Comparative Intestinal Histomorphology of Five Species of Phyllostomid Bats (Phyllostomidae, Microchiroptera): Ecomorphological Relations with Alimentary Habits

Histomorfometria Comparativa de Intestino de Cinco Espécies de Murciélagos Phyllostomídeos (Phyllostomidae, Microchiroptera): Relaciones Ecomorfológicas con Hábitos Alimentarios

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SUMMARY: The intestines of *Sturnira lilium*, *Phyllostomus hastatus*, *Carollia perspicillata*, *Glossophaga soricina* and *Desmodus rotundus* were analyzed through macroscopic, morphometric and light microscopy studies. The species studied presented some common characteristics generally found in bats, such as the absence of a caecum and an appendix. The frugivorous bat *S. lilium* has a longer intestine than the other species. The intestinal epithelium is of the simple columnar type, constituted of absorptive cells characterized by microvilli and goblet cells, which in all the species proved to be PAS + and AB +. These cells presented some differences in quantity and in distribution among the species. The intestinal mucosa presented morphologic and morphometric differences, such as the shape and size of villi as well as the length of the crypts of Lieberkühn. Histologically the different intestinal portions could be distinguished: in the middle portion we found few goblet cells and long villi; in the distal portion we found an increase in goblet cells and a decrease in villi height; and in the large intestine no villi were found, but rather abundant intestinal glands with numerous goblet cells. In *C. perspicillata*, *P. hastatus* and *G. soricina* we could observe Peyer's patches in the distal portion near the large intestine, whereas in *D. rotundus* and *S. lilium* we found aggregations of lymphoid nodulous tissue distributed along the tube. In all species we observed the presence of Paneth cells at the base of the crypts of Lieberkühn. We could observe differences among the species in the distribution of collagen in the small intestine submucosa and serosa. The outer muscular layer has one circular layer and a longitudinal layer, the circular layer increasing in thickness along the tube. Large intestine characteristics are uniform among the species. Structures such as the taenia coli and the appendices epiploicae were absent. These results should contribute not only to improve understanding of bat morphology, but also to provide grounds for the evaluation of evolutionary models on the adaptive radiation of phyllostomid feeding habits.

KEY WORDS: Intestines; Bats; Phyllostomidae; Histology; Histochemistry; Micrometry; Ecomorphology.

INTRODUCTION

The family Phyllostomidae, endemic to the Americas, constitutes the most diverse and most widely distributed family of Neotropical bats. It is represented by the New World leaf-nosed bats, and is considered the third biggest family of Chiroptera, with 50 genera and 145 species grouped in several subfamilies and tribes (Koopman, 1993; Giménez, 1998). The evolutionary history of these bats is marked by a great adaptive radiation associated with feeding habits, including

insectivorous, frugivorous, nectarivorous, carnivorous, omnivorous and sanguivorous diets (Gardner, 1977).

The first detailed study of the chiropteran gastrointestinal tract morphology dates from the end of the 19th century. Robin (1881) presented information which was new for the time, in addition to an excellent review of the literature published until then. In the 20th century, advances

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in histological techniques and the betterment of microscopes led to a boom in microscopic studies.

The macro- and microscopic (histological) anatomies of the gastrointestinal tract or its parts have been well reported for numerous species of Microchiroptera, e.g. Schultz (1965); Rouck & Glass (1970); Forman (1971, 1972, 1973), Kamiya & Pirlot (1975); Madkour (1977); Okon (1977); Forman *et al.* (1979); Ishikawa *et al.* (1985). However, these works represent a scarce body of information, in view of the as yet unstudied diversity of Neotropical chiropterans.

Although there is a body of literature dealing with morphological descriptions of the chiropteran gastrointestinal tracts, it is not only insufficient, but in addition almost totally lacking in a comparative analysis consistent with the existing diversity of food habits.

Comparative analysis of chiropteran gastrointestinal tract morphology can undoubtedly evidence important features to further our knowledge on the phylogenetic relations of this group, as well as to better understand the evolutionary process as a whole, by means of comparative data on the relation between adaptative radiation and availability of resources in the environment (Forman *et al.*). These comparative studies can additionally subsidize hypotheses for the understanding of the relations between feeding habits and the digestive physiology of Neotropical bats (Bhide, 1979).

In the present work we carried out a comparative study on the intestine histomorphology of five representatives of family Phyllostomidae, so as to acquire more knowledge on the structural components which make up these tissues. Such results will contribute to a better understanding of these bats' ecomorphology and thus provide grounds to assess evolutionary models on the adaptative radiation of phyllostomid feeding habits.

