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Morphological adaptation of the eutherian gastrointestinal tract to diet

PETER LANGER¹, MARCUS CLAUSS²

¹ Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität, Aulweg 123, 35385 Giessen, Germany — ² Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zürich, Winterthurerstr. 260, 8057 Zürich, Switzerland — *Corresponding authors: peter.langer@anatomie.med.uni-giessen.de, mclauss@vetclinics.uzh.ch

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Abstract

Although adaptations of the gastrointestinal tract to diet have been widely documented, statistical evaluations of corresponding correlations between diet and morphology are scarce. We use a dataset that scores the complexity of the stomach, caecum and colon in 599 Eutherian species, with a higher complexity score indicating a higher degree of macroanatomical differentiation, and link these data to information on body mass and the estimated fibre content of the natural diet, controlling for phylogeny. The results indicate that dietary niche differentiation occurs along, rather than within, major Eutherian lineages, and that stomach and large intestine complexity are often positively correlated. Large intestine complexity represents a convergent adaptation to high-fibre diets across lineages (although not all species ingesting high-fibre diets have complex large intestines). By contrast, stomach complexity cannot be linked to diet, but represents a taxon-specific signal in the sense of homoplasies. In particular, the functions of stomach complexity in the smallest and the largest Eutheria with complex stomachs (the Myomorpha and the Cetacea) remain to be elucidated.

Key words

Foregut, hindgut, forestomach, trophic niche, digestion, mammals.

Introduction

Of the various soft tissue organs of the vertebrate body, the gastrointestinal (GI) tract has particularly fascinated comparative anatomists (HOME, 1814; FLOWER, 1872; MITCHELL, 1905; MITCHELL, 1916; GORGAS, 1967; VORONTSOV, 1967/1969; BEHMANN, 1973; HOFMANN, 1973; CHIVERS & HLADIK, 1980; NAUMOVA, 1981; LANGER, 1988; STEVENS & HUME, 1995). It is well accepted that herbivores have more voluminous and complex GI tracts than carnivores (STEVENS & HUME, 1995), requiring larger body cavity volumes (CLAUSS *et al.*, 2017), in order to host a symbiotic microbiome for the digestion of plant fibre. Yet, quantitative evaluations of this adaptation remain scarce. CHIVERS & HLADIK (1980) showed that the relationships between body mass and GI tract volume or surface area differed between faunivores, frugivores and folivores, although substantial overlap occurred between the latter two and between all groups with low body mass.

Since then, the relationship between dietary habit and GI tract morphology has not been assessed in a large scale across mammals, and in particular not with a comparative approach accounting for phylogenetic relationships.

Here, we use a qualitative description of the eutherian GI tract that indicates the degree of differentiation of the stomach, caecum and colon, as well as a characterisation of dietary habits using an ordinal scale, and the species' average body mass, all compiled in LANGER (2017), to test for statistical correlations. By performing these tests with and without accounting for the phylogenetic structure of the data, we test whether potential correlations occur both across and within major phylogenetic lineages. Our hypotheses were that:

1. There is a general dichotomy of fibre content with body mass, where very large animals consume mostly

very high or, if they are predators, very low levels of fibre (HIEMAE, 2000);

2. There is a trend of increasing GI tract complexity with increasing fibre content of the natural diet (CHIVERS & HLADIK, 1980). This pattern was hypothesised to emerge more clearly after exclusion of aquatic mammals, because the large group of cetaceans is exclusively carnivorous, i.e. feeding on a low-fibre diet, yet characterized, possibly due to evolutionary history, by highly complex stomachs (LANGER, 1996; BÜKER, 2009).

3. Animals either evolved to be ‘foregut fermenters’ with a complex stomach or ‘hindgut fermenters’ with a complex large intestine, resulting in a negative correlation between stomach and large intestine indices (LANGER, 2003).

Abbreviations

- GI tract** gastrointestinal tract
- GLS** generalised least squares (‘conventional statistics’)
- PGLS** phylogenetic generalised least squares (‘phylogenetically controlled statistics’)

Methods

The data compilation in LANGER (2017; Table 1.6 of the monograph and Table S1 in the supplementary material) was used in the present study. Species nomenclature follows WILSON & REEDER (2005). Body mass was collected from various sources during the compilation of anatomical descriptions, and sources are listed in detail in LANGER (2003). As explained and referenced in detail in LANGER (2003), the crude fibre content of the natural diet of species was derived from quantitative estimates of diet composition and nutrient composition tables for domestic herbivores and carnivores. The coding for complexity of the GI tract used was introduced by LANGER (2003) and accounts for 18 different qualitative characteristics. Stomach complexity ranges from 1–6 and reflects the presence of various stomach epithelia, a forestomach, compartmentalisation, haustration (haustra: pouch-like diverticles along the wall of the GI tract that lie between longitudinal muscular or fibrous band and are separated from each other by transversal semilunar folds), and peculiar mucosal structures. Caecum complexity ranges from 0–3, reflecting the presence of a caecum, and the presence of haustra, an appendix, a spiral fold, or paired caeca (in sirenians); note that scores higher than 3 are not attained because no species combines all possible macro-anatomical characteristics. Colon complexity varies from 0–1, considering haustration and presence of diverticula (in hyracoidea). Large intestine complexity is the sum of caecum and colon complexity (range 0–4) and the to-

Table 1. Eutherian groups included in the study

Major group	Subgroup 1	Subgroup 2
Afrotheria	Afrosoricida	Tenrecomorpha
	Afrosoricida	Chrysochloridea
	Macroscelidea	
	Tubulidentata	
	Hyracoidea	
	Proboscidea	
	Sirenia	
Xenarthra	Cingulata	
	Pilosa	Folivora
	Pilosa	Vermilingua
Euarchontoglires	Scandentia	
	Primates	Strepsirrhini
	Primates	Haplorrhini
	Rodentia	Sciuromorpha
	Rodentia	Castorimorpha
	Rodentia	Myomorpha
	Rodentia	Anomaluromorpha
	Rodentia	Hystricomorpha
	Lagomorpha	
Laurasiatheria	Erinaceomorpha	
	Soricomorpha	
	Pholidota	
	Chiroptera	
	Carnivora	Feliformia
	Carnivora	Caniformia
	Perissodactyla	
	Artiodactyla	
	Cetacea	Mysticeti
	Cetacea	Odontoceti

tal GI tract complexity is the sum of all individual indices (range 1–7). The scoring of species is based on the sources in LANGER (2017) and is strictly limited to fully described species, with no extrapolation to non-described relatives. From the original 601 species of LANGER (2017), two (*Sciurus aberti*, *Dusicyon australis*) were not represented in the mammalian supertree by FRITZ *et al.* (2009b), and were therefore excluded from all analyses. Following the subdivision into four supergroups by WILSON & REEDER (2005), the 599 species included in this study represent 24.1% (19 of 79) of all Afrotheria species, 28.6% (10 of 35) of all Xenarthra, 8.8% (244 of 2765) of all Euarchontoglires, and 14.8% (326 of 2203) of all Laurasiatheria, and hence 11.8% of all Eutheria. All data are supplied, with additional explanations, in the supplementary material. The subgroups within the four major groups included in the dataset are listed in Table 1. We tested whether the number of species in a higher-level phylogenetic group had an influence on the diversity in morphology scores by summarizing data on the level of orders (WILSON & REEDER, 2005), correlating the number of species (per order) with the minimum, maximum and the range of GI tract and stomach complexity scores within orders by simple nonparametric Spearman’s correlation coefficient (ρ).

Table 2. Summary of relationships of body mass with the estimated level of crude fibre in the natural diet (as a proxy for dietary habits) in eutherian groups in generalised least squares (GLS) and phylogenetic generalised least squares (PGLS) based on the tables in the supplementary material. Positive (+), negative (–) or non-significant (*n.s.*) relationships were detected.

