

## RESEARCH ARTICLE

## Gross intestinal morphometry and allometry in primates

Amanda McGrosky<sup>1\*</sup>  | Carlo Meloro<sup>2</sup>  | Ana Navarrete<sup>1</sup> | Sandra A. Heldstab<sup>1,3</sup>  |  
Andrew C. Kitchener<sup>4</sup>  | Karin Isler<sup>1</sup>  | Marcus Clauss<sup>3</sup> 

<sup>1</sup>Department of Anthropology, University of Zurich, Zurich, Switzerland

<sup>2</sup>Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool, United Kingdom

<sup>3</sup>Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland

<sup>4</sup>Department of Natural Sciences, National Museums Scotland, Edinburgh, United Kingdom

## Correspondence

Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland.  
Email: mclauss@vetclinics.uzh.ch

## Present address

School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona.

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## Abstract

Although it is generally assumed that among mammals and within mammal groups, those species that rely on diets consisting of greater amounts of plant fiber have larger gastrointestinal tracts (GIT), statistical evidence for this simple claim is largely lacking. We compiled a dataset on the length of the small intestine, caecum, and colon in 42 strepsirrhine, platyrrhine, and catarrhine primate species, using specimens with known body mass (BM). We tested the scaling of intestine length with BM, and whether dietary proxies (percentage of leaves and a diet quality index) were significant covariates in these scaling relationships, using two sets of models: one that did not account for the phylogenetic structure of the data, and one that did. Intestine length mainly scaled geometrically at exponents that included 0.33 in the confidence interval; Strepsirrhini exhibited particularly long caeca, while those of Catarrhini were comparatively short. Diet proxies were only significant for the colon and the total large intestine (but not for the small intestine or the caecum), and only in conventional statistics (but not when accounting for phylogeny), indicating the pattern occurred across but not within clades. Compared to terrestrial Carnivora, primates have similar small intestine lengths, but longer large intestines. The data on intestine lengths presented here corroborate recent results on GIT complexity, suggesting that diet, as currently described, does not exhaustively explain GIT anatomy within primate clades.

## KEYWORDS

anatomy, diet, digestive tract, phylogeny, primate

## 1 | 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 & Langer, 1994). Illustrations of the digestive tracts of herbivores and carnivores make it evident that the digestive tracts of herbivores are more complex (Stevens & Hume, 1998) due to the less digestible nature of their natural diets. Though statistical evidence is lacking (Lavin, Karasov, Ives, Middleton, & Garland, 2008; Smith, Parker, Kotzé, & 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 & 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 & Hladik, 1980; Lambert, 1998; Martin, Chivers, MacLarnon, & Hladik, 1985). Understanding aspects of the anatomy of primates' digestive systems are thought

to provide information about the diet to which a particular taxon may be adapted (Ferrari & 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 inter-specific, 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 & Martins, 1992; Ferrari, Lopes, & Krause, 1993 in callitrichines), and some studies (e.g., Hill, 1958) provide illustrations of primate gastrointestinal tracts, but do not provide measurements. The paucity of recent gross intestinal morphology research may be in part related to the perception that the proportions of different components of the gastrointestinal tract can vary intraspecifically with age (Langer, 1988) or with dietary shifts (Gross, Wang, & Wunder, 1985). Nevertheless, the use of relative dimensions can provide information about the relative role of different portions of the tract in a particular subset of species (Caton, 1998; Chivers & Hladik, 1980) and can inform hypotheses about adaptations to different dietary regimes. The enlarged caecum and colon of some strepsirrhines, new world monkeys, cercopithecines, and hominoids (Chivers, 1994; Hladik, Charles-Dominique, Valdebouze, Delort-Laval, & Flanzky, 1971), for example, act as fermentation chambers to aid in the digestion of plant foods.

On the other hand, it has also been recognized that the gastrointestinal form alone is not sufficient to predict diet (Milton, 1987), even though general relationships between gross digestive morphology (e.g., relative gut proportions) and broad dietary categories are expected. Chivers and Hladik (1980) demonstrated an increase in the ratio of the combined stomach, caecum, and colon volume to small intestine volume across a continuum of faunivores to frugivores to folivores, although there was substantial overlap between the groups. When Chivers and Hladik considered the surface area of the small intestine, however, no differences between trophic groups were evident. Notably, these analyses were performed before the arrival of statistical methods that account for phylogenetic nonindependence. When controlling for phylogeny, Langer and Clauss (2018) did not find diet-associated differences in gut complexity among primates.

Despite these various lines of research, quantitative data on the digestive tracts of primates are scarce. To provide data on intestine length for a larger number of primates, we used the opportunity to take photographs of the digestive tracts of a number of specimens during dissections performed for a study on mammalian body composition (Navarrete, van Schaik, & Isler, 2011), and provide photographic evidence for the gross digestive tract morphology of 32 species. Because with any absolute measure, body size will be the main driver of the magnitude, we first investigate the allometric relationship of intestine length with body mass (BM). Based on the general geometric relationship between a length and a volume measure, one would expect intestinal lengths to scale approximately with BM to the power of 0.33. However, three previous data compilations—on mammals in

general (Lavin et al., 2008), on mammalian carnivores (McGrosky, Navarrete, Isler, Langer, & Clauss, 2016) and on ruminants (McGrosky et al., 2019)—unexpectedly yielded higher exponents. The explanation for this phenomenon was, to our knowledge, first proposed by Woodall and Skinner (1993), who suggested that animals should evolve so that their intestinal surface retains a geometric or metabolic scaling (i.e., at an exponent between 0.67 and 0.75), but so that the diameter of the intestine should scale less-than-geometrically to maintain short diffusion distances, and that hence, to compensate, intestinal length should scale more-than-geometrically. Therefore, a corresponding scaling was expected in primates as well.

