

Comparative histology of the digestive tract in three new world marsupials

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Abstract

We compare the main histological features of the digestive tract of three selected New World didelphid marsupials (Mammalia, Metatheria, Didelphimorphia, Didelphidae): the White-eared Opossum *Didelphis albiventris* Lund, 1840, the Short-tailed Opossum *Monodelphis dimidiata* Wagner, 1847, and the Patagonian Opossum *Lestodelphys halli* Thomas, 1921. The three species have a geographic distribution restricted to south-eastern and southern South America, and have quite distinct body masses, adaptations and life histories. Our observations include the following: (i) submucosal glands are present throughout the oesophagus of *D. albiventris*, only in its first third in *M. dimidiata*, and are lacking in *L. halli*; (ii) in the stomach and duodenum, the serous coat in *D. albiventris* is cuboidal (simple, squamous mesothelial layer in the other two species); (iii) the duodenum in *L. halli* has large folds, short crypts and Brunner's glands (the other species lack folds and Brunner's glands); (iv) the colon's mucous membrane has short, scarce villi in *D. albiventris* (villi absent in the remaining species). Some of the observed differences can be due to ecological adaptations, especially in the relatively large-sized, extremely omnivorous *D. albiventris* (e.g., colon villi).

KEYWORDS

Didelphis, digestive tract, histology, *Lestodelphys*, *Monodelphis*

1 | INTRODUCTION

Contrary to an extended perception, living New World marsupials (Mammalia, Metatheria) are not “living fossils” (Goin, 2003). The Didelphidae, (Order Didelphimorphia), which constitute the most diverse group of living opossums (the remaining ones being the Microbiotheria and the Paucituberculata), have their oldest undoubted record in the early Miocene of Patagonia, ca. 20 million years before present (Goin et al., 2007). Notwithstanding, the more generalized peradectoid didelphimorphians are much older, with

their oldest record extending far down to the Late Cretaceous of North America (Williamson, Brusatte, Carr, Weil, & Standhardt, 2012) and the early Palaeocene (ca. 63 Ma) of South America (Muizon, 1991). A review of South American metatherians, including their major Cenozoic lineages and their phylogenetical, biogeographical, palaeoenvironmental, palaeogeographical and adaptive contexts, is given in Goin, Woodburne, Zimicz, Martin, and Chornogubsky (2016). Voss and Jansa (e.g., 2009) made a detailed account of the phylogenetic relationships and classification of living New World didelphids. Brown (2004) updated the distribution of

all New World metatherians. Gardner (2008) summarized aspects of the specific taxonomy, distribution and natural history of living South American mammals, including marsupials. Canevari and Vaccaro (2007) offer a similar account for the mammals of the Southern Cone.

In spite of their “modernity” in the fossil record, living didelphids have been generally regarded as representative of early metatherian (or even therian) mammals in many anatomical aspects (e.g., Wible, 2003). This explains much of the interest among mammalogists in the study of specific organs, or whole anatomical systems, of representatives of this marsupial family. Because of its peculiar reproductive pattern, additional interest was put in the consideration of some of its species (e.g., *Monodelphis domestica* J. A. Wagner, 1842) as laboratory animals for biomedical research (see, e.g., Jurgelski, 1984; Saunders & Hinds, 1997).

Within the Didelphidae are included around a hundred living species ranging from southern Canada to southern Patagonia in Argentina. In South America, the bulk of these species are distributed in Amazonian and peri-Amazonic areas, while the remaining few inhabit different biomes along the Andean Cordillera and South America’s Southern Cone (Brown, 2004; Goin et al., 2016; Martin, 2010, 2011; Martin, Goin, & Forasiepi, in press). Species of this family occupy a large diversity of biomes, biotopes, niches and diets, and have developed a variety of sizes and types of locomotion (see, e.g., Gardner, 2008, Martin et al., in press).

