

# Histologic features of the gastrointestinal tract of *Laonastes aenigmamus* (Rodentia: Diatomyidae)

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## Abstract

We have carried out histological studies of the gastrointestinal tract of Laotian rock rat *Laonastes aenigmamus*. Most of the inner surface of the stomach is a cardiac region having reduced glands. Generally the cardiac glands are located near the esophagus. The esophagus and the ventricular groove are lined by keratinized stratified squamous epithelium. The region containing fundic (proper gastric) glands occupies a small area of the stomach. The maximum thickness of the gastrointestinal wall has been determined for the hindstomach and duodenum. The minimum wall thickness has been determined for ileum, colon, and cecum. In the large intestine, the glands are weakly developed and this can mean that there is not an active digestion in this gut site. Our results confirm the fact that foregut fermentation is crucial in digestion for this rodent. The topography of the regions, occupied by different types of mucosa in the stomach, has a convergent similarity to ones that are found in ruminant-like marsupials and points to similar adaptations to the consumption of plant foods. Owing to the small body mass of the rodents, the distribution of foregut fermentation is exceptionally rare in evolutionary history.

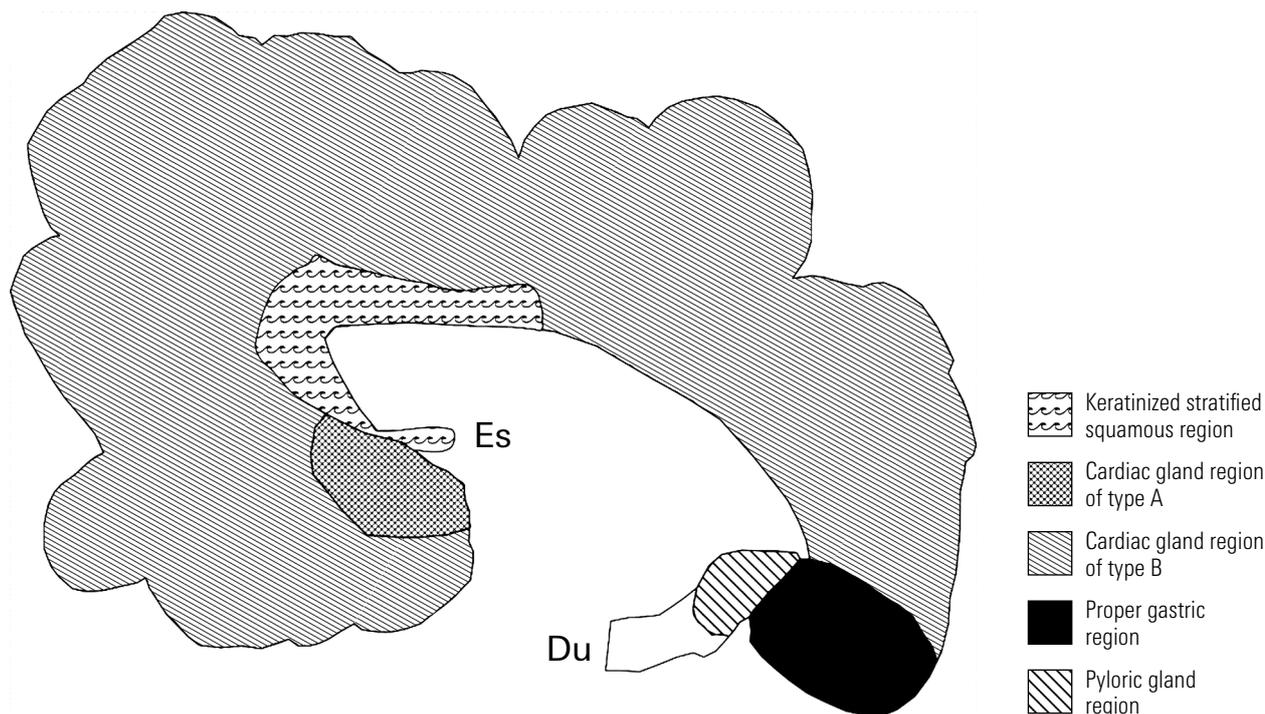
## Key words

Digestive system, anatomy, histometry, evolution, *Laonastes aenigmamus*.

## Introduction

The Rodentia is the largest of all mammalian orders that is characterized by wide morphological diversity of its constituent species occupying various ecological niches (MERRITT 2010). The forms and functions of the digestive system are not yet fully explored in rodents, despite the fact that the comparative morphology of the gut structures has been the subject of many reviews (TULLBERG 1899, GORGAS 1967, BEHMANN 1973, CARLETON 1973, VORONTSOV 1979, NAUMOVA 1981, LOVEGROVE 2010). Recently, a new enigmatic rodent – the Laotian rock rat *Laonastes aenigmamus* has been described (JENKINS *et al.* 2005). It differs significantly from all other members

of Rodentia and is considered a «living fossil» having sciurognathous and hystricognathous characters (JENKINS *et al.* 2005, DAWSON *et al.* 2006, HUCHON *et al.* 2007, HAUTIER *et al.* 2011, STEFEN 2011, HERREL *et al.* 2012, COX *et al.* 2013). «Living fossils» have always attracted the attention of scientists because their study sheds light on the origin and rates of evolution in the different taxonomic groups (JANIS 1984, FISHER 1990). Only the study of a «living fossil» can give an opportunity to explore the structures of the internal organs and their physiological significance in ancient animals. The digestive tract represents an evolutionarily conserved pattern in a certain



**Fig. 1.** Topography of epithelial regions in the stomach of *Laonastes aenigmamus*. (Es) – esophagus, (Du) – duodenum.

systematic group of mammals (GORGAS 1967, VORONTSOV 1979). The Laotian rock rat is the smallest foregut mammal possessing the enlarged stomach with a sacculated structure on the greater curvature. It is the unique digestive structure in rodents. To date, the gross anatomy of the digestive system was only described (SCOPIN *et al.* 2011; LAAKKONEN *et al.* 2014). However, to perform a detailed anatomical analysis of the digestive tract it is necessary to complement this with histological studies (LANGER 2002). Our study aimed to conduct the histological investigation of the digestive tract to obtain more information and to facilitate the understanding of the mechanisms of food fermentation in this rare rodent.

## Methods

Rock rats were procured from the food market in Khammouane Province of Lao PDR in 2008. We selected three animals, which had been dead for less than one hour. No pathological disorders were found in these individuals. The gastrointestinal tract was fixed in 70% ethanol immediately after the dissection. We cut off sections of esophagus, stomach, duodenum, jejunum, ileum, cecum, colon, and rectum. From each section we were obtained 10 to 25 samples. The histological specimens were prepared by standard methods using alcohol-xylene scheme and embedded in paraffin (BANCROFT & GAMBLE, 2002). The paraffin blocks were then dissected in the longitudinal and transverse planes. The slides for the micro-

scopic studies were stained by hematoxylin & eosin. For quantitative analysis we used metric parameters of *tunica mucosa*, *lamina muscularis mucosae*, *tela submucosa*, *tunica muscularis*, *tela subserosa*, *lymphonoduli solitarii*, *lymphonoduli aggregati*. We calculated the ratio of *tunica mucosa* : *tunica muscularis*. The stomach glands arrangement was drawn in accordance with the guide by STEVENS & HUME (1995). The measurements obtained from samples were then averaged within sections. The reliability of the results was determined by Student's test ( $t_{st}$ ) using Statistica 6.0. The nomenclature of the gastrointestinal tract was used in accordance with 'Nomina Anatomica Veterinaria' (2012).

## Results

Histological patterns of the digestive tract of *Laonastes* resemble those of other herbivorous mammals, but specific features have also been observed.

The luminal surface of the esophagus is lined by keratinized stratified squamous epithelium (KSSE). The average thickness of the keratinized layer of KSSE (the *stratum corneum*) is  $14.0 \pm 1.95\%$ , and the thickness of the nonkeratinized layer of KSSE (the *stratum basale* plus the *stratum spinosum*) is  $20.1 \pm 2.53\%$  of the thickness of the esophageal wall. *Lymphonoduli aggregati* are absent. There is *lamina muscularis mucosae* that is separated from *tunica muscularis* by *tela submucosa*. *Tunica muscularis* is represented by two layers of muscles. The

inner layer of the striated muscle is predominant. The average thickness of *tunica muscularis* is  $53.3 \pm 1.51\%$  of the thickness of the esophageal wall. The esophagus performs the transit of ingesta into the stomach.

The internal part of a stomach is lined by the various types of mucosa (Fig. 1). At the place where the esophagus enters into the stomach, the inner surface is lined by KSSE. The ventricular groove is also lined by KSSE. The main difference is that the thickness of a keratinized layer of KSSE is greater in the ventricular groove ( $18.92 \pm 2.61\%$  of the wall thickness) as compared with the esophagus, and conversely the thickness of a nonkeratinized layer of KSSE is significantly lower  $-13.17 \pm 0.95\%$  ( $t_{st} = 2.07$ ,  $P = 0.049$ ). The thickness of *tunica muscularis* is  $56.55 \pm 2.83\%$  of the wall thickness in the ventricular groove, this is not significantly different with the esophagus ( $t_{st} = 0.62$ ,  $P = 0.544$ ). The thickness of keratinized epithelium may indicate a high intensity of the passage of rough plant foods in this stomach region.

