=== **ANIMAL AND HUMAN PHYSIOLOGY** ===

Functional Diversity of Morphologically Similar Digestive Organs in Muroidea Species

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Abstract—We examine possible ways of functional adjustment of morphologically similar alimentary tracts in rodents with different dietary specializations. We study the structure of stomach and gut epithelial surface as well as the features of its colonization with microorganisms in five gerbil species: *Psammomys obesus, Meriones crassus, Gerbillus henleyi, G. andersoni*, and *G. dasyurus*. Data on the morphological diversity of mucosa-associated microbiota have been obtained and confirmed by the results of previous microbiology studies. Species differences in chymus acidity associated with dietary specialization have been determined. Variations in the activity of the endoglucanase microbial enzyme, which is crucial for rodents fed on cellulose-containing food, have also been detected. The importance of microbiota for functional adaptations to various food types in rodents with morphologically similar digestive tracts has been evaluated.

INTRODUCTION

A semiglandular stomach is a mandatory attribute of the digestive tract of all muroid rodents (Muroidea), regardless of their dietary specialization. Cornification of a part of the gastric epithelium in rodents results from the evolutionary interaction of animals with microorganisms obligatory for the digestion of plant food. The morphology of the semiglandular stomach is extremely diverse and is usually associated with the role of cellulose-containing food in the diet of rodents (Vorontsov, 1967, 1982). Voles (Microtinae), highly adapted to herbivory, have a bilocular stomach; the nonglandular part of it is isolated into a separate chamber, and the glands either occupy the entire right half of the stomach or are concentrated in the central part (discoglandular stomach). However, sometimes voles do not show an obvious association between the structure of the stomach and intestines and food specialization. For example, *Microtus arvalis* and *Ellobius talpinus* with the discoglandular stomachs consume food with different fiber contents (Naumova, 1981; Naumova et al., 2018).

Dietary specialization of the other group of rodents, gerbils of the family Gerbillidae, also did not significantly affect the morphology of the stomach and intestines (Behmann, 1973; Naumova, 1981; Snipes, 1982; Naumova et al., 2011). All gerbils are characterized by a single-chamber semiglandular stomach and a cecum with the same structure of the ileocecal junction. The main morphological features that ensure the adaptation of individual species of the group to certain food include the size of the intestinal parts (Naumova et al., 2011). Despite the fact that gerbils are similar to voles in the range of dietary specialization, although they live in environmental conditions of limited food resources, high temperature, and moisture deficit, functional aspects for their food adaptations have not yet been disclosed. It is obvious that it is impossible to decipher the adaptation of animals to changing environments using only morpho-ecological approaches. An understanding of the functional role of the intestinal microbiota in different aspects of the host's life has emerged only in the past two decades due to the use of microbiological, biochemical, and other research methods (Kohl et al., 2011; Kohl and Carey, 2016).

The aim of this work is to specify the functional features of the microbiota that ensure the assimilation of different types of food with the example of gerbils, a group of rodents with a homogeneous structure of the digestive tract and different food specialization.

MATERIALS AND METHODS

Five gerbilline species inhabiting the Negev Desert have been studied: *Psammomys obesus*, *Meriones crassus*, *Gerbillus henleyi*, *G. andersoni*, and *G. dasyurus* (2–4 individuals of each species). These rodents are classified as granivorous (Bar et al., 1984), with the exception of *P. obesus*, which consume exclusively green parts of plants (Daly and Daly, 1975). On a JSM 840 Å scanning electron microscope (Japan), the macro- and microrelief of the surface of the mucous

membrane of the forestomach, cecum, and colon were studied. Tissue samples were washed with isotonic sucrose solution and fixed with 3% glutaraldehyde. After treatment with alcohols and acetone, the samples were dried in air and sprayed with gold. The acidity of the gastric content was determined with a universal indicator paper at the apex of the fundus, in the nonglandular part of the stomach near the border fold, in the area of the fundus glands, and in the pylorus, as well as in the cecum body.

