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Duque-Correa, MJ, Codron, D, Meloro, C, McGrosky, A, Schiffmann, C, Edwards, MS and Clauss, M (2021) Mammalian intestinal allometry, phylogeny, trophic level and climate. Proceedings of the Royal Society B: Biological Sciences, 288 (1944). ISSN 0962-8452

Proceedings of the Royal Society B: Biological Sciences *Mammal intestinal length*

doi https://doi.org/10.1098/rspb.2020.2888

Mammalian intestinal allometry, phylogeny, trophic level and climate

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Abstract

An often-stated ecomorphological assumption that has the status of ‘textbook knowledge’ is that the dimensions of the digestive tract correlate with diet, where herbivores – consuming diets of lower digestibility – have longer intestinal tracts than faunivores – consuming diets of higher digestibility. However, statistical approaches have so far failed to demonstrate this link. Here, we collated data on the length of intestinal sections and body mass of 519 mammal species, and test for various relationships with trophic, climatic and other biological characteristics. All models showed a strong phylogenetic signal. Scaling relationships with body mass showed positive allometry at exponents >0.33, except for the caecum, which is particularly large in smaller species. Body mass was more tightly linked to small intestine than to large intestine length. Adding a diet proxy to the relationships increased model fit for all intestinal sections, except for the small intestine when accounting for phylogeny. Thus, diet has a main effect on the components of the large intestine, with longer measures in herbivores. Additionally, measures of habitat aridity had a positive relationship with large intestine length. The small intestine was longer in species from colder habitats at higher latitudes, possibly facilitating the processing of peak intake rates during the growing season. This study corroborates intuitive expectations on digestive tract anatomy, while the dependence of significant results on large sample sizes and inclusion of specific taxonomic groups indicates that the relationships cannot be considered fixed biological laws.

Keywords: anatomy, digestion, diet, scaling, ecomorphology, convergence.

Background

Ecomorphological diversity is considered the main driver of species diversity, and diet is considered as one of the most important components of an animal's niche [1]. Across mammalian taxa, the gastrointestinal tract (GIT) exhibits great variation in length, area, volume, and shape. Several hypotheses have been formulated to explain this morphological diversity. The most widely accepted one is that there is a link between the trophic niche and GIT morphology, a concept almost universally accepted as 'textbook knowledge' [2-4]. Mammals consuming highly digestible diets, such as faunivores (carnivores, insectivores) do not need complex or long GITs; mammals that feed mainly on vegetable matter, especially on the leaves and stems of grass or browse, require large fermentation chambers to digest plant fibre [5]. Therefore, it has been widely claimed that herbivores' intestines are longer than those of carnivores [2, 3, 5-8].

Typically, this claim has been supported by graphical representations of the gut anatomy of strict herbivores, such as a sheep, compared to strict faunivores, such as the domestic cat (Fig. 1AB); the difference in length and apparent complexity between the two is striking. However, not all species follow this rule: the giant panda *(Ailuropoda melanoleuca)*, which consumes an exclusive diet of bamboo, has a simple stomach and a short intestine; on the other hand, dolphins feed mainly on fish and squid but have complex stomachs and very long intestines (Fig. 1CD).

Statistical evaluations of the hypothesis that GIT morphology reflects trophic niche in mammals are seldomly reported. The most often-cited work to back this claim is that of Chivers and Hladik [5]; in citing this study, the large overlap in GIT morphology between trophic groups and several other issues (see Supplement 1) are often not mentioned, as well as the fact that these analyses were done without accounting for phylogeny. A large number of original studies that investigated digestive tract anatomy came to supportive conclusions, albeit always necessarily on very small datasets [9-14], and generally also without accounting for phylogeny. By contrast, large-scale studies that accounted for phylogeny did not confirm an association between diet and intestinal length [15-19] or GIT complexity [20]. Other factors than diet thought to influence GIT anatomy include special adaptations to a volant [15, 21, 22] or a marine [23-25] lifestyle, or the aridity of the habitat [16, 26, 27].

Given that digestive tract anatomy and function have been instrumental in mechanistically linking mammalian ecology and evolutionary diversification [3], we sought to resolve the contributions of trophic and habitat niche components to GIT variation. Based on previous findings, we expected a significant phylogenetic signal; a scaling at an exponent higher than expected from geometry (i.e., positive allometry); an effect of diet particularly on parts of the large intestine with shorter lengths in more faunivorous species; and longer large intestines in animals from xeric habitats.

Methods

Relevant publications were collated using published datasets [15-18, 23] as starting points, and traced back to the original articles cited in the publications. Additionally, publications were actively searched for using the search engines Google Scholar, PubMed and Web of Science, with taxon names and ‘anatomy’, ‘morphometry’, ‘digestive tract’ ‘intestine’, ‘length’, as search terms. Data were only used if the publication included body mass and provided length measurements of the gut that included the small intestine (SI), the caecum, the colon-rectum-complex (‘colon’), the large intestine (LI, colon and caecum) and/or the total intestine (TI). Publications that reported estimated body masses were generally not included; however, some data on bats were included even when the body masses were not from the same animals as the intestine lengths [28, 29], as this appeared the only way to include these species. If the literature included data for juveniles and adults, juvenile data were excluded. Additional unpublished data were obtained from post-mortem examinations carried out by MC and MSE over the last decade, and more recently by MD.

Information included number of sampled animals, body mass and length of the total intestine, small intestine, large intestine, caecum, and the colon/rectum. The sum of caecum and colon/rectum was taken as 'large intestine', and the sum of small and large intestine as 'total intestine'. Not all data were available for each species, with total intestine information reaching the largest sample size. Weighted means (correcting for sample size) were calculated of each morphometrical parameter and the corresponding body mass. For example, if more data were available for small intestine than for caecum length of a species, then the body mass used for associations with small intestine length was different from the one used in the same species for associations with caecum length.

Various biological traits were added to the dataset. Data on the diet consumed in the wild was obtained from [30]. If a species was not included in that dataset, the diet of the closest taxonomic relative was used. The dataset gives quantitative information (in %) on the amount of prey animals, fruits, nectar, seeds and other plant parts. In addition to these quantities, we classified species into faunivore, omnivore or herbivore using two different cutoffs. One classification ascribed an extreme category (faunivore or herbivore) if 90% or more of the diet consisted of the corresponding sources, with omnivores being all other species. The second classification used 70% as the respective cutoff. The diet for *Laonastes aenigmamus* was taken from [31] and [32].

All species were categorized into volant (only those that perform active flying) or non-volant, terrestrial or marine [33], and whether their digestive system includes a non-glandular forestomach or not [34]. Environmental variables for the habitat occupied by each species included mid-latitude (used as absolute latitude), precipitation, temperature, and actual evapotranspiration (AET), were obtained from the PanTHERIA database [35]. The fully referenced dataset is provided as an online supplement.

The phylogenetic tree was built following Upham, Esselstyn [36]. A consensus supertree inclusive of 5911 mammalian species with time calibration (MamPhy_fullPosterior_BDvr_Completed_5911sp_topoCons_NDexp_MCC_v2_target.tre) was directly downloaded from (http://vertlife.org/phylosubsets/). The supertree was pruned in R using scripts from the library 'ape' [37] and 'tidyverse' [38] in order to obtain a final tree inclusive only of the 519 species for which GIT data and body masses were available.

Statistical analyses were done on (i) all available data (i.e., at different sample size for the different intestine sections – generally larger samples for the total intestine than for individual sections), and on two subsets that comprised (ii) those species for which both small and large intestine length was available and (iii) those species for which small intestine, caecum, and colon/rectum data were available, and (iv) various individual taxonomic groups. Analyses were done for full datasets, and for those species for which climate information was available. The factors volant, marine and forestomach presence were only assessed in the larger datasets comprising total and small intestine.

First, the allometric relationships with body mass were determined, and it was assessed which intestine section showed the best fit with body mass. Scaling exponents were termed 'more' or 'less than geometric' if they were above or below the expected isometry of 0.33 [39]. Then, the effect of diet was evaluated, using different dietary descriptors as cofactors or covariables with total intestine length, to decide which diet proxy would be used from there onwards (leading to the use of %faunivory, see supplement). Next, the effect of being a volant or marine species, and forestomach presence was evaluated, together with the effect of adding the diet proxy to body mass relationships. Finally, in the subset with climate proxies, the additional effect of these was assessed. Allometric regressions were performed as linear regressions on log-transformed data, because we are not aware of another method to which we can apply phylogenetic generalized least squares (see below). Linear regression on log-transformed data has been criticized [40]; therefore, we inspected the fit of the resulting equations to the un-transformed data.

Comparative analyses need to consider the phylogenetic structure of the datasets that are analyzed [41-43]. Here, all analyses were performed using generalized least squares (GLS) and phylogenetic generalized least squares (PGLS), recording the 95% confidence interval for parameter estimates, using the R packages 'caper' [44] and 'nlme' [45]. In all PGLS models, as phylogenetic signal, lambda (λ) was estimated by maximum likelihood. Additionally, we used the R package 'phytools' [46] to estimate the phylogenetic signals Blomberg's K [47] and Pagel's λ [48] for the complete datasets and the dataset of those species for which small intestine, caecum, and colon/rectum data were available. The significance level was set to 0.05. Different models applied to a certain dataset (separately for GLS and PGLS) were compared using the small sample corrected Akaike's information criterion (AIC_c) [49], considering models that differed by more than 2 ($\Delta AIC_c > 2$) as providing a different fit to the data.

Results

A final database comprised length data for the total intestinal tract (519 species), the small intestine (397 species), the large intestine (387 species), the caecum (352 species) and the colon/rectum (370 species). Generally, the small intestine represented the longest intestinal section, followed by the colon/rectum, and the caecum (Fig. S1). These data were regressed against a set of predictor variables including body mass, trophic niche, and climate and other characteristics of the natural habitat. Both Pagel's λ (at values of 0.97 to 0.99) and Blomberg's K (0.58 to 0.76) indicated a distinct phylogenetic pattern in the data; the two methods differed only for the caecum length, for which K, but not λ, indicated lower values than for the other intestinal sections (Table S1). In all PGLS analyses, there was a strong phylogenetic signal ($\lambda > 0.9$), indicating significant phylogenetic structure in all datasets (Tables S2-S12). There was no evident spacing in intestinal length between marsupials and placentals (Fig. S2A). Afrotheria and Xenarthra had comparatively short intestines (Fig. S2B), and phylogenetic clustering was evident both within the Laurasiatheria and the Euarchontoglires (Fig. S2C-E).

Allometry. Regardless of the dataset analysed, intestinal lengths scaled more-than-geometrically (positive allometry) throughout, except for the caecum, which scaled less-than-geometrically (negative allometry). Regardless of the phylogenetic signal, the simple scaling relationships were generally similar in generalized least squares (GLS) and PGLS (Table S2, Fig. S3). A visual inspection of the fit of the regression line on non-transformed data for the total intestine did not indicate a relevant mismatch (Fig. S4). When using only species for which all respective data were available, the small intestine-body mass relationship achieved lower AIC_c than the large intestine-body mass relationsip (ΔAIC_c GLS=357, PGLS =135), or than the caecum-body mass and colon/rectum-body mass relationships (ΔAIC_c GLS>308, PGLS>178), suggesting that the large intestine is more subjected to additional influence factors (Table S2). Body mass was part of all subsequent models.

Trophic level. Any trophic proxy increased the data fit for the total intestine, with %faunivory showing the best fit (Table S3). The addition of %faunivory yielded a far better data fit (ΔAIC_c 19-316) for all intestinal sections in GLS; the difference from the model without trophic proxy was least for the small intestine (Table S4). In PGLS, the same was true for the large intestine (ΔAIC_c 15-25), but for the small intestine, the model including the trophic proxy was even slightly less supported than the one without it ($\Delta AIC_c = 1.7$), and the trophic proxy was not significant, suggesting that phylogeny accounted for differences in small intestine length between trophic groups (Table S4). For all intestine sections, %faunivory was negatively related to length (Fig. 2).

The effect of trophic level was not consistent across different taxonomic groups. For the total intestine, the large groups of Eutheria, Boroeutheria, Euarchontoglires and Laurasiatheria showed significant effects of diet in GLS but not PGLS, indicating that taxa within these groups differ systematically by total intestine length and diet. By contrast, the large intestine showed a clear diet relationship in all these groups (Table S5). Clear diet effects for the total and large intestine were evident in the samples of Marsupialia and Afrotheria, and for the total intestine only (as large intestine data were lacking for this group) in Chiroptera. No effect for the total intestine but an effect on the large intestine was observed in Rodentia. No diet effect at all was evident within Primates, Eulipotyphla, Carnivora, and Artiodactyla (Table S5) – groups with comparatively uniform diets at the level of diet resolution of the present study.

Volant / Marine / Forestomach. When assessed individually with body mass, being volant had a negative relationship with total intestine length in both GLS and PGLS (Fig. S5A); being marine was not a significant factor; and having a forestomach had a positive relationship with total intestine length in GLS but not in PGLS (Fig. S5B; Table S6). In GLS, a model that included diet and all three factors (volant, marine, forestomach) was the best-supported (ΔAIC_c to the next-best model = 9), with all factors being significant (here, being marine had a positive effect on length). In PGLS, this model had similar support as other models that included diet and being volant ($\Delta AIC_c < 2$); neither being marine nor having a forestomach was significant in these or other PGLS models (Table S6).

For the small intestine, for which hardly any data for bats existed, models including diet, being marine and having a forestomach were the best-supported in GLS (ΔAIC$_c$ to next-best model = 8); both factors were positively related to length. In PGLS, the best-supported model only included being marine (ΔAIC$_c$ to next-best model = 2; Table S7). The pattern, however, does not appear convincing at visual inspection, being based on rather few species (Fig. S6).

Environment. For the total intestine, the best model included diet and absolute latitude in GLS (ΔAIC$_c$ to next-best model = 4 [temperature] and > 17 to other models). In PGLS, the best model included diet and temperature (ΔAIC$_c$ to next-best model = 7 [latitude] and > 18 to other models) (Table S8). Latitude was positively related to intestine length (Fig. 3A), and temperature negatively. For the small intestine, the models with diet and either latitude or temperature were equally supported in GLS (ΔAIC$_c$ < 2; ΔAIC$_c$ to other models > 7). In PGLS, the model with temperature had more support than the one with latitude (ΔAIC$_c$ = 3; ΔAIC$_c$ to other models > 8) (Table S9).

For both the large intestine and the colon/rectum, the best models included diet and either AET or precipitation in GLS (ΔAIC$_c$ < 2; ΔAIC$_c$ to other models > 5). In PGLS, the best models included diet and either AET or temperature for the large intestine (ΔAIC$_c$ < 2; ΔAIC$_c$ to precipitation = 2, to other models > 4), but only diet and AET for the colon/rectum (ΔAIC$_c$ to other models > 2) (Tables S10 and S11). Higher precipitation or AET (i.e., a habitat with more moisture) were linked to shorter intestinal lengths (Fig. 3B).

For the caecum, the models including latitude and temperature were equally supported in GLS (ΔAIC$_c$ < 2; ΔAIC$_c$ to other models > 10). In PGLS, the model with diet only, with AET, and with precipitation were all equally supported (ΔAIC$_c$ < 2), yet the models with temperature and latitude nearly had equal support ($\Delta AIC_c = 3$); none of the environmental parameters were significant in these models (Table S12).

Discussion

The present study provides a comprehensive data collection on mammalian intestinal length, which corroborates previously stated concepts on intestinal allometric scaling, and intuitive concepts about the relationships between digestive tract anatomy, diet, and environmental aridity. Additional, existing concepts on the effect of being a volant or marine species are also supported, and some new findings on associations are provided with having a forestomach, and with the mid-latitude of the species current geographic range. Throughout, the results emphasize that it is reasonable to consider different sections of the intestinal tract individually, as they are linked to the different biological factors to varying degrees. The scatter evident from plots recommend that while macroevolutionary trends can be stated, they should not be considered fixed biological laws, and that results may depend to a large extent on the size and composition of the investigated sample.

Limitations of the present study. The typical constraints of large literature compilations apply [50] that are not re-iterated here. Given the state of both the published literature and the information available on dissected specimens, it was not possible to account for the diet actually ingested by the animals either within the last months before measurements, or during their ontogeny. Intestinal anatomy has varying degrees of flexibility in different species; this has particularly been investigated in small mammals [51], whereas there is less evidence in larger mammals [52]. In a recent study on intra-specific variation of intestinal length measurements linked to material stored frozen or in formalin, no difference between the methods was evident [53]. However, given probable differences between individual studies, it is recommended that the present data compilation is used to investigate broad patterns across many species, but should not form the basis of a comparison of a specific pair of species.

