

# Skull Sizes and Proportions in Western Palearctic Wood Mice (*Sylvaemus*, Muridae, Rodentia) from Eastern Europe: 1. Interspecific Variability

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**Abstract**—Cranio-metric features (measurements, indexes) in several species of the genus *Sylvaemus* (*S. sylvaticus*, *S. flavicollis*, and *S. uralensis* from Eastern Europe and some adjacent territories, as well as *S. ponticus* and *S. witherbyi* from the Caucasus) have been studied using multivariate statistical analysis. For the first time, craniometric characters of the genus *Sylvaemus* are considered in relation to the feeding ecology of species. A total of 614 skulls were studied. Based on original material, discriminant keys have been developed using skull measurements. The keys appear to be suitable for the diagnostics of the studied *Sylvaemus* species, including sibling ones. The largest skulls are shown to be characteristic of *S. flavicollis*, and the smallest ones, of *S. uralensis*. Cluster analysis of the absolute measurements of the skull cumulative selection has revealed the greatest isolation of *S. flavicollis* and the similarity of coexisting but phylogenetically remote *S. ponticus* and *S. witherbyi*. Factor analysis showed that, within the genus *Sylvaemus*, the general sizes are less essential than the characters related to food smashing (the length of the lower jaw and rostrum, the width of the occipital part of the skull), and possibly also to the thickness of the incisors. Comparative analyses of the relative skull measurements (the indexes related to the food preferences of the animals, granivory or folivory) allow us to conclude that the food adaptations to granivory in the structure of the skull and teeth increase in the series *S. uralensis*–*S. sylvaticus*–*S. witherbyi*–*S. flavicollis*–*S. ponticus*. The cranial evolution in species within the genus *Sylvaemus* is suggested to have been directed to increased adaptations in the mechanisms in seed peeling and processing.

**Keywords:** *Sylvaemus*, sibling species, craniometry, measurements, indices, multivariate statistical analysis, diagnostics, feeding ecology, adaptive strategy, evolution

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## INTRODUCTION

The distribution of mice of the genus *Sylvaemus* covers the mountain and flat landscapes of Europe, the Caucasus, North Africa, and also the Near East, Middle East, and Southwestern Asia, where these rodents are often common species (Pavlinov et al., 1995). Until recently, all species of wood and field mice were united into a single transpalearctic genus *Apodemus* Kaup 1829, consisting of four subgenera: the Western Palearctic wood mice *Sylvaemus* Ognev 1924 and *Karstomys* Martino 1939, as well as the Eastern Palearctic *Apodemus* Kaup 1829 and *Alsomys* Dukelski 1929 (Musser et al., 1996). The generic status

of *Sylvaemus* including the subgenera *Sylvaemus* and *Karstomys*, was substantiated by biochemical data (Bonhomme et al., 1985; Mezhzherin and Zykov, 1991; Mezhzherin, 1997), and later it was both supported (Zagorodnyuk, 1993; Pavlinov et al., 1995; Zagorodnyuk et al., 1997; Kartavtseva, 2002; Chelomina and Suzuki, 2006; etc.) and not recognized (Vorontsov et al., 1992; Lavrenchenko and Likhnova, 1995; Gromov and Erbaeva, 1995; Frynta et al., 2001; Baskevich et al., 2004; Musser and Carleton, 2005; etc.). In the latest taxonomic report (Pavlinov and Lissovskii, 2012), the Western Palearctic wood and field mice are given the generic rank *Sylvaemus* Ognev 1924, and we accept this point of view in this communication. Paleontological data date the formation of

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the Western Palearctic species of wood mice to the Pleistocene (Gromov et al., 1963). According to molecular (Michaux et al., 2002; Chelomina and Suzuki, 2006; etc.) and genetic and biochemical data (Mezhzherin, 1997), the genus *Sylvaemus* appeared before the Pleistocene. Mezhzherin (1997) dates this event to the Pliocene. Obviously, subsequent events have led to intense morphogenesis in the taxon, which, as is commonly believed, is still ongoing. As a result of large-scale genetic studies (Vorontsov et al., 1989, 1992; Mezhzherin and Zagorodnyuk, 1989; Mezhzherin, 1991, 1997a; Mezhzherin and Zykov, 1991; Orlov et al., 1996; Michaux et al., 2002; Filip-pucci et al., 2002; etc.), the genus was substantially revised and supplemented, mainly by identifying the sibling species of Eastern Europe and the Caucasus. Currently, the majority of researchers recognize in the genus *Sylvaemus* nine species: the wood mouse (*S. sylvaticus* Linnaeus 1758), the yellow-necked mouse (*S. flavicollis* Melchior 1834), the alpine mouse (*S. alpicola* Heinrich 1952), the pygmy wood mouse (*S. uralensis* Pallas 1881), the steppe field mouse (*S. witherbyi* Thomas 1902 = *S. fulvipectus* Ognev 1924, *S. arianus* Blanford 1881, *S. hermonensis* Filip-pucci, Simson et Nevo 1989), the Caucasus field mouse (*S. hyrcanicus* Vorontsov, Boeskorov et Mezhzherin 1992), the Black Sea wood mouse (*S. ponticus* Sviridenko 1936), the eastern broad-toothed field mouse (*S. (Karstomys) mystacinus* Danford et Alston 1877), and the western broad-toothed field mouse (*S. (K.) epimelas* Nehring 1902). Until now, the position of individual taxa in the structure of the genus has been controversial. Thus, some researchers have given species status to the ciscaucasian and vohlynensis forms (Orlov et al., 1996), with which other zoologists disagree (Zagorodnyuk, 1993; Mezhzherin, 1997a; Bogdanov, 2001, 2004; Bogdanov et al., 2009, 2012). Not all mammalogists agree (Gromov and Erbaeva, 1995; Frynta et al., 2001) with the majority of authors recognizing the species rank of *S. ponticus*, which is a sibling species of *S. flavicollis* (Mezhzherin, 1991; Musser and Carleton, 1993, 2005; Pavlinov, 2003; etc.). There is still no morphological and taxonomic interpretation of genetically discrete intraspecific groups identified as part of certain species (Bogdanov, 2001, 2004; Filip-pucci et al., 2002; Michaux et al., 2002; Bogdanov et al., 2009, 2012, 2014; Klempa et al., 2008); depending on the trait used, the interspecific and intraspecific relations of *Sylvaemus* are considered ambiguous (Mezhzherin, 1997; Chelomina and Suzuki, 2006; Bogdanov et al., 2012; etc.).

To solve controversial issues in the construction of the taxonomic system of *Sylvaemus*, as well as for the diagnosis of species and intraspecific forms, researchers used different signs: allozymes (Mezhzherin, 1987, 1990; Vorontsov et al., 1989, 1992; Mezhzherin and Zykov, 1991; Lavrenchenko and Likhnova 1995; Macholán et al., 2001; Bogdanov, 2004; etc.), features of the differential staining of chromosomes and FISH

(Kozlovsky et al., 1990; Bulatova et al., 1991; Vorontsov et al., 1992; Boeskorov et al., 1995; Orlov et al., 1996, 1996a; Bogdanov, 2001; Bogdanov and Rozanov, 2005; Kartavtseva, 2002; Baskevich et al., 2004; Karamysheva et al., 2010; Rubtsov et al., 2011), molecular genetic markers (Chelomina, 1998, 2005; Chelomina et al., 1998, 1998a, 2007; Chelomina and Suzuki, 2006; Balakirev et al., 2007; Bogdanov et al., 2009, 2012, 2014; Amshokova et al., 2015; etc.), as well as behavioral (Stopka, 1999, cit. ex Baskevich et al., 2004), morphological, based on a comparative analysis of the features of the generative system of males (Baskevich et al., 2004a), and nonmetric signs of the skull (Orlov and Okulova, 2001).