As a second step, we tested whether proxies of the natural diet influenced the scaling relationships with BM. Following broad mammalian trends and Chivers and Hladik (1980), we expect both small and large intestine length to increase along a dietary continuum from insectivores to frugivores to folivores.

## 2 | METHODS

During the data collection for a different study (Navarrete et al., 2011), a large number of mammalian specimens originating from various sources were dissected by AN; some additional specimens were contributed by MC. Most specimens derived from zoological collections. The specimens were either dissected directly after death or, in the majority of cases, after storage by deep-freezing and thawing. BM was recorded, and the gastrointestinal tracts were dissected by removing mesenteries. The intestinal tract was laid out according to common practice for anatomical documentation (Stevens & Hume, 1995), placing the intestine as a straight line without stretching, and photographs (with scale) were taken for later measurement. For measurements, the caecum served as the defining border between the small and the large intestine. Length of the different sections was determined using the polyline VOI tool of the MIPAV biomedical imaging software (version 14.0, National Institutes of Health), which facilitated tracing the length of the intestine directly on the digital photo and converting pixel length into centimeters.

For some large-sized specimens, the intestine was cut into several pieces before photography. Photographs of these specimens were not manipulated to create the impression of an uninterrupted intestine. The only photo manipulations included the deletion of background and, in some cases, adjustment of the brightness and color of the images and mirroring to achieve a consistent position of the stomach.

Additional data were collected from the literature, but only if the original BMs of the specimens investigated were reported together with the length measurements; this led to the exclusion of many published intestine length measurements. When several specimens were available for a species, averages for both BM and the respective measurements were calculated; in doing so, we

**TABLE 1** Average ( $\pm$ SD) body mass (g) and intestinal length (cm) measurements of primate species

Species (Clade <sup>a</sup> )	Source	n	Body mass	Small intestine	Caecum	Colon	Large intestine <sup>b</sup>	Total intestine	%leaves in natural diet <sup>c</sup>	Diet quality index <sup>c</sup>
<i>Alouatta sara</i> (P)	1	2	3,950 ( $\pm$ 636)	123 ( $\pm$ 11)	6 ( $\pm$ 5)	74 ( $\pm$ 3)	80 ( $\pm$ 1)	202 ( $\pm$ 10)	50	NA
<i>Alouatta seniculus</i> (P)	2	1	635	239	12	58	70	309	48	328
<i>Ateles paniscus</i> (P)	1	1	8,070	211	13	60	73	283	8	456
<i>Callithrix argentata</i> (P)	1	1	242	43	4	23	28	70	0	NA
<i>Callithrix jacchus</i> (P)	1,3	5	323 ( $\pm$ 30)	58 ( $\pm$ 14)	5 ( $\pm$ 1)	25 ( $\pm$ 13)	30 ( $\pm$ 12)	88 ( $\pm$ 27)	0	519
<i>Cebuella pygmaea</i> (P)	1	1	163	41	5	24	29	69	0	599
<i>Cebus apella</i> (P)	1	1	1,750	145	5	34	39	184	16	543
<i>Cheirogaleus medius</i> (S)	1	2	197 ( $\pm$ 49)	114 ( $\pm$ 0)	5 ( $\pm$ 0)	16 ( $\pm$ 3)	21 ( $\pm$ 3)	135 ( $\pm$ 3)	4	549
<i>Chiropotes satanas</i> (P)	2	1	3,130	282	19	48	67	349	1	504
<i>Chlorocebus pygerythrus</i> (C)	1	1	5,300	176	7	67	74	250	10	526
<i>Colobus guereza</i> (C)	1	2	9,750 ( $\pm$ 354)	278 ( $\pm$ 57)	8 ( $\pm$ 0)	104 ( $\pm$ 22)	112 ( $\pm$ 22)	390 ( $\pm$ 79)	61	348
<i>Eulemur coronatus</i> (S)	4	1	1,580	99	14	55	69	168	3	493
<i>Eulemur fulvus</i> (S)	1	1	2,500	91	16	57	73	164	25	396
<i>Eulemur macaco</i> (S)	1	2	1,875 ( $\pm$ 530)	125 ( $\pm$ 20)	26 ( $\pm$ 6)	66 ( $\pm$ 1)	92 ( $\pm$ 5)	217 ( $\pm$ 15)	45	454
<i>Gorilla gorilla</i> (C)	1,5	2	154,648 ( $\pm$ 102,032)	810 ( $\pm$ 299)	18 <sup>d</sup>	139 <sup>d</sup>	162 ( $\pm$ 8)	972 ( $\pm$ 307)	61	359
<i>Haplemur griseus</i> (S)	6	4	648 ( $\pm$ 106)	86 ( $\pm$ 16)	7 ( $\pm$ 4)	50 ( $\pm$ 6)	57 (N.R.)	144 (N.R.)	100	296
<i>Homo sapiens</i> (C)	9	6	65,300 ( $\pm$ 14,471)	678 ( $\pm$ 138)	8 ( $\pm$ 2)	146 ( $\pm$ 16)	154 ( $\pm$ 15)	831 ( $\pm$ 144)	30	NA
<i>Lemur catta</i> (S)	1	3	2117 ( $\pm$ 144)	156 ( $\pm$ 43)	24 ( $\pm$ 7)	86 ( $\pm$ 24)	111 ( $\pm$ 28)	267 ( $\pm$ 71)	32	432
<i>Leontopithecus chrysomelas</i> (P)	1	3	642 ( $\pm$ 98)	101 ( $\pm$ 12)	5 ( $\pm$ 1)	27 ( $\pm$ 4)	32 ( $\pm$ 4)	133 ( $\pm$ 15)	0	490
<i>Macaca arctoides</i> (C)	1	4	14,525 ( $\pm$ 3,495)	297 ( $\pm$ 51)	7 ( $\pm$ 2)	125 ( $\pm$ 47)	132 ( $\pm$ 45)	429 ( $\pm$ 95)	40	NA
<i>Macaca cyclopis</i> (C)	7	6	119,667 ( $\pm$ 1,783)	230 ( $\pm$ 29)	6 ( $\pm$ 1)	79 ( $\pm$ 7)	85 ( $\pm$ 7)	315 ( $\pm$ 30)	23	470
<i>Macaca fuscata</i> (C)	1	1	11,970	434	5	121	126	560	32	372
<i>Macaca nigra</i> (C)	1	1	5,600	295	8	113	121	415	2	596
<i>Macaca sylvanus</i> (C)	1	1	9,625	334	7	163	170	504	11	430
<i>Mandrillus sphinx</i> (C)	1	1	23,000	515	8	189	197	713	8	482
<i>Mirza zaza</i> (S)	1	1	336	82	4	34	38	120	38	420
<i>Nomascus leucogenys</i> (C)	1	1	6,550	449	13	83	96	545	59	356
<i>Pan paniscus</i> (C)	1	1	37,730	527	12	234	245	773	24	415
<i>Papio hamadryas</i> (C)	1	2	23,250 ( $\pm$ 8,132)	426 ( $\pm$ 161)	10 ( $\pm$ 2)	148 ( $\pm$ 12)	158 ( $\pm$ 10)	585 ( $\pm$ 172)	28	401
<i>Pithecia pithecia</i> (P)	1,2	3	1,467 ( $\pm$ 339)	191 ( $\pm$ 25)	11 ( $\pm$ 4)	56 ( $\pm$ 17)	67 ( $\pm$ 21)	258 ( $\pm$ 46)	9	492
<i>Pongo pygmaeus</i> (C)	9	1	56,250	559	23	328	351	910	48	458
<i>Propithecus tattersalli</i> (S)	6	1	2,760	362	37	252	289	651	39	378