Group (Body mass)	Crude fibre	
	GLS	PGLS
Eutheria	+	+
Eutheria (terrestrial)	+	+
Eutheria (aquatic)	<i>n.s.</i>	<i>n.s.</i>
Afrotheria (terr.)	+	<i>n.s.</i>
Xenarthra	<i>n.s.</i>	<i>n.s.</i>
Euarctontoglires	+	+
Primates	+	<i>n.s.</i>
Rodentia	+	<i>n.s.</i>
Sciuro- & Castorimorpha	+	<i>n.s.</i>
Mymorpha	<i>n.s.</i>	<i>n.s.</i>
Hystricomorpha	<i>n.s.</i>	<i>n.s.</i>
Laurasiatheria (terr.)	+	+
Carnivora (terr.)	+	<i>n.s.</i>
Chiroptera	+	<i>n.s.</i>
Cetartiodactyla	–	<i>n.s.</i>
Artiodactyla	+	<i>n.s.</i>
Ungulata (Artiod./Perissod.)	+	<i>n.s.</i>

We used ranked data (with continuous ranks and higher ranks for higher values) for all analyses because of the ordinal nature of the GI tract complexity indices and the dietary fibre levels, and the non-normal distribution of body mass data. Ranking was performed for each individual dataset (i.e., the rank of a species differed when it was part of a larger and a smaller dataset). Using linear models, we tested for relationships between individual measures (body mass and crude fibre, body mass and GI tract indices, crude fibre and GI tract indices, stomach index and hindgut indices), as well as for a combined effect of body mass, fibre level and their interaction (to test for shifts in effects of fibre level across the body mass spectrum) on GI tract indices. We used generalised least squares (GLS) in R 2.15.0 (R Core Development Team) using the package *nlme* (PINHEIRO *et al.*, 2011). Ranking as well as adjusted R^2 calculation for GLS were performed in SPSS 22.0 (IBM, Armonk, NY, USA).

To account for the phylogenetic structure of the dataset, data were linked to a phylogenetic tree (FRITZ *et al.* 2009). The general structure of the tree (indicating the taxonomic levels ‘order’ and ‘suborder’) is shown in Fig. S1. Data were also analysed in phylogenetic generalised least squares (PGLS) with the phylogenetic signal λ estimated by maximum likelihood, using the package *caper* (ORME *et al.*, 2010). A λ significantly different from 0 indicates the presence of phylogenetic structure in the dataset (REVELL, 2010). In contrast to a common recommendation for comparative studies (FRECKLETON, 2009), we display results of both GLS and PGLS analyses, because discrepancies between the two can yield impor-

tant insight into the data patterns (CLAUSS *et al.*, 2014; DITTMANN *et al.*, 2015). With respect to our hypotheses, a significant relationship in GLS at no significant relationship in PGLS indicates that the effect is due to the fact that different phylogenetic lineages occupy distinct combinations of morphological and ecological niches; significance in both GLS and PGLS indicates that a similar pattern of morphology-ecology associations can be observed across as well as within different lineages; non-significance (or a different directionality of associations) in GLS but significance (or different directionality) in PGLS indicate that the pattern observed across all species masks another pattern within phylogenetic lineages.

Analyses were performed for a series of species sets: for all eutherian orders combined, separately for terrestrial and aquatic Eutheria (as indicated in Table S1), for Cetartiodactyla, and within terrestrial Eutheria for various phylogenetic lineages (as indicated in Table 2). Additionally, because the ecological literature often focuses on ungulates as a functional herbivore group, the non-phylogenetic, gradistic group of Ungulata (here: Artiodactyla and Perissodactyla) was also included separately. Note that it has been suggested that Cetartiodactyla and Perissodactyla represent sister taxa and can be summarized in the phylogenetic group of Euungulata (ASHER & HELGEN, 2010; ESSELSTYN *et al.*, 2017); in contrast, our species set of ‘Ungulata’ does not comprise the Cetacea.

Detailed results including P -values and adjusted R^2 measures are listed in the supplementary material. For a summary of results, P -values above 0.050 were considered not significant, and relationships were indicated as positive (+) or negative (–).

Results

The number of species per order was significantly correlated to both the range of body mass ($\rho = -0.95$, $P < 0.001$; Fig. 1A) and the range of crude fibre ($\rho = -0.86$, $P < 0.001$; Fig. 1B). It was not significantly correlated to either the minimum or maximum complexity score for the total GI tract or the stomach (ρ from -0.30 to 0.38 , $P > 0.100$). In contrast, the number of species per order was highly correlated to the range of complexity scores for both the total GI tract ($\rho = 0.74$, $P < 0.001$; Fig. 1C) and the stomach ($\rho = 0.64$, $P = 0.002$; Fig. 1D).

Generally, the phylogenetic signal λ was always significantly different from 0, and had high values between 0.9–1.0, indicating a strong phylogenetic signal in all analyses.

Body mass vs. dietary crude fibre

There was a significant, positive relationship between body mass and dietary crude fibre in both conventional statistics (GLS) and phylogeny-informed statistics