The main part of the stomach is a region of cardiac glands. The cardiac region is divided into two types - A and B. The cardiac region of type A (CRA) includes typical glands that are common for rodents. The CRA has a small area and is located around the *pars cardiaca*. This region has well-developed columnar glandular epithelium and wide *tunica mucosa* (Fig. 2a). The surface layer of epithelial cells is lined with a significant layer of lymphocytes. The average thickness of this layer is 6.0–6.5% of the height of the wall thickness (maximum - up to 13%). *Tunica muscularis* of the CRA consists of two muscle layers. In esophagus and CRA, there are thick *lamina muscularis mucosae*. In other sections of gut, the *tunica muscularis* was also present in only two layers.

The main part of the forestomach (sac-like compartments) is a cardiac region of type B (CRB). CRB is a kind of simplified and reduced part of CRA. CRB is located in *fundus ventriculi* and *corpus ventriculi*. It is lined with the glandular mucosa that is a complex of simple epithelial glands likely cardiac and fundic origin. In glands of CRB, parietal cells are virtually absent. In CRB the cardiac glands are prevail. These glands have the form of short tubes and are also covered with a layer of lymphocytes that demarcates the gut contents from the wall of the stomach. In *corpus ventriculi* there are glands without visually visible lumen that perhaps are reduced fundic glands. The glands of CRB are rarely distributed on the inner surface of the stomach and do not form a continuous layer (Fig. 2b). The glands can be absent in some parts of the CRB. As a consequence of the disappearance of cardiac glands within some parts of CRB, there is reduction of mucosa and *lamina muscularis mucosae* (Fig. 3, 4). The disappearance of the glands within the CRB was an evolutionary adaptation to reduce the secretion of enzymes that degrade the symbiotic microorganisms. Further histochemical studies may provide an answer to the origin of the glands of CRB.

*Corpus ventriculi* has two rows of large lymph patches (*lymphonoduli aggregati*) occupying a large area and it

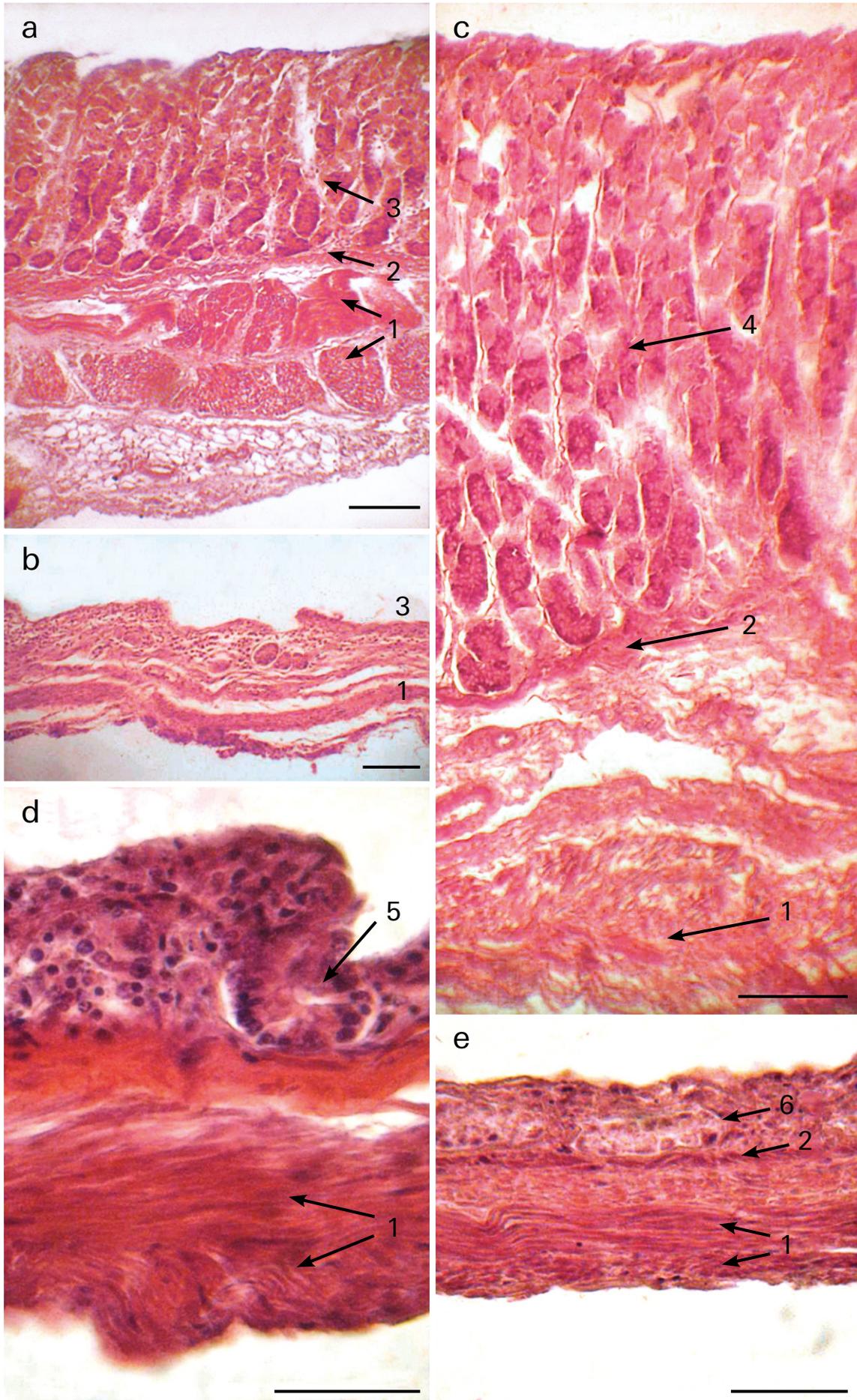
is an important organ for gut-associated lymphoid tissue (GALT). A feature of CRB is extremely low thickness of the gastric wall (Fig. 3). The thickness of the muscle layers, in the CRB, is  $22.23 \pm 1.17\%$  of the stomach wall. This is significantly less than in the CRA ( $t_{st} = -3.65$ ,  $p = 0.002$ ) and this suggests the possibility that the stomach wall significantly dilates at filling with ingesta.

Sac-lake compartments of the stomach are separated by *plicae*. *Plicae* are both temporary and permanent. The form and the thickness of *plicae* greatly vary. The network of *plicae* contribute to the maintenance of the form of a stomach and its affixing to the abdominal cavity. The first type of *plicae* is the temporary folds formed by the heterogeneity of the mucosa. These folds are able to stretch and can disappear. The second type is the permanent one-sided folds that always retain their form. They start from the lesser curvature and run along the stomach and are directed perpendicular to the side of the greater curvature, where they end. These folds often ramify near the greater curvature and this contributes to covering of a larger surface of the forestomach. The folds of the third type are the full permanent transverse folds. Both the beginning and the ends of which lie on the lesser curvature of the stomach i.e. the folds are located around the stomach in the transverse plane. These folds contains well-developed layer of *tunica muscularis*. The full permanent transverse folds have a wall thickness of  $533.45 \pm 19.84 \mu\text{m}$ , compared with the permanent one-sided folds ( $127.50 \pm 13.80 \mu\text{m}$ ). These differences are significant ( $t_{st} = 14.54$ ,  $p = 0.000$ ).

The main function of folds is to facilitate the transit of food and to maintain the internal volume of the stomach. The function of the full permanent transverse folds is an analogous to the function of taeniae that there are in other non-ruminant foregut fermenters. As *Laonastes* is a relatively small sized animal, the rapid evacuation of digesta from the stomach into the small intestine is an important task. The internal structure of the folds is formed of two muscle layers. The reduction in the thickness of stomach muscle layers contributes to the greater ability to dilate the stomach wall and correspondingly to the increase in the volume of ingesta entering into the stomach. This is an important for processes of microbial digestion.

The fundic (proper gastric) gland area occupies not more than 10% of the total area of the stomach (SCOPIN *et al.* 2011) depending on the stomach fullness and expansion of its walls. Mucosa is well developed (Fig. 2c, 3, 4). The thickness of the muscle layers is less than 10% of the whole wall. The fundic glands are characterized by a lot of parietal cells that are located in the apical part of *tunica mucosa*. The pyloric region is almost not expressed within the stomach. The region with pyloric-like glands is located in mainly in *ampulla duodeni*.

