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DIGESTIVE SYSTEM OF THE LAOTIAN ROCK RAT *LAONASTES AENIGMAMUS* (RODENTIA: DIATOMYIDAE) FROM THE EVOLUTIONARY VIEWPOINT

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ABSTRACT

A preliminary study of the gastrointestinal tract of *Laonastes aenigmamus* Jenkins et al., 2005 has been carried out. We have revealed that *Laonastes* is the smallest folivorous mammal with the enlarged forestomach, which is similar to that of certain herbivorous marsupials. The stomach of this rodent contains 70% of the digesta and performs the main role in storing and digesting of plant foods. *Laonastes* is a unique rodent having such the digestive system, and its herbivory is confirmed by the enlarged *ampulla duodeni*, small dimensions of the hindstomach (*pars pylorica*), the absence of *vesica fellea*, the presence of colon spiral loops, the well-developed lymphoid tissue of stomach, and the gut mass making up to 25–27% of the entire body mass. Such the gastrointestinal tract might have evolved as a result of a general digestive strategy of the foregut mammals that inhabited tropical forests in the Miocene. This strategy involved an adaptation to the nutrition on leaves of tropical dycots which apparently contributed to the convergent evolution of the digestive system in different folivorous mammals.

Key words: *Laonastes,* rodents, stomach, digestive system, foregut, folivory, evolution

ПИЩЕВАРИТЕЛЬНАЯ СИСТЕМА ЛАОССКОЙ ГОРНОЙ КРЫСЫ *LAONASTES AENIGMAMUS* (RODENTIA: DIATOMYIDAE) С ЭВОЛЮЦИОННОЙ ТОЧКИ ЗРЕНИЯ

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РЕЗЮМЕ

Проведено первичное изучение желудочно-кишечного тракта *Laonastes aenigmamus* Jenkins et al., 2005. Установлено, что *Laonastes* является самым мелким по размеру листоядным млекопитающим, обладающим

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объемным желудком с большим количеством расширений (камер). В желудке этого грызуна содержится 70% перевариваемого корма, и он имеет наибольшее сходство с желудком некоторых травоядных сумчатых. *Laonastes* является единственным известным грызуном с подобной структурой пищеварительного тракта. Растительноядность грызуна подтверждается наличием увеличенной *ampulla duodeni*, мелкими размерами *pars pylorica*, отсутствием *vesica fellea*, присутствием спиралей ободочной кишки, хорошо развитой лимфоидной тканью кишечника и значительной массой желудочно-кишечного тракта, составляющего 25–27% от общей массы тела животного. Происхождение подобной пищеварительной системы могло быть результатом общей трофической стратегии млекопитающих, обитавших в тропических лесах миоценовой эпохи. Эта стратегия была результатом адаптации к питанию листьями тропических покрытосеменных растений, что способствовало конвергентной эволюции пищеварительной системы у различных растительноядных млекопитающих.

Key words: *Laonastes,* грызуны, желудок, пищеварительная система, листоядность, эволюция

Limestone rocks and karst caves of Southeast Asia are the examples of unique ecosystems characterized by a high species endemism (Clements et al. 2006). Many new mammal species have been found here during the last decade (Jenkins and Robinson 2002; Jenkins et al. 2005; Musser et al. 2006). In 2005, a new rodent species, the Laotian rock rat (*Laonastes aenigmamus*), was found here (Jenkins et al. 2005). This species was assigned to a separate family Laonastidae within the hystricognathous rodents. Later, *Laonastes* was reassigned to the family Diatomyidae, which was earlier considered extinct in the Late Miocene, 11 million years ago (mya) (Dawson et al. 2006). Therefore, the Laotian rock rat is a good example of pseudoextinction and is a kind of “living fossil” or “Lazarus taxon” (Dawson et al. 2006). Nowadays, a close similarity of the Diatomyidae and Ctenodactylidae has been revealed (Huchon et al. 2007). Both families belong to the infraorder Ctenodactylomorphi and the suborder Hystricomorpha (Wilson 2009), and both seemed to have diverged approximately 44 mya (Honeycutt 2009).

The Laotian rock-rat inhabits karst caves located in Khammouane Province, Lao PDR (Jenkins et al. 2005). To date, the rodent’s exterior, peculiarities of its cranium structure and a muscular system have been described; a multigene molecular analysis has been performed (Jenkins et al. 2005; Huchon et al. 2007; Hautier and Saksiri 2009). Yet, many aspects of the anatomy, physiology and ecology of *Laonastes* remain unknown. It is necessary to carry out studies on other morphological characteristics and ecology of the Laotian rock rat in order to see the level of species’ adaptation to the life in tropical ecosystems and its relationships within the hystricognaths.

The structure of a digestive system of extinct mammals can be estimated only on the basis of indirect indicators. Until now there is no published information about the nutrition and structure of the gastrointestinal tract of the Laotian rock rat. Therefore, a study of the rodent’s gastrointestinal tract may help to understand the functions of a digestive system of extinct rodents. Among a great number of extant rodents, herbivorous species predominate. They can be characterized by a variety of gastrointestinal tracts, each specializing to consuming and digestion of certain vegetable foods (Behmann 1973; Carleton 1973; Vorontsov 1979, 1982; Perrin and Curtis 1980; Stevens and Hume 1995). A digestive system has been sufficiently well-studied in the hystricognathous rodents, which are widespread in the Old and New Worlds, giving an opportunity to analyze possible ways of trophic adaptation in a given taxon (Tullberg 1899; Gorgas 1967; Stevens and Hume 1995). The aim of the present study is to carry out gross anatomy studies of the gastrointestinal tract of the Laotian rock rat and to compare it with guts of other herbivorous mammals.