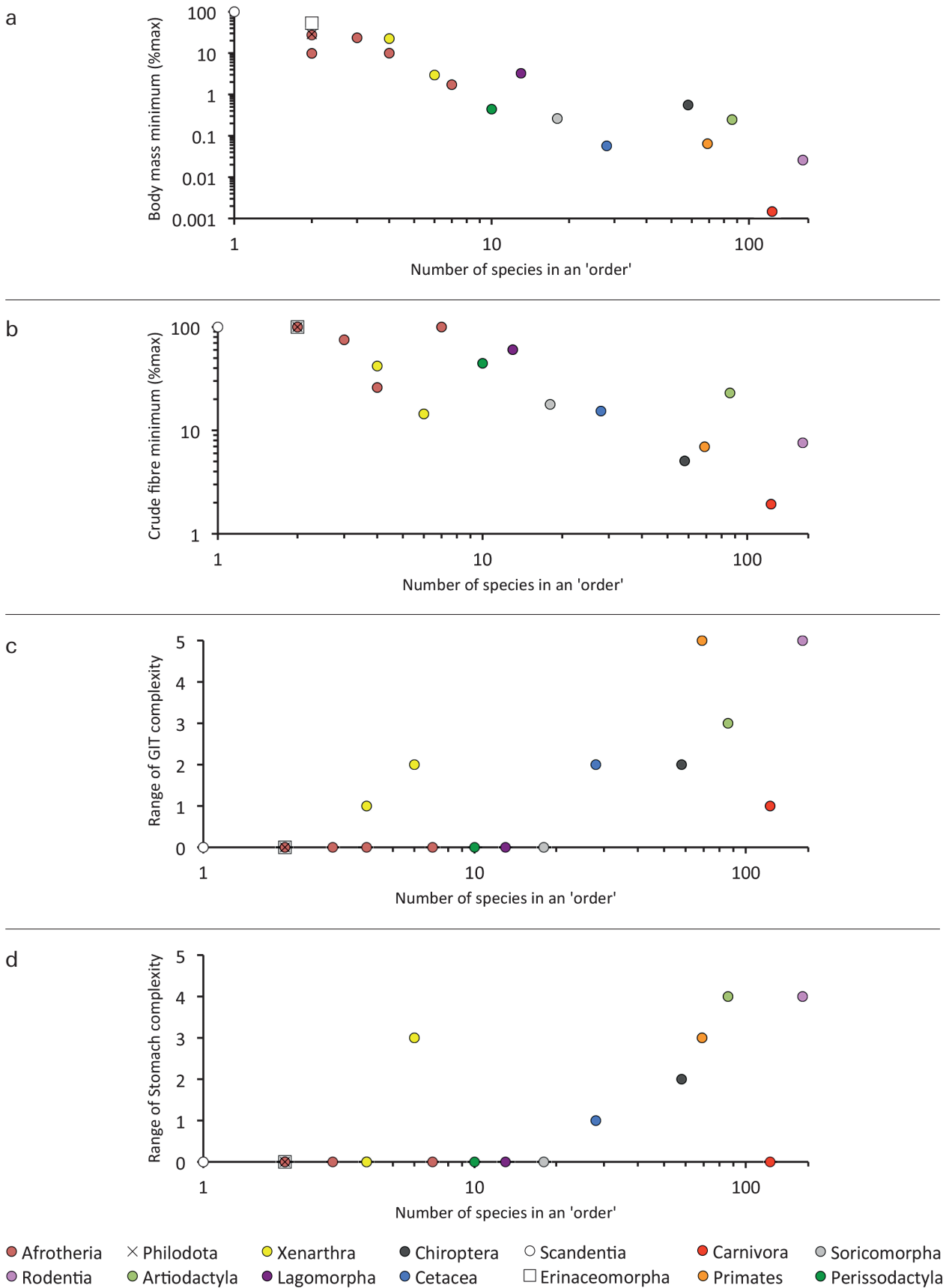


Fig. 1. Relationship between the number of species included in an 'order' in the present study and the range of (a) body mass, (b) dietary crude fibre, (c) total gastrointestinal tract (GIT) complexity and (d) stomach complexity; note that in (a) and (b), the range is indicated as the minimum in % of the maximum, so that lower values indicate a larger range. Afrotheria include Afrosoricida, Macroscelidea (with the largest crude fibre range), Tubulidentata, Hyracoidea, Proboscidea and Sirena; Xenarthra include Cingulata and Pilosa (with the higher diversity). Data from Table S1.

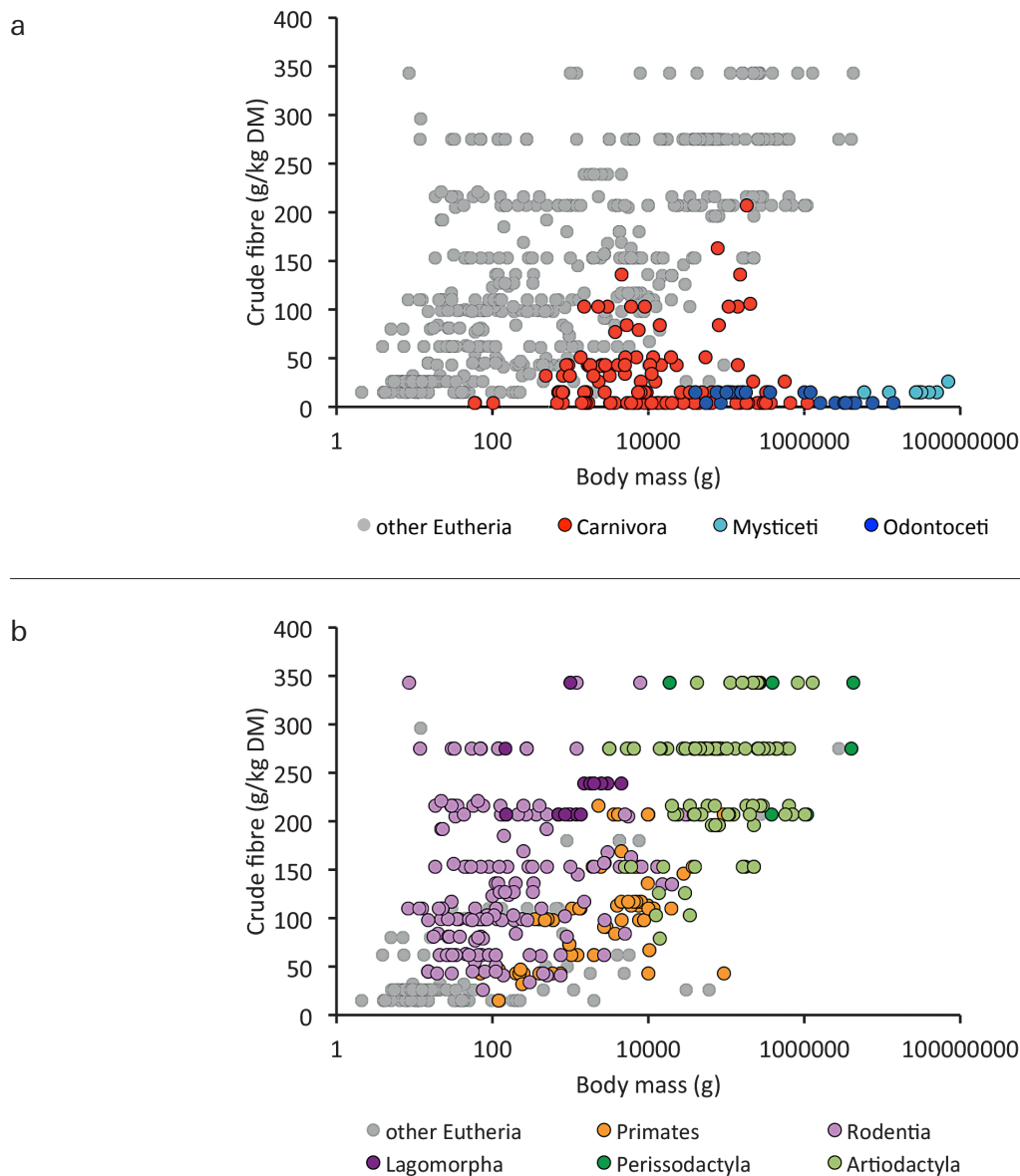


Fig. 2. Relationship between body mass (g) and estimated crude fibre levels of the natural diet (g/kg dry matter) for (a) all Eutheria, with Carnivora and Cetacea displayed individually, and (b) for all Eutheria except Carnivora and Cetacea, with several orders displayed individually. Data from Table S1.

(PGLS) across Eutheria (Table 2; Fig. 2); visually, a dichotomy existed, with very large mammals having diets either very high or very low in fibre, a dichotomy particularly evident when inspecting Carnivora and Cetacea (Fig. 2a). In the dendrograms for body mass and dietary fibre, the deviation of Carnivora and Cetacea from the general pattern is also evident (Fig. 3a, b). The relationship between body mass and dietary fibre was significantly positive within the larger species sets of Euarchontoglires and Laurasiatheria (Table 2). This relationship was also significant in GLS in many phylogenetic subgroups, but not in PGLS (Table 2), suggesting that within these subgroups, diet differentiation occurred mainly in parallel to phylogenetic differentiation (Fig. 2b). Similarly, the relationship was negative in GLS for Cetartiodactyla but not in PGLS, reflecting the fact that the largest Cetartiodactyla – the Cetacea – are exclusively carnivorous.