The activity of the microbial enzyme endoglucanase was measured in *P. obesus*, *M. crassus*, *G. andersoni*, and *G. dasyurus* by a viscosimetric method (Sinitsyn et al., 1990). The use of this method in studies of the activity of enzymes of the cellulase complex allows us to compare the results obtained with previously published data. Samples of the chyme from the forestomach, cecum, and colon were transferred in preweighed Eppendorf tubes containing 1 mL of 86% glycerol (in total, nine individuals were examined); the sample weight was determined by repeated weighing. The analysis of the results of endoglucanase activity determination was carried out in the software environment R (R Core Team, 2019) using the RKWard graphical interface (Friedrichsmeier, 2018). For primary data processing, both basic and additional R packages were used: dplyr (Wickham et al., 2019) and tidyr (Wickham and Henry, 2019) for primary data processing; ggplot2 (Wickham, 2016) for graph creation; and also original designed functions.

RESULTS

Epithelial Surface and Associated Microbial Communities

The surface of the keratinizing epithelium of the forestomach of gerbils forms folds of various sizes. The large ones change their configuration due to peristalsis and smooth out as the stomachs fill. Small folds, formed by the surface layers of the epithelium, are constantly present and create a fine mesh relief (Fig. 1), which can change due to the desquamation of superficial epithelial cells. Such an architectonics of the epithelial surface of the forestomach is typical for all the gerbil species studied.

The forestomach of rodents, as well as the cecum and colon, are abundantly populated with symbionts, some of which are attached to the epithelial surface in order to avoid washing out by the contents passing through the digestive tract. A review of studies on normal microbiota of rodents (carried out mainly on mice and rats), maintained on commercial pelleted foods, showed that its composition was ubiquitous (Tannock, 1997). According to the available data, in the muroid species studied the proximal parts of the digestive tract are usually dominated by lactobacilli with a developed mechanism of attachment to the keratinizing epithelium. The distal parts are dominated by various representatives of the genera *Enterococcus* and by *Escherichia coli*. Although detailed studies of the microbiota in various species of wild rodents have rarely been carried out, there is reason to believe that many muroid species have a specific microbiota (Perrin and Kokkinn, 1985; Naumova, 1990). A visual examination on a scanning electron microscope of the associations of bacteria colonizing the epithelium of the digestive tract of gerbils showed their great diversity even just in morphological features.

In *P. obesus*, the epithelium-associated microbiota of the forestomach is represented mainly by bacilli and fusiform bacteria. Bacilli 1−2 µm long are present in all gerbils studied, but most abundantly they colonize the epithelium in *M. crassus* and *G. henleyi*. In the forestomach microbiome associated with the epithelium, corynemorphic bacteria were recorded in *G. andersoni* and cocci, in *G. dasyurus*. In general, in all gerbils, epithelium-associated bacilli predominate in the forestomach.

There are open crypts on the surface of the mucous membrane of the cecum (Fig. 2); the mucous membrane around the crypt openings forms concentric folds. In all gerbils the microbiota of the cecum mucous membrane is represented mainly by fusiform bacteria and cocci, while filamentous bacteria are found in *G. andersoni*. In the colon, the highest density of bacteria is observed on the surface of the mucous membrane of the mesenteric wall; on the oblique folds, bacteria are concentrated in the crypt openings (Fig. 3). In *P. obesus*, the colon microbiota is more diverse in comparison to those in the forestomach and cecum. In this species, large (4−5 µm) bacilli and curved rod-shaped bacteria predominate in the colon; in *M. crassus*, fusiform bacteria and cocci do. In three species of the genera *Gerbillus*, the mucous membrane is colonized by the most shape-diverse bacteria; in *G. andersoni* and *M. crassus,* very large (>19 µm) rod-shaped bacteria are also found.

