Comparative lengths of digestive tracts of seven didelphid marsupials (Mammalia) in relation to diet

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ABSTRACT. The relative proportions of the digestive tract were rarely explored to understand the behaviour and the ecology of neotropical marsupials. In this study, proportions of the digestive tract and diet were compared in seven opossum species. The animals studied were *Didelphis albiventris* Lund, 1840, *D. aurita* Wied-Neuwied, 1826, *Metachirus nudicaudatus* (Desmarest, 1817), *Philander frenatus* (Olfers, 1818), *Lutreolina crassicaudata* Desmarest, 1804, *Monodelphis sorex* (Hensel, 1872) and *Caluromys lanatus* (Olfers, 1818). Segments of digestive tracts of marsupials were measured and differences were statistically tested by Analysis of Variance and Covariance. Caecum and hard guts were responsible for the main differences among opossums, although all segments differed significantly. *Caluromys lanatus* was the most specialised species, with a large hard gut and caecum, small stomach and shorter small gut. The large caecum of *M. nudicaudatus* and the shortest hard gut of *M. sorex* were also noticed. The arboreal *C. lanatus* has a well different feeding habit and life style regarding other marsupials studied, such as *M. sorex* and *M. nudicaudatus* which are terrestrial, corroborating the results reached.
KEY WORDS. Caecum, *Caluromys lanatus*, digestive tract proportions, hard gut, *Metachirus nudicaudatus.*

RESUMO. **Dimensões comparadas de tratos digestivos de sete marsupiais didelfídeos (Mammalia) em relação à dieta.** Proporções relativas do trato digestivo são raramente exploradas para entender o comportamento e a ecologia de marsupiais neotropicais. Neste estudo, proporções relativas do tubo digestivo e dieta de sete espécies de marsupiais são comparadas. Os animais estudados foram *Didelphis albiventris* Lund, 1840, *D. aurita* Wied-Neuwied, 1826, *Metachirus nudicaudatus* (Desmarest, 1817), *Philander frenatus* (Olfers, 1818), *Lutreolina crassicaudata* Desmarest, 1804, *Monodelphis sorex* (Hensel, 1872) e *Caluromys lanatus* (Olfers, 1818). Posteriormente, cada segmento do tubo digestivo destes marsupiais foi medido e as diferenças encontradas foram estatisticamente testadas usando a Análise de Variância e de Covariância. O ceco e o intestino grosso foram responsáveis pelas principais variações observadas, embora todos os segmentos alcançaram diferenças significantes. *Caluromys lanatus* foi a espécie mais especializada, apresentando grandes intestino grosso e ceco, pequeno estômago e intestino delgado mais curto. Destacou-se também o relativamente longo ceco de *M. nudicaudatus* e o intestino grosso mais curto de *M. sorex*. *Caluromys lanatus*, de hábito arborícola, apresenta alimentação e estilo de vida bem diferentes, considerando os outros marsupiais estudados, como *M. sorex* e *M. nudicaudatus* que são terrestres, confirmando os resultados alcançados.
PALAVRAS CHAVE. Ceco, proporções do trato digestivo, *Caluromys lanatus*, intestino grosso, *Metachirus nudicaudatus*.

Marsupials are a rich group of mammals in the neotropics with about 70 species. Among them, didelphids have the most wide distribution of species in the Neotropical region, many of them ranging from Mexico to Argentina. Didelphid marsupials occupy a variety of habitats, such as the tropical, submontane and montane forests, the arboreal, terrestrial and aquatic environment (Emmons & Feer 1997) and present a continuum of feeding habits, from those species deeply omnivore to those more frugivore, insectivore or carnivore (Leite *et al*. 1994, Santori *et al*. 1995a, Cáceres *et al*. 2002, Astúa de Moraes *et al*. 2003, Cáceres 2004, Santori *et al*. 2004, Vieira & Astúa de Moraes 2004).

The digestive tract is important in the determination of the dietary type of marsupials (Crowe & Hume 1997). In general, the form and size of its parts are functionally adapted. For example, carnivorous animals show larger stomachs and shorter guts whereas herbivorous-frugivorous animals often show smaller stomachs, long hard guts and developed caeca (Hildebrand 1995). Few studies have compared relative proportions of digestive tract or skulls (*e.g.* Medellín 1991, Santori *et al*. 1995b, Sánchez-Villagra & Smith 1997) to answer questions related to feeding habits of didelphid marsupials. One of them is how didelphids, having only slightly different diets, adjust structurally to these differences. This is the question that this paper intends to answer by comparing the relative proportions of digestive tracts of seven species of didelphid marsupials from southern Brazil.

