation chambers to aid in

79   the digestion of plant foods.

80   On the other hand, it has also been recognized that gastrointestinal form alone is not

81   sufficient to predict diet (Milton, 1987), even though general relationships between gross

82   digestive morphology (e.g., relative gut proportions) and broad dietary categories are

83   expected. Chivers and Hladik (1980) demonstrated an increase in the ratio of combined

84   stomach, caecum, and colon volume to small intestine volume across a continuum of

85   faunivores to frugivores to folivores, although there was substantial overlap between the

86   groups. When Chivers and Hladik considered the surface area of the small intestine, however,

87   no differences between trophic groups were evident. Notably, these analyses were performed

88   prior to the arrival of statistical methods that account for phylogenetic non-independence.

89   When controlling for phylogeny, Langer and Clauss (2018) did not find diet-associated

90   differences in gut complexity among primates.

91   Despite these various lines of research, quantitative data on the digestive tracts of

92   primates are scarce. In order to provide data on intestine length for a larger number of

93   primates, we used the opportunity to take photographs of the digestive tracts of a number of

94   specimens during dissections performed for a study on mammalian body composition

95 (Navarrete, van Schaik and Isler, 2011), and provide photographic evidence for the gross

96 digestive tract morphology of 32 species. Because with any absolute measure, body size will

97 be the main driver of the magnitude, we first investigate the allometric relationship of

98 intestine length with body mass. Based on the general geometric relationship between a

99 length and a volume measure, one would expect intestinal lengths to scale approximately

100 with body mass to the power of 0.33. However, three previous data compilations – on

101 mammals in general (Lavin et al., 2008), on mammalian carnivorans (McGrosky, Navarrete,

102 Isler, Langer and Clauss, 2016) and on ruminants (McGrosky et al., 2019) – unexpectedly

103 yielded higher exponents. The explanation for this phenomenon was, to our knowledge, first

104 proposed by Woodall & Skinner (1993), who suggested that animals should evolve so that

105 their intestinal surface retains a geometric or metabolic scaling (i.e., at an exponent between

106 0.67 and 0.75), but that the diameter of the intestine should scale less-than-geometrically to

107 maintain short diffusion distances, and that hence, to compensate, intestinal length should

108 scale more-than-geometrically. Therefore, a corresponding scaling was expected in primates

109 as well.

110   As a second step, we tested whether proxies of the natural diet influenced the scaling

111 relationships with body mass. Following broad mammalian trends and Chivers and Hladik

112 (1980), we expect both small and large intestine length to increase along a dietary continuum

113 from insectivores to frugivores to folivores.

114

115 **Methods**

116 During the data collection for a different study (Navarrete et al., 2011), a large number of

117 mammalian specimens originating from various sources were dissected by AN; some

118 additional specimens were contributed by MC. Most specimens derived from zoological

119 collections. The specimens were either dissected directly after death or, in the majority of

120   cases, after storage by deep-freezing and thawing. Body mass (BM) was recorded, and the

121   gastrointestinal tracts were dissected by removing mesenteries. The intestinal tract was laid

122   out according to common practice for anatomical documentation (Stevens and Hume, 1995),

123   placing the intestine as a straight line without stretching, and photographs (with scale) were

124   taken for later measurement. For measurements, the caecum served as the defining border

125   between the small and the large intestine. Length of the different sections was determined

126   using the polyline VOI tool of the MIPAV biomedical imaging software (version 14.0,

127   National Institutes of Health), which facilitated tracing the length of the intestine directly on

128   the digital photo and converting pixel length into centimeters.

129   For some large-sized specimens, the intestine was cut into several pieces prior to

130   photography. Photographs of these specimens were not manipulated to create the impression

131   of an uninterrupted intestine. The only photo manipulations included the deletion of

132   background and, in some cases, adjustment of the brightness and color of the images and a

133   mirroring to achieve a consistent position of the stomach.

134   Additional data were collected from the literature, but only if the original BMs of the

135   specimens investigated were reported together with the length measurements; this led to the

136   exclusion of many published intestine length measurements. When several specimens were

137   available for a species, averages for both BM and the respective measurements were

138   calculated; in doing so, we always ensured the averaged BM matched the averaged gut

139   section measure.

140   Data on the natural diet of the investigated species, as the percentage of leaves in the

141   overall diet (as generally the diet items most requiring microbial fermentation) and the diet

142   quality index (to account not just for one but the range of diet items), were taken from a

143   literature collection based on three publications (Van Woerden, van Schaik and Isler, 2010,

144   2014; Van Woerden, Willems, van Schaik and Isler, 2012), supplemented with additional

145   information (for a full set of sources, see Table S1). The diet quality index represents a sum

146   of each dietary item, multiplied by a factor that is higher for more digestible diet items (8 for

147   insects, 5 for fruits/seeds/flowers, 3 for young leaves, 1 for mature leaves) and is weighted

148   for the proportion of these items in the diet (Van Woerden et al. , 2010). All species-specific

149   data are given in Table 1.

150   Allometric relationships were investigated using linear regressions on log-transformed

151   data according to Length = a BM^b, with 95% confidence intervals for parameter estimates,

152   for the whole dataset and for individual clades. Additionally, the same analysis was

153   performed with clades as cofactors, and the clade x BM interactions, to directly test for

154   differences between the clades. Proxies of the natural diet were added to the linear

155   regressions on log-transformed data as covariates (only one proxy per model, i.e. either the

156   percentage of leaves, or the diet quality index). Initially, models including the BM x diet

157   proxy interaction were also included, but because there were no significant interactions,

158   results are only presented here for models without interactions. Analyses were performed

159   using Generalized Least Squares (GLS) and Phylogenetic Generalized Least Squares (PGLS),

160   using a consensus phylogenetic tree downloaded from the 10kTrees Project (version 3;

161   Arnold, Matthews and Nunn, 2010). The phylogenetic signal (Pagel's λ) was estimated using

162   maximum likelihood (Revell, 2010). λ can vary between 0, indicating no phylogenetic signal,

163   and 1, indicating a strong phylogenetic signal and that similarity among species scales in

164   proportion to their shared evolutionary time (Pagel, 1999; Freckleton, Harvey and Pagel,

165   2002). Statistical tests were performed using the package caper (Orme et al., 2010) in *R*

166   2.15.0 (Team, 2011). The significance level was set to 0.05.