Body mass vs. gastrointestinal tract complexity

Total GI tract complexity (Fig. 4a), large intestine complexity (Fig. 4b) and colon complexity were positively related to body mass in both GLS and PGLS across Eutheria and Laurasiatheria, and also in GLS (but not PGLS) in several phylogenetic subgroups (Table 3). For caecum complexity, there was a similar pattern, but no significant relationship in PGLS in Laurasiatheria (Table 3). Stomach complexity (Fig. 4c) only had various significant relationships with body mass in GLS but never in PGLS, indicating that stomach morphology is a major correlate of phylogenetic differentiation, which is also clearly evident in the dendrogram (Fig. 3f). Whereas the GLS relationship was typically positive, indicating that within some lineages, larger species typically had more

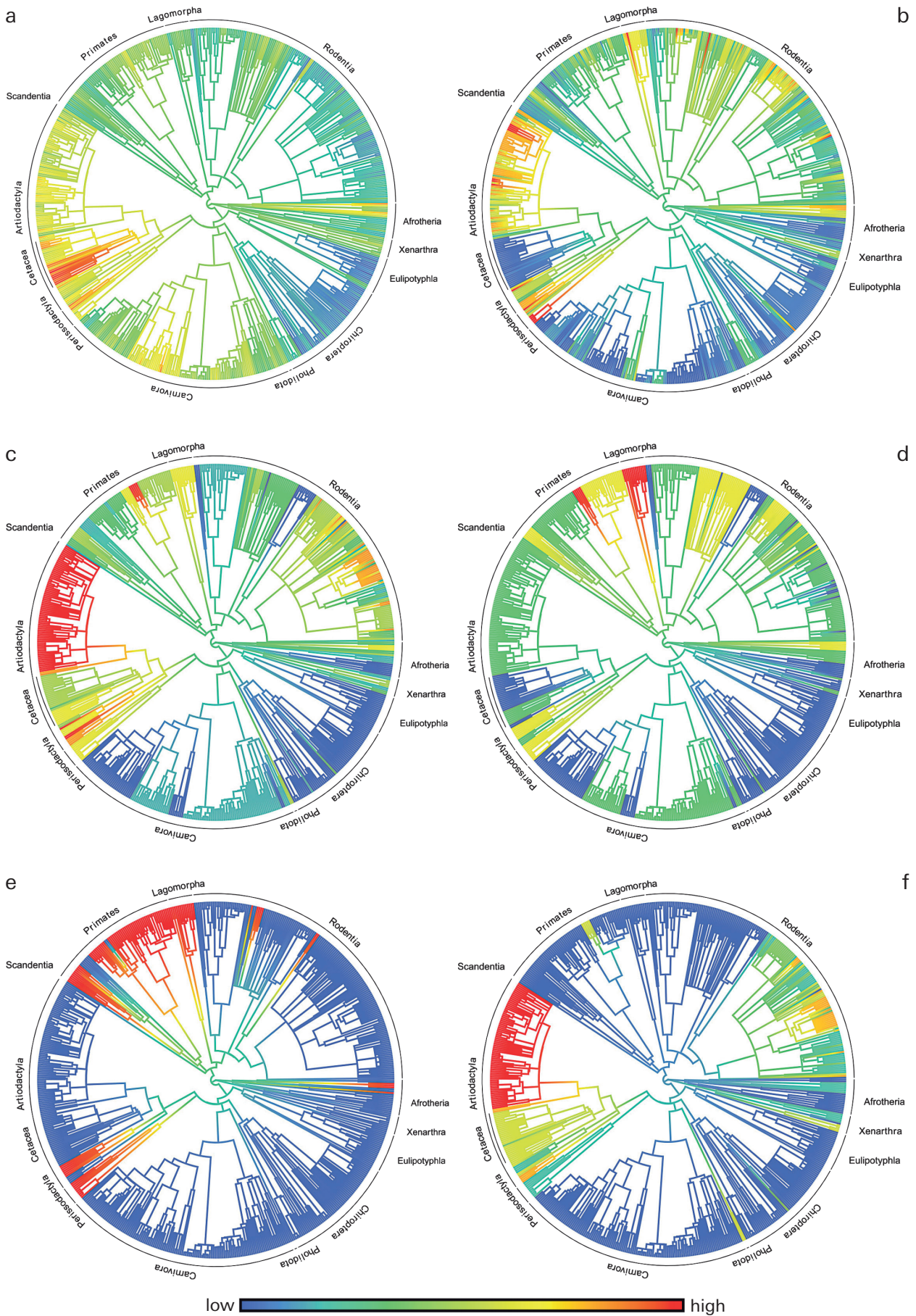


Fig. 3. Dendrograms illustrating the distribution of (a) body mass, (b) dietary crude fibre, (c) total gastrointestinal tract (GIT) complexity, (d) caecum complexity, (e) colon complexity, (f) stomach complexity across the Eutherian phylogenetic tree (from FRITZ et al., 2009b).

Table 3. Summary of relationships of body mass with the complexity indices of individual components or the whole gastrointestinal (GI) tract in eutherian groups in generalised least squares (GLS) and phylogenetic generalised least squares (PGLS) based on the tables in the supplementary material. Positive (+), negative (–) or non-significant (*n.s.*) relationships were detected.

Group (Body mass)	Stomach		Caecum		Colon		Large intestine		GI tract	
	GLS	PGLS	GLS	PGLS	GLS	PGLS	GLS	PGLS	GLS	PGLS
Eutheria	+	<i>n.s.</i>	+	+	+	+	+	+	+	+
Eutheria (terrestrial)	+	<i>n.s.</i>	+	+	+	+	+	+	+	+
Eutheria (aquatic)	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>
Afrotheria (terr.)	+	<i>n.s.</i>	+	+	+	<i>n.s.</i>	+	+	+	+
Xenarthra	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Euarchontoglires	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Primates	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Rodentia	–	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Sciuro- & Castorimorpha	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Mymorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Hystricomorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	+	+	<i>n.s.</i>	+	<i>n.s.</i>
Laurasiatheria (terr.)	+	<i>n.s.</i>	+	<i>n.s.</i>	+	+	+	<i>n.s.</i>	+	+
Carnivora (terr.)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Chiroptera	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Cetartiodactyla	–	<i>n.s.</i>	–	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	–	<i>n.s.</i>	–	<i>n.s.</i>
Artiodactyla	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Ungulata (Artiod./Perissod.)	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>

complex stomachs or GI tracts, this relationship was negative in Rodentia as well as Cetartiodactyla (Table 3), indicating that in these species sets, smaller phylogenetic lineages had more complex stomachs or GI tracts (the Myomorpha in the Rodentia, and the Ruminantia in the Cetartiodactyla).

Dietary crude fibre vs. gastrointestinal tract complexity

Total GI tract complexity and large intestine complexity were positively related to dietary crude fibre levels in both GLS and PGLS across Eutheria and Laurasiatheria, and also in GLS (but not PGLS) in several phylogenetic subgroups (Table 4); the dendrograms of dietary fibre (Fig. 3b) and total GI tract complexity (Fig. 3c) indicate a high degree of matching, again with the exception of the Myomorpha and the Cetacea. Stomach complexity only had various significant relationships with crude fibre in GLS but never in PGLS, again indicating that stomach morphology is a major correlate of phylogenetic differentiation. In both Carnivora and Artiodactyla, the GLS relationship of caecum and large intestine complexity with crude fibre was negative.

Body mass and dietary crude fibre vs. gastrointestinal tract complexity

In models that relate both body mass and crude fibre to GI tract complexity, both factors (or the interaction) were significant across Eutherian subgroups in GLS but very

rarely in PGLS (Table 5). For these models, PGLS only indicated that across terrestrial Eutheria, large intestine and total GI tract complexity was positively associated with body mass.

Stomach complexity vs. large intestine complexity

There seemed to be a clear dichotomy between either complex stomachs or complex large intestines in the raw data (Fig. 5a). Stomach complexity was not related to caecum or large intestine complexity and negatively to colon complexity in GLS across Eutheria (and several subgroups), but it was *positively* related to caecum and large intestine complexity in PGLS, and PGLS indicated no significance for the relationship with the colon (Table 6). The generally positive relationship can be gleaned from displays of subsets of the data (Fig. 5b–g). The only species sets with a significantly negative relationship between stomach complexity and some large intestine element were the aquatic eutherians, Cetartiodactyla, and Artiodactyla. If, however, Artiodactyla and Perissodactyla were considered together as ‘Ungulata’, the negative relationships between stomach and large intestine element complexity were significant in both GLS and PGLS.

