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Dimensions of the Body and Molars in the Mole Vole (*Ellobius talpinus*, Rodentia, Cricetidae) Depending on the Age and Environmental Conditions

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Abstract—We determined the body size and the size of molars (m/1) in mole voles (*Ellobius talpinus* Pallas 1770) collected in a laboratory colony (n = 35), in natural habitats (Orenburg oblast, n = 34; Chelyabinsk oblast, n = 42), and in two Holocene-dated horizons in Alekseevskaya Cave (n = 51; n = 66). It was found that the individual absolute age determined based on the molar root length (measured between the tooth neck and the end of the root) corresponds to the age intervals determined in labeled animals from natural habitats. The individual age of samples collected in Alekseevskaya Cave varied from several months to four years; the age group of one year was dominant, and animals younger than one year composed the second most abundant age group. The samples of the laboratory colony had the most pronounced morphological traits (greater height and length of the molar crown). We observed no significant differences in all the parameters studied between the animals collected in natural habitats and in the cave. Although there are no differences in the size parameters of the teeth, we cannot definitively conclude that the body size of mole voles in the Holocene was the same as that in recently collected samples, since the correlation of the body length and m/1 in animals from natural habitats and the laboratory colony was low.

Keywords: molars, age determination, body size, mole vole, Holocene

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INTRODUCTION

The body size is one of the parameters that reflect a number of ecological, physiological, and other characteristics of animals (Schmidt-Nielsen, 1987). The secular variability of body size in mammals can be studied based on subfossil remains and old museum collections (Paaver, 1965). Fluctuations in the body size of some mammals in warm and cold epochs of the Pleistocene and Holocene have been investigated in paleozoological studies (Kurten, 1968).

Regression analysis is one of the methods used widely for modeling of the body size based on the size of skeleton parts (Martin, 1996; Borowski et al., 2008; Balciauskas and Balčiauskienė, 2011; etc.). The most accurate modeling is based on the use of several large cranial (Balciauskas and Balčiauskienė, 2011) or postcranial (Balčiauskienė and Balciauskas, 2016) structures; however, separate teeth have also been used (Martin, 1996; Borowski et al., 2008). Fossil and subfossil skeletons are rarely complete enough to determine the body size of mammals. Body size modeling is usually based on the size of separate remains. In rodents, teeth are mainly used as such remains. In the mole voles (*Ellobius talpinus* Pallas 1770), as well as in some other rodents, the roots of cheek teeth are developed at a certain age, and the development rate of these roots can be used as an indicator of the individual age. The literature-based methods for the determination of age in voles with cheek tooth roots involve the measurement of the length of roots and the index of the root length (the ratio of the length of the root and the tooth) (Koshkina, 1955; Clevezal, 2007). The length is measured from the point of root bifurcation or from the borderline of the enamel (Koshkina 1955; Viitala, 1971; Gustafsson et al., 1982; Borodin et al., 2012). N.G. Evdokimov developed a method for dividing mole voles into age groups based on the length of the roots measured from the point of bifurcation to the apex of the longest root (Evdokimov, 1997). The processes of tooth growth and development have been investigated in detail under laboratory conditions. The purpose of this study is to investigate the ratio of the sizes of the first molar (m/1) and the body length in postjuvenile mole voles for further paleozoological studies. We studied the following parameters: (1) correlation between the length of tooth roots in the voles of the laboratory colony, (2) the age of samples studied and the age structure of fossils from Alek-

Table 1. Material

No. of the group of samples	Amount of teeth	Group of samples	Geographical location	Studied parameters	Age of fossil remains, year of collection
1	51	Alekseevskaya Cave, horizon 1	Orenburg oblast, Kvarkenskyii district	Size parameters of teeth and their integrity	1470 (±90) years from nowadays
2	66	Alekseevskaya Cave, horizon 4			8100 (±240) years from nowadays
3	39	Laboratory colony	Kurgan oblast, Kurtamyshskii district; Chelyabinsk oblast, Kunashakskii district (founders)	Individual age, body length, size parameters of teeth	2000–2008
4	42	Natural habitats	Chelyabinsk oblast, Kunashakskii district	Body length, size parameters of teeth	1998–2000
5	34	Natural habitats	Orenburg oblast, Kuvandykskii district		2001

seevskaya Cave, (3) the duration of the time period of intense body and m/1 growth in the postjuvenile ontogeny of voles in the laboratory colony, and (4) the size parameters of samples collected in natural habitats, the laboratory colony and fossil samples, and the dependence of these parameters on age.