Histological studies of New World opossums are relatively scarce throughout the literature. One exception is the Virginia Opossum, *Didelphis virginiana* Kerr, 1792; relevant to our work on the digestive system, are worthy of mention the studies by Acuff, Krause, and Cutts (1989); Krause and Leeson (1969a,b); Krause (1972, 1973, 1987, 1991); Krause, Cutts, and Leeson (1976a,b,c); Krause, Yamada, and Cutts (1989) and Marklin, Krause, and Cutts (1979), among others. In general terms, research has focused on a few species thought to be interesting for experimental, biomedical purposes (e.g., Barnes, 1977). Among South American marsupials, several histological reports made around the last couple of decades have focused on the South American opossum *D. albiventris*. Histological studies of the palate, tongue, oesophagus and pancreas are worth mentioning (Abdulnour–Nakhoul, Nakhoul, & Orlando, 2000; Cáceres, 2005; Countinho, Beck, Pessoa, Pinheiro, & Coutinho, 1982; Martínez, Martínez, & Pinheiro, 1998; Martínez et al., 1997). In turn, Moreno–Durán, López–Hurtado, and Ruiz–Sanchez (2007) considered all the digestive tract in their histological study of this species. As mentioned, most of these studies dealt with single species, not being their main focus the comparative histology of all, or selected, taxa of New World marsupials. Here, we begin such an attempt; our purpose was, first, to compare the histological anatomy of the digestive tract of

selected species with rather similar distribution but quite different life histories. In second place, we attempt to correlate such differences with their distinct ecological adaptations and modes of life. This is the first of a series of studies whose ultimate purpose was to correlate the anatomy, histology, physiology, ecology and diet of selected species of New World marsupials.

2 | MATERIALS AND METHODS

Studied specimens were sampled in different locations within the Pampean and Patagonian regions of Argentina (Buenos Aires and Chubut provinces, respectively). *Didelphis albiventris* was captured near La Plata City (north-eastern Buenos Aires Province); captures of *Monodelphis dimidiata* specimens were done near Balcarce City in central Buenos Aires Province; finally, specimens of *Lestodelphys halli* were captured in western Chubut Province near the town of Esquel. Specimens were anaesthetized and sacrificed by ether inhalation. Samples of oesophagus, stomach, small intestine and colon organs were obtained and fixed in 10% buffered formalin. They were processed routinely for histology by colouration of Haematoxylin and Eosin. In one colon sample of *D. albiventris*, we made Masson trichromatic colouration for a better observation and differentiation of muscle and connective tissues from mucosae. Digital images of the studied tissues were obtained using software by Micrometrics S.E. Premium Program. All histological specimens are housed at the Cátedra de Histología A, Facultad de Ciencias Médicas, Universidad Nacional de La Plata.

3 | RESULTS

3.1 | Oesophagus

In the three studied species, the mucosae membrane is composed of a stratified squamous non-keratinized epithelium. The *lamina propria* is made of loose connective tissue. The *mucosae muscularis* consists of smooth muscle running in a longitudinal direction and with some inner circular fibres (Table 1).

The submucosa of *D. albiventris* is composed of connective tissue with submucosal glands (Figure 1a,b). Typical mucous alveoli are observable throughout the oesophagus. In *M. dimidiata*, the submucosal glands are present only in the first third of the oesophagus (Figure 2a); finally, in *L. halli* submucosal glands were not observed.

The muscular coat is composed of two layers of smooth muscle, an inner circular layer and an outer longitudinal one.

The serosa coat consists of a mesothelium and a layer of loose connective tissue.