MATERIAL AND METHOD

We studied 54 bats representing the 5 Phyllostomidae subfamilies: *Sturnira lilium*, *frugivorous* (Stenodermatinae); *Phyllostomus hastatus*, *omnivorous* (Phyllostominae); *Carollia perspicillata*, *frugivorous*, but also insectivorous (Carollinae); *Glossophaga soricina*, nectar-polinivorous, but also consuming insects and fruits (Glossophaginae); and *Desmodus rotundus*, *sanguivorous* (Desmodontinae). These animals were captured in a joint effort with the team of researchers from the Laboratory of Mammalian Systematics and Evolution from the National Museum/UFRJ, through collections carried out in Carmo Municipality, Rio de Janeiro

State (July 1999/ October and November 1999), and in Serra da Bodoquena and Bonito regions in Mato Grosso do Sul State (July 2000 / January and February 2001).

Samples of the gastrointestinal tract for microscopic study were obtained following a protocol consisting of anesthesia, sorting, weighing, measuring and dissecting. The abdominal cavity was opened through a ventromedian incision beginning roughly at 1 cm from the external genitalia and extending to the cervical region, followed by two lateral incisions towards the anterior and posterior limbs. The entire gastrointestinal tract was removed, sectioned into its anatomic portions, and washed in biological saline. Samples of the small and large intestines were cut out and fixed in buffered 10% formalin (24 to 48 hours), followed by routine histological technique down to final embedding in paraffin. The material was sectioned into 5- μ m slices in a microtome and stained by the routine haematoxylin and eosin staining technique and by the PAS, Alcian-blue pH 2.5 and Picrosirius red histochemical techniques.

The animals were fixed in 10% formalin, stored in 70% alcohol and placed in the scientific collection of the Mastozoology Sector at the National Museum/ UFRJ.

For morphometric analyses the Image Pro Plus software (Media Cybernetics, USA) was used.

RESULTS

Macroscopic study. The intestine of all species studied showed itself displaced to the right within the abdominal cavity, presenting itself extremely curved (Fig. 1A, B). In *D. rotundus* this curvature is less noticeable, and the largest part of the intestine is folded back upon itself in a compact series of numerous winding folds (Fig. 1C).

On analyzing the intestine macroscopically we could not distinguish the delimitation between the small and large intestines, in spite of the presence of Peyer's patches. These can be small and difficult to visualize, as in *G. soricina*. In *S. lilium* and *D. rotundus* we found nodular lymphoid tissue aggregates distributed along the tube. The duodenum can be identified by its diameter, which is bigger than the rest of the gastrointestinal tract.

In *P. hastatus* and *C. perspicillata* we could observe an increase in the diameter of the junction of the small and large intestines, as a result of the presence of Peyer's patches at the end of the distal portion. The large intestines of the analyzed species have neither caeca nor appendices, consisting only of a descending colon.

Fig. 1. Photomacrograph of *Sturnira lilium* showing the (A) anatomic position of the intestine: displaced to the right within the abdominal cavity, extremely curved (B), in detail. Photomacrograph of *Desmodus rotundus* (C) presenting most of the intestine folded upon itself in a compact series of numerous winding folds.

The intestinal length varies greatly among the species: *S. lilium* possessing a very long intestine, *P. hastatus*, *D. rotundus* and *C. perspicillata* having intestines of moderate length, and *G. soricina* presenting a very short intestine. All measurements were related to body length (Table I).

If the intestine is cut open longitudinally, we observe a series of definite folds in its internal surface. These are Kerckring's folds, which generally run parallel to one another and occupy from half to two-thirds of the tube's perimeter. These folds include the mucosa and part of the submucosa. In the bats studied, these folds are absent in the upper region of the duodenum and in the distal portion as it approaches the colon.

Microscopic study. Histologically, the small intestine wall of the species studied is composed of the typical layers: mucosa, submucosa, muscularis mucosae and serosa.

We observed in all species a mucosa with villi covered by a simple columnar epithelium constituted of absorptive cells, characterized for possessing microvilli (Fig. 2). Scattered among the absorptive cells, the goblet cells can be found. In the middle portion they are less numerous, but distally they increase in number. *D. rotundus* presented fewer numbers of goblet cells throughout the small intestine than the other species.