To test whether these findings were due to an increase from minimum complexity to any degree of complexity across the dataset, the analyses were repeated for all Eutheria after excluding all species with a combination of minimum stomach complexity and minimum hind-gut complexity (i.e., the group in the lower left corner

Table 4. Summary of relationships of the estimated level of crude fibre in the natural diet (as a proxy for dietary habits) with the complexity indices of individual components or the whole gastrointestinal (GI) tract in eutherian groups in generalised least squares (GLS) and phylogenetic generalised least squares (PGLS) based on the tables in the supplementary material. Positive (+), negative (-) or non-significant (*n.s.*) relationships were detected.

Group (Crude fibre)	Stomach		Caecum		Colon		Large intestine		GI tract	
	GLS	PGLS	GLS	PGLS	GLS	PGLS	GLS	PGLS	GLS	PGLS
Eutheria	+	<i>n.s.</i>	+	+	+	+	+	+	+	+
Eutheria (terrestrial)	+	<i>n.s.</i>	+	+	+	<i>n.s.</i>	+	+	+	+
Eutheria (aquatic)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Afrotheria (terr.)	+	<i>n.s.</i>	+	+	+	<i>n.s.</i>	+	+	+	+
Xenarthra	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>
Euarchontoglires	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Primates	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Rodentia	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Sciuro- & Castorimorpha	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Mymorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Hystricomorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Laurasiatheria (terr.)	+	<i>n.s.</i>	+	<i>n.s.</i>	+	+	+	<i>n.s.</i>	+	+
Carnivora (terr.)	<i>n.s.</i>	<i>n.s.</i>	-	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	-	<i>n.s.</i>	+	<i>n.s.</i>
Chiroptera	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Cetartiodactyla	+	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	<i>n.s.</i>	+	<i>n.s.</i>
Artiodactyla	+	<i>n.s.</i>	-	<i>n.s.</i>	-	<i>n.s.</i>	-	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Ungulata (Artiod./Perissod.)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>

of Fig. 5). While after this exclusion, all relationships of stomach complexity with large intestine elements were negative in GLS, both caecum and large intestine complexity were still positively related to stomach complexity in PGLS (Table 6).

Discussion

The reader will identify limitations of this study: Estimates concerning diet characteristics and morphological differentiations of sections of the gastrointestinal tract, as presented in Table S1 of the supplementary material, are approximations. These are useful and suitable for a large-scale comparative overview, but for a comparison of individual species, more detailed information should be sought. Note that such detailed comparisons are not the aim of the present study. Similarly, while the mammalian supertree used for the phylogeny is appropriate for comparative analyses across a large scale of taxa, it may not reflect the most recent phylogenetic relationships within certain taxa. The supertree does not contain most recent information about the position of large phylogenetic groups as in TARVER *et al.* (2016) or ESSELSTYN *et al.* (2017), where it is suggested that Perissodactyla and Cetartiodactyla can be joined as sister taxa in the group of Euungulata (but a lower number of species is included in the respective trees). Rather than resorting to constructing our own tree, we used an existing consensus tree. While it is difficult to predict to what degree our results would change with other trees, we consider it

unlikely that the large-scale overall result of our analysis would change in a relevant way.

Diversity

The analyses corroborate the common sense assumption that a higher species diversity in a phylogenetic group also results in a higher morphological and ecological diversity. Eutherian orders with a low number of species had a low degree of diversity in body mass and dietary crude fibre range as well as a low degree of diversity in GI tract complexity (Fig. 1). The order Pilosa from the Xenarthra represented an outlier because this order contains, with sloths and anteaters, two phylogenetic groups of extreme morphological and ecological differences. Such an observation raises the evident question why these two groups are not given, each for itself, order status, and reminds us of the arbitrariness involved in assigning a certain hierarchical status such as ‘order’ or ‘genus’ to a certain group of taxa. The order Carnivora represented another outlier, with a high body mass and ecological diversity as expected based on their high species diversity, but a surprisingly low diversity in GI tract and stomach complexity. Reasons for these deviations from the general pattern beyond the invocation of ‘contingency’ remain to be elucidated.

Eutherian feeding ecology

Our analyses demonstrate that body size, diet niche and GI tract complexity are mainly a property of ma-

Table 5. Summary of models that link the complexity of a compartment of the gastrointestinal (GI) tract with both body mass (BM), the estimated level of crude fibre in the natural diet (as a proxy for dietary habits) (CF), and their interaction (int) in eutherian groups in generalised least squares (GLS) based on the tables in the supplementary material. Significant terms (BM, CF, int) or absence of any significance (*n.s.*) are noted.

Group	Stomach		Caecum		Colon		Large intestine		GI tract	
	GLS	PGLS	GLS	PGLS	GLS	PGLS	GLS	PGLS	GLS	PGLS
Eutheria	BM int	<i>n.s.</i>	BM CF int	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	BM CF int	<i>n.s.</i>	BM CF int	<i>n.s.</i>
Eutheria (terrestrial)	BM int	<i>n.s.</i>	BM CF int	<i>n.s.</i>	BM CF	<i>n.s.</i>	BM CF int	BM	CF int	BM
Eutheria (aquatic)	<i>n.s.</i>	<i>n.s.</i>	int	int	<i>n.s.</i>	<i>n.s.</i>	int	int	<i>n.s.</i>	<i>n.s.</i>
Afrotheria (terr.)	<i>n.s.</i>	<i>n.s.</i>	CF	CF	<i>n.s.</i>	<i>n.s.</i>	CF	<i>n.s.</i>	CF	<i>n.s.</i>
Xenarthra	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Euarchontoglires	BM	<i>n.s.</i>	BM	<i>n.s.</i>	BM	<i>n.s.</i>	BM	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Primates	<i>n.s.</i>	<i>n.s.</i>	BM	BM	BM CF	<i>n.s.</i>	BM	<i>n.s.</i>	BM	<i>n.s.</i>
Rodentia	<i>n.s.</i>	<i>n.s.</i>	BM	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	BM	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Sciuro- & Castorimorpha	<i>n.s.</i>	<i>n.s.</i>	BM CF int	<i>n.s.</i>	int	<i>n.s.</i>	BM	<i>n.s.</i>	BM	<i>n.s.</i>
Mymorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Hystricomorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	BM	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Laurasiatheria (terr.)	CF int	<i>n.s.</i>	BM	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	BM	<i>n.s.</i>	BM CF	<i>n.s.</i>
Carnivora (terr.)	<i>n.s.</i>	<i>n.s.</i>	BM int	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	BM int	<i>n.s.</i>	BM int	<i>n.s.</i>
Chiroptera	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Cetartiodactyla	CF	<i>n.s.</i>	CF	<i>n.s.</i>	BM	<i>n.s.</i>	CF	<i>n.s.</i>	CF	<i>n.s.</i>
Artiodactyla	CF	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Ungulata (Artiod./Perissod.)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>

Table 6. Summary of relationships of the stomach complexity index with the complexity indices of individual components or the whole large intestine in eutherian groups in generalised least squares (GLS) and phylogenetic generalised least squares (PGLS) based on the tables in the supplementary material. Positive (+), negative (–) or non-significant (*n.s.*) relationships were detected.