An important limitation in the current dataset is that the functional units of the colon cannot be separated. Just like the caecum, to which it is adjacent, the proximal colon is a site of microbial action (fermentation). The major function of the subsequent parts of the colon, however, is water reabsorption [8]. In most species, it is not possible to distinguish these two colon parts macroscopically, and therefore, the length of the colon/rectum might reflect adaptations to both herbivory and arid environments.

Making absolute statements, even based on comprehensive datasets, is something our results caution against. Based on the complete dataset of 519 species, the PGLS model that related total intestinal length to body mass and diet had better support than the model with body mass alone (ΔAIC = 3, Table S3). However, in the reduced datasets of 387 or 351 species, both models were equally supported (ΔAIC=1.9 and 0, respectively, Table S3). Thus, a comparatively large dataset (351 species) did not indicate an effect of trophic level on total intestinal length, whereas a yet distinctively larger dataset (519 species) did. Although the result of the model using the larger sample size corresponds to our expectations, one might question how generalizable a result is that requires such immense sample sizes.

Our results also indicate that it is important to reference the taxonomic level on which a statement is based. The fact that there is a diet effect on the total intestinal tract length across all mammals, or within Chiroptera, contrasts with the absence of such an effect in Primates, Carnivora or Artiodactyla (Table S4). Hence, depending on the sample composition, the diet hypothesis would be confirmed or rejected. The problem of defining ‘diet’ in a way that is applicable across taxa is evident. Whereas in the Carnivora, a distinction between large- and small-prey feeders might be appropriate [54], in the Artiodactyla a separation along the browser-grazer-spectrum would make more sense [55].

Phylogeny. Both phylogenetic signals, K and λ, indicated that closely related species share a common intestinal morphology. Although it has been recommended that only results using PGLS or another method to account for phylogeny should be considered [56], a comparison between GLS and PGLS can often be instructive [43, 57, 58]. A factor that contributes significantly to variation in GLS, but does not do so in PGLS, is likely distributed unequally across the phylogeny; phylogenetic diversification then reflects the diversity in this factor. A relationship that is significant in GLS but not in PGLS shows no convergence across taxa; however, the functional association between the variables should not be discarded based on the PGLS result alone. Whereas in GLS, all diet descriptors were significantly related to total intestine length, this was not the case for several of them in PGLS (Table S2), suggesting phylogenetic specialization on either easily digestible or less easily-digestible plant parts. Whereas in GLS, having a forestomach was a significant factor for a longer small intestine, this was not significant in PGLS, most likely because the presence of a forestomach is not evenly distributed across taxa but represents a hallmark of specific taxa [34, 59]. For the same reason, we expected that a volant lifestyle, which was exclusively represented by bats in the mammalian dataset, should not yield a significant signal in PGLS – similar to other examples where a dichotomous distribution of traits across a phylogeny led to nonsignificance when accounting for that phylogeny [58, 60]. However, it has been stated that methods like PGLS are sometimes susceptible to indicating significant relationships even in such dichotomic cases; in these instances, "*unreplicated differences colocalized on a single* [phylogenetic] *branch provide only weak evidence of a causal relationship between traits*" [61]. Yet, that the evolution of flight requires a body plan with light organs, including a short intestinal tract, is physically plausible, and gains support from the convergence with birds [15, 21, 22].

Allometry. As previously described for different datasets [15-17, 23, 26] except for a study in rodents [18], intestinal lengths scale at a higher exponent than expected based on simple geometry (i.e., positive allometry at an exponent > 0.33). This applied to the small intestine, the colon/rectum, and the summative measures large and total intestine. This has been explained by geometry – that intestinal surface scales geometrically – and the necessity to keep diffusion distances short, so that intestinal diameter should not scale geometrically, but lower. Consequently, length must scale higher than geometrically to compensate [26]. A comprehensive dataset on intestinal diameter would be required to test this.

The scaling of the caecum differed from that of the other intestinal sections, with a lower exponent than expected (i.e., negative allometry at an exponent < 0.33). Based on these scaling relationships, larger mammals have, on average, a relatively shorter caecum. We hypothesize that the reason for this is not to be sought in a constraint on caecum length at higher body masses. Rather, we suggest that the ‘shallower’ scaling is an effect of particularly long caeca in small species of the Lagomorpha and Rodentia (Fig. S6). In these species, the digestive strategy of coprophagy is common [62-64], for which a voluminous caecum is one of the prerogatives. This strategy is dependent on a colonic mechanism that separates microbial matter from indigestible components of the digesta [65], which most likely is limited by colonic diameters and hence not feasible above a certain body size.

Reasons for intestine length. Two basic arguments are used to explain the need for a longer intestinal section: (i) a niche that constantly requires more of the intestine’s action, like a diet of lower digestibility [2, 3, 5-8], an arid environment [16, 26, 27], or a functional link with the strategy of coprophagy outlined above; or a niche that does not allow a long intestine due to other constraints, as in volant animals; (ii) a niche that does imply the intestine to function consistently, but requires it to adapt to peak bursts of action. This second explanation has so far only been applied to the exceptionally long small intestines of diving marine predators [23-25]. Our results suggest the hypothesis that major constant differences in dietary or humidity niches are mainly reflected in the length of the caecum and colon, whereas differences in the constancy in intake and digestion are reflected in the length of the small intestine.

Consistently different modes of action – Diet niches. In broad terms, faunivores as well as herbivores specialized on nectar or seeds have highly digestible diets (80-90%), while herbivores consuming leaves and stem parts of plants have poorly digestible diets (50-70%) [2, 3]. The lower digestibility is mainly an effect of the plant cell wall (fibre). Overall digestibility is typically negatively related to the diet's fibre content [4, 66]. When considering the intestine, fibre is fermented with assistance of a microbiome (allo-enzymatically) in the caecum and the proximal colon. Therefore, it is plausible that in animals that consume higher proportions of plant material, these sections are generally longer, as documented in the present study, and more complex [20]. As a side effect, mammalian herbivores require more voluminous body cavities [67] to harbour the longer, more complex digestive tract.

By contrast, the digestive action in the small intestine is not related to fibre fermentation, but to auto-enzymatic digestion of proteins, fats, and easily digested carbohydrates. Available data does not suggest a difference in digestive processes for protein and fat between herbivores, omnivores or carnivores [68], and therefore, major differences between the trophic guilds need not to be expected for the small intestine. Possibly, plant fibre here only acts as a dilutant, for which herbivores might compensate with longer small intestines. However, the finding that diet did not significantly explain small intestine length in PGLS indicates that within taxonomic groups, no such relationship was evident.

The GLS finding that animals with a forestomach had longer small intestines was surprising. Forestomachs do not only occur in large mammalian herbivores of various taxa [59], but also in muroid rodents [34, 69, 70]. The presence of a forestomach follows clear phylogenetic boundaries, which explains the absence of a significant signal in PGLS. We can only speculate that the enzymatic digestion of microbes, which grow in the forestomach and ultimately pass through the glandular stomach into the small intestine, requires additional intestinal capacity.

Consistently different modes of action – Xeric environments. The findings that both precipitation and actual evapotranspiration were negatively related with colon/rectum and hence large intestine length support the concept that animals in more xeric environments need more intestinal capacity for water reabsorption [16, 26, 27], even though this pattern may not be consistent within specific mammal groups [18]. Future work could assess whether renal adaptations to aridity [71] occur in parallel, or in compensatory manner, with colon length.

Consistently different modes of action – Volant lifestyle. Similar to previous findings, volant mammals had shorter total intestines than terrestrial mammals [15, 21, 22], most likely to reduce the overall weight. In birds, this does not necessarily apply to the caecum [72]. Yet, active flight is an energetically demanding form of locomotion [73] for which sufficient energy must be absorbed from the shorter intestines. Therefore, flying mammals acquired morpho-physiological adaptations such as an enlarged intestinal absorptive area by increased microvillous amplification and epithelial folding [74]. Additionally, increased paracellular absorption compared to other mammals compensates for shorter intestines [22].

Irregular modes of action – Marine habitats. Similar to previous reports, marine mammals were indicated to have longer small intestines in the present study. This additional capacity is required to compensate for a lack of intestinal function during diving [23-25].

Irregular modes of action – Seasonal habitats. A similar logic might apply for animals living in seasonal habitats. Small intestine length increased at increasing (absolute) latitude. In seasonal environments, many mammals have to incur the costs of reproduction in the growing season and also build up body reserves, which are then used in the dormant season [75]. Rather than experiencing a constant food intake, their digestive tract thus has to be able to cope with seasonally high intakes. On the one hand, it has been proposed for small mammals that increased plasticity in the digestive tract is linked to high-latitude habitats, so that more intestinal tissue can be made available when required [51]; on the other hand, our findings might indicate that a long small intestine itself is an adaptive feature for life at high latitudes. Given that seasonal environments have been linked to an increase in the pace of life [76], increased intestinal capacity might thus facilitate intense resource processing during periods of resource limitation.

Conclusions

Our investigation demonstrates associations between intestinal anatomy and dietary niches that have been claimed in the biological literature for long. At the same time, they indicate that these associations – or convergences – cannot be considered ubiquitous or 'fixed laws'. Rather, data scatter suggests that different morphophysiological solutions exist for the same ecological challenge – a typical finding of ecomorphological studies. The effects of dietary niches are particularly evident in sections of the large intestine, the caecum and the colon, whereas a trophic differentiation of the small intestine follows mammalian phylogeny, and yields no significant signal when accounting for phylogeny. Increased habitat aridity is linked to a longer colon, and habitats with colder temperature at higher latitudes are linked to longer small intestines. Our findings emphasize that different sections of the intestinal tract fulfil different functions during digestion.

Acknowledgements

We thank Barbara Schneider and Jacqueline Wick for tireless support in literature acquisition. The contributions to this project by the Disease Investigations and Animal Care staff at San Diego Zoo Global, Charles Paddock Zoo and Pacific Wildlife Care, as well as numerous student assistants, are greatly appreciated. We thank Emilia Clauss for drawing Fig. 1.

Funding

This work was supported by the Science National Foundation as part of the project CRSII5_189970 / 1.

Data, code and materials

The data collection including all individually recorded data and the species average values, together with the biological characteristics, the corresponding literature references, and the phylogenetic tree used are publicly available [77].

The R code used in the statistical procedures has been fully referenced in the method section and is given in the Supplementary Material.

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Author contributions

M.J.D.C participated in data collection and manuscript writing. D.C. performed the statistical analyses and critically revised the manuscript. C.M. compiled the phylogenetic tree and critically revised the manuscript. A.M., C.S. and M.S.E. participated in data collection and critically revised the manuscript. M.C. conceived of the study, designed the study, participated in the data collection and manuscript writing. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

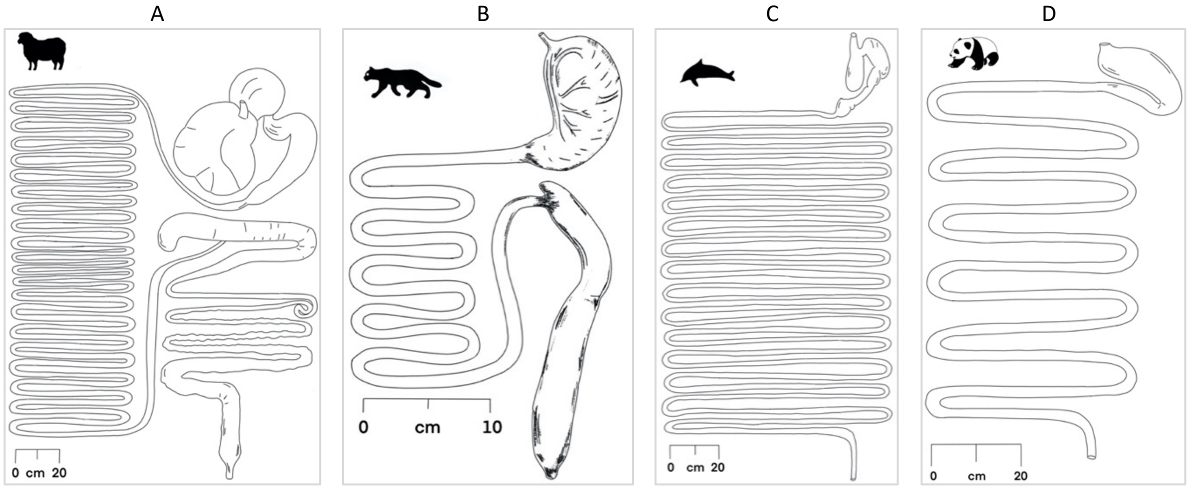

Figure 1 Examples of digestive tracts of mammals. (A) the domestic sheep (*Ovis aries*), a ‘typical’ herbivore, with a long intestine; (B) the domestic cat (*Felis catus*), a ‘typical’ faunivore, with a short intestine; (C) a dolphin (*Larnorhynchus acutus*), an ‘atypical’ faunivore with a long intestine; (D) a giant panda , an ‘atypical’ herbivore with a short intestine. Modified from [78] and [79]. Note that phylogeny groups the more similar cat and panda (Carnivora) and sheep and dolphin (Cetartiodactyla) together.

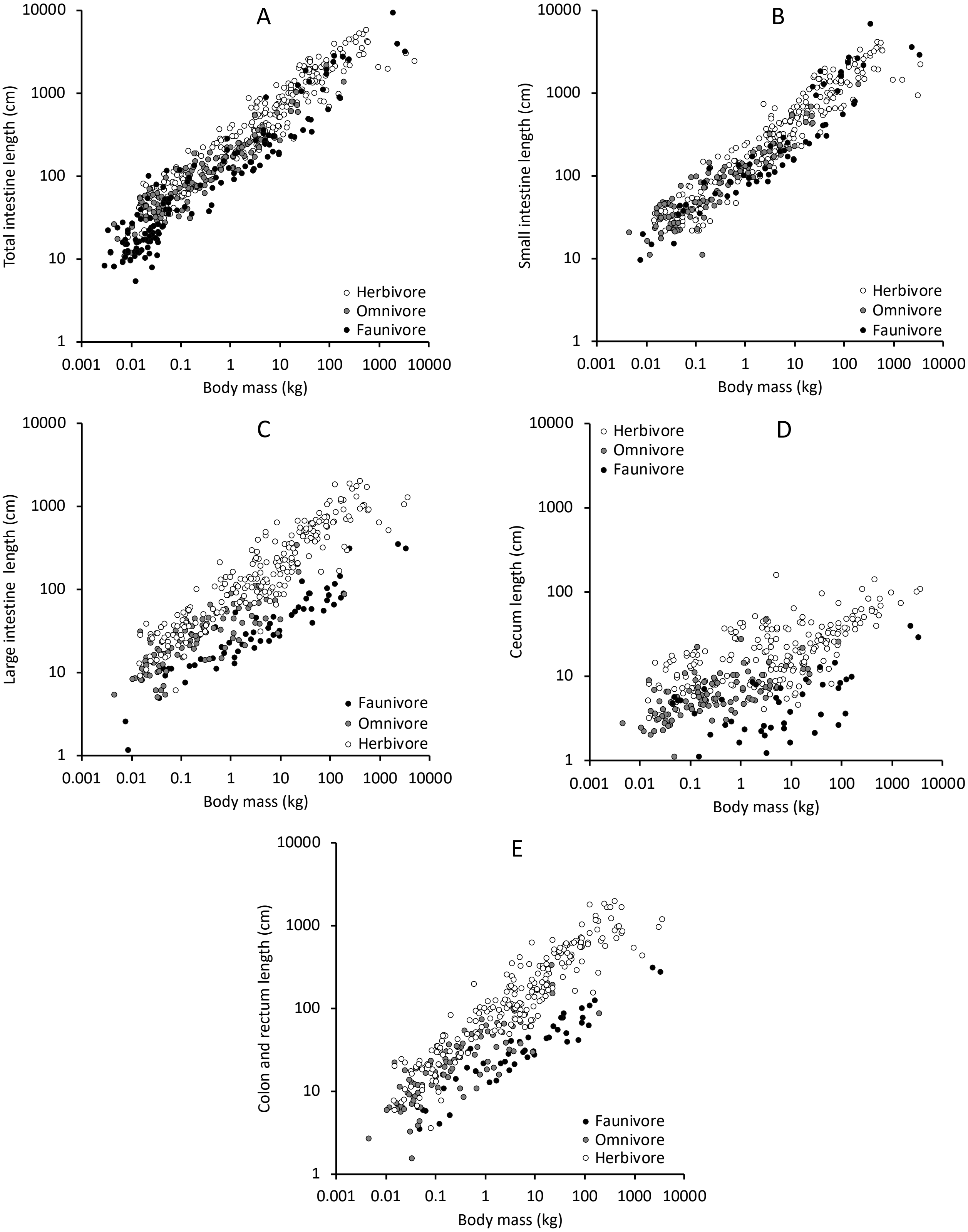

Figure 2 Relationship of body mass and intestinal length for (A) total intestine (n=519 species), (B) small intestine (n=397), (C) large intestine (Caecum, colon and rectum) (n=387), (D) caecum (n=352), (E) colon and rectum (n=370) by trophic groups. For statistics, see Table S4. Note that for statistics, %faunivory was used as a continuous variable, whereas it is depicted for different groups here, using a 10 and 90% threshold to separate herbivores, omnivores and faunivores.