(Continues)

TABLE 1 (Continued)

Species (Clade <sup>a</sup> )	Source	n	Body mass	Small intestine	Caecum	Colon	Large intestine <sup>b</sup>	Total intestine	%leaves in natural diet <sup>c</sup>	Diet quality index <sup>c</sup>
<i>Propithecus verreauxi</i> (S)	6	2	3,890 (±438)	365 (±38)	39 (±7)	364 (±42)	403 (N.R.)	767 (N.R.)	53	302
<i>Saguinus fuscicollis</i> (P)	1	1	330	81	2	22	25	106	0	614
<i>Saguinus oedipus</i> (P)	1	4	460 (±211)	75 (±8)	5 (±1)	29 (±9)	33 (±10)	109 (±17)	0	NA
<i>Saimiri boliviensis</i> (P)	1	1	1,003	144	5	18	22	166	0	500
<i>Saimiri sciureus</i> (P)	1,2,8	22	678 (±117)	104 (±17)	4 (±1)	12 (±4)	16 (±4)	120 (±21)	0	684
<i>Symphalangus syndactylus</i> (C)	1	1	8,500	298	5	60	65	362.46	45	435
<i>Theropithecus gelada</i> (C)	1	1	11,400	227	4	121	125	352	94	313
<i>Trachypithecus vetulus</i> (C)	1	1	5,000	305	9	83	92	397	45	300
<i>Varecia rubra</i> (S)	1	1	4,200	162	35	72	108	269	12	454
<i>Varecia variegata</i> (S)	1	1	3,520	102	25	51	75	178	9	472

Abbreviations: NA, not available; SD, standard deviation.

<sup>a</sup>C Catarrhini, P Platyrrhini, and S Strepsirrhini.

<sup>b</sup>Including caecum length.

<sup>c</sup>For sources, see Table S1.

<sup>d</sup>Caecum and colon length only obtained from the present study.

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 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 mammal digestive tract anatomy (Chivers & 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 specimens.

always ensured the averaged BM matched the averaged gut section measure.

Data on the natural diet of the investigated species, as the percentage of leaves in the overall diet (as generally the diet items most requiring microbial fermentation) and the diet quality index (to account not just for one but the range of diet items), were taken from a literature collection based on three publications (Van Woerden, van Schaik, & Isler, 2010; Van Woerden, van Schaik, & Isler, 2014; Van Woerden, Willems, van Schaik, & Isler, 2012), supplemented with additional information (for a full set of sources, see Table S1). The diet quality index represents a sum of each dietary item, multiplied by a factor that is higher for more digestible diet items (eight for insects, five for fruits/seeds/flowers, three for young leaves, and one for mature leaves) and is weighted for the proportion of these items in the diet (Van Woerden et al., 2010). All species-specific data are given in Table 1.