167   Finally, the data of primates were compared visually to data from terrestrial Carnivora

168   including canids, mustelids, ursids, mephitids, procyonids, felids, hyenids, herpestids and

169   viverrids, but excluding pinnipeds (McGrosky et al., 2016).

170

Results

172 Among the Strepsirrhini, lemurs appear to have particularly long caeca (Fig. 1) compared to

173 the gummivorous cheirogalids (Fig. 2). The latter have smaller caeca, although their caeca

174 still appear proportionally larger than those of the gummivorous callitrichids (Fig. 3). The

175 non-gummivorous cebids studied here all have similar digestive tracts (Fig. 4). Atelids have

176 an unremarkable caecum that appears part of a large proximal colon (Fig. 5), whereas the

177 caecum of the pitheciids is more distinct (Fig. 5). Among the Catarrhini, colobines have a

178 voluminous forestomach, as well as a distinct caecum and an enlarged proximal colon (Fig.

179 6). The hindgut of many non-colobine Catarrhini is voluminous and haustrated, with a short,

180 broad caecum (Fig. 7-10). In the apes, the caecum bears a clearly visible, vermiform

181 appendix (Fig. 10).

182 When using the complete gastrointestinal morphology dataset, as well as Strepsirrhini-

183 and Platyrrhini-specific datasets, there was a strong, significant phylogenetic signal,

184 indicating that the data scatter is guided by the phylogenetic structure in the datasets.

185 However, this strong phylogenetic signal was generally not observed within Catarrhini (Table

186 2). Across all species, the scaling exponent typically included 0.33 in the 95% confidence

187 interval, indicating geometric scaling (Table 2). The 95% confidence intervals for the

188 allometric factors (a) and scaling exponents (b) generally overlapped between the clades,

189 with the exception of both the factor and exponent of the caecum, which were higher in the

190 Strepsirrhini (Table 2). This observation was corroborated by the models that tested the

191 scaling including the clade and clade x BM interactions, where the Strepsirrhini x BM

192 interaction was significant both in GLS ($P = 0.009$) and PGLS ($\lambda = 0.73$; $P = 0.017$),

193 indicating a steeper scaling of the caecum with BM for this clade (Fig. 11). Additionally,

194 although the corresponding 95% confidence intervals for a overlapped, the analyses for small

195   intestine length and total intestine length indicated significantly smaller values for Platyrrhini

196   (small intestine: GLS $P = 0.015$; PGLS $\lambda = 0.73$, $P = 0.018$; total intestine: GLS $P = 0.032$;

197   PGLS $\lambda = 0.80$, $P = 0.035$; in all cases, with non-significant interaction terms; Fig. 11).

198   While the scaling exponent of GLS models was generally very similar to that of PGLS

199   models (Table 2 and S2), the GLS scaling exponent for the caecum in the complete dataset

200   was very low (due to the long caeca of small-bodied strepsirrhines) and excluded geometric

201   scaling in the confidence interval (0.16; 95%CI 0.04-0.29; Fig. 11). However, PGLS analyses

202   indicated a generally geometric scaling of the caecum (0.41; 95%CI 0.25-0.56; Table 2).

203   Neither the percentage of leaves in the diet nor diet quality index exhibited a significant

204   effect on intestinal length in any of the models, including models of caecum length (P always

205   > 0.05). The only exceptions to this trend included significant GLS models of colon and total

206   large intestine length for the percentage of leaves dataset and the diet quality index (GLS:

207   colon – leaves $P = 0.045$; colon – diet index $P = 0.008$; large intestine – leaves $P = 0.066$;

208   large intestine – diet index $P = 0.011$). In PGLS, these dietary effects were no longer

209   significant, indicating that variation in large intestine length with diet occurred mainly across

210   and not within clades (PGLS: colon – leaves $P = 0.402$; colon – diet index $P = 0.075$; large

211   intestine – leaves $P = 0.648$; large intestine – diet index $P = 0.231$). Using the diet quality

212   index and the relative colon length (in cm/BM$^{0.33}$), Figure 12 illustrates how the phylogenetic

213   structure of the dataset explains the colon – diet index relationship: within clades, there is

214   little correlation between the measurements, and any trend within Strespirrhini or Platyrrhini

215   is due to a particular genus, not due to similar variation in several genera; the position of the

216   clades, however, suggests the expected negative relationship. For a more detailed graph

217   including the phylogenetic tree and the distribution of these two measures across it, see Fig.

218   S1.

219   When compared to terrestrial Carnivora, the total intestines of primates are generally

220   slightly longer (Fig. 11). This holds particularly true for the colon, and the caecum of the

221   Strepsirrhini. By contrast, the caecum of the Catarrhini was of a magnitude also observed in

222   many terrestrial Carnivora.

223

224   **Discussion**

225   Using what is to our knowledge the most comprehensive dataset on primate intestine lengths

226   directly linked to the body mass of the same specimens, the present study largely

227   corroborates well-known features of different primate groups and in part confirms broad

228   macroanatomical concepts about differences in intestinal length between carnivores and

229   herbivores. However, it also demonstrates that, in primates, correlations of length measures

230   of the different intestinal sections with the natural diet may not be as clear-cut as is often

231   assumed.

232   The photographic evidence provided can be compared to drawings and reports from the

233   literature. While we do not want to dwell on this in detail here, some points of interest shall

234   be mentioned. Fisher (2000) explained a reliable classification of species with respect to

235   whether they have a true 'appendix' or not requires more than visual inspection, including

236   histology, and ontogenetic series. Several species that have been classified as having an

237   appendix in comparative datasets (e.g., Smith et al., 2017), including *Eulemur* spp. (Fig. 1)

238   and *Callithrix* spp. (Fig. 3), did not have a vermiform structure that was clearly

239   distinguishable. For *Papio hamadryas*, a variable disposition with respect to the presence of

240   an appendix has been assumed (Smith et al., 2017), with our specimen not showing

241   macroscopic evidence of a vermiform structure (Fig. 9). With respect to *Varecia* spp. or

242   *Lemur catta*, it is evident that the macroscopic appearance could be interpreted both ways

243   (Fig. 1), and that further investigations as recommended by Fisher (2000) would be required

244   for a reliable assessment.