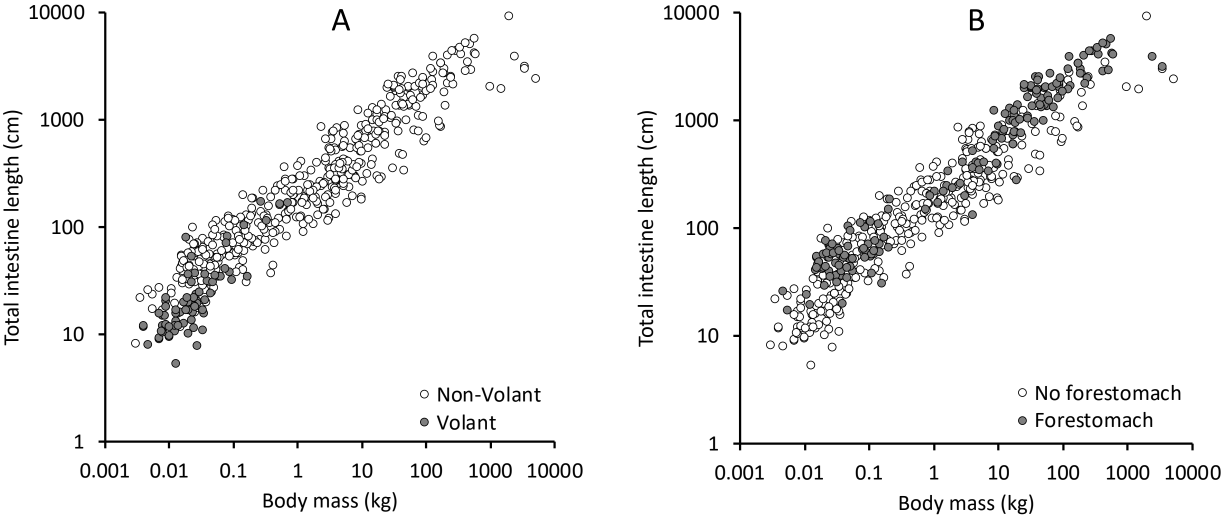

Figure 3 Relationships between total intestine length and body mass (A) nonvolant vs. volant mammals, (B) mammals without and with a forestomach. For statistics, see Table S6.

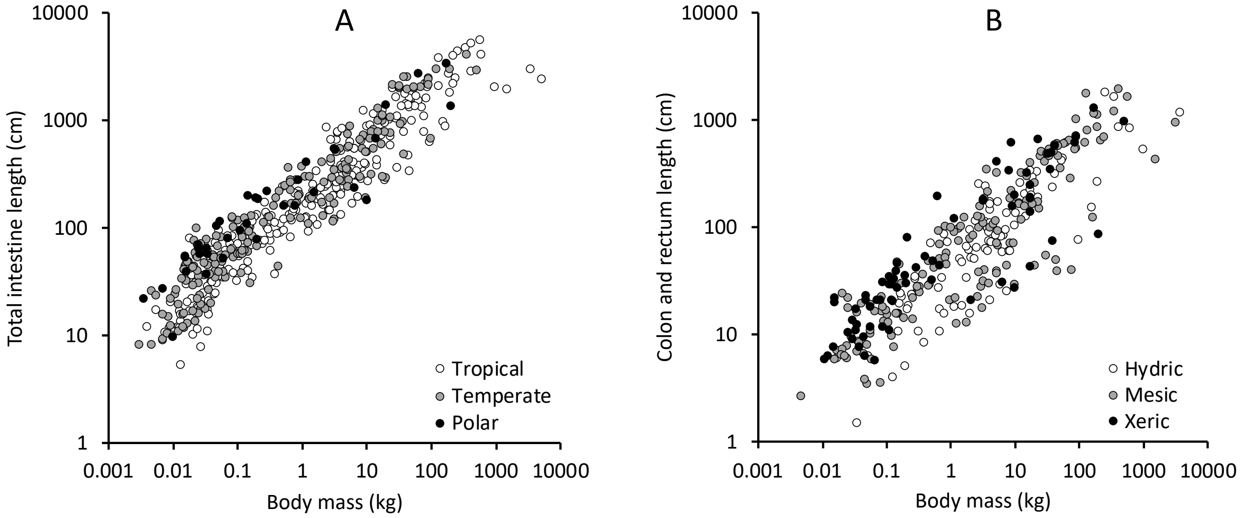

Figure 4 Relationships between mammalian intestinal length and body mass (A) for the total intestine with species separated by mean latitude of origin, (B) for the colon/rectum and species separated by the dryness of their habitat. For statistics, see Table S8 and S11. Note that for statistics, latitude and AET were used as a continuous variable, whereas they are depicted for different groups here, using 1400 mm- and 500 mm thresholds to separate animals from hydric (moist), mesic (intermediate), and xeric (arid) climates.

Supplementary material

Proceedings of the Royal Society B

doi https://doi.org/10.1098/rspb.2020.2888

Mammalian intestinal allometry, phylogeny, trophic level and climate

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Additional thoughts on the very influential publication by Chivers and Hladik (1980)

Additional analyses regarding the trophic level proxy

Tables S1-S12

Figures S1-S6

R Code

References

Additional thoughts on the very influential publication by Chivers and Hladik [5], where not only a plethora of digestive tracts are given as illustrations, but where digestive tract measures are also submitted to statistical analyses.

In that dataset, the overlap between diet groups is substantial – a fact typically not mentioned when it is cited. Various details of this work might lead to the conclusion that the methods are not robust: There is a dramatic difference in measures between the – ecologically, physiologically and anatomically similar – sheep (*Ovis aries*) and goat (*Capra hircus*) in the dataset, with sheep having less 'fermentation' capacity, tending towards the frugivores (Fig. 17, 18,); the rabbit (*Oryctolagus cuniculus*) is placed on the borderline between frugivores and folivores (Fig. 17, 18); the golden cat (*Profelis aurata*) and the domestic pig (*Sus scrofa*) have similar measures on the border between faunivores and frugivores (Fig. 17), and the domestic cat (*Felis catus*) is classified as more of a frugivore than the domestic pig and dog, which are both classified as fauni-/frugivores (Fig. 18); dietary classifications are not consistent across the analyses, e.g. the group of colobine monkeys is classified as both frugi- and folivorous in one display (Fig. 18) and as only folivorous in another (Fig. 20); whether a surface area of a haustrated structure like the colon of a pig or horse or gorilla can be really approximated using 'length and a series of breadths' (p. 356) appears questionable. Some of these problems are proactively addressed, e.g. in the legend of Fig. 20.

Additional analyses regarding the trophic level proxy. The proportion of animal matter (i.e., the reciprocal of the proportion of all plant matter) in the diet yielded the best fit for the total intestine-body mass relationship in GLS (ΔAIC to models with other diet proxies >8); in PGLS, it was equally supported as the faunivore-omnivore-herbivore classification with the 70% threshold (ΔAIC<2; ΔAIC to models with other diet proxies >3; Table S3). However, in the latter analysis, omnivores were not significantly different from faunivores. The proportion of more readily digestible plant parts (fruits, nectar, seeds), or of the less digestible plant parts (leaves and stems) did not yield a better data fit, and only had a significant effect in GLS but not PGLS (Table S3). Therefore, %faunivory was used as a trophic proxy throughout.

Table S1 Phylogenetic signals (K and λ) in the main datasets of the present study

	All available data					**Consistent species dataset**				
		body mass		intestine length			body mass		intestine length	
	n	K	λ	K	λ	n	K	λ	K	λ
Total intestine	519	0.76	0.99	0.76	0.98	351	0.61	0.99	0.62	0.98
Small intestine	397	0.63	0.99	0.58	0.98	351	0.61	0.99	0.59	0.98
Large intestine	387	0.64	0.99	0.66	0.99	351	0.61	0.99	0.64	0.99
Caecum	352	0.61	0.99	0.34	0.97	351	0.61	0.99	0.34	0.97
Colon	370	0.62	0.99	0.65	0.99	351	0.61	0.99	0.64	0.99

analyses performed in 'phytools' [46] using 9999 simulations per analysis and log-transformed values; all analyses significant at $P < 0.001$

Table S2 Summary statistics for allometric scaling as log(y) = a + b log(body mass), or y = (10^a) BM^b (significant parameters in **bold**)

			GLS				**PGLS**			
Dependent	**Model**	**n**	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
All data										
Total intest.	BM	519	-	-	a	**2.26 (2.24 to 2.28)**	0.93 (0.88 to 0.96)	-	-	**2.17 (1.85 to 2.49)**
					b	**0.48 (0.46 to 0.49)**				**0.40 (0.38 to 0.43)**
Small intest.	BM	397	-	-	a	**2.13 (2.11 to 2.15)**	0.93 (0.88 to 0.96)	-	-	**2.04 (1.69 to 2.39)**
					b	**0.46 (0.44 to 0.47)**				**0.40 (0.38 to 0.43)**
Large intest.	BM	387	-	-	a	**1.75 (1.71 to 1.78)**	0.97 (0.95 to 0.99)	-	-	**1.57 (1.09 to 2.06)**
					b	**0.41 (0.39 to 0.44)**				**0.37 (0.34 to 0.41)**
Caecum	BM	352	-	-	a	**0.98 (0.95 to 1.02)**	0.96 (0.94 to 0.98)	-	-	**0.71 (0.23 to 1.20)**
					b	**0.21 (0.18 to 0.24)**				**0.28 (0.25 to 0.32)**
Colon/Rect.	BM	370	-	-	a	**1.65 (1.61 to 1.68)**	0.97 (0.95 to 0.99)	-	-	**1.47 (0.94 to 2.01)**
					b	**0.45 (0.42 to 0.48)**				**0.39 (0.35 to 0.43)**
Consistent data (species for which both small and large intestinal length are available)										
Total intest.	BM	387	-94.9	4.3	a	**2.31 (2.29 to 2.33)**	0.92 (0.86 to 0.96)	-399.8	0.0	**2.20 (1.90 to 2.50)**
					b	**0.44 (0.43 to 0.46)**				**0.40 (0.37 to 0.42)**
Small intest.	BM	387	-99.2	0.0	a	**2.14 (2.11 to 2.16)**	0.94 (0.89 to 0.97)	-349.6	50.2	**2.04 (1.70 to 2.39)**
					b	**0.46 (0.44 to 0.47)**				**0.40 (0.38 to 0.43)**
Large intest.	BM	387	257.8	357.1	a	**1.75 (1.71 to 1.78)**	0.97 (0.95 to 0.99)	-214.9	184.8	**1.57 (1.09 to 2.06)**
					b	**0.41 (0.39 to 0.434)**				**0.37 (0.34 to 0.41)**
Consistent data (species for which small intestine, caecum and colon/rectum length are available)										
Total intest.	BM	351	-82.5	4.0	a	**2.31 (2.29 to 2.33)**	0.94 (0.90 to 0.97)	-391.7	0.0	**2.19 (1.88 to 2.51)**
					b	**0.44 (0.42 to 0.46)**				**0.39 (0.36 to 0.41)**
Small intest.	BM	351	-86.4	0.0	a	**2.13 (2.11 to 2.15)**	0.96 (0.92 to 0.98)	-347.5	44.2	**2.04 (1.68 to 2.40)**
					b	**0.45 (0.44 to 0.47)**				**0.40 (0.37 to 0.43)**
Large intest.	BM	351	182.5	268.9	a	**1.77 (1.74 to 1.81)**	0.97 (0.94 to 0.98)	-223.4	168.4	**1.59 (1.13 to 2.05)**
					b	**0.41 (0.38 to 0.43)**				**0.36 (0.33 to 0.40)**
Caecum	BM	351	234.9	321.3	a	**0.98 (0.95 to 1.02)**	0.96 (0.94 to 0.98)	-169.0	222.7	**0.71 (0.23 to 1.20)**
					b	**0.21 (0.18 to 0.24)**				**0.29 (0.25 to 0.32)**
Colon/Rect.	BM	351	222.2	308.6	a	**1.67 (1.63 to 1.70)**	0.97 (0.95 to 0.99)	-132.0	259.7	**1.48 (0.95 to 2.02)**
					b	**0.45 (0.42 to 0.47)**				**0.38 (0.34 to 0.42)**

AIC_c: small sample corrected Akaike's information criterion (for analyses using the same species set, indicated by the same n, a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S3 Summary statistics for models assessing different diet proxies with mammalian total intestine length (n = 519 species) as dependent variable according to log(total intestine length) = a + b log(BM) + c (diet proxy); (significant parameters in **bold**)

	GLS				**PGLS**			
Diet proxy	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
(none)	-54.8	135.7	a	**2.26 (2.24 to 2.28)**	0.93 (0.88 to 0.96)	-479.3	3.1	**2.17 (1.85 to 2.49)**
			b	**0.48 (0.46 to 0.49)**				**0.40 (0.38 to 0.43)**
Trophic70	-181.9	8.5	a	**2.11 (2.08 to 2.15)**	0.92 (0.86 to 0.95)	-482.4	0.0	**2.15 (1.84 to 2.46)**
			b	**0.45 (0.44 to 0.47)**				**0.40 (0.38 to 0.42)**
			70Herbivore	**0.24 (0.20 to 0.28)**				**0.08 (0.01 to 0.14)**
			70Omnivore	0.02 (-0.05 to 0.10)				0.00 (-0.07 to 0.07)
Trophic90	-182.3	8.1	a	**2.09 (2.06 to 2.13)**	0.92 (0.87 to 0.95)	-479.1	3.3	**2.15 (1.83 to 2.46)**
			b	**0.45 (0.43 to 0.46)**				**0.40 (0.38 to 0.43)**
			90Herbivore	**0.27 (0.23 to 0.32)**				**0.07 (0.00 to 0.14)**
			90Omnivore	**0.15 (0.10 to 0.19)**				0.04 (-0.02 to 0.10)
%faunivory	-190.5	0.0	a	**2.37 (2.34 to 2.39)**	0.92 (0.87 to 0.95)	-482.2	0.2	**2.23 (1.92 to 2.54)**
			b	**0.45 (0.44 to 0.46)**				**0.40 (0.38 to 0.42)**
			c	**-0.28 (-0.32 to -0.23)**				**-0.09 (-0.16 to -0.01)**
%less digestible plants	-167.1	23.4	a	**2.15 (2.12 to 2.17)**	0.92 (0.87 to 0.95)	-478.6	3.8	**2.16 (1.84 to 2.48)**
			b	**0.44 (0.42 to 0.45)**				**0.40 (0.38 to 0.43)**
			c	**0.29 (0.24 to 0.34)**				0.04 (-0.03 to 0.11)
%digestible plants	-60.2	130.3	a	**2.24 (2.22 to 2.27)**	0.93 (0.88 to 0.96)	-478.1	4.4	**2.17 (1.85 to 2.49)**
			b	**0.48 (0.47 to 0.49)**				**0.41 (0.38 to 0.43)**
			c	**0.10 (0.03 to 0.16)**				0.03 (-0.04 to 0.11)

Trophic70 / 90: species classified as faunivores (>70 or 90% faunivory), omnivores, or herbivores (<30 or 10% faunivory); less digestible plant parts = leaves and stems; digestible plant parts = fruit, nectar, seeds

$\mathrm{AIC_c}$: small sample corrected Akaike's information criterion (a lower $\mathrm{AIC_c}$ indicates a better model fit); $\Delta\mathrm{AIC_c}$: indicates the difference in $\mathrm{AIC_c}$ to the model with the lowest $\mathrm{AIC_c}$ (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that $\mathrm{AIC_c}$ cannot be compared between GLS and PGLS models.