Group (Stomach)	Caecum		Colon		Large intestine	
	GLS	PGLS	GLS	PGLS	GLS	PGLS
Eutheria	<i>n.s.</i>	+	–	<i>n.s.</i>	<i>n.s.</i>	+
Eutheria (terrestrial)	<i>n.s.</i>	+	–	<i>n.s.</i>	<i>n.s.</i>	+
Eutheria (aquatic)	–	–	<i>n.s.</i>	<i>n.s.</i>	–	–
Eutheria (without 1/0) ¹	–	+	–	<i>n.s.</i>	–	+
Afrotheria (terr.)	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+	+
Xenarthra	–	–	<i>n.s.</i>	<i>n.s.</i>	–	–
Euarchontoglires	–	+	–	<i>n.s.</i>	–	+
Primates	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Rodentia	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+
Sciuro- & Castorimorpha	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	+	+
Mymorpha	<i>n.s.</i>	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+
Hystricomorpha	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Laurasiatheria	+	+	<i>n.s.</i>	<i>n.s.</i>	+	+
Carnivora	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Chiroptera	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Cetartiodactyla	+	<i>n.s.</i>	–	–	+	<i>n.s.</i>
Artiodactyla	–	<i>n.s.</i>	–	–	–	<i>n.s.</i>
Ungulata (Artiod./Perissod.)	–	–	–	–	–	–

¹ excluding species with a combination of minimum stomach and minimum hindgut complexity

for groups and subgroups across Eutheria, and that these characteristics show only limited parallel evolution *within* Eutherian lineages. Thus, the results corroborate previous findings that phylogenetic differentiation in mammals is closely linked to dietary specialisation (ANDREWS *et al.*, 1979; EISENBERG, 1981; PINEDA-MUNOZ

& ALROY, 2014). With respect to the interplay of body mass and diet, the data pattern corroborates the general interpretation that larger species tend to be more herbivorous in terrestrial environments (PRICE & HOPKINS, 2015). However, rather than supporting the interpretation of an approximately linear correlation, the shape

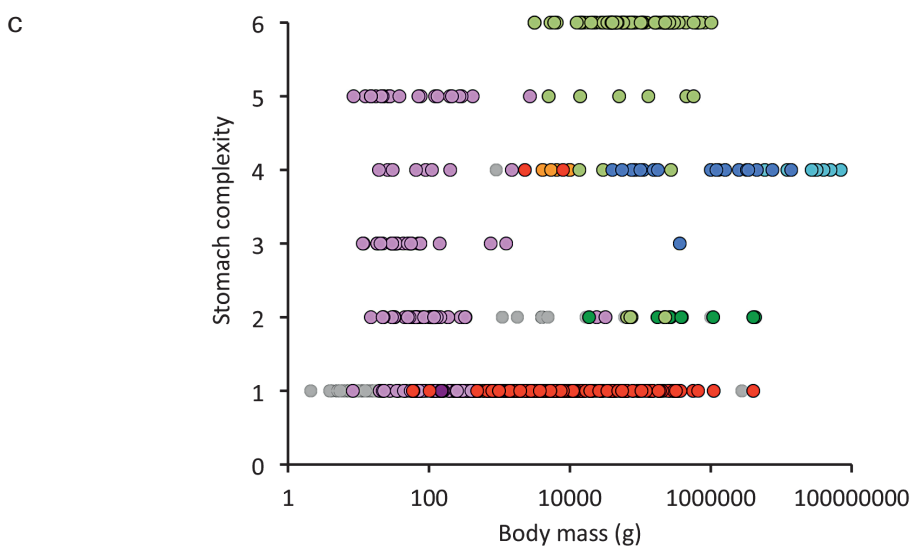
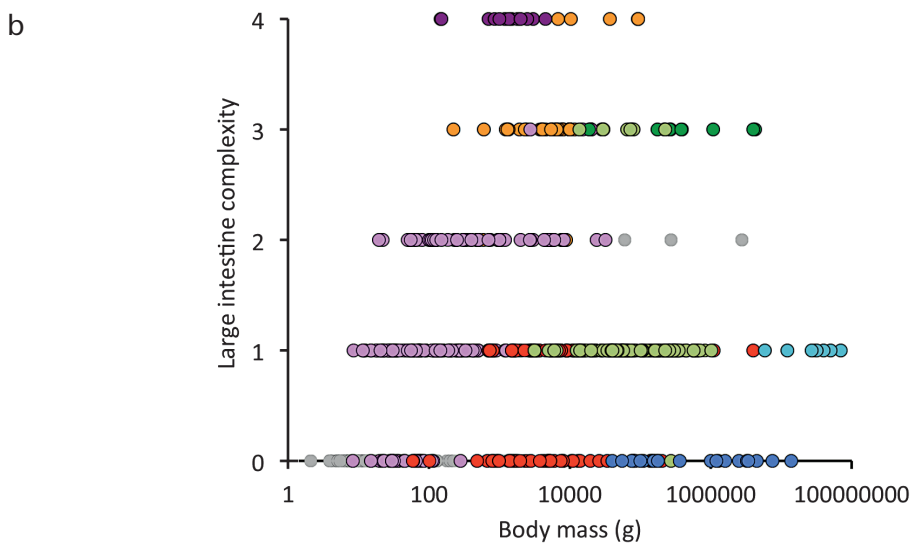
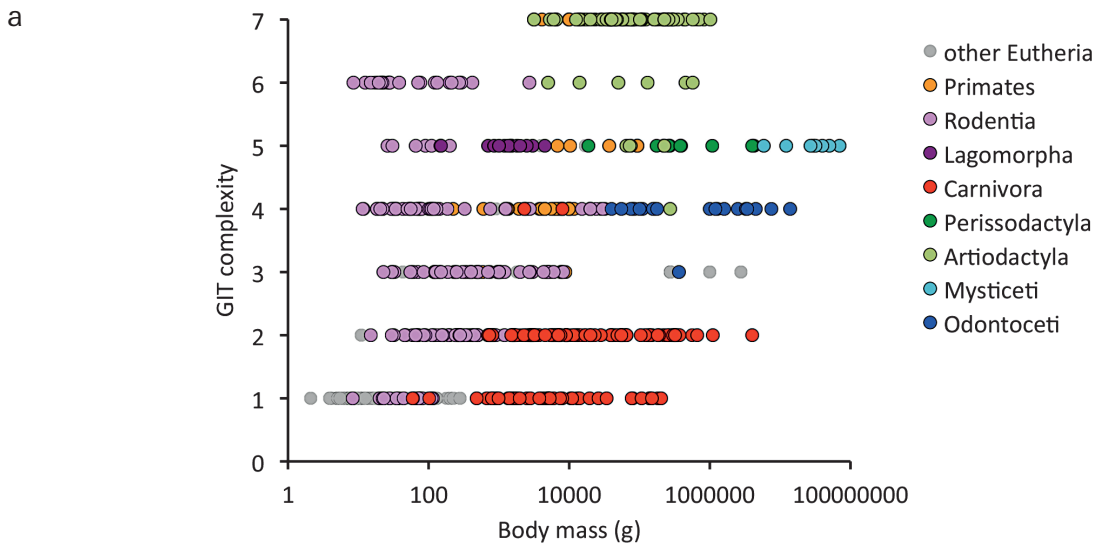


Fig. 4. Relationship between Eutherian body mass (g) and the complexity indices of (a) the total gastrointestinal tract (GIT), (b) the large intestine and (c) the stomach, with several taxa displayed individually. Data from Table S1.