245   A series of limitations applies to the present study. Our own and the literature data

246   represent a mixture of measurements taken from freshly dissected specimens and specimens

247   dissected after frozen storage and thawing. While we do not think that this has a relevant

248   effect on macroscopic length measurements, readers that question this assumption should

249   therefore consider the results with extra caution. In our view, it needs to be mentioned that

250   length measurements of intestinal structures should rather be considered as indicating

251   magnitudes, and not precise data (hence, we give no decimals in Table 1). When laying out

252   intestines for length measurements, details such as the dryness of the organ and the

253   smoothness of the surface used for measuring can influence whether an unintentionally

254   stretched organ can contract again or retains the stretched disposition, for example. A further

255   kind of caveat that needs to be mentioned refers to the use of a consensus tree (here, from the

256   10kTrees Project) rather than testing a whole distribution of trees. The standpoint, adopted

257   intuitively in the present study, that absence of a signal when using the consensus tree is

258   meaningful, could of course be questioned, and the data could be explored using the whole

259   distribution of trees available.

260   However, the main limitations of the present study are its reliance on mainly captive

261   specimens, and the low sample size for the majority of the included species that also

262   precludes tests of ontogenetic changes. Freckleton, Harvey, & Pagel (2002) demonstrated

263   that at lower species numbers below 20, a phylogenetic signal may not be always detected

264   reliably, whereas a wrong detection of a phylogenetic signal is rare. In our analyses, this was

265   also reflected in the finding that confidence intervals for λ could often not be calculated

266   (Table 2). Among the Strepsirrhini (n=11) and Platyrrhini (n=14), the limited number of

267   species might have been responsible for the finding that small intestine length and colon

268   length (and hence also large intestine and total intestine length) showed a phylogenetic

269   signal. This phylogenetic signal indicates that variation in these measures and clades was

270   mainly an effect across, and not within, the included taxonomic subgroups. Notably, this did

271   not apply to the Catarrhini, for which we obtained a larger sample size (n=17). In contrast,

272   the fact that no phylogenetic signal was evident in strespirrhine caecum length suggests that a

273   long caecum that increases in length with body mass is a common feature across various

274   strepsirrhine subgroups. For more confidence in the phylogenetic signal of intestinal length

275   measurements, a larger species sample would be required. This would also help to clarify if

276   primates are really different from carnivores, ruminants or mammals in general (Lavin et al.,

277   2008, McGrosky et al., 2016, 2019), which all show a more-than-geometrically scaling of

278   intestine length, possibly to achieve geometrical constancy of absorptive intestinal surface

279   while keeping diffusion distances in the instestine small by increasing the intestinal diameter

280   at less-than-geometrically scaling (Woodall and Skinner, 1993). The large 95% confidence

281   intervals for the scaling exponents in the present study do not allow a clear answer to this

282   question.

283   Another limitation becomes evident given the absence of a clear dietary signal in

284   intestinal length measurements, and is inherent to our study design: intestinal length is

285   possibly poorly correlated with diet. Other measures, notably the volume or the actual gut fill

286   (Clauss, Schwarm, Ortmann, Streich and Hummel, 2007; Müller et al., 2013), are most likely

287   more meaningful correlates with diet, as mammalian herbivores generally have more

288   voluminous (yet not necessarily longer) intestines. Chivers and Hladik (1980) addressed this

289   fact by using intestinal surface area rather than length for some of their analyses. Notably,

290   they did not find a significant difference in small intestine surface area between diet groups,

291   and they did not report results for the large intestine or caecum in isolation, as done in the

292   present study, where any dietary signal that derives from the anatomy of the stomach and

293   forestomach was excluded. The often-cited patterns between gut morphology and diet

294   described by Chivers and Hladik (1980) always represent a composite signal in which the

295   volume or surface area of the (fore)stomach and the large intestine are summed up before

296   evaluation. However, even using this composite signal, their study revealed substantial

297   overlap between faunivores, frugivores and folivores. Additionally, affiliation to dietary

298   groups varied, depending on whether anatomical surface or volume measurements were used;

299   while colobine monkeys were exclusively grouped as folivores in terms of volume measures

300   (Fig. 20 in Chivers and Hladik, 1980), they were also depicted within the range of frugivores

301   in terms of surface measures (Fig. 18 of their study).

302   Nevertheless, the present study provides evidence for the functional relationship between

303   colon or large intestine length and diet, as postulated previously (Hladik, 1978; Chivers,

304   1994). Similar to the findings on gastrointestinal complexity of Langer and Clauss (2018),

305   GLS models revealed a significant relationship between diet and large intestine length.

306   However, in both Langer and Clauss (2018) and the present study, these effects were not

307   significant when accounting for the phylogenetic structure of the data using PGLS. This

308   indicates that these effects do not occur within the different primate clades and therefore

309   cannot be considered convergent between them in the respective datasets. Rather, the pattern

310   occurs at deeper nodes of the phylogeny in each dataset, to the extent that clades as a whole

311   differ in both, the GIT and the diet measure. The lack of significance in PGLS, or, in other

312   words, the lack of evidence for dietary convergence, should not encourage the interpretation

313   of a lack of a functional relationship. The relationship is just not evident *within* clades, but

314   only *across* the clades included in this study. This could lead to the traditional interpretation

315   often applied to non-significant findings when accounting for phylogeny, i.e. clade-specific

316   characteristics other than diet (represented by 'phylogeny') led to the evolution of longer or

317   more complex large intestines in those taxa that also ingest more leaves. Alternatively, it

318   suggests that clade diversification in primates followed, to a large extent, dietary niche and

319   concomitant intestinal adaptations, but that diet diversification within clades left less reliable

320   marks on intestinal anatomy. Reporting only one result, such as – in the case of a significant

321   phylogenetic signal – the PGLS result while ignoring the GLS result, as sometimes

322   recommended in the biological literature (Freckleton, 2009), would leave this observation

323   unrecognized.