The use of predominantly genetic research methods made it possible to clarify the boundaries of a number of species and intraspecific groups of animals. Within this context, several questions arise: what features of the structure and way of life of animals distinguish the selected groups? What mechanisms of evolution cause the revealed differences? Do they have adaptive meaning, and if so, which one? What could explain the emergence of such groups? Answers to these questions can be obtained by comparing the morphological features and ecology of groups. However, investigations of the ecological and morphological differences of species of the genus advance slowly. The ecology of the former polytypic species was studied in detail, but the latest scientific achievements such as identifying sibling species (*S. ponticus*, *S. flavicollis*, etc.), as well as intraspecific chromosomal, allozyme, molecular-genetic forms, drive a significant review of this work. Craniometric approaches with the use of multidimensional statistics methods have had limited application and have mainly concerned regional samples of individual species in particular sites or areas of ranges where species are sympatric (Mezhzherin and Mikhailenko, 1991; Boeskorov, 1992; Zagorodnyuk, 1993; Lavrenchenko and Likhnova, 1995; Reutter et al., 1999; Frynta et al., 2001; Stakheev, 2009; etc.). The degree of coincidence of molecular-genetic variability with morphological and morphometric variations and ecological peculiarities of the identified sibling species and intraspecific genetically discrete groups has not been studied. Methods for species diagnostics for practical purposes are not always developed. At the same time, craniometric studies are certainly of interest because they expand the range of diagnostic features in identifying sibling species and intraspecific forms of *Sylvaemus* and open up new possibilities for studying the problems of evolution and ecological dependencies in the formation of the morphological variability of *Sylvaemus*.

The aim of this report is to compare, on the basis of methods of multidimensional statistics, the craniometric features of the following species of the genus *Sylvaemus*: *S. sylvaticus*, *S. flavicollis*, and *S. uralensis* from Eastern Europe, as well as *S. ponticus* and *S. witherbyi* from the Caucasus.

## MATERIALS AND METHODS

We used our own original data on representatives of the genus *Sylvaemus* (*S. flavicollis*, *S. ponticus*, *S. witherbyi*, *S. sylvaticus*, and *S. uralensis*) from Southeastern and Western Ukraine, Northwestern Caucasus, the Republic of Dagestan, and Ivanovo oblast. In addition we involve craniometric data on our measurements of the skulls from the collections of the Zoological Museums of Moscow State University and the Zoological Institute, Russian Academy of Sciences (ZI RAS). Table 1 represents the material on these species. The skulls of adults and semiadult individuals of both sexes were used in this work. Individual laboratory diagnostics of specimen species affiliation were not carried out, with the exception of animals from Dagestan (Lavrenchenko and Likhnova, 1995). Genetic confirmations of the presence of a particular species in the study areas were obtained for *S. uralensis* from Ivanovo oblast (protein electrophoresis was carried out by S.V. Mezhdzherin), for the same species and *S. ponticus* from Krasnodar krai (karyological analysis was provided by V.N. Orlov and M.I. Baskevich; protein electrophoresis and molecular-genetic analysis, by A.E. Balakirev, A.S. Bogdanov, and B. Klempa), for *S. uralensis*, *S. witherbyi*, and *S. ponticus* from Dagestan (protein electrophoresis by O.N. Likhnova), and for *S. sylvaticus* and *S. uralensis* from Dniprovsko Orilskii Nature Reserve (karyological analysis were done by A.I. Kozlovskii).

The measurements were made for 309 skulls of the representatives of the genus *Sylvaemus* from our original summer–autumn samplings and for 305 skulls from the materials of Moscow State University and ZI RAS; in total 614 skulls were processed (Table 1). Our collections from the Northwestern Caucasus relate to the area of the municipal district of the city of Sochi, including the vicinity of the town Krasnaya Polyana. Descriptions of the environmental conditions and fauna of small rodents were reported previously for the Dniprovsko Orilskii Nature Reserve (Okulova and Antonets, 2002, 2007; Antonets and Okulova 2014), for the Northwestern Caucasus (Okulova et al., 2005), and for Dagestan (Lavrenchenko and Likhnova, 1995). In Ivanovo oblast animals were collected by N.M. Okulova and her assistants in the Privolzhskii (near the town of Plyos) and Zavolzhskii (settlement of Krasnogor'e) districts, in the subzone of coniferous–deciduous forests (for a description of the area, see Okulova and Khelevina, 1989). The sampling localities are presented in Fig. 1.

The animals (except for representatives of *S. witherbyi*) were caught mainly at the end of summer and at the beginning of autumn, usually over two or more years, which, in our opinion, eliminates the variability in the age and sex composition. Special studies are needed to assess fully the role of this factor in craniometric variability. The intraspecific geographical vari-

ability of widespread species (mainly *S. uralensis* and *S. flavicollis*) will be discussed in Report 2.

Measurement of the skulls in millimeters was performed using an MBS microscope and an ocular micrometer at magnifications of  $\times 04$ ,  $\times 7.5$ , and  $\times 25$ . The measurement scheme is shown in Fig. 2, and the results are presented in Table 2. Twenty-one signs were measured on the skull: (1) Cbl, condylobasal length; (2) Zyg, zygomatic width; (3) Hmax, height of the upper jaw in front of  $M^1$ ; (4) Lmd, length of the lower jaw; (5) Iob, interorbital width; (6) Lna, the length of the nasal bones; (7) Bna, the width of the nasal bones; (8) Lbull, the length of the auditory bulla; (9) Lfi, the length of the incisor foramen; (10) Bfi, the width of the incisor foramen; (11)  $Lm^{1-3}$ , the length of the upper dentition; (12)  $Lm_{1-3}$ , the length of the lower dentition; (13)  $Lm^1$ , the alveolar length of the first upper molar; (14)  $Bm^1$ , the width of the first upper molar; (15) D1, upper diastema length; (16) D2, lower diastema length; (17)  $M^{1-1}$ , minimum distance between the first upper molars; (18) Bcra, the width of the skull in the area of the auditory bulla; (19) Hcra, the height of the skull in the area of the auditory bulla; (20) Li, the length of the incisor from the alveoli; (21) Bi, the width of the incisor in the lateral direction at the end of the tooth. For Dagestan specimens, 17 cranial signs were measured (all except Hmax, Li, Bi, and D2).

Based on these measurements, 24 indices were calculated.

Statistical data processing was carried out on a computer using Statistic software in modules: descriptive statistics, arithmetic average  $M$ , its error  $m$ , and the standard deviation of data  $\sigma^2$ . To analyze the differences in the indices, the maximum and minimum species values were compared by Student's criterion ( $t \geq 2$ ). We also used cluster analysis (one linkage method and calculation of Euclidean distances) and factorial and discriminant analyses. The construction of clusters was carried out according to average values for all signs or their separate group; for factor analysis, the axes were rotated using the varimax row method. In discriminant analysis,  $R_{can}$ , the canonical correlation coefficient in the system was also determined. The reliability of the coefficients of the equations and the canonical correlation coefficients in the discriminant analysis were estimated using the Fisher criteria  $F$ ,  $W\lambda$ ,  $\chi^2$ ,  $F$  with  $p < 0.05$ . Only those calculations were considered reliable that had significant coefficients for all the terms of the equation with eigenvalues of two or more. We aimed for 100% separation of species, but in some cases it was necessary to use and consider convincing results with an average accuracy of identification of more than 95%. As a result of the calculations, the animal was attributed to the species for which the maximum value of the discriminant function was obtained.