MATERIAL AND METHODS

Killed rock-rats were obtained from the food market in Ban Doy village in November 2008. The village (17°33´26´´N, 104°49´28´´E, at an altitude of 140 m) is located approximately 18 km to the north of Thakhek in Khammouane Province of Lao PDR. We selected five animals, which had been dead for less than 2–3 hours. No pathological disturbances were found while dissecting the animals. The gastrointestinal tract was put into 70% ethanol immediately after the dissection. Alcohol was proven to be a reliable fixative by other researchers of the digestive system of hystricognathous rodents (Tullberg 1899; Gorgas 1967; Kotze et al. 2010). The nomenclature of the gastrointestinal tract follows “Nomina Anatomica Veterinaria” (2005). Photos, measurements and weighting were taken from the preserved material. The length, width, weight of filled and empty compartments of the gastrointestinal tract (stomach, duodenum, jejunum, ileum, cecum, colon, and rectum) were measured. The gut volume was calculated using the formulae: (1) compartments of the stomach were measured as a sum of the spheres’ volume; (2) small and large intestines were measured as a volume of the cylinders (Chivers and Hladik 1980). The surface area needed for calculation of volumes was determined by a direct method (Young Owl 1994). The number and area of aggregative lymphatic nodules were calculated in all gut sections. Before an analysis, the mesentery was removed, and the gut was washed in 10% acetic acid solution. Linear characters were measured to an accuracy of 1.0 mm, the mass – of 0.01 g. The ratio of certain parts of the digestive system was calculated based on the wet mass, length and volume. These indices were considered as 100% for the gastrointestinal tract as a whole.

RESULTS

The Laotian rock rat is a small-sized rodent. In average, its body length is 258.0 mm (238.0–290.0 mm). The whole length of the gastrointestinal tract is some 1500 mm (Table 1), exceeding the animal body length by 4.8–6.0 times. The whole gut mass with the content is 25–27% of the body mass. The oesophagus is rather short and resembles a narrow pipe. At rest, it is in a depressed condition and its length does not usually exceed 50 mm, width – 6 mm. The stomach is compactly located in the body cavity and there is a sacculated organ along *curvatura ventriculi major* (Figs. 1, 2). In a natural state, in the abdominal cavity, the stomach length is 2.7–3.0 times less than in a straightened state. Outwardly, the stomach is a bulky organ, but the voluminous stomach consists of small pouches caused by sacculation (Fig. 2), resembling the forestomach of some marsupials and primates. A sac is the chamber’s broadening within the stomach. Such the broadenings are not closed formations, having an inner passage sequentially connecting all of them. Sacs with the content adjoin each other in a similar way as bellows of an accordion. A number of such sac-like compartments of the stomach can reach 9–10. They differ in sizes and are positioned in different planes. Sac divisions include the plicae and permanent transverse folds. The fold structure favours the folding up of the stomach approaching both *pars cardiaca* and *pars pylorica*. There are no sphincters and valves between the sacs, only cardiac narrow orifice and pyloric sphincter present. Therefore, it would be a mistake to treat this rat’s stomach as the plurilocular one. In fact, it is the unilocular stomach possessing sacculation, should the terminology used for the marsupials is adopted (see Langer 1980, 1988). If so, the left side of the stomach from *pars cardiaca* can be treated as the sacciform forestomach, whereas the right one up to *pars pylorica* should be the tubiform forestomach (Fig. 2C). The sacciform forestomach (*fundus ventriculi*) and tubiform forestomach (*corpus ventriculi*) are positioned in different anatomical planes. Yet the structure of their tissues is similar, so the subdivision of the forestomach into two parts is rather arbitrary. *Ostium cardiacum* is directed to the largest sac. Depending on a volume of the ingesta being added to the stomach, various chambers can change their shapes and consequently dimensions of the entire stomach. The stomach volume of mature individuals exceeds 70 cm^3, the inner surface area is 280 cm^2. An empty stomach weights approximately 12 g (Table 1), which is about 3% of the body weight. A filled stomach is about 16–21% of the total body weight that emphasizes its importance as a basic digestive organ. This is also confirmed by a strong development of the gut-associated lymphoid tissue. The forestomach has got a large number of aggregative lymphatic nodules or Peyer’s patches (*lymphonoduli aggregati*), situated in two rows (each consisting of 20 or more lymphatic nodules). The size of biggest nodules exceeds 10 mm. The total area of aggregative lymphatic nodules is rather large (Table 1). The oesophagus enters the stomach from the left side of *curvatura ventriculi minor*. Two *diverticulum ventriculi* are located at the point of entry of the oesophagus into the stomach. They can be rather large (15.0–17.0 mm long). *Pars pylorica* of the stomach is narrower and shorter as compared with other parts. In average, its length is 43.75±5.15 mm and width 4.28±0.17 mm. The shape of *pars pylorica* resembles the hindstomach of certain marsupials and folivorous primates. The surface area of the *pars pylorica* is about 4 to 10% of the total inner surface area of the stomach depending on a volume of digesta. The

Table 1. Characteristics of digestive system of *Laonastes aenigmamus*.