Shape of villi of the intestinal mucosa presented differences among the species. *C.*

perspicillata presented fingerlike villi all over the small intestine, which were longer, arched and arranged in oblique rows in the middle portion, while distally their height decreased (Fig. 3A). In *P. hastatus* the villi are fingerlike, arched, oblique and long in the middle region (Fig. 3B) whereas, in the distal portion, they were short, more spaced and with not very sharp apices. *S. lilium* showed villi in two shapes, pyramidal in the middle-proximal portion of the duodenum (Fig. 3C), and fingerlike in the other portions (Fig. 3D). The villi are quite long in the middle portion and decrease in the distal portion. *G. soricina* showed a mucosa with compact, fingerlike villi (Fig. 3E), long in the middle portion and shorter in the distal portion. *D. rotundus* possesses pyramid-shaped villi (Fig. 3F), longer in the middle portion than in the distal portion.

Fig. 2. Photomicrograph of *Desmodus rotundus* mucosa with villi covered by a simple cylindrical epithelium (Ep) composed of absorptive cells, also known as enterocytes (E), characterized for having striated border (SB). Scattered among the absorptive cells are the goblet cells (GC) AB+ (AB 1000x). LP – lamina propria.

Table I. Mean ± SD intestinal length and body length of the analyzed species.

Species	n	Intestinal	Body length	Intestinal length/body
<i>C.perspici</i>	5	52.4 ± 12.9	142.6 ± 3.3	2.7
<i>D.</i>	5	76.9 ± 13.9	208.5 ± 4.6	2.7
<i>G.</i>	5	52.6 ± 6.5	99.8 ± 1.7	1.9
<i>S. lilium</i>	5	59.7 ± 24.5	209.6 ± 1.7	3.5
<i>P.</i>	5	96.7 ± 9.9	265.6 ± 4.1	2.7

Fig. 3. Villi patterns. (A) *Carollia perspicillata*, villi fingerlike, long, arched and arranged in oblique rows (H&E 100x). (B) *Phyllostomus hastatus*, villi fingerlike, arched, oblique and long in the middle region (H&E 100x). (C) *Sturnira lilium*, villi in two shapes, pyramidal in the middle portion close to the duodenum (PAS 100x) and (D) fingerlike in the other portions (H&E 100x). (E) *Glossophaga soricina*, mucosa with compact and fingerlike villi (H&E 100x). (F) *Desmodus rotundus*, villi with very sharp apices (H&E 100x).

Fig. 4. (A) Panoramic photomicrograph of the small intestine of *Desmodus rotundus* showing presence of Peyer's patches (PP) (H&E 10x). (B) Photomicrograph of *Carollia perspicillata* villi showing the presence of a central lacteal vessel (LV) in the lamina propria (LP) and goblet cells (GC) PAS+ (PAS 400x). (C) Photomicrograph of the crypts of Lieberkühn (CL) of *Sturnira lilium* with Paneth cells (P) at the base. (H&E 400x). SB – striated border, Mm – muscularis mucosae, ICM – inner circular muscle layer, E – enterocytes, GC – goblet cell.

In the distal portion, next to the junction with the large intestine, we found clustered lymphatic nodules, forming the lumps called Peyer's patches (Fig. 4A). In the lamina propria of the villi we could see the presence of a discontinuous lacteal vessel, a central lymphatic vessel (Fig. 4B).

Among the villi we found simple tubular glands, the crypts of Lieberkühn (Fig. 4C). These glands are separated by the conjunctive tissue of the lamina propria and their extremities reach the muscularis mucosae. In all the studied species we found, deep in the crypts of Lieberkühn, groups of granular cells known as Paneth cells (Fig. 4C).

Goblet cells were also found in the crypts and, as in the villi, they increase in number in the distal portion. *C. perspicillata* distally presented few goblet cells in its crypts, being more concentrated in the villi (Fig. 4B).

The muscularis mucosae is a very thin tissue layer, and we could not visualize it in the middle portion, but distally it was a little thicker. The submucosa proved to be formed by slack conjunctive tissue possessing blood and lymphatic vessels. In *D. rotundus* the submucosa was denser than in the other species (Fig. 5).

Fig. 5. Photomicrograph of the small intestine showing (A) the very thin submucosa (SM) of *Sturnira lilium* with blood vessels (BV) (HE 100x) and the (B) thicker submucosa of *Desmodus rotundus* (H&E 100x). ICM – inner circular muscle layer, GC – goblet cell, CL – crypts of Lieberkühn, OLM – outer longitudinal muscle layer.