**Table 1.** Material on the craniometry of representatives of the genus *Sylvaemus* used in the work

Site no.	Sampling location	Species of the genus <i>Sylvaemus</i>					Total	Collector, collection
		<i>uralensis</i>	<i>sylvaticus</i>	<i>witherbyi</i>	<i>ponticus</i>	<i>flavicollis</i>		
1	Dniprovske Orilskii Nature Reserve, 1998–2000	55	31	—	—	—	86	Okulova, Antonets
2	Northwestern Caucasus, 2001–2005	23	—	—	78	—	101	Okulova
3	Republic of Dagestan (vicinity of the village of Dylm), 1988	53	—	9	18	—	80	Lavrechenko, Likhnova
4	Roztochya Biosphere Reserve, Lviv oblast, Ukraine, 2000	—	—	—	—	23	23	Okulova, Antonets
5	Sweden, vicinity of Malmö, 1964–1968	—	—	—	—	12	12	Zoological Museum, Moscow State University
6	Tver oblast, vicinity of Maksatikha, 1941	—	—	—	—	23	23	"
7	Republic of Bashkiria, 1906, 1933–1937	—	—	—	—	35	35	"
8	Leningrad oblast, 1920–1970, 1987, 1995	—	—	—	—	40	40	Zoological Museum, ZI RAS
9	Belovezhskaya Pushcha National Park, Belarus, 1948–1953	—	—	—	—	58	58	Zoological Museum, Moscow State University
10	Temnikovskii district, Republic of Mordovia, 1936	—	—	—	—	19	19	"
11	Moscow and Ryazan oblasts, 1935–1946	—	—	—	—	9	9	"
12	Ivanovo oblast, 1996–1993	19	—	—	—	—	19	Okulova
13	Moscow oblast, 1926–1948	21	—	—	—	—	21	Zoological Museum, Moscow State University
14	Yaroslavl oblast, 1930	18	—	—	—	—	18	"
15	Ryazan oblast, 1973	36	—	—	—	—	36	"
16	Tellerman Forestry, Voronezh oblast, 1948	—	—	—	—	34	34	"
Total		225	31	9	96	253	614	

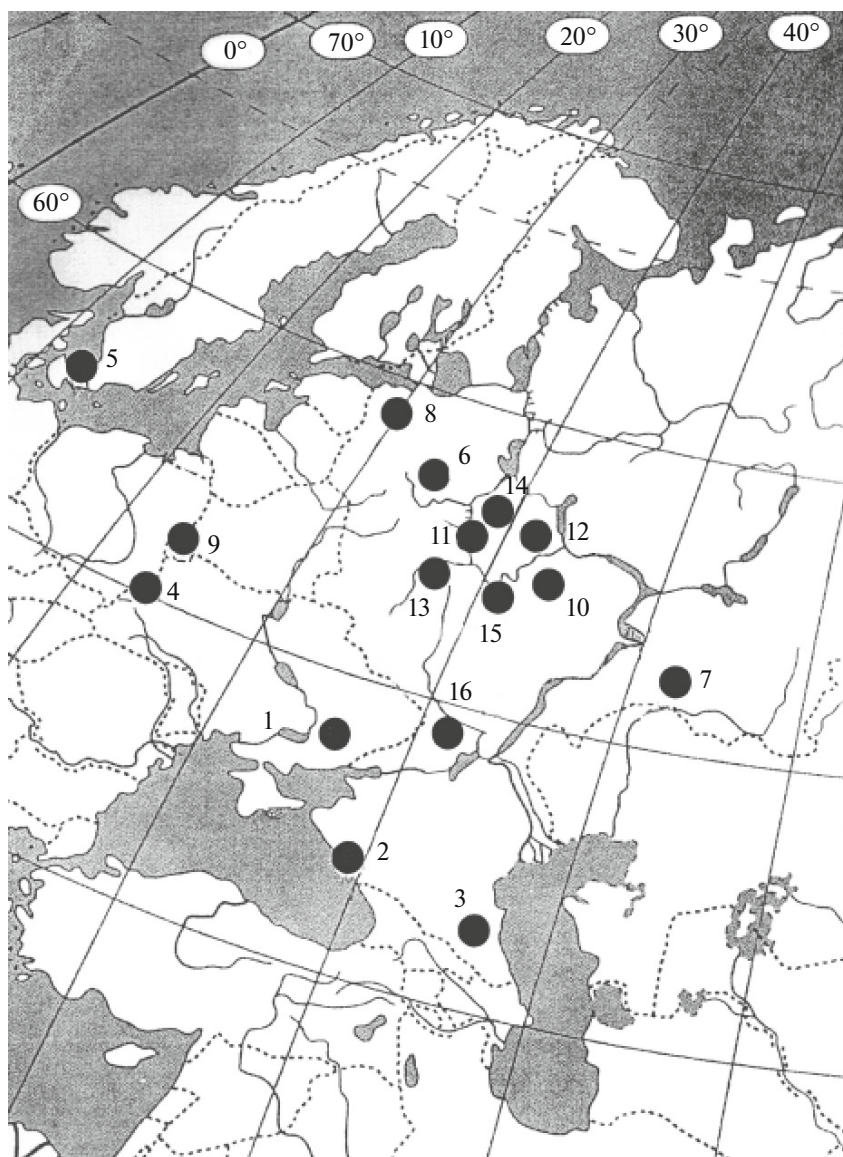
## RESULTS AND DISCUSSION

### *Species Variability*

Table 2 shows that among the five species of *Sylvaemus*, the largest skulls are characteristic of *S. flavicollis*, and the smallest, of *S. uralensis*. Accordingly, the dentition ( $Lm^{1-3}$ ,  $Lm_{1-3}$ ) is usually larger in the first species and smallest in the latter. However, reliably maximum values of Zyg, Lmd, D1,  $M^{1-1}$ , Li, and Bi were noted not in *S. flavicollis*, in which the skull is the longest, but in *S. ponticus*. Four features are maximal in *S. sylvaticus* (Bfi,  $Lm^1$ , Bcra, and Hcra), and two features, in *S. witherbyi* (Lna and Bna). The minimum values of the features according to the average

indicators for the species were observed in the smallest *S. uralensis* in 12 cases out of 21 (Zyg, Lmd, Lna, Lfi,  $Lm^{1-3}$ ,  $Lm_{1-3}$ ,  $Lm^1$ ,  $Bm^1$ , D1,  $M^{1-1}$ , Bcra, and Bi); in one case, in *S. sylvaticus* (Hmax); in three cases, in *S. ponticus* (Bna, Iob, and Bfi); and in one case, in *S. flavicollis* (Li).