Acidity of the Stomach and Cecum Content

The fundus is characterized by a close to neutral pH in the herbivorous and largest gerbil *P. obesus*. This pH is maintained relatively uniformly throughout the forestomach, slightly increasing near the border with the glandular part. In the zone of the fundus glands, acidity rises sharply and reaches a maximum (pH 1.0) in the antral part, providing a very high gradient (Table 1). In other species, the forestomach is characterized by a weakly acidic pH level (pH 4.0−5.0), but high acidity is also maintained in the antral part. Only in the small granivorous *G. henleyi* is there no dramatic change in acidity from the fundus to the antrum, as well as a sharp border that creates different environmental conditions in the forestomach and the glandular part of the stomach. The zone of the fundus glands and the antrum in all species is characterized by high acidity (pH 1.0−2.0). In the cecum the pH is very stable and
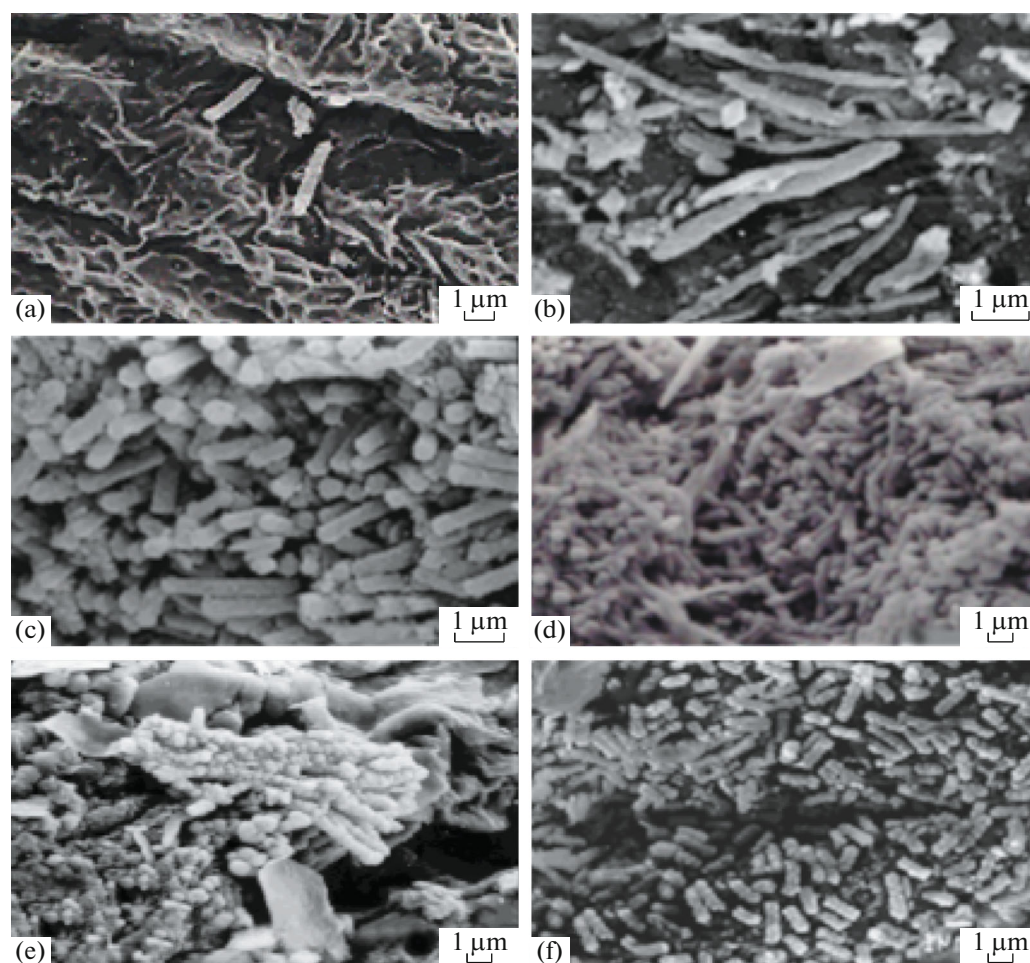
Fig. 1. Forestomach epithelium of the gerbils. (a, b) *P. obesus*; (c) *M. crassus*; (d) *G. dasyurus*; (e) *G. andersoni*; (f) *G. henleyi*; for Figs. 1 and 3.

is slightly alkaline in all gerbils studied. Only *G. henleyi* has a lower pH in the cecum.

Endoglucanases

Endoglucanase activity (EA) characterizes the hydrolysis of amorphous β-glucans, topographically associated with fibers, and makes these fibers available for further hydrolysis. The diagram (Fig. 4) presents the EA values of microsymbionts inhabiting the forestomach, cecum, and colon in four gerbil species and, for comparison, similar data for two species of *Microtus* sp. obtained on large samples (Varshavskii et al., 2004). As the sample size was quite small, the averaged data allows us to compare results only at the order level of values. Nevertheless, some general characteristics of EA in voles and gerbils can be noted. In the forestomach of all the species studied, except for *G. dasyurus*, EA values were 0.85−2.15 μmol/min, which is close to the average values for the *Microtus* voles. The absence of EA in the forestomach is common for all the species studied. EA values in the cecum vary from 1.07 to

8.01 μmol/min. Unexpectedly, high EA values, comparable to those in highly specialized herbivorous voles, were found in *P. obesus*. EA values in all species studied are the highest in the cecum.