FIGURE 1 (a) *Didelphis albiventris*, oesophagus, H-E, 4x. (b) *Didelphis albiventris*, oesophagus, submucosa, 10x

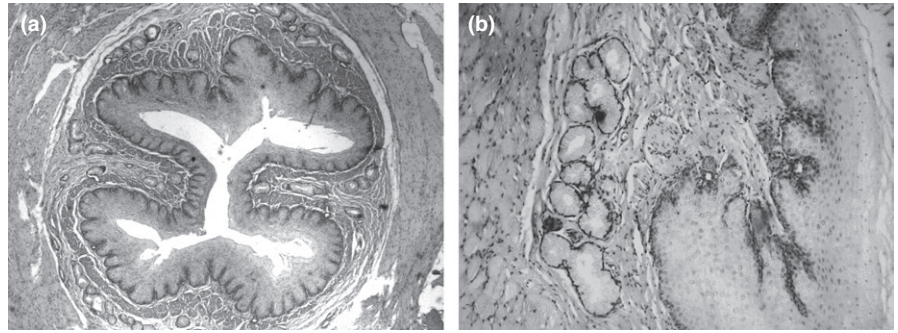


FIGURE 2 (a) *Monodelphis dimidiata*, oesophagus, general view, H-E 10x. (b) *Monodelphis dimidiata*, stomach (fundus), mucous membrane, H-E, 10X [Colour figure can be viewed at wileyonlinelibrary.com]

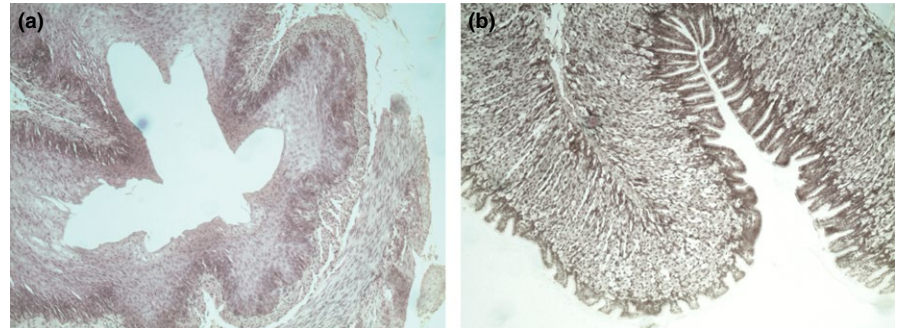


TABLE 1 Salient microanatomical and histological aspects of the digestive tract in three South American marsupials: *Didelphis albiventris*, *Monodelphis dimidiata* and *Lestodelphys halli*

Organ	Coat	<i>Didelphis albiventris</i>	<i>Monodelphis dimidiata</i>	<i>Lestodelphys halli</i>
Oesophagus	Submucosa: oesophageal glands	Throughout the oesophagus	Present only in the first third	Absent
Stomach	Mucous membrane	The entire mucosa coat has folds which have an axis of muscular mucous fibres	The entire mucosa coat has folds which have an axis of muscular mucous fibres	The folds have the two coats: mucous and submucous membranes
	Epithelium of serous coat	Simple, cuboidal epithelium	Simple squamous mesothelial layer	Simple squamous mesothelial layer
Duodenum	Mucous membrane	Without folds, only villi and crypts	Without folds, only villi and crypts	Large folds and short crypts
	Submucosa	Brunner's glands absent	Brunner's glands absent	Brunner's glands present
	Serous coat	Covered by a simple cuboidal epithelium	Cover is a squamous mesothelial layer	Cover is a squamous mesothelial layer
Jejunum and Ileum	Epithelium of mucous membrane	Fewer goblet cells than duodenum	Fewer goblet cells than duodenum	More goblet cells number than duodenum
Colon	Mucous membrane	Very short and scarce villi	Villi absent	Villi absent

3.2 | Stomach

The main body of the stomach (fundus) of *D. albiventris*, *M. dimidiata* and *L. halli* has a mucous membrane which is entirely occupied by a mass of gastric glands that open on the surface by gastric foveolae (Figure 3a, 2b). These glands are

simple and extend deeply to reach the *mucosae muscularis*. Between them displays the *lamina propria* which consists of loose connective tissue. In *D. albiventris* and *Monodelphis dimidiata*, the entire mucosa coat has folds which have an axis of muscular mucous fibres, while in *L. halli*, the folds have the two coats: mucous and submucous membranes.