Thus, according to the absolute terms, the length of the skull and the length of the upper and lower dentitions are maximal in the yellow-necked mouse (*S. flavicollis*), but the length of its incisors is minimal. The Black Sea field mouse (*S. ponticus*) is distinguished by a rather large, but not maximal skull length, with a significantly maximal width of the archus zygomaticus, lengths of mandible and upper diastema, and width of



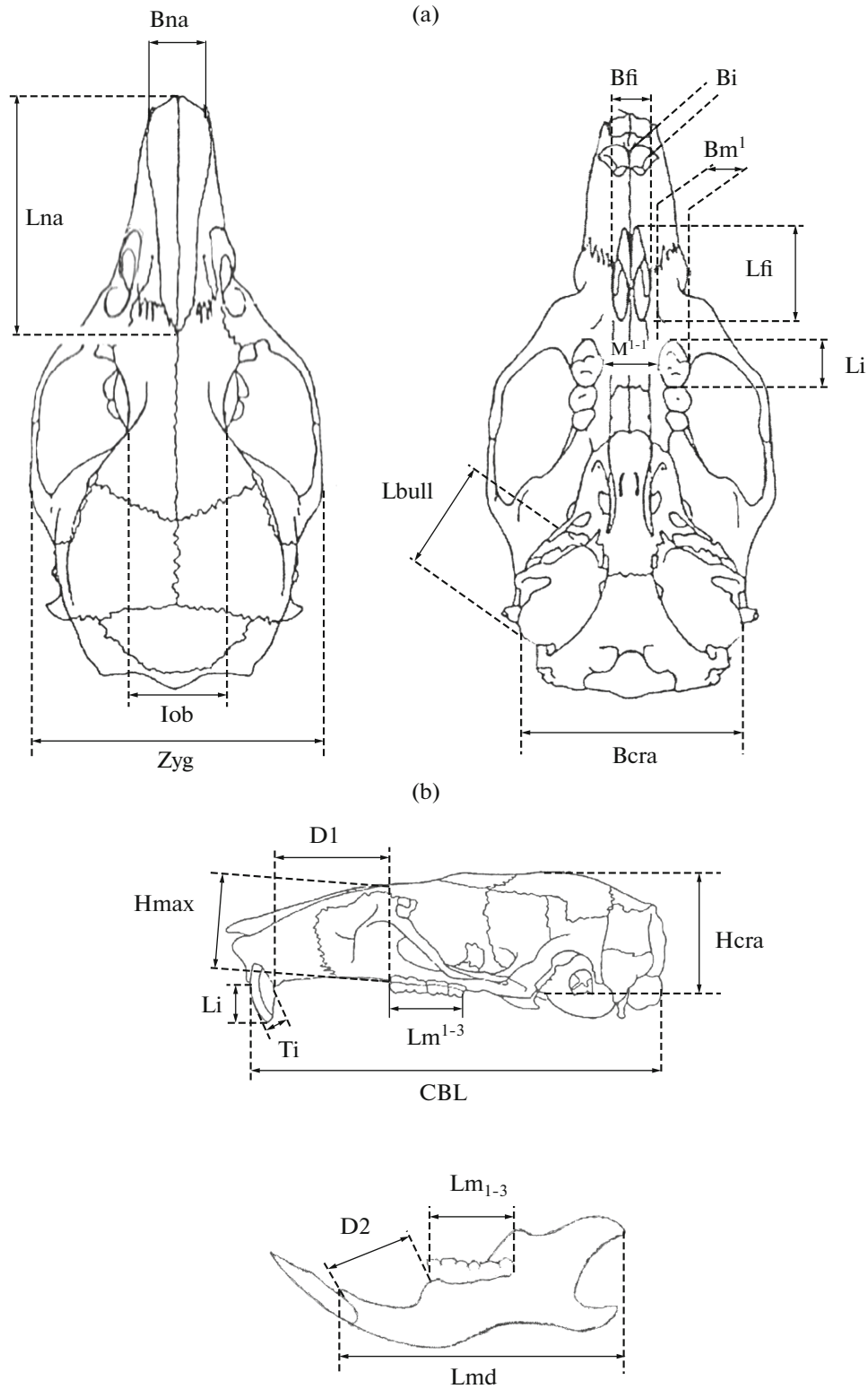
**Fig. 1.** Sampling localities (their numbers correspond to Table 1): 1, Dniprovsko Orilskii Nature Reserve (*S. uralensis* and *S. sylvaticus*); 2, Northwestern Caucasus, the region of the municipal district of the city of Sochi (*S. ponticus* and *S. uralensis*); 3, Republic of Dagestan (*S. uralensis*, *S. ponticus*, and *S. witherbyi*); 4, Roztochya Biosphere Reserve, Ukraine (*S. flavicollis*); 5, Sweden (*S. flavicollis*); 6, Tver oblast (*S. flavicollis*); 7, Bashkirskii Nature Reserve (*S. flavicollis*); 8, Leningrad oblast (*S. flavicollis*); 9, Belovezhskaya Pushcha National Park, Belarus (*S. flavicollis*); 10, Republic of Mordovia (*S. flavicollis*); 11, Moscow oblast (*S. uralensis*); 12, Ivanovo oblast (*S. uralensis*); 13, Prioksko-Terrasny Nature Biosphere Reserve, Moscow oblast (*S. flavicollis* and *S. uralensis*); 14, Yaroslavl oblast (*S. uralensis*); 15, Ryazan oblast (*S. uralensis*); 16, Tellerman Forestry, Voronezh oblast (*S. flavicollis*).

the incisor and of the interorbital space. At the same time, this species has the narrowest muzzle (the width of the nasal bones and the incisor foramen are minimal).

The steppe wood mouse (*S. witherbyi*) has an average length of the skull, but at the same time, elongated and enlarged nasal bones. The wood mouse (*S. sylvaticus*) with a smaller skull has a maximum width of the incisor foramens and skull in the area of the auditory bullas, as well as the maximum  $M^1$  length with a minimum height of the upper jaw before the start of denti-

tion. The pygmy wood mouse (*S. uralensis*) was characterized by half of the minimum values of the skull parts with a minimum length of the skull; maximum values were not found at all.

The similarity of species and groups of the genus in the dimensions of the skull and its parts was studied by cluster analysis methods. We used our original own materials. To assess the degree of similarity, we used the absolute values of dimensions and the one-linkage method. Euclidean distances were used as linkage dis-



**Fig. 2.** Scheme of skull measurements of representatives of the genus *Sylvaemus*: (a) dorsal and ventral view; (b) lateral view and lower jaw.

**Table 2.** Absolute values (mm) of the dimensions of the skull and parts in various species of the genus *Sylvaemus* ( $M \pm m$ )