Allometric relationships were investigated using linear regressions on log-transformed data according to  $\text{Length} = a \text{ BM}^b$ , with 95% confidence intervals (CIs) for parameter estimates, for the whole dataset and for individual clades. In addition, the same analysis was performed with clades as cofactors, and the clade  $\times$  BM interactions,

to directly test for differences between the clades. Proxies of the natural diet were added to the linear regressions on log-transformed data as covariates (only one proxy per model, i.e., either the percentage of leaves, or the diet quality index). Initially, models including the BM  $\times$  diet proxy interaction were also included, but because there were no significant interactions, results are only presented here for models without interactions. Analyses were performed using Generalized Least Squares (GLS) and Phylogenetic Generalized Least Squares (PGLS), using a consensus phylogenetic tree downloaded from the 10kTrees Project (version 3; Arnold, Matthews, & Nunn, 2010). The phylogenetic signal (Pagel's  $\lambda$ ) was estimated using the maximum likelihood (Revell, 2010).  $\lambda$  can vary between 0, indicating no phylogenetic signal, and 1, indicating a strong phylogenetic signal and that similarity among species scales in proportion to their shared evolutionary time (Freckleton, Harvey, & Pagel, 2002; Pagel, 1999). Statistical tests were performed using the package caper (Orme et al., 2010) in R 2.15.0 (Team, 2011). The significance level was set to 0.05.

Finally, the data of primates were compared visually to data from terrestrial Carnivora including canids, mustelids, ursids, mephitids, procyonids, felids, hyenids, herpestids, and viverrids, but excluding pinnipeds (McGrosky et al., 2016).



**FIGURE 1** Digestive tracts of various lemur species. Note the long caecum in all species

### 3 | RESULTS

Among the Strepsirrhini, lemurs appear to have particularly long caeca (Figure 1) compared to the gummivorous cheirogalids (Figure 2). The latter have smaller caeca, although their caeca still appear proportionally larger than those of the gummivorous callitrichids (Figure 3). The nongummivorous cebids studied here all have similar digestive tracts (Figure 4). Atelids have an unremarkable caecum that appears part of a large proximal colon (Figure 5), whereas the caecum of the pitheciids is more distinct (Figure 5).

Among the Catarrhini, colobines have a voluminous forestomach, as well as a distinct caecum and an enlarged proximal colon (Figure 6). The hindgut of many noncolobine Catarrhini is voluminous and haustrated, with a short, broad caecum (Figures 7–10). In the apes, the caecum bears a clearly visible, vermiform appendix (Figure 10).

When using the complete gastrointestinal morphology dataset, as well as Strepsirrhini- and Platyrrhini-specific datasets, **there was a strong, significant phylogenetic signal**, indicating that the data scatter is guided by the phylogenetic structure in the datasets. **However, this strong phylogenetic signal was generally not observed within**



**FIGURE 2** Digestive tracts of two cheirogalid species

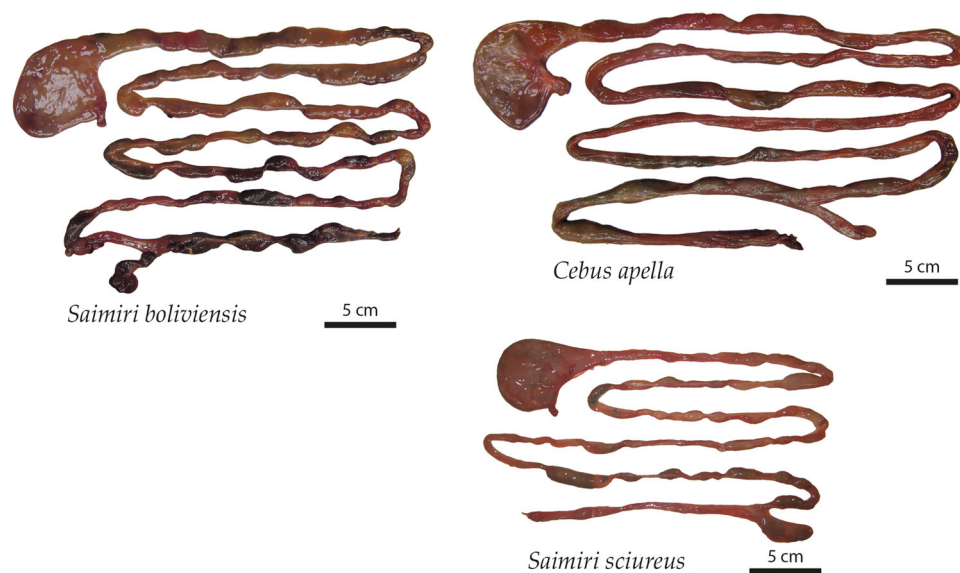




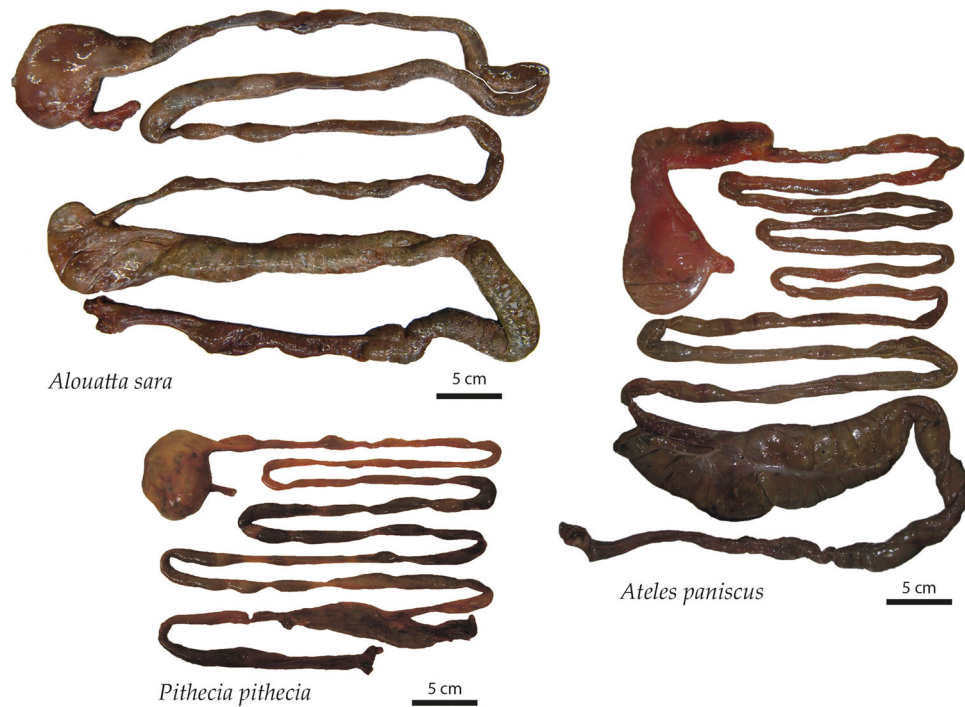
**FIGURE 3** Digestive tracts of five callitrichid species