The structures of the small intestine of *Laonastes* resemble those in other herbivorous mammals. They perform one of the main roles in digestion. This section of the intestine has the most well developed layer of mucosa (Fig. 3, 4), which indicates that there is the intensive



absorption of nutrients here. The maximum wall thickness was shown in the duodenum. In the ileum, there is a sharp reduction of the mucosa. Both the duodenum and jejunum have a well developed GALT. There are a large number of *lymphonoduli aggregati* and *lymphonoduli solitarii*. In the jejunum, the number of *lymphonoduli aggregati* is huge, but it is less than in the stomach (Fig. 5). *Lymphonoduli solitarii* are large and interrupting *lamina muscularis mucosae*. In consequence of this fact, the lymphocytes penetrate into lumen through gastric pits.

The large intestine is characterized by a thinner wall than in other gut parts. The mucosa is underdeveloped, but its glands are present (Fig. 2d, 2e). Papillae are absent in the cecum and colon. The intestinal wall is an average of 15 times thinner in the colon than in the duodenum. In the colon, the mucosa is better developed but muscle layers are weaker comparing with the cecum (Fig. 3, 4). These differences are statistically significant ( $t = -2.11$ ,  $P = 0.05372$ ). Thus the colon and the cecum are not involved in the processes of active digestion. These gut sections are shortened in comparison to other parts of intestines (SCOPIN *et al.* 2011), and this promotes more rapid transit undigested food residues. There is thickening of the rectum wall mainly due to the development of musculature for the evacuation of feces.

## Discussion

### Adaptive significance of the gut structures

Any compartmentalization of the digestive tract of herbivorous mammals is necessary for the existence of symbiotic microorganisms that promote the digestion of food structural carbohydrates (LANGER 2002). In the course of evolutionary history, the voluminous mammalian forestomach as a core element of foregut fermentation appears repeatedly in different taxonomic groups. This convergence of the foregut structures has been noted in five groups of mammals (ungulates, sloths, some herbivorous marsupials, primates, and rodents) and is taken as an adaptation to herbivory (KARASOV & MARTINEZ DEL RIO 2007).

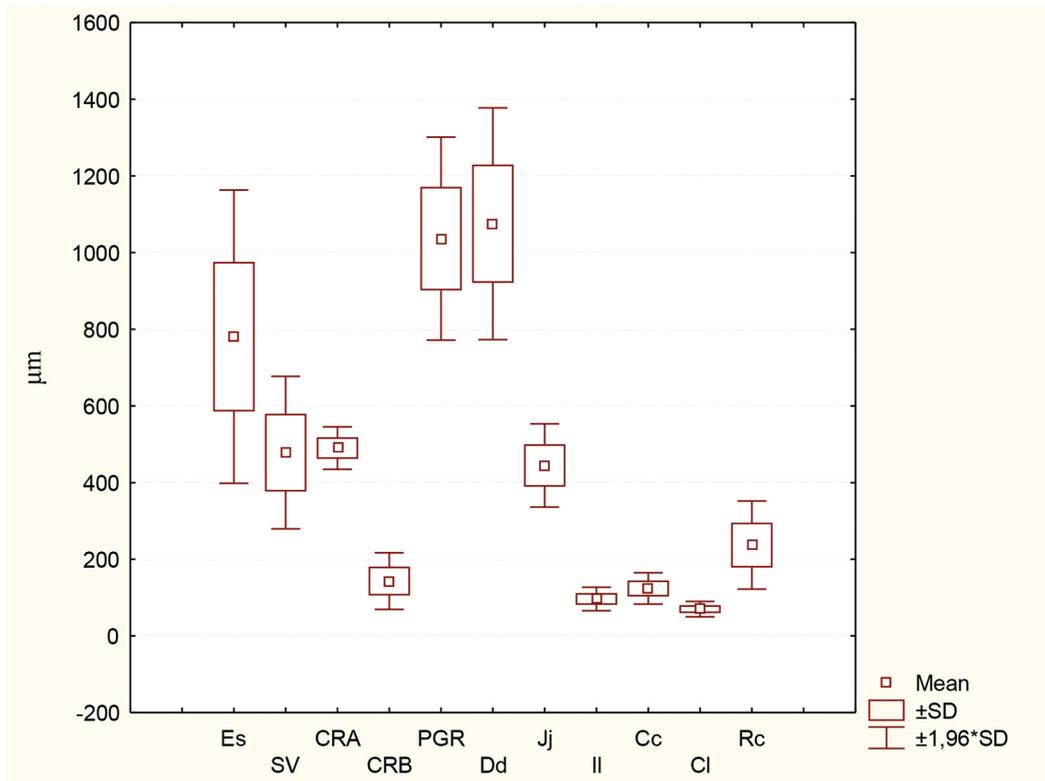
*Laonastes* is definitely a foregut fermenter with peculiar characteristics. Amongst other hystricognaths, it has long been known that there is the most developed stomach in *Mysateles melanurus* (DOBSON 1884), which is a plant-eating rodent. It feeds mostly on leaves, but it can also consume fruit and gnaws bark (SILVA *et al.* 2007). In the stomach of this rodent there is probably a partial

digestion of plant foods. Similar enzymatic and probably microbial activities take place in the foregut in some herbivorous cricetids and murids (KARASOV & MARTINEZ DEL RIO 2007). However, in all of these mammals, the stomach is not the primary digestive organ. In rodents, the hindgut fermentation is predominant. In the cecum and colon, the high activity of microbiota is accompanied by the increased size of this gut sites (STEVENS & HUME 1995). For example, in cricetids as hindgut fermenters, the colon has a thick layer of the mucosa and *tunica muscularis* (NAUMOVA 1981). In the hystricognathous rodent *Myocastor coypus*, the cecum is a large haustrated construction and the mucosa of the proximal colon has columnar epithelium with goblet cells (SNIPES *et al.* 1988). For *Laonastes* only the foregut fermentation is essential. There is no active digestion in the large intestine of *Laonastes*: within the cecum and colon, the glands are rare.

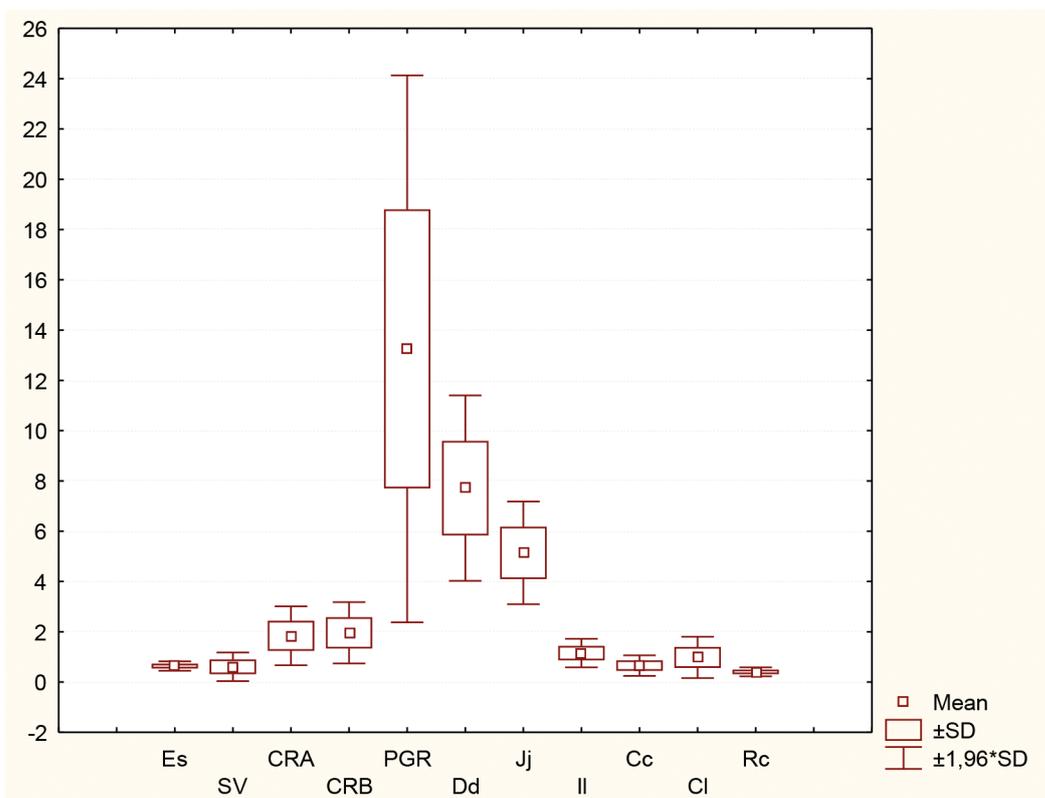
Surprisingly, the closest relative of *Laonastes* – *Ctenodactylus gundi* has a dissimilar digestive system. It has a simple unilocular stomach and large cecum (GORGAS 1967). The presence of a simple stomach is a reflection of the small body size and the reason why there is a limitation in the development of active foregut fermentation (KAY 1984, FLEAGLE 1988). Most likely, these gut differences have originated due to the specific niches occupied by these rodents. The gundi is a dweller of the deserts, where it is necessary to maintain water balance. Because of this, the gundi has a strongly developed large intestine, where there is high reabsorption of water and consequently the output of very dry pellets (GOUAT 1993). The hindgut fermentation is most effective when the diet contains large amounts of fibrous plant foods (KARASOV & MARTINEZ DEL RIO 2007) and this is a common component in desert communities. On the contrary, *Laonastes* lives in humid tropical forest. Feces of this rodent are soft, due to the lack of water reabsorption in the colon. This may be the consequence of the presence of a huge foregut. It is a fact that a large stomach confines the space available for the other organs of the viscera. Thereby the volume of colon and water-absorbing surface are reduced (CLAUSS *et al.* 2004).