MATERIALS AND METHODS

We studied the tooth collections (m/1) of the mole voles collected in the laboratory colony and the natural habitats and fossil remains of Alekseevskaya Cave (Kuzmina et al., 2001; Kuzmina, 2009) (Table 1). Laboratory animals were kept in containers with sawdust litter. The diet included carrots, grains, and willow branches; during the vegetation season (from May to September), the diet additionally included a grass mixture. The temperature was 13 to 23°C depending on the season. Detailed description of Alekseevskaya Cave and the fossil remains found there is provided in (Kuzmina et al., 2001). The methods used for collection of mole voles in the Trans-Urals and long-term data on their biological parameters are described in (Evdokimov, 2001). The samples studied are stored in the zoological museum of the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences, Yekaterinburg, Russia).

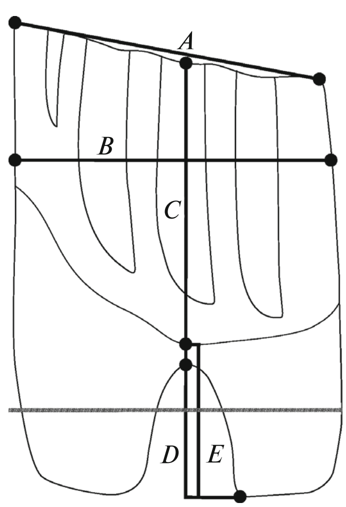

Fig. 1. The measurement of the first lower molar (m/1) in mole voles: *A*–*E*, see Materials and Methods.

We used the following parameters of teeth (letters in Fig. 1 are given in brackets): the maximal length of the grinding surface (*A*), the length of the tooth crown between the most prominent points of the lateral sides (*B*), the height of the tooth crown (*C*), and the length of roots measured from the point of root bifurcation (*D*) or from the borderline of enamel (*E*). We mainly used the right molars; both the right and left molars were analyzed in subfossil samples. A binocular microscope with a micrometer eyepiece was used for measurements; the measurement error was 0.1 mm. The values were measured twice, and then the mean value was calculated. We also measured the body length in the samples collected in natural habitats and the laboratory colony.

The data on the growth of m/1 roots in laboratory samples of known age were compared with the same data for samples obtained in natural habitats (Evdokimov, 1997). The determination of the age using the method proposed by Evdokimov (Evdokimov, 1997) is based on the length of tooth roots and the month of sample collection. This parameter was impossible to determine in the subfossil samples. Therefore, we had to adapt the method to our samples. In order to assess the correlation between the length of tooth roots and the age of voles, we used a regression equation fit. The

Table 2. Age intervals determined by the length of tooth roots in the animals of the laboratory colony

Length of roots, mm	Age in laboratory colony, months	Age group	Age-related morphological parameters of body and m/1
0–0.1	<3	0	Body growth, increase in the grinding surface of teeth, root formation
0.2–0.5	3–5	1	The tooth roots are formed. Intense growth of the body is over. Further increase in the grinding surface of teeth
0.6–0.9	6–11	2	Stabilization of the length of grinding surface
1.0–2.2	6–37	3	The length of grinding surface can vary slightly due to grinding angle
2.3–3.4	30–62	4	