The outer muscular layer is composed of two layers, one circular and another longitudinal. Between them we could visualize the myenteric plexus. In the middle portion the circular and longitudinal layers are very thin, but distally the circular layer becomes much thicker than the longitudinal one (Fig. 6).

Finally, we found the serosa which is the thin, outermost layer, formed by slack conjunctive tissue covered by a mesothelium.

The large intestine of the bats presented uniform characteristics, being formed by only a descending colon and

the rectum. All four layers were present: mucosa, submucosa, muscular and serosa.

The mucosa is smooth, without the presence of villi or folds as in the small intestine. The whole thickness of the mucosa is filled with intestinal glands (crypts of Lieberkühn) which are long, straight and tubular.

The superficial epithelium as well as the glands epithelium is of the simple columnar type and contains absorptive cells and innumerable goblet cells. The submucosa is formed by a slack conjunctive tissue containing blood vessels. The muscularis layer is divided in two, one very thick

Fig. 6. Large intestine of *Phyllostomus hastatus* in (A) a panoramic photomicrograph (PAS 10x) and (B) a photomicrograph. Note the absence of villi in the mucosa. The crypts of Lieberkühn (CL) occupy the entire mucosa. Numerous goblet cells (GC) are found and the inner circular muscular layer (ICM) is thicker than the outer longitudinal one (OLM) (H&E 100x). SM – submucosa.

Fig. 7. Photomicrographs of the small intestine of (A) *Phyllostomus hastatus*, showing abundant conjunctive tissue (CT) in the submucosa (SM) and of (B) *Carollia perspicillata*, showing scarce conjunctive tissue (CT) in the submucosa (SM) (Picro-sirius 100x). BV – blood vessels. (C) Photomicrographs of the large intestine of *Glossophaga soricina* showing abundant conjunctive tissue (CT) in the submucosa (SM) and around the blood vessels (BV). (Picro-sirius 400x).

and circular, and the other thin and longitudinal. The serosa is very thin, with abundant conjunctive tissue around the vessels.

Structures that are characteristic of the large intestines of mammals, like taeniae coli and appendices epiploicae, were not found in the species studied.

In the present work we used methods of routine staining as well as some special dyes (histochemistry). We used the Periodic Schiff Acid (PAS) to detect the presence of glycoproteins in the goblet cells of the small and large intestines. These cells tested positive for all regions of the small and large intestines of all studied species.

In all species the alcian blue pH 2.5 method tested positive for the carboxylated proteoglycans of the goblet cells all over the intestine (small and large).

The collagen distribution in the small intestine presented differences among species, being abundant in the submucosa and around the serosa vessels in *P. hastatus*, *G. soricina* and *D. rotundus*, but scarce in the submucosa of *C. perspicillata* and *S. lilium*. In the large intestine collagen was abundant in all species. This analysis was done using the picro-sirius method without polarization (Fig. 7A, B and C).

Under a polarized light we could notice the organization of the collagen network, which appeared to be type-I for being birefringent and displaying red-orange shades in the small and large intestine of all species studied.

The length of the crypts of Lieberkühn and of the villi both in the middle portion of the small intestine were morphometrically analyzed (Table II and III; Fig. 8). In *P. hastatus* the crypts were longer than in the other species, and in *D. rotundus* they were shortest (Table II and Fig. 8A). The villi presented differences in length. *S. lilium* and *C. perspicillata* presented longer villi than *P. hastatus*, *D. rotundus* and *G. soricina* (Table III and Fig. 8B).

Fig. 8. Morphometric values for each of the specimens studied, regarding (A) the crypts of Lieberkühn lengths (µm) and (B) villi length (µm). Cp (*Carollia perspicillata*), Dr (*Desmodus rotundus*), Gs (*Glossophaga soricina*), SI (*Sturnira lilium*), Ph (*Phyllostomus hastatus*).

Table II. Morphometric measurements of the Lieberkühn crypts lengths (µm).

Specimen	<i>Carollia</i>	<i>Desmodus rotundus</i>	<i>Glossophaga</i>	<i>Sturnira lilium</i>	<i>Phyllostomus</i>
	<i>perspicillata</i>		<i>soricina</i>		<i>hastatus</i>
1	172.792	79.499	155.580	119.477	424.286
2	147.999	146.956	168.801	124.504	536.448
3	144.177	108.335	342.970	188.853	688.676
4	-	-	-	-	548.211
Mean	154.989	111.597	222.450	144.278	549.405
SD	15.535	33.846	104.580	38.685	108.350

Table III. Morphometric measurements of villi length (µm).