324   With respect to length, primates do not appear to differ from terrestrial carnivores for the

325   small intestine where auto-enzymatic digestion occurs. However, as also described by Martin

326   (1990) and Lambert (1998), primates generally have a longer large intestine (a site of allo-

327   enzymatic digestion), which coincides with their generally higher reliance on diets that

328   contain plant cell walls compared to carnivores. The difference in the intestinal segment by

329   which primates achieve a longer large intestine resembles the pattern observed between other

330   large (e.g., perissodactyl) and small (e.g., rodents and lagomorphs) hindgut-fermenting

331   herbivores (Stevens and Hume, 1998); while smaller species typically have particularly large

332   caeca and are often called 'caecum fermenters', larger species also possess a voluminous

333   colon for allo-enzymatic digestion. This pattern is reflected in the differences between the

334   larger Catarrhini and the smaller Strepsirrhini and Platyrrhini, which both have larger caeca

335   compared to the Catarrhini (Fig. 12D). The difference in caecum size and shape between

336   these groups has been known for some time (Reider, 1936; Scott, 1980). One can only

337   speculate that for smaller species, the retention times necessary for allo-enzymatic fiber

338   digestion are more easily achieved by a larger dead-end structure such as the caecum rather

339   than by a larger colon.

340   Ultimately, primate clades have a typical mammalian macroscopic appearance of their

341   gastrointestinal tracts. The measure of intestinal length in primates matches broad statements

342   about differences between carnivorous and herbivorous species mentioned in the

343 Introduction, and, in the case of the large intestine, about the effect of natural diets on primate

344 intestinal length. Within primates, however, dietary effects are found only across but not

345 within clades, as models of the effect of diet on intestine length are only significant if the

346 phylogenetic structure of the dataset is not accounted for. Within primate clades, dietary

347 specialization as measured in our dataset has little power to explain intestinal length

348 measures.

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495 **Table 1** Average (±S.D.) body mass (g) and intestinal length (cm) measurements of primate species

Species (Clade[a])	Source	n	Body mass	Small intestine	Caecum	Colon	Large intestine[b]	Total intestine	%leaves in natural diet[c]	Diet quality index[c]
Alouatta sara (P)	1	2	3950 (±636)	123 (±11)	6 (±5)	74 (±3)	80 (±1)	202 (±10)	50	NA
Alouatta seniculus (P)	2	1	635	239	12	58	70	309	48	328
Ateles paniscus (P)	1	1	8070	211	13	60	73	283	8	456
Callthrix argentata (P)	1	1	242	43	4	23	28	70	0	NA
Callithrix jacchus (P)	1,3	5	323 (±30)	58 (±14)	5 (±1)	25 (±13)	30 (±12)	88 (±27)	0	519
Cebuella pygmaea (P)	1	1	163	41	5	24	29	69	0	599
Cebus apella (P)	1	1	1750	145	5	34	39	184	16	543
Cheirogaleus medius (S)	1	2	197 (±49)	114 (±0)	5 (±0)	16 (±3)	21 (±3)	135 (±3)	4	549
Chiropotes satanas (P)	2	1	3130	282	19	48	67	349	1	504
Chlorocebus pygerythrus (C)	1	1	5300	176	7	67	74	250	10	526
Colobus guereza (C)	1	2	9750 (±354)	278 (±57)	8 (±0)	104 (±22)	112 (±22)	390 (±79)	61	348
Eulemur coronatus (S)	4	1	1580	99	14	55	69	168	3	493
Eulemur fulvus (S)	1	1	2500	91	16	57	73	164	25	396
Eulemur macaco (S)	1	2	1875 (±530)	125 (±20)	26 (±6)	66 (±1)	92 (±5)	217 (±15)	45	454
Gorilla gorilla (C)	1,5	2	154648 (±102032)	810 (±299)	18[d]	139[d]	162 (±8)	972 (±307)	61	359
Hapalemur griseus (S)	6	4	648 (±106)	86 (±16)	7 (±4)	50 (±6)	57 (N.R.)	144 (N.R.)	100	296
Homo sapiens (C)	9	6	65300 (±14471)	678 (±138)	8 (±2)	146 (±16)	154 (±15)	831 (±144)	30	NA
Lemur catta (S)	1	3	2117 (±144)	156 (±43)	24 (±7)	86 (± 24)	111 (±28)	267 (±71)	32	432
Leontopithecus chrysomelas (P)	1	3	642 (±98)	101 (±12)	5 (±1)	27 (±4)	32 (±4)	133 (±15)	0	490
Macaca arctoides (C)	1	4	14525 (±3495)	297 (±51)	7 (±2)	125 (±47)	132 (±45)	429 (±95)	40	NA
Macaca cyclopis (C)	7	6	119667 (±1783)	230 (±29)	6 (±1)	79 (±7)	85 (±7)	315 (±30)	23	470
Macaca fuscata (C)	1	1	11970	434	5	121	126	560	32	372
Macaca nigra (C)	1	1	5600	295	8	113	121	415	2	596
Macaca sylvanus (C)	1	1	9625	334	7	163	170	504	11	430
Mandrillus sphinx (C)	1	1	23000	515	8	189	197	713	8	482
Mirza zaza (S)	1	1	336	82	4	34	38	120	38	420
Nomascus leucogenys (C)	1	1	6550	449	13	83	96	545	59	356
Pan paniscus (C)	1	1	37730	527	12	234	245	773	24	415
Papio hamadryas (C)	1	2	23250 (±8132)	426 (±161)	10 (±2)	148 (±12)	158 (±10)	585 (±172)	28	401
Pithecia pithecia (P)	1,2	3	1467 (±339)	191 (±25)	11 (±4)	56 (±17)	67 (±21)	258 (±46)	9	492
Pongo pygmaeus (C)	9	1	56250	559	23	328	351	910	48	458
Propithecus tattersalli (S)	6	1	2760	362	37	252	289	651	39	378
Propithecus verreauxi (S)	6	2	3890 (±438)	365 (±38)	39 (±7)	364 (±42)	403 (N.R.)	767 (N.R.)	53	302
Saguinus fusicollis (P)	1	1	330	81	2	22	25	106	0	614
Saguinus oedipus (P)	1	4	460 (±211)	75 (±8)	5 (±1)	29 (±9)	33 (±10)	109 (±17)	0	NA
Saimiri boliviensis (P)	1	1	1003	144	5	18	22	166	0	500
Saimiri sciureus (P)	1,2,8	22	678 (±117)	104 (±17)	4 (±1)	12 (±4)	16 (±4)	120 (±21)	0	684
Symphalangus syndactylus (C)	1	1	8500	298	5	60	65	362.46	45	435
Theropithecus gelada (C)	1	1	11400	227	4	121	125	352	94	313
Trachypithecus vetulus (C)	1	1	5000	305	9	83	92	397	45	300
Varecia rubra (S)	1	1	4200	162	35	72	108	269	12	454
Varecia variegata (S)	1	1	3520	102	25	51	75	178	9	472