The closest external resemblance to the stomach of *Laonastes* is found in marsupials. In the main, the topography and the sequence of the gland regions in the stomachs of ruminant-like marsupials (potorids and macropodids) (GEMMEL & ENGELHARDT 1977, HUME 1999) and *Laonastes* have a clear functional similarity. The order of gland distribution in sac-like compartments contributes to the activity of gut microbiota in the stomach of *Laonastes*. Microbial activity is high in the voluminous forestomachs (STEVENS & HUME, 1995). The main part of

← Fig. 2. Structures of some gastrointestinal regions of *Laonastes aenigmamus*. (a) cardiac region of type A (CRA) in the stomach; scale bar = 100  $\mu$ m. (b) cardiac region of type B (CRA) in the stomach; scale bar = 100  $\mu$ m. (c) proper gastric region in the stomach; scale bar = 100  $\mu$ m. (d) cecum; scale bar = 50  $\mu$ m. (e) colon; scale bar = 50  $\mu$ m. (1) *tunica muscularis*, (2) *lamina muscularis mucosae*, (3) cardiac glands, (4) proper gastric glands, (5) cecum glands, (6) colon glands.



**Fig. 3.** Thickness of the intestinal wall of *Laonastes aenigmamus* along the alimentary canal. (Es) – esophagus, (sv) – sulcus ventriculi, (CRA) – cardiac region of type A, (CRB) – cardiac region of type B, (PGR) – proper gastric (fundic) region of stomach, (Dd) – Duodenum, (Jj) – jejunum, (II) – ileum, (Cc) – cecum, (Cl) – colon, (Rc) – rectum.



**Fig. 4.** Ratio of *tunica mucosa* to *tunica muscularis* along the alimentary canal. (Es) – esophagus, (sv) – sulcus ventriculi, (CRA) – cardiac region of type A, (CRB) – cardiac region of type B, (PGR) – proper gastric (fundic) region of stomach, (Dd) – Duodenum, (Jj) – jejunum, (II) – ileum, (Cc) – cecum, (Cl) – colon, (Rc) – rectum.

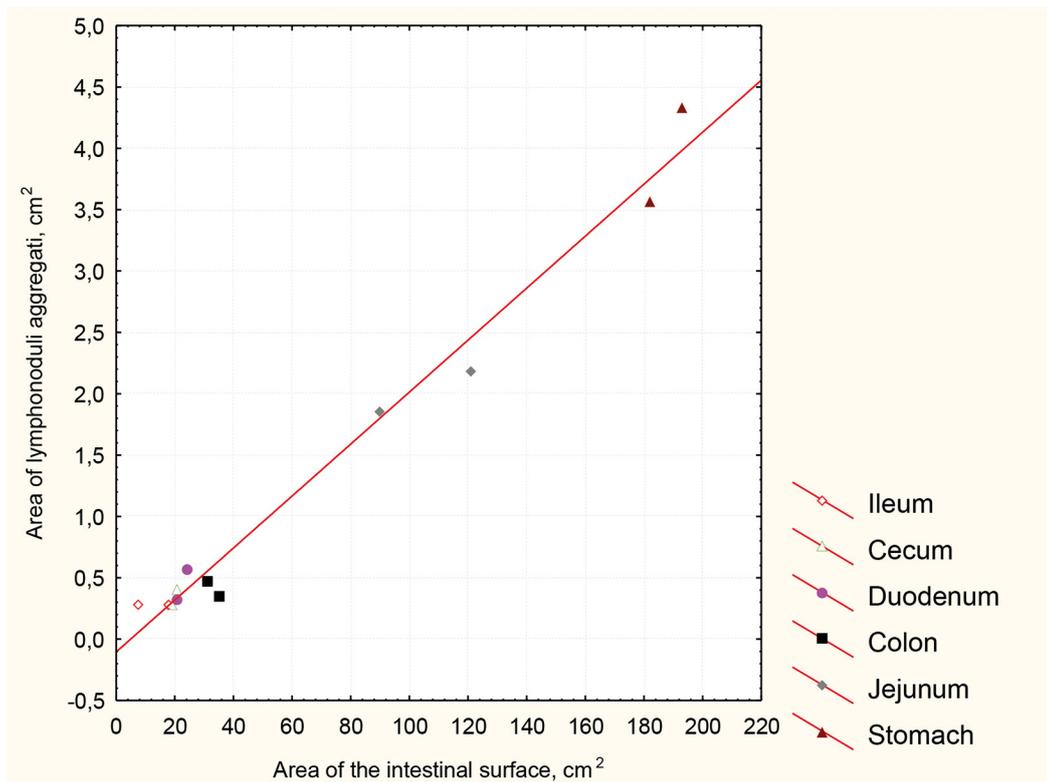


Fig. 5. The relationship between the lymph patches and the intestinal surface in *Laonastes aenigmamus*.

such forestomachs is the cardiac region that is common for non-ruminant foregut mammals: marsupials, camelids, suids (CUMMINGS *et al.* 1972, HUME 1999, LEUS *et al.* 1999, 2004). The existence of foregut fermentation in small mammals is aimed at selection of food with more nutrients; for example, highly soluble carbohydrates which can easily be absorbed directly into the stomach (BARBOZA *et al.* 2009). Moreover, the forestomach of various rodents has a set of amylases, lipases, chitinases to contribute the utilization of highly digestible nutrients of plant and animal origin (GARTNER 2001).

Additionally, the fundic region in *Laonastes* occupies only 10% of the stomach area to maintain microbial and enzymatic fermentation. A similar tendency was noted for ruminant-like marsupials where the fundic region is within 5.8–15.6 % of the stomach area (LANGER 1988). Probably in the Miocene when there was the wide diversification of mammalian herbivorous taxa, the similarity in the structure of the stomach arose because it was the most optimal adaptation to digest leaves and shoots of tropical plants through microbial fermentation (SCOPIN *et al.* 2011).

The presence of KSSE in the foregut is common for ungulates, ruminant-like marsupials and sloths (CHIVERS & HLADIK 1980, OBENDORF 1984, HOFMANN 1989). The esophagus and a large part of the stomach in many rodents are lined by stratified squamous epithelium (CARLETON 1981, NAUMOVA 1981). The variability of cornification (keratinization) may depend on the consumption of fibrous and rough diets (CARLETON 1973, VORONTSOV 1979,

EURELL & FRAPPIER 2006). However, in sciurognaths, the keratinized layer of KSSE is thinner (NAUMOVA 1981), than that in *Laonastes*. Perhaps, *Laonastes* eats rough forage. It has been noted that this rodent consumes dry leaves (LAAKKONEN *et al.* 2014). In ruminants, a thicker cornified layer is inherent to grazers (roughage eaters) and a thinner stomach cornification is inherent to concentrate selectors (HOFMANN 1989).

The cornification is absent in the cardiac region of *Laonastes*' stomach, except the ventricular groove. The ventricular groove plays an important role in the weaning period. But adult rats only have a vestigial ventricular groove. This may be explained by the fact that the weaning period is longer in small herbivorous mammals that produce large amounts of methane and require a long period for the settlement of gut bacterial microbiota, that it is especially true for histricognaths (LANGER 2002). The presence of a ventricular groove in the nonruminant mammalian herbivores (*Colobus*, *Dendrolagus*) is typical (BAUCHOP 1978). In many ways, the presence of stratified squamous epithelium is an adaptation to the preservation of food in the stomach of rodents (PERRIN & CURTIS 1980). For example, in *Lophiomys*, the sacculated stomach is lined by KSSE (NAUMOVA & ZHAROVA 2003).

We can assume that plant foods are not stored long in the sacculated stomach of *Laonastes*, because it is not lined by stratified squamous epithelium. Probably, the digestion in the stomach of the rat occurs mainly by amyolytic fermentation as is observed in the smallest ruminants: easily digestible substances are absorbed; un-

digested particles are quickly removed from the stomach (HOFMANN 1989). The active absorption of nutrients in the stomach is confirmed by the presence of *lymphonoduli aggregati*. However, the greatest degree of absorption is observed in the jejunum and duodenum. The *ampulla duodeni* has a great number of villi and is in essence a pyloric part of the stomach.