MATERIAL AND METHODS

The digestive tracts of seven species of didelphid marsupials (N = 29 individuals, family Didelphidae) were obtained from adult individuals collected in the Paraná and Santa Catarina States. Species used were the white-eared opossum *Didelphis albiventris* Lund, 1840 (1500 g, N = 5 individuals), the southern black-eared opossum *D. aurita* Wied-Neuwied, 1826 (1200 g, N = 4), the grey four-eyed opossum *Philander frenata* (Olfers, 1818) (250 g, N = 3), the brown four-eyed opossum *Metachirus nudicaudatus* (Desmarest, 1817) (290 g, N = 5), the short-tailed opossum *Monodelphis sorex* (Hensel, 1872) (45 g, N = 6), the woolly opossum *Caluromys lanatus* (Olfers, 1818) (300 g, N = 3) and the thick-tailed opossum *Lutreolina crassicaudata* (Desmarest, 1804) (600 g, N = 3). All animals used were deposited in the Capão da Imbuia Museum of Natural History (MHNCP) collection, in Curitiba, Brazil. Nomenclature follows Fonseca *et al.* (1996).

The complete digestive tract of fresh individuals, from pharynx to anus, was removed through a longitudinal section from the abdomen (beginning at the anus) to the throat. Latter, each digestive tract was extended on a salver with flat surface and the caecum, hard gut, small gut, stomach and oesophagus were measured with a 1 mm precision ruler. The length of each segment was measured after removing all mesenteric attachments but only when the tissue stopped contraction after its distension on the salver. For stomachs, after emptying all food material through a small incision, their areas were estimated by measuring their length on the longer stomach axis, and width on the shorter axis, perpendicularly.

The relative dimension of each portion of the digestive tract was obtained by dividing each measure (*e.g.* the caecum length) by the total length of the respective digestive tract. For comparison to other measures, the stomach area was transformed to its square root (Medellín 1991).

The coefficient of variation of each segment of the digestive tract was calculated based on arithmetic means and standard deviation for each species (CV = standard deviation / mean x 100). Differences observed in digestive tracts of species were analysed statistically by two-way Analysis of Variance (ANOVA) and the Analysis of Covariance (ANCOVA), using the total digestive length as covariate, in order to increase the statistical power. Species that contributed more to differences in proportions of digestive tracts were tested by the *post-hoc* HSD Tukey test for samples of different sizes (Zar 1984, Statistica 1993). To avoid the variance heterogeneity associated with percentages (Zar 1984), arcsin transformations were performed on relative proportions (Crowe & Hume 1997).

RESULTS

The caecum was the segment of the digestive tract that varied more among species (average CV = 36%), followed by the hard gut (23%). The longer segment in all species, the small gut, was the one that varied less (8%). Stomach and oesophagus lengths varied at percentages of 16% and 20%, respectively.

However, the Covariance analysis, a more robust analysis, showed that hard gut (F = 74.7; g.l. 6, 21; $p < 0.0001$) and small gut (F = 70.3; g.l. 6, 21; $P < 0.0001$) were the most important for general variations (see F values), although all segments differed significantly among species (for caecum: F = 39.2; g.l. 6, 21; $p < 0.0001$; for oesophagus: F = 27.0; g.l. 6, 21; $p < 0.0001$, and for stomach: F = 22.3; g.l. 6, 21; $p < 0.0001$).

Using the Analysis of Variance, all relative measures of digestive tracts differed significantly between species but with a weaker *P* value for the stomach (Tab. I). HSD Tukey test showed that *C. lanatus* differed from other species mainly because the small and hard intestines and caecum, *M. nudicaudatus* only because of the caecum (except in comparison with *C. lanatus*) and *Monodelphis sorex* because the hard intestine (Tab. I). Stomach, in general, did not differ between species. Thus, *C. lanatus* was the most different species, with a longer relative hard gut length (29%), a large relative caecum (8%), and short relative dimensions of the small intestine (51%) and stomach (3.8%) (Tab. II). *Metachirus nudicaudatus* had the longer relative caecum length (10%) in relation to other species. In contrast to *C. lanatus*, *M. sorex* had the shortest relative hard gut length (13%). Species of *Didelphis* were similar in all segments (Tabs I and II).