Catarrhini (Table 2). Across all species, the scaling exponent typically included 0.33 in the 95% CI, indicating geometric scaling (Table 2). The 95% CIs for the allometric factors ( $a$ ) and scaling exponents ( $b$ ) generally overlapped between the clades, with the exception of both the factor and exponent of the caecum, which was higher in the

Strepsirrhini (Table 2). This observation was corroborated by the models that tested the scaling including the clade and clade  $\times$  BM interactions, where the Strepsirrhini  $\times$  M interaction was significant both in GLS ( $p = .009$ ) and PGLS ( $\lambda = .73$ ;  $p = .017$ ), indicating a steeper scaling of the caecum with BM for this clade (Figure 11). In



**FIGURE 4** Digestive tracts of three cebid species



**FIGURE 5** Digestive tracts of two atelid and one pitheciid species

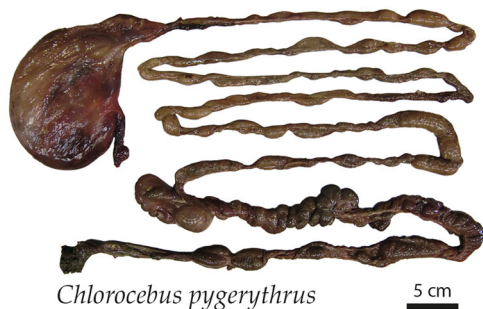
addition, although the corresponding 95% CIs for  $a$  overlapped, the analyses for small intestine length and total intestine length indicated significantly smaller values for Platyrrhini (small intestine: GLS  $p = .015$ ; PGLS  $\lambda = .73$ ,  $p = .018$ ; total intestine: GLS  $p = .032$ ; PGLS

$\lambda = .80$ ,  $p = .035$ ; in all cases, with nonsignificant interaction terms; Figure 11).

While the scaling exponent of GLS models was generally very similar to that of PGLS models (Tables 2 and S2), the GLS scaling



**FIGURE 6** Digestive tracts of two colobine species



**FIGURE 7** Digestive tract of *Chlorocebus*

exponent for the caecum in the complete dataset was very low (due to the long caeca of small-bodied strepsirrhines) and excluded geometric scaling in CI (0.16; 95% CI 0.04–0.29; Figure 11). However, PGLS analyses indicated a generally geometric scaling of the caecum (0.41; 95% CI 0.25–0.56; Table 2).

Neither the percentage of leaves in the diet nor diet quality index exhibited a significant effect on intestinal length in any of the models, including models of caecum length ( $p$  always  $> .05$ ). The only exceptions to this trend included significant GLS models of colon and total large intestine length for the percentage of leaves dataset and the diet quality index (GLS: colon–leaves  $p = .045$ ; colon–diet index  $p = .008$ ; large intestine–leaves  $p = .066$ ; large intestine–diet index  $p = .011$ ). In PGLS, these dietary effects were no longer significant, indicating that variation in large intestine length with diet occurred mainly across and not within clades (PGLS: colon–leaves  $p = .402$ ; colon–diet index  $p = .075$ ; large intestine–leaves  $p = .648$ ; large intestine–diet index  $p = .231$ ). Using the diet quality index and the relative colon length (in  $\text{cm}/\text{BM}^{0.33}$ ), Figure 12 illustrates how the phylogenetic structure of the data set explains the colon–diet index relationship: within clades, there is little correlation between the measurements, and any trend within Strespirrhini or



**FIGURE 8** Digestive tracts of four macaque species. \*Indicates where the small intestine was linked before dissection





**FIGURE 9** Digestive tracts of three baboon species. The \* marks where the small intestine was linked before dissection

Platyrrhini is due to a particular genus, not due to similar variation in several genera; the position of the clades, however, suggests the expected negative relationship. For a more detailed graph including the phylogenetic tree and the distribution of these two measures across it, see Figure S1.

When compared to terrestrial Carnivora, the total intestines of primates are generally slightly longer (Figure 11). This holds particularly true for the colon, and the caecum of the Strepsirrhini.

By contrast, the caecum of the Catarrhini was of magnitude also observed in many terrestrial Carnivora.

#### 4 | DISCUSSION

Using what is to our knowledge the most comprehensive dataset on primate intestine lengths directly linked to the BM of the same



**FIGURE 10** Digestive tracts in four ape species. The \* marks where the small intestine was linked before dissection. Note the caecal appendix in all four species

specimens, the present study largely corroborates well-known features of different primate groups and in part confirms broad macroanatomical concepts about differences in intestinal length between carnivores and herbivores. However, it also demonstrates that, in primates, correlations of length measures of the different intestinal sections with the natural diet may not be as clear-cut as is often assumed.