Sign no.	Index	Species of the genus <i>Sylvaemus</i>				
		<i>uralensis</i>	<i>sylvaticus</i>	<i>witherbyi</i>	<i>ponticus</i>	<i>flavicollis</i>
1	Cbl	23.17 ± 0.11	24.73 ± 0.50	23.55 ± 0.16	24.35 ± 0.20	27.23 ± 0.16
2	Zyg	11.35 ± 0.10	12.21 ± 0.20	12.87 ± 0.15	14.23 ± 0.16	12.16 ± 0.11
3	Hmax	6.77 ± 0.07	6.22 ± 0.13	N.d.	7.20 ± 0.10	7.45 ± 0.10
4	Lmd	12.52 ± 0.10	13.54 ± 0.17	14.59 ± 0.15	14.60 ± 0.12	13.33 ± 0.11
5	Iob	3.63 ± 0.05	4.41 ± 0.04	4.33 ± 0.04	2.55 ± 0.09	3.86 ± 0.03
6	Lna	7.97 ± 0.06	8.61 ± 0.17	9.18 ± 0.01	8.85 ± 0.11	8.86 ± 0.09
7	Bna	2.65 ± 0.03	2.89 ± 0.05	2.94 ± 0.04	1.81 ± 0.07	2.83 ± 0.03
8	Lbull	5.11 ± 0.22	4.71 ± 0.11	4.55 ± 0.05	5.19 ± 0.05	5.94 ± 0.24
9	Lfi	4.68 ± 0.04	5.25 ± 0.09	5.06 ± 0.09	5.06 ± 0.05	5.04 ± 0.04
10	Bfi	1.50 ± 0.02	1.84 ± 0.06	1.67 ± 0.03	1.14 ± 0.04	1.83 ± 0.02
11	Lm <sup>1-3</sup>	3.39 ± 0.02	3.78 ± 0.03	3.79 ± 0.03	3.72 ± 0.04	3.92 ± 0.04
12	Lm <sub>1-3</sub>	3.71 ± 0.03	4.09 ± 0.08	N.d.	4.14 ± 0.04	4.72 ± 0.08
13	Lm <sup>1</sup>	1.64 ± 0.01	1.93 ± 0.04	1.84 ± 0.01	1.92 ± 0.02	1.87 ± 0.02
14	Bm <sup>1</sup>	1.13 ± 0.02	1.29 ± 0.02	1.23 ± 0.01	1.32 ± 0.01	1.25 ± 0.04
15	D1	6.35 ± 0.05	6.73 ± 0.13	7.02 ± 0.07	7.37 ± 0.06	6.60 ± 0.07
16	D2	3.77 ± 0.04	3.64 ± 0.07	N.d.	3.95 ± 0.04	4.24 ± 0.09
17	M <sup>1-1</sup>	2.70 ± 0.02	2.88 ± 0.04	2.83 ± 0.06	3.10 ± 0.05	2.70 ± 0.03
18	Bcra	10.22 ± 0.07	12.38 ± 0.20	11.21 ± 0.08	11.68 ± 0.07	10.72 ± 0.10
19	Hcra	7.54 ± 0.09	9.9 ± 0.26	8.05 ± 0.13	9.83 ± 0.11	7.40 ± 0.05
20	Li	2.73 ± 0.08	3.26 ± 0.18	N.d.	4.65 ± 0.07	2.40 ± 0.06
21	Bi	0.60 ± 0.01	0.61 ± 0.01	N.d.	0.81 ± 0.02	0.67 ± 0.01

For data volume see Table 1; N.d., no data.

tances. The results are presented in Fig. 3. It is seen clearly that *S. flavicollis* differs greatly from other species. *S. uralensis* is distinguished from the others; *S. ponticus* and *S. witherbyi* are most similar (among others), and *S. sylvaticus* is somewhat separated. The alpine mouse (*S. alpicola* Heinrich 1952), which is close to *S. flavicollis* (Reutter et al., 1999) according to its dimensions, appeared to be closer to *S. ponticus*.

#### *Proportions (Indices) of Signs in Different Species*

Calculation of the proportions (indices) allows us to compare the dimensions of individual parts, regardless of the size of the whole. Consideration of the skull proportions of *Sylvaemus* species (Table 3) leads to the following conclusions. *S. flavicollis* differs from other species in a number of features. More than half of the indices (13 out of 24: 3/1, 4/1, 6/1, 9/1, 14/1, 14/13, 11/1, 15/1, 15/11, 17/11, 13/12, 18/1, and 19/1) in this species are distinguished by minimal values (in comparison with other species of the genus).

The skull of *S. flavicollis* is characterized by the following features: the lowest upper jaw and the shortest

lower jaw, the shortest nasal bones and incisor foramina relative to the condylobasal length, the narrowest M<sup>1</sup> relative to its length, the shortest upper dentition, and both diastemas short relative to Cbl (and the upper diastema, also relative to the length of the upper dentition), narrowed interdental space M<sup>1-1</sup>, and shortened Lm<sup>1</sup> relative to Lm<sup>1-3</sup>, narrowed width Bcra/Cbl, and a minimum height of the skull in the area of the auditory bullas Hcra/Cbl. No maximum values of indices for this species were identified.

Thus, the skull of *S. flavicollis* is maximally elongated, narrowed, and flattened. The lengths of the mandible, the upper dentition, the upper diastema, the interdental space, the nasal bone, and the incisor foramina are relatively short. M<sup>1</sup> is narrowed; its proportion in the length of the upper dentition is minimal.

For *S. ponticus*, five minimal-value indices were found (5/1, 10/9, 7/6, 21/20, and 12/4) and 12 out of 24 were maximum (2/1, 4/1, 14/1, 14/13, 15/1, 15/11, 17/11, 13/12, 14/13, 12/1, 19/1, and 20/1). In other words, in the Black Sea wood mouse (*S. ponticus*) the zygomatic width and height of the skull, the length of

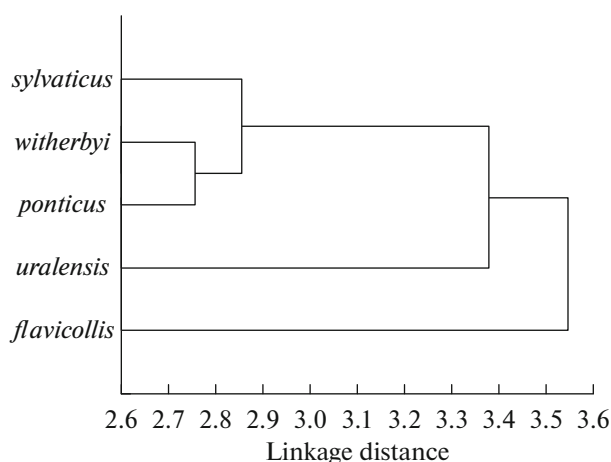


Fig. 3. Cluster analysis of craniometric features of species of the genus *Sylvaemus*.

the lower jaw and upper diastema relative to Cbl and the upper dentition, and the interdental space and the length of the 1st upper molar relative to the upper dentition are maximum. The incisors are the longest and narrowest relative to Cbl and Li, respectively; the 1st upper molar is widest relative to its length; the nasal bones, the interorbital space, and the incisor foramens are narrowed.

Thus, the skull of *S. ponticus* is somewhat shorter than in *S. flavicollis*, but the highest, with the widest zygomatic part, while the interorbital space is minimal. The upper diastema and interdental space are the largest,  $M^1$  is wide and the  $M^1$  proportion in the length of the upper dentition is maximal, while the nasal bones and incisor foramens are narrowed. The skull of *S. ponticus* in comparison with the skulls of other species seems to be the largest.

In *S. witherbyi* five minimum values of indices were revealed (5/1, 5/2, 8/1, 20/1, and 14/13); i.e., it has the minimum length of the auditory bullas, the minimum interorbital space relative to Cbl and the zygomatic width, and the smallest incisors relative to the length of the skull. This species also has a minimum width of the 1st upper molar relative to its length. At the same time, four features are of maximum values: 4/1, 6/1, 10/9, and 12/4; i.e., the nasal bones and lower jaw are the longest relative to the condilobasal length of the skull and the incisor foramens are the widest relative to their length. In addition, the length index of the upper dentition relative to the length of the lower jaw is maximal. In general, with the average size of the skull of *S. witherbyi*, the lower jaw, nasal bones, and upper dentition are elongated relative to the length of the lower jaw, but the interorbital space is narrowed relative to the length of the skull and its zygomatic width; the zygomatic bullas and incisors are shortened.

In *S. sylvaticus* with a rather small skull size, minimal indices were not found, but there were revealed six

maximal indices relative to the average values: 5/1, 7/1, 9/1, 18/1, 5/2, and 7/6. In general, this means that *S. sylvaticus* is characterized by an extended interorbital space (in two proportions) and the nasal bones, the longest auditory bullas and incisor foramens, and the maximal skull width in the area of the auditory bullas relative to the condylobasal length.

In *S. uralensis*, one minimal index (11/1) and one maximal index (3/1) were revealed; i.e., with the minimum size, the skull of *S. uralensis* is distinguished by a minimum dentition and maximally high upper jaw in front of the molars.