DISCUSSION

Caluromys lanatus and *M. nudicaudatus* were the species that have the larger variation observed in segments of digestive tracts, mainly regarding the caecum and hard guts. Despite of a long caecum, these two species have opposite life strategies, with *C. lanatus* having a strictly arboricolous habit and *M. nudicaudatus* being strictly terrestrial (Malcolm 1991, Cunha & Vieira 2002). The great caecum and hard gut of *C. lanatus* may be related to a diet based on plant material, as occurs in other frugivorous-herbivorous mammals (Chivers & Hadlik 1980, Charles-Dominique *et al.* 1981, for *C. philander*; Schieck & Millar 1985). The genus *Caluromys* Allen, 1900 is relatively more specialized in the consumption of fruits, gums and twigs (Grand 1983, Leite *et al.* 1994, Julien-Laferrière 1999), similarly to some primates (Chivers & Hadlik 1980, Passos 1999). A more frugivorous diet is associated to a small stomach chamber (Hildebrand 1995), just as observed here for *C. lanatus*.

A large hard gut may also function in the re-absorption of water from fruits (see Atramentowicz 1988), as is probably the case of species of *Caluromys* that live mostly in the forest canopy, rarely descending to the ground (Malcolm 1991, Leite *et al.* 1994). Low levels of water deficit should occur seasonally even in tropical forests (such as the forested savannahs) during drier months (*e.g.* Smithe 1970), and *C. lanatus*, a species distributed in seasonal forests in central and southern Brazil (Emmons & Feer 1997), could be benefited by exploring water from fruits, as suggested for the scansorial marsupial *D. albiventris* in the same region (Santori *et al.* 2004).

Table I. Analysis of Variance (ANOVA) between relative measures of digestive tracts of seven didelphid marsupial species and post-hoc test of Tukey HSD showing the main genera that differed in the analyses.

Digestive tract	g l	F	p	Tukey HSD test
Oesophagus	6, 24	12.2	< 0.001	*Lutreolina* ≠ all species, except for *Philander* and *Monodelphis*
Stomach	6, 24	3.2	< 0.050	NS
Small intestine	6, 24	21.6	< 0.001	*Caluromys* ≠ all species
Caecum	6, 24	28.4	< 0.001	*Metachirus* ≠ all species, except for *Caluromys*
Hard intestine	6, 24	47.6	< 0.001	*Caluromys* and *Monodelphis* ≠ all species

Tukey test is significant at p < 0.05 level. The symbol ≠ indicates the term "differed of". NS indicates no significant difference.

Table II. Distribution of total digestive tract lengths among segments (in % for relative size; in cm for raw data) in seven species of didelphid marsupials from southern Brazil.

Relative Size	N	Oesophagus	Stomach	Small intestine	Caecum	Hard intestine
Caluromys lanatus	3	7.9 ± 1.1	3.8 ± 1.0	51.0 ± 1.7	8.1 ± 1.5	29.2 ± 0.9
Didelphis albiventris	5	8.9 ± 0.6	5.1 ± 0.5	64.6 ± 0.8	4.4 ± 0.5	17.1 ± 1.1
Didelphis aurita	4	7.9 ± 1.4	4.3 ± 0.8	65.1 ± 2.4	4.2 ± 0.5	18.6 ± 1.2
Lutreolina crassicaudata	3	13.0 ± 0.2	5.4 ± 1.2	60.9 ± 1.6	3.0 ± 0.1	17.8 ± 0.6
Metachirus nudicaudatus	5	9.6 ± 0.5	5.5 ± 1.0	56.7 ± 1.3	10.3 ± 0.8	18.0 ± 0.3
Monodelphis sorex	6	10.7 ± 1.4	5.9 ± 0.9	64.5 ± 1.9	5.7 ± 1.2	13.3 ± 1.0
Philander frenatus	3	11.5 ± 0.7	5.4 ± 0.8	60.2 ± 4.6	5.3 ± 1.2	17.5 ± 3.0
Raw Data						
Caluromys lanatus	3	9.3 ± 0.7	4.5 ± 1.3	60.5 ± 5.8	9.5 ± 1.3	34.8 ± 3.8
Didelphis albiventris	5	15.8 ± 1.6	9.1 ± 1.2	114.9 ± 8.0	7.8 ± 1.1	30.4 ± 3.4
Didelphis aurita	4	14.2 ± 1.7	7.6 ± 1.2	117.7 ± 10.4	7.5 ± 1.1	33.6 ± 2.5
Lutreolina crassicaudata	3	11.8 ± 2.8	4.8 ± 0.6	55.6 ± 14.0	2.7 ± 0.6	16.1 ± 3.3
Metachirus nudicaudatus	5	8.5 ± 1.2	4.9 ± 0.9	50.6 ± 7.0	9.1 ± 0.6	16.0 ± 1.9
Monodelphis sorex	6	5.4 ± 0.4	3.0 ± 0.5	32.6 ± 3.9	2.9 ± 0.8	6.7 ± 0.7
Philander frenatus	3	9.8 ± 1.0	4.6 ± 0.2	51.5 ± 8.4	4.6 ± 1.0	15.0 ± 3.0

N is the sample size. Means of species are given with standard deviation.