	Wet mass of a organ$^{\#}$, g M±m (lim.) n=5	Length, mm M±m (lim.) n=5	Maximum width, mm M±m (lim.) n=5	Relative volume, cm^3 M±m (lim.) n=3	Distribution of gut contents mass, % M±m (lim.) n=5	Quantity of aggregative lymphatic nodules on inner gut walls, n=2	Total area of aggregative lymphatic nodules on inner gut walls, cm^2 n=2	Ratio of digestive sections by wet mass , % M±m (lim.)	Ratio digestive sections by length, % M±m (lim.)	Ratio digestive sections by relative volume, % M±m (lim.)
Stomach	11.77±0.51 10.61–13.60	321.6±26.16* 260.0–418.0 16.20±0.69** 14.0–18.0	79.40±3.90 70.00–88.00	98.18±33.91 58.41–169.31	70.86±3.44 64. 10–75.32	20–24	4.38–5.52	60.29±1.18 57.95–62.92	24.03±1.54*** 21.2–26.5	67.73±5.92 57.3–77.8
Duodenum	0.80±0.06 0.70–0.97	97.2±8.68 75.00–120.00	18.00±0.70 16.00–20.00	2.57±0.39 1.72–3.82	0.38±0.02 0.35–0.40	5–13	0.41–0.72	4.28±0.26 3.71–4.96	5.93±0.84 5.0–7.6	1.53±0.17 1.2–1.7
Jejunum	3.68±0.32 2.77–4.60	590.00±50.25 530.00–710.00	17.8±0.58 17.00–20.00	14.67±0.77 12.19–16.33	9.69±1.00 7.70–10.83	15–24	2.36–2.84	18.45±1.70 14.47–22.71	39.27±2.47 36.0–44.1	11.90±2.26 7.5–15.0
Ileum	0.26±0.04 0.20–0.39	61.40±7.68 50.00–90.00	18.00±0.89 15.00–20.00	1.64±0.33 0.80–2.86	0.59±0.06 0.47–0.68	1–2	0.35–0.45	1.50±0.22 1.11–2.10	3.9±0.45 3.0–4.4	1.20±0.25 0.7–1.5
Caecum	0.94±0.10 0.65–1.14	61.40±3.03 50.00–68.00	43.40±3.68 30.00–50.00	10.80±1.42 7.02–13.53	8.39±1.36 6.68–11.08	1–2	0,35–0,51	4.63±0.52 3.36–5.56	4.57±0.52 4.0–5.6	9.50±1.66 6.4–12.1
Colon	1.22±0.18 0.90–1.30	201.20±26.78 121.00–277.00	17.80±1.32 13.00–21.00	4.32±1.04 3.23–7.14	6.31±0.76 5.50–7.83	2–4	0.45–0.60	6.29±1.07 5.00–9.50	12.90±1.68 10.7–16.2	4.27±0.91 3.3–6.1
Rectum	0.87±0.08 0.79–1.09	99.25±14.40 80.00–142.00	20.00±2.48 13.00–24.00	4.25±1.97 2.86–6.51	3.81±0.96 2.08–5.38	0–1	0–0.25	4.58±0.44 3.71–5.79	9.40±1.10 7.5–11.2	3.87±1.23 2.3–6.3
Total	19.36±0.63 18.31–21.74	1451.7±170.0*** 1134.0–1715.0	–	139.43±36.7 102.0–212.8	100	49–65	9.1–10.2	100	100	100

Designations: # – mass of an organ without contents; (*) – length of the stomach with contents has been calculated by *curvatura ventriculi major*; (**) – length of the stomach with contents has been calculated by *curvatura ventriculi minor*; (***) – length of the empty stomach and other digestive sections has been calculated after complete removal of mesenterium.

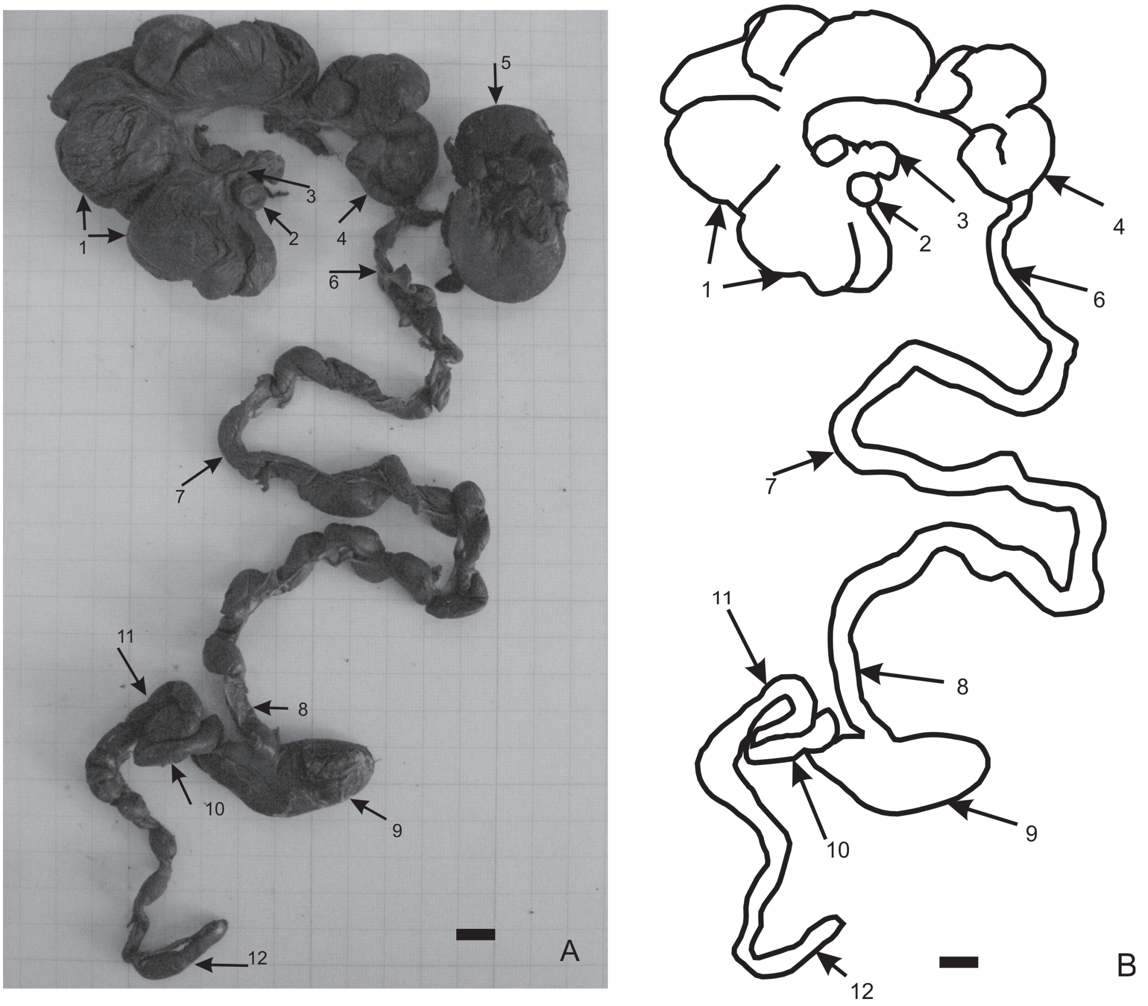

Fig. 1. Digestive system of *Laonastes aenigmamus*: A – appearance; B – scheme.