In general, endoglucanase activity in the digestive tract of the gerbils studied corresponds to the previously obtained data on the distribution and localization of cellulases in other small mammalian phytophagous species: the minimum activity is in the forestomach; the maximum, in the cecum, while intermediate is in the colon. *P. obesus* is an exception.

DISCUSSION

Diet

The range of diet specialization within the group of gerbils is quite wide, from strictly granivorous to herbivorous. Most species of gerbils inhabiting the deserts of Asia Minor and Central Asia belong to the group of consumers of concentrated feed, but occasionally consume small amounts of grass (Abramsky, 1989). Exceptions are *Rhombomys opimus* and *P. obesus*,
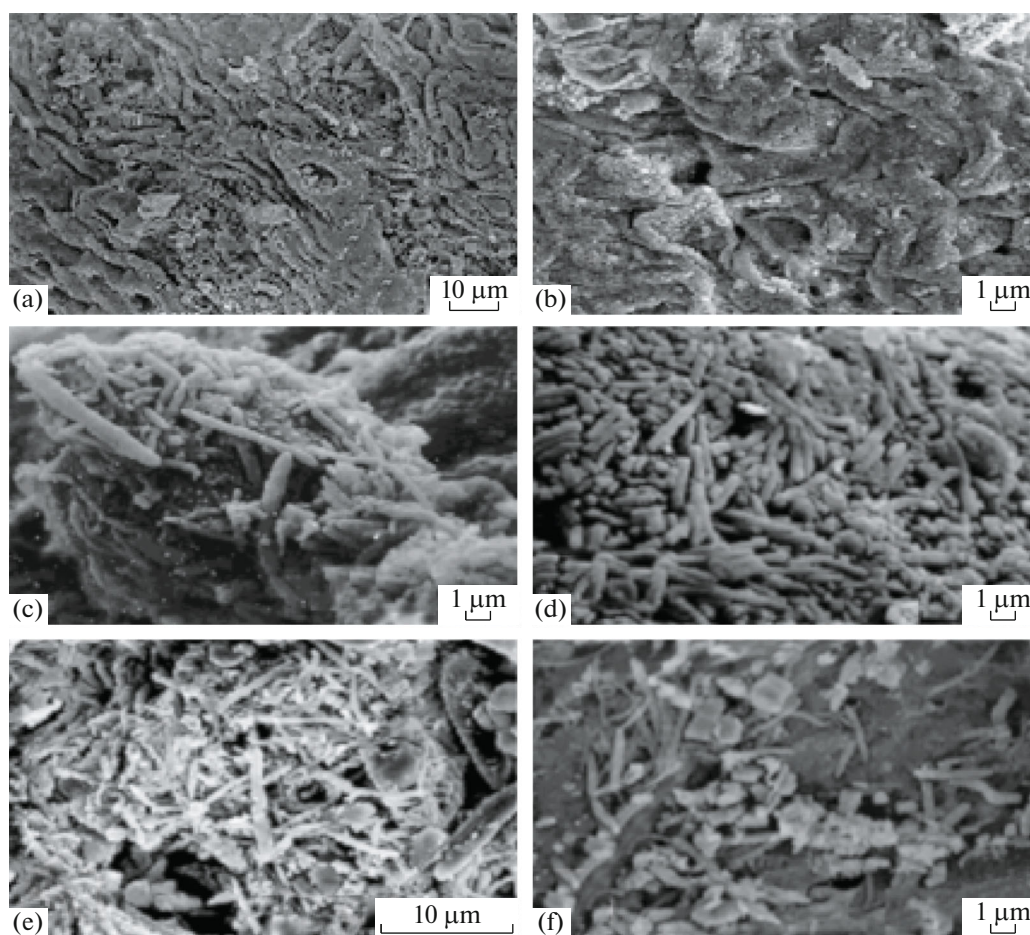
Fig. 2. Cecum epithelium of the gerbils. (a) *P. obesus*; (b, c) *M. crassus*; (d) *G. dasyurus*; (e) *G. andersoni*; (f) *G. henleyi*.