Specimen	<i>Carollia</i>	<i>Desmodus rotundus</i>	<i>Glossophaga</i>	<i>Sturnira lilium</i>	<i>Phyllostomus</i>
	<i>perspicillata</i>		<i>soricina</i>		<i>hastatus</i>
1	568.800	368.520	338.230	564.860	423.360
2	509.050	424.070	273.080	594.030	334.020
3	444.620	396.290	415.080	564.000	445.340
4	-	-	-	-	326.430
Mean	507.490	396.293	342.130	574.296	382.287
SD	62.105	27.775	71.080	17.095	60.862

DISCUSSION

Intestines in the analyzed species are located in the same position as in the different species of Chiroptera studied by Park & Hall, (1951); Forman *et al.*; Tedman & Hall, (1985).

The intestine of *D. rotundus* is similar to that described by Forman *et al.*, displaying very little noticeable curving, while in the other species the shape was arched, as reported by Schultz, (1965).

Special techniques like light and scanning electron microscopy have been used to distinguish the different portions of bat intestines, e.g. by Okon (1977); Ishikawa *et al.* (1985); Tedman & Hall (1985); Makanya & Maina (1994); Makanya (1997), Makanya *et al.* (2001).

External morphology does not allow a clear distinction between the small and large intestines in all bat species. Tedman & Hall (1985) stated that the intestine of *Pteropus alecto* and *P. poliocephalus* is a continuous tube without separation between the small and large intestines. Forman, (1974a, b) states that the junction of the small and large intestine is formed by a small ampulla, resulting from

abundant lymphoid tissue (Peyer's patches). He revealed differences in the abundance, distribution and morphology of these tissues in phyllostomids which are possibly diet related. He also noted that frugivorous bats have more Peyer's patches than nectarivorous, carnivorous or insectivorous ones, and that they can occur anywhere along the tract. In insectivorous and carnivorous species, the patches are small, showing a low state of activity, and usually restricted to the ileum submucosa. In *S. lilium* and *D. rotundus* we noticed a greater number of aggregates of lymphoid nodular tissue, which are well distributed along the tract. In *P. hastatus* and *C. perspicillata* Peyer's patches were observed in the distal portion next to the large intestine, and the two portions of the intestine (small and large) could be distinguished. In *G. soricina* we could not visualize Peyer's patches externally, and so it was not possible to delimit the small/large intestine junction, as also observed by Ishikawa *et al.*, in the insectivorous bat *Myotis frater*.

The absence of the caecum and of the appendix is considered characteristic of the gastrointestinal tract of chiropterans (Tedman & Hall), another feature being the absence of the ascending and transverse colons, the large

intestine as a result being restricted to a descending short colon (Forman *et al.*). This absence is well described in the literature for several species of bats (e.g. Park & Hall, Ishikawa *et al.*; Tedman & Hall; Makanya & Maina; Makanya; Makanya *et al.*, 2001), and this also applies to all species studied in the present work.

Most bats have a smaller intestine than do terrestrial mammals of comparable size (Klite, 1965). Several comparisons of bat intestinal length measurements (Robin 1881; Eisentraut 1950, Park & Hall; Forman *et al.*; Tedman & Hall; Makanya) reveal that frugivorous species have a longer intestine, relative to body length, than species with other feeding habits.

Eisentraut, observed a great number of bat species with a variety of feeding habits and noted that those with intestines four times longer than the body were always frugivorous species. Among the species with a longer intestine were *Chiroderma villosum*, *Vampyrops vittatus* and several species of *Artibeus*. Vampire bats presented intestines of moderate length and insectivorous ones a short gastrointestinal tract. Comparable measurements were taken in this work and we noted that *S. lilium*, frugivorous, has a long intestine relative to body length. In *D. rotundus*, *P. hastatus* and *C. perspicillata* intestine length is moderate, and in *G. soricina* it is short. The latter is similar to the insectivorous species in that it supplements its diet with insects. The short intestine observed in this species is probably an adaptation to reduce weight for improving flight. Physiological studies made by Keegan (1975, 1977) indicated that long intestines would not hamper the flight of frugivorous bats, since food transit and absorption time is quite rapid.

The disposition of Kerckring's folds, absent in the upper region of the duodenum and in the distal portion as it approaches the colon, are similar to that generally found in mammals.