The photographic evidence provided can be compared to drawings and reports from the literature. While we do not want to dwell on this in detail here, some points of interest shall be

mentioned. Fisher (2000) explained a reliable classification of species with respect to whether they have a true 'appendix' or not requires more than visual inspection, including histology, and ontogenetic series. Several species that have been classified as having an appendix in comparative datasets (e.g., Smith et al., 2017), including *Eulemur* spp. (Figure 1) and *Callithrix* spp. (Figure 3), did not have a vermiform structure that was clearly distinguishable in our study. For *Papio hamadryas*, a variable disposition with respect to the presence of an appendix has been assumed (Smith et al., 2017), with our specimen not showing macroscopic evidence of a vermiform

**TABLE 2** Phylogenetic signal ( $\lambda$ ) and allometric relationships between intestinal length measures (in cm) and body mass (BM, in kg) according to length =  $a \text{ BM}^b$  with 95% confidence intervals (CI) for parameter estimates from analyses using Phylogenetic Generalized Least Squares

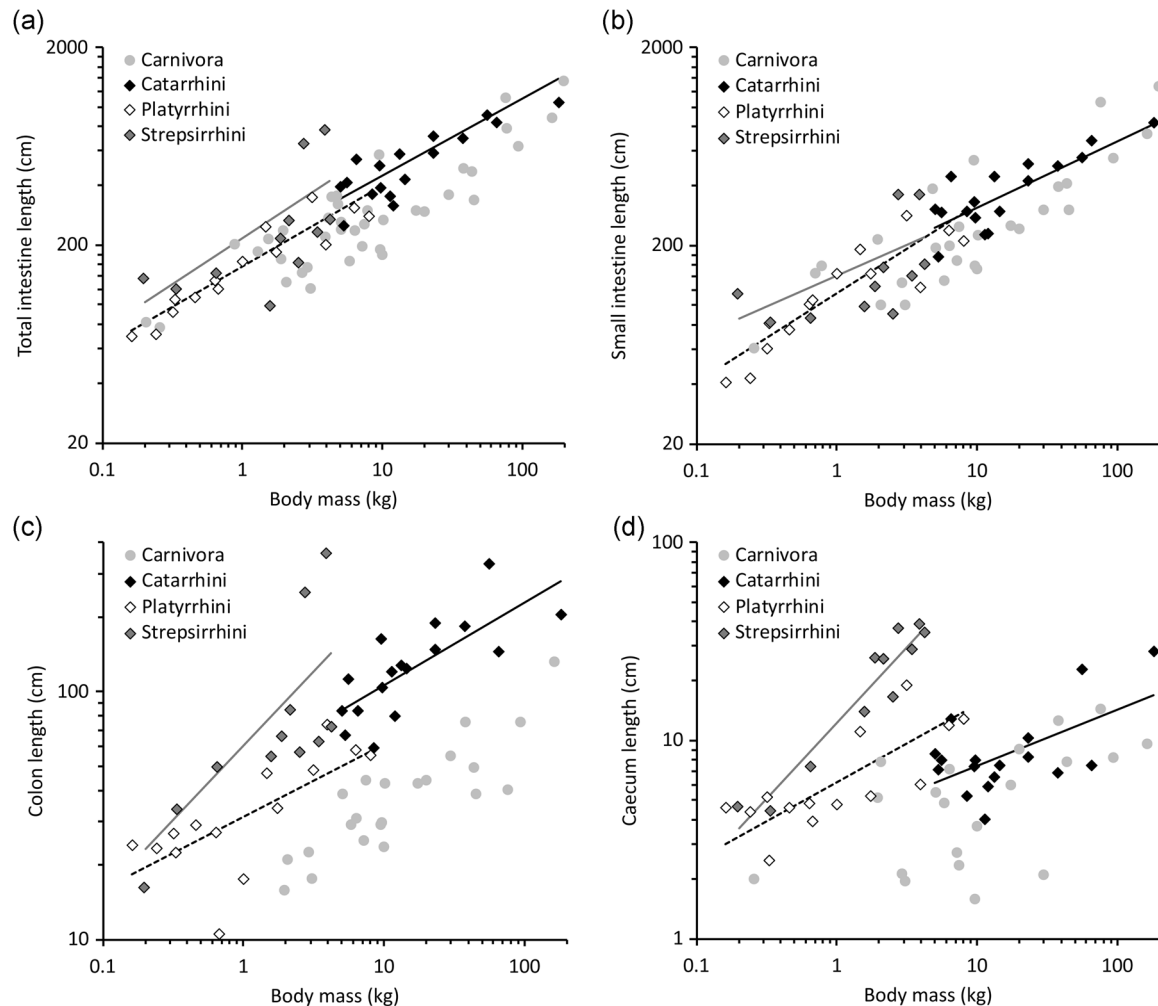
Length of	n	$\lambda$ (95%CI)	$a$ (95% CI)	$b$ (95% CI)
Total intestine	42	0.82 (0.47; 0.96)	187 (123; 287)	0.38 (0.30; 0.47)
<i>Strepsirrhini</i>	11	1.00 (0.40; NA)	217 (127; 371)	0.47 (0.15; 0.79)
<i>Platyrrhini</i>	14	0.72 (NA; NA)	156 (134; 181)	0.41 (0.30; 0.51)
<i>Catarrhini</i>	17	0 (NA; 0.46)	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)
<i>Strepsirrhini</i>	11	1.00 (0.57; NA)	141 (94; 213)	0.31 (0.07; 0.56)
<i>Platyrrhini</i>	14	0.66 (NA; 0.97)	115 (93; 142)	0.45 (0.30; 0.60)
<i>Catarrhini</i>	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)
<i>Strepsirrhini</i>	11	0 (NA; 0.79)	12.3 (10.5; 14.5)	0.76 (0.61; 0.91)
<i>Platyrrhini</i>	14	0.77 (NA; NA)	6.2 (4.5; 8.4)	0.39 (0.18; 0.61)
<i>Catarrhini</i>	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)
<i>Strepsirrhini</i>	11	1.00 (0.77; NA)	61 (37; 100)	0.60 (0.30; 0.89)
<i>Platyrrhini</i>	14	0.75 (0.07; NA)	31 (23; 42)	0.29 (0.09; 0.49)
<i>Catarrhini</i>	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)
<i>Strepsirrhini</i>	11	1.00 (0.60; NA)	75 (47; 120)	0.64 (0.35; 0.92)
<i>Platyrrhini</i>	14	0.82 (0.20; NA)	38 (29; 49)	0.31 (0.13; 0.48)
<i>Catarrhini</i>	17	0 (NA; 0.76)	54 (36; 82)	0.33 (0.19; 0.47)