which are tolerant to structural carbohydrates in plants (Daly and Daly, 1973; Fedorova and Dubrovskii, 1987; Degen et al., 2000). The development of digestive organs in this group of rodents was associated with the exploitation of the poor plant food reserves in deserts and semi-deserts under conditions of water restriction. The single-chamber semiglandular stomach, typical for gerbils, was considered less adapted for

Table 1. Acidity of the stomach and cecum contents in gerbils (pH)

Species	n	Stomach				Cecum
		fundus	border zone	fundus gland zone	antrum	
P. obesus	4	5.88 (5.0–7.0)	5.00 (4.0–6.0)	1.00 (1.0)	1.00 (1.0)	7.00 (7.0)
M. crassus	4	4.75 (4.0–5.0)	4.25 (4.0–5.0)	1.50 (1.0–3.0)	1.50 (1.0–3.0)	7.00 (7.0)
G. dasyurus	3	4.33 (4.0–5.0)	4.50 (4.0–5.0)	1.83 (1.0–2.5)	1.00 (1.0)	7.00 (7.0)
G. andersoni	2	5.00 (5.0)	5.00 (5.0)	1.50 (1.0–2.0)	1.00 (1.0)	7.00 (7.0)
G. henleyi	2	4.00 (4.0)	–	3.00 (3.0)	1.50 (1.0–2.0)	6.25 (6.0–6.5)

n is the number of animals.
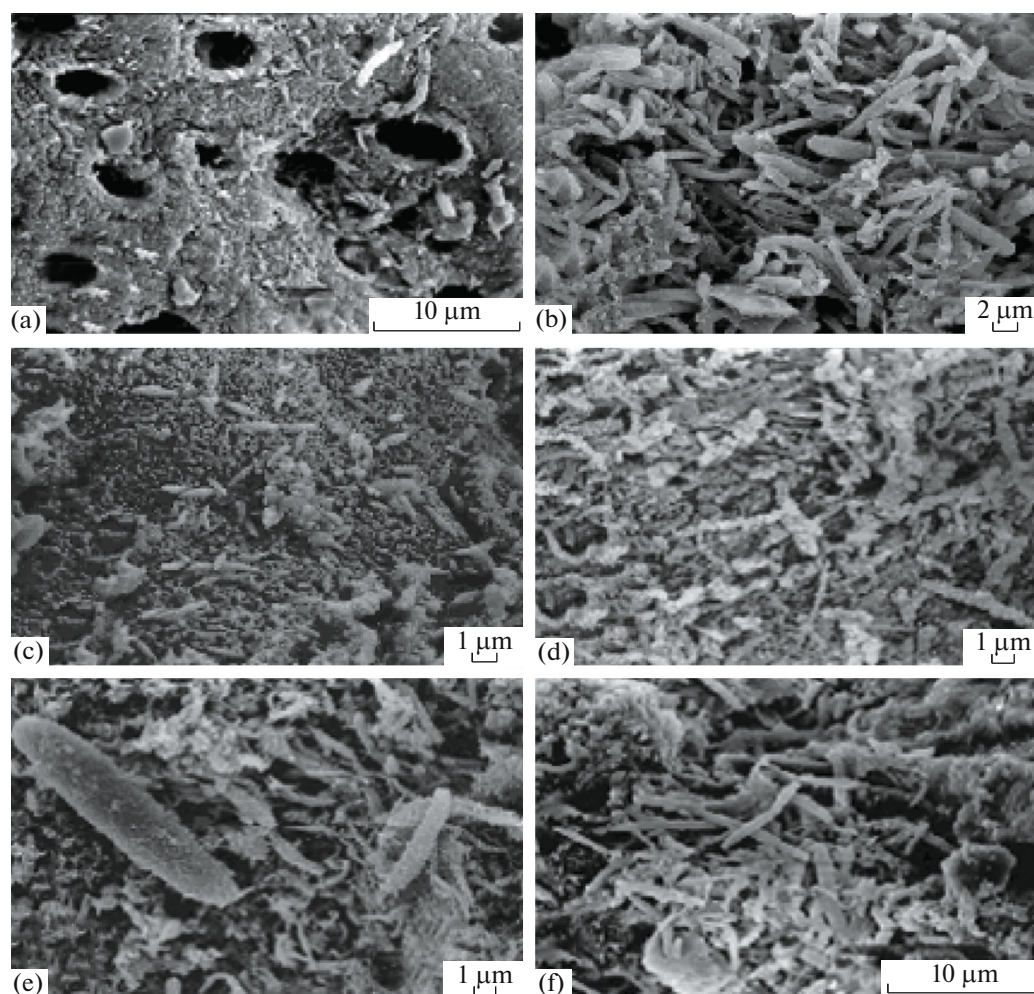
**Fig. 3.** Epithelium of the colon of the gerbils.