The gland of Brunner is easily found in the duodenum of bats, but the taenia coli and the appendices epiploicae are absent in the large intestines of the species analyzed in this work, as well as in the ones studied by Tedman & Hall; Makanya & Maina; Makanya; Makanya *et al.* (2001).

We can distinguish the intestine segments by the increase of the goblet cells and the absence of villi, which are typical of the chiropteran large intestine. The middle and distal portions can be distinguished by decrease of the villi and increase of the goblet cells in the distal portion, also observed by Ishikawa *et al.*; Tedman & Hall; Makanya & Maina in other species.

The villi of the small intestine mucosa presented differences, similar to the ones described by Mathis (1928); Schultz; Forman *et al.* The mucosa epithelium, similar to that found in other mammals, is of the simple columnar type, which was also observed in *Myotis frater* by Ishikawa *et al.*, in *Pteropus alecto* and *P. poliocephalus* by Tedman & Hall and in *Epomophorus wahlbergi* by Makanya *et al.* (2001).

The cell types found in the small intestine of the bats studied are basically the same found in mammals in general, i.e. absorptive cells which microvilli and goblet cells which become more numerous along the tube. This was observed in other species of bats by Ishikawa *et al.*; Tedman & Hall; Makanya & Maina; Makanya; Makanya *et al.* (1995, 2001). *D. rotundus* presented less goblet cells than the other species, a fact also observed in *Pteropus alecto* by Tedman & Hall. This can be associated to the type of food consumed, which is liquid and easily absorbed. *D. rotundus* is sanguivorous.

Paneth cells were observed by Schaaf (1970) in the insectivorous species group: *Artibeus jamaicensis*, *Bachyphylla nana*, *Phyllonycteris polyi* and *Monophyllus redmani*. These cells were also observed in all the analyzed species.

The presence of glycoproteins and carboxylated proteoglycans in goblet cells is a common characteristic in mammals, including man.

The muscularis mucosae and submucosa are not highly developed in the species here described, a fact also observed in *Myotis frater* by Ishikawa *et al.*, but blood and lymphatic vessels were well observed in the submucosa. In *D. rotundus* this layer was thicker than the others, a characteristic previously observed by Forman *et al.*, in vampire bats.

Many characteristics generally found in mammals were also seen in bats, such as the presence of central lacteals in the lamina propria of the villi, and an outer muscular layer composed of a circular and a longitudinal layer, the former increasing in thickness as it approaches the large intestine. A myoenteric plexus was observed between them and the outermost layer, the serosa, was formed by slack conjunctive tissue covered by a mesothelium.

The presence of collagen fibers in the intestine of mammals is common. It is believed that in the large intestine this collagen layer regulates the transport of substances which are absorbed. In the small and large intestines of all studied species a dense collagen network was found, seemingly of type I. The characteristics of the large intestine are uniform in the studied species, as well as in the ones already described in the literature.

Morphometric studies of the bat gastrointestinal tract are scarce in the literature. These studies are essential to determine important functional parameters, such as the absorption surface area available in different kinds of bats.

We may conclude that the patterns of morphological variation observed in the small intestine suggest adaptations to the different feeding habits of the bat species here studied. These results can be used as a new and promising systematic approach for formulating rules of variation concerning the histological patterns observed, to corroborate existing hypotheses or to create grounds for new studies.

List of specimens used.

- *Phyllostomus hastatus* (Subfamily Phyllostominae): MN 56210, MN 56233, MN 56234, MN 56235, MN 56236, MN 56238, MN 59715, MN 59835.
- *Carollia perspicillata* (Subfamily Carolliinae): MN 56262, MN 56289, MN 56292, MN 56293, MN 56324, MN 56352, MN 59694, MN 59696, MN 59721, MN 59732, MN 59739, MN 59803, MN 59810.
- *Desmodus rotundus* (Subfamily Desmodontinae): MN 56164, MN 56190, MN 59710, MN 59711; MN 59724, MN 59743, MN 59766, MN 59778; MN 59823; MN 59830.
- *Sturnira lilium* (Subfamily Stenoderminae): MN 56186, MN 56194, MN 56342, MN 56344, MN 56345, MN 59697, MN 59716, MN 59749, MN 59750, MN 59755, MN 59761, MN 59817.
- *Glossophaga soricina* (Subfamily Glossophaginae):

MN 56156, MN 56157, MN 56278, MN 56278, MN 56302, MN 56308, MN 56309, MN 56310, MN 56333, MN 56335, MN 59758.