Previously (Lebedkina, 1949; Vorontsov, 1967; Okulova, 2000) it was shown that dental indices (the ratio of the upper dentition, diastema, and the proportions of teeth) in rodent families are quantitatively related to nutrition: some indices increase with folivory increasing, others increase with the bias to granivory. For Dniprovsko Orilskii Nature Reserve (Okulova and Antonets, 2002; Antonets and Okulova, 2014), we noted the relation of some dental indices to the feeding preferences of mice. However, being clearly pronounced in the comparison of rodents of different genera or species, these patterns are not significant within the genus *Sylvaemus*. It turned out that the proportion of seeds in the autumn feeding of the mice studied by us does not correspond to the average values of the indices related to nutrition in these species.

Quite possibly the strength of seed shells, which animals have to crack, also plays a significant role in the nutrition of the species studied. In this case, differences in nutrition may also appear in other indicators, such as the width of the skull (the wider the skull, the greater the area for attachment of the masticatory muscles), the strength of the bones, and the thickness of the incisors. It is possible that for this reason, the yellow-necked mouse (*S. flavicollis*) has a narrower and flatter skull, since they mainly feed on acorns with relatively soft shells; for cracking hazelnuts, as well as other nuts, the thickness of the incisors may be important. Unfortunately, we did not measure this parameter in most of the species. The widest in the zygomatic part skull ( $Zyg/Cbl$ ), apparently due to the large volume of muscles associated with the incisors, were found in *S. ponticus*, the food of which often contains nuts of hornbeam and beech with very strong shells.

#### Factor Analysis

To understand the features that have the greatest value in the divergence of mice of the genus studied, we conducted a factor analysis based on our own data. Two groups of factors (axes) were distinguished: the 1st axis has an eigenvalue of 5.365 and explains 67.06% of the dispersion of characters, and the 2nd axis is characterized by values of 1.09 and 12.61%, respectively. Overall, the system explains 79.67% of the variance. Table 4 shows that the greatest loads bear signs



**Table 3.** Relative values (indices) of the dimensions of the skull in different species of the genus *Sylvaemus*

Index values		Species of the genus <i>Sylvaemus</i>				
		<i>uralensis</i>	<i>sylvaticus</i>	<i>witherbyi</i>	<i>ponticus</i>	<i>flavicollis</i>
2/1	Zyg/Cbl	0.490 ± 0.004	0.489 ± 0.005	0.434 ± 0.02	0.587 ± 0.005	0.446 ± 0.003
3/1	Hmax/Cbl	0.299 ± 0.004	0.267 ± 0.009	N.d.	0.296 ± 0.003	0.262 ± 0.003
4/1	Lmd/Cbl	0.536 ± 0.005	0.562 ± 0.010	0.619 ± 0.005	0.600 ± 0.004	0.486 ± 0.003
5/1	Iob/Cbl	0.157 ± 0.002	0.184 ± 0.006	0.184 ± 0.001	0.105 ± 0.004	0.141 ± 0.001
5/2	Iob/Zyg	0.317 ± 0.004	0.364 ± 0.007	0.151 ± 0.002	0.183 ± 0.007	0.317 ± 0.002
6/1	Lna/Cbl	0.343 ± 0.003	0.353 ± 0.011	0.390 ± 0.004	0.365 ± 0.004	0.322 ± 0.002
8/1	Lbull/Cbl	0.343 ± 0.007	0.356 ± 0.029	0.193 ± 0.002	0.214 ± 0.002	0.208 ± 0.002
9/1	Lfi/Cbl	0.201 ± 0.002	0.219 ± 0.009	0.215 ± 0.003	0.208 ± 0.001	0.184 ± 0.001
14/11	Bm <sup>1</sup> /Lm <sup>1-3</sup>	0.332 ± 0.004	0.343 ± 0.005	0.323 ± 0.015	0.357 ± 0.004	0.320 ± 0.011
14/1	Bm <sup>1</sup> /Cbl	0.048 ± 0.002	0.053 ± 0.002	0.052 ± 0.0004	0.054 ± 0.0004	0.045 ± 0.002
11/1	Lm <sup>1-3</sup> /Cbl	0.146 ± 0.001	0.157 ± 0.004	0.111 ± 0.02	0.153 ± 0.002	0.144 ± 0.001
15/1	D1/Cbl	0.273 ± 0.002	0.261 ± 0.006	0.298 ± 0.003	0.303 ± 0.002	0.242 ± 0.002
15/11	D1/Lm <sup>1-3</sup>	1.880 ± 0.012	1.778 ± 0.35	1.853 ± 0.024	2.004 ± 0.025	1.693 ± 0.012
17/11	M <sup>1-1</sup> /Lm <sup>1-3</sup>	0.803 ± 0.005	0.760 ± 0.010	0.747 ± 0.014	0.843 ± 0.015	0.693 ± 0.005
13/11	Lm <sup>1</sup> /Lm <sup>1-3</sup>	0.484 ± 0.002	0.511 ± 0.012	0.486 ± 0.004	0.522 ± 0.007	0.480 ± 0.003
14/13	Bm <sup>1</sup> /Lm <sup>1</sup>	0.688 ± 0.008	0.674 ± 0.015	0.669 ± 0.007	0.689 ± 0.006	0.675 ± 0.021
12/1	Lm <sub>1-3</sub> /Cbl	0.159 ± 0.002	0.160 ± 0.006	N.d.	0.171 ± 0.002	0.162 ± 0.005
10/9	Bfi/Lfi	0.305 ± 0.005	0.354 ± 0.013	0.302 ± 0.063	0.223 ± 0.007	0.360 ± 0.002
7/6	Bna/Lna	0.314 ± 0.004	0.338 ± 0.006	0.319 ± 0.054	0.200 ± 0.006	0.324 ± 0.002
18/1	Bcra/Cbl	0.442 ± 0.003	0.498 ± 0.012	0.476 ± 0.004	0.481 ± 0.004	0.396 ± 0.003
20/1	Li/Cbl	0.111 ± 0.004	0.132 ± 0.015	0.08 ± 0.01	0.192 ± 0.003	0.090 ± 0.002
21/20	Bi/Li	0.241 ± 0.006	0.218 ± 0.020	0.302 ± 0.06	0.175 ± 0.004	0.290 ± 0.005
19/1	Hcra/Cbl	0.326 ± 0.004	0.373 ± 0.010	0.284 ± 0.03	0.406 ± 0.004	0.274 ± 0.002
11/4	Lm <sup>1-3</sup> /Lmd	0.271 ± 0.001	0.280 ± 0.004	0.260 ± 0.003	0.255 ± 0.002	0.294 ± 0.002

associated with an increase in the longitudinal dimensions of the rostral part of the skull and lower jaw in the absence of tendencies to an increase in the overall size of the skull (factor 1, length of the lower jaw, nasal bones, incisor foramina, and upper diastema) and dental system (upper dentition and 1st upper molar); in addition, there is an increase in the occipital width of the skull (factor 1) and the width of the interorbital space (significantly weaker factor 2). Elongation of the lower jaw and diastema indicates the predominance of the gnawing type of food processing (Vorontsov, 1967) and the increase of granivory; at the same time, there is a weaker tendency toward an increase in the dimensions of the upper dentition, which may indicate an increase in folivorous mood in some species. The width of the interorbital space is most likely related to the age variation of the feature.

Thus, the skull of Western Palearctic wood mice, without a directional change in the overall size, tends to narrow the rostral part and expand the occipital part with an increase in the interorbital space and the pre-

vailing development of signs characterizing the granivory type of diet. At the same time, in some forms there seems to be a tendency towards an increase of folivory.