According to Chivers & Hadlik (1980) and Schieck & Millar (1985), hard gut size is one of the best indicators of diet in small mammals: the greater its dimension, the more herbivorous is the diet, and in contrast, the smaller the dimension, the more carnivorous (in a *latu sensu*, including all animal matter, *sensu* Vieira & Astúa de Moraes 2003) is the diet. Accordingly, one could conclude that *M. sorex* is the more insectivore amongst the marsupials studied. Previously, Charles-Dominique *et al*. (1981) reached this conclusion for *M. brevicaudata* (Erxleben, 1777) (Didelphidae) by analysing gut proportions and contents. On the other hand, Chivers & Hadlik (1980) and Schieck & Millar (1985) also pointed out that the small gut length does not help to elucidate the actual diet of an animal.

A large caecum is utilized in the storage and fermentation of food (plant material), or in the storage of vitamins (Hildebrand 1995). Hundreds of small seeds were seen concentrated into the caecum of an individual of *C. lanatus* analysed (Cáceres & Casella in preparation) and this could be related, possibly, to storage of fruit components or vitamin extraction from them. Anyway, the diet of *Caluromys* is thought to be more herbivorous than previously known (Julien-Laferrière 1999, Santori *et al*. 2004), based on the proportion of its caecum (Crowe & Hume 1997).

Despite the diet of *M. nudicaudatus* be more insectivore (Santori *et al*. 1995a, Cáceres 2004), its caecum had a long relative dimension, though less complex (and smaller in volume; personal observation) than that of *C. lanatus* (Santori *et al*. 2004). This could be related to the absorption of water and electrolytes, as hypothesized for insectivorous mammals (Anderson *et al*. 1992). Alternatively, it may be related to the metabolism of large volumes of chitin ingested, which would occur in the stomach and caecum of *M. nudicaudatus* hypothetically, through specific enzymes, as in other insectivorous mammals such as bats (Webb *et al*. 1993). With such enzymes, bats may extract a reasonable quantity of carbohydrates from the chitinous skeleton of insects.

The presence of a caecum in most didelphid marsupials is in agreement with the omnivory of the group (Astúa de Moraes *et al*. 2003, Santori *et al*. 2004). Even the more carnivorous-omnivorous marsupial *Lutreolina crassicaudata* has a relatively developed caecum when compared to other carnivorous marsupials (Santori *et al*. 2004, Vieira & Astúa de Moraes 2004). Material plant such as fruits could be ingested since the first months of young opossums after their independence of the mother (Cáceres 2002, 2004). Furthermore, plant-eaters herbivorous or folivorous will have greater caeca for microbial fermentation than those frugivorous animals (Crowe & Hume 1997), which will have larger caeca than more carnivorous marsupials.

The grey four-eyed opossum, *P. frenatus*, differently of the expected based on its more carnivorous diet (Santori *et al*. 1995b, 1997, 2004, Cáceres 2004), did not show significant differences in the stomach chamber size among other opossum species. According to Hildbrand (1995), specialized carnivorous animals tend to have big and elastic stomachs to eat and temporarily store large quantities of meat in each meal. *Philander frenatus* appears to be a omnivorous mammal not well adapted to the function of carnivory but with trends to this (Santori *et al*. 2004). Tests of laboratory food preferences indicated the same trend for this species (Astúa de Moraes *et al*. 2003).

Dimensions of digestive tracts of didelphid marsupials may hide phylogenetic characteristics that mask functional adaptations, becoming difficult to detect them. For example, the neotropical kinkajou *Potos flavus* (Schreber, 1774) (Procyonidae) (Charles-Dominique *et al*. 1981, Julien-Laferrière 1993) and the African hyena *Proteles cristatus* (Spaarman, 1783) (Hyenidae) (Anderson *et al*. 1992) exhibit digestive tracts of carnivores (resembling their ancestral) but today their diets are frugivorous and insectivorous, respectively. Also, the gastrointestinal morphology of Pseudocheiridae Australian marsupials is conditioned by phylogeny rather than diet or habitat (Crowe & Hume 1997). Phylogeny may have constrained the form of digestive tract of didelphid marsupials, yet differences between species with opposite life strategies suggest that there was space for adaptations in the group. Taxa such as *Caluromys* and *Monodelphis* appear to differ much more in form, differences that are in agreement with their opposite diets.

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