496 NA not available

497 [a] C Catarrhini, P Platyrrhini, S Strepsirrhini
498 [b] including caecum length
499 [c] for sources, see Table S1
500 [d] caecum & colon length only obtained from the present study
501 Sources: 1 present study; 2 Fooden (1964); 3 Caton, Hill, Hume and Crook (1996); 4 Schwitzer (2009); 5 Steiner (1954); 6 Campbell, Eisemann, Williams and Glenn (2000); 7 Makita et al. (1984); 8 Beischer and
502 Furry (1964); 9 Chivers (pers. comm.): for a previous study on mammal body composition (Navarrete et al. 2011), handwritten notes of Dr. Chivers were obtained of files used in preparation of his publication on
503 mammal digestive tract anatomy (Chivers and Hladik 1980); while these notes did not record the lengths of the intestines for the species included in that publication, they contained measurements of some additional
504 specimens.

505 **Table 2** Phylogenetic signal (λ) and allometric relationships between intestinal length
506 measures (in cm) and body mass (BM, in kg) according to Length = a BM^b with 95%
507 confidence intervals for parameter estimates from analyses using Phylogenetic Generalized
508 Least Squares

Length of	n	λ (95%CI)	a (95%CI)	b (95%CI)
Total intestine	42	0.82 (0.47; 0.96)	187 (123; 287)	0.38 (0.30; 0.47)
Strepsirrhini	11	1.00 (0.40; NA)	217 (127; 371)	0.47 (0.15; 0.79)
Platyrrhini	14	0.72 (NA; NA)	156 (134; 181)	0.41 (0.30; 0.51)
Catarrhini	17	0 (NA; 0.46)	198 (146; 269)	0.34 (0.24; 0.45)
Small intestine	42	0.80 (0.37; 0.94)	130 (86; 198)	0.38 (0.29; 0.47)
Strepsirrhini	11	1.00 (0.57; NA)	141 (94; 213)	0.31 (0.07; 0.56)
Platyrrhini	14	0.66 (NA; 0.97)	115 (93; 142)	0.45 (0.30; 0.60)
Catarrhini	17	0 (NA; 0.58)	143 (101; 203)	0.34 (0.22; 0.46)
Caecum	42	0.92 (0.62; NA)	7.1 (3.2; 15.9)	0.41 (0.25; 0.56)
Strepsirrhini	11	0 (NA; 0.79)	12.3 (10.5; 14.5)	0.76 (0.61; 0.91)
Platyrrhini	14	0.77 (NA; NA)	6.2 (4.5; 8.4)	0.39 (0.18; 0.61)
Catarrhini	17	0 (NA; 0.69)	3.9 (2.1; 6.9)	0.29 (0.09; 0.48)
Colon	42	0.94 (0.76; 0.99)	46 (23; 93)	0.38 (0.25; 0.51)
Strepsirrhini	11	1.00 (0.77; NA)	61 (37; 100)	0.60 (0.30; 0.89)
Platyrrhini	14	0.75 (0.07; NA)	31 (23; 42)	0.29 (0.09; 0.49)
Catarrhini	17	0 (NA; 0.81)	49 (32; 76)	0.33 (0.19; 0.48)
Large intestine	42	0.94 (0.74; 1.00)	55 (28; 106)	0.38 (0.26; 0.50)
Strepsirrhini	11	1.00 (0.60; NA)	75 (47; 120)	0.64 (0.35; 0.92)
Platyrrhini	14	0.82 (0.20; NA)	38 (29; 49)	0.31 (0.13; 0.48)
Catarrhini	17	0 (NA; 0.76)	54 (36; 82)	0.33 (0.19; 0.47)

509 NA - no respective confidence limit available
510 for GLS results, see Table S1

Eulemur fulvus

5 cm

Eulemur macaca

5 cm

Varecia rubra

5 cm

Varecia variegata

5 cm

Lemur catta

5 cm

511
512   **Figure 1** Digestive tracts of various lemur species. Note the long caecum in all species.

Cheirogaleus medius   5 cm   *Mirza zaza*   5 cm

513
514   **Figure 2** Digestive tracts of two cheirogalid species.

Callithrix argentata   5 cm

Callithrix jacchus   5 cm

Leontopithecus chrysomelas   5 cm

Saguinus fusicollis   5 cm

Saguinus oedipus   5 cm

515
516   **Figure 3** Digestive tracts of five callitrichid species.

Saimiri boliviensis   5 cm

Cebus apella   5 cm

Saimiri sciureus   5 cm

517
518   **Figure 4** Digestive tracts of three cebid species.