maximal share of the explained regression was obtained with a quadratic equation, since the dependence of the length of tooth roots on the age was found to be nonlinear. The growth rate of teeth decreases with age (Evdokimov, 1997). We obtained two equations that used different methods for the measurement of tooth roots (Figs. 1, *D*; 1, *E*). Due to the conditions of bone tissue accumulation in fossil deposits, the teeth do not always remain unchanged (Andrews, 1990; Kuzmina et al., 2001). Bones and teeth found in pellets and excrement are affected by digestive enzymes. The parts of teeth that are not covered by enamel are digested first. Even in the case of a low resorption rate, the neck of teeth is usually damaged, which makes it difficult to measure the distance between the root and the point of bifurcation. Thus, in order to minimize the measurement error caused by differences in the position of the bifurcation point, we measured the length of tooth roots from the borderline of the enamel (Fig. 1, *E*). In this case, the absolute age of mole voles from laboratory colony coincides with the predicted age determined according to Evdokimov (Evdokimov, 1997).

The correlation between the grinding surface and the body length of animals collected in natural habitats and the laboratory colony was estimated using the Pearson correlation coefficient and quadratic regression equation. The maximal share of explained regression was obtained with a quadratic equation. We produced logistic curves in order to assess the duration of intense growth based on the length of the body and molars in the mole voles of the laboratory colony. We calculated the points of inflection of these curves (Zaitsev, 1984; Kropacheva, 2013). The samples were divided into age groups according to the length of tooth roots (Evdokimov, 1997) and the data on changes in the size of the body and grinding surfaces of m/1 (Table 2). We performed two-way analysis of variance with the factors of "age group" and "the group of samples." The size of molars and the body length were used as dependent variables. Primary analysis was performed for all samples. In the case of significant differences for the factor of "the group of samples," we performed a pairwise comparison of groups. For analysis of data and for comparison of samples, we used the StatSoft STATISTICA package for Windows 8.0.

RESULTS

The correlation between the length of tooth roots (the distance between the root end and the borderline of enamel) and the age is described by the following equation: $y = 0.92 + 8.03x + 3.26x^2$ ($R = 0.96$, $R^2 = 0.93$, $p < 0.001$, $n = 39$), where y is the age (months) and x is the length of roots (mm) (Fig. 2). The age of samples from Aleskeevskaya cave calculated using this equation varies from two months to four years. The age of animals from both horizons of the cave was usually 12–24 months (60% of animals from the first horizon and 45% of animals from the second horizon). These are the animals that overwintered one year and are considered as yearlings (Evdokimov, 1997). The age of a significant part of animals from the fourth horizon was 2–6 months (30% of animals). These are the animals that were born in the same year, i.e., underyearlings.

The length of the grinding surface increases significantly with age in all groups of animals ($F = 33.44$, $p < 0.001$). The body length increases with age in the samples from natural habitats and the laboratory colony ($F = 5.08$, $p < 0.001$). The height of the tooth crown decreases with age ($F = 179.01$, $p < 0.001$). The length of the tooth crown does not differ between the age groups ($F = 1.27$, $p = 0.28$).

According to the data obtained in the laboratory colony using the equations of logistic curves, intense body growth is completed, on average, by the age of 2.5 months. The length of the grinding surface increases over eight months due to the grinding of the tooth crown and the formation of a grinding angle. The correlation between the body length and the length of the grinding surface is described by the following equation: $y = -302.81 + 250.0x - 37.66x^2$ ($R = 0.68$, $R^2 = 0.46$, $p < 0.001$, $n = 104$), where y is the body length (mm), and x is the length of the grinding surface of m/1 (mm). Due to the low percentage of explained variance, we did not use the regression equation for modeling of the body size of mole voles