Designations: 1 – sac-like compartments; 2 – diverticulum of a stomach; 3 – oesophagus; 4 – *pars pylorica*; 5 – liver; 6 – duodenum; 7 – jejunum; 8 – ileum; 9 – caecum; 10 – *colon ascendens*; 11 – *colon discendens*; 12 – rectum. Scale bar = 10 mm.

ventricular groove (*sulcus ventriculi*) along *curvatura ventriculi minor* is surrounded by well-marked ridges (Fig. 2C). This groove runs from the oesophagus to the middle of the stomach only and it does not reach the hindstomach. The groove is likely to be reduced in adults. There is a region resembling the squamous epithelium between ridges of the ventricular groove. The area of this region is about 5 cm^2, and there is a maximum dilation (up to 30 mm) in the largest chamber of the stomach. *Pars pylorica* and enlarged *ampulla duodeni* are of great importance in digestion. The spleen is situated on the stomach surface close to the colon joining. It is of a boomerang or crescent shape, and of a triangular shape on a transverse incision. Its average, its weight is 0.25 g, being approximately 2% of the empty stomach weight. The liver has 4 lobes, its weight is about 3.5% of the total body weight. There is no gallbladder (*vesica fellea*). The weight of pancreas is approximately 0.3% of the body weight.

The rat's intestine is not as long as that of other hystricognathous rodents. Its length is only 73–81% of the whole gut and exceeds the body length just by 4–5 times. The content of intestines is about 30% of the total gut content. Intestines make up only 50% of the aggregative lymphatic nodules surface (Table 1). Small intestines are developed most. Their length is

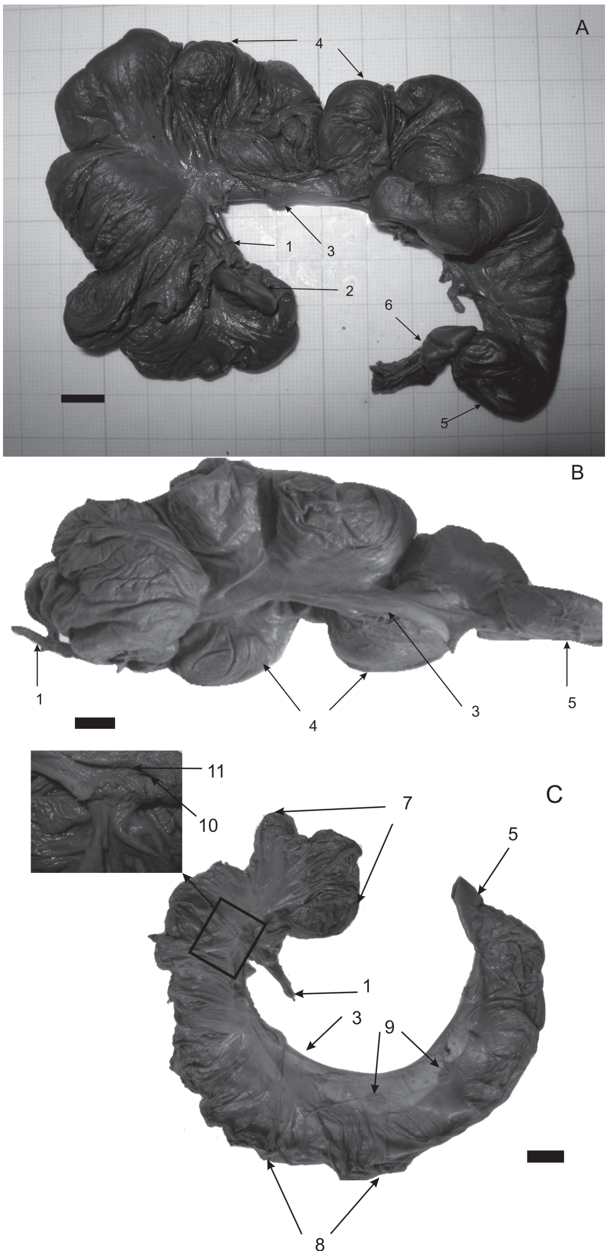

Fig. 2. Stomach of *Laonastes aenigmamus*: A – full stomach from the left side; B – full stomach from *curvatura ventriculi minor*; C – empty stomach after removing of mesenterium.

Designations: 1 – oesophagus; 2 – diverticulum of a stomach; 3 – *curvatura vetriculi minor*; 4 – sac-like compartments; 5 – *pars pylorica* (hindstomach); 6 – *ampulla duodeni*. 7 – *fundus ventriculi*; 8 – *corpus ventriculi*; 9 – Peyer's patches; 10 – *ostium cardiacum*; 11 – *sulcus ventriculi*. Scale bar = 10 mm.

68% of the whole length of intestines. The average weight of small intestines is 24% of the whole wet mass of the empty gut (Table 1). Duodenum is comparatively short but characterized by the strongly pronounced *flexura duodeni* and *ampulla duodeni*. Jejunum is the longest part of the gastrointestinal tract and the second one regarding the inner volume and the surface of aggregative lymphatic nodules (Table 1). The shortest part of small intestines is ileum. Large intestines play a secondary role in digestion of plant foodstuffs in the Laotian rock rat. Their length does not exceed 25% of the total gut length. Caecum is only 6% as to the gut length and, regarding its wet mass, is 12% of the general indices of intestines. It has a shape of a simple pouch (Fig. 1B). There are no *apex ceci* and *haustra ceci*. No more than two Peyer's patches were found in the caecum. The colon is the longest part of large intestines, however, its volume normally does not exceed 6% of the total volume of the gut (Table 1). Faeces formation in this part of intestines determines unevenness of its width throughout its whole length. The colon forms *ansa spiralis coli*, which consists of three spiral loops. *Colon ascendens* makes up 20–25% and *colon transversum* only 6% of the whole length of the colon. A proximal part of the colon has a small enlargement. The longest part is *colon descendens*. The rectum is comparatively small, differing from the colon by apparent longitudinal folds located on its inner surface.