the fiber forage assimilation in comparison to the bilocular stomach of the voles. The increase in the area of the keratinizing epithelium in the single-chamber stomach was considered for a long time as an adaptation to the increasing role of cellulose feed in the diet of rodents. However, a survey of a large number of stomachs of gerbils showed that the ratio of the areas of the glandular and keratinized epithelium is quite variable and largely depends on the nature of the filling of the stomach and the distribution of the food mass in it. In gerbils, adaptations to the forage with differ chemical compositions and nutritional value are realized not only by optimizing the size of the intestinal parts responsible for the assimilation of concentrated or fiber feed, but also due to the specific functioning of microbial communities and endogenous secretions.

One of the main indicators influencing the structure of microbial communities is the quality composition of the food. Thus, dietary changes in laboratory mice significantly alter the microbial diversity (Carmody et al., 2015). Up to 64% of the innate microbiota species was preserved in the wild rodents after being

transferred to captivity (Kohl and Dearing, 2014). More than that, the composition of microbial communities is largely determined by the colonization of the digestive tract by transit bacteria associated with the plants consumed (Kuznetsova at al., 2013). A similar relationship between the microbiota and characteristics of the food consumed is confirmed by the visualization of the morphological diversity of epithelium-associated bacteria in the gerbils and the enzymatic activity of microbial communities.

Composition of Microbial Communities

Mammals, depending on their food specialization, are hosts for microbial communities of different taxonomic composition and functions (Ley et al., 2008; Muegge et al., 2011). The keratinizing epithelium of the forestomach and the mucous membrane of the large intestine form an optimal microrelief for bacterial colonization. Microcells of the forestomach epithelium and oblique folds of the Kerckring relief prevent bacteria from being washed out during the move-
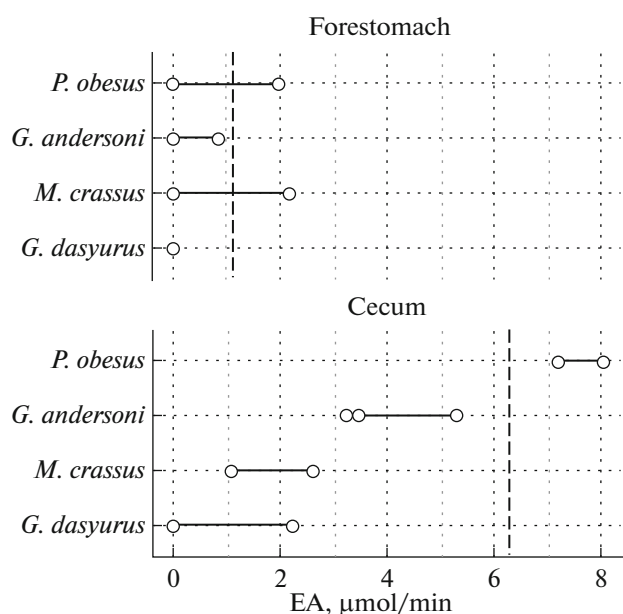
Fig. 4. Endoglucanase activity in the forestomach and cecum of gerbils *P. obesus*, *G. andersoni*, *M. crassus*, and *G. dasyurus*. The vertical dashed line shows the median EA values of *Microtus* sp.

ment of the contents. The morphological diversity of the microbiota of the stomach and intestines demonstrated in gerbils was also confirmed by microbiological studies (Kuznetsova et al., 2013). Representatives of the genera *Bacillus*, *Arthrobacter,* and other corynemorphic bacteria, cellulolytic bacteria of the genera *Myxobacterales*, *Staphylococcus*, *Micrococcus*, *Bacteroides*, and *Aquaspirillum* were isolated from various organs of the gerbils' digestive tract. All these bacteria were isolated as dominant members of the communities, while *Lactobacillus*, representatives of the family Enterobacteriacea, genus *Bifidobacterium*, and some others made up 1% of all microorganisms found in the digestive tract of gerbils. *B. megaterium* and *Bacteroides* spp. are common inhabitants of the digestive tract of animals (Naumova et al., 2005).