Note: NA—no respective confidence limit available for GLS results, see Table S1.

structure (Figure 9). With respect to *Varecia* spp. or *Lemur catta*, it is evident that the macroscopic appearance could be interpreted both ways (Figure 1), and that further investigations as recommended by Fisher (2000) would be required for a reliable assessment.

A series of limitations apply to the present study. Our own and the literature data represent a mixture of measurements taken from freshly dissected specimens and specimens dissected after frozen storage and thawing. While we do not think that this has a relevant effect on macroscopic length measurements, readers that question this assumption should, therefore, consider the results with extra caution. In our view, it needs to be mentioned that length measurements of intestinal structures should rather be considered as indicating magnitudes, and not precise data (hence, we give no decimals in Table 1). When laying out intestines for length measurements, details such as the dryness of the organ and the smoothness of the surface used for measuring can influence whether an unintentionally stretched organ can contract again or retains the stretched disposition, for example. Or a freshly dissected intestine may have some residual contractility, in contrast to one that had been frozen in between. A further caveat that needs to be mentioned refers to the use of a consensus tree (here, from the 10kTrees Project) rather than testing a whole distribution of trees. The standpoint adopted intuitively in the present study, that absence of a signal when using the consensus tree is meaningful, could, of course, be questioned, and the data could be explored using the whole distribution of trees available.

However, the main limitations of the present study are its reliance on mainly captive specimens and the low sample size for the majority of the included species that also precludes tests of ontogenetic changes. Freckleton et al. (2002) demonstrated that at lower species numbers below 20, a phylogenetic signal may not be always detected reliably, whereas a wrong detection of a phylogenetic signal is rare. In our analyses, this was also reflected in the finding that CIs for  $\lambda$  could often not be calculated (Table 2). Among the *Strepsirrhini* ( $n = 11$ ) and *Platyrrhini* ( $n = 14$ ), the limited number of species might have been responsible for the finding that small intestine length and colon length (and hence also large intestine and total intestine length) showed a phylogenetic signal. This phylogenetic signal indicates that variation in these measures and clades was mainly an effect across, and not within, the included taxonomic subgroups. Notably, this did not apply to the *Catarrhini*, for which we obtained a larger sample size ( $n = 17$ ). In contrast, the fact that no phylogenetic signal was evident in *strepsirrhine* caecum length suggests that a long caecum that increases in length with BM is a common feature across various *strepsirrhine* subgroups. For more confidence in the phylogenetic signal of intestinal length measurements, a larger species sample would be required. This would also help to clarify if primates are really different from carnivores, ruminants or mammals in general (Lavin et al., 2008; McGrosky et al., 2016, 2019), which all show a more-than-geometrically scaling of intestine length, possibly to achieve geometrical constancy of absorptive intestinal surface while keeping diffusion distances in



**FIGURE 11** Relationship between body mass and (a) total intestinal length, (b) small intestinal length, (c) colon length, and (d) caecum length in primates as compared to terrestrial carnivorans (from McGrosky et al., 2016). Regression lines from Phylogenetic Generalized Least Squares (Table 2). Straight black line = Catarrhini; black dotted line = Platyrrhini; grey line = Strepsirrhini. The two outlier lemurs in (a–c) are sifakas (*Propithecus* spp.)

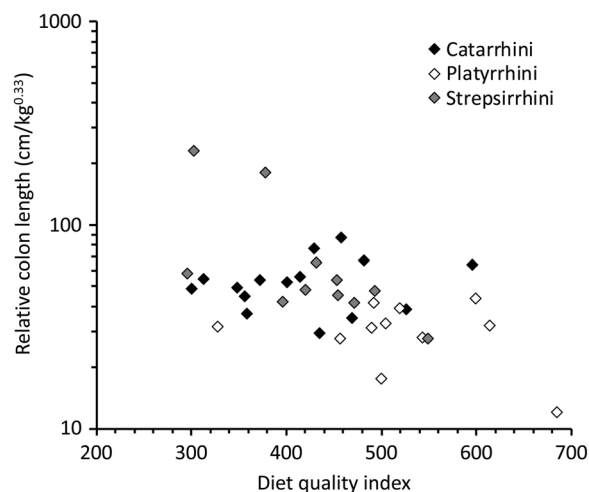
the intestine small by increasing the intestinal diameter at less-than-geometrically scaling (Woodall & Skinner, 1993). The large 95% CIs for the scaling exponents in the present study does not allow a clear answer to this question.