DISCUSSION

The Laotian rock rat is the smallest folivorous foregut mammal

The gastrointestinal tract of herbivorous animals is always characterized by its significant capacity. It is very importance for the microbial degradation of plants in the gut (Karasov and Martinez del Rio 2007). Vegetable food remains longer in the gastrointestinal tract of large herbivores as compared with small ones. Therefore, nutritional strategies of small mammals is often directed to a greater feeding selectivity when consuming certain parts of plants and to the restriction of the rate of food passing through the gastrointestinal tract by means of the extension of digestive organs (Barboza et al. 2009). The maximum volume of the gastrointestinal tract usually does not exceed 25% of the body weight of mammalian herbivores (Barboza et al. 2009). The volume of gastrointestinal tract of the Laotian rock rat corresponds to this indicator, thus corroborating its absolute herbivory. This is also proved by a small surface of *pars pylorica*, the absence of *vesica fellea*, the enlarged *ampulla duodeni*, and the presence of colon spiral loops, all traits being typical for herbivorous rodents (Vorontsov 1979; Perrin and Curtis 1980).

The hystricognathous rodents as herbivores have a specific gastrointestinal tract with the developed hindgut fermentation. However, the structure of the digestive system of Laotian rock rat differs from all extant rodents (Gorgas 1967; Behmann 1973; Vorontsov 1979; Stevens and Hume 1995). Such the large foregut system has never been found in other rodents except for the Laotian rock rat. The large forestomach is absent from the hystricognathous rodents, including the close relative *Ctenodactylus gundi* Rothmann, 1776. This plant-eating rodent has the unilocular stomach (Gorgas 1967). Among the hystricognathous rodents small sacculations have been found only in the unilocular stomach of capybara *Hydrochoeris hydrochoeris* Brisson, 1762 (De Barros Moraes et al. 2002). However the succulations in capybara have an absolutely different structure. Within the suborder Myomorpha there are certain rodents that possess the composite stomach. For instance, the Malagasy short-tailed rat *Brachyuromys betsileoensis* Bartlett, 1879 has sacculated sections on the cardiac gland region of its stomach. The maned rat *Lophiomys imhausi* Milne-Edwards, 1867 has a four-chamber stomach (Vorontsov 1979, 1982; Naumova and Zharova 2003). The external stomach characters of these rodents much more resemble those of the Laotian rock rat than of other rodents. However, these digestive tracts have been studied insufficiently yet, and their parts are likely to have a different structure and origin than those of the Laotian rock rat.

As was speculated by Gilyarov (1985) and Fisher (1990), it is highly probable that a lower rate of speciation in a “living fossil” may have resulted in preserving of an ancient complex of characters with minimal morphological changes. The gastrointestinal tract is one of the conservative systems of an organism (Gorgas 1967). Consequently, we suspect that the alimentary tract of the Laotian rock rat may have remained evolutionary unchanged. Therefore, it would be important to carry out a comparative study of herbivorous mammals possessing an analogous digestive system. The digestive system of the relict Laotian rock rat is based on foregut fermentation, though for the majority of extant rodents the hindgut fermentation is more typical. The foregut fermentation is also typical for ungulates, but is rare in other mammals. Such the foregut fermentation is frequently called the ruminant-like fermentation (Kinnear et al. 1979; Langer 1980; Stevens and Hume 1995). There is a principal difference in the stomach chamber structure between foregut nonruminants and true ruminants. The nonruminants do not have sphincters or filters (narrow orifices) that separate stomach compartments from each other. In the ruminants, these stomach filters (especially reticulo-omasal orifice) contribute to the separation of food particles and limit the volume of consumed food. The latter fact is evidently the main reason why such physiological mechanism does not exist in small foregut fermenters, to which many of the nonruminant mammals belong. In small herbivorous mammals, a rapid turnover time of plant food and large gut capacity are the important mechanisms that are essential for a digestion (Foley and Cork 1992; Veloso and Bozinovic 1993).

The nonruminant foregut with pregastric fermentation has been found in the primate subfamily Colobinae, the three-toed sloths Bradypodidae, the rock hyrax *Procavia*, the Syrian hamster *Mesocricetus auratus* Waterhouse, 1839, the marsupials of the families Macropodidae and Potoroidae, and the maned rat (Bauchop and Martucci 1968; Langer 1980, 1988; Kay and Davies 1994; Stevens and Hume 1995; Hume 1999; Naumova and Zharova 2003; Karasov and Martinez del Rio 2007). The foregut system’s functioning is based on a prolonged retention time and microbiological fermentation of digesta in the voluminous stomach. The stomach of the Laotian rock rat is significantly enlarged due to a number of sacs along its entire length. It is possible that the extension of sac-like stomach compartments is a consequence of the adaptation of alimentary tract to storage and digestion of low-quality vegetable food. This assumption is additionally supported by a considerable quantity of aggregative lymphatic nodules in the stomach walls. The presence of the ventricular groove may be directly connected to regurgitation, which is common in foregut mammals (Langer 1988), and/or to using it during the lactation period. A multi-chamber structure of the rodents’ stomach was shown (Vorontsov 1963, 1979) to be a direct species adaptation to consuming food containing a great proportion of structural carbohydrates.

The stomach of the Laotian rock rat is most similar to that of the extant direct descendants of Miocene mammals, viz. the diprotodonts, in particular, representatives of the genera *Macropus, Thylogale, Petrogale, Dendrolagus, Lagorchestes, Aepyprymnus*, and *Potorous* (Langer 1988; Hume 1999). A similar structure of the stomach has also been found in some folivorous primates (Stevens and Hume 1995; Caton 1999). All the aforementioned mammals have the three-partite stomach, containing *saccus gastricus* (sacciform forestomach), *tubus gastricus* (tubiform forestomach), and *pars pylorica* (hindstomach) (Caton 1999; Langer 1988). The entire stomach of the Laotian rock rat practically consists only of the tubiform forestomach following Langer's terminology. *Pars pylorica* and sacciform forestomach are small.

The structure of intestines confirms a leading role of the stomach in rat's digestion. Small intestines become strongly developed when the stomach plays a basic role. This is expressed in the extension of the length and absorbing surface area of small intestines (Chivers and Hladik 1980; Chivers 1989; Barboza et al. 2009). Indeed, compared with other intestine sections, this section is mostly developed in the Laotian rock rat. In total, a relative length (body length/intestine length*100%) of the Laotian rock rat's intestine lies within the limits of 500–600%. Such the proportion is common in many herbivorous rodents and is higher only in the voles (*Myodes, Microtus*) that have minimal body sizes among all herbivorous mammals (Shvarts et al. 1968; Panteleyev et al. 1990). A small caecum without *haustra* is an ancient feature of the herbivorous rodents (Perrin and Curtis 1980), and this type has been found in the Laotian rock rat. A simple caecum is also typical for the marsupials and primates having the forestomach (Hill and Rewell 1948, 1954).