In previous studies, it was found that gerbil species differ in the quantitative ratio of the representatives of different bacterial genera detected (Kuznetsova et al., 2013). In *M. crassus*, the number of representatives of the order Myxobacterales in the forestomach and colon was quite high; in all parts of the gastrointestinal tract examined, a large number of gram-negative bacteria of the genus *Aquaspirillum* were found. *Staphylococcus* and *Micrococcus* have also been found in the forestomach, cecum, and colon of *M. crassus*. Perhaps one of the reasons for the poor colonization of the forestomach epithelium in *P. obesus* is the localization of cellulolytic bacteria in the organ cavity directly on the substrate. A similar low level of bacterial colonization was observed in the stomach of the herbivorous *R. opymus* (Naumova, 1999). This fact could be con-

sidered as an important mechanism of adaptation to the food composition. The differences in the microbiota composition in phytophagous mammals of different taxa were also found using molecular genetic methods (Kohl et al., 2011). Microbial communities of the digestive tract are also known as a natural buffer for digestion under conditions of seasonal fluctuations in the quality of forage plants (Fon and Nsachlai, 2012). Specific relationships between hosts and their microbial communities can be formed during seasonal changes in the environmental conditions (Carey and Duddleston, 2014).

Acidity

Microbial colonization can be influenced not only by the nutrient composition and physical properties of the contents of the digestive tract and oxygen availability, but also by the pH level. The acidity of the gut content in rodents largely depends on the structure of the stomach (Kohl et al., 2013). The bilocular stomach of voles better than the single-chambered one provides a contrasting pH gradient, which is necessary to create different digestive conditions, alloenzymatic and symbiotic. A noticeable acidity gradient was noted for the herbivorous *Microtus brandtii* with a bilocular stomach (Naumova and Zharova, 1984). However, in the single-chambered semiglandular stomach in gerbils, a significant acidity gradient also can be created; in the largest gerbil *P. obesus* it amount to 7 pH units. The high acidity gradient in gerbils results from the dividing role of borderline and angular folds (Naumova et al., 2011), as well as the upper position of the forestomach relative to the glandular part in a living animal. The acidity gradient in small *Gerbillus* is not as sharp as in larger species due to the lesser morphological differentiation of the stomach.

The different pH levels in the forestomach of different gerbils ensure the fermentation of various plant substrates. In particular, a pH of 6−7, noted in the forestomach content of *P. obesus*, is optimal for glycan fermentation; at pH 4−5, the initial hydrolysis of the protein takes place. The differences in the morphology of bacteria colonizing the nonglandular epithelium and the different levels of EA correspond to these facts.

Enzymes

Structural carbohydrates are found in greater or lesser amounts in any plant food. In the digestive tract of most herbivorous mammals, a complex of symbiotic microorganisms has evolved. It is capable of hydrolyzing fiber to simple bioavailable sugars. The increased interest in the study of EA is explained by the high content of amorphous β-glucans in plant food (Rabinovich et al., 2001) and their availability for bacterial degradation, which makes them an easily digestible nutrient for the host. Bacteria decompose cellulose with the help of high-molecular-weight

extracellular structures called cellulosomes (Rabinovich and Melnik, 2000). Cellulosomes can be considered as molecular complexes consisting of many different enzymes that decompose ordered forms of cellulose and endoglucanase, which hydrolyzes glucan chains of cellular fibrils (Tokuda et al., 2005). Our results illustrate the high lability of the cellulase enzyme systems associated with the nutritional and metabolic characteristics of the hosts. Thus, in the diet of granivorous small gerbils, glycans are not an important nutrient, which corresponds to the low EA in representatives of the genera *Meriones* and *Gerbillus*, in contrast to *P. obesus*, in the cecum of which the EA is comparable to that in herbivorous voles.