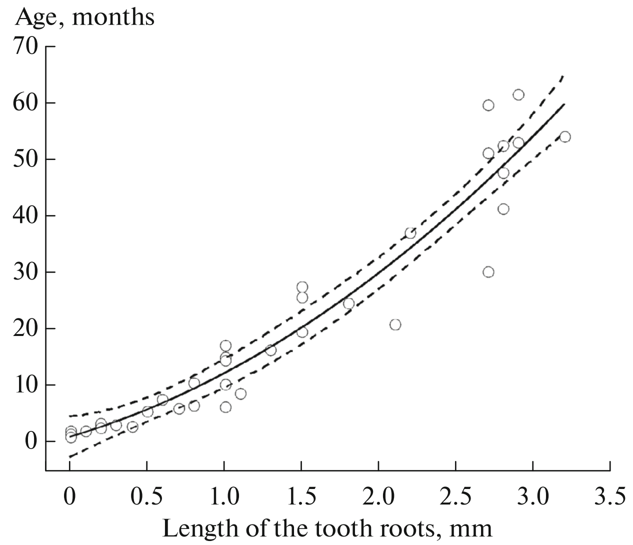

Fig. 2. The length of tooth roots in the mole voles from the laboratory colony.

found in Alekseevskaya Cave. We only compared the size parameters of recent and Holocene samples of mole voles.

The size parameters of the samples studied are presented in Table 3. The analysis of variance with "the group of samples" and "age group" used as factors showed that there are no significant differences in the length of the grinding surface of m/1 between all groups of samples ($F = 1.21$, $p = 0.31$). We found some differences in the height and length of tooth crowns ($F = 21.24$, $p < 0.001$, and $F = 6.75$, $p < 0.001$, respectively), which is due to the specific parameters of the laboratory animals. The height and length of tooth crowns in the voles of laboratory colony are significantly higher ($F = 58.46$, $p < 0.001$, and $F = 25.71$, $p < 0.001$, respectively) as compared with the voles from natural habitats. The animals from natural habitats and fossil remains did not differ significantly in the height and length of tooth crowns ($F = 1.11$, $p = 0.33$, and $F = 1.14$, $p = 0.87$, respectively). The body length did not differ significantly between the animals from natural habitats and the laboratory colony ($F = 1.73$, $p = 1.18$).

DISCUSSION

The age structure of samples from two horizons of Alekseevskaya Cave can be explained by the pattern of deposit formation (Kuzmina et al., 2001). A significant part of the samples found consists of yearlings and underyearlings, i.e., the age groups that provide the dispersal of mole voles, especially in the spring (Evdokimov, 2001). We can conclude that these ani-

Table 3. Size parameters of the mole voles, mm

Size parameter	No. of the group of samples	Number of samples	Age group		
			1	2	3
Body length	3	23	106.4 (94.0–120.0) ± 9.62	109.5 (103.0–115.0) ± 4.93	111.15 (110.0–115.0) ± 1.67
	4	31	109.2 (104.0–112.0) ± 3.11	110.67 (105.0–116.0) ± 4.32	108.83 (99.0–120.0) ± 5.10
	5	23	107.67 (106.0–110.0) ± 1.41	111.67 (105.0–115.0) ± 4.18	111.22 (105.0–115.0) ± 3.07
Length of the grinding surface	1	40	2.90 (2.80–3.10) ± 0.14	3.0 (2.90–3.20) ± 0.13	3.21 (2.90–3.40) ± 0.11
	2	41	3.0 (2.70–3.20) ± 0.15	3.17 (3.10–3.20) ± 0.58	3.28 (3.0–3.60) ± 0.19
	3	23	2.84 (2.70–3.10) ± 0.13	3.10 (2.90–3.20) ± 0.14	3.21 (3.10 –3.30) ± 0.08
	4	30	3.0 (2.90–3.10) ± 0.08	3.25 (3.10–3.30) ± 0.08	3.28 (2.80–3.50) ± 0.18
	5	24	2.93 (2.70–3.10) ± 0.14	3.12 (3.0–3.20) ± 0.08	3.15 (3.0–3.30) ± 0.10
Length of the tooth crown	1	40	3.13 (3.0–3.30) ± 0.15	3.18 (3.10–3.30) ± 0.08	3.21 (3.0–3.40) ± 1.11
	2	41	3.16 (3.0–3.30) ± 0.10	3.17 (3.10–3.30) ± 0.11	3.27 (3.0–3.60) ± 0.17
	3	23	3.26 (3.10–3.3.) ± 0.07	3.47 (3.30–3.60) ± 0.13	3.33 (3.20–3.50) ± 0.11
	4	31	3.22 (3.10–3.40) ± 0.11	3.18 (2.90–3.30) ± 0.15	3.25 (2.90–3.50) ± 0.16
	5	26	3.20 (3.0–3.30) ± 0.09	3.16 (3.0–3.30) ± 0.10	3.14 (2.90–3.30) ± 0.12
Height of the tooth crown	1	40	4.47 (4.10–4.70) ± 0.26	4.04 (3.05–4.30) ± 0.32	3.31 (2.70–4.0) ± 0.30
	2	41	4.30 (4.0–4.70) ± 0.22	3.63 (3.40–3.90) ± 0.25	3.03 (2.40–3.60) ± 0.34
	3	24	5.08 (4.60–5.50) ± 0.26	4.93 (4.50–5.30) ± 0.39	4.08 (2.50–5.20) ± 0.72
	4	31	4.56 (3.80–4.90) ± 0.45	4.17 (3.40–4.40) ± 0.38	3.26 (2.20–4.10) ± 0.57
	5	25	4.59 (4.20–4.90) ± 0.23	4.18 (3.80–4.40) ± 0.20	2.79 (2.0–3.30) ± 0.43