Table S4 Summary statistics for models assessing different mammalian intestinal sections only with body mass (BM) or additionally with a diet proxy according to log(length) = a + b log(BM) + c (diet proxy); (significant parameters in **bold**)

			GLS					**PGLS**				
Dependent	**Model**	**n**	**AICc**	**ΔAIC (trophic)**	**ΔAIC (all)**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC (trophic)**	**ΔAIC (all)**	**parameter (95% CI)**
All data												
Total intest.	BM	519	-54.8	135.7	-	a	**2.26 (2.24 to 2.28)**	0.93 (0.88 to 0.96)	-479.3	2.9	-	**2.17 (1.85 to 2.49)**
						b	**0.48 (0.46 to 0.49)**					**0.40 (0.38 to 0.43)**
Total intest.	BM + %faunivory	519	-190.5	0.0	-	a	**2.37 (2.34 to 2.39)**	0.92 (0.87 to 0.95)	-482.2	0.0	-	**2.23 (1.92 to 2.54)**
						b	**0.45 (0.44 to 0.46)**					**0.40 (0.38 to 0.42)**
						c	**-0.28 (-0.32 to -0.23)**					**-0.09 (-0.16 to -0.01)**
Small intest.	BM	397	-96.0	18.9	-	a	**2.13 (2.11 to 2.15)**	0.93 (0.87 to 0.96)	-339.9	0.0	-	**2.04 (1.69 to 2.39)**
						b	**0.46 (0.44 to 0.48)**					**0.40 (0.38 to 0.43)**
Small intest.	BM + %faunivory	397	-114.9	0.0	-	a	**2.17 (2.14 to 2.20)**	0.94 (0.89 to 0.97)	-338.2	1.7	-	**2.02 (1.67 to 2.38)**
						b	**0.46 (0.44 to 0.47)**					**0.40 (0.38 to 0.43)**
						c	**-0.13 (-0.19 to -0.08)**					0.03 (-0.07 to 0.13)
Large intest.	BM	387	257.8	316.1	-	a	**1.75 (1.71 to 1.78)**	0.97 (0.95 to 0.99)	-214.9	24.8	-	**1.57 (1.09 to 2.06)**
						b	**0.41 (0.39 to 0.44)**					**0.37 (0.34 to 0.41)**
Large intest.	BM + %faunivory	387	-58.3	0.0	-	a	**1.94 (1.91 to 1.97)**	0.95 (0.92 to 0.98)	-239.7	0.0	-	**1.77 (1.34 to 2.20)**
						b	**0.39 (0.38 to 0.41)**					**0.37 (0.33 to 0.40)**
						c	**-0.70 (-0.77 to -0.64)**					**-0.33 (-0.45 to -0.21)**
Caecum	BM	352	236.6	177.5	-	a	**0.98 (0.95 to 1.02)**	0.96 (0.94 to 0.98)	-168.5	15.2	-	**0.71 (0.23 to 1.20)**
						b	**0.21 (0.18 to 0.24)**					**0.28 (0.25 to 0.32)**
Caecum	BM + %faunivory	352	59.1	0.0	-	a	**1.14 (1.10 to 1.17)**	0.95 (0.92 to 0.97)	-183.7	0.0	-	**0.90 (0.45 to 1.36)**
						b	**0.19 (0.17 to 0.22)**					**0.27 (0.24 to 0.31)**
						c	**-0.63 (-0.71 to -0.55)**					**-0.32 (-0.46 to -0.17)**
Colon/Rect.	BM	370	264.1	254.9	-	a	**1.65 (1.61 to 1.68)**	0.97 (0.95 to 0.99)	-126.8	15.7	-	**1.47 (0.94 to 2.01)**
						b	**0.45 (0.42 to 0.48)**					**0.39 (0.35 to 0.43)**
Colon/Rect.	BM + %faunivory	370	9.3	0.0	-	a	**1.83 (1.80 to 1.86)**	0.96 (0.92 to 0.98)	-142.5	0.0	-	**1.66 (1.17 to 2.16)**
						b	**0.43 (0.41 to 0.45)**					**0.38 (0.34 to 0.41)**
						c	**-0.69 (-0.76 to -0.62)**					**-0.32 (-0.46 to -0.18)**

Table S4 ctd. Summary statistics for models assessing different mammalian intestinal sections only with body mass (BM) or additionally with a diet proxy according to log(length) = a + b log(BM) + c (diet proxy); (significant parameters in **bold**)

			GLS					**PGLS**				
Dependent	**Model**	**n**	**AICc**	**ΔAIC (trophic)**	**ΔAIC (all)**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC (trophic)**	**ΔAIC (all)**	**parameter (95% CI)**
Consistent data (species for which both small and large intestinal length are available)												
Total intest.	BM	387	-94.9	96.4	96.4	a	**2.31 (2.29 to 2.33)**	0.92 (0.86 to 0.96)	-399.8	1.9	1.9	**2.20 (1.89 to 2.50)**
						b	**0.44 (0.43 to 0.46)**					**0.40 (0.37 to 0.42)**
Total intest.	BM + %faunivory	387	-191.3	0.0	0.0	a	**2.38 (2.36 to 2.41)**	0.91 (0.84 to 0.95)	-401.7	0.0	0.0	**2.25 (1.96 to 2.55)**
						b	**0.44 (0.42 to 0.45)**					**0.39 (0.37 to 0.42)**
						c	**-0.28 (-0.33 to -0.23)**					**-0.09 (-0.18 to -0.00)**
Small intest.	BM	387	-99.2	21.8	92.1	a	**2.13 (2.11 to 2.16)**	0.94 (0.89 to 0.97)	-349.6	0.0	52.1	**2.04 (1.70 to 2.39)**
						b	**0.46 (0.44 to 0.47)**					**0.40 (0.38 to 0.43)**
Small intest.	BM + %faunivory	387	-121.0	0.0	70.3	a	**2.17 (2.15 to 2.20)**	0.94 (0.89 to 0.97)	-347.6	2.0	54.1	**2.04 (1.69 to 2.39)**
						b	**0.45 (0.44 to 0.47)**					**0.40 (0.38 to 0.43)**
						c	**-0.14 (-0.20 to -0.09)**					0.01 (-0.09 to 0.11)
Large intest.	BM	387	257.8	316.1	449.1	a	**1.75 (1.71 to 1.78)**	0.97 (0.95 to 0.99)	-214.9	24.8	186.7	**1.57 (1.09 to 2.06)**
						b	**0.41 (0.39 to 0.44)**					**0.37 (0.34 to 0.41)**
Large intest.	BM + %faunivory	387	-58.3	0.0	133.0	a	**1.94 (1.91 to 1.97)**	0.95 (0.92 to 0.98)	-239.7	0.0	162.0	**1.77 (1.34 to 2.20)**
						b	**0.39 (0.38 to 0.41)**					**0.37 (0.33 to 0.40)**
						c	**-0.70 (-0.77 to -0.64)**					**-0.33 (-0.45 to -0.21)**

Table S4 ctd. Summary statistics for models assessing different mammalian intestinal sections only with body mass (BM) or additionally with a diet proxy according to log(length) = a + b log(BM) + c (diet proxy); (significant parameters in **bold**)

			GLS					**PGLS**				
Dependent	**Model**	**n**	**AICc**	**ΔAIC (trophic)**	**ΔAIC (all)**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC (trophic)**	**ΔAIC (all)**	**parameter (95% CI)**
Consistent data (species for which small intestine, caecum and colon/rectum length are available)												
Total intest.	BM	351	-82.5	92.2	92.2	a	**2.31 (2.29 to 2.33)**	0.94 (0.90 to 0.97)	-391.7	0.0	0.0	**2.19 (1.88 to 2.51)**
						b	**0.44 (0.42 to 0.46)**					**0.39 (0.36 to 0.41)**
Total intest.	BM + %faunivory	351	-174.7	0.0	0.0	a	**2.38 (2.36 to 2.41)**	0.93 (0.89 to 0.97)	-391.3	0.4	0.0	**2.23 (1.92 to 2.55)**
						b	**0.43 (0.42 to 0.45)**					**0.38 (0.36 to 0.41)**
						c	**-0.31 (-0.37 to -0.25)**					-0.07 (-0.17 to 0.04)
Small intest.	BM	351	-86.4	26.5	88.3	a	**2.13 (2.11 to 2.15)**	0.96 (0.93 to 0.98)	-347.5	0.0	44.2	**2.04 (1.68 to 2.40)**
						b	**0.45 (0.44 to 0.47)**					**0.40 (0.37 to 0.43)**
Small intest.	BM + %faunivory	351	-112.9	0.0	61.8	a	**2.17 (2.15 to 2.20)**	0.96 (0.92 to 0.98)	-345.8	1.8	45.5	**2.02 (1.65 to 2.39)**
						b	**0.45 (0.43 to 0.47)**					**0.40 (0.37 to 0.43)**
						c	**-0.18 (-0.24 to -0.11)**					0.03 (-0.08 to 0.15)
Large intest.	BM	351	182.5	270.6	357.2	a	**1.77 (1.74 to 1.81)**	0.97 (0.94 to 0.98)	-223.4	18.0	168.4	**1.59 (1.13 to 2.05)**
						b	**0.41 (0.38 to 0.43)**					**0.36 (0.33 to 0.40)**
Large intest.	BM + %faunivory	351	-88.1	0.0	86.6	a	**1.94 (1.91 to 1.97)**	0.95 (0.90 to 0.97)	-241.3	0.0	150.0	**1.78 (1.37 to 2.19)**
						b	**0.39 (0.37 to 0.41)**					**0.36 (0.32 to 0.39)**
						c	**-0.68 (-0.75 to -0.62)**					**-0.33 (-0.46 to -0.19)**
Caecum	BM	351	234.9	179.7	409.6	a	**0.98 (0.95 to 1.02)**	0.96 (0.94 to 0.98)	-169.0	16.9	222.7	**0.71 (0.23 to 1.20)**
						b	**0.21 (0.18 to 0.24)**					**0.29 (0.25 to 0.32)**
Caecum	BM + %faunivory	351	55.2	0.0	229.9	a	**1.14 (1.10 to 1.17)**	0.95 (0.92 to 0.97)	-185.8	0.0	205.5	**0.91 (0.46 to 1.37)**
						b	**0.19 (0.17 to 0.22)**					**0.27 (0.24 to 0.31)**
						c	**-0.64 (-0.72 to -0.55)**					**-0.33 (-0.48 to -0.19)**
Colon/Rect.	BM	351	222.2	242.3	396.9	a	**1.67 (1.63 to 1.70)**	0.97 (0.95 to 0.99)	-132.0	16.5	259.7	**1.48 (0.95 to 2.02)**
						b	**0.45 (0.42 to 0.47)**					**0.38 (0.34 to 0.42)**
Colon/Rect.	BM + %faunivory	351	-20.2	0.0	154.5	a	**1.84 (1.80 to 1.87)**	0.95 (0.90 to 0.98)	-148.5	0.0	242.8	**1.70 (1.22 to 2.18)**
						b	**0.43 (0.41 to 0.45)**					**0.37 (0.33 to 0.41)**
						c	**-0.70 (-0.77 to -0.62)**					**-0.36 (-0.51 to -0.21)**

AIC_c: small sample corrected Akaike's information criterion (for analyses using the same species set, indicated by the same n, a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models. ΔAIC_c (trophic) compares a model with BM and the same model with the additional trophic signal; ΔAIC_c (all) compares all models using the same species set.

Table S5 Summary statistics for models assessing total or large intestinal length in different mammal subgroups with body mass (BM) or additionally with a diet proxy according to log(length) = a + b log(BM) + c (diet proxy); (significant parameters in **bold**)

Taxon	**Dependent**	**Model**		**GLS**				**PGLS**			
			n	**AICc**	**ΔAIC**		**parameter (95% CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95% CI)**
Marsupials	Total intest.	BM	36	30.0	7.5	a	**2.15 (2.05 to 2.26)**	0.88 (0.16 to 0.99)	13.8	4.6	**2.17 (1.59 to 2.75)**
						b	**0.44 (0.34 to 0.55)**				**0.28 (0.16 to 0.40)**
		BM + %faunivory		22.5	0.0	a	**2.38 (2.23 to 2.53)**	0.46 (NA to 0.97)	9.1	0.0	**2.44 (2.09 to 2.80)**
						b	**0.32 (0.20 to 0.43)**				**0.29 (0.17 to 0.40)**
						c	**-0.50 (-0.76 to -0.23)**				**-0.46 (-0.78 to -0.15)**
	Large intest.	BM	33	48.8	12.7	a	**1.60 (1.45 to 1.75)**	0.97 (0.84 to 0.99)	16.6	2.8	**1.60 (0.79 to 2.42)**
						b	**0.50 (0.33 to 0.68)**				**0.24 (0.10 to 0.38)**
		BM + %faunivory		36.1	0.0	a	**1.95 (1.76 to 2.14)**	0.95 (0.70 to 0.99)	13.8	0.0	**2.02 (1.23 to 2.80)**
						b	**0.32 (0.17 to 0.48)**				**0.21 (0.07 to 0.34)**
						c	**-0.79 (-1.13 to -0.45)**				**-0.63 (-1.17 to -0.09)**
Eutheria	Total intest.	BM	483	-73.0	123.0	a	**2.27 (2.25 to 2.29)**	0.91 (0.87 to 0.95)	-523.9	1.3	**2.17 (1.82 to 2.53)**
						b	**0.48 (0.46 to 0.49)**				**0.42 (0.39 to 0.44)**
		BM + %faunivory		-196.0	0.0	a	**2.37 (2.35 to 2.39)**	0.91 (0.86 to 0.94)	-525.2	0.0	**2.22 (1.87 to 2.57)**
						b	**0.45 (0.44 to 0.46)**				**0.42 (0.39 to 0.44)**
						c	**-0.27 (-0.31 to -0.22)**				-0.07 (-0.14 to 0.00)
	Large intest.	BM	352	219.6	292.4	a	**1.76 (1.73 to 1.80)**	0.93 (0.88 to 0.97)	-243.4	22.8	**1.62 (1.42 to 1.81)**
						b	**0.41 (0.38 to 0.43)**				**0.39 (0.36 to 0.43)**
		BM + %faunivory		-72.8	0.0	a	**1.94 (1.91 to 1.97)**	0.89 (0.80 to 0.94)	-266.2	0.0	**1.76 (1.59 to 1.94)**
						b	**0.39 (0.38 to 0.41)**				**0.39 (0.35 to 0.42)**
						c	**-0.70 (-0.76 to -0.64)**				**-0.31 (-0.43 to -0.20)**
Afrotheria	Total intest.	BM	23	6.3	4.2	a	**2.11 (2.02 to 2.20)**	0.80 (0.34 to 0.97)	-16.6	2.6	**2.10 (1.92 to 2.29)**
						b	**0.41 (0.35 to 0.47)**				**0.36 (0.27 to 0.44)**
		BM + %faunivory		2.1	0.0	a	**2.35 (2.18 to 2.52)**	0.72 (0.13 to 0.96)	-19.2	0.0	**2.34 (2.08 to 2.61)**
						b	**0.31 (0.23 to 0.39)**				**0.31 (0.23 to 0.40)**
						c	**-0.43 (-0.69 to -0.16)**				**-0.40 (-0.77 to -0.04)**
	Large intest.	BM	12	12.4	7.2	a	**1.75 (1.61 to 1.89)**	0.97 (0.72 to NA)	-8.9	3.3	**1.78 (1.48 to 2.09)**
						b	**0.45 (0.37 to 0.53)**				**0.40 (0.28 to 0.52)**
		BM + %faunivory		5.2	0.0	a	**2.03 (1.88 to 2.18)**	0.93 (NA to NA)	-12.2	0.0	**2.10 (1.74 to 2.45)**
						b	**0.32 (0.25 to 0.40)**				**0.32 (0.20 to 0.43)**
						c	**-0.61 (-0.88 to -0.33)**				**-0.68 (-1.24 to -0.11)**
Boroeutheria	Total intest.	BM	453	-80.8	125.3	a	**2.28 (2.26 to 2.30)**	0.83 (0.75 to 0.89)	-515.1	0.9	**2.28 (2.17 to 2.39)**
						b	**0.48 (0.47 to 0.49)**				**0.42 (0.40 to 0.45)**
		BM + %faunivory		-206.2	0.0	a	**2.38 (2.35 to 2.40)**	0.82 (0.73 to 0.89)	-516.0	0.0	**2.31 (2.20 to 2.43)**
						b	**0.46 (0.45 to 0.47)**				**0.42 (0.40 to 0.44)**
						c	**-0.28 (-0.32 to -0.23)**				-0.07 (-0.14 to 0.01)
	Large intest.	BM	337	213.0	284.9	a	**1.77 (1.73 to 1.80)**	0.93 (0.87 to 0.97)	-237.6	19.8	**1.62 (1.43 to 1.82)**
						b	**0.40 (0.38 to 0.43)**				**0.39 (0.36 to 0.43)**
		BM + %faunivory		-71.9	0.0	a	**1.94 (1.91 to 1.97)**	0.89 (0.80 to 0.94)	-257.4	0.0	**1.74 (1.56 to 1.92)**
						b	**0.40 (0.38 to 0.42)**				**0.39 (0.35 to 0.42)**
						c	**-0.73 (-0.80 to -0.66)**				**-0.30 (-0.42 to -0.18)**