#### Discriminant Analysis

We used our original measurements of the skulls of five *Sylvaemus* species on the entire complex of characters (absolute values) in the discriminant analysis. The results are presented in Tables 5 and 6.

Equations for the identification of five species in a single system were compiled using 12 signs with an eigenvalue of 26.4 and a canonical correlation coefficient of 0.98. Figure 4 shows that *S. flavicollis*, *S. sylvaticus*, and *S. ponticus* are distinguished in the best way, while *S. uralensis* interferes with other species.

We used from two to nine signs for pairwise comparison of species, usually around five (Table 5). In all pairwise comparisons, the results were located on the

**Table 4.** Factor analysis of cranial features of representatives of the genus *Sylvaemus*

Variables (skull measurements)	Factor loads (principal component method)	
	factor 1	factor 2
Lmd	0.9128	0.08834
Iob	0.0909	0.9791
Lna	0.8047	0.3839
Lfi	0.7786	0.3899
Lm <sup>1-3</sup>	0.8012	0.3285
D1	0.8966	0.0041
Lm <sup>1</sup>	0.8107	0.1291
Bcra	0.8793	0.1075

same canonical axis. The eigenvalues did not reach two in two cases (*S. flavicollis*–*S. witherbyi* and *S. sylvaticus*–*S. uralensis*); in the same cases, the minimal canonical correlation coefficients were obtained (0.72–0.75).

Most combinations of pairs of species exist in nature sympatrically: *S. sylvaticus* and *S. flavicollis* or *S. uralensis* and *S. flavicollis* in different biotopes of Rostov oblast (Stakheev, 2009; Stakheev et al., 2011), *S. uralensis* and *S. flavicollis* in the forests of the black earth regions and the southern non–black earth regions (Okulova et al., 2007a), *S. uralensis* and *S. ponticus* in the Northwestern Caucasus (Okulova et al., 2005, 2007), etc. A system for determining species by craniometric characteristics was developed using discriminant equations for three Dagestan field mouse species (Lavrenchenko and Likhnova, 1995). The same systems were developed for pairs of species

in two other studied sites, Dniprovsko Orilskii Nature Reserve and the Northwestern Caucasus (Table 7). Therefore, these equations can be used to create local diagnostic systems and practical definition of species.

#### *Ecological and Morphological Interpretation of the Data*

In general, within the genus *Sylvaemus*, according to the data of factor analysis, the overall dimensions of the skull are less significant than the signs associated with food crushing: the length of the mandible and the rostrum (as a pressure lever of incisors) and the width of the occipital part of the skull (as a place of the muscles attaching, the increase in volume of which causes an increase in the pressure of the incisors). Dispersion of the features occurs mainly in accordance with the change in the food preferences. It is also possible that changes in the dispersion will be noticeable during comparison of the thickness of the incisors, which helps to increase the strength and potency of their cracking movements. Unfortunately, we do not have full data on the thickness of the incisors.

In vertebrate ecology, the separation of ecological niches according to the body size of animals has often been reported (Dzhiller, 1988). In particular, it was noted in the work (Dickman, 1988) for common shrews of the genus *Sorex* (order Lipothyphla). A similar phenomenon was observed by us for the representatives of the family Muridae in the Dniprovsko Orilskii Nature Reserve (Okulova and Antonets, 2002). Species of mice coinhabiting this area have a ratio of sizes that corresponds to the proportions determined by the Hutchinson rule. A similar phenomenon was noted for representatives of *Sylvaemus* in Rostov oblast (Stakheev, 2009).

**Table 5.** Results of discriminant analysis of *Sylvaemus* species in the general system (according to all our data for each species)

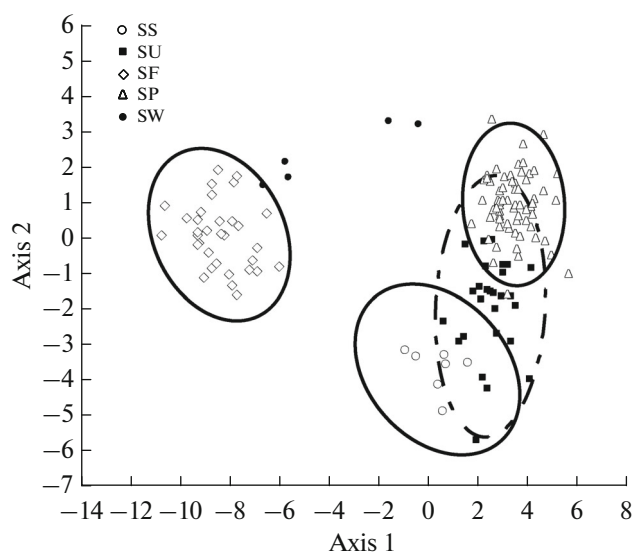
Species	Equation	% c.i.*
<i>sylvaticus</i>	$-271.608 - 10.586Zyg + 26.519Iob - 5.416Lbull + 30.815Lm^{1-3} + 31.659M^{1-1} + 50.434Lm^1 + 8.245Lm_{1-3} - 7.868Bfi - 2.211Bna + 18.657Bcra + 7.174Li + 2.17Hcra$	100
<i>uralensis</i>	$-221.144 - 8.324Zyg + 18.746Iob - 4.003Lbull + 32.182Lm^{1-3} + 28.656M^{1-1} + 40.841Lm^1 + 9.083Lm_{1-3} - 17.635Bfi + 1.184Bna + 16.666Bcra + 6.992Li + 1.009Hcra$	100
<i>flavicollis</i>	$-418.647 - 11.011Zyg + 29.948Iob - 11.505Lbull + 46.576Lm^{1-3} + 43.831M^{1-1} + 65.004Lm^1 + 10.622Lm_{1-3} - 13.509Bfi + 8.951Bna + 23.768Bcra + 12.817Li - 8.283Hcra$	100
<i>ponticus</i>	$-71.608 - 10.586Zyg + 26.519Iob - 5.416Lbull + 30.815Lm^{1-3} + 31.659M^{1-1} + 50.434Lm^1 + 8.245Lm_{1-3} - 7.868Bfi - 2.211Bna + 18.657Bcra + 7.174Li + 2.17Hcra$	96.9697
<i>witherbyi</i>	$-271.608 - 10.586Zyg + 26.519Iob - 5.416Lbull + 30.815Lm^{1-3} + 31.659M^{1-1} + 50.434Lm^1 + 8.245Lm_{1-3} - 7.868Bfi - 2.211Bna + 18.657Bcra + 7.174Li + 2.17Hcra$	100

\* c.i., correct identification.