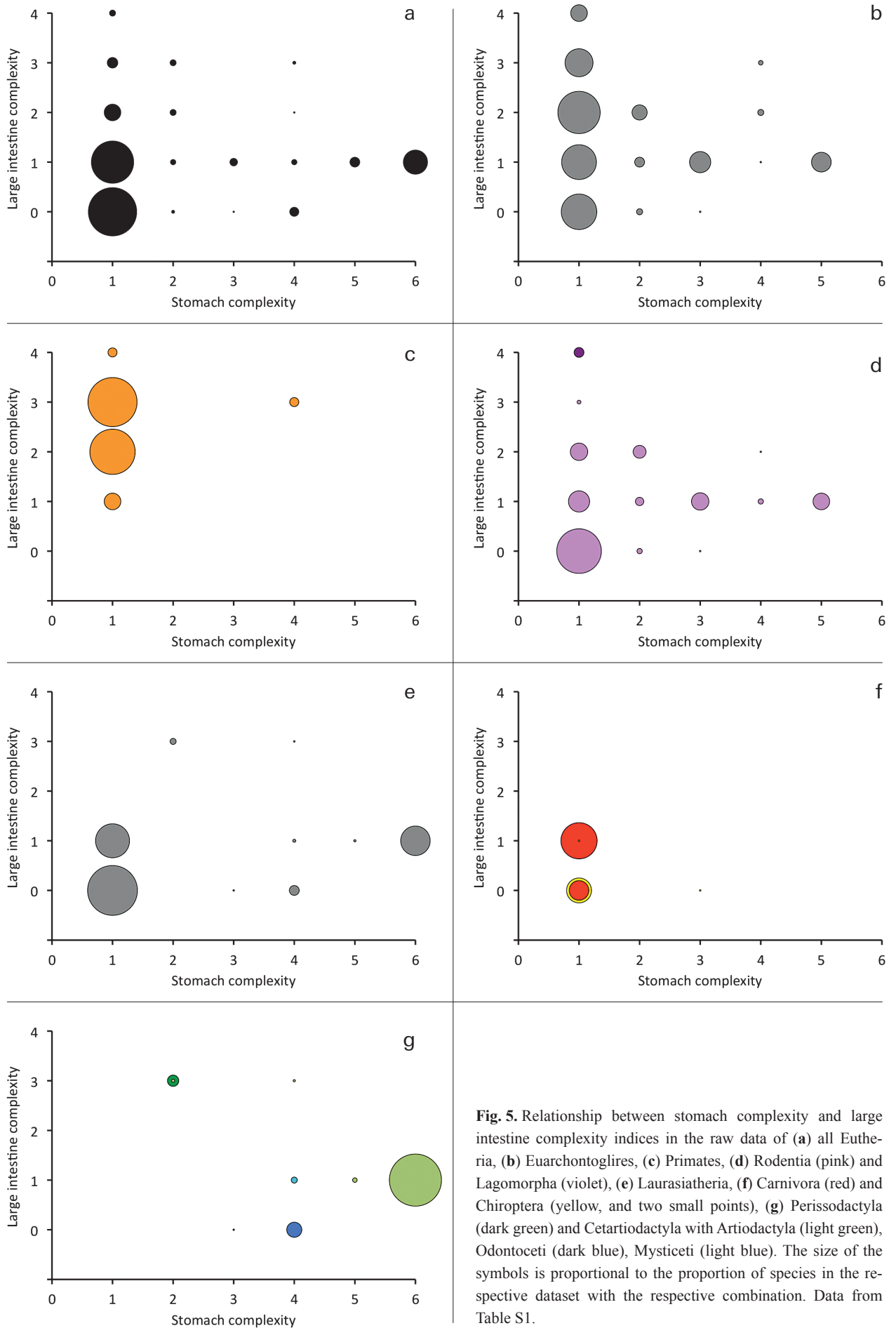


Fig. 5. Relationship between stomach complexity and large intestine complexity indices in the raw data of (a) all Eutheria, (b) Euarchontoglires, (c) Primates, (d) Rodentia (pink) and Lagomorpha (violet), (e) Laurasiatheria, (f) Carnivora (red) and Chiroptera (yellow, and two small points), (g) Perissodactyla (dark green) and Cetartiodactyla with Artiodactyla (light green), Odontoceti (dark blue), Mysticeti (light blue). The size of the symbols is proportional to the proportion of species in the respective dataset with the respective combination. Data from Table S1.

of the body size-diet data scatter indicates underlying ecological constraints. On the small end of the body size spectrum (from 10 g upwards), any dietary option appears open to mammals (Fig. 1), although the opportunity to feed selectively on high-quality feeds, which are accessible in sufficient abundance at this size scale, may lead to a higher proportion of species feeding on high-quality (low-fibre) diets (HIEMAE, 2000; CLAUSS *et al.*, 2013). At increasing body size, animals have to ingest food that is more abundant at larger spatial scales and hence inherently of lesser quality (cf. lack of low-fibre diets at increasing size in Fig. 1b), or they have to specialize on exclusive carnivory (Fig. 1a), being mostly limited to large prey in terrestrial ecosystems but free to use large or small prey in aquatic environments (HIEMAE, 2000; CARBONE *et al.*, 2014).

Hindgut convergence with diet and stomach homoplasmy

A basic assumption underlying the hypothesis of a link between diet and GI tract complexity is that descriptions of complexity actually reflect physiological function. The relationship between dietary fibre and large intestine complexity – and hence also total GI tract complexity – at the levels of all Eutheria, Afrotheria and Laurasiatheria (Table 3) suggests such functionality at this GI tract section. Even if microbial digestion can occur at relevant magnitudes in large intestines of low complexity, as in camelids or ruminants (Artiodactyla), and some herbivores can lack a caecum altogether, such as sloths (Pilosa-Folivora) or Hippopotamidae (Artiodactyla), more complex large intestines are mainly linked to more fibrous diets, and hence also to body mass. The only major exception to this rule is in the Carnivora where those species with a high dietary fibre intake (Ursidae, including the totally herbivorous giant panda, *Ailuropoda melanoleuca*) lack a caecum (LIU, 1984). In contrast, many strictly carnivorous species from other Carnivora taxa have a caecum (MCGROSKY *et al.*, 2016). For example, a caecum is present in the pinniped families Otariidae (fur seals and sea lions), Odobenidae (walrus) and Phocidae (true seals), but also in Canidae, in Hyaenidae, Felidae, Herpestidae and Viverridae (LANGER, 2017). Yet, when considered beyond the presence or absence of a caecum, increased large intestine complexity represents a convergent, albeit not obligatory, adaptation to fibrous diets.

By contrast, stomach complexity is neither linked to fibre nor body mass across all Eutheria or individual subgroups. Although stomach complexity is often linked to herbivory (ALEXANDER, 1993), this relationship does not hold for the smallest (Myomorpha) and largest (Cetacea) taxa with highly complex stomachs. Complex stomachs hence represent only a taxon-specific characteristic (Fig. 3f), without global convergent function. Actually, while the general function of the complex stomachs of mammalian herbivores is generally well understood (LANGER,

1988; STEVENS & HUME, 1998), the Cetacea and Myomorpha still challenge our functional understanding of complex stomachs.

Cetacea: phylogenetic inertia or/and functional adaptation?

This challenge of functional understanding can be met with a certain ease in Cetacea, where the complex stomachs can be understood as examples of phylogenetic inertia – because their closest relatives among the Artiodactyla, the Hippopotamidae (NIKAIDO *et al.*, 1999; GATESY *et al.*, 2013), also have complex stomachs (LANGER, 1975, 1976), as do other artiodactyl groups (Tayassuidae, Camelidae and all Ruminantia subgroups) (LANGER, 1973). Even though Cetacea stomachs are, in their detailed anatomy, more dissimilar to the stomachs of other artiodactyl groups than those are amongst themselves (LANGER, 2001), it is assumed that Cetacea derived from an Artiodactyl lineage that had adapted to herbivory and underwent a secondary transition to carnivory (THEWISSEN *et al.*, 2011; WANG *et al.*, 2016). GINGERICH (2015) suggested that various reports of predominantly herbivorous Artiodactyla feeding opportunistically on nestling or fish adds credibility to the concept that a herbivore could transition to a carnivorous feeding habit. A recent compilation of a larger number of observations where Hippopotami either scavenged carcasses or hunted themselves further supports this concept (DUDLEY *et al.*, 2016). That the transition from herbivory to secondary carnivory occurred in a group with complex stomachs could be considered a sheer coincidence, making the stomachs of cetacea an example of evolutionary contingency (ERWIN, 2006) rather than convergence.