Another limitation becomes evident given the absence of a clear dietary signal in intestinal length measurements, and is inherent to our study design: intestinal length is possibly poorly correlated with diet. Other measures, notably the volume or the actual gut fill (Clauss, Schwarm, Ortmann, Streich, & Hummel, 2007; Müller et al., 2013), are most likely more meaningful correlates with diet, as mammalian herbivores generally have more voluminous (yet not necessarily longer) intestines. Chivers and Hladik (1980) addressed this fact by using the intestinal surface area rather than length for some of their analyses. Notably, they did not find a significant difference in small intestine surface area between diet groups, and they did not report results for the large intestine or caecum in isolation, as done in the present study, where any dietary signal that derives from the anatomy of the stomach and forestomach was

excluded. The often-cited patterns between gut morphology and diet described by Chivers and Hladik (1980) always represent a composite signal in which the volume or surface area of the (fore) stomach and the large intestine are summed up before evaluation. However, even using this composite signal, their study revealed a substantial overlap between faunivores, frugivores, and folivores. In addition, affiliation to dietary groups varied, depending on whether anatomical surface or volume measurements were used; while colobine monkeys were exclusively grouped as folivores in terms of volume measures (Fig. 20 in Chivers & Hladik, 1980), they were also depicted within the range of frugivores in terms of surface measures (Fig. 18 of their study).

Nevertheless, the present study provides some limited evidence for the functional relationship between colon or large intestine length and diet, as postulated previously (Chivers, 1994; Hladik, 1978). Similar to the findings on the gastrointestinal complexity of Langer and Clauss (2018), GLS models revealed a significant relationship between diet and large intestine length. However, in both Langer and Clauss





**FIGURE 12** Relationship between the diet quality index and the relative length of the colon in species of three different primate clades. Note that while there is a negative relationship in the overall data, this is not the case in the individual clades, leading to a nonsignificant result when accounting for the phylogenetic structure of the data (see Section 3). The two outliers with a high relative colon length in the Strepsirrhini are from one genus (*Propithecus* spp.); the two outliers in the Platyrrhini with a low relative colon length are also from one genus (*Saimiri* spp.). For a more detailed graph including the phylogenetic tree and the distribution of these two measures across it, see Figure S1

(2018) and the present study, these effects were not significant when accounting for the phylogenetic structure of the data using PGLS. This indicates that these effects do not occur within the different primate clades and therefore cannot be considered convergent between them in the respective datasets. Rather, the pattern occurs at deeper nodes of the phylogeny in each dataset, to the extent that clades as a whole differ in both, the GIT and the diet measure. The lack of significance in PGLS, or, in other words, the lack of evidence for dietary convergence, should not encourage the interpretation of a lack of a functional relationship. The relationship is just not evident within clades, but only across the clades included in this study. This could lead to the traditional interpretation often applied to nonsignificant findings when accounting for phylogeny, that is, clade-specific characteristics other than diet (represented by 'phylogeny') led to the evolution of longer or more complex large intestines in those taxa that also ingest more leaves. Alternatively, it suggests that clade diversification in primates followed, to a large extent, dietary niche and concomitant intestinal adaptations, but that diet diversification within clades left less reliable marks on intestinal anatomy. Reporting only one result, such as—in the case of a significant phylogenetic signal—the PGLS result while ignoring the GLS result, as sometimes recommended in the biological literature (Freckleton, 2009), would leave this observation unrecognized.

With respect to length, primates do not appear to differ from terrestrial carnivores for the small intestine where auto-enzymatic digestion occurs. However, as also described by Martin (1990) and Lambert (1998), primates generally have a longer large intestine

(a site of allo-enzymatic digestion), which coincides with their generally higher reliance on diets that contain plant cell walls compared to carnivores. The difference in the intestinal segment by which primates achieve a longer large intestine resembles the pattern observed between other large (e.g., perissodactyl) and small (e.g., rodents and lagomorphs) hindgut-fermenting herbivores (Stevens & Hume, 1998); while smaller species typically have particularly large caeca and are often called 'caecum fermenters', larger species also possess a voluminous colon for allo-enzymatic digestion. This pattern is reflected in the differences between the larger Catarrhini and the smaller Strepsirrhini and Platyrrhini, which both have larger caeca compared to the Catarrhini (Figure 12d). The difference in caecum size and shape between these groups has been known for some time (Reider, 1936; Scott, 1980). One can only speculate that for smaller species, the retention times necessary for allo-enzymatic fiber digestion are more easily achieved by a larger dead-end structure such as the caecum rather than by a larger colon.

Ultimately, primate clades have a typical mammalian macroscopic appearance of their gastrointestinal tracts. The measure of intestinal length in primates as compared to carnivores matches broad statements about differences between carnivorous and herbivorous species mentioned in the Introduction, and, in the case of the large intestine, about the effect of natural diets on primate intestinal length. Within primates, however, dietary effects are found only across but not within clades, as models of the effect of diet on intestine length are only significant if the phylogenetic structure of the dataset is not accounted for. Within primate clades, dietary specialization as measured in our dataset has little power to explain intestinal length measures.

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## CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest.

## ORCID

Amanda McGrosky <http://orcid.org/0000-0002-1110-4310>

Carlo Meloro <http://orcid.org/0000-0003-0175-1706>

Sandra A. Heldstab <http://orcid.org/0000-0002-5909-1870>

Andrew C. Kitchener <http://orcid.org/0000-0003-2594-0827>

Karin Isler  <http://orcid.org/0000-0002-2391-1523>

Marcus Clauss  <http://orcid.org/0000-0003-3841-6207>

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