The gastrointestinal tract of *Laonastes* has a strong development of GALT, including a large number of Peyer's patches in the stomach and a small intestine (SCOPIN *et al.* 2011). GALT is developed in areas where there are the strongest antigenic effects on the body and therefore GALT plays a key role in a host defense (WILLIAMS 2012). Commensal microflora is of great importance in the development of mucosa-associated lymphoid tissue (RAKOFF-NAHOUM & MEDZHITOV 2006). Unlike *Laonastes*, Peyer's patches are absent in the stomach of *Mysateles melanurus*. In *M. melanurus* Peyer's patches appear in the duodenum and a lot of them, like other rodents, in the cecum (DOBSON 1884). Probably, in the stomach and small intestine of *Laonastes*, there are the most highly developed processes of intestinal nutrient absorption and neutralization of foreign microbes and plant toxins. Strong development of the lymphoid tissue and the presence of lymphocyte layer covering the luminal stomach surface implies strong exchange processes between the contents and the cell wall, and is also likely to contribute to microbial fermentation of ingesta. This helps to maintain acid-base balance of the digestive process and the tolerance to microbiota (NAUMOVA 1981, LENTLE & JANSSEN 2011, WILLIAMS 2012). Similar development of GALT in the stomach and the penetration of lymphocytes into lumen were observed only in the pyloric region of sciurognathous rodent - *Spermophilopsis leptodactylus* (NAUMOVA 1981). There is also GALT in nonruminant primate stomachs. But in the stomach of *Colobus*, *lymphonoduli aggregati* are not formed, and there are many diffusely located *lymphonoduli solitarii* which have large size, interrupting *lamina muscularis mucosae* that contributes to a strong immune protection of the mucosa (KUHN 1964).

The structure of intestinal muscles of *Laonastes* is a very interesting phenomenon. In *tunica muscularis*, there are two layers of muscles. For example, this pattern was noted for rodents from the family Bathyergidae (NAUMOVA 1981), Nesomyidae (MADDOCK & PERRIN 1981), Cricetidae (DEARDEN, 1969). However, in other rodents, including sciurognaths, the gut can have three muscle layers (NAUMOVA 1981). Two muscle layers within *tunica muscularis* plus *lamina muscularis mucosae* are typical for the esophagus of herbivorous macropodids (OBENDORF 1984). The body of sac-like compartments, that forms the stomach, has a thin wall that contributes to being stretched to a great extent. This fact was noted for other rodents (GENEST-VILLARD 1968). *Laonastes* as an herbivorous rodent must consume a lot of food. In general, the intake rate of dry food matter in foliage-eating herbivores is more than three times that of omnivorous mammals (McNAB 2002, KARASOV & MARTINEZ DEL RIO

2007). The folds facilitate the adjustment of the digesta passage in the stomach. The secretion of enzymes is reduced by weak development of the cardiac glands in sac-like compartments (CRB). A similar phenomenon occurs in ruminants where production of digestive gland components may be attenuated at the enlargement of the duodenum (KRAUSE 1981). It is probably need to maintain a pH environment in the stomach, which is important for the functioning of the microbiota, and also supports a longer effect of salivary amylases on the ingesta (CARLETON 1981). In rodents with a high level of herbivory, the reduction of the glandular mucosa has been observed (VORONTSOV 1979).

The stomach of *Laonastes* separated by the folds is similar to the enlarged forestomach (the sacciform and tubiform forestomach) of marsupials (LANGER 1988, HUME 1999). The stomach of these marsupials has been described as plurilocular and composite haustrated structure (LANGER 1988). However, this still does not mean that the stomach of *Laonastes* is a true multi-chambered stomach. There are no orifices between compartments in its forestomach and the sac-like compartments do not differ from each other by morphological features. The folds act as taeniae to preserve the form of a stomach and to affix it to an abdominal cavity (SCOPIN *et al.* 2011). There are no differences in the size of the food particles in sacculated compartments (LAAKKONEN *et al.* 2014). Interestingly, the particle-sorting mechanism is also poorly developed in other nonruminant mammals (SCHWARM *et al.* 2009). Nevertheless, the differentiation of food particles was observed in the stomach of *Lophiomys*, which is described as multi-chamber (NAUMOVA & ZHAROVA 2003).

In fact, the stomach of *Laonastes* is essentially a maximum modified construction of the unilocular-hemiglandular stomach by sacculatation. A unilocular-hemiglandular structure of the stomach is common amongst rodents (CARLETON 1981). If it can be taken into account that there is a division of the whole stomach into a few sac-like compartments by deep folds, as argued by LANGER (1988), then in accordance with this, the stomach of *Laonastes* must be plurilocular, because there are such permanent folds. The number of the compartments is 9 or 10 (SCOPIN *et al.* 2011). However, in herbivorous mammals, each of the chambers within a true multi-chamber stomach has specific morphological and physiological characteristics (LANGER 1988, DEHORITY 1997). On this basis the stomach of *Laonastes* can not be a truly multi-chamber in the strict sense. For example, the presence of the constant *plica praepyloricus* gives no ground to assume that a single-chamber stomach with such fold is to be considered as two-chambered (VORONTSOV 1979). In the stomach of *Lophiomys*, there are also many folds and it is difficult to determine the number of individual sacs. But there is nevertheless the presence of the ventricular groove which gives us the opportunity to consider the separate compartments as a whole chamber through which the ventricular groove is passing (NAUMOVA & ZHAROVA 2003). This position could be also considered

for *Laonastes*. If in foregut fermenters, the limitation of food intake is due to a multi-chamber stomach (CLAUSS *et al.* 2007), then, in small herbivorous mammals, the origin of any multi-chamber stomach could slow down a retention time of ingesta which would be incompatible with the maintenance of energy balance.

In *Laonastes*, the small intestine plays a significant role in the digestion and absorption of nutrients. Both the duodenum and jejunum have a considerable length and a large area of absorptive surface due to well-developed villi and the thick mucosa. This is common for mammalian foregut fermenters (STEVENS & HUME 1995). The active role of the large intestine is not so obvious in the digestive processes of *Laonastes*. They have reduced *tunica muscularis* and mucosa. The digestive glands often are absent. Therefore, it can be argued that these gut parts do not participate in active digestion. The cecum tissue reduction has also been observed in *Lophiomys* (NAUMOVA & ZHAROVA 2003). In nonruminant foregut marsupials, there are no villi in the hindgut, however the microbial fermentation is there (HUME 1999). On the other hand, in mammalian hindgut fermenters, the presence of villi, thick *tunica muscularis* and mucosa and GALT was noted. For example, these are the characteristic attributes for sciurognathous and hystricognathous rodents (BEHMANN, 1973, NAUMOVA 1981, GABELLA 1981, STANOJEVIC *et al.* 1982, SNIPES *et al.* 1982, 1988, KOTZE *et al.* 2009).

In general, in herbivorous rodents, the morphologic specialization of foregut structures occurs in different ways: by increase of the size and the complexity of an unilocular stomach (through increased forestomach) like in *Laonastes*, or by increase of the number of chambers in the stomach like in *Lophiomys* (NAUMOVA & ZHAROVA 2003) or by the development of the stomach papillae which are necessary for the attaching of symbiotic bacteria as in *Mystromys*, *Cricetomys* and *Tachyoryctes* (VORONTSOV 1979, PERRIN & KOKKIN 1986, KNIGHT & KNIGHT-ELOFF 1987, NAUMOVA *et al.* 1995).

Our results imply the greatest functional development of the stomach, duodenum, jejunum and confirm their important functional role in digestion. In these parts of the gut, the thickness of the intestinal wall and mucosa is the most developed, especially in the proper gastric region of the stomach (Fig. 3, 4). On the contrary, the minimum thickness of the intestinal wall is registered in the ileum, cecum, colon (Fig. 3, 4), which emphasizes the smaller importance of these sections in digestion.

## Remarks on foregut evolution in rodents

The diatomyids have originated in the Miocene (HUCHON *et al.* 2007, FLYNN & WESSELS 2013), although the beginning of the ancestral *Ctenodactyloidea* dates back to an earlier time – Eocene (FABRE *et al.* 2012). There is a great interest in the question – how prevalent was the foregut system amongst rodents? In general, foregut fermentation is not typical for this mammalian group.

Mismatch of the chemical composition of plant-based diet in the tropics and morpho-physiological structure of the digestive system in rodents leads to extremely low levels of food intake that does not exceed 10% of body weight per day (KUZNETSOV & NAUMOVA 2004). It would be interesting to determine the level of feed conversion in *Laonastes*, perhaps its foregut is more efficient at nutrition of tropical plant mass than in rodents with hindgut fermentation.