Table S5 ctd. Summary statistics for models assessing total or large intestinal length in different mammal subgroups with body mass (BM) or additionally with a diet proxy according to log(length) = a + b log(BM) + c (diet proxy); (significant parameters in **bold**)

Taxon	**Dependent**	**Model**		**GLS**				**PGLS**			
			n	**AICc**	**ΔAIC**		**parameter (95% CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95% CI)**
Euarchontoglires	Total intest.	BM	210	-162.8	2.7	a	**2.31 (2.29 to 2.33)**	0.80 (0.63 to 0.90)	-285.0	0.0	**2.33 (2.23 to 2.43)**
						b	**0.41 (0.39 to 0.43)**				**0.38 (0.34 to 0.41)**
		BM + %faunivory		-165.6	0.0	a	**2.33 (2.31 to 2.36)**	0.80 (0.63 to 0.90)	-284.1	0.9	**2.34 (2.24 to 2.44)**
						b	**0.40 (0.38 to 0.42)**				**0.37 (0.34 to 0.41)**
						c	**-0.15 (-0.25 to -0.05)**				-0.05 (-0.16 to 0.05)
	Large intest.	BM	204	-24.2	39.7	a	**1.81 (1.77 to 1.84)**	0.88 (0.73 to 0.96)	-140.7	14.8	**1.81 (1.64 to 1.97)**
						b	**0.39 (0.36 to 0.42)**				**0.37 (0.32 to 0.42)**
		BM + %faunivory		-63.9	0.0	a	**1.87 (1.84 to 1.91)**	0.82 (0.62 to 0.93)	-155.5	0.0	**1.88 (1.73 to 2.02)**
						b	**0.37 (0.34 to 0.39)**				**0.36 (0.31 to 0.41)**
						c	**-0.47 (-0.60 to -0.34)**				**-0.30 (-0.45 to -0.16)**
Primates	Total intest.	BM	62	-75.6	0.0	a	**2.24 (2.21 to 2.27)**	0.92 (0.73 to 0.99)	-110.9	0.0	**2.28 (2.09 to 2.46)**
						b	**0.39 (0.34 to 0.43)**				**0.37 (0.31 to 0.43)**
		BM + %faunivory		-70.6	5.0	a	**2.25 (2.19 to 2.31)**	0.93 (0.72 to 0.99)	-109.2	1.8	**2.29 (2.10 to 2.49)**
						b	**0.38 (0.33 to 0.43)**				**0.36 (0.30 to 0.43)**
						c	-0.03 (-0.20 to 0.13)				-0.04 (-0.23 to 0.14)
	Large intest.	BM	62	-15.3	0.0	a	**1.71 (1.66 to 1.76)**	0.98 (0.89 to NA)	-61.1	0.0	**1.76 (1.41 to 2.11)**
						b	**0.36 (0.29 to 0.43)**				**0.31 (0.21 to 0.40)**
		BM + %faunivory		-13.9	1.4	a	**1.78 (1.68 to 1.87)**	0.93 (0.72 to 0.99)	-59.9	1.3	**1.81 (1.41 to 2.21)**
						b	**0.32 (0.23 to 0.40)**				**0.25 (0.14 to 0.36)**
						c	-0.23 (-0.50 to 0.04)				-0.14 (-0.33 to 0.06)
Rodents	Total intest.	BM	140	-108.0	0.0	a	**2.38 (2.35 to 2.42)**	0.67 (0.42 to 0.84)	-165.6	0.0	**2.35 (2.25 to 2.44)**
						b	**0.46 (0.43 to 0.50)**				**0.39 (0.34 to 0.43)**
		BM + %faunivory		-105.6	2.3	a	**2.39 (2.36 to 2.43)**	0.66 (0.42 to 0.84)	-164.2	1.4	**2.35 (2.25 to 2.45)**
						b	**0.46 (0.42 to 0.49)**				**0.39 (0.34 to 0.43)**
						c	-0.12 (-0.25 to 0.01)				-0.05 (-0.19 to 0.08)
	Large intest.	BM	135	-34.2	28.2	a	**1.90 (1.86 to 1.95)**	0.67 (0.42 to 0.84)	-81.2	18.7	**1.87 (1.74 to 2.00)**
						b	**0.46 (0.42 to 0.50)**				**0.39 (0.33 to 0.45)**
		BM + %faunivory		-62.4	0.0	a	**1.94 (1.90 to 1.99)**	0.56 (0.26 to 0.81)	-99.9	0.0	**1.93 (1.81 to 2.04)**
						b	**0.43 (0.39 to 0.46)**				**0.39 (0.34 to 0.45)**
						c	**-0.48 (-0.64 to -0.33)**				**-0.40 (-0.56 to -0.23)**

Table S5 ctd. Summary statistics for models assessing total or large intestinal length in different mammal subgroups with body mass (BM) or additionally with a diet proxy according to $\log(\text{length}) = a + b \log(\text{BM}) + c\,(\text{diet proxy})$; (significant parameters in **bold**)

Taxon	**Dependent**	**Model**		**GLS**				**PGLS**			
			n	**AICc**	**ΔAIC**		**parameter (95% CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95% CI)**
Laurasiatheria	Total intest.	BM	243	-10.4	55.8	a	**2.21 (2.18 to 2.24)**	0.86 (0.76 to 0.93)	-247.1	0.0	**2.24 (2.09 to 2.39)**
						b	**0.52 (0.50 to 0.53)**				**0.45 (0.42 to 0.48)**
		BM + %faunivory		-66.3	0.0	a	**2.36 (2.32 to 2.41)**	0.85 (0.73 to 0.92)	-246.8	0.3	**2.29 (2.12 to 2.46)**
						b	**0.48 (0.46 to 0.50)**				**0.45 (0.41 to 0.48)**
						c	**-0.27 (-0.33 to -0.21)**				-0.07 (-0.18 to 0.04)
	Large intest.	BM	133	148.0	169.7	a	**1.46 (1.34 to 1.58)**	0.94 (0.85 to 0.98)	-102.8	3.2	**1.37 (1.11 to 1.64)**
						b	**0.57 (0.50 to 0.64)**				**0.41 (0.37 to 0.46)**
		BM + %faunivory		-21.7	0.0	a	**1.94 (1.86 to 2.02)**	0.92 (0.79 to 0.98)	-106.0	0.0	**1.52 (1.25 to 1.78)**
						b	**0.43 (0.39 to 0.47)**				**0.41 (0.36 to 0.46)**
						c	**-0.82 (-0.90 to -0.73)**				**-0.27 (-0.49 to -0.05)**
Eulipotyphla	Total intest.	BM	18	7.6	0.0	a	**2.33 (2.07 to 2.58)**	0.67 (0.10 to NA)	-7.3	0.0	**2.35 (2.04 to 2.67)**
						b	**0.46 (0.32 to 0.61)**				**0.45 (0.26 to 0.63)**
		BM + %faunivory		8.5	0.9	a	**2.02 (1.03 to 3.00)**	0.75 (0.15 to NA)	-6.5	0.8	**1.92 (1.05 to 2.79)**
						b	**0.48 (0.32 to 0.64)**				**0.46 (0.26 to 0.65)**
						c	0.36 (-0.75 to 1.46)				0.48 (-0.40 to 1.36)
Chiroptera	Total intest.	BM	73	-23.4	19.9	a	**2.27 (2.12 to 2.43)**	0.92 (0.73 to NA)	-79.5	5.0	**1.93 (1.73 to 2.12)**
						b	**0.58 (0.49 to 0.67)**				**0.38 (0.30 to 0.46)**
		BM + %faunivory		-43.4	0.0	a	**2.25 (2.12 to 2.39)**	0.86 (0.57 to 0.99)	-84.5	0.0	**2.14 (1.92 to 2.36)**
						b	**0.45 (0.36 to 0.54)**				**0.39 (0.31 to 0.47)**
						c	**-0.28 (-0.37 to -0.18)**				**-0.23 (-0.39 to -0.07)**
Carnivora	Total intest.	BM	60	-9.1	0.0	a	**2.09 (2.01 to 2.16)**	0.71 (0.43 to 0.91)	-68.3	0.0	**2.08 (1.93 to 2.23)**
						b	**0.48 (0.43 to 0.54)**				**0.47 (0.41 to 0.52)**
		BM + %faunivory		-4.1	5.0	a	**2.09 (1.93 to 2.25)**	0.69 (0.41 to 0.90)	-67.0	1.3	**2.03 (1.84 to 2.22)**
						b	**0.48 (0.43 to 0.54)**				**0.47 (0.41 to 0.52)**
						c	0.00 (-0.18 to 0.17)				0.07 (-0.10 to 0.24)
	Large intest.	BM	40	-34.6	0.0	a	**1.25 (1.18 to 1.32)**	0.22 (na to 0.75)	-50.6	0.0	**1.26 (1.17 to 1.35)**
						b	**0.35 (0.30 to 0.40)**				**0.35 (0.29 to 0.40)**
		BM + %faunivory		-30.1	4.5	a	**1.24 (1.03 to 1.45)**	0.69 (0.41 to 0.90)	-48.8	1.8	**1.22 (1.00 to 1.43)**
						b	**0.35 (0.30 to 0.40)**				**0.35 (0.29 to 0.41)**
						c	0.01 (-0.22 to 0.23)				0.05 (-0.17 to 0.27)
Artiodactyla	Total intest.	BM	81	-80.4	0.0	a	**2.50 (2.41 to 2.59)**	0.39 (NA to NA)	-96.0	0.0	**2.40 (2.26 to 2.55)**
						b	**0.43 (0.38 to 0.49)**				**0.44 (0.39 to 0.50)**
		BM + %faunivory		-79.0	1.4	a	**2.51 (2.42 to 2.60)**	0.38 (NA to NA)	-94.0	2.0	**2.41 (2.25 to 2.56)**
						b	**0.43 (0.38 to 0.48)**				**0.44 (0.39 to 0.50)**
						c	-0.32 (-0.86 to 0.23)				-0.03 (-0.73 to 0.67)
	Large intest.	BM	79	-58.3	0.0	a	**1.94 (1.83 to 2.04)**	0.82 (0.31 to 0.97)	-78.9	0.0	**1.79 (1.53 to 2.04)**
						b	**0.45 (0.39 to 0.51)**				**0.47 (0.40 to 0.54)**
		BM + %faunivory		-56.8	1.5	a	**1.95 (1.84 to 2.06)**	0.82 (0.31 to 0.97)	-76.9	2.0	**1.78 (1.52 to 2.05)**
						b	**0.45 (0.39 to 0.51)**				**0.47 (0.40 to 0.54)**
						c	-0.31 (-0.94 to 0.31)				0.02 (-0.85 to 0.89)

AIC$_c$: small sample corrected Akaike's information criterion (for analyses using the same species, indicated by the same n, a lower AIC$_c$ indicates a better model fit); ΔAIC$_c$: indicates the difference in AIC$_c$ to the model with the lowest AIC$_c$ (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC$_c$ cannot be compared between GLS and PGLS models.

Table S6 Summary statistics for models assessing the total mammalian intestinal length (n = 519 species) with body mass (BM), or additionally with a diet proxy and other biological factors (being volant Vol, being marine Mar, having a forestomach FStom) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factors); (significant parameters in **bold**)

	GLS				**PGLS**			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	-54.8	197.1	a	**2.26 (2.24 to 2.28)**	0.93 (0.88 to 0.96)	-479.3	5.9	**2.17 (1.85 to 2.49)**
			b	**0.48 (0.46 to 0.49)**				**0.40 (0.38 to 0.43)**
BM + %faunivory	-190.5	61.4	a	**2.37 (2.34 to 2.39)**	0.92 (0.87 to 0.95)	-482.2	2.9	**2.23 (1.92 to 2.54)**
			b	**0.45 (0.44 to 0.46)**				**0.40 (0.38 to 0.42)**
			c	**-0.28 (-0.32 to -0.23)**				**-0.09 (-0.16 to -0.01)**
BM + Vol	-110.2	141.6	a	**2.29 (2.27 to 2.31)**	0.92 (0.87 to 0.95)	-481.9	3.2	**2.18 (1.87 to 2.49)**
			b	**0.45 (0.43 to 0.46)**				**0.40 (0.38 to 0.42)**
			c	**-0.24 (-0.30 to -0.18)**				**-0.32 (-0.60 to -0.03)**
BM + Mar	-53.3	198.6	a	**2.26 (2.24 to 2.28)**	0.93 (0.88 to 0.96)	-478.0	7.1	**2.17 (1.85 to 2.49)**
			b	**0.48 (0.46 to 0.49)**				**0.40 (0.38 to 0.43)**
			c	-0.04 (-0.15 to 0.07)				0.06 (-0.07 to 0.18)
BM + Fstom	-121.3	130.6	a	**2.20 (2.18 to 2.23)**	0.93 (0.88 to 0.96)	-478.0	7.1	**2.17 (1.85 to 2.49)**
			b	**0.46 (0.45 to 0.48)**				**0.40 (0.38 to 0.43)**
			c	**0.17 (0.13 to 0.21)**				0.05 (-0.06 to 0.15)
BM + %faunivory + Vol	-227.3	24.6	a	**2.38 (2.36 to 2.40)**	0.91 (0.85 to 0.95)	-484.6	0.6	**2.24 (1.93 to 2.54)**
			b	**0.43 (0.42 to 0.44)**				**0.40 (0.37 to 0.42)**
			c	**-0.25 (-0.29 to -0.21)**				**-0.08 (-0.16 to -0.01)**
			d	**-0.18 (-0.23 to -0.12)**				**-0.30 (-0.57 to -0.02)**
BM + %faunivory + Mar	-206.3	45.6	a	**2.37 (2.35 to 2.39)**	0.91 (0.85 to 0.95)	-482.7	2.5	**2.24 (1.93 to 2.55)**
			b	**0.44 (0.42 to 0.45)**				**0.40 (0.37 to 0.42)**
			c	**-0.31 (-0.36 to -0.27)**				**-0.11 (-0.18 to -0.03)**
			d	**0.22 (0.12 to 0.33)**				0.10 (-0.02 to 0.23)
BM + %faunivory + FStom	-206.7	45.1	a	**2.32 (2.29 to 2.35)**	0.92 (0.86 to 0.95)	-480.6	4.6	**2.22 (1.91 to 2.54)**
			b	**0.45 (0.43 to 0.46)**				**0.40 (0.38 to 0.42)**
			c	**-0.23 (-0.28 to -0.19)**				**-0.09 (-0.16 to -0.01)**
			d	**0.09 (0.05 to 0.12)**				0.03 (-0.07 to 0.13)
BM + %faunivory + Vol + Mar	-243.2	8.6	a	**2.38 (2.36 to 2.41)**	0.90 (0.84 to 0.94)	-485.2	0.0	**2.25 (1.95 to 2.54)**
			b	**0.42 (0.41 to 0.43)**				**0.39 (0.37 to 0.42)**
			c	**-0.29 (-0.33 to -0.24)**				**-0.10 (-0.18 to -0.03)**
			d	**-0.17 (-0.23 to -0.12)**				**-0.29 (-0.56 to -0.03)**
			e	**0.22 (0.12 to 0.32)**				0.10 (-0.02 to 0.23)
BM + %faunivory + Vol + FStom	-236.4	15.4	a	**2.34 (2.31 to 2.37)**	0.91 (0.85 to 0.95)	-482.7	2.4	**2.23 (1.92 to 2.54)**
			b	**0.43 (0.42 to 0.45)**				**0.40 (0.37 to 0.42)**
			c	**-0.22 (-0.27 to -0.17)**				**-0.08 (-0.16 to -0.01)**
			d	**-0.16 (-0.22 to -0.10)**				**-0.29 (-0.57 to -0.01)**
			e	**0.07 (0.03 to 0.11)**				0.02 (-0.08 to 0.12)