Alouatta sara

5 cm

Ateles paniscus

5 cm

Pithecia pithecia

5 cm
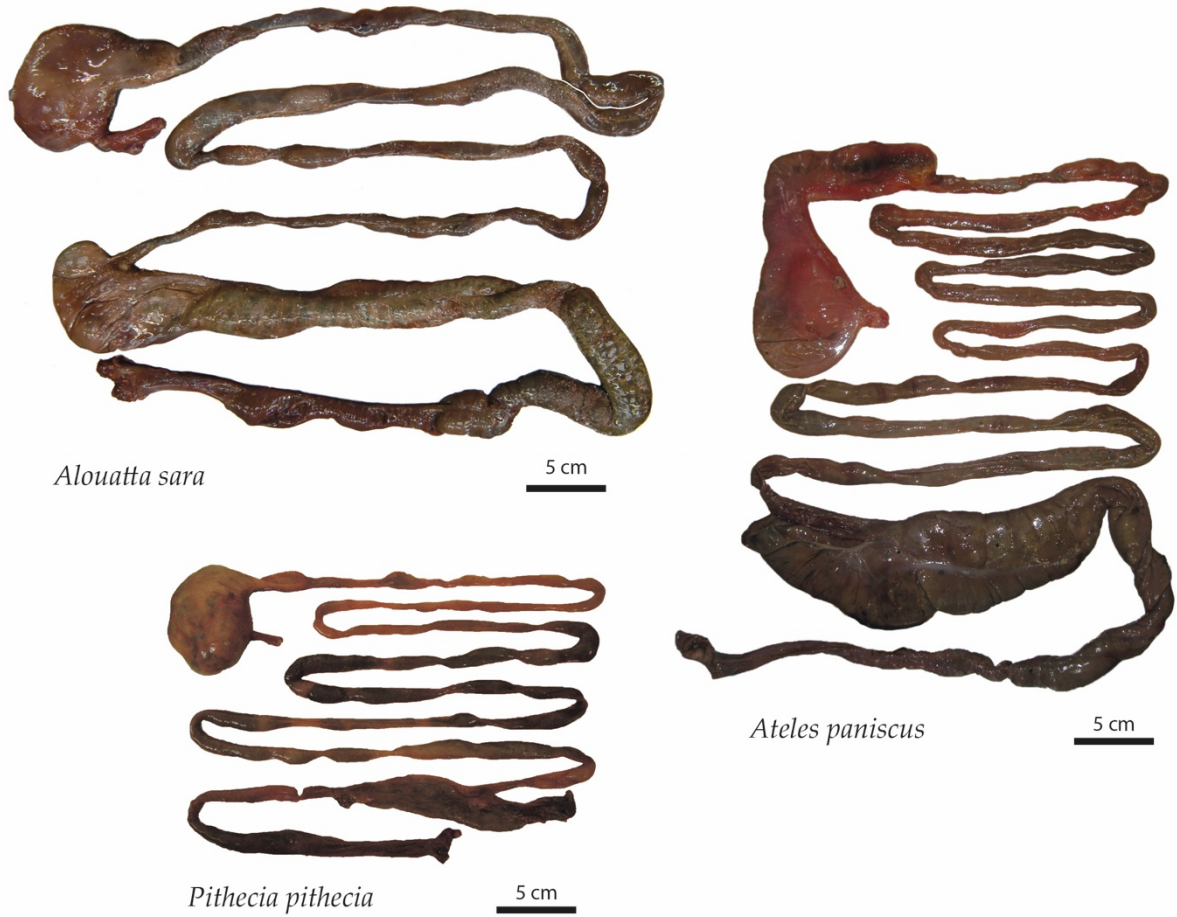
519
520   **Figure 5** Digestive tracts of two atelid and one pitheciid species.

Colobus guereza

5 cm

Trachypithecus vetulus

5 cm

521
522 **Figure 6** Digestive tracts of two colobine species.

Chlorocebus pygerythrus

5 cm

523
524   **Figure 7** Digestive tract of *Chlorocebus*.

Macaca arctoides

5 cm

Macaca fuscata

5 cm

Macaca sylvanus

5 cm

Macaca nigra

5 cm

525
526 **Figure 8** Digestive tracts of four macaque species. The * indicates where the small intestine
527 was linked before dissection.

Papio hamadryas

5 cm

Mandrillus sphinx

5 cm

Theropithecus gelada

5 cm

528
529 **Figure 9** Digestive tracts of three baboon species. The * marks where the small intestine was
530 linked before dissection.