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GADELHA-ALVES, R.; ROZENSZTRANCH, A. M. S. & ROCHA-BARBOSA, O. Histomorfometría comparativa de intestino de cinco especies de murciélagos phyllostomideos (phyllostomidae, microchiroptera): relaciones ecomorfológicas con hábitos alimentarios. *Int. J. Morphol.*, 26(3):591-602, 2008

RESUMEN: Los intestinos de *Sturnira azucenas*, *Phyllostomus hastatus*, *Carollia perspicillata*, *Glossophaga soricina* y *Desmodus rotundus* se analizaron a través de estudios macroscópicos, morfométricos y de microscopía de luz. Las especies estudiadas presentan algunas características comunes en general encontradas en murciélagos, tales como la ausencia de un ciego y un apéndice. Murciélagos frugívoros *S. azucenas* tienen un intestino más largo que el de otras especies. El epitelio intestinal es de tipo columnar simple, constituido por células de absorción que se caracterizan por microvellosidades y células caliciformes, que en todas las especies resultó ser PAS + y AB +. Estas células presentan algunas diferencias en cantidad y en la distribución entre las especies. La mucosa intestinal presenta diferencias morfológicas y morfométricas, como la forma y el tamaño de las vellosidades, así como la longitud de las criptas de Lieberkühn. Histológicamente las diferentes partes intestinales pueden ser distinguidas: en la parte media encontramos pocas células caliciformes y largas vellosidades, en la porción distal encontramos un aumento de células caliciformes y una disminución en la altura de vellosidades, y en el intestino grueso no se encontraron vellosidades, sino más bien abundantes glándulas intestinales con numerosas células caliciformes. En *C. perspicillata*, *P. hastatus* y *G. soricina* podemos observar placas de Peyer en la porción distal, cerca del intestino grueso, mientras que en *D. rotundus* y *S. azucenas* se encontraron agrupaciones de tejido linfóide nodular distribuido a lo largo del tubo. En todas las especies se observó la presencia de células Paneth en la base de las criptas de Lieberkühn. Hemos podido observar diferencias entre las especies en la distribución de colágeno en el intestino delgado y submucosa serosa. La capa muscular exterior tiene una capa circular y una capa longitudinal, la capa circular en el aumento de espesor a lo largo del tubo. Las características del intestino grueso son uniformes entre las especies. Estructuras como la taenia coli y los apéndices epiploicos estuvieron ausentes. Estos resultados deben contribuir no sólo a mejorar la comprensión de la morfología del murciélago, sino también para sentar las bases para la evaluación de los modelos evolutivos adaptativa de la radiación en los hábitos alimenticios de filostómidos.

PALABRAS CLAVE: Intestinos; Murciélagos; Phyllostomidae; Histología; Histoquímica; Micrometría; Ecomorfología.