BM + %faunivory + Mar + FStom	-221.9	30.0	a	**2.33 (2.29 to 2.36)**	0.91 (0.85 to 0.95)	-480.8	4.3	**2.23 (1.93 to 2.54)**
			b	**0.44 (0.42 to 0.45)**				**0.40 (0.37 to 0.42)**
			c	**-0.27 (-0.32 to -0.22)**				**-0.10 (-0.18 to -0.02)**
			d	**0.22 (0.11 to 0.32)**				0.10 (-0.03 to 0.23)
			e	**0.08 (0.05 to 0.12)**				0.02 (-0.08 to 0.12)
BM + %faunivory + Vol + Mar + FStom	-251.8	0.0	a	**2.35 (2.32 to 2.38)**	0.90 (0.84 to 0.94)	-483.2	2.0	**2.24 (1.94 to 2.54)**
			b	**0.42 (0.41 to 0.44)**				**0.39 (0.37 to 0.42)**
			c	**-0.26 (-0.30 to -0.21)**				**-0.10 (-0.18 to -0.02)**
			d	**-0.16 (-0.21 to -0.10)**				**-0.29 (-0.56 to -0.02)**
			e	**0.21 (0.11 to 0.31)**				0.10 (-0.02 to 0.23)
			f	**0.06 (0.03 to 0.10)**				0.01 (-0.08 to 0.11)

AIC_c: small sample corrected Akaike's information criterion (a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S7 Summary statistics for models assessing mammalian small intestinal length (n = 397 species) with body mass (BM), or additionally with a diet proxy and other biological factors (being volant Vol, being marine Mar, having a forestomach FStom) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factors); (significant parameters in **bold**)

	GLS				PGLS			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	-96.0	49.6	a	**2.13 (2.11 to 2.15)**	0.93 (0.89 to 0.96)	-339.9	2.9	**2.04 (1.69 to 2.39)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.38 to 0.43)**
BM + %faunivory	-114.9	30.7	a	**2.17 (2.14 to 2.20)**	0.94 (0.89 to 0.97)	-338.2	4.6	**2.02 (1.67 to 2.38)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.38 to 0.43)**
			c	**-0.13 (-0.19 to -0.08)**				0.03 (-0.07 to 0.13)
BM + Vol	-94.0	51.6	a	**2.13 (2.11 to 2.15)**	0.93 (0.89 to 0.96)	-338.2	4.7	**2.05 (1.70 to 2.39)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.37 to 0.43)**
			c	0.00 (-0.21 to 0.22)				-0.10 (-0.48 to 0.27)
BM + Mar	-100.6	44.9	a	**2.13 (2.11 to 2.15)**	0.93 (0.88 to 0.96)	-342.8	0.0	**2.04 (1.70 to 2.38)**
			b	**0.45 (0.44 to 0.47)**				**0.40 (0.37 to 0.43)**
			c	**0.16 (0.04 to 0.27)**				**0.20 (0.02 to 0.38)**
BM + Fstom	-117.2	28.4	a	**2.09 (2.06 to 2.11)**	0.93 (0.89 to 0.96)	-338.6	4.2	**2.03 (1.69 to 2.38)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.38 to 0.43)**
			c	**0.10 (0.06 to 0.14)**				0.05 (-0.06 to 0.16)
BM + %faunivory + Vol	-113.2	32.4	a	**2.17 (2.14 to 2.20)**	0.94 (0.89 to 0.97)	-336.5	6.4	**2.03 (1.67 to 2.38)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.37 to 0.43)**
			c	**-0.14 (-0.19 to -0.08)**				0.03 (-0.07 to 0.13)
			d	0.07 (-0.14 to 0.28)				-0.11 (-0.49 to 0.27)
BM + %faunivory + Mar	-137.1	8.5	a	**2.18 (2.15 to 2.20)**	0.93 (0.88 to 0.96)	-340.8	2.0	**2.04 (1.67 to 2.38)**
			b	**0.44 (0.43 to 0.46)**				**0.40 (0.37 to 0.43)**
			c	**-0.20 (-0.26 to -0.13)**				0.00 (-0.10 to 0.10)
			d	**0.31 (0.19 to 0.43)**				**0.20 (0.02 to 0.38)**
BM + %faunivory + FStom	-124.7	20.9	a	**2.12 (2.09 to 2.16)**	0.94 (0.89 to 0.96)	-337.0	5.8	**2.01 (1.66 to 2.37)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.38 to 0.43)**
			c	**-0.10 (-0.16 to -0.04)**				0.03 (-0.07 to 0.14)
			d	**0.08 (0.03 to 0.12)**				0.05 (-0.06 to 0.17)
BM + %faunivory + Vol + Mar	-135.6	9.9	a	**2.18 (2.15 to 2.20)**	0.93 (0.88 to 0.96)	-339.0	3.8	**2.04 (1.69 to 2.38)**
			b	**0.44 (0.43 to 0.46)**				**0.40 (0.37 to 0.43)**
			c	**-0.20 (-0.26 to -0.14)**				0.00 (-0.10 to 0.11)
			d	0.08 (-0.12 to 0.28)				-0.10 (-0.47 to 0.27)
			e	**0.31 (0.19 to 0.43)**				**0.20 (0.02 to 0.38)**
BM + %faunivory + Vol + FStom	-123.3	22.3	a	**2.12 (2.09 to 2.16)**	0.94 (0.89 to 0.96)	-335.2	7.6	**2.02 (1.66 to 2.37)**
			b	**0.46 (0.44 to 0.47)**				**0.40 (0.37 to 0.43)**
			c	**-0.10 (-0.16 to -0.04)**				0.04 (-0.07 to 0.14)
			d	0.09 (-0.12 to 0.29)				-0.09 (-0.47 to 0.28)
			e	**0.08 (0.03 to 0.12)**				0.05 (-0.06 to 0.17)

BM + %faunivory + Mar + FStom	-145.6	0.0	a	**2.14 (2.10 to 2.17)**	0.93 (0.88 to 0.96)	-339.3	3.6	**2.03 (1.68 to 2.38)**
			b	**0.44 (0.43 to 0.46)**				**0.40 (0.37 to 0.43)**
			c	**-0.16 (-0.22 to -0.09)**				0.01 (-0.10 to 0.11)
			d	**0.30 (0.18 to 0.42)**				**0.19 (0.01 to 0.37)**
			e	**0.07 (0.03 to 0.11)**				0.04 (-0.07 to 0.15)
BM + %faunivory + Vol + Mar + FStom	-144.4	1.2	a	**2.14 (2.10 to 2.17)**	0.93 (0.88 to 0.96)	-337.4	5.4	**2.03 (1.68 to 2.38)**
			b	**0.44 (0.43 to 0.46)**				**0.40 (0.37 to 0.43)**
			c	**-0.16 (-0.22 to -0.10)**				0.01 (-0.10 to 0.11)
			d	0.10 (-0.10 to 0.30)				-0.09 (-0.46 to 0.28)
			e	**0.30 (0.18 to 0.42)**				**0.19 (0.01 to 0.37)**
			f	**0.07 (0.029 to 0.11)**				0.04 (-0.07 to 0.15)

AIC_c: small sample corrected Akaike's information criterion (a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S8 Summary statistics for models assessing mammalian total intestinal length (n = 466 species) with body mass (BM), or additionally with a diet proxy and environmental factors (latitude LAT, precipitation Prec, temperature Temp, actual evapotranspiration AET) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factor); (significant parameters in **bold**)

	GLS				**PGLS**			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	-27.8	186.4	a	**2.26 (2.24 to 2.28)**	0.94 (0.89 to 0.97)	-437.0	24.8	**2.17 (1.83 to 2.50)**
			b	**0.47 (0.46 to 0.49)**				**0.39 (0.36 to 0.41)**
BM + %faunivory	-175.7	38.5	a	**2.37 (2.35 to 2.40)**	0.93 (0.87 to 0.96)	-441.8	20.0	**2.24 (1.92 to 2.56)**
			b	**0.44 (0.42 to 0.45)**				**0.38 (0.36 to 0.41)**
			c	**-0.32 (-0.37 to -0.27)**				**-0.11 (-0.19 to -0.03)**
BM + %faunivory + Lat	-214.2	0.0	a	**2.29 (2.25 to 2.32)**	0.92 (0.87 to 0.96)	-455.3	6.6	**2.19 (1.88 to 2.5)**
			b	**0.44 (0.43 to 0.46)**				**0.39 (0.36 to 0.41)**
			c	**-0.31 (-0.35 to -0.26)**				**-0.11 (-0.19 to -0.03)**
			d	**0.0035 (0.0025 to 0.0046)**				**0.0021 (0.0011 to 0.0032)**
BM + %faunivory + Prec	-191.2	23.0	a	**2.43 (2.40 to 2.47)**	0.93 (0.87 to 0.96)	-441.2	20.6	**2.25 (1.93 to 2.573)**
			b	**0.44 (0.43 to 0.46)**				**0.38 (0.36 to 0.4102)**
			c	**-0.31 (-0.36 to -0.27)**				**-0.11 (-0.19 to -0.0292)**
			d	**-0.0007 (-0.0011 to -0.0004)**				-0.0002 (-0.0005 to 0.0001)
BM + %faunivory + Temp	-210.2	4.0	a	**2.48 (2.44 to 2.52)**	0.93 (0.87 to 0.96)	-461.8	0.0	**2.33 (2.01 to 2.64)**
			b	**0.44 (0.43 to 0.46)**				**0.38 (0.36 to 0.41)**
			c	**-0.31 (-0.36 to -0.27)**				**-0.11 (-0.19 to -0.03)**
			d	**-0.0063 (-0.0083 to -0.0043)**				**-0.0046 (-0.0066 to -0.0027)**
BM + %faunivory + AET	-197.1	17.1	a	**2.46 (2.42 to 2.50)**	0.93 (0.87 to 0.96)	-443.3	18.5	**2.27 (1.95 to 2.59)**
			b	**0.44 (0.43 to 0.46)**				**0.39 (0.36 to 0.41)**
			c	**-0.31 (-0.36 to -0.27)**				**-0.11 (-0.19 to -0.03)**
			d	**-0.0001 (-0.0002 to -0.0001)**				0.0000 (-0.0001 to 0.0000)

AIC_c: small sample corrected Akaike's information criterion (a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S9 Summary statistics for models assessing mammalian small intestinal length (n = 351 species) with body mass (BM), or additionally with a diet proxy and environmental factors (latitude LAT, precipitation Prec, temperature Temp, actual evapotranspiration AET) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factor); (significant parameters in **bold**)

	GLS				**PGLS**			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	-87.1	46.1	a	**2.13 (2.10 to 2.15)**	0.94 (0.88 to 0.97)	-316.6	7.5	**2.04 (1.70 to 2.38)**
			b	**0.45 (0.43 to 0.47)**				**0.39 (0.36 to 0.42)**
BM + %faunivory	-124.9	8.4	a	**2.18 (2.15 to 2.20)**	0.94 (0.88 to 0.97)	-314.8	9.3	**2.03 (1.68 to 2.38)**
			b	**0.44 (0.42 to 0.46)**				**0.39 (0.36 to 0.42)**
			c	**-0.21 (-0.27 to -0.14)**				0.03 (-0.08 to 0.1317)
BM + %faunivory + Lat	-131.5	1.7	a	**2.12 (2.08 to 2.17)**	0.94 (0.89 to 0.97)	-321.4	2.7	**1.98 (1.63 to 2.33)**
			b	**0.45 (0.43 to 0.47)**				**0.39 (0.36 to 0.42)**
			c	**-0.19 (-0.25 to -0.13)**				0.03 (-0.07 to 0.13)
			d	**0.0021 (0.0001 to 0.0035)**				**0.0019 (0.0006 to 0.0032)**
BM + %faunivory + Prec	-125.1	8.2	a	**2.20 (2.16 to 2.24)**	0.94 (0.88 to 0.97)	-312.8	11.4	**2.03 (1.67 to 2.38)**
			b	**0.44 (0.43 to 0.46)**				**0.39 (0.36 to 0.42)**
			c	**-0.20 (-0.26 to -0.15)**				0.03 (-0.08 to 0.13)
			d	-0.0003 (-0.0007 to 0.0001)				0.0000 (-0.0004 to 0.0004)
BM + %faunivory + Temp	-133.2	0.0	a	**2.24 (2.19 to 2.29)**	0.94 (0.89 to 0.97)	-324.1	0.0	**2.10 (1.75 to 2.45)**
			b	**0.45 (0.43 to 0.47)**				**0.39 (0.36 to 0.42)**
			c	**-0.19 (-0.26 to -0.13)**				0.03 (-0.08 to 0.13)
			d	**-0.0040 (-0.0065 to -0.0016)**				**-0.0039 (-0.0061 to -0.0016)**
BM + %faunivory + AET	-126.0	7.2	a	**2.21 (2.17 to 2.26)**	0.94 (0.89 to 0.97)	-313.1	11.0	**2.04 (1.68 to 2.39)**
			b	**0.45 (0.43 to 0.46)**				**0.39 (0.36 to 0.42)**
			c	**-0.20 (-0.26 to -0.13)**				0.03 (-0.08 to 0.13)
			d	0.0000 (-0.0001 to 0.0000)				0.0000 (-0.0001 to 0.0000)

AIC_c: small sample corrected Akaike's information criterion (a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S10 Summary statistics for models assessing mammalian large intestinal length (n = 343 species) with body mass (BM), or additionally with a diet proxy and environmental factors (latitude LAT, precipitation Prec, temperature Temp, actual evapotranspiration AET) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factor); (significant parameters in **bold**)

	GLS				PGLS			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	208.4	260.7	a	**1.77 (1.73 to 1.80)**	0.97 (0.95 to 0.99)	-181.3	29.8	**1.57 (1.08 to 2.05)**
			b	**0.43 (0.40 to 0.46)**				**0.37 (0.33 to 0.41)**
BM + %faunivory	-40.1	12.2	a	**1.94 (1.91 to 1.97)**	0.95 (0.91 to 0.98)	-205.2	5.9	**1.78 (1.34 to 2.21)**
			b	**0.39 (0.37 to 0.41)**				**0.36 (0.32 to 0.39)**
			c	**-0.69 (-0.76 to -0.6201)**				**-0.35 (-0.47 to -0.22)**
BM + %faunivory + Lat	-46.5	5.8	a	**1.88 (1.83 to 1.93)**	0.95 (0.91 to 0.98)	-207.1	4.0	**1.74 (1.31 to 2.17)**
			b	**0.40 (0.38 to 0.42)**				**0.36 (0.32 to 0.39)**
			c	**-0.67 (-0.74 to -0.60)**				**-0.34 (-0.47 to -0.22)**
			d	**0.0023 (0.0008 to 0.0039)**				**0.0015 (0.0000 to 0.0030)**
BM + %faunivory + Prec	-51.7	0.6	a	**2.00 (1.96 to 2.05)**	0.95 (0.91 to 0.98)	-208.8	2.3	**1.81 (1.39 to 2.2)**
			b	**0.40 (0.38 to 0.42)**				**0.36 (0.33 to 0.40)**
			c	**-0.67 (-0.74 to -0.60)**				**-0.34 (-0.47 to -0.22)**
			d	**-0.0009 (-0.0013 to -0.0004)**				**-0.0005 (-0.0009 to -0.0001)**
BM + %faunivory + Temp	-47.3	5.0	a	**2.01 (1.95 to 2.06)**	0.95 (0.91 to 0.98)	-209.8	1.2	**1.84 (1.41 to 2.27)**
			b	**0.40 (0.38 to 0.42)**				**0.36 (0.32 to 0.39)**
			c	**-0.68 (-0.75 to -0.61)**				**-0.35 (-0.47 to -0.22)**
			d	**-0.0043 (-0.0070 to -0.0015)**				**-0.0035 (-0.0061 to -0.0008)**
BM + %faunivory + AET	-52.3	0.0	a	**2.02 (1.97 to 2.08)**	0.95 (0.91 to 0.98)	-211.1	0.0	**1.84 (1.41 to 2.27)**
			b	**0.40 (0.38 to 0.42)**				**0.36 (0.32 to 0.39)**
			c	**-0.67 (-0.74 to -0.60)**				**-0.34 (-0.46 to -0.21)**
			d	**-0.0001 (-0.0002 to -0.0001)**				**-0.0001 (-0.0001 to 0.0000)**