Nomascus leucogenys   5 cm

Symphalangus syndactylus

Gorilla gorilla   15 cm

Pongo pygmaeus   10 cm
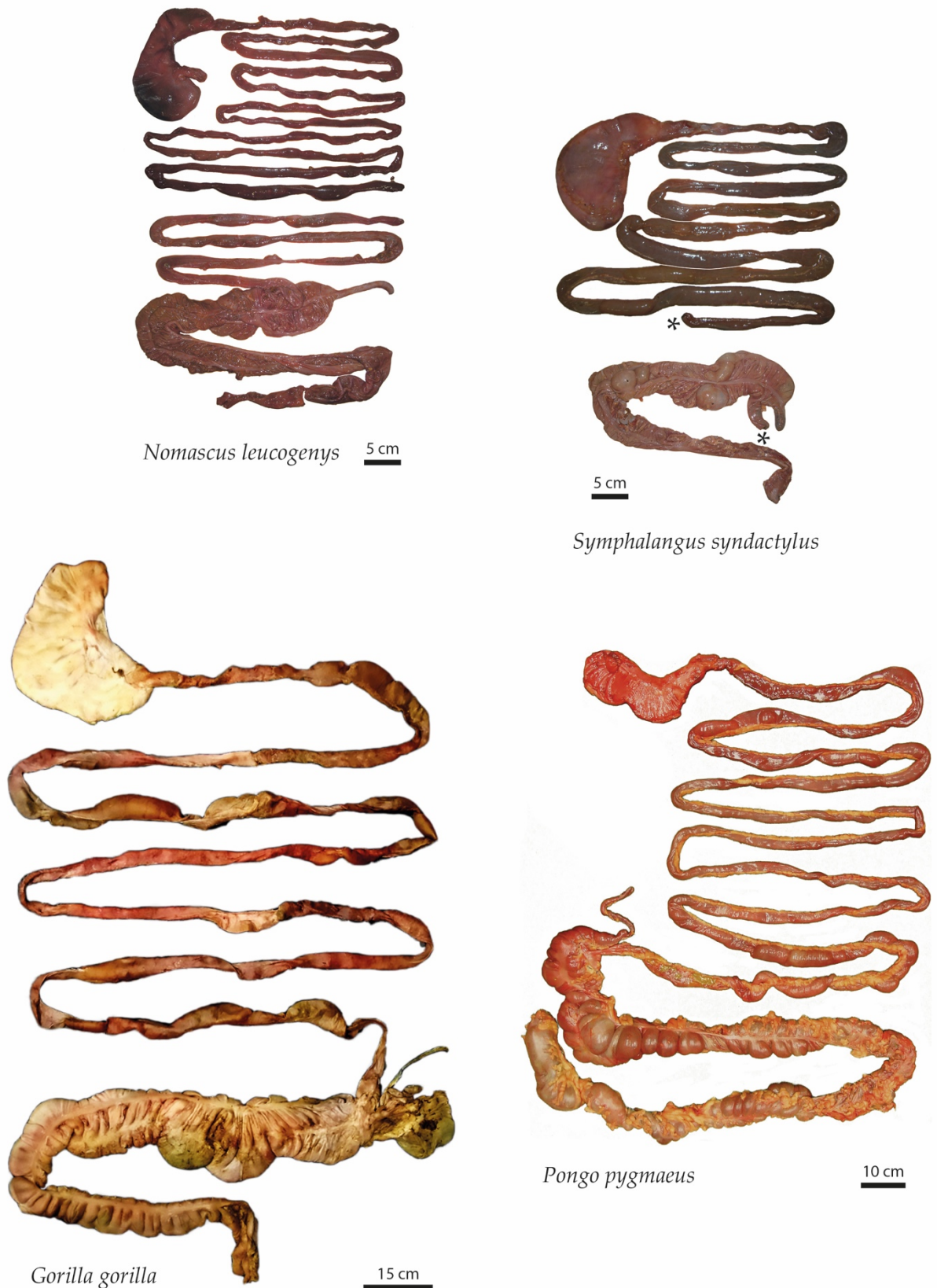
531
532   **Figure 10** Digestive tracts in four ape species. The * marks where the small intestine was
533   linked before dissection. Note the caecal appendix in all four species.
534
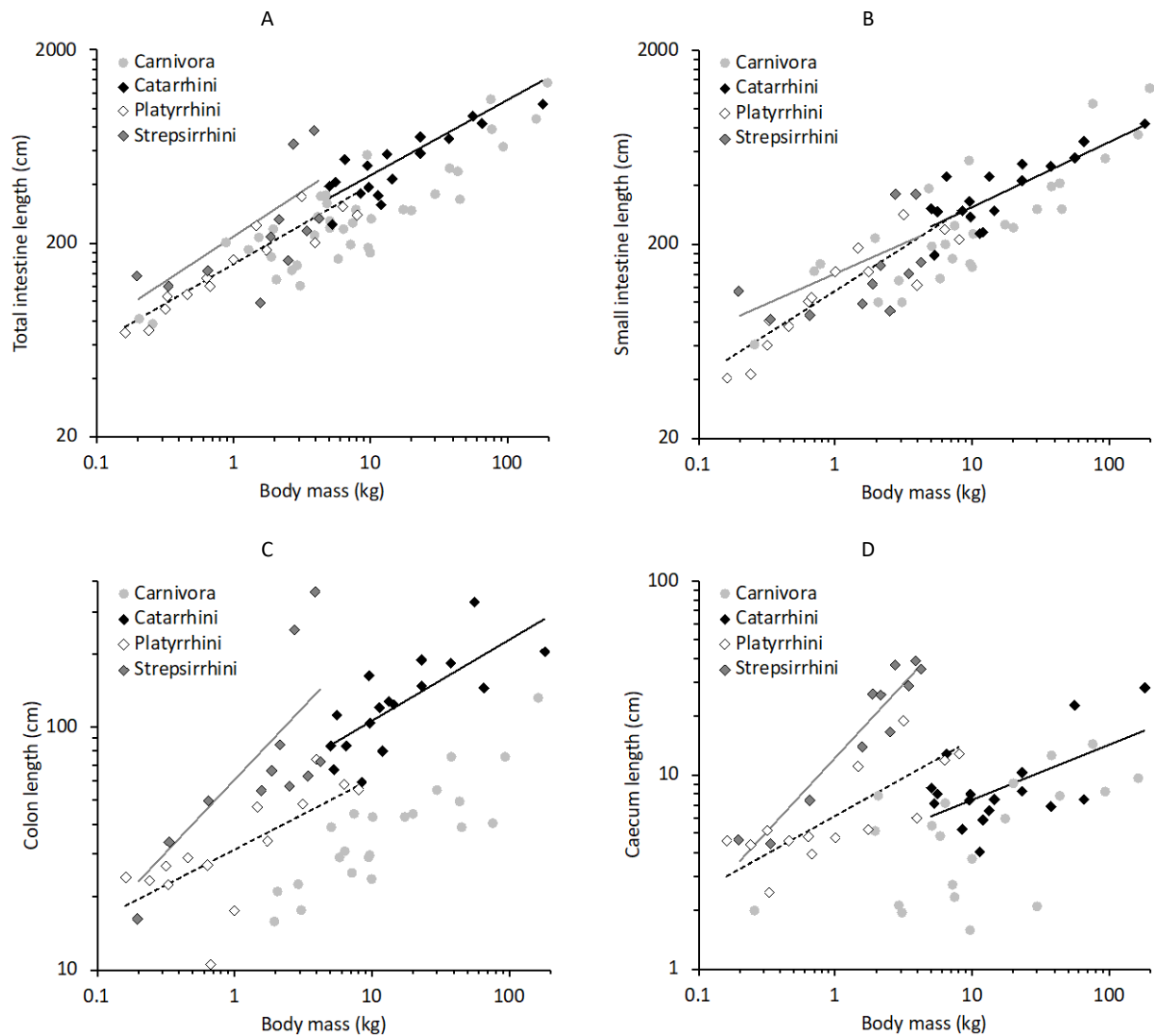
535
536 **Figure 11** Relationship between body mass and A) total intestinal length, B) small intestinal
537 length, C) colon length and D) caecum length in primates as compared to terrestrial
538 carnivorans (from McGrosky et al., 2016). Regression lines from Phylogenetic Generalized
539 Least Squares (Table 2). Straight black line = Catarrhini; black dotted line = Platyrrhini; grey
540 line = Strepsirrhini. The two outlier lemurs in (A-C) are sifakas (*Propithecus* spp.).