But there is the paradox that the efficiency of digestion in foregut fermenters only increases with increasing body weight, that changes the retention time of ingesta (MCNAB 2002). Maybe like other small folivorous mammals *Laonastes* maintain its energy balance by means of other more nutritious foods, like fruits or invertebrates, or it has a specific microflora. For example, the hamster *Lophiomys imhausi* has a voluminous stomach but it is not the main digestive organ (NAUMOVA & ZHAROVA 2003). In small ruminants, the efficiency of fermentation within the foregut is also increased by a highly selective diet (PARRA 1978). Most important is perhaps the point that *Laonastes* consumes mainly dicots, which are much more nutritious than monocots although dicots also are more toxic plants. The plants of tropical rainforest produce huge amounts of secondary compounds for protection against numerous herbivores, but these plants have many nutrients (JANZEN 1975). Therefore, mammals often are faced with the need for detoxification of caloric food resource (LINDROTH 1989, CORK & FOLEY 1991). By foregut fermentation *Laonastes* has the opportunity to detoxify eaten forage plants, like that in the rumen of ungulates (MCNAB 2002, KARASOV & MARTINEZ DEL RIO 2007). In addition, with animals of smaller body size the detoxification will be more effective (FOLEY & MCARTHUR 1994).

There is an assumption that the large foregut structures must have emerged after of development the hindgut because the foregut mammals have some fermentation in the hindgut (HUME & WARNER 1980). It is not surprising that hindgut fermenters are widely spread currently. Most rodents have a small body size and the most of them are omnivores (LANDRY 1970) thereby these circumstances contributed to the physiological constraints on the development of foregut fermentation. However in Miocene the global changes of the productivity of terrestrial ecosystem have led to the progressive evolution of foregut mammals therefore the foregut and hindgut ways of fermentation could have originated contemporaneously in some new-emerging taxonomic groups (LANGER 1991). The different evolution of the digestive systems of closely related species (foregut fermenter - *Laonastes* and hindgut fermenter – *Ctenodactylus*) confirms this statement.

Additionally, the evolutionary trophic strategies are often different within certain mammalian groups. That is, if in a recent taxonomic group the dominant strategy is herbivory it does not mean that all extinct species which had a larger size were herbivores. Likewise, not all representatives of macropodids – a herbivorous group

with greater convergent similarity in gut structures with *Laonastes* – were herbivores in the past (BLACK *et al.* 2012).

Nevertheless, taking into account the variability of body weight in the group Ctenodactyloidea we can assume the possibility of the presence of foregut fermentation in related species of extinct rodents with the same or greater weight than for *Laonastes*. The reconstruction of body weight, physiological functions and characteristics of soft tissue in extinct vertebrates is largely built on the basis of information about the morphology and physiological functions in recent animals (REYNOLDS 2002, HOPKINS 2008, SCHACHNER *et al.* 2009, BRUSATTE 2012). Although the tooth system demonstrates a rodent's adaptation to diet to a lesser degree compared with the morphology of the intestinal tract (VORONTSOV 1979), it is in most cases the sole opportunity to evaluate their weight (GINGERICH & SMITH 1984, HOPKINS 2008). Correct forecasts of body weight have been given using allometric scaling of such morphological parameters as the length of the tooth row and the first molar (HOPKINS 2008). We used these tooth parameters for analysis of published paleodata. It has been revealed that most taxonomic groups of Ctenodactyloidea were small animals. The extinct genera of the families Diatomyidae and Ctenodactylidae (*Ageitonomys*, *Baluchimys*, *Birbalomys*, *Bounomys*, *Diatomus*, *Distylomys*, *Euryodontomys*, *Fallomus*, *Hodshibia*, *Huangomys*, *Karakoromys*, *Lindsaya*, *Lophibaluchia*, *Marymus*, *Prodistylomys*, *Prosayimys*, *Sayimys*, *Willmus*) have smaller teeth compared with *Laonastes* (KOWALSKI 1974, HARTENBERGER 1982, FLYNN *et al.* 1986, BASKIN 1996, WANG 1997, MARIVAUX & WELCOME 2003, MARIVAUX *et al.* 2004, JENKINS *et al.* 2005, FLYNN & MORGAN 2005, FLYNN 2006, 2007, WANG 2010) therefore these mammals probably had no foregut system to sustain the digestion, because the body weight of folivorous mammals is no less than 500-700 g (CORK & FOLEY 1991, CORK 1994). In contrast, other representatives of Ctenodactylidae (*Confiniummys*, *Ottomania*, *Tataromys*, *Yindirtemys*) were significantly larger than *Laonastes* (LI & QIU 1980, WANG 1997, BRUIJN *et al.* 2003, SCHMIDT-KITTLER *et al.* 2007, BENDUKIDZE *et al.* 2009). If these rodents were herbivores, it is quite possible, the foregut fermentation was essential for them. Thus, within the group Ctenodactyloidea, the foregut fermentation as the main way of digestion is a fairly rare occurrence and it was not widespread in evolutionary history.

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## References

- BANCROFT, J.D. & GAMBLE, M. (2002): Theory and Practice of Histological Techniques. – Churchill Livingstone, London, 768 pp.
- BARBOZA, P.S., PARKER, K.L. & HUME, I.D. (2009): Integrative Wildlife Nutrition. – Springer Verlag, Berlin and Heidelberg, 342 pp.
- BASKIN, J.A. (1996): Systematic revision of Ctenodactylidae (Mammalia, Rodentia) from the Miocene of Pakistan. – *Palaeovertebrata*, **25**: 1–49.
- BAUCHOP, T. (1978): Digestion of leaves in vertebrate arboreal folivores. – *In*: Montgomery, G.G. (ed.): The Ecology of Arboreal Folivores. – Smithsonian Institution Press, Washington. Pp. 195–204.
- BEHMANN, H. (1973): Vergleichend- und funktionell-anatomische Untersuchungen am Caecum und Colon myomorpher Nagetiere. – *Zeitschrift für wissenschaftliche Zoologie*, **186**(3/4): 173–294.
- BENDUKIDZE, O.G., BRUIJN, H. & VAN DEN HOEK OSTENDE, L.W. (2009): A revision of Late Oligocene associations of small mammals from the Aral Formation (Kazakhstan) in the National Museum of Georgia, Tbilissi. – *Palaeodiversity*, **2**: 343–377.
- BLACK, K.H., ARCHER, M., HAND, S.J. & GODTHELP, H. (2012): The Rise of Australian marsupials: a synopsis of biostratigraphic, phylogenetic, palaeoecologic and palaeobiogeographic understanding. – *In*: TALENT J. (ed.): Earth and Life: Global Biodiversity, Extinction Intervals and Biogeographic Perturbations through Time. – Springer, Dordrecht, Pp. 983–1078.
- BRUIJN, H. DE, ÜNAY, E., SARAC, G. & YILMAZ, A. (2003): A rodent assemblage from the Eo/Oligocene boundary interval near Süngülü, Lesser Caucasus, Turkey. – *Coloquios de Paleontologia*, **1**: 47–76.
- BRUSATTE, S.L. (2012): Dinosaur Palaeobiology. – Wiley-Blackwell. 322 pp.
- CARLETON, M. (1973): A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. – *Miscellaneous publications of Museum of Zoology, University of Michigan*, **146**: 1–43.
- CARLETON, M. (1981): A survey of gross stomach morphology in Microtinae (Rodentia: Muroidea). – *Zeitschrift für Säugetierkunde*, **46**: 93–108.
- CHIVERS, D.J. & HLADICK, C.M. (1980): Morphology of gastrointestinal tract in Primates: comparisons with other mammals in relation to diet. – *Journal of Morphology*, **166**: 337–386.
- CLAUSS, M., LECHNER-DOLL, M. & STREICH, W.J. (2004): Differences in the range of faecal dry matter content between feeding types of captive wild ruminants. – *Acta Theriologica*, **49**: 259–267.
- CLAUSS, M., SCHWARM, A., ORTMANN, S., STREICH, W.J. & HUMMEL, J. (2007): A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. – *Comparative Biochemistry and Physiology, part A*, **148**: 249–265.
- CORK, S.J. (1994): Digestive constraints on dietary scope in small and moderately-small mammals: how much do we really understand? – *In*: CHIVERS, D.J. & LANGER, P. (eds.): The Digestive System in Mammals: Food, Form and Function. – Cambridge University Press, Pp. 337–369.