Cetacea have adapted to their new feeding niche: In a comparative molecular study positive selection for proteinase and lipase enzymes was found in Cetacea, as is appropriate for a carnivorous diet, as well as a loss of pancreatic RNASE1 that is considered a requirement for herbivory (WANG *et al.*, 2016). Similarly, Cetacea have reduced numbers of genes, or nonfunctional genes, coding for bitter, umami, sweet or sour taste receptors compared to herbivores (FENG *et al.*, 2014; KISHIDA *et al.*, 2015; LIU *et al.*, 2016). Just as many taste receptors may be of no use to Cetacea, there is no evident benefit of a complex stomach; the simple-stomached Pinnipedia cover a nutritional range similar to that of Cetacea, including filter-feeding in the pinniped *Lobodon carcinophaga* (MÄRTENSSON *et al.*, 1994). Early propositions that complex stomachs of Mysticeti are functionally similar to those of Ruminantia due the detection of volatile fatty acids, equating the chitin component of krill to plant fibre (HERWIG *et al.*, 1984), did not explain the adaptive value of the similarly complex stomachs of the closely related Odontoceti. Actually, the energy derived from microbial fermentation in a baleen whale's forestomach is dramatically lower than that typically measured in a herbivorous foregut fermenter (OLSEN & MATHIESEN, 1996). However,

one can speculate that complex macroanatomical structure such as a composite stomach may be more difficult to lose than enzymes or taste receptors. A comparison of the stomach capacity (measured by gut fill) allows the speculative assumption of a comparative reduction in size in the Cetacea as compared to Artiodactyla (PÉREZ *et al.*, 2017), facilitating the hypothesis that retrogression is taking place to a certain extent. The lack of a nonglandular forestomach in the odontocete Iniidae (river dolphins) and Ziphiidae (beaked whales) (LANGER, 2017), potentially a secondary loss based on limited embryological evidence (JUNGKLAUS, 1897), might point into the same direction. However, even though simple stomachs can also expand enormously to accommodate a gorging food intake strategy in large terrestrial carnivores, the volume capacity that comes with a forestomach may be beneficial for Odontoceci and Mysticeci alike: The nutritional ecology of the Mysticeci, with spatially lumped, large packages of krill available during limited periods of time may make a forestomach with a certain voluminous capacity adaptive. Odontoceci, which do not chew their food but may swallow large numbers, or even large pieces of prey, may similarly benefit from capacious forestomachs.

Even if the general presence of complex stomachs in Cetacea was considered an example of phylogenetic inertia, this would not necessarily rule out new adaptive functional relevance of these structures. Even though some authors consider functional interpretations a vain effort (e.g., MEAD, 2007), the adaptive value of complex stomachs in Cetacea has traditionally focussed, apart from the mentioned emphasis on fermentative microbial digestion of krill, either on the function of storage or trituration. MORIMOTO *et al.* (1921) delivered a detailed discussion why convincing evidence for a trituration or ‘gizzard’ function is lacking. These authors already mention another macroanatomical observation on the stomach of the beaked whales that appears difficult to reconcile with a mere concept of phylogenetic inertia. In this group, a series of compartments in the so-called ‘connecting stomach’ have evolved that vary in number, up to 10 in *Mesoplodon bidens* and *M. europaeus* (MEAD, 2007). While these structures are still not described in a conclusive or satisfactory manner (LANGER, 2017), they represent new morphological features without equivalent in non-Cetacea. Other potential functions of cetacean stomachs, apart from the evident food storage and the debated trituration and microbial fermentation, may be related to feeding during deep dives under extreme pressure. For example, *Mesoplodon densirostris* – with only 3–5 connecting chambers (MEAD, 2007) – habitually does not dive as deep as *Ziphius cavirostris* (BAIRD *et al.*, 2006; TYACK *et al.*, 2006) with its 8–9 connecting chambers (MEAD, 2007), and diving depths for *Berardius bairdii* with its 7–10 connecting chambers (MEAD, 2007) were also spectacularly deep (MINAMIKAWA *et al.*, 2007). Whether this is a spurious finding or describes a relevant pattern, and what adaptations are required for feeding and stomach storage and digestion under high pressure, remains to be explored.

Myomorpha: enigmatic stomach complexity

The adaptive value of the complex stomachs of Myomorpha cannot be explained by phylogenetic inertia. It appears unlikely that Myomorpha forestomachs serve for the digestion of plant fibre as suggested by VORONTSOV (1967/1969), because microbial fibre digestion rather occurs in the caecum of Myomorph rodents (SAKAGUCHI *et al.*, 1981). CARLETON (1973) elaborated two additional hypotheses. The first suggests that a nonglandular stomach compartment might serve for additional trituration of the food bolus (comparable to the hypothesis mentioned above in Cetacea); however, given the high chewing efficiency of myomorph rodents (LEE, 1993; FRITZ *et al.*, 2009a), a relevance of such additional trituration might be questionable. The second hypothesis suggests that an aglandular stomach compartment might allow a more thorough digestion of the food by salivary enzymes, in particular amylase (CARLETON, 1973). Another aspect is the storing function of an extended gastric volume – although, as mentioned above for the Cetacea, simple stomachs can easily accommodate large volumes of food by simple expansion, so that the evolution of a forestomach does not appear as a stringent necessity for an increased intake capacity. A more recent set of hypotheses is linked to putatively protective microbial effects. For example, forestomach microbiota might neutralize specific dietary toxins (KOHL & DEARING, 2012; KOHL *et al.*, 2014b). Compared to herbivorous foregut fermenters, myomorph forestomachs harbour a different microbiome with more lactobacilli (KOHL *et al.*, 2014a; SHINOHARA *et al.*, 2016). Because these might have antifungal properties, SHINOHARA *et al.* (2016) hypothesized that complex stomachs in Myomorpha could be an adaptation to granivory and scatter hoarding, as seeds are susceptible to mould (JANZEN, 1976). These hypotheses await comprehensive comparative evaluation.

Relations between stomach and large intestine

The typical classification of herbivores into foregut or hindgut fermenters (JANIS, 1976; VAN SOEST, 1996; STEVENS & HUME, 1998), together with the observation that many eutherian groups have an emphasis on either one of these fermentation sites, leads to the intuition that stomach and large intestine complexity should be correlated negatively. However, this expectation was only met in conventional statistics (Table 6), whereas statistics including phylogeny indicated that within lineages or among closely related lineages, increases in stomach complexity are rather positively than negatively linked to increases in large intestine complexity, regardless of whether all species with a combination of non-complex stomachs and non-complex large intestines were excluded or not. Only if the dataset is artificially constrained to the “Ungulata” – Perissodactyla + Artiodactyla – did we find the expected relationship. These results caution

against transferring observations from a phylogenetically limited dataset, intuitive as they may appear.

Conclusion and outlook

With respect to macroscopic anatomy, the capacity of the GI tract (CHIVERS & HLADIK, 1980; LANGER & SNIPES, 1991) may be a more relevant proxy for GI tract functionality than a scoring of complexity. However, such measures are inherently more difficult to determine than complexity indices that reflect (dimensionless) shape, and they require simultaneous documentation of the body mass of the respective specimens. Until such data on capacities are widely available, the present study represents a comprehensive test of macroanatomical patterns of the GI tract of most eutherian taxa.

Our scores of complexity yield different results for the stomach and the large intestine. Complex large intestines can be linked to high-fibre diets, and while this is not necessarily true the other way round, they therefore represent an example of convergent evolution. Correspondingly, there are only relatively few morphological changes that produce diversity in the large intestinal morphology, in particular, the taeniae, haustra and semilunar folds that facilitate a volume increase of, and influence digesta transit through, the large intestine (LANGER, 1991; LANGER & TAKÁCS, 2004), which are shared by a large number of different taxa. By contrast, stomach morphology displays an intriguing, apparently unsystematic array of arrangements and shapes (LANGER, 1988; LANGER, 2017). As homoplasies, these structures characterize phylogenetic lineages, to the extent of being diagnostic indicators of the respective phylogenetic groups.

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Authors' contributions

PL performed the data collection over years, and initiated the study. MC analysed the data. Both authors drafted the manuscript together.

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