AIC_c: small sample corrected Akaike's information criterion (a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S11 Summary statistics for models assessing mammalian colon/rectum length (n = 330 species) with body mass (BM), or additionally with a diet proxy and environmental factors (latitude LAT, precipitation Prec, temperature Temp, actual evapotranspiration AET) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factor); (significant parameters in **bold**)

	GLS				**PGLS**			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	230.0	216.1	a	**1.66 (1.62 to 1.70)**	0.97 (0.94 to 0.99)	-95.2	21.7	**1.47 (0.94 to 2.00)**
			b	**0.46 (0.43 to 0.49)**				**0.39 (0.35 to 0.43)**
BM + %faunivory	22.2	8.3	a	**1.83 (1.80 to 1.87)**	0.95 (0.90 to 0.98)	-111.4	5.4	**1.69 (1.20 to 2.17)**
			b	**0.43 (0.41 to 0.45)**				**0.37 (0.33 to 0.41)**
			c	**-0.69 (-0.76 to -0.61)**				**-0.35 (-0.50 to -0.20)**
BM + %faunivory + Lat	19.4	5.5	a	**1.78 (1.73 to 1.84)**	0.95 (0.90 to 0.98)	-113.5	3.3	**1.64 (1.16 to 2.13)**
			b	**0.44 (0.42 to 0.46)**				**0.37 (0.33 to 0.41)**
			c	**-0.67 (-0.75 to -0.59)**				**-0.35 (-0.50 to -0.19)**
			d	**0.0020 (0.0002 to 0.0038)**				**0.0018 (0.0001 to 0.0036)**
BM + %faunivory + Prec	15.8	1.9	a	**1.89 (1.84 to 1.94)**	0.95 (0.90 to 0.98)	-113.3	3.6	**1.7 (1.24 to 2.21)**
			b	**0.44 (0.42 to 0.46)**				**0.37 (0.33 to 0.42)**
			c	**-0.67 (-0.75 to -0.59)**				**-0.35 (-0.50 to -0.19)**
			d	**-0.0008 (-0.0013 to -0.0002)**				**-0.0005 (-0.0010 to 0.0000)**
BM + %faunivory + Temp	18.6	4.7	a	**1.90 (1.83 to 1.96)**	0.95 (0.90 to 0.98)	-114.7	2.2	**1.76 (1.27 to 2.24)**
			b	**0.44 (0.41 to 0.46)**				**0.37 (0.33 to 0.41)**
			c	**-0.68 (-0.76 to -0.60)**				**-0.35 (-0.50 to -0.20)**
			d	**-0.0039 (-0.0070 to -0.0007)**				**-0.0037 (-0.0069 to -0.0006)**
BM + %faunivory + AET	13.9	0.0	a	**1.91 (1.85 to 1.97)**	0.95 (0.90 to 0.98)	-116.8	0.0	**1.76 (1.28 to 2.24)**
			b	**0.44 (0.42 to 0.46)**				**0.37 (0.33 to 0.41)**
			c	**-0.67 (-0.75 to -0.59)**				**-0.35 (-0.50 to -0.19)**
			d	**-0.0001 (-0.0002 to 0.000)**				**-0.0001 (-0.0002 to 0.0000)**

AIC_c: small sample corrected Akaike's information criterion (a lower AIC_c indicates a better model fit); ΔAIC_c: indicates the difference in AIC_c to the model with the lowest AIC_c (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that AIC_c cannot be compared between GLS and PGLS models.

Table S12 Summary statistics for models assessing mammalian caecum length (n = 316 species) with body mass (BM), or additionally with a diet proxy and environmental factors (latitude LAT, precipitation Prec, temperature Temp, actual evapotranspiration AET) according to log(length) = a + b log(BM) + c (diet proxy) + d ... (factor); (significant parameters in **bold**)

	GLS				PGLS			
Model	**AICc**	**ΔAIC**		**parameter (95%CI)**	**lambda (95%CI)**	**AICc**	**ΔAIC**	**parameter (95%CI)**
BM	191.3	165.5	a	**0.99 (0.96 to 1.03)**	0.96 (0.93 to 0.97)	-168.4	13.3	**0.72 (0.27 to 1.17)**
			b	**0.21 (0.18 to 0.24)**				**0.30 (0.26 to 0.33)**
BM + %faunivory	36.0	10.2	a	**1.14 (1.10 to 1.17)**	0.94 (0.91 to 0.97)	-180.7	1.0	**0.90 (0.47 to 1.32)**
			b	**0.19 (0.16 to 0.21)**				**0.28 (0.24 to 0.32)**
			c	**-0.63 (-0.71 to -0.54)**				**-0.30 (-0.44 to -0.15)**
BM + %faunivory + Lat	25.8	0.0	a	**1.05 (0.99 to 1.11)**	0.94 (0.91 to 0.97)	-178.7	3.0	**0.90 (0.47 to 1.33)**
			b	**0.20 (0.18 to 0.22)**				**0.28 (0.24 to 0.32)**
			c	**-0.60 (-0.69 to -0.52)**				**-0.30 (-0.45 to -0.15)**
			d	**0.0033 (0.0015 to 0.0052)**				-0.0002 (-0.0018 to 0.0014)
BM + %faunivory + Prec	36.1	10.3	a	**1.17 (1.11 to 1.22)**	0.94 (0.91 to 0.97)	-181.0	0.7	**0.87 (0.44 to 1.30)**
			b	**0.19 (0.17 to 0.21)**				**0.28 (0.24 to 0.32)**
			c	**-0.62 (-0.71 to -0.53)**				**-0.30 (-0.45 to -0.15)**
			d	-0.0004 (-0.0009 to 0.0002)				0.0004 (-0.0001 to 0.0008)
BM + %faunivory + Temp	28.0	2.2	a	**1.2 (1.16 to 1.29)**	0.94 (0.91 to 0.97)	-178.9	2.8	**0.91 (0.48 to 1.34)**
			b	**0.19 (0.17 to 0.22)**				**0.28 (0.24 to 0.32)**
			c	**-0.61 (-0.70 to -0.53)**				**-0.30 (-0.45 to -0.15)**
			d	**-0.0054 (-0.0087 to -0.0021)**				-0.0008 (-0.0037 to 0.0021)
BM + %faunivory + AET	36.2	10.4	a	**1.17 (1.11 to 1.24)**	0.94 (0.91 to 0.97)	-181.7	0.0	**0.85 (0.43 to 1.28)**
			b	**0.19 (0.17 to 0.21)**				**0.28 (0.24 to 0.32)**
			c	**-0.62 (-0.70 to -0.53)**				**-0.30 (-0.45 to -0.15)**
			d	0.0000 (-0.0001 to 0.0000)				0.0001 (0.0000 to 0.0001)

$\mathrm{AIC_c}$: small sample corrected Akaike's information criterion (a lower $\mathrm{AIC_c}$ indicates a better model fit); $\Delta\mathrm{AIC_c}$: indicates the difference in $\mathrm{AIC_c}$ to the model with the lowest $\mathrm{AIC_c}$ (i.e., a value of 0.0 indicates the best-supported model amongst those using the same dataset). Note that $\mathrm{AIC_c}$ cannot be compared between GLS and PGLS models.

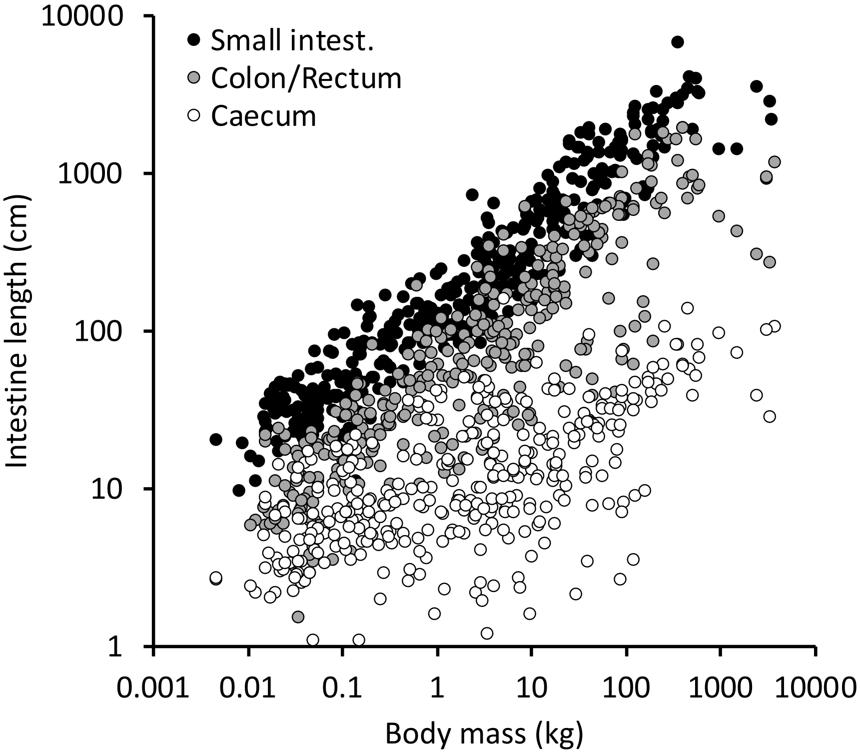

Figure S1 Magnitude comparison of the length of the small intestine, the colon/rectum, and the caecum in mammals. Note that while the relationship between the small and the large intestine stays similar, the caecum becomes relatively shorter at increasing body mass.

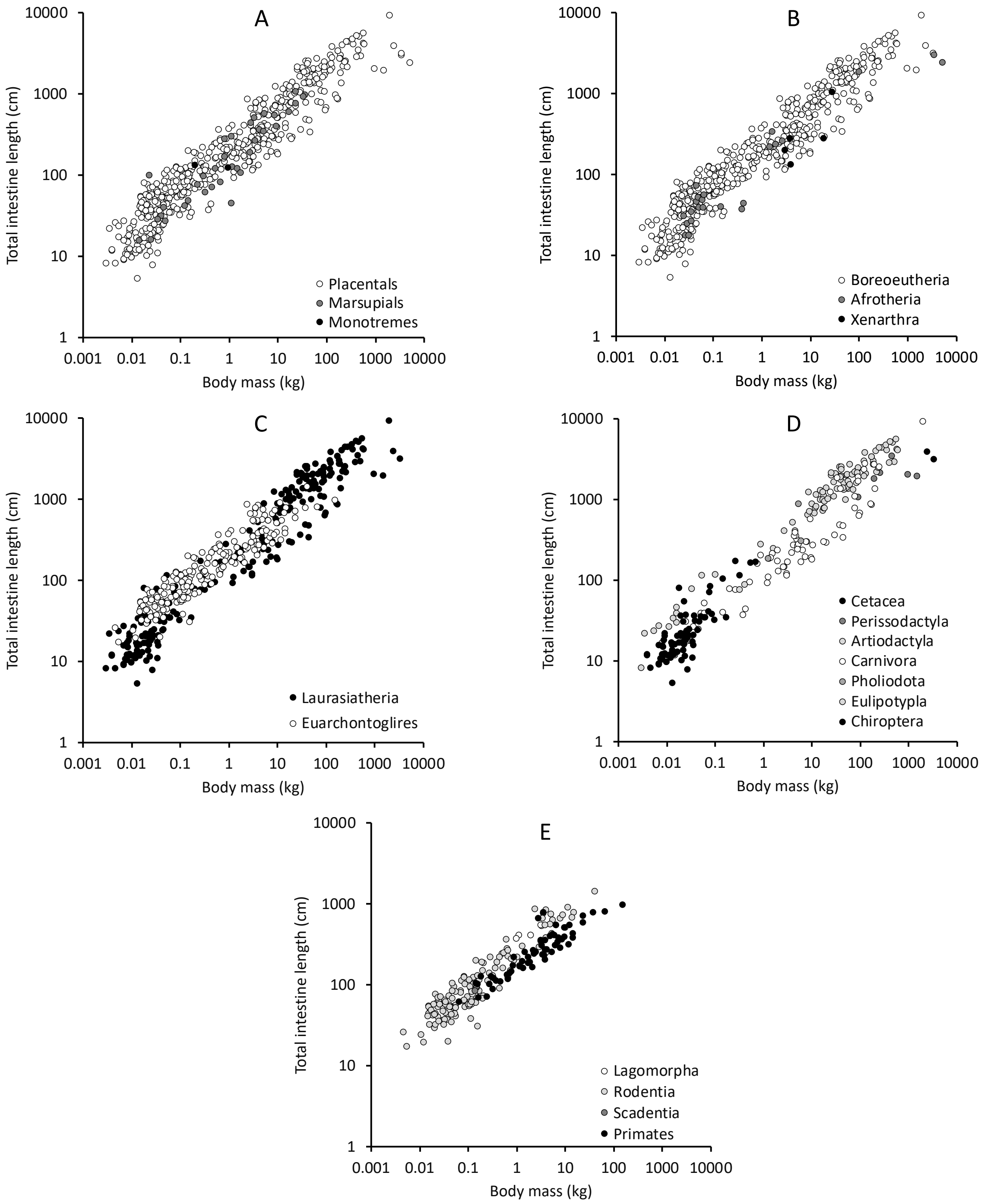

Figure S2 Relationships between mammalian intestinal length and body mass for taxonomic groups (A) Mammalian infraclasses, (B) The major Eutherian groups, (note that Laurasiatheria and Euarchontoglires are grouped as Boroeutheria), (C) two bigger Eutherian groups Laurasiatheria and Euarchontoglires, (D) Laurasiatheria, (E) Euarchontoglires.

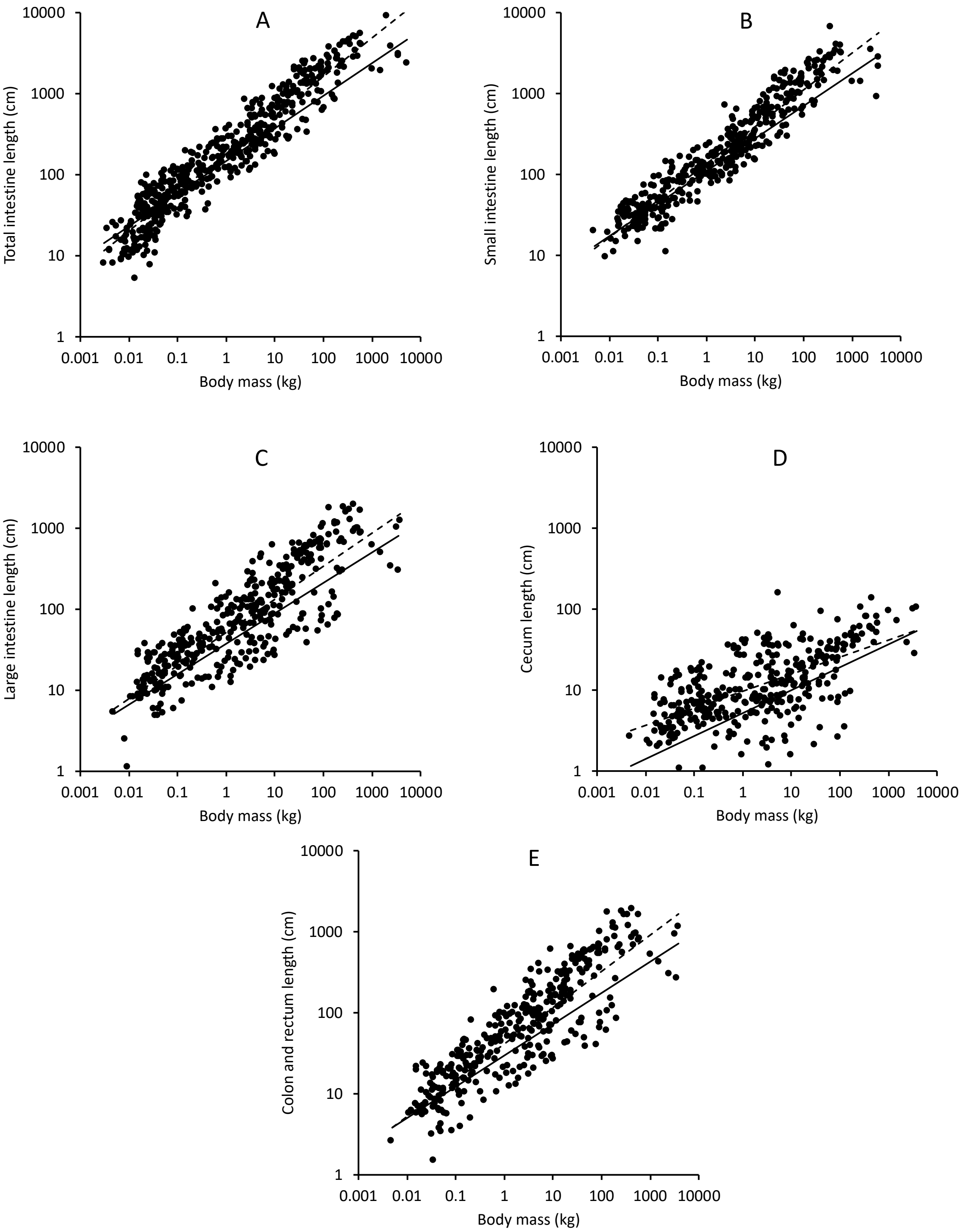

Figure S3 Relationships between mammalian intestinal length and body mass for (A) Total intestine (n=519 species), (B) Small intestine (n=397), (C) Large intestine (Caecum, colon and rectum) (n=387), (D) caecum (n=352), (E) colon and rectum (n=370). Dotted regression line in GLS using raw data; black regression line from PGLS accounting for phylogeny. For statistics, see Table S2.