- CORK, S.J. & FOLEY, W.J. (1991): Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. – In: PALO, R.T. & ROBBINS, Ch.T. (eds.): *Plant Defenses Against Mammalian Herbivory*. – CRC Press, Boca Raton, Pp. 133–166.
- COX, Ph. G., KIRKHAM, J. & HERRELL, A. (2013): Masticatory biomechanics of the Laotian rock rat, *Laonastes aenigmamus*, and the function of the zygomaticomandibularis muscle. – Peer J. 1:e160 DOI: 10.7717/peerj.160
- CUMMINGS, J.F., MUNNELL, J.F. & VALLENAS, A. (1972): The mucigenous glandular mucosa in the complex stomach of two new-world camelids, the llama and guanaco. – *Journal of Morphology*, **137**: 71–109.
- DAWSON, M.R., MARIVAUX, L., LI, C., BERAD, C. & METAIS, G. (2006): *Laonastes aenigmamus* and the “Lazarus effect” in recent mammals. – *Science*, **311**: 1456–1458.
- DEARDEN, L.C. (1969): Stomach and pyloric sphincter histology in certain microtine rodents. – *Journal of Mammalogy*, **50**(1): 60–68.
- DEHORITY, B.A. (1997): Foregut fermentation. – In: MACKIE R.I. *et al.* (eds.): *Gastrointestinal Microbiology*. – Chapman and Hall, London, Pp. 39–83.
- DOBSON, G.E. (1884): On the myology and visceral anatomy of *Capromys melanurus*, with a description of the species. – *Proceedings of the Zoological Society of London*, **52**(2): 233–250.
- EURELL, J.A. & FRAPPIER B.L. (2006): *Dellmann’s Textbook of Veterinary Histology*. – Blackwell Publ., Ames-Oxford, 405 pp.
- FABRE, P.-H., HAUTIER, L., DIMITROV, D. & DOUZERY, E.J.P. (2012): A glimpse on the pattern of rodent diversification: a phylogenetic approach. – *BMC Evolutionary Biology*, **12**(88): 1–19.
- FISHER, D.C. (1990): Rates of evolution – living fossils. – In: BRIGGS, D.E.G. & CROWTHER, P.R. (eds.): *Palaeobiology: a synthesis*. – Blackwell Science Ltd., Oxford, Pp. 152–159.
- FLEAGLE, J.G. (1988): *Primate Adaptation and Evolution*. – Academic Press, San Diego – New York, 486 pp.
- FLYNN, L.J. (2006): Evolution of the Diatomyidae, an endemic family of Asian rodents. – *Vertebrata Palasiatica*, **44**(2): 182–192.
- FLYNN, L.J. (2007): Origin and evolution of the Diatomyidae, with clues to paleoecology from the fossil record. – *Bulletin of Carnegie Museum of Natural History*, **39**: 173–181.
- FLYNN, L.J., JACOBS, L.L., & CHEEMA, I.U. (1986): Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. – *American Museum Novitates*, **2841**: 1–58.
- FLYNN, L.J. & MORGAN, M.E. (2005): An unusual diatomyid rodent from an infrequently sampled Late Miocene interval in the Siwaliks of Pakistan. – *Palaeontologia Electronica*, **8**(1): 17A. 10pp.
- FLYNN, L.J. & WESSELS, W. (2013): Paleobiogeography and South Asian small mammals: Neogene latitudinal faunal variation. – In: WANG, X., FLYNN, L.J., FORTELIUS, M. (eds.): *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. – Columbia University Press, New York, Pp. 445–460.
- FOLEY, W.J. & McARTHUR, C. (1994): The effects and costs of allelochemicals for mammalian herbivores: an ecological perspective. – In: CHIVERS, D.J. & LANGER, P. (eds.): *The Digestive System in Mammals: Food, Form and Function*. – Cambridge University Press, Pp. 370–391.
- GABELLA, G. (1981): On the musculature of the gastrointestinal tract of the guinea pig. – *Anatomy and Embryology*, **163**: 135–156.
- GARTNER, K. (2001): The forestomach of rats and mice, an effective device supporting digestive metabolism in muridae (review). – *Journal of Experimental Animal Science*, **41**: 1–20.
- GEMMEL, R.T. & ENGELHARDT, W.V. (1977): The structure of the cells lining the stomach of the tamar wallaby (*Macropus eugenii*). – *Journal of Anatomy*, **123**(3): 723–733.
- GENEST-VILLARD, H. (1968): L’estomac de *Lophuromys sikapusi* (Temminck) (Rongeurs, Murides). – *Mammalia*, **32**: 639–656.
- GINGERICH, Ph.D. & SMITH, B.H. (1984): Allometric scaling in the dentition of primates and insectivores. – In: JUNGERS, W.L. (ed.): *Size and Scaling in Primate Biology*. – Plenum Publishing, Pp. 257–272.
- GOUAT, P. (1993): Biometrics of the digestive tract of three species of Ctenodactylidae: comparison with other rodents. – *Zeitschrift für Säugetierkunde*, **58**: 191–193.
- GORGAS, M. (1967): Vergleichend-anatomische Untersuchungen am Magen-Darm-Kanal der Sciuromorpha, Hystricomorpha und Caviomorpha (Rodentia). – *Zeitschrift für wissenschaftliche Zoologie*, **175**: 237–404.
- HARTENBERGER, J.-L. (1982): A review of the Eocene rodents of Pakistan. – *Contributions from the Museum of Palaeontology the University of Michigan*, **26**(2): 19–35.
- HAUTIER, L., LEBRUN, R., SAKSIRI, S., MICHAUX, J., VIANEY-LIAUD, M. & MARIVAUX, L. (2011): Histricognathy vs sciurognathy in the rodent jaw: a new morphometric assessment of hystricognathy applied to the living fossil *Laonastes* (Diatomyidae). – *PloS ONE*, **6**(4): e18698. doi:10.1371/journal.pone.0018698.
- HERREL, A., FABRE, A.-C., HUGOT, J.-P., KEOVICHIT, K., ADRIAENS, D., BRABANT, L., VAN HOOREBEKE, L. & CORNETTE, R. (2012): Ontogeny of the cranial system in *Laonastes aenigmamus*. – *Journal of Anatomy*, **221**: 128–137.
- HOFMANN, R.R. (1989): Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. – *Oecologia*, **78**: 443–457.
- HOPKINS, S.S.B. (2008): Reassessing the mass of exceptionally large rodents using tooththrow length and area as proxies for body mass. – *Journal of Mammalogy*, **89**(1): 232–243.
- HUCHON, D.E., CHEVRET, P., JORDAN, U., KILPATRICK, C.W., RANWEZ, V., JENKINS, P.D., BROSIUS, J., & SCHMITZ, J. (2007): Multiple molecular evidences for a living mammalian fossil. – *Proceedings of the National Academy of Sciences, U.S.A.*, **104**: 7495–7499.
- HUME, I.D. (1999): *Marsupial Nutrition*. – Cambridge University Press, 434 pp.
- HUME, I.D., WARNER, A.C.I. (1980): Evolution of microbial digestion in mammals. – In: RUCKEBUSCH, Y., THIEVEND, P., (eds.): *Digestive Physiology and Metabolism in Ruminants*. – MID Press, Lancaster, Pp. 665–684.
- JANIS, C.M. (1984): Tragulids as living fossils. – In: ELDRIDGE, N. & STANLEY, S.M. (eds.): *Living Fossils*. – Springer Verlag, New York, Pp. 87–94.
- JANZEN, D.H. (1975): *Ecology of Plants in the Tropics*. – Edward Arnold, London, 66 pp.
- JENKINS, P.D., KILPATRICK, C.W., ROBINSON, M.F. & TIMMINS, R.J. (2005): Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hy-