Nutritional features of animals indicate the most probable reason of the origin of homoithermic foregut animals. Most of these species, including the Laotian rock rat, are highly selective herbivores of tropical forests, namely, frugivores and browsers. Leaves, shoots and fruits of tropical plants are the main food of these animals (Hume 1999; Bodmer and Ward 2006; Kuznetsov 2006; Hohmann 2009; Hayssen 2009, 2010). Leaves of dycotyledonous plants form the dietary basis of the examined Laotian rock rats. Remains of seeds and underground vegetable parts have also been regularly recorded. Animal food in the form of insect larvae was exceptionally seldom. Thus, the Laotian rock rat is a partially folivorous rodent. Generally, folivorous mammals have small home ranges (Fleagle 1988), and it is likely that this peculiarity allows the Laotian rock rat population to survive in a limited territory.

Certain small foregut mammals accomplished a complete turn to using high-caloric foods. The digestive system of small diprotodonts, such as the bettongs and potoroos, resembles that of the Laotian rock rat. However, they are larger than the rat. These potorid species are micophagous (fungus-eating) mammals (Seebeck and Rose 1989; Hume 1999; Claridge et al. 2007). They inhabit arid regions, and therefore feeding on subterranean fungi, tubers and rhizomes is only a nutritional adaptation of this group. The smallest and most primitive representative of diprotodonts – musky rat-kangaroo (*Hypsiprymnodon moschatus* Ramsay, 1876) – is similar to the Laotian rock rat in its weight and it also inhabits tropical rain forests (Claridge et al. 2007). However, the musky rat-kangaroo eats mainly fruits, seeds and litter-dwelling invertebrates; this is why its simple unilocular stomach retained unchanged (Langer 1988; Claridge et al. 2007).

The nutrition on low-caloric vegetable food imposes significant limitations in the development of organism's form and functions. While studying body weight of arboreal folivores, its lowest limit has been defined. It is the so-called Kay's threshold, stating that the body weight of folivorous mammals must be no less than 700 g (Kay 1984; Cork and Foley 1991; Cork 1994). This rule is based on the negative correlation: viz, if body weight of homoithermic mammals decreases, heat loss and metabolic rates per the body weight increase sharply (Bradley and Deavers 1980; Clutton-Brock and Harvey 1983). Such metabolic increase cannot be compensated by a low-caloric vegetable diet which is imperfectly digested in non-ruminant foregut mammals. In these animals, maximally effective digestion of vegetable food and nutrient absorption depend largely on the time of digesta retention in the foregut and accordingly on its size (Mackie 2002; Brown and Sibly 2006; Karasov and Martinez del Rio 2007; Barboza et al. 2009). The latter depends on the size of mammals themselves. Small herbivorous rodents with the hindgut fermentation can overcome this dimensional threshold not only due to the extension of the inner gut surface, but also due to the increase of passage time, the amount of food consumed and a higher efficiency of its use (Foley and Cork 1992; Lee and Houston 1995).

A long-term evolution of the foregut under conditions of wet tropic forests resulted in obtaining of significant advantages to digest browse. This is associated with a greater effectiveness of the foregut system than the caecum-colon system in the detoxication of plant leaves and other vegetable food that contain lots of toxic secondary metabolites (Janis 1989; Cork and Foley 1991; Mackie 2002; Iason and Villalba 2006). Thus, with rare exceptions, small mammals having the colon-caecum system cannot use foliage of tropical trees as a basic source of their food. On the contrary, small foregut fermenters cannot effectively digest grasses, and this is why these mammals do not live in open-habitats where monocots prevail (Cork and Foley 1991).

The lowest threshold of body weight among the folivorous rodents was found in the rodents with hindgut fermentation, such as *Petaurista* and *Anomalurus* (Cork and Foley 1991), and in the rodent *Lophiomys imhausi* with the foregut one (Naumova and Zharova 2003). Among other folivorous mammals, the lowest threshold was determined for the New Guinean ringtail possums (*Pseudochirulus mayeri* Rothschild et Dollman, 1932*, P. canescens* Waterhouse, 1846) that weight less than 500 g. Yet they also belong to the hindgut fermenters and consume mosses, lichens, fungi, and pollen more often than leaves (Hume et al. 1993; Hume 1999). The maned rat also feeds on various plant forages (Naumova and Zharova 2003). The body weight of the Laotian rock rat is less than 500 g (Jenkins et al. 2005). It is the smallest folivorous rodent and the smallest herbivorous mammal possessing the enlarged forestomach. In order to maintain metabolism at such body weight, folivorous mammals should have a number of physiological and digestive adaptations. To date, such adaptations of this rodent have not been studied yet. A maximally possible stomach development in small foregut mammals seems to be the main adaptation required for increasing the digestion time of vegetative plant parts and to retain temporally the ingesta during the period when an animal does not consume. Small foregut marsupials have the stomach not exceeding 10–16% of the total body weight (Langer 1988). For the smaller Laotian rock rat this index is higher by 1.5–2.0 times. The maximal stomach weight reaching 25–30% of the body weight has been found only in large mammals, such as ungulates with the better developed foregut fermentation (Langer 1988).

The merycism, low basal metabolic rates, a low mobility and locomotion can be considered additional adaptations that maintain the metabolism, energy balance and functioning of digestive system in the Laotian rock rat. Many of these adaptations are well-known and are typical for certain leaf-eating marsupials, edentates and primates (Chapman and Chapman 1991; Hume 1999, 2006). Such the adaptations are a direct consequence of low digestive effectiveness while fermenting leaves. In small mammals, lowering of the metabolic rate may also lead to enhanced digestive efficiency (Veloso and Bozinovic 1993).