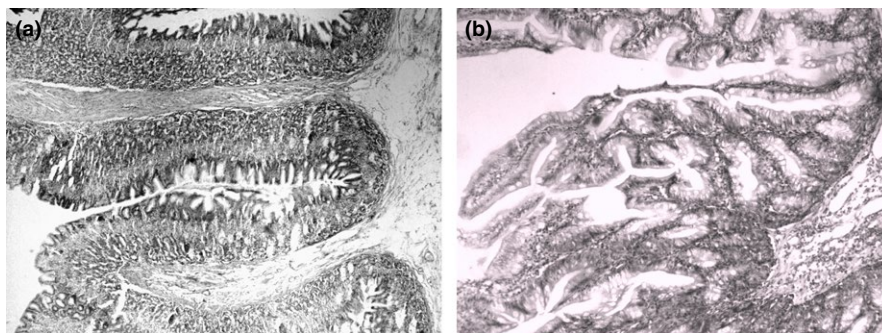


FIGURE 3 (a) *Didelphis albiventris*, stomach (fundus), mucous membrane and submucosa, H-E, 4x. (b) *Didelphis albiventris*, duodenum, mucous membrane, H-E, 10X [Colour figure can be viewed at wileyonlinelibrary.com]

The fundic glands have three portions: a basal region, a middle region and an upper isthmus. In the isthmus, only surface epithelial cells and parietal cells are present. In the middle region, the main cell type is the mucous neck cell, very abundant, between which parietal cells are displayed. The basal portion is mostly composed of main cells with some parietal cells.

The *mucosae muscularis* is relatively thin; a few slips from it extend into the *lamina propria* between gastric glands up to the gastric folds.

The submucosa tunic is made out of a relatively dense fibroconnective tissue.

The muscular coat in *D. albiventris* has two layers of smooth muscle, the inner one being thick and circular, and the outer one thinner and longitudinal. *M. dimidiata* and *L. halli* show a similar pattern, with layers having the same thickness (Figure 4a).

The serous of *D. albiventris* consists of layer of loose areolar tissue covered by a simple, cuboidal epithelium: the peritoneum (Figure 5). In turn, in *M. dimidiata* and *L. halli*, it consists of a squamous mesothelial layer.

3.3 | Gut

The small intestine extends from the pyloric orifice to the large intestine. It is divided into three parts with the similar histological structure: the first is the duodenum, and the remainder is divided into the jejunum and the ileum.

3.4 | Duodenum

In the three species, the duodenum has a *mucosae membrane* with villi and crypts. The epithelium is simple and

columnar, with scattered goblet cells. In *D. albiventris*, these goblet cells are abundant and then increase in number along the digestive tract. The villi are long projections of the mucous membrane which are covered by the epithelium and have a core of *lamina propria* and *muscularis mucosae*. The crypts or glands of Lieberkuhn are short tube-like structures opening between the bases of villi. The *lamina propria* extends between the crypts and into the cores of villi. It shows lymphocyte infiltration. The *muscularis mucosae* have two layers of muscle cells: an inner one, circular, and an outer one, longitudinal (Figure 3b). Only in *L. halli*, we could observe large folds and short crypts in the mucosae membrane. The muscles of the “small intestine” increase in thickness posteriorly in the caudal direction.

The submucosa coat is composed of fibroconnective tissue; Brunner's glands are absent in *D. albiventris* and *M. dimidiata*, while they are present in *L. halli*.

The muscular coat consists of two well-defined layers of smooth muscle, an inner one, circular, and an outer one, longitudinal.

The serous coat in *D. albiventris*, as we observed in the stomach, consists of loose connective tissue covered by a simple cuboidal epithelium (Figure 5). In *M. dimidiata* and *L. halli*, the cover is a squamous mesothelial layer.

3.5 | Jejunum and ileum

The three species have similar features as in the duodenum. The epithelium in *D. albiventris* has less goblet cells; *M. dimidiata* has the same amount, while *L. halli* has a larger number of goblet glands than in the duodenum (Figure 6a).