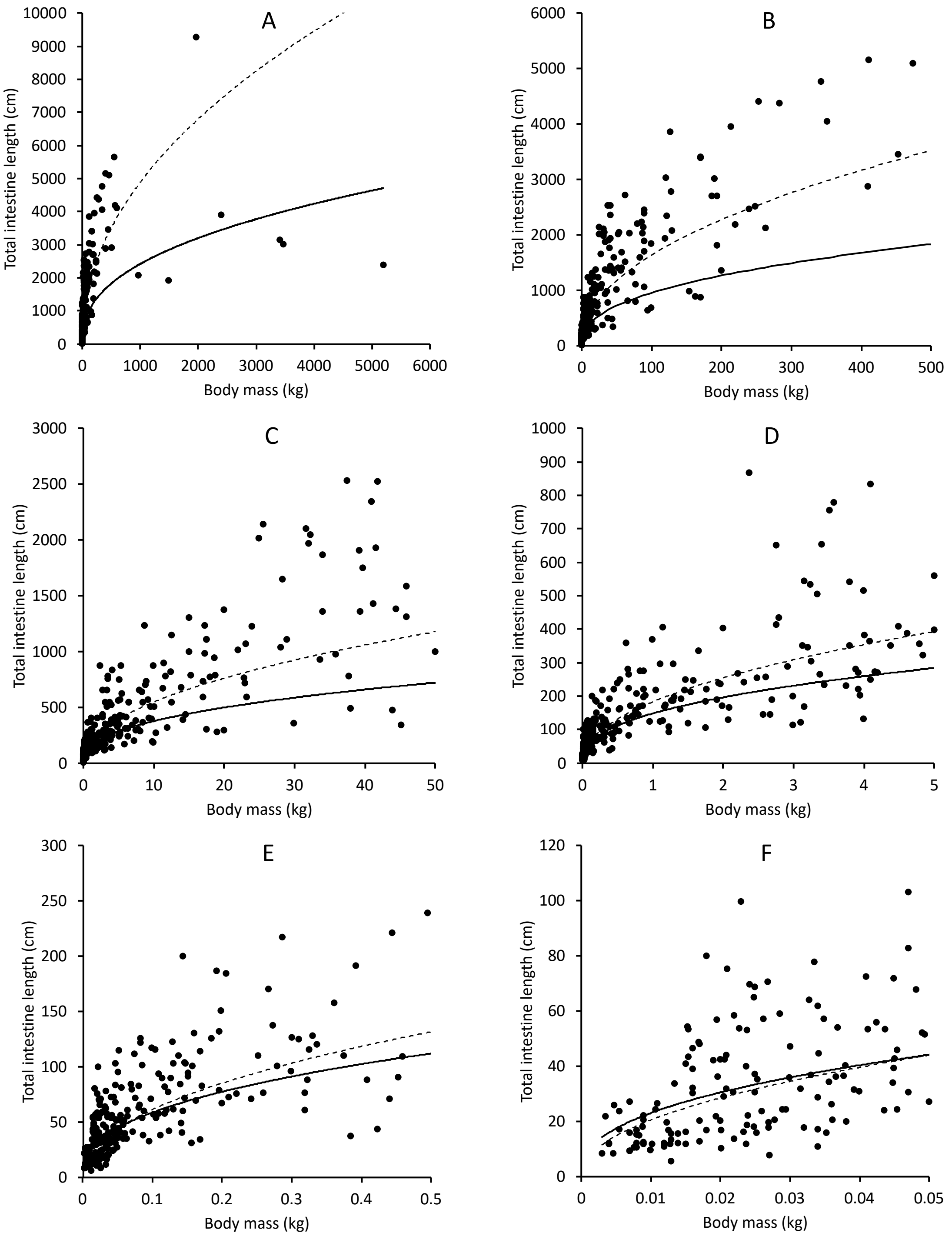

Figure S4 The same data and GLS and PGLS regression equations as in Fig. S3A, displayed (A) as the complete dataset, non-transformed, (B-F) data subset in the lower body mass range, non-transformed. Dotted regression line in GLS using raw data after log-transformation; black regression line from PGLS accounting for phylogeny after log-transformation.

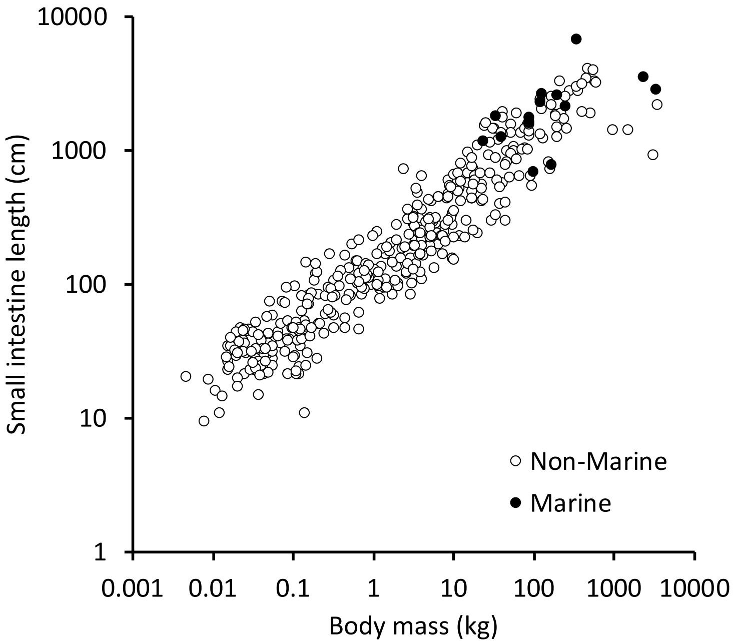

Figure S5 Relationship between small intestinal length and body mass for marine and non-marine mammals. Most data points refer to Carnivora, where one phocid had a surprisingly short small intestine; another short small intestine is from the afrotherian dugong (*Dugong dugon*); the two largest species are baleen whales, which have, compared to other Cetartiodactyla, rather short small intestines.

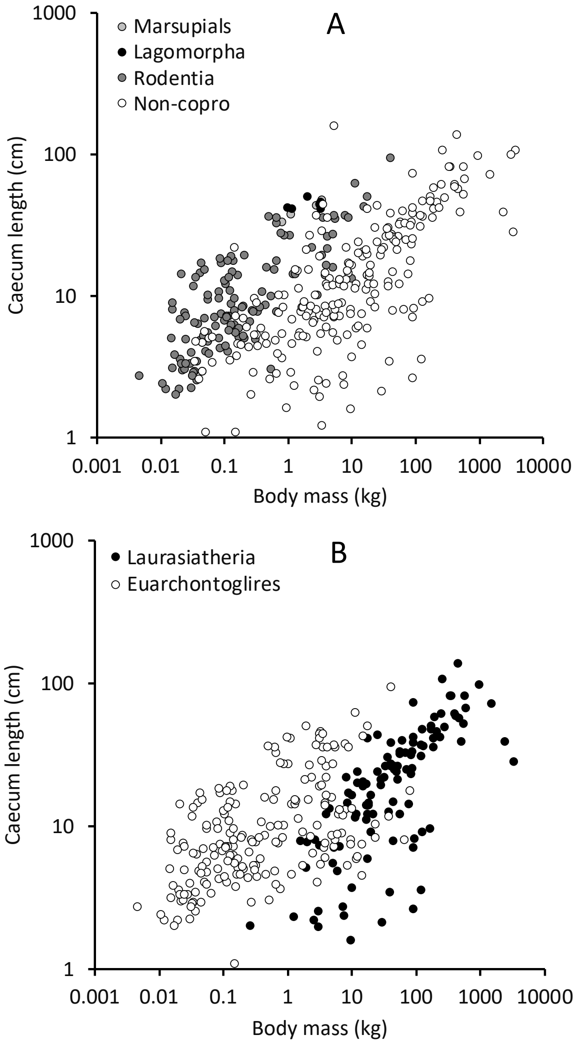

Figure S6 Relationship between caecum length and body mass (A) across mammals separated into orders in which coprophagy is a frequent digestive strategy (Lagomorpha, Rodentia) plus individual coprophageous marsupial species, and other groups in which it is not reported. The species with the very long caecum among the non-coprophageous mammals, is the koala (*Phascolarctos cinereus)*, a species that is known to use caecum contents for feeding its young [80]. Using GLS, the scaling between the two functional mammal groups had different confidence intervals for both the factor and the exponent, and geometric scaling was included in the confidence interval for non-coprophageous species (non-coprophageous: caecum length = 6.4 [5.6 to 7.3] BM$^{0.29\ [0.25\text{ to }0.33]}$; coprophageous: caecum length = 10.0 [9.1 to 10.9] BM$^{0.20\ [0.17\text{ to }0.23]}$); using PGLS, geometric scaling was included in the confidence interval for both groups, there were no differences in the scaling exponent, and the numerical difference in the factor was not maintained by the confidence intervals (non-coprophageous: caecum length = 4.5 [1.3 to 15.5] BM$^{0.29\ [0.24\text{ to }0.33]}$; coprophageous: caecum length = 7.8 [2.5 to 24.1] BM$^{0.29\ [0.25\text{ to }0.33]}$); (B) across Laurasiatheria and Euarchontoglires (because more evolutionary changes in the caecal appendix occurred in the latter compared to the former [19]). Euarchontoglires have longer caeca, and a shallower scaling, but confidence intervals overlap in PGLS (GLS: Lauras. caecum length = 4.1 [3.0 to 5.7] BM$^{0.40\ [0.32\text{ to }0.49]}$, Euarch. caecum length = 10.7 [9.7 to 11.9] BM$^{0.20\ [0.16\text{ to }0.25]}$; PGLS: Lauras. caecum length = 5.6 [2.8 to 11.1] BM$^{0.30\ [0.24\text{ to }0.36]}$, Euarch. caecum length = 11.6 [7.7 to 17.6] BM$^{0.29\ [0.24\text{ to }0.35]}$).

R Code

Generic descriptors in CAPITAL letters

GLS and PGLS analyses

```
# R packages ‘caper’ [44] and ‘nlme’ [45]
# Data tables are prepared in Excel from the original data file, including log-transformation;
note that in R, commands that read like ‘log-transform’ may perform a ln-tranformation;
tables saved as txt files

# Loading the data
Data <- read.table("TABLE.txt", header=T)

# ensuring variables (NAME) that are coded by numbers (such as 0,1 for dichotomous
variables or 0,1,2 for three possible states) are used as factors and not as continuous variables
NAMEfactor <- as.factor("NAME")
Data$NAMEfactor <- as.factor(Data$NAME)

# Loading the phylogenetic tree; Linking the data and the phylogenetic tree; both the data file
and the tree file contain the descriptor ‘Species’, and the corresponding species names are
identical in these two files
Tree <- read.tree("TREE.txt")
matrix <- comparative.data(Tree, Data, Species)

# Checking the link; this command will indicate the number of species in tree not used (in
example: 10), the number of species that occurred both in the tree and the data file (in
example: 519), and the number of species that occurred in the datafile but not in the tree (in
example: 0); example: tree { 10 ( 519 } 0) Data; the latter number must be zero
matrix

# GLS models using various dependent (e.g., a log-transformed intestine length measure) and
independent variables (e.g., log-transformed body mass, or additionally %faunivory) or
factors
model1 <- gls(DEPENDENT ~ INDEPENDENT, data=Data)
# or
model1 <- gls(DEPENDENT ~ INDEPENDENT1 + INDEPENDENT2, data=Data)
# or
model1 <- gls(DEPENDENT ~ INDEPENDENT1 + NAMEfactor, data=Data)
# etc.

# calling the GLS model results, which are then copied into e.g. an Excel file
summary(model1)
# the standard error SE from the model summary is then used to calculate the 95% confidence
interval (as the estimate ‘value’ minus/plus 1.96 * SE); note that depending on results
display, the ‘intercept’ estimate (a) might require de-logging as =10^a, e.g. when displaying
the scaling result as an allometric equation y = a x^b; the information given includes the AIC,
which is subsequently used to calculate differences in AIC between appropriate models in
Excel
```

```
# PGLS models using various dependent (e.g., a log-transformed intestine length measure) and independent variables (e.g., log-transformed body mass, or additionally %faunivory) or factors
model2 <- pgls(DEPENDENT ~ INDEPENDENT, data=matrix, lambda="ML")
# or
model2 <- pgls(DEPENDENT ~ INDEPENDENT1 + INDEPENDENT2, data=matrix, lambda="ML")
# or
model2 <- pgls(DEPENDENT ~ INDEPENDENT1 + NAMEfactor, data=matrix, lambda="ML")
# etc.

# sometimes, a PGLS model does not work; in this case, it needs to be repeated with excluding 0 as a solution for lambda, but with very small lambdas possible:
model2 <- pgls(DEPENDENT ~ INDEPENDENT, data=matrix, lambda="ML", bounds=list(lambda=c(0.000001,1))
# this step might have to be repeated with different zero-decimals for the lower bound (e.g., 0.000001, 0.00001, 0.0001)

# calling the GLS model results, which are then copied into e.g. an excel file; this includes output for lambda; as the normal summary call does not yield AIC values, these have to be called individually; calculate 95% confidence interval and AIC differences as above; note that you must not compare AIC between GLS and PGLS models but only within the respective model group
summary(model2)
AIC(model2)
```

Analyses for Phylogenetic Signal

```
# R package ‘phytools’ [46]
# prepare the datasets with species and the variables that shall be submitted to analysis (e.g., log-transformed body mass and log-transformed intestinal section length), but ensure that the first column with the species names does not have a column heading (the other ones with the variables should have their heading); tables saved as txt files

# Loading the data and the phylogenetic tree
Data <- read.table("TABLE.txt")
Tree <- read.tree("TREE.txt")

# link the data rows to the species names
row.names(Data) <- Data[,1]
Data <- Data[,-1]

# select the trait you want to analyse; if it is in the first column after the species names, use “1”, if it is in the second column after the species names, use “2”, etc., and link them to the species names
trait <- Data[,1]
names(trait) <- rownames(Data)
```

```
# calculate the phylogenetic signal (either K or lambda) with the number of simulations you want (here, 9999); the result is displayed automatically, as is the number of species in the tree that is not used in the specific calculation
phylosig(Tree, trait, method="K", test=TRUE, nsim=999)
# or
phylosig(Tree, trait, method="lambda", test=TRUE, nsim=999)
```

Supplement References (in this document, they are lumped with the main text references; in the individually submitted files, these are properly separated)