If the Laotian rock rat really has such types of adaptations, then this species is likely to be rather vulnerable. The main restricting factors for the rodent could be: its diet limited only to leaves and fruits of tropical dicotyledonts; its low fertility; its ability to live exceptionally in warm climate; and the need of shelters to be safe from bad environmental conditions and predators and where the young can raise.

Digestive system of the Laotian rock rat in the light of evolution of foregut mammals

The origin of herbivorous mammals and their active radiation initially took place in the Eocene when angiosperms began to dominate in tropical and subtropical forests (Kemp 2005). Originally, tropical herbivorous mammals were represented by frugivores only (Bodmer and Ward 2006). Later on, they started to adjust to vegetable food. In the Eocene, there were favorable conditions for the emergence of true folivorous mammals, because the warm period of this epoch was shown (Collinson and Hooker 1991; Janis 2000) to have contributed to a diversification among smallish terrestrial herbivores in tropical forest habitats.

The suborder Hystricomorpha has been presented in its evolutionary history by a high species diversity: viz., the Hystricidae in Eurasia, the Caviomorpha group in South America, and the Phiomorpha group in Africa. The Hystricognathi group originated in Asia, though its early evolutionary history has been poorly studied yet (Marivaux et al. 2002; Sallam et al. 2009). The Diatomyidae group was formed and evolved in the late Eocene – early Oligocene in South Asia (Marivaux et al. 2004; Dawson et al. 2006). At that time, a wide radiation of browsers started in tropical forests, many of them were tree-dwellers (Collinson and Hooker 1991; Kemp 2005). Tropical forests extended through African and Asian territory, therefore representatives of the Diatomyidae and their putative relatives Ctenodactylidae inhabited vast areas during Oligocene-Miocene. Their remains have been found in Pakistan, India, Thailand, China, Mongolia, Japan, Saudi Arabia, Morocco (Baskin 1996; Dawson et al. 2006; Schmidt-Kittler et al. 2007). These rodent groups diverged rather early from the general stem of Rodentia, therefore they differed greatly from other recent rodents in a considerable number of features (Beintema et al. 1991; Dawson et al. 2006).

Paleontological records revealed that the hystricognathous rodents had a wide morphospace and occupied various ecological niches. Some representatives of this group were of tremendous size and weighted up to several hundred kg, that, in its turn, contributed to consuming large amounts of low-quality vegetable food (Alexander 2003; Sanchez-Villagra et al. 2003; Millien 2008). The increase of body dimensions simultaneously with simplified dentition and bilophodonty was also common for the later Diatomyidae (Flynn 2007). The primary trophic trend of rodents' evolution was a transition from rich – caloric to low-caloric vegetable forages (Vorontsov 1963, 1979).

It was the period when the Diatomyidae group was forming, specific conditions which induced the origin of such morphological structure as the enlarged forestomach emerged. Most of recent foregut ruminants and non-ruminants were browsers. Thus, it is safe to assume that if the majority of Miocene herbivorous mammals of all systematic groups were browsers, they should have had foregut fermentation. Although primary rodents and primates were fruit- and seed-eaters, it is likely that the emergence of forestomach became one of the first adaptations of these mammals to eating plants, principally soft vegetable foodstuffs (Benefit 2000; Agusti and Anton 2002). It could have appeared only in the tropical climate where energy costs maintaining metabolism are minimal. Perhaps, this is why the earliest foregut mammals had small body sizes (Clauss et al. 2003) and a great adaptive radiation of the Diatomyidae in tropical forests took place at that historical period. However, a subsequent extinction of the Diatomyidae at the end of Miocene caused an isolation of the Laotian rock rat in a small tropical refuge, which resulted in conservation of the form and functions of its digestive system. As was argued by Shvartz (1977), morpho-physiological modifications of fully settled animals are sharply limited under stable environmental conditions. The latter generalization could explain an irreversibility of cardinal changes of the digestive tract of the Laotian rock rat, though certain morphological modifications could apparently have emerged. Such modifications are usually associated with changes of body and organ dimensions rather than with a radical change of the principal structure of organism systems, which has been demonstrated for island mammals (Berry 1996; Millien 2006).

It is known that many morphological features of mammal groups emerged convergently, for instance, the origin of hystricognath taxonomical characters in different rodent groups (Simpson 1980). There are many paleontological examples of convergence and parallelisms of morphological characters at early evolutionary stages among certain groups of mammals (Perrin and Curtis 1980; Vorontsov 1982; Agadjanian 2009). A convergent origin of some structures of various digestive systems can be hidden (Gorgas 1967). However, morphological adaptations to the herbivory and gut microbiota composition proved to represent a convergent evolution among the mammals with a similar gut occupying similar trophic niches (Ley et al. 2008).

Different systematic positions and origin of mammals possessing the foregut with pregastric fermentation can also be evidence of the convergent evolution of such digestive systems (Chivers and Hladik 1980; Langer 1988; Karasov and Martinez del Rio 2007; Arendt and Reznick 2008). The convergent evolution seems to explain the fact that structure of the digestive system of the Laotian rock rat is most similar not to extant rodents, but to representatives of other mammalian groups, such as marsupials. Such parallelism seemed to have been caused by the similarity in trophic niches occupied by these animals during the historical period when analogous changes in the structure of gastrointestinal tract started to emerge. The convergent similarity in stomach structure of marsupials, edentates, primates and ancient rodents appeared simultaneously in the Miocene when a strong adaptive radiation of folivorous mammals had occurred (Langer 1988; Chivers 1989). The bilophodont pattern of cheek teeth has been discovered in the Laotian rock rat, kangaroos, and the cercopithecoid monkeys (Benefit 2000; Dawson et al. 2006; Janis 2008), i.e. the convergence in tooth structure of the descendants of Miocene folivorous mammals is also evident in the initial section of digestive system. Usually, convergent development is a response of certain populations/species to similar environmental conditions constituting the adaptive zone of these animals. Animals of various origin inhabiting similar adaptive zones in different continents can have likeness of morphological features that is connected with the ability of genotype to change unidirectionally in compliance with similar variability of the environment (Simpson 1944).