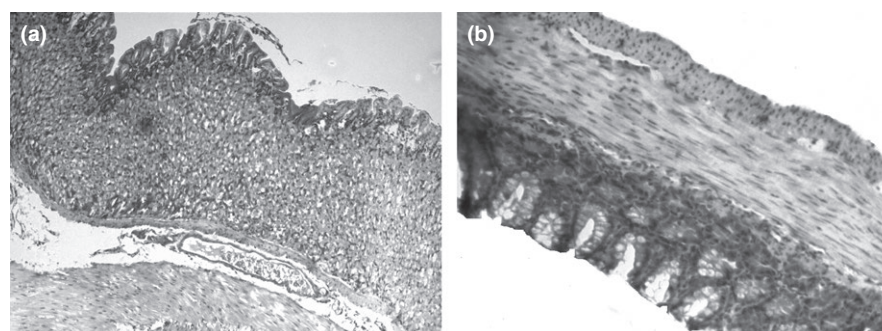


FIGURE 4 (a) *Monodelphis dimidiata*, stomach (fundus), mucous membrane, submucosa and muscular coat, H-E, 10x. (b) *Monodelphis dimidiata*, colon, mucous membrane (lacking villi), submucosa and muscular coat, H-E, 10x

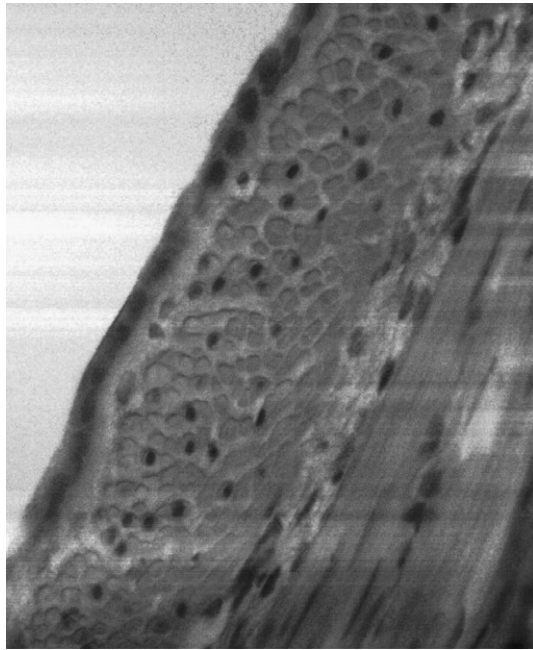


FIGURE 5 *Didelphis albiventris*, stomach and duodenum, serous coat covered by a simple cuboidal epithelium, H-E, 40x

3.6 | Colon

The mucosae membrane of *D. albiventris* has very short and scarce villi (Figure 6b), which are absent in *M. dimidiata* and *L. halli*. In the three species, the crypts are short. These coats form folds with an axis of connective tissue in the three species. In *L. halli*, the goblet cells are more abundant than the small intestine. The rest of the coats are similar to those described for the small intestine (Figure 4b).

4 | DISCUSSION

For this study, we selected three South American species, representative of quite different body sizes, adaptations and life histories. *Didelphis albiventris* Lund, 1840, the White-eared Opossum is widely distributed in peri-Amazonian, forested or open environments from south-eastern Brazil to central Argentina (Cerqueira & Tribe, 2008). The species

has one of the largest sizes among living New World marsupials (500–2,000 g of body mass); it has scansorial habits, an opportunistic, omnivorous diet, and it is nocturnal. *M. dimidiata* Wagner, 1847 (the Yellow-sided, Short-tailed Opossum) inhabits mostly open, grassland environments of the Pampean phytogeographic province, ranging from central and northern Argentina to Uruguay and south-eastern Brazil (Brown, 2004; Pine & Handley, 2008). It is small-sized (40–84 g), cursorial, insectivorous and diurnal to crepuscular in habits. Finally, *L. halli* Thomas, 1921 (the Patagonian Opossum) is the southernmost living opossum, ranging from central to southern Argentina (Santa Cruz Province; Martin, De Santis, & Moreira, 2008). This small-sized species (60–90 g) has low-density populations and inhabits mostly xeric, bushy environments (Patagonian and Monte phytogeographic provinces). It is nocturnal, terrestrial, probably also semifossorial and has a faunivorous diet consisting mostly of small vertebrates (especially rodents) and arthropods (Martin & Udrizar Sauthier, 2011; Martin et al., 2008; Zapata, Procopio, Travaini, & Rodríguez, 2013).