- stricognatha) from Lao PDR. – Systematics and Biodiversity, **2**(4): 419–454.
- KARASOV, W.H. & MARTINEZ DEL RIO, C. (2007): Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins. – Princeton University Press, Princeton-Oxford, 741pp.
- KAY, R.F. (1984): On the use of anatomical features to infer foraging behavior in extinct primates. – In: RODMAN, P.S. & CANT, J.G. (eds.): Adaptation for Foraging in Nonhuman Primates. – Columbia University Press, New York, Pp. 21–53.
- KNIGHT, M.N. & KNIGHT-ELOFF, A.K. (1987): Digestive tract of the African giant rat, *Cricetomys gambianus*. – Journal of Zoology (London), **213**: 7–22.
- KOTZE, S.H., VAN DER MERWE, E.L., NDOU, R., O'RIAIN, M.J. & BENNETT N.C. (2009): The colonic groove or furrow: a comparative morphological study of six species of African mole-rats (Rodentia, Bathyergidae). – Journal of Morphology, **270**: 966–975.
- KOWALSKI, K. (1974): Middle Oligocene rodents from Mongolia. – Palaeontologia Polonica, **30**: 147–178.
- KRAUSE, W.J. (1981): Morphological and histochemical observation on the duodenal glands of eight wild ungulate species native to North America. – The American Journal of Anatomy, **162**: 167–181.
- KUHN, H.-J. (1964): Zur Kenntnis von Bau und Funktion des Magens der Schlankaffen (Colobinae). – Folia Primatologica, **2**: 193–221.
- KUZNETSOV, G.V. & NAUMOVA, E.I. (2004): On feeding specialization of tropic mammals. – Zoologicheskii Zhurnal, **83**(2): 175–184. In Russian.
- LAAKKONEN, J., KANKAANPAA, T., CORFE, I. J., JERNVALL, J., SOVERI, T., KEOVICHIT, K. & HUGOT, J.-P. (2014): Gastrointestinal and dental morphology of herbivorous mammals: Where does the Laotian rock rat fit? – Annales Zoologici Fennici, **51**: 153–161.
- LANDRY, S.O. (1970): The Rodentia as omnivores. – Quarterly Review of Biology, **45**: 351–372.
- LANGER, P. (1988): The Mammalian Herbivore Stomach. Comparative Anatomy, Function and Evolution. – Gustav Fischer, Stuttgart – New York, 557 pp.
- LANGER, P. (1991): Evolution of the digestive tract in mammals. – Verhandlungen der Deutschen Zoologischen Gesellschaft, **84**: 169–193.
- LANGER, P. (2002): The digestive tract and life history of small mammals. – Mammal Review, **32**(2): 107–131.
- LENTLE, R.G. & JANSSEN, P.W.M. (2011): The Physical Processes of Digestion. – Springer, New York, 279 pp.
- LEUS, K., GOODALL, G.P. & MACDONALD A.A. (1999): Anatomy and histology of the babirussa (*Babyrousa babyrousa*) stomach. – C.R. Acad. Sci. Paris, Sciences de la vie, **322**: 1081–1092.
- LEUS, K., MACDONALD, A.A., GOODALL, G., VEITCH, D., MITCHELL, S. & BAUWENS, L. (2004): Light and scanning electron microscopy of the cardiac gland region of the stomach of the Babirussa (*Babyrousa babrussa* – Suidae, Mammalia). – C.R. Biologies, **327**: 735–743.
- LI, CH. & QIU, ZH. (1980): Early Miocene mammalian fossils of the Xining Basin, Qinghai Province. – Vertebrata Palasiatica, **18**(3): 198–209.
- LINDROTH, R.L. (1989): Mammalian herbivore-plant interaction. – In: ABRAHAMSON, W.G. (ed.): Plant-Animal Interaction. – McGraw Hill B.C., New York, Pp. 163–206.
- LOVEGROVE, B.G. (2010): The allometry of rodent intestines. – Journal of Comparative Physiology, B, **180**: 741–755.
- MADDOCK, A.H. & PERRIN, M.R. (1981): A microscopical examination of the gastric morphology of the white-tailed rat *Mystromys albicaudatus* (Smith, 1834). – South African Journal of Zoology, **16**: 237–247.
- MARIVAUX, L., CHAIMANEE, Y., YAMEE, C., SRISUK, P. & JAEGER, J.-J. (2004): Discovery of *Fallomys ladakhensis* Nanda & Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications. – Geodiversitas, **26**(3): 493–507.
- MARIVAUX, L. & WELCOME, J.-L. (2003): New diatomyid and baluchimyine rodents from the Oligocene of Pakistan (Bugti Hills, Balochistan): systematic and palaeobiogeographic implications. – Journal of Vertebrate Paleontology, **23**(2): 420–434.
- MCNAB, B. (2002): The Physiological Ecology of Vertebrates: a View from Energetics. – Cornell University Press, Ithaca – London, 576 pp.
- MERRITT, J.F. (2010): The Biology of Small Mammals. – The Johns Hopkins University Press, Baltimore, 313 pp.
- NAUMOVA, E.I. (1981): Functional Morphology of Rodent and Lagomorph Digestive Systems. – Nauka Publ., Moscow, 262 pp. In Russian.
- NAUMOVA, E.I., NESTEROVA, N.G., KHOLODOVA, M.V. & ZHAROVA, G.K. (1995): Morphological and physiological adaptations of digestive system of African mole rat *Tachyoryctes spendens*. – In: SOKOLOV, V.E. (ed.): Theriological Investigations in Ethiopia. – Nauka Publ., Moscow, Pp. 118–126. In Russian with English summary.
- NAUMOVA, E.I. & ZHAROVA, G.K. (2003): Structure and functions of the digestive tract in the maned hamster (*Lophiomys imhausi*). – Zoologicheskii Zhurnal, **82**(11): 1368–1374. In Russian with English summary.
- NOMINA ANATOMICA VETERINARIA. 2012. 5th ed. Publ. Edit. Comm. I.C.V.G.A.N., Hannover, 160 p.
- OBENDORF, D.L. (1984): The Macropodid oesophagus. I. Gross anatomical, light microscopic, scanning and transmission electron microscopic observation of its mucosa. – Australian Journal of Zoology, **32**: 415–435.
- PARRA, R. (1978): Comparison of foregut and hindgut fermentation in herbivores. – In: MONTGOMERY, G.G. (ed.): The Ecology of Arboreal Folivores. – Smithsonian Institution Press, Washington, Pp. 205–229.
- PERRIN, M.R. & CURTIS, B.A. (1980): Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. – South African Journal of Zoology, **15**: 22–33.
- PERRIN, M.R. & KOKKINN, M.J. (1986): Comparative gastric anatomy of *Cricetomys gambianus* and *Saccostomus campestris* (Cricetomyinae) in relation to *Mystromys albicaudatus* (Cricetinae). – South African Journal of Zoology, **21**: 202–210.
- RAKOFF-NAHOUM, S., MEDZHITOV, R. (2006): Role of the innate immune system and host-commensal mutualism. – In: HONJO, T. & MELKERS, F. (eds): Gut-Associated Lymphoid Tissues. – Springer Verlag, Berlin, Pp. 1–18.
- REYNOLDS, P.S. (2002): How big is a giant? The importance of methods in estimating body size of extinct mammals. – Journal of Mammalogy, **83**: 321–332.

- SCHACHNER, E.R., LYSON, T.R. & DODSON, P. (2009): Evolution of the respiratory system in nonavian theropods: evidence from rib and vertebral morphology. – *The Anatomical Record*, **292**: 1501–1513.
- SCHMIDT-KITTLER, N., VIANEY-LIAUD, M. & MARIVAUX, L. (2007): Oligocene–Miocene vertebrates from the Valley of Lakes (Central Mongolia): morphology, phylogenetic and stratigraphic implications 6. The Ctenodactylidae (Rodentia, Mammalia). – *Annalen des Naturhistorischen Museums in Wien*, **108 A**: 173–215.
- SCHWARM, A., ORTMANN, S., WOLF, CH., STREICH, W. J. & CLAUSS M. (2009): Passage marker excretion in red kangaroo (*Macropus rufus*), collared peccary (*Pecari tajacu*) and colobine monkeys (*Colobus angolensis*, *C. polykomos*, *Trachypithecus johnii*). – *Journal of Experimental Zoology*, **311A**: 647–661.
- SCOPIN, A.E., SAVELJEV, A.P., SUNTSOVA, N.A., GNOPHAXAY, S., TIKHONOV, A.N. & ABRAMOV, A.V. (2011): Digestive system of the Laotian rock rat *Laonastes aenigmamus* (Rodentia: Diatomyidae) from the evolutionary viewpoint. – *Proceedings of the Zoological Institute RAS*, **315(1)**: 3–18.
- SILVA TABOADA, G., SUAREZ DUQUE, W. & DIAZ FRANCO, S. (2007): Compendio de los Mamíferos Terrestres Autoctonos de Cuba: vivientes y extinguidos. – Museo Nacional de Historia Natural, Habana, 465 pp.
- SNIPES, R.L. (1982): Anatomy of the guinea pig cecum. – *Anatomy & Embryology*, **165**: 97–111.
- SNIPES, R.L., HÖRNICKE, H., BJÖRNHAG, G. & STAHL, W. (1988): Regional differences in hindgut structure and function in the nutria, *Myocastor coypus*. – *Cell Tissue Research*, **252**: 435–447.
- STANOJEVIC, D., NIKOLIC, Z. & DREKIC, D. (1982): The alimentary canal in the ground squirrel (*Citellus citellus* L.) II. Oesophagus, ventriculus, duodenum, jejunum, ileum, caecum, colon and rectum. – *Acta Veterinaria (Beograd)*, **32(4)**: 205–216.
- STEFEN, C. (2011): On the hair cuticle structure of the rodent *Laonastes aenigmamus* (Mammalia: Rodentia: Diatomyidae). – *Vertebrate Zoology*, **61(3)**: 373–376.
- STEVENS, E. & HUME, I.D. (1995): *Comparative Physiology of the Vertebrate Digestive System*. – Cambridge University Press, 400 pp.
- TULLBERG, T. (1899): Ueber das System der Nagethiere: eine Phylogenetische Studie. – *Nova Acta Regiae Societatis Scientiarum Upsaliensis (Upsala)*, **18**: 1–514.
- VORONTSOV, N.N. (1979): *Evolution of the Alimentary System in Myomorph Rodents*. – Smithsonian Institution Publ., Nat. Sci. Foundation, Washington, 346 pp.
- WANG, B. (1997): The Mid-Tertiary Ctenodactylidae (Rodentia, Mammalia) of Eastern and Central Asia. – *Bulletin of the American Museum of Natural History*, **234**: 1–88.
- WANG, B.-Y. (2010): *Ageitonomys neimongolensis* gen. et sp. nov. (Ctenodactyloidea, Rodentia, Mammalia) from Early Oligocene of Nei Mongol, China. – *Vertebrata Palasiatica*, **48(1)**: 179–183.
- WILLIAMS, A.E. (2012): *Immunology: Mucosal and Body Surface Defences*. – Wiley Blackwell, 380 pp.