The high morphological diversity of epithelium-associated bacteria of the digestive tract suggests the possibility of bacterial synthesis of a wide range of enzymes essential for the host. The microbiocenosis of the gerbils' digestive tract is important not only for the carbohydrate diet of gerbils. One of the main recently elucidated functions of microbial communities in the digestive tract of rodents was nitrogen fixation (Naumova et al., 2000; Kuznetsova et al., 2010, 2013). Nitrogenase producers of different taxa were found in several species of murid rodents, including three species of gerbils with different dietary specialization. Until now, the role of nitrogen-fixing microorganisms in providing the host with nitrogen has not been fully elucidated, but their participation in maintaining the nitrogen balance in the biosphere is obvious.

The digestive tract is abundantly populated by urealytic prokaryote symbionts, which hydrolyze urea. In the predominantly granivorous *Meriones meridianus*, the urease activity in all parts of the digestive tract was significantly higher than in herbivorous *Microtus socialis* (Stepankov et al., 2018). The functioning of urealytic microorganisms can provide a significant contribution to the water balance of animals by reducing the loss of water during urine excretion. In an arid climate, nitrogen recyclization reduces the mass of excreted urea and, consequently, the mass of excreted water (Brosh et al., 1987; Freudenberger and Hume, 1993).

Herbivorous gerbils of the deserts cover their water requirements by feeding on plant foliage (Degen, 1997; Degen et al., 1997) and having a sufficiently capacious cecum. Small granivorous species obtain water by oxidizing high-calorie nutrients, during which urea is released, which serves as a substrate for urealytic bacteria.

Adaptive Role of Microbiota

The absence of vivid specific features in the gut structure of gerbils is largely covered by the functional specificity of microsymbionts. Although gerbils' microbiota functions are not well understood, it is clear that the accumulation of a microbial mass in the stomach and intestines reduces the animal's requirements for dietary protein. The complex architectonics of the mucous membrane surface of the cecum and colon increases the efficiency of absorption of microorganism metabolites and water. According to the constitution of the colon mucosa, this gut part, like in other Muroidea, has a high separator activity, especially in *P. obesus* (Naumova et al., 2019). This function reduces the loss of microbial protein by the host due to the accumulation of microorganisms between the oblique folds of the mucous membrane, which prevents them from being washed out.

In phytophagous mammals interactions with microorganisms play an important role in the life of the hosts. The microbiota participates in the synthesis of microbial protein, which increases the nutritional value of food, which can occur both by nitrogen fixation (Naumova et al., 2000; Kuznetsova et al., 2010) and by urea recycling (Kennedy and Hume, 1978; Vecherskii et al., 2015). The most important function of microorganisms is the use of structural carbohydrates as a nutrient, which is confirmed by the data on the digestibility of cellulose-containing food by *P. obesus*, the most active consumer of the green parts of desert plants. This indicator in *P. obesus* is somewhat lower than in other herbivorous rodents (Batzli and Cole, 1979; Hammond and Wunder, 1991; Foley and Cork, 1992; Justice and Smith, 1992; Degen et al., 2000). In addition to nutrients, the succulent green parts of plants contain sufficient moisture to maintain life in arid conditions. Water deficit in the habitats of gerbils is one of the most important factors that affect the structural and functional specifics of the gerbils' digestive tract.

Structural transformations of the digestive tract of two widespread groups of small mammals (gerbils and voles) associated with the consumption of plant food have both similarities and differences. The similarities lay in formation of the nonglandular part of the stomach, the ileocecal junction, which partially isolates the cavity of the cecum, and the separator mechanism of the colon, which is the most important regulator of the movements of various food fractions. Against the background of this similarity, the less pronounced structure of the gerbils' digestive tract in comparison to the voles' makes it possible to consider gerbils as a generalized group of phytophagous rodents to a lesser extent than voles specializing in feeding on cellulose-containing food. Gerbils, which do not have clearly expressed species-specific differences in the structure of the digestive tract, use their own microbiota to adapt to the peculiarities of the food supply in arid regions, characterized by instability of vegetation and fruiting of food plants and, which is especially important, to water deficit (Degen, 1997). Therefore, physiological adaptations to the seasonal changes in the food quality and water retention in the body play an important role in formation of their nutrition and

digestion strategy. These adaptations are carried out through symbiosis with microorganisms.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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