It is striking that, even though most mammals have a simple squamous epithelium in the serosa membrane (peritoneum), the serosa of *D. albiventris* has an epithelium of cuboidal simple cells throughout all the digestive tract. Whether this is a unique feature of *D. albiventris* or it is present in other South American marsupials is still unknown.

In the oesophagus of *D. albiventris*, we observed in the submucosa glands throughout the organ, while in *Monodelphis*, the submucosal glands appear only in the first third of this organ. These findings could be due to the different diets in both species. *D. albiventris* has a strongly seasonal, opportunistic diet which includes many items, from fruit to insects, small vertebrates; seeds, sap, etc. (see Cáceres, 2002; Rodrigues da Silva, Dias Forneck, Loretto Bordignon, & Vargas Cademartori, 2014; and literature cited). On the other hand, *Monodelphis* and *Lestodelphys* have more insectivorous and carnivorous diets, respectively.

The muscular coat has two layers of smooth muscle. Contrary to this, the oesophagus of *Marmosa robinsoni* (Didelphidae) shows three muscle layers and no mucous glands; it contains striated muscle in its initial segment, which is replaced by smooth muscle caudal to the trachea (Barnes, 1977).

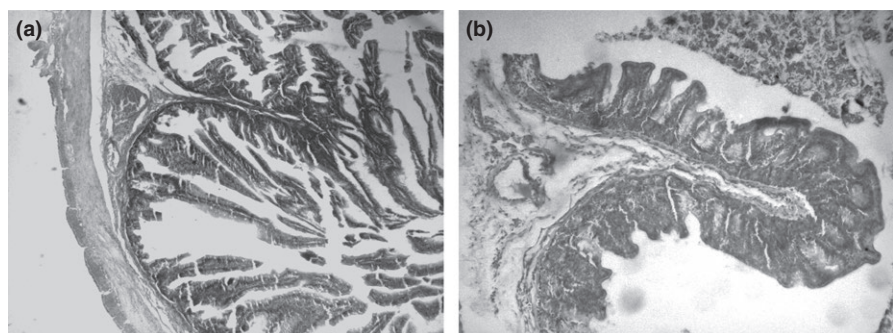


FIGURE 6 (a) *Didelphis albiventris*, jejunum (general view), H-E, 4x. (b) *Didelphis albiventris*, colon, H-E, 10x

The stomach of the three species study in this work has the same characteristic as the *Caenolestes*, which present a stomach lined with a tall columnar epithelium. The cardiogastric and gastric regions contain a large number of enzyme-producing chief cells and hydrochloric acid-producing parietal cells, most of them in the cardiogastric glands (Richardson, Bowden, & Myers, 1987).

The duodenum of *D. albiventris* and *M. dimidiata* lacks Brunner's glands, while they are present in *Lestodelphys*; in contrast, there are many goblet cells in the first two species. It could be argued that these cells replace the activity of the secretion of Brunner's glands. An explanatory framework of their absence in the former species requires a larger taxonomic sample to be analysed.

The colon of *D. albiventris* has short villi, while *Monodelphis* and *Lestodelphys* lack them, like most other mammals. It could be argued that the overall intestinal length in *D. albiventris* is proportionally shorter, relative to its body size, than in other didelphids; therefore, the villi would provide extra surface for intestinal absorption.

Barnes (1977:402) state that the caecum of *Marmosa robinsoni* is "... histologically identical to the upper colon." Its mucosa is formed by crypts lined with abundant goblet cells, as in *Lestodelphys*, and the villi are absent, as it happens in *Monodelphis* and *Lestodelphys*.

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