The Early Miocene was characterized by significant warming that caused the expansion of tropical forests (Kemp 2005). Probably, these environmental conditions predetermined the emergence of first eutherian foregut fermenters and such phenomenon as folivory (Fleagle 1988; Hume 1999). The peak of global warming took place in the Middle Miocene and, as a result, the productivity of plant communities increased and mammal diversity culminated, including the foregut mammals (McFadden 2000b; Kemp 2005). Namely, at that time, the highest species richness of browsing ungulates, woodland savanna inhabitants, was recorded (Janis et al. 2004). Yet the divergence of foregut marsupials, the large browsing macropodids and smaller potoroids occurred (Hume et al. 1989). These two groups were direct descendants of the possum-like arboreal mammals, dwellers of tropical rain forests (Hume 1999; Claridge et al. 2007). It is possible that other ancient folivorous rodents, for instance, *Melissodon* hamster (Vorontsov 1982; Agusti and Anton 2002), could have had foregut fermentation. Later, the descendants of foregut animals dispersed to other climatic zones and adapted to other ecological niches. However, nowadays the majority of these mammals inhabit forest and forest-like ecosystems within the tropic zone (Langer 1988).

The end of the Miocene was characterized by the beginning of global cooling, drying and seasonality of the climate (Dutton and Barron 1997; MacFadden 2000a,b; Agusti and Anton 2002; Kemp 2005). Those changes affected the composition and distribution of vegetation. In the Miocene, the zone of tropical forests began to sharply reduce. Consequently, the area of mammal species with foregut fermentation, of which basic foods consisted of plant leaves and fruits, also declined. First of all, this is relevant for small-sized species. Changes of plant communities occurred in the Miocene under climate fluctuations, which occurred at the beginning of dominance of the C_4-type open-habitat plants (Cerling et al. 1997; MacFadden 2000a; Janis 2008; Edwards et al. 2010). Towards the Late Miocene, approximately 7–11 mya, the plant communities consisted mainly of open-habitat grasses began to dominate in landscapes of different continents (Jacobs et al. 1999; MacFadden 2000a; Retallack 2001; Janis et al. 2004; Stromberg 2005). This resulted in changes of the composition and abundance of herbivores species, as well as in the modification of their habitus and the structure of alimentary tract. A number of the frugivorous and obligate arboreal mammals also reduced (Janis 2000). Probably, the dentition and foregut system of micromammalia turned out to be ineffective for grinding and digestion of monocots which accumulate great quantities of lignin, cellulose and grit. Therefore, the foregut mammals with pregastric fermentation were less competitive as far as food resources concern (Kinnear et al. 1979). This is why under the conditions of savanna-like landscapes only large mammals with the foregut digestive system could have survived and evolved. They had to increase their body size and also the size and number of chambers in their composite stomach. At that time, ungulates with highly-specialized grazing adaptations emerged and became widespread in the open savannas (Janis 2008). Only thanks to their large body dimensions large marsupials such as macropodids could have survived and adapted to new landscapes and forage resources. Yet, it was partly possible because there was no competition with other large herbivorous mammals. Besides, a series of physiological and morphological adaptations (e.g., low turnover rates of proteins and water, the flexibility of cardiovascular system and lung functions) contributed to their success. Many other representatives of marsupials with the sacculated stomach had become extinct by the end of the Miocene (Hume 1999), and the number of ungulates sharply reduced (Janis et al. 2004). Almost all the representatives of Diatomyidae, many folivorous and frugivorous primates, sloths and other mammals also vanished completely (Janis 1993; Benefit 2000; Kemp 2005; Dawson et al. 2006). By the end of the Miocene, the colon-caecum fermenters had began to occupy trophic niches of the plesiadaptiforms, small ungulates, and other small forestomach mammals (Fleagle 1988; Chivers 1989; Langer 1991; Stevens and Hume 1995; Janis 2000).

Nowadays, a few species of Ctenodactylidae closely related to the Laotian rock rat still exist in North Africa. Small body dimensions precluded the *Ctenodactylus* ancestors from forming of the enlarged forestomach, and these animals retained the simple unilocular stomach. Due to a weak specialization of their foregut region, later on these rodents developed the colon-caecum system of intestines adapted to digest vegetable diets.

Descendants of some small mammals with the foregut fermentation were also able to survive within those areas where tropical forests used to grow originally. However, in order to survive, the bettongs and potoroos had to adapt to living in arid climate and to feeding on the available forages of fungi and plant tubers only. All the other non-ruminant foregut fermenters remained only within the territory of extant tropical forests.

CONCLUSION

The Laotian rock rat is an example of the evolution of foregut fermenters among the rodents. It is a unique representative of the mammalian folivores with the enlarged forestomach. Only few rodent species use foliage as food. The environment conditions of the Miocene determined the basic features of the digestive system of all the folivorous mammals. The digestive system of the Laotian rock rat is determined and stabilized by its environment. This animal seems to have survived to date due to anatomic and physiological adaptations that guarantee its fitness in the ecological niche currently occupied by this species. However, a narrow specialization in the structure of its digestive system determines limitations of further evolutionary development of the taxon and even its survival. For instance, the large and highly specialized forestomach might be a reason for species' extinction, should sharp changes of environmental conditions leading to changes in available forage resources take place. Reduction of the area of occurrence and extinction of the majority of Diatomyidae seemed to have been the main reason for isolation of the Laotian rock rat within the current limits of small refuge with limestone rocks and karst caves. Here the rodent could avoid a competition with other herbivorous mammals and a threat from predators. Thus, the Laotian rock rat practically as if transformed into an "island species". Many island species are known to maintain derivations from the baseline of evolution within their systematic group for rather long time (Shvartz 1977). Since the end of the Miocene, the majority of rodents quickly developed the hindgut fermentation in order to adapt to the changing climate, new landscapes and nutrition on low-quality vegetable foods. However, the Laotian rock rat, as a "living fossil", probably retained its digestive system unchanged. This is why its digestive system differs greatly from other recent rodents. As unique genetic and biochemical parameters of the hystricognaths have been found, the common monophyletic system of the rodents' origin is now in doubt (Graur et al. 1991, 1992; Luckett and Hartenberger 1993). It is safe to conclude that further studies on the digestive and other systems of the Laotian rock rat will enable us to re-consider the systematic status and phylogenetic position of the Hystricomorpha.

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