The table contains mean values, range and standard deviation for each group.

mals were caught by predators during their spring dispersal.

The data on the duration of intense growth obtained in the laboratory colony correspond with the literature data (Letitskaya, 1984). The growth rate after the age of 2.5 months is slow. In natural habitats the mole voles reach their maximal size by the age of 2–3 years (Evdokimov, 2001). The correlation between the length of the grinding surface of molars and the body length, which was observed in the voles from natural habitats and the laboratory colony, is not strong enough for accurate modeling of the body size. We can only obtain an approximate picture and propose a hypothesis on the size of mole voles in the Holocene based on comparison of the size parameters of their teeth with the parameters of other samples. The comparison of groups showed that the size parameters of teeth in Holocene samples did not differ from those in samples obtained from natural habitats. The mole voles have some physiological traits typical of a burrowing animal (Novikov et al., 2007) and a small rate of geographical size variability (Panteleev et al., 1990; Evdokimov, 2001). Their range has changed to a relatively small extent simce the Late Holocene (Smirnov et al., 2016). These data suggest that the size parameters of mole voles are rather conservative.

The comparison of the size parameters of all studied groups of samples showed that the laboratory colony was the only group that differed significantly from the others. The specific conditions of laboratory colonies include a smaller interseasonal range of temperatures as compared with natural conditions, lower diet diversity, lower abrasive ability of feeds, and the absence of ground (soil) in cages. The founder effect, domestication, and artificial formation of mating pairs have a certain effect as well. The high percentage of individuals with a long tooth crown in the laboratory colony is apparently caused by the founder effect. Such a length of the tooth crown in laboratory animals can also result from a lower attrition rate.

After analysis of the data obtained, we made the following conclusions: (1) The analysis of correlations between the length of teeth and the age of mole voles showed that the correlation of these values is most accurate when measuring the root length from the borderline of the enamel to the end of roots. (2) The data on the age of samples from Alekseevskaya Cave helped to determine the age structure of mole voles consumed by carnivorous animals and birds inhabiting this cave. The age of samples in fossil remains varies from two months to four years. The dominant age group consists of yearlings; underyearlings are the second most abundant age group. (3) The correlation between the size parameters of teeth and the body length is not strong enough for accurate modeling of the body length based on isolated molars. (4) The comparison of size parameters of teeth with regard to individual age did not show any differences between the samples collected in natural habitats and the Holocene remains from two horizons of Alekseevskaya Cave. The mole voles from laboratory colony had higher values of the height and length of tooth crowns.

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