541
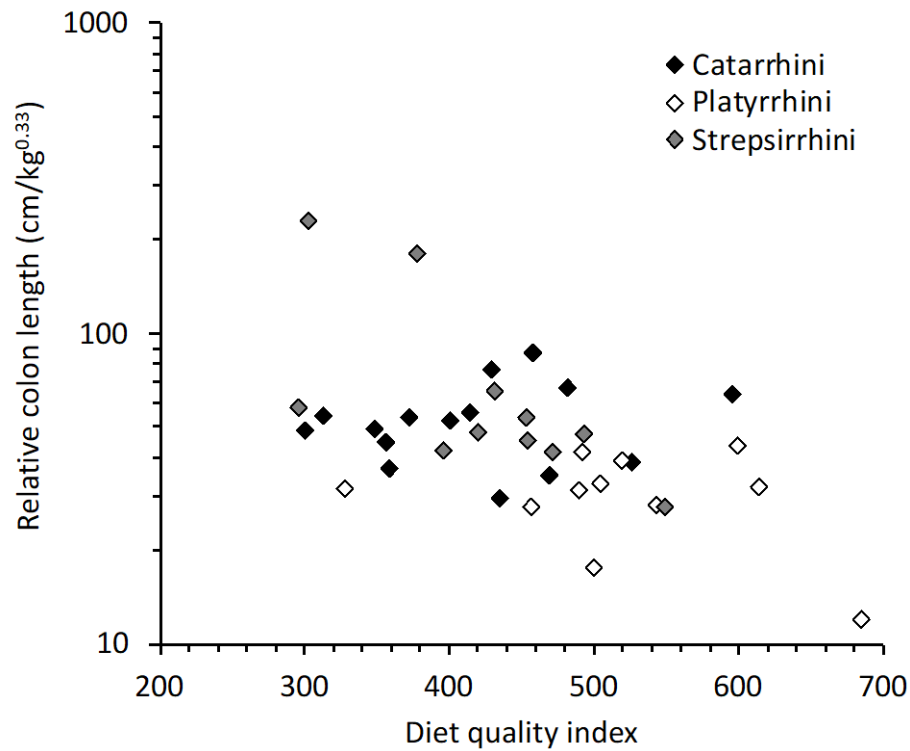
542
543 **Figure 12** Relationship between the diet quality index and the relative length of the colon in
544 species of three different primate clades. Note that while there is a negative relationship in
545 the overall data, this is not the case in the individual clades, leading to a non-significant result
546 when accouting for the phylogenetic structure of the data (see Results). The two outliers with
547 a high relative colon length in the Strepsirrhini are from one genus (*Propithecus* spp.); the
548 two outliers in the Platyrrhini with a low relative colon length are also from one genus
549 (*Saimiri* spp.).

550   **Supporting Information**

551   # Gross intestinal morphometry and allometry in primates

552   Amanda McGrosky • Carlo Meloro • Ana Navarrete • Sandra A. Heldstab • Andrew C.

553   Kitchener • Karin Isler • Marcus Clauss

554   **Table S1** Sources for diet information

555

556   ACHTUNG: alles normal ist aus den Van Woerden Papers bzw. aus der Excel-Tabelle; gelb = keine Ahnung, woher (incl. der Angabe im

557   Excel); blau = Angabe aus Excel, obwohl Quelle in Van Woerden Papers; pink = all the worlds primates – kann man da die direkte quelle

558   rausziehen?

Species (Clade[a])	Source
Alouatta sara (P)	Neville, M. K., Glander, K. E., Braza, F., & Rylands, A. B. (1988). The howling monkeys, genus *Alouatta*. In *Ecology and behavior of neotropical primates, vol 2* (ed. R. A. Mittermeier, A. B. Rylands, A. Coimbra-Filho, G. A. B. Fonseca). Washington DC: World Wildlife Fund.
Alouatta seniculus (P)	Julliot, C., & Sabatier, D. (1993). Diet of the red howler monkey (*Alouatta seniculus*) in French-Guiana. Int J Primatol 14:527-550. Di Fiore, A., & Campbell, C. J. (2007). The atelines: variation in ecology, behavior, and social organisation. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Ateles paniscus (P)	van Roosmalen, M. G. M. (1980). *Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (Ateles paniscus paniscus Linnaeus 1758) in Surinam*. PhD thesis. Landbouwhogeschool Wageningen: Leersum. Di Fiore, A., & Campbell, C. J. (2007). The atelines: variation in ecology, behavior, and social organisation. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Callthrix argentata (P)	xxx (Willems and van Schaik 2015?)
Callithrix jacchus (P)	de Castro, C. S. S., & Araújo, A. (2007). Diet and feeding behavior of marmoset, *Callithrix jacchus*. *Brazilian Journal of Ecology*, 7, 14-19. Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). Callitrichines: the role of competition in cooperatively breeding species. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Cebuella pygmaea (P)	xxx (Van Woerden 2010?)
Cebus apella (P)	Zhang, S. Y. (1995). Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French-Guiana. *International Journal of Primatology*, 16, 489-507.
Cheirogaleus medius (S)	Fietz, J., & Ganzhorn, J. U. (1999). Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? *Oecologia*, 121, 157-164.
Chiropotes satanas (P)	Norconk, M. A. (1996). Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In *Adaptive radiations of neotropical primates* (ed. M. A. Norconk, A. L. Rosenberger, P. A. Garber). New York: Plenum Press.
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Leontopithecus chrysomelas (P)	xxx (Willems and van Schaik 2015?)

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559   [a] C Catarrhini, P Platyrrhini, S Strepsirrhini

560 **Table S2** Allometric relationships between intestinal length measures (in cm) and body mass
561 (BM, in kg) according to Length = a BM^b with 95% confidence intervals for parameter
562 estimates from analyses using Generalized Least Squares (i.e., not accounting for phylogeny)

Length of	n	a (95%CI)	b (95%CI)
Total intestine	42	168 (148; 190)	0.40 (0.34; 0.46)
Strepsirrhini	11	188 (133; 367)	0.40 (0.08; 0.73)
Platyrrhini	14	152 (137; 168)	0.40 (0.32; 0.49)
Catarrhini	17	198 (146; 269)	0.34 (0.24; 0.45)
Small intestine	42	117 (103; 132)	0.41 (0.35; 0.46)
Strepsirrhini	11	125 (93; 167)	0.29 (0.01; 0.56)
Platyrrhini	14	111 (96; 128)	0.44 (0.32; 0.56)
Catarrhini	17	143 (101; 203)	0.34 (0.22; 0.46)
Caecum	42	7.5 (5.7; 9.7)	0.16 (0.04; 0.29)
Strepsirrhini	11	12.3 (10.5; 14.5)	0.76 (0.61; 0.91)
Platyrrhini	14	6.1 (5.0; 7.4)	0.34 (0.18; 0.51)
Catarrhini	17	3.9 (2.1; 6.9)	0.29 (0.09; 0.48)
Colon	42	41 (34; 49)	0.41 (0.32; 0.50)
Strepsirrhini	11	54 (37; 79)	0.62 (0.26; 0.98)
Platyrrhini	14	31 (25; 38)	0.31 (0.14; 0.47)
Catarrhini	17	49 (32; 76)	0.33 (0.19; 0.48)
Large intestine	42	49 (41; 59)	0.38 (0.29; 0.47)
Strepsirrhini	11	69 (48; 98)	0.66 (0.34; 0.98)
Platyrrhini	14	38 (31; 45)	0.32 (0.17; 0.47)
Catarrhini	17	54 (36; 82)	0.33 (0.19; 0.47)

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