Table 6. Results of discriminant analysis of species pairs of the genus *Sylviaemus* (according to all our data for each species)

Species pairs	Equation	F (d.f.)	Eigenvalue	R <sub>can</sub>	Wλ	χ <sup>2</sup> (d.f.)	% c.i.*
<i>sylvaticus</i> – <i>flavicollis</i>	–340.597 + 4.890Hmax + 18.057Lbull + 20.299Lm <sup>1-3</sup> + 10.361Lm <sup>1</sup> + 44.624Hcra –298.597 + 14.433Hmax + 8.040Lbull + 45.96Lm <sup>1-3</sup> + 39.202Lm <sup>1</sup> + 16.896Hcra	194.35 (5.37)	26.2636	0.981	0.0367	127.3 (5)	100 100
<i>flavicollis</i> – <i>uralensis</i>	–139.950 + 18.911Lm <sup>1-3</sup> + 5.652Cbl + 5.307Lmd + 2.588Lbull – 14.573Bfi – 20.607Li – 2.468D1 + 14.614M <sup>1-1</sup> + 27.587Lm <sup>1</sup> –102.775 + 12.609Lm <sup>1-3</sup> + 4.678Cbl + 4.445Lmd – 1.027Lbull – 6.985Bfi – 17.372Li – 1.599D1 + 19.856M <sup>1-1</sup> + 20.279Lm <sup>1</sup>	109.89 (9.342)	2.892	0.862	0.257	469.49 (9)	97.7 95.93
<i>uralensis</i> – <i>witherbyi</i>	–33.2257 + 17.6082M <sup>1-1</sup> + 2.6905Hcra –95.1359 + 49.11962M <sup>1-1</sup> – 4.2288Hcra	38.259 (2.139)	2.3167	0.836	0.362	166.660 (2)	100 100
<i>flavicollis</i> – <i>witherbyi</i>	–122.153 + 9.942Zyg + 82.256Bm <sup>1</sup> – 2.349Bna + 21.225M <sup>1-1</sup> – 6.853Li –237.649 + 14.278Zyg + 111.24Bm <sup>1</sup> – 14.268Bna + 37.658M <sup>1-1</sup> – 9.55Li	45.484 (5.207)	1.10	0.724	0.476	154.6 (5)	100 100
<i>sylvaticus</i> – <i>uralensis</i>	–214.695 – 1.614Zyg + 31.193Lm <sup>1</sup> + 15.624Bcra + 52.765D2 –200.013 + 0.069Zyg + 21.096Lm <sup>1</sup> + 12.614Bcra + 58.361D2	13.08 (4.42)	1.215	0.745	0.4453	34.79 (4)	88.89 100
<i>sylvaticus</i> – <i>witherbyi</i>	–119.070 + 2.689Cbl + 2.426Lna + 3.723Lbull + 22.699Lfi –155.42 + 6.274Cbl + 22.361Lna – 6.193Lbull – 7.81Lfi	38.259 (4.9)	17.004	0.972	0.0555	28.906 (4)	100 100
<i>uralensis</i> – <i>poncticus</i>	–118.902 – 0.412Zyg + 32.133Lm <sup>1-3</sup> + 29.617Lm <sub>1-3</sub> + 4.367Bna –127.690 + 1.786Zyg + 25.962Lm <sup>1-3</sup> + 32.813Lm <sub>1-3</sub> – 0.754Bna	68.988 (4.106)	2.603	0.850	0.2775	137.16 (4)	95.35 97.06
<i>poncticus</i> – <i>witherbyi</i>	–154.443 + 55.083Iob – 8.490Lfi + 58.862M <sup>1-1</sup> – 3.3016Bna + 5.677Hcra –321.566 + 75.644Iob – 21.790Lfi + 106.403M <sup>1-1</sup> + 17.710Bna + 1.059Hcra	96.061 (5.70)	6.862	0.934	0.127	147.424 (5)	100 100
<i>flavicollis</i> – <i>poncticus</i>	–162.548 + 7.169Cbl – 7.507Zyg + 44.332Iob – 5.713Lna + 13.617Hcra –128.090 + 2.222Cbl + 1.446Zyg + 15.75Iob – 2.14Lna + 15.870Hcra	323.04 (5.286)	5.648	0.922	0.1504	544.60 (5)	99.03 98.84
<i>sylvaticus</i> – <i>poncticus</i>	–364.922 + 13.816Cbl – 23.578Zyg – 11.384Lmd + 38.214Iob + 10.884Bm <sup>1</sup> + 55.906M <sup>1-1</sup> – 37.397Bna – 47.228Bcra –258.637 + 9.873Cbl – 17.248Zyg – 4.813Lmd + 22.54Iob + 34.948Bm <sup>1</sup> + 44.115M <sup>1-1</sup> – 24.372Bna – 34.360Bcra	29.495 (8.83)	2.843	0.860	0.260	115.775 (8)	100 100

\* c.i., correct identification.



**Fig. 4.** Distribution of individuals of different species of the genus *Sylvaemus* in accordance with two canonical axes. SU, pygmy wood mouse *S. uralensis*; SP, Black Sea field mouse *S. ponticus*; SW, steppe field mouse *S. witherbyi*; SS, wood mouse *S. sylvaticus*; SF, yellow-necked mouse *S. flavicollis*.

The mice of this genus are characterized by a joint habitat of several species, and the segregation of ecological niches occurs in accordance with the Hutchinson rule by the size of individuals: for the coliving species, the overall size or body parts of the smaller one are approximately 0.7–0.8 of the length of the larger one. In addition, it is important for the structure of mammalian communities that species share biotopes, being confined to certain types of landscape, food, and abiotic environmental conditions. Sometimes, the

even smaller house mouse (*Mus musculus*) or Eurasian harvest mouse (*Micromys minutus*) joins the *Sylvaemus* species. They have lower food requirements and subsist on small seeds, and their requirements for abiotic conditions also differ (Okulova et al., 2016). Field and house mice inhabiting the same area often compete with each other for resources, as was noted, for example, in the forests and protecting forest belts of the northern foothills of the Caucasus (Tarasov, 1989) or in the lowlands of the Northwestern Caucasus (Okulova et al., 2005, 2007). The advantage is obtained by those species the needs of which are better fulfilled by the region's natural resources. Thus, according to Lindeman and coauthors (2005), house mice for a long time dominated man-made forests in western Kazakhstan, while plantings were young and did not produce the proper amount of seeds. But as plants matured and fruiting increased, the pygmy wood mouse prompted them to leave this biotope. In the years of abundance peaks of *S. uralensis*, there are almost no house mice in the Northern Ciscaucasia, and in the years of their depression, the house mouse dominates. The same was noted in the lowlands of the Northwestern Caucasus for *S. ponticus* and *S. uralensis*. It can be assumed that within the genus *Sylvaemus* during the process of species evolution there was a quantitative increase in differences in the mechanisms of peeling seed shells and seed processing, as well as a change in dietary patterns: an increase in the proportion of vegetative fodder and seeds of trees or lower forest levels. Thus, the group of large consumers of tree seeds, representatives of which are more closely related to the tree layer of vegetation, should be considered more ancient. It is known that the grassy layer in the forest zone evolved much later than the woody one.

**Table 7.** Discriminant equations for identifying *Sylvaemus* species of the sites studied: 1, Dniprovsko Orilskii Nature Reserve; 2, municipal district of the city of Sochi

Site	Species pairs	Equation	$F$ (d.f.)	Eigenvalue	$R_{can}$	$W\lambda$	$\chi^2$ (d.f.)	% c.i.*
1	<i>sylvaticus</i> – <i>uralensis</i>	$-340.597 + 4.890H_{max} + 18.057L_{bull} + 20.299L_m^{1-3} + 10.361L_m^1 + 44.624H_{cra}$	194.35 (5.37)	26.2636	0.981	0.0367	127.3 (5)	100
		$-298.597 + 14.433H_{max} + 8.040L_{bull} + 45.96L_m^{1-3} + 39.202L_m^1 + 16.896H_{cra}$						100
2	<i>ponticus</i> – <i>uralensis</i>	$-150.246 + 51.255I_{ob} - 13.85B_{fi} + 2.775B_{na} + 16.983B_{cra}$	311.60 (4.87)	14.33	0.967	0.0652	240.2	100
		$-159.324 + 23.413I_{ob} + 43.76B_{fi} + 32.29B_{na} + 10.475B_{cra}$						

\* c.i., correct identification.

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## 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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