REFERENCES

- Bhide, S. A. Observations on the anatomy, histology and histochemistry of the stomach of the vespertilionid bat *Miniopterus schreibersii* (Kuhl). *Proc. Indian Acad. Sci.*, 88b:1-12, 1979.
- Eisentraut, M. Die Ernährung der Fledermäuse (Microchiroptera). *Zool. Jahrb.*, 79:114-7, 1950.
- Forman, G. L. Gastric morphology in selected mormopid and glossophagine bats as related to systematic problems. *Trans. Illinois Acad. Sci.*, 64:273-82, 1971.
- Forman, G. L. Comparative morphological and histochemical studies of the stomachs of selected American bats. *Univ. Kansas Sci. Bull.*, 59:591-729, 1972.
- Forman, G. L. Studies of gastric morphology in North American Chiroptera (Emballonuridae, Noctilionidae, and Phyllostomatidae). *J. Mammal.*, 54:909-23, 1973.
- Forman, G. L. Comparative studies of organized gut-associated lymphoid tissue in mammals with diverse food habits. Distribution, size, and organization of Payer's patches in New World bats. *Trans. Illinois Acad. Sci.*, 67:152-6, 1974a.
- Forman, G. L. The structure of Peyer's patches and their associated nodules in New World bats in relation to food habits. *J. Mammal.*, 55:738-46, 1974b.
- Forman, G. L.; Phillips, A. J. & Rouk, C. S. *Alimentary tract*. p. 205-227. In: Baker, R.J., Jones Jr., J.K., Carter, D.C., eds. *Biology of bats of the New World Family Phyllostomatidae*. Part III. Spec. Publ. Mus. Texas Tech. Univ., 16:1-441, 1979.
- Gardner, A. L. *Feeding habits*. pp.293-350. In: Baker, R.J., Jones Jr., J. K., Carter, D.C., eds. *Biology of bats of the New World Family Phyllostomatidae*. Part II. Spec. Publ. Mus. Texas Tech. Univ., 13:1-364, 1977.
- Gimenez, E. A. *Análise cladística e sistemática da família Phyllostomidae e outros Noctionoidea (Mammalia: CHIROPTERA)*. PhD thesis. Botucatu, SP: Universidade Estadual Paulista, 1998. p168.
- Ishikawa, O. K.; Matoba, M.; Tanaka, H. & Ono, K. Anatomical study of the intestine of the insect feeder bat, *Myotis frater kaguae*. *J. Anat.*, 142:141-50, 1985.
- Kamiya, T. & Pirlot, P. Comparative gastric morphology of Old World bats. Part 1. In light microscopy. *J. Mammal. Soc. Jap.*, 6:145-54, 1975.
- Keegan, D. J. Aspects of absorption of fructose in *Rousettus aegypticus*. *S. Afri. J. Med. Sci.*, 40: 49-55, 1975.
- Keegan, D. J. Aspects of the assimilation of sugars by *Rousettus aegypticus*. *Comp. Biochem. Physiol. Part A Comp. Physiol.*, 58:349-52, 1977.
- Klite, P. D. Intestinal bacterial flora and transit time in three neotropical bat species. *J. Bacteriol.*, 90:375-9, 1965.
- Koopman K. F. Order Chiroptera In: Wilson D. E. & Reeder, D. M., eds. *Mammal species of the world: a taxonomic and geographic reference*. 2nd ed. Washington & London, Smithsonian Institution Press, 1993, pp.137-241.
- Madkour, G. A. A comparative study of certain features of the alimentary canal and disposition of the viscera in Egyptian bats. *Ann. Zool. (Agra)*, 13:63-81, 1977.
- Makanya, A. N. The morphology of the intestine of the entomophagous longfingered bat, *Miniopterus inflatus*: mucosal topography and possible landmarks. *Acta Biol. Hung.*, 48:15-27, 1997.
- Makanya, N. A. & Maina, J. N. The morphology of the intestine of the insectivorous horseshoe bat (*Rhinolophus hildebrandti*, Peters): a scanning electron and light microscopic study. *African J. Ecology*, 32(2):158-68, 1994.
- Makanya, A. N.; Mayhew, T. M. & Maina, J. N. Stereological methods for estimating the functional surfaces in the chiropteran small intestine. *J. Anat.*, 187:361-8, 1995.
- Makanya, A. N.; Self, T. J.; Warui, C. N. & Mwangi, D. K. Gut morphology and Morphometry in the epauletted Wahlberg's fruit bat (*Epomophorus Wahlbergi*, Sundervall, 1846). *Acta Biol. Hung.*, 52(1):75-89, 2001.
- Mathis, J. Beitrag Zur Kenntnis des Fledermausdarmes. *Z. Mikrosk. Anat. Forsch.*, 192(8):595-647, 1928.
- Okon, E. E. Functional anatomy of the alimentary canal in the fruit bat, *Eidolon helvum* and the insect bat, *Tadarida nigeriae*. *Acta Zool. (Stockh.)*, 58:83-93, 1977.

Park, H. & Hall, E. R. The gross anatomy of the tongues and stomachs of eight New World bats. *Trans. Kansas Acad. Sci.*, 54:64-72, 1951.

Robin, H. A. Recherches anatomiques sur les Mammifères de l'ordre des Chiropteres. *Ann. Sci. Nat. Zool.*, 12:1-180, 1881.

Rouk, C. S. & Glass, B. P. Comparative gastric histology of five North and Central American bats. *J. Mammal.*, 51:455-76, 1970.

Schaaf, V. P. Untersuchungen über das histochemische Verhalten der Panethschen Kornerzellen bei mittelamerikanischen Fledermausarten mit unterschiedlichen Ernährungsweisen. *Anat. Anz. Bd.*, 126:275-7, 1970.

Schultz, W. Studien über den Magen-Darm-Kanal der Chiropteren. *Z. Wiss. Zool.*, 171:240-391, 1965.

Tedman, R. A. & Hall, L. S. The morphology of the gastrointestinal tract and food transit time in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Aust. J. Zool.*, 33